

AKADEMIYA NAUK SSSR
INSTITUT ISTORII ESTESTVOZNANIYA I TEKHNIKI
INSTITUT MORFOLOGII ZHIVOTNYKH IM. A.N.
SEVERTSOVA

Academy of Sciences USSR
Institute of the History of Science and Technology
A. N. Severtsov Institute of Animal Morphology

L. Ya. Blyakher

HISTORY OF EMBRYOLOGY IN RUSSIA
FROM THE MIDDLE OF THE EIGHTEENTH
TO THE MIDDLE OF THE NINETEENTH CENTURY

(Istoriya Émbriologii v Rossii
s serediny XVIII do serediny XIX veka)

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Editor: G. A. Shmidt

With an Introduction by
Jane Maienschein

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GENERAL

When Dr. Robert Multhauf asked me if I would consider editing this translation of Blyakher's volume, he warned that this was part of what seemed to him a most unusual scholarly project. Thanks to a somewhat mysterious and complicated government exchange program, the Smithsonian Institution and the National Science Foundation had been charged with overseeing the translation into English of several foreign language texts in the history of science. Upon the recommendation of experts, the volumes chosen included two by L. Blyakher, a Russian biologist. In particular, these Russian volumes, including THE HISTORY OF THE INHERITANCE OF ACQUIRED CHARACTERISTICS, edited by Frederick Churchill, and this one, were thought to present a valuable exposure to a Russian point of view in the history of science and to detail important episodes of Russian scientific history. Therefore, the translation began.

Following someone's recommendation, this particular volume went to Egypt to be translated by an anonymous translator. I admire the translator's patience in working through the detailed embryological descriptions. Unfortunately, however, the style of the English translation was infelicitous at best, and the translator evidently had trouble with proper names, German references, and embryological terms. My task, then, became to turn the prose into an acceptable style, to correct the names and terms to conform with standard English usage, and to check the references.

The fact that I do not read Russian, except for word-by-word translation with a dictionary, could have posed a fatal problem. But fortunately, the Dickinson College Library and work study office generously donated the services of work study student Lauri Wiener, who reads Russian and possesses the requisite active curiosity and healthy sense of humor. Together, Lauri and I checked the questionable phrases as well as a random sample of other passages to determine the accuracy of the translation. Except for some of the discussion

of German philosophy and a few embryological descriptions, the translation appeared to us to be accurate. The fact that Blyakher's style is straightforward and essentially descriptive undoubtedly helped, since the translator could thus provide a rather literal translation without losing the content or warping the style significantly. The fact that many of the embryological terms had simply been transliterated from Latin or German into Russian and then back in accordance with standard international scientific terminology to make this translation meant that the terms usually remained recognizable. Thus, although I make no pretense of certifying the precision of every detail of this translation, to my knowledge it is reasonably accurate at all points and represents Blyakher's content and style fairly closely. I very much appreciate Lauri Wiener's help in verifying and improving the translation.

Identifying some of the intended proper names and dates required a bit of detective work. Double transliteration or translation into Russian and then into English created much more trouble with some of the names than did translation of embryological terms. Names such as Isidore Geoffroy Saint-Hilaire or Cuvier produced mysterious and occasionally hilarious results, as the former became Izedor Zhefwar Tzent Iler, and the latter Kyuve. Joseph Needham became Nidzhem, Leeuwenhoek became Lev'nhk, and so on. As might be expected, the more obscure names created the greatest difficulties, but with the help of the extraordinarily helpful and competent Dickinson College Interlibrary Loan staff, I managed to track down all but a couple of minor Russian figures to check spellings and dates. In questionable cases, I have used spellings from the Library of Congress National Union Catalog. And some names are left in Russian style, such as Karl Maksimovitch Baer (alias Karl Ernst von Baer, of course) to reflect the importance of Blyakher's claim that these men are essentially Russians. In this case, Karl Maksimovitch Baer is closer to the man's given name when he was born in Estonia.

References to published and unpublished materials provided even more trouble in some cases, though here, too, I was able to check and correct all except a few Russian references. A project of this type and magnitude naturally encourages some errors to creep in, so I expect that there

may be some imperfections in citations. Nonetheless, with the exception of some of the Russian articles, I have been able to verify dates, page numbers, and other significant reference data. Readers with access to a superior library should be able to locate most of the material Blyakher cites, though some of the unpublished Russian materials may well prove inaccessible as they did to me.

My other task in editing this volume lay in making the descriptive chapters on von Baer's *UBER ENTWICKELUNGS-GESCHICHTE* useful, since Blyakher's page number references to the Russian translation of von Baer's work would obviously not be particularly relevant for most readers of this English translation. Therefore, for the passages Blyakher quotes or cites, I identified page numbers of the German original edition, which has been reprinted recently. And where necessary I checked, corrected, and added the section references to *ÜBER ENTWICKELUNGS-GESCHICHTE*. The references are thus: (volume, section, German page number) or (volume, section, Russian page number (German page number)). In addition, I corrected translation of the quotations where necessary to accord with more common English versions.

For other references to or quotations from German or English works, I made necessary corrections and substituted standard English versions where available since some passages had been distorted in the double translation.

At this point, the first round of editing was complete. Here Rosemary Regan enters the story. Ms. Regan, a marvelously competent and intelligent assistant to Dr. Multhauf, helped with typing some of the longer and messier chapters; she corrected errors in the entire draft, and she used her knowledge of editing and the history of science to polish details of style and terminology. I thank Rosemary for her considerable help and both Rosemary and Robert Multhauf for their continued encouragement and good humor.

With these acknowledgements and with the above caveats, I feel assured that this descriptive volume should be accurate and usable. Editing this has proven to be an unusual project, as Dr. Multhauf warned, but I feel, as he has felt,

that the translated and edited volume can prove useful, as indicated in more detail below.

OUTLINE OF BLYAKHER'S WORK

In fact, this book represents only half of Blyakher's HISTORY OF EMBRYOLOGY IN RUSSIA, covering only the mid-eighteenth to the mid-nineteenth century. A brief discussion of the second volume, covering the mid-nineteenth to the mid-twentieth century, appears in a review by Charles Bodemer in ISIS. While that second volume describes material less well-known to western historians of science and while it might therefore seem more valuable, this volume is intriguing in part precisely because it deals with apparently familiar figures and works from a different perspective which is distinctly, though on the whole not zealously, patriotically Russian. Blyakher claims that those recognized great embryologists, Kaspar Friedrich Wolff, Khristian Pander, and Karl Maksimovich Baer - heretofore considered German embryologists - were in fact distinctly Russian, and that their Russian connections define their scientific characters and help explain their successes in important ways. This Russian viewpoint is the first of the book's two major offerings.

The second lies in the description and catalog of essentially inaccessible works and the compiling of several descriptions into a single narrative index of sorts. Blyakher discusses works of major embryologists which can be located only with difficulty. For example, even though they appeared in German (which can be read by more English speakers than Russian can), many of the papers cited appeared in some of the little-circulated publications of the St. Petersburg Academy of Science. Thus, Blyakher provides new descriptions which he combines with discussion of other both major well-known and relatively rare sources. Since many of these sources are little known, little circulated, inaccessible, or difficult to read because of the archaic scientific detail or descriptive style, Blyakher has performed a valuable service by describing them.

I will outline the chapters briefly as a guide to Blyakher's work, since this is a descriptive study which could use some index, and its indices have not been translated into English for logistical reasons.

In the INTRODUCTION, Blyakher explains that he will give "a detailed account of the history of Russian embryological investigations" to provide "exhaustive evidence (for) the frequently repeated claim that Russia is the fatherland of embryology as a science, that it developed from Russian soil and became one of the most important foundations of the evolutionary and historical view of the organic world." Embryology - meaning Russian embryology, of course - fell into three distinct periods, according to Blyakher: that of establishing epigenesis and making embryology possible as a science (Wolff), that of discovering the embryonic layers and establishing the prerequisites for comparative embryological development (Pander and Baer), and that of evolutionary embryological development (Alexander Kovalevsky and I.I. Mechnikov). The first two periods form the focus of this volume, while the third is subject of his second volume. The following chapters amass "evidence" for his claim for Russian fatherhood primarily by describing the many accomplishments of native (and adopted) Russians and by showing how these actually were in some essential way Russian accomplishments.

CHAPTER 1 considers the early period, beginning with the late seventeenth and the early eighteenth century, the time of Peter I's reorganization in Russia. Peter wanted to encourage native-born and trained scientists, Blyakher tells us, and so the ruler established a significant teratological and embryological collection in the Kunstkamera to support native medical studies. Peter I initiated Russian interest in embryology, according to the author. And Mikhail Lomonosov stimulated serious embryological studies, drawing on those teratological and embryological collections. Lomonosov, like Wolff and other followers, began the modern era of experimentation, materialism, empiricism, and historical explanation, Blyakher asserts, without fully explaining what he means by each of those recurring terms. Despite his infrequent lapses into enthusiastic excesses, Blyakher convincingly establishes that there was early embryological

interest in Russia, which has not been widely studied, and that historians of science should therefore explore the subject more seriously.

CHAPTER 2 discusses the preformation and new formation (alias epigenesis) exchanges. This chapter offers few new insights into these debates, but the reader should recall that Blyakher was writing in the early 1950's and that his Russian audience was likely unfamiliar (or only recently familiar) with material which a western audience might find much more familiar. Blyakher's listing of partisans on either side and his discussion of the issues here and in later chapters are essentially clear and potentially useful even if not profound.

CHAPTER 3 introduces that great adopted Russian, Kaspar Friedrich Wolff, who then provides the subject of Chapters 5-8 as well. Wolff deserves more credit than he has received (by 1955, remember), Blyakher asserts; everyone from Russian historians to German historians to Wolff's contemporaries have reportedly been consistent in their underestimation of Wolff's significance. Here, Blyakher becomes a bit zealous in his efforts to make Russian everyone and everything which seems good or important. He faults the Russian historian and biographer Boris Evgen'evic Raikov, for example, for suggesting that Wolff felt ideologically isolated after his move to Russia in 1767. Not the case, Blyakher insists. ". . . in Germany Wolff was not evaluated as a first class investigator and advanced thinker. This forced him to move to Russia, and therefore Germany does not have the right to claim Wolff's glory."

While Blyakher's claim is silly as stated and while it might seem exaggerated and annoying to the modern historian of science, it may also reveal valuable insight. It would be well for historians of biology to recall that Wolff was little known in Germany; that he did move from Germany to Russia in 1767, albeit after much of his major embryological work had been completed and published; that his biographers have found the reasons for his move unclear; but that St. Petersburg did offer important collections of embryological and teratological specimens and that Wolff seems to have used them to advantage. Thus, perhaps St. Petersburg

did offer an especially congenial environment for an embryologist who was an epigenesist, and perhaps the reasons should be better examined.

CHAPTER 4 provides a useful outline of Wolff's dissertation - both the original Latin of 1759 and the German, more "popular" version of 1764. The Latin criticized earlier epigenetic suggestions and reflected a great deal of respect for Haller, but Blyakher claims that Wolff appealed to Haller only because he sought the latter's support and that Wolff consistently rejected any tendency toward Haller's preformationist views. In the German, Wolff provided an epigenetic discussion of development and expressed opposition to rigorously mechanical understandings of vital phenomena. Blyakher's description of Wolff's work is valuable, but the reader should be aware that Blyakher has probably had to strain the data here more than elsewhere to support his thesis about Russian priorities in embryology and his view that Wolff was one of the Russian "good guys" on the progressive path to modern scientific embryology. Again, the reader should recall that this was published in 1955, just shortly after other Russian publications of histories of embryology and translated embryological works.

CHAPTER 5 remains somewhat more descriptive, providing a valuable discussion of Wolff's relatively rarely read *ON THE FORMATION OF THE INTESTINE*. Here begins Wolff's articulated disagreements with Haller over whether development occurs gradually and epigenetically or by unfolding of preformed material. "I consider it proven that the intestine is doubtlessly thus formed (by rolling of material) and did not exist previously in an invisible form, ready to appear at the appropriate moment," wrote Wolff in opposition to Haller. Just because he could not see the parts early on does not mean that they could not exist already, Wolff realized, but he believed that in fact the parts are only formed as the result of a gradual process. Unfortunately, Wolff's work was little known, even after a translation into German appeared. Only much later was Wolff appreciated, according to Blyakher, and it took figures such as von Baer, the American biologist William Morton Wheeler, and the embryologist-historian of science Joseph Needham to evaluate properly Wolff's "fatal blow for preformation."

CHAPTER 6 considers Wolff's teratological work, performed after his move to Russia and based on the St. Petersburg collections in the Kunstkamera. These studies, published in Latin, have remained essentially unknown until recently. After arguing that God would not have created monsters, Wolff maintained that abnormalities must occur by epigenesis rather than preformation. Blyakher asserts that Wolff's discussion of God reflected his desire to "eliminate God from nature" and that any impression otherwise stems from Wolff's necessary conformity to prevailing popular opinion. But the reader should consider this claim sceptically, a warning reinforced by awareness of Blyakher's efforts through the last few pages of the chapter to make Wolff a predecessor of modern embryology.

CHAPTER 7 presents Wolff's "essential power" as discussed in his commentary for the 1782 St. Petersburg Academy of Science prize competition for understanding nutritional power. In a paper of his own, Wolff responded to papers by Blumenbach and Born by discussing attractive and repulsive forces and the importance of forces as well as structure for organic animal development.

CHAPTER 8 addresses evaluation of Wolff's work by Kirchoff (Wolff brought development from mystery to a science by establishing that organic life follows laws) and Raikov (Wolff was a materialist and denied the existence of Stahl's mystical "soul," an idealist but not a vitalist, stressing the primacy of material over soul). Interestingly, given his retrospective tendencies elsewhere, Blyakher believes that Raikov distorts the proper historical perspective, and he sees Wolff as fluctuating between materialism and idealism. Consistently, Blyakher tries to show how major figures were predecessors of modern science even though they were side-tracked by errors of their day. Thus he is Whiggish in his history, but he is not completely ahistorical. It is not Wolff's fault that he could not do more, Blyakher apologizes; the backward times slowed Wolff's progress in Blyakher's assessment. Thus, like earlier chapters, this chapter begins with useful description and references to relatively little-known material and ends with a claim for Russian priority.

CHAPTER 9 argues that Wolff was essentially ignored but that Russian embryologists nonetheless began to accept

epigenesis by the late eighteenth century. Blyakher discusses such figures as Johannes Beseke, Matvei Pekken, Nestor Maksimovich-Ambodik, and Aleksandr Radishchev, providing a valuable, though brief, introduction to each of these scientists.

CHAPTER 10 is perhaps the most significant in introducing a cast unfamiliar characters and unfamiliar material, and in providing original theoretical discussion. After establishing what Naturphilosophie means to him, Blyakher assesses the impact of German Naturphilosophie on Russian science; he concludes that Russians were generally not receptive to Schelling's philosophy or to idealistic Naturphilosophie in general, even though some embryologists such as Danil Vallanski, Michael Pavlov, and others endorsed seemingly idealistic views. The Russian intelligentsia recognized the unreality of Naturphilosophie and the importance of materialism, Blyakher argues, and thus they moved toward a progressive empirical philosophy. Despite apparent flirtations with Naturphilosophie, therefore (as for von Baer), Blyakher concludes that "the successful aspects of embryology in Russia were thus not connected with Naturphilosophie." Although once again consistently retrospective and apologetic for the seemingly imperfect progress of Russian science, Blyakher has in this chapter addressed the suggestion by others that Naturphilosophie may have directed Russian science and argues that it may have been seriously considered but then rejected or refined in "successful" Russian science. His discussion of those who did accept some form of idealistic philosophy is useful, as is his interpretative assessment of its limits.

CHAPTERS 11 AND 12 sketch, respectively, the contributions of transition figures Louis Treder and Ludwig Bojanus. Treder admittedly "was not a Russian, was not born in Russia, and lived there only six years." Yet he was an honorary Russian in Blyakher's view. Treder did produce an influential dissertation, reportedly inspired by the Russian Wolff and by Treder's visit to St. Petersburg; there he outlined the preliminary story of the avian egg and its hatching and early development. Bojanus introduced study of the embryonic layers in mammals, which influenced Pander and von Baer, according to Blyakher.

CHAPTER 13 discusses Khristian Pander, von Baer's fellow student at Würzburg studying under Döllinger. Döllinger and von Baer convinced Pander to apply his apparently significant financial resources to procure the necessary large number of eggs in order to trace details of chick development during the first five days of life. Pander's work, despite criticism by Lorenz Oken which Blyakher discusses in detail, provided a starting point for future study in epigenetic developmental biology, and especially notably, it served as a foundation for von Baer's work. At one point, Blyakher almost perversely manages to make Pander's weaknesses sound like strengths. He says that Pander's errors were valuable and that they were important in part because they later "allowed Baer to give the true interpretation." As before, Blyakher's interpretation remains retrospective and frustrating at times, but his data are useful for an introduction to this material.

CHAPTER 14 THROUGH 24 deal with Karl Ernst von Baer, here Karl Maksimovich Baer. 14 provides biographical information and outlines his professional career. 15 presents Baer's discovery of the mammalian ovum and reveals concern both with establishing Baer's priority and with opposition to Baer's work. CHAPTERS 16 THROUGH 22 describe Baer's opus, *UBER ENTWICKELUNGSGESCHICHTE*. Originally published in Germany (volume 1 1828, volume 2 1837, volume 2 part 2 1888), Baer's work appeared in Russian translation only in 1950 and 1953, which may have provided one stimulus to Blyakher to publish his historical study. Blyakher evidently relied on the Russian translation, so I have had to provide references to the German original (as mentioned above). Few people have read through Baer's long and detailed study completely, so Blyakher's discussion of all five scholia and corollaries and of the rest of the work, of which many are aware but which few read, will prove useful.

Most important, though, is the discussion of Baer's volume 2, and especially in CHAPTER 22 of the fourth part which forms the second part of volume 2. This section was published not by Baer himself but by Ludwig Stieda, after Baer's death. Baer had not completed the work, and Stieda discovered the manuscript while working through Baer's materials in order to produce a biography. Baer had begun his

study of human development, discussed in this part four, in Königsberg in 1834, but his move to St. Petersburg that year disrupted his work and he never completed his examination of human normal and abnormal development.

Human development also forms the subject of part of CHAPTER 23, which deals with Baer's teratological work in St. Petersburg. Here Blyakher addresses Baer's complaints about "lack of consideration or unfair attacks, with which his remarkable discoveries were met in Prussia." The Russians were more sympathetic, of course, according to Blyakher. In part because the Germans did not fully acknowledge the importance of his work, Blyakher establishes convincingly, Baer returned to Russia and gave up his systematic embryological studies, turning instead to anthropology and other scientific and family ventures.

The few studies of fertilization and embryological development which Baer did perform after his move, Blyakher discusses, including several papers detailing what is essentially meiosis and mitosis, according to Blyakher. If fertilization and cell-division initiate development, then there could be no pre-existence of individuals; the unfertilized ovum must contain latent but not pre-formed life, Baer had concluded in a paper of 1847. Some of Baer's teratological and fertilization studies reveal that Baer accepted a limited version of evolution - an evolution of the individual within his system of types. Blyakher neatly illustrates the transition between his second and third historical periods of embryology with the example of St. Petersburg Academy of Science's establishment of a prize for Biological Science in 1864. Kovalevsky and Mechnikov won that prize, thus bridging the move from Baer's older epigenetic work to the new evolutionary embryological science.

CHAPTER 24 considers Baer's theoretical views, including a very brief look at Baer's version of the history of science. This chapter offers intriguing suggestions, but most are incompletely developed and hence do not significantly extend our understanding of Baer. As with the rest of the book, the chief value of these lengthy chapters on Baer lies in the potential of their suggestions, in the descriptions of more well-known sources and of unfamiliar material alike against a background of other familiar works. The

references provided certainly suggest that Baer is as yet poorly understood, despite the several biographical sketches, and that historians of science would do well to explore his complex Russian connections - both before his move to and after his return from Germany.

CHAPTER 25 serves as a transition to the third stage of world and hence Russian embryology (featured in Blyakher's second volume). It considers figures after Baer but before Mechnikov and Kovalevsky. The focus is on Grube, Nordmann, Warnek, and Krohn in particular. These men made way for Kovalevsky and Mechnikov, according to Blyakher, and these latter men effected the revolution from comparative-descriptive to comparative-evolutionary embryological science.

NOTES - These notes have not been translated, obviously. Some offer biographical information, others provide references to additional scientific and other works, while still others elaborate on the text. These notes are cited in the text by the numbers enclosed in square brackets: (#).

The above brief outline sketches Blyakher's volume. Throughout, the work remains descriptive. Each chapter thus provides details of the works and people it considers. Some of these descriptions are so extremely thorough as almost to reproduce the original sources being considered, while others provide essentially an index or overview of their subjects. To my knowledge, the descriptions seem consistently reliable and useful.

VALUE OF THE WORK

As suggested above, Blyakher's work contributes both useful description of little-read source materials and a particularly Russian perspective. The latter, which clearly directs what interpretation Blyakher does offer, only occasionally intrudes on the narrative. As noted earlier, Blyakher does at rare times become fervent in his attempts to establish that "Russia is the fatherland of embryology as a science." Yet he would appear to have considerable evidence that his claim should at least be taken seriously. Western

scholars often tend to dismiss Soviet scholarship and its fiercely patriotic perversions. But Blyakher, despite his effectively cold war context, remains relatively restrained and reasonable.

The author's concern with establishing scientific priorities, with establishing who first discovered such-and-such, seems equally open to objection from the perspective of current history of science. Yet this orientation clearly does not result strictly from Blyakher's Russian point of view; most historians of science in the 1950's sought to establish priorities and to document high points of scientific "progress."

In sum, then, Blyakher does provide a very useful descriptive guide to major works in the history of embryology, many of which happen to be Russian in some sense. His interpretative discussion, which seeks to establish that the Russian connection in important embryological work was not merely coincidental needs to be questioned, dissected, and then explored further to discover just what the essential Russian influences were. We should thank Blyakher for his suggestions and use his volume as a guide for that further exploration.

Because the materials are so widely known, I have decided not to provide a full bibliography of works relevant to the subjects Blyakher discusses. See the DICTIONARY OF SCIENTIFIC BIOGRAPHY entries for the key figures and standard sources in the history of developmental biology for additional references and for discussion of similar materials from various non-Russian perspectives.

July 1981

Jane Maienschein
Arizona State University

PREFACE

Embryology occupies a notable position among the biological disciplines of Russian science, as noted by K. A. Timiriazev.¹ Separate stages of the history of Russian embryology are presented in journal articles, collected biographical essays, and commentaries which have accompanied the recently published works of the Russian scientists K. F. Wolff, K. M. Baer, A. O. Kovalevsky, and I. I. Mechnikov. There is no systematic treatise of the history of embryology, either here or abroad.² Joseph Needham's HISTORY OF EMBRYOLOGY, which was translated in 1947 into Russian,³ cannot satisfy any exacting reader. (1)⁴ For exhaustive evidence of the frequently repeated claim that Russia is the fatherland of embryology as a science, that it developed from Russian soil and became one of the most important foundations of the evolutionary and historical view in the organic world, therefore, it is necessary to give a detailed account of the history of Russian embryological investigations.

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1. K(liment) A(rkadevich) Timiriazev, "Istoricheskii metod v biologii" (Historical methods in biology) SOCH., V.VI.M., Selkhozgiz (1939), p. 32.
 2. This confirmation is correct now only in relation to the history of embryology of animals. After the manuscript of this present book was given to the press, there appeared P(avel) A(leksandrovich) Baranov's monograph, ISTORIYA EMBRIOLOGII RASTENII V SVYAZI S RAZVITIEM PREDSTAVLENII O ZAROZHDENII ORGANIZMOV (History of plant embryology in connection with developmental ideas on the generation of organisms) (Moscow: Akademii Nauk, 1955, 439 pp.). In the first part of this book its author presented the prehistory of the embryology of plants, to the nineteenth century, against the background of development of general ideas on the generation of organisms, both plant and animal (p. 8).
 3. J. Needham, HISTORY OF EMBRYOLOGY, translated from the English by A. V. Yudinaya, preface by V. P. Karpov (IL, 1947), 342 pp.
 4. Numbers in square brackets are related to the comments at the end of the book.

The first observations of embryonic development date back 2,500 years; however, the onset and development of embryology as a science is connected with the general progress of the natural sciences in the eighteenth and nineteenth centuries. There are three main stages in the history of embryology. The period of the substantiation of the theory of epigenesis, making possible the existence of embryology, is connected with the Russian academician K. F. Wolff. The period of the discovery of the embryonic layers, when the prerequisites for comparative embryology appeared, is the period of activity of the Russian academicians Kh. I. Pander and K. M. Baer. Finally, the period of the creative development of embryological problems in the light of Darwin's work is inseparably united with the Russian investigators A. O. Kovalevsky and I. I. Mechnikov and the brilliant zoologists who followed their footsteps.

The present book reviews the first two periods of the history of embryology, including the epoch directly preceding the scientific activity of A. O. Kovalevsky and I. I. Mechnikov. The history of Russian embryological investigations, from the beginning of comparative embryology to the present time, is embodied in the contents of the books discussed here. One is dedicated to the history of embryology of invertebrates and another book elucidates the history of the embryology of vertebrates.

At the time of writing the present book, no work of Wolff or Baer had been published in Russian except for the incomplete and inaccurate translation of the second part of the first volume of Baer's *UBER ENTWICKLUNGSGESCHICHTE*.⁵ In 1950, in the academic series "Klassiki nauki," the translation of Wolff's "Theory of Generation" appeared, as did the translation of the two volumes of Baer's "History of Animal Development" in 1950 and 1953. An article by Gaissinovich⁶ (in an appendix to Wolff's book) clearly presents

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5. K. M. Baer, *IZBRANNYE RABOTY* (Selected works), from the series *KLASSIKI ESTESTVOZNAANIYA*, translated with comments and preface by Yuri A(leksandrovich) Filipchenko (Moscow: GIZ, 1924), 114 pp.
 6. A. E. Gaissinovich, "K. F. Wolff and Studies on Development," in an appendix to K. F. WOLFF: *THEORY OF DEVELOPMENT* (Moscow: Akademii nauk, 1950), pp. 363 - 477.

this embryologist's ideas against the historical background of studies of evolution. An analogous article by B. E. Raikov concluded the first volume of Baer's work.⁷ The appearance of these articles has reduced the corresponding chapters of the present book, but the author considers it necessary to give a brief, thorough review of the basic works of Wolff and Baer in connection with their other embryological and teratological works.

The works of Russian embryologists of the eighteenth and the beginning of the nineteenth centuries—Wolff, Tretern, Pander, M. G. Pavlov, and Baer—are, in part, written in Latin and cannot be read in the original by the majority of our young contemporaries. The literary legacy of Baer is extremely vast and difficult to review.

It seemed to the author that it is important to explain not only the most important works of the Russian embryologists of the second half of the eighteenth century and the first half of the nineteenth century, but also their less important works, in order to present the contribution which Russian investigators made to world science. The activity of the Russian embryologists coincided closely with the development of world embryological science. The importance of the Russian investigations can be correctly evaluated only in comparison with the works of the foreign embryologists, which are explained by short comments in the present book. Expansion of these excursions into the history of world science did not seem possible without significantly increasing the size of the book.

In presenting the contents of the Russian embryological works, sometimes sufficiently long extracts are presented that the reader can form an impression not only about the contents, but also about the scientific literary style of the investigations discussed.⁸

7. B(oris) E(vgen'evich) Raikov, "On the Life and Scientific Activity of K. M. Baer," in an appendix to K. M. BAER: THE HISTORY OF ANIMAL DEVELOPMENT, Vol. I (Moscow: Akademii nauk, 1950), pp. 383 - 438.

8. All the citations printed are underlined by the authors of the discussed works permitting the reader to see exactly what the authors, themselves considered most essential in their works.

The drawings are considered to be the most important part of the morphological works. The pictures, reproducing the studied objects as they were seen either with the naked eye or with the aided eye, reveal the level of the technique and the exactness of the observations. The schematic drawings are considered the graphic expressions of the authors' theoretical opinions. Therefore the original drawings speak about the scientific priorities and facilitate the description in words of the corresponding discoveries. In reference to this, we must not forget the authors of revisions and educational textbooks; although they occasionally reprint the illustrations of the foreign authors, often they are not a bit better than the drawings of the Russian investigators published earlier. The reprinting of the original drawings of Wolff, Tredern, Boyanus, Pander, Baer, Grube, Nordman, Warnek and Krohn in the present book is to present the level of their morphological investigations, and also to defend the priority of the Russian embryologists.

The present book was finished in 1950. Its contents, and also the plan for its continuation to subsequent stages of embryology in our country, were reported in the meeting of the sector of the history of biology in the Institute of Natural Science History of the Academy of Science of USSR and in the Academic Council of this Institute.

The author is deeply grateful to T. D. Detlaf; L. D. Lioznera, S. R. Mikulinsky, S. L. Sobol and G. A. Shmidt, who listened to the reports about the contents of this book or read the manuscript and made critical comments. The author particularly thanks the collective of the library of the Moscow Society of Naturalists, who willingly helped during the search for literary sources and illustrated materials.

CHAPTER 1

THE BEGINNING OF EMBRYOLOGICAL INVESTIGATIONS IN RUSSIA IN LOMONOSOV'S EPOCH

The end of the seventeenth century and the beginning of the eighteenth century are considered a turning point in the history of Russian culture, connected with the reorganizing activity of Peter I. To overcome economic backwardness and to consolidate the powerful State, specialists in the fields of industry, military affairs, and medicine were necessary. But the existing seventeenth-century Russian educational institutions—Slavic, Greek, and Latin academies in Kiev, Mogilyanskaya, and Moscow—offered religious-scholastic education which could not insure the preparation of such specialists. In the beginning, different specialists were invited from abroad; however, the need to prepare their own was clear. At the beginning of the eighteenth century in Moscow, and later in Petersburg, the schools of mathematical and navigational sciences (1701), preparatory (1703), surgery (1706), engineering (1712), and others were therefore established.

Medical education required materials, first of all for the study of anatomy, the basis of medical science. Besides the preparation of these anatomical demonstrations for training future physicians, natural-historical demonstrations were collected to illustrate the normal and deformed development of the human and animal embryo. The formation of the embryological and teratological collection was carried out by nominal decrees.

On February 13, 1718 Peter I gave the following decree:

It is known that monstrosities are born of freak humans, animals and birds, which are collected in all conditions for their interest. A decree had been established many years previous

that those who gave birth or contributed a freak received a payment for the above mentioned. Two which were brought were described as babies, each with two heads that were attached to their bodies. It is possible that many were born in this condition. The ignorant believed that these monsters were born from the devil's influence, that it was impossible for the single creator of all creatures, God, to be responsible. Actually, the deformity was caused by damage to the interior, by fear or maternal conditions at the time of pregnancy, examples of which were the frightened mother, the mother who was hurt or in pain, etc.

From the contents of this decree, it is clear that a similar decree had preceded some years earlier, but its text was never found. This revised decree specified payment for every human, animal and avian monster brought to the Commandant in every town. Payment for dead monstrosities included: for the human, ten roubles; for animal, five roubles; and for avian, three roubles. For living monsters, payment for the human was 100 roubles; for animal, 15 roubles; and for the avian monster, 7 roubles. But if it was highly unusual higher payment was given, and less if there was little change from the ordinary. In addition, if birth was intentional and because of shame over the monster they did not want to bring it, the Commandant innocuously asked them—whose? By relinquishing the monstrosity, the person received his money and was set free. When the monsters died, they were put in spirits. Or if preservatives were unavailable, then they were placed in strong ordinary wine and closed tightly, in order not to deteriorate. Payment for this wine was made to the pharmacy.¹

Earlier, January 28, 1704, Peter had declared the following nominal decree for Moscow and for the Moscow district of boyar Musiny-Pushkin:

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1. POLNOE SOBRANIE ZAKONOV ROSSIISKOI IMPERII S 1649 (The Complete Collection of Laws of the Russian Empire from 1649) (1830), v. V, pp. 541 - 542.

The Great Sovereign decrees.... in all parishes of His Great Majesty, under penalty of death, that midwives delivering babies who are born with any deformed characteristics or appearance, or immature in form or strange, must not kill and must not hide them. They must declare them to the priests of the monastic order of these parishes, and the priests must declare them to boyar Ivan Alekseevich Musiny-Pushkin and his assistants.²

The prohibition against killing monsters and the request for information about them indicated that before 1704 there had been no systematic collection of teratological and embryological material. Related to the latter was the nominal decree of May 30, 1705, which stated: "To all ranks of people whose pregnant wives deliver embryos of babies from five to nine months and whose wives die: the hour of death of these wives must be reported in person to the monastic order, to be reported to boyar Ivan Alekseevich Musiny-Pushkin and his assistants."³

The collected materials at first were added to the collections of Peter I, brought by him from the journey of the "Great Embassy" to Western Europe in 1697 - 1698. The anatomical and embryological preparations from this collection were kept in the main pharmacy of Moscow, where the preparations from the hospital dissecting room, opened in 1703, were transmitted. In 1714 these collections were transported to the building of the Summer Palace in Petersburg, to the so-called "Imperial Cabinet," and from there, in 1718, to a special building, "Kunstkamera," in the house of A. Kikin.

The embryological collections were at first exhibited in the form of pictorial compositions (2), like the famous collection of the Dutch anatomist Ruysch, which Peter purchased from him during the second journey to Holland in 1717. Besides this, according to one foreign eye-witness,

2. Ibid., v. IV, p. 243.

3. Ibid., p. 308.

systematic embryological collections were present in the Kunstkamera: "bottles with specimens of human fetal development, from the earliest form of the embryo to the complete mature fetus. There are also different monsters both human and animal."⁴

The reading public in Russia at the end of the eighteenth and beginning of the nineteenth centuries was informed about the richness of the collections of the Kunstkamera, in particular about the presence there of the embryological preparations, by "Pismovnik," which was a widely distributed popular work of Professor N. G. Kurganov.⁵ The author of the first work on the history of medicine in Russia, Professor V. M. Richter, characterized these collections by writing:⁶

that among these preparations primary attention is given and astonishment is produced by the representation of the birth of man, the constant formation and development of the fetus from the earliest beginning to complete maturation. This collection is composed solely of 110 embryos (embryos and fetuses) representing the constant growth of the infant from the size of a grain to complete formation of the infant. Here also the embryo which has just come from the fallopian tube is present . . . The last is so delicate and transparent, that one can easily see in the first months the position and also the formed organs. The rich collection of monsters must be added to this.

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4. Petersburg, 1720. "A Polish Eye-witness' Notes," OLD RUSSIA, X, June 1879, pp. 263 - 290, quotation p. 271.
 5. N(ikolai Gavrilovich) Kurganov, PISMOVNIK, containing science of Russian language with many adherences of different educational and useful amusing words. 1802. (The first edition appeared in 1777.) (7)
 6. V. M. Richter, HISTORY OF MEDICINE IN RUSSIA, I (1814), pp. 30, 31.

Another foreign eye-witness who visited the Kunstkamera in 1721 wrote that, "Among many other subjects . . . I especially noticed . . . the gradual development of the human embryo from the first conception. In bottles filled with spirits, you can see a uterus and in its opening a baby with a completely formed head and face, many forms of babies removed from the uterus, with skin or without skin, with one head but with two faces, other monsters with two heads, four hands, four legs, many fingers and, in addition, a gradual alteration of frogs and their generation from tadpoles...."⁷ The teratological and embryological materials were given to the Kunstkamera (3) either by physicians or by people from different sections of Russian society responding to the famous decree of 1718 (4). After the establishment of Petersburg Academy of Science in 1725, the Kunstkamera was transmitted to its authority, and in 1728 a special building opened for visitors on Vasilevsky island.

The first attempts to study the teratological collections of the Kunstkamera were made by academician Dyuvernuia (5), who, as seen from the following document, had been instructed to investigate the newly received material: "On September 16, 1728 the wife of a Saint Petersburg garrison soldier gave birth to two sons Ivan and Voka, and Ivan had no hands. By the decree of the Academy of Science it was determined that the above mentioned infant be examined by professor of Anatomy Dyuvernuia along with other academy members."⁸ Dyuvernuia made a report on his results: "In the conference Professor Dyuvernuia showed the dead monsters sent from the Admiral board and reported his works on this observation."⁹

Information about monsters received from distant outskirts sometimes showed the extremely serious view of monstrosities by simple Russian people. For example, one

7. F. V. Berkhgol'tsa, DIARY (1721 - 1725). First part, translated from the German by I. F. Ammona. New edition. (Moscow, 1902), quotation on pp. 107 - 108.

8. "Materialy dlya istorii Imper. Akademii nauk" (Materials for the history of the Imperial Academy of science) v. 1, No. 617. October 1728, p. 404, 1885.

9. Ibid., No. 687, March 18, 1729, p. 474.

letter gave a detailed description of a deformed kid. The copy of this letter was received from the office of the main board of Siberian and Kazan factories, and was sent from Samara to the Empress Anna Ivanovna.

On December 10, of this year in the house of the foreman Fedor Elkin, a goat gave birth to a monster kid.... It was certified by the office of the main factory board and also of the pharmacist Krestyan Menders as a monster. It had two heads, white wool, a goatlike body, two separate faces, four eyes, two under the ears, two in the middle of the face, two mouths, four nostrils, two strange ears,....the lower lip was divided on the right side, the left side of the mouth was like that of the natural goat, the lips were curved, and the above mentioned were connected at the sides—left to right and right to left; thus they stood separately and were not connected together. The first side of the face looked to the right, the second to the left; in each mouth the tongue was similar to that of the natural animals. Its nourishment from the mother was not seen but when the pharmacist gave milk in one mouth from a feeding-bottle, it took more in the right mouth than in the left one. But both mouths reacted when one mouth was given food that passed to only one belly. Both mouths could cry, and therefore it seemed as if it had two throats; when one kept silent, the other cried, but if they were free, they cried together... A drawing is given of this kid. In the original the following is written: Major Leontei Ugrimov. Nikifor Kleopin. Timofei Burtsov.

The drawing of the monster-kid is followed by the inscription: "This figure in toto resembles the kid which was born from a goat with white wool, in Ekaterin time, on December 10, 1738. Miron Avramov drew and shaded it."¹⁰

The reorganizing activity of Peter I was expressed, in particular, by sending young people abroad to receive general

10. Ibid., v. IV, No. 1, pp. 1 - 2.

and special education. The first Russian doctor of philosophy and medicine was P. V. Posnikov, who was sent on a mission to Italy in 1692 and received the scientific degree from the University of Padua. Beginning in 1696, going abroad for educational purposes became more frequent. Contact with the Dutch working in Moscow and his visits to Holland in 1697 - 1698 prompted Peter to use the industrial and educational institutions of that country for training the Russian people who were sent abroad.

The journey of Moscow-born Arnold van der Hulst to Holland for medical education is interesting for the present purposes (6). In 1717 in Leyden, he defended a dissertation on the subject "Blood circulation in the fetus"¹¹ (Figure 1). The dissertation opens with an interesting two pages dedicated to Russian Czar Peter Alekseevich. Among other praises the author spoke of Peter as the "tireless prospector and liberal distributor of all arts and sciences, whose cause truly benefits mankind."

The process of conception was regarded by Hulst, from the point of view predominating at that time, as preformationist. He assigned importance to seminal animalcules (which spermatozooids were called); he considered then the true rudiment of the fetus and in the presence of the necessary heat as responsible for its origin (p. 3). Hulst was convinced of the importance of seminal animalcules by his observation of chick embryos, which after some hours of incubation have, according to him, the same structure as that of cock embryos. Both possess swollen heads and curved small bodies. Malpighi had described this as a result of the changes by which they were transformed into chickens. "Similarly," Hulst wrote, "nature acts during the formation of the human body from the semen of men." And he referred to the observations of Ryusch, who during the dissection of a woman's corpse a short time after conception, saw, for the first time, a human embryo, completely similar in form with those worms which Leeuwenhoek had discovered in male semen. "We are not afraid to conclude," Hulst wrote, "that animalcules, which were observed by

11. Arnold van der Hulst, DISPUTATIO MEDICA INAUGURALIS DE CIRCULATIONE SANGUINIS IN FOETU, June 1717, Ludini Batav, 26 pp.

Leeuwenhoek in the semen of men, also are considered the base for the formation of the human fetus" (p. 4).

Turning to the role of woman in reproduction, Hulst, in accordance with current opinions, accepted that the mother "gives the semen a comfortable shelter, warms it and defends it against unsuitable effects" (p. 4). The ovaries were considered the organ of reproduction in women; vesicles formed on their surface. These vesicles (ova) were fertilized by the semen which penetrated into their fluid contents, and they were carried through the fallopian tube to the uterus. Hulst noticed that the changes which the semen caused in the ovum and in the woman's body after conception remained unclear. In any case he considered it established that the internal surface of the uterus, having received the fertilized ovum, became soft because of the outflow of blood from the open ends of the vessels. The ovum sank into this blood-enriched superficial layer, held firmly to it by an outgrowth of rootlets. Near the embryo, over the membrane which covered it (chorion), a plexus of arterial and venous vessels formed, giving origin to the placenta.

Hulst's discussions of the embryonic structure were more or less in accordance with the preformists' presentations, although not in the current primitive form of absolute preformation. Hulst confirmed that:

the body of the extremely delicate embryo, united with the placenta by means of the so-called umbilical cord, represents not an accidental union of parts, but a production of divine art according to high mathematical law. It is composed of two kinds of parts—compact and fluid. The compact parts contain the delicate and weak vessels, which are so small that they are difficult to see even with the aided eye. A transparent fluid flows in them, its movement stimulated by the heat of the mother.... From this originally transparent fluid arises pinkish moisture, which eventually becomes red and acquires the characteristics of true blood which is similar in the yolk. In that moment, when this purple-colored fluid appears, the complicated machine arises. This machine is called the heart, with the auricles, two veins, and two arteries belonging to it. (p. 9)

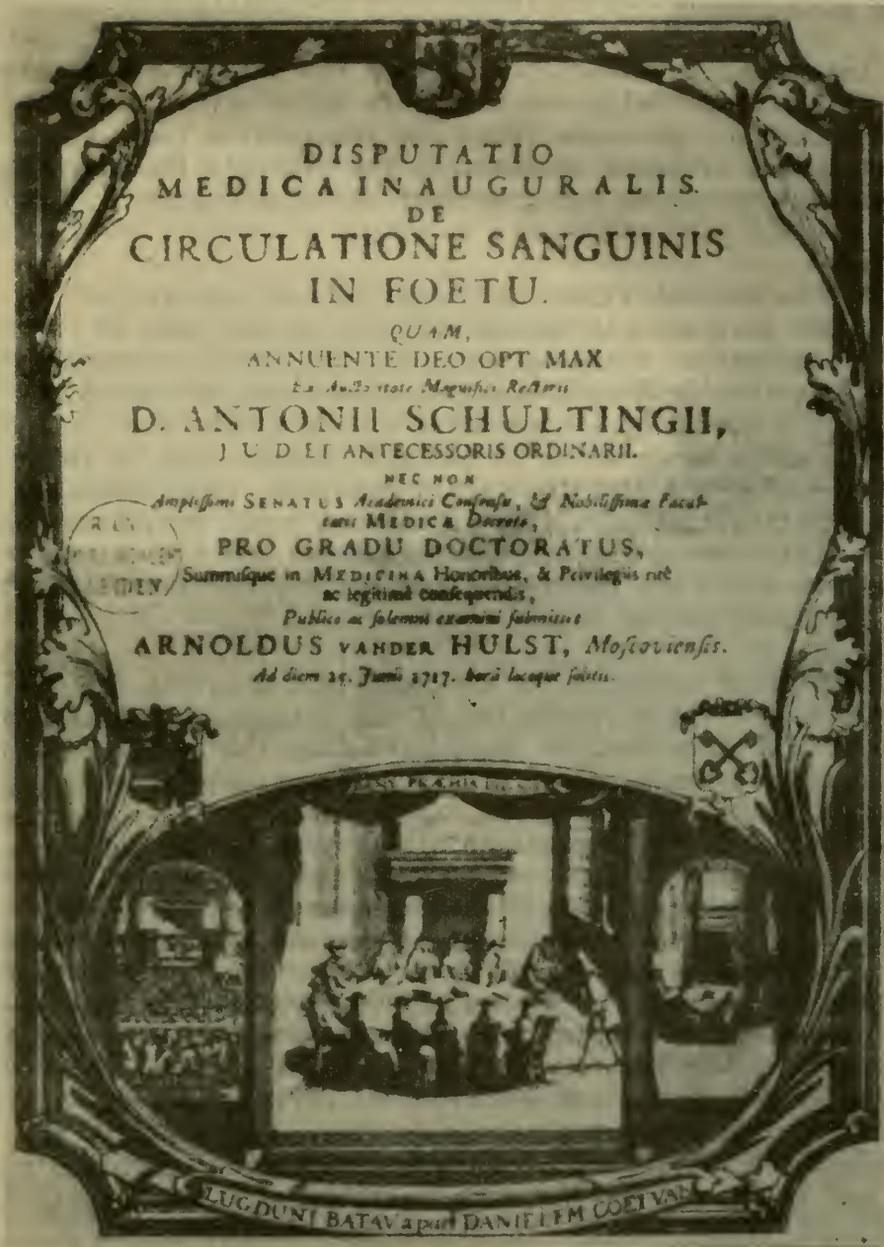


Figure 1. The title page of the dissertation of Arnold van der Hulst.

The subsequent life of the fetus depends on the start of blood circulation.

Later, Hulst discussed at length the anatomy of the heart and vessels, especially the structure and activity of the blood system of the human fetus. He returned to the participation of blood movement in the system's formation in one of the concluding paragraphs of his dissertation. "Thus," Hulst wrote,

when contemplating the origin of our life it is not difficult to understand that at the time of conception, when the semen of the father is shared with the mother, mechanical structures pre-exist. As a result of the movement of the fluid, the pumping heart later on becomes visible. Due to its beating and distribution of moisture, which provides nutrition, the vessels expand and grow. The fetus increases by insensible increments, and all that was fluid and hardly visible shortly before becomes compact and is easily observed. (p. 25)

From these extracts, it is clear that Hulst on the one hand voted for the preformation of the fetus in a spermatozoid, while on the other hand he considered that the formation of the fetus is accomplished by the new formation of these important parts, including the heart, blood vessels, and blood. Thus, the theoretical opinions of the young Moscow doctor of medicine did not move beyond the traditional opinions of the beginning of the eighteenth century, although he did avoid the incorrect extreme of preformation.

The journeys abroad of Russian young people in the eighteenth century were either for preparation of specialists and practical workers, or for replenishment of national science personnel for two principal scientific centers—the Academy of Science in Petersburg and Moscow University. In its first ten years, Moscow University followed Lomonosov's plan and filled all its vacancies with Russian professors.¹²

12. N. A. Penchko, OSNAVANIE MOSKOVSKOGO UNIVERSITETA (The foundation of Moscow University), Moscow, 1953, 190 pp.

In the Academy of Science, the struggle against the dominant foreign specialists was more difficult and lasted for a long time. Among the foreign academicians and those who had come to Russia only out of mercenary inducements and opportunism, a group of authentic scientists was quickly distinguished. They gave their adopted land all their strength and abilities. In this group, besides Eiler, Pallas, Gmelin and others, we must include Kaspar Friedrich Wolff, who arrived in Russia in the spring of 1767.

The arrival of Wolff in Petersburg coincided with the return of the academic museum, the Kunstkamera, to its previous building, which was re-established after its 1747 fire. The zoological collections of the Kunstkamera were entrusted to Pallas, the botanical to Gmelin, and the anatomical (and embryological) to Wolff.¹³ When the first two academicians left for an expedition to study Russia's natural resources, the guidance of all natural history collections of the Kunstkamera was placed under Wolff. In addition he was delegated to receive the collections of the expeditions and to assure the safety of those scientific materials.¹⁴ This vast organizational work did not prevent Wolff from starting his serious study of the continuously growing anatomical and embryological collections of the Kunstkamera. While in Russia he devoted himself to this ongoing activity.

The years before Wolff's arrival in Petersburg, the Academy of Science suffered a heavy loss. Mikhail Vasilevich Lomonosov died at the prime of his creative power. Strong traditions of strict investigation and materialism are connected in Russian sciences with the name and genius of Lomonosov. "One experiment," Lomonosov wrote, "I prefer to six hundred opinions, born only by imagination."¹⁵ Along

13. T. V. Stanyukovich, KUNSTKAMERA PETERBURGSKOI AKADEMII NAUK (Kunstkamera of Petersburg Academy of Science) (Moscow: Akademii nauk, 1953), p. 142.

14. *Ibid.*, pp. 149, 154.

15. Mikhail Vasil'evich Lomonosov, IZBRANNYE FILOSOFSKIE SOCHINENIYA (Selected philosophical works), edited and preface by G. Vasetsky (Moscow, 1940), p. 109. In the Latin original Lomonosov wrote "sexcenti," which means not only "six hundred" but "a great number." Thus, of course, this expression must be translated.

with the confirmation of the importance of empirical investigations for science and its practical applications, Lomonosov tirelessly showed the necessity of materialistic explanations for all phenomena of nature. He rejected the interference of the supernatural and underlined the changeability of all existing things. "And at least it must not be attributed to miracles," he wrote at the beginning of 1760. In his work, "The first fundamentals of metallurgy or mining," Lomonosov spoke in 1763 about the necessity of historical study of natural bodies, and he caustically made fun of the supporters of metaphysical opinions about the unchangeability of any body of nature.

It must be little understood that the visible corporeal or terrestrial substances of the world are not in this condition from the beginning of their creation....but that great changes took place in them.... Thus many think wrongfully, that....from the beginning the creator built not only mountains, valleys and water, but also the different kinds of minerals, and therefore, it is not necessary to investigate the causes, for their internal nature and different places of location. These discussions are extremely harmful to the advancement of all sciences,...although it is easier to be a clever man and philosopher by learning by heart three words: 'God thus built,' and giving them as the answer for creation.¹⁶

Simultaneously, Lomonosov sought the material structure of all natural bodies. In "The course of true physical chemistry," (1752 - 1754) he wrote the following:

All bodies are divided into organic (organized) and non-organic. The organic parts of bodies appear interconnected so that all mutually united parts have one casual origin.... We consider organic... the natural bodies, namely animal and plant kingdoms in which fibers, ducts, vessels, juices are known and must be regarded as one whole. In addition, although the organs of the animals and plants are delicate, they are composed of smaller particles. These are from the non-organic, i.e. from mixed

16. Ibid., p. 270.

bodies, because during chemical operations their organized structure is destroyed and then produce mixed bodies. In this way, all that is produced from the animal and plant bodies by nature or art constitutes mixed bodies, or chemical materials.¹⁷

These brief extracts show the way Russian sciences advanced and how scientific work developed from the middle of the eighteenth century.

K. F. Wolff was considered one of the brilliant representatives of Russian science during Lomonosov's epoch. Although tributes to Lomonosov's traditions in the Petersburg Academy of Science were counteracted by some foreigners, Lomonosov's ideas had become rooted deeply in Russian public opinion of that time. The consequence of this negative feeling was the cautious selection of foreign scientists. Preference was given to those who were determined to explore new ideas in Russia permanently. K.F. Wolff unquestionably satisfied these conditions.

Wolff's dissertation, "Theoria generationis," and the popular statements of its underlying principles in a German book of the same name, came prior to his move to Russia in 1767. At the Petersburg Academy of Science, Wolff continued to work out embryological problems. From 1766 to 1768, he published in Russia his vast memoirs "About the formation of the intestine," which had almost the same significance as his above-mentioned works.

After this, Wolff turned to the study of monsters, using the teratological collection of the Kunstkamera and carrying out extremely thorough investigation of the materials collected there. He published only three works on this subject. The greater part of his description, together with the theoretical considerations concerning human and animal monsters remained unpublished. Only recently, a part of these manuscripts was published, in extracts, by B. E. Raikov.¹⁸

17. *Ibid.*, p. 214.

18. B. E. Raikov, OCHERKI PO ISTORII EVOLYUTSIONNOI IDEI V ROSSII DO DARVINA (Essays on the history of evolutionary ideas in Russia before Darwin) (Moscow: Akademii nauk, 1947), pp. 46 - 94.

The significance of the works of Wolff, who in fairness is considered the founder of embryology as a science, can scarcely be exaggerated. His advanced ideas about embryonic development found favorable ground in the Petersburg Academy of Science and received a practical base in the embryological and teratological collections of the *Kunstkamera*.

One of Wolff's most important services, as is known, is the substantiation and the empirical proof of the epigenesis principle. The establishment of the epigenetic character of individual development made the existence of embryology as a science possible, because the preformation theory predominating before disclaimed any qualitative change in the organism from the ovum to the fully formed condition. The principle of epigenesis as a study of the qualitative changes during the individual life of the organism consequently set up the basis of evolutionary, historical views of organic nature.

In his lectures on general zoology,¹⁹ K. F. Rulé was almost the first to connect the epigenesis principle with an historical viewpoint. The following extracts are from these lectures. "In nature, in the world of phenomena," Rulé wrote, "there is nothing that existed from the beginning; all existing things are formed from non-existing things; all the following are formed from repetitions of the foregoing with the addition of the new; all is formed by constant slow development (Epigenesis)" (p. 11). And later on: "In order to understand how the animal is organized now, one must first understand how it has been up to the present moment; its formation in space becomes understood by appreciating its origin in time. Zoognosis is based on Zoogenesis" (p. 12). "...all Zoogenesis is only an expression of the common fact of genetic development: epigenesis directly opposes the present view of investment of the embryo (*Emboîtement des germes*) or preexistence of the embryo (*Préexistence des germes*), which was held by (Georges Cuvier) himself" (pp. 12 - 13). In the following pages Rulé gives brilliant

19. K(arl) F(rantsovich) Rulé (Charles Rouillier), "Chteniya ekstra-ordinarnogo professora Rulé, 1850. Obshchaya zoologiya" (Lectures of Extraordinary Professor Rulé, 1850, General Zoology) (Litografir. izdanie), pp. 11 ff. The author has to thank S. R. Mikulinsky for indication of this source.

criticism of the idea of preformation and shows how the principle of epigenesis, the "law of intercourse of the animal with the world," (p. 16) is realized in the historical development of organisms.

Later on, Wolff's observations that the embryo in the early stages is composed from layers, later called embryonic layers, gained great importance. The study of the embryonic layers, as the common form of development of all multicellular animals, in the second half of the nineteenth century became the base of comparative embryology. Creation and detailed elaboration of this progressive direction in the study of ontogenesis constitute the glory of Russian science.

In order to evaluate to the necessary extent the greatness of Wolff's scientific exploits, especially his development of the theory of epigenesis, it is necessary to give a brief essay of the history of the struggle between supporters of preformation (preexistence) and epigenesis (new formation), which represented a struggle of two outlooks, two metaphysical and historical opinions of the world of living creatures.

CHAPTER 2

PREFORMATION OR NEW FORMATION?

The clash of the two mutually incompatible points of view on the development of the organism: preformation, or the doctrine of preexistence; and epigenesis, or the doctrine of new formation, can be traced far back in history. Epigenetic opinions had been stated by Aristotle, who knew well from his own observations on the developing chick embryo, that the organs of the latter appear not all at once, but in determined succession. He criticized what came, apparently from the authors of the "Hippocratic collection," who stated that all parts of the embryo appear simultaneously. (8)

Aristotle's ideas possess epigenetic and materialistic contents. However, Aristotle's epigenetic opinions and his materialism, as is known, were inconsistent. His fluctuations between materialism and idealism, about which V. I. Lenin wrote,¹ appear in his opinions about development, and the materialistic idea contradicts his opinion that all epigenesis is an idealistic doctrine. This latter erroneous view also appears throughout the works of the founder of recent epigenesis, K. F. Wolff.

The epigenetic point of view on vertebrate development was also stated distinctly by W(illiam) Harvey (1651) in his book "On the Origin of Animals." He, to a significant extent, followed Aristotle. Harvey, like Aristotle, accepted epigenesis for the perfect animals, while the imperfect animals, in his opinion, originated from mold. Harvey differentiated three distinct modes of generation and development of animals: epigenesis, metamorphosis, and spontaneous generation, the last two ways, according to Harvey, inherent in insects.

1. See (Vladimir Ilyich Ulyanov) Lenin, FILOSOFSKIE TETRADI (Philosophical notebooks) (Gospolitizdat, 1947), pp. 263 - 270.

Harvey's merits are undoubtedly overstated by his British compatriot J(oseph) Needham,² who dedicated several enthusiastic pages to him. Needham was obliged to admit that Harvey "did not break with Aristotelianism, . . . but on the contrary lent his authority to a moribund outlook"

Harvey's opinions were much more objectively evaluated by an early historian of biology, J. Beseke, in his book published in Russia at the end of the eighteenth century.³ Beseke noted that "the plastic power" by which Harvey tried to explain Aristotelian epigenesis, in fact did not explain anything, and that Harvey, with his presentation about the three ways of generation, was in fact far from his own principle that "An egg is the common origin of all animals." Proof of this latter general conclusion does not belong to Harvey but to (Francesco) Redi, who proved experimentally that the larvae of meat flies develop not from rotten meat, but from eggs laid by the flies.

In the middle of the seventeenth century the defense of epigenetic opinions, as J. Needham correctly noted, was a step backwards towards Aristotle. It did not require the courage and independence of ideas which proved necessary at the middle of the eighteenth century, when the ideas of preformation became predominant. The emergence of these preformationist ideas began in the second half of the seventeenth century, connected with the oblivion of Descartes' philosophical opinions and Harvey's theoretical propositions. Descartes' biological opinions, mechanical and epigenetic in character, had an acknowledged influence on the development of embryology. His presentations about the embryonic development of animals are stated in the treatise, "Treatise on the Human Body." (9)

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2. J(oseph) Needham, A HISTORY OF EMBRYOLOGY, pp. 166 - 167. (Ed.: References are to the German edition, p. 149 of 2nd ed., New York: Abelard-Schuman, 1959.)
 3. J(ohann) M(elchior) G(ottlieb) Beseke, VERSUCH EINER GESCHICHTE DER HYPOTHESEN ÜBER DIE ERZEUGUNG DER THIERE, WIE AUCH EINER GESCHICHTE DES URSPRUNGS DER EINTEILUNG DER NATURKÖRPER IN DREY REICHE. Mitau, Steffenhagen, 1797 (12 unnumbered + 130 pp.).

Apparently the only great biological theory generated in the seventeenth century was the theory of preformation. According to that theory, the embryonic organism is minute at the earliest period of its existence. (10) One of the earliest defenders of this theory was Marcello Malpighi, who considered that in the egg, in a coagulated condition, there is a completely prepared animal which needs for its unfolding a flow of nutrition.

The preformationists explained that the difficulty or impossibility of seeing parts of the adult creature in the embryo occurs because the organisms are small in number, transparent, and rolled up like balls of thread. The transformation from the apparently uniform homogeneity of the microscopically small embryo to the perceptible polymorphism of the formed organism, i.e. development, was interpreted by the preformists as a thickening of parts and organs, and their development (evolutio) was the untangling of the clew. The etymology of "development" (the origin of this word has been completely lost) undoubtedly finds its origin in preformationist representations.⁴

Malpighi's preformationist theory was keenly received by his contemporaries. Embryological works and philosophical writings appeared, their conclusions coinciding to a degree with Malpighi's. The factual data for supporting preformation was achieved by Jan Swammerdam (1637 - 1685); he reached his conclusions from investigation of metamorphosis in insects and some other arthropods. Apparently, Swammerdam was one of the first to revive the idea of generations of embryos enclosed one within the other.

The logical consequence of the preformation theory, the doctrine about "enclosing" of embryos, is not considered a creation of the seventeenth century. Its sources can be traced back to the fourth century of our era.⁵ The philosophers

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4. The Russian word "razvitie" for "development" (also Latin, "*evolutio*"; German, "Entwicklung"; English and French, "development" and "développement"; Italian, "svillupo") means unrolling of anything which was originally wrapped up.
 5. See A. D. Nekrasov, OPLODOTVORENIE V ZHIVOTNOM TSARSTVE. ISTORIYA PROBLEMY (Fertilization in the animal kingdom. Historical problems), Moscow, 1930, p. 67.

at the end of the seventeenth century, in particular Malebranche and Leibnitz, interpreted the theory of preformation and the idea of "enclosing." Nicolas de Malebranche, as seen in his main work, "Search for Truth," did not see any improbability in the idea of the eternally great number of embryos wrapped within each other. (11) Malebranche, however, cannot be related to the contemporary preformationists, since he took for granted the changes which originate in the fetus under influences felt by the mother during pregnancy. (12) From Malebranche's example it can be seen that the doctrine of "enclosing" did not necessarily connect the thinkers of the seventeenth century with the complete theory of preformation, but more often the two were nonetheless connected.

Preformism lies at the base of Leibnitz's opinions. Leibnitz imagined that the existence of the individual substances and bodies of nature proceed from the assumption about the substantial forms or monads, from which is realized the idea of unity of contents and form, material and power, body and soul. The acting powers of nature or monads are primordial and indestructible. From this comes the conclusion that life is also primordial, and therefore there is no basis for supposing that any dead body can become living. Leibnitz decidedly objected to the assumption of spontaneous generation. (13) The impossibility of spontaneous generation and the preexistence of the formed organism nearly led Leibnitz to the idea of the "enclosing." (14) According to Leibnitz, the beginning and the end of the individual do not exist; the origin of the organism consists of extension and development of the preexisting organs, and death is rolling up of the individuality. Leibnitz's understanding of development (*evolutio*) was not historical (change in time), but rational, i.e. a doctrine about the succession of ideas.

Biology of the eighteenth century adopted Leibnitz's idea, which was equal to his other proposition known as the law of continuity of natural phenomena. The biologist-Leibnitzians used the idea of continuity for the foundation of their doctrine of "the chain of being." The internal connection between the idea of preformation and the idea of a continuity of bodies of nature, resulting from Leibnitz's general philosophical conceptions (15), sometimes was kept

(Haller, Bonnet) and sometimes was broken. At that time the idea of "the steps" was combined with the epigenetic opinions on development (Radishchev).

The preformation of the eighteenth century heavily leaned on two trends developed in the previous one hundred years, concerning the bearer of the preformation—whether spermatozoid or ovum. The supporters of spermatozoid preformation were called animalculists (from animalculum = animals, which the spermatozoids were called; these were discovered in the seminal fluid by Ham and Leeuwenhoek in 1677). The supporters of preformation of the embryo in the ovum were named the ovists;⁶ these latter were more numerous and include Haller, Bonnet, Vallisneri and others.

If Vallisneri, as fairly suggested by A. D. Nekrasov, is considered not more than a compiler, Albrecht von Haller and Charles Bonnet were undoubtedly the original investigators. Their theoretical opinions on the development of the organism did not rise, however, above the level of Vallisneri's presentations.

Haller, who was an early supporter of epigenesis, arrived at the idea of preformation from his own investigations of chick development. (16) These investigations do not give any proof of pre-existence of the organism in the egg, because Haller assumed a close connection of the chicken embryo with the yolk and erroneously took the yolk sac for the yolk membrane. Consolidating the position of preformation, Haller took this doctrine up the hypothesis of "enclosing" (17) and denied the possibility of the new formation in embryonic development. Haller's aphorisms, "No epigenesis exists" and "No part of the animal appears before the others, and all are simultaneously created," were extremely popular in the second half of the eighteenth century. Haller formulated his discussions more cautiously than Bonnet, and he was willing to discuss the arguments for epigenesis; he positively evaluated wolff's dissertation although he did not agree with his final conclusions.

6. For details about the animalculists and ovists of the 18th century see the books of A. D. Nekrasov, FERTILIZATION IN THE ANIMAL KINGDOM (1930) and Joseph Needham, HISTORY OF EMBRYOLOGY.

Bonnet was distinguished, on the contrary, by his extreme straightforwardness and his intolerant relations with his theoretical opponents. Bonnet became a supporter of preformation mainly on the basis of his discovery of parthenogenesis in aphids, i.e. the development of their ova without fertilization, and many other observations, in particular of reproduction of the colonial flagellate Volvox. These data, especially about virginal reproduction in aphids *Aphis rosae*, were taken by the supporters of the theory of "enclosing" as grounds for the triumph of ovists over animalculists. (18)

Bonnet, more decidedly than Haller, defended the hypothesis of "enclosing" and spoke about it as the greatest triumph of reason over sensual perception. Bonnet objected to epigenetic presentations, which judged the moment of organ formation to be when these organs become visible. Bonnet suggested that "inactivity, a state of quiescence, or transparency of some of these parts can make them invisible to us when, in fact, they do exist."⁷ To the hypothesis of "enclosing" Bonnet added one more arbitrary assumption, calling for explanation of the phenomena of vegetative reproduction and regeneration: he considered that in animal bodies there are preformed organ rudiments for the restoration of any disturbed unity of the organism.

The idea of "enclosing" was strongly related by the animalculists to spermatozoids, and was related by the ovists to the ova. The fantasy of animalculists was repeatedly ridiculed by the contemporaries, including ovists such as Vallisneri. Greater material for mockery than these fantasies, especially the idea of "enclosing" of countless generations in each other, is reflected by one who was not directly connected with science, but who soberly evaluated the scientific theories of his time. Jonathan Swift's immortal book, which has provided favorite reading for nearly three hundred years of adults and children, satirizes the imaginations of his contemporary microscopists, hinting at the hypothesis of "enclosing" as:

7. Ch(arles) Bonnet. CONSIDERATIONS SUR LES CORPS ORGANISES (Amsterdam: Chez Marc-Michel Rey, 1762), part 1, p. 87.

Fleas, so naturalists say,
Have smaller fleas that on them prey.
And these have smaller still to bite 'em,
And so proceed *ad infinitum*.⁸

Georges Buffon was an inconsistent opponent of the preformation theory. He objected to the theory of "enclosing" and considered that "the organism is something organized in all its parts, developing from an infinite number of similar figures and similar parts into an aggregate of embryos or small embryos or small individuals of its kind." Buffon reached this conclusion by considering the vegetative reproduction of plants and the results of Trembley's experiments on hydra, which showed the possibility of restoring the whole individual from any part of the polyp. Buffon's assumption about the existence of "living particles," from which complicated organisms are composed, is considered an echo of Leibnitz's doctrine on monads. The embryo, according to Buffon, is built from particles and nutrients which are distributed in it according to some internal form or model (moûle intérieur). This opinion represents an attempt to reconcile preformation (presence of a preexisting internal model) with epigenesis (gradual formation of the developing organism from the nutrients received from without).

Buffon's opinions were widely known to readers because of the great popularity of his works, which were written in lively and picturesque language.⁹ Because of their inconsistencies, however, Buffon's opinions did not show the essential clash between the ideas of preformation and epigenesis. The theory of preformation along with the hypothesis of "enclosing" of the embryos remained predominant to the end of the eighteenth century, despite K. F. Wolff's works which had already struck a shattering blow.

8. (Ed.: "On Poetry" (1733). Actually a well-known ditty by Jonathan Swift.)

9. Pushkin called Buffon "the great pictorialist of nature." "The style of his blooming always will be an example of descriptive prose" (A. S. Pushkin, POLNOE SOBRANIE SOCHINENII (Complete collected works) in 6 volumes, (Moscow, 1936), v. VI, p. 24).

CHAPTER 3

KASPAR FRIEDRICH WOLFF AND SUBSTANTIATION OF THE THEORY OF EPIGENESIS

If in the works of Buffon and other naturalists of the eighteenth century it is possible to find timid attempts to oppose the idea of preformation in its indistinctly formulated and inconsistent form, the predominating doctrine of preformation met a decisive and courageous opponent in K. F. Wolff. Wolff presented logically complete and well-founded facts of the theory of epigenesis, i.e., that the development of individuals involved a new formation.

With great effort B. E. Raikov extracted from undeserved oblivion Wolff's great manuscript and, in addition, included in his book the contents of some of Wolff's published works. However, he was interested mainly in Wolff's transformist presentations, and, supposing that Wolff's embryological works were well known,¹ Raikov elucidated the latter only briefly. He considered in particular Wolff's remarkable embryological work on the development of the chick's digestive canal. He insufficiently reviewed Wolff's last published theoretical work, "About the Essential Power." Therefore, in order to form an appreciation of Wolff's importance as the forefather of embryological science, it is necessary to elucidate his work in more detail, particularly that on embryonic development. This is also necessary because the biographical and critical literature about Wolff is scanty (19), and sometimes his life and scientific activity is misrepresented.

Even Goethe was interested in Wolff's personality and works, because Wolff was his direct predecessor in the doctrine of the metamorphosis of parts of plants. In relation to the epigenesis theory, Goethe collected only scanty data on Wolff, and,

1. The printed works of Wolff were little known even by his contemporaries.

following Kant, Goethe incorrectly evaluated wolff's true role, crediting undeserved recognition to (Johann Friedrich) Blumenbach. (20)

Wolff's biographer A. Kirchhoff² called him the great German physiologist. More than fifty years before this Johann Friedrich Meckel, Jr., in his preface to his translation from Latin to German of Wolff's work, "On the Formation of the Intestinal Canal in the Incubated Chicken Egg," sought to attract attention to the author's work. Wolff is considered German by nationality and one "whom the Germans can speak about with pride and can compare with any great names of any other country."³ K. F. Wolff was born in Berlin in 1734.⁴ He studied medicine in Berlin and then in Halle, where he finished at the university in 1759. In the same year he published his dissertation, "Theoria Generationis." His work on the same subject, in a more popular form, was published in German in 1764. After this, in early 1767, he moved to Russia, at the invitation of the Petersburg Academy of Science. There he remained to the end of his life. The period of Wolff's scientific activity in Germany covered eight years only. For more than two years he lost touch with his research work because he participated in the Seven Years War as a doctor in a field hospital. The publication of his dissertation, in which Wolff came out against the universally recognized authorities, turned the representatives of official German science against him; his aspiration to become a professor in the Berlin Medico-Surgical Institute was rejected in an insulting way, and this removed all possibility of continuing his scientific work in his motherland.

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2. A. Kirchhoff, "Caspar Friedrich Wolff: sein Leben und seine Bedeutung für die Lehre von der organischen Entwicklung," in JENAISCHE ZEITSCHRIFT FÜR MEDIZIN UND NATURWISSENSCHAFT, 4 (1868), pp. 193 - 220.
 3. Introductory article of Meckel, p. 3.
 4. This date is considered more exact than that usually indicated, 1733. See J. Schuster, "C. Fr. Wolff. Leben und Gestalt eines deutschen Biologen," SITZ. BER. GES. NATURF., Berlin, 1936 (cited by G(eorg) Uschmann, CASPAR FRIEDRICH WOLFF, EIN PIONIER DER MODERNEN EMBRYOLOGIE (Leipzig: Urania-Verlag, 1955).)

The Petersburg Academy of Science selected Wolff as a member. It gave him those material conditions which he needed for his work, and for twenty-seven years it supported him in his scientific work. He was ensured the right to prepare his works for publication and to publish them. In the year following his arrival at the Petersburg Academy, Wolff began to publish, in "New Commentaries of the Petersburg Academy," his vast work (nearly 150 pages in quarto) in Latin on the development of the intestine. In 1789 the Academy published Wolff's great theoretical work on the essential power (about 100 pages in quarto), and also in the period from 1770 to 1780, fourteen anatomical and teratological works. What about the great manuscripts of Wolff which remain unpublished? These manuscripts were not completed for print by the author himself and were fragments of a larger work, the work which was interrupted by his sudden death in 1794. The supposition of B. E. Raikov that Wolff's main manuscripts remained unpublished because the representatives of the Russian scientific world, in particular academicians A. P. Protasov and I. I. Lepekhin, did not want to support him, and that Wolff in Russia "lived in ideological loneliness," is a supposition only. It is insufficiently grounded because at that time in Russia, the academicians S. Ya. Rumovsky and F. Epinus, who worked on physiological investigations to which Wolff referred in his work about the essential power (1789), and also professors M. M. Terekhovskiy, N. M. Maksimovich-Ambodich, A. M. Shumlyansky and other investigators, were able to understand Wolff's ideas and to evaluate the significance of his investigations.

There is reason to believe that the educated Russian people were seriously interested in these problems, which constituted the subject of Wolff's scientific investigations and reflections. The discussions of these people, as recorded by Antiokh Dmitrevich and historian Vasily Nikitich Tatishchev, serve as evidence of this. Tatishchev's work, "Conversation about the benefit of sciences and schools,"⁵ was begun in 1733 and continued for many successive years; it was published after more than 150 years. It stated, for example, these advanced

5. V. N. Tatishchev, RAZGOVOR DVYKH PRIYATELEI O POL'ZE NAUK I UCHILISHCH (Conversation of two friends about the benefit of science and schools), with preface and index by Nil Popov (1887).

conclusions about scientific proofs: "In physiological and natural matters no proof is needed; they are proved by themselves, i.e. the natural circumstances must be confirmed" (answer to the 97th question, p. 133). There also, Tatishchev was concerned about the question of the origin of the soul in the developing fetus, and he attempted to find its origin in the "enclosing" of the preformation hypothesis. He wrote:

Earlier an opinion existed about weeds, that in the semen of each, something is found which is capable of producing growth of all organs and semen. Leeuwenhoek, through his extremely intricate work with the microscope or magnifying glass, examined the male outpouring of animalcules which are similar to newly born frogs or tadpoles: wide, circular, or oblong bodies with tails, many of which are present in one drop. In real semen they constitute the living things which reach the female ovum where they find nutrition. The body begins to grow, and later on all the parts, although extremely small and immature, grow completely as in man. Adam's semen included all souls that are created. (Answer to the 14th question, p. 8)

Kantemir, on the contrary, announced himself as a supporter of the epigenetic point of view. In work neither published nor completely finished during his life, which in posthumous publication conditionally received the name, "Letters about Nature and Man,"⁶ Kantemir presented the following discussion:

They (animals) can, in endless ages, extend their kind; their creator put this possibility into them from the beginning. Let us say that the multiplication of their kind begins with the semen of the species which eternally abides in them and prepares a special messenger which exists in them at birth The embryos or semen in animals and cattle which have been prepared through infinite ages must possess the form of their bodies according to kind. Through growth

6. SOCHENENIYA, PESMA I IZBRANNYE PEREVODY KNYAZYA ANTIOKHA DMITRIEVICHA KANTEMIRA (Works, letters and selected translations of Prince Antiokh Dmitrievich Kantemir), edited by P(etr) A(leksandrovich) Efremov, vol. 2, 1868.

in the womb they will be born. There will be further creation of the above mentioned which is impossible to understand. The basis of all that is animal needs, comprehensive wisdom, and art. However, if it is thus, then: first, the basis of this animal has in its smallest stage all internal and external parts; and, second, it is necessary that each embryo has, in itself also, the possibility to be propagated into infinite kinds. Is it possible that the mind understands the complex preparation in one embryo of a number of creatures? (pp. 43 - 44)

To this extract it must be added that Wolff's time in Petersburg coincided with that of A. N. Radishchev, who returned from abroad in 1771 and was arrested in 1790. Radishchev, due to his unusual and wide scientific interests and enormous erudition, was acquainted with Wolff's works and related to him with sympathy. It is clear that, in a treatise "About man, his death and immortality," Radishchev definitively stated his epigenetic view (as discussed later).

From the foregoing, the conclusion can be reached that in Germany Wolff was not evaluated as a first class investigator and advanced thinker. This forced him to move to Russia, and therefore Germany does not have the right to claim Wolff's glory. In fairness he must be considered a Russian scientist. He must not be compared in any case with those foreign academicians of Petersburg, who moved to Russia for a short time for material considerations and did not firmly involve themselves with Russian science. Unjustly, Kirchhoff wrote about Wolff's decision to move to Russia that: "Of course, this was a decision connected with renunciation; he must then live far from his native country, in a cold northern country, without constant renewal from enthusiastic students and intimate contact with European science."

It is well known that the representatives of European science, in the persons of Bonnet, Haller, Meckel Sr. and others, did not wish to admit Wolff into their midst; about these opinions Meckel Jr. and Kirchhoff passed over in silence. Also, B. E. Raikov's⁷ statement that in Russia Wolff had no

7. Raikov, ESSAYS ON THE HISTORY OF EVOLUTIONARY IDEAS IN RUSSIA, p. 70.

students or supporters is not completely accurate. (21) Below (see Chapters 9 and 11) it will be shown that epigenetic opinions, based on Wolff's theoretical propositions and observations, enjoyed in Russia at the end of the eighteenth century and at the beginning of the nineteenth century sufficiently wide distribution. S. G. Zybelin, D. A. Golitsyn, I. Beseke, M. Kh. Peken, N. M. Maksimovich-Ambodic, A. N. Radishchev, and later on L. Tredern, all stated them.



Figure 2. Silhouette of Kaspar Friedrich Wolff made by F. Anting (1784); the only existing picture of Wolff

CHAPTER 4

THE "THEORY OF GENERATION" OF K. F. WOLFF

Wolff's first work, with which he began to found the epigenetic theory and his struggle against preformation, was his Latin dissertation, *THEORIA GENERATIONIS*,¹ to which his German book under the same title is related.² Wolff's factual data and his opinions appear strictly and systematically in *THEORIA GENERATIONIS*. *THEORIE VON DER GENERATION* provides necessary additions and explanations.

Wolff's dissertation begins with the established plan of the whole work. First, Wolff determined "the development of the organized body" as the appearance of all parts of this body (§ 1). He sent a compliment to the "famous Haller," who, in Wolff's words, discovered the laws of development, i.e. found the influence of the power of the living body by which its formation is accomplished (§ 2). The compliment to Haller cannot be explained by the real merits of the latter in the creation of the development theory. But its purpose can be seen from Wolff's letters to Haller, in which Wolff hoped to attract the famous physiologist to his side and to convince him of the correctness of his own opinions. This phrase about Haller stands in direct contradiction with the contents of the following thesis, in which Wolff spoke directly against the preformation (predelineation) theory, i.e. in fact against Haller. This famous thesis runs as follows (§ 3): "The defenders of a predelineation system do not explain the phenomenon of generation, but confirm that this does not exist." In his dissertation, Wolff clearly,

1. Kaspar Friedrich Wolff, *THEORIA GENERATIONIS*, Halae ad Salam, 1759, 146 pp. In the present work the Latin text is used and also its German translation, Leipzig, 1896, 95 + 98 pp.

2. Kaspar Friedrich Wolff, *THEORIE VON DER GENERATION. IN ZWO ABHANDLUNGEN ERKLART UND BEWIESEN*, Berlin: F. W. Birnstiel, 1764, 16 + 284 pp.

concisely, and completely expressed the correct idea that the preformation theory, assuming the preformation of the organism in the early embryo, as a matter of fact denies the real development formation of living creatures. Wolff made it his task to produce a theory of development, based upon principles and laws (§ 5), and which "can show sufficient basis of the origin of the living creature" (§ 6). The true theory of development must show the causes of development of the organism, i.e. must represent its philosophical cognition, that being the real science of organized bodies (§ 10). According to Wolff, the doctrine about development, as related to anatomy, is purely a descriptive understanding of living bodies and the philosophical cognition of substances related to their historical cognition; therefore the theory of development can be called "rational anatomy" (§ 11). In his German volume, Wolff detailed the contrast of historical and philosophical cognitions. The explanation of composition of a whole from parts and the description of these parts represents the task of the historical cognition. If the knowledge comes not only from direct experiment, but also from causes and bases, then this gives grounds for concluding that the substance must be this and not another, and that it necessarily possesses determined characters. If this is the case, then it will not be historical knowledge, but philosophical cognition.³ The theory of development must explain the phenomena of nutrition and growth, and also the formation of the constituent parts of the organism (§ 24). It must take into consideration all essential and also less essential conditions, and it must investigate why this or that process of development proceeds in one way and not in another way (§ 25).

Already from Wolff's program, it is clear that he took upon himself a task of extraordinary importance: to give the general theory of the formation and development of living creatures and its contrast to the false theory of ontogenesis, which was unconditionally doctrinaire about preformation. He underlined the importance of a theory founded upon facts rather than upon groundless discussions. "I cannot agree in any case," he wrote, "that it can be performed by those.... who hold speeches about this subject, as if there were no science, truth and grace" (§ 4, Introduction).

3. THEORIE VON DER GENERATION, p. 8.

The first part of the dissertation is dedicated to plant development. In this part Wolff postulated in plants the presence of "power, which is fluid collected from earth, forced to act in the root, and distributed throughout the plant, part of which is consumed in different places, and part of which leaves the plant" (§ 1). He called this power "the essential power of the plant" (§ 4).

Before speaking about the effect of the essential power on development, Wolff considered the structure of the young rudiments of leaves, derived from buds. Using imperfect optical means, he could nonetheless see distinctly that this rudiment was derived from those structural formations which exist in the formed leaf, namely the fibers and vessels. The rudiment consists of transparent vesicles or, as in the seed of a bean, of a light, homogenous substance. At the beginning, vesicles are so few in number that they can be easily counted, and Wolff found not more than twenty in the young rudiments of the leaf. The number of vesicles increases ("soon they become innumerable" § 8), while the size of each vesicle remains as before. Very early, a few vessels appear in the apex of the stem, the number later increasing visibly.

The formation of new vesicles and new vessels takes place, according to Wolff, in the following way. The delicate homogenous substance filling the spaces between the vesicles is extended by the flowing nutritive juices. As a result of this, rounded cavities are formed, producing newly formed vesicles which are distributed between the early vesicles. This same movement of the nutritive juices builds canals in the homogenous mass which are transformed subsequently into vessels (§ 21). The formative ability of the nutritive juice occurs during cessation of its movement, when it is transformed by evaporation into a thick, then viscous, and finally a solid substance. Wolff called this character of the nutritive juice the solidification ability (§ 27).

Wolff pointed out that there is no preexisting structure in the young rudiments of plant organs, because from the beginning their formed substance, consists of a simple mixture of substances and is deprived of any internal organization. Only after this, the vesicles and vessels are formed in

this substance (§ 33). The thickening and formation of the walls of the vesicles and vessels Wolff considered the result of the above mentioned movement of juices, which gradually lose their volatility. As a result, the solid substance is deposited in the walls of the extended rounded cavities (vesicles) and canals (the future vessels). Simultaneously, new vesicles and new rudiments of vessels appear (§ 29). Wolff did not find any internal organization in the vesicles constituting the organs of the plant, and he objected against the fantasy of microscopists who described non-existing structures. In the second remark (to § 38) he wrote:

The extremely unreal substances, which Malpighi, (Nehemiah) Grew, and (Anthony van) Leeuwenhoek mentioned, are the fruits of their rich imaginations. Thus, for example, they assumed that those vesicles which I have described and interpreted are similar to the glands of animals; vessels must enter them, which because of their small size cannot be seen by any microscope. These glands discharge their juice in the vessels, which similarly occurs in the glands of animals. Why do we imagine that which has no trace in nature? Why, timidly, do we search everywhere for a miracle? Maybe for the reason that the clever production and wisdom of the Creator is revealed. It must not be forgotten that the quality of the machine can be judged, not by the number of its constituent parts, but by the excellence and the simplicity of its result.

The description of the emergence of the internal organization of plants is considered an argument in favor of epigenesis and against preformation. That same idea stands out in all statements on the development of plants, including consideration of the final formation of the leaves, formation of stem, roots, flowers, fruits, and seeds. For example, the leaves, which still do not possess their final form, finally become formed, and in their place new young non-formed leaflets originate. They are formed from the structureless substance of the vegetational bud; that is why in the place of the substance used for the formation of leaves, new structureless substance appears (§ 53).

In the second part of the dissertation there are factual data and considerations concerning animal development. The

object of Wolff's investigation was the development of the chick embryo in the first stages of incubation. As in plants and in animals, the cause of development, according to Wolff, is the essential power and the ability of solidification of the living substance.

Wolff noticed in the 28-hour embryo a characteristic external form and position of the yolk. Concerning the internal structure, he found at this stage only the presence of globules scarcely connected with each other; the embryo was transparent and of semifluid consistency. It was impossible to differentiate either heart, vessels or red blood in it (§ 166). In the commentary to this paragraph Wolff dwelled on the fundamental argument of preformationists, who explained the invisibility of the preexisting structures by the insufficiency of their optical means, and also by the characteristics of the embryo itself, beginning with its transparency. First of all he took notice of the accusation he anticipated from his scientific opponents, and admitted that it is impossible to consider non-existing that which is beyond direct perception. That is why he also had mentioned that this principle has a character of sophism rather than truth. Since the particles from which all early rudiments of animal organs originate are globules visible by average magnification of the microscope, then it is impossible to say that the parts of the body of the embryo, if they are preformed, are beyond perception. "Thus," Wolff wrote, "the confirmation that the parts of the body of the embryo are latent due to their infinitely small size, and that they only become visible gradually later on is considered a fable." Continuing, he noticed that it is accurate to explain the way nature produces the parts of the organism, particularly in the formation of the extremities (§ 217 and following), kidney (§ 220 and following), and so on. The transparency, which truly disturbs observation, he did not consider insurmountable. The body looks transparent in this case if it lies on another body, in it or under it. If the transparent formation is placed so that it will not be connected with other parts, then it cannot escape observation.

Undoubtedly, Wolff's claim that even "with the help of stronger lenses no one discovered those parts which are not

perceived by the weaker magnification," is controversial. These words must not be considered as an expression of a scornful attitude on Wolff's part to the microscope as an instrument of scientific investigation.⁴ Wolff apparently meant only that magnification by the microscope does not always find in the embryo the preformed organism, because the latter is not always present. Thus, Wolff declared in the German THEORIE that "the seminal animals (spermatozoa)—these are not the production of philosophy, but the result of Leeuwenhoek's polished glass" (p. 73). Here the sharp polemics are turned, of course, not to Leeuwenhoek's technical achievement in improving the microscope, but to the idea of animalculism, which supposes that in the spermatozoid, an animal exists preformed.

Wolff returned again to the question of whether it is possible to confirm the existence of unperceptible substances. His point of view is completely definite: the investigation must take into consideration only that which can be perceived and must judge the existence of substances by their detectable manifestations. Wolff's idea is presented in the following form:

I can, for example, very easily prove that in my bag there is no "fridrikhsdor"⁵ and no Dorida is present now in my room. You easily see that these determined substances are connected with determined manifestations, which in conformity with their nature cannot remain secret. The "fridrikhsdor" in my bag must be seen or be felt, and if Dorida is now present, then other signs of her presence must be available.

Comparing the embryo after 28 and 36 hours of incubation, Wolff discovered in the latter the beginning of the heart, in the form of a tube. This tube has the form of a third of a ring, still not pulsating and not connected with the arteries and veins. He, with surprise, noticed that during the short

4. Thus, apparently, S. L. Sobol was ready to consider in his main work, *ISTORIYA MIKROSKOPA I MIKROSKOPICHESKIKH ISSLEDOVANII V ROSSII V XVIII VEKE* (History of the microscope and microscopical investigations in Russia in the 18th century), Moscow: Akademii Nauk, 1949.

5. A golden coin.

period between 28 and 36 hours essential changes in embryonic development take place (§ 167).

The increase of size and the progressive formation shows that the embryo feeds on the egg substance. From here it follows, according to Wolff, that the nutritional particles pass from the egg to the embryo. And all of this is accomplished by means of a power. As this power is not the contraction of the heart and arteries or the muscles, since all these parts do not yet function or do not yet exist, and since the power acting here sends away the nutritional substances by a canal, then it, is consequently analogous to the essential power (§ 168). Wolff considered that the nutritional juices in the embryo of the chicken move, as in plants, stimulated by the essential power, through the substance built from globules and deposited between these globules, and by this movement they increase the size of the embryo (§ 169).

Animal substance, as plant substance, is characterized by the ability to solidify. This substance is soluble in water. While standing and during simultaneous slight heating, it gradually loses water and is transformed at the beginning into a more or less thick, and then hard body (§ 171). Wolff considered that the ability of solidification of the animal substance is expressed in a lesser degree than that of the plant; its solidification occurs more slowly and it never reaches that degree which is characteristic for the plant substance. He confirmed this for the cellular tissue of animals, which never possesses that compactness and solidity possessed by the wood of even young trees (§ 172).

Returning to his description of phenomena, Wolff turned attention to the moment which precedes the beginning of heart pulsation. In the umbilical vascular area (area vasculosa), the substance of the embryonic disc disintegrates into islets. Their number progressively increases, and their color changes from white to dark-yellow to red. It follows from that, that in other eggs practically in the same stage of development, where the fluid in the islets is slightly more red, the heart pulsates extremely animatedly (§ 179). This description, stated nearly in Wolff's actual words, shows that he distinctly saw the formation and development of blood islets

and the blood in them prior to the formation of the heart and to the beginning of its activity.

"Of the number of my most fortunate observations," Wolff wrote in a commentary to this paragraph, "I relate that which I am reprinting in Figures 7 and 8.⁶ I suppose that here it is possible to overhear nature when it is engaged in very important work, namely to see the transformation of fluid, stealing between the islets, into blood." The observation of the blood movement in the vascular area creates the impression that the vessels already existed (Fig. 3, 7). Examining this region under the microscope, Wolff did not see anything, however, except distintegrated heaps similar to those represented in Fig. 3, 4 aa. At this moment the true vessels are still not formed. Somewhat later on, head of the embryo and the first outlines of the brain, cerebellum and eyes are outlined, and "the rudiments of the vertebral column in the form of a chamber, filled with a homogenous substance are visible; but the rudiments of the extremities have not yet appeared" (Fig. 3, 10). At this point "the outlined cavities, filled with blood bodies are clearly visible" (§ 180). The next step in the development of the vessels is the widening of their cavities at the expense of the increasing amount of blood and the increased thickening of the vascular walls; the globules making up the wall of the vessel appear more compressed. The most compact structure is possessed by the part of the wall near its opening; the farther from the axis of the vessel, the more the substances become softer and, finally, are transformed into the ordinary loose cellular tissue, filling the spaces between the vessels (§ 181).

The processes of development of the chick embryos are distinctly connected with heat, obtained during incubation; if giving heat is discontinued, then all formative processes stop. Wolff considered that heat cannot be one of the specific causes of organic development, however, because "all physical changes in the world, to a certain extent, are in need of heat, as to a resolving power. Without heat all will be turned into lifeless chaos" (§ 183). Wolff saw the role of heat in embryonic development as leading to the dissolution of yolk,

6. Here and later on, in the present chapter the references to figure are related to Table 11 of Wolff, reprinted in Figure 3.

which then can be assimilated by the embryo (§ 186). From these considerations this conclusion follows: "We do not know any other power, except heat and essential power, which shares in the formative processes... Therefore there is no basis for doubt that the supply of nutritional substances to the fetus... takes place under the influence of the essential power" (§ 187).

The subsequent statement was dedicated to the detailed description of how the vascular branches originate and the difference in formation of the veins and arteries; later Wolff addressed the development of vessels, nourishing of vessels, venous valves and anastomosis (§ 215 and 216). It is impossible not to agree with Wolff in these special observations, because in the discussion above, his method of embryological investigations and his fundamental opinions about developmental regularity have already become clear. In the conclusion, he compared development in plants and in animals; then he concluded that here and there the same formative principle acts. Any differences are expressed by the following: animals have a heart, which is absent in plants, and the latter have a central core and point of growth, which are absent in animals; but these differences do not constitute the main point of plant and animal organisms. The peculiarities of animals and plants are the expression of their form and structure only to the extent that these are machines. The essence of the animal and plant depends not so much upon the structure, as upon the activity of the essential power (§ 216).

Then Wolff turned to the formation of organs, beginning from the development of the extremities. After 36 hours of incubation, even the rudiments of the extremities are absent (Fig. 3, 5). In this stage the outlines of the eyes, brain, cerebellum, medulla oblongata and spinal chord are visible in the vertebrae; only the spinal vertebrae are clear, while the lumbar vertebrae are slightly outlined. The periphery of the embryo is occupied by a "light substance," which Wolff called cellular and which he saw as composed of globules (§ 218). This substance gradually combines from both sides of the embryo in two definite points—on the level of the lumbar vertebrae and on the level of the heart. In these places prominences form (Fig. 3, 11), at the end of which the extremities develop. These prominences "truly are the first rudiments of the extremities" (§ 219).

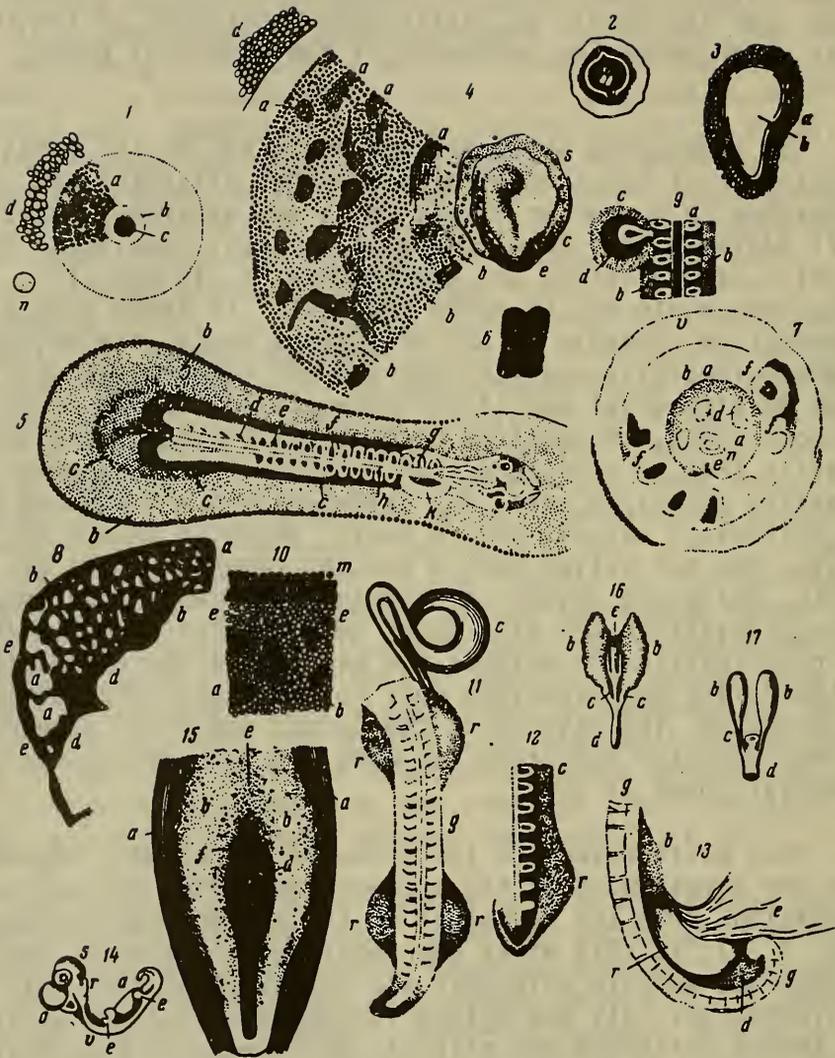


Figure 3. Table of drawings from K. F. Wolff's dissertation illustrating the development of the chicken.

Figure 3. Table of drawings from K. F. Wolff's dissertation illustrating the development of the chicken.

1. The embryonic spot (n) from the non-incubated egg in its natural size; b, c—circular position of the globules around the "center of conception" of the embryo (a); d—granules of yolk.
2. The embryonic spot after 28 hours of incubation in its natural size.
3. The same, under magnification; a—yolk membrane; b—embryo, included in saccule of water membrane.
4. The same, under somewhat less magnification; saccule (c) on the embryo extends and the last shines (e); a and b in correct rings and islets around the embryo; s—stretched membrane in fold.
5. The embryo at 36 hours; in the head "something of a beak," parts of brain and eyes with optic nerves; h—the spinal cord; d, e, f, g—vertebrae; c—substance surrounding the spinal cord; b—cavity of embryo membrane; k—heart.
6. Part of the vertebrae of the embryo represented in Figure 5, under greater magnification.
7. The embryonic spot in the ovum after 64 hours of incubation, in its natural size; v—yolk; d, f—islets: a—umbilical disc; b—rudiments of the vessels; n—mobile particle ("membrane" of Malpighi); e—embryo.
8. Region of embryonic spot of the previous embryo, in greater magnification; a—'island of "white matter"; e, b—red fluid; d—boundary of the islet, as in Figure 7.
9. Part of the spinal column (a) and heart (c) of embryo of 64 hours; b—substance surrounding the vertebrae; d—cavity of the heart with blood globules.
10. Part of umbilical area after 72 hours of incubation; magnification larger than Figures 7 and 8; e, b—ducts, forming the vessels; m—boundary of the yolk.

(Caption of Figure 3, continued)

11. Embryo after 96 hours of incubation; the vertebrae are visible (g); rudiments of extremities (r) and heart (c).
12. Half of vertebra of embryo of 34 hours; c—substance surrounding the column; r—rudiment of the extremity.
13. Posterior part of the vertebra of the embryo of the fifth day; g—vertebra; r—extremity; b—condensation of substance, giving the origin of the rectum between extremities and the tail, and also kidney (d); e—remnants of urinary sac and membrane of the umbilical vessels.
14. Spirit preparation of chicken embryo, slightly magnified; O—occiput; S—forehead; r—beak; v—vertebra; e—extremities; a—abdomen.
15. Pelvis and lower part of the abdomen of the embryo represented in Figure 14; covers of the abdomen; b—red fluid, the same as under letter b in Figure 13; d—place of removed rectum; f—place where intestine passes in the still unformed substance e; c—substance giving the origin of the ureter.
16. Kidneys (b) and rectum (e) with caecum of embryo somewhat later than in Figure 14; c—ureters; d—the lower part of the rectum.
17. Nearly formed kidneys (b); c—ureters; d—rectum.

Wolff began his description of kidney development with demonstrations that up to the fourth and fifth days of incubation the embryos are deprived of any trace of the kidney. Only at this stage their first rudiments appear in the form of accumulated cellular tissue in the area of the lumbar vertebrae, joining the vertebral column from the front (Fig. 3, 13). From these rudiments, oval bodies of the kidneys are later formed. The ureters develop from their posterior end leading into the rectum (Figs. 3, 17, § 220 - 221). Since Wolff made the first description of kidney development, the kidney in this stage of formation, or mesonephros, received the name Wolffian body. Wolff emphasized that the substance from which the organs form contains nothing except the slightly formed globules (§ 230).

From the first two parts of Wolff's dissertation, which are almost without polemical discussions, it is clear that his task was to demonstrate with factual data how the development of plant and animal organisms is accomplished. Each of the examples he mentioned show satisfactorily that there is no pre-existence or preformation, and that the parts of the developed organism are formed anew from structureless material. To summarize: The first step is the formation of vesicles or globules which, through nutrition, increase in number and in this way form cellular tissues, the material for building organs. The generalization that these globules are the basis for both the rudiments of organs and the actual organs in both plants and animals holds paramount importance. It represents the basic doctrine about the composition of all the organic bodies from cells, i.e. the cell theory, which was formulated only eighty years later. Wolff's significance as one of the early contributors to the cellular theory has been repeatedly presented in literature⁷ and need not be discussed here in further detail.

The third part of Wolff's German THEORIE, titled "On the organic bodies of nature and on their development

7. See, for example, Z(akharie) S(aulovich) Katsnel'son, STO LET UCHENIYA O KLETKE. ISTORIYA KLETOCHNOI TEORII (Hundred years study about the cell. History of the cellular theory), Moscow: Akademii Nauk, 1939, and B. E. Raikov, pp. 54, 64 - 65. A. E. Gassinovich in the above-cited article about Wolff rightly warns against the categorical confirmation of Wolff's role in the substantiation of the cellular theory.

generally," provides some concluding generalization. In order not to repeat what others had stated previously, Wolff considered it necessary to provide a summarized theory of development, briefly formulated in the form of definite propositions, and to confirm the correctness of the system with his own microscopical investigations. "Only at this time," Wolff wrote, "when all was completed and prepared for publication, did I read books which by chance proved to be identical to the conclusions in my dissertation" (§ 231). Of his predecessors who wrote about epigenesis, Wolff mentioned C. G. Ludwig and (John Turberville) Needham. All the others, according to Wolff, either agreed with Ludwig or defended clear error. Harvey, according to Wolff, adopted his opinion from Ludwig. He confirmed that the male semen affects the uterus in a way analogous to the way impressions arise in the brain of a painter who creates the likeness of the source of his impressions (§ 232).

Wolff pointed out that the first principle of development, its moving power which he called the essential power, is a necessary condition of existence of animals and plants. Many authors and investigators had known this power for a long time, although they did not consider it the principle of development. Thus Ludwig, denying the necessity of this power for plants, suggested that the distribution of fluid in the plant organism was due to external causes. Later, Wolff noticed that the expansive and vegetative power, and also the power of resistance, which Needham had mentioned, were not identical with his own principle of development. In his work, "New observations on development, building and destruction of animal and plant substances" Needham called the expansive power of growing matter. Under the influence of this power, each separate point of matter attempts continuously to move away from its neighboring points, and Needham considered growth as extension. However, Wolff designated the essential power to be the ability to distribute and move the fluids somewhere else in the plant, i.e. something more determined than simple extension. Speaking about the extension of plant substance in vesicles and canals, he attributed the extension of substance not having the essential power to a mechanical pressure of penetrating fluid in this substance (§ 233). Wolff later noted that the necessary character of plant and animal substance (here he called this character the decisive cause)

is its solidification ability, expressed in plants and animals in different degrees. His predecessors also mentioned this character, although they did not consider it as the principle of development. Thus, Needham spoke about the power of resistance, by means of which the particles of matter joined together. Wolff wrote: "In one unbearably tangled book, I could not find the author's reference to the power of resistance that sharply differs from the power of linkage, which is characteristic for all bodies of nature" (§ 234). Wolff hurled reproaches at authors who wrote about the development of an epigenetic spirit, who did not give any definite formative principle, and who "spoke about it as Galen had about digestion, when he confirmed that the last is conditioned by digestible power" (§ 235).

Contrary to his Latin dissertation, where Wolff criticized his epigenetic predecessors, in the German he considered in detail the opinions of opponents of the epigenesis theory, the supporters of preformation. Without touching upon the opinions of Haller, whom he respected, he directed his polemical discussion mainly at Bonnet, whose book was published two years before the publication of Wolff's German work. Wolff sharply attacked the theory of preformation, calling it a chimera, an idea taken from air. The nature of preformation he called pitiful and even simply rubbish. He decidedly rejected the idea; instead, in the German book, he defended the theory of epigenesis. The understanding of epigenesis, only casually mentioned in the Latin work, is widely used in the German. Characterizing epigenesis as formation of organic bodies, Wolff represented it as the real antithesis of preformation. While the latter hypothesis denies that the body undergoes formation (Ed.: since it is already preformed), epigenesis confirms this formation. Recognition that the hypothesis of predelineation is false at the same time confirms the truth of epigenesis (pp. 61 and 62). Epigenesis is real development in characteristics of all natural phenomena, including inorganic phenomena. The rainbow appears suddenly, but it does not pre-exist in latent form. Epigenesis, as true development, appears in the organized bodies of nature, as is clear in examples of plant development from seeds and animals from ova.

Great interest is represented by Wolff's perspicacious discussion about the philosophical source of the predelineation hypothesis. He considered pre-established harmony to be Leibnitz's idea. Censure of the idea of preformation is, at the same time therefore, censure of Leibnitz's idealistic proposition. It is important to be aware of this, because the literature demonstrates the succession of the idea from Leibnitz to K. F. Wolff, and through philosophy, physics and botany from Leibnitz to Christian Wolff. If the influence of Leibnitz on K. F. Wolff cannot be denied completely, then Wolff's doctrine of essential power is not free from traces of this influence. The independence of Wolff's philosophical opinions must therefore not be overstated or overevaluated.

From the early facts and considerations already mentioned Wolff concluded the general laws of development, the most important of which are formulated as follows: the appearance of parts of the body and its organization are different processes; first, the part is isolated, and then organized. Essential for understanding Wolff's outlook is his confirmation that "all parts of any organic body are formed by means of this or that natural process" (§ 240). He consequently denied the role of any unknown principle in development. The second chapter of his third part, summing up the investigation of development, begins with a definition of this understanding. Development is considered to be extremely general: Wolff includes all changes, either appearance of new parts and their formation by the extension of the substance of fluids in particular, or simple growth and maintenance of existing structures by means of nutrition (§ 241).

The different forms of development in plants and animals represent manifestations of fundamental principles—the essential power and ability of solidification of the nutritional juices. Wolff again stresses the primacy of this essential power. "The essential power," Wolff stated, "together with the ability of solidification of the nutritional juices, forms the acting principle of all development, either in plants, or in animals" (§ 242). All other conditions or principles of development Wolff called accessories; in some way they promote the course of developmental process. Thus: "Except for the essential power and the ability of the developing substance to solidify, no other determining

principle shares in the process of development. It follows that the developing organic bodies are not machines, but consist of non-organic substance" (§ 253). In the commentary to this paragraph he puts the question, why does development need this non-organic substance? Because it possesses definite characters or because it builds in a definite way? Wolff, without deviation, assumed the first alternative, and as a proof he referred to the growth of plants in which the arising parts are composed only of non-organized mass. The organization, the structure in this non-organized matter, is manifested later on (§ 253).

From these considerations appears the general relation of Wolff to the mechanical explanation of vital phenomena, either normal or pathological. The title of paragraph 255 directly asks the question: "What is thought on this basis about the mechanical medicine?" The answer is given as follows: "If mechanical medicine is labelled that which explains the vital processes of the human body...., then it is clear that mechanical medicine is an imagined system, i.e. that which does not correspond to any thing in nature."

Commenting on this conclusion, Wolff characterized the opinions of the supporters of mechanical medicine: "The little which they have established hardly penetrates through the surface of matter, and the great part of that which concerns animal nature is either completely hypothetical or simply unknown" (§ 255, remark 1). Below (Remark 2) Wolff indicated that the mechanical interpretation of vital phenomena only gives that explanation deceptive clarity. In the conclusion to this paragraph, Wolff turned to the characteristics of his own view, warning against hurried conclusions, because "If you, favorable reader, want to guess my opinion, then you easily can make a mistake. Further you can approach my opinions, if you think about Stahl's opinion . . . according to which the functions of our body must be attributed to a non-material spirit" (§ 255, Remark 4).

This declaration of Wolff must be considered carefully, and it must not be hastily concluded that he was a supporter of Stahl's animistic vitalism. Wolff's idea is greater in that he declared himself as a decisive opponent of mechanical understanding of vital phenomena and objected against the

mechanists' consideration of non-organic processes. In order to imagine clearly Wolff's opinions, we must pursue a thought from one of the concluding paragraphs: "The basis for formation of the plant bud and animal embryo is contained only in the available substance capable of development, which is supplied by the essential power." And later: "For the appearance of the organized body of nature nothing is needed except a substance capable of development, which by some means is produced by nature."

In the last (third) chapter of the dissertation, Wolff's remark that attracts attention is that the working out and proofs of his assumed principles of development (the essential power and ability of solidification) must be continued in the future. Wolff pursued this in the investigations and theoretical explanations in both his *THE FORMATION OF THE INTESTINE* (1766 - 1768) and "On the Special Essential Power" (1789).

CHAPTER 5

WOLFF'S TREATISE

"ON THE FORMATION OF THE INTESTINE"

This work, as already stated, represents one of the most important stages in the history of embryology. It was published and distributed in a limited edition in "New Commentaries of the Petersburg Academy of Science." It was known to few contemporaries, until Meckel translated it into German in 1812. After that, the biologists interested in the history of science acquainted themselves with Wolff's works. They turned to the distributed edition of the German translation of *THEORIA GENERATIONIS*, and these readers were able to form their own opinions about Wolff, concluding that his ideas were not always expressed in comprehensible language, were abstract, and were not very convincing discussions about development.

Wolff's work dedicated to the development of the intestine produced another impression completely. It is a systematic statement of thorough and impartial observations on the development of the chick embryo during the first four days of incubation. The conclusions which the investigator reached clearly arose from his informed facts and therefore were completely convincing. This truly classical work fairly deserved the high evaluation of the leader of embryological science, K. M. Baer.

The complete title of Wolff's work is "Observations carried out on incubated eggs, mainly on the formation of the intestine, and also on the false amnion and other parts of chick embryo that are still not observed today."¹ The

1. C. F. Wolff, *DE FORMATIONE INTESTINORUM* praecipue tum et de amnio spurio, aliisque partibus embryonis gallinacei, nondum visis observationes, in ovis incubatis institutae.

(... contd on next page)

work begins with a comparison of development in plants and animals. Wolff first noticed that the different parts from which the plant organisms are composed are extremely similar to each other, and therefore the ways of their development are easily established. Truly, as Wolff said, great depth of thought is not required to notice, especially in some plants, that in many composites in which the leaves gradually become smaller and more incomplete and adjoin nearer to each other the higher they are situated on the stem, at the end the last leaves, which are present directly under the flowers, turn out to be extremely small and are firmly adjacent to each other. They form the leaves of the calyx, and together constitute the calyx itself. Concerning the petals of the flower, Wolff did not doubt that they are also modified true leaves. He made the same conclusion for other parts, which in some flowers are transformed into petals, and vice versa. As a result of these observations Wolff concluded the following: if all parts of the plant, except the stem, are similar in their morphology to the leaves and are nothing other than modification of the latter, then it is not so difficult to formulate the theory of development in plants.

(Footnote No. 1, contd)

NOVI COMMENT. ACAD. SCIENT. IMP. PETROPOLITANAE,
v. XII (pro Anno 1766 - 1767), 1768, pp. 403 - 507, v. XIII
(pro Anno 1768), 1769, pp. 478 - 530.

This title is situated in the first part of work, without an independent subtitle; second and third parts are called accordingly "Second part, Cardiac fossa; commissure of false amnion, lower fossa; beginning, increase and disappearance of these formations" and "Third part. Internal phenomena and false amnion, which at the same time stated the formation of mesentery, thorax, abdomen, wings and legs". Meckel in his translation gave the work a briefer general title ON THE FORMATION OF THE INTESTINAL CANAL IN THE DEVELOPING CHICKEN (KASPAR FRIEDRICH WOLFF ÜBER DIE BILDUNG DES DARMKANALS IM BEBRÜTETEN HÜHNCHEN. Übersetzt und mit einer einleitenden Abhandlung und Anmerkungen versehen von Johann Friederich Meckel, Halle, 1812).

Repeatedly, it was noticed that Wolff pioneered the idea of unity of the morphological structure of plants, brought together to a general form in the leaf, which was later worked out in detail by Goethe. This side of Wolff's scientific interests is indirectly related to the basic direction of his activity.

Passing to the morphology of animals, Wolff noticed that the analogy cannot be established between the individual parts which exist in plants, and the different organs which exist in the animal body. The organized body of the animal is a very complicated whole; it originates as a result of interaction of many interconnected dependent causes.² One of the forms of development characteristic for animals is similar to the development of plants; it appears in the formation of the extremities. Wolff wrote the following:

The extremities, i.e. wings and legs of birds, first appear in the form of protuberances, and then elongate; at their ends new protuberances appear which are the rudiments of the fingers, and gradually they acquire the form and structure of the formed leg and wing. Something similar occurs in vegetation, as the leaves of plants are formed; this common mode of formation I stated in the theory of generation.³

This process of development is realized when, at the beginning, the nutritional fluid collects in the already existing parts and causes a protuberance to appear, which is the first rudiment of a new part. This fluid is gradually transformed into a more compact substance. Simultaneously with this, vessels appear in it, through which new nutritional juices flow. By this means a new part is organized, i.e. acquires structure. Similarly new protuberances appear in different places, being the rudiments of new parts.

In animals, other types of generation and development of parts of the body also exist. Thus, a different type of development than that just described characterizes the intestine, the fundamental object of Wolff's observations

2. DE FORMATIONE, p. 410.

3. Ibid., pp. 411 - 412.

in the discussed work. Already in the beginning of the work (§ 2), Wolff confirmed that he could understand the initial stages of the genesis of the intestinal canal only because he traced the entire process of development of the intestine from the moment of its formation to its final completion. Wolff expressed a hope that his theory about formation of the intestinal canal would be acceptable for experienced naturalists, as it is nearly wholly taken from observations.

In another place (§ 81) Wolff described his method of studying the developing eggs, which he considered the only suitable method, in order to make the description of the phenomena completely understandable; thus: "I selected the following order in the description of the phenomena in the incubated egg. From the beginning I described the phenomena at that time when they attain the highest development.... then I followed them to the moment of appearance, described the changes which occur from their first appearance to that time when their essence can be determined. Finally I explained the other changes, which occur in the period up to the full completion of the process."

Passing to the statement of the basic results of his work, Wolff turned attention to the previously insufficiently studied membranes which already surround the embryo in the first days. He gave the study of the membranes special significance because according to his data the intestinal canal originates from these peculiarly structured membranes.

From the subsequent text it is clear, without doubt, that Wolff still could not differentiate the true preliminary membranes (serosa and amnion), formed from the extra-embryonic parts of the ectoderm and mesoderm, from the embryonic layers, from which the embryo itself developed. According to his description, the condition of the egg about the middle of the third day of incubation is seen in Figure 6. A part of the yolk membrane, as Wolff called it, very rich in vessels, and the center of which is called the vascular area (area vasculosa) is where the embryo is found. This part is composed of two layers; the external layer is delicate, transparent and is deprived of vessels. It goes above the embryo and is loosely united with the internal layer so that during immersion in water it separates from it and comes to the surface. And the

internal layer, together with the embryo, goes to the bottom. As a result, the embryo, which is still not surrounded by amnion, appears open. The thin transparent film, easily separated from the embryo, which Wolff called the external layer, is nothing other than the yolk membrane, and the internal layer represents the blastodisc, actually composed of all three embryonic layers.

To the end of the third day and slightly later, according to Wolff's description, the vascular area also is composed of two layers: upper—thin—and lower—thicker and softer. But at this time they are so closely connected that they appear as one membrane. Near the embryo there is a transparent region; in its range both of these membranes begin to separate and the embryo becomes distinct. It appears between them so that the upper membrane passes above the embryo, and the lower passes under it.

Interpreting the description from the context of present knowledge about chick development, it can be suggested that the picture of separation of the two "membranes" corresponds to the formation of the exocoelom, i.e. the extra-embryonic space, limited by the parietal and visceral layers of the mesoderm, so that Wolff's "upper membrane" is probably the ectoderm together with the parietal layer of the mesoderm, and "the lower membrane" is the visceral layer of the mesoderm together with the endoderm.

Wolff described the subsequent fate of the lower layer of the vascular area (Figure 7) as follows:

This layer goes from all sides of the vascular area in the direction of the embryo ... at a higher level, than the embryo and amnion ..., as if it wants to pass through the amnion lying below with the embryo in it and to cover it. Only a small space remains in the middle of the upper surface of the amnion which is not covered with the internal layer ... After that, when the internal layer reaches this place, it is immediately turned in an acute angle, directed downwards, and lies around the embryo with the thin amnion surrounding it. After this, on the lower surface

of the vascular area around the embryo, or more exactly around the amnion covering it, a vesicle must be formed

Wolff noticed that this vesicle can be seen distinctly, although it is not expressed identically in all eggs, and he considered that the other investigators did not notice it, because, in the first stages of incubation, they never examined the lower surface of the embryo lying on the yolk. In addition, he did not see this formation himself up to 1764, although he had investigated the developing eggs during the five previous years.

"All," Wolff continued, "who did not see the true amnion during its first appearance, or at least in the third or fourth day of incubation, assumed that this vesicle is the amnion, because the described vesicle is swollen and distended with fluid. It seems directly adjacent to the embryo, while the amnion itself, due to its extreme thinness and transparency, may remain unnoticed. Therefore, I called this formation the false amnion, although it does not properly possess any similarity with the true amnion."⁴

It is not easy to translate into the language of recent embryology his description. Here, apparently, the descriptions of different formations are combined: on one hand Wolff dealt with the trunk folds, the apex of which was submerged inside the embryo. Finally this apex separates from the yolk sac. On the other hand, he saw a deepening of the endoderm, submerged from below in the embryo. All of this composed a picture of what Wolff described as the false amnion.⁵

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4. Cited places in § 36 and 37 under title "Vesicle, appearing in the lower surface of the transparent zone, or false amnion" (pp. 434 - 437).
 5. Nearly the same, K. M. Baer evaluated the idea of the Wolffian term as "false amnion," when he cited the work of Wolff in his classical work, HISTORY OF ANIMAL DEVELOPMENT (UBER ENTWICKELUNGSGESCHICHTE DER THIERE. BEOBACHTUNG UND REFLEXION, v. I, part I, 5 c).

DE

FORMATIONE INTESTINORVM

PRAECIPVE, TVM ET DE AMNIO SPVRIO,
ALIISQVE PARTIBVS EMBRYONIS GALLI-
NACEI, NONDVV VISIS

OBSERVATIONES, IN OVIS INCV-
BATA INSTITVTAE.

Auctore

C. F. WOLFF.

Pars I.

§. I.

Generalem hactenus in theoria generationis huius negotii naturae ideam exhibui; leges enodavi, secundum quas partes corporum organicorum naturalium, quae vtrisque eorum generibus, vegetabilibus et animalibus, communes sunt, vasa nempe et partes, ex his compositae, formantur et causas viresque detexisse puto, quibus haec formatio peragitur. Tum praeterea in plantis diuersas partes plerasque, quae fere similes sibi sunt, cognituque ideo faciliores, folia puta, calycem, petala, pericarpium, semina, caulem, radicem, ex suis causis efficientibus explicare tentavi; in animalibus autem

Introdu-
ctio. In-
stitutum.

E : c 2

prae-

Figure 4. The first page of Wolff's work "On the Formation of the Intestine."

Caspar Friedrich Wolff
über die
Bildung des Darmkanals
im bebrüteten Hühnchen.

Uebersetzt
und mit einer einleitenden Abhand-
lung und Anmerkungen
versehen
von
Johann Friedrich Meckel.

Fischer


Mit zwei Kupfertafeln.

Halle 1812
In der Rengérschen Buchhandlung.

Figure 5. The title page of Meckel's translation of Wolff's work. Copy belonging to the first president of the Moscow Society of naturalists G. I. Fisher; kept in the library of the Society.

The further description of behavior of the lower layer, i.e. endoderm, is extremely important because it makes clear that Wolff truly saw the initial stages of formation of the digestive canal. This lower membrane of the vascular area, Wolff wrote, "ascending and forming the vesicle which was described by me, is considered that membrane from which the intestinal canal is formed. How it takes place, how it is generally possible that from the simple membrane a canal is formed, will be explained later on." This description makes up the contents of the second part of the work discussed.

In this zone, which Wolff called the false amnion and described in the form of a closed vesicle, first of all a fossa is formed, situated at the level of heart. Wolff called this fossa, because of its location, the cardiac fossa.⁶ The form of this fossa is nearly oval. Upwards and laterally it is rounded and wider, downwards it is gradually compressed, and later it passes downwards into the amnion commissure. To this description Wolff added an explanation that here upper and lower mean correspondingly anterior and posterior ends of the embryo.

This cardiac fossa, or cardiac opening, is the first rudiment of the stomach. The result of the process shows this exactly. The vesicle is subsequently changed in this way: its part which forms the fossa is transformed into the stomach . . . Which parts of the stomach in this condition are already present, which parts are still absent . . . can then be explained in this way, that from here it is easy to receive clearer proof of epigenesis.

This general conclusion is supported by the following interesting argument.

From here it is clear without doubt that it does not occur in nature that parts of the organized bodies exist from the beginning, infinitely small and

6. Meckel in his translation called it "gastric fossa" which maybe represents its role in development, but all this also may be unexactness of translation.

invisible but perfect and complete, and not thus, as if they were created instantly by the Most High Creator (22), and that finally, under the influence of accidental causes, as if stimulated, they begin to expand, extend and grow to the normal size of the adult body. Not so. I say that what I saw in nature occurs, but sooner, so that the formation of natural bodies in general is pre-established only by one natural power, existing in animal or plant matter. (§ 56, p. 453) (23)

"Similarly, if from a small and invisible but complete and fully formed stomach it becomes large and visible, then it will be clear that the stomach then has the form of the adult stomach, but only smaller in size. In any case it will be seen that it is not half, not in any case opened or united with other parts" (§ 57, pp. 454 - 455). And later on: "I more often saw embryos with cardiac fossa and without the whole heart; this means that the stomach appeared earlier than the heart—a fact contradicting the general opinion and hypothesis of evolution" (p. 455).

Later Wolff moved to a description of the false amnion commissure. He used this name for the deep groove going along the ventral side of the embryo; it appears in the third day of incubation, beginning from the lower, gradually compressed end of the cardiac fossa and, not being interrupted, extends backwards, ending in the edge of the membrane cover of the tail. The edges of the commissures at this time are adjacent and united so closely that they do not admit a probe. Shortly before this, in the second day of incubation, "the edges of the groove not only are separated from each other, but are widely separated. The entire anterior surface of the vertebral column, which at first seems astonishing, is not covered by anything. The embryo is uncovered totally in the anterior surface, except the most anterior part, lying in front of the cardiac fossa." This part in front of the cardiac fossa (future stomach) represents a tube which, according to Wolff, is not the thoracic cavity, but the anterior part of the digestive canal. On the contrary, the part lying behind the cardiac fossa represents a cavity in the form of a half cylinder. Later, the edges of this cavity gradually move closer, accrete and, by these means, about the third day of incubation the above mentioned commissure appears, which closes with the abdominal

side of the new-formed intestinal canal. "It must be noticed," Wolff wrote later, "that the intestinal canal, even when it is completely formed is so similar to the intestine that it may be mistaken for it; it also significantly differs from the intestinal canal in the mature condition" (§ 62, p. 450).

In his first works, even in the polemical part of the German "Theory of Generation," Wolff had not touched on the disagreement with Haller. Only here, in the work about the development of intestine, he for the first time noticed a divergence from Haller concerning the periods of appearance of the formed parts of the intestinal canal, which the "famous Haller" saw first in the fifth to seventh day. Later, however, Haller informed Wolff about earlier periods—about the fourth day. Wolff also observed the formed digestive canal within three and a half days after the beginning of incubation. The deep divergence lies, however, not in what Haller said but in the moment when the organs of digestion become visible. Haller gave no information about their development, while Wolff showed the gradual formation of the intestinal canal.

"The first rudiment of intestine and stomach," Wolff wrote, "can be recognized . . . by successive changes and by the processes of development, which appear much earlier" (p. 460). "The part of the membrane forming the commissure is the internal or villous skin of the intestine. Thus, the intestine regarded as a whole is the opened intestine. In order for it to become a whole canal, its lateral parts must come together from the front and be accreted" (§ 63, p. 460).

After this description the following "thoughts about epigenesis" are significant.

I suggest that if the described way of intestine formation is correctly understood, then no doubt can remain of the truth of epigenesis. Because if the intestine, from the beginning, is a simple membrane which is then rolled up; . . . if the flat membrane swells, acquires a cylindrical form, and becomes similar to primary intestine, then I consider it proven that the intestine is doubtlessly thus formed and did not exist previously in an invisible form, ready to appear at the appropriate moment. (pp. 460 - 461)

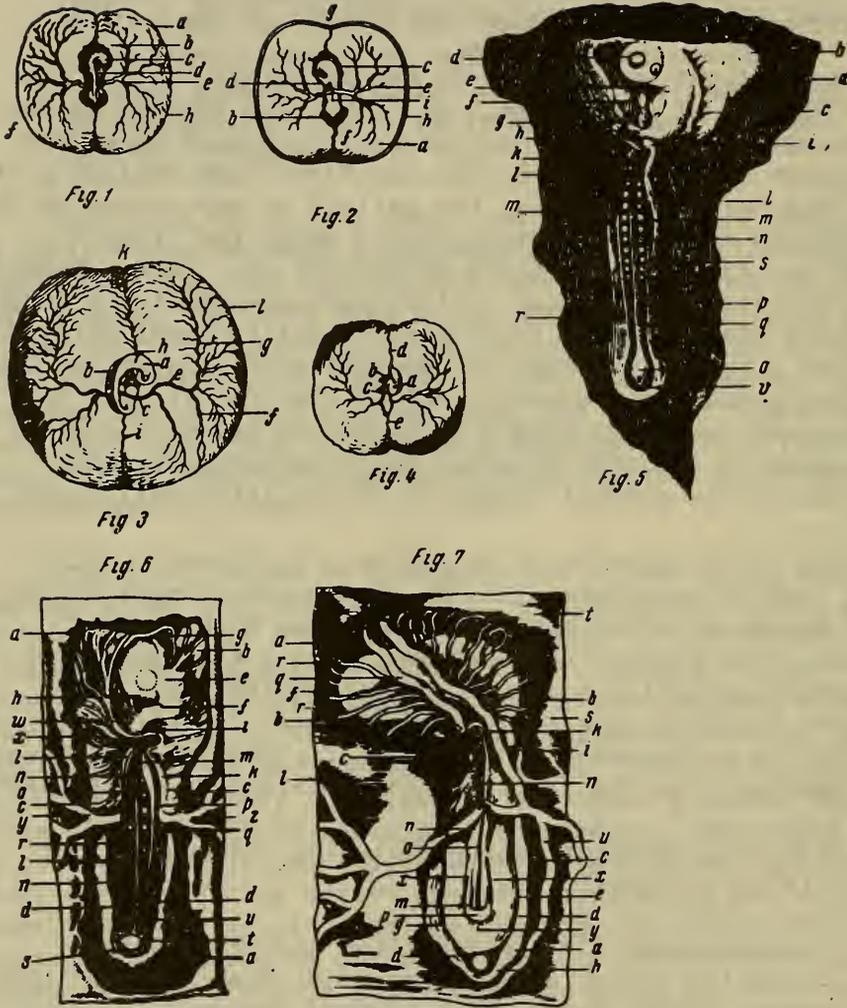


Figure 6. Table 1 illustration from Wolff's "On the Formation of the Intestine."

Figure 6. Table 1 illustration from Wolff's "On the Formation of the Intestine."

1. Vascular area (area vasculosa) from upper surface after three days of incubation; a—vascular area; b—transparent place (area pelludica); c—embryo; d—heart; e—lateral yolk veins; f—descending vein; k—boundary vein.
2. Lower surface of the vascular area and on it the vesicle or false amnion; a—lower surface of the vascular area; b—transparent place; c—false amnion and on it (from c to d) cephalic branch; di—middle part of it; i to b—caudal membrane; d—cardiac fossa, from d to i, commissure; i—lower fossa; e—lateral veins; f—descending vein; g—ascending vein; h—boundary vein.
3. Upper surface of the vascular area in living embryo of three and a half days of incubation; a—embryo; b—fossa, which it forms in yolk; c—origin of yolk veins; d—their lower branches; f—middle branches; g—branching of the upper branches; h—ascending vein; k—its branches; i—descending vein; l—terminal vein.
4. Vascular area in living condition; a—chamber of heart; from above, bulb of aorta, from downwards, auricle of the heart; b—aorta; c—hollow vein; d—ascending vein; e—descending vein.
5. Transparent place in the embryo from lower surface, under microscope, 54 hours of incubation; a—transparent place; b—cephalic branch; c—part of the embryo above the cardiac fossa; d—anterior part of the head; e—heart; f—first rudiment of the true amnion; g—ascending vein; h—origin of cephalic branch; i—swollen edge of the ventricle opening; k—opening of the stomach still is not closed, but has narrowed; l—abdominal folds; m—intestinal folds; n—rudiments of vertebrae; o—end of vertebrae; p—the beginning of formation of amnion opening; q—spinal cord; r—marked lateral parts of the vesicle; s—traces of retiform, derived from red blood, vessels; v—first rudiment of the caudal membrane.
6. Part of lower surface of the vascular area with the transparent place and embryo, after two days of incubation.

(Caption of Figure 6, contd)

a—the transparent place; b—cephalic branch; c—upper, swollen region of the lateral part of the vesicle; d—lower, still not swollen part; e—part of the embryo over the cardiac fossa; f—heart; g—occiput; h—anterior part of the head; i—edge of the cardiac fossa; k—left abdominal fold; l—right lower abdominal fold; m—internal intestinal fold; n—right intestinal fold; o—spinal cord; p—cavity of the intestinal canal; q, r—lateral deepenings, rudiments of cavity of the body; from s to t—rudiment of caudal membrane; s—united abdominal folds; t—union of the intestinal folds, origin of rectum; u—slightly bending end of the spinal chord; w—ascending vein; x—its branches; y—right lateral vein; z—left lateral vein.

7. Part of the vascular area, containing the embryo, covered by the false amnion, after 60 hours of incubation. a—immovable false amnion; b—cephalic branch; c—lateral parts of the vesicle; d—caudal membrane; e, f, i, g—embryo, translucent through the vesicle; f—occiput; g—protuberance of right leg; h—rudiment of tailbone; i—protuberance of left wing; k—cardiac fossa; l—commissure; m—lower fossa; n—fold of commissure; o—opening between abdominal and intestinal folds; p—fold of lower fossa; q—ascending vein; r—its branches; s—vein associated with the ascending; t—its branches; u—descending vein; x—abdominal fold; y—area formed by the union of trunk folds.

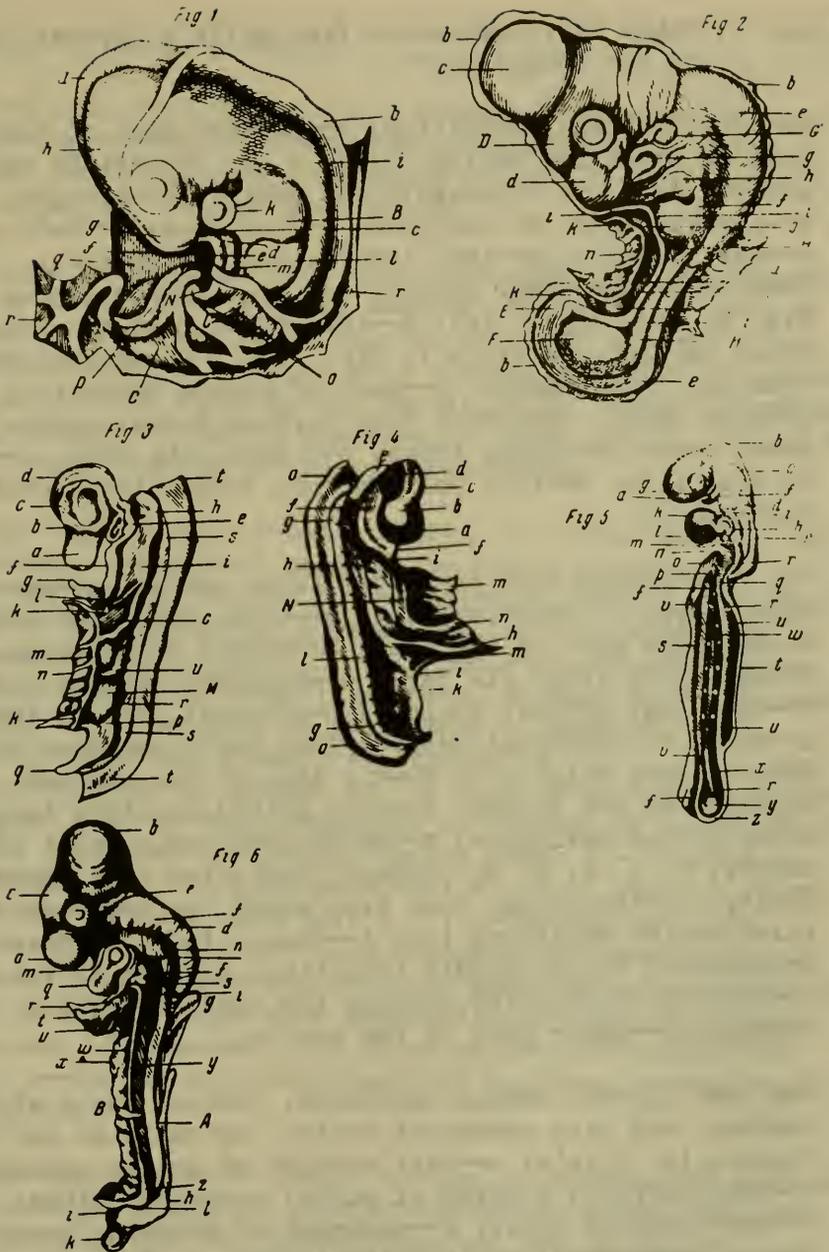


Figure 7. Table II illustration from Wolff's .
 "On the Formation of the Intestine."

Figure 7. Table II illustration from Wolff's "On the Formation of the Intestine."

1. Embryo of 4 days incubation; r—excised part of the vascular area on which the vesicle lies; a, b, c—vesicle or false amnion; g, h, i, l—translucent embryo; h—occiput; g—anterior part of the head; i—vertebra; l—left wing; k—left auricle; B—left lateral part of thorax; C—fold of abdominal opening and true amnion (Table I, Fig. 2, ii, Fig. 7, xx); e—intestinal fold and fold of false amnion (see Table I, Fig. 7, n); m—opening between true and false amnion; d—part of middle intestine; f—rounded fossa, appearing from cardiac fossa, groove and lower fossa; N—lower fossa; p—right yolk vein; o—artery of that side; n—left yolk artery; q—umbilical vesicle (allantois).
2. The same object with extracted false amnion; a—part of upper layer of vascular area; b—true amnion; c—occiput; d—anterior part of the head; D—middle protuberance, disappearing after six days; e—vertebra; f—left wing; F—left leg; g—left auricle; h—lateral part of thorax; i—folds of abdominal opening from which membrane of true amnion takes origin; H, H—the area of the abdomen, adjacent to the thighs, forming paired cavities in the sides of the vertebrae; E—backwards-bending part of this cavity; k, l, m, n, o, p—parts beginning from abdominal cavity; k—intestinal fold from which the membrane of the false amnion continues (n); l—deeper fold of intestine; m—parts of folded middle intestine; n—part of false amnion; o—its part continuing through the cardiac fossa to the stomach; p—upper part of the rectum.
3. The same object; amnion destroyed, lateral parts of thorax removed; and also abdominal cavity, extremities and head; viscera is visible; a—left chamber of heart; b—aural canal; c—left auricle; d—arch of aorta; v—venous sinus; f—left lobe of liver; g—rudiment of abdomen; h—digestive tract; i—stomach; k—intestinal fold; l—duodenum; MM—middle intestine; n—part of membrane of false amnion; o—part of this membrane covering the intestinal canal; p—upper funnel-shaped part of the rectum; q—lower part of rectum, which, like the stomach, also already has

(Caption of Figure 7, contd)

cylindrical form, while lying between them a part of intestine opened; r—mesentery—continuation of false amnion and intestinal membranes; s—left kidney; t—part of vertebrae; u—left yolk artery.

4. The same preparation from the right side; a—left chamber of the heart; b—its right chamber; c—aorta; d—arch of aorta; e—rudiment of left lung; f—right lobe of liver; g—right kidney; h—right yolk artery; i—right intestinal membrane, from which middle intestine is formed; k—rectum; l—mesentery; m—right membrane of false amnion; n—right yolk vein; N—trunk of vein; o—vertebrae.
5. Embryo represented in Table 1, Fig. 6, liberated from all membrane; a—anterior part of the head; b—occiput; c, d—occipital region; d, e—region of thorax; e-z—the rest of the vertebrae; g—left part of the lower jaw; f—process (first rib); h—left auricle; i—aural canal; k—left chamber of heart; l—aorta; m—membrane represented in Fig. 3, g; n—part of false amnion from which the cardiac fossa and stomach are formed; o, p, q, s, t, z—first rudiment of abdomen in the form of bending membrane; o—upper part of this membrane; p, s—edge of abdominal fold; q—its upper left, strongly curved part; t—its edge in the place where it becomes wider; v—right lateral abdominal membrane; u—left membrane; s, r, z—intestinal canal (fistula intestinalis)—first rudiment of mesentery with still divided membranes; s—right mesenterical membrane with right kidney; r—the same also—left; w—opening between membranes of mesentery, in which uncovered vertebra is seen; x—vertebrae; y—rudiment of tailbone; z—rudiment of the pelvis.
6. Embryo represented in Table I, Fig. 7; a—anterior part of the head; b—posterior part of the head; c—protuberance (see Fig. 2, D); d—thoracic part of the vertebrae; e—occipital region; f—rudiments of ribs; g—rudiment of wing; h—rudiment of leg; i—hip region; k—region of tailbone; l—rudiment of pelvic cavity; m—rudiment of true amnion; n—part of thorax; o—left auricle; q—middle chamber; r—abdomen; s—stomach; t—ascending vein; u—part

of cephalic branch; v—edge of the stomach (see Table I, Fig. 7, k); w—intestinal fold; x—part of false amnion; y—completely formed mesentery; z—upper, funnel-shaped part of the rectum; A—left kidney, later on separated from the mesentery; B—yolk artery.

Wolff illustrated the principle of gradual establishment of parts in the process of development with many examples. He referred to the description and drawings of Rezel, according to which in the tadpoles of frogs, there are no legs at the beginning. The extremities are developed later. He said later that, according to Réaumer, the accidentally destroyed chelae of crayfish grow again and that Trembley saw simple polyyps which later became branched and complicated (his report, apparently, is about the regeneration of antennae and about the budding of hydra).

Describing the gradual formation of the intestinal canal from the rolled-up and accreted edges of the membrane, Wolff noticed, though obscurely, the similar formation of the central nervous system. In fact, his analogy confirms the general principle of gradual development for the commissure of the false amnion, for the primary intestine, for the brain and spinal cord, and even for the embryo as a whole. Wolff's discovery of the common manner of development led to his assumption of the transformation of that which is flat by means of closure of its edges, into a hollow cylindrical body. Apparently Wolff could not observe directly the process of rolling up of the medullary membrane in a canal. In any case, the propagation of the described principle of development on the central nervous system, even if an assumption at the time, was an excellent discovery which Baer made sixty years later.

In addition Wolff turned attention to the successive formation of the different systems of organs, the first of which, in his opinion, is the central nervous system. Then, he supposed, the muscles are isolated. The third to become clear is the circulatory system, and, finally, the digestive system (p. 472).

From the third part of the reviewed work we must consider only the general conclusions, which partly repeat those above, but which deserve further mention because here Wolff brought a final summation of the theory of epigenesis as opposed to the idea of preexistence of the parts of the embryo. Thus, he wrote:

We see that many parts of the body, for example the thorax, at a certain moment of time not only do not exist completely, but also cannot exist at that time. We conclude that it did not exist not because we do not observe it, but because we see in this place, where the thorax must appear, the appearance of true amnion; from here we conclude that the thorax, which is not revealed, cannot exist and as a matter of fact does not exist.

These arguments of Wolff also concern development of the pelvis and the digestive tract. "I consider," he concluded, "that this is the most important evidence in favor of epigenesis."

From here it can be concluded that the parts of the body do not always exist, but are formed gradually; during this it is not important by what means formation is accomplished; I do not say that the parts are formed by the accumulation of particles, or by any kind of fermentation, by means of mechanical causes or by powers of soul; I only say that the parts are truly formed Instead of the center of the intestine, i.e. the entire intestinal tract from duodenum to rectum, there are two plates with rolled up anterior edges, and in the rest plates divided are falling behind each other I ask, therefore, are these plates the formed intestine? No one, of course, will confirm this. Thus, I conclude that the complete and formed parts do not always exist, but are formed in a determined period after conception. (§ 155)

This necessarily brief and selective statement of Wolff's ideas gives a clear view of the means of exact investigation of embryonic development by which he finally consolidated and confirmed the truth of epigenetic opinions and the fruitlessness of the preformation idea.

Wolff was insufficiently evaluated by contemporaries. Forty years later the majority of them had no idea about the existence of his main work. Meckel's merit is not only that by publishing his translation he made Wolff's work general property, but also that he helped restore Wolff's priority

and credited him with "contributing to the history of development in general and development of the intestine in particular."

The evaluation of Wolff's work was given by Meckel in the following statements:

This exactness of observation, this step-by-step tracing of organs from their first appearance to their final development, only this could lead to creation of a true history of embryonic development. The author did not follow preconceived opinions, did not report more than he saw, and did not promote only probable propositions as law. The work is considered a model in all respects, so that I do not think that I can be reproached for translating the work of 1768. Knowing that it remained almost completely unknown, and also that it was found in a journal, available to only a few readers, completely eliminates my indecision.

"This work until this time remained unknown to the physiologists," Meckel continued, "as attested to by the fact that Oken, who published in 1806 an article about intestine formation, did not possess any knowledge of Wolff's work, as he did not mention it anywhere" (Introductory article, p. 5). In many following pages Meckel compared Oken's results with Wolff's data and showed that Wolff had established much long before Oken.

Wolff's discoveries were much ahead of his time; he remained misunderstood by the majority of his contemporaries. About forty years after Wolff's death, his great successor in the Petersburg Academy, K. M. Baer, said the following: "Not only superiority of work assured its success Academician Wolff, after untiring work, discovered the law of organic transformation; but at that time the time had not yet come to investigate this law, and science disregarded him (24). After half a century, others succeeded with little reinforcement in obtaining laurels themselves in this same field, noticed his existence, and exalted the memory of Wolff."⁷ As is well known, Baer praised Wolff's work on the intestine.⁸

The American zoologist Wheeler, in the past century, wrote about the significance of Wolff's embryological works in the following poetic words: "The Siegfried destined to overcome this monstrous theory of emboîtement, a theory not only false in itself, but one jealously guarding the problem of development, and preventing all access to it, as the dragon guarded the treasure of the Niebelungen, was CASPAR FRIEDRICH WOLFF."⁹

The contemporary historian of embryology J. Needham also highly evaluated the significance of Wolff's work for refuting the idea of preformation of the embryo. Needham, repeating the expression of Claude Bernard,¹⁰ considered that "this was a fatal blow for the theory of preformation."¹¹

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7. Opinion about the development of science, speech read October 24, 1835 at the public meeting of the Academy of Science by Baer. JOURN. MIN. NAR. PROSV., May 1836, pp. 190 - 245 (citation p. 218).
 8. K. E. V. Baer, UBER ENTWICKELUNGSGESCHICHTE DER TIERE. BEOBACHTUNG UND REFLEXION, 1837, v. II, part 3, 7 (footnote).
 9. W. M. Wheeler, "Caspar Friedrich Wolff and Theoria generationis." BIOL. LECTURES, Mar. biol. lab. Wood's Hole, 1898 - 99, p. 271.
 10. Claude Bernard, LÉCONS SUR LES PHÉNOMÈNES DE LA VIE COMMUNE AUX ANIMAUX ET AUX VÉGÉTAUX. (Paris: J. B. Baillièrè et fils, 1878 - 1879), p. 316.
 11. J. Needham, A HISTORY OF EMBRYOLOGY, p. 258.

CHAPTER 6

WOLFF'S TERATOLOGICAL WORKS

On publishing the work discussed above about the development of the intestine, for which the main objective was to establish the theory of epigenesis, Wolff never considered his task accomplished. He always sought new material for the question in which he was interested.

The actual arguments against preformation and in favor of epigenesis he drew from teratology, which he continued studying extensively throughout his long years of work in Petersburg. From Raikov's work it is clear that Wolff had collected a large amount of material in which he investigated in detail the structure of human monsters or malformations, which, along with his theoretical judgments concerning a number of general biological problems, were never prepared for publication.

In addition to human monstrosities, Wolff was interested in the development of animal monstrosities, as evidenced by his three publications on the subject. Two of them, "About chicken monstrosities" and "Description of a double-headed chicken," are included in the list of Wolff's printed works attached to Raikov's book, although their inclusion in this book is not highlighted, and a third, "A single egg carrying twins," is not included in the list. These works of Wolff, in Latin, remain almost unknown. Thus it becomes essential to give a short account of their contents; moreover, interesting factual data is in all of these works, and to the second, the most commonly known, is attached an independent report, "About the origin of monsters."

Wolff's first published teratological work, his "A single egg carrying twins"¹ (Fig. 8 - 10), begins with the reminder

1. Wolff, "Ovum simplex gemelliferum," NOVI COMMENT. ACAD. SCIENT. PETROPOLIT. v. XIV pro Anno MDCCLXIX, 1770, pp. 456 - 483.

that eggs bearing twins were known by Harvey and Fabricius Aquapendente and even Aristotle. However, all these authors worked not with single eggs which contain one simple yolk with two embryos developing in it, but with eggs containing two yolks, each of which gives rise to a separate embryo. Wolff wrote that he also saw many eggs with double yolks; he suggested naming them the twin-eggs in distinction from the single eggs carrying twins (p. 457). He considered the methods of development of this and other types of eggs. For the formation of twin eggs it is necessary that two yolks be separated in the ovary and be passed separately along the oviduct, after which in the lower part of the oviduct they are surrounded by a common white mass and covered with a common shell. Two yolks in one egg could be closely adjacent to each other; however, they remain separated and represent at the end two different eggs in one shell. Something else completely is represented by the egg carrying twins, which contains a single and is actually single in every sense. Such an egg is single throughout its entire existence but nevertheless produces two embryos.

The egg described in this work, which carried twins, was incubated for six days. Wolff gave a short description of the situation of the parts in a normal egg. At this time of incubation the albumin is separated from the yolk and is located at the pointed end of the egg. The vascular zone (area vasculosa) occupies half of the surface of the yolk and is supplied with rare vascular branches. The transparent zone (area pellucida), which represents the central part of the vascular zone, i.e. the place where the embryo is located, disappears by the sixth day of incubation in normal eggs.

In the egg carrying twins, the albumin is single and common for both embryos and normal in size and location. The yolk also is single and does not show anything abnormal (p. 465). The vascular zone is also single; however, the vessels present in it form a double system of branching which is considered the first sign of doubling of the embryo. The strange property of this egg is the absence of the amnion; thus both embryos look entirely unusual: they are free, covered with nothing, and lie movable on the yolk (p. 469). Skin of the abdomen in both embryos gets across in the

membrane of the yolk, as a result of which there are independent yolk ducts for each embryo. The latter lie so close to each other that a third one cannot be situated between them; their head ends are especially close.

Later, Wolff described the folds on the surface of the yolk between the embryo and the openings of their intestines into the yolk. In the structure of the embryos themselves he did not notice anything deviating from the normal.

In a special section of the work (*Corollaria quaedam*) Wolff turned particular attention to the folds of the yolk membranes, which are located between the embryos. He believed these to be the remnants of the false amnion, which from the first to the fifth day was present there. Therefore his opinion was that the false amnion and area pellucida were common for both embryos at the preceding stages. Comparing the described case with examples of joined twins in the literature, Wolff expressed his belief that the growing twins do not result from the growth of the already formed embryos, admitting at the same time that they are a product of incomplete division of the embryo at the early stage.

In the work Wolff reached no general conclusions. However the distinction of the egg with two yolks, where the presence of two embryos is entirely natural, from the twins originating from one yolk is very obvious. Wolff undoubtedly wanted to demonstrate a phenomenon which supported the theory of epigenesis. The presence of two embryos connected with one yolk indicates that the preformation of a ready embryo in the egg does not exist and that the development occurs of epigenesis.

Wolff's second teratological work again is concerned with the disturbance in the development of the chicken embryo.² This is a small note with the following content. In the spring of 1777, some of the eggs under a sitting hen did not hatch chickens. On opening such eggs, it was revealed

2. Wolff, "De pullo monstroso, quatuor pedibus, totidemque alis instructo, ACTA ACAD. SCIENT. PETROPOLITANAE, 1783, pp. 203 - 207.

that they either were sterile or they contained dead embryos. From one of these eggs Wolff extracted a monster chicken, which provided the subject of the following description (Figs. 11 - 12). The chicken looked completely ready for hatching. It had a single head, neck, thorax and abdomen, but the extremities were four pairs in number: two pairs of legs and wings. The situation of the extremities was such that it was easy to distinguish the natural from the additional. The additional legs were attached to the thighs at the sacral region and directed to the head end of the chicken, i.e. in a situation opposite the natural legs. The origins of the additional wings were located backwards from the origin of the additional legs in the coccyx region. The impression is that the additional wings and legs belong to another undeveloped chicken, which is located on the original chicken. The underdeveloped chicken is positioned as if the head and neck of the first are hidden in the pubic region of the formed partner, and the chest and abdomen are embedded in the sacral region of the latter, so that externally only the legs and wings appear.

On opening it, Wolff found that the abdominal protuberance contained a single yolk. In the structure of the internal organs of the primary chicken, no deviations from normal were seen with the exception that instead of the two blind out-growths of the intestine there were three. All of the internal organs related to the primary chicken, and in the second there was nothing except the extremities—neither neck, nor head, nor abdomen, nor thorax nor an internal cavity.

The article is terminated by a quick comparison with the monsters described in literature and does not contain any general conclusions. This is entirely natural, because earlier Wolff had published another teratological work about the double-headed calf,³ which was accompanied with a theoretical chapter containing conclusions related to the above-described monstrosity. The material described in the last mentioned work is a calf which died at birth. It had two heads and two necks, but a single chest, abdomen and a normal number of extremities.

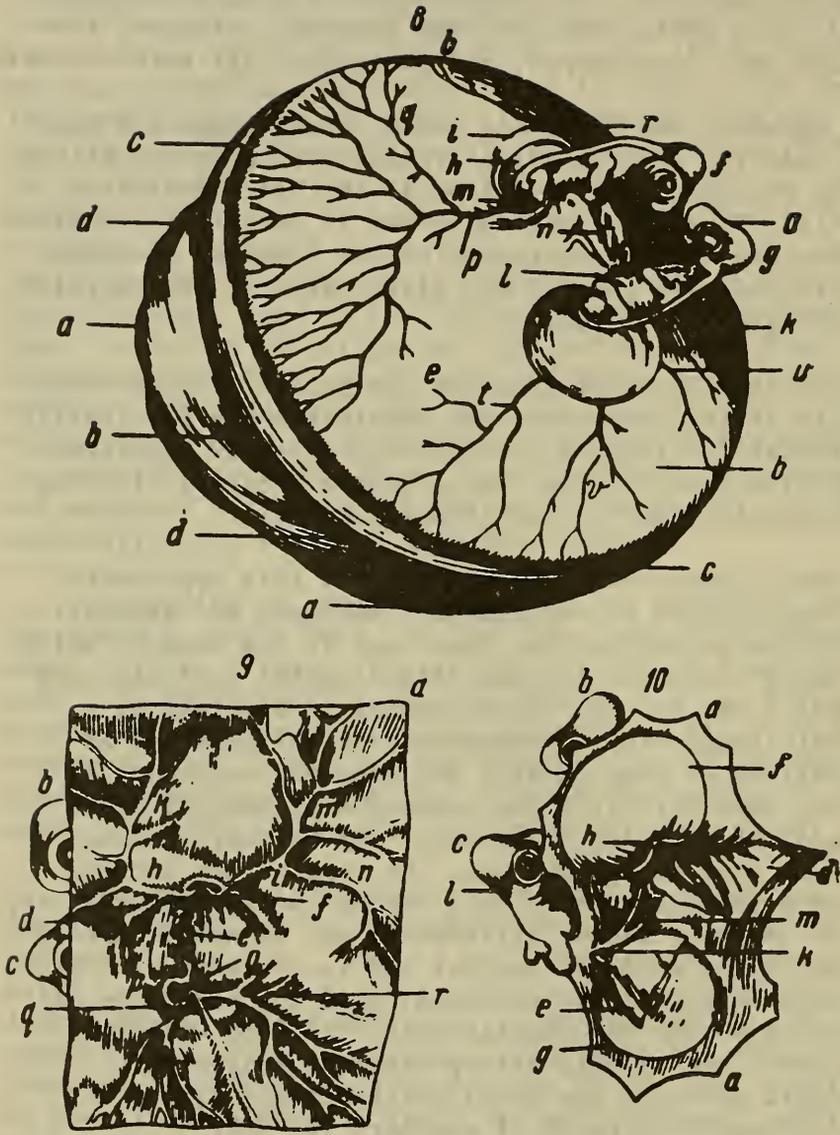
3. Wolff, "Descriptio vituli bicipitis cui accedit commentatio de ortu monstrorum," NOVI COMMENT. ACAD. SCI. PETROP., XVII, 1773, pp. 540 - 573.

The vertebral column was duplicated at the level of the second-third thoracic vertebrae; from here anteriorly it extended in duplicate, and posteriorly; a single vertebra extended. As a whole, the calf was somewhat deformed, the thorax and back were humped, the posterior legs were deformed.

On opening, one heart was found, three lungs and two trachea, and the corresponding presence of two heads with a change in the number and location of the blood vessels (Figure 13). The latter are described in detail with Wolff's usual accuracy. This description can be bypassed in order to come to the main part of the given subject, the article "On the Origin of Monsters."

First of all, Wolff compared two points of view about the origin of twin monsters. One considered the possibility of accidental collision and union of previously separated embryos. "The famous Haller and (Jacques Bénigne) Winslow, who are equally great persons," Wolff wrote,

have turned the arguments against this hypothesis . . . They noticed in the monsters accuracy and regularity of the structure, not less than in the normal, which could not occur in case of accidental collision and union, or in case of accidental transmutation. This regularity is recognized in our monsters as well as in many others. Why does the esophagus of one calf join with the esophagus of another calf, and not with any other part; why do they accrete with each other? Why does the lung of one accrete with the lung of another; why is the anonymous artery in the same manner attached to the anonymous artery or to the aorta of another and is accreted with it? Why, in any of the monsters, does the esophagus not accrete with the jugular vein, the lung with the liver, the carotid artery with the hollow vein? Could parts of one fetus instinctively find the corresponding parts of another? (p. 550)



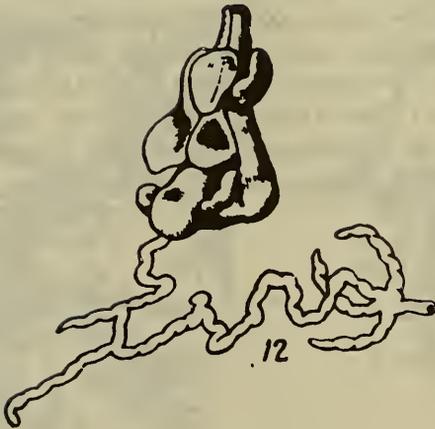
Figures 8 - 10. Illustrations of Wolff's work "Single egg carrying twins."

Figures 8 - 10. Illustrations of Wolff's work "Single egg carrying twins."

8. Egg extracted from the shell; a—albumin; b—yolk; c—the part of the terminal vein; d—the part of the yolk which is devoid of vessels; e—area vasculosa; f, g—upper and lower embryo; h—the part of the umbilical vesicle of the upper embryo; i—a depression in the yolk which is produced by this vesicle; k, m—umbilical vesicle of the upper and lower embryos; n, o—folds of the yolk membrane; p, q, r—yolk vessels of the upper embryo; t, u, v—the same vessels of the lower embryo.

9. The part of the membrane adjacent to the embryo, from the internal aspects; a—border of the cut membranes; b, c—upper and lower embryos; d, e—folds of the membranes; f, o—openings of the intestinal canal of the upper and lower embryos; p, q—border of the abdominal umbilical opening which is transparent throughout the membranes; h, i, k, m, n—yolk vessels of the upper embryo; r—same vessels of the lower embryo.

10. Internal surface of the external membranes which is seen after being separated and turned internally; a—external yolk membrane; b, c—lower and upper embryos; d, e—part of the internal membrane which extends into the intestines of both embryos; f, g—their umbilical bladders; h—opening of the umbilicus through which the internal yolk membrane, which is a continuation of the intestine, leads out from the abdomen; k—vessels; l, m—folds of the membranes.



Figures 11 - 12. Illustration for Wolff's "On the monstrous chicken" (11—External view of the chicken; 12—Viscera).

Wolff came to the conclusion that it is impossible to explain the given condition as the union of two embryos. As a result of that, he raised another question: could it be possible that the monsters originate from embryos which are created monstrously and are prompted to develop like the normal, but which by the powers of nature grow incorrectly? "None of the famous authors writing about monsters," Wolff said, "discuss this question, but rejecting the hypothesis of collision and accidental transmutation, they all now talk about embryos which are created monstrously, as if it is necessary that they begin from predestined embryos" (p. 553).

Thus Wolff formulated the solution of the question, "How do monsters develop—under the effect of the modified powers of nature causing the development, or are their embryos directly created by God and only changed by the powers of nature?" (pp. 553 - 554).

First of all he rejected the accidental development of monsters, because in their structure it is possible to recognize features of beauty, regularity and expediency. From another aspect, monsters occur so faultily organized, so imperfect, that it is impossible to believe that this was created directly by the action of God. As an illustration Wolff gives the case of the duplicated monstrosity which was described by Winslow, where the union of two babies in the pelvic region led to such impairment of the urogenital system of one of the partners that the seminal ducts opened in the urinary bladder. Wolff concluded that: "The rudiments of such deviations from natural structures are to a great extent imperfect, and hence are deserving of deep sorrow from people. They could not have been created and predetermined." (p. 556)

Wolff was not satisfied with this example and gave others; each additional example should increasingly confirm the opinion he held. For example, he referred to the human fetus described by (Jean de) Méry in 1700 in which the region of the lumbar vertebrae was twisted in such a way that its knees and feet were directed backwards. The skull cavity, thorax and stomach were opened, the auricles joined in one cavity receiving in itself all the veins, and so on. On the basis of that and some other monsters he mentioned which were still more imperfect, Wolff stated: "I consider it is

impossible that any individual animal species of this type could have been logically thought to exist in such a way that the species could not possibly live." (p. 560) Further on, Wolff gave the case of the sheep embryo monstrosity described by Antonelli in 1703, which consisted of an abdomen with an umbilicus and hind legs, but without head, anterior legs and thoracic cavity; in the abdominal cavity there was nothing except a mesentery with the intestine and a deformed stomach, i.e. there was neither a liver, nor a kidney and moreover no heart and lungs.

The monster described by Barfolome Zeifart, in addition to its other imperfections, was characterized by the presence of one well-formed eye at the base of the forehead, which was at the same time devoid of the optic nerve. "What is the purpose of such an eye," Wolff asked. "If it could see, why was there not an optic nerve? If it could not see, why, in this monster, was such an incomplete eye formed?" The general conclusion Wolff reached is stated in the following sentences: "I am sure that these examples are sufficient for proving that monsters are not the production of God, but of nature; however, there are productions which have developed unsuccessfully." (p. 567) The report is terminated by short statements showing the importance of studying monsters in order to establish the historical theory of development, i.e. for the substantiation of epigenesis.

Not in any other single report did Wolff mention God so frequently and constantly as in this work, where he names Him as the High Power, sometimes as the High Creator, or as the very wise Founder, or as the Essence of intelligence. All these names were set up in capital letters and were sharply pronounced throughout the text. The work is produced in such a way as to create the impression that it is theological in origin. Actually it was evaluated as such by observers in the period of Queen Catherine II when the latter actively pursued the representatives of progressive thought in Russia.

Wolff's argument itself does not look usual here. In the letter of Wolff to Haller,⁴ written in answer to Haller's

4. The translation of this letter is given in B. E. Raikov's book, pp. 67-78.

preference for preformation over epigenesis, which is in agreement with religious presentations, the subtle irony concerning such arguments sounds bad. And in the work just described, "About the origin of monsters," as if referring to an argument of the same nature, Wolff referred relating the intentional creation of these monsters to God as doubting His wisdom. It is sufficient, however, to consider all those "devout" sentences of Wolff to realize that his main task was to eliminate God from nature. He makes that goal applicable mainly to the development of monsters, but he also relates these discussions to normal development. The results are in complete agreement with his observations in other works, in which he frequently stressed the relationship of the processes of development to natural true reasons.

Besides the above-mentioned teratological works, Wolff published also a small work "Note, concerning the double monsters, whose two bodies are connected by the posterior parts."⁵ In this note, Wolff related that on May 21, 1778 Senat notified the Academy about the birth of a live double monster by a woman in the province of Tversk. The accreted twins lived for two months and were then given to the Academy. They were united at the posterior surface of the pelvic region from the upper edge to the coccyx; the posterior secretory opening was general for both. The remaining parts of the trunk, heads and extremities were entirely separated. The note is terminated by the statement that detailed description of this monster would be published later. Apparently Wolff meant to include the description of this case in a large teratological monograph, but that work was interrupted by his death. Wolff's drawing, which is published by A. E. Gaisinovich from the archive of the Academy of Science of USSR and which is reproduced here (Fig. 14), undoubtedly illustrates the case described.⁶

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5. Wolff, "Notice touchant un monstre biforme, dont les deux corps sont réunis par derrière," ACTA ACAD. SCIENT. PETROPOL. pro anno 1770, part 1, 1780, pp. 41 - 44.
 6. A. E. Gaisinovich, "K. F. Wolff and the study of development," in K. F. WOLFF: THEORY OF CONCEPTION (Academy of Science USSR, 1950). The mentioned drawing is located between pp. 472 and 473.

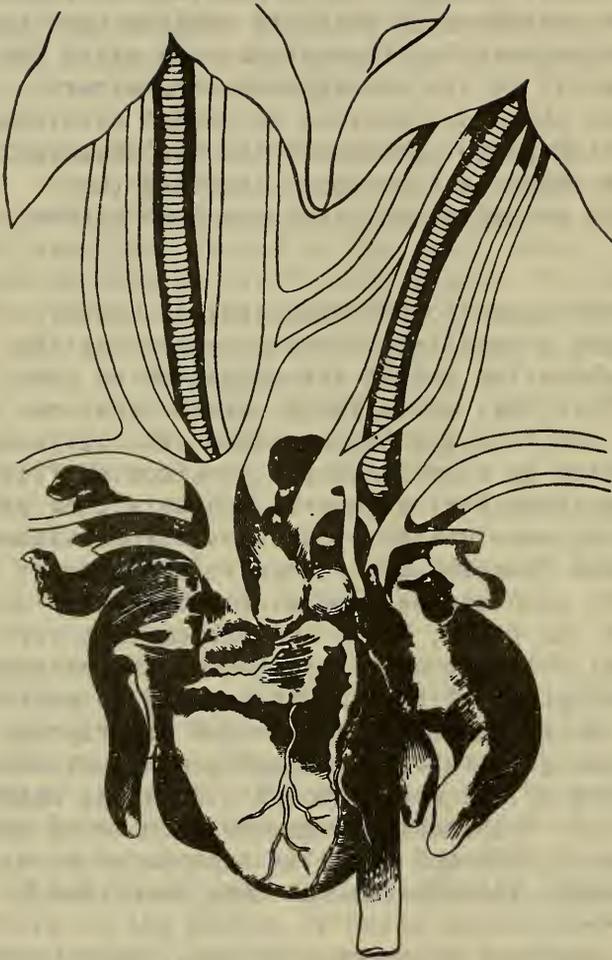


Figure 13. Illustration to Wolff's "Description of double-headed calf."



Figure 14. Illustration of Wolff, showing accreted twins.

In regard to opinions concerning monstrosities as a result of sharp deviations from normal development, there are Wolff's judgments about the variable features in general, which are observed in particular in human anatomy. The latter was elucidated by Wolff's special work, "About the instability of the structure of the human body and about the examples selected for the demonstration of this

instability."⁷ The article contains numerous examples of anatomical variations in man. Wolff noted that not only small venous branches whose variability is endless and is not defined, not only large veins and arterial vessels, not only nerves, but also bones, muscles and the internal organs are characterized by instability. This is related, according to Wolff, even to the "most precious parts of the body as the heart and brain to the extent that it is hardly possible to find even two human bodies in which these precious internal organs are identical in their form, situation and proportions" (p. 217 - 218). The variability of organs in the adults depends on their more distinctly expressed variability in the embryonic period. For the illustration he referred to the fact of the deep differences in the structure of the chick embryos, which "are sometimes so unequal that they could have been mistaken as other animals if it was not known that they had been taken from chicken eggs" (p. 223).

Wolff's epigenetic ideas, which he based on study of ontogenetic development and on variability in individual development, should certainly have led Wolff to question the origin of diversity of organic forms, i.e. to the problem of evolution in the modern understanding of this word. Actually, if development is a new-formation and not growth from the beginning of existence; the variability of creatures could not be primordial, could not be a sequence of a creative action. In the published reports Wolff did not consider this question himself; however, the significance of the principle of epigenesis did not escape Engels' insight into the problems of species evolution. In DIALECTICS OF NATURE the following very significant paragraphs were dedicated to Wolff: "... K. Wolff produced in 1759 the first attack on

7. Wolff, "De inconstantia fabricae corporis humani, de eligendis ad eam representandum exemplaribus," ACTA ACAD. SCIENT. PETROP. pro anno 1778 (1781), pp. 217 - 235. The judgment about this subject can also be found in others of Wolff's anatomical works (see list in Wolff's THEORY OF CONCEPTION, Academy of Science USSR, 1950, pp. 478 - 480).

the theory of the stability of the types as species, proclaiming the study of their development."⁸

An identical opinion about the significance of Wolff's investigations was stated by Ya. A. Barzenkov in a posthumously published outline of the history of comparative anatomy.⁹ On characterizing the theory of "evolution" of Haller and Bonnet and the study connected with it about "inserting of the embryos," Barzenkov wrote: "From this theory, by the way, one sequence developed which is very important for the theoretical natural sciences: the stability, and the invariability of the types." (p. 96) "As a very young man, Wolff ... came to the belief that this theory is not possible." (p. 97) Proving the falseness of preformation and turning instead to the principle of epigenesis, Wolff consequently disproved also the idea of the stability of types. The quotations from Wolff's manuscripts which were recently published by B. E. Raikov undoubtedly indicate that he was sure of the support for the changeability of the types and, therefore, can be truly considered one of the predecessors of Lamarck and Darwin.

Giving credit to Wolff's efforts to proving epigenesis, his idea about the origin of the parts of the embryo from folds having the form of plates or leaves must be noted in particular, because this observation influenced Pander and Baer.

The previously discussed list of Wolff's works undoubtedly indicates that he actually had seen these structures and called them leaves or membranes. It is possible also to give another example, from which it can be concluded that he had seen not only layers in the embryo itself, but that he also recognized that by their means the embryo and all the remaining blastodisc are united into a single unity. Describing the structure of the "cardiac fossa" which represents, according to Wolff's description,

8. F. Engels, Old introduction to DIALECTICS OF NATURE (STAROE VVEDENIE K DIALEKTIKE PRIRODY), K. MARX AND F. ENGELS. SOCH., v. XIV, p. 483.

9. Readings of Ya. A. Barzenkov about comparative anatomy. Uch. Zap. Mosk. un-ta, vyp. 4, 1884, p. 242.

the fold of the stomach, he noted that the 'membrane constituting the substance of the stomach does not break down at the border of the fossa . . . , and leads into the internal layer of the transparent part of the vascular area and then into the internal layer of the yolk itself."¹⁰

There is no doubt that this observation should have been discussed as showing the continuity of the layers of the embryonic and extra-embryonic entoderm which is connected with the visceral layer of the mesoderm. Wolff saw the embryonic layers, but he did not understand their significance. The theory of the embryonic layers represents the product of the first half of the nineteenth century and is connected with the names of the Russian academicians Pander and Baer. Wolff only established the factual basis on which this theory could be later constructed.

10. DE FORMATIONE INTESTINORUM, p. 454.

CHAPTER 7

THE WORK OF WOLFF: "ON THE SPECIAL ESSENTIAL POWER"

In order to conclude a summary of Wolff's activities in embryology and to characterize them completely, it is necessary to stop at the idea which he frequently considered central to development and which was so differently evaluated subsequently. The idea is that of the essential power. In Wolff's works reviewed above, the essential power was mentioned either generally or sometimes in a very hazy form, or it was mentioned casually without sufficient explanation. Apparently, at the end Wolff found it necessary to explain his point of view on this subject more definitely, and he felt the need to examine scientifically the power's control over the activities of organisms.

In 1782 the Petersburg Academy of Science, under Wolff's initiative (25), announced competition (26) for a prize on the question about the nature of the feeding powers. The subject of this work was formulated in the following manner.¹ In the introduction to the question, it was asserted that the nutritional juices were distributed among even those parts of the animal organism, such as the epidermis, nails, hairs, and horns, which, it was claimed at the time, were devoid of blood vessels. Further, it was noted that in the early stages of development of the embryo, in which there was not yet a heart, the blood vessels and the nutritional juices were also distributed homogeneously. From this it was concluded

1. The questions for the competition were given in Latin and submitted to the below-discussed manual "Zwo Abhandlugen etc." Here a shortened statement of the introductory part of the question is given. The text of the questions themselves is given in literal translation.

that the movement of the nutritional fluids, under the effects of such a power, is not dependent on the movement of the heart. Because juices similarly assimilate, grow, and form new parts throughout their life in plants, and because at the same time there is no other power comparable to the power of the heart movement, the movement of plant juices should also be described under the special power.

Therefore the following is asked:

What is the nature of that power, and in particular, is it identical with the commonly known powers, or is it, as they think distinguished from those and innate only to animals and growing plant substances? If the latter is true, the next question follows: of what general character is the effect of this power and by what properties is it distinguished from the general magnetic powers, indicating its exceptional nature?

In this competition, work from different countries was submitted. Among the twenty-four submitted works a large number were not worth serious consideration. Wolff reviewed all these works and, based on his opinion, two works were published: the article of J. F. Blumenbach (27), professor of medical sciences in Göttingen,² and that of K. F. Born, doctor of medicine and surgery and ordinary lecturer at the medical-surgical institute in Kronshtadt.³ Wolff combined his own article with these two articles, and they were printed together in one manual; Wolff's work presented his opinion about Blumenbach's and Born's articles, but it mainly contained the statement of his own ideas.⁴

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2. The article by (Johann Friedrich) Blumenbach is entitled, "Attempt to answer the competition question, for the third time proposed by the Improvisator of the Academy of Science in Petersburg: Uti nutritio aequalibus etc.?"
 3. Born's article does not have a title, but was simply called "Second article on the feeding power."
 4. The general topic of the manual appears on the title page as, "Zwo Abhandlungen über Nutritionskraft, welche von der Kaiserlichen Academie der Wissenschaften in St. Petersburg den Preis getheilt erhalten haben. Die erste von Herrn Hofrath Blumenbach und zwote von Herrn Prof. Born. Nebst einer ferneren Erläuterung eben derselben Materie." Von C. F. Wolff, der Akademie Mitglied, 1789.

Wolff's article is called "About the inherent essential power of the plant as well as of the animal substance."⁵ Its introduction compared Blumenbach's and Born's opinions. It is written in quite a friendly tone and is concerned more with Blumenbach's theses, because Born's article was less original and to a certain extent full of citations from the previous work of Wolff and Blumenbach.

Wolff remarked that according to Blumenbach, the power or force which moves the nutritional juices is related, primarily, to the selective properties of the feeding tissues and, secondly, to the delivering force of the vessels or generally to the cavities containing those juices. On the contrary, Born found in the nutritional juices themselves the basis of the movement of the juices during feeding, growth, regeneration of the lost parts and healing of wounds. In other words the juices themselves acquire, in his opinion, the property of moving in definite directions. Without disproving any of the authors' opinions, he came to his understanding of the question.

First Wolff developed the idea (§ 1 - 5) that the nourishing power could not be related only to the hard or solid nourished parts of the body or only to the nourishing juice itself, but in his opinion, "it is inherent in the solid or hard, as well as in the fluid parts." (§ 4, p. 5) Turning to the character of the powers inherent in the living body (§ 6 - 8), Wolff stated his belief that these powers or forces are as such: reciprocal attraction of the homologous parts and repulsion of the heterologous parts in the nourishing juices, and also attraction between homologous solid and fluid parts and reciprocal repulsion of the heterologous parts (§ 7; p. 7). Consequent to that, there is an important observation that "defining and distinguishing the forces from each other cannot be done other than by their actions." (§ 8, p. 7)

Next comes a detailed justification of the existence of attractive (§ 9 - 16) and repulsive (§ 17 - 29) forces in the

5. "Von der eigenthumlichen und wesentlichen Kraft der vegetabilischen sowol als auch animalischen Substanz" (pp. 3 - 94).

organisms. Then, after comparing his conclusions with Blumenbach's and Born's (§ 30 - 36), Wolff discussed, in detail, the question about the means of movement of the nourishing juices, and he arrived at the conclusion that in the nourished parts there are no intervals and that the juices penetrate through a confluent substance (§ 37 - 66 and 69 - 71). With that, he considered it as beyond doubt that the nourishing force could not be anything other than an attractive power (§ 67 - 68).

Wolff identified the attractive and repulsive power with the specific essential force of the plant and animal substance; hence, all the preceding represents only an introduction to two basic parts of the work which consider the particularities of the essential force in the two living kingdoms. In the first part, which he entitled "About the distinguishing features of the specific essential force in the plant substance," Wolff confirmed that plants and their characteristic plant life do not develop as a result of attractive and repulsive forces which are common for all nature or of forces connected with the organization of the plant bodies. Hence the essential force, in his opinion, should be distinguished from those forces (§ 72 - 79).

In the light of the conference works, published in 1784, this was a basic question: if the attractive force represents the cause of movement of the nutritional juices, then is it identical with the general attractive force which is inherent to all the bodies of nature, or if it is distinguished from it? Wolff remarked that this question was not even mentioned in any of the submitted works, although two of them contain a note that the authors considered the nourishing force as the usual force of attraction. "This question is of great importance and is easily solved," Wolff wrote. If the subject was as the authors thought, then plants, which are fitted with a general attractive force and acquire organization, could only be machines, distinguished from artificial machines only by their structures. In this case it would have been possible to construct from any material which is provided with a general attractive force, a model which not only in its external form but also in its internal structure could have been similar to one or another plant, such as the *Tragopan pratensis* L. This model must grow like

a living Tragopanon, give similar flowers and seeds, i.e. reproduce, because it acquires the properties of this plant's organization and the same force. In other words it could have been the same machine. "I think, however," Wolff wrote,

that even the strongest defenders of mechanical medicine do not prescribe models of such function. Consequently, the nourishing force of the plants and animals should be distinguishable from the general force of attraction, which is characteristic of all the bodies of nature. This nourishing force should be inherent only in the plant and animal substance, because no other material except the plant and animal feeds, grows and multiplies. Because the entire life of the plants—their nourishment, growth, vegetation and multiplication—depends on the nourishing force, it would be possible to call it inherent and an essential force ... Since animals eat, grow and vegetate (although the latter process extends not too long after development) and reproduce ... and since their life depends on the nourishing force, this force must be considered an essential force which is characteristic of all vegetating bodies. (§ 72, pp. 38 - 39)

Further, Wolff stressed that for the vegetative life of plants and animals their structure is not essential. As proof he cited the boundless diversity of forms and the presence of living creatures (lichens, sponges, moulds) which do not have a defined external form and are devoid of structure (composed of either vesicles or of granular masses). "All these living creatures simply could be accepted as living or vegetative material, and it is too difficult to consider them as organized bodies" (§ 73, p. 40). Another point in favor of the independence of the organism's vegetative function from its structure Wolff considered to be the decrease of the regenerative property with the increase of organization.⁶ "It is known," he wrote, "that the more perfect the regenerative

6. The belief that the degree of the regenerative property is in a strictly inverse relationship to the height of the (... contd on next page)

property is in animals, the more imperfect is the organization of their body. How then could the vegetative functions be dependent on the organization?" (§ 74, p. 40).

Admitting that the forces characteristic of organized bodies promote the functions of vegetative life—in particular nourishment, vegetation, and multiplication—Wolff considered that these forces are sufficient bases for the functions mentioned. From this he concluded that "the mechanical causes interfere (where they exist) only accidentally in the activities of the proper vegetative forces and modify the activity, changing . . . in particular the results of the form-making (vegetation), which hence could reach an endless diversity" (§ 75, p. 41).

Wolff's general conclusion he formulated in the following words, in which he simultaneously determined his relationship to animistic vitalism:

The essential force which is characteristic of plant and animal substance promotes vegetative functions without the participation of organization and without the effect of additional forces. This specific actual force is, apparently, particularly that force which was sought by (Bernhard Siegfried) Albinus, and its existence was admitted by Stahl and is ascribed without basis as its spirit. It represents a special defined relation to the attractive and repulsive forces.
(§ 77, p. 42)

Later, however, Wolff wrote the following:

So far as the vegetative life of plants and animals depends only on a force, because the organization does not add anything, it is fair to consider this

(Footnote No. 6, contd)

organism was dominant in the literature until recently. Only recently, M. A. Vorontsov has given essential indicators of the incorrectness of this prevalent belief (M. A. Vorontsov, "Regeneration of organs in animals" (Regeneratsiya organov v zhivotnykh), 1949, SOV. NAUKA, pp. 82 - 88).

force as distinguished from the general attractive and repulsive forces of all the other bodies. It should be characteristic only for developing bodies, including, as we know, only plants and animals. This force acquires the property of attraction as well as repulsion. It must, therefore, get a particular definition, i.e. must represent special kinds of attractive and repulsive forces. (§ 79, p. 42)

Then Wolff considered in detail the character of the actual force. He considered it to be established that the plant substance attracts the homologous substance and replaces the heterologous substance (§ 81 - 82), on which property is based, in both plants and animals, the capability of producing the plant and animal substances (§ 83 - 84). According to Wolff, the main vegetative functions of the animal organism are connected with the essential force: the digestion and formation of the milky juice (§ 85), blood formation (§ 86 - 87), and finally the secretions. This latter function he particularly reviewed in detail (§ 89 - 105). Wolff subsequently mentioned another feature of the essential force on which the plant substance depends, not only to attract to itself the homologous substances, but also to mix with them (§ 110). This feature Wolff considered important and indicative that the attractive force of the plants and animals becomes a nourishing force (§ 111 - 115). Comparing the appearance of the essential force in plants and animals led Wolff to a conclusion that "Therefore, in plants and animals there is only one essential force" (p. 65).

Reaching the conclusion that the essential force is single, Wolff again turned to the question about the nature of this force. "It was possible," he wrote,

to call it the spirit of the plant and the vegetative part of animals, but not, of course, in the philosophical meaning of this word, but only in a general sense of force which determines all features which taken together constitute the life of things. If I am not mistaken this is the same spirit which was acutely observed by Stahl and the defenders of his opinion in the vegetative functions, but which they mixed, without basis, with the spirit of animals

Because in nature all can be related to attraction and repulsion, and both of these primary actions originate from the same force, it seems to me, if I may express my opinion, that in all nature only one single force exists, namely the force of attraction and repulsion . . . and there are not many forces, but only one force. (§ 124, pp. 69 - 70)

Coming to the animal functions, the study of which constitutes the second part of the work, Wolff remarked that his opinions have a less conclusive character. First of all he drew attention to animal functions which are effected by stimulation of the nerve substance and muscular action and which, at first glance, are promoted by special forces: the first is sensitivity, and the second is irritability. "Both of these forces should be completely distinctive and distinguishable from the essential forces of plant substance; they must constitute the essential force of the animal substance, i.e. on which all the animal functions depend" (§ 137, p. 77). From the analysis of these features, Wolff formulated a cautious conclusion that a relationship exists between irritability and the repulsive force (§ 138), and he discussed the initiating cause of irritability as identical to the essential repulsive force (§ 141, p. 79). (Sigismund) Kohlreuter carried out investigations based on this opinion, which he described in an article sent to the Petersburg Academy of Science. (28)

Wolff concluded from these data that "It is more than evident that irritability is inherent in the plant substance in general, as in the animal, and that irritability by any means does not represent the essential force of only the animal substance" (§ 150, p. 85). From this he drew the conclusion of the single nature of the essential force in plants and animals; it is distinguished only by a different animation effect (§ 152, p. 86). The analogy allowed Wolff to think that irritability is based on the force of repulsion, as sensitivity is on attractive force.

The concluding paragraph begins with the statement: "Considering that the essential force of the plant and animal substance is inherent to these substances, no one will doubt that the initial existence of the force itself has

been shown." On the question, "does the essential force depend on the entire aggregation of the substance with which it is characterized, i.e. on all the substance, or does it depend mainly on one constitutive part, or on individual substance which can be considered as the constituent part of the living animal and plant substance, but separated from it?" Wolff answered that "for me the latter, for many reasons appears much more evident." (§ 178, p. 94) Remarking that in regard to the essential force of the animal substance there were yet many things which were not clear, Wolff ended his work with the following words: "Concerning the essential force of the plant substance, I do not believe that I have made a mistake on any important point."

CHAPTER 8

THE IDEOLOGY OF WOLFF

The comparison of Wolff's thoughts about the essential force, which he stated throughout a thirty-year period from the time of his dissertation up to the work which has just been discussed, with his other principal reports, could serve as material for conclusions about Wolff's theoretical ideas.

To formulate a conclusive opinion is not easy, as evidenced by the diversity of the opinions in literature. Apparently, the first methodical evaluation of Wolff's opinions was given by Kirchhoff,¹ in whose article there was a special section under the title of "Wolff's Materialism." Comparing Wolff to Haller, Kirchhoff wrote that the latter extracted the "mystery of the invisible existence" of preformed rudiments "from the mystery of the act of creation in Adam's time." In contrast, "Wolff's epigenesis transferred the miracle of development of the organism from the provisional subjects of the world and gave it to the authority of the rational science. By means of exhausting investigations and by means of the sharpness of logic, Wolff made the development of organisms an unquestioned truth." However, in Kirchhoff's opinion another important service also belongs to Wolff: "He established the route for the only possible explanation of life, namely for the mechanical or materialistic explanation, which is based on the solid, rock-like foundation that life phenomena can be explained as originating from material and

1. However, much earlier Haeckel remarked that "vis essentialis" represented to Wolff not something mythical but simply a suitable name for the identification of two real phenomena, namely the autonomic movement of the nourishing solution in the organism and the independent development of the typical forms and structures (BRITISH AND FOREIGN MEDICO-CHIRURGICAL REVIEW, v. 12 (1853) pp. 285 - 314).

the power which is not separated from it."² Reviewing the contents of Wolff's article, "About the special essential force," Kirchhoff extracted from it the following conditions. Organic life, according to Wolff, is situated under the control of universal natural laws which do not know exceptions. The law of organic life is the effect of the power of attraction and repulsion, which does not, however, correspond identically to the manifestations of the inorganic world. The organic power of attraction is the particular nourishing power of living creatures which Wolff called the essential force or power. In it, the existence of the organism is expressed; it is inherent to each of its particles which is capable of attracting some substances and repulsing others, as in the magnet where each point acts in an attracting and repulsing manner simultaneously. The nourishing of organisms is similar to the development or growth of crystals, because in this case only certain substances are attracted; however, there are differences because the crystal acquires new material from the surface while the organism swallows it internally. The selective property of nourishing substances could be comparable to the activities of the soul, but, it is impossible in any case to mix it with the properties of the animal soul as Stahl did. On stating these opinions, in a fairly simple rewording of Wolff's own, expression, Kirchhoff exclaimed: "How clearly without base are these views about nature...!"³ Kirchhoff later developed his own view as follows: "There is a solid line for the mechanical biology of our and all times: the movement of material, by the eternal law of physics and chemistry, promotes the circulation of substances through air, water and earth and also through living bodies; hence their birth, life and death represent a surrender to the natural law of the link in this wonderful complex... Wolff says that to accept Blumenbach's educational type of force means to agree with his incapacity to relate life to its reasons, i.e. to interpret in accordance with the laws of nature. Whoever behaves like that tries to help himself by a big voluminous word which gives a cheap explanation to all

2. A. Kirchhoff, "C. F. Wolff: Sein Leben und seine Bedeutung für die Lehre von der organischen Entwicklung," JENAISCHE ZEITSCHRIFT FÜR MEDIZIN UND NATURWISSENSCHAFT, Leipzig, 4 (1868), p. 214.

3. Ibid., p. 216.

existence." Kirchhoff concluded Wolff's critique of Blumenbach by citing Goethe's words: "Where comprehension is lacking, there a word fills in at the right time."⁴ E. Haeckel similarly praised Wolff's methodology, labelling him a "great natural-philosophy scientist in the best and highest understanding of this word."⁵

Kirchhoff evaluated Wolff's ideology as materialistic, naturally identifying it with the "mechanical" understanding of nature. This conclusion is not understandable, if we remember how definitely Wolff, as early as 1759, had objected to the principles of "the mechanical medicine," which he called an "imagined system." Contrary to Kirchhoff, the majority of authors who have written about Wolff and who were interested in his ideology have characterized him as a vitalist. This was manifest when (Emile) Ràdl, in his first edition of HISTORY OF BIOLOGICAL THEORIES,⁶ wrote that Wolff, following J(ohn) T(urberville) Needham, had borrowed Leibnitz's idea of the monad which, by the effect of a specially developed force, is turned into an organism. Hence, Ràdl concluded, Wolff had added this conception to Stahl's idea about the soul as a continuing superphysical power in nature. And although Ràdl, in the second edition of his book, considered Wolff's evaluation as incorrect,⁷ such an opinion has appeared in recent literature without any reservation, for example by J. Needham in HISTORY OF EMBRYOLOGY (p. 256).⁸ It is entirely natural, of course, that (Hans) Driesch⁹ considered Wolff to be a complete vitalist because in his HISTORY OF VITALISM Driesch had joined the vitalists, and for the most part, although without sufficient basis, so had almost all the leading biologists.

4. "Faust," fourth scene, translation of N. A. Kholdokovskogo.

5. E(rnst) Haeckel, ANTHROPOGENIE; ODER ENTWICKLUNGSGESCHICHTE DES MENSCHEN. (Leipzig: Engelmann, 1874), p. 36.

6. E(mile) Ràdl, GESCHICHTE DER BIOLOGISCHEN THEORIEN, v. I, 1905.

7. Ibid., 2nd ed., 1913, p. 243.

8. (Ed.: Joseph Needham, A HISTORY OF EMBRYOLOGY (2nd ed., 1959), pp. 207 - 208. This claim represents a misreading of Needham.)

9. H. Driesch, DER VITALISM ALS GESCHICHTE UND ALS LEHRE (Leipzig: Johann Ambrosius Barth, 1905), pp. 50 - 55.

Referring to Rádl, P. A. Novikov¹⁰ also considered Wolff an idealist, calling his system of opinions physiological vitalism. Novikov said that Wolff's opinions, from the philosophical viewpoint, oppose Cartesian ideology and are related to Leibnitz's teachings about monads. At the same time they are in opposition with other conditions of the latter, particularly with the teachings about pre-established harmony. Somewhat later, Novikov remarked that Wolff's theory is vitalistic only from the formal point of view and undoubtedly could have been favorably accepted in France where "materialism, at that time, was becoming a popular philosophy and where Diderot, applying the epigenesis of Maupertuis, has placed the materialistic foundation under it." In another place in his book, Novikov placed the vitalistic epigenesis of Stahl and van Helmont against the ideas of Wolff and Blumenbach, which he characterized by the absence of animism.

B. E. Raikov, in the book repeatedly cited here, has made an attempt to review Wolff's theoretical ideology. Translating the corresponding parts from Wolff's different works, especially from both books devoted to the theory of generation, and from the article "On the special essential force," Raikov concluded that Wolff's scientific method is materialistic, that his "essential force" is contrary to Stahl's "soul" and does not have a mystical supernatural character. Raikov referred also to Wolff's handwritten work, "First outline of the theory of the soul," in which Wolff confirmed that the soul does not precede the body; Wolff acknowledged what is expressed in modern language as the primacy of the material over the soul. "Therefore," Raikov wrote, "Wolff cannot by any means be listed in the category of the vitalists—he has many idealistic ideas."¹¹ Wolff's opinion against "The mechanical medicine" Raikov considered as Wolff's opposition to "This diverse materialism, which has got the name of mechanism."¹² This conclusion, in

10. P. A. Novikov, THEORY OF EPIGENESIS IN BIOLOGY (1926), pp. 18 - 19, and 62.

11. B. E. Raikov, OUTLINES OF THE HISTORY OF EVOLUTIONARY IDEAS IN RUSSIA BEFORE DARWIN, 1947, p. 72.

12. Ibid., p. 73.

agreement with Wolff's opinions about the eighteenth century, represents, to a certain extent, a modernization of his ideology which distorts the historical perspective.

The connection of Wolff's opinions with philosophical presentations undoubtedly have had an effect on modern science. It has already been noted above that some of his ideology was dependent upon Leibnitz's ideas which were predominant in the eighteenth century. It must be remembered that with Leibnitz's philosophical presentations, the persons opposing Wolff—those who were supporting the idea of preformation—had a greater basis to attack Wolff, because Leibnitz was himself inclined to the idea which he expressed as his idealistic doctrine about the pre-established harmony. In the literature, it was repeatedly noted that K. F. Wolff had learned Leibnitz's ideas from his teacher Christian Wolff, who had tried to reject the most idealistic aspects of the doctrines, in particular the existence of pre-established harmony. As mentioned above, K. F. Wolff himself considered these teachings about the pre-established harmony a philosophical source of the idea of preformation. No, strictly speaking there is no basis to assume that Wolff had accepted Leibnitz's doctrines about monads. In his theory of development, Wolff followed only Leibnitz's ideas on the understanding of the forces or powers as the source of life processes in general, and development or growth in particular, which are central for Leibnitz and his independent successors.

Apparently, it is not an exaggeration to say that Wolff had made an attempt to establish a special system guided by a concrete study of the manifestations of nature and, above all, the manifestations of life. He could not put his system in order. If Wolff's materialistic tendency in his opinions about the possibility of knowing the world, about the subordination of all its manifestations including all the features of life to natural law, about the subordination of psychical processes to materialistic features and so on are unquestionable, so his fluctuations between materialism and idealism on the question about the moving force of vital processes (29) are without doubt. In an analogous context, he hurried to make the reservation that the essential force is entirely distinctive and inherent only to the organic body. With his opinions, he sometimes moved close to Stahl's presentations and sometimes decisively shut himself off from them.

In his fluctuations between materialism and idealism, Wolff was undoubtedly closer to the former. In any case, he repeatedly urged strict and careful investigations of nature. It is not his fault that the general level of philosophy and knowledge of nature at that time did not allow him to develop his efforts into materialistic judgments. It is not his fault that he sometimes was obliged to argue theologically, which, judging from his letters to Haller, did not satisfy him deeply. Now it is impossible to know accurately why Wolff behaved as he did, either because he hoped to convince his opponents with such arguments, or because he was obliged as a result of external circumstances to give his thoughts a form that did not correspond to theirs. In any case it is clear that Wolff never retreated from his scientific beliefs.

Unrecognized in Germany where he was born and where he spent his youth, Wolff was acknowledged in Russia which can be fairly considered his second motherland. On Wolff's sudden and early death, the Petersburg Academy of Science praised him in a short but condensed obituary, which clearly stated the outstanding services of the late Russian academician.¹³

13. An obituary in French is published in NOVA ACTA ACAD. SCIENT. PETROPOL., XII (1794), 1801. A translation of a significant part of this document is given in A. E. Gaissinovich, "K. F. Wolff and teachings about development," pp. 472 - 473.

CHAPTER 9

THE THEORY OF EPIGENESIS IN RUSSIA AT THE END OF THE 18TH CENTURY

It is impossible to believe that the scientific effect of Wolff's ideas was not realized until many years after his death. During his life his scientific opinions were cited and discussed. Thus the epigenetic ideology was held by Zybelin (30), a professor of the medical faculty of Moscow University and Wolff's contemporary. Beginning with Lomonosov's materialistic principles, Zybelin established that all living creatures come from fluid. "All of mankind, even legendary giants as solid and strong as Hercules, whales and elephants all started from fluid. At their beginning they were nothing but one drop of fluid, from which fibers, membranes, muscles, cartilage and hard bones developed into man, the eternal astonishment of human intellect."¹ Solving the question about the beginning of individual development from the point of view of epigenesis, Zybelin did not see the necessity for explaining "the union of the parts" by assuming a particular "attractive force." He considered it "not appropriate to exaggerate things and ideas unnecessarily and hence only make science difficult."²

In the eighteenth century in Russia, an attempt was made to interfere experimentally in the process of embryogenesis.

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1. The thoughts about the reason behind the internal union of the parts and about the resulting strength in the human body were expressed when Semen Zybelin received the title of Professor in the Imperial Moscow University of Medicine on August 23, 1768. These words had not been previously published. (*Opyt trudov vol'nogo sobraniya pri imp. Moskovskom universitete, Chast' vtoraya*, 1775, pp. 152 - 185 (citation on pp. 160 - 161)).
 2. Zybelin, p. 180.

Acceptance of the possibility of some outside effect on its course signifies the assumption of the epigenetic nature of embryonic development, because from the point of view of preformation the development of the fetus is predetermined in every detail from the beginning. The experimental investigation mentioned above is that of the physicist D. A. Gallitzin (Evdokiia Golitsyna) (31). In his letter to the Petersburg Academy of Science, "On Some Electric Objects,"³ Gallitzin reported his experiments on electric manifestations. In conclusion, he wrote the following: "I cannot hold to . . . , or state here the results of a particular single experiment which was carried out in the last year. Because this experiment is a single one, it is completely possible that its results are of an accidental nature; I am hoping that this year I will have the opportunity to repeat it. On July 5, I electrified for half an hour, eight eggs which had been incubated for nine days and left four eggs without electrification. A hen continued to sit on the eggs. On the 17th day of that month, at midday, the young chicks started to hatch; by evening all had appeared and all had black feathers. On the evening of the 18th only one chick hatched from the four non-electrified eggs. One egg was found broken and contained a white chick. The two remaining eggs were found to be nonfertilized. The brood hen was white" (p. 15).

What is interesting here, of course, is not the result of the experiment itself but the idea, indicating the spread of epigenesis among Russian scientists. Wolff's ideas had gained significance in one of the early manuals of the history of biology—in the presentation of J. Beseke's AN ATTEMPT AT A HISTORY OF THE HYPOTHESIS ABOUT THE GENERATION OF ANIMALS, which appeared in Russia in 1797.⁴ This book and its author deserve to be extracted from the injustice of oblivion (32).

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3. Lettre sur quelques objets d'électricité adressée à l'Académie Impériale des Sciences de St. Pétersbourg par S. E. Mr le prince Dimitri de Gallitzin, St. Pétersb., De l'imprim. de l'Acad., 1778, 16 pp. in quarto.
 4. Beseke, VERSUCH EINER GESCHICHTE DER HYPOTHESEN ÜBER ERZEUGUNG DER THIERE . . . , Mitau, 1797.

Johann Beseke (1746 - 1802), during the last twenty-eight years of his life, was professor of law in the academic high school in Mitau (now Elgava, Latvian SSR). Besides his philosophical, juridical and educational presentations, three fragments of his common works (33) were published; these were devoted to his thoughts on the history of all natural sciences throughout twenty centuries and more. The work on these subjects was interrupted by the author's death.

In the book of 1797, Beseke reviewed all the different hypotheses proffered up to the middle of the eighteenth century for the explanation of animal regeneration and development. He divided them into two groups, because one of the hypotheses confirms that organic bodies actually are the outgrowth of other organic bodies, and others consider that organic bodies exist from the beginning of the world. The first group of hypotheses is related to epigenesis, or the true conception and development, and the last to the system of evolution in the broad meaning of the word, which does not allow for the possibility of true development. Some representatives of the second point of view claimed that the preformed organic rudiments are not actually identified from the beginning with the organic bodies and that only by interpenetrating with the latter do they acquire the capability of turning into formed organic bodies (system of dissemination); others presumed that these rudiments are contained in the organic bodies themselves (system of evolution in the narrow meaning of the word). In agreement with the latter theory, the preformed rudiments are situated, one into the other, either in the male or in the female body. The first assumption is the theory of preformation, or the system of Leeuwenhoek, and the second is the system of evolution in the narrowest sense of the word, or the system of Malpighi.

Against all these preformation theories, Beseke with great feeling decidedly set the epigenetic doctrines of Wolff. Wolff, according to Beseke, "has acted against the theoretical possibility of preformation as well as against its factual existence and has confirmed that everywhere in nature there is a true education of what previously was not present." (p. 62) Beseke reproached Wolff only because the latter did not try to declare the contents of the "essential force" which manages the development. Wolff, in Beseke's view proved that

development is accomplished epigenetically, and this is his most important achievement; but he did not give the features of development its necessary explanation. "Was it possible," Beseke asked, "to explain what is called the essential force by using the hydrostatic, aerostatic and chemical laws, or by using the laws of attraction, gravity, chemical affinity, dissolving, precipitation, elastic fluids and so on?" (pp. 65 - 66) Beseke's raising of these questions itself shows that he considered it necessary to make concrete the materialistic understanding of the "essential force," which Wolff did not actually try to do.

His criticism of Wolff's ideas did not keep Beseke from acknowledging the progressive importance of the opinions of the Russian academician, whose system, according to Beseke, "was so insightful and was based on such accurate observations that it had exceptional success and was highly evaluated even by Haller, who himself was the head of the new evolutionary sect" (p. 70).

Summarizing Wolff's discussion with Bonnet, who was the most candid supporter of the doctrines about the preformed body and rudiments inserted into each other, Beseke remained sympathetic to Wolff's opinions. "None of the thinking natural investigators," Beseke wrote, "after what Wolff taught would dare to sway him ... The nature-investigators who have been trying to explain philosophically the mystery of nature have, for a long time, fluctuated between truth and confusion; however more and more they are inclined towards the side of epigenesists, whose new detachment was headed with dignity by the excellent genius Wolff." (pp. 75 - 76)

Even in the educational manuals, which usually give only the commonly accepted theories, Wolff's ideas received equal consideration with the opposing ideas of such well known authors of the time as Haller. Professor M. K. Pekken's manual of physiology (34)⁵ can serve as an illustration. In one of his concluding chapters, Pekken discussed the questions of

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5. THE ELEMENTARY BASICS OF PHYSIOLOGY OR SCIENCES OF THE NATURE OF HUMANS. The Works of Matvei (Khristianovich) Pekken, outside consultant and professor in the Kronshtadt Medical School, 1787.

embryology; hence he gave the students an idea about the existing theories. He did not commit himself openly to any of the opinions and presented them as not more than "intellectual conditions and conjectures." "Not adhering to them and not getting into the discussions resulting from these teachings," Pekken wrote, ". . . I only intend to present briefly the most important opinions and studies about the beginning and origin of animals, about which (Albrecht von) Haller so elegantly wrote in the entire sense of natural science" (§ 495, pp. 323 - 324).

The new living existence originates, in the opinion of some, in the maternal organism under the influence of natural creative force (by epigenesis), and, in the opinion of others, exists in the parent organism from the beginning. This latter opinion exists in the basic studies about the pre-existence (praeexistentia), or predesignation (praedelineatio), or the assessment and development of the fetus (evolutio). (§ 498, pp. 324 - 325)

It is wonderful that Pekken mentioned epigenesis in the first place. No less important is the fact that he considered epigenesis that theory of development which is concerned with the influence of natural conditions, at the same time quietly confirming that the studies about preformation, or evolution, cannot be managed without the influence of the other forces. Next he stated the opinions of the animal investigators, "the famous man from Delft, Leeuwenhoek," Swammerdam, and Malpighi. Turning to the question about the motivating forces of development and labelling as "ridiculous opinions" all the talk about this subject of "complicated sophistications," Pekken rejected such opinions as those about "the accidental attraction of the nutritional particles, about the internal patterns, and also about the concurrence of the spontaneous beginning, about the soul-foundation, and others."⁶

Stahl's animistic vitalism is especially antipathetic to Pekken, who wrote the following: "The famous Stahl has confirmed that in the human, the soul itself organizes the body; hence it must be in the embryo endlessly more intelligent

6. Here, not mentioned by name, Descartes, Buffon, and Stahl are considered.

than in maturity. The birth marks, whose origin is still in question, serve as the main evidence by which this idea is confirmed and defended." (§ 499, p. 328)

Mentioning J. T. Needham as one of the supporters of epigenesis, who acknowledged "in the same substance the diffusing and the opposing force," Pekken turned to Wolff's opinion. "K. F. Wolff, a member of the Imp. Russian Academy of Science, proposed a certain essential force (*vis essentialis*), which acts on the unformed initial substance, distributes it, forms the vessels, constructs and creates the body. His opinion has many defenders and successors; however those opposing him also disprove it with important evidence." Presenting Haller's idea ("scientific sophistication") which he characterized as "conventional, although it was disproved by many important arguments," and Blumenbach's studies about "the formative efforts (*nisus formativus*)," Pekken concluded as follows: "However, all that is known about creation is not covered by true studies and is higher than the human intellect." (§ 501, p. 331)

Mundir, who was a bureaucrat and professor, evidently obliged Pekken, especially in the manual, by being careful in expressing opinions in a certain way so that they appeared as opposing the official approbated church opinions. This, apparently explains Pekken's conclusive agnostic declarations. However, from all that he had said previously it appears that his scientific sympathy is on the side of epigenesis, on the side of explaining the manifestations of development by essential reasons.

Within four years after Pekken's book appeared, a manual of natural science appeared in the Russian language. This was issued in Petersburg by the academician, N. Ozeretskovskii.⁷ Although this work is not original but a translation of the

7. THE INITIAL BASICS OF NATURAL HISTORY CONCERNS THE ANIMAL KINGDOM, PLANTS AND INSECTS. THE ANIMAL KINGDOM, issued by the Academician Nikolai Ozeretskovskii for the systematics of the animals, translated by G. Leske into German and written in St. Petersburg, 1791.

German textbook of N. Leske,⁸ it played an important role in the spread of natural-scientific knowledge in Russia. In the second section of this book, which was devoted to the general properties of organized ("constructed") bodies, Leske, and following him, Ozeretskovskii, discussed three methods of multiplication (and development) of living creatures—"accidental (spontaneous—L. B.) birth," gradual formation (Wolff's theory of epigenesis and Buffon's theory of panspermia) and unfolding, and the theory of evolution of Haller, Leeuwenhoek and others. In this manual not a single one of these presentations about the multiplication or reproduction and development ("generation") of living creatures is considered "universal," but the most widespread idea in the organic world is considered by the authors to be that of gradual formation, i.e. epigenesis (§ 33 - 42).

Great interest is due to the famous Russian obstetrician N. M. Maksimovich-Ambodik's book (35), PHYSIOLOGY OR THE NATURAL HISTORY OF MAN, which was printed in 1787.⁹ Even as a popular work geared to the young reader, this presentation is entirely scientific. Embryological questions are discussed in Chapter II ("About the Rudiments of the Infant") and in Chapter III ("About Pregnancy").

Noticing that the process of conception has appeared unclear to many, and refusing to discuss the "many diverse theories," Ambodik gave the following: "The opinion of the majority of scientists about human conception is closer to the truth."

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8. Nathanael Gottfried Leske, ANFANSGRUNDE DER NATURGESCHICHTE. ZWOTE VERBESSERTE UND VIEL VERMEHRTE AUSGABE (Leipzig, 1784).
 9. PHYSIOLOGY OR THE NATURAL HISTORY OF MAN CONCERNING HIS CONCEPTION, BIRTH NATURE, STRUCTURE OF THE BODY AT DIFFERENT AGES, ACTS OF LIFE, THE DIFFERENCE IN THE HUMAN GENUS, DISEASES, AGEING OR GETTING OLD, AND DEATH. FOR THE SAKE OF RUSSIAN YOUTH. By the efforts and independence of Nestor Maksimovich-Ambodik, Doctor of medicine and professor, in his first publication. With typography by the Naval Gentry Military School. In the city of St. Peter, 1787, CLII pp.



Nestor Maksimovich Maksimovich-Ambodik

The most successful semen of the male penetrate through the cervix of the uterus into its most internal cavity and from there they rush ... through the gaping openings of the uterine tubes and particularly to that one,.... which is raised upwards with a wide termination bending to the ovary itself, and firmly fitting closely to it with its wide mouth. The ovum in the female ovary, or in the nest, matures and is fertilized by the male sperm; from there it separates and is freely nurtured by the corresponding tube, and there it is freely acquired and little by little it is carried to the hollow of the uterus itself, where with its greatest part facing towards the internal bottom, its surface grows first to a very thin hold, by which it is rooted. Little by little it receives a new increment by which the new uterine fetus impartially grows and assumes its personification. (p. IV - V).

Here almost every sentence causes a feeling of amazement for such accuracy and correct description of the features which would be for some years the subject of unjustified guesses and fantastic imagination. Right before 1827, when K. M. Baer discovered the ovum of mammals and man, the most inaccurate assumptions about the process of fertilization were developed, especially by the supporters of speculative nature philosophy.

Ambodik talked, presumably, about the earliest stages of development of the embryo, but here he approached quite closely the actual relationships which were also recognized with certainty significantly later.

"Hopefully, and it is highly probable, the new embryo in the first days of its existence in the uterus has the shape of a vesicle like a small ball. After three or four days from conception this ball takes a rounded shape with a diameter of about ten millimeters" (p. IV). His description of the subsequent stages does not leave any doubt that Ambodik stuck to the epigenetic idea, because he described the organs developing one after the other from undifferentiated rudiments.

After a lapse of seven days it is possible to see some small fibers which are mutually connected among

themselves. These are nothing but the initial parts of the embryo in an acceptable form. All that, at first, appears to be of a semitransparent composition, sticky like jelly. After two weeks it is possible to distinguish in it the head and even the features of the face. The nose is represented in the form of a small raised perpendicular line, the eyes appear in the form of two small black points, the ears in the form of small orifices, the mouth opens, the internal structures appear in the form of soft and delicate parts In six weeks the embryo has a length of about two inches; at that time movement of the heart is noted in the form of a moving spot, and the signs of its sex are clearly distinguished. In two months ... the bones start to form in the shape of rounded cartilaginous spots appearing in the middle of the clavicle, elbows, hips, and others. Bones serving for the enclosing and protection of the body's sense organs get their form more quickly than the others. (pp. IV - V)

In the given extract it is possible to observe without doubt the attempt to describe the processes of bone histogenesis; in particular, the appearance of ossification is noted.

In still more detail Maksimovich-Ambodik described bone histogenesis in another work, his ANATOMICAL-PHYSIOLOGICAL DICTIONARY, which had seen the light of day four years before. The corresponding place in this book reads as follows:

It is impossible to determine for certain that time in the embryo in which the conversion of the soft parts into hard bones starts. It is only known that in each embryonic body, in the parts where bones are located, in the middle of the soft substance a white spot first develops, from which fibers gradually extend in different directions. Hour by hour they get new extension in length, width and thickness; then in an unrecognizable manner they are turned into actual bones.¹⁰

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10. ANATOMICAL-PHYSIOLOGICAL DICTIONARY, in which are named all parts of the human body which relate to anatomy
(... contd on next page)

Wolff's embryological as well as his teratological investigations did not remain without effect on the Russian sciences at the end of the eighteenth and beginning of the nineteenth century. The academician V. F. Zuiew described the shark embryo from the collection of the Academy of Science.¹¹ The Petersburg physician H. Knakshtedt (37) issued a separate report describing a monster without brain or skull.¹² In this small memorandum containing Russian and German texts, its authors "did not get into the investigation of the specific explanations . . . of monsters." It gives an honest anatomical description of onencephalia which he had encountered in his practice.

(Footnote No. 10, contd)

and physiology from the works of different physicians. They are collected in Russian, Latin and French, and are clearly and briefly stated with short description. For the benefit of Russian youth, it was first printed by the efforts and independence of Nestor Maksimovich-Ambodik, Doctor of Medicine and professor of the medical arts. In the typography of the Naval Gentry of the military school. In the city of St. Peter, 1783. xviii + 160 + 136 pp. (36)

11. V. F. Zuiew, "Foetus squali singularis. Dorso mutico, dentibus acutis; cum pinna ani. Linnaei Syst. Nat. Descriptus" a Bas. Zuiew, NOVA ACTA ACAD. SC. IMP. PETROPOL., V, 1789, pp. 239 - 242.
12. "Anatomical Description of Monsters Born Alive without Brain or Cephalic Skull, in the form of an invitation letter reported by Kristofer Elias Knakshtedt, Doctor of Medicine and Surgery and well known Professor of Sciences of the bones and their diseases in the Medico-Surgical Institute, and translated into the Russian language by Karl Meisner, who is a student of this institute." With accompanying figures. In the city of St. Peter, 1791, 23 pp.

ФИЗИОЛОГІЯ

или

ЕСТЕСТВЕННАЯ ИСТОРИЯ О ЧЕЛОВѢКѢ

КАСАТЕЛЬНО

Его зачатія, рожденія, природы, строенія тѣла, различныхъ возрастовъ, дѣяній жизни, различій въ чловѣческомъ родѣ примѣчаемыхъ, бо-лѣзней, старости и смерти.

Для пользы Россійскаго юношества.

трудами и вживденіемъ

Нестора Максимовича-Амбодика

Медицины Доктора и Профессора

въ первые напечатанная.

При Типографіи Морскаго Шляхетнаго
Кадетскаго Корпуса,
Во градѣ Св. Петра 1787 года.

Figure 15. Title-page of Maksimovich-Ambodik's PHYSIOLOGY.

Figure 15. Title-page of Maksimovich-Ambodik's **PHYSIOLOGY**.

PHYSIOLOGY, OR NATURAL HISTORY OF MAN, CONCERNING HIS CONCEPTION, BIRTH, NATURE, STRUCTURE OF BODY AT DIFFERENT AGES, ACTS OF LIFE, REMARKABLE DIFFERENCES IN THE HUMAN GENUS, DISEASES, AGEING, AND DEATH. For the benefit of Russian youth, by the efforts and independence of Nestor Maksimovich-Ambodik, Doctor of Medicine and Professor. First edition. In the Typography of Naval Gentry of the Military School, in the City of St. Petersburg, 1787.

Wolff's unpublished notes and drawings on teratology interested the academicians V. Tilezius and P. A. Zagorskii (38). The first informed the conference of the Academy about the presence in the archive of Wolff's handwritten manuscript, and in 1814 the latter requested permission to "take it from the archive to review the notes and drawings remaining after the death of Professor Wolff." Permission was obtained, and Zagorskii got involved in studying the archival materials as well as the human monsters or anomalies in the anatomical museums of the Academy of Science and the Medico-Surgery Academy. The result of these investigations was a series of work about monsters, anatomical anomalies and variations, of which the first, of 1805, concerns the time of discovery, and carries the name "Anatomical Report, containing descriptions and drawings of the rare monstrous human abortions."¹³

This article is illustrated by the description of the monstrous human fetus which was devoid of head and upper extremities. There was extreme interest in P. A. Zagorskii's report, "Formation of different human monsters,"¹⁴ in which he gives a specific teratological classification dividing the monsters into the following groups: 1) Changes in the body or its relevant parts in type, color, size and location; 2) Imperfection in the structure or deficiencies; 3) Absence of parts; 4) Complicated monsters, i.e. composed or appear to be composed of two accreted bodies. Zagorskii stopped at the essential sources of monsters, which develop "by accidents and also by errors of nature." He claimed that the reasons for development of monsters have a mechanical basis and that monstrosity does not depend "on forces of imagination and indignation of the soul, to which many people relate the errors." (38a)

At the turn of the nineteenth century, philosophical and scientific thought in Russia after Lomonosov again rose

13. Zagorskii, "Commentatio anatomica abortus humani monstrosi rarissimi descriptionem ac delineationem sistens," NOVA ACTA ACAD. SCIENT. PETROPOLITANAE, v. xv (1805), pp. 473 - 482.

14. SPECULATIVE INVESTIGATIONS OF THE IMP. ST. PETERSBURG ACADEMY OF SCIENCE, v. III, 1812, pp. 265 - 277.

to great heights in the reports of A. N. Radishchev. Here is not the place to review in any detail Radishchev's significance in the history of Russian and world philosophy.¹⁵ It is sufficient to say that Radishchev, whose ideas were established under the influence of acute social dispute in Russia in the second half of the eighteenth century, had extended Lomonosov's materialistic traditions to Russian philosophy. Radishchev represented the establisher of the revolutionary-democratic directions of Russian philosophical thought. He independently established and solved a number of important problems about the relationships between material, consciousness, the development of psychics and so on. Being deeply and broadly educated, in particular in the natural sciences, Radishchev saturated his main philosophical treatise, "About man, his death and immortality," with numerous examples from different branches of the biological science. Relevant to the content of the present chapter, Radishchev's discussions hold particular interest. Those discussions handled the acute conflict between the already obsolete ideas of preformation and the developing theory of epigenesis.

Studying Bonnet's report, Radishchev quoted the idea of the unity of natural bodies ranging from the inorganic to common human existence. Bonnet's chain of being which represents, in his opinion, only an expression of "Law of Continuity," for Radishchev acquired a significantly deeper materialistic meaning

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15. In 1949, 200 years after the day of his birth, A. N. Radishchev was widely mentioned in Soviet scientific literature. It is possible to cite the book of M. A. Gorbunov, PHILOSOPHICAL AND SOCIO-POLITICAL OPINIONS OF A. N. RADISHCHEV and his article "Philosophical and Sociological Ideas of Radishchev" (UCHENYE ZAP. AKAD. OBSHCH. NAUK, 5, 1949, pp. 36 - 38) and the article of I. Ya. Shchipanov, "Socio-political and Philosophical Ideas of Radishchev" (from the history of Russian philosophy IZ ISTORII RUSSKOI FILOSOFII, 1949, pp. 181 - 226). The scientific opinions of A. N. Radishchev are stated also in: Kh. S. Koshtoyants, OUTLINES OF PHYSIOLOGY IN RUSSIA, (Ocherki po istorii fiziologii v Rossii), Edition of the Academy of Science USSR, pp. 37 - 43, and S. L. Sobol; HISTORY OF THE MICROSCOPE (Istoriya mikroskopa), pp. 376 - 377.

and, in contrast to Bonnet, an evolutionary sense. Radishchev wrote about what he called "the steps of being"¹⁶ the following inspired words:

Staring at everything, you see your environment is alive. Direct your curiosity to what we consider inanimate: from the stones where the power of coupling seems to be clearly single, . . . to man whose composition is so skillful, in whom the elements are represented in different compositions, in whom all the influences which are known in nature work together, an organization of the highest sense . . . from stones to man the graduation is evident, which deserves reverential amazement. The substance of the steps is evident; the graduation is already known in that all genera have little individuality, even though they can confidently be distinguished one from the other; the steps or graduation of ruby, iron, mercury, and gold are homogenous or identical with aloe, tulip, cedar, oak; these successions are in essence analogous to butterfly, snake, eagle, lark, sheep, elephant, man; the steps on which crystallization and mineralization become the forces of plants, the steps on which coral, lips, moss grow and are conceived, the steps by which force the plants extend their energy into other compositions, are transferred little by little into an irritation and from that into sensitiveness.¹⁷

The most difficult, of course, is the question about the rightful situation of man in one continuous line with other living creatures. The acceptability of that does not cause Radishchev any doubt. "The interior of man," he wrote, "is homogeneously identical with the interiors of animals." Reviewing in this connection the structure of different systems of organs

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16. A(leksandr) N(ikolaevich) Radishchev talks not about the stairs of creatures (*échelle des êtres*) but about the stairs of substance, stressing by this the materialistic content.
 17. Radishchev, ON MAN, HIS DEATH, AND IMMORTALITY. A complete collected work, vol. 2, issued by the Academy of Science, USSR, 1941, p. 110.

of man and animals, he concluded: "We do not underestimate man if we say that beasts have the capability of reflecting or meditating; and there is not in man any inclination or any virtue which we do not find in animals."¹⁸ For Radishchev, man's mental activity did not constitute any difficulty when compared with animal behavior because he held a materialistic view about the unity of body and mental features, based on the view that the appearance of spiritual activities represent the functions of the brain.¹⁹

Using Bonnet's idea about the graduation of creatures and materialism, Radishchev rejected the preformation idea of the Swiss naturalist and joined the epigenetic opinion about individual development which had been established by the Petersburg academician K. F. Wolff.

The basic philosophical question about the nature of man and his mental (spiritual) activities Radishchev proposed solving through the study of human development. "Previously (as though a certain new prophet) I said that man will be or could be present before birth Where were you until your organs were formed; before you reached daylight?"²⁰

Man is conceived in the uterus of woman. This is the essential event. He is conceived in the uterus of the wife; in it he grows, and ripens in nine months in the uterus of the mother, goes out to light provided with his organs of sensation, action and thinking, which can improve gradually; this is known to everyone. But before birth the embryo is formed, grows, improves; there is a secret motivation. Our curiosity to know this secret is satisfied by the possibility that we can see how gradually the animal grows after its conception. The happy coincidence was that, by unquenchable curiosity, the observations were scientific. In Russia we have a wonderful collection of embryos from almost the first day of conception

18. Ibid., p. 48.

19. Ibid., pp. 88, 89.

20. Ibid., pp. 39 - 40.

up to birth.²¹ By what means does conception and nutrition or the increment of growth occur? Another question remains, which with some assumptions has a solution We see that the sperm from which the embryo is conceived exists in some animals in the uterus before fetal development; but for explaining unfolding or growth, this explanation is weak. This we see clearly in feathered animals. The ovum is a seed, and before fetal formation it contains in itself the same essentials of its composition, the parts of albumin and yolk About plants and birds it is possible to say, not with probability but with definite clarity, that sperm exist not only before conception but also before fetal formation From this conclusion, according to the rule of similarity, it is possible to say the same about all animals and about man himself. Thus we conclude that man existed before his conception, or more correctly that the seeds containing the future man existed; but life, i.e. the capability to grow and formulate, is absent.²²

If it is not certain, but probable, that man existed prior to conception in the sperm, then in essence there are two possibilities where these sperm existed. The probability that they started in the wife is the most probable of the assumptions. But let us say a word about the sperm. Either the sperm were contained in one which had existed before and which contained all sperm, one containing the next endlessly. Or the later sperm are a part of the earlier, which were a part of those which had appeared prior to them and which could divide into as many new parts or sperms as possible: the uniform and separated parts which can be packed and divided endlessly.²³

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21. Radishchev means the preparations of the Cabinet of Natural History, the basic stock of which is composed of the collection acquired by Peter I (see p. 14).
22. A. N. Radishchev, ON MAN, HIS DEATH, AND IMMORTALITY, pp. 40 - 41.
23. Ibid., p. 43.

The first of those possibilities which Radishchev rejected is obviously the hypothesis of "emboîtement," and the second, as S. L. Sobol' correctly noted,²⁴ was very similar to Weismann's idea about the continuity of germ plasma. Radishchev's agnostic base for these opinions is obvious. "Continuity . . . how senseless we are! All that cannot be defined by its limits is eternal."²⁵

Radishchev opposed another idea: "But why can we not confirm, as we have said above, that the sperm are formed in the wife? For if sensitivity, thought, and all the properties of man (not talking about animals and plants) are formed in him gradually and are improved, why do we not say that the life which is in the sperm and which can exist in a depository until it appears in development, is formed in the organs of man?"²⁶

Therefore, Radishchev posed the question about embryonic development epigenetically. In the same epigenetic understanding, he interprets growth of the individual as illustrating his opinion of development of avian egg:

Take the egg as an example; you know that by means of incubation it can survive and become a bird. But is the chick seen in the egg, although there is no doubt that it is contained there? And if we want to trace the transfer of the egg into a chick and if we will observe it daily, so we shall see its gradual growth. At first the beginning of life appears—heart, then eyes, then waist and other parts gradually up to that hour, after 21 days, when it breaks the egg shell and appears to the creator of light already alive, crying as if to say: to the glorification of you! From this example you recognize how many conditions the egg must pass through before it become a chick. From that you see that all these conditions are continuous and come essentially out of one another. Consequently, the egg and chick essentially develop from one another;

24. Sobol', p. 377.

25. Radishchev, p. 43.

26. Ibid.

by incubation the chick hatches from the egg if nothing hinders that process. In this manner there is a procession of essential forces; once they begin, they continue and produce the gradual changes which we see in time.²⁷

Thus, this progressive theory of developmental events by essential causes, i.e. the epigenetic character of individual development which was suggested, worked out and defended by the establisher of the Russian and world embryology K. F. Wolff, had gained the support of the advanced materialistic philosophy of that time, as represented by A. N. Radishchev.

27. Ibid., p. 99.

CHAPTER 10

THE DEVELOPMENT OF EMBRYOLOGY IN THE EPOCH OF THE STRUGGLE OF RUSSIAN EMPIRICAL SCIENCE AGAINST NATURPHILOSOPHIE

The beginning of the nineteenth century in Russian and world embryology was characterized by the activities of H. C. Pander and especially the brilliant activities of K. M. Baer, both of whom afterwards were members of the Petersburg Academy of Science. After K. F. Wolff's work and general conclusions became available and understandable to contemporaries, but prior to Pander and Baer, it is impossible to name any other embryologist who was comparable in accuracy, breadth and depth of investigation.

Pander's and Baer's works will be reviewed in the following chapters with the necessary detail. The present chapter will be devoted to the characteristics of the ideas of Naturphilosophie which were generated in Germany and which for thirty years made their effect (mainly negative) on Russian biological science, including embryology. These ideas, which attracted some investigators, were abstracted on the way so that they sometimes developed unusual constructions. From the beginning they were rejected by representatives of the progressive materialistic trend in Russian science, which was supported by the brilliant achievements of natural science, including the activities of the Petersburg Academy of Science.

The excitement over Naturphilosophie was, to a certain extent, a sign of the times. The epoch of the eighteenth-century French Enlightenment and the liberation of the French Revolution were replaced by years of political and ideological reaction, expressed particularly by the German idealistic philosophical systems. Among them is Schelling's system.

Schelling himself, by changing his opinions, demonstrated the movement from advanced ideas to reactionary political and philosophical ideas. The young Schelling began with the study of the unity of all features of nature. He anticipated the idea of the community of physical forces. He stated in teleological form the idea of organic development and the idea of the origin of living creatures from one initial form. He ended with the revelation of God as his approach. Engels described this evolution of Schelling's ideas in the following lively and poetic passage:

When he (Schelling—L. B.) was still young, he was different. His charming intellect at that time gave rise to brilliant thoughts. Some of them served their role in the struggle of the younger generation. He, at that time, freely and courageously swam in the open sea of thoughts in order absolutely to open the Atlantic The fire of youth took him to the flames of enthusiasm . . . he announced the approach of a new time He opened wide the doors of philosophy, and in the halls of abstract thought the fresh smell of nature appeared: a warm spring ray fell on the seeds and awakened in them all the sleeping forces. But the fire died; the courage changed; the grape, in the process of fermentation, did not become clear wine but turned into vinegar. The ship dancing with courage and joy on the waves fell asleep. It entered into a small harbor of belief and dashed the keel onto the sand, so that it could not move from its place. There it lies now and no one can distinguish that old useless ship from the previous ship, which had never, with its flags turned down, sailed in the sea with full sails.¹

Schelling's Naturphilosophie, originating from his subjective-idealistic ideas, is based on the idea that all living creatures on earth form a complete unity, the kingdom of the development of life, whose reason for creation develops

1. F. Engels, "Schelling and Revelation: The Critics of the Newest Reactionary Attempt upon Free Philosophy" (1842).
K. Marx and F. Engels, WORKS, Vol. 11, 1931, pp. 163 - 164.

from nature itself and initially from the inorganic world. From this comes the conclusion about the unity of the organic and inorganic worlds which is recognized by the corresponding forces. Hence, the basis of this unity is the spirituality of all bodies of nature. In the inorganic world, Schelling distinguished three forces—magnetic, electric, and chemical—which are capable of conversion into one another. In the world of living creatures, these forces correspond to reactivity, sensitivity, and productivity. This last idea Schelling borrowed from the anatomist Kielmeyer. (39) In the living, as well as in the non-living, Schelling searched for the development of opposing forces, which are identical, in his opinion, in the absolute into which merge subject and object, existence and consciousness, forces of attraction and forces of repulsion, positive and negative. The ideas of opposition or polarity in natural phenomena also belong to (Karl Friedrich von) Kielmeyer. In living creatures Schelling assumed the presence of opposition between interior and exterior, i.e. between the organism itself and the surrounding environment. The exterior and interior in living nature also merge in a harmonious identity. Harmony of the organism, as expressed by Schelling, "is the charm characteristic of organic nature," is the result of the unity of the opposition between the blind mechanical forces acting in the organism and the expediency inherent in it. According to Schelling, each living creature is single and integral and simultaneously represents part of nature which is considered an organism of a high order. Life, according to Schelling, is a process of continuous creation. In connection with that, he decidedly rejected the idea of preformation and considered that the problem of development of the individual should be solved from the point of view of epigenesis.

It is not surprising that the ideas of the young Schelling particularly fit the Naturphilosophie constructions which he developed in the university through brilliant and spiritual improvisations which delighted the young people who were coming, literally, from all ends of Europe to listen to him. The numbers of Schelling's students and followers were not few. Among those serious scientists applying Schelling's ideas of Naturphilosophie, the first mentioned should be Lorenz Oken.

Oken's main work, *MANUAL OF NATURPHILOSOPHIE*, begins with a statement of theological questions because, in his opinion, "Naturphilosophie is the science of eternal conversion of God into the universe."² Discussing, from Naturphilosophie's point of view, the meaning of positive and negative sizes and ciphers, Oken defined the essence of deity as follows: God is absolute self-knowledge. Self-knowledge is nothing, and, being nothing, "self-knowledge is God."³ Such a beginning does not foreshadow anything good. However, later on Oken's work included a discussion of a number of wonderful suppositions which were to be confirmed, in one degree or another, by the subsequent development of the biological sciences. Among these is the belief that the basic substance of the organic world is carbon, which by uniting with water and air forms mucous-like fluid. The primary fluid appeared, according to Oken, in the sea, and from this primary mucous-like fluid all living creatures were formed. Oken described organic development in the following manner: the primary spots or vacuoles of mucus, which he named infusoria, can be combined in different ways and therefore give rise to the various higher organisms. Oken thus acknowledged the development of the organic world from the simplest creatures up to complex man. This development of the world of living creatures takes place, he thought, in the development of organisms into more complex creatures during their lives.

In Oken's examples it is possible to foresee a range from protoplasm and cell to the cellular structure of higher organisms, to the evolution of the organic world, and finally to the biogenetic law according to which the process of individual development repeats the stages through which the species had passed in evolution. Oken reached that understanding, not by means of direct study of the facts, however, but by intellectual methods, the essential aspects of which are instinct and argument by analogy. By way of setting up an analogy, Oken established an entirely imaginary classification of living creatures, by dividing the animal world into intestinal, vessel, respiratory, and meat animals, the latter of which (to which he related the vertebrates) he

2. L(orenz) Oken, *LEHRBUCH DER NATURPHILOSOPHIE*, I (1809), p. vii.

3. *Ibid.*, p. 14.

divided further into animals of tongues, noses, ears, and eyes. In another place Oken stated that molluscs correspond to the organs of touch, insects to the organs of vision, amphibia to that of taste, and birds to that of hearing. Inside the organism some parts are analogous to others: skull to pelvis, mouth opening to posterior-excretory, and so on. These imaginative analogies played a role in the history of science, because they attracted biologists' attention to the problems of comparative anatomy and comparative physiology.

One of the achievements of comparative anatomy of that time, which was based on the general conclusions of Naturphilosophie, was the establishment of what is called the "vertebral nature of the skull." The authors of this theory were the great poet Johann Wolfgang Goethe and the naturalist Oken. In 1791 Goethe discussed the idea that the skull of the vertebrate animal was formed by the growth of four greatly modified vertebrae; however, he did not publish his speculations on this subject for a long time. (Ed.: Not until 1820 in ZUR MORPHOLOGIE.) Hence the initiative in establishing the vertebral theory of the skull is usually credited to Oken, who came to the same conclusions independently of Goethe and who reported them in a publication in 1807. Comparative anatomical work up to the second half of the nineteenth century found no significant objections to Goethe's and Oken's conclusions, if we disregard (Thomas) Huxley's remarks about the non-correspondence of the vertebral theory of the skull to the facts relating to the head of lower vertebrates. Huxley also briefly mentioned that the embryonic cartilaginous skull did not have segments comparable to the vertebrae. Only in 1871 did one of the founders of comparative embryology, Mechnikov, approach this problem from an embryological, evolutionary point of view and show the lack of correspondence of this theory to the facts.

In a speech devoted to the vertebral theory of the skull, Mechnikov gave an interesting opinion about its origins in Naturphilosophie. It is thus necessary to include here some quotations from this speech, which was published in a poorly distributed and apparently unknown journal.⁴

4. I. I. Mechnikov, "Vertebral Theory of the Skull." Speech prepared to be read at the celebration of Novorossiiskii University, August 30, 1871. NOTES OF NOVOROSSIISKII UNIVERSITY, 7 (1871), pp. 1 - 20.

"The vertebral theory of the skull," Mechnikov said,

was inherited by science from Naturphilosophie, that strange mongrel that resulted from the union of metaphysics with positive knowledge, and which, in general, had significantly slowed the progress of natural science. A whole generation of first-class scientists was needed to purge the science of living creatures of Naturphilosophie rubbish and to establish a stable basis of that science. Regardless of the antagonism between scientists and Naturphilosophie scientists, the former took some theories gotten from the latter, among which the vertebral theory of the skull played an important role. Already you see that it represents nothing significant in the line of thought of the Naturphilosophie school. It is sufficient to name one of the authors of the vertebral theory to show whether one should believe its generalizations.

Mechnikov mentions Goethe and then Oken, and tells about the circumstances of the establishment of this theory. After that he gives embryological data about the sequence of appearance of embryonic skull parts in vertebrates; these data are incompatible with the vertebral theory.

Mechnikov's statement on Naturphilosophie is excessively strict. Engels, reflecting on the history of science, has written the following concerning German Naturphilosophie:

In it there were many absurd and imaginary things, but not more than in the contemporary non-philosophical theories of the empiricists. It included many intelligent ideas which were beginning to be understood when the theory of evolution started to spread. Thus, Haeckel accurately recognized the services of Treviranus and Oken. In his conception of the primary mucus and the infusoria, Oken suggests as a postulate of biology what was later actually discovered in the protoplasm and cell.⁵

5. Engels, ANTI-DÜHRING. Gospolitizdat, 1953, p. 11.

In another place Engels talked about Oken as the first in Germany to acknowledge the theory of development.⁶ Such a general evaluation of Naturphilosophie was given by Engels in "Ludwig Feuerbach":

. . . with the help of data obtained by the most empiricistic natural science, it is possible to give fairly systematically a general picture of nature as a complete unity. To give such a general picture of nature was previously the task of what is called Naturphilosophie, which could only fill the gap with imaginary connections of the yet unknown actual group of phenomena. It substituted ideas for unavailable facts, replenishing the actual gaps only by imagination. In this case many clever thoughts emerged and many of the latest discoveries were foreseen, but also a lot was said which was nonsense. Otherwise it could not have existed at that time.⁷

Noting, therefore, the historical importance of Naturphilosophie at the beginning of the nineteenth century, Engels warned against useless attempts to raise it again in contemporary natural science. Such an attempt, Engels wrote, "is not only unnecessary, but also could be a step backward."⁸

Giving great significance to solving biological problems of embryonic development, Oken turned to the independent study of the embryology of vertebrate animals and made a number of important factual discoveries. Their significance was depreciated by Meckel's translation of K. F. Wolff's work, "On the Formation of the Intestines,"⁹ where it was revealed that Wolff had achieved Oken's most important data forty years before in his paper in the "New Commentaries of the Petersburg Academy of Science," which was completely unknown to Oken.

6. See Engels, DYNAMICS OF NATURE. Gospolitizdat, 1952, p. 161.

7. Engels, "Ludwig Feuerbach and the End of Classical German Philosophy," K. Marx and F. Engels, WORKS, Vol. II. Gospolitizdat, 1952, p. 370.

8. Ibid.

9. See Chapter 5.

Oken's popularity as a professor and author of scientific and popular books, and also as the publisher of the scientific-philosophical journal *ISIS*, was very great.

The passion for Schelling's work, especially his *Naturphilosophie*, also attracted Russians travelling to study in the German universities, or those sent to Germany "for advancement" after their completion of high school. The young followers of idealistic German philosophy and its abstract presentations on the good and the beautiful, on the unity of all the phenomena of the world, soul, body, God and nature, were met on their return by a reality very different from "the harmony" which Schelling taught. His ideas necessarily clash with the most gloomy ideological and political reactions of the landlord government guided by Golitsyn, Magnitskii, Runich and others, "in whose dirty hands," according to Pushkin, "the unfortunate sciences were flung."¹⁰ A section of Russian society resisted this reaction, the section from which the great Pleiadic Decembrists came. Although the latter grew up on the philosophical and social opinions of A. N. Radishchev and the ideas of the French Revolution and could not oppose Schelling's followers with a completed system, the majority retained deistic and even materialistic (atheistic) ideas. It is sufficient to remember the anti-religious poems of Pushkin, the closest to the Decembrists, and his feelings about Radishchev's atheism. Free-thinking was particularly spread among the members of the more radical Southern Secret Society, where the most decisive judgments in this regard were stated by A. P. Baryatinskii.

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The followers of German philosophy in Russia did not represent an entirely homogenous group. Among them were people who later actually participated in the December revolt, such as V. K. Kyukhel'beker, and people of liberal opinions such as D. V. Venevitinov. However, the majority of them voluntarily or involuntarily played a reactionary role, and these latter displayed an inclination to mysticism (V. F. Odoevskii, P. Ya. Chaadoev), or to political reaction (I. V. Kireevskii, S. P. Shevryev, M. P. Pogodin, and others).

10. "Second Message to the Censor."

The effect of Schelling's philosophy on Russian philosophical and scientific thought became manifest at the beginning of the nineteenth century with the organization in Moscow of groups to study German philosophy. One of these groups carried the lofty name of "The Society of Wisdom Lovers," at the head of which stood V. F. Odoevskii. Among Schelling's readers who showed his influence to some degree were Moscow University professors M. G. Pavlov and I. I. Davydov, and in particular, Professor D. M. Vellanskii of the Petersburg Medical-Surgical Academy.

Danil Mikhailovich Vellanskii had worked for Oken for three years and had attended Schelling's lectures, after which, in 1805, he returned to Russia believing in Schelling's views. All his subsequent educational and scientific-literary activities represented continuing propaganda for those ideas. There is no necessity to be concerned here with Vellanskii's ideology;¹¹ hence, only some of his general opinions are stated, and, in more detail, his opinions about embryonic development, contained mainly in the book, THE BIOLOGICAL INVESTIGATION OF NATURE,¹² and partly in the manual issued almost a quarter of a century later, BASIC OUTLINE OF GENERAL AND SPECIAL PHYSIOLOGY.¹³

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11. A detailed description of the scientific activities of Vellanskii, especially his physiological opinions, is given in the book by Kh. S. Koshtoyants, OUTLINE OF THE HISTORY OF PHYSIOLOGY IN RUSSIA (1946). See also the article by A. M. Levin, "D. M. Vellanskii and Schellingism in Russian Medicine at the Beginning of the 19th Century," VRACH, vol. 16, No. 28, 1895.
 12. THE BIOLOGICAL INVESTIGATION OF NATURE IN ITS CREATING AND CREATED QUALITY, CONTAINING THE MAIN OUTLINES OF GENERAL PHYSIOLOGY, the work of the doctor of medicine and surgery and Extraordinary Professor of Physiology and Anatomy of the Imperial Medical-Surgical Academy, Danil Vellanskii (1812), xvi + 461 pp.
 13. BASIC OUTLINE OF GENERAL AND SPECIAL PHYSIOLOGY, OR PHYSICS OF THE ORGANIC WORLD, the work of the Academician and active professor of the Imperial St. Petersburg Medical-Surgical Academy, the Real Councillor Soviet, Danil Vellanskii, for the supervision of the teaching of physiology lectures. St. Petersburg, 1831. x + 502 pp.

Vellanskii's scientific method completely corresponds with the main principle of Naturphilosophie. "True knowledge of nature and the essence of the human" could be, in his opinion, achieved only by means of speculation and analogy. Since all the bodies of organic and inorganic nature completely correspond to each other, the mathematical relations (line, circle, parabola and so on) as well as the physico-chemical processes (magnetism, chemism, and others) and the geological elements (water, air, metals, and so on) should be completely analogous to this corresponding formation of the living organism. Vellanskii developed in detail the Naturphilosophic idea that the organism is like the planet.

Next Vellanskii turned to an entirely arbitrary analogy of the organs of living creatures with geometric forms. It is not necessary to stop at Vellanskii's examples illustrating the analogy of the organs with inorganic bodies and geometric concepts. It is necessary only to give examples of the internal similarities among the organs of the animal organisms. He wrote that::

Corresponding to three parts of the body—chest, pelvis, and head—there are three pairs of extremities: hands, legs, and jaws The lungs correspond to the bladder in the pelvis; and in the head the nose is the neural lung. The tongue is the head's intestinal tract. Kidneys and the large intestine are related to the genital system and comparable to the liver and small intestine; and the sexual organs, male and female, are equivalent to the swallowing organs. Hands come from the chest which is formed separately as the animal organ of movement It is composed of seven chest ribs separated from the vertebrae and connected with the breast bone. The radial and the elbow bone, in essence, are two upper ribs of the chest which are divided into five fingers corresponding to the five lower ribs. The arm tassel is the chest cage turned externally, since the chest cage is also comparable to the hand tassel turned internally.¹⁴

14. Ibid., pp. 37 - 46.

With similar arbitrary and imaginary analogies, Vellanskii gave an entirely speculative analogy between the skeletal elements of the arms and legs.¹⁵ He also stated the basics of the vertebral theory of the skull: "The elementary form of bones is the vertebra . . . and the entire bone system is composed of one vertebra, in different variations. Each head has one vertebra, and three vertebrae: ear, tongue, and eye constitute the skull, and the nose enters into the composition of the face."¹⁶

Vellanskii's physiological imaginings are also based on Naturphilosophie, in particular on the principle of polarity.

Levin, in an article on Vellanskii, said the following: "The scanty source of physiological data in his time did not hinder him from giving himself over to real, frenzied reflection."¹⁷ That this is not an exaggeration is evidenced by the following: "The nourishing juice (chyle) moves in the lymphatic vessels by polar tension between the lungs and intestines, and rushes from the intestines to the lungs as a result of the nutritional juice, which is composed of hydrogenated carbon and is of different polarity than the lungs which contain oxidated nitrogen From the opposite, due to its oxidized constitution which is of the same polarity as the lungs, the nourishing juice is pushed off by the lungs and passes downwards into the large intestine."¹⁸

It is not surprising that Ivan Pavlov, head of the Department of Physiology of the Military Medical (previously the Medical-Surgical) Academy, in which Vellanskii had never been, spoke of him in a mocking manner. Thus:

Vellanskii was a very talented man, brilliantly educated abroad, but he was not a real physiologist. Due to his being abroad, he became a nature-philosopher,

15. Ibid., p. 39.

16. Ibid., pp. 34 - 35.

17. A. M. Levin, "D. M. Vellanskii and Schellingism," p. 790.

18. Vellanskii, BASIC OUTLINE, pp. 50 - 52.

i.e. he discussed all phenomena without considering reality. Now such Naturphilosophie seems so amusing that it can be humorous or entertaining as after-dinner talk. But at that time Vellanskii benefited from popularity among the public, and many people crowded into his room.¹⁹

The principle of analogy, which had frequently interested Vellanskii as well as other nature-philosophers, is an unfounded fantasy, but at the same time represents the basis of the comparative anatomical imagination. This principle of analogy was beloved in a strange way.

The basic idea of comparative anatomy has been expressed by Vellanskii in the following words:

The animal kingdom is one common organism, whose special members are in essence all animals, and man constitutes the general unity The origin of land animals in the organic world and the formation of external sensations in the human organism is in essence of one significance, and the six external sensations of man correspond to the six classes of lower animals, where each sensation is expressed separately in its specific significance. In worms the sensation of feeling is represented; in molluscs, touch; in fish, vision; in insects, smell; in amphibia, taste; and in birds, hearing. Thus the worm is equivalent to the lips of the human, the mollusc to the fingers, the fish to the eye, the insect to the nose, amphibia to the tongue, and birds to the ear. Mammals constitute a seventh class, which corresponds to the general unity of external sensations.

These extracts of Vellanskii's thoughts concerning general questions of the structure and life activities of animals and men he adopted from Oken's anatomical analogies and, in particular, his vertebral theory of the skull and

19. I(van) P(etrovich) Pavlov, LECTURES ON PHYSIOLOGY (1912 - 1913), issued by Academy of Medical Sciences (1949), p. 269.

other physiological ideas. Vellanskii added to these many, essentially unfounded, peculiarities of thought, which he defended in a letter to M. G. Pavlov soliciting comments on his physiological lectures.²⁰

Vellanskii presented his embryological ideas in the book, BIOLOGICAL INVESTIGATIONS, the thirteenth chapter of which is "Birth and Death." For discussion of the natural development of the individual which starts at birth and ends at death, Vellanskii used the favorite principle of the nature-philosophers, the principle of polarity. He gave comparisons of opposing phenomena: "The moment of birth, in essence, is the conception and development of the fetus in the maternal uterus death begins with disease and ends with decomposition. Therefore conception is equal to decomposition, and development of the embryo corresponds to disease of the formed organism."²¹

For understanding individual development, Vellanskii considered it necessary to analyze the minute structure of the formed organism, which he described in agreement with Oken's ideas: "In order to see the process of birth and death of certain organisms, it is necessary to look first at complexes in organic nature, in which unity is confirmed and its usual stability is found. This complex consists of infusoria, which are formed by the decomposition of any substance in water."²²

Describing in detail the way to obtain a culture of infusoria in an infusion of grass or meat, Vellanskii rejected the possibility that these creatures develop from eggs:

Infusoria in essence are the primary monads of the organic world But the consideration of these as preformed creatures which undergo aggregation and thereby give rise to all animals and plants could

20. This letter of May 29, 1834 is given in the book by Kh. J. Koshtoyants, OUTLINE OF THE HISTORY OF PHYSIOLOGY IN RUSSIA.

21. Vellanskii, BIOLOGICAL INVESTIGATION, p. 402.

22. Ibid., p. 403.

have been a crude understanding by the atomists, who assumed a mechanical composition of the visible world from pre-existing atoms. Nothing organic could ever actually originate and disappear, but only its form of existence is changed The materialistic existence of the organism . . . always changes according to the positive idea constituting its essences; the point is to geometric physics what the infusoria is to the organism.²³

He continued:

Just as the meaning of figures does not depend on the constituent points but on a combination, so the essence of any organism does not consist of infusoria but is a reflection of ideas discussed here.

A strange opinion, accepted as true, is that all living organisms originate from ova or eggs (omne vivum ex ovo); Oken proved satisfactorily that every living organism originates from a living organism.

Of physiological problems, birth is the most important, most difficult, and the one causing the most scientific curiosity . . . but, perceiving the subject from only one side, it is not possible to understand it appropriately. One light, Naturphilosophie, has driven away the darkness, and if not illuminated by it, it would be impossible to see this subject. Although many people have discussed theories of the evolutionists, panspermists, and epigeneticists, nothing but contradictions and disproofs have resulted.²⁴

As was recognized, Vellanskii rejected preformation ("the theory of evolutionists, panspermists") as well as epigenesis. Preformation in the form of ovism and animalculism had no supporters at the beginning of the nineteenth century after Wolff had proved, in the second half of the eighteenth century, the absence of preformation in fertilized eggs. Yet

23. Ibid., p. 405.

24. Ibid., pp. 405 - 406.

epigenesis as Wolff conceived it was unacceptable for nature-philosophers because, according to the principles of Naturphilosophie, no organic body develops; rather it presents only a modification of previously existing living bodies.

A necessary constituent of Naturphilosophie is the idea of spontaneous generation, which nature-philosophers discussed metaphysically and idealistically. Their discussions were not about the development of the living from the non-living, i.e. not about the progressive development of the material, but about the continuous transformation of animated material—of the unchanged organic monads, which are different organic bodies and which exist primordially.

That this particular understanding of spontaneous generation was characteristic for Vellanskii is seen in his following statements:

Generation from undifferentiated creatures (*generatio aequivoca*) must be the beginning in the origin of organic creatures and characteristic for the lower types of animals and plants. These include, in essence: helminths, which originate and live in the interiors of animal bodies; worms originating from decomposing substances; and some insects which originate in the skin of a living body, such as crab lice, lice, ulcerative acarus (*Acarus exulcerans*). Originating in other substances at a special temperature and humidity, there are: fleas, some types of flies, mosquitoes, and many others. All these originate directly from specific organic monads, which are everywhere present and ready. The intestinal helminths do not find food or drink in the interiors in which they live, but they are conceived from infusoria which are present in the intestinal juice. Their worm shape corresponds to the structure of the intestines themselves; there are three types of helminths in man: round, which correspond to the small intestine; flat, the large intestines; and small worms, the rectum Therefore lice generate a disease called phthyriasis; and crab lice are frequently found in pimples of the skin which no outside eggs can penetrate.²⁵

25. Ibid., pp. 407 - 408.

Thus, the simplest structured living creatures are formed from living monads—infusoria by means of spontaneous generation. How do variations develop among living creatures leading to so many multiformed organic shapes? By what means were the two kingdoms of the organic world, plants and animals, distinguished from each other? Vellanskii answered these questions by stating that this distinction begins with the development of primary creatures which still carry general properties but which at the same time have already acquired rudiments of the properties of plants or of animals.

The predecessors of animals, in his opinion, are polyps, and the predecessors of plants are the fungi. Simultaneously, there is observed in the polyp a characteristic property of the male sex (the creative property of man), and that of the female sex (the creative quality of woman) is seen in the fungi. This idea is confirmed by the following, which compares the capability of regeneration in the coelenterata and fungi: "Not any branch of a polyp grows into a whole polyp; but each grain, by its jelly-like material, produces from itself directly such an organic body. Therefore all jelly-like material in the coral is a fruitful seed, which is characteristic in all known creatures of the male sex. Contrary to that, not any part of the fungus develops into a whole fungus, and consequently there is no creative force in it such as that produced by the polyp."²⁶

Vellanskii followed successfully the analogy of the origin of the male in higher organisms with the polyp and the female with fungus. He used the process of fertilization, which precedes the conception of a new organism, to demonstrate the weakness of empirical science, and he contrasted it with Naturphilosophical attempts to explain the process of conception and development. Thus:

The necessity of the male and female sex for the conception of all animals which are born from males and females is known; but the proper force and the effect of each in the production of the embryo, which might be discovered through studies of sex, remain an unsolved problem in empirical physiology. Evolutionists, assuming prepared embryos in the mother, attribute some help in their development to the father. Panspermists, considering the embryo as being ready in

26. Ibid., p. 410.

the male sperm, consider the woman only necessary to receive and contain it until the appropriate stage of development is reached. But the evident likeness of one child with the father and another with the mother contradicts these theories which impute the essential force of conception either to the father or to the mother alone. Epigenesis, according to which the embryo originates from the mixing of male sperm with female, is also incorrect; for it was proved long ago, by de Graaf, that women do not have true sperm.²⁷

Noting that in animals having external fertilization, particularly fish, the milt cannot mix with the roe because the roe are covered with a jelly-like membrane, Vellanskii concluded that fertilization of the sperm is not represented mechanically or chemically, but dynamically, and he applied this conclusion to the higher vertebrates, in which "conception takes place by the effect of the male sperm on the follicles which are present in their maternal ovaries, where the sperm are present giving life, and the follicles are given life, the first being equivalent to the polyp, and the second corresponding to the fungus."²⁸

Vellanskii could not, of course, avoid the well known fact that in the seminal fluid there are numerous active bodies with tails. He called the spermatozoids cercariae, assigning to them "the fertilizing property of the semen."

Cercariae . . . reach the ovary in the manner of polyps; they find there the Graafian follicles like the fungus corresponding to them; and these together produce a single creature, the embryo of the animal The follicles given life by the polyp swell and blow up, and the polyp within the flowing fluid forms the embryo, which does not originate from the mixing of sperm with the fluid of the follicle, but is a transformation of many cercariae into one organism.²⁹

27. Ibid., pp. 413 - 414.

28. Ibid., p. 417.

29. Ibid., p. 421.

According to Vellanskii, this is the Naturphilosophie theory of fertilization. It was possible to establish such a theory because the mammalian ovum was not yet detected, and because the essential content of the Graafian follicle was considered to be the fluid filling it. The demonstration of the presence of the egg or ovum in the Graafian follicle, by K. M. Baer in 1827, made it evident that Naturphilosophie was without grounds with respect to fertilization.

Turning to the phenomena of embryonic development, Vellanskii gave only the most primitive outline of factual data, since he was interested mainly in repeating the features of ontogenesis which are characteristics for a complex ascending series of animals, i.e. Naturphilosophie's problem of analogy.

Higher animals, after conception, must pass through all the periods which are characteristic for the development of the lower classes, where they have a prolonged stay in their proper formation. Man, representing the perfect unity of the earthly world, after conception passes through periods which are characteristic of the development of all classes of the animal kingdom; therefore the proper development of his organism is the most prolonged.³⁰

The human embryo develops linearly at the beginning into a worm, along which form its membranes reach out . . . ; among them the external membranes (chorion) are highly shaggy. It touches the uterus with its filaments and assumes the fetal place (placenta). The internal membrane (amnion) includes the embryo itself, with its fluid (liquor amnii). Almost one month after conception the embryo remains invisible; then it appears in a moving spot (punctum saliens), from which in some days it grows to two and a half millimeters and has the form of a worm.³¹

In the first day, according to Avtenrit, the embryo . . . hangs on a very short umbilical cord . . .

30. Ibid., pp. 422 - 423.

31. Ibid., p. 424.

On its face is the lower jaw with the large structure of the mouth; two dark half-circles here designate the eyes; two small holes on the sides of the head indicate the place of the future ears; and four small pimples, two upwards and two downwards of the body, are the beginning of the arms and legs In the period of the fourth day . . . development of the tactile and visual organs begins; subsequently, the embryo is transformed from a worm into a mollusc and a fish.³² In subsequent periods of development, the embryo passes on to the condition of insects, amphibia and birds, as this observation shows. After fifty-two days . . . two depressed points appear at the place of the nose, and the ear helix formation begins as cut-out knots. By the fifty-fifth day, the sides of the nose appear somewhat raised, with closed openings . . . ; thus the basic formation of the nose as an organ of smell is equivalent to the insects, and ear formation starts as equivalent to the birds.³³

In concluding his digressions on embryology, Vellanskii turned his attention to how parental features are given to children, and criticized Buffon's "atomistic theory," according to which

particles (les molecules) from each organ of the body are related to the (testicles) and ovaries; and each of them, representing a certain part, unites at the place of conception with others, and together they produce a new animal like the parents. But material organs and the particles themselves are in essence only transient features of life and not the parent's transitory body giving birth to offspring. The idea of immortality thus produces a reflection of itself. Consequently there is no need to assume that the sperm contain the miniature of all the parts of the body in order to produce a whole embryo³⁴

32. Ibid., pp. 425 - 426.

33. Ibid., pp. 426 - 427.

34. Ibid., pp. 422 - 423.

And next: "Although sperm do not contain particles from each member separately, there is no such production of the organism which has fulfilled all the conditions of its process, and where the idea of life appears possible to the extent that the organism is represented in reality."³⁵

All that was stated represents a complete idealistic system of opinion on development and heredity, which takes its root directly from Schelling, which in turn represents, to a certain extent, a revival of the Platonic view of the material world as an imperfect reflection of the world idea.

The anatomical, physiological, and particularly the embryological ideas of Vellanskii are given here with the aim of showing an example of the expressed effect of German Naturphilosophie on individual representatives of Russian biological science. Strictly speaking, this example is unique in its type. Vellanskii did not find enough like-minded persons in his mother country for him to continue. His efforts to call attention to the ideas of Naturphilosophie remained useless. Only in Moscow University, under the influence of M. G. Pavlov, did a certain interest in Naturphilosophie appear, and its weak outgrowths can be traced up to the middle of the 1830s.

Michael Grigor'evich Pavlov (1793 - 1839) participated in 1813 in a spiritual seminar at Moscow University. He finished outstandingly in two faculties at once—mathematics and medicine—and in 1818 obtained the degree of Doctor of Medicine. He devoted his dissertation to the embryological problem of nourishment of the human fetus.³⁶

35. *Ibid.*, p. 424.

36. DISSERTATIO INAUGURALIS PHYSIOLOGICO-OBSTETRICIA DE NUTRITIONE FOETUS HUMANI, QUAM . . . PRO GRADU DOCTORIS MEDICINAE . . . ELABORAVIT ET PUBLICE DEFENDET Michaël Pavlov. Moscow, 1818, 87 pp.



Michael Grigor'evich Pavlov.

M. G. Pavlov's dissertation does not contain particular observations. It is composed of critical reviews of the literature and the author's arguments about the sources of nutrition in the human fetus. This work is interesting because it gives a clear idea about the level of embryological knowledge at that time. The work begins with an address to the Dean of the faculty of medicine of Moscow University, the anatomist E. O. Mukhin (41), and represents an aphorism: "In arduis audere juvat" (in difficulties it is pleasant to be daring). The dissertation is composed of three chapters, the first of which carries the name "The Appearance and Growth of the Fetus." It starts with a statement that no obstetrician accurately knows how long the time is between conception and the first appearance of the fetus, and, for this reason, there are significant disagreements. Thus, Moriss, Monro, and others have stated that on the third day after conception they have seen in the human ovum an embryo like a worm (*vermiculi speciem*). Haller never recognized the fetus before the seventeenth day. The same period is indicated by the "superior and most famous professor, V. M. Richter." (42) Pavlov, here and below, cited the text and drawings of the first edition of Richter's book, *MANUAL OR GUIDE TO THE MIDDLE SKULL* (Moscow, 1801). In a short description of the formation of the human fetus, Pavlov to a certain extent follows Richter: "The embryo appears in the form of a dull mucoid cloud, which is swimming in the cleanest fluid of the ovum; it is composed of three vesicles denoting the rudiments of the head, the chest, and the lowest part of the belly" (§ 7). About the third week after conception, in an aborted ovum, it is possible to see a crumpled fetus in the form of a small white body with a small rounded head. It is devoid of all signs of the extremities. It swims on the surface of a completely transparent, colorless fluid, and is connected by means of an umbilical canal with the umbilical sac. In a footnote, Pavlov remarked that specimens of these fetuses, which were obtained by E. O. Mukhin, were present in the anatomical rooms of Moscow University and the Medical-Surgical Academy. About the fourth week of pregnancy, the body of the fetus looks bloodless, white, and semi-transparent; the head is entirely smooth; on it there is only a small slit denoting mouth formation. The umbilical canal becomes thicker. The rudiments of the extremities appear between the thirty-fifth and fortieth days. During the sixth week, according to Richter,

the fetus is equal in size to a bee; its head is large in comparison to the body. Next to the mouth the eyes are visible, but there is still no trace of the nose. On each side, near the corners of the mouth, is seen a very small opening, which is the future aural canal; the extremities are short and thick, the upper are developed more than the lower; the fingers on these and the others are rudimentary. Between the end of the second and the beginning of the third month, the size of the embryo is about two Parisian inches; the forehead is rounded; the eyes are closed; the nose shows up; the mouth is closed; the lips are not yet turned back; the digits of the hands and feet are in the form of distinct rudiments. Between the tenth and eleventh weeks the umbilical vessels are strongly twisted and yet there is no trace of the placenta, which appears between the twelfth and sixteenth weeks of pregnancy. The second stage of development of the fetal membranes occurs in this period, and in particular the disintegrating membrane appears and the vessels outside the embryo aggregate in one spot. The amniotic fluid increasingly accumulates and becomes non-transparent, resembling milky serum.

Pavlov skipped the descriptive details of the fetal ovum's structure and cited "the brilliant work of the famous professor J. Wenssowitsch (43), entitled, 'On the Structure and Role of the Fetal Membranes and Placenta.'"³⁷ Next, Pavlov considered the processes of fetal growth, denoting that in different periods of life the rate of growth is not the same; it becomes slower with the approach of the moment of birth. The increase in body size of all living creatures is a result of nutrition; the same thing relates to the fetus growing in the uterus. "From ancient times," Pavlov wrote, "the question of how the fetus feeds was raised; this question was solved differently in different times, because each school of physiologists had its own hypotheses" (§ 23).

These words represent a transition to the second chapter, "Investigation of Opinions about the Nutrition of the Human

37. (Joannes Wenssowitsch), DISSERTATIO OBSTETRICIO-MEDICA DE STRUCTURA ET USU SECONDIRARUM, QUAM . . . PRO GRADU DOCTORIS IN AUDITORIO MAJORE UNIVERSITATIS CAES. Moscow, 1803, 65 pp.

Fetus." It begins with arguments on the use of hypotheses by citing Condillac's words: "It happens when they reach for evidence; in all sciences and arts they begin with the sense of touch." Concerning nutrition of the fetus, Pavlov divided the nutritional sources into three groups: the blood of the mother, the serum chyle (serum chylosum), or the amniotic fluid. Turning to the first hypothesis, Pavlov remarked:

If the fetus feeds on the mother's blood, so it is necessary that his blood vessels be anastomosed with the mother's vessels; however, recently the existence of these anastomoses have been denied. It is natural to assume that the place where the maternal vessels could unite with the vessels of the fetus is the placenta; however, its structure speaks against such union. (§ 27, 28)

Giving the description of placental structure (§ 29 - 32), with citations to Wenssowitsch's work, suggesting differentiation of the placenta into distinct parts—maternal (pars placento-uterina) and fetal (pars placento-umbilicalis)—Pavlov made a reminder about the attempts to solve the question experimentally. Wax introduced into the umbilical artery or vein sometimes does not pass into the uterine placental cells, even if they are not destroyed, and remains in the placental umbilical part. A wax injection from the side of the uterine vessels does not pass into the fetal vessels of the placenta. Therefore, despite Meckel's opinion, Pavlov accepted Mukhin's view that fetal blood vessels do not anastomose with maternal vessels. Next, he stated in detail other arguments against fetal nutrition by the blood of the mother, based on the observation of the rhythm of vascular pulsation in experiments with their ligation in animals and so on. Pavlov concluded with: "And so, if we accept that the blood vessels of the fetus do not have any communication with those of the mother, if the maternal blood cannot reach the fetus by any means, so it is concluded that the fetus does not feed from the blood of the mother" (§ 54).

The second point of view, according to which the fetus feeds from the milky serum which is extracted from the maternal blood, Pavlov stated in the words of Wenssowitsch: "From the beginning of pregnancy . . . the capillary vessels of the

embryo extract a serous-lymphatic whitish nutritional serum from the maternal arterial blood vessels which are located between the placenta and the uterus. By attaining this stage of development when the fetus is increasing to a size that requires a large stock of blood, it begins preparing special blood from the chyle juice" (chylus).³⁸ In Pavlov's opinion, Wensowitsch's hypothesis did not resolve all the doubtful questions and did not reject the third point of view of fetal nutrition (nutrition by the amniotic fluid). This latter point of view assumes the intake of amniotic fluid through the mouth, through the skin, or through both. Pavlov compared arguments for and against the different opinions, in two columns divided longitudinally on the page. There is reason to trace this entire discussion, as it is sufficient to illustrate individual points.

- | | |
|-----------------------------------------------------------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| 1. Fetus does not breathe, and without breathing, swallowing is impossible. | 1. In case of absence or interruption of breathing, the possibility of swallowing is not excluded (the opinion of Maksimovich-Ambodik). |
| 2. Mouth of the fetus, in the natural condition, is closed. | 2. Observations of Meerheim are given stating that on the introduction of the finger into the uterus after the destruction of the fetal membrane, the fetus takes this finger in its mouth and compresses its lips. Besides, if the mouth of the fetus is closed, then the amniotic fluid can penetrate through the nostrils. |

38. Wensowitsch evidently considered, however, that the amniotic fluid serves also to protect the fetus; and of its nutrition he said in the fourth thesis of his dissertation: "Probabile est, liquorem amnii, praeter defensionem foetus inservire quoque ad nutritionem ejusdem."

DISSERTATIO
INAUGURALIS
PHYSIOLOGICO-OBSTETRICIA
DE
NUTRITIONE FOETUS HUMANI,
QUAM,
EX AUCTORITATE
AMPLISSIMAE FACULTATIS MEDICAE
CAESAREAE UNIVERSITATIS
MOSQUENSIS,
PRO
GRADU DOCTORIS MEDICINAE
summisque in Medicina honoribus ac immuni-
tatibus legitime capessendis, elaboravit et puh-
lice defendet

Michaël Pawlow.

MOSQUAE, 1818.

Týpis Universitatis Mosquensis.

Figure 16. Title-page of Pavlov's "On the Nutrition of the Human Fetus"

3. There are cases of birth of fetuses devoid of mouth or missing a head.
3. This means that the fetus is nourished not only on the amniotic fluid.
4. If the fetus was fed by swallowing amniotic fluid, then his intestines should have been filled with feces.
4. Amniotic fluid is light food, from which only very little fecal matter remains.

As to arguments in favor of nutrition by the amniotic fluid, Pavlov reported the evidence of investigators who had found amniotic fluid and also hairs of the embryonic fur in the fetal stomach, confirmed by chemical analysis. Favoring the intake of amniotic fluid by the skin are, in Pavlov's opinion, observations about the filling with fluid of the distended subcutaneous lymphatic vessels of the fetus. After giving these data, he moved to the following cautious conclusion: "It must not, however, be thought that the fetus feeds exclusively on amniotic fluid, because it is impossible to neglect the nutritional value of the milky serum" (§ 84).

After reviewing different opinions about the sources of fetal nutrition, Pavlov moved to the considerations which make up the third chapter of his dissertation. First of all, setting aside the possible accusation of presumption and vanity, he defended his right to "dispute the opinions of scientists and to build his own path, leading to the truth." In his justification he said: "I am seeking the truth and, for this reason, I do not want to swear by the words of the teachers" (§ 87).

For solving the question raised, Pavlov chose the path of comparative investigation. He noted that different living creatures are characterized by different degrees of development, man and infusoria forming the extremes between which there is gradual transition. The different degrees of perfection of organization correspond to the complexity of organization: the simpler the organization, the less it is improved, and the reverse. The organization of the human is the most complicated, hence it is considered the most improved of all animals. So for the explanation of the function of any organism, the more difficult it is, the more complex it is. And "the physiology

of the human body, if looked at by itself, could have constituted a problem that nobody could approach" (§ 90). Pavlov recommended to proceed always from simple phenomena to the more complicated. Man, Pavlov said, is a microcosm; in him, as in the depth of nature, where there are four life forms, there is a fourfold life period, namely the life of minerals, plants, animals, and finally the intellectual life, or the human life. In a footnote (§ 92), Pavlov said that for the most brilliant work reviewing this question we are indebted to the great professor of the Petersburg University, Jakob Kaydanow (44). This work was published under the title, "The Fourfold Property of Life, of the differences and reciprocal connections of the four main types of life, which are discussed in general and in relation to man in particular."³⁹ Following him in importance is I. M. Boldryev (45), at that time professor of anatomy and physiology of the Imperial Moscow Medical-Surgical Academy, with his dissertation "On the Features of Plant or Organic Life."⁴⁰ Speaking of man as a microcosm for the depth of nature, Pavlov followed the terminology of Kaydanow. Human nature, Pavlov said, citing Kaydanow, could have remained much less available to our understanding if animals did not exist, whose nature is discovered in the life of plants, and the nature of the latter in the life of minerals. "And so," he continued, "there is no doubt that for the thorough investigation of the truth there is a route leading from the simple to the complex, i. e. as if from the known to the unknown" (§ 93). So far as man and infusoria designate the extreme degrees in the limits of perfection of the animal organism, and so far as in nature nothing is done by leaps, so "it is hardly possible to imagine that man had occupied the highest of these steps without going through (not touching) the lower" (§ 94).

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39. Jacob Kaydanow, TTRACTYS VITAE SEU DE DIFFERENTIA MUTUAQUE CONTINUITATE IV CARDINALIUM FORMARUM VITAE, GENERATIM CONSIDERATAE, HOMINIS PRAECIQUE. St. Petersburg, 1813, 107 pp.
40. J. Boldryev, "De characteribus vitae vegetativae seu organicae principalibus ejusque praecique et animalibus in homine differentia." Moscow, 1815, 27 pp.

The presentation of his idea in the form of the chain of being is much closer, of course, to the evolutionary argument in the spirit of Radishchev and Lamarck than to Bonnet's metaphysical version. The graduation of structural complexity which is recognized in a series of living creatures (from infusoria to man) is, as Pavlov claimed, reflected in embryonic development. "The formation and growth of the fetus," he wrote, "represents a line which, beginning from the lower animals and passing almost through all the steps of the animal organism, reaches up to man" (§ 94).

Pavlov suggested dividing the embryonic period into its two stages: the stage of evolution or metamorphosis, during which the development of the fetus is carried out, and the stage of ripening or perfection, when the developing structures reach maturity. Going back to the idea of the production in ontogenesis of progressive levels of creation, he stated that, so far as there is corresponding difference in the structure of infusoria and mammals, their nutrition is also different; is it not possible that during the first stage of fetal development, when the organism becomes gradually more perfect and complex, that nutrition has similarly become more complex? The more complex the nutrition, the more perfect the animal; hence the nutrition of the fetus during the first developmental stage becomes more complex.

With the second stage, when development ends, the type of nutrition is stabilized. "In order to explain more properly fetal nutrition from its beginning, comparative physiology is recommended, beginning from simple creatures to the more complex" (§ 98). "If you carefully trace the nature of formation," Pavlov continued, "it is possible to see that body rudiments originate in water. Crystals develop from the fluid; the green material of Priestley is the beginning of plant life. The infusoria, as the rudiments of animal life, also begin with water" (§ 99). "From here it is easy to understand why the fluid condition represents a necessary condition for the formation of all bodies" (§ 100). Agreeing with the physicists, Pavlov wrote that the fluid state of the body undoubtedly precedes the solid state; thus the cellular tissue itself, which is the basis of solid development in the organism, initially develops from fluid.

Later on, he put this thought in the form of an aphorism: "I expect not to stray from the truth if I change the law—that all that lives comes from the egg—to another law—that all that lives comes from fluid" (§ 102). In agreement with Lamarck, Pavlov imagined that fluid appears at the beginning, by whatever means. It then forms into cellular tissue, and from that a living body develops. For life to appear requires an organic interaction between fluid and the cellular tissue. This organic movement occurs through the stretching of the cellular tissue, and the latter responds to the pressure under whose effect displacement of the fluid takes place.

The fluid contained in the cellular tissue Pavlov, following Lamarck, called the essential moisture (in higher animals, this is the blood; in lower animals, uncolored fluid; according to Pavlov, this latter is ichor). The first organic movement, according to Pavlov, makes possible the appearance of the basic life function—nutrition, which he considered the application of assimilated particles on dense formations, in which there are always cavities or canals containing the circulating essential moisture. This last disperses continually, and the organism needs its replacement through nutrition. The essential moisture must be variable in different animals, becoming more complex in composition as the animal's organization increases. Thus, in infusoria and polyps, the essential moisture is represented in a fluid watery jelly; in insects it is thicker; in crustacea, annelids, and molluscs, it has a more complex constitution and contains little protein; in fish and reptiles there is not only protein but also fibrous material in the blood.

The process of assimilation of food is also related, Pavlov continued, to organization; hence more complex processes of assimilation correspond to complexity of the digestive tract. Likewise with the intake of oxygen, which Pavlov believed participates in the final stage of assimilation, especially in the formation of blood, which is not directly contained in the food. The source of development for these substances, Pavlov thought, can hardly be sought in oxygen alone. "Undoubtedly," he said, "such an extremely effective force, which is considered vital, can be called an assimilating force" (§ 118).

Continuing the ontogenetic-phylogenetic parallel related above, Pavlov stated that the fetus is at first similar to the infusoria, not only in organization, but also in the character of nutrition. The infusorian extracts food and oxygen from drops of water in the mouth. At the beginning the fetus is constructed quite simply; it has the shape of a vesicle, devoid of any organs and composed of gelatin ("does not this structure simulate the organic infusoria?" Pavlov asked). The source of food and water for the fetus is an insignificantly small portion of the transparent amniotic fluid. When natural development moves upward from plants to animals, the digestive canal acquires great importance. In general, it is considered the first special organ. Digestion is the first function necessary for the continuation of existence. "Does not the same occur in the fetus?" Development of the fetal digestive canal is gradual; hence it is impossible that digestion develops suddenly. Pavlov suggested that the digestive canal in the early fetus is insufficiently developed and for this reason cannot accomplish its function. He noted that nobody doubted that the digestive canal in polyps, radiates, and insects can digest food. The developing fetus, according to his analysis, behaves as those animals do; why then does its digestive canal not function? As in higher animals the organs of digestion appear more perfected, so in the fetus the digestive system improves in the process of development.

Between the twelfth and sixteenth weeks, when, according to Pavlov, metamorphosis ends, the amniotic fluid provides insufficient food and oxygen to meet the requirements of the fetus. "Therefore nature seeks new means to complete the deficiency, and thus the placenta is formed" (§ 134). Between the fetus and the mother there is a juice, richer in nutritional substances than the amniotic fluid, which is extracted by the vessels of the umbilical canal.

Pavlov's third chapter, on human fetal nutrition, includes the assumptions which partially form his dissertation's conclusions. In summary, these include: 1) "All that is living is from fluid" (Thesis 1); 2) "Fetal life can be divided into two stages—the stage of metamorphosis and the stage of perfection" (Thesis 111); 3) The method of embryonic changes in nutrition repeats the changes in the transition from lower animals ("infusoria") to higher animals.

The processes of assimilation, according to Pavlov, are governed by a special power. This statement perhaps echoes Wolff's studies on the essential force. In general, Pavlov's bibliographic citations are rich. Wolff's work is not cited, so it is difficult to assess any possible effect of Wolff's ideas on Pavlov.

It is not possible to judge M. G. Pavlov's dissertation by contemporary standards concerning embryonic development and physiology of intrauterine nutrition. A few speculations are listed which produced an effect on German Naturphilosophie, but Pavlov's dissertation also contains a number of additional interesting thoughts and general conclusions. Particularly valuable in this regard are his onto-phylogenetic parallels, which Haeckel later combined to form his biogenetic law. Pavlov worked out in detail a comparison between embryonic stages of development and the degrees of structural and functional organization in the digestive organs of the animal world.

In his subsequent scientific and educational activities, M. G. Pavlov did not return to embryological studies. In 1820, after two years abroad, he went to lecture at Moscow University in physics, mineralogy, and agriculture. Besides that, he lectured publicly on the general subject, "About Nature," in which he treated Schelling's ideas, and he also delivered popular lectures on improved agricultural methods. It is possible to judge the importance of Pavlov's professional activities through A. I. Herten's memoirs.

German philosophy, Herten wrote, was transferred to Moscow University by M. G. Pavlov. The department of philosophy was closed from 1826, and Pavlov taught introductory philosophy instead of physics and agriculture. It was difficult to learn physics from his lectures, and impossible to learn agriculture, but his courses were nonetheless extremely useful. Pavlov stood within the physico-mathematic division and presented students with the question: "Do you want to know nature? But what is nature? What is there to know?" This was extremely important. Young men entering the university were entirely devoid of philosophical preparation; some had an understanding of philosophy, but usually completely wrong. As an answer to these questions, Pavlov quoted Schelling and Oken with a clarity

that had never been present in other nature-philosophers. If he did not attain explicitness in everything, it was because of Schelling's weakness.⁴¹ (46) Pavlov's brilliant lectures had attracted listeners from every direction, and their construction and content kept his audience enthusiastic. (47)

Critically stating the basic principles of German Naturphilosophie and the theory of knowledge, Pavlov concluded that speculative intuition by itself is entirely insufficient, and that for the study of the phenomena of nature it is necessary also to apply empirical investigation. The evolution of Pavlov's opinions could be traced by his articles in the manual MNEMOSIN, by V(ladimir) F(edorovich) Odoevskii and V. K. Kukhel'beker, and in an issue of the journal ATENEI. The articles in MNEMOSIN⁴² reflect Pavlov's earlier period of philosophical development, when he had accepted, almost without reservation, Schelling's and Oken's principles of Naturphilosophie. The effort to discover the main reason for the countless phenomena in the harmony of nature, and to establish their general theory, Pavlov said, starts from two contradictory points—the experimental and the speculative. Nature is investigated by two methods: by the analytical-empirical method and by synthetic speculation; which method is more perfect? (pp. 8 - 9). Pavlov answers his question in the following manner. Because the truth is indivisible, all essential sciences must be based on a single unified theory. However, empirical sciences such as mineralogy, pharmacology and therapy have not just one, but many theories. "On what, then, does imperfection of the empirical sciences depend? Are their representatives deceived concerning the importance of experiment?" (p. 12). Many theories are based on the fact that material existence is accidental, imaginary, and actually exists only ideally. The experiment—analytical or empirical investigation—can perceive that which is only

41. A(leksandr) I(vanovich) Herten, MY PAST AND THOUGHTS (Byloe i dumy), 1946, p. 215.

42. "On Methods for the Investigation of Nature," MNEMOSIN, 4 (1825), pp. 1 - 34. The article is signed with two Greek letters.

externally subject to sensation, i.e. the nonessential, while the ideal is not subject to experiment.

The external aspect of nature is the region of empirics, consequently the field of intellect; the internal is the aspect of speculation and the field of thought. Those following the first find only a reflection, which is a print of the ideal. Those following the second try to contemplate the idea which is reflective by itself. (p. 29)

And: "Empirics from the surroundings (i.e. from external manifestations—L. B.) strive to the center (i.e. to the main point—L. B.) at random, and speculation from the center goes out to the exterior—most likely" (p. 30).

It seems that from these idealistic judgments there must be an inevitable conclusion that only speculation can give true knowledge. However, Pavlov showed caution in his conclusions. At the end of the article he wrote the following: "However, speculation with all its advantages is insufficient. Each phenomenon (and nature—their combination) is a union of contradictions (synthesis oppositorum), a combination of the ideal with the material. Hence, individually, speculative knowledge and empirical knowledge are incomplete."

Still more defined in this respect are Pavlov's considerations stated in his article in ATENEI.⁴³ This work is simplified in the form of a conversation between the "wisdom-lover" Polist and his supporter Kenofon on one side, and Menon on the other. (48) The latter, who is expressing Pavlov's own point of view, demands a reasonable combination of speculation and empiricism. He argues: "In order to know philosophy, it is necessary first to know science; philosophy judges the possibility of what science considers to be present. Is it possible to make judgments about what we do not know?"

43. M. Pavlov, "On the Reciprocal Relation of Speculative and Experimental Knowledge," ATENEI, Part 1, No. 1 (1828), pp. 3 - 15; No. 2 (1828), pp. 1 - 19.

Consequently, speculative information, which constitutes philosophy, is possible only in the face of scientific experimental information. It is clear now that the sciences could exist without philosophy and not be complete nonsense, but philosophy without science is impossible. If one seeks to philosophize without knowing science, his wisdom will be delirium, shameful for the intellect, harmful for science. (pp. 17 - 18)

Despite the reasonable tone of these discussions, it must be acknowledged that M. G. Pavlov could not overcome the idealistic ideas that he had met in his youth.

The effect of Naturphilosophie was also shown in the opinions of those Russian zoologists and physicians interested in the development of the internal and external human parasites. This subject has an acknowledged relation to embryology, because the authors writing about the spontaneous development of parasitic forms also approached the phenomena of development in all other living creatures.

Studies about the spontaneous generation of parasites spread in Germany, where it was supported by those authoritative helminthologists, Rudolf and Bremser. From Germany this study penetrated into Russia. Bremser's book was translated into Russian in 1839,⁴⁴ accompanied by an article by J. Spassky supporting the idea of arbitrary or undefined development of parasites. Spassky himself, fifteen years prior to that, had published a dissertation devoted to the parasitic helminths⁴⁵ which also concentrated on their spontaneous generation. He expressed his idea in the following theses:

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44. (Johann Gottfried) Bremser, ON THE HELMINTHS PRESENT IN THE HUMAN BODY, OR A MANUAL FOR THE IDENTIFICATION AND TREATMENT OF HELMINTHIC DISEASES. Translated from the German. 1839. xxii + 384 pp. (49)
 45. Johannes Spassky, "Entozologiae historiae progressus, et status hodierni brevis expositio." St. Petersburg, 1824. ii + 50 pp.

IV. The origin of interior animals in the human body is explained by means of primitive generation.

V. We deny that there exist in air or water seeds of worms which penetrate the animal body, and that interior animals multiply as such.

VI. We deny that interior animals can transfer from the mother to the fetus. (p. 49)

That same point of view is given in the dissertation which A. Kosminsky⁴⁶ defended at Moscow University in the same year as Spassky's. Concerning the origin of parasitic worms, Kosminsky gave various points of view. The possibility of introducing the parasites into man through food or drink, either in mature form or as eggs, is equivalent to the transfer of parasites or their embryos from the human parents through the egg from which the human fetus develops, or by means of infection through the placenta, milk, saliva, etc.; Kominsky decisively rejected all of this. His arguments included: "Regarding previous discussions . . . , it is sufficient to say that all the new authors collectively state that worms find a shelter in the intestines of people and beasts, and they get their start from spontaneous or sudden generation or development."⁴⁷ Kosminsky assumed that not only molds, fungi, lichens, and infusoria could develop this way, but also intestinal worms. Kosminsky envisioned the process of their spontaneous development as follows. In those parts of the organism which, for some reason, are weakened and consequently secrete abnormal serum, lymph, or mucus, there appear organic particles which represent rudiments of future parasitic worms. The mucus, serum, and lymph accumulate in the intestine, where the nutrient fluid, which was earlier converted into animal matter, thickens and coagulates. Covered with epidermis, it can easily give rise to the development of worms.⁴⁸

46. Alexander Kosminsky, "Dissertatio inauguralis medico-practica de entozois s. vermibus in intestinis hominum praecique nidulantibus, de remediis anthelminticus et methodis eadem exhibendi." Moscow, 1824. 24 pp.

47. Ibid., p. 28.

48. Ibid., p. 23.

In the theses submitted for his dissertation, Kosminsky expressed the same ideas more briefly and yet with more definition:

Thesis 4. The idea that the worms are conceived from eggs which get into the human body appears to be false.

Thesis 5. The development of worms is best explained by what is called spontaneous conception.

In 1841 in Dorpat, the doctoral dissertation of the physician Ivan Kramarenkov, from Sum, was published as "Something about the Flatworm, and Some Means of Its Expulsion."⁴⁹ Kramarenkov, with detailed study of the literature, discussed further the development of worms in the human body, and had come to accept the idea of their spontaneous conception. The first section, titled "Something about the Origin of Worms in the Body," begins:

The question of how worms are conceived in the body can be solved in two ways: either they develop from some organic material and not from pre-existing creatures similar to them, which would suggest spontaneous development, or else new organisms develop as a result of the coupling of bodies similar to each other, consequently by propagative development.
(p. 1)

Comparing the opinions supporting each point of view, Kramarenkov wrote that "Pallas deduced from his experience that from the eggs of cestodes, introduced into the abdominal cavity of a puppy, new small worms are formed. With some passion, he tried to explain the origin of worms as a result of eggs dispersed in nature (p. 4). Pallas' opinion, according to Kramarenkov, was completely disproved by Bremser; Kramarenkov himself considered that "the most probable is that human worms develop in the organism in the beginning neither from water, nor soil, nor from eggs or larvae, nor from food or drink. They develop by means of spontaneous generation" (p. 16). To confirm his point of

49. Johannes Kramarenkov (Medicus primi ordinis Sumensis), "Nonnulla de Bothriocephalo lato ejusque expellendi quibusdam methodis." Dorpat, 1841. iii + 51 pp.

view, Kramarenkov referred to such authors as Johannes Müller and Hufeland, citing appropriate quotations from their reports.

To characterize the biological ideas from the department at Moscow University over a twenty- to thirty-year period, we must give the opinions of A. L. Lovetskii, who was considered at that time to be its leading professor. His book, INITIAL INSCRIPTION OF NATURAL HISTORY, had for a long time been well regarded as a guide for students. A. L. Lovetskii (1787 - 1840), a physician and naturalist, gave presentations mainly for courses of zoology and mineralogy. In MY PAST AND THOUGHTS⁵⁰ Herten wrote disrespectfully about him, from which a negative impression could be formed about his scientific and teaching activities. Lovetskii suggested the spontaneous development of organisms, which appears to express the Naturphilosophie idea of the development of organisms from the products of decomposition of living creatures.

Lovetskii's and Vellaskii's ideas came from the idealistic and metaphysical notion of eternity and the unchangeable nature of the organic monads as germs or embryos of living creatures.

In 1824 Lovetskii published a paper "On the Initial Conception of Worms in Animal Bodies."⁵¹ Concerning opinions on the spontaneous development of parasitic worms, Lovetskii wrote:

The observations of some scientists give grounds for the assumption and the defense of those ridiculous opinions affirming that they have seen intestinal worms outside the animal body. These opinions are disproved by the following conditions: a) there are no true and exact observations about the presence of these worms living outside the body; b) worms that are discharged from the body soon die; c) the genera and types of worms are as variable as the types of the animals in which they live; d) the worms are found

50. Herten, MY PAST AND THOUGHTS, section VI, p. 68.

51. Lovetskii, in NEW MAGAZINE OF NATURAL HISTORY, PHYSICS, CHEMISTRY, AND ECONOMIC INFORMATION, edited by I. A. Ovigubskii, Part 2 (1830), pp. 17 - 34, 87 - 108.

not only in the newly-born infant, but also in the fetus; e) the character and type of life of the worms is specific and entirely distinguished from that of other animals.

Opponents of the spontaneous development of worms asserted that worms outside the host's body take another shape from that inside it. Lovetskii rejected this view with two arguments: "a) land and water animals which accidentally get into an animal's stomach die very soon either from digestion or from extreme heat; b) transformations, with the exception of insects and frogs, are not characteristic of any other animals."

Similarly, Lovetskii was not convinced that infection with worms could occur through their eggs' getting into food or drinking water. Thus, "the original material of their initial development should be in the animals themselves . . . and this development occurs in certain conditions as though a necessary sequence of their organization." Spontaneous conception, Lovetskii proposed, also occurs in arthropods. "The observations indicate," he wrote,

that they frequently appear suddenly in people in whom they were not previously present What are those internal conditions which promote the formation of worms? A scrofulous condition of the juices, copious and sticky sweat remaining on the skin surface, putrefactive hemolysis of the blood, and others are the conditions under which a watery organic material, in a condition of putrefactive fermentation . . . is converted into such bodies as lice.

In no less clear a form, Lovetskii stated his corresponding opinions in his article, "Properties and Sources of Infection in General, and of Cholera in Particular."⁵² There he described in particular detail the mechanism of spontaneous infection. The Naturphilosophical character of the idea of spontaneous infection appears clear from his words: "That destroyed animals and even plant materials are capable of conversion into embryos of new living creatures is evidenced by the fact that they

52. Lovetskii, in TELESCOPE, Part 2 (1831), pp. 52 - 74, 235 - 239, 354 - 382.

are in essence materials which are not dead but only dying, i.e. they are devoid only of their previous form and not of the property of living in another form. The most important example of conversion of destroyed organic material into creatures that are alive and organized is the birth or development of animals and primitive plants (Protozoa, Protophyta) with which the organic kingdom began."

In relation to the vertebrate animal, Lovetskii rejected the possibility of spontaneous development. He stated his reasons in a special article, "On the Larvae of Insects and Frogs Living inside the Human Body."⁵³ He cited cases described by Professor Spassky where, according to the observations of a Doctor Gubchenko, a nineteen-year-old girl in a period from "July to October 13, vomited up to thirty live toads of different sizes." Assuming that she had swallowed developing toad eggs, Lovetskii wrote: "To confirm that the toads initially could develop in the intestinal canal of man by spontaneous generation is highly ridiculous and not in compliance with any understanding of things. Only the invisibles (infusoria, worms, lice, and mites) could appear by spontaneous generation in the animal organism."

Lovetskii's ideas about fertilization and embryonic development stand close to his opinions about spontaneous development. In the above-cited article, "On the Initial Development of Worms," Lovetskii handled these issues with the following: "The plant grain and animal eggs, being still in an undefined and immature condition, do not have any defined shape. Essentially they are featureless material, which changes after fertilization by means of vital chemical fermentation. This material forms a mucous bladder (the initial point of body-development), with later development of organs and equilibrium maintained by the same fluid materials from which it received its physical beginning."⁵⁴

53. Lovetskii, in NEW MAGAZINE, Part 2 (1828), pp. 265 - 275

54. Quotations from the work of Lovetskii were adopted from A. P. Borgdanov, CARL FRANTSOVICH RULE AND HIS PREDECESSORS IN THE IMPERIAL MOSCOW UNIVERSITY (Izv. Obsh. Lyub. Estestv., Antrop. i Etnogr., 43, 1885).

The idea of spontaneous development, actually in somewhat variable form, found support at a later time between 1840 and 1850, for example in the work of the amateur naturalist Gros,⁵⁵ who was interested mainly in the origin and development of parasitic worms. He published his articles in the BULLETIN OF THE MOSCOW SOCIETY OF NATURE INVESTIGATORS in the period from 1845 to 1855.

Gros' earliest work⁵⁶ began with various microscopic investigations; besides observations on ticks, ascarids, tapeworms taken from snipe intestines, blood filaria, vaginal and intestinal trichomonads, and vibrions from the mouth cavity and human feces, there is a section on the development of the worm, in which Gros assumed that rotifers could develop from particular eggs. In the same report Gros described the embryonic development of the filaria, and gives explanations of the early stages of division.

A paper he published in 1849,⁵⁷ like the previous one, began with a variety of parasitological and embryological observations. He described a worm with five openings, a nematode from a tortoise intestine, an amoeba from a human mouth cavity, observations on blood parasites and infusoria, and, finally, some embryological data. Gros described his observations on the development of the eggs of human ascarids and pinworms, and he described briefly the structure and development of fresh-water moss and his observations on embryonic chick development. In this section he reported work on the structure of the yellow granules, on the differentiation of embryonic

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55. Biographical information about George Gros was not available. In the card index of the members of the Moscow Society of Nature Investigators, in which he was named Egor Egorovich Gro, it was recorded that Gros was considered an active member of the Society from March 16, 1844, and frequently participated at the meetings with introductory presentations, and that his articles were printed in the BULLETIN of the Society.
56. Gros, "Observation et inductions microscopiques," BULL. SOC. NAT. MOSCOW, 18 (1845), pp. 380 - 428.
57. Gros, "Fragment d'helminthologie et de physiologie microscopique," BULL. SOC. NAT. MOSCOW, 22 (1849), pp. 549 - 573.

feathers, on the development of the crystalline lens, on the appearance of the gall bladder in the fetus, and on the development of the lungs.

His embryological observations led Gros to certain conclusions about spontaneous development, published in an article of 1847.⁵⁸ In this report, after a history of the speculative study of spontaneous development, Gros reported with no hesitation the spontaneous development of the tape-worm. He described in detail the conversion of vacuoles in the digestive glands into worm eggs, the appearance of embryonic vacuoles in the eggs, and their disappearance before the beginning of division.

Gros stated his opinions most completely in a long article (130 pages) published in 1851.⁵⁹ This work holds interest also for the history of the theory of evolution. His main objective was to affirm that organisms at successive steps of creation are genetically connected with each other. Thus: "Borders between the animal and plant kingdoms do not exist; on the contrary, they cross each other." "A cell can make a plant or an animal." "Conversion of types is proved by observations." "A cell is capable of multiplication as a plant (filament) or as a pseudo-animal cell (euglena); its daughter cells could multiply later as plant or as animal cells." "The cell developing as a plant provides the beginning of more complex plant types"—however, some of those cells, in Gros' opinion, constantly produce their specific type, and others go in the direction of regressive evolution (p. 458). "Filaments are capable of dividing into vacuoles, which can be turned into animal cells and converted into a number of transitional forms." "Euglena cells are related to both kingdoms and, apparently, form a cross between them" (p. 549). "Euglena cells demonstrate in a very clear form the relationship of the two kingdoms and form the beginning of two branches, one of which forms an ascending plant line,

58. Gros, "De la génération spontanée ou primitive en générale et en particulier de Helminthes," BULL. SOC. NAT. MOSCOW, 20 (1847), pp. 517 - 540.

59. Gros, "De l'embryologie ascendante des espèces, ou génération primitive, équivoque et spontanée et métamorphoses de certains animaux et végétaux inférieurs," BULL. SOC. NAT. MOSCOW, 24 (1851), pp. 283 - 340, 429 - 502.

and the other an ascending line or generation of animals." Gros considered the effect of the surrounding environment—temperature, time of year, light, quantity and quality of matter—as the source of heterogenic multiplication ("whims of reproduction"). Gros illustrated his understanding of conversion of types by examples; he discussed the conversion of amoeba into ciliated forms, of euglena into solar forms, while infusoria, in his opinion, are converted into rotifers and sloths.

The problem of spontaneous development or conception is part of the concept of evolution for Gros. But evolution was not understood by Gros as the arising of live creatures from "chaos and rotten stuff," as many of his predecessors had held. Rather, new forms began as animal-molecules.

Gros considered the possibility of the conversion of one species into another in an article under the title, "Primary Development of Round Worms,"⁶⁰ in which he gave examples of metamorphoses, larvae of worms, and also the conception of the infusorian *Torquatina* from the cells of the mucous membranes of the urinary bladder of frogs.

The study of the spontaneous conception of parasitic worms in the first third of the nineteenth century reflected the negative effort of the idealistic principles of German Naturphilosophie. It is no accident, therefore, that the supporters of spontaneous generation directly connected the beginning of life with the life power.

There is no need to stipulate that the study of spontaneous development of highly organized living creatures, which was widespread at the beginning of the nineteenth century, had nothing in common with Engels' materialistic idea of the origin of the living from the non-living.

The question of the development of living creatures was solved by the supporters of spontaneous generation, and especially A. L. Lovetskii, without the traditional reference to God as creator. It is possible to think that Lovetskii was inclined towards materialism, but the strong root of his opinions was under the obscuring veil of Naturphilosophie.
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60. Gros, "Génération primitive de Nématoides," BULL. SOC. NAT. MOSCOW (1885), pp. 204 - 226.

The signs of the effects of Naturphilosophie could also be observed in the biological ideas of Shchurovskii. Grigori Efimovich Shchurovskii, (1803 - 1884) graduated from Moscow University's Faculty of Medicine, and became a teacher of physics and natural history in the Moscow Educational House. He was a lecturer on natural history in the Faculty of Medicine at the University. A great part of his later work was devoted to geology and mineralogy, but in his earliest scientific activities Shchurovskii was interested in general biological issues. In his "Organology of Animals" (1834) and three other works, he considered the questions of embryology.

In the first of the above-mentioned works, he touched on Pavlov's Naturphilosophical ideas. In particular:

Man by his physical formation lives a double life: private, in which he passes all the periods of his relative existence; and a general life, in which, along with all similar animals, he constitutes one undivided, gradually improving organism. In his life generally, he experiences changes induced by the natural sequence of ages. Radiate animals represent his uterine condition or embryo, which is not yet differentiated into the various organs. In the slugs or molluscs he has his infancy; in animals having external articulation he has his youth; in fish, reptiles, birds, and beasts he reaches maturity, which in turn is replaced by sensible and experienced old age. And thus man is the final development of the animal kingdom, and the last step of existence.⁶¹

For Shchurovskii, the regularity of repetition in stages of individual development of all the animal kingdom takes a distinct Naturphilosophical form, without concern for empirical confirmation of these stated ideas.

The data for his lectures on heart development⁶² are more distinct. Here Shchurovskii used the data he had available,

61. Cited by A. P. Bogdanov, CARL FRANTSOVICH RULÉ, pp. 86 - 87.

62. G. E. Shchurovskii, "On the Individual Development of a Bird Heart and its Similarity with the General Development (... contd on next page)

especially that for the embryonic development of birds (he himself apparently did not make observations), but he drew his conclusions both from data and from selected works of Naturphilosophie.

"Nature is an organic body, a part of which, in essence, is development, or perhaps it is better to say the repetition of one and the same beginning" (p. 192). Referring to Saint-Hilaire, who called this repetition or identity "unity in the formation of organization," Shchurovskii formulated the following law:

Each organ of the animal body, moving from the non-existent to the existent, from primary embryo to the most perfect form, represents a number of private developments which become complicated. Sometimes the private development of an organ in one animal reflects, in general, the development of the same organ in the whole kingdom. Thus, gradual development noted in the hearts of birds corresponds to different epochs of formation of this organ in the whole animal kingdom. (p. 193)

An explanation of the agreement between the stages of development of the embryo and the group of all animal forms, Shchurovskii sought in Plato's and Schelling's ideas of the universe of ideas materially realized in the universe of objects. Thus: "The life of the organic body which is still not enveloped in material form is called its concept or possible constitution Thus in the egg is included the concept or the possible constitution of the bird, which enters into actual existence at the time of incubation, when materialistic forms and organs of the future animal begin to form" (p. 193).

(Footnote No. 62, contd)

of the Same Organ in the Whole Animal Kingdom," in SCIENTISTS OF WESTERN MOSCOW UNIVERSITY, Part I (1833), pp. 192 - 210. A year later Shchurovskii published two more articles relating to embryology: "On the Head Vertebrae of Higher Animals," SCIENTISTS OF WESTERN MOSCOW UNIVERSITY, Part III (1834), pp. 256 - 268, 466 - 276, and "On the Structure of the Cloaca in Birds and the Theory of Egg Formation," *ibid.*, Part II (1834), pp. 37 - 61.

In order to substantiate his ideas, Shchurovskii referred to the observations of "Malpighi, Haller, Wolff, Spallanzani, Pander, Prévost, and Dumas." He distinguished six stages or steps of development in the heart of the chick. The first (about twenty-seven hours after fertilization) produces an elongated straight tube, both ends of which disappear in a transparent fluid. In the second stage (about thirty-one hours), the heart already has two venous and three to four arterial branches, and there is marked movement of colorless blood. In the third stage (thirty-six hours), the heart is characterized by the curvature of the heart tubing and two interceptors, "one of them separating the first cavity from the second, which is called the atrial system, and the other going from the second cavity along the span of the descending trunk, which is named the ventricular system." The first cavity he called the auricle; the second, the left ventricle; and the originating stem, the aorta, which by the end of the thirty-ninth hour is divided into two stems, each of which develops side branches. In the fourth stage (forty-eight hours) the heart changes from its elongated form to an oval or spherical form. At this time the heart appears "with one auricle and one ventricle," and the colorless fluid is replaced by red blood. In the fifth stage (fifty-eight hours) the right ventricle is formed through the extension of the vessel which runs from the right part of the auricle to the ventricle. In this period the heart has one auricle and two ventricles. Finally, at the sixth stage (third day), the cavity of the auricle is divided into two and forms a two-auricle, two-ventricle heart.

The essential error of this description is in the statement that the ventricle is divided into two before the auricle. This mistaken assumption of the presence of a one-auricle, two-ventricle heart, as will be seen later, caused Shchurovskii serious difficulty.

For a description of the development of the avian heart, we can compare its embryonic stage with the development of the heart of different animals. This is based on evidence that "the different periods of formation of this organ have a separate, independent life, and in their combination represent one organ, whose gradual development takes place in separate special organs in the different classes of animals" (pp. 197 - 198).

The most interesting of Shchurovskii's postulates starts with the confirmation that all lower animals are analogous to the egg. Just as the formation of an organism is included in the egg, so in the lower animals "the possible development of the animal kingdom, for reasons not yet discovered, is included in the formation of the organs, Therefore in infusoria, polyps, and zoophytes, the ideas of the heart and other organs have not yet materialized," Shchurovskii assumed that the heart was first formed in insects, where it has the shape of an elongated unbranched vessel and is analogous to the heart of the chick embryo twenty-seven hours after fertilization. In spiders and annelids (annulated worms), arteries and veins appear. "This second stage of development corresponds with the thirty-first hour after fertilization" (p. 199).

If in insects (first stage) the heart extends in a straight line, and if in the second stage it is stretched in its surface, then in the third stage, to which Shchurovskii related the molluscs, the heart "merges and closes up in a sphere." In "shell" molluscs it forms two widenings, "of which one (the auricle) . . . receives the veins, and the other (the ventricle) returns the arterial blood to all the body" (p. 200). Molluscs are thus analogous to the chick embryo in the thirty-sixth hour after fertilization. Shchurovskii located the heart of the cephalopod molluscs between the third and fourth stages, noting that, for example, in the cuttlefish there are three muscular widenings, to which correspond, in the more highly organized animals, the auricle, ventricle, and the descending aorta. Similarly, the hearts of fish correspond with the fourth stage of development of the bird embryo, i.e. to the forty-eighth hour after fertilization.

The heart of the lower reptiles (i.e. amphibia) is similar to the heart of fish, according to Shchurovskii. As "in tortoises, snakes, and lizards, which are considered of a higher class, it takes a special form of development The reptilian heart is of two-auricle, one-ventricle structure. This fifth stage of development corresponds to the fifty-eighth hour after fertilization, but with the difference that the duplication of the ventricle in birds precedes the duplication of the auricle" (p. 202). This stipulation interfered with the harmony of the postulate and is, as was mentioned before, a result of the mistaken description of the development of the chick heart.

In reptiles, as well as in the embryos of the higher vertebrates, the right and left heart, the vein pouring into it, and the pulmonary vein all have communication; therefore the blood can pass more easily through the oval opening between the auricles or through the valves directly to the aorta. According to Shchurovskii, reptiles are characterized by flexibility, a "cartilaginous composition," quick development, almost non-stop growth, abundance of blood, and other features characteristic of avian and mammalian infancy. "Reptiles are always young, always found in embryonic condition, swimming in the waters of the mother," Shchurovskii repeated (p. 205).

All this discussion concluded with the confirmation that the successive periods of heart development represent a fight between the powers of "dilation" and of "contraction. The first stretches the heart into a straight shape, and the second tries to compress it into a round form. This play of opposing powers is entirely similar to the systole and diastole of the heart of the great organism of the animal kingdom" (p. 206). And furthermore, all the nuances in formation of the various hearts are inspired by one understanding, so that, regardless of external variability, they are combined in internal unity. "Could it be otherwise? In nature each organ, each part, is necessary, an additional complementary voice to the general harmony of the universe" (pp. 207 - 208). Hence in Shchurovskii's work, embryological facts and suppositions were fantastically entangled in the substance of the latest ontogenetic-phylogenetic parallels, along with the Naturphilosophical snares of Oken and Vellanskii.

Regardless of such efforts by a few Russian followers of German idealistic philosophy, they did not succeed in establishing it firmly in Russia. The famous Russian physician Matvei Yakovlevich Mudrov (1776 - 1831), the founder of national internal medicine, who had heard in Germany a lecture about Naturphilosophie, criticized its ideas. The following is a quotation from one of his letters:

Dazzled by the brilliance of the high-flown sophistications born in the depths of Naturphilosophie, the young physicians search for new causes of disease in the structure of the universe and do not want to accept the empirical heights of the non-materialistic world,

not seeing what is under their eyes and what is confirmed by direct healthy understanding. Also, in pathology, instead of explaining the disease from the affected structure, which is not easy, they think it easier to look for sophisticated reasons abstracted from the material form.⁶³

The incidents of December 1825, after which not only unrestricted but also unclear ideas became dangerous to Nicholas's government, led to the dissolution of the "Society of Philosophy-Lovers," that weak bulwark of Naturphilosophie in Russia. Persecution trials sought to eliminate German idealistic philosophy from university departments. However, the failure of idealistic and Naturphilosophical ideas in Russia did not depend on government regulations. The government was trying to restrict philosophical thought by limiting orthodox theology. The decisive resistance which met Naturphilosophie in the environment of the advanced Russian intelligentsia persuaded the "philosophy-lovers" of their separation from reality, and of the idealistic character of their opinions.

It is possible to draw that judgment from a letter to V. F. Odoevskii from his cousin A. I. Odoevskii,⁶⁴ the poet of the December Revolution, and from the literary and philosophical controversy which appeared in the pages of the newspapers "Son of the Motherland," "Moscow Telegraph," "Moscow Herald," and others. A negative view of speculative German philosophy was expressed frequently by Pushkin. P. V. Amekov, in "Materials for a Biography of Pushkin," stated that the poems "Poet," "Niello," "To the Poet," and others indicating the influence of German idealistic philosophy, were actually propaganda from the editorial staff of the "Moscow Herald." One of the managers of this newspaper, S. P. Shevysev, says in his memoirs that Pushkin "has declared vivid feelings to those young

63. Matvei Yakovlevich Mudrov, cited in the introduction of an article by A. G. Gukasyan on the "Selected Works of M. Ya. Mudrov," PUBLICATION OF THE ACADEMY OF MEDICAL SCIENCE (1949), p. 30.

64. See Kh(achatur) S(edrakovich) Koshtoiants, OUTLINE OF THE HISTORY OF PHYSIOLOGY IN RUSSIA, pp. 70 - 71.

writers who have been fascinated especially by the new artistic theory of Schelling."⁶⁵ Actually the matter was entirely different. Pushkin's agreement to participate in the "Moscow Herald," as seen from his letter to Ugazemskin and Tumanskii, did not exclude completely his negative view of the ideas of this newspaper's managers. Pushkin declared, for example, in his letter to Delvig of March 2, 1827, that: "You blame me for the 'Moscow Herald,' and for German metaphysics. God sees how I hate and despise it; but what can I do? Hot-headed boys have gathered, they are straight; the priest or the Devil with them. I say: Gentlemen, do you want to take from the empty and pour into the more empty? All that is good for the Germans, who are already saturated with positive knowledge, but we . . . the 'Moscow Herald' people, sit in a hole and ask: What faith is that?"⁶⁶

Regarding the idealism of German Naturphilosophie, the foremost Russian thinkers opposed the materialistic understanding of natural conditions, including processes taking place in the human organism. Fighters for the materialistic ideology, in particular, came from the environment of the participants in the December uprising.

Among the Decembrist members of the Northern Society, more than others with similar materialistic and atheistic ideas, Ivan Dmitrievich Yakushkin was distinguished. He was the author of the well known "Memorandum" and a philosophical treatise hand-written in the 1830s in Yalutorovsk and kept in the archives of the Yakushkin family.⁶⁷

65. Cited in the book PUSHKIN IN THE MEMOIRS AND STORIES OF CONTEMPORARIES, Gospolitizdat (1936), Government-Literature Issue (1936), p. 462.

66. See B. Heilach, "Pushkin and Russian Romanticism," ISSUE OF THE ACADEMY OF SCIENCE USSR (1937), p. 177.

In this article there also were given evidences of the negative relation of Pushkin to German philosophy.

67. This treatise carries the title, "What Is Man?," published in the paper VOPROSY FILOSOFII (Questions of Philosophy) (1949, No. 3), pp. 291 - 298, again in

(... contd on next page)

"One of the most important and interesting manifestations in nature," Yakushkin wrote in the treatise, "is of course life phenomena in general' and the life phenomena of man in particular" (pp. 156 - 157). For the investigation of life phenomena, it is necessary to determine the features of similarity and variation between man and other living creatures. "What distinguishes man from other animals? The answer to this simple question can be heard from all sides. The child, learning a short catechism by heart, and even those who did not learn it and cannot read, know that man has a non-dying root which is not present in any other animal" (p. 154). "The legend or tradition from old times is deep," and ironical, in the words of Pushkin. Yakushkin concluded with a narrow statement based on religious dogma. In brief but meaningful words, he gave the history of philosophical views on the nature of man, starting with Descartes, who said that "not under force can medieval wisdom be washed off the face of the earth" (p. 154), and Kant, with his agnostic criticism of the human capacity for knowledge.

Yakushkin suggested that "if man is convinced that he constitutes only a link of an endless chain of creation . . . then it is not difficult to trace from all the manifestations of nature, by studying nature's manifestations and trying to determine their interrelationships, their relation to man and the relation of man to nature, and in this way to clarify what man is" (p. 156).

The way to a materialistic understanding of human nature and the relation of man to other animals Yakushkin saw in the features of development. He made an interesting excursion into embryology, demonstrating his diverse education.

All life (Yakushkin wrote of the chick) goes out from the egg . . . which itself is formed from a small

(Footnote No. 67, contd)

manuscript, with corrections of inaccuracies in the previous publication in the book SELECTED SOCIOLOGICAL AND PHILOSOPHICAL WORKS OF THE DECEMBRISTS, Vol. I, Gospolitizdat (1951), pp. 153 - 170. In this last edition is the article called "What Is Life?".

bladder included in the membranous sac of the hen's ovary When it reaches the size of the yolk . . . it (the bladder) destroys the membranes surrounding it in the ovary. At the same time the included animal or the primary bladder bursts, leaving on the surface of the yolk, under the membrane, its enveloping white speck or paunch, designating the place where the embryo begins its development. The egg, containing in itself the life conditions of the future chicken, can stay for some time unchanged; . . . for the development of life in the egg only warmth is necessary If you put the fertilized egg under a brood hen, or in a warm place, significant changes constantly take place. In the first day, in the middle of the elongated paunch, between both membranes of the yolk, a whitish streak is observed with thickenings at the ends and surrounded by a membranous fold This streak is the rudiment of the head, the spinal brain, from which develops all the brain and sensation apparatus On succeeding days the one-cavity heart appears separate from the brain apparatus. Soon the left auricle forms, after which the auricle is divided by a ring of membrane into two cavities. After three days, the right ventricle becomes clear, but the heart beats before its complete formation and contains at that time uncolored fluid. The red blood appears primarily in the vessels which form at a distance from the embryo in the membranes of the yolk; these vessels spread, become entangled, and push the blood to the heart. Soon after the appearance of the head and spinal brain, some pairs of spots appear close to it, representing the vertebrae After the appearance of the head, all the other external parts of the chicken gradually form. But that part of the abdomen which at the beginning is entirely opened, gradually shrinks, so that by the twentieth day it is absorbed by the remaining fluid and becomes entirely closed." (pp. 157 - 158)

"The development of the child takes place in a manner similar to, but not identical with, the development of the chick," Yakushkin added, giving the features of development in the human embryo. "And thus," he continued, "observations

on embryos obviously indicate that the initial formation of all animals takes place in general in the same order; but in this case each of them varies infinitely in the details and stages of his development. Each animal exists separately from all other animals yet represents a link of the unbroken chain of all creatures" (p. 160).

Yakushkin compared the regularity of development of the chick in its egg and the human fetus in the uterus, with the idea, which was circulating at the beginning of the nineteenth century, of the successive formation in man of features characteristic of lower animal forms. That the character of Yakushkin's argument had a historical and not a Naturphilosophical point of view is clear. He accepted the idea of recapitulation of the physical organization of thinking as a function of the brain, and talked about the gradual development of this function in animals. Affirmation of the gradual development of intellectual activities in the animal world, based on comparative embryology, led Yakushkin to the recognition of the primacy of matter over the soul, i.e. it revealed to him the basic scientific materialistic solution of the main question of philosophy. This ideology permeated his embryological ideas: to explain the phenomena of development he did not need the assistance of any special power or any unified world power, but would refer only to the material properties of the growing embryo and the effect of physical factors of the surrounding environment.

Evidence of the continuing struggle of the progressive (Ed.: materialistic, positivistic) ideology with idealism is found in a paper by that courageous nature investigator, the materialist Iustin Evdokimovich Diadkovskii (1784 - 1841).⁶⁸ Professor of Moscow University and the Moscow Medical-Surgical

68. The significance of the work of Diadkovskii for the history of Russian philosophy and science was elucidated recently in an interesting small monograph by S. P. Mikulinskii, "I. E. Diadkovskii (1748 - 1841): Ideology and Common Biological Views," Mosc. Obshch. Isp. Prir. (1951), 117 pp., and also in S. L. Sobol', "I. E. Diadkovskii—A Russian Materialist-Biologist at the Beginning of the 19th Century," TRUGY UN-TA IST. ESTESTV., v (1953), pp. 145 - 156.

Academy, I. E. Diadkovskii came from the national lower classes. He was born in the village Diakove of the Ryasanskii Province, into a poor family. In 1809 he finished the Ryasanskii Spiritual Course, where already at his young age he had shown an independence of thought. This apparently caused some worry to the priests giving the course. "In the course, Diadkovskii" succeeded, according to his biographer K. Lebedev, "in all the sciences, and showed a high level in his power of reasoning; frequently his teachers themselves suffered from his fascinating syllogisms."⁶⁹ In 1812 Diadkovskii completed with excellence the course at the Medical-Surgical Academy and, with the financial assistance of Professor E. O. Mukhin, remained in the Academy to prepare for scientific and teaching activities. After time spent as a physician volunteer in Moscow during the Napoleonic invasion, Diadkovskii returned to the Medical-Surgical Academy, where, as a result of opposition from the foreign professors, he did not at once receive the responsibility of teaching.

From 1814 Diadkovskii lectured for several years in the Academy's courses in botany and pharmacology, and later in general pathology, general and special therapy, and clinical therapy. As a naturalist, Diadkovskii was always interested in the common questions of natural science, considering them the basis of medicine. "His beloved interest," Lebedev wrote, "was the study of zoology, mineralogy, botany, and the collection of the natural products of all three kingdoms of nature, in particular the plant kingdom."⁷⁰ According to the same biographer, Diadkovskii was distinguished by an extraordinary memory, and as an adult he independently studied French, German, English, and Italian. Of the ancient languages, he knew Greek well, and especially Latin, which he could speak fluently.

In 1816, as a result of being involved in pharmacology and medication, J. E. Diadkovskii wrote his doctoral

69. "A Discussion on the Effect of Drugs on the Human Body, with a Biography of Professor Iustin Diadkovskii," by Doctor of Medicine Kosmoe Lebedev. Moscow, 1845. 48 pp.

70. Ibid., p. 3.

dissertation, "The Methods of Action of Drugs on the Human Body,"⁷¹ which after his death was translated into Russian by K. V. Lebedev.

This dissertation was considered an extraordinary contribution to the scientific literature of that time. Diadkovskii appeared as a fearless opponent of spreading idealistic ideas. He demolished the challenges by foreign authorities and successfully defended materialistic ideology, continuing the glorious traditions of Lomonosov and Radishchev.

The first section of Diadkovskii's dissertation, "General Understanding about Drugs and the Circumstances Promoting an Explanation of the Methods of Their Action on the Human Body," begins with a dialectic: "Nature did not create anything that is absolutely useful, absolutely harmful, or completely useless."⁷² Rather, drugs and poisons act, depending upon their nature, on the condition of the organism. At the end of the first section, Diadkovskii, having developed and illustrated this idea, lifted it to the level of a biological generalization. "There is nothing like the continuous tendency toward the destruction of the organism; however, in its recovery undoubtedly the useful becomes harmful, and the harmful becomes useful."⁷³

The second and most important section of the dissertation was entitled "Discussion of the Related Powers of Nature in General and the Life Powers in the Narrow Understanding of the Word." He started with opinions of nature-investigators, according to which there are two types of bodies in nature, living and non-living. The first, from this point of view, is characterized by the presence of individual life powers. Diadkovskii decisively confirmed that "the ideas about the differentiation of the bodies and their powers do not agree with their (the nature-investigators, confirming the existence

71. Diadkovskii, DISSERTATIO INAUGURALIS MEDICA DE MODO, QUO AGUNT MEDICAMENTA IN CORPUS HUMANUM. Moscow, 1816. 87 pp.

72. Russian translation edited by Lebedev, p. 159.

73. Ibid., p. 162.

of these differences) specific experiments, and in general with the proper method of decision and judgment about things."⁷

Diadkovskii based his objection on his opinion that living bodies could form from the non-living. In general, he objected to the terms "dead bodies" and "dead powers." The use of these terms could lead to the conclusion that "all these bodies are considered products from the beginning of the world and are considered to exist without activity. But daily experience shows that these bodies have appeared in more recent years. The dead bodies act like those which are called living and, like the latter, are subjected in their actions to laws."⁷⁵ Diadkovskii asked "how this dead nothing, this absolute nothing, could reactivate dead, inert bodies and prompt them to activity?"

Instead of fruitless argument about the life power, Diadkovskii suggested careful investigation of the conditions necessary for the creation, formation, and preservation of bodies. In characterizing the condition of life, Diadkovskii gave some postulates and a general conclusion which was considered a decisive confirmation of materialism. He wrote that:

All the mystery of the development and preservation of bodies is included in certain materials that combine in certain quantity and are present in a defined relationship to the chemical and mechanical powers of surrounding bodies. If that is the case, then it is clear that the primary source must include and explain all the phenomena of nature.⁷⁶ The primary source should not be considered a power or a particular beginning, which until now we

74. Ibid., p. 163.

75. Ibid., p. 164.

76. The translator Lebedev has inserted at this point an interlinear note relating the materialistic confirmation of Diadkovskii. To the phrase "all the phenomena of nature," Lebedev add "Apparently, materially, nature is also spiritually related to another, higher world." It is difficult to say whether that was a compromise to meet the requirements of censorship or "a correction" of the specific ideas of Lebedev.

could not research and which we can now reject as an entirely useless product of imagination, but only as a material which is a definite cause of these manifestations.⁷⁷

Formulating a materialistic ideology free from any compromises, Diadkovskii approached idealism in its several forms. He objected to Erasmus Darwin's animism and Schelling's philosophy of the general animation of nature, and to their dualism. Considering that his statement came at the time of the "Treaty of the Holy Alliance," his own words should be reproduced.

There is no . . . need to agree with Darwin⁷⁸ to animate matter with such a life spirit, or, following transcendental philosophy, to reanimate it with the idea of universal life, or to divide it into objective and subjective parts.⁷⁹ As matter (51) is, in our opinion, alive, matter contains in itself the beginning and the basis of all its actions; matter itself acquires the capability of all those actions which we observe in it, because it is not homogeneous but variable. And, particularly from this variation of its properties, we can explain the different manifestations of affinity and striving, the different types of hardness, viscosity, and heaviness of the material, and also the differences between the kingdoms of nature. These are the differences between individual classes, genera and species in relation to their method of birth or development, construction, conditions of life, properties, etc. We explain the main difference between individual organic bodies and their organs in relation to their structure and properties.⁸⁰

77. Lebedev ed., p. 176.

78. Present in the opinion of Erasmus Darwin.

79. Diadkovskii referred to Vellanskii's BIOLOGICAL INVESTIGATIONS OF NATURE IN ITS CREATING AND CREATED QUALITIES (1812). K. Lebedev omitted to mention that Diadkovskii's objection to the national Schellingians do not appear to be addressed to anybody in particular.

80. Lebedev ed., p. 176.

The third section of Diadkovskii's dissertation is called "On the Powers that Form and Activate the Human Body." Concluding the diversity of matter and its capability of combining into different bodies, Diadkovskii believed that nature could undoubtedly create the human organism by the same method as it did other bodies, by combination of materials.

In accordance with the level of materialism at that time, Diadkovskii related all life manifestations, including the development of the embryo, to chemical reactions, and he considered that conception, growth, retrospective development, and the final destruction of the organism correspond with the different stages of chemical processes, whose character changes at different stages of development. He illustrated this idea with the following statements:

We know that males and females join together and regenerate, forming a body (namely that of the embryo) with the capability of achieving entirely different combinations than those they could achieve separately. We can seek the reason for this change only in their reciprocal affinity. We know that a child has capabilities for combinations different from those of youth, and the adult has the capability for combinations different from those of old age. Nature itself prepares and at once provides substances for the nourishment of the body soon after conception, and after some months other substances are provided. In the uterus there are certain substances; outside there are others.⁸¹

At the end of the third section, when he had related all the life-activities of the organism and most all the opinions on this, he included some words about the spirit of man. Diadkovskii gave up the useless struggle to combine materialistic ideas with religious dogma. He concluded that "Because its (the spirit's) activities do not relate to our subject, I assume that it is not my problem to explain either that such spirit, by some means, is combined with or acts on the body,

81. Ibid., p. 180.

or the converse, how the body affects it."⁸² In concluding this section of his dissertation, Diadkovskii considered the different external forces affecting the human organism, especially the mechanical, chemical, thermal, and electrical influences. He concluded that "Continuous reciprocal influence of these powers in the human body, the influence of the external powers on the internal, and the internal powers on the external, constitute life. Without this reciprocal effect, it is impossible even to imagine the life of the human body."⁸³

In 1836 Diadkovskii published a manual of general therapy.⁸⁴ In the introduction, he established himself as a strong supporter of natural science, defending its progressiveness and independent character.

Russia has just recently stepped onto the route to enlightenment, moving by gigantic steps, quickly competing with other kingdoms which started far earlier Especially among teaching physicians, the Russians have achieved such progress that they are not only at the level of the people preceding them, but also have pushed ahead of some of them.⁸⁵

Diadkovskii reproached his contemporaries for an insufficiency of "that noble national pride, that high patriotic love, that alone can give life to the spirit of national

82. Ibid., p. 185. Lebedev gives an underlined note, the object of which is entirely obvious. The translator strove not to soften the impression of Diadkovskii's materialistic conclusions. Deciding not to introduce a distortion into the text of the dissertation itself, Lebedev translated, in a note, the words of Hufeland on the immortal soul, spirit, and understanding, which are not material, that the immortal soul is combined with the body and in particular with the brain, and so on.

83. Ibid., p. 186.

84. GENERAL THERAPY, Issued for Guiding the Audience, by the Ordinary Professor at the Imperial Moscow University and Moscow Department SPB of the Medical-Surgical Academy, Iustin Diadkovskii. Moscow, 1836. 121 pp.

85. Ibid., p. iii.

enterprise." He reproached them because they were "filled with some extraordinary spirit of cosmopolitanism suppressing competition in learning," because they are "indifferent to the progress of national education and, on the contrary . . . prejudiced in favor of all that is foreign."⁸⁶

About himself, Diadkovskii wrote that he was trained "from youth not to accept any mental attitude as truth unless I was convinced of its truth by its faithfulness and by its logical, moral, and physical usage."⁸⁷ He sought freedom from all predilections toward foreign teachings, which were so frequently logically ridiculous, morally deformed, and physically unsuitable for use. "For twenty years I have been proving that, with their present knowledge, Russian physicians have the capability of throwing off the yoke of foreign teachers and behaving independently."⁸⁸

In "General Therapy," Diadkovskii noted the bases of his theory ("physical," i.e. materialistic, studies) and the work of his students. From this humble information it is possible to conclude that Diadkovskii was not alone in his fight. His students continued to develop his ideas, though not always successfully. Diadkovskii paid great attention to his numerous listeners at the University and at the Medical-Surgical Academy; hence he was not driven away from teaching because of his progressive ideas. Two of his listeners later on became professors at Moscow University and played a great role in the development of progressive science in Russia. One was Professor of Physiology I. T. Glebov, under whom I. M. Sechenov

86. Ibid., pp. v - vi.

87. This aphorism of Diadkovskii, which was set by the translator and publisher Lebedev in the form of an epigraph to "Practical Medicine," displayed the direct influence of Lomonosov, who wrote, in "Notes on Physics and the Corpuscular Philosophy," the following: "I do not accept any fabrication or any hypothesis, however probable it may seem, without accurate evidence, subordinate to the rules, controlled by the arguments." (M. V. Lomonosov, WORKS, Vol. I (1950), publication of the Academy of Science USSR.)

88. Diadkovskii, GENERAL THERAPY, p. vi.

studied, and Professor of Zoology K. F. Rulé, a leading naturalist and one of Darwin's Russian predecessors.

Rulé frequently⁸⁹ opposed Schelling's Naturphilosophie, and never returned to the question of the correlation between experiment and theory in the study of nature; he decisively rejected empiricism as well as idealistic rationalism. "Natural history," wrote Rulé,⁹⁰

is the clean experimental science in which everything begins and ends with the experiment Observations and experiments are mute; they must be explained . . . if not, they will stay without use in science. In its turn each speculation should be checked and reflected by some fact What will result from such clean experimentation and clean speculation?— a clean paradox." (pp. 28 - 29)

The struggle between empirical (materialistic) ideology, whose supporters included Diadkovskii and his successors, and the speculative (idealistic) ideology of Naturphilosophie caused V. G. Belinskii and, almost simultaneously, Herten to resolve the issue of the significance of the true relationship of experiment and speculation in science. In 1844, Belinskii wrote the following:

All that he (Faust in the Epilogue of "Russian Nights") says about the predominance of experimental observations and analysis in the natural sciences is partly true. Nevertheless, it is impossible to agree that this could originate from moral corruption, from the fading life. It is possible instead to think that the general philosophical bases of natural science had not yet

89. For example, in the course GENERAL ZOOLOGY (lithographed edition, 1850; reissued in the book, K. F. RULÉ: SELECTED BIOLOGICAL WORKS, ed. with commentary by L. Sh. Dovitashoili and S. R. Mikulinskii. Published by the Academy of Science USSR, 1954).

90. K. F. Rulé, "Doubts in Zoology as Science," "Native Notes," Vol. XIX, Part II, pp. 1 - 13 (1841) (cited in K. F. RULÉ: SELECTED BIOLOGICAL WORKS, 1954).

arrived because of the deficiency of facts, which could be obtained only by experimental observations, and that this contemporary empiricism should with time prepare the philosophical development of the natural sciences.⁹¹

Hertzen subjected this collision of science with speculative philosophy to detailed and deep analysis in "Letters on the Study of Nature." He first of all noted the fruitlessness of empirical science, which when separated from philosophy is equal to the fruitlessness of idealistic philosophy itself. "Philosophy without the study of nature is impossible, as is the study of nature without philosophy," Hertzen wrote.⁹² In another place; "Without empiricism there is no science, but there is no science in one-sided empiricism. Experiment and speculation are two necessary, true, actual stages of one and the same knowledge If taken in opposition, they do not lead to anything, such as analysis without synthesis and synthesis without analysis."⁹³ And also; "Empiricism provided an open objection, and a loud one, against idealism. What idealism did was rejected by empiricism. It did not concede a step." Applicable to this phrase is another statement: "Is it necessary to repeat that empiricism was extremely ridiculous, that its uses in the 1840s was as ridiculous as the flights of idealism; one extreme created a similar extreme on the opposite side."⁹⁴

Hertzen showed that empirical investigations had accumulated numerous assorted facts:

So long as natural science . . . remains within the limits of empiricism . . . it becomes stronger,

91. Belinskii, COLLECTED WORKS (Kiev, 1911), Vol. III, p. 194.

92. A. I. Hertzen, "Letters on the Study of Nature. First Letter: Empiricism and Idealism" (1845), in COLLECTED WORKS in thirty volumes, Publication of Academy of Science USSR, Vol. III (1954), p. 93.

93. Ibid., p. 97.

94. Ibid., p. 120.

partially producing a common language, a systematic and necessary registry of the estate of science; this is material capable of subsequent development To remain within the limits of such empiricism in reality is difficult, almost impossible; for that, a great deal of temperance is necessary, a great deal of selflessness, the greatness of Cuvier or the stupidity of any dull-witted specialist.⁹⁵

There were two ways of searching for those common things which were so necessary for the intellectual nature-investigator, embodied, Herten saw, in the names of Schelling and Goethe.

Schelling's science . . . was not practical, not real nature; all this is more clearly seen from the fact that he was engaged with the advantages of Naturphilosophie and had never been involved in the actual study of any branch of the natural sciences. His erudition was great, and he knew the encyclopedia of natural knowledge. He was a genius amateur.

The naturalists, Schelling's successors, took the formal aspect of his studies They built from his ideas a strange metaphysical-sentimental structure they took two to three general formulas which were strong and abstract, and from them they drew all phenomena and all the universe Oken was above all of them, but it is impossible to separate him from them entirely. Oken was awkward and narrow and no less dogmatic than others. His wide and voluminous work included the mistaken idea that nature is a thought.⁹⁶

Goethe was immeasurably superior to Schelling. "He taught that the object, to the highest level, was practical; he went into detail, not losing sight of the totality He knew that without speciality general therapy would be rejected by idealism, that the specific was part of the study of nature also, that the reading of the sources was history. From that he suddenly revealed to the world an entirely new side of his

95. Ibid., pp. 101 - 102.

96. Ibid., pp. 115 - 116.

subject. Empiricists accepted all of Goethe's great thoughts and evaluated them." Herten noted the vertebral theory of the skull, the metamorphosis of all parts of the plant from the original organ—the leaves—and a number of Goethe's osteological discoveries.⁹⁷ Goethe, according to Herten, "was endowed to a high degree with the direct view of things; but he knew that, and he himself looked through everything; he was not a university professor or a department scientist; he was a thoughtful artist; he established, for the first time, the actual, true relationship of man to the world and his surroundings; by himself he gave the naturalists a great example."⁹⁸

However, Goethe did not establish a complete materialistic synthesis of philosophy and the empirical study of nature; moreover, this was not done, and could not be done, by the nature-philosophers. "Every success in the study of nature has been achieved outside Naturphilosophie."⁹⁹

In Russia, German Naturphilosophie does not appear to have had a marked effect on the development of the natural sciences.

Why, in the first half of the nineteenth century, K. A. Timiryasev asked, did

the waves of metaphysical speculation, barely touching German science, hardly coming into contact with our borders, not leave traces on our sciences? I assume that all of that was not accidental, that in the selection of their teachers, as well as worldwide brilliance and distinction of results, Russians had shown their natural tendency to go more willingly and successfully along the tracks of Newton, than along the route of Plato.¹⁰⁰

With these words K. A. Timiryasev underlines the materialistic tradition persisting in Russian science from the time of Lomonosov. The successful aspects of embryology in Russia were thus not connected with Naturphilosophie.

97. Ibid.

98. Ibid., p. 114.

99. Ibid., p. 118.

100. K(liment) A(rkad'evich) Timiriasev, "The Festival of Russian Science," ASSEMBLY, Vol. V (1939), p. 43.

CHAPTER 11

LOUIS TREDERN—THE FORGOTTEN EMBRYOLOGIST OF THE BEGINNING OF THE NINETEENTH CENTURY

Before going into the characteristics of this turning point in the history of embryology, which is known by Baer's classical investigations and Pander's earlier work, it is appropriate to review the dissertation of L. Tredern, published in 1808.

The personality of this embryologist, who so brilliantly began his investigative work and then unexpectedly disappeared from the scientific horizon, had long remained veiled. K. M. Baer, who was always actively interested in the history of science in Russia, and particularly in his homeland in the Prebaltic, took pains to clarify the conditions of Tredern's life and work; Baer published the results of his search in a special article.¹ In 1901 the late professor of Dorpat University, Ludwig Stieda, who is known for his review of Russian work in histology and embryology, printed the Latin text of Tredern's dissertation translated from the German. He prefaced this with an introductory article containing a biography of Tredern, which drew additional information, particularly from Baer's papers.² In 1927, M. M. Solovev gave

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1. K. E. v. Baer, "Biographische Nachrichten über den Embryologen Grafen Ludwig Sebastian Tredern," BULL. ACAD. SCI. ST. PETERSB., 19 (1874), pp. 67 - 76.
 2. L. Stieda, "Der Embryologen Graf von Tredern und seine Abhandlung über das Hühnerei," ANAT. HEFTE. BEIT. U. REFERATE Z. ANAT. U. ENTW., Part I, Bk. LVIII, Vol. XVIII (1901), pp. 1 - 69.

some new data about Tredern, contained in a letter from K. M. Baer to the famous Russian teacher I. F. Krusenshtern.³

In his article about Tredern, Baer mentioned how in 1817 he was engaged in comparative anatomy with Döllinger and assisted in the organization of Pander's embryological studies. On becoming acquainted with the dissertation of the Count Tredern, he was surprised by its thoroughness and accuracy in observations and drawings. Being interested in the personality of this investigator, Baer asked Döllinger about him and received the answer, "You know him; you know that he is also from Estonia." Slightly surprised that he did not know a fellow countryman, Baer decided that on returning home he would get information. However, in Estonia there was no trace of the Count Tredern. Doctor Vetersstrand, working on the "Biographical Dictionary of the Activities of Liflyandi, Estlyandi and Kurlyandi," could not tell anything about Tredern, and explained only that some years before, when the Russian fleet was stationed in Revel, a naval officer lived there who had on his ship a brood hen and diligently watched the growth of chickens. The people of Revel remembered this strange naval officer, but nobody could remember his name. This gave Baer his first clue. After that, the search for Tredern yielded no results. In Petersburg, Baer wrote on April 7 and June 24, 1836, two articles for the Prebaltic newspaper DAS INLAND,⁴ in which a short account of Tredern's dissertation was given and its significance noted. He expressed surprise that Count Tredern's family had disappeared in little Estonia without any trace, and that nobody could remember anything about them. In the first of these articles, Baer appealed to his fellow countrymen, especially

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3. M. M. Solovev, "Correspondence of the Academician K. M. Baer with Admiral I. F. Krusenshtern. First Collection of the Memoirs of Baer." Publications of the Academy of Science USSR, 1927. pp. 10 - 59.
 4. K. E. v. Baer, "Bitte um eine Nachricht über die Litteraturgeschichte unseres Vaterlandes, besonders an die jenigen Herren gerichtet, welche in den Jahren 1806 - 1808 in Jena oder Göttingen studiert haben," DAS INLAND. EINE WOCHENSCHRIFT FÜR LIV-, ESTH- UND KURLÄNDISCHE GESCHICHTE, GEOGRAPHIE, STATISTIK UND LITTERATUR (1836), No. 15, pp. 253 - 256. "Wegen des Grafen von Tredern zweite Aufforderung," ibid. (1836), No. 23, pp. 391 - 392.

to those who during 1806 to 1808 had studied in Jena and Göttingen, to ask whether they knew anything about Count Tredern. The information he received led, according to Baer, only along a false trail. In 1874, when Baer wrote his article on Tredern, he obviously forgot completely that in 1836, undoubtedly in answer to his call, he had received a letter from the notary Shtender from Libava with very useful information about Tredern. Enclosed in the letter was even an autograph of the mysterious embryologist. The contents of this letter are mentioned below.

Baer also called upon Admiral I. F. Krusenshtern for help, and in a letter of May 26, 1836, he requested his assistance. In this Baer mentioned, incorrectly, the later assumption that the senior Tredern had stayed in Revel with his ship. There his son was born, who considered Estonia his country. Because the young Tredern was later a Russian naval officer, it was natural to assume that he studied in the Petersburg Navy Corps.

"Would Your Excellency," wrote Baer to Krusenshtern, "with the advantage of your post, please search in the registers and archives of the Russian fleet 1) for an officer with the family name of Tredern who may have spent some time in Revel. 2) Did he father a son there and what was his name?" In an article on Tredern in 1874, Baer indicated: "in the files of the navy, which were reviewed according to my request, this given name was not known."

Continuing with the story of his search, Baer described how in 1839 or 1840 he got his first clue, when in the populous community of Petersburg he again asked if anybody knew Count Tredern, accidentally pronouncing this family name with the accent on the last syllable. One of the ladies present, daughter of the statistician, the academician Shtorkh, said that they knew Count Tredern in the house of the banker Ralle, whose widow lived at Vasilev Island, and even mentioned in what house. The widow Ralle was found, and she remembered well the father of the missing embryologist. He was a French emigré who was in Russia in Tsar Paul I's time, from whom, apparently, he had received the title of count. Later Baer corresponded with Gebenbaur and Katfazh and received from them some documentary data on Tredern.

On the basis of the available materials, biographical data about Tredern can be briefly stated as follows. The family of Tredernov, whose name indicates their Celtic origin, previously lived in Brest. The younger line of this family, to which the embryologist belonged, was named Tredern de Lézérec. The embryologist's father, Jean Louis Tredern de Lézérec, was a captain in the French fleet and a mathematician. On September 14, 1780, when Captain J. Tredern was inspector of the naval college in Brest, he became father of a son who received the name Louis Sebastien Marie. The elder Tredern participated in the War of the Vendée on the side of the mutineers and royalists, and after the defeat at the Quiberon peninsula in the summer of 1795 he emigrated to Russia with his son Louis Sebastien, who at this time was not yet fifteen years old. Nothing reliable is known about the years of education of the future embryologist in Petersburg. There is reason to assume that he studied in the Petersburg boarding school Abbot Nicollia, where his father apparently was teaching mathematics, and then went into the Navy. In any case, it is known that on October 4, 1797, Louis Sebastien Tredern enlisted as a naval cadet in the Russian fleet on the ship "Pimen," which was stationed for a long time in Revel. The young Tredern lived in Revel for four years, information on his presence there existed from individuals who knew him personally and who confirmed the fact that this young man, besides serving in the fleet, had studied and was occupied with investigations in natural history. Thus a certain person named Gamper, from whose father Tredern had hired a flat, stated that this remarkable sailor had turned his room into a true open-air cage for birds, which lived there on specially placed saplings. Another person living in Revel, a retired Russian general of Livron, said that he was a neighbor of Tredern's and frequently helped him to watch dogs, cats, rats, and other animals.

In the summer of 1801, warrant officer Louis Tredern resigned in order to accompany his ailing father abroad, and both of them left Russia in August. The father returned to France, where he died after some years, and the son involved himself with medicine and the natural sciences in Germany. It is not known in which university he studied. It is known only that in October 1804 Candidate of Science Count Sebastian Tredern was enrolled in Würzburg University. In

this period he worked with Döllinger, which Döllinger later reported to Baer. Having missed the opportunity of conducting an inquiry about Treder in Würzburg, Baer was uncertain about him, because fifty years later, at the moment when Baer was working on his article on Treder, there was no one still living who could remember him there.

In the introduction to his dissertation, Treder stated that in the summer of 1807 he was busy studying comparative anatomy (obviously, in Würzburg in Döllinger's laboratory), and in the autumn he travelled to Göttingen, where he consulted with Blumenbach about his embryological and comparative anatomical investigations.

Treder wrote further that he had, at the beginning, the intention to publish an extensive work on avian embryonic development, but he had heeded Blumenbach's advice and instead began writing a dissertation to obtain a doctoral degree, including in it only a small part of his data and prepared drawings. With Blumenbach's recommendations and assistance, Treder, in the winter of 1807 - 1808, studied embryology in Göttingen's rich library and at the same time continued his study of incubated eggs, overcoming the great difficulties of such wintertime study. In his dissertation, Treder mentions with gratitude the official prefect Tsakhar and his wife, who assisted him in getting the material for his investigations. Tsakhar's son had told Baer in 1865 that Treder, whom they thought Swedish, had passionately pursued the study of chick embryos, and frequently came to them at home with opened eggs and showed them the course of development of the chick. The famous zoologist K. Siebold wrote to Baer that in the winter of 1825 - 26, he heard in Göttingen Blumenbach's lecture favorably defending Treder's work and, with his characteristic humor, added that the Göttingen housewives were claiming that Treder was causing the price of eggs to rise.

In April 1808, Treder left for Jena, apparently with a prepared dissertation. It is not known if he associated with Oken there. At any rate, Oken, talking about Pander's dissertation, wrote that "Treder's dissertation . . . was accomplished in our laboratory," so "in our laboratory" could

mean only in Jena.⁵ But it is not evident, first, that Treder's dissertation was accomplished in Jena, and, second, that Oken had any connection to it. In 1808 Oken was not in a position to evaluate the significance of Treder's dissertation, so that even after ten years he could write about Pander's dissertation in statements indicating a complete misunderstanding of the subject. (52)

In the spring of 1808, Treder passed the examination *rigorosum* honorably, and, after defending his dissertation on April 4, he received the degree of Doctor of Medicine and Surgery. Treder thereupon returned to Göttingen, where he continued working intensively on the study of avian development. It was about that second period of Treder's life in Göttingen that the notary Shtender had the memories mentioned above. This letter, lost by Baer and recovered by Stieda, is interesting enough for us to extract detailed quotations.

Treder, my friend from student years, will always live in my memories. I cannot give a convincing answer to the question as to where he disappeared. In autumn, 1808, nearly within half a year after my arrival in Göttingen, Treder also was present.

He was a man of strong physique, 5 feet 3 inches tall, with dark hair, large whiskers, brown eyes, and a fairly large, slightly arched nose. He was, according to our judgment, about twenty-four years old.⁶ He had a quiet and at the same time an active character. He lived very economically, did not indulge in any vices, and constantly wore a suit of dark brown cloth, gray trousers, and a black cloth hat with a sharp, downward-hanging brim. He carried a brush like those carried by our military people thirty years ago. He was present only with small groups of people, especially with Blumenbach. He spent all of his time on the incubation of the eggs of different birds, mainly chickens, and in drawing the embryos from the beginning of incubation to the time the chick hatched from the

5. Oken, *ISIS*, No. 192 - 193 (1817), p. 1531.

6. In 1808 Treder was actually twenty-eight years old.

shell. However, he displayed an almost incredible endurance, was literally skin and bones because he forgot about eating, drinking, and sleeping, and was sustained only at the pipe which he rarely took from his mouth. For his observations he had some tin and clay containers fitted with a thermometer and usually heated by oil or alcohol lamps, or, rarely, with charcoal; the eggs were placed there in clean white sand. Because my presence did not interrupt him, I frequently visited him. We smoked and talked, and during this time he moved from one container to another carrying out drawings of the opened eggs. He was capable of doing that with thoroughness. Since the drawings and the features represented were similar from one egg to another, the speed and easiness with which he drew frequently left me in amazement.

Shtender enclosed with his letter a paper from an album which Treder had given him as a farewell gift, showing a view of Jena and the embryologist's autograph (Figure 17). On the above right was written: "Kennst du das Land, wo die Kartoffeln blühen? Lebe wohl und denke an mich. Dein Freund und Bruder S. G. Treder."⁷ On the left is the inscription "Memoria der Fuchse."⁸ Below the picture is the date: 17/3 1809 Göttingen. "A country where potatoes grow," in Treder's words, "by which you must mean Göttingen, where potatoes are extensively cultivated and where poor students feed mainly on them," giving it a humorous nickname pointing out their gastronomical predilection.

Where was Treder in the period from 1809, when he left Göttingen, to 1811, when he appeared in France? Again it is not known. In the summer of 1811 in Paris, Treder passed the government examinations, obtaining the right to practice medicine in France. He based his thesis on the subject of the organization of hospitals. After that, he joined the French fleet as a physician. He travelled to Guadaloupe, where he died unmarried. The date of his death is unknown.

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7. "Do you know the place where the potatoes grow? Live well and remember me. Your friend and brother S(ebastian) G(raf) Treder."
 8. "Memory of fuchse." "Fuchse" are incoming students, frequently subjected to the mocking of the members of the student corporations.

This quick and incomplete biographical account indicates a rich life. It draws a portrait of a man who was capable of untiring and selfless activity in his scientific interests, together with a tendency towards wandering. He was transferred as a child from Brittany to distant Petersburg. From there in his youth, with an already developed scientific interest, he travelled to Revel. As an adult he went to Germany where he moved from one university city to another: Würzburg, Göttingen, Jena, and again Göttingen. Later he was in Paris and, at the end, in Guadaloupe, on the shores of America. This biography could be material for an interesting story, but it does not give more than a picture of the life of a wonderful, independent investigator. Yet in 1836 Baer noted, in comparing Treder's life story with the fate of the mysterious foundling Kaspar Hauser, that his dissertation was as amazing as the author himself. "I would have doubted," wrote Baer, "the existence of this dissertation if it were not directly in front of me."

Treder's dissertation finds a place in the history of embryology in Russia, despite the fact that the author was not a Russian, was not born in Russia, and lived there only six years. There are two reasons for this. First, while living in Petersburg, Treder developed a deep interest in the problems of comparative anatomy, and especially embryology, which he worked on first at Revel, and then in Germany. It is hard to believe that there was a source for this interest other than the work of K. F. Wolff, who had died one year prior to Treder's arrival in Russia. Especially in Petersburg, Treder could have been acquainted with Wolff's classical work, which had elucidated the embryonic development of the chick intestines, and he might have found in this work the impulse for similar study.

The second reason for listing Treder among Russian embryologists is the fact that he considered himself as such. The title page of his dissertation clearly identifies the author as "L. S. Treder, Estonia—Rossus." After losing his motherland, Treder obviously considered Russia his country, the place where he successfully started his investigations. It is highly probable that his designation of national affiliation in the dissertation implied an intention to return to Russia. It has been explained why this intention was not accomplished.

The aim of Tredern's dissertation was to tell the preliminary story of the avian egg and its hatching. He submitted his dissertation for open public discussion by scientists on April 4, 1808.⁹ The introduction contained an important statement specifying the extensive material to which the author had referred, presented in several divisions. These divisions are:

I. NATURAL HISTORY OF THE EGG. Color, form, size, weight, and taste of the egg, properties of the shell, the behavior of birds during incubation and its duration, the number of eggs, and so on.

II. ABNORMALITIES OF EGGS (deviations from normal structure). Information was included about eggs becoming luminous in the dark, about eggs turning into glass and amber, and even about cocks laying eggs. The last case, obviously, deal with hens displaying feathers like those of cocks, or having voices like those of cocks, features which are not rare, but which promote superstition.

III. CHEMISTRY OF EGGS. This division included investigations about the effect of different reagents and physical agents (temperature and humidity) on individual constituents of the egg.

IV. INCUBATION OF THE EGG. Tredern wrote that he had carefully investigated eggs from the first hours of incubation, from the appearance of a recognizable embryo to the hatching of the chick, partly with the naked eye, partly with the aid of a lens, accompanied by descriptive, life-size drawings. In this section he reported changes in the egg membranes, including the amnion and chorion, during the whole period of incubation, the changes in the yolk and the egg white, and also in the amniotic fluid and the blood-carrying vessels (obviously those

9. Tredern, DISSERTATIO INAUGURALIS MEDICA SISTENS OVI AVIUM HISTORIAE ET INCUBATIONIS PRODROMUM, QUAM PRO GRADU DOCTORIS SUMMISQUE IN MEDICINA ET CHIRURGIA HONORIBUS, PRIVILEGIIS AC IMMUNITATIBUS RITE CAPESSENDIS, A.D. IV Aprilis MDCCCVIII publico eruditorum examini subjecit Ludovicus Sebast. Comes ab Tredern, Estonia—Rossus, Jena.

outside the embryo). There is also an explanation of fetal development; hence the changes of the individual organ systems were followed. The dissertation mentioned that many systems of the growing embryo had not been investigated by previous authors, especially the muscular, circulatory, and nervous systems. On the development of the skeleton, there was an earlier book by Haller. With regard to the internal organs, Tredern noted that many authors had thoroughly studied heart development; other organs were investigated with more or less detail, but he found no data about some, such as the fibrous sac, uropygial glands, and the pancreas. Tredern sought to correct mistakes and to fill gaps in his predecessors' investigations. He modestly observed that his beginning should receive support through verification by other scientists.

V. THE CHICKEN AFTER HATCHING FROM THE EGG. Here he mentioned only a few areas subjected to study, such as the disappearance of the yolk and the yolk duct.

VI. This division was entitled "Notes about Books," and was composed of explanatory notes on the list of works on embryology and related questions in the Göttingen library.

The above list of problems represented such an extensive plan of work that, according to Baer, no individual could have accomplished it without achieving immortality. "This report," Baer continued,

occupies four pages (of sixteen), and inevitably the suspicion creeps in that the author gave only the list of what he planned to investigate. But later he provided accurate descriptions and defined observations with abundant references to his predecessors, indicating that the author knew the literature of his subject completely. The references include K. F. Wolff's work on the intestines, which almost nobody had known until Meckel made his well-known German translation in 1812. The same observations in Tredern's dissertation are stated very briefly and accurately, which requires us to acknowledge the author's unquestionable talent in minute anatomical investigations. An outstanding feature is a table engraved on brass (Figure 18). It is very simple, almost just outlines, but in accuracy and richness of detail it surpasses the brevity of the

text. I could have characterized the table best by saying that with the exception of the earliest period of life of the embryo, which was not presented there, the table was richer in its content than all that was published earlier concerning this question. The later series of engravings by the Englishman Ham do not give one-fourth the clarity presented by this outlined drawing. It is as if the author wanted to be provocative, using line drawings and leaving to posterity the question of who he was and where he had gone. It is necessary to remember that he wrote in 1808, for four years after which not a single significant work on the development of the chicken appeared. He was considered the principal founder of a new series of investigations. Being the first in this respect, he had no guide, because there were none who could have assumed this leadership.¹⁰

It will be useful to give a brief statement of those sections of the dissertation in which are described those more or less complete observations and the wonderfully specific drawings. These observations concern the paunch (cicatrice), the albumin ligaments, the development of the jaws and beak with its hillock, the yolk-intestinal duct, the digestive tract, and the extremities. Below are given Tredern's data, references, and comments in the form of notes at the end of the book.

THE PAUNCH, OR CICATRICE, was called by the old embryologists the cock's trace or cover. It later received the name embryonic layer or embryonic disk. Tredern only mentioned that he could observe this formation on the surface of the egg yolk while they were still in the ovary, something that none of his predecessors had succeeded in doing (Figure 18, 1).

10. The stated opinion of Baer was taken from two of his articles about Tredern, in DAS INLAND (April 7, 1836) and in BULL. ACAD. SCI. ST. PETERSBURG, 19 (1874).

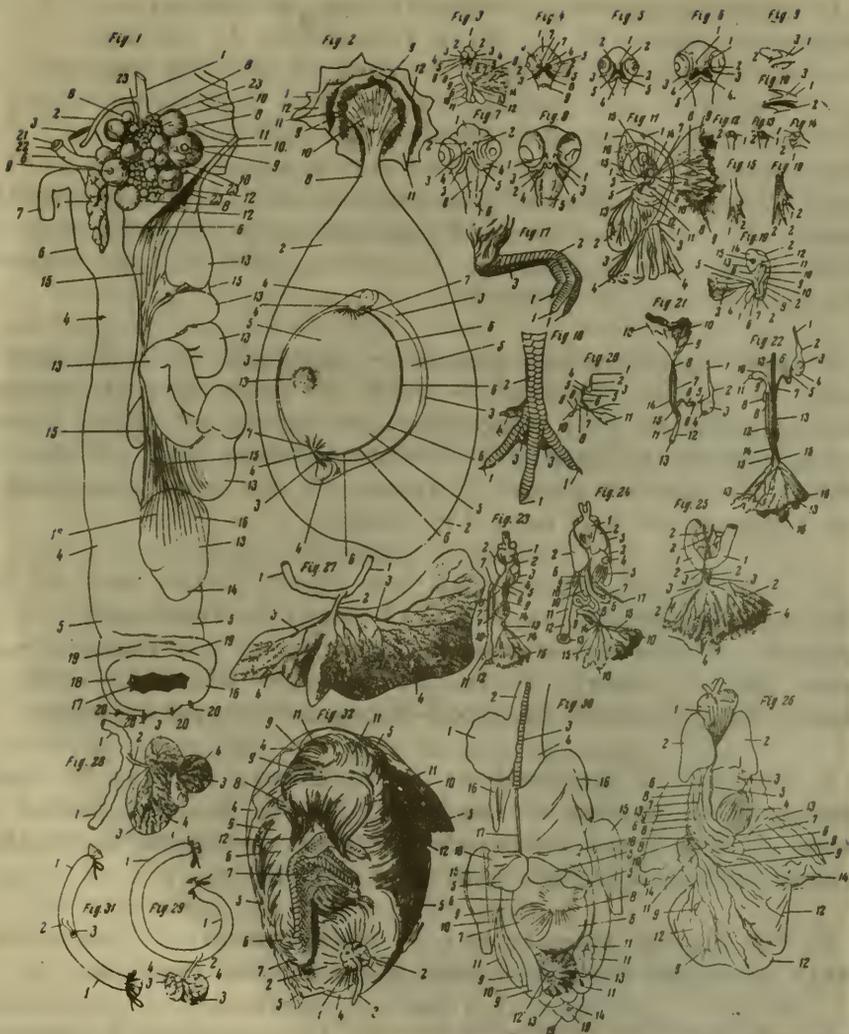


Figure 18. Table of illustrations from Tredern's DISSERTATIO . . . OVI AVIUM HISTORIAE ET INCUBATIONIS PRODROMUM.

Figure 18. Table of illustrations from Treder's DISSERTATIO
. . . OVI AVIUM HISTORIAE ET INCUBATIONIS
PRODROMUM. .

Key:

Fig. 1. Internal parts of domestic hen: 1- aorta; 2- mesenteric vessels; 3- large intestine; 4- rectum; 5- cloaca; 6- caccum; 7- fat; 8- yolk of the egg in the ovary; 9- groove; 10- vessels of the yolk membrane; 11- attachments of round ligament; 12- infundibulum; 13- curvature of the uterus; 14- cervix of uterus; 15- peritoneal ligament of the uterus; 16- stretched uterine ligament; 17- anal opening; 18 and 19- its external and internal pulp; 20- feathers; 21- faeces; 22- villous membrane of the intestines; 23- bowl;

Fig. 2. egg, opened under water: 1- shell; 2- second white; 3- third white; 4- chalaza; 5- yolk; 6- belt of yolk membrane; 7- corrugations of yolk membranes; 8- cervic of white ligament; 9- stretched white ligament; 10- transparent part of the ligament; 11- second proper ligament of the egg; 12- first proper ligament of the egg; 13- groove;

Fig. 3. view of the embryo from the front. Third hour of the 4th day of incubation: 1- brain; 2- eye; 3- forehead; 4- rudiment of the upper jaw; 5- opening of the beak; 6- upper jaw; 7- heart; 8- vertebrates; 9- wing; 10- legs; 11- tail; 12- chorion; 13- yolk duct; 14- vascular zone;

Fig. 4. 6th day of incubation: 1- forehead; 2- eye; 3- opening of the beak; 4- dorsum of the beak; 5- its lateral parts; 6- basis of the upper parts of the beak; 7- fissures of the future nostrils; 8- upper jaw; 9- trachea;

Fig. 5. 8th day of incubation: 1- beak dorsum; 2- nostrils; 3- basis of upper jaw; 4- lower jaw; 5- beak opening;

Fig. 6. twelfth hour of the 9th day: 1- nostrils; 2- node on beak dorsum; 3- lateral parts of the upper jaw; 4- opening of the beak; 5- lower jaw;

Fig. 7. 1- forehead; 2- nostrils; 3- node of the beak; 4- lateral parts of the beak; 5- lower jaw; 6- trachea, visible through tectum;

Fig. 8. 13th day: 1- nostrils; 2- beak node; 3- parts of the upper jaw; 4- lower jaw; 5- trachea;

Fig. 9. 16th day; cartilaginous capsule of the beak from the side: 1- beak node; 2- nostrils; 3- upper capsule;

Fig. 10. 19th day: 1 and 3- as in Fig. 9; 2- lower part of the lower jaw;

Fig. 11. domestic goose, 8th day of incubation: 1- amnion with corrugations, caused by the effect of water; 2- chorion; 3- place of union of proper membrane of yolk with chorion and amnion; 4- cut membrane of yolk; 5- opening of amnion, or navel; 6- small intestine; 7- yolk duct; 8- vascular zone; 9- its lateral parts; 10- left leg; 11- rudiments of fingers; 12- uropiges; 13- tail; 14- heart; 15- forehead; 16- brain with vessels; 17- eye;

Figs. 12-15. 8th, 10th, 11th and 12th day: 1- fingers; 2- membrane;

Fig. 16. 1- swimming membrane; 2- claws;

Fig. 17. 17th day: 1- claws; 2- elongated scales; 3- wart-shaped scales;

Fig. 18. 21st day: 1- claws; 2- elongated scales; 3- remnants of swimming membrane; 4- wart-shaped scales;

Fig. 19. sixth hour of the 4th day: 1- chorion; 2- amnion; 3- vascular zone; 4- yolk membrane; 5- intestines; 6- navel; 7- tail; 8- leg; 9- wing; 10- aorta; 11- heart; 12- lower jaw; 13- forehead; 14- brain; 15- eye;

Fig. 20. 6th day: 1- oesophagus; 2- craw; 3- stomach; 4- duodenum; 5- pancreas; 6- small intestines; 7- yolk-intestinal duct; 8- rudiment of caecum; 2- rectum; 10- cloaca; 11- vascular zone;

Fig. 21. 9th day: 1- oesophagus; 2- craw; 3- tendinous part of the stomach; 4- muscular part of the stomach; 5- duodenum; 6- pancreas; 7- small intestines; 8- yolk duct; 9- vascular zone; 10- yellow vessels; 11- rectum; 12- cloaca; 13- anal opening; 14- large intestines; 15- caecum;

Fig. 22. 1- oesophagus; 2- craw; 3- tendinous part of the stomach; 4- muscular part of the stomach; 5- duodenum; 6- pancreas; 7- small intestine; 8- caecum; 9- rectum; 10- cloaca; 11- anal opening; 12- large intestine; 13- vessels of the yolk; 14- yolk duct; 15- its infundibulum; 16- yellow vessels;

Fig. 23. 12th day: 1- heart with pericardium; 2- liver; 3- tendinous part of the stomach; 4- muscular part of the stomach; 5- duodenum; 6- pancreas; 7- caecum; 8- large intestine; 9- small intestine; 10- rectum; 11- cloaca; 12- anal opening; 13- yolk duct; 14- yolk vessels; 15- yellow vessels;

Fig. 24. 16th day: 1- heart with pericardium; 2- liver; 3- craw; 4- tendinous part of the stomach; 5- muscular part of the stomach; 6- duodenum; 7- pancreas; 8- small intestine; 9- large intestine; 10- caecum; 11- rectum; 12- cloaca; 13- anal opening; 14- yolk duct; 15- yolk vessels; 16- yellow vessels; 17- chorion vessels;

Fig. 25. the twelfth hour of the 18th day: 1- intestines; 2- yolk vessels; 3- yolk duct; 4- yellow vessels;

Fig. 26. 18th day: 1- heart; 2- liver; 3- tendinous part of the stomach; 4- muscular part of the stomach; 5- chorion vessels; 6- duodenum; 7- pancreas; 8- small intestine; 9- yolk vessels; 10- yolk-intestinal duct; 11- yolk duct; 12- yolk membrane; 13- cut amnion; 14- cut navel;

Fig. 27. 28 hours after hatching: 1- intestines; 2- yolk-intestinal membranes; 3- yolk vessels; 4- yellow vessels;

Fig. 28. 1- intestines; 2- yolk-intestinal duct; 3- yolk vessels; 4- yellow vessels;

Fig. 29. 4th day after hatching; the same legends;

Fig. 30. 4th day after hatching: 1- craw; 2- oesophagus; 3- trachea; 4- neck; 5- lever; 6- stomach; 7- muscular part of the stomach; 8- tendinous part of the stomach; 9- duodenum; 10- pancreas; 11- small intestine; 12- remnants of the navel;

13- yolk; 14- anal opening; 15- thigh (femur); 16- wing;
17- sternum; 18- remnants of cut abdominal muscles;
19- feathers;

Fig. 31. 16th day after hatching: 1- intestines; 2- yolk-
intestinal duct; 3- remnants of the yolk;

Fig. 32. 20th day of incubation: 1- navel; 2- corrugations of
covers around navel; 3- umbilical vessels; 4- shell;
5- chorion; 6- right femur; 7- right leg; 8- beak; 9- basis
of wing; 10- wing; 11- neck; 12- head.

THE ALBUMIN LIGAMENT (*Ligamentum albuminis*) is the structure located, so Tredern thought, on the border between the external fluid and the internal thick egg albumin. These two layers of egg albumin Tredern called the primary and secondary egg albumin respectively (*Albumen primum* and *Albumen secundum*). In detail he described the different parts of this ligament and its relation to water and acid; in short, he did not doubt its constant existence. Later, however, Baer showed that the structure did not represent an independent membrane or ligament, but only the surface layer of the second (middle) layer of the albumin which was connected with the first (external) layer at the pointed end of the egg. This membrane, according to Baer,¹¹ appeared only in an egg opened in water. Upon removal of the membrane formed in water, it developed again. Baer agreed with Purkinje, who considered the reproduction of the membrane as evidence that it was not a constant structure but only a result of water acting upon the surface of the thick albumin.

DEVELOPMENT OF THE JAWS AND BEAK. Some earlier authors had noted the presence of the beak at about the fifth day of incubation (Haller, Wolff, Malpighi) (53) and some had related its appearance to different periods of embryonic life (Koiter, Vesling, Stenon, Lengli, and Shrader) (54). Tredern concluded that on the fifth day (rarely, on the fourth day) it was possible to see the first beginnings of the beak. Occasionally the lower jaws appeared earlier than the fourth day, when along the sides of the neck two branches appeared. The upper jaw is usually seen somewhat earlier than the lower, but its halves remain disconnected longer. The central growths of the upper jaws from the forehead have at first the shape of a cluster (Figure 18, 36, 46). They are separated from smaller blunt growths by two slits (Figure 18, 4), which later are converted into the nostrils. These blunt growths later (at the fifth day) join with the side parts of the upper jaw (Figure 18, 36, 45). The forehead cluster gradually forms the back of the upper jaw (55) (Figure 18, 44, 51). On the seventh or eighth day the beak starts to be covered with a cartilaginous case, which is almost always more constructed in the upper jaw than in the lower (56). This cartilaginous capsule gets its beginning from one small

11. Baer, *UBER ENTWICKLUNGSGESCHICHTE*, Vol. 2 (1953), p. 22.

white spot, which later is converted into the top of the beak. Simultaneously with the conversion of the beak into a cartilaginous mass, an elevated white spot appears on it (57), having a top which on the tenth day is the size of a small pinhead. On the eighteenth day the top of this elevation has the shape of a spike, which the chick uses at the time of hatching to break the membranes and perforate the shell. Within one to two days after hatching, the prominence on the beak falls off; however, its remnants can be seen for some time.

INTESTINAL YOLK DUCT. This formation Treder called the stem or the apophysis. According to his data, the intestinal yolk duct is formed on the fourth day of incubation, after the closing of the intestinal canal, as a delicate extension as of a narrow gut through the opening to the abdominal cavity (58) (Figure 18, 19(5)). Later, the length of the duct increases, and apparently it is composed of a membrane and a gut. The connection between the yolk and the intestine through this duct shows that it is possible to blow into the intestine from within the yolk sac. Because this is not always possible, some authors doubted the existence of an opening in the yolk intestinal duct (59). However, other investigators, for example Vicq d'Azyr and Blumenbach, regarded this experiment as successful. The remains of the yolk intestinal duct are seen after hatching in the form of a narrow mesentery (Figure 18, 27(2)). The remains of the mesentery can be observed up to the seventeenth day after hatching, and in some birds, especially swimming birds, throughout its life (Figure 18, 31(2)).

INTESTINAL CANAL. Treder considered the digestive canal only from the stomach to the anus, and he described its changes during incubation. On the fourth day it is possible to see the intestinal canal with a lens (60). In this period it has an equal diameter throughout its extension. Treder noted the great accuracy of Wolff's work in the NEW COMMENTARY OF THE PETERSBURG ACADEMY OF SCIENCE, especially in his third section. Because Wolff had studied intestinal development under a microscope, and not with a lens as Treder did, the latter did not consider that he could add anything to Wolff's description.

Referring to Wolff's work, Trederen said that the intestine is formed of the mesentery (61). On the sixth day, part of the intestinal canal forms something like a loop (Figure 18, 20(5)), which is designated as the blind intestine (Figure 18, 20(8)). When other parts of the digestive tract are already distinguishable to the naked eye, this loop thrusts out a little bit from the abdominal cavity (Figure 18, 21(7)). It is more clearly seen on the eleventh day, when the size of the intestines increases (62) (Figure 18, 22(12)). From the sixteenth day the loop starts to extend into the abdominal cavity, and this process ends by the nineteenth day. During this time all parts of the digestive canal acquire a defined shape.

This section of the dissertation ends with observations characteristic of the entire work.

EXTREMITIES OF THE WINGS AND LEGS. Trederen began by giving credit to Wolff, who had given the first and undoubtedly the best description of the early stages of development of the extremities. Trederen indicated that his own data were only a confirmation of Wolff's. Noting the different opinions of different authors concerning the time of appearance of the extremities (63), Trederen gave the following description of their development. On the second and third days in that place where the extremities appear, cellular material accumulates. By the end of the second or the beginning of the third day, suddenly and perfectly distinctly, the foundation of the extremities appears, so that on the fourth day they have the shape of sacs (Figure 18, 3(9 - 10)) as though filled with a transparent material, in which no structure can be seen. On the fifth day, the central part of this foundation becomes whitish and much wider than before; there is a white cartilaginous material which is divided in separate parts. From the sixth day it is possible to see fingers, composed of this same transparent material, which cover the extremity in the form of a glove (Figure 18, 11(10 - 11)) (64). A drawing illustrates the fingers of a goose embryo at the eighth day of incubation. In the chick embryo at the eighth day, the joints appear distinctly. On the tenth or eleventh day, the transparent material covering the fingers starts to move toward their tips, and something like the swimming web is formed, which on the twelfth and

thirteenth days grows longer as the fingers grow. (Figure 18, 14 - 16). The remains of this web then shortens (Figure 18, 18). At this same time appear rudiments of the scales which will later cover the legs; the scales at the beginning are completely transparent. On the seventeenth day all the scales are finally formed, but so thinly that one can see all the vessels (Figure 18, 17) through them. The posterior surface of the fingers is not covered by scales, but by something of a horny wart (Figure 18, 12(3), 18(4)). The claws are first apparent as of the eleventh or twelfth day. In this period they are straight and soft (Figure 18, 16(2)); later they gradually become curved, and on the sixteenth day they acquire their final form (Figure 18, 13). Only later do they enlarge and get harder (Figure 18, 18(1)).

In this section, Tredern suggested new facts and significant corrections to the descriptions given by previous embryologists. Tredern's poor optical facilities (he frequently points out that he made observations with his naked eye or with a lens) did not allow him to investigate the early stages of development or the more delicate structure of embryonic parts. In this respect he could not go beyond Wolff, whose name Tredern always mentioned with deep respect. Generally it is thought that Wolff's outstanding work on intestinal development was overlooked by his contemporaries and only rediscovered by Meckel. Even Baer, who knew Tredern's dissertation well, argued so. But it must be acknowledged that Tredern and not Meckel was the first to give credit to the classical work of that Russian academician. Tredern also considered mainly the later stages of chick development which had not been investigated prior to him. These related to the fate of the yolk intestinal duct, the development of the facial parts of the skull and beak, and the development of the extremities. Baer rightly noted that Tredern's observations were repeated by other embryologists many years later.

Against the background of neglect for Tredern's work, his strict and serious study of the facts was readily overwhelmed by the attractive but unsubstantial fantasy of Naturphilosophie. Not without reason did the young Baer, feeling a decided hostility towards the influence of Naturphilosophie, become immediately fascinated by the small notebook of the unknown embryologist .

All knew and honored the great Baer; many remembered his fellow and direct predecessor, H. C. Pander. It is important to remember the name of that first embryologist of the nineteenth century, L. Treder, who links Wolff and Baer in the history of Russian and world embryology. As the work of Wolff was apparently a model for Treder and a stimulus to his continuation of research from the point at which Wolff had stopped, so Treder's humble work played a similar role as stimulus and model for Baer, though Baer surpassed that model significantly.

CHAPTER 12

THE STUDY OF THE EMBRYONIC MEMBRANES OF MAMMALS: THE INVESTIGATIONS OF LUDWIG HEINRICH BOJANUS

Wolff frequently mentioned but did not give a comprehensive description of the embryonic membranes and organs. Later authors tried to explain the nature and reciprocal situation of the mammalian embryonic membrane and embryonic organs—Meckel, Cuvier, Dutrochet, Oken, Emmert, and others. The most significant attempts were undoubtedly, however, those investigations accomplished at the beginning of the nineteenth century in Russia, at Vilna University by Professor of Veterinary and Comparative Anatomy Ludwig Bojanus.¹

Ludwig Bojanus (1776 - 1827), born in Elzas, accepted in 1806 an offer to occupy the department in Vilna, where he spent the last twenty years and more of his life. Bojanus was a brilliant, talented lecturer and investigator. Besides his work in veterinary science, Bojanus published a number of reports on the comparative anatomy of molluscs, annulated (annelida) and flat worms, fish, reptiles,² and mammals, and also investigations of vertebrate embryology. In his special

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1. Biographical data concerning Bojanus is contained in Raikov, RUSSIAN BIOLOGISTS AND EVOLUTIONISTS BEFORE DARWIN (1952), which gives the most complete bibliography of his works.
 2. From the anatomical work of Bojanus. His work "Anatomy of the European Tortoise" (ANATOME TESTUDINIS EUROPAEA, Vilnae, 1819 - 1821) is especially significant. The more detailed descriptions of the structure of EMYS ORBICULARIS are furnished with wonderful drawings by the author. This work received the enthusiastic opinion of Cuvier and Oken.

work, his capability as an extraordinarily thorough investigator and acute observer is recognized. He also undertook more theoretical investigations, as seen in articles on the vertebral origin of the skull and in his academic lectures, particularly in his introduction to comparative anatomy. In this last work, he discussed ideas on the reciprocal relationship of organisms. This gave B. E. Raikov the basis for including Bojanus in the list of Russian evolutionists and forerunners of Darwin. (65)

Bojanus' embryological work considered the embryonic membranes and embryonic organs of the vertebrate animals, mainly mammals. His first work, accomplished in 1813 and published in 1815,³ was entitled "On the Fetal Membranes of Dogs, Mainly concerning the Allantoic Membrane." The author sought to address the unclear question of whether the amnion was surrounded from all sides by the allantois. He effected detailed and accurate description of canine fetal membranes by applying a method of opening which guaranteed the membranes' completeness and retained their normal location.

According to Bojanus, the fetus extracted from the uterus with its membranes has a cylindrical shape and is covered on all sides by the chorion. In the middle, above the surface of the chorion, a dominant zone of thicker fibrous vascular tissue is limited by a fold-like border. This zone, which is near the internal surface of the uterus, is in contact with the maternal placenta. If an opening is carefully cut in the chorion, the fetal fluid does not escape, and consequently its receptacle remains intact.

3. L. Bojanus, "De foetus canini velamentis imprimis de ipsius membrana allantoide," MEM. ACAD. SCI. ST. PETERSB., 5 (1815), p. 3021. This work was later published in German (with indication to the original place of publication) in the journal edited by L. Oken. At the beginning, in the form of a short abstract, was a review of a number of comparative anatomical works. "Verzeichnis meiner Arbeiten in der vergleichenden Anatomie," ISIS, 7 (1817), pp. 876 - 884, attached to the article, L. Bojanus, "Anatomie des Blutegels," *ibid.*, pp. 874 - 876, and then in detail: L. Bojanus, "Abhandlungen über die Hüllen des Hundefoetus, insbesondere über dessen Allantoides," *ibid.*, 10 (1818), pp. 1616 - 1623.



Ludwig Heinrich Bojanus

Bojanus opened only the external membrane of the chorion, and hence he was able to see the actual location of the embryonic membranes and organs. His predecessors had not taken the necessary precautions and had come to a number of incorrect conclusions, in particular to the determination that the umbilical sac is located inside the allantois. Bojanus accurately determined the shape and topography of the umbilical vesicle (tunica erythroides, vesicula umbilicalis). The latter has the shape of a folded, reddish (due to a great number of vessels), thin stem which extends from the umbilical cord and is stretched between the main vessel stems which connect the umbilical cord with the belt of placenta. The umbilical vesicle spreads along the fetus to the end of the fetal sac, where it is joined with chorion (and not with the amnion, as was thought by Needham and Oken). Daubenton likewise did not understand the nature of this formation and wrongly considered it to be the allantois, which is not surprising because he did not find any connection with the urinary bladder. Besides the umbilical vesicle, at this stage the allantoic canal appears, though its detection is not easy.

In order to reach the allantois and the amnion, it is necessary to open the internal membrane of the chorion with its thin blood vessels. With careful preparation, the removal of this membrane does not lead to the pouring off of the fetal fluid. Such a careful opening of the internal membrane of the chorion is difficult to accomplish, however, because the deep membranes are firmly attached with it and are very thin.

Successful opening allowed Bojanus to correct the prevailing wrong belief in that time, that the amnion and the embryo are located in the allantoic cavity and swim in the fluid filling it. The displacement of the fetus in the amnion by pressing on it from the outside and by blowing the allantois with air after releasing its fluid through a small cut, allowed Bojanus to determine that the amnion is not surrounded on all sides with the allantois. Instead, the latter forms around the fetus which lies in the amnion.

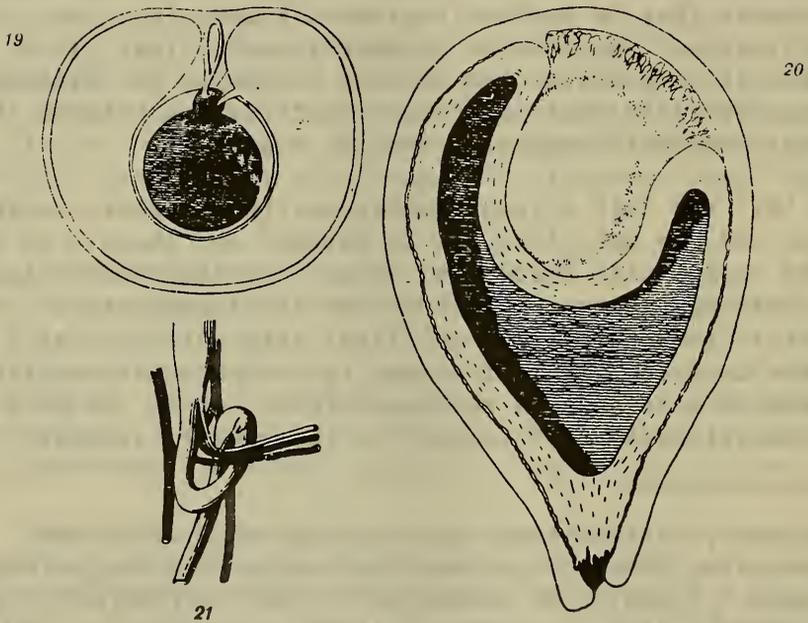
The results of Bojanus' investigations are summarized in the following manner. The fetus of the dog has four membranes: the amnion, allantois, umbilical sac and chorion. The amnion lies not in the cavity of the allantois, but near the sac formed by it; the amnion is surrounded by the allantois

except for a small part. The allantois is provided with a canal which goes to the urinary bladder of the embryo. The umbilical sac lies outside the allantoic cavity; it is not joined with the allantois; its stem is connected with the umbilical cord; and both the free ends of the sac are connected with the chorion. The chorion forms a closed cavity around all the other parts and is composed of two layers, of which the thicker external one is enveloped by the placenta as a belt and is connected with the uterine wall. The internal layer covers the allantois, and the amnion is covered with the allantois. Figure 19 shows the transverse section through the fetus. The scheme shows the topographic relationship of the fetal membranes and their cavities. In explaining the drawing, Bojanus wrote that he omitted the blood vessels and the internal layer of the chorion to make it more clear. It is not difficult to realize that Bojanus succeeded in delineating very accurately the most important relationships between the individual embryonic membranes and the organs.

In 1817 and 1818 Bojanus published three reports on the allantois and the umbilical sac in horses⁴ and sheep.⁵ In the first, he argued with Dutrochet, whose investigations Bojanus saw as creating greater confusion than they eliminated. Dutrochet indicated that the umbilical sac, with the fetus and the amnion covering it, is included in the allantoic cavity. He considered also that in the human fetus, as in the mare fetus, the allantois fits closely to the entire internal

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4. L. Bojanus, "Allantoides und vesicula umbilicalis des Pferdefoetus. Bemerkungen aus dem Gebiete der vergleichenden Anatomie," *RUSSISCHE SAMMLUNGEN FÜR NATURWISS. U. HEILKUNST*, Riga u. Leipz., 2 (1817); reprinted in *ISIS* (1818), pp. 1426 - 1427. L. Bojanus, "Über die Darmblase des Pferdefoetus," *ISIS* (1818), pp. 1633 - 1636. In this last work a teaching scheme is included for the reciprocal relationship of the embryonic membranes and organs, similar to that given above for the dog embryo.
 5. L. Bojanus, "Über die Darmblase des Schaafsfoetus, zum Beweise, dass die vesicula umbilicalis mit dem Darm unmittelbar zusammenhängt," *ISIS* (1818), pp. 1623 - 1633; also in Meckel's *ARCH. ANAT. PHYSIOL.* (1818).

surface of the chorion. Bojanus considered the first of these to be disproved by his work published in 1815.



Figures 19 - 21. Illustrations from Bojanus' work.

- 19—transverse section of a dog fetus;
- 20—discorded membrane of a human fetus;
- 21—yolk duct of an adder.

The second Bojanus correctly considered inaccurate because the embryonic organs of man and horses have different structure. In order to explain, Bojanus gave the following description of the topography of the fetal membranes and embryonic organs of horses. The fetus is covered with the amnion, which with the umbilical vessels goes out from the allantoic duct and widens, forming the voluminous allantoic-sac. This sac bends around the amnion and lines the entire chorion, with the exception of that place where the blood vessels go out. "Therefore," Bojanus said "the amnion and its fetus lie in the allantois exactly as the intestines in the peritoneum." This accurate comparison shows that the intestines lie not in the cavity of the peritoneal sac, but outside it and are covered with folds of the peritoneum. Bojanus concluded with the following words: "The amniotic sac does not swim in the allantoic fluid entirely; the allantois and the amnion forms an independent closed sac, located between the amnion and chorion and next to the external wall of the amnion and the internal wall of the chorion." This, according to Bojanus, is characteristic for the fetus of the horse as well as for other mammals—dogs, cats, and ruminants.

In another place (ISIS, 1817, p. 877), Bojanus entered into controversy with Emmert. Emmert stated that the duct of the umbilical sac (yolk duct) is formed apparently only at the end of development, being formerly unconnected with the cavity of the intestinal canal. Bojanus referred to his data, and to what "Wolff had forty years earlier already showed to the contrary, so obviously that the subject could be considered completed."

In sheep embryos Bojanus found basically the same situation as in the embryos of dogs and horses. In an article about the embryonic membrane and organs of sheep, Bojanus determined that the allantoic duct entered into the posterior end of the peritoneal cavity. Near the duct, both the umbilical arteries and the umbilical veins extended into the peritoneal cavity, divided, and turned toward the liver. The stem of the umbilical sac in the embryonic body was directed straight toward the intestinal canal.

In 1820 Bojanus again returned to the embryology of dogs and gave an anatomical description of a twenty-four-day-old

fetus and its embryonic membranes.⁶ A year later in *ISIS*, Bojanus considered the membranes of the human fetus.⁷ In that work he is considered to have corrected the main mistake in the description of the sloughed-off membranes, which remained from Hunter's time. Bojanus showed that the ovum, going out from the Fallopian tube, passes between the wall of the uterus and the sloughed-off membrane. By increasing in size, it separates the membrane from the uterine wall to the extent that the hillock which is covered with the sloughed-off membrane protrudes increasingly into its cavity. In the place where the fertilized ovum contacts the uterine wall, the maternal placenta forms. In the same place, the uterus forms a new sloughed-off membrane (Bojanus calls it decidua serotina), in which the vessels grow from the chorion and the maternal placenta. And thus, at the beginning the decidua bends through the fertilized ovum and covers it only in those places where it is not in contact with the uterine wall. The end of the ovum appears to be surrounded with the sloughed-off membrane. Schematic illustrations (Figure 20), further elucidate the description.

In the same *ISIS* article is a small note,⁸ addressed to the editor of this journal, L. Oken. There Bojanus cited Oken's unjustified attack and proposed that Oken should more accurately formulate his point of view on the nature of the sloughed-off membrane. Bojanus' dissatisfaction is entirely justified, because against Bojanus' accurate observations Oken had opposed only the dim ideas of *Naturphilosophie*.

A year later Bojanus published a work in which, by extending his previous material, he gave a description of the relationship of the umbilical sac to the membranes in the hare.⁹

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6. Bojanus, "Observatio anatomica de foetu canino 24 dierum ejusdem velamentis," *NOVA ACTA ACAD. LEOPOLD.-CAROL.*, 10 (1820), p. 139.
 7. Bojanus, "Ein Wort über das Verhältniss der membrana decidua und decidua reflexa zum Ei de menschlichen Embryo," *ISIS* (1821), pp. 268 - 271.
 8. Bojanus, "Anfrage und Bitte wegen der membrana decidua," *ISIS* (1821), p. 1174.
 9. Bojanus, "Über die Darmblase des Haasefoetus," *ISIS* (1822), pp. 1228 - 1230.

Not being restricted to investigations on mammals, Bojanus performed his basic conclusions also on reptile embryos, mainly on the adder (*Coluber berus*, or, according to the present systematic terminology, *Vipera berus* L.). Emmert confirmed that in the reptile embryo the yolk duct is not present, i.e. the duct connecting the yolk sac with the intestine.

Concluding from the comparative embryological work, Bojanus doubted that this observation was correct; his investigations led to other conclusions. The main part of his work consists of thorough drawings with detailed explanations.¹⁰ The articles are summarized in the following:

- 1) In the fetus of *Coluber berus* there is a yolk duct;
- 2) this yolk duct is connected with the intestinal canal not far from the origin of the appendix, i.e. it has the same topographic relationship as the horse embryo;
- 3) the yolk-mesentery vessels are situated primarily as in other animals.

Of the illustrations accompanying this work, Figure 21 is particularly remarkable. It shows the connection of the yolk duct with the intestine at the early stage of intestinal development when parts of the intestinal canal are still undifferentiated. The yolk duct enters a region between the stomach and the beginning of the intestine. Also shown is that connection of the yolk-mesentery artery with the descending aorta and the yolk-mesentery vein with the flooding vein.

This short account of Bojanus' embryological investigations confirms that he succeeded in settling a number of important questions about the structure and reciprocal situation of the embryonic membranes and embryonic organs in mammals and reptiles. The results of his distinct investigations led him to argument with known authors of that time, especially with Cuvier. Only later was it determined that Bojanus' descriptions and discussions were much closer to the truth.

10. Bojanus, "Dottergang im Foetus des *Coluber berus*," ISIS (1818), pp. 2093 - 2094.

In embryology Bojanus could be considered a continuation of Wolff, of whose work he always spoke with great respect. In the epoch preceding the appearance of the classical work of Pander and especially Baer, the investigations of Ludwig Bojanus undoubtedly had remarkable importance.

CHAPTER 13

THE DISCOVERY OF EMBRYONIC LAYERS: THE DISSERTATION OF KH. I. PANDER

While Wolff's investigations represented an epoch in the history of embryology, those works found considerable continuity in the work of the Russian academicians Kh. I. Pander and K. M. Baer. K. A. Timiryazev has emphasized Wolff's significance for the second half of the eighteenth century and Pander's and Baer's for the beginning of the nineteenth century, in his brilliant essay on the history of biology. He wrote that:

Along with the static method of comparison in the first years of the century, Karl Ernst von Baer (and Pander) originated the "formative" method, i.e. the investigation of the organism in its sequence of developmental stages from the ovum. Thereafter the wide study of the history of development began. Here the word "history" was used for the first time, not in that undefined sense as in "natural history," but in the strict sense of specifying the facts in time and not in space. Embryology has grown particularly in zoology, and the most remarkable role has fallen to Russian zoologists (Baer and Pander in the beginning of the century, and Kovalevsky and Mechnikov in the second half).¹

Thus, the three stages of embryology are connected with Wolff, then with Pander and Baer, and finally with Kovalevsky and Mechnikov. As Timiryazev pointed out in his familiar work, "The Historical Method in Biology,"

1. K. A. Timiryazev, "THE MAIN FEATURES OF THE HISTORY OF DEVELOPMENT OF BIOLOGY IN THE 19TH CENTURY," INVESTIGATION, vol. 8 (1939), p. 98.

From the second half of the past century the use of the systematic method of investigation was begun on an organism in successive stages of its embryonic existence; this was later directly called the history of development or embryology. This new science . . . had a special meaning to Russia. Its simultaneous achievements obviously characterize three stages in the fate of Russian science in general. In Petersburg, the brilliant Kaspar Friedrich Wolff, whose courageous and innovative ideas did not find a response among his compatriots, mapped with his brilliant embryological work the route for a new science. Another Russian academician, a student of the famous Dorpat University which was performing such great services to Russian science, Karl Ernst von Baer, was considered the founder of modern embryology. The classical investigations of Baer and his fellow countryman Pander established, with many others, the high standard of science on the Baltic coast. Finally, the names A. Kowalevsky and Mechnikov remain connected with the era of development of that new science.²

A well-known role in the preparation of the new period in the history of biology, the period of removing the fantasy of the nature-philosophers, was played by a professor of Würzburg University, I. Döllinger, who taught Pander and Baer. Both spoke warmly of Döllinger's influence on their scientific endeavors and of his kind relations with them when they started their work in his laboratory. In his youth Döllinger had been fond of the ideas of Kant and Schelling. Later he sceptically stuck to *a priori* structures and gave great consideration of the direct empirical study of nature. Pander's and Baer's presence in his laboratory was important, though Döllinger did not himself have a significant effect in science. Baer wrote that the school of Döllinger had done much for the understanding of nature through the investigations of Pander. Baer humbly underestimated himself.

In his autobiography, published on the occasion of the fiftieth anniversary of obtaining his doctoral degree,³

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2. K. A. Timiryazev, "THE HISTORICAL METHOD OF BIOLOGY," INVESTIGATION, vol. 6 (1939), p. 32.
 3. Baer, NACHRICHTEN UBER LEBEN UND SCHRIFTEN DES HERRN GEHEIMSRATHS DR. KARL ERNST VON BAER, 1864. St. Petersburg, 1865. 674 pp.

K. M. Baer said how he, in the spring of 1816, had convinced his Dorpat friend Pander to move from Göttingen to Würzburg to work with Döllinger, with whom Baer himself had studied comparative anatomy. Döllinger long cherished a plan to perform a systematic investigation of the chick embryo, but he had neither time nor materials to conclude the work. For this work, a great number of fresh eggs were required. And incubators, because of the lack of thermoregulating facilities, required observation twenty-four hours a day. Further, it was also necessary to invite a graphic artist and an engraver to prepare drawings suitable for reproduction into prints. On a country walk Döllinger, with Baer and Pander, decided that Pander would perform this work and provide the necessary material requirements.

Here it is appropriate to give some biographical information about him, however scanty. Khristian Ivanovich Pander was born on May 12, 1794 in Riga to the family of a bank director. In 1812 he entered Dorpat University, and from 1814 he continued studying medicine in Berlin and Göttingen. In 1816 he worked in Würzburg with Döllinger. After finishing his dissertation in embryology (1817), he worked for about ten years with the artist d'Alton in the comparative osteology of contemporary and fossilized animals, and then turned exclusively to paleontological investigations. In 1821 Pander was selected a member of Petersburg Academy of Science; he was from 1822 a scientific senior assistant, and then an academician. In 1827 he resigned because "he did not agree with the internal regulations in the Academy and with the leaders of this organization,"⁴ After that, Pander became an official of special commissions in the scientific section of the mining department. His responsibilities included processing the paleontologic collection brought into the department, which gave him material for his monograph on paleozoic fish. The work of Pander and his contemporary E.I. Eichwald provided the basis of paleontologic studies in Russia. Having, according to his contemporaries,

4. Biography of Pander in MATERIALS FOR THE HISTORY OF SCIENTIFIC AND APPLIED ACTIVITIES IN RUSSIA IN ZOOLOGY AND THE BRANCHES OF SCIENCE RELATED TO IT, PRIMARILY DURING THE LAST THIRTY-FIVE YEARS (1850-1887), collected by Anatol Bogdanov, Vol. 2 (1889), p. 55).



Kristian Ivanovich Pander.

an extreme modesty and a complete absence of private interest for all science outside his own, Pander remained outside the official world of science. His life was so devoid of scientific honors that even after death he was forgotten. Not one scientific organization kept his obituary or a list of his numerous works Many of the results of his scientific investigations were published in the work of others.⁵

Pander died in 1865.

Concerning Pander's working conditions in Würzburg, Baer reported the following: Döllinger gave Pander the procedures of investigation which he had worked out for early chicken embryos, namely the method of separating the blastoderm from the yolk under water. This method had been previously employed, apparently, by Malpighi and Wolff, but they did not give a description of it. For this reason, it was not known to Haller and Ham, whose achievements therefore were consequently insignificant. Of Ham's work Baer wrote, for example, that "Ham is significantly later than Wolff, even later than Pander. He has offered us investigations of the chick embryo from which it is not possible to know more than that the embryo gets larger and larger."⁶ "And thus," Baer continued,

Pander could use Döllinger's experiments and more expedient methods. But in order to obtain true impressions about this progress (Baer means the most important question in chicken embryology—the formation of the intestines and peritoneal cavity) it is necessary to start from the beginning and follow all the stages of the chick successively. This was done by nobody else but Pander.⁷

Already on July 10, 1816 Baer wrote to his friend Dietmar:⁸

Because you have shown such interest in Pander's work, I cannot postpone telling you about it,

5. Ibid.

6. Baer, NACHRICHTEN, p. 210.

7. Ibid., p. 211.

8. Later published in BALTISCHE MONATSSCHRIFT (1893). Cited in R. Stölzle, KARL ERNST VON BAER UND SEINE WELTANSCHAUUNG (Regensburg, 1897), xi + 687 pp.

(citation on p. 15).

although Pander does not want that. So look: In all the sciences of nature there is no point more important than the formation of the organism from the original mass; that should hold the key for all physiology and biology. For the lower organisms this formation can be investigated at the emergence of the pouring in animals and water-plants. For the higher animals, only the history of the incubated eggs is available. Although it has been frequently investigated, this has been done partially because of previous ideas, especially the crazy theory of evolution;⁹ and partially because attention was directed only towards the development of individual parts, for example in Wolff's work. No engravings have appeared since Malpighi in the seventeenth century, and now Pander has decided to investigate the history of development of the incubated egg and give this work with engravings, perhaps as a dissertation, or as an independent work. In order to get enough eggs, two machines were prepared in which, following Döllinger's recommendations, the eggs are incubated by artificial heating. Paying for a specialist graphic artist and engraver, Pander, by means of these egg shells, stands on the path toward adorning his brow with a laurel wreath. I am proud to be the main stimulus to this action. Be quiet, however, until everything is finished.

Pander worked extremely intensively, and within a year he published his work in Latin, without illustrations, as "Dissertation on the History of the Development of the Incubated Egg throughout the First Five Days. Author Chr. Pander, a Russian from Riga."¹⁰ A German version soon followed, organized along a somewhat different plan and with numerous excellent illustrations, entitled "History of the Development of the Chicken in the Egg."¹¹ In the preface to

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9. It must be remembered that at the beginning of the nineteenth century, the term evolution was used to mean the development of performed materials (see Chapter 2).
 10. Pander, DISSERTATIO INAUGURALIS SISTENS HISTORIAM METAMORPHOSEUS, QUAM OVUM INCUBATUM PRIORIBUS QUINQUE DIEBUS SUBIT (Würzburg, 1817), 69 pp.
 11. Pander, BEITRÄGE ZUR ENTWICKLUNGSGESCHICHTE DES HUHNCHENS IM EIE (Würzburg, 1817), 42 pp.

the Latin dissertation Pander warmly referred to Döllinger's kind treatment and to the readiness with which he gave him assistance, and also referred to the friendly conditions and group discussions in the laboratory.

In the introduction, Pander described his method of investigation. First, he cited the necessity of having available extensive material, since earlier disagreements about chick development originated from the fact that the disputants could not investigate controversial data because of a lack of material. In order to obtain a sufficient number (up to forty) of embryos at one stage, Pander rejected the use of brood hens and instead used an incubating machine of Colman's system, about which Blumenbach had spoken favorably. Pander objected to the current prejudice against incubators, referring to the fact that egg development occurs normally in them and that chickens, as usual, hatch out on the twenty-first day. According to Pander, the temperature in the incubator should not be lower than 28° nor higher than 32°C. A total of more than two thousand developing chicken eggs were used.

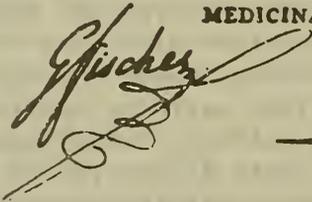
The least understood period of chick development was considered to be the earliest. For this reason, Pander limited his investigations to the first five days of incubation. "In this period," Pander wrote, "when the basics of all parts were laid, we did not find anything special that deserves mentioning."¹² Opening the egg, Pander said, should be done in water. To study the early stages (up to the fifth day), it is necessary to watch for complete separation of the blastoderm from the surrounding parts, because there the processes of embryonic formation actually take place. With this objective, around the cicatrice or, at later stages, along the terminal sinus, Pander cut a segment of the yolk membrane, after which the egg submerged in water separates by itself from the blastoderm. Soon after that, Pander continued, we must begin observing with different types of complex and simple microscopes, with greater or smaller magnification. He recommended placing the observed object on a dark background; then it is comfortable to use the glasses which cover pocket watches. To prepare the blastoderm with instruments, Pander used saucers covered with a layer of wax.

12. Pander, DISSERTATIO, p. 12.

DISSERTATIO INAUGURALIS
SISTENS
HISTORIAM METAMOR-
PHOSEOS,
QUAM
OVUM INCUBATUM
PRIORIBUS QUINQUE DIEBUS
SUBIT.

AUCTORE
CHR. PANDER,

RIGA RUTHENO,
MEDICINAE DOCTORE.



A handwritten signature in cursive script, likely belonging to G. I. Fisher, is written over a horizontal line. The signature is written in dark ink and is somewhat stylized.

Wirceburgi 1817⁴⁵
Typis Francisci Ernesti Nitribitt, Universitatis
Typographi.

Figure 22. Title page of Pander's Latin dissertation. A copy, belonging to G. I. Fisher, from the library of the Moscow Society of Nature Investigators.

Among his predecessors, Pander spoke first of "Malpighi, who in his 'Epistolary Dissertation on the Formation of the Chicken in the Egg,' has given us wonderful presentations accompanied by brief explanations." Pander gave no less consideration to Haller's work, especially to two French memoirs on the development of the heart, and to a Latin paper on this subject. "However, with the greatest praise," Pander discussed Wolff's wonderful observations which are partially stated in the book *THE THEORY OF GENERATION*, and partially in his treatise "On the Formation of the Intestines" presented in the twelfth and thirteenth volumes of the *COMMENTARIES* of the St. Petersburg Academy of Science.¹³ In regard to circulation in the vessels and the movement of blood there, Pander referred to Spallanzani's "Features of Circulation" ("Dei fenomeni della circolazione," 1773). In concluding his review of the literature, Pander briefly stated: "It is impossible to ignore the careful observations of the most famous master of graphs, Tredern."¹⁴

The first paragraph of Pander's dissertation is devoted to the earliest developmental stages of the incubated egg. On the surface of the yolk and hanging in the egg albumin, Pander saw the small whitish spot, the cicatrice, saying that "Different authors called it by different names (66), but nobody tried to determine how it is situated, where it is located and from where it originates."¹⁵ Pander himself stated that the yolk membrane near this spot is thin and transparent and that egg cicatrices suitable for incubation are distinguished from the formations found in nonfertilized eggs. In the latter the spot is smaller, whiter, granulated, and not completely rounded. In fertilized eggs, the spot is larger in size, leaden-whitish and entirely rounded. The surrounding yolk forms an intensively colored zone, and the spot itself is edged with a paler border and has in the center a white spot. On lifting the yolk membrane, Pander found that the spot is composed of one layer of light granules and has the shape of a disk located between the yolk and the yolk membrane. The central part of the disk is attached to the lump underneath, to which the whiter color

13. *Ibid.*, p. 16.

14. *Ibid.*, p. 17.

15. *Ibid.*, pp. 18 - 19.

in the center of the spot is related. Thus, Pander distinguished two parts in the cicatrice—the disk, or membranous layer, and the central lump situated below it, to which he gave the name nucleus¹⁶ of the cicatrice. Pander gave great consideration to the membranous layer and called it the blastoderm (67).

At the eighth hour of incubation (§ 2) (68) the nucleus of the disk is more easily separated from the yolk, but it remains attached to the blastoderm. The latter increases insignificantly in size, its center somewhat clarified.

The twelfth hour of incubation (§ 3) is characterized by further spreading of the blastoderm; its transparent central part also increases and changes the round form into a pear-shaped form. In the blastoderm at that time it is possible to differentiate two regions: the internal region called the transparent area (*area pellucida*) (69), surrounded by a non-transparent region, called "the opaque area" (*area opaca*). Through the transparent area the nucleus of the cicatrice is visible, "giving Malpighi a reason for his strange mistake and imaginary picture."¹⁷ "The greatest importance," Pander wrote, "is that the blastoderm itself is composed of two layers. This membrane before incubation consists of a single layer of granules. In the process of incubation the second very thin layer appears, however, it is so firm that by prolonged maceration it is possible to separate the blastoderm into two layers." (70) "The internal of these layers," Pander continued, "is connected with the yolk. We will call it later the mucous membrane, and the external homogenous and smooth layer the serous membrane. Both these membranes spread over all the blastoderm and are present in the transparent as well as in the opaque area, with only the difference that in the transparent area the mucous membrane is much more delicate than in the opaque area."¹⁸

16. Called "Pander's nucleus" by subsequent authors.

17. Pander, DISSERTATIO, p. 25.

18. Ibid., p. 27.

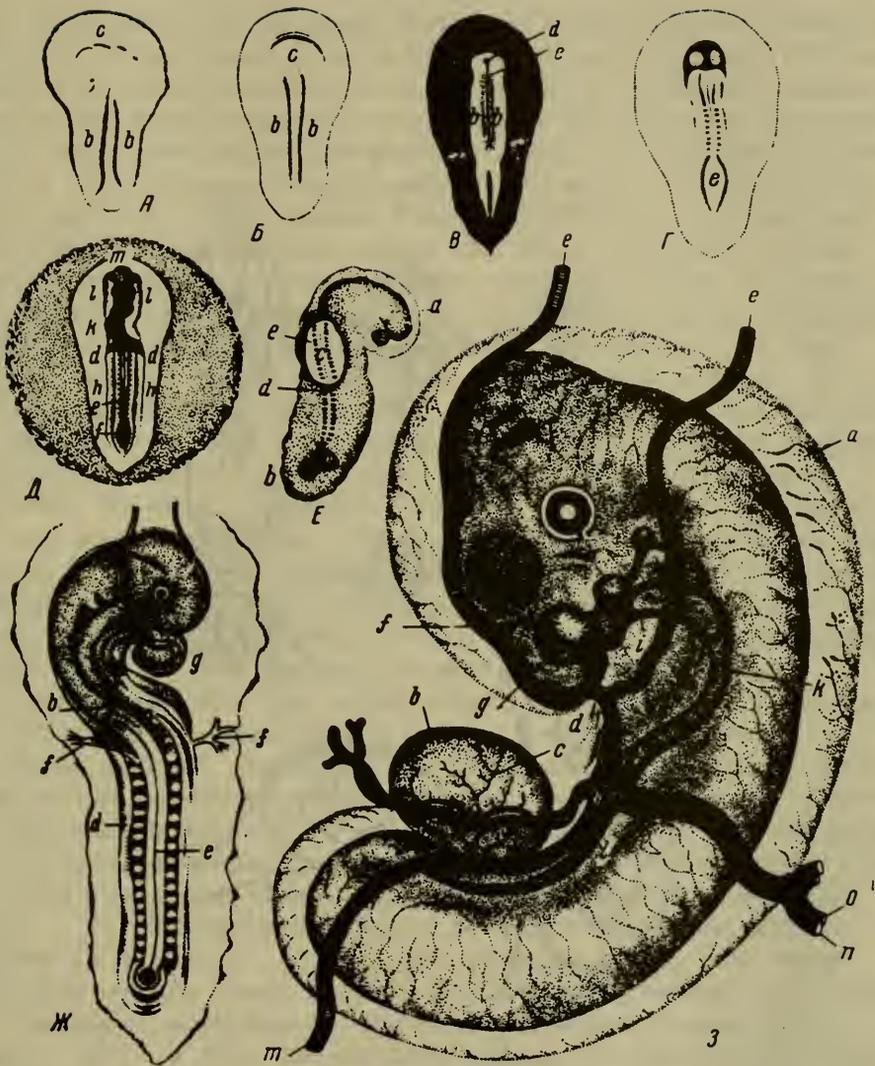


Figure 23. Pander's illustrations from "History of Development of the Chicken in the Eggs."

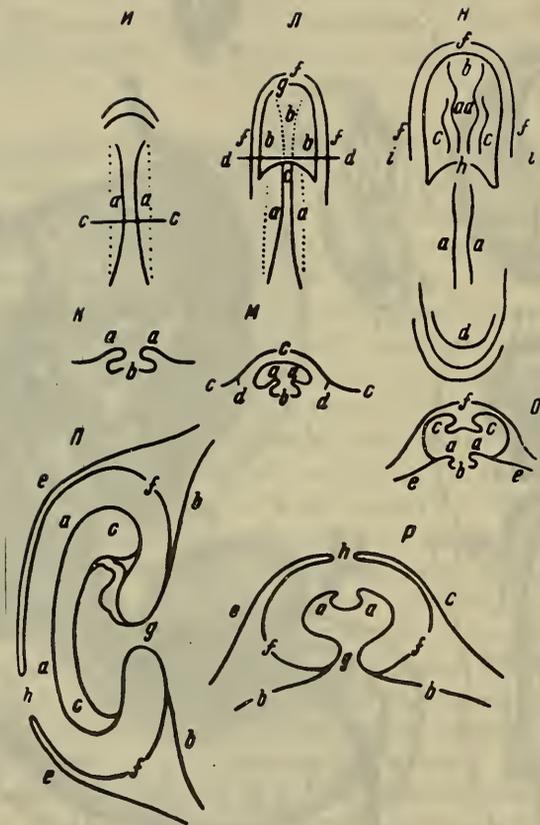


Figure 23 (continued).

Figure 23. Pander's illustrations from "History of Development of the Chicken in the Egg."

A(1) Back side: *bb*—primary folds in their earliest condition; *c*—fold of the fetal area above the primary folds. *b*(2) Back side: *bb*—primary folds; at *c* they are arch-shaped, joined at the future head end, and, conversely, separated at the tail end. *B*(3) Back side: *bb*—primary folds; *e*—filament of the spinal cord between the primary folds; *d*—knot-shaped end.

(4) Primary folds closer, especially in the central part of the fetus, where on both sides the first rudiments of the spinal vertebrae are laid; below, where the thin filament of the spinal cord terminates at *e* in a lancet shape, they again disperse.

(5) The peritoneal side: *dd*—end of the head portion at which the lower edge of the heart is seen (*k*); *ef*—spinal cord; *h*—intestinal folds, appearing as lateral borders to the head portion; *ll*—lateral borders of the head portion; *m*—head. *E*(6) Fetus from the side of the shell:

a—head; *b*—tail; *c*—spinal column, seen through the opening of the amnion; *d*—same, under the amnion; *e*—opening of the amnion.

(7) Fetus from the side of the yolk: *b*—border of the head portion; tail portion; *d*—intestinal folds; *e*—spinal cord; *ff*—arterial stems; *g*—heart in form of twisted canal.

(8) Fetus in the amnion: *a*—amnion; *b*—chorion sac; *d*—place where all the veins enter the fetus; *c*—vessels of the chorion; *ee*—descending veins; *m*—ascending vein; *f*—upper arch of the heart; *g*—lower arch; *h*—bulb of aorta, from which go out three arch-shaped curved arteries *i*, uniting in descending aorta *k*; *l*—left artery with its lateral branch *n*; *o*—vein, accompanying this branch.

(9) *aa*—primary folds; *cc*—the cut place (see 10). *K* (10) Transverse section (see 9): *aa*—primary folds; *b*—place where the spinal column is situated.

(11) *aa*—primary folds; *bbb*—head portion; *c*—its lower border; *g*—its upper border; *fff*—borders of the upper membrane of the head portion: *dd*—cut place (see 12).

M (12) *aa*—primary folds; *b*—location of spinal cord; *ccc*—upper layer of the head portion; old intestinal folds. *H* (13) *aa*—primary folds; *b*—place where the spinal cord is formed; *cc*—folds of the internal layer of the head portion, forming the heart; *h*—lower border of the head portion; *fff*—border of the upper layer of the head portion;

d—tail portion; *ii*—place of the cut (see 14). *O* (14) *aa*—primary folds; *b*—location of the spinal column;

cc—folds, forming the heart; *cc*—the vessel layer covering the yolk; *f*—the upper layer of the head portion. (15)

Longitudinal section made in the amnion of the fetus:

aa—external side of the primary folds; *cc*—lateral parts of the fetus; *ee*—serous layer of the blastoderms forming the false amnion; *h*—opening which later closes; *ff*—internal layer of these serous layers (especially the amnion); *g*—opening by which the intestines are connected with the yolk; *bb*—blastoderm. *P* (16) Transverse section on the lines of (15). The explanations are the same.

Next Pander referred to the galoons, the white concentric spheres bordering the cicatrice. In a footnote he indicated that until now nobody could explain their structure. Especially Oken, in his "Manual of the Natural History," said that he did not know their nature, and suggested their connection with the vascular system. This suggestion Pander considered devoid of basis. He himself distinguished two types of galoons, one related to the blastoderm, which exists even before the incubation, and another which appears on the second and third day and develops in the yolk itself; the most external of these corresponds with the border of the blastoderm.¹⁹

Until the sixteenth hour of incubation (§ 4) the transparent area has an elongated pear-shaped form. In it are two opaque parallel lines, which in Pander's opinion are the folds forming the blastoderm in the direction of the shell (Drawing 23, 1 - 2). "These first traces of the developing embryo are called the primary folds, and what is found between them we, with Malpighi, call the intermediate careen,"²⁰ (71).

In one part of the transparent area the primary folds very early turn up to the center and join each other in an arch; and in the opposite area they, on the contrary, become separated. Until this takes place, the transparent area gradually changes its shape from pear-shaped into biscuit-form (Blumenbach) or, Pander suggested, they acquire the shape of sandals. Between the primary folds, Pander saw a quickly developing delicate whitish filament, which he considered the spinal cord. The spinal cord turns into the brain. The opaque area is divided into two zones: the internal repeats the sandal shapes of the transparent area, and the external zone has an elliptical form. The nucleus of the embryonic disk swells, is easily separated from the yolk, and then below it a pit is observed.

In the twentieth hour, embryos (§ 5) are "composed of primary folds and spinal cord, which develop from the blastoderm and in an unknown way are connected with the place of formation," according to Pander. He distinguished two ends—the upper, or the head end, where the folds coincide,

19. The term galoon is not employed in later embryological literature, because the rings designated by it are not permanent formations.

20. Pander, DISSERTATIO, pp. 28-30.

and a lower, or tail end, where they are bifurcated. "The cephalic end is somewhat curved inside the egg above the spinal cord and forms in this way a very small half-moon fold."²¹ Describing in detail the structure and situation of this fold, Pander gets to the characteristics of the conditions of the blastoderm. After dividing it by maceration into two layers, he saw under the microscope that under the internal surface of the serous layer, which is lying on the mucous layer, there is a delicate semi-transparent layer of minute granules. This layer is distributed not all over the blastoderm, but occupies only the region of the transparent area and the internal zone of the opaque area, making by itself a division of the opaque area into two zones. Pander especially draws attention to the process of development of this new layer. At about the twelfth hour it is composed of small groups of dispersed granules, forming aggregations in the form of islets; the latter merge in each other but do not form a continuous layer because from them blood islets and blood vessels develop. This layer, the third and middle layer of the blastoderm, Pander called the vascular layer.

In the German version of Pander's work, it is explained distinctly that the blastoderm, which is composed of the embryonic membranes or layers, is considered the origin of the future embryo. All development is nothing other than "like the metamorphosis of the membrane (blastoderm)... and its layers."²²

To the end of the first days, according to Pander, the primary rudiments of the vertebrae appear, which in his words are as if hung to the primary folds in the form of nearly quadratic spots of a pale-yellowish color, separated by spaces and situated in two parallel lines. The primary folds at first are straight, then become serpent-shaped, curved and wavy. To the tail the folds disperse, and in the spinal cord they form a convex arch.

21. Ibid., p. 31.

22. Pander, BEITRÄGE ZUR ENTWICKLUNGSGESCHICHTE
DES HUHNCHENS IM EIE, p. 6.

The thirtieth hour of incubation (§ 7) is characterized, according to Pander, by the following: "Primary folds previously were opened with the spinal cord situated between them; now they approach each other mainly at the central distance between the head and tail. The edges of the folds move closer; they cover the spinal cord and after that they accrete. When this approach and accretion of the edges occurs along the whole length, the mentioned folds remain apart, and in the head region they keep the serpent-shaped curves and form a number of three or four chambers of larger sizes."²³ The transverse fold becomes a little widened and stretched to the tail end, forming the head portion, as Wolff called it. Pander does not believe that this fold is duplicated, but suggested that the upper one depends on the bending of the embryonic body, and the lower depends on the bending of the blastoderm. At this stage Pander saw the heart rudiment situated under the head as an elongated, not clearly defined sac. The granulated layer, facing from inside to the serous layer, acquires the shape of a net.

Within thirty-six hours after the beginning of incubation (§ 8) the anterior ends of the primary folds get together and accrete with each other, forming the forehead and the facial parts of the embryo. "From each side of this rounded area develops one rounded portion. They are situated a little bit backwards, appearing to be the primary rudiment of the eyes and appear as lateral widenings of the primary central rounded area."²⁴ The heart, according to Pander, becomes a narrowed, straight, cylindrical canal which extends from the heart depression to the head. The granular layer disintegrates into separate islets; these have a yellowish color, while the granules forming the bordering ring are already stained a red color.

By the forty-second hour of incubation (§ 9) the end of the head, formerly adjacent to the blastoderm, now is inserted into a small depression formed by the blastoderm, whose fold extends above the head. The fold, forming the border of this depression, represents the rudiment of the amnion. The heart at this stage appeared as an arch curved to the left

23. Pander, DISSERTATIO, p. 35.

24. Ibid., p. 37.

and divided into three cavities. The head portion now reaches the place of bifurcation of the heart; here also is formed "the heart depression," leading to the esophagus. The lateral borders of the head portion are strongly stretched towards the tail. At the posterior (the lower, according to Pander) end of the fetus appears the wrapped-up part of the blastoderm, which later forms the tail portion, whose borders go along the sides of the embryo and get into the folds near the heart depression. The blood islets at this stage acquire a red color.

By the end of the second day (§ 10) the depression, in which the free anterior part of the embryonic body is situated, increases; the head portion, which is outlined by a half-moon border, is distinctly formed. Then the fetus turns to the left side. The granular layer is converted into the vascular plate, which is situated between the two layers of the blastoderm; the latter, therefore, becomes three-layered. The blood islets of the middle layer have now the shape of vessels with their own walls, i.e. they are converted into blood vessels. The spaces, formed by the bent primary folds in the head region become filled with vacuoles and are converted into cavities from which the brain is formed. The posterior (first) space gives the origin to the medulla oblongata, the second to the rounded body of the four hillocks, and the third the narrower part of the brain, while the stems and protuberances of the optic nerve and the most anterior (fourth) is converted into the hemispheres. Pander gave special attention to the fate of the lower space which is adjacent to the yolk surface of the blastoderm. He described two pairs of folds there, the external and internal. The external are formed from all the layers of the blastoderm; and the internal only from the vascular and mucous layers. The external folds, in Pander's opinion, form the peritoneal walls and share in the formation of the intestines. He calls them the peritoneal and intestinal folds. To the internal folds, in correspondence with their subsequent fate, he gave the name of the mesenteric folds. Undoubtedly, these paired folds correspond with those of the embryonic formations which Baer later called the peritoneal and intestinal layers. In this place Pander made a general footnote of several pages devoted to Wolff's investigations and the evolution of Oken's work.

Indicating that Tiedemann, in his manual of zoology, and Meckel, in his translation of Wolff's work, had given credit to Wolff, Pander remarked that Oken instead had attacked Wolff sharply. Oken reproached Wolff for lack of clarity and requested that Tiedemann "follow up completely the development of the intestinal canal, or otherwise there will be a gap . . . in Wolff's descriptions. Now we must put an end to all discrepancies."²⁵ Pander declared also that Oken was not entirely correct in his complaints against Wolff's lack of clarity and in indicating some of his mistakes. "The reason for most of Wolff's mistakes," Pander wrote, "is mainly . . . in his assumption that the blastoderm is a single layer . . . and that the origins of the developing changes and their course are connected with it."²⁶ Pander did not claim to have studied all the layers of the blastoderm completely. He did, however, determine that "these layers, either separated, or connected, are the only origin of the different organs."²⁷ Pander concluded with a long quotation from Wolff, in which he discussed the formation of the closed intestinal canal from the original bifurcating layers, in order to show his agreement with Wolff.

Pander's observations on the development of the digestive tract revealed the following. The heart depression (Wolff's term, which Pander adopted) forms a wide cavity with a gaping opening. The latter has an oval form; anteriorly it is wider, and posteriorly the intestinal and mesenteric folds, get lost in the posterior part of the tail covers. The colon is formed when the walls of the tail portion move close to each other. Concerning the mesenteric folds, Pander agreed with Wolff that they are the rudiments not only of the mesentery, but also of the kidneys. By the end of the second day the heart bends more and more into the form of a horse-shoe, or parabola," developing on the left side.

Chapter 11 of Pander's dissertation is devoted to the incidents of the third day. At that time the blastoderm occupies half of the yolk surface; the form of the transparent area loses its regularity, but in the anterior it remains wider than posteriorly. The blood-carrying system emerges

25. Ibid., p. 42 (footnote).

26. Ibid.

27. Ibid.

as follows: The net of the previously developing blood vessels is converted into a system of vascular stems and branches, "highly refined decoration of the vascular membranes"; the stems reach the fetus, and the smallest branches reach the peripheral circulation. The arterial stems go out from the fetus in a straight angle, soon divide into three or four branches, while an endless number of small branches fall into the terminal series and also form numerous anastomoses with the thin venous branches. The terminal or peripheral blood circulation, which is called terminal venous circulation, is devoid of vessel walls. From the terminal venous circulation, two or three veins originate, directed to the fetus along its longitudinal axis. The upper descending vein, which is usually duplicated, is a continuation of the terminal sinus; it descends to the head of the fetus, lies on the head portion, and moves close to the heart. The lower ascending vein begins with numerous small branches from the opposite end of the terminal sinus, ascends beside the tail of the embryo, and joins the descending veins near the heart.

The heart, which is located on the left side of the fetus and covered with the head portion, is composed of three connected cavities. The first of these cavities is the auricle, the second is the ventricle, and the third is the aortic bulb. The ball-shaped auricle is connected with veins backwards, and anteriorly connected with the continuation of the ventricle. The latter is connected by means of a narrow duct to the widest aortic bulb, from which a narrow cylindrical canal passes into two or three aortic stems. The aorta goes along in a large arch to the heart hole, forming a single trunk which then divides into two, each of which covers a vertebra. By getting narrower, it is lost in the tail region. From these arterial trunks, somewhat further to the middle of the fetus, originate two arteries of the vascular area.²⁸ Blood flow in the vessels begins from the ventricle, where the blood passes along the aorta into two lateral arteries. From their smallest branches it goes partially into the terminal sinus and partially into minute branched veins, and

28. This place in the dissertation is accompanied by an extensive footnote, in which Pander talks about the erroneous description of the embryonic vessels in the works of Tiedemann, Wolff, and especially Oken.

then blood reaches the heart through the descending and ascending veins. Pander described the terminal sinus, and the blood flow in this network.

Turning to the digestive tract, Pander remarked that the stomach on the third day is already an elongated form, narrowing anteriorly in the direction of the esophagus. Posteriorly, it has an opening corresponding to the heart depression; the borders of the opening continue posteriorly into the intestinal folds. The mesentery above the stomach, which previously consisted of two layers, now becomes a single layer. The posterior intestine has the form of a cone, with an anterior opening. The body wall, surrounding the cone of the colon, represents the rudiment of the pelvis, which forms by connection with the peritoneal folds. From the pubis, the blastoderm turns to the spinal surface of the fetus. The rudiment of the true amnion is still unclosed above the middle of the back. Along the border of this part, the serous membrane continues in the blastoderm. In a footnote Pander mentioned Treder's mistake of considering this continuation as the amnion. He noted later that the formation which he called the "false amnion" is not identical with that which Wolff designated by that name. In the posterior part of the embryo, Pander indicated the presence of a lentil-sized cavity which is filled with a transparent fluid; it originates from the surface of the colon and holds the umbilical artery. This cavity, Pander said, is usually called the chorion, and Oken compared it with the mammalian allantois. Pander's observations of development of the liver, lungs and kidneys at this stage correspond with Wolff's descriptions.

Section 12 concerns the embryonic characteristics after four days. The yolk membrane is exhausted and falls behind the blastoderm; the blastoderm surrounds almost all the yolk. Arteries and veins are filled with more intensely colored red blood. In the vascular membrane the arteries are accompanied with the corresponding veins. In the auricle it is possible to see an interceptor in the form of two half-rings, i.e. the beginning of the separation of the left and right auricles. The left is larger than the right and always contains drops of blood seen through its wall. In the ventricle a separation is also observed: above the aortic bulb a reddish oval hillock develops which is situated across

the originally existing ventricle. This is the foundation of the right ventricle. From the aortic bulb, closely adjacent to the ventricle, two or three branches go out, and from their base the aorta is formed, which later is bent in the form of an arch. The amnion is only slightly open and includes the whole fetus, which already has rudiments of the legs and wings. The peritoneal folds, which by bending back form the actual amnion, spread along the sides of the fetus, and near the region of the heart and around the borders of the pelvis constitute the borders of the chest and abdominal cavities. The opening of this cavity is the rudiment of the umbilicus.

These observations, which were completely novel, can only suggest that Pander's contemporaries could not understand those features they discovered. Such misunderstandings were displayed not only by Oken, but even by Baer, to whom Pander tried to explain his observations. In his autobiography (p. 212) Baer reports:

Pander had performed his investigations for some months, and I requested that he give me an idea of the method by which the closed body develops from a flat rudiment. Apparently, Pander had at that time a complete, and obviously a correct, idea about that. I remember well that he ran for the assistance of a handkerchief, spread it on his hand, and by bending the fingers tried to give me a visual idea of the formation of the gizzard. But the process remained unclear to me, perhaps because I could not, as I think now, clearly imagine the formation of the intestines.

The subsequent formation of the internal organs Pander described as follows. The stomach is completely closed; it goes into the duodenum to the extent that it is the duodenum rather than the stomach that opens in the regions of the former heart depression. From the duodenum, the middle intestine begins to form. It is at that time composed of two layers, joined at the dorsal borders, which continue into the mesentery. The peritoneal borders of these layers are still separated and extend along the sides into the vascular and mucous layers of the blastoderm. The lungs are located near the heart; they have the shape of extremely

delicate semitransparent bodies almost cylindrical in form, terminating in very thin vacuoles. Between the heart and the lungs, below the auricles, the right lobe of the liver is situated, continuing with convex peritoneal and concave dorsal surfaces which are adjacent to the heart; the portal vein goes through this lobe. The left lobe of the liver is narrow; it is located near the stomach and the duodenum. The kidneys are very long, with a lobed structure. They start at the chest region near the lungs and extend along the posterior end of the colon, to which they are connected to the urinary canal. Legs and wings appear as distinct hillocks. On the development of the mandibles, Pander referred to Tredern's observations. The cavity of the chorion as Pander called it, increases in size. In a footnote, Pander mentions the controversy about this organ and refers to Haller's unsuccessful attempts to blow air into the allantois through the intestines, or vice versa. Tiedemann gave more accurate data about the allantois, and Pander quoted him: "This sac is hung on a stem which is rich in vessels including both the umbilical arteries. The sac is composed of two layers—the external layer which is rich in vessels, and the internal which is thin and without vessels, containing transparent fluid. The cavity of the sac, through a canal extending between the umbilical arteries, connects with the terminal part of the colon or the cloaca The external layer of the sac is analogous to the vascular layer (chorion), and the internal layer could correspond to the allantois."

The last paragraph of the dissertation (§ 13) is concerned with the condition of the chick embryo at the fifth day of incubation. The yolk membrane has disappeared. The false amnion, i.e. the serous membrane in Baer's terms, becomes adjacent to the shell membrane. The true amnion is completely closed. The spreading chorion is connected internally with the false amnion. The descending and ascending veins of the vascular area are in the process of disappearing. The middle intestine is almost closed. Between the intestinal layers, there remains only "a small yolk intestinal canal connecting the intestine with the yolk. The serous and mucous layers are entirely separated from each other, the first of which . . . above the back forms the amniotic membrane; the latter together with the mucous layer include the yolk." Pander considered neural

development very little. The spinal cord, curved at a straight angle, continues in the medulla oblongata. As a result of the divergence of the lateral parts of the latter, the opened fourth ventricle is formed. The four hillocks are seen in the form of a divided sac. Pander was not sure whether what he had seen was brain material or its membranes. It is difficult to know, he wrote, because "the brain mass even on the sixth day of incubation is still so soft that it flows like tears."²⁹

At the end of 1817, in Oken's journal *Isis*,³⁰ there appeared an extensive review of Pander's dissertation. The review was not signed, but there is reason to believe that it came from Oken himself. The review first of all expressed satisfaction that the publication of these long-awaited investigations was "accomplished with unprecedented diligence, monetary expenditure, and talent." Oken, if indeed he is the author, implied that Pander was not the sole author of his work, but only a participant in a collective with Döllinger and d'Alton. Baer decisively disproved this interpretation. (72)

Oken quite fairly and in detail reviewed the dissertation, alternating statements and extracts with his notes and questions. First he wanted to know what the chalazae are. He expressed the idea that they are tubes through which the food materials pass into the yolk, because, in his opinion, during incubation the albumin and not the yolk diminishes; but it is not directly connected with the embryo. This fantastic assumption is confirmed, in Oken's opinion, by turning the eggs many times. This twists the chalazae, and their assumed pathways close; hence those long-living eggs, i.e. turned many times, do not hatch.

Oken rightly indicated the novelty and importance of the discovery of the embryonic layers. He was only unsatisfied with the description of their development and did not understand how they connect with the yolk membranes. In this respect Oken suggests three possibilities: 1) The layers are mechanically connected with each other, "as drops of wax on paper"; such structures, in his opinion, do not correspond with the nature of living substances, 2) The yolk membrane

29. Pander, *DISSERTATIO*, p. 68.

30. *ISIS* (1817), No. 192, pp. 1529 - 1540.

itself is composed of two layers, and the embryonic membrane separates the internal layer from the external; this suggestion is contrary to the fact of the disappearance of the yolk membrane above the vascular area. 3) The blastoderm is formed from the submerged yolk membrane. This possibility Oken considered the most probable, but it is an entirely arbitrary suggestion, not confirmed by direct observation.

Oken continued to remark that he did not understand the formation of the two-layered blastoderm, and asked what is present between it and the yolk membrane.

Referring to Pander's description of the formation of the primary folds, Oken considered the most important part of the dissertation to be that on the *punctum saliens*.³¹ He expressed regret only that these parts of the embryo are not illustrated in the schematic ("ideal") drawings. (73) He stated in this respect that "Each prepared anatomical drawings should follow the rule of depicting things not as they look, but as they exist. The so-called drawing from nature is always an expression of what seems to be. The true vision is not that of the artist, but that of the philosopher" (p. 1533). Concerning the drawings accompanying Pander's German text, Oken said that they allow no understanding of the work because they are not schematic.

A number of details remained unclear to Oken: for example, the topography of the layers or folds in relation to the blastoderm, and the yolk to the shell. To him the method of formation of the spinal cord is not clear; is it a tube or a groove? Oken's perplexity is completely logical for Pander described the gradual closing of the spinal folds, between which from the beginning there is already a thread-like spinal cord. The solution to this confusion was achieved only by Baer, who showed that the thread is not the spinal cord, but a cord where the brain is formed as a

31. *Punctum saliens*—a springing point. This is what Aristotle named the rudiment of the heart of the chick embryo, from which, in his opinion, the processes of formation begin. See Aristotle, THE DEVELOPMENT OF ANIMALS, Second Book, 4 (Academy of Science, USSR, 1940), p. 109.

result of the closing and accretion of the spinal layers ("primary folds" of Pander).

Concerning Pander's ideas for the period from the twentieth to the thirtieth hour of incubation, Oken accepted the description of blood vessels development and asked only about how the heart develops.

The most perplexing ideas for Oken related to the forty-second hour of incubation. Giving a literal description from Pander concerning the depression in which the head of the embryo is submerged and also concerning the folds forming the borders of this depression and representing the rudiment of the amnion, Oken said "We do not understand that. Also, as with Wolff's description . . . we want to know, can anybody understand that?"

Further on, Oken referred to the following: "The head portion extends to the place of the division of the heart into two stems, and in this region forms the heart depression which leads to the esophagus, the lateral angles of this portion extending forward strongly to the tail." It is not completely clear from the quotation why Oken burst into this tirade: "It is impossible to understand a single letter. All is stated as Wolff stated it, and therefore it is completely unclear. How could the digestive canal be, say, cut off downwards and have the shape of a blowing tube with a gaping empty opening?" (p. 1535).

Concerning the formation of the rectum from the walls of the tail, Oken again said that this cannot be understood. Then moving from the individual details of the formation of the digestive canal to Pander's general ideas, he wrote: "It cannot all occur like that. The body develops from cavities or sacs, and generally not from layers." Pander and his colleagues, Oken continued, "write as if they completely forget that the yolk and the yolk membrane (which is a cavity or sac) represent an actual part of the body, and that the embryo does not swim in the yolk, as the fish in water."

The source of these comments, freely expressed in a controversial form characteristic of Oken, are the wrongly interpreted observations on the development of mammals,

and especially his *a priori* natural philosophical ideas about the beginning rounded form inherited by all the bodies of nature.³²

Concerning the structure of the blood-carrying vessels of the blastoderm, described by Pander, Oken again stated that they must be looked at as "two cords, whose arteries and veins are connected with each other. Next Oken says that the neighboring vessel is nothing other than the uterus. Aside from these natural philosophical fantasies, Oken suggested a reasonable idea, that the yolk of the chick embryo corresponds to the umbilical sac of the mammalian embryo. Talking about the embryonic vessels he expressed his wish to see a schematic drawing illustrating the connection of the umbilical vessels with the body vessels.

Below (p. 1539), Oken again returned to the question about the development of the intestine, confirming with certainty that he himself had investigated this process and did not understand Wolff's and Pander's descriptions. Having only the drawings for the yet unpublished German text, which were sent to him ahead of time to consider, Oken commented that the "engravings were accomplished so clearly that the figures, it seems, can be judged from the papers" (pp. 1539 - 1540).

Oken's review ends with praise for Pander's unselfish services to science and with Oken's wishes for productive and continuing efforts for the popularization of scientific progress. "We heard," he wrote,

that Pander is going to issue a German edition, not for sale but to offer the nature investigators. This, in any case, is an incomparable offer. It is impossible to neglect the need to serve science, so that such sacrifice, with and without the monstrous expenses which Pander has invested on his own, should be highly appreciated. We can, however, advise printing copies for sale also. There are many friends of science whom Pander may not know and who undoubtedly desire to acquire such work. (p. 1540)

32. More details about that in Chapter 10.

Oken's article was apparently one of the very few responses to Pander's work, aside from K. M. Baer's. (74)

Pander acquainted himself with Oken's review, and his detailed answer soon appeared in ISIS.³³ Oken in turn was interested in Pander's reply; hence in printing it he added his own observations, which he put directly into the text. (75) Expressing his delight for Oken's interest, Pander said that he hurried to answer the questions posed in the review.

Concerning "chalazae," Pander referred to the German text of his work, in which the investigation is given in a different way than in the Latin text, not in regard to the periods of development but in regard to the organ system. There the chalazae are explained as twisted growths of the yolk membrane. The twisting of the chalazae is not a result of frequent turning of the eggs, as Oken thought, because the chalazae are twisted even in eggs that are just laid. There is no cross canal in the chalazae; they do not participate in the suction of the albumen and disappear early, along with the yolk membrane. The albumen, in general, is not used at the beginning of incubation as a food material; its diminution simply depends upon the drying which takes place in the fertilized as well as in the unfertilized egg, as the following data shows. One fertilized egg weighed 805 grains before incubation, and after the lapse of twenty days it lost 131 grains; another unfertilized egg, at the beginning, weighed 785 grains, and within the same period in the incubator lost 121 grains. The loss in weight is observed in eggs kept at room temperature. For two months one of two investigated eggs lost 96.5 grains, and the other lost 63.5 grains. To Oken's unsubstantiated suggestion about the nature of the chalazae, which ascribes to them a role in feeding the embryo, Pander responded with a simple but convincing experiment.

Oken's next question concerned the formation of the blastoderm, which Pander addressed by dismissing Oken's error on the genetic connection of the blastoderm and the yolk membrane. "The blastoderm," Pander wrote, "is an entirely isolated part, existing already in the non-incubated

33. Pander, "Entwicklung des Küchels," ISIS, v. 3 (1818), p. 512-524.

egg. It lies on the nucleus and is sharply distinguished from the yolk membrane by its non-transparency and by its loose structure. By lifting the yolk membrane from the yolk it remains lying there. The blastoderm grows hourly under incubation. Later it is composed of three layers—the serous, vascular, and mucous—and finally, after the disappearance of the yolk membrane, it contains the yolk in itself" (p. 514). Oken's response indicated that Pander's clear description had reached his consciousness. "This means that the blastoderm and cover do not have any relationship to the yolk membrane."³⁴

On Oken's question about the nature and destiny of the nucleus, Pander answered that the nucleus is represented in the form of a whitish cap and corresponds with the cover of the non-incubated egg. At the time of incubation, along with the growth of the blastoderm, it loses its regular form. By the seventh day it gradually disappears.

Oken asked what is situated between the blastoderm and the yolk membrane. Pander's response was: "Nothing; they are directly connected."³⁵

Concerning the relationship of the primary folds to the spinal cord, which Oken did not understand, Pander was not able to give a satisfactory explanation.

The next two questions, about the development of the heart and the digestive organs, Pander answered together. He noted Oken's mistaken idea about digestive canal formation as a blowing tube with a gaping opening. He objected to the non-empirical nature of Oken's stress on a sac-shaped beginning stage of development. "In order to understand the formation of the heart and the intestinal canal," Pander wrote, "it must be considered that the blastoderm is composed of three layers."

The lower one, membrana pituitosa, takes upon itself the formation of the intestinal canal;

34. Pander, "Entwicklung des Kùchels," p. 514.

35. Ibid.

the membrana vasculosa gives rise to the heart and blood vessels; and the membrana serosa is the source of the spinal cord, sides of the body, and amnion. All of this is made clearer by the drawings and descriptions given here.³⁶
(Figure 24)

Pander explained the blood system as corresponding to the four stages of its embryonic formation. The first stage, illustrated in Table VIII of the German version, leads to the formation of three blood passages: along the circle at the border of the vascular area (the border vein), along the branches connecting the border vein with the fetus, and along the vascular stem in the main body of the fetus. The upper or the descending vein (usually double) appears in the form of a stem from the heart-shaped curve of the border vein. The lower or the ascending vein always begins with many branches, passes above the arterial stem and, taking many lateral branches, connects with the upper vein near its entrance in the heart.

The second stage of blood-circulation development is characterized by gradual disappearance of the upper and lower veins. For this, particularly on the fifth day, veins develop and pass along the route of the arteries; however, the arteries are under the veins. This structure remains to the ninth day, and by the fifteenth day of incubation the vessels of the blastoderm become insignificant and then disappear. The arch of the aorta is formed from two or three branches which go out from the bulb (76). In the region of the heart depression, this single stem divides into two equal arterial stems, descending in parallel along both sides from the spinal column to the tail. The arteries going out from them at right angle Pander considered vessels corresponding to the iliac arteries of the developing animal. This, of course, is not accurate; this is the umbilical-mesenteric artery. Later all three veins join in the heart, which they enter by a common stem.

36. Ibid., p. 515.

Figure 24. "Ideal cross-section" by Pander.

- 1—*xxx*—a passage of the yolk membrane in the chalazae, in the nucleus of the cover; "blastoderm of non-incubated . . . (a gap in Pander's text);
- 2—blastoderm of the second day, composed of three layers; *cc*—the mucous layer; *dd*—vascular layer; *ee*—serous layer; *f*—fetus;
- 3—here the layer of the blastoderm is drawn so as to show the change of the serous layer, which at *gg* has formed the primary folds;
- 4—schematic presentation of the vessels of the layers of the blastoderm. The serous layer forms a fold on the tail at *n* and a fold on the head at *m*, and then together with other membranes it spreads in order to cover the yolk, which they cover more and more. The umbilical ring (*lk*) here is still very wide. Parts of the serous membrane *l* and *i* form the amnion, which will later extend through the back of the embryo and close by means of the adhesion of the borders of the folds (77). The vascular layer, following behind the serous layer, at *f* forms the heart and the large arteries which are its continuation, and at *g* (Pander is not sure about this) the sac of the chorion or the allantois. The mucous layer at *f* forms the food canal, and at *g* the colon, and between *g* and *f* it forms the middle intestine of Wolff (78);
- 5—A—longitudinal section, *c*, *d*, *e* designating the same as before; *hh*—level of the transverse section presented in 5B; *v*—area in which the heart and food canal develop; *w*—place of formation of the colon and apparently the chorion; *z*—spinal cord; *G*—view from below (from the side of the yolk) the embryo of 5A; *aaa*—area between *kk* in Fig. A (i.e. the umbilicus); *bbb*—the head portion (*gk* in Fig. A); *c*—the tail portion (*fk* in Fig. A); *dd*—the translucent spinal cord with the primary folds;
- 6—A and B—the same as Fig. 5A and 5B; at *ah* the vascular membrane has formed the heart (*y*); *z*—spinal cord; *x*—head depression of the yolk;

- 7—A—the same as Fig. 6A; the serous layer begins the formation of the amnion at the head (*f*) and tail (*g*) ends; B—*i*—the posterior end of the umbilicus; *g*—posterior end of the tail folds of the amnion; *h*—sac of the chorion;
- 8—later fetus; *a*—heart, transition into the vascular layer *dd*; *bb*—intestine, connected by means of the yolk—intestinal duct (which corresponds with the wide previous opening *kk*) with the amniotic layer *cc*, from which it is formed (79); *gh*—the gradually closing amnion;
- 9—still later stage; all the previous designations; between the intestine and the body of the embryo is the mesentery.

The blood movement takes place, according to Pander, in the following manner. The arterial division of the heart, "with surprising speed and strength" of contracting, sends the blood into the aorta. The push caused by the contraction spreads the blood along the arteries, it then moves to the venous branches and the terminal sinus. From the latter, the blood returns to the heart through the descending and ascending veins.

"The features of blood circulation," Pander wrote,

are so unusually magnificent that we invite everybody who has any desire to investigate nature not to miss the excellent chance given by the incubated egg to try to enjoy this excellent performance For this purpose it is recommended to take an egg of three days incubation, to open it in warm water, and to transfer quickly the blastoderm into a glass plate a little submerged in water under a complex microscope with a large optical field, and to observe under dripping warm water which preserves the movement of the blood.³⁷

At the stage described, Pander thought that there was still no portal vein. Oken responded that if the portal vein is not actually present, then there should be mesenteric vessels, or umbilical arteries; he reasonably asked whether the veins accompanying them are to be considered the mesenteric veins.

The third stage of development of blood circulation begins with the appearance of the chorion sac (h in 7B) in which the umbilical vessels mainly develop. When this organ dies off, the fourth stage of blood circulation begins.

Turning to the development of the amnion, Pander cited his drawings, which yield explanations as "the descriptions of the ideal sections." The explanations are given here in

37. Ibid., p. 520.

the form of a footnote to Figure 23, with few interpreted observations to interfere.

To a certain extent, the report of Kazan University Professor E. I. Eichwald (80), "Physiological investigations of the Human Ova,"³⁸ is considered a response to Pander. It was preceded by an extensive introduction in the form of a letter to Pander, in which Eichwald mentioned his studies on embryology ("Observations of the Developing Chicken Egg") performed in Petersburg under Pander's supervision. His interest in embryology led him to the comparative study of the ova of different animals and humans. His work contains few original observations and indicates insufficient acquaintance with the literature, but it has significance in that Eichwald tried to apply a comparative embryological method. He compared parts of the egg, especially the egg membranes³⁹ and provisory organs in different vertebrates (lizards, bony fishes, amphibia, reptiles, birds and mammals, and also in man), and he even tried to compare the eggs and embryos in vertebrates and invertebrates (insects, crustacea and worms). On comparing the structures of eggs or ova of different animals, Eichwald came to the conclusion that "if the yolk in birds is, like that of quadrupeds, amphibia, fish, crabs and insects, composed of numerous balls, then we can presumably conclude that the human ovum is composed of these same balls" (p. 7). Later Eichwald wrote in detail about the fact that all the layers of the blastoderm and the organs of the embryo developing from them "gradually develop from these primary balls, i.e. all the embryo from the beginning is composed of a granular mass." Thus Eichwald anticipated the cellular structure of the embryo, study of which became widespread in embryology under the later influence of the work of Remak, Reichert, Kölliker, and others.

Pander's embryological investigations had some effect on some of his countrymen working in entomology. Thus, a member

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38. Eduard Eichwald, "In ovum humanum disquisitio physiologica, Casani," (1824), ix + 29 pp.
 39. Eichwald refers, by the way, to the work of the great Professor L. Bojanus (L. Bojanus, "Über das Verhältniss der membrana decidua und reflexa zum Ei des menschlichen Embryo," Vilna, 1820).

of the Moscow Society of Nature Investigators, Gimmerthal, several times reported from Riga about his observations on the metamorphosis of flies (genus *Tachina*) and butterflies (*Naetua occulata*).⁴⁰

Another native of Riga, V. Sodovskii, later published a fairly extensive article about the development of butterflies, with comparative data on the structure of eggs of caterpillars and butterflies and of different scaly-winged insects. In the embryological part of this article Sodovskii discussed especially the process of covering the yolk with the blastoderm, and the development of two embryonic membranes—the amnion and the chorion.⁴¹

Pander's significant contributions begin with his definition of the meaning of the blastoderm. He was the first to define that each of the layers or sheets of the blastoderm (he frequently called them membranes) represent the rudiment of a certain system of organs of the developing chick. Therefore Pander must be considered the establisher of studies about the embryonic membranes. The Latin names which Pander gave the membranes—membrana pituitosa, vasculosa, serosa—remained in embryology for a long time; eventually the terms were replaced by the current non-expressive Greek terms—endoderm, mesoderm, and ectoderm—which do not allow such easy and clear translation.

Next, Pander discovered the primary folds which constitute the first signs of embryonic formation. In fact, Pander did not succeed in connecting these with the formation of the spinal cord, but his wrong interpretation played its positive role. Pander's observations allowed Baer to give the true interpretation. They were sufficiently accurate to eliminate confusion in the description of features, and only the interpretation happened to be wrong. Baer, on another occasion, sympathetically cited Bacon, who said that a mistake leads to the truth more quickly than to confusion.

40. "Métamorphose des insectes. Observations extraites des lettres de M. Gimmerthal à Riga," BULL. SOC. NAT. Moscow, I (1829), pp. 136-141.

41. W. Sodofsy, "Über die Metamorphose des Schmetterlings," ARBEITEN DES NATURFORSCHENDEN VEREINS ZU RIGA, I (1847), pp. 61-82.

To Pander belongs the immortal merit of extracting from oblivion Wolff's outstanding investigations. Wolff's report "On the Development of the Intestines" Pander understood more correctly than Meckel had in his German translation. Pander's controversy with Oken on intestinal formation had great significance and affected Baer's later work in this direction. Pander's schematic drawings showing the formation and closing up of the amniotic folds and his work on the vascular system are extremely close to Baer's corresponding results published eleven years later. It deserves astonishment that Baer, in his basic work "On the History of Development of Animals," does not even mention Pander's article in ISIS and its accompanying drawings. Knowing Baer's unusual kindness and his efforts to protect Pander's priority, it has to be assumed that he did not read it. That later on he became acquainted with this work is clear from his reference to the article in his autobiography (p. 302).

A comparison of the historical significance of Pander and Baer could be expressed in the words of Cuvier, which Baer quoted in his biography of the French naturalist: "I am only a Preparator, said he (Cuvier) in one of his lectures. Preparator is a predecessor to Raphael I am collecting material for the future great anatomist, and if this happens I want to be taken by him into his service in order to make for him the preparatory work." Such a Preparator was Pander for the great embryologist Baer. By this, his place in the history of embryology is determined.

CHAPTER 14

OUTLINE OF THE LIFE AND SCIENTIFIC ACTIVITIES OF KARL MAKSIMOVICH BAER

If K. F. Wolff is considered the central personality in embryology in the second half of the eighteenth century, then in the first half of the nineteenth century the Russian academician K. M. Baer was most significant. Baer devoted his long life totally to the service of science. Starting with questions of zoology, comparative anatomy, and especially embryology, Baer later concentrated on geographic problems, applied zoology and especially ichthyology, ethnography, and finally the methodology of the natural sciences, especially biology (81). The limitations of the present book permits us to judge only Baer's embryological work, with which he left the deepest and most permanent mark. A short biographical sketch will preface discussion of Baer's embryological investigations and his related theoretical ideas.

Karl Maksimovich Baer was born on February 17, 1792 in Pip in the neighborhood of Jerwen in Estonia. Receiving his early education at home, Baer then spent four years in the middle school in Revel (now Tallin). In 1810 he was admitted to the medical faculty of the university in Dorpat (now Tartu). Among the professors of Dorpat University who had an influence on the young Baer were (Karl Friedrich von) Ledebour, who taught zoology, botany, geology and mineralogy, and especially Karl Friedrich Burdach, who taught physiology and the history of evolution

In 1812, during the Napoleonic wars, where the army of Napoleon's General Macdonald besieged Riga, Baer and other Dorpat medical students volunteered to go to the fighting area, where they worked under very difficult conditions. They struggled with a typhus epidemic, and Baer himself nearly died of the disease. In 1814 he finished his medical education,

and on August 24, he presented his dissertation on "The Endemic Diseases of Estonians," after which he went abroad for advanced courses in practical medicine.

On travelling through Berlin in 1814 he met Pander, with whom he had studied at Dorpat University, and Pander warmly urged him to stay in Berlin to study natural science. "In Berlin," Baer wrote in his autobiography,¹

I met Pander, the future embryologist and paleontologist. He had been there already for one or two semesters and strongly urged me to stay in Berlin. He talked with admiration about the zoological museum, about the botanical garden and about the lectures he had heard. All that was very tempting, but I wanted to be a true practical physician and was afraid that these fascinations would be distracting. Hence I became hard and decided not even to look at these sirens. (pp. 205 - 206 (163) (150))

Instead, Baer decided to carry out his intended plan and departed to Vienna, where he was admitted to clinical studies. But soon he felt dissatisfaction with this work and learned that his true interests were the biological sciences. He then left Vienna to seek a German university where he could study comparative anatomy, in which he was

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1. NACHRICHTEN ÜBER LEBEN UND SCHRIFTEN. See footnote on p. 136. This was first given in the Russian language in 1950 (Academician Baer, K. M., AUTOBIOGRAPHY, edited by Academician E. N. Pavlovskii, Translation and commentary by Prof. B. E. Raikov, Edition of AS USSR, 544 pp.). After that the chapters of the present book devoted to Baer were written. On referring to AUTOBIOGRAPHY, citations are given to the pages in the Russian translation and the German original (in rounded brackets). (Ed.: Corrected page references to NACHRICHTEN ÜBER LEBEN UND SCHRIFTEN, 1864; Hannover-Döhren: Verlag Hannov. Hirschheydt, 1972, reprint of 1886 printing.)

especially interested. In the town of Wasserburg (Ed.: on one of his botanical expeditions in the Alps) Baer met the naturalists Hoppe and Martius; they advised him to go to Würzburg, to Döllinger.

When he reached Würzburg, Baer was depressed to learn that Döllinger would not teach comparative anatomy in that autumn semester of 1815. Döllinger, noticing the young man's depression, said to him: "Why do you want lectures? Bring some animal and dissect it, and another, and study their structure." Next morning Baer appeared in the laboratory with leeches bought from the pharmacy, and under Döllinger's supervision he started studying their anatomy. After that, he explored other invertebrates and read the monographic literature. Baer later remembered with gratitude Döllinger's assistance at the first stages of his independent studies.² In fact, in 1815 Döllinger had directed Baer's interest to embryology, although the circumstances were such that Baer's studies of the history of evolution came later on and were done entirely independently.

Besides working with Döllinger, Baer visited the obstetrical clinic of Siebold and listened to the course of Professor Wagner "which the students called Naturphilosophie, because all general ideas were considered Naturphilosophie and depended on a less solid basis," Baer wrote ironically in his memoirs.³ "I was very curious," he continued,

to follow the systematic work of Schelling's philosophy; one heard about Naturphilosophie everywhere and found it referred to in many books, without being able to understand it if one did study Schelling's systematically. I therefore registered with Wagner, although Döllinger had told me that I would not find too much there. Actually, I found a high-level, wonderful schema for all things and all relationships, to the extent that at the beginning I was attracted by its novelty. Soon, however, it seemed so empty

2. Baer, NACHRICHTEN, p. 227 (193) (168).

3. Ibid., p. 232 (182) (170).

and artificial that I could not listen to the course to the end⁴. . . . My thirst was quieted for a long time. Döllinger was himself in favor of Naturphilosophie; however, he was strict and substantial.⁵ (82)

On characterizing the ideas of his teachers, Baer wrote about Döllinger that

With philosophical views he looks at imperfections in understanding, without being able to fill the holes, which should be slowly begun by chemical and minute physical investigations. He never tries to fill these holes by means of philosophical deduction He had earlier diligently studied Kant, then was in admiration of Schelling, with whom he was particularly familiar Later he unwillingly spoke of this time and looked forward to the successful synthesis of physiology of specific observations with a philosophical spirit.⁶

It is possible to think that Döllinger's influence to a certain extent helped Baer to overcome the fashionable temptation of Naturphilosophie and to return to the strict and accurate studies of the features of nature. In this case he reached the ideas expressed in the following words: "The route from the particular to the abstract is not only the natural way, but also the most fruitful route, because only through the correct understanding of particular phenomena is it possible to come to correct abstraction."⁷ In another section of his autobiography, Baer again returned to his philosophical searching. At the beginning of his twentieth year, Baer sought a solid general basis for the problems of anthropology, psychology, and embryology. At one time he apparently thought that Schelling's philosophy could serve as such a foundation. About his search Baer wrote that

4. Ibid., pp. 232-233 (182) (170).

5. Ibid., p. 233 (182-183) (171).

6. Ibid., p. 252 (196) (184).

7. Ibid., p. 248 (193) (181).

Schelling's philosophy, I thought, cannot be so entirely empty as it was decried by some, because many scientists have felt the warmth of its rays. I have tried to study it, but by a short route, partly because my profession was far from philosophy and did not allow time to study all the series of Schelling's works or other natural philosophers, but partly because I was repulsed when I realized the foggy uncertainty The great distinctness of this expression and the sequence of the outstanding ideas in this work attracted me, but also often stimulated my decided opposition, for example with the negation of all limits and the absence of all quality.⁸

Naturphilosophie proved important for much of Baer's later work, especially his studied in anthropology and the history of evolution.

Before considering those later works, however, it is necessary to return to an earlier period. In the spring of 1816, Pander arrived in Würzburg, called there by Baer's cheerful description of the working conditions in Döllinger's laboratory. On Baer's recommendation, Pander accepted Döllinger's suggestion that he study chick development.⁹ Baer himself was very interested in this work but could not participate in it because he felt he did not have sufficient funds or time. At that time his former Dorpat professor, Karl Burdach, arrived in Königsberg and invited Baer to take up the responsibilities of a prosector there. Baer accepted in July 1817 and travelled to Königsberg.

In Königsberg, Baer first read the practical course of invertebrate comparative anatomy and by 1819 was considered an Extraordinary Professor of the zoology course. In subsequent years, the organization of the department of comparative anatomy and the zoology museum took much of his time (83). By 1826 Baer was already an Ordinary Professor of anatomy and director of the anatomy museum. His administrative

8. Ibid., p. 248 (193) (181).

9. See Chapter 12.

and teaching responsibilities did not hinder Baer from his unparalleled capability to study the development of different vertebrates, and also to perform a number of special investigations in zoology, comparative anatomy, and anthropology (84). In 1826 Baer, during the course of his embryological investigations, made a wonderful discovery by observing the ovum in the ovary of mammals. This discovery he reported the following year in an extensive letter to the Petersburg Academy of Science,¹⁰ which in answer selected Baer as corresponding member.

In 1827 the Petersburg academician, botanist (Karl Bernhard Trinius, suggested to Baer that he occupies Pander's position as an academician, since Pander had left his post. In 1828 Baer's election as a member of the Petersburg Academy of Science occurred, and by the end of the next year he arrived in Petersburg. Apparently, once there Baer could not satisfy what he considered the necessary conditions for work, and he returned to Königsberg, apologizing for his refusal of the academic post. In the following three to four years, Baer continued with his highly intensive study of embryology, and as a result the first volume of his classical work, ÜBER ENTWICKLUNGSGESCHICHTE DER THIERE, came to light in 1828. In order to accomplish this work Baer had to overcome considerable organizational and material difficulties created by the unfriendly attitudes of the Ministry of Education towards him. This strengthened his desire to return to Russia. Travel to the mother country and his family estate in Estonia corresponded with the second selection of Baer to the Petersburg Academy of Science, and from 1834 he remained permanently in Russia.

In Petersburg Baer was involved in various studies, which to a considerable extent drew him away from his embryological investigations. At this time he accomplished and published only some special work in embryology; his attention was particularly drawn to mutations, which he considered as interesting with the normal course of development. The study of mutations he considered important for promoting understanding

10. Baer, DE OVI MAMMALIUM ET HOMINIS GENESI. EPISTOLA AD ACAD. IMP. SCIENTIARIUM PETROPOLITANAM. Leipzig, 1827.

of the normal course of embryogenesis. Baer devoted much more time in Petersburg to geographical investigations, however, and he made a number of trips, with great difficulty, to Nova Zembla, to Chudov Lake, to the Volga, and to the coast of the Black and Caspian seas. From 1841 to 1852 Baer was a professor of anatomy and physiology in the Medical-Surgical Academy, giving much attention and time to his teaching activities. He also performed considerable work as director of the library of the Academy of Science. In the summer months of 1845 and 1846, Baer travelled to the Mediterranean (Genoa, Venice and Trieste), where he again studied embryology and made a number of interesting observations on the development of marine invertebrates.

Many times Baer gave public lectures and speeches. Among the latter, the speech entitled "A View of the Development of Science" given to the Academy of Science in 1836 had considerable importance. Similarly important was his speech, "The Correct View on Living Nature and the Application of This View to Entomology," given May 10, 1860 at the opening of the Russian Entomological Society, of which Baer was first President. These two speeches and others were later included in two collections of speeches and articles.¹¹

In 1862 Baer retired and was selected a member of honor in the Academy of Science. On August 18, he solemnly celebrated the fifty-year jubilee of receiving his doctoral degree. The hero of the anniversary, then seventy-three years old, gave a concluding speech at the ceremony interspersed with jokes. He invited all the participants to his next jubilee after another fifty years.

In 1867 Baer arrived in his native university city of Dorpat. Being unburdened there by any official responsibilities, he gave himself up to literary work by commenting on current biological science, particularly Darwin's theory, which already had received wide distribution. He also continued some historical work.

11. Baer, REDEN, GEHALTEN IN WISSENSCHAFTLICHEN VERSAMMLUNGEN UND KLEINERE AUFSÄTZE VERMISCHTEN INHALTES. Part I: REDEN, GEHALTEN IN WISSENSCHAFTEN VERSAMMLUNGEN, pp. vi + 296. Part II: STUDIEN AUS DEM GEBIETE DER NATURWISSENSCHAFTEN, pp. xxv + 480. Braunschweig, 1886.

On November 16, 1870, Baer died, after a short illness. He was only three months short of his eighty-fifth birthday. On the tenth anniversary of his death, the sculptor A. M. Opekushin, who also did the well-known statue of Pushkin in Moscow, designed a statue of Baer in Dorpat.

In his speech, "Features of the Activities of K. M. Baer and the Significance of His Work,"¹² the academician (Filipp Vasil'evich) Ovsianikov said the following:

The activities and work of this scientific genius, who died at the end of the past year in Dorpat, the Member of Honor of the Academy K. M. Baer, . . . must represent a great interest to all people of intellect. We have lost in him not only a first-class scientist, not only a great founder of scientific embryology, but also a man of the highest spiritual qualities, a man of deep interest to our country. (p. 1)

Highlighting the significance of Baer's most important scientific work, Ovsianikov in conclusion once again pointed out his greatness as a scientist and his grandeur as a man who had given all his life to the service of science, which he had considered the source of prosperity to people. "He lived not for himself, not for his family- he lived for science, for his country, and for civilization. He was not of Russian origin, yet it is rare to meet anyone who could have been as faithful to Russia and her interests as he was" (p. 24).

A concise but pithy outline of Baer's scientific activities was given by Dorpat University Professor E. Rosenberg, in a speech at the dedication of Baer's statue.¹³

A discussion of Baer's work in embryology should begin with his discovery of the mammalian ovum, then turn to review his greatest accomplishment, his ÜBER ENTWICKLUNGSGESCHICHTE, and also his remaining embryological and teratological work. At the conclusion, this account will consider his theoretical reports related to problems of the history of development.

12. Given at the beginning of 1877, published in 1879.

13. E. Rosenberg, FESTREDE AM TAGE DER ENTHÜLLUNG DES IN DORPAT ERRICHTETEN DENKMALS FÜR KARL ERNST VON BAER. Dorpat, 1886, 33 pp.



Die Wissenschaft ist ewig in ihren Quellen,
mehr erfindlich in ihrem Ursprung, eudoch in ihrer Ausprägung,
wenn sie nur in ihrem Geiste

Baer Blume auf die Entdeckung der Wissenschaft

Karl Maksimovich Baer

CHAPTER 15

BAER'S TREATISE DE OVI MAMMALIUM ET HOMINIS GENESI¹

From the time of Hippocrates and Aristotle to the seventeenth century, the idea predominated that the source for development of a new individual is some "generative material" which is present in the female sexual organs. It was considered analogous to the male sperm and was frequently called the female sperm. By extension, the ovaries were named the "female testicles." Following Harvey's statement that "all that is living comes from the ovum," the idea that the source of development for all animals, including mammals, is the ovum, received a wide distribution. Johann van Horn and Nicholas Stensen claimed that the ova of mammals are those early-opened follicles of the ovary. They contended that the ova (follicles) represent generative material for future generations, an idea supported in particular by the anatomist Ruysch. In accordance with the new point of view, the female sexual gland was named the ovary.

In 1672 (René) de Graaf played a very important role with his detailed study of the structure of the ovary. He actually discovered the ovarian cycle, i.e. the interrelation between the follicle and the corpus luteum. De Graaf thought that the ovum exists below the membranes of the mature follicle (Graafian vesicle); however, the nature of the latter remained unknown to him. From his investigations, de Graaf concluded that: "All animals in general, and in the same respect man himself, get their beginning from the ovum which is present (in the female testicles) prior to copulation." This statement formed the anatomical basis of Harvey's thesis, and at the same time was in agreement with predominating earlier ideas.

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1. (Ed.: Baer, DE OVI MAMMALIUM ET HOMINIS GENESI (Leipzig, 1827); translated by Charles Donald O'Malley, ON THE GENESIS OF THE OVUM OF MAMMALS AND OF MAN (Cambridge, Mass.: History of Science Society, 1956).)

Even within 150 years after de Graaf's work, when Baer began to study the initial stages of development, nothing had been added to the understanding of the nature of the ovum.

As mentioned above, Baer's report DE OVI MAMMALIUM was published in 1827 in Latin (Figure 25) as a letter to the Petersburg Academy of Science. The next year Baer published it in a reworked form in German.²

In the introduction to the jubilee edition in 1927, the translator (Ed.: into Russian), B. Ottov, confirmed that "among all the results of Baer's investigations, the discovery of the mammalian ovum occupies the most significant position." It is impossible to agree with this contention only because the classical work ÜBER ENTWICKLUNGSGESCHICHTE has still more significance. In the latter work, Baer actually established the basis for comparative vertebrate anatomy. Yet this assessment, of course, does not in any degree depreciate the value of the wonderful discovery of the true ovum in the mammalian ovary.

Baer gave a detailed account in his autobiography of the history of his embryonic investigations, explaining how he discovered the mammalian ovum. The main method of his work, which he frequently substantiated in his reports, was to trace the process of development in reverse chronological order; that is, to work from the already formulated condition of any system or organ back to its more primitive beginning. With his approach to the whole embryo, he could detect in the incubated bird egg the already developing rudiment, which had been named by previous embryologists the cock's trace or the cover (in recent terminology, the embryonic disk). He admitted that "how the cock's trace or rudiment is formed did not become completely clear to me, and it is, so far as I know, still not."³

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2. Baer, "Commentar zu der Schrift De ovi animalium et hominis genesi," ZEITSCHRIFT FÜR ORGANISCHE PHYSIK, v. 2, pp. 125-192. (85)
 3. Baer, NACHRICHTEN, p. 413 (309) (Ed.: p. 300 in German 2nd ed.).

Trying to clarify differences in development of different animals, after detailed studies of chick embryology, Baer turned to the study of development in invertebrates (isopodous crustacea, fresh-water and land molluscs) and also the lower vertebrates (salamanders and frogs). Baer wrote that "the development of mammals had especially attracted me in regard to the formation of the embryo itself as well as in regard to the formation of the ovum."⁴

Working first on dog embryos and concentrating on the early stages, Baer found very small semi-transparent vesicles at the end of the oviducts. Under the microscope he could detect rounded patches like that of the cock's trace, or even smaller non-transparent rounded bodies of a granular structure. "Thus I was led to find the ovum in this form as it lies in the ovary before fertilization. In order to show the importance of detecting the ovum, and in order to explain why I could not start the investigation from this end, I am allowing myself to refer to an older investigation."⁵

Recalling the greatest anatomist and physiologist of the eighteenth century, Albrecht von Haller, "a man of very extensive knowledge and almost incomprehensible diligence," Baer gave him credit for the investigation of heart and vascular development and also for the study of the formation of the skeleton. Haller's study of development of the mammalian ovum was unsuccessful, however; the investigations of Haller's student, the Russian physician J. C. Kuhlemann, conducted on forty sheep, were also without results.⁶ From these unsuccessful investigations Haller concluded that "the formation of the embryo takes place by coagulation of the fluid similar to crystallization." This point of view persisted because of Haller's almost unquestioned authority.

In the 1820s, some investigators supported the previously dominant idea that the origins of the primary ova are the Graafian vesicles, which are entirely separated from the

4. *Ibid.*, p. 421 (313) (306).

5. *Ibid.*, p. 422 (314) (307-308).

6. *Ibid.* (308). Johann Christian Kuhlemann, DISSERTATIO INAUGURALIS ANAT.-PHYSIOLOGICA EXHIBENS OBSERVATIONES QUASDEM CIRCA NEGOTIUM GENERATIONIS IN OVIBUS FACTAS (Göttingen, 1753), 60 p.

ovary and received in the oviducts. (86) Other observers considered this incorrect but could not find an accurate solution. Also, in 1797 (William) Cruikshank (87)⁷ reported that he saw the ovum in the oviduct of a rabbit within three days after mating. There, the ova were much smaller than the Graafian vesicles. At first, he was not believed, and Prévost and Dumas⁸ (88) in 1824 failed to confirm his observations on dogs and rabbits. Baer highly regarded the work of the French embryologists,⁹ but he contended that they were not concerned with the ova but with the early embryos.

Already in 1826, Baer had seen many times small transparent ova (1 - 3 mm in diameter) in the horns of the uterus and in the oviducts; in spring 1829, he observed significantly smaller and less transparent ova. He did not doubt that these bodies actually were ova, because he assumed that the yolk of the mammalian egg is non-transparent as it is in birds. Thus, Baer described how he accomplished this last step:

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7. William Cruikshank, "Experiments in which, on the third day after impregnation, the ova of rabbits were found in the fallopian tubes, and on the fourth day after impregnation in the uterus itself; with the first appearance of the foetus," *PHILOSOPHICAL TRANSACTIONS of the Royal Society of London*, 87 (1797), pp. 129 - 137.
 8. J. L. Prévost et J. A. Dumas, "Nouvelle théorie de la génération." *Deuxième mémoire*, "Rapports de l'oeuf avec la liqueur fécondante. Phénomènes appreciables, résultant de leur action mutuelle. Développement de l'oeuf des batraciens," *ANN. SCI. NAT.*, 2 (1824), pp. 100 - 121, 129 - 149. *Troisième mémoire*, "De la génération dans les mammifères et des premiers indices du développement de l'embryon," *ibid.*, 3, pp. 113 - 138.
 9. However, in the introduction to the second volume of *UBER ENTWICKLUNGSGESCHICHTE*, Baer talked about the mistakes of Prévost and Dumas in a fairly ironical tone.

DE
OVI
MAMMALIUM ET HOMINIS GENESI

EPISTOLAM

AD
ACADEMIAM IMPERIALEM SCIENTIARUM
PETROPOLITANAM

DEDIT
CAROLUS ERNESTUS A. BAER
ZOOLOGUS PROF. PUBL. URIS REGIOMONTANUS.

CUM TABULA Aenea

LIPSIÆ. SCULPTURUS LEOPOLDI VOSSII
MDCCCXXVII

Figure 25. Title page of Baer's treatise "De ovi."

In April or the first days of May, I discussed with Burdach that I could no longer doubt the origin of the ova from the ovary and that I very much wanted to obtain a bitch mated a couple of days earlier for the investigation Burdach had such a bitch in his house and sacrificed it. Opening it, I found some burst Graafian follicles and others that were close to bursting. On examining the ovary, I noticed in one follicle a yellow spot, and then saw the same in many others, but always only one spot. It was wonderful! I thought, what could this be? I opened a follicle and carefully carried the spot by a knife to a watch glass filled with water, then put it under the microscope. Looking into it, I jumped; how surprising the discovery was, because evidently I had seen a very small, distinctly formed, yellow yolk ball. I had to take a breath before being able to look again into the microscope, because I was afraid that my vision may have deceived me I saw in front of me a sharply outlined, regular small ball within a thick membrane, which was distinguished from the bird's yolk only by this rough shape, somewhat falling behind the external membrane. And thus the primary ovum of the dog was found! It does not float in an undefined position in the fairly viscous fluid of the Graafian vesicle, but is attached to its wall and held to it by a wide row of very large cells.¹⁰

With his report of this discovery, Baer wrote to the members of the Petersburg Academy of Science to express his happiness that he could publish his discovery under the auspices of the Petersburg Academy.

It is for whoever does not know how far Your Academy exceeds all others in its services to the study of the secrets of nature related to the formation of new organic bodies. The investigators who established

10. Baer, NACHRICHTEN, pp. 427-428 (311-312).

the first sound basis for the history of development of animals were members of Your Academy. First was Caspar Friedrich Wolff, the father of eternal glory, of whom in all the world I have seen very few so clever, nor have I seen his equal in decisiveness in investigating the most delicate things. I cannot pronounce his name without such reverence as we feel when we talk about the idea of the origin of good. Next, Christian Pander: it has always been my pride that I could give, though insignificant, a push to his wonderfully illuminating investigations on chick development. (p. 1).

In § 1, entitled "The Origins of the Canine Fetus," Baer gave a description of a three-week-old dog embryo, accompanied by life-size illustrations (Figure 26, 7), in 10x magnification from the side (Figure 26, VII a), and in transverse section (Figure 26, VII b). The description is accompanied by a comparison with the analogous stages of bird, reptilian, and amphibian development. Baer also referred to Wolff's treatise on the development of the intestine, to the German text of Pander's dissertation, and to the work of Prévost and Dumas.

In § 2, entitled "Primary Development of the Canine Ovum," he described still earlier ova extracted from the uterus.

Section 3 he entitled "Ovules in the Ovary of Dogs." It must be noted that Baer called the early rudiment of the developing embryo by the term ovum, still having a follicle form. The previous section was particularly concerned with those "ova." That which in modern literature is frequently called the ovum-cell Baer designated by the term small ovum, or ovule. First, he expressed his belief that the very ovules which he observed in the oviducts and uterus could not be made up from the ovary by the Graafian vesicles. He considered it unlikely that very compact bodies develop in the tubes as a result of coagulation of the fluid which comes out of the Graafian vesicles.

By examining the ovary with the naked eye, Baer saw in the intact Graafian vesicles a pale yellowish spot which, it seemed to him, swam freely in the fluid of the follicle and could be disturbed by pressing with a probe. His experiences are associated with the detection of the ovule, which he

explored by looking at it under the microscope, and Baer described it alive subsequently in his autobiography. Here, he only talked about how he was surprised at seeing the ovum in the ovary, which he already had observed in the ducts "so clearly that it can be seen by a blind man" (p. 12). The ovule had a diameter of one-thirtieth to one-twentieth of a Parisian line. On the surface of the ovule, there is a ring-shaped plate, which Baer called the *discus proligerus*.

In § 4, "How the Graafian Vesicles are Constructed and General Considerations on the Mammalian Ovule," Baer stated that, besides the ovaries of dogs, he had investigated the ovaries of cows, pigs, sheep, rabbits, hedgehogs, dolphins, and man. He was convinced that in all the mammals studied, the Graafian vesicles have an identical structure. Each Graafian vesicle has two parts—an enveloping part, or the shell (putamen), and the part included inside its nucleus. The first is composed of membranes, not related to the Graafian vesicle but to the ovary, and only a little raised by the follicle.

The membrane (indusium) covers only part of the follicle; it is composed of peritoneal epithelium (Figure 26, IX, 1) and of what is called cellular tissue, termed by some authors albuginea. This theca consists of two layers, an external and an internal layer. The external is thin and transparent, composed of compact cellular tissue. It receives the blood vessels and sends their terminal branches into the next layer. The internal layer is thicker, softer and darker; its internal surface is covered with delicate fibers. The external surface is firmly connected with the external layer. In the place of the future rupture, a thinning of the theca occurs as a transparent spot.

Related to the nucleus are the following: granular membrane, follicle fluid, embryonic disk, and the ovule itself. The granular membrane is composed of a thin layer of granules and includes the fluid content of the Graafian vesicles. The humor consists of fluid and granules swimming in it. In natural follicles, the fluid is yellow-colored, perhaps because of the yellow color of the granules. Boiling the fluid and the effect of alcohol cause the fluid to coagulate, which indicates its protein nature. The embryonic disk and the cumulus are in the fluid or on its surface. They consist of

white granules, distinguished by this color from the yellow granules of the fluid. With the maturation of the follicle, the embryonic disk gets closer and closer to the periphery. Finally, in the cumulus and in the embryonic disk it is sometimes possible to see the ovule itself. In all animals the round formed mass of the ovule has a dark center, and the transparent periphery is surrounded by a membrane (membrane corticalis). The size of the ovule in different mammals is different: the largest are in cows, sheep and swine; they are smaller in the rabbit and dogs; the smallest are in humans.

It is difficult not to be amazed by the accuracy of Baer's microscopical studies, which he accomplished not by the modern use of paraffin sections and selective stains, but by means of preparations with needles and examinations under the microscope. Comparison of Baer's data with modern ideas about the structure of the Graafian follicle leads to the conclusion that he succeeded in seeing all the constituent parts of the mature follicle. As a matter of fact, the terminology has changed only insignificantly. Baer's cellular membrane (indusium) is now called the external theca; the internal layer of Baer's theca, which contains the vessels, is called the internal or vascular theca. The transparent layer of Baer's theca presently is called the hyaline membrane. Baer claimed that the cumulus swims on the surface of the follicular fluid, while now it is known that it represents one unit with the granular membrane forming its thickening. The membrane, directly covering the ovum itself, which Baer called the cortical membrane, is now named the transparent zone.

Section 5 is called "A Brief Review of the Development of Mammals," since Baer considered it important to compare the development of mammals with the development of other animals. Because the ovule is invisible in the early stages of formation of the Graafian vesicle, and since investigations during that period **are** very difficult, Baer was limited to a hypothetical conclusion that the ovule exists in the Graafian vesicle before it is possible to detect it. He assumed that the ovule of mammals could be comparable with the Purkinje vesicles of other animals, such as molluscs and worms, in which features preceding the development of the ovum are observable.

Continued.

Key:

1* - ovum from the ovary of bitch with embryonic disc
(enlarged in 30 times):

6- 12th-day ovum of bitch with embryo (natural size) (from
Prevo and Dum):

VI - enlarged embryo of the same ovum;

7- nearly three weeks ovum of bitch (natural size);

VII a- embryo of the bitch; located on left side, after
removal of right half of cephalic vagina and right half of
intestinal sac (zaccus intestinalis): ab- passage of mucous
plate of the intestinal sac in the cephalic vagina; acde- cut
cephalic vagina; ef- right descending vein, recurved backwards;
f"- its original position; e g- auricle of the heart;
h- ventricle; ii- pericardium; k- bulb of the aorta; l- aorta;
mno- brain; m- ear and medulla oblongata; ep- commissure or
groove of middle intestine; arep- left side of the intestine;
step- its right side; gr- angle, in which the left wall of
the intestine passes to the intestinal sac; uvw- vascular
area; grw- transparent area; us- ascending vein; xy**- amnion;
2- urinary sac or allantois:

VII b- transverse section of the same embryo in the middle
of the back: -a- upper part of the back; ab- spinal (dorsal)
plate; bc- ventral plate; d- intestinal sac; e- passage of
the wall of intestine in the wall of intestinal sac;
de- limb, according to Wolff; f- intestinal commissure, by
Wolff; g- laying of spinal column; h- notochord; i- amnion;
k- spinal chord;

IX- middle sizes of swine Graafian follicles (enlarged
10 times): 1- peritoneal epithelium; 2- formative cover of
the theca; 3- external layer of the theca; 4- internal layer
of the theca; x- stigma; 5- granular membrane of the nucleus;
6- fluid of the nucleus; 7- embryonic disc; 8- ovary:

*In lettering on table of Baer, there is an explanation of
some parts of his illustrations only.

- X- Embryonic disc of the swine;
- XII- ovary of cow with embryonic disc magnified by 10 times);
- XIII- ovary of woman with embryonic disc and granular membrane (magnified by 10 times);
- XIV- corpus luteum of bitch (magnified by 10 times):
1- peritoneal epithelium; 2- formative cover; 3- external layer of the theca; 4- corpus luteum; 5- its opening;
6- albuminous mass; 7- scar of corpus luteum;
- XV- stigma of Graafian follicle (magnified by 10 times);
- XVI- embryonic layer from mature ovum of grass-snake (magnified by 5 times);
- XXIV- nearly mature ovum of *Rana temporaria*, sealed in diluted nitric acid and cut by longitudinal axis (magnified by 10 times);
- XXV- mature ovum of *Rana temporaria* with moved embryonic vesicle (magnified by 10 times);
- XXVI- the same ovum with driven out embryonic vesicle (magnified by 10 times).

At a later stage of development of the Graafian vesicle, its fluid content corresponds to the compact part of the protein in the chicken egg. Then polar differences in the fluid appear: on one side it is more transparent, and on the other there appears an aggregation of granular material. Thus, the cumulus is formed with the embryonic disk, and the ovule situated there becomes increasingly separated by the forming membrane. Next, the central area appears in the ovule since its granules become attached to the periphery. In this, according to Baer, the general principle of development in the centrifugal direction becomes apparent.

On the question about the origin of the corpus luteum, Baer disputed the current opinion that this was a new formation, unrelated to the Graafian vesicle. Instead, he tried to establish an indication that the corpus luteum resulted from growth of the internal layer of the theca in the empty Graafian vesicle. This completely corresponds with modern ideas, but now it is known that the hypertrophy of the corpus luteum walls takes place at the expense of the follicular epithelium, and not at the expense of the internal theca as Baer thought. The elements of the internal theca are only preserved in the radial connective tissue partitions, which correspond to the folds of the rupturing vesicle.

The ovule separated or released from the Graffian vesicle falls into the funnel in the fallopian tube and then into the uterus, where it is covered with fibers. The development of the embryo in the mammalian ovum, according to Baer, "was in the same manner as in birds." First of all, he claimed, the spina dorsalis appears.¹¹ From it grow the spinal plates (laminae dorsalis), which correspond to the primary or primitive folds (plicae primitivae) of Pander, and soon the ventral or abdominal plates (laminae ventrales). All vertebrates undergo one type of development, namely growing centrifugally; hence the two plates are directed upwards and form a plane for the spinal and head brain, and two plates are directed downwards. A plane for the internal parts and vascular stems forms there.

11. By this term Baer designated that formation to which, in ÜBER ENTWICKLUNGSGESCHICHTE, he gave the name accepted in modern embryology, primary region.

Baer followed these phenomena also in frogs, snakes, lizards, and birds. Although in fish he could not see the early stages, he nevertheless claimed that they do not constitute an exception. With Burdach, Baer observed development extending from the abdominal side to the spinal side in fish. These data Baer did not publish at the time, but in 1824, under the heading, "What Did the Notebooks of My Listeners Indicate?" (p. 24).

The last paragraph (§ 6) is entitled "Comparison of the Mammalian Ovule with the Ova of Other Animals." Regardless of the differences seen in the ova of different animals, there may also be significant similarities, according to Baer. It is common, for example, for the ova of all animals to have a nucleus, or, as Baer called it at that time, the Purkinje vesicle, named for the famous Czech physiologist who discovered this formation. Purkinje had described this formation in his HISTORY OF THE BIRD'S EGG BEFORE INCUBATION, which he dedicated to J. F. Blumenbach in connection with his fiftieth anniversary of scientific activity (89).

Baer indicated that in all the ova investigated, the Purkinje vesicle persists until the end of ovum development. In mammals, the vesicle is included in the cumulus. In the deposited ova and in the ova located in the oviduct, he never observed the follicle. According to Baer's observations, the follicle disappears earlier. For example, in insects it disappears while it is still in the ovary. Concerning the significance of the Purkinje vesicle, Baer suggested that "the Purkinje vesicle is the effective part of the ovum, by which the female faculty exerts its power, as the male faculty resides in the male sperm." Concerning the disappearance of the Purkinje follicle, which Baer designated as "throwing out" and "dissolving," it is "dependent upon the maturity of the ovum and upon the irritation After fertilization the blastoderm grows in the same place where the fluid content of the follicle was poured off" (p. 29).

Baer's words appear striking, especially his anticipation of the discovery of division of maturation and the theory of polarity of the mature ova. Actually, the expression "throwing out" of the Purkinje vesicle successfully describes the theory of separation of the polar bodies

which actually acts as if they are thrown out of the ovum. The expression "dissolving" of the vesicle indicates the disappearance of the nuclear membrane in the nucleus of the ovum in the metaphase of the division of maturation.

Baer's contention that the blastoderm develops in the place of the release of the Purkinje follicle is also quite correct. In the overwhelming majority of cases, the place of separation of the polar bodies is close to the animal pole of the ovum, i.e. to the same place where, in particular in the mesoblastic ova, the first blastoderms are settled.

Less accurate are Baer's discussions concerning the nature of the Graafian follicle. He called it an ovum and equated it to that follicle-shaped stage which is already observed in the fallopian tube or uterus, identifying the ovule as the Purkinje vesicle. However, on describing the ovule, Baer mentioned in one place (p. 18) the darker central and transparent peripheral parts of the ovule; in another place (p. 19), he said that a central area appears in the ovule which is free from granules, which remain at the periphery. From these descriptions it is clear that Baer had seen the nucleus in the mammalian ovum but was not sure if this formation were identical to the Purkinje vesicle of other animals.¹²

12. The modern terminology was introduced by P. G. Svetlov in a commentary on the second volume of ÜBER ENTWICKLUNGSGESCHICHTE (note 139, pp. 476 - 480).

CHAPTER 16

APPEARANCE AND SIGNIFICANCE OF BAER'S MAIN WORK ÜBER ENTWICKLUNGSGESCHICHTE DER THIERE

There is no doubt that the most remarkable incident in the history of embryology in the first half of the nineteenth century was the appearance of Baer's excellent work, ÜBER ENTWICKLUNGSGESCHICHTE DER THIERE, BEOBACHTEN UND REFLEXION. The first volume appeared in 1828; the second volume, not completely edited by the author, appeared in 1837; and the concluding notebook of the second volume was published by L. Steida after Baer's death in 1888.¹ Until recently all three parts of this work represented a bibliographical rarity, because they were never republished and they were not translated completely into Russian. Only in 1924 did a partial translation of part of the first volume appear.² In 1950 and 1953, the publishing house of the Academy of Science USSR issued translations of the first and second volumes.³

Following the title page of the first volume comes a dedication: "To the friend of my youth, Christian Pander."

1. Baer, ÜBER ENTWICKLUNGSGESCHICHTE DER THIERE. BEOBACHTUNG UND REFLEXION. Erster Theil. Königsberg, 1828, 271 pp. Zweiter Theil, 1837, 315 pp. Schlussheft, 1888, 84 pp.
2. Baer, SELECTED WORKS. TRANSLATION WITH INTRODUCTION AND NOTES. Yu. A. Filipchenco, GIS, 1924, 114 pp.
3. K. M. Baer, HISTORY OF ANIMAL DEVELOPMENT. OBSERVATIONS AND REFLECTIONS. First volume, Edition by academician E. N. Pavlovskii. Comments by Prof. B. E. Raikov. (ISTORIYA RAZVITIYA ZIVOTNYKH. NABLYUDENIYA I RAZMYRHLENIYA. Tom pervyi. Redaktsiya akad. E. N. Pavlovskogo. Kommentorii prof. B. E. Raikova). 150, 466 pp. Second volume. Edition of academician E. N. Pavlovskii and Prof. B. E. Raikova (Tom vtoroi, Redaktsiya akad. E. N. Pavlovskogo i prof. B. E. Raikova), 1953, 625 pp. Translation of the first volume was performed by I. I. Kanaev,

(... Continued on next page)

To him also was directed an extensive preface describing the history of the book and explaining the principles and terminology employed. In his preface, Baer recalled the happy time of his work with Pander in Döllinger's laboratory in Würzburg.

After his arrival in Königsburg in 1818, Baer received both the texts (Latin and German) of Pander's dissertation and noted there several conditions which appeared doubtful to him. In particular, he questioned Pander's ideas about "primary folds" and about the formation of the amnion. In the summer of 1819, Baer conducted an independent study of chick development, first with the objective of explaining to himself some obscure areas in Pander's work. He attained the desired clarity only after continuing his work during the next summer; already his investigations yielded so much profound material that he went on with embryological research, extending it from birds to other vertebrates, especially amphibia and mammals. One of the most important conclusions, which, in his words, "penetrated like rays of light," was "the idea that gradually in the embryo the vertebrate type structure develops." This idea was based on the theory of four types, established independently by Baer and by Cuvier.

His study of chick development led Baer to conclude that the course of embryonic development experiences strict regularity, an idea so simple that it causes surprise that no one had detected it previously. "Now one can be sure," Baer wrote,

when the course of development appears so simple that all is clear by itself and hardly requires confirmation through investigation. But the story of Columbus' egg is repeated every day, and what matters to me is only once to have placed it in the ring. How slowly one advances to gain knowledge of what is obvious, especially if the

B. E. Raikov and I. I. Skolov, with the cooperation of Yu. I. Polyanskii and P. G. Svetlov; translation of the second volume, Yu. M. Olenov, I. I. Skolov and B. E. Raikov, with the participation of P. G. Svetlov (90).

respected authorities object to it, I was sufficiently convinced of my personal experience.⁴

Baer continued his embryological investigations after an interruption for vast organizational work for the establishment of a zoological museum in Königsberg. His resumption of embryological work Baer credited to his colleague in the University of Königsberg, Professor Karl Burdach. Burdach undertook an extensive study under the title, DIE PHYSIOLOGIE ERFAHRUNGSWISSENSCHAFT (1826 - 27), and he suggested that Baer include his data in this work about the development of vertebrate animals. Baer agreed and gave Burdach a note containing the results of his investigations on frog and hen development, accompanied by a member of general considerations (91). These articles in Burdach's manual represent the first version of the ÜBER ENTWICKLUNGSGESCHICHTE.

Furthermore, in his preface Baer hesitated at some terms. In particular he spoke about the "embryonic membrane" (KEIMHAUT, or extra-embryonic blastoderm in modern terminology), then about the terms "dorsal and abdominal plates" which have significance for the comparison of vertebrate and invertebrate development, and finally about the replacement of the name "spinal cord" with the term "vertebral cord" in order to give it a more definitive localization and embryological importance.

Baer devoted several pages of his preface to explaining that he was little concerned with the investigations of other authors and referred to them only in cases of actual gaps in specific data. This does not mean, however, that he underestimated the value of his predecessors such as Wolff, Oken, Purkinje, and others. Detailed citations of others' works could have diverted him from his own specific details and systematic data, to which Baer aimed his fundamental work.

4. K. M. Baer. ÜBER ENTWICKLUNGSGESCHICHTE, I, p. 12 (p. viii). (Ed.: References are evidently to the Russian edition. The brackets represent pages in ÜBER ENTWICKLUNGSGESCHICHTE (Brussels: Culture et Civilisation, 1967, reprint of 1828 Königsberg edition). Hereafter listed without further specification as (v. #, section # (if any), p. #).)

He introduced controversy only on occasions of utmost importance. Then he disputed the opinion of only the most authoritative investigators, such as Wolff and Pander. "To object to work which disappears quickly without any trace is entirely useless . . . ," he wrote. "If it comes to frequently returning to any such work, confirming it or, on the contrary, disputing it, this only indicates the importance of this work."

Turning to the drawings accompanying his work, Baer remarked on the difficulty of combining in them documentary accuracy and clarity, and he confessed that he could not completely achieve such a combination. In difficult cases he sacrificed accuracy in favor of clarity. At that time, the difficulty of understanding the still very insufficiently investigated ideas of embryological development required clear, schematized illustrations.

In the conclusion to his preface, Baer justified including in his work a special section devoted to general subjects and representing a statement of his scientific belief in the history of animal development. The objective of publishing these general views was an attempt to promote other investigators to make more detailed studies of embryological problems. Even of Oken's fantastic ideas, Baer wrote: "Regardless of the fact that many of them now should be considered wrong, they have invaluable affected the history of development, because they led naturalists to a clearer understanding of the question."⁵

Possibly, more detailed study is no less important than achieving generality, especially for the earliest stages of development, Baer suggested. Thus:

That an understanding for the first days of development still lacks something, . . . you will at least suspect. And whoever remains in this difficult field, in which each branch seeks to be individual and carefully united, does not achieve all even if he tries hard all his life for the harvest; and who would not take away empty ears of corn for full ones? Kaspar Friedrich Wolff, who truly

5. (I, xvii-xviii).

performed the most complete anatomical investigations, made mistakes. Lucky is that person who succeeds in collecting the ripened shafts, which give fruit for future sowing I would be satisfied if my contributions were seen as having proven that the type of animal organization stipulates its development. Scientific accomplishments of others will be many. However, the palm of superiority will be attained by that lucky person who will relate the developmental powers of animal organisms to the general powers of life laws of the world. But the tree still does not grow of which this cradle will be made!⁶

With these deep and poetical words, the preface concluded.

F. Engels in DIALECTICS OF NATURE, speaking about the stages of establishing evolutionary theory, put Baer's name in one line with Oken and Lamarck; he considered Baer a predecessor of Darwin.⁷ Not without reason did Darwin's talented associate Thomas Huxley, who translated into English part of Baer's important publication, note that "it seemed a great pity that works which embody the deepest and soundest philosophy of zoology, and indeed of biology generally, which has been given to the world, should be longer unknown in this country."⁸

The embryologist Wilhelm Waldeyer, characterizing the condition of embryology at the beginning of the nineteenth century, wrote that,

6. (I, xxii).

7. Engels' authentic words about Baer are given on p. 204. (Ed.: Engels, DIALECTICS OF NATURE (New York: Publications, 1940), p. 13, intro.)

8. "Fragments Relating to Philosophical Zoology. Selected from the Works of K. E. von Baer," SCIENTIFIC MEMOIRS, edited by Arther Henfrey and Thomas Henry Huxley, art. 7, London, 1853, pp. 176-238. (Ed. Quotation p. 176.)

in those times there was a shortage of scientific investigations to cover all the history of development of one species; no comparative embryology was established, that valuable relation of embryology to morphology in general, as well as a sufficiently clear understanding of the great significance of this branch of knowledge for all studies about organic life. In this case there was also no commonly implemented terminology, and also no easily concluded and understood statement of the history of development such as the *Systema Naturae*, from which they could implement further follow-up investigations. All of that was given by Baer, and he can with great fairness more than anyone else be called the father of scientific embryology.⁹

Another known embryologist and histologist, Albert von Kölliker, in *GRUNDRISS DER ENTWICKLUNGSGESCHICHTE DES MENSCHEN UND DER HOHEREN TIERE*, has expressed the following about Baer's work: "Baer went on along the way of Wolff and Pander, and in the richness of the excellent he studied the facts as well as the reliable and broad generalizations; his work represents the best of what is available in the embryological literature of all times and people.¹⁰

In 1927, on the centenary of Baer's election to the Petersburg Academy of Science, the academician V. I. Verandskii wrote that

Of course the naturalist does not create a new branch of science from his mind; . . . He takes his and others' material, adds to it his impression, and under his steam the unformulated

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9. W. Waldeyer, "Über K. E. von Baer und seine Bedeutung für die Naturwissenschaften," *AMTL. BERICHT D. 50. VERSAMML. DEUTSCH. NATURFORSCH. U. ARZTE IN MUNCHEN, 1877*, p. 10.
 10. A. Kölliker, *GRUNDRISS DER ENTWICKLUNGSGESCHICHTE DES MENSCHEN UND DER HOHEREN TIERE. FÜR STUDIERENDE UND ARZTE* (Leipzig: W. Engelmann, 1880), 1884.

material becomes a constructed system, and the odd facts appear as a part of a unity of the whole critical thing This is what Baer accomplished in his uncompleted basic work about the development of animals which came out in the German language in 1828 - 37; the last part came out only at the end of the past century.

It is not surprising, therefore, that Verandskii put Baer on a continuum with Aristotle, Harvey, Lamarck, Cuvier, and Darwin, and among the Russian academicians Lomonosov and Eiler.¹¹

Baer's greatest contribution, which until now has still not been sufficiently evaluated in the history of science, appears in his *UBER ENTWICKLUNGSGESCHICHTE*. There he exhibited a tendency towards Naturphilosophie, to the extent that reaction to it was expressed as complete renunciation of his theoretical arguments and conclusions. The Naturphilosophie of Schelling and Oken proclaimed that the task of science was to look for the unified features of the world by thinking, through the creative activities of the mind.¹² "This situation," as noted later by Ya. A. Borzenkov,¹³ "had a very strong and highly ruinous effect on the study of nature. If nature is only an apparent object (discerned only by the impression of thinking, of the creative spirit), then . . . the nature investigator may not try hard to make observations and perform experiments,"¹⁴ because he is in a condition to understand nature regardless of his empirical activities. In contrast, empirical natural investigators such as Cuvier were opposed to Naturphilosophie *a priori*, resulting in their "nominating, classifying, and describing"¹⁵ without making any theoretical generalization.

11. V. I. Verandskii, "Memories of the Academician K. M. von Baer. First collection of the Memoirs of Baer." Moscow: Akademii Nauk, 1927, pp. 1-9.

12. To philosophy, nature means creative nature.

13. The historical outline of the directions existing in the zoological sciences in the nineteenth century. Speech given in ceremonial meeting of the Imperial Moscow University on January 12, 1881, by Ordinary Professor Ya. Borzenkov, pp. 1-61.

14. Borzenkov, p. 15.

15. Borzenkov suggested replacing this "slightly long motto by a shorter and more energetic one: Do not discuss!", p. 27.

In systematic zoology and comparative anatomy, the attempts to establish theoretical ideas depended not on arbitrary *a priori* assumptions, but on critical comparisons of strictly tested facts, performed by Lamarck and Geoffroy Saint-Hilaire from the beginning of the nineteenth century. In embryology, Baer solved this problem by achieving unsurpassed results. It is not accidental, therefore, that as a subtitle to ÜBER ENTWICKLUNGSGESCHICHTE he put the words "Observations and Reflections." In his book, Baer applied the richest empirical material, obtained by thorough observations, to his theoretical discussions, and thus suggested how investigators could delve into other aspects of biology.

In order to be convinced without doubt as to the correctness of the judgments of Baer and his work, it is necessary to have sufficient detail of his scientific heritage. The following chapters, 17 through 23, contain the actual contents of Baer's embryological and teratological works, and his most important theoretical general conclusions. The last chapter, 24, devoted to Baer considers his ideology.

CHAPTER 17

FIRST PART OF ÜBER ENTWICKLUNGSGESCHICHTE: DEVELOPMENT OF THE CHICKEN IN THE EGG

In discussing the history of chick development, Baer began with the first period of development of the incubated egg. To this description he prefaced a short introduction. Following Pander, Baer indicated that the temperature necessary for chick embryo development ranges from approximately 28° to 32° C. The temperature conditions distinctly affect the speed of development. Apparently contradictions in the data of different authors about the periods of development result from that difference; for even Wolff, who in Baer's words was an extremely accurate observer, had such contradictions.

Baer differentiated two types of deviations from typical development: irregularity of the general course of development in different eggs, and irregularity in the realization of different features in the same egg. Greater or less speed of development may depend upon the time of the year as well as the temperature of incubation, and especially upon how long the egg is kept before incubation.

Depending on how long the egg is kept, slowing of development may be fairly significant, especially during the first five days of incubation. Taking into consideration the existing variations, Baer divided development into three periods. The first period lasts approximately two days and ends with the complete formation of blood circulation. The second period has a duration of three days and involves circulation of the blood through the vessels of the yolk sac. The third period continues through the appearance of blood circulation in the lungs, that is, until hatching.

FIRST PERIOD OF CHICK DEVELOPMENT

Baer's description of the first period began with the events of the first day of incubation (§ 1) (Figure 27). He knew that development of the chick embryo begins even before incubation. Therefore he described the developmental process as a continuation of the separation, already begun, of the embryo from the yolk and the primordial membrane. (92) The embryo at that time becomes more compact and thin, and its center is raised in the form of an overgrowth. At about the twelfth hour of incubation one can detect the division of the primordial membrane into two layers: the surface layer, which is thin and dense, and a deeper layer, thicker and looser. Baer, in agreement with Pander, named the first layer "the serous layer" and the second "the mucous layer." Simultaneous with that separation, separation is also observed along the surface, so that the center becomes lighter than the borders. The light part (the area pellucida) changes form from rounded to oval, and then into a pear shape.

With the continuing separation of the rudiment from the underlying yolk, as a result of which the sub-embryonic cavity forms,¹ further separation in the rudiment membrane occurs: the dark border, surrounding the transparent embryonic area, is divided into concentric rings. At the same time, between the serous and mucous layers, a third "vascular layer" develops; therefore, Baer gave it the name vascular area (area vasculosa). The external ring adjoining the yolk he designed "the yolk area" (now called the "area opaca").

After the fourteenth or fifteenth hour of incubation, the first sign of embryonic organization appears, which leads to the appearance of the dark zone. Baer gave this formation the

1. It is possible not to stop at Baer's wrong idea about nutrition of the embryo by the fluid which, in his opinion, collects in the cavity of the white yolk, but which actually does not exist.

name it still has, the "primary zone";² it represents, in his opinion, the structure of the vertebral column and defines, by its location, the longitudinal axis of the embryo. (93)

From the primary zone, two longitudinal cylinders develop, called Pander primary folds. In Baer's opinion, these require another name, however, because they do not represent primary formations of the embryo and they do not represent true folds. A transverse section shows that these cylinders at first have internal and external slopes of similar form. Then the internal slope becomes sheer, while the external remains gentle. The tops of the cylinders become sharp, like a blade, and incline to each other above their division by a fissure; they merge so that the fissure becomes a closed tube. Baer called these cylinders "spinal plates or disks," from which develop the axial parts of the embryo, namely the central nervous system, the axial skeleton and the muscles. At the same time, the spinal plates develop; at the bottom of their dividing groove the spinal string or cord develops in the form of a central dark zone, situated along the axis of the embryo. This detection of the spinal cord is considered one of Baer's most important embryological discoveries, as he recognized. He likened the identity of the embryonic cord to the rods which a cartilaginous fish has throughout its entire life. The spinal cord, Baer said, "is not only an axis around which the first parts of the embryo develop, but also a true scale for the whole body and all its main system" (I, 1 1; p. 44 (15))³. With a preparation method using the thinnest dissecting needles, Baer could separate the spinal cord from its transparent but firm case and pull it out like a lace.

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2. Baer especially stressed that particularly the control zone, and not two parallel folds as Pander thought, represents the first organization of the developing embryo.
 3. Here and next; the Roman number means the volume, the arabic number and latin letter refer to the paragraph and its subdivision; the pages are related to the Russian issues of UBER ENTWICKELUNGSGESCHICHTE. (Ed.: references to German edition (p. #).)

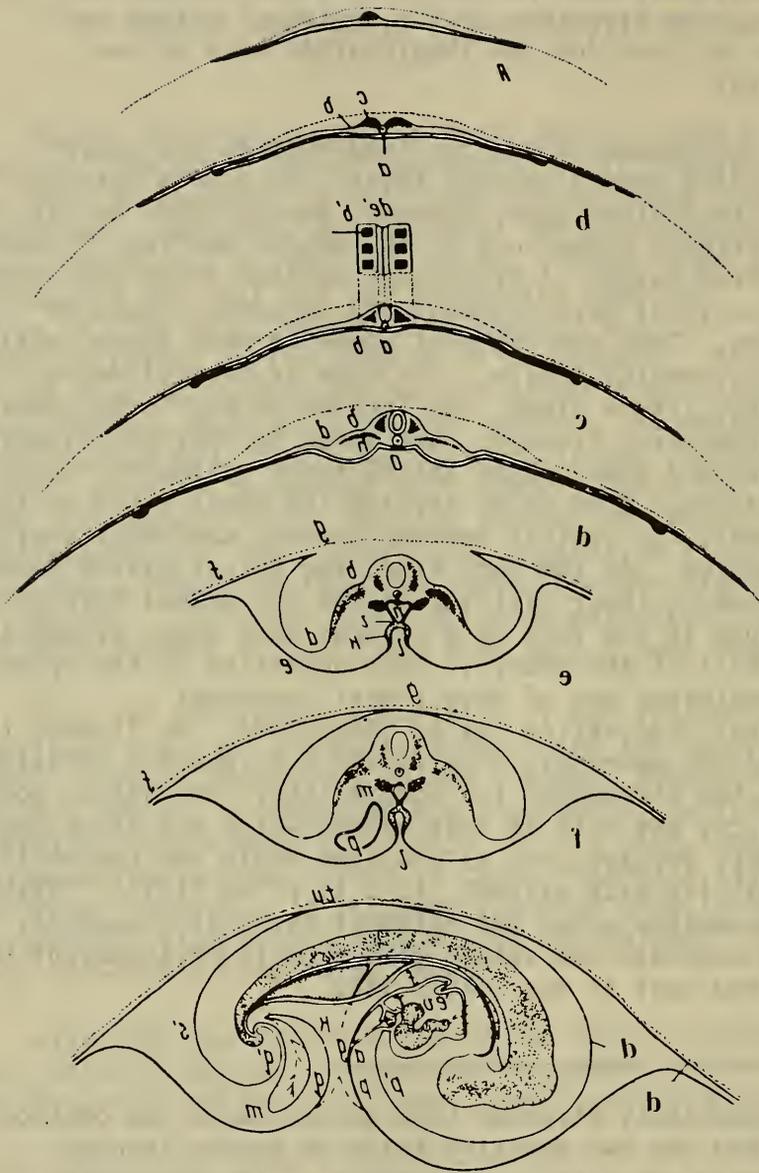


Figure 27. Baer's illustration from the first part of UBER ENTWICKLUNGSGESCHICHTE.

Figure 27. Baer's illustration from the first part of ÜBER
ENTWICKLUNGSGESCHICHTE.

1. Transverse section of the embryo in the middle of the first day.
2. Transverse section of the embryo in the second half of the first day.
3. Transverse section of the embryo in the beginning of the second day.
4. Transverse section of the embryo at the end of the second day.
- 5 and 6. Transverse section of the embryos in the fourth day (earliest and latest).
7. The same as in 6, longitudinal section. The designations on all the figures of the transverse sections (1-6):
a—spinal cord; b, b'—external border of the spinal plate; c—upper border of it; bc—spinal plate;
d—external, later lower border of the abdominal plate;
bd—abdominal plate; e—the bend of the serous layer;
de—skin part of the abdominal wall; f—border of the lateral folds; g—lateral part of the amnion folds; deg—amnion; h, i—upper and lower angles of the mesenteric plates;
k—vascular layer of the intestine; l—mucous layer of the intestine; lf—the false amnion of Wolff; m—Wolff's body;
o—aorta; p—urinary sac; n—opening the mesentery.
The designations on the figure of the longitudinal section (7): f—stomach; g—anterior entrance into the digestive canal; gk—the unclosed part of the intestine; e—respiratory apparatus; m—urinary sac;
p, p'—the band of the vascular, mucous, and serous layers; q—the transfer of the embryo into the caudal fold; pr—the head or cephalic fold; qs—caudal fold; tu—the closed anterior and posterior fold of the amnion; r, t, u, s—serous membrane, or the false amnion of Pander; v—auricle; γ—stem of the body vein.

On the first day of incubation, the growth of different parts of the embryo is already regular. Baer noted that the curving of the anterior end of the embryo does not represent a direct consequence of the intensified growth of the spinal plates. Instead, he wrote that "this change depends upon the deeper general foundation which is observed at every moment of embryonic formation to separate it from the surrounding parts of the rudiment and from the remaining egg."

"The (separation) thus depends: 1) on the growth of the embryo, which grows faster than its base (i.e. the region of the union of the embryo with the rest of the blastoderm—L.B.), as well as 2) on the regions of the initial narrowing, connecting the embryo with the primordial membrane; this narrowing becomes noticeable only in the second day" (I, 10; p. 47 (17)).

Further development of the spinal plates concludes with the final closure of the slits called by Baer the closure of the back, and their breaking up into separate straight-angle parts, described by Baer as the foundation of the vertebrae. This process, it is now known, does not represent the formation of the vertebral column, but the segmentation of the axial mesoderm into parts called somites. From the somites, or the primary vertebrae as they were named not too long ago, the vertebrae and the hard brain membrane develop, and also the muscles, the connective tissue layer of the skin, the kidneys and the sexual glands.

Summarizing the processes occurring during the first day of incubation, Baer then described the condition of the embryo at that time. The embryo has the shape of an inverted boat. Only the spinal part is distinct, with some pairs of the primary vertebrae; the abdominal side is still entirely unseparated from the primordial membrane. The separation of the embryo from the neighboring parts of the blastoderm takes place only in the anterior part. From all sides the embryo, which has no defined borders, is joined with the primordial membrane and contains the same layers as the latter. The mucous layer lies freely under the primary vertebrae, the region of which represents the most compact part of the embryo. The serous layer of the blastoderm continues into the smooth surface of the spinal plates. The loose layer of the vascular layer continues from the

vascular area outside the embryo into the embryo between the serous and mucous layers, indistinctly delineated from both. "All the rudiment," Baer wrote, "can be considered as the unformulated body of the whole animal, which appears as nothing other than a large unclosed intestinal sac" (I 1t, p. 51 (20)).

The spinal plates Baer considered the expansion of the serous layer; in a footnote (I 1t (20)), he discussed Pander's terms "serous layer" and "vascular layer" and approached a modern subdivision of the embryonic layers. Baer remarked that Pander's experiment "distinguishing the layers of the rudiment membrane was a turning point in the study of the history of development and was a true light for the latest investigation." Baer, however, considered that the early separation of the layers only serves as a preparation for future development.

Running somewhat ahead, he stated that at the end of the second day he could already clearly distinguish in both the embryo and the rudiment membrane the animal and its plastic or vegetative parts. The first consists of two layers, the future skin and the animal part of the body, and the second is composed of the vascular and mucous layers. And thus, the most characteristic picture for the first day of incubation, besides the separation of the layers, is the "growth of the embryo from the primordium which is yet on the anterior end, as a result of which the primordium is divided into the embryo and the primordial membrane" (I 1u, p. 52 (21)).

The extensive second section Baer devoted to the events of the second day of incubation which completes the first period of development. During the second day, the separation of the embryo from the yolk continues, which leads to the lifting of the anterior half of the body.

The previously described accretion of the spinal plates does not occur at the same time along the entire length; rather, it starts in the region behind the head and continues to the region of the future sacrum. The number of primary

vertebrae gradually increases so that by the end of the second day the number ranges from 10 to 12. In the head or cephalic region, the knitting spinal plates leave a wider canal, which indicates the location of skull cavity formation. At about the thirtieth hour, the separation of three divisions of this cephalic expansion corresponds to the frontal brain, the four-hillock ("VIERHUGEL"),⁴ and the medulla oblongata. On the sides of the posterior part of the frontal expansion, projections form which are the first rudiments of the eyes; at about the thirty-third hour, the frontal end of the embryo assumes a similarity to the head of a fly.

Baer concluded that the rudiments of the cephalic brain and eyes are hollowed vesicles, formed from an initially homogeneous tube. He asked, "What is the stimulus in that process of development?" The answer required an explanation of the further question, "What preexists in the canal prior to the appearance of the cephalic and spinal brain, and when and how do the central parts of the nervous system appear?" (I 2e, p. 56 (24)). Making sure that the spinal plates and even the brain vesicles do not contain "a compact primary mass," Baer concluded that "originally in the place of the cephalic and spinal brain, there is only fluid in the cavities. Under its effect, the initial bulging out of the eyes occurs" (I 2e, p. 57 (25)).

The abdominal plates begin closing under the vertebral column; this process takes place slowly and continues during the whole period of incubation. In the anterior part of the embryo, where its body is already closed, the abdominal plates form the lateral walls of the body. Wolff named this belt the abdominal plates, more appropriate than Pander's term of abdominal folds.

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4. (Ed.: It is not quite clear what Baer meant by these parts of the early developmental stage. Today embryologists refer to the 33-hour chick as having a prosencephalon (probably Baer's forebrain), a mesencephalon, rhombencephalon (perhaps together forming the "Vierhugel"?), and no medulla as yet.)

In connection with the bending of the anterior end of the embryo, under the head part an increasing deepening of the blastoderm appears in the form of folds. Baer called this formation the "head cap" (Kopfkappe) (I 2h (26)). The displacement of the top of the cap backwards denotes the separation of the head end of the embryo. The deepening of the mucous layer extends, forming the first rudiment of the digestive canal in the form of a blind sac. This sac opens downwards and backwards with a wide opening into the stomach. Baer called this opening the "anterior entrance into the alimentary canal,"⁵ suggesting his rejection of Wolff's inappropriate term *Fovea cardiaca*.

Between the close anterior ends of the abdominal plates, the vascular layer becomes thick and a granular mass appears in it, forming two lateral projections whose ends are directed backwards. This is the material for the formation of the heart. In the middle of the second day, the central part of the described rudiment becomes transparent; internally its contents become blood, and the external layer becomes the heart wall. At the same time, the central nervous system becomes independent. On the second half of the second day, at the internal surface of the spinal plates, a layer forms a hollow cylinder, the lateral walls of which are thickened. This is the fold of the cephalic and spinal brain. In the head division the future parts of the brain are originally one unclear mass. They then become separated by weak interceptors, which begin dividing into two hemispheres. The canal from the brain to the eye, which is the future optic nerve, remains hollow at this stage. The primary foundation of the ear begins to occur, according to Baer, in the same way as the formation of the eye rudiment, i.e. as a hollow outgrowth from the medulla oblongata.⁶

Turning to the foundation of the vascular system, Baer referred to Wolff's and Pander's observations on vascular growth. Confirming their observations, he remarked that the

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5. The term is kept also in the modern embryology.
 6. Actually, the rudiment of the internal ear (auditory vesicle) is formed from the unlaced deepening of the ectoderm.

fluid moving in the fetal area is colorless at first, even when the heart is already contracting. Only after pulsation begins is it possible to see the movement of red blood from the vascular area. Baer, however, was somewhat doubtful as to the accuracy of his observations. He was unsure whether he could talk about the movement of blood in canals which are still devoid of walls and therefore provide no clearly outlined route (I 2r, p. 69 (34)).

In the rudiment of the heart, the anterior canal grows into two thin branches, which disappear without reaching the roof of the digestive sac. The pulsation of the heart still pushes a colorless blood anteriorly, as in the heart of insects. In this period the heart is located directly under the future head and from both sides is enclosed by the anterior parts of the abdominal plates. Later on, it stretches forward from these plates and protrudes downwards. The canals coming out from the anterior end of the heart, Baer indicated, joint later, forming the beginning of the aorta. The heart becomes curved by the middle of the second day; by the end of this day it curves downwards and anteriorly even more, so that its ends come close together. Three pairs of arterial arches form, one after the other. Nearly in the middle of the embryonic body at that time, the entry point of the veins appears.

The initial condition of the other parts of the vascular system Baer described as follows. At the border of the vascular region, a blood receptacle forms as two semi-circles, at first without defined walls. This is the blood circle, which embryologists later called the border vein. Blood enters the middle of each semi-circular sinus and moves anteriorly and posteriorly. Anteriorly from the sinus go many vessels, flowing into a common stem which reaches the embryo (frequently there are two such stems). Vessels from the posterior part of the sinus merge into an ascending vein, which with the anterior vein pours into the left heart protrusion. The blood goes into the heart anteriorly and, passing through the stem, it goes out through three pairs of arterial arches which curve upwards and pour into two stems. These merge together at first, then they divide again along the way to the posterior end of the embryo. In the middle part of the body, they form two thick branches which reach to the border sinus.

Because of its expansion, the serous layer of the head cap completely covers the heart at the end of the second day. At the same time as the increase of the head cap, a caudal cap appears as a fold of the blastoderm; hence, in the posterior part of the embryo the mucous layer forms a pit which is the rudiment of the posterior part of the digestive canal.

The dropping of the abdominal plates leads to the subsequent separation of the embryo from the blastoderm. By the end of the second day, the place of the future mouth opening is seen; the head end of the embryo still bends downwards.

The general characteristic of the first period of development, Baer stated in § 3: "(The history of the first period shows that) the embryo is a part of the primordium which arises to a higher independence; that as this independence becomes expressed, the vertebrate type and development above and below that family stem emerges; and that there appears in the animal part the articulation which is characteristic of the . . . type" (I 3, p. 38).

SECOND PERIOD OF CHICK DEVELOPMENT

Baer considered the second period to begin with the appearance of blood circulation through the yolk vessels and to end with the development of the urinary sac, as the organ of respiration. This period extends from the third to the fifth day of incubation, and during this period the separation of the embryo and the formation of the temporary embryonic membranes also occurs (§ 4).

The events of the third day of incubation are stated in § 5. In this period only the separation of the embryo occurs, leading to the development of the chest and the lower part of the body, and at the same time the formation of the intestine and mesentery. The chest as well as the abdominal cavities form by the changing situation of the abdominal plates; the external borders of the abdominal plates become inclined increasingly downwards. At the same time the abdominal

plates split into two layers, the external and internal. Wolff described the corresponding changes completely and correctly but not perfectly clearly. Thus misunderstandings later occurred, caused mainly by Wolff's term "intestinal fissure." Actually this fissure represents the slit between the layers of the mesentery which later close up. Even Pander understood Wolff incorrectly, and did not know the fact.⁷ The results of Baer's specific investigations led him to conclude that Wolff's description was unclear only because he did not distinguish the mucous from the vascular layer. If Pander's discovery of the division of the embryonic layers was applied to Wolff's description, then everything would have become clear.

After the division of the abdominal plates into two layers, it is possible to see that the internal layer in its turn is composed of two layers—an external vascular, and an internal mucous (endoderm and visceral layer of the mesoderm). Subsequent to that in the external layer, two layers also become prominent: the serous sheet and the "generating tissue," forming, in Baer's opinion, the fibrous tissue, bones, muscles, nerves, and walls of the body (the ectoderm and the parietal layer of the mesoderm). This external layer of the abdominal plates, together with the spinal plates, form the animal part of the body. The internal layer of the abdominal plates forms the beginning of the vegetative part. Protrusion of the internal layer toward the yolk along the middle line where the vascular is not separated from the mucous layer, produce a longitudinal gutter, whose borders bend from the sides under the body of the embryo. These lateral plates Wolff had named the "false amnion," and the gutter itself "the mouth of the false amnion." Because the lateral plates join together anteriorly and move into the head cap, and posteriorly they join in the caudal cap, these lateral folds Baer called the lateral caps, or folds, which represent a part of the united common fold.

The parts of the internal layer of the abdominal plates, descending vertically to the yolk, form the layers of the mesentery which comes together shortly below (Fig. 27, 5).

7. Baer refers to this on page 22 of Pander's German dissertation.

The line of this union Wolff named a "junction." Wolff erred only in his indication that before the formation of the junction the space between the layers of the mesentery opens downwards, whereas actually it is covered by a mucous layer. Gradually the layers united below the mesentery begin to accrete with each other. This process proceeds along the long axis of the embryo, so that its variable stages can be seen on different levels of the same individual. In the anterior part of the body, where the digestive canal is already present, the layers of the mesentery envelop it, so that it is composed of the internal mucous canal and the external canal formed by the vascular sheet.

After the closure of the mesentery junction, the mucous and the vascular layers protrude upwards along the middle line of the body and form a gutter, the walls of which Baer called "the intestinal plates" (Fig. 27, 5) and the gutter itself the "intestinal gutter." It closes below but, as Baer wrote, "not by means of the middle junction, but in such a way that from both ends a lengthening of the already closed beginning and end parts of the food canal takes place to the middle" (I 5e, p. 84 (45)). By the end of the third day, only the third part of the length of the digestive canal remains, in the form of unclosed gutter.

Baer warned against the simplification of the process of intestinal formation which could be concluded from Wolff's description and his specific data. "It is logical by itself," he wrote, "that this protrusion must not represent a pure mechanical process through which the layers of the rudiment membrane, which were located earlier on one plane, must be later made up into folds; soon this protrusion is accompanied by organic growth . . ." (I 5f, p. 85 (46)). This warning is important because a half century later in embryology, the simple mechanical interpretation of formative processes was still widely distributed. For example, gastric invagination was understood as a simple protrusion of the vegetative hemisphere of the blastula, and the formation of the embryonic folds as a mechanical protrusion of the previously planar parts of the embryonic layers.

Baer considered the formation of the intestine, and the formation of the mesentery which precedes it, and at the same time the approach of the abdominal plates to each other as a

process of gradual separation of the embryo from the yolk, "as if an unseen hand outbalances the places of communication among the embryo, embryonic membrane and yolk" (I 5f, p. 86 (47)). In this case the protrusion of the mucous and serous layers takes place, and also the growth of the ends of the digestive canal.

At the same time as the described separation, the external edges of the lateral plates form the fold extending above the surface of the blastoderm, which spreads into the peripheral part of the blastoderm at first under a blunt, then under a straight, and finally under an acute angle. At the cephalic and caudal ends, this fold appears earlier and gradually becomes sharper. Baer considered that Wolff's term "false amnion" referred especially to this ring of the common fold.

The true amnion forms, according to Baer, from the serous layer (he gave it the still current name "amniotic fold"⁸). The ring of this fold becomes narrow above the back of the embryo, then by the end of the third day it closes, and the embryo appears included in a sac which is the true amnion.

At the time of the formation of the amnion, the head end of the embryo bends increasingly downwards. At the same time the head turns to the right, and gradually the whole embryo lies on its left side. The lateral projections of the heart, described previously (I 2q), are now transformed into lateral veins of the vascular area, and the common stem into which they pour forms the posterior end of the heart. The heart still has the form of a canal, which grows wide and bends a bit to the left, then strongly to the right and down. This canal continues to narrow, then moves left and upwards, where it divides into four pairs of arches. Between the vascular arches, the substance of the abdominal plates becomes thin, and three pairs of slits appear, leading from the outside into the digestive cavity or the future gullet. The crescent-shaped space between the slits Baer called "the branchial arches"

8. In fact the amniotic fold is composed from the ectoderm and the parietal layer of the mesoderm.

because "of their correspondence with the branchial arches of fish" (I 51, p. 94 (53)) (94). The arches of each side join at the dorsal side of the gullet in one vessel, which Baer called "the root of the aorta."

At this stage one can already give names to the individual parts of the vascular system. The veins going from the vascular areas in the abdominal cavity of the embryo are the umbilical-mesenteric veins; they represent the general system of the portal vein. In the embryo itself, at this time, the veins are not yet distinguishable. The heart is yet not divided into chambers. The arteries going out from the embryo are the umbilical-mesenteric arteries. The aorta branches first, beginning with the carotid arteries, and its terminal branches enter the urinary sac developing at that time. In the embryo veins appear, the jugulars appearing first.

The most important changes occur in the heart: 1) it gets displaced backwards; 2) as a result of its ends coming close together, the heart protrudes downwards more, moving between the abdominal plates; 3) it bends increasingly to the right; and 4) it begins dividing into chambers. In the venous part of the heart, two lateral widenings of the anterior part appear. These are the primordia of the auricles, actually ears, but the cavity of the auricles is not yet divided. Where the common venous stem contacts the digestive canal on the sides of the vein, pyramid-shaped hollow projections grow and acquire a leaf-shaped form enveloping the vein.

Turning to the development of the digestive canal, Baer objected to Wolff's and Pander's idea that "each part of the digestive canal acquires its individuality in the formative process and ... the stomach forms, the duodenum and so on." In contrast, he considered that the intestine "in the beginning becomes separated from all the other body by its common individuality; however, it still remains homogeneous in all its extension, and only later are the differences in its individual parts observed" (I 5r, p. 103 (60)).

Baer further described how the vascular layer of the digestive canal becomes swollen and gives rise during the third day to the lungs, liver, the pancreas, caecum and urinary sac, in whose formation the protrusions of the mucous sheets also

take part. Thus, the rudiments of the lungs appear in the form of two hollow cone shapes. They develop by the same method as the liver and the pancreas. The protrusions of the caecum do not appear earlier than the end of the third day; somewhat earlier, from the posterior end of the digestive canal a single projection, the future urinary sac (allantois), grows out. It is formed of two layers, an external vascular and an internal mucous layer.

In the second half of the third day, Baer detected the appearance of "Wolff's bodies," as they were called. They appear in the form of knotted thread-like cylinders in the corner between the mesenteric and the abdominal layers (Drawing 27, 6 m). At the same time, on the abdominal layer, the primary rudiments of the extremities appear with the initial form of narrow cylinders.

The spinal brain or cord during this period remains compressed from the sides, but the walls become thicker and subdivided into upper and lower layers. The divisions of the cephalic brain are still poorly differentiated. Backwards toward the marked hemispheres, the outlet of the optic nerves appears. At the lower surface of the hemisphere arises the basis of the olfactory nerve. In the eye, one can distinguish the retina and the lens.

The separation of the embryo becomes more and more distinct, because the ring-shaped interceptor between it and the rest of the egg becomes narrow, forming an opening which Baer called the umbilicus. A comparison of the successive stages shows that the umbilicus was previously the wide opening of the body. Even earlier, the umbilicus formed the whole circumference of the opened body. The external layer of the umbilicus is formed by the serous layer (Drawing 27, 7 p', q'), which from one side of the embryonic skin represents a continuous extension and from the other side a surrounding fold, i.e. the amnion. Inside the serous canal, which Baer called "the skin umbilicus" or "abdominal umbilicus," there is a tube composed of vascular and mucous layers, "the intestinal umbilicus." The mucous and serous walls of this tube form the passage of the vascular and mucous layers of the blastoderm into the corresponding layer of the digestive canal.

The cavity of the intestinal umbilicus connects with the intestine, and the gap of the skin umbilicus connects with the cavity of the embryonic body. Baer explained the origin of the abdominal cavity of the embryo with unusual perspicacity, stating that "it is nothing other than the union of both the gaps which were formed in the abdominal plates in the third day" (II 6e, p. 112 (67)).

Directly after the splitting of the abdominal plates, two abdominal cavities form as narrow slits (Fig. 27, 5). Then these slits become wide and between them a communication develops in the anterior part of the embryo near the heart. The separation into layers spreads from the abdominal plates through the umbilicus to the fold surrounding the body of the embryo. Therefore, the abdominal cavity at first was, to a considerable degree, outside the embryo and contained only the heart; later it included the intestine also.

On the fourth day, the embryo already has distinct rudiments of the extremities and tail. Its neck curves so strongly that the most anterior part of the head represents the transition of the spinal cord into the medulla oblongata. The heart and even the liver still are found in the neck region.

The digestive tube remains almost completely straight. In its anterior part, the throat cavity is defined, after which comes a narrowed short part, the esophagus, transferring into an elongated widening, the stomach. The duodenum ends at the "anterior passage." In the posterior part, the large intestine still cannot be distinguished from the small one, which ends anteriorly at the "posterior passage"; the posterior-entrance opening in this period has not yet appeared.

The lungs still connect with the digestive canal by means of a short respiratory tube. The liver plates increase in size, then envelope the portal vein. Inside the liver, the liver ducts branch and the veins undergo ramification. The urinary sac grows quickly in the second half of the fourth day and enters between the serous and vascular layers of the caudal and then of the lateral folds. Now it is transparent, and in its vascular layer the arterial network is distinctly seen. Inside each Wolff's body passes a longitudinal vessel with branchings.

In the vascular system during the fourth day, the following changes occur. The system of the portal vein clearly separates from the system of the hollow vein. The ears (auricles) of the heart increase in size, open into the common venous sac, whose walls are thickened and can now be called the auricle. Inside the ventricular chamber of the heart, a strongly marked fold appears.

Two primary arterial arches in the branchial arches become reduced, and the third and fourth ones are enlarged. In addition, the fifth arch appears. The first branchial slit closes, but posteriorly to the fourth arch a new slit appears, so there again appear to be three. The aorta branches laterally into the intervertebral spaces.

The extremities acquire the form of plates, situated in the space between the spinal and abdominal plates.

The changes in the nervous system during the fourth day are as follows. The lateral walls of the spinal cord still thicken; the upper and lower layers are divided by a groove. The cerebellum is already distinctly marked. The largest bladder in the cephalic brain corresponds to the four-hillock parts, in which a cavity appears. The third brain cavity goes down to the base of the skull and forms the cone of the brain. In the frontal and sincipital regions, one can distinguish, although still not completely, the lateral ventricles from each other by an upward hanging fold. The lower layers of the spinal cord clearly extends also into the brain at the bottom of the fourth ventricle and the cavity there, forming the cone of the third ventricle. The sensory nerves still have the shape of hollow tubes. In the entrances into the corresponding brain ventricles are seen the auditory nerve (in the fourth ventricle), the optic nerve (in the third), and the olfactory (in the lower surface of the lateral ventricle).

Summarizing his observations on sensory nerve development, Baer concluded, that they represent protrusions of the brain into the body mass, and the sensory organs represent a modification of the ends of the sensory nerves. This conclusion he presented most clearly, in eye development. The retina on the fourth day represents a thick-walled rounded structure, connected by a canal to the third brain cavity. Under the eye, there is a thickening, which represents the rudiment of the upper jaw.

The marked thickening of the first branchial arch indicates the beginning of its conversion into the lower jaw. The vascular area occupies somewhat more than half of the yolk circle by the end of the fourth day.

During the fifth day (§ 7), the separation of the embryo reaches the greatest degree, and the urinary sac becomes the organ of respiration. The intestinal umbilicus becomes narrow and is transferred into the yolk duct. The anterior and posterior entrances into the digestive canal join together so that the gutter-shaped part of the intestine disappears. The urinary sac, very rich in blood vessels and on the right side of the embryo between the amnion and the serous membrane lying above it, extends to the surface of the yolk in the form of the serous layer of the ectoderm. At this point, the embryo is so distorted that the head and tail come in contact with each other. The body cavity still forms somewhat at the neck, but the liver is already placed in the body.

One can easily distinguish the esophagus, stomach and intestines, and the respiratory tube from the esophagus. In the region of the developing pancreas, the primary intestinal loop corresponding to the duodenum forms. The caecum and large intestines are still poorly developed, but the posterior passage opening is already present in the form of an umbilical slit. The Wolff's bodies are strongly enlarged and extremely rich in blood. On their internal surface, the rudiment of the sexual glands appears as a longitudinal strip.

In the heart, at the "central venous sac" (auricle), the beginning of the extension is marked. A partition divides the "heart chamber" (ventricle) into two parts connected by an elongated opening. In the stem of the aorta are two orifices.

The extremities lose their leaf-shaped form and become chisel-shaped. In the shoulder and thigh, dark patches form the rudiments of skeletal elements; correspondingly, in the forearm and shank two dark strips appear. The upper jaw has

the form of a shield, which becomes elongated opposite the frontal projection; thus it appears doubly split.⁹

A special membrane covers the spinal cord. The cerebellum in the embryo at that age projects considerably farther. The canal between the cerebellum and the four-hillock structure extends more than before; this corresponds with the posterior part of the water passage (urethra). The vesicle of the four-hillock structure is strongly enlarged. The cavity, corresponding to the third brain vesicle, grows insignificantly, but its bottom becomes elongated. The brain stalks become more prominent than before, and become the brain stems. The external membrane of the eye splits into two layers: a hard membrane whose continuation is the cornea, and a vascular membrane.

Section 8 concludes the second period of development. Here, Baer distinguished three types of processes: a continuing separation of the embryo and its envelopment by membranes; the separation of the vegetative from the animal part; the turning of the embryo to the left and the displacement of the blood supply to the left side. The final process represents the progressive process of internal differentiations, which are entirely characteristic of the vertebrate type.

The separation (unlacing) of the embryo from the blastoderm outside the embryo takes place by the appearance of folds— anterior, caudal and lateral, all representing parts of one common fold, which is transformed at the final end into the umbilicus.

The turning of the embryo to the left side, and the corresponding displacement of the vessels, Baer compared to the particularities of development in molluscs. Observing the similarity, Baer made a reservation: "It is impossible, however, to say that the chick embryo is now present at the level of development of molluscs. Against that, the presence of the vertebral column, the spinal cord, and the brain are a definite proof" (I 8 c, p. 142 (89)).

9. This fits the description of the development of the face skeleton of the chicken embryo given by Tredern and his drawings (see pp. 125 - 126 and drawing 18).

At the beginning of the third day, the chick embryo contains all the existing features inherent to the vertebrate animal in general. By the formation of the urinary sac, the embryo already shows the features of the land vertebrates.

THE THIRD PERIOD OF CHICK DEVELOPMENT

Baer divided the third period of chick development into six stages. The first, described in § 9, continues through the sixth and seventh days. At this time the size of the air cavity increases further. The allantois passes the embryo in growth, penetrating between the serosa and the amnion.

The beginning of the third period corresponds to the first movements of individual embryonic parts. Its form changes somewhat, the curvature in the neck region particularly decreasing. The trunk grows wide as the liver increases and the heart drops, but the volume of the head remains not less than the size of the trunk. The umbilicus now represents not a single opening or ring, but a short canal, which gave Baer the basis to discuss the presence of an umbilical cord in birds.

The vascular area of the yolk occupies more than half its surface; its vessels (border, ascending and descending veins) begin to disappear. The part of the umbilical vein, which goes to the hollow vein after branching into the liver is comparable, according to Baer, to the ductus venosus Arantii in mammals.

In the abdominal plates, covering not more than half the walls of the cavity, the rudiments of the ribs assume the form of dark strips. At the upper arches of the vertebrae, bony protuberances form.

The extremities increase in dimension and distinctly break into four divisions. The elbow and knee joints are directed externally ("as in the majority of amphibia"). With the exception of the terminal divisions, the anterior and posterior extremities are similar, as are the terminal parts, except for differences in the wing, where there are three fingers, and the leg, where there are four or five fingers.

The facial parts undergo the following changes. The frontal projection between the olfactory depressions elongates. The projections of the upper jaws grow, reaching the frontal projection by the seventh day. Since the upper jaw projections do not reach the end of the front projection, wide slits form and connect from both sides with the mouth opening. The lower jaw forms from the primary branchial arch, then becomes enlarged and pointed at the end. The foundation of the tongue appears.

The esophagus becomes elongated; the gizzard is displaced to the left; the glandular stomach is already marked separately, but not sharply limited from the gizzard. The intestinal loop sits behind the stomach (the duodenum). The next loop, the beginning of the small intestine, enters the umbilicus. Part of the small and the large intestine forms the last curve of the intestine, or the whole remaining intestine. The respiratory tube elongates; the lungs are completely distinguished from the esophagus and are divided into anterior (larger) and posterior divisions. The larynx appears in the place of the passage of the respiratory tube into the throat.

From each Wolff's body, Baer observed a sudden appearance of a thickly walled canal, which passes along the Wolff's body and parallels that canal in many fishes which extends from the abdominal cavity to the sexual orifice. This canal, thin at the anterior part, becomes lost somewhere near the auricle. Its posterior end can be traced to the point where it falls into the cloaca. Baer concluded from an error that the Wolff's body forms the blood-carrying vessels. Observing on the seventh day the presence of many ducts going from the Wolff's body into the canal mentioned earlier, Baer stated the possibility that this canal also represents a modified blood vessel. Since the walls of this canal are very thick and its diameter is large, Baer came to the conclusion that the described canal represents a sexual duct. Baer did not resolve the contradictions of the vascular origin of the Wolff's body with other peculiarities. Thus he stated that "the method of forming the Wolff's body remains so far unclear"(I 9 q; p. 154 (98)).

In this place, Baer's investigations reveal with great clarity his thoroughness of observation, his carefulness in conclusion, and his readiness to withdraw inaccurate conclusions.

In the vascular system at the start of the third period, Baer noted the change in the heart as well as its location and structure. Further development of the partition extends to the stem of the aorta; at the end of the seventh day, the stem widens and reveals two canals coming from the right and left chambers of the heart.

The nervous system has the following features. The hard and soft brain membranes remain distinctly separated from each other. The trunk part of the spinal cord has thickenings where nerves exist from the extremities; however, the thickenings which correspond to the anterior and posterior extremities directly cross each other. The spinal cord nerves, regardless of their insignificant thickness, could extend a fairly great distance. In the brain, the predominant part is the four-hillock structure, connected with the cerebellum. The deepening of the fissures between the divisions of the brain leads to their great separation. Inside the brain, the lateral ventricles appear. The funnel of the brain is well developed, the brain appendage still not clearly separated from it. Anterior to the funnel, there is a projection from which the optical nerves go out, which do not yet form the actual crossing. Baer investigated the condition of the visual organs in detail. He noted a cored entrance in the optical nerve, the nerve itself already compact. The retina remains very thick, thicker than the cover of the brain hemisphere. The vascular membrane of the eye is completely separated from the still very thin hard membrane, whose continuation is the cornea. The openings of the external ear lie above the mouth slit. The openings of the Eustachian tubes lie close together. The olfactory depressions become deep; the nostril passages go to the outside from the space between the upper jaws and frontal projections into the mouth cavity.

The second stage of the third period of development is described in § 10, continued throughout the eighth, ninth and tenth days of incubation. At this stage, the vascular area covers about three fourths the surface of the yolk. The border vein disappears entirely; the veins and especially the arteries of the vascular area narrow considerably.

The urinary sac, in the form of a closed vesicle, covers a great part of the yolk sac. One surface of the allantois lies adjacent to the amnion and yolk sac; the other surface, richer in blood, is adjacent to the serous and shell membrane.

At the ninth and tenth day, the feather appears on the skin cover, at first on the middle of the back and thighs; the rudiments of the rudder feathers are especially marked. The differences between the anterior and the posterior extremities become more distinct. The elbow now is directed backwards, and the knee anteriorly; after the eighth day, the fingers are differentiated; on the tenth day, the terminal divisions of the extremities completely acquire the features of the wings and legs.

The abdominal plates in the anterior part of the trunk become closed. At the place of the closure or junction, the chest becomes established. Baer followed the trunk nerves throughout their extension during this period. In connection with the study of the development of nerves, he raised the question, do they grow out of the spinal cord or grow into it? The centrifugal direction of development of the head nerves ("nerves of the sensory organs"), Baer presumed, does not suggest that the same method of development occurs in the spinal cord nerves. He suggested that the development of the nerves does not take place in either the central nervous system or in the muscles. He wrongly concluded that the nerve develops along all its extension at once by its separation from the producing tissue.

The muscle fibers become noticeable after formation of the cartilage. At the beginning, they appear in the region of the thighs and shoulders, and then in the forearm and shanks. Ossification begins in the extremities, first in the large tibial bone, then somewhat later in the femur and fingers of the feet.

The internal structures change in this stage more than in others as a result of the backward displacement of the heart, liver and stomach.

The glandular stomach is still not clearly distinct from the gizzard, which in general is characteristic of wild birds. The distinct separation of these parts, characteristic of

grain-eating birds, appears later. Starting with the eighth day, the crop appears clearly as a widening in the esophagus. The liver becomes less red in color than before as a result of the growth of the parenchyma and the narrowing of the blood vessels. The gall bladder then appears. As a result of the intensive growth and branching of the respiratory tube, the lungs develop quickly. "All their dispersion," Baer wrote, "represent on the tenth day an extensive picture" (I 10n, p. 173 (112)). Next he observed the foundation of the air sacs, the lower and upper larynxes.

The kidneys become shorter, as a result of which the ureters are clearly seen. Simultaneously, the Wolff's bodies decrease in size. In male embryos the Wolff's bodies are symmetrical, and in female the right one is somewhat smaller than the left. The testicles acquire a bean-shaped form, and the ovaries the shape of a triangular plate.

The vascular system does not undergo major changes. From the five pairs of arches existing from the beginning, the first disappears. Then the second disappears. Later, the fifth left arch disappears; the aorta still has two roots which are somewhat shorter than before.

Among the parts of the brain, one sees the most intensive growth in the region of the large hemispheres, which increase in size in all directions, especially in the direction of the four-hillock body. Behind the latter, the cerebellum has a clearly seen central lobe (the little worm). The brain takes the appearance of a fibrous structure, in the form of separated thick bundles. The brain base also has crossing fibers. This study of the optic nerves led Baer to the conclusion that sensory nerves grow from the brain.

The skull maintains the skin consistency. The regions of the wedge-shaped and occipital bones appear more compact, and so does the auditory capsule.

The eyes, whose size Baer considered "almost monstrous," occupy more than half of the whole head. By the end of the tenth day, a skin edge surrounds them with a little fold, which later provides the beginning for the nictitating membrane. The hard membrane of the eye is very thin. The retina forms a growth immersed in the hyaline body; the iris remains colorless.

The third stage of the third period of development (§ 11) covers days 11 through 13. The yolk sac starts to diminish as a result of yolk consumption. The vascular area occupies nearly the entire surface of the yolk and forms wrinkled folds immersed in the yolk mass. Baer considered these folds analogous to the intestinal folds of the lower vertebrates; they play the role of intestinal fibers. The urinary sac surrounds the yolk and the amnion. Hence, its opposing borders coincide and accrete together. The internal wall of the allantoides protrude into its cavity in the form of a fold-structure rich in vessels, sometimes called the chorion. The fluid of the allantoides contain flake-shaped lungs of the urinary precipitates. In the walls of the amnion, narrow vessels are distinguishable. The embryo moves more actively. The beak and the claws become horny.

Through the umbilical orifice, a twisted loop of the intestine hangs over, its length at that time significantly increasing. The abdominal plates have almost grown to the umbilicus, leaving around it an elliptical area covered only by the peritoneal membrane. From the substance of the abdominal plates themselves, cartilage, muscles and nerves are already formed. Ossification of the skeleton progresses quickly; however, Baer could not determine regularity of this process. The points of ossification in the vertebrae lie inside their bodies. The narrowing of the spinal cord relates to the ossification of the spinal column, which occurs backwards from the anterior end.

The organs of digestion intensively show the processes of differentiation. In the wall of the esophagus, longitudinal folds appear; the wall of the crop thickens and is accompanied with mucous glands. From the right of the muscular stomach (gizzard) the duodenum proceeds, and the loop envelops the pancreas. The growing liver pushes the remaining part of the intestine backwards and downwards, as a result of which the small intestine moves into the umbilical orifice. The gall bladder assumes a gray color, while the bile penetrates the stomach and the duodenum. The cloaca acquires a folded internal surface and is joined by the stem of the urinary sac.

The lungs firmly join the chest cavity, with deep marks of the ribs noticeable. The surface of the lungs begins as broom-shaped or velvety, because the terminal tubules hang

above it. At the thirteenth day, the ends of the tubules become welded together, while the surface of the lungs becomes smooth again.

Further differentiation of the vascular system leads to the anterior part of the body, which becomes supplied with arterial blood from the left ventricle; both ventricles supply the posterior part.

In the brain, the four-hillock body has the shape of two widely separated follicles. Anterior to them lies the big brain, and the cerebellum is situated posteriorly; as a result, the whole brain, according to Baer, resembles the outlines of the ace of clubs.

The iris of the eye begins pigmentation from the side of its pupil border.

The auditory canal is situated in the open furrow of the wedge-shaped bone and is covered in obliquely located drum membranes.

During the fourth stage, from the fourteenth through the sixteenth day of incubation (§ 12), the urinary sac covers practically the entire egg contents: the greatly wrinkled yolk sac, the embryo and most of the albumen. It represents an intact membrane adjoining the shell membrane and carries the name "chorion."

Since it will soon move out of the shell, the embryo undergoes active respiratory movements. Some intestinal loops hang from the umbilicus, which soon begin to be gradually drawn backwards into the abdominal cavity. The feather rudiments elongate but still do not appear clearly.

The organs of respiration, the kidneys, the central nervous system and the eyes continue developing, not undergoing remarkable quantitative changes. Differences in the sexual apparatus become more distinct. At the entrance to the nostrils, the scales characteristic of the chicken family appear.

The stage before the last stage (fifth) of the period described (17 - 19th day) is characterized by the following features (§ 13). The yolk sac becomes empty and divided by one or several deep folds. The quantity of the urinary precipitates in the cavity of the chorion (allantoic cavity) increases. The albumen is almost completely absent, while the amniotic fluid also diminishes. The loops of the intestine situated outside the abdominal cavity continue retraction backwards, attracting the yolk surrounding the mucous and vascular sacs. The feather rudiments are very long, but the feathers do not yet appear.

The last stage (twentieth and twenty-first day of incubation; § 14) is considered the preparatory stage for hatching. The fluid from the cavity of the amnion and chorion has almost disappeared. The embryo occupies nearly all of the egg cavity with the exception of the air sac. The yolk sac is gradually pulled into the abdominal cavity. It is possible to observe the stage when the yolk sac is present half in the abdominal cavity and half outside it, and they are connected by a narrow neck, situated in the umbilicus. At that time, the umbilical orifice becomes tightened and begins healing.

The arteries which connect the aorta with the pulmonary arteries contract, forming a boat-like duct.

The movement of the chick's head ruptures the chorion. In this case, the end of the beak penetrates the air chamber, which makes breathing possible. A first squeak accompanies the breathing. Baer sometimes heard the cheep of the chick still in the unbroken egg shell two days before hatching. Sometimes the movement of the head breaks the shell, after which breathing and the first squeak occur. After that, breathing begins with atmospheric air; the vessels of the

chorion, which were previously filled with blood, then become abated. The chorion becomes separated from the umbilicus, and the chick breaks out of the egg.

The general characteristics of the third period of development of the chick embryo Baer gave in his concluding section (§ 16) of the first part. His first concluding point leads to the assumption that during the third period of embryonic development the embryo gains predominance over the remaining parts of the egg. If at the beginning the embryo represented a part of the rudiment, then the latter now becomes a part of the embryo. The parts of the egg from which the embryo became separated in the second period now gradually become embedded in it. Baer identified the same three stages of separation: the separation of the embryo from parts outside itself, their retraction inside, and, finally, life outside the egg, in which the animal is no longer part of the egg, but becomes dependent on the outside world.

Another important point of the concluding paragraph established that development represents a transition from the general to the special. While in the second period the embryo acquires features which are general to all vertebrates, in the third period it reveals the particularities of birds ("the chicken becomes a bird") in the features of its respiratory system, extremities (wings) and covers (feather rudiments). "However, from the beginning it is a bird in general, and not a bird from the family of chickens." Gradually, the features of land birds appear (shortening of the interdigital web or membrane); then, the features of chickens can be distinguished (form of the head, the separation of the glandular stomach from the gizzard, blunt claws and scales above the nostrils). At the time of hatching, the generic feature appears (the comb on the head) while the individual particularities develop outside the egg as the chick reaches its maturity. The general conclusions given here by Baer are very briefly illustrated in the second part of the work.

CHAPTER 18

SECOND PART OF ÜBER ENTWICKLUNGSGESCHICHTE: SCHOLIA AND COROLLARIES TO THE HISTORY OF CHICKEN DEVELOPMENT IN THE EGG

Baer called the second part of the first volume of his work "Scholia and Corollaries" (95). In spite of that name familiar to medieval students, it does not contain dogmatism originating from any preconceived point of view, but penetrating thoughts on the basic regularities of chick development. These represent generalizations of those observations stated in the first part.

The first scholium, "On the certainty of observations on embryos," poses a question basic to arguments by embryologists from the seventeenth century. Specifically, is it possible to confirm that the embryo exists only from that time when it, as a whole, and its component parts become accessible for observation? Because of the narrowness of investigative means, Baer asked "whether all the embryo with all its parts can be there, but so finely structured that it is not accessible to the knife and microscope" (I 212 (143)).

With the example of muscle development, Baer proved that the embryo as a whole does not acquire parts with minute structure, and dimensions are beyond the limits of microscopic powers. While the muscular fibers of the adult chicken can be split into very minute fibers, seen only at very high magnification, the embryonic muscle fibers are accessible for observation under lenses, although they are still not formulated and can be separated from each other only with difficulty. The same thing applies to the nerve fibers and other component structures of the embryo. Baer's general conclusion opposed the opinions of the preformationists, leading to the assumption that the large size of the embryonic component elements "undoubtedly makes

impossible the existence of the embryo in a preformed shape in the second and third generations" (I Sch Ia 214 (145)).

The second scholium, "The formation of the individual in relation to its surrounding," discusses two questions, concerning the essence which manages the development of the animal, and about the most essential result of development, the progressive independence of the embryo. Desiring to "clarify the essence of development," Baer stated that "although each new step in development becomes possible only because of the pre-existing condition, nevertheless the entire development is directed towards the prevailing essence of the animal" (I Sch IIa, p. 217 (147)).

This situation is illustrated by the significantly greater variability of the embryo than of the adult organisms of the same species. Noticing the frequently deep differences between embryos of one age, Baer wrote that "one must conclude that the differences are compensated for, and each abnormality, as much as possible, will return to the norm" (I Sch IIa, p. 218 (148)).

From the fact of this remarkable regularity which is inherited by developing embryos, Baer concluded that "not every stage is like the others with all its particularities determining the future stages of development, but here more general and higher relationships predominate." And further: "Natural science, which is readily identified in that it feeds and supports materialistic ideas, can, as a result of observations, disprove the strict materialistic studies and lead to the evidence that not the material but the essence (the idea according to the new school) of the developing life form governs the development of the fetus" (I Sch IIa 148).

Commenting on this point in the Russian version of Baer's work (pp. 218 - 219 and note 43, pp. 450 - 451), B. E. Raikov considered that "Baer's presentation clearly reveals the idealistic character of his view about the factors of development." This requires an explanation, however, in order to reject the charge of the influence of Naturphilosophie and followers of Schelling on Baer during the early years when this science was very popular. Objecting to the "strict materialistic studies" of life phenomena, Baer addressed the

materialism of the beginning of the nineteenth century, which is now called mechanical or metaphysical materialism. It is not surprising that Baer's deep intellect could not be reconciled with the primitive simplified ideas about development coming out of the general principles of this materialism.

Baer's negative relationship to materialism was characterized by his concern about complex life processes, for which he sought other than dead mechanical schemes. The possibility of real scientific solution to the questions interesting him in the first half of the nineteenth century was not yet available, however. Instead, Baer was faced with idealistic ideas, diligently propagated by the departments of German universities. From Baer's endorsement of idealism comes the beginning of his views about "The general and superior attitudes" about the "essence" or "notion" governing the development of individuals. Baer's idealistic discussions frequently go against his specific ideas about ontogenic development, which are based on strict and accurate observations.

On a much greater level, Baer's idealistic opinions on the evolution of the organic world remain consistent. Admitting the natural origin and development of living creatures, because otherwise a miracle would be required, Baer limited the evolutionary process to lower systematic groups and did not extend the idea to his types. In relation to the mobile powers of evolution, Baer, especially in later years, decisively objected to Darwin's materialistic point of view. His question about evolutionary opinions extends, in general, beyond the limits of the present book and requires further specialized study.

The second question discussed in Baer's second scholium concerns the most important result of development as a whole, "the increasing independence of the developing animal."

The main stages of chick embryo development, discussed in detail in the first part of the work, include the following: 1) growth of the rudiment (blastoderm), whose unlimited part constitutes the embryo; 2) separation of the embryo from the remaining rudiment, but with the embryo remaining subordinated to and supplying the rudiment with nutrient materials; 3) the separation of the embryo from the egg parts outside the embryo,

but with the embryo still supplying nutrition and constituting one unit with those extra-embryonic parts; 4) the inclusion of the individual extra-embryonic parts of the rudiment within the embryo (by immersing the remaining yolk in the embryo's abdominal cavity) and the separation of the embryo from the remaining parts (amnion and allantoides) upon hatching. By this, according to Baer, "the last stage of the growing independence" is attained.

His comparison of the development of birds, amphibia, fish and mammals led Baer to conclude that in amphibia from the beginning, the embryo is very large in comparison to the yolk mass; to achieve independence, it does not require separation (unlacing) as other embryos do. Bony fish hold an intermediate position between the birds and amphibia in this respect, with only insignificant unlacing. In mammals, the separation and the covering with membranes takes place more quickly than in birds and results in an especially long umbilical cord in the most highly organized representative of mammals, the human.

This early separation of the mammalian embryo from the yolk sac does not contradict the truth that for all vertebrates the embryo constitutes a single unit with the blastoderm and yolk. Fertilization of the egg, which was previously a part of the mother, produces an independent unit, similar to the parents; the features of this unit appear during the process of development.

In lower animals, according to Baer, there is no separation of sexes, and reproduction occurs only by growth beyond the limits of the individual. Baer developed this erroneous idea in the special supplement to his second scholium in "Corollaries about reproduction." There he tried to discredit the data about parthenogenesis in vertebrates, and with perplexity he dealt with facts about the parthenogenetic development in the plant louse and certain butterflies. The difficulties which Baer met in the interpretation of features of fertilization he explained with the standard knowledge of the time.

The third scholium, "Interior transformation of individuals," concerns those routes along which the embryo develops. Baer stressed that individual development at all stages proceeds from the homogeneous to the heterogenous, from the general to

the specific. Baer distinguished three forms of transition from the general to the specific in ontogenetic development, or three forms of differentiation: the primary, histological, and morphological differentiations.

The first type, primary differentiation, comprises the division of the blastoderm into layers, which Pander had called plates. At first, two layers appear. The external layer Baer called the animal layer, and the internal layer he called the vegetative, or the plastic layer. In the animal layer, a skin layer and muscular layer become differentiated; they are composed of the spinal and abdominal plates "which include in a nondifferentiated shape the bony, vascular and muscular systems with the corresponding nerves." The vegetative part also differentiates into two layers, the vascular and the mucous.

In an article supplementing the translation of the first volume of ÜBER ENTWICKLUNGSGESCHICHTE, B. E. Raikov¹ successfully compared the subdivision of the blastoderm into embryonic layers as suggested by Pander, Baer, and later by Remak; illustrating his comparison with a table² (96). The comparison reveals that Baer's identification of the rudiment layers with the embryonic layers, in the modern meaning of that term, constitutes an incorrect interpretation of primary differentiation. Bischoff³ and Filipchenko also discussed this issue.⁴

It must be added that Baer's designation of two embryonic layers between the skin layer (ectoderm) and the mucous layer (endoderm), and not only one "mobile-rudiment layer," as Remak later identified it ("mesoderm," according to modern embryology), indicate Baer's cleverness in observation. He was capable of

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1. B. E. Raikov, "On the life of scientific activities of K. M. Baer" (Ozhizni inauchnoi deyatel'nosti K. M. Baer), in K. M. BAER (1950), pp. 383 - 438.
 2. *Ibid.*, p. 419.
 3. Theodore Bischoff. ENTWICKLUNGSGESCHICHTE DER SÄUGETHIERE UND DES MENSCHEN (Leipzig: Voss, 1842) (Vol. VII of "Anatomie" edited by Zemmering).
 4. Translator's note: K. M. Baer, SELECTED WORKS, translation with introduction and comments by Yu. A. Filipchenko.

distinguishing the two layers of the lateral plates of the mesoderm, which are now named somatic and splanchnic mesoderm. (97)

Baer also related the separation of the vertebrate central nervous system rudiment into layers to primary differentiation. Baer remarked that the skin and nervous layers originate from the upper surface of the embryo, so his point of view concerning the source of the central nervous system remains unclear.

The second type of differentiation, histological differentiation, already occurs inside the layers, as a result of which the skeleton, muscles, nervous system, and blood form.

The third type of differentiation, the morphological, produces the external shape of the embryo. After that occurs the embryonic layers are transformed into tubes; the separated parts of these tubes acquire different configurations and serve as a source for the organs. Thus, the neural tube subdivides into the spinal and cephalic membranes and the organs of sense. The mucous tube gives rise to the mouth cavity,⁵ the esophagus, stomach, intestine, respiratory organs, liver, allantoides, and so on. Morphological differentiation takes place, according to Baer, due to the irregular growth of individual parts of the nervous, mucous and other tubes. By irregular growth, Baer could explain the apparent demarcation of one section of the tube from another; for example, the divisions of the brain from each other, the stomach from the intestine, and also the localized protrusions giving rise to the sensory organs, respiratory organs, liver, and allantoides.

The three forms of differentiation described represent, according to Baer, a source of heterogeneity of the organism. Early in development, heterogeneity of the organs and their constituent histological elements is less marked. "Observations," Baer said, "show more than any description can that

5. It was not known to Baer that the mucous membrane of the mouth cavity originates from the ectoderm.

all individuality is at first contained in the general" (I Sch IIIa 156). This pre-existence of individuality in the general, though not of course in the sense of primitive preformation, others might consider an argument against studies of new formation. But Baer disputed this point of view.

Study of histological differentiation shows that new structures form not at an empty place, but by transformation of the previously existing simpler and homogeneous formations. The modern embryologist could describe the phenomenon of cartilage formation in the extremities, for example, as the transformation by condensation of mesenchymal cells into cartilage. The same also relates to morphological differentiation, because "each organ is a changing part of the more general organism." Baer illustrated this with the example of respiration development. When the lungs develop as outgrowths of the mucous tube, there is already an elevation between them which, after stretching, forms the trachea.

Another example concerns the development of the extremities. Their first appearance could be called a new formation; however, the skin layer which is separated from the spinal and abdominal plates in the region of the future extremities already contains primitive structures which initiate the formation of extremities.

In opposition to Serres, who considered that organic growth is represented by the union of initially isolated elements, as with crystal development, Baer confirmed that the formation of an organ, like the formation of the whole embryo, involves a sense of preformation. "The absolute beginning of the process," he asserted, "is always imperceptible" (I Sch IIIf, 157 - 158).

The development of the whole embryo and its organs universally occurs, in Baer's opinion, from the center to the periphery, but the universality of this idea seemed similar to the constructions of Naturphilosophie which were in general so foreign to his thinking. In his next scholium, Baer objected to this centrifugal character of development. This fourth scholium, with its two corollaries, is called "On the scheme which vertebrate development follows."

Turning to the first step of development (Sch. IV, § 1), Baer remarked that the breakdown in the rudiment and embryo follows one plan, but in different directions. Thus, in the rudiment and the rudiment membrane, differentiation of thickness develops along the surface and the length. Finally, the fetal area is most developed in the anterior region, and the vascular in the posterior region.

The differentiation in thickness leads to the separation of the animal part of the embryo, and also the vascular and mucous layers. Differentiation along the surface delimits the embryonic body and the vascular and yolk fields from each other; in length such important parts as the brain and skull, heart and intestines becomes separated. The transformation of the layers of the rudiment into the embryonic body, according to Baer, proceeds from the surface to the interior. At first, parts of the serous layer are differentiated, then formation of the heart and aorta begins in the vascular layer, and only later the mucous sheet begins to form the digestive tube. Along the length and breadth of the embryo, differentiation proceeds in defined succession from the anterior backwards and from the middle to the periphery. The successive processes of separation of the embryo occur in the same order. The conversion of the layers into tubes is accomplished in vertebrates by a double symmetric development from one axis (I Sch. IV 2a, 143).

Baer first stated the idea basic to comparative embryological investigation, that the three methods of differentiation just mentioned are apparently inherent to all animals except the simplest. Also, for the vertebrates, in his opinion, it is characteristic that the processes of formation follow the principle of double symmetry in relation to the longitudinal axis of the body. The upper or animal layer forms a tube by rolling up this layer above the axis of the body. Describing this idea in the chick embryo, he also confirmed it in the frog embryo and expressed his certainty that in the other amphibia, fish and mammals development follows that same scheme.

After formation of the spinal tube under the cord, which lies along the axis of the body, the abdominal tube forms by the union of two symmetrical halves. In transverse section, the vertebrate embryo assumes the form of a figure eight.

In the process of fusion of the upper as well as the lower parts of the embryo, the layers separate and acquire the form of tubes inserted into each other, which Baer called the basic of fundamental organs.

The mucous layer forms the internal tube of the abdominal half of the embryo. This fundamental organ Baer called the mucodermal tube. It begins material exchange with the external environment, specifically with the organs of digestion and respiration. The vascular layer in the abdominal half covers the mucodermal tube and forms two tubes: one lies above the intestine and the other surrounds the intestine. From this duplicated vascular-dermal tube, the blood vessels form. The lower muscular layer of the animal layer also forms two tubes: the spinal one includes the neural tube, and the abdominal includes the previously mentioned two vascular-dermal tubes. By means of histological differentiation, the muscular layer divides into the dermofibrous and the specific muscular layer. The central nervous system and skin also form tubes: the skin tube envelops both muscular tubes. Both have a common origin in the separated upper layer of the animal part of the germ. Part of this initially single formation appears in the interior (the neural tube) and part remains at the periphery.

The fact that these tubular basic organs are located one inside the other, but become separate as different parts undergo different activities, Baer tried to explain by the polar opposition of their vital properties. This idea of opposition as a source of formation undoubtedly has a nature-philosophie character, and Baer considered it an echo of the effect of Schelling and Oken on him. Baer, being sufficiently sceptical about Naturphilosophie, nonetheless tried to find in such ideas a rational seed and to use them for the discussion of the phenomena he sought to understand.

Baer used his scheme of embryonic development from systems of tube-shaped basic or fundamental organs to establish a general plan for the organization of vertebrates. Still more important for this plan of organization Baer considered the axes and planes of symmetry. Referring to his schematic drawings, Baer described the relation of the basic (fundamental) tubes to the main axis of the body.

Baer considered the irregular growth of fundamental organs as the basic differentiating factor (§ 3 (173)), and he illustrated this idea in particular with examples of development of the skull, cephalic brain and heart. The source of irregular growth Baer saw as in the direction of the flow of nutritional materials, on which depend the separation of: surface layers of the blastoderm from the layers adjacent to the yolk, the central parts from the peripheral parts, and the cephalic part of the embryo from the caudal or tail part. In judgments of this kind, Baer showed his inherent scientific carefulness and stipulated that he did not so much search for the reasons of development as he paid attention to coordinating the processes of development, "that it is for us in the beginning more important to gain knowledge of the deepest basis of the process, because the latter at the beginning of investigations is difficult to clarify in all completeness." This carefulness, moreover, gives credit to Baer that he, in all discussions of the dependence of development on movement of nutritional materials, moved beyond the wrong impression that the nutrition of the embryo passed through a canal which connects the central yolk cavity with the blastoderm lying on it.

Besides the separation of the basic or fundamental organs in the process of development, formations appear which connect the main organs with each other. According to this plan, the sensory organs develop (they connect the nervous system with the skin) and the derivative mucodermal tubes pass outwards (mouth, anus and branchiate slits).

About histological differentiation, Baer said very little, considering only the differentiation of bones and nerves from muscles. He reasonably objected to Serres, who suggested that nerves grow from the periphery to the center. Yet he also adopted the inaccurate view that nerves are formed at once along their length "from the muscular layer by means of histological separation." Baer did not promote this idea, remarking that the essence of the histological separation remained unknown to him.

The fifth scholium, entitled "On the relation of forms which the individual takes at the different stages of its development," is most widely known, and most frequently cited.

Baer began (§ 1) with the formulation of the contemporary idea that "the embryo of the higher animals passes through the permanent forms of the lower animals." He underlined

that the higher animals in single stages of individual development, from the first origin to completed development, respond to the permanent forms of the animal series, and that the development of individual animals follow the same laws as that of the whole animal series. Therefore, the more highly organized animal in its individual development passes through the most important permanent stages lower than its own, so that the periodical differences of the individual may be related to the differences in the permanent animal forms. (I Sch. V 1a, 286 - 287 (199))

The development of this idea Baer attributed to the time when systematic investigations of early embryogenesis were absent, with the exception of the work of Malpighi and Wolff. It was developed by Johann Friedrich Meckel, Junior, whom Baer did not name and only mentioned as a person who "acquired a highly serious knowledge about the history of development of the higher organisms" (I Sch. V 1a, 200). Baer remarked next on those evolutionary conclusions based on the similarity of embryos of higher animals to the adult lower animals. Ridiculing these hurried evolutionary conclusions, Baer caricatured the transformation of fish into land vertebrates and the elongation of the heron's neck as a result of its trying to reach to catch fish. His objections were directed not so much against the principle of evolution in general, or even against Lamarck's principle of inheritance of acquired characteristics, as against "the permanent arrangement of animal forms in one series" (I Sch. V 1a,b, 200).

In section 2, therefore, Baer turned to his doubts and objections to the repetition of the phylogenetic history in ontogenesis. The comparative study of adult animal forms made him sceptical of the idea of ontogeny following phylogeny. Insofar as

his first embryological investigation led Baer to conclude that in chick development the features of the vertebrate animal appear very early, he had already referred to his doubts in his dissertation published five years earlier.⁷

The similarity between the individual embryonic stages and the adult stages of others Baer considered as unquestionable, but without major significance. Against the view that development of the individual passes through constant forms, which are characteristic of lower animals, Baer promoted the following objections. If it were true, there should not be in the embryo any characters that are absent in lower adults (for example, the reserve of nutritional materials in the yolk or the intestinal loops hung externally). Besides, there might be similarity in just one feature or aggregate of features. According to the structure of the heart and extremities, bird embryos are similar to those of fish; but the other series of features inherent to early fish development are not present. The similarities of embryos with animals which are more highly organized also argues against the recapitulation idea. Finally, those organs which are inherent only to the higher animals appear very early. For example, the foundation of the vertebral column appears when the vertebrate animal, according to the idea of repetition of the species' history, would only have passed the stage of invertebrates (I, Sch. V 2b, 204 - 206).

All of Baer's argument against the repetition of the species history in ontogenesis, he mobilized for his theory of types. The theory of types played, in the history of science, a dual role: a positive one, insofar as it represented the basic natural classification system, and a negative role, insofar as the theory of types represented an antithesis to the theory of one origin, the evolution of the organic world. To the theory of types, Engels' familiar words relate directly: ". . . from that time, when they began working in biology in the light of evolutionary theory, one rigid boundary line for

7. Baer, DE FOSSILIBUS ANIMALIUM RELIQUIIS IN PRUSSIA REPERTIS DISSERTATIO. Regiomontii, 1823, 40 pp. (98).

classification after another has been swept away in the domain of organic nature . . . the distinguishing characteristics, which are almost becoming articles of faith, are losing their absolute validity"8

Baer's theory of types was more flexible than Cuvier's, because Baer assumed, though very cautiously, that all animals develop from one general original form, and, more confidently, that there is variability of organisms within the limits of each type. Although it is impossible to consider Baer a consistent evolutionist, his services in the preparation of the evolutionary idea are unquestionable.

Engels further defined Baer's historical significance. Remarking that the first assault on the theory of species constancy and proclamation of evolution was accomplished in 1759 by K. F. Wolff, Engels continued: "But what he had was a genius' anticipation which took a defined form in Oken, Lamarck and Baer, and was victoriously carried through by Darwin in 1859, exactly one hundred years later."9 In another place, on enumerating the gaps opened by science, Engels wrote: "(Natural science, at the outset revolutionary, was confronted by an out-and-out conservative nature) in which everything remained today as it was at the beginning of the world, and in which, right to the end of the world, everything would remain as it had been at its beginning."10

The urge to find out the most essential in the processes of individual form-production led Baer to establish the true relationships in the organization of different animals;

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8. F. Engels, ANTI-DÜHRING, Gospolitiedat, p. 13, 1952. (Ed.: English page numbers are from ANTI-DÜHRING, Moscow? Foreign Language Publishing House, 1959, p. 21.)
 9. F. Engels. DIALECTICS OF NATURE. Gospolitiedat, p. 11, 1952. (Ed.: English version page numbers are from DIALECTICS OF NATURE, New York: International Publications, 1940, ed. and trans. by Clemens Dutt, p. 13.)
 10. F. Engels. DIALECTICS OF NATURE, pp. 153-154 (186).

however, he suggested distinguishing the degree of development of the animal body and the type of organization¹¹ (Sch. V 3 a,b, 207, 208).

By degree of differentiation Baer meant the degree of heterogeneity of its component parts or the degree of histological and morphological differentiation. Baer considers a higher organization where "the different divisions of systems of organs are not similar to each other, and each part has a more remarkable individuality," in contrast to forms in which "all the organization as a whole is more homogeneous." Comparing the lower vertebrates (fish) with the higher arthropods (insects) reveals a greater heterogeneity of structure in the latter, although fish are a higher type in organization.

By type, Baer meant the character of distribution of organic elements and organs, which represent an expression of "the main relations between individual features of life of the organisms." The possibility of distinguishing "type" from "degree of differentiation" leads to the conclusion that one type can cover different degrees of development, and, on the contrary, one stage of development can be reached by different types. The combination of the type with a particular degree of differentiation or degree of development produces the major groups of the animal kingdom, the classes.

The confusion of the type and degree of development represented, in Baer's opinion, the source of incorrect classification. Clear demarcation leads to the conclusion that the different forms of animals could not be put in one line of development "from the monad to the human."

Between the main types, in Baer's words, there are "intermediate forms, in which the characteristic features of

11. On the necessity of differentiating these two understandings, Baer remarked in a more easily understood report—"Beiträge zur Kenntniss der niedern Thiere." (NOVA ACTA PHYSICO-MEDICA ACADEMIAE CAESAREAE LEOPOLDINA CAROLINAE NATURAE CURIOSORUM, 13 (1827), pp. 525-762), especially in the article "Über die Verwandtschaftsverhältnisse der niedern Thierformen" (pp. 731-762).

the main types are combined in one middle type, or in which one half of the body represents one type, and the other half represents another." But Baer did not review these intermediate forms in the present work, in order to set off the peculiarities of the four main types ("Haupt-Typen"): the peripheral or radiate, the articulated or elongated, the massive or mollusc, and the vertebrate.

Baer studied the types of organization for analysis of individual development (219 4a). Embryonic development involves an increase of the "degrees of development, or histological and morphological differentiation. It is possible to show that between the embryos of higher animals and the constant forms of the lower animals there exists a certain relationship. This, however, does not represent evidence that "each embryo of the higher animal form gradually passes through the form of the lower animals," according to Baer. On the contrary, "the type of each animal from the beginning is fixed in the embryo and governs all development."

All work on chick development Baer considered "only a long comment to this confirmation." Before anything else the spinal column is separated, then the spinal and abdominal plates, and also the spinal cord. All these rudiments appear very early, and after their appearance "there could not be any speech about the correspondence of the embryo to any invertebrate animal." On the contrary, the first recognized are the properties characteristic of the vertebrate animal. This is true not only for the bird embryo but also for all classes of vertebrates, from which Baer concluded that "the embryo of the vertebrate animals is from the first a vertebrate." Because no adult vertebrate animals exist which could be characterized with no little histological and morphological differentiation as the young chicken embryo, Baer concluded that "the vertebrate embryo in its development does not pass through the stages . . . of adult animal form."

In the formation of individuals, it is possible to establish a general regularity characteristic of the type. Such a rule is represented by the greater early similarity of embryos of different vertebrates and the approach of a later moment of original development. The peculiarities,

characteristic of the large divisions of the vertebrate type, appear earlier, and the features of the smaller systematic groups appear later. In other words, "from the more general type the more specific is formed." This same regularity is true for the development of the vertebrate, as well as invertebrate animals, such as the Crustacea.

At the very early stages, both vertebrates and invertebrates have what is called the primary zone. This raises a question, "are not all animals basically identical at the beginning of their development, and is there not for all of them one general primary form," Baer confirmed that such a general form actually exists, represented by the vesicular stage. Birds constitute no exception because the blastoderm, gradually growing over the yolk, is completed by the yolk membrane, and in mammals the vesicle surrounds the yolk from the first.

Yet in the German commentary to the treatise on the origin of the mammalian and human ovum,¹² Baer confirmed that "the simple form of the vesicle is the general basic form, by which all animals develop, not only in idea, but also historically." This vesicle-shaped embryonic stage, which Baer considered common to all animals, corresponds in modern terminology to the blastula. It is difficult to say with confidence whether this echoes Oken's idea about the round-shaped original form of all the bodies of nature, or if it indicates Baer's unusual perspicacity which was capable of discovering this important regularity through comparative anatomy.

Bringing in his results about the similarity of early embryos of different animals and about the divergent character of their subsequent development, Baer formulated four fundamental conclusions:

12. "Commentar zu der Schrift: DE OVI MAMMALIUM ET HOMINIS GENESI," p. 173.

1. "In each large group the general is formed earlier than the special." The most general for all animals is considered to be that opposition between the external surface, directed towards the surrounding media, and the internal surface. Therefore it is absolutely natural that the general original form represents a hollow circle, or vesicle.
2. "From the general the less general is formed and so on, until at the end the very special appears."
3. "Each embryo of a certain animal form, instead of passing through other defined forms, deviates from them."
4. "The embryo of higher forms is similar not to the other animal form, but only to its embryo."
(320 - 321 (224))

The superficial similarity of the embryos of higher animals to the adult lower animals depends on the fact that the latter are little differentiated and therefore not so far from the embryonic condition.

The transition in individual development by means of divergence from the more general form to the more special Baer illustrated by his schema, "Illustration of the course of development" (227).

The structure of the scheme is as follows:

(key on the following page).

Key:

1. In the egg occurs
2. Radiant development (?)
3. Sprial development
4. Symmetrical development
5. Double symmetrical development
6. Animals of peripheral type
7. Animals of massive type
8. Animals of elongated type
9. Vertebrate animals have vertebral column, spinal plates, nervous tube, branchiate slits and acquire
10. Branchiate fringe; the latter
11. Do not form actual lungs
12. Form lungs
13. Skeleton does not ossify
14. Skeleton ossifies
15. Carlilaginous fish
16. Bony fish Amphibia
17. Growing urinary sac
18. No umbilical cord
19. There is umbilical cord
20. No wing and air sacs
21. There are wing and air sacs
22. Reptiles
23. Birds
24. Mammals.

Baer's table continues also to the left, where it shows that the ovum is a consequence of the dichotomy of asexual and sexual multiplication, and to the right, where it presents the divergence of the amphibia and mammals according to peculiarities of later development. The text (p. 321 and on (225 ff.)) gives a detailed commentary to this table. One of its main purposes is to show clearly that the embryo in the course of development sometimes does not pass from one main type to another. From the point of view of modern embryology, Baer's scheme could have included a series of corrections, such as that spiral development is inherent not only to molluscs (to the massive type), but also to the annelid worms (representatives of Baer's elongated type), and so on. Baer himself stipulated the imperfection of his scheme, as also all others, but his main idea about the divergent character of development need not fluctuate with particular corrections.

Baer considered it absolutely natural that the erroneous point of view that transmission to embryonic stages correspond to simply constructed animals had acquired many supporters. Since fish deviate less from the basic type than mammals, it is natural that the embryo of mammals is more similar to fish than the embryo of fish is to mammals.

To the fifth scholium Baer attached four corollaries, which begin with the wonderful aphorism so frequently cited thereafter: "The history of development is a real light for the study of organic bodies. At each step it finds its application, and all ideas which we have about the reciprocal relations of organic bodies will experience the influence of our knowledge of the history of development" (p. 328 (231)).

The first corollary is entitled "The application of this scholium to the study of arrested development (Hemmungsbildung)."¹³ It begins with the confirmation that arrested development can be understood only by knowing the process of normal development. After that comes a controversy with those authors who considered that arrested development illustrates the repetition of ancestral

13. (Ed.: "Hemmungsbildung" means structural defects, malformations, or arrested development, but Baer seems to have meant the last.)

features in ontogenesis. If similarity is recognized between the developmental stage and the adult stages of lower organized animals, then this, Baer considered, occurs most frequently because the given adult form is closer to the original type. As a result, arrested development of the more highly organized animal will certainly draw these forms closer to each other.

The second corollary, called "Application of the present opinion to the determination of individual organs in different animal forms," concerns rational nomenclature for comparative anatomy, which can be constructed only with consideration of the history of development. Thus, the series of abdominal nerve knots of articulated animals cannot be called a spinal cord and compared to the nodes of the vertebrate sympathetic nervous system. The anterior pair of nodes in articulated animals cannot be called the cephalic brain. The supporters of such suggestions refer to these nodes, but Baer showed, illustrating his idea by a simple graphical scheme, that these nodes lie not above but anteriorly to the gullet. Thus the nerve ring near the gullet represents a secondary formation, dependent on the breakdown of the mouth at the abdominal surface of the body. Equally, one cannot compare the respiratory tubule of insects with the respiratory tube of vertebrates, because the latter develop from the mucodermal tubes, and the former represent a result of the protrusion of the external covers. At the same time, in a number of types there are organs of identical purpose and origin. Thus, "the digestive canals in all animals are formed from the membrane facing the yolk." This example and a number of others, Baer put as basic to the study of analogous and homologous organs; the demarcation of these understandings are attributed usually to a later period of the history of biology and connected with the name Richard Owen.

In the third corollary, "Application to the knowledge of animal affinities," Baer again returned to the idea of the linear or stair-like succession from the cephalopods or crustacea to fish, from the echinodermata to the molluscs, the impossibility of knowing which stands higher—the articulated animals or the molluscs—and so on. If the current idea about the ladder of animals were renounced,

every form could be considered a type-change from a more general form; even the last is a modification of the basic type. Hence in individual representatives of a type, some organs are more developed, and in others, other organs. Baer's rejection of the linear succession of developing individual organs led him to deny the possibility of reverse development. In some undefined form he stated, at the end of this corollary, an idea about the fact that development is always progressive and in the animal world leads to the foremost developed system, the cephalic brain.

The extensive fourth corollary, entitled "The division of animals according to their method of development," is devoted first, to the developmental difference between plants and animals, and secondly, to the differences of individual groups of animals based on processes of development. Such differences correspond to the animal type. Thus, for the vertebrates it is characteristic, according to Baer, to have a double symmetrical development, which he himself studied in detail. Typical for vertebrate development is the formation of two tubes, which are closed at the spinal and abdominal ends and divided at the longitudinal axis by the spinal or vertebral cord. To the elongated animal the symmetrical type of development is inherent, which leads to the formation of one symmetrical tube closed along the abdominal side to the spinal side. It is right to compare symmetrical development with double symmetrical development, but not to deduce one type from the other.

The preliminary data, obtained by Baer from his embryological study of bivalved molluscs and snails, led him to conclude that this development proceeds according to the principle of transference of the developing parts into spirals; therefore the molluscs have a waved form of development. Baer had little data concerning development of the peripheral or radiate type.

From comparing the methods of development of animals of the four main types, Baer concluded that "each main type follows a peculiar plan of development." The connection between the character or plan of development he designated by the following aphorism: "The plan of development is nothing other than the emerging type, and the type the result

of the plan of development." Baer continued, "the type can be known best by its method of development. This conveys the difference in the existing relationship of the initially agreeing germs" (Sch. V C4k, 257 - 258).

The given confirmation must be considered as recognition of the initial unity and general origin of all the animal world. Here Baer returned to the idea about a single method of acquisition of independence for all animals, by formation of the vesicle-shaped stage in which the most general character is recognized. The unity of the original form, inherent to each of the four types, has as a consequence the similarity between the representatives of the different types, which are preserved throughout life. Baer specifically said that the initial similarity of the embryos of all animals does not disappear absolutely in the adult form.

In Baer's study of differences but also of similarities in the types of development, one can perceive reflections of Naturphilosophie. In distinction from the principles of German Naturphilosophie, which originated almost completely from *a priori* understandings, Baer's opinion depended on thoroughly checked observations; therefore they stand in close connection with the evolutionary ideas of the second half of the nineteenth century.

From the assertion that the type of animal depends on that form of development which is inherent to its type, Baer concluded that a rational classification of animals should be based on embryological data. This idea he illustrated by examples. That the insects are organized higher than the arachnids and crustacea, and that amphibia and reptiles are considered differentiated from each other by classes can only be established by studying the history of their development.

The last, sixth scholium briefly sums up the others. In the process of multiplication, a part becomes a whole, and in the process of development the independence of the organism from its surrounding medium increases. The definition of its form also increases; internally, from the most general parts, the most specific develop and their originality becomes more distinct. All these conclusions

Baer generalized in the following words: "The developmental history of individuals is the history of growing individuality in every respect" (Sch. VI, 263).

The first volume of ÜBER ENTWICKLUNGSGESCHICHTE established the bases of embryology. Baer's contemporaries were not, however, in a position to evaluate such an immense contribution to science. Evidence of how far Baer preceded his times is clear from the almost complete silence with which his book was received. In his autobiography, written thirty-five years later, Baer could not cite any single serious objection to his work. He wrote only that within three years (actually within eight years) a French edition of his book appeared in a translation by Breschet.¹⁴ And only after a quarter of a century did Huxley publish an English translation of the fifth scholium.¹⁵

In a supplement to the German edition of his NACHRICHTEN, commenting on the purpose of his major work, Baer wrote:

Soon after my publishing of this work, Oken's critique appeared in his ISIS (1829, pp. 206-212) which pleased me greatly. Notwithstanding many friendly acknowledgements, it becomes very lively and pointed as soon as a statement deviates from his prevailing opinion. This in particular relates to the presentation about the development of the intestine, which in Oken's opinion is completely formed from the yolk sac and grows in the direction of the embryo. In the supplements (Baer means "the studies and corollaries."—L.B.), I made it my main task to correct the currently dominant opinion that the more highly organized forms, during their formation, gradually pass the stages of the lower forms, correcting this assertion with the idea that the early stages

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14. Baer, HISTOIRE DU DÉVELOPPEMENT DES ANIMAUX, Part I, trans. by G. Breschet, Paris, 1836. Complete, 1846.
 15. Thomas Henry Huxley in SCIENTIFIC MEMOIRS (full citation Chapter 16, fn. 8).

correspond more to the intermediate forms, from which all the peculiarities of the different classes, families; genera, and species have gradually appeared. The earlier idea was especially created by Meckel and Oken. The examples and expressions selected for characterizing this opinion I took directly from Meckel without designating him by name. Oken believed himself directly insulted and courageously defended his point of view, which rested only on assertions.¹⁶

It must be thought that Baer was particularly cheered by Oken's notice.

Baer, of course, did not accidentally pause in his memories at Oken's article. When ÜBER ENTWICKLUNGSGESCHICHTE had just gone into print, he waited with impatience to see how his colleagues would accept his work. During the following years, apparently, he did not lose the feeling of disappointment and injury that his main life effort was not evaluated and credited to him during his lifetime.¹⁷

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16. Baer, NACHRICHTEN ÜBER LEBEN UND SCHRIFTEN . . . , p. 609 (447).
 17. See Chapter 23.

CHAPTER 19

THEORETICAL INTRODUCTION

TO THE SECOND VOLUME OF ÜBER ENTWICKLUNGSGESCHICHTE

The second volume of Baer's basic work includes the third part, "Lectures on the origin and development of organic bodies, read to physicians and prospective students of nature in the form of an introduction to a deeper study of the history of development," and the fourth part, "Studies of the history of human development,"¹ The third part begins with a theoretical introduction, which presents the basic principles of the history of development. Baer then moved to a systematic statement of the embryological data for all classes of vertebrates.

A superficial acquaintance with the third part can give the impression that he repeated the first part. Such a conclusion is not fair, because the first part stresses the chronology of development and the individual steps characterized by the condition of the different organs. The **third part** represents a related description of development of the organs and their systems.

For the characteristics of Baer's general opinions, the fairly extensive theoretical introduction, entitled "Statement of the Task," holds great interest (§ 1). Baer began with the cardinal question about what organic life is, remarking that scientific information about life is incomplete because of the impossibility of accurately indicating the beginning of this process. When the question, "What, in essence, is the life of the organic body," is asked, a typical

1. The fourth part is not included in the second volume of the Russian version; in it are listed only the human embryos investigated by Baer. (Ed.: Nor is the fourth part in the original German edition. It was printed later, as explained in Chapter 21.)

answer would conclude that life derives from something different, possibly from some sharply outlined individuality. To the layman such explanations, which relate life either to the long running oxidation process or to an electric phenomenon, will cause great delight. This delight is fed by the belief that such information brings understanding of the essence of life, because such unique processes of inorganic nature are considered accessible to complete apprehension. By this means, it would be possible to indicate accurately life's beginning and end.

All such explanations Baer considered absolutely unsatisfactory for the physiologist, because they are concerned with only one particular phenomenon of the life process. The physiologist should teach that life should be explained not from something else, but from life itself. Turning to the inorganic world, Baer noted that the time will come when the physicists themselves should recognize that on performing their experiments they remove individual physical phenomena from the context of the general nature of life. It is known that "not a single chemical process takes place without galvanic activity, nor any galvanic without magnetic activity, that light and heat are mutually dependent; and therefore, it is to be hoped that, as until now the physiologist compares the complex phenomena of organic life to physical processes, some day he will compare physical phenomena with those in the living organism and will gain understanding from them" (II 1a 3). At that time, Baer predicted that the complaint concerning unclear life phenomena should end. It is customary to look at their reciprocal relations and take them as they are, without forced, frequently laughable explanations and references to the unique phenomena in inorganic nature.

Baer's statements reflect his ideology, which was not free from the effect of the, to him modern, idealistic philosophy. But his ideas reflected a protest against the simplified mechanical understanding of processes, the inorganic as well as the organic, and the spontaneous approach to the idea about the general or universal connection of all phenomena.

The difficulties in investigating inorganic phenomena are not so great, but understanding organic life is more

imperfect because it is not possible to determine accurately the moment of its appearance in each separate individual. Hence the origin and development of organic bodies seems particularly obscure and strange. However, Baer noted, the beginning of individual life is not more obscure than any other life phenomenon, but what is directly apprehended seems to be much more understandable than that unavailable for perception. Every year the tree gives rise to buds, and sprouts grow from them. This fact, for people who do not study nature, does not arouse curiosity, while the quick growth of the tree from the seeds creates an unsolved enigma. In a similar way they do not see anything strange in that each man, each animal and plant feeds and grows over time. However, the nourishment is nothing other than a constant change; man today is not man of yesterday. It is possible to say that growth is nourishment with the formation of a new mass, that it is a continuation of conception, and that conception in its turn is nothing other than the origin of individual growth.

In the spiritual constitution of man, it is common to search for an entirely defined origin of all things, a defined border between being and not being, when it is actually possible that in nature there is nowhere an absolute beginning. Nature is characterized only by eternal change. With living beings it is natural to assume that the beginning of a new organism corresponds with the moment of fertilization. In order to pursue this beginning moment, writers had resorted to wit and imagination. They had assumed that at the time of fertilization the new creature appears as a result of an electric shock, or through the union of two heterogenous substances, or by means of some magic power. However, since the microscope had not been improved or vision extended, after fertilization it was possible to see only what was seen before fertilization. Only after some time was a new plant or new animal recognized, but already in a condition of later growth. Undoubtedly, however, before fertilization nothing had existed that represented the primary form of the emerging animal or plant; so an independent organic body resulted from its conversion. Consequently, the beginning of the individual does not correspond with fertilization, and the rudiment of the fetus already preexists in the parents. At fertilization the conditions allow it to grow quicker. In other words, the initial existence of the

fetus should have been sought either in the mother's or in the father's body.

The ovary of the mother contains parts, such as the ova, which give the beginning to a new individual. It was possible to assume preformation in the ova. From the other side, after the invention of the magnifying lens, observers found in the male an enormous number of small, spontaneously moving animals, i.e. live bodies. This observation was extremely welcomed by the supporters of preformation. The fact of the enormous quantity of these bodies in the male testicles was difficult to explain. Defenders of preformation believed that the moment of fertilization millions of the male bodies (called cercaria) violently fight with each other, until those lucky few live conquerors penetrate into the vesicle of the female ovary. It is only a pity, Baer speaks ironically, that these bodies do not have jaws to bite each other. In general they do not have even the most remote similarity to the higher animals, but consist only of a small head and a long tapering tail.

"After a brief flourishing," Baer continued, "this hypothesis, like the hypothesis of preformation in the egg, was forgotten and faded throughout half a century. Only recently two very accurate observers, Prévost and Dumas, have revived it as a result of a thorough investigation of the testicular beasts." About the cercaria, Baer cited the words of Prévost and Dumas that "not the complete hen or cow is formed from the cercaria, but only the nervous system, while the others grow from the female reproductive material" (II 1d, 5). Actually, Baer continued, the cephalic brain, in combination with the spinal cord, has a form somewhat similar to the cercaria magnified a million times" (II 1d, 6). The first part of Prévost's and Dumas's work² was received, according to Baer, with complete confidence. However, when

2. J(ohn) L(ouis) Prévost and J(ean-Baptiste) Dumas, NOUVELLE THEORIE DE LA GÉNÉRATION (New theory of generation) (Paris, 1824). ANNALES DES SCIENCES NATURELLES, 1 (1824), pp. 1-29, 167-187, 274-292.

Prévost found similar bodies in the reproductive organs of snails and the cockle-shell,³ in which there is neither a cephalic brain nor a spinal cord, then the authors

were required to have oratorical art to explain that they were incorrectly understood; they say that they did not affirm that the narrow system is directly formed from the testicular bodies which penetrate into the ovum, and considered that this penetration is necessary as a preparation to its formation. By this explanation, however, they themselves frustrated their hypothesis. (II, Id, pp. 12-13 (p. 6))

Next Baer strove to show that the task of explaining the defined beginning of individual development will not be solved if we assume the preexistence of future generations in the bodies of the parents, because, in this case, we must assume that all living creatures, right up to the last generation, were created at the same time as the first individuals. Consequently, in the chick ovary all the chicks that are to be formed must be present, and in the ovary of each one of them must be again all their future offspring, and so on. These offspring included in each other, because of their infinitely small sizes, are unavailable for observation by our optical facilities. Although the hypothesis, as Baer said, is next to nonsense, nevertheless it was defended by many famous naturalists. This represents a clear example of the confusion into which one can fall if he bases opinions on suggestions and not on observations. If this point of view were correct, then it should have been recognized that inevitably the time would come when all life on earth would end because all creation had been already formulated. Continuing ironically this "theoretical argument," which in part relies on religious belief, Baer wrote that after the exhaustion of preformed generations the Creator would then begin his work again, since the first effort of creation appeared to be so

3. J. L. Prévost, "On the Generation of Painters Mould," ANN. SCI. NAT., 7 (1826), p. 447-455.

imperfect. From the characteristics of preformation, Baer drew his listeners' attention to the fact that, in spite of the slowly progressing accumulation of facts in the history of development and the great difficulties in extracting such facts, the accomplishments of science are highly significant. Observations show the incorrectness of the aforementioned ideas about reproduction and development. Baer expressed his belief that already there was enough data to recognize nature's methods for forming new organisms. The new investigations of the history of development, Baer said, were still poorly known, and the old ones obscured by preconceived ideas; therefore it is necessary to present the facts from the history of development.

Baer considered his task as giving the combined work of the history of reproduction and development and showing that they, in one sense, are not preformed and, in another sense, do not develop as was usually thought, all at once from a formless mass.

Baer noted in this case that he recognized well the difficulty of talking about an object still so alien to contemporary scholastic and university education. He feared that he would not be understood on the level that he wished, because his listeners had more experience with hypotheses rather than with facts. Knowing how the classical trend of education had fenced German students off from studying the phenomena of nature, Baer, not without irony, said that he even assumed the structure of the bird's egg to be unknown to his listeners.

For among my respectful listeners there are probably few who do not know that the cackle of geese once saved the Capitol. With the exception of medical persons, there are probably few who are aware of the contents of a goose egg, and a qualified German teacher, above all, would not know that poultry lay eggs if he did not have it from Pliny or Phaedrus. (II, 1f, 8).

About birds' eggs, Baer continued,

the basis of our knowledge of growth and development of animals is obtained from the fortunate opportunity of continued studies. What we know of the development of other animals is for most classes, especially the mammals, to which the physical aspects of man also belong, so isolated, that it can only be understood by comparison with the development of birds. (II, If, p. 16 (p. 8))

And although Baer, as a result, anticipated that the features of similarity of birds and other vertebrates, as well as their specific peculiarities, might be inherent only to avian development, he later did not pay attention to his own warning. Describing the development of the egg in the ovary, the structure of the fertilized egg, the formulation of embryonic organs and membranes and so on in reptiles, birds, and mammals, Baer strove not to keep finding complete parallels. Sometimes he did not see those new formations characteristic of the higher classes of vertebrates. Note that it is impossible to forget about Baer's great service. He was the first to show with complete distinctness the fruitful comparative method in embryology, although he himself used it only within the class of vertebrates and did not see the possibility of comparing regularity of development in animals belonging to different morphological types.

In order that his listeners could establish an objective judgment, and in order that they would not draw general conclusions for their own dogmatism, Baer suggested the following. He intended to begin by stating the history of bird development, then to compare the most essential from the history of development of other classes of animals in order to get to the most important problem—the elucidation of reproduction and development.

The last division of the book, treating general questions of embryology, was never written, and because the second volume of ÜBER ENTWICKLUNGSGESCHICHTE was printed without the author's participation, the missing part remained only a reference in the introduction.

CHAPTER 20

THIRD PART OF ÜBER ENTWICKLUNGSGESCHICHTE: DEVELOPMENT OF THE BIRD EGG AND EMBRYO

Turning to the structure and formation of the bird's egg, that is, its history prior to hatching, Baer considered the structure of the laid but not yet hatched egg (§ 2). He successively described the parts of the laid egg, starting with the shell and the underlying two-layered shell membrane. These layers are only separated at the blunt end of the egg, with the air chamber between them. The external layer carries papillae on the external surface, which penetrate into the shell. In the albumen, Baer distinguished three layers under the shell membrane—an external, middle, and internal or third albumen. Concerning what was called the middle membrane of albumen, Baer referred to it as a solitary layer on the surface of the middle albumen, and noted that it is not seen in live eggs and appears only with the effect of water. The same thing apparently also occurs with another formation, the albumen ligament, which Treder had described in detail (see Chapter 11). Next, Baer briefly referred to the chemical composition of the albumen. In the center of the albumen mass sits the yolk ball, ellipsoid in form; its longitudinal axis corresponds to the longitudinal axis of the shell.

On the surface of the yolk there is a yolk membrane, composed of a single layer. Of the two layers of the yolk membrane which Wolff had thought existed, the internal one actually represents the embryonic pollicle (blastoderm). The yolk itself is composed of granules of equal size, irregularly shaped whitish masses and bright light fat droplets. The central cavity in the yolk communicates with the surface by a canal.¹ In front of its external end on the yolk surface

1. Actually the center of the yolk ball is occupied with what is called the white yolk.

is found the most important part of the egg, the cocks' trace or cover (cicatricula). It consists of a thin surface disk, which Pander had called "the rudiment pellicle" (Keimhaut, blastoderma), but which Baer preferred to label the rudiment (Keim, blastos). The rudiment is composed of firmly laid small whitish granules, under which lies the rudiment layer, whose whitish-yellow mass Pander called the nucleus of the cover. Baer considered all this to be only layers of the yolk, which connect with the rudiment and merge with the remaining yolk. Only in the middle is the nucleus of the cover separated from the yolk by fluid to form the hillock of the rudiment layer.

The formation of the yolk ball (§ 3) Baer traced from its presence in the nonsexually mature hen; such a hen's ovary contains vesicles with transparent fluid. Reaching the size of a millet grain or seed, the vesicles sharply increase in size and become filled with a milky white, then yellowish content at copulation. The yolk is connected to the ovarian stem and is covered with a capsule composed of firmly adjoined layers. These layers have openings for vessels which do not, however, penetrate the yolk; thus the yolk membrane remains intact. At the emerging part of the yolk, which is still in the ovary, an arch-shaped white zone—cicatrice—appears. When the yolk is ready for separation, the ovarian membrane ruptures in the region of the cicatrice. After the yolk exits from the capsule, its remains and stem form a deepening, called the cup. The membrane directly covering the yolk appears on its surface before maturation. Also long before maturation, near a small yolk equator (beside the cup stem, sometimes at the cicatrice), a white spot appears, corresponding to the cover of the laid egg. But in the ovarian egg it does not acquire such clear outlines. This part is called the rudiment layer. In its middle there is a light spot, an extremely delicate vesicle filled with a transparent fluid, called the embryonic vesicle or Purkinje vesicle.

The term "embryonic vesicle" (for the egg nucleus) was widely employed in embryological literature until recently, and even in current works. Baer noticed that in hens the embryonic vesicle is revealed very early, while the corresponding transference of the nucleus takes place at a much

later stage of egg development in other animals. With the transference of the egg nucleus comes the formation of the central cavity of the yolk and its canal. In the frog egg, where the transference of the embryonic vesicle occurs late, Baer observed it with greater distinctness than in the bird's egg.

After copulation, the cicatrice is ruptured and the yolk falls from the cavity of the capsule. For the release of the yolk, copulation is not necessary, but it stimulates this process. Many authors after Baer described the disappearance of the embryonic vesicle upon maturation of eggs of many types of animals. But only after the investigation of N. A. Warnek (see Chapter 25) did this phenomenon become connected with maturation division and the formation of the polar bodies. Baer considered the appearance of the rudiment (KEIM) from the rudiment layer a direct consequence of fertilization, and without fertilization the rudiment is not formed.

Describing the further formation of the egg, which is already occurring in the oviduct (§ 4), Baer first considered the organization of the sexual conducting routes and described the structure of the funnel, especially the oviduct and uterus, from which a narrow passage leads to the cloaca. The pressing of the yolk ball by the funnel and its passage along the oviduct is accomplished by active movement of the latter; hence the yolk, passing by the oviduct, turns around the longitudinal axis so that the rudiment layer always remains on one side. After passage of the egg, the walls of the oviduct produce albumen, which gradually envelops the yolk ball. The shell membrane forms, in Baer's opinion, from the surface layer of the albumen, because the latter rolls up when the egg reaches the uterus. In this division of the oviduct the "hail-stones" (HAGELSCHNÜRE) and the shell are formed. In the uterus the egg remains nearly a day. Concerning the formation of the rudiment, Baer assumed that it develops from the content of the embryonic vesicle, indicating a contradiction because there is no rudiment in the unfertilized eggs even though the embryonic vesicle may have ruptured even without fertilization.

Not deciding beforehand the question of whether the embryo is produced only from the egg nucleus, Baer accorded the latter

great significance and strived to explain its origin and subsequent fate. His comparative investigations led Baer to believe that the embryonic vesicle exists at the earliest stages of egg formation in the ovary. Thus, in hens he saw the embryonic vesicle in ovarian eggs with a diameter of not more than half an inch (about 1.3 mm); the remaining egg parts, including the yolk, are apparently formed later. (Baer had already stated in his DE OVI his belief in the primary existence of the embryonic vesicle.)

G. Rathke, studying salmon eggs,² objected against Baer and confirmed that the "Purkinje vesicle arises . . . considerably later than the yolk." To resolve this dispute, Baer referred to the other objects investigated by Rathke, the river crayfish and fishes. He reported in a later section of his main work (§ 11, footnote pp. 392-394 (11 Bw, 296)) that in the autumn, when the eggs increase in size and acquire a color, it is easy to extract the embryonic vesicles included in the voluminous yolk mass. In immature eggs, containing considerably less and still uncolored yolk, the embryonic vesicles are also seen, but they are smaller in size. Even in the smallest eggs with few granules, the embryonic vesicles already exist. In such eggs, there is also a substance dissimilar to yolk, and a few fluid vesicles. Baer concluded that the yolk of eggs which acquire embryonic vesicles is formed only in the period of egg maturation. In the fish Baer also observed that such egg has a nucleus; however, in younger eggs the nucleus is larger and is surrounded with less substance.

In the process of incubation, the egg loses weight as a result of evaporation, but during the same period unincubated eggs lose less weight than incubated eggs. Simultaneously with the development of the embryo, the volume of the air chamber increases, and the air present in it contains oxygen which the embryo uses. (99) Due to the loss of water, the egg albumen thickens. Changes in the yolk are especially

2. Rathke, "Über das Ei einiger Lachsarten," ARCH. ANAT. PHYSIOL. (Martin Heinrich Rathke, "Darstellung der spätern Umbildung," in NEUESTE SCHRIFTEN DER NATURFORSCHENDEN GESELLSCHAFT IN DANZIG, VI, Heft 4.)

distinct: to the fifth day of incubation the yolk increases in volume, arises to the shell, becomes thin, and its granules become more obvious or distinct. These changes were observed by the Kazan professor Eikhval'd. In the process of development not only morphological, but also chemical transformations occur, and new chemical substances appear.

Structural changes in the egg lead to the disappearance of the yolk membrane and to the development of the rudiment. The latter enlarges in size and begins gradually to cover the yolk; the central part of the rudiment becomes the embryo, and the large peripheral region remains thin and has the shape of a pellicle. Baer called it the rudiment pellicle or blastoderm. It represents a continuation of the embryo, with which it is directly connected, and eventually most of it becomes part of the embryo. The rudiment pellicle contains the blood-carrying vessels which receive the nutritional materials from the yolk and transfer them to the embryo. And thus, as the rudiment becomes enlarged, it divides into two parts distinguished by the external shape but connected by a common vital process: its center becomes the embryo, and the periphery becomes the blastoderm. At the beginning the rudiment lies on the surface of the yolk in the form of a plate, and then, on growing, it gradually covers the yolk and acquires a sac form. Already on the fourth day between the embryo and the underlying sac a narrow communication remains. The vesicle containing the yolk is called the yolk sac, or the intestinal or yolk vesicle.

In the process of development, the rudiment is divided into two incompletely separated layers. From the surface layer the animal parts of the embryo form, and from the internal layer the vegetative or plastic parts. Therefore Baer named them the animal and vegetative layers. At the same time Baer recalled that this animal layer is nothing other than Pander's serous layer, and the vegetative layer corresponds to Pander's vascular and mucous layers. Pander's terms had been worked out during his time in Würzburg and had spread since that time. Baer considered the names vascular and mucous layers appropriate but the designation serous layer inappropriate, because the covers of the embryo form only from its peripheral parts, while the middle gives rise to the most important internal organs. Besides that,

it represents a division from both other layers, and the animal part of the embryo develops from it.

This division of the animal and plastic layers Baer distinctly implemented in his first volume (§ 1) and in the fourth scholium of the second part of ÜBER ENTWICKLUNGS-GESCHICHTE. Here he noted the importance of such opposition for the comparison of embryonic development of different vertebrates and for the comparison of development of the vertebrates and the lower animals. "The vegetative layer," Baer wrote, "contains the layer of the mucous membrane and the vascular layer, but the animal layer at first corresponds with Pander's serous layer. Later it divides in the middle into two layers, the lower of which I call the fleshy layer and the upper the skin layer" (II, 51, pp. 46 - 47 fn. (64)).

The embryo, on separating from the yolk, connects with the remaining parts of the egg by means of the umbilicus. The external umbilicus represents the border between the embryonic and extra-embryonic parts, which previously represented the periphery of the animal layer. The internal umbilicus, the yolk duct, represents the transition of the internal vegetative parts into the vegetative layer of the embryonic sac. In the vegetative layer of the yolk sac there are two subordinated layers, a vascular and a mucous layer. The blood-carrying vessels, present only in the former, are transferred into the embryonic vessels. In mammals they are called the umbilical-mesenteric vessels because they go through the umbilicus from the mesentery. The animal layer of the rudiment undergoes transformation upon the appearance of the amnion on the third or fourth day, when the blastoderm is divided into two main layers.

Baer's description of amnion development is very unclear. He proposed to withdraw Wolff's idea of the "false amnion" (see Chapter 5) from use, especially since Pander did not employ it in the same sense (see Chapter 12); this produced some confusion.

Baer designated the cephalic fold of the animal layer the cephalic cap; it gradually enlarges and forms the cephalic vagina. Slightly later, this same process takes place at the caudal or tail end (the caudal cap becomes the caudal vagina)

and at the sides. By this means develops the circular fold,³ whose top fuses to form the amnion which thus grows from the animal layer.

When the opening of the amnion closes, the lower layer of its forming fold contributes to the construction of the amnion, while the upper is not connected with amnion formation. For this part, Baer suggested keeping Pander's name serous vesicle or serous membrane. The serous vesicle includes the amnion with the embryonic and yolk sac. Between the serous membrane, amnion and the yolk sac there remains an interspace connected with a gap between the dermal and intestinal umbilicus. This ring-shaped gap leads into the embryonic abdominal cavity and could be named the abdominal umbilicus. Therefore, the cavity of the serous vesicle is an extra-embryonic part of the abdominal cavity, as the yolk sac is the continuation of the digestive canal situated outside the body.

Turning to the development of the allantois, Baer described how on the third day from the most posterior end of the digestive canal, i.e. from the future cloaca, a small rounded sac protrudes. Upon elongating, it passes through the abdominal umbilicus and appears in the space between the amnion, yolk sac and serous membrane. Later it spreads, covers the amnion, penetrating between it and the serous membrane, and then also grows over the yolk sac. Baer called this formation the urinary sac, not only because it develops from the cloaca, into which the urinary tracts flows, but also because urine collects in it the second half of incubation. (100) The stem of the urinary sac is called the urinary duct (urachus). Because the intestine consists of two layers (internal-mucous and external-vascular), these same layers should be present also in the urinary sac, and they actually can be distinguished there very early. In the external layer of the urinary sac a network of vessels develop to receive the blood from the two branches of the aorta, the umbilical arteries. Through the single umbilical vein, the blood goes from the urinary sac backwards into the body of

3. Its cavity represents the extra-embryonic part of the complete circular cavity.

the embryo. These vessels had been named "umbilical arteries" because they go through the umbilicus, but in Baer's opinion they would better be called the vessels of the urinary sac. The external half of the urinary sac represents the embryonic organ of respiration. It firmly adjoins the shell membrane, then gradually separates from the shell and forms the chorion. The internal half of the urinary sac becomes thin and fits close to the amnion and yolk sac.

Baer summarized changes in the incubated egg as follows. In the process of incubation the quantity of albumen decreases partly from evaporation and partly as a result of its use by the embryo; thus the volume of the air chamber enlarges at the blunt end of the egg. The yolk mass at first increases, then decreases as the embryo uses it; the membranes of the yolk and chalazae disappear. The middle part of the rudiment is transformed into the embryo, and the periphery into the blastoderm covering the yolk. Upon separation of the embryo from the blastoderm, the umbilicus forms, and the extra-embryonic blastoderm forms the yolk sac hanging from the embryo. In the latter, the blood-carrying vessels of the yolk sac branch and become the vessels of the mesentery along the yolk duct. The animal layer of the rudiment membrane forms two vesicles (or membranes), the amnion and the serous vesicle, of which only the amnion remains to the end of development. From the vegetative region of the embryo, the urinary sac, rich in vessels, protrudes and is gradually overgrown by the embryo with its appendages, the yolk sac and the amnion. The external part of the urinary sac forms the chorion adjoining the shell membrane. The parts of the extra-embryonic formations (albumen, yolk membranes, chalazae, the yolk itself, the peripheral zone of the blastoderm, the internal half of the urinary sac) are reduced at different times. Only the embryo develops and grows continuously.

At the end of incubation, the yolk sac enters through the umbilicus to the embryonic abdominal cavity, where the remains of the yolk are used for some weeks after hatching. During the nineteenth and twentieth days of incubation, the umbilicus narrows, which leads to blockage of blood circulation in the umbilical vessels. The chicken tries to breathe with its lungs by penetrating its beak into the air chamber or by breaking the shell. Then the movement of the blood in the

umbilical vessels stops completely; the umbilicus closes and isolates the chick from its embryonic appendages. On hatching, the chick leaves its membranes, amnion, and chorion with the shell membrane and the shell.

The next division of Baer's work, entitled "General Method of Formation of the Bird Embryo," (§ 6) concerns the previously established forms of differentiation: the primary, morphological, and histological. In the organization of all vertebrates, Baer considered essential, not the specialized organs of blood-carrying, nervous or digestive system, but the parts similar for all vertebrates. According to Baer, a generalized understanding such as that of the body layers spreading along the entire extension of the body could be useful. These layers lie one above the other, as if they develop each other. They become noticeable in the earliest developmental stages, but can also be recognized in the adult. (101)

Baer prefaced his scheme of the structure of all vertebrates with the characteristics of primary differentiation. Along the longitudinal axis extends the stem (vertebral column), above which is the spinal part of the animal and below which the abdominal part of the animal. The spinal part consists of the neural tube, the vascular layer, the muscular layer and skin. All these layers have the form of a tube, which forms the primary organs of the vertebrate animal. If we do not take into consideration the extremities, it is possible to consider that the body of the vertebrate animal forms the following parts or layers:

1. The firm or solid part, which never extends beyond the surface of the trunk.
2. The spinal part, composed of:
 - 1) the closed neural tube;
 - 2) the muscular tube surrounding it;
 - 3) half of the dermal tube, covering the muscular tube.

3. The abdominal part, composed of:

- 1) the closed mucous tube, which forms the internal surface of the abdominal part;
- 2) the vascular tube which surrounds the mucous tubes, goes above the muscular tube to the trunk, and adjoins to its lower surface;
- 3) the muscular tube which is closed upwards by the trunk;
- 4) the second half of the dermal or skin tube which covers the muscular tube.

Therefore, with a transverse section, such a figure is obtained: the two opposing tubes of the muscular layer form a figure eight, in the middle of which is the trunk; in the upper circle of the figure eight is a tube of neural material, and in the lower circle is the tube of the mucous membrane, surrounded by the vascular layer which continues to the trunk. The muscular layer forms two tubes—the spinal and abdominal—both of which are covered by the common skin cover. The spinal and abdominal tubes represent primary organs and are initially strictly symmetrical. Deviations from symmetry, observed in some vertebrates, have a secondary character.

The source of symmetry of the primary, tube-shaped organs is their formation from curved and accreted paired plates. All the paired plates (those of the spinal cord, spinal, abdominal, mesenteric and intestinal) which give rise to the aforementioned tubes, could be converted into two pairs of the main plates, the spinal (dorsal) and the abdominal (ventral). Previously, all these plates formed one general plate composed of heterogenous layers. Earlier the different layers were not recognized.

Thus gradually the grounds of development occur, "but only in reverse succession" (II, 6(Ah) p. 90. (63)) With these words, Baer stated his method of embryological investigations. He considered that in the beginning it is necessary to study the general organization of the formed animal, that end to which the long chain of developmental processes leads. Later it is possible to pass gradually along the links of this chain

to its beginning, to trace development retrospectively, and then it is possible to establish the succession of events in actual chronological order.

The beginning phase of primary differentiation Baer described in the following words: "Initially there are no separable differentiated layers, but only the surfaces of the rudiment, in which one can see differences, as in polyps, indicating the opposition between external and internal surfaces. The space between these surfaces, as in the polyps, is occupied by an indifferent mass" (II, 6(4)i, p. 91 (67-68)). The given quotation indicates with complete clarity that the idea of comparing the embryonic layers in vertebrate embryos with the body layers of the coelenterates belongs to Baer, and not to Thomas Huxley,⁴ as is frequently claimed.⁵ Baer was ahead of the English zoologist by not less than twenty years, if we take into consideration that the printing of his second volume began in 1829.

In the embryo, Baer continued, the opposition of external and internal surfaces results in differentiation of the upper skin and lower mucous layers. Simultaneously, a differentiation occurs along the surface: the middle of the rudiment becomes thin, giving rise to the transparent zone (Wolff's area pellucida), and the periphery forms the dark zone (Pander's area opaca). The vascular layer reaches only the middle of the dark zone. Because the vessels are present only in the vascular layer, the periphery is broken up into the internal, vascular zone (Wolff's area vasculosa) which is separated from the yolk zone (area vitellaria) by the broad terminal vein (vena terminalis, which Baer called the sinus terminal). The transparent zone is also divided: the middle

4. Thomas Huxley, "On the anatomy and the affinities of the family of the Medusae," PHIL. TRANS. ROY. SOC., 2 (1849), pp. 413-434.

5. See, as an example: I. I. (Ilia or Elias) Mechnikov, EMBRYOLOGISCHE STUDIEN AN MEDUSEN. EIN BEITRAG ZUR GENEALOGIE DER PRIMITIV-ORGANE (Wien: A. Hölder, 1886; Moscow: Akademii Nauk, 1950), pp. 284, 418.

is raised in the form of a shield (the future embryo), and the periphery forms what is called the fetal zone. The shield elongates at straight angle to the egg axis, outlining the axis of the embryo along which forms the primary zone.

As a result of the fusion or closure of the embryonic layers, they are converted into tubes. The beginning of this process Baer described as follows. Along both sides of the primary zone two unremarkable thickenings arise which appear as a line of dark small balls. This line, the spinal cord, forms the middle part of the trunk. The lateral thickenings, the spinal plates (*Laminae dorsalis*), contain only the skin and muscular layers. They correspond to what Pander had called primary folds (*plicae primitivae*) and what Burdach had called "mirror plates." The crests of the spinal plates deviate from each other and accrete, forming the back of the embryo. The internally folded part of the skin layer is separated from the muscular layer, and quickly thickens to form the central part of the nervous system as a somewhat laterally compressed neural tube. Soon after the formation of the spinal folds, curving of the wide abdominal folds or the abdominal plates (*Laminae ventrales*) begins downwards. Wolff had called them *Fasciae abdominales*, because he assumed that they do not reach the posterior part of the body.

This process is concluded along both sides of the spinal cord where, in the vascular layer, two thickened bands form; their external borders incline to each other and accrete. The mucous layer in the region of the cord separates from it, so that the bands of the vascular layer, called the mesenteric plates (*laminae mesentericae*), appear in that free space between the cord and mucous layer. The place of fusion of the mesenteric plates Baer, like Wolff, called the suture of the false amnion. Soon after the formation of the suture, along the sides two other bands separate from it, composed from vascular and mucous layers. They thicken, acquire the form of plates, incline to each other and accrete; hence each intestinal plate (*lamina intestinalis*) represents a half-canal, and they together form the intestinal tube. The fusion of the intestinal plates downwards represents a simultaneous separation of the embryo from the blastoderm.

A double conversion of the plates into tubes leads to the formation of the primary organs of the embryo. In all

the primary tube-shaped organs it is possible to distinguish, first, a central line and, second, a fusion line by which accretion takes place. The fusion lines of each primary organ correspond to the peripheral borders of these plates, from which the organ is formed. The central line of each primary organ had occupied the center while in the stage of the plates. All the central lines lie in the middle plane, one above the other and close to each other. Only the skin, which has two fusing lines, has no central line. At an early stage of development, all the central lines of the future primary organs are concentrated in the primary zone.

Turning to the development of the extremities, Baer suggested that both pairs of vertebrate extremities are connected with broad muscular belts and that the basic segments of the extremities and the adjoining muscles form the external muscular layer, including both muscular tubes of the trunk. The formation of the first fold of the extremity, in Baer's opinion, confirmed that suggestion, because it appears from each side as a long common fold which constitutes part of the external muscular tube; this in turn represents a primary organ.

The described relations Baer illustrated with a schematic drawing (Figure 28). If we lay flat the plane of the layer of the spinal plates ab'' and that of the abdominal plates ac'' , they will look like ab and ac . When the plates of the extremities $b''c''$ are located in the plane $ab\ bc$, then the transverse section shows that they extend from the closing line of the back (b'' or b) to the closing line of the abdomen (c'' or c). From the scheme it appears that in the zone of the rudiment, through the rise of the spinal plates, the plates of the extremities will be the continuation of the back plates. (II 6A, 77-78)

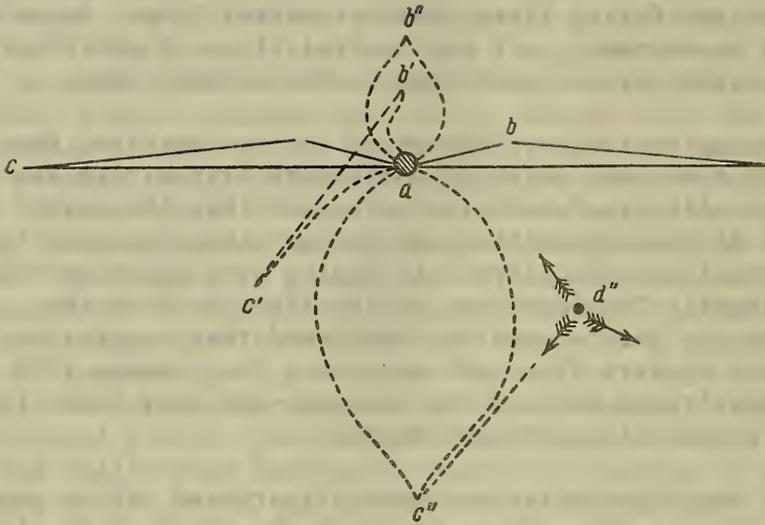


Figure 28. Baer's scheme of vertebrate development and structure
(explanation is in the text)

Further breakdown of the primary organs leads by indirect morphological differentiation to the formation of definitive organs. Thus, in the cephalic part of the mucous tube, the entrance is differentiated into the respiratory system and the entrance into the anterior part of the digestive canal. In the latter, the esophagus is narrowed and serves only for transferring food; the second (stomach) is wide and provides digestion for the food. Individual areas of the mucous tube protrude and branch away, forming glands (salivary, liver, and the pancreas). The same principle is implemented also in the development of other tubes such as the neural tube, in which the anterior end thickens in the form of the brain, and the posterior end narrows to form the spinal cord; individual parts of the brain in turn develop into subordinated parts.

The processes or morphological differentiation, which occur after primary organ formation, conform to some general regulations. Individualization is implemented gradually by irregular growth, such as narrowing, branching and so on. Morphological differentiation spreads from the inert region of the central line toward the fusing line; this route, recognized also in the development of the most primary organs, Baer called the generating arch.

The form-generating process does not proceed directly from the central lines to the fusing or closing lines; it differentiates the similar morphological elements one after the other. The entire vertebrate body consists of a combination of such morphological elements. Thus, the vertebra with its upper and lower arch is a morphological element of the bone system; the double ring nerves, with part of the central nervous system, represent a morphological element of the nervous system; the blood-carrying system is also composed of morphological elements.

Along the longitudinal axis, the morphological elements, such as vertebrae of different regions, are not identical. The group of morphological elements with similar features, such as the neck vertebrae, Baer called a morphological segment. By the principle of dividing it into morphological segments, the whole vertebrate body is divided into

the head and trunk, the latter of which is further divided into the thoracic and abdominal parts. The morphological elements are established very early in the embryo, and the differences between them develop late; much later the morphological segments develop. The morphological elements and segments stand in a different relationship to the particular organs.

Assuming that understanding of organs is devoid of morphological content, Baer found it necessary to introduce a more complete understanding of morphological elements and segments. Thus he held that the eyeball belongs to one morphological element, while the brain occupies a whole segment, which in turn consists of elements. The liver, regardless of its size, is a product of one morphological element, and the small thyroid gland belongs to two elements. In adults, the breakdown of vegetative organs into morphological elements is not noticeable. The younger the animal, the more this division is obvious; thus, the branchiate slits with their five vascular arches undoubtedly relates to the division of the throat cavity into five parts. In the arthropods there is an obvious breakdown of the whole intestine.

Baer considered this morphological analysis a very important task which had not previously attracted the attention of embryologists. He expressed his belief that it would be possible to explain the factors upon which all the particular properties of animal structure depend. But this has not yet been accomplished. Nonetheless, interest in problems of animal structure, in particular the phenomena of metamerism which is characteristic of contemporary morphology (investigations of A. N. Severtsov, B. S. Matveev, D. P. Filatov, P. P. Ivanov, N. A. Livanov, V. N. Bekhemishev, and others), bears witness to Baer's insight.

The actual properties of each primary organ are determined by the character of its morphological division. In particular, cored growths or protrusions form from the neural or intestinal tubes, but the other primary organs only form compact growths. The cored or hollow organs such as the heart and blood vessels can develop not only by means of protrusion (morphological differentiation), but also by means of histological differentiation, particularly due to the development of hollow passages

in the vascular layer. By these observations, Baer established the beginning of a theory of development of the vascular system. This theory gained embryological use much later, and Baer's role in its establishment is not always evaluated fairly.

Turning to histological differentiation, Baer introduced histological elements. At first the embryo is composed of a nearly homogenous mass, partially consisting of dark or light small globules or vesicles, and partially of a transparent formless mass. Individual organs at first are also almost entirely homogenous, and only later do fibres, plates and hollow passages appear in them. Baer stated that "modern anatomists called the study of tissue histology, in contrast to anatomy, or the study of the external form. Therefore, in the embryo, the development of separations into multiformed tissues is called histological differentiation, represents not a new formation, but a change in what already exists, particularly by separation of the homogenous into variable histological elements. Histological differentiation usually develops later than morphological differentiation; however they are not completely distinct temporally (II 6(c) 11, pp. 122-123 (92)).

Blood forms, according to Baer, by a thinning of certain parts of the organism, but the walls of the blood-vessels appear with the movement of the blood. All this occurs at first in the vascular layer and then throughout the embryo.

The processes of histological differentiation are very distinct in muscle formation. At first they look extremely soft, like unclearly formulated, fairly thick fibers with alternating widened and narrowed portions. These fibers do not grow from other muscles and do not connect one bone with others, but develop in a formless mass located between the bones. Baer objected to Ham's view, that muscles form from small blood globules in a row. Muscle bundles develop by splitting of the initially developing fibers, as a result of which the latter become thinner.

Concerning nerve formation, Baer believed that nerves do not represent growths from the neural tube. Only the nerves going to the sensory organs represent a growth from

the brain, while the other nerves develop by means of histological differentiation in other primary organs.

From his comparison of the three types of differentiation Baer generated the following aphorisms. "Primary, morphological and histological differentiations repeat the same distinctions, the first above the others, the second behind the others, and the third in the others" (II 6D, p. 126 (94)). Therefore, these distinctions are not absolute, but only relative, because the distinctions, which are essential in the primary organs, are repeated as subordinated distinctions in individual parts of the body. (102)

The divisions concluding the description of bird development (§ 7) considers the formation of individual systems and organs. Baer first addressed the histological differentiation of the skeletal parts of the bony or osseous system. According to his description, all the bones are composed of cartilage, which comes from closely arranged small dark globules. The mass of these globules becomes light and forms a soft cartilaginous material; the periphery of the cartilage becomes a cartilaginous membrane, and the middle becomes a firmer cartilage. The cartilaginous parts at first remain formless and only later develop defined features, acquire appendages, and so on. In other words, for the skeletal elements, morphological differentiation is preceded by histological. Ossification in individual cartilage proceeds from the middle to the surface, frequently beginning in several spots at the same time. The joints appear simultaneously with the cartilage by similar histological differentiation, as distinctly observed by Treder on the fingers of the anterior and posterior extremities. From the parts of the body system, the axial skeleton is established earliest. Along the embryonic axis, dark granules form a thin string, the vertebral cord. Baer reminded his readers that in *De ovi* he gave this formation the name spinal cord and later concluded that it should have been named the vertebral cord. It must be noted that in embryological literature after Baer his first choice gained distribution.

By means of histological differentiation, the cord is separated from its lighter membrane, the cord sheath.

Ossification of the vertebrae proceeds from the anterior backwards, as described in detail in the first part (I 17, 2c, 2d and 11f). The body of each vertebra has an independent point of ossification. The upper arches of the vertebrae form from two halves, the opposing aggregations of dark granules in both the spinal plates.

Baer's ideas of the development of the osseous skeleton and the skeleton of the extremities were perceptive. Thus, the first steps of skull formation in connection with the developing brain constitute the form-producing interactions of parts in embryonic development. Talking about the order of ossification of the skeletal elements, Baer noted that this histogenetic process begins earliest in the fastest growing parts of the skeleton.

The transverse appendages of the vertebrae and ribs are initially established as an entity and then separated by joints. In respect to the development of the skull, Baer stuck to "the vertebral theory" formulated by Oken and Goethe. The skull, in Baer's opinion, is "the sum of the most anterior vertebral arches." It develops like the other vertebrae, only the development here is "modified by the strong extension of the brain" (II 7d, p. 132 (99)). The bones, of the facial part of the skull "are formed from the most anterior end of the ventral plates and represent, in this way, the lower arches of the cephalic vertebrae" (II 7c, p. 133 (100)).

The extremities are formed by the expansion of the layer lying above the spinal and abdominal plates and which becomes observable only at the third day of incubation. The fold from which the extremities form spreads upwards, downwards and externally; development upwards and downwards produces the trunk part of the extremities, shoulder girdle and pelvis. In Drawing 28 the original point of development of the extremities is shown by the spot d". The growth externally raises the crest of the fold in the form of a layer, after which the foundation of the extremities is divided into a stem and plate, the middle and the terminal segments of the extremities.

Concerning the development of the jaws, Baer leaned towards the nature-philosophical analogy identifying the jaws with the extremities.

As already noted, the central part of the nervous system develops, in Baer's opinion, by primary differentiation through exfoliation from the internal surface of the spinal plates, while the peripheral part is formed through histological differentiation of the muscular layer. At the beginning, the tissue differentiating into the neural tube is characterized by histological homogeneity, but soon differences in the structure of the surface and in deeper layers appear; particularly in the latter which connects with brain tissue. The division of the neural tube into rudiments of the brain and spinal cord takes place before the fusion of the spinal plates, insofar as the anterior part of the tube appears wider than the posterior.

The spinal cord and its extension maintains a regular thickness, with the exception of the places of formation of the extremities, where there are thickenings of the spinal-brain tube. The internal structure of the spinal cord becomes visible gradually. In it there appear four main main structures, which are particularly obvious at the internal surface. The number of structures increases, and still later fibers become recognizable in it. The internal part becomes grey, and the external white, while the grey matter at the transverse section acquires the form of a cross.

The cephalic brain at the early stages of development is little different from the spinal cord. Yet, it must not be thought, Baer said, that the cephalic brain represents an anterior extension of the spinal cord into the skull cavity, or the reverse. They both represent a modification of one primary organ, the brain tube, and are formed from it by means of morphological differentiation. The earliest part of the cephalic brain soon divides into separate portions, each of which expands to form brain vesicles; between them interceptors form. At first the anterior vesicle separates from the most elongated posterior one, then the latter subdivides into two and produces the stage of the three vesicles; the anterior, middle and posterior. The anterior vesicle represents the future large brain, the posterior becomes the cerebellum and the medulla oblongata, and the middle becomes the four-hillocked mass. The anterior

vesicle soon divides into two, and its anterior part becomes paired. The posterior vesicle also is converted into two, so the number of brain vesicles increases to five. The cavity of the anterior vesicle is the beginning of the lateral ventricles of the brain, and its walls become the hemispheres. Inside the second vesicle, the cavity of the third ventricle appears. The third vesicle is the rudiment of the four-hillocked mass. The fourth vesicle becomes the cerebellum, and the fifth is the medulla oblongata. All the brain vesicles which communicate among themselves at first lie in one line, where the curving of the cephalic brain and the reciprocal displacement of its division begins. The subsequent development of the brain is described in the first part (I 2m, 5aa, 9v, 10t, 11p, 12g). All sensory organs are formed from the anterior part of the cephalic brain.

Prior to other sensory organs, the eyes develop. They are already detectable on the second day as two prominences on the sides of the intermediate brain. Their connection with the brain is narrowed, and at that time the eye rudiments have the shape of vesicles which are situated on cored stems; from the latter the optic nerves form, and from the vesicles the eye balls. The vascular and hard eye membranes develop with the splitting into layers of the initial single cover of the eye, the same that takes place in the brain, the cornea represents a part of the hard membrane; later the anterior chamber of the eye develops under it (see v. I, 2n, 5bb, 6v, 7w, 9w, 10u, 11q, 12h).

The ear is founded at the end of the second day; its primary rudiment, according to Baer, is a protrusion of the posterior part of the cephalic brain.⁶ By what means the auditory vesicle turns into a labyrinth remained unknown to Baer; undoubtedly the auditory nerve forms like the optic nerve. From the throat cavity to the ear, a protrusion covered with mucous membrane grows, forming the eustachian tube and the drum cavity.

6. It is difficult to imagine how such a sharp-sighted and careful observer as Baer could allow such a mistake. The auditory vesicle (rudiment of the internal ear) is formed from the increasing unlacing of the ectoderm.

For the formation of the organ of smell, the anterior brain forms protrusions, against which olfactory depressions appear on the surface; the nasal passages develop later, after the formation of the palate and upper jaw. Thus, Baer wrote, "the eye is a protrusion of the brain tube through the muscular layer, and the nose is a protrusion from the brain to that bony region" (II 7q, p. 156 (117)). The organ of taste stands by itself. "I could not recognize," Baer wrote, "whether for the formation of the tongue a part of the brain protruded" (II 7r, p. 157 (118)).

Recalling that the abdominal plates of the mucous layer approach each other along the length of the embryo, forming an internal tube at the same time as the unlacing of the embryo, Baer described the subsequent changes. In agreement with Rathke, in the anteriormost part of the tube, which Baer called the mouth part of the intestine, the mouth slit bursts open. In the posterior, the mouth part of the intestine opens by an orifice, which Wolff called the fossa cardiaca, facing the yolk. Because it is not connected with the heart and does not correspond with the future stomach, Baer suggested calling it "the anterior entrance into the intestinal canal." At the posterior end of the embryo, upon initiation of unlacing a blind hole is formed; this is converted afterwards into a tube whose end later opens. Instead of Wolff's name, "lower hole" (foveola inferior), Baer suggested the term "posterior entrance into the digestive canal." The posterior portion of the intestine, he called the posterior-communicating intestine, in agreement with Rathke. The middle portion of the intestine, located between the anterior and posterior entrances, at first remains flat. Upon development of the mesentery, it is converted into a gutter, the borders of which are formed by the intestinal plates. By continuation of the unlacing, the anterior and posterior portions of the intestine pull up to each other, their entrances become nearer and form a general passage from the intestine into the yolk sac (the intestinal umbilicus); at the fifth day this passage draws up in a narrow canal, the yolk duct (see v. 1, 5e, f, r; 6g, 7h).

Baer noted the historical study of digestive canal development, writing that

Wolff was the first who understood this method of development and explained it in the greatest

work which we know in the field of description in the natural sciences, in his treatise. *DE FORMATIONE INTESTINARUM*. It was published in the twelfth and thirteenth volumes of the *NOVI COMMENTARII ACADEMIAE PETROPOLITANAE*. Meckel performed this work and issued it in the form of an individual book under the name of C. F. Wolff, *ÜBER DIE BILDUNG DES DARMKANALS IM BEBRÜTETEN HÜHNCHEN* (Halle, 1812), accompanied by an introduction, in which he discussed the concurrence of mammalian and avian development. I refer to Wolff's book not only for the study of the development of the intestine, but also for the early history of development in general This book had an unfortunate fate, because its main content, the discovery of the method of intestine formation and physiology, in great part was incorrectly understood. To Wolff an opinion was added, that the intestinal plates grow out from the vertebral column and are put together with each other. However, Wolff, in many places, says definitely that the intestinal plates represents parts of his false amnion, and the false amnion of Wolff is our "title cap," i.e. part of the vegetative layer of the blastoderm.⁷ (II 7s, fn. 161 (121))

Baer's words testify to his high evaluation of his predecessor's classical work, as well as in the work of the Petersburg Academy of Science.

It is known that Oken, not understanding Wolff's work, considered intestine formation as if both ends of the intestine grow into anterior and posterior regions of the embryo. Arguing with Oken, Baer affirmed that the embryo develops not from parts isolated at the beginning, but from a common rudiment; the anterior and posterior intestines from the beginning occupy fixed places in the embryo. Before the connection of the mouth and posterior-communicating

7. About this work of Wolff see Chapter 5.

portions of the intestine, the digestive canal remains straight and does not show a structural difference along its length. For this stage of development of the intestine, Baer considered acceptable Wolff's term "primitive intestine." Along its length, it consists of two layers, the internal mucous and the external vascular; above the intestine, the vascular layer extends towards the vertebral column. Between the mesentery plates, there remains a space which Baer named the mesenteric aperture. "This aperture," Baer remarked "represents what Wolff named the fistula intestinalis, because he did not distinguish it from the aperture of the intestine. There is his main mistake" (II, 7s fn.p. 164 (123)).

The intestine at the described stage of development represents a primitive organ not only for all the digestive apparatus, but also for the respiratory and some urinary and sexual organs. The most anterior part of the digestive canal, the gullet, after jaw development, is directed downwards to form the mouth cavity, from which the nose cavities are separated by the palate. In the posterior part of the gullet cavity at the third day, three pairs of slits appear which, as in fish, should be named the branchiate slits. On the third or fourth day the first slit usually becomes covered, and posteriorly the fourth is formed. On the fifth or sixth day, as a rule, the other slits are closed. The portions of the gullet walls between the slits are called branchiate arches.

The intestinal tube develops somewhat later than the gullet, and the crop significantly later. The stomach at the beginning is not distinguished by width from the other parts of the digestive tube, but later it widens. The intestine gradually elongates. The small intestine, forms many loops, some of which pass through the umbilicus from the abdominal cavity and then extend internally with the remnants of the yolk sac, which in some birds such as nightingales never disappear. The posterior part of the intestine (cloaca) continues.

The liver is a protrusion of the intestinal walls, which forms externally and downwards two blunt hollow appendages enveloping a venous stem. The bases of the protrusion gradually narrow. The protrusions of the mucous layer branch into the vascular layer, which is raised in the form of a

mound. On the subsequent formation of the liver, its ducts and gall bladder appear. The enlarging mass of the vascular layer forms the parenchyma of the liver, and the vein which is jammed between the liver rudiments branches in the parenchyma as the portal vessels. Similarly, but without that much close contact with the vessels, the pancreas develops. Baer wrongly considered that it develops as a single structure.

All the respiratory apparatus develops by protrusion from the digestive tube. Directly behind the last branchiate slit, on the eighth day a pair of small hollow elevations appear; these are converted into sacs along a common narrow base. These sacs represent the lung rudiments from whose stem-like base the respiratory tube develops. Subsequently the lungs form a system of branching tubes, and the air sacs develop to penetrate the entire cavity of the body and bones.

Histological differentiation of the vascular system Baer described as follows: Blood forms earlier than the vessels as a result of the dilution or thinning out of the previously compact or firm parts. This occurs only in the vascular layer. The fluid is initially colorless, then it becomes yellow and finally it becomes red blood. Under the effect of the movement of blood, the permanent passages form and soon acquire firmer walls.

The process of morphological differentiation in the vascular system Baer divided into four periods, each involving small changes which prepare for the subsequent period. The first period, in which the vascular system appears, continues during the first two days of incubation. On the second day, between the anterior ends of the ventral plates, two elongated granular masses appear forming a figure called the cardiac canal. Proceeding from it anteriorly are two vascular arches, which Baer correctly noted are only like veins at first; Wolff was incorrect when he considered that all the vessels of the first arch are veins. These arches soon become less detectable, then the second pair of arches is formed, later the third, and finally, between the second and third days the fourth pair is formed. The arches of each side pour into canals (roots of the aorta) above the gullet, which are fused into the impaired aorta passing under the vertebral column; its branches give rise to the arteries of the yellow sac.

Simultaneously, vein formation occurs, and the veins join into two main stems in the posterior and anterior halves of the vascular field; both stems enter the left bend of the cardiac canal. The posterior part of the heart forms a horseshoe-shaped elevation directed to the right. At that time the heart does not yet appear in the region of the future chest cavity, but in the region of the neck.

The second period of vascular development is characterized by a circular blood movement, which is connected with the blastoderm. The blood moves primarily anteriorly and in two great stems is transferred into one or two anterior veins of the blastoderm. From the posterior part of the blastoderm, blood collects initially in one (left) posterior vein of the blastoderm, and only later the right posterior vein appears. All venous blood enters both bends of the heart, but mainly the left. From the two stems of the aorta go the posterior vertebral arteries and the blastoderm arteries. The latter, branching, reach the border sinus. In the second period the vessels of the blastoderm become vessels of the yolk sac.

The blood-carrying system at this stage has been demonstrated in a distinct and refined schematic drawing, with letter designations as mentioned below in the text.⁸ (Drawing 29) The vascular system of the embryonic body is composed of the following vessels. The vein of the yolk sac N begins in the mesentery; both arteries of the blastoderms join to make a common stem, the artery of the yolk sac p. The embryonic veins pour into a vessel which passes between the liver and heart and produces the liver branchings (the portal system). The veins going from the head along the lateral sides of the neck collect blood from the brain and neck region (the anterior vertebral veins g) and pour into a common venous stem o. From the posterior end of the body,

8. The relationship of Baer's idea by the vascular system in the amniotes to the contemporary data given by P. G. Svetlov in the note to the Russian translation of the second volume of HISTORY OF ANIMAL DEVELOPMENT (see note 85 on pp. 468 - 469).

the blood flows in the vessels, passing at the upper border of the mesenteric plates. In these vessels (posterior vertebral veins hi) veins pour in from the tail h and posterior extremities, cloaca, pelvic region, the posterior end of the kidneys and small branches of each intervertebral space. The general stems, in which the anterior and posterior vertebral veins join, are named the umbilical venous stems K; both these stems go to the heart ab. Only later is the posterior hollow vein m separated. From the union of the vessels going along the lower border of each abdominal plate, in the third period the umbilical vein forms.

The changes in the heart in the second period are as follows. From the posterior part of the cardiac canal the common venous stem forms, from the anterior part, the arterial stem, and from the middle, the whole heart chamber. Behind the passage from the venous stem, two sacs protrude into the heart chamber; these are the nondivided auricles. In the cavity of the middle part of the cardiac canal, from the convex side a lower fold grows inside and separates the single blood current into two. The arterial division of the heart widens into the trunk of the aorta. The first branchiate vascular arch disappears on the fourth day, and in replacement the fifth arch develops. Simultaneously, in the place of the union of the first arterial arch with the spinal aorta, the rudiment of the vertebral artery d is formed; and from the place of union of the first arch with the stem going from the root of the aorta, the cephalic artery c forms. The spinal aorta at the posterior end of the kidney divides into two vertebral arteries. "For blood circulation of the second period, it is characteristic that the blood in the whole route does not pass through the differentiated organs of respiration," Baer asserted (II 7gg, p. 188 (132)).

The third period is characterized by blood circulation through the external respiratory organ, whose role is responding to the quickly growing urinary sac. The branches of the aorta going into it, the umbilical arteries, enlarge. Consequently, the umbilical veins also enlarge, especially the left vein and the posterior hollow vein. The posterior vertebral veins are reduced into an unpaired vein. The

anterior end of the venous stem is increasingly converting into the auricle. The route of the umbilical vein from its branching in the liver to its union with the posterior hollow vein Baer called the venous passage (*ductus venosus*); the latter disappears in the fourth period. The common auricle is further divided into two by a septum. The cardiac chambers (ventricles) are already separated by the beginning of the third period. The vessel going from the right ventricle is the stem of the pulmonary artery, and that going from the left ventricle is the stem of the aorta. The passages from the vascular arch into the root of the aorta (Botallo's ducts) narrow. Both anterior arches of this period remain in connection with the cephalic and vertebral arteries, and also with the arteries of the anterior extremities. In the place of the middle arch only the Botallo's ducts remain; from the external half of the last vascular arch the stem of the aorta forms, and from the internal half, the right pulmonary artery. The left root of the aorta soon is converted into a thin vessel, the direct continuation of the Botallo's duct of this side. "In this period," Baer concluded,

the blood, which shares in respiration, passes to the body through the umbilical vein, . . . is mixed with the blood from the rest of the body, and goes into the heart together with blood returning from the liver. It (the blood—L. B.) is divided into two streams, one of which goes into the pulmonary artery, and the other, the stranger, into the aorta Respiration takes place in the urinary sac The physiologists call such blood circulation an incomplete double circle (II 7hh, pp. 194-195 (147))

The fourth period after hatching is characterized by the formation of a complete double circle of blood circulation. The auricles are completely separated, and all the blood from the body goes through the right half of the heart into the lungs for gas exchange, and from them through the left half of the heart, then into the whole body for nutrition. Respiration through the urinary sac stops. The umbilical arteries and veins become empty. The yolk artery becomes a branch of the portal vein, and finally disappears.

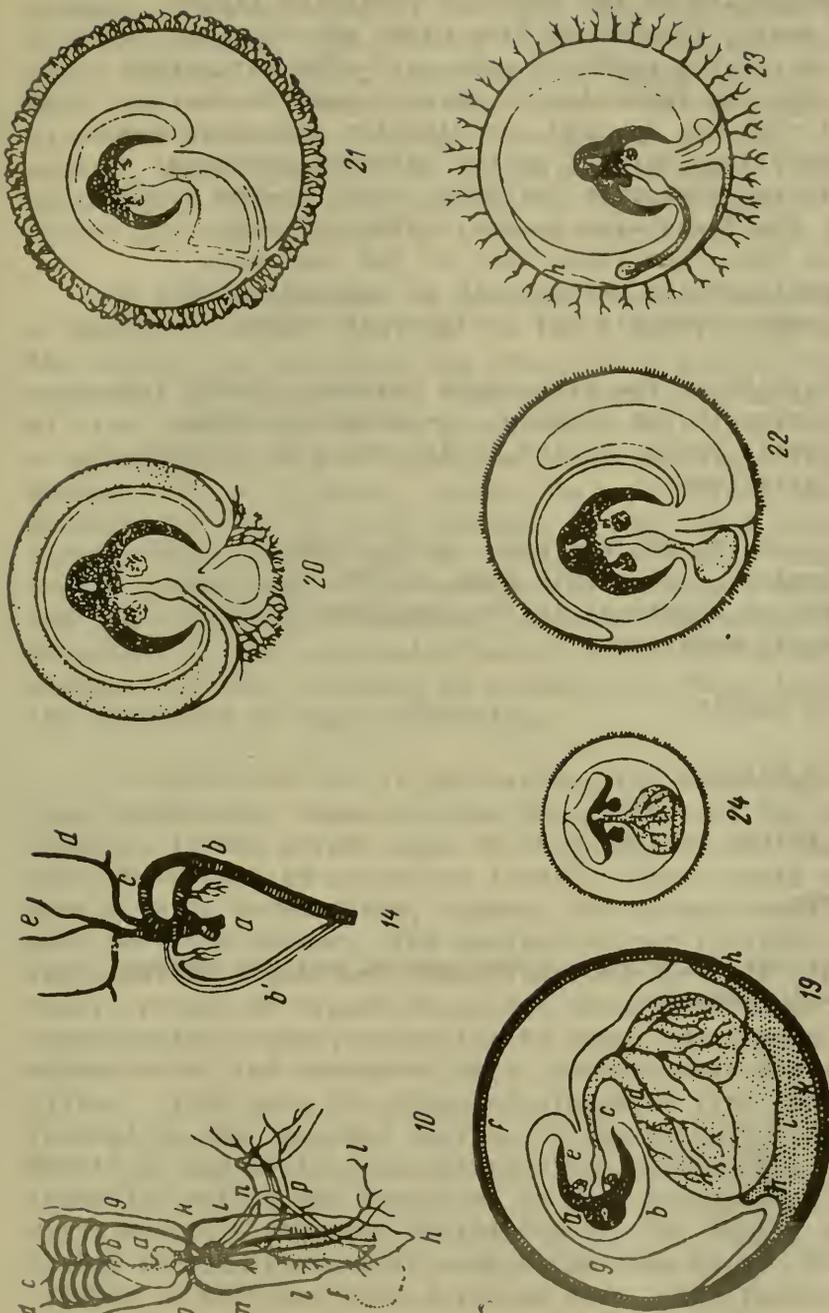


Figure 29. Baer's illustration from the third part of ÜBER ENTWICKLUNGSGESCHICHTE

(Caption on the following page).

(Figure 29, Caption)

10. A representation of the vascular system of birds: ab--the heart, from which five pairs of arterial arches go; c--the cephalic artery; d--the vertebral artery, for the formation of which a part of the arterial root (e) is used; f--division into branches in the umbilical artery; g--the anterior vertebral vein; h--the posterior vertebral vein; i--the caudal vein; k--the transverse venous system; ll--the umbilical vein (the lower vein of the stomach); m--the hollow vein; n--the vein of the yolk sac; o--the common venous stem; p--the yolk artery.
14. The conversion of the branchiate vascular system into constant arteries in mammals: a--arterial stem; b--the aortic roots; c--the aortic arch; d, c--the carotid arteries.
19. A section of the chicken egg: a--the embryo; b--the amnion; c--the yolk duct; d--the yolk sac; h--the serous membrane; i--the condensed albumen; k--the shell membrane.
20. Ovum of a rabbit.
21. Ovum of a bitch.
22. Ovum of swine.
23. Human ovum.
24. Scheme of the formation of the amnion and the serous membrane in mammals.

The predecessors of the permanent kidneys, which exist at a later age, are temporary organs carrying the name of primary or false kidneys; in birds they are named the Wolffian bodies. The primary kidneys form from the mesenteric plates; however, the method of their initial development Baer considered insufficiently clear. These organs have a glandular character. Along them extends a duct, the false ureter, which opens in the cloaca. This duct, in Baer's opinion, is formed by histological differentiation of an intact structure, which is transferred later into a tube.

In the development of primary kidneys, Baer discovered a regularity other than that of the digestive glands. For the latter, he described the determining role of the mucous membrane, which initially forms an excretory duct, and then all the branchings of the gland which only later receives a network providing it with the blood vessels. The primary kidneys, in his opinion, develop in a different manner, particularly in the first changes in the blood vessels. Already under the effect of the blood vessels, secretory canals are formed. This combination of Baer's wrong ideas has great historical interest, because they show his great attention to the interrelations of parts of the developing organism and his striving to explain, by these interrelations, the processes of organ formation.

On the sixth day of incubation, the mesenteric plates form extensions; these are the foundations of the permanent kidneys, in the border zone of which Müller had seen vesicles with their tubules extending inward. These small urinary canals later become thin, branch, and through smaller stems pour into the ureter. The genital system (divided into reproductive organs and conducting passages) is formed from other systems of organs which are detectable later. The reproductive organs, according to Baer, are formed by the expansion of the abdominal part, particularly the mesenteric plates. They have the shape of elongated flat bodies, located on the internal surface of the primary kidneys and devoid of any defined structure. The sexual organs are initially paired and identical in both sexes; then the right ovary in chickens diminishes in size fairly early, though in wild birds both remain the same size. The right oviduct in chickens also develops less. The testicles change

the rounded form into a bean-shaped form. Histological differentiation occurs there also, but not in the form of vesicles as in the ovaries but in the form of small canals, whose terminal parts go through the external layer of the primary kidneys and reach the excretory duct.

The essay on bird development Baer terminated with a short summary. There he gave the differences between the two aspects of the individual development, the development for oneself and development for the species. The first begins early but quickly progresses, while the second begins only near the end of development of the individual, and then is renewed annually. At the time of embryonic development in the egg, vital functions differentiate by the contents of the egg taking their origin from the maternal body. But after release from the egg membranes, the organism enters into an interaction with the external world. In development of the methods of nourishment, it is possible to distinguish three periods: the use of the yolk, then the fetal fluid and finally nourishment from the external world. The four periods of respiratory and circulatory development Baer designated by the terms: blood formation, simple circle, incomplete double and complete double circle of blood-circulation. These periods of development follow each other, and in each period one can observe "preparation for what is produced in the subsequent periods"⁹ (II, III, 7u, 153).

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9. To Baer belongs, in this way, the first attempt to divide chick development into periods depending upon the different interrelations with the conditions of the surrounding medium, in particular depending on the character and sources of nutrition.

CHAPTER 21

THIRD PART OF ÜBER ENTWICKLUNGSGESCHICHTE (Continued):

DEVELOPMENT OF REPTILES, MAMMALS, AND ANIMALS DEPRIVED OF AMNION AND YOLK SAC

Baer based his presentation of reptile development on data concerning turtles, monotremes, and viviparous snakes and lizards (§ 8). The aim of his detailed study, according to Baer, was comparison of the peculiarities of development characteristic of the separate classes with features characteristic of all vertebrates.

Baer's information about turtle development was limited. His attempts to receive more or less late stages of development were unsuccessful, as described in detail in his specialized study.¹ (103) The peculiarities of early turtle development, which Baer observed up to the tenth day of development, showed that interpretation of the embryo was an error of observation (Figure 30). In ÜBER ENTWICKLUNGSGESCHICHTE, Baer referred to the observations of Tiedemann,² who saw a turtle embryo surrounded by amnion. The urinary sac is connected with the urinary bladder and by the right side rather than in the body of the embryo. The yolk sac, by the help of the yolk duct, is united with the intestine. As in birds, towards the end of embryonic life, the yolk sac passes through the umbilicus to the abdominal cavity. Bending of the embryo and its internal organization is the same as that of birds.

Concerning the monotremes, snakes and lizards, Baer enumerated in detail the similarities of their embryonic

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1. K. E. v. Baer. "Beitrag zur Entwicklungsgeschichte der Schildkroten." ARCH. ANAT. PHYSIOL. U. WISS. MED. (1834), pp. 544-550 (104).
 2. (Ed.: Friedrich Tiedemann, ZU SAMUEL V. SÖMMERINGS JUBELFEIER. Heidelberg, 1828, pp. 23 ff.)

development with the development of birds. The ova of reptiles are supported by a small amount of albumen and deprived of chalazae. Their development elapses more slowly than in birds, so that the heart, for example, although generally similar to the heart of birds, is delayed in early stages of development; the same holds for the development of extremities. The ova are laid when development is sufficiently advanced. The development of the ova outside the maternal body corresponds to the third period of avian development. The difference between the embryos of reptiles and birds are these: the vascular arches, coming out from the aorta, are longer in lizards and snakes than in birds, and their aorta in the post-embryonic period retains two roots, from which the right is much larger than the left. The cardiac chamber remains without septum. Thus, Baer concluded, "with respect to circulation, the reptiles remain in an embryonic condition, so the circulation system remains in an incomplete double form. In contrast, most birds do not acquire external genital organs. In this regard, the birds thus remain in a more embryonic condition in comparison with reptiles" (II, 8b. 213 (141)). In the development of viviparous snakes and lizards Baer did not notice any essential peculiarity.

Turning to the development of mammals (§ 9 (164) and 10 (233)), Baer first noticed that in different representatives of his class, the moment of birth coincides not with one or another stage of embryonic development, but in accordance with the fact that there can be both early and late-born mammals. Immediately after birth in the former, the young are incapable of independent movement, while in the latter the young are actively moving. "The early-born mammals," Baer wrote, "are, thus, transitory forms, and the late-born mammals constitute a proper branch of this class" (II, 9a, p. 218 (164)). The development of early-born mammals Baer did not study himself. Rather he referred to the limited literature of his time on monotremes and marsupials.

Concerning the late-born mammals, Baer first noticed great differences in the external form of the embryonic ova³

3. Embryonic vesicles, by recent terminology.

and the embryos themselves. The existence of the umbilical cord, amnion, chorion, allantois and placenta in mammals had been known for a long time. In the human embryo, according to Baer, until recently the importance of the small vesicle between the chorion and amnion and connected with the umbilicus by a long stalk could not be interpreted.

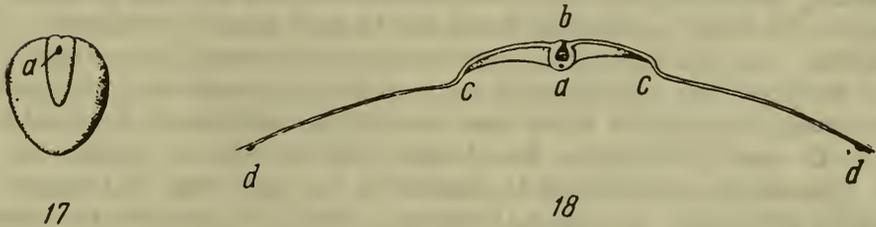


Figure 30. Baer's illustration of the development of turtles.

17 - embryonic corselet "Emys europeae," view from above; a- entrance in the spinal canal;
 18- the same also, in transverse section (enlarged 10 times); ab- spinal plates; bc- abdominal plates;
 d- boundary vessel.

In the first and second decades of the nineteenth century, however, it was learned that in the mammalian embryo the yolk sac is actually present. Thus the umbilical vesicle of man and other mammals and similar to the yolk sac of birds, is connected with the intestine. In a special report, Baer carried out on different mammals studies that showed that the formation of allantois and chorion changes with changes in uterine structure.⁴ In the initial period of development of

4. K. E. v. Baer, "Untersuchungen über die Gefäßverbindung zwischen Mutter und Frucht in den Säugethieren," EIN CLÜCKWUNSCH ZUR JUHELFEIER S. T. SÖMMERING, Leipzig, 1828, pp. 30 ff.

the human ovum, the entire uterus is covered by a thick layer of coagulated matter, the caudal membrane. Baer, following Hunter,⁵ repeated that this membrane forms a pocket in which the ovum lies in an open sac, a peculiarity which distinguishes humans from other mammals.

Returning to the question about the origin of the ovum, Baer recalled the unsuccessful searches for mammalian ova by Haller and his student Kuhlemann, the observations of Cruikshank, and his own investigations, leading to the discovery of the ovum in the Graafian follicles. The history of this discovery is considered above (in Chapter 14).⁶

After a description of the female genital system in mammals, Baer addressed the characteristics of the ovum in the ovary. On this question, Baer could not reach complete clarity. In his opinion, the follicle content is a fluid rich in protein, surrounded by a granular membrane, which he erroneously compared with the vitelline membrane of bird's egg. In the albuminous fluid Baer saw vitelline globules and therefore considered it possible to call the follicle content an ovum, noticing, however, that it represents something more than the yolk ball of a bird's egg, because not all the mass covered with the granular membrane is converted into the fetus. The embryo of mammals is developed from a small vitelline globule situated at the inner surface of the follicle and ejected after the latter bursts. This globule Baer compared with the embryonic vesicle in the eggs of birds and reptiles. He recognized, however, some consequences of this comparison, noticing that in birds and reptiles the embryonic vesicle in the fertilized egg disappears, while in mammals it is the beginning of the embryo.⁷ Further Baer

5. Baer referred to a treatise by (William) Hunter, ANATOMIA UTERI HUMANI GRAVIDAE TABULIS ILLUSTRATA, Birmingham, 1774.

6. See also Baer, NACHRICHTEN, p. 331(323). There Baer stated his polemics with Plagga, attempting to ascribe to himself the priority of the discovery of the ovum of mammals.

7. Detailed analysis of Baer's errors connected with the study of the mammalian ovum is given by P. G. Svetlov in his remarks on the translation of the second volume of ÜBER ENTWICKLUNGSGESCHICHTE (remark 139, pp. 476-479).

spoke about the movement of the ovum in the tubes and the formation of the corpus luteum (II, 9 g-k (176-183)). He supposed that "in the ovum of mammals following entry into the uterus or shortly after that, the embryo is isolated" (II, 91; p. 244 (184)). The ovum, which is composed of vitelline globules soon becomes diluted, quickly grows at the expense of the liquid composing parts of the surrounding albumen, and hence becomes covered by a membrane closely adjacent to the ovum reservoir. This membrane, which Baer studied in swine and sheep, was called the outer ovum membrane. Under it was present that membrane directly covering the yolk (vitelline membrane), which later dissolved.

The primary form of the embryo Baer described as follows: When the yolk becomes liquid and transparent, it is clear, that the sac-like rudiment is composed of two unequal parts: the smaller is the embryo, in the middle; the larger part surrounding it is the embryonic membrane. The part that is the origin of the embryo first has a rounded form, then it changes to the form of a shield, becoming transparent and deprived of all organization" (II 9p, p. 252 (189-190)). Later the shield elongates, and along the edge appears a strip similar to the primary strips in the bird's egg.

Just after embryonic formation begins, it is untwisted from the rest of the blastoderm by formation of the umbilicus. As a result of this, the embryo itself and the yolk sac are formed. During the study of development of dogs, rabbits, swines and sheep, Baer noticed that the yolk duct connects the yolk sac with the intestine. In mammals, as in birds, the yolk sac and intestine represent two parts of the vegetative part of embryo, which are only untwisted from each other. Their connection by means of the yolk duct in different families of mammals is kept for different lengths of time: the longer the time, the greater the size of the yolk sac. Not in any mammal does the yolk sac enter the body of the embryo. It is torn away with the ovum membranes or it disappears earlier. The yolk sac of mammals and of birds is composed on the outside of a vascular layer and inside of a mucous layer, which are never completely separated. The form and size of yolk sacs of different mammals are very different. For example, in carnivora it is large, the form changes from spherical to ellipsoidal and then to

fusiform, and for a long time it remains connected with the intestine. In human beings the yolk sac, called here the umbilical sac, remains spherical. In rodents it is very large and rounded, winding under the serous membrane around the amnion.

Before the beginning of the untwisting of the embryo from the yolk sac, the embryo is split into two layers—animal and vegetative—connected in the region of the primary stripe. The abdominal layers, after separation, turn upwards. Because of this the formation of the amnion quickens to the extent that the moment of its formation is difficult to recognize. "However," Baer wrote, "I was lucky enough to see in dogs, and more frequently in swine and sheep, embryos completely uncovered by the amnion. Therefore I can assure absolutely that the amniotic sac is formed as that of birds. Following amnion formation, all other parts of the outer layer of the blastoderm, as in birds, form the serous membrane, in which the amnion and yolk sac are included" (II 9r, 255-256 (192)) (Figure 29, 24). Baer noticed that attention was not given to the serous membrane, and thus it was impossible to understand the development of membranes.

The urinary (allantoic) sac of mammals, Baer observed, grows when body of the embryo is opened nearly the whole length. It represents the growth of cloaca and is composed of two layers: an internal layer which is the continuation of the serous layer, and an external or vascular layer. Into the latter enter two branches and ends of veins, passing by the lower edge of abdominal layers. These vessels are the future umbilical arteries and veins, which share in the formation of chorion and placenta. The subsequent development of the allantoic sac of carnivora (similar to birds) leads to its growth, so that it extends through the back of the embryo from right to left and meets with its opposite part, leaving free only the place for the vitelline vesicle. In the internal half of the allantoic sac, adjacent to the amnion, the blood vessels are few, and in the internal half which intergrows with the superficial membrane, forming the chorion, the vessels grow and form the vascular network of the placenta. The case is different in hooved animals. The allantoic sac widens a little and lies near the amnion. Because it is more elongated, it digs through the external layer and goes beyond its limits. The layers of the allantoic

sac of hooved animals are situated far apart, so the two inserted sacs are in each other, the internal one deprived of vessels and assumed to be the urinary outlet. Even before Baer, it was called specifically the allantois. The allantoic sac of rodents does not extend through the amnion, situated against it on the ventral side of the embryo. Finally, the allantoic sac of human beings is very small (Figure 29, 23).

Baer called the outer vascular layer of the mammalian embryonic vesicle the chorion. It is formed originally from that external embryonic layer deprived of vessels. The placenta, according to Baer, was considered growths of the chorion, which served to create conditions for the maternal blood to influence the embryonic blood. On the basis of observations Baer suggested broadening understanding of the placenta to include all the blood-containing villi present on the surface of the ovum. When the flow of blood to the uterus is strengthened, a structureless material is distinguished on its internal surface; later vessels penetrate it and there arises the caducous membrane, which Baer favored calling the uterus cover or uterine placenta.

Concerning embryonic respiration and nutrition, Baer noticed that the maternal blood vessels nowhere communicate with the fetal vessels. In the blood of both mother and fetus, which pass in close proximity, "changes must take place, and these changes must be called respiration" (II 9x, p. 275 (205)). The feeding of the ovum at the beginning, when there are still no vessels, takes place by absorption at its surface. Later, with the appearance of blood vessels, this absorption occurs through them.

Turning to the details of mammalian development, Baer first established the great similarity to avian development in organ formation. For example, in the skeletal system, the spinal column and tail form as in birds. At early stages, the limbs are similar to those of birds, and at first a long fold forms, from which the basic segments of limbs, articulated joints, and digits are formed. The last is at first undifferentiated, so the four hooves of sheep are basically indistinguishable from the digits of dogs and the hooves of swine. Jaw development takes place from the

same rudiments as in birds. The lower jaw is a derivation of the first and second branchial arches. Peculiarities of formation of upper jaws in mammals result because the middle does not extend into a long neck like the bird's beak. Every upper jaw develops an inside crest, which gives rise to the corresponding half of the hard palate and nasal septum. Only after this do the jaws of the mammalian embryo begin to extend. In connection with brain development in the previous stages, the facial parts of sheep and swine are very similar to the human face.

For the digestive canal, the abdominal cavity of mammals closes as in birds, but somewhat later. At first the intestine is connected with the yolk vesicle by a very wide space, the construction and extension of which forms the vitelline duct of the cutaneous umbilicus. The short and non-differentiated digestive canal divides into parts, quickly elongates and moves aside from the backbone, especially in the middle part as a result of the growth of the mesentery. In this place the intestine forms a projection, into which the vitelline duct falls. As in birds, from the digestive tract develop the salivary glands, organs of respiration, liver, pancreas and urinary bladder. A part of the intestinal loop for some time lies in the umbilical branch.

Differences in the structure of the digestive organs which are inherent to different families of mammals, appear gradually. Furthermore Meckel saw that in the earlier period of development of ruminants, the stomach is single. Notches appear in it, and then the parts of the stomach become separated. Baer noticed Meckel's mistake here, pointing out that Meckel, in support of his opinion that embryos of higher animals pass through the stages corresponding to organization of the lower organisms, confirmed that the stomach of man passes, as in ruminants, the stage of the sac divided into parts.

In the vascular system, the heart is initially similar to birds and has the form of a double-branched canal. Becoming shorter, it gains the beginning of five vascular arches, which are transformed into two aortae. Further features appear which are characteristic of mammals. The ventricle turns more to the right side, which is why both ventricles from the

beginning appear close together. The current of blood from the right ventricle moves into the fifth left arch more than in the fourth. From the fourth left ventricle, it passes into the fourth left arch more than in the fourth right. Therefore, in mammals the movement of blood in the left side is more intensive, and the arch of aorta forms from the left root, while in birds it is from the right.

In a footnote Baer objected to Allen Thomson's scheme (II cc, pp. 212-213). The latter had taken Baer's drawing of the blood vessels in a chick embryo, transferred the right parts to left and vice versa, and proposed that it is thereby possible to represent the vessels of the mammalian embryo. To prevent such erroneous interpretations, Baer made a new drawing (Figure 29, 14) of the mammalian transformation of the branchial vascular system into constant arteries. This drawing makes clear that from the anterior bifurcated end of a primarily single arterial trunk, five pairs of vascular arches proceed to the two roots of aorta b. Early disappearing arches are represented by a dotted line, and those remaining are represented by a thin contour, while the final vessels are black. In the venous system of the mammalian embryo, the same vessels which appear in birds are present. Vessels of the yolk sac and the boundary vein are also present. The coincidence between birds and mammals is especially great with the venous vessels of the embryo itself. In those and others, there are anterior and posterior vertebral veins. The posterior vein trunk in mammals, as in birds, unites with the posterior veins of the body; after that the diameter of the vertebral veins decreases. The jugular veins only at first are connected with the anterior vertebral veins and then are separated from it.

The formation of the neural tube and differentiation of its anterior part into five cerebral sacs takes place in mammals as in birds. However, in mammals the middle cerebrum is not so high and sac-formed, while in birds it is more elongated and curved. Unlike that in birds, the predominance of the anterior cerebrum over the other parts appears very clearly in mammals. But the head cerebrum, is more bent in mammals than in any other class of vertebrates. The transformation of the spinal cord to the medulla oblongata takes

place nearly at right angles. Owing to this, a clear occipital projection is seen from the outside. Baer considered the bends of the brain to be the result of its intensive growth, which the skull cavity has no time to follow. The organs of sensation develop as in birds.

The primary kidneys, similar to those in birds, appear and disappear. Toward the outside the constant kidneys originate; at first they are stretched in length, then they become rounded and move away from the vertebra than in birds.

The transformations of the genital system are very complicated. The genital glands have the form of spindles in the internal sides of the primary kidneys; in the external convex edge of the primary kidneys, simultaneous with the genital glands, a thread-like conducting canal appears. This is the future seminal duct or oviduct. In the cloaca, two lateral folds form, which then unite. They separate the rectum from the part which gives rise to the allantoic sac. Besides this, the external orifice divides into two parts for the formation of perineum. Further, the genital glands become rounded, and by histological separation in males the canalicules are developed, and in females the Graafian follicles later develop. The conducting genital ducts in females are widened and supplied by an orifice in the abdominal cavity; the uterus and vagina develop later on.

Baer described in detail the development of the external genital parts, cavernous bodies, urethra, uterus and vagina, and also the descending of testicles from the abdominal cavity to the scrotum.

Baer mentioned little about the development of the diaphragm, noting that he could not give it special attention. He did, however, establish the facts of gradual backwards displacement of the diaphragm, of elongation of the embryonic thoracic cavity, and of the growth of muscles from the wall of the body. Baer described the serous membranes briefly, whereas he described development of the mesentery in more detail. He described its displacement during the formation of intestinal loops and mentioned the turning of the stomach and the origin of omentum.

The formation of the umbilicus of the mammalian embryo takes place as in birds. Concerning the umbilical cord, in the majority of mammals the yolk duct dies off early and the vessels of the yolk sac disappear. The length of the umbilical cord is not equal in different mammals; man's is the longest, it is slightly shorter in monkeys, followed by that of hooved animals, and with the rodent's shortest.

Description of mammalian development he concluded by counting the embryonic parts lost during birth, the chorion, amnion, yolk sac and placenta with the umbilical cord. These parts in mammals are correspondingly larger than those in birds.

In a special section, Baer described the structure and development of the embryonic sac in different mammals, especially in humans. The preliminary remarks which open this paragraph stress the importance of comparative embryological investigation of the embryonic sac and the history of development of embryonic membranes. Thus "exact knowledge of the different mammalian forms of ovarian membranes can help the understanding development of human embryonic membranes. The first steps of their formation are unavailable for investigation" (II 10 a, p. 313 (235)). For explanation of the text, Baer offered diagrammatic illustrations. The first of these (Figure 29, 19) represents a transverse section of a bird's egg about the eighth day of incubation, with which the embryonic ova of different mammals are compared. In this drawing, *a* is a section of the embryo, *b* the amnion. In the body of the embryo are seen the primary kidneys, mesentery and intestine, with the yolk duct leaving at *c*, which passes to the yolk sac *d*. On the latter the distribution of vessels and the boundary vein are shown. The allantoic sac still occupies only part of the ovum; its external half *f*, adjacent to the shell membrane, marks the beginning of the chorion, and the internal half *g* surrounds the amnion. The allantoic sac already extends over the back of the embryo on the opposite side. Further, the allantoic duct *e*, remnants of the serous membrane *h* and the albumen of the egg *i* are also represented.

The embryonic sac of carnivores (Figure 29, 21) is shown in the stage of the already-formed chorion and developing placenta. The yolk sac, with an elongated form, is surrounded

by the remnant of the serous membrane *h*, separated from the yolk sac. The fate of the serous membrane becomes clear upon comparison with the earlier stage when the amnion is in contact with the serous membrane, and when the allantoic sac remains very small. The allantoic sac of a dog's embryo, developing from the cloaca at the age of about three weeks, covers the embryonic body touching the external surface of the amnion and internal surface of the chorion. The vessels of the external layer of the allantoic sac form the villi. Later, the embryonic sac stretches into the form of cylinder with rounded ends, and the villi forms the belt-like placenta. The yolk sac of carnivores is rich in vessels, and its duct remains open for a long time.

The embryonic sac of swine (Figure 29, 22) is represented at the moment when the formation of chorion continues (up to the end of the second week); the formed embryo is seen with the allantoic sac coming out from it. The latter appears earlier in thick-skinned animals than in carnivores and grows very quickly. Umbilical arteries enter the allantoic sac from the two sides of the embryo, and the umbilical veins go out into ramifications in the abdominal wall. After the formation of anastomosis between the umbilical veins, the right vein gradually disappears. In the external membrane of the embryonic sac the blood vessels appear only when the chorion is formed, or after the accretion of the membrane with allantoic sac. In swine embryos, Baer followed in detail the development of villi of the chorion. At first the beginning skin transverse fold lines appear with a height of 0.1; the free edges of folds are covered by cuts that lead to the formation of many villi. The same process takes place in the internal surface of the placenta, while between its villi arise the villi of the chorion. Also, Baer followed up the process of the union of the allantoic sac with the external membrane of the embryonic vesicle and the intergrowth of blood vessels in the embryonic vesicle with the formation of vascular networks in the villi. After the end of the fourth week, the network of the chorion's blood vessels increases, filling all the villi and spaces between them; a denser network of vessels develops in the internal wall of the uterus.

The embryonic sac of ruminants is in the essential features similar to the ovum of the thick-skinned animals, with the difference that the placentae of the ruminants are multiple and differ in form in different species. The embryonic sac of rodents (Figure 29, 20) is characterized by a single placenta, confined to part of the ovum surface.

In sloths (Baer mentioned the data of Carus and Rudolphi) the placenta is elongated and rounded, consisting of multiple placentae adjacent to each other. This forms a remarkable transition between extremely unlike forms, namely between ruminants and monkeys.

The embryonic sac of the monkey is very similar to the human sac, but more elongated in accordance to the form of the uterus. The monkey umbilical sac is larger than that of man, is also kept until birth, and possesses a similar long stalk. The length of the umbilicus, which in monkeys is larger than in all other mammals, also brings the monkey nearer to man.

Considering that he had to rely on the observations of others for questions of human development more than for other parts of his work, Baer at first refused to enter into arguments concerning the nature of human beings. "We shall," he maintained, "regard man only as a member of the great animal kingdom" (II 10k, pp. 351-352 (264)). Thus Baer determined his role as a naturalist with respect to opinions on human nature. "Comparison with the development of animals, and namely with the mammals," Baer continued, "is considered the most reliable guiding star . . . without the flame of the comparative history of development we cannot clarify the significance of the separate parts of early embryonic sac of man" (II 10.k, p. 352 (264)). And further: "You know the history of development of the mammalian egg and can imagine that the history of the human egg represents only a special case of the general history of the mammalian egg" (p. 353 (II 10L 265)).

The cover of the uterus is developed in human beings earlier than in other animals; Baer claimed that he saw the dropping off of the membrane on the eighth day of pregnancy. This cover is supplied by fossae, in which the villi of embryonic vesicle grow. The investigation of two-week-old

human embryos showed that the embryo begins to form in the internal sac, as all other mammals do. Then the embryo untwists, so that the remaining part of the sac produces the beginning of the yolk sac, which is called in human beings the umbilical sac. It quickly moves away from the embryo, while connected with it by the yolk duct. The umbilical sac usually disappears in the third month of uterine life. It may be inferred by analogy with birds and mammals that the amnion of the human embryo grows extremely quickly, even though the formation of the human amnion was not observed. Baer asserted that in human beings its development "must not take place differently" (II 10 q, p. 363 (233)). Direct observations, showing the ingrowth of blood vessels from the wall of the allantoic sac to the external membrane of embryonic vesicle, forced Baer to consider the comparative embryological suggestion that the human chorion is formed as in other mammals. Baer considered the question about the structure of the human allantoic sac controversial, but he did not doubt that, here also, the principal stages of its development are the same as those of other vertebrates. The villi of the human chorion are longer, thinner and more ramified than those of other mammals. They are entwined by a network of vessels to form placenta. The development of the umbilicus and the human embryo itself was not described by Baer, who referred this aspect of humans to other mammals (105).

The concluding section of his third part, Baer entitled "Development of animals which have no amnion and no yolk sac" (II § 11, p. 280). Mentioning the similarity characterizing development of reptiles, birds and mammals, Baer indicated that fish and amphibia possess essential differences in the structure of the ovum and membranes. This forced him to recognize that the lineal group of amphibia must be divided into two classes, amphibia and reptiles.

The main peculiarity of fish and amphibia is that they are always deprived of the amnion and allantoic sac. Instead of the latter, fish and reptiles develop other organs of respiration, the external gills.

In spite of this difference of fish and amphibia from the other vertebrates, the formation of their embryo follows the general scheme for all vertebrates: from the embryo two spinal arches arise, two abdominal layers form, and by the closure of these and others the dorsal and ventral sides of the animal form.

Further, Baer described the ova and their development in amphibia and fish, and devoted separate published works to the embryology of these two classes of vertebrates.⁸

In the ovum of amphibia, which is present in the ovary, the embryonic vesicle appears early. From the beginning it is large and is present in the middle of the ovum. At the time of maturation it ascends to the surface at the place where the embryonic layer is present from outside, not clearly demarcated from the yolk. The embryonic layer with the vesicle present inside it ascends slightly in the form of an embryonic hillock. In a footnote Baer said that he represented this stage in his *Epistola de ovi mammalium genesi* (see Figure 26, XXIV-XXVI). Covered by a thin layer after maturation, the ova fall into the abdominal cavity, and from there into the funnel of the oviduct. Embryonic vesicles are not found in the ova, which are present in the abdominal

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8. Baer, "Die Metamorphose des Eies der Batrachier vor der Erscheinung des Embryo und Folgerungen aus ihr für die Theorie der Erzeugung," MÜLLER'S ARCHIV ANAT. PHYSIOL. (1834), pp. 481-509; "Entwicklungsgeschichte der ungeschwänzten Batrachier," BULL. SCIENT., publié par l'Acad. Imp. d. Sciences de St. Petersb., No. 1 (1835), pp. 4-6, No. 2, pp. 9-10; "Untersuchungen über die Entwicklung der Fische nebst einem Anhang über die Schwimmblase," Leipzig (1835), iv + 42 pp. in quarto; "Beobachtungen über die Entstehungsweise der Schwimmblasen ohne Ausführungsgang," BULL. SCIENT., publié par l'Acad. Imp. d. Sciences de St. Petersb., 1, No. 2 (1836), pp. 15-16; "Über Entwicklungsweise der Schwimmblase der Fische," FRORIEP NEUE NOTIZEN, 39, No. 12 (1846), pp. 177-180.

cavity. During the passage through the oviduct, the ovum is covered by gelatinous material secreted by the walls of the oviduct, which Baer equated to the albumen of a hen's egg.

Fertilization in the tailless amphibia is external; the sperm cover the ova falling into water. In salamanders the sperms also are ejected into water before they penetrate the genital apparatus of the female.

The structure of the deposited ova and the early stages of development Baer described in Müller's ARCHIV in 1834 and below.⁹ The freshly deposited ova closely adjoin each other and are covered by compact albumen. In water the latter is swollen and becomes transparent. Meanwhile the ovum becomes spherical and begins to turn in its membrane, directing the dark side upwards. Baer called the upper and lower regions of the frog ovum the dark and light surfaces; their centers he called the dark and light poles and the line joining the poles the axis of the ovum.

Concerning the first stages of development of the fertilized frog ovum, Prévost and Dumas¹⁰ reported their observations. According to them, "astonishing division" takes place on the surface of ovum as Baer had said. These observations, Baer reported, "caused a lively interest in all directions, partly due to the unexpectedness of the fact that the yolk sphere, which will become a frog, is preliminarily covered by a network of geometrically and regularly situated fissures. It was due, also, to the apparent improbability that such a noticeable phenomenon had escaped the attention of many observers of the development of the frog ovum, including Swammerdam" (106). Although Prévost and Dumas did not understand the essence of the division phenomenon, Baer accurately stated that they "remained on the surface of the phenomenon" (MÜLLER'S ARCHIV, 1834, pp. 482-483). Rusconi¹¹ also saw the same

9. Baer, "Die Metamorphose des Eies der Batrachier vor der Erscheinung des Embryo und Folgerungen aus ihr für die Theorie der Erzeugung."

10. J. L. Prévost et J. A. Dumas, "Nouvelle theorie de la generation," ANN. SC. NATUR., 2 (1824), pp. 100-121, 129-149.

11. M(auro) Rusconi, DÉVELOPPEMENT DE LA GRENOUILLE COMMUNE DEPUIS LE MOMENT DE SA NAISSANCE JUSQUE À SON ETAT PARFAIT (Milan: Giusti, 1826).

picture of fissures on the ovum surface; also Baumgärtner, who incompletely described the phenomenon. The merit of final discovery of the secret of ovum division undoubtedly belongs to Baer (107). The study of the developed ova of brown and green frogs led him to the conclusion that fissures, which are seen on the surface of the yolk, represent nothing more than the boundaries of the divisions which are manifested by the whole embryonic sphere. Baer gave to embryological terminology names for the fissures of division. He named the fissures connecting the poles of the ovum, the planes of which pass through the axis of the ovum, the meridional fissures; the fissure crossing the axis of the ovum at a right angle, he called equatorial if it divided the axis approximately in half and parallel if it was situated near one of the poles. In addition to the accurate description of division, Baer thought he saw non-existent phenomena in the frog ovum. Thus he referred to an orifice which seemed to be present in the region of the dark pole and which he thought led through a canal into the deeper cavity and remained there even after the disappearance of the embryonic vesicle. This description came, evidently, from the penetration by the spermatozoa, which leave behind the dark trace that Baer erroneously took for a canal.

The phenomenon which Baer called transformation is externally detected by the development of the first meridional fissure. He described it in extreme detail, since he clearly recognized its importance. Five hours after oviposition, the first meridional fissure forms beginning from the dark pole and it gradually moves from there along a spherical arch in the direction of the light pole, where its ends are united. This process of fissure formation, Baer asserted is not continuous, but takes place in separate stages as if the movement of the fissure were overcoming some resistance. The essence of this first transformation in the developing ovum is that the "yolk sphere is divided into two hemispheres or, more accurately, into two spheres, which become attached to each other" (p. 487).

After the closure of the first fissure, according to Baer, "apparent quiescence begins. However it only seems to be, because the cleavage is imperceptibly distributed from the inside surface" (pp. 487-488).

The following stage in transformation consists of the appearance of a second meridional fissure, appearing six to seven hours after fertilization. It goes also from the dark region to the light, and its plane is situated under and at right angle to the first. The process leads to "cleavage of the sphere into four quarters," as can be confirmed by cutting the compact ovum.

In the third stage of transformation, the equatorial fissure appears and division into eight spherical parts attached to each other begins, followed by two parallel fissures (above and below the equator) producing sixteen yolk masses. Further division continues until there are sixty-four. All previous divisions were performed in vertical (meridional), or horizontal (equatorial or parallel) planes.

Baer hinted at the difference in the rhythms of division of the upper and lower halves of the ovum. "It must also be noticed," he pointed out, "that the first and also the second meridional fissures in the light region move slower and fit in less deeply" (p. 489). However, in his drawings the inequality of division of the animal and vegetative halves of the ovum is clearly represented. Later, the division of yolk regions into central and peripheral regions takes place. At this time there are already so many fissure-separated regions, that the surface seems shagreen (leathery), and after a little time when the total number of the separated yolk masses is approximately 3,000, the surface is very finely granulated, resembling grains of sand. Finally, the divided parts of the ovum become microscopic, their surface seems to be smooth, and a great number (many thousands) of yolk aggregations can be found in one section. In the following stage of development, the formation of the embryo (KEIM) takes place, according to Baer, and the demarcation of the embryo begins.

His description shows that Baer could clearly follow the process of complete division of the ovum and establish its various stages. In the following pages of his outstanding work, "General Observations of the Mechanism of Division," he attempted to reveal the regularity of division processes and to understand their purpose. First, he objected to formal

geometrical interpretation, because the geometrical regularity of distribution of the fissures is frequently misrepresented without violation of the following notion of development. Further Baer established the following general rule: "... If in the separated yolk mass (or blastomers, as they are now called—L.B.) one side is significantly longer than the other, then it also undergoes division. According to this rule, the equatorial regions must be divided by vertical fissures, and the circumpolar regions by horizontal fissures. However, deviations from this rule are possible" (p. 499).

After more than forty years, the established regularity of the axis of division was identified as Hertwig's law,²² while, in fact, it must be called Baer's law.

The succession of the planes of division in the frog ovum Baer explained in the following way. The first fissure, beginning from the dark pole, is meridional. It divides the ovum into two parts with identical vertical and horizontal diameters; that is, at these parts, according to Baer's law, the second division in vertical and horizontal planes is equally possible. However, it always takes place only in the vertical plane and it, as the first, also begins from the dark pole. In the four parts of the ovum, the vertical diameter is twice greater than the horizontal; they are divided in accordance with Baer's law, in the equatorial plane. Then again eight blastomeres ("yolk masses") appear. Every one of them is bound on three sides by equal planes, and on the fourth side by an identical part at all the spherical surfaces. Here again it would not seem to matter in which plane the division of these parts of the divided ovum takes place. The division regularly begins from the dark pole, however, and the fissures of division appear again meridionally. Later, strict regularity of division is lost, but the tendency to

12. It is known under this name everywhere, including the Russian handbooks (see for example A. Maksimov, OSNOVY GISTOLOGII (THE BASIS OF HISTORY), Part 1: UCHENIE O KLETKE (Study of the cell) (1917), p. 334.

distribute the division from the dark pole towards the light pole is retained; therefore in the region of the latter the blastomeres are always larger and distributed less regularly. "All this indicates," Baer concluded, "that the determination of division must originate from the rudimentary orifice¹³ and its canal. The exact geometrical characteristics of the first divisions depend on the rudimentary orifices and forms the initial point of division. The canal marks the axis. This confirmation, apparently, is based on those cases where the rudimentary orifice is sufficiently distant from the center of the region. All fissures of division preserve the usual position to the rudimentary orifice and its canal, and therefore the equatorial fissure on one side advances deeply towards the light region (p. 501).

Interpreting the "determinations of division originating from the rudimentary orifice and its canal," Baer considered it unquestionable that "divisions are performed under direct influence of a producing substance" (he means the substance of sperms). It is true that Baer erroneously indicated that in fertilization "not the seminal animals, but the fluid or even the more delicate parts of sperms play the role" (p. 503), because he could not discover the penetration of spermatozoa in the ovum.

Baer's extremely interesting analyses of development begin from the division of the ovum into its separate parts. An initial individual ovum is divided into countless numbers of individualities, each of them with negligible importance which proves to be only an elementary component of the new individual. "A vital process (the process of development) which dissolves the initial individuality is not quite destroyed, because from its fragments the new individual originates. In the latter, when the process of division has gone sufficiently far, the rudiment separates from the yolk, and in the rudiment the embryo of the future frog is set apart" (p. 504).

13. For example, from place of entry of the spermatozoan and its way into ooplasm.

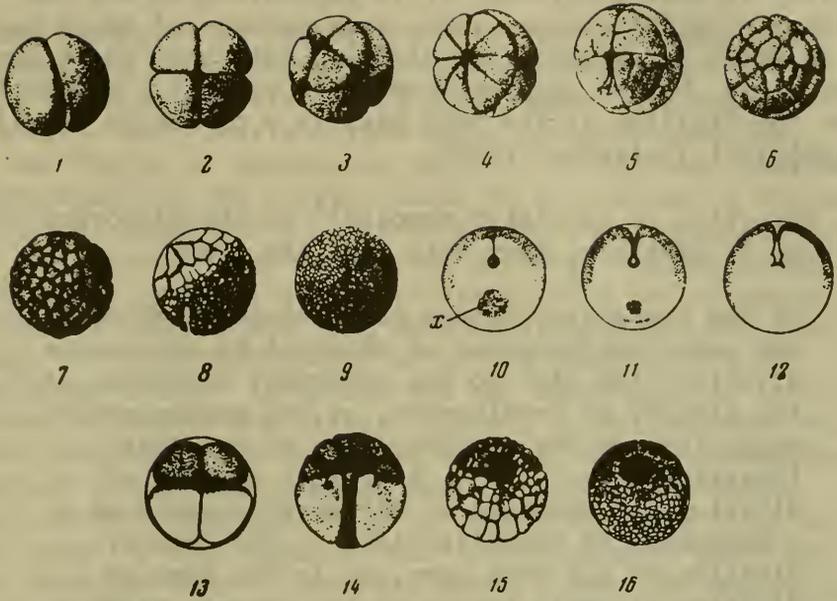


Figure 31. Baer's illustration of "Transformation of the ovum of amphibia"

1- First division; 2- second division; 3- third division; 4- typical fourth division; 5- atypical fourth division; 6- stage of blackberry; 7- stage of raspberry; 8- stage of leathery surface; 9- stage of sandy surface; 10- section in first meridional fissure, the rudimentary orifice with its canal is seen; x- the remaining place of union of the hemisphere of the ovum; 11 and 12- formation of second meridional fissure; 13- vertical section after third division; 14- vertical section through ovum in blackberry stage; 15- section through ovum in stage of leathery surface; 16- the same also in stage of the sandy surface.

Baer understood that the discovery of ovum division, from which the development of amphibia begins, represented a fundamental discovery in embryology. Against the importance of this phenomenon, he admitted that an objection might be raised "if in other animals there is nothing which is similar. We, however, suspect that they have these phenomena" (p. 505). In fish, in Baer's opinion, it is impossible to see the division clearly because of the transparency of their eggs, and in birds he assumed that division into many small grains takes place, but in another form. "I consider," he concluded, "that the division of the yolk mass is a prototype of all histological isolation" (108).

Returning in his later memoirs¹⁴ to the discovery of ovum division in amphibia, Baer said that the study

of the preparatory stage of development which is the autotransformation of material by continuous division (led him) to the innermost sanctuary of the history of development, as was subsequently shown through the corroboration of countless investigations A similar process of division was observed in different animals as a consequence of fertilization, in the form of division of all yolk mass, or in the form of division of small layers of the latter, which I called the rudiment.

Further in his autobiography, Baer discussed the behavior of nuclei during division. At first the nucleus has a rounded form, then is enlarged and stretched. Its center becomes narrower and the nucleus takes a biscuit form; then the substance of the nucleus disperses into different directions, forming two small bodies. The division of the ovum itself follows the division of the nucleus. Baer wrote that the situation is like that of two rulers, originating by division, each of whom collects around itself part of the kingdom in order that after a short period of quiescence it may again separate,

14. Baer, NACHRICHTEN, pp. 381-383 (377).

but only in another direction. Is the nucleus causing the division? Baer confirmed that "this I could not establish conclusively in the frog, because its nuclei are excessively dark and large. Later this process was clarified for me in the ova of the sea-urchin, which I investigated in Trieste during a journey from Petersburg" (see Chapter 23).

The phenomena of division of the frog ovum gave Baer the grounds to speak decisively about preformation. "The history of metamorphosis of the yolk sphere in amphibia," Baer wrote, "had clearly solves this important question, which was for me an unexpected joy."¹⁵ He did not consider it appropriate in the special works of his volume to discuss the old moot point about the preexistence, or epigenesis of a new individual. Baer noted that although studies about preformation, assuming the preexistence of a new organism up to fertilization, had long been considered an unfounded fantasy, all questions cannot be solved conclusively by direct observation. In truth, the new embryological investigations supported the status that all separated parts of the new individual are formed as a result of transformation of earlier formed more general parts. Hence, the animal section of the vertebrate body is formed from the outer or animal layer of the rudiment, and the vegetative parts are formed from the lower (internal) layer. Thus the embryo is considered the result of isolation of a part of the rudiment. It seems that the rudiment is, without question, the undeveloped animal. However, the formation of the rudiment up to fertilization precedes the formation of the less determined organized mass, which clearly differs from the proper yolk. Baer called this mass the rudimentary layer; in the non-fertilized frog ovum, the dark cover in one of the sides of the ovum is considered this rudimentary layer. The rudimentary layer is used for the formation of rudiment as a single unity, and not as a substance. The rudimentary layer in the frog ovum up to fertilization is continuous, but from the beginning of development its continuity is disturbed with each division of the ovum.

15. Baer, "Die Metamorphose des Eies der Batrachier," p. 506.

If one turns to the history of theoretical ideas about development, Baer said, then it can be confirmed that some used observations on frog development for the idea of preexistence. Specifically, on the ova of the frog Swammerdam had tried to show that the dark cover of the ovum is directly transformed into the tadpole. Swammerdam was so imbued with this certainty that he declared that the formed frog embryo which he discovered had preexisted before fertilization. Referring to his statement about the disturbance of continuity of the rudimentary layer during division, Baer confirmed that the frog ova provides a basis for refutation of the theory of preformation.

For examination of Baer's data concerning the subsequent development of amphibia, it is necessary to return to the concluding section (Volume II 11) of his ÜBER ENTWICKLUNGS-GESCHICHTE. Following the scheme of development he had presented for birds and mammals, Baer assumed that in amphibia, division of the rudiment into two vegetative layers takes place. In this primary stripe which forms from the vegetative layer (if we speak according to the language of recent embryology, then we speak about the roof of the primary intestine), the spinal cord forms, which is so thick that from embryos condensed in nitric acid it can be removed by the fingers. Next Baer described the formation of spinal shafts, which are widely spaced at first, and narrowly spaced later; they ascend as high edges and bend towards each other. At the time of closure of the spinal shafts their internal layer is separated, so that the cerebrospinal canal is formed from two intergrowing layers. In the anterior part of this canal, until its accretion, are seen dilations which represent the future cerebral cavities. All these processes, Baer noticed, can be seen more clearly in amphibia than in birds and mammals.

Baer undoubtedly saw the phenomenon of epiboly of the ectoderm, since he comments on how "the rudiment till the formation of the embryo (that is to say up to neuralization) covers nearly all the yolk sphere." In connection with this, he questioned the comparison with the meroblastic ova, asking "Is the entire rudiment becoming the embryo, or is the rudiment divided into two parts, the embryo and the blastoderm?"

The answer to this question is: "since the umbilicus is not formed, then gradually all the rudiment becomes the

embryo, so that for the following stage of life nothing remains excessive, contrary to mammals, birds and reptiles.¹⁶ Therefore the entire rudiment must be considered as the embryo" (II 11 f; p. 380 (286)).

At the time of closure of the back, the embryo changes from a spherical to an elongated form. In the anterior part of the trunk, in the region of abdominal layers of both sides, the branchial protuberances appear stretched downwards; there the parallel fissures form. Towards them from the inside, deeper fissures grow, and the branchial slits originate in this way. Earlier observers saw only three branchial slits, but in his monograph published in Bardach's "Physiology," Baer proved the existence of four slits.¹⁷ Rusconi saw the same, and also found a questionable fifth slit. The surface of the branchial arches has nodules, which are transformed into delicate branched protuberances supplied by blood vessels and then transformed into external gills on three branchial arches.

The development of brain and organs of sensation takes place as in higher vertebrates, only the bends are less pronounced.

When the tail reaches the length of the trunk and the external gills are already well branched, the embryo ruptures the yolk and gelatinous membranes. Hatching occurs at a very early stage of development in comparison with birds.

The larvae coming out from the membrane are attached to the jelly covering the spawn, or to other objects in the water by special suckers, which disappear shortly afterwards. Initially, the larvae eat the jelly and frequently the dead bodies collected by it, and with the appearance of extremities they move to plant food. At this time the internal gills are formed, and the opercular fold covering them grows with an orifice to the outside.

16. In Baer it stands—"amphibia." This is either a misprint or an application of Linneaus' designation of a group which includes amphibia and reptiles.

17. (Ed.: Karl Friedrich Burdach, DIE PHYSIOLOGIE ALS ERFABUNGSWISSENSCHAFT, Bd. I (1826), Bd. II (1828).)

In amphibia, during the process of development a greater part of the primary vascular system remains than in mammals and birds. Both roots aortae are kept; the ventricle of the heart remains undivided.

Concerning the development of extremities, Baer mentioned that the anterior pair suddenly appears outwards as a result of breaking the intact branchial skin fold. Later he noticed the disappearance of the tail as a result of absorption of the mass filling its skin. The development of the central nervous system of amphibia takes place as in higher animals with specified differences, which depend upon the peculiarities of the brain structure. With nerves, Baer repeated the earlier mistake that their appearance is caused by histological separation from the surrounding parts. Baer stated the development of the digestive system very briefly, noticing that the digestive canal of amphibia is formed without the untwisting of the yolk sac. The development of the urinogenital system he also awarded a small place. The primary kidneys, described by Müller, are situated in the innermost part of the trunk; they are kept until the disappearance of the tail, when the permanent kidneys appear. The genital organs develop later on, while the genital glands' appearance precedes the formation of the fatty body.

Turning to fish,¹⁸ Baer noted that their development is similar to the development of amphibia, because there is no amnion and no allantoic sac in these two classes. Incidentally, the history of development of different fish is not completely equal; the differences partially depend on the greater or smaller quantity of yolk ("and on the peculiarity of albumen," Baer added), and also on peculiarities of organization. The ova of fish are formed in the ovary; in its rudimentary layer can be found yolk spheres containing embryonic vesicles and surrounded by a membrane. In connection with this, Baer entered a long controversy with Rathke and other authors about the question of which forms earlier in the ovum—the embryonic vesicle or the

18. The development of fish was described earlier in a separate edition of a very well known work (see footnotes). In future when referring to this work, the pages of its text will be shown. Illustrations are taken from it and mentioned here (Figure 32).

yolk. Baer indicated that in young ovarian ova the embryonic vesicles are very large, and the bigger they become the less the nourishing materials in the ovum. The details of this controversy have not been established.

Fertilization in fish takes place in the same way as in the frog, at the moment of depositing the egg in the water; in the viviparous fish, for example (*Blennius viviparous*), the four-eyed (anableps) and some silurids, the fertilizing substance penetrates from the water into the genital orifice of the female, and in some fish (Selachians), the fertilizing substance is introduced there by the male, as occurs in mammals.

The structure of the ovum membrane of fish is variable; it is a fine-grained or cartilaginous membrane (for example in perch) or even shelled with four edges (egg-laying selachians). The rudimentary layer occupies a smaller space on the surface of yolk in the fish which Baer investigated than in amphibia, but relatively larger than in birds. Thus, in *Cyprinus blicca*¹⁹ and pike the rudimentary layer occupies a quarter of the yolk surface. In the center it is thicker than at the edges, denser than the yolk and very transparent. The embryonic vesicles in the deposited ova are not detected. The rudimentary layer, according to Baer, after fertilization is transformed into a rudiment without the preliminary division of the yolk sphere, which he described in the amphibia. In a footnote Baer referred to Baumgärtner, who apparently saw something similar in trout²⁰. Although Baer could not directly observe segmentation in the ova of fish, this did not prevent him, as mentioned above, from recognizing that the process of segmentation is a principal and universal phenomenon, with which development begins. Later, referring to his work on fish development, Baer remarked that he had not noticed divisions taking place after fertilization. These divisions, he thought, took place at night, and the protuberances on the surface of

19. *Cyprinus blicca*, an old classification used by Baer, which corresponds to the present name ABRAMIS (BLICCA) BJÖRKNA, or ABRAMIS BRAMA.

20. (Ed.: Baumgärtner, "Beobachtungen über die Nerven und des Blut," p. 13.).

the rudiment appearing after artificial insemination he assumed to be a sign of death and the beginning of destruction.

The rudiment gradually begins to be covered by the yolk; in three to four hours after oviposition it occupies nearly one third of the surface of the ovum; in seven hours, half the surface (Figure 32, 3); and within nine hours, three quarters (Figure 32, 4). After that, as in the rudiment, the division takes place in the thin animal and vegetative layers, the separation of the embryo begins, which at the beginning is not distinguished on the surface of the ovum. Shortly after formation of the embryo, the spinal fissure becomes noticeable (Figure 32, 6). The shafts ascend over the surface and move nearer to each other, at the same time the very delicate vertebral cord can be distinguished between them. At nineteen hours after oviposition the spinal shafts are high and the fissures between them become deeper (Figure 32, 7 and 8). By the end of the first day the back is closed and separation of the primary vertebrae begins (Figure 32, 9 and 10), and the spinal cord becomes noticeably thicker. The head at this time is equal in length to the trunk, rounded projections appear, formed by the cerebral vesicles. An examination from the side shows formation of the transparent projection of the eye in the middle of the cerebral vesicle. Somewhat later the ear rudiment is seen; the eyes at this time are beginning to bulge and the first rudiments of abdominal layers are distinguished. At the end of the second day the embryo becomes pear-shaped (Figure 32, 13); its ventral part consists of two divisions: the anterior is rounded and the posterior is in the form of a curved tube (Figure 32, 14 and 15). Then the embryo begins to straighten (Figure 32, 16). The separation from the yolk in different fish takes place differently. In those cases where the mass of yolk is not large, the abdominal layers envelop it; in fish with voluminous yolk matter, the embryo from which the yolk sac hangs disconnects (for example in selachians and batrachidae). In those cases, where the yolk mass is not large, the abdominal layers envelop it; while in fish with voluminous yolk mass, an unfastening of the embryo takes place and the yolk sac is attached to it (for example in selachians and batrachidae).

The branchial protuberances are expressed less clearly than in amphibiae, but they are divided also by four fissures.

Because these five pairs of arches are separated, the anterior pair provides the beginning of the lower jaw and hypoglossal bone, and the other four become the branchial arches. On the surface of the latter the branchial platelets develop, situated in two rows.

The development of the vascular system of the fish embryo can be very easily observed due to its transparency. The rudiment of the heart at first is very similar to the cardiac canal of birds and all other vertebrates. Its two branches are united, and a curved canal is formed to the right from which the vascular arches are subsequently separated. They meet above, as usual in two-root aortae. In the posterior end of the heart two venous branches flow. The rudiments of anterior extremities have the form of small triangular elevations (Figure 32, 18).

In the moment of hatching the length of the tail constitutes about two-fifths of the total length. The eyes are pigmented, but the iris membranes have no metallic brightness, which appears in the second or third day after hatching. The ear is large and transparent, with the auditory drums visible in it. Parts of the brain are clearly differentiated, especially the cerebellum, the cavity of the middle and intermediate brain. The structure of the vascular system one day after hatching is illustrated in Figure 32, 20. The auricle of the heart is curved to the left, formed by the accretion of the two venous branches. The first vascular arch goes to the eye and branches in the slit of the iris membrane, while its other branch is the vertebral artery. The aorta develops intravertebral branches, passing into branches. The caudal vein passes through the kidneys, forming ramifications in them. The posterior vertebral veins (Baer equated the right posterior vertebral vein to the posterior hollow vein) flow together with anterior veins (from brain, ear, and occipital region in a transverse branch); both transverse branches run around the yolk sac and flow into the auricle.

In a special work on the development of fish of 1835, Baer described in detail the changes of the arterial and venous systems of *Cyprinus blicca* in the days after hatching, and carried out comparisons with cyclostomes and skates (adults and embryos), and also with the embryos of birds and mammals

(pp. 24-31). In a section about ÜBER ENTWICKLUNGSGESCHICHT (II, 11 bb), also in detail, he reviewed the transformation of cerebral vesicles of the embryo into the part of the definitive brain as in *Cyprinus blicca*, and as also in other carps (*Cyprinus erythrophthalmus*) and cartilaginous fishes.

Baer gave limited information on the digestive system. The oral orifice opens at the end of the first day after hatching. The intestinal canal up to the fifth day is very wide, completely direct and easily distinguished from the yolk sac, which is diminished. The mesentery appears later on (at the beginning, the intestine is adjacent to the spinal column); however, its development undoubtedly takes place exactly as in birds and mammals.

More briefly, Baer mentioned the development of the excretory system, noticing that kidneys of fish do not undergo that transformation which is characteristic of the higher vertebrates. In connection with this, the corresponding reconstruction of the circulatory system does not take place.

Later Baer gave a fluent description of the development of the paired extremities and unpaired fins. He noted that at the beginning, the unpaired fins in all fish, regardless of the future structure of fins with dense edgings, are situated from the back through the tail to the ventral side. Then the fringes are broken into as many parts as there are separated unpaired fins in the given fish. Between these regions the fringes disappear, and in the remaining fins cartilaginous or bony arms develop.

The development of the swimming sac was given special detailed attention by Baer in separate works (see footnote 8). The posterior swimming vesicle of carp fish, according to Baer, is analogous to the underdeveloped lung because, like the latter, it arises from the protruding anterior region of the digestive canal. In hatching embryos there are no traces of the swimming vesicle and only near the end of the first day in the material, condensed in nitric acid can two protrusions be seen, one from the back and the other from the ventral side, each of them about 0.1 inch in size (Figure 32, 24). On the second day the dorsal protrusion acquires a finger-like form and is elongated backwards (Figure 32, 25).

Later it becomes longer, the ventral becomes rounded and its internal cavity is situated on a lobule (Figure 32, 27). The first protrusion represents the rudiment of the swimming vesicle, and the second the rudiment of the liver. By the fourth to fifth day the swimming vesicle consists of two parts, an elongated sac and a hollow stalk similar to the branchus of the simple lung. The vesicle, when seen under the microscope or in live fish, still does not contain air. After the fifth day the swimming vesicle fills with air and thereby becomes significantly larger and distinguishable by the naked eye.

The anterior swimming vesicle in adults is connected with the posterior one and with the auditory organ. It is formed later than the anterior, after four weeks, when the body of the fish is already opaque and its formation is thus very difficult to follow. Nevertheless, on the basis of his direct observations Baer presented an astute discussion of development of the anterior swimming vesicle with the auditory apparatus. The last question is discussed in a special addition to the above-mentioned work of 1835 on fish development, in which he classified the swimming vesicles of the different fish in connection with the history of development of those organs.

Two earlier works, especially illustrating the study of branchial slits and branchial vessels in different vertebrates, serve as an addition to the third part of ÜBER ENTWICKLUNGS-GESCHICHTE. They represent a continued essay of the comparative embryology of vertebrates.²¹ The first of these works he began with "Not long ago my dear friend Dr. Rathke (109) wrote me. Finally I found in the human embryo hints of gills, in particular in one six or seven-week-old aborted embryo. From each side there were two gills, the anterior

21. Baer, "Über die Kiemen und Kiemengefäße in den Embryonen der Wirbelthiere," ARCH. FÜR ANAT. U. PHYSIOL. (1827), pp. 556-568; "Über die Kiemenspalten des Säugethier-Embryonen," IBID. (1828), pp. 143-148.

large and the posterior significantly smaller. They were clearly seen, because between them there were slits penetrating up to the pharynx; thus there was no doubt of their existence. This information reminded me of the investigations which I had carried out the previous winter on human embryos. In the smallest of them, I did not discover branchial slits, which were also absent in the embryos of other vertebrates, although I frequently saw them in birds, frogs and snakes. In those human embryos I investigated, I saw them more clearly in that five weeks old embryo, than in the embryos which I knew to be six weeks old" (p. 556).

In the first specimen Baer saw three pairs of branchial slits; the posterior pair was significantly shorter than the others. The branchial slits were especially well seen from inside the pharyngeal cavity. Based on comparison of available data Baer concluded that in humans and maybe in all land vertebrates, there are primarily four pairs of branchial slits, but they appear and disappear at separate times. In his work illustrating the branchial slits of vertebrates, Baer referred to investigations of Huschke,²² who discovered in bird embryos that a vascular arch passes in every branchial arch. This vascular arch begins from a general stem and comes out from the heart; it then flows into the aorta which consists of two roots. Thus every root of the aorta receives the vascular arch of its side. Huschke, however, did not see all the vascular branchial arches of the embryo. Baer himself clearly saw in the three-week-old embryo of a dog four arches filled with vascular blood, and he assumed that there was also a fifth pair of very delicate arches not filled with blood. He also distinguished four pairs of vascular arches in chickens.

Baer stated with certainty that the transformation of the vascular system of mammals and birds is very similar because the four pairs of vascular arches, which he saw in the dog embryo, had great similarity to the four pairs of arches of the bird embryos in the first half of the fourth day after hatching. The comparison of the vascular system of adult lizards and snakes, on one hand, and of embryos

22. E. Huschke, "Über die Kiemenbögen im Vogelembryo," *ISIS* (1828), pp. 160-164.

of birds before hatching, on the other hand, shows that in both the aorta begins with two roots. But only in birds is this condition transitory (kept only to hatching), whereas in reptiles it is permanent. Baer found an interesting comparison in the embryo of a lizard which had five functioning branchial vascular arches. In *LACERTA AGILIS* a similar condition is found before oviposition (110).

In the embryo of a lizard, according to Baer, blood circulation can sometimes be observed under a microscope, and he confirmed the presence of all mentioned vessels. From his data Baer concluded that in all embryos of vertebrates developing outside water there are five pairs of vascular branchial arches. In addition, they are present at the same time in lower forms, but in higher organized forms they appear and disappear in a known sequence. Amphibian larvae have four pairs of vascular arches, which remain for a longer time than in higher animals. Baer considered it necessary to clarify whether there was a fifth (outermost) arch in an earlier period under the formation of the lower jaw. The means of formation and the situation of vascular arches in amphibia are the same as in birds and mammals, but the distance between the anterior branchial slit and oral orifice of amphibia is more significant. In bony fish, throughout life four vascular arches remain in the gills. In plagiostomes there are five pairs of vascular branchial arches, and in cyclostomes more, but the cyclostomes, Baer noticed, generally strongly deviate in structure from other vertebrates. The last note is interesting, because in it, on the basis of comparative embryology, Baer presented a well-founded discussion of the systematic situation of cyclostomes. The separate situation of cyclostomes was recognized later, and they were distinguished from the class of fish in the dependent class of vertebrates.

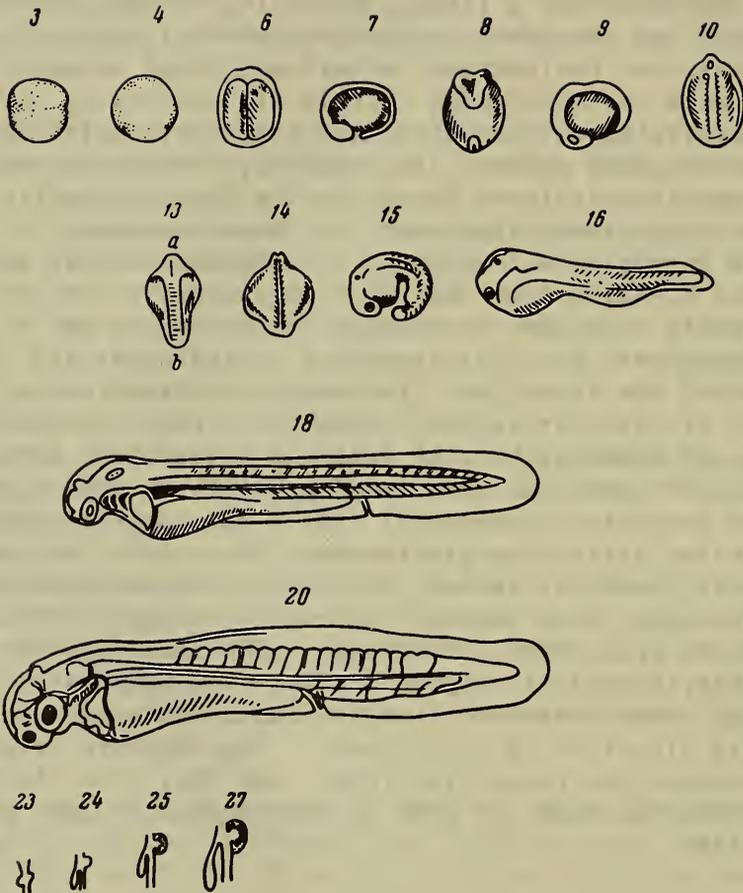


Figure 32. Baer's illustration from "Investigations on the development of fish"
 (Caption on the following page).

(Caption to Figure 32)

3--The shape of the ovum from the side; embryo covers half of the yolk sphere. 4--The same; embryo covers three-quarters of the yolk sphere. 6--The embryo with wide spinal fissure, the shape from above. 7 and 8--The embryo with well-defined ascending spinal shafts, shape from the side and from above. 9 and 10--The embryo with closed back in the beginning of the formation of vertebrae, lateral and upper view. 13--Pear-shaped embryo with closed spine at the beginning of vertebrae formation, lateral and upper views. 14 and 15--Twisted embryo, lateral and upper view. 16--The beginning of straightening of the embryo, 18--The embryo before hatching. 20--Second day after hatching. 23-27--The anterior part of the digestive tract, the first to fourth day after hatching.

CHAPTER 22

FOURTH PART OF ÜBER ENTWICKLUNGSGESCHICHTE: STUDIES ON THE DEVELOPMENT OF MAN

The final, fourth part of ÜBER ENTWICKLUNGSGESCHICHTE¹ was published fifty-one years after the appearance of the previous parts. Because of conditions which prevented this work from appearing at the proper time, L. Stieda stated the following: "I am publishing the termination of work which the scientific world has awaited for more than fifty years."

It is known that Baer's study of the history of animal development remained unfinished. The publishing of the second part, begun in 1829, stopped for five years due to incompleteness of the manuscript. The publisher Bornträger, in Königsberg, waited three years for the promised completed work, and finally published the incomplete second volume without a preface, table of contents, or explanation of the tables.

When Baer left Königsberg in October 1834, the manuscript of the final part was, apparently, already prepared. He intended to compare his results of the study of human embryos with the analogous observations of other authors upon his arrival in Petersburg. He sent extracts of his manuscript from Königsberg to Siebold, who published them under the name "Observations on the History of Development of Man. Portions from a letter to the Publisher."² In this letter Baer wrote:

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1. Karl Ernst von Baer, ÜBER ENTWICKLUNGSGESCHICHTE DER THIERE. BEOBACHTUNG UND REFLEXION. Zweiter Theil. Schlussheft. Herausgegeben von Prof. Dr. Ludwig Stieda, Königsberg, 1898. v + 84 pp. After Stieda's preface on the second "title" page appeared: "IV Studien aus der Entwicklungsgeschichte des Menschen."
 2. Baer, "Beobachtungen aus der Entwicklungsgeschichte des Menschen," Aus einem Schreiben an den Herausgeber JOURN. FÜR GEBURTSHILFE, 14 (1835), pp. 400-411.

My observations on the history of development of man . . . are intended for the second volume of the book. I made up my mind to publish the history of development now before changing my place of residence. However, these materials remained unfinished for a long time because I could not complete description of the development of the lower classes of animals (111) . . . therefore I am not confident of completing this manuscript in five years.

When Baer arrived in Petersburg and wanted to resume the work, he did not have the necessary books, because his own library still was not available. During resettlement he did not take his library with him and received it only a year later in late autumn of 1835. He began unpacking the books and putting them in order in the winter of 1835/36. Since Baer could only outline his section on man, Bornträger grew impatient and published the second volume incomplete. Following this, Baer left the manuscript unchanged and turned to other scientific work. In his autobiography he wrote: "I am sorry, that in the hope of filling these gaps in the history of the development of invertebrates I did not print the other work, 'The Special Investigation of the Earlier Stages of the Human Ovum'."

Stieda wrote that "directly after Baer's death in November 1876, when I was busy putting his remaining literature in order, I found this manuscript together with the titled volumes." Stieda could not devote time to the manuscript then either and only prepared it for press twelve years after Baer's death. The published text, as Stieda wrote, exactly repeats the contents of the manuscript. The publisher did not make any changes or additions but only put Baer's outlines next to the text. Explanation of the drawings and Tables IV-VII published in the second volume of ÜBER ENTWICKLUNGSGESCHICHTE were without explanation. The first two tables (IV and V) relate to the text of the second volume, and the other two (VI and VII) illustrated the final fourth part. Stieda included in his preface the suggestion that the reader understands that the work had been written fifty years earlier. This note of Stieda's was more significant for the reader of the second half of the twentieth century since more than hundred years had elapsed after Baer's writing on his embryological work.

The contents of Baer's work do not require a detailed account. The work is a collection of materials for the future connected with the history of the human embryo. Baer himself wrote in the introduction that his suppositions were to be considered as observations relevant to the study of the history of human fetus, and not as complete descriptions of the later stages of human formation. He noted later that the earlier stages of different human ova so strongly differed from each other that no investigator could be absolutely correct in his observations, but that which was considered normal, and that which was considered a deviation from normal was beginning to be made clear. Therefore, Baer continued, it is very important that one observer has the possibility to compare a large number of ova. He conveyed his satisfaction with the fact that he, by investigation, could confirm that aborted ova are frequently abnormal.

Baer's descriptions of human fetuses follow their ages, which can be judged by data of a preliminary case study and by features of the embryos and their membranes.

Unquestionable interest is represented by case 1, relating to an extremely early stage. Because early diagnosis of pregnancy is very difficult, Baer considered it necessary to include for this case the following data concerning the duration of pregnancy: "In the summer of 1826 in the Anatomical Institute of Königsberg the corpse of a servant was obtained, found in Pregel. It was learned that the young girl had spent half a day with a young man eight days earlier. She returned home very sad and anxious. Her death by drowning was not accidental but deliberate. Anatomical investigation showed the presence of a recent pregnancy. I supposed, that the determination of the duration could be considered correct" (p. 5).

On the convexity of one of the ovaries, Baer found a slit-shaped opening of crescent form which was beginning to grow. Cutting the ovary he found there a cavity covered with a yellow mass; from outside the yellow body was covered by a layer of cellular tissue, the outer layer of the capsule of the evacuated Graafian follicle. The uterus was not increased in size, but was somewhat swollen; its anterior wall was farther from the posterior than normal. The internal surface

of the uterus was rough. Under a microscope, villi and ends of blood vessels were distinguished with the ends of the blood vessels situated not in the villi but between them; the vessels formed a network, submerging in the coagulated nearly transparent mass, which filled the spaces between the villi. Baer considered this condition to be the beginning of formation of the caducous membrane. How the ovum of mammals and man looks, Baer did not know. "If I knew," he wrote, "that these ova represent opaque small bodies, then I may have found also the ovum, although as far as I searched in the oviduct and in the uterine wall for a vesicle with villi or without them, all efforts were useless" (p. 8).

Case 2 related to pregnancy which ended due to the mother being scared or frightened in the fourteenth day. The embryonic vesicle was not more than three inches in diameter and covered by delicate villi. From outside, the embryo was not observable. "During the dissection of the ovum," Baer wrote, "I found two slipped combined vesicles; the internal one was smaller than the outer. The rudiment of the embryo was found between them, having the form of an open boat, the length of about $\frac{2}{3}$ inch" (p. 9). From the general form of the embryo, it was seen that the back was already formed, and the ventral side was still opened wide. Near the embryo, a cudgel-shaped vesicle, was the allantoic sac. Baer could not find the umbilical vesicle and considered the yolk sac or umbilical vesicle to be the internal vesicle of the embryonic ovum, although it was not clear for him whether it was united with the embryo or not.

Case 3 presented a three-week-old embryo studied by Baer in detail. He described the general view of the embryonic ovum, the chorion, its villi, the connection of the embryo with other parts of the embryonic vesicle (Figure 33, 5), the amnion, umbilical vesicle and allantoic sac (Figure 33, 9). The embryo and its situation, form and structure are seen in Figure 33, 11. The back of the embryo is closed in all its extension; the occipital protuberance is clear but not strongly protruding. The vesicle of the fourth hillock protrudes significantly and is nearly transparent, since the top of the skull remains very thin there. The lateral fissure is clearly seen, dividing the dorsal and ventral plates. Two convexities are present on the ventral

side of the embryo, which Baer at first suggested as the heart and liver, but he then indicated an error, against which he warned other investigators. The anterior projection proved to be the lower jaw, which together with the hypoglossal bone formed from the anterior pair of the branchial arches, protruding more than the others. Behind the projection of the lower jaw, two dark cavities appear. Doubtless these are the branchial slits, which do not yet penetrate the cavity of the pharynx. The posterior projection of the ventral side is the heart, to which a semi-canal is affixed, representing the rudiment of the digestive tract, separated during the preparation from the union with the yolk duct; the passage of the abdominal layers into the amnion is also torn. The embryo still has no trace of extremities. The age of the embryo cannot be determined with complete exactness. In any case, Baer assumed it related to a somewhat later stage of development than did the embryo described by Pokel's and was sixteen to twenty days after conception.

Cases 4 and 5 were described briefly due to the unknown length of pregnancy, both approximately three weeks.

Case 6, an embryo three to four weeks old, (Fig. 4 and 6) is described in more detail. The mouth of the embryo was closed, and the branchial slits were not seen, neither from outside nor from the cavity of the pharynx, which was considered an abnormally slow development at this age. The wide stomach, without limits, entered the intestine, while there was an impression that the stalk of the umbilical vesicle was united with the stomach. In the embryo the cord and brain were clearly seen; the ventricle of the heart remained single, but in it the dividing fold had begun to form. In the described case, for the first time in the human embryo, both roots of the aorta could be seen. The lungs were clearly divided into lobes. In the posterior part of the abdominal cavity the urinary bladder was present, extending into the stalk of the allantoic sac. Beside the vertebrae, the posterior halves of primary kidneys were seen.

Case 7, an embryo of five weeks, was very superficially investigated in 1822, because it was obtained in very damaged condition.

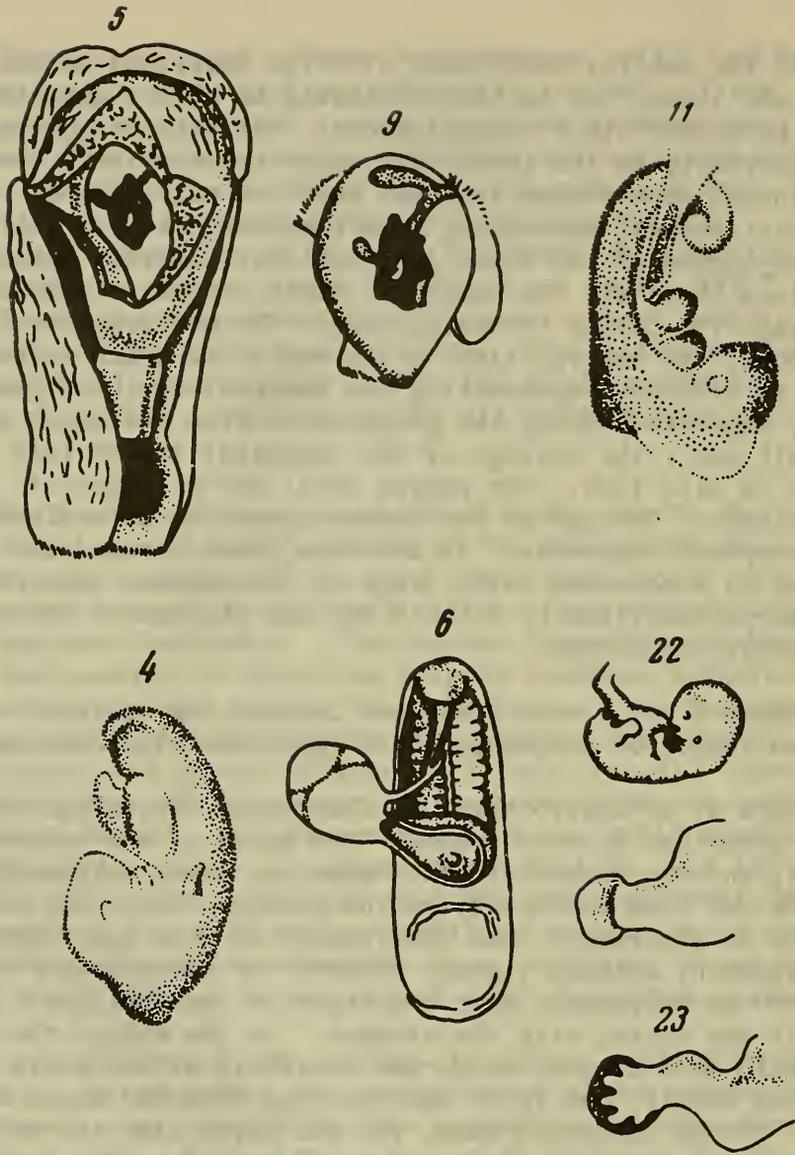


Figure 33. Illustration by Baer for the fourth part of
 ÜBER ENTWICKLUNGSGESCHICHTE.

5 (Table VI)—embryo first month of pregnancy; 9 (Table VI)—
 liberated amnion; 11 (Table VI)—embryo, from left side;
 4 (Table VII)—dog embryo from the side; 6 (Table VII)—embryo
 with dissected abdominal cavity; 22 (Table VII)—embryo, from
 the side; 23 (Table VII)—anterior and posterior extremities
 of the embryo.

Case 8 was also in the fifth week of development. The length of the embryo was five inches, well formed. The length of the extremities was about one inch, each extremity consisted of a short stem and a rounded thick end part without traces of fingers. The posterior extremities were much shorter than the anterior,³ with their end part not separated. Behind the head three pairs of branchial slits were seen, of which the anterior pair was more developed. The branchial slits were very clearly seen from the side of pharyngeal cavity. The degree of development of the lower jaw suggested to Baer that the most interior pair of the branchial slits was already closed. In the spinal cord in the transverse section four strands were distinguished. Half the vertebral arches were not united either among themselves or to the bodies of vertebrae. The auricles were very large in comparison with the ventricles. The latter were still united with each other near the bulb of the aorta. The liver was significantly smaller than the heart, clearly divided into three lobes. The stomach was clearly delineated from the intestine, giving a small bend only in the region of its union with the hollow yolk stalk. After the removal of liver and stomach, the primary kidneys were seen in the cavity of the body along its extension.

Case 9, an embryonic vesicle of five weeks age, Baer obtained in damaged condition. The embryo was destroyed, thus only the embranes could be examined.

In case 10, the embryo was somewhat younger than the previous one, but was slightly more formed than in case 8, as seen in particular in the end parts of the extremities and by the presence of the elbow joint.

Case 11 presented a five-week-old embryonic vesicle (Figure 33, 22-23) with chorion and densely shrunken branched villi. The wall of the chorion consisted of two layers.

3. It must be noted that Baer named them anterior and posterior and not upper and lower extremities, as if he were underlining the identity of man's extremities with the extremities of other vertebrates.

The embryo was very small, although it was well formed. Its head constituted about two-fifths of the total length. The eyes were surrounded by rudiments of eyelids. In the cavity of the pharynx appeared the orifices of the Eustachian tube. The structure of the upper jaw of the embryo shows a similarity to amphibia and tortoises, and the nasal passages of the posterior orifices opened in the most anterior part of the oral cavity. Behind the lower jaw, a pair of branchial slits appeared. Baer considered this a second pair, which remained in all animals for a longer time than the other pairs. In the anterior extremities the shoulder and elbow joints were very clearly seen. The wrist was not separated by a joint from the forearm; it had the form of a rounded blade with five fingers of nearly equal length, except for the noticeably shorter large finger. The spaces between the fingers were narrow, with a semitransparent connecting mass very similar to the swimming membrane. In the posterior extremities the same could be differentiated, but with the fingers less clear. From this Baer could conclude

that the fingers of hands and feet formed not as a result of a simple thickening of the forming mass into separated arms, but because the existing mass collected in these arms, and because the thickness of space between the fingers was less than the thickness of undifferentiated plates. But the most interesting was the similarity of the extremities. The general agreement presented by them was at once striking to the eye. (p. 51)

The liver occupied nearly half of the abdominal cavity. The stomach was well isolated from the intestine, with the form of a blind sac, displaced to the left from the middle plane of the body. Behind the great curvature of the stomach was the spleen. The intestine near the stomach (the duodenum) was slightly curved, which led directly to the place of fixation of the umbilical cord, where the loop forms. The caecum was short, but completely and clearly formed. The left ventricles of the heart in this stage were noticeably larger than the right. The roots of the aorta were only slightly separated from each other. The larynx was barely visible; the rings of trachea were still undifferentiated. The ducts of the primary kidneys opened in the nearly cylindrical allantoic sac. The rudiments of the primary kidneys

were shapeless. The relatively differentiated genital organs could not yet be distinguished between ovary or testis. The external genital organ was large, with a fissure at its base where the urinary canal flows.

In case 12, a five-week-old embryonic vesicle with very voluminous amnion, the embryo was invisible. Possibly, here there was a lack of conformity in the degree of development of embryo and its membranes, examples of which Baer had found earlier. For illustration, he presented the following case. A woman who had given birth several times was inclined to spontaneous abortion. At the time of her pregnancy she was subjected to a nervous convulsion, after which she became ill. She was afraid of abortion. Although abortion did not take place, the abdomen from that time increased very little. Forty days before the time of parturition the birth pains began and she gave birth to a fetus very small for the duration of gestation. During the dissection of the fetal ovum, it was found that all ovum membranes were very thick, and the placenta reached in thickness three inches. The embryo itself was flabby, and its size and degree of development corresponded to the age of nine to ten weeks. It was clear that in this case the embryo died after the several mental suffering of the mother, but the membranes continued to develop.

The described observations were accompanied by many general notes. First Baer noticed that only five of the former cases in his illustrations (1, 2, 7, 10 and 12) represented normal features, and the others to some extent were anomalies (especially 4, 5, 6 and 9). The relation of the dimensions of the embryonic vesicle to the size of embryo varied strongly. For example, in case 5 a relatively large vesicle developed in which the embryo was hardly recognized. There are known cases of detection of embryonic vesicles without embryos which, in Baer's opinion, showed a fixed degree of independence in the development of the embryonic membranes. The embryo can grow sickly and even die, but the life of the membranes is not disturbed; Baer frequently noticed these phenomena in other mammals, in particular in swine in which there are cases of suffocation of certain foeti by thread-like processes from the yolk sac. The embryos during this are underdeveloped, their sizes

reaching four to five inches, whereas the embryonic vesicles, while also not reaching the normal size, nonetheless grow to eight inches (20 cm) and more (112). In addition, during normal development in swine the embryonic vesicles in different stages may be of different sizes. From these data it follows that when determining the age of embryos, one must draw attention to the formation of the embryo itself, rather than to the size of the embryonic vesicle.

In concluding notes, Baer considered the structure and development of embryonic membranes. Undoubtedly, his historical interest is represented by the discussions of the most important question at that time, the relation of the pear-like vesicle, given by Pokel the name Erythrois, to the intestine and to the formation of the chorion. Baer considered that the vesicle, which in the human embryo corresponds to the Erythrois of other mammals, is nothing other than the urinary bladder, or since the intestine arises from it, it is considered to be the cloaca.

The formation of the chorion in mammals Baer described as a result of concrescence of the urinary bladder with the outer embryonic membranes and receiving vessels growing near the allantois. Baer was positive that the chorion in man is formed in this manner also. Here he gave a very interesting footnote: "I consider that it is an honor for me," Baer wrote,

that this opinion was repeated by Weber, Frorin and Bischoff. Nearly in the same words they called it a serious and brilliant hypothesis. In my work, "On the Vascular Connection between Mother and Fetus in Mammals,"⁴ I suppose, I have shown in detail in different animal forms the gradual formation of the chorion by the union of the urinary sac with the outer membranes of the embryonic ovum. Without drawings, doubt arises because of difficulty in understanding these

4. Baer, "Untersuchungen über die Gefäßverbindung Zwischen Mutter und Frucht in Säugethieren," 1828, 305 ff (113).

relationships. Or perhaps it is thought that in dogs, sheep, swine, and rabbits the process occurs in a particular way while in humans it occurs differently. Is not man a mammal? Are not the embryonic vesicles in man the same as in other mammals?

The same idea of the similarity of development of man with the development of other mammals was mentioned further in the text, when Baer turned to the question about the formation of extremities. "Observations No. 9, 10 and 11 confirm that extremities of man are formed by the same law as in other mammals."

Thus, bearing in mind the report on the subject of the described human embryos and in great part limited to the commentaries of the observed facts, Baer did not avoid giving a conclusion of great significance: that man, as representative of the mammal class, in his structure and embryological development obeys the regularities which are general for all this class.

The concluding section of Baer's major work does not contain theoretical reviews and generalized conclusions. This is not surprising, if we remember the history written at the beginning of this chapter. Circumstances had existed to prevent conclusion of the work, which led to Stieda's discovery of the papers in unfinished condition after Baer's death. The work of Baer undoubtedly would have been crowned with theoretical conclusions. However, the impatient publisher waited in vain for thirty years of the past century.

CHAPTER 23

BAER'S TERATOLOGICAL WORKS AND HIS EMBRYOLOGICAL REPORTS, RELATED TO THE PERIOD OF HIS WORK IN PETERSBURG

Baer was not a pioneer of teratological investigations in Russia. By the middle of the eighteenth century the Anatomical Museum of the Academy of Science had available a significant collection of preparations demonstrating the abnormal development of man and different animals. Before the arrival of K. F. Wolff in Russia, the materials of these collections had been little investigated, excepting the more or less accidental descriptions performed by A. Kau-Burgav. Wolff very energetically undertook the investigation and description of the abnormalities in the Academy's collection, connecting to them the material personally collected by him. However, because he was involved with vast anatomical investigations, he published only some of his observations. **A great part of them were to have been included in the great work which was left unfinished due to his unexpected death, and which consequently did not appear.** At the beginning of the nineteenth century the teratological collections were put in the reliable hands of Academician P. A. Zagorsky, organized, and again studied intensively. Zagorsky had time to investigate and describe only a small number of interesting teratological cases.

Eventually Baer settled in Petersburg. Despite his varied activities connected with investigations in different spheres, and with administrative, educational, and experimental work, he found time for teratological investigations. At this time he was not a beginner in this sphere. He was still a professor in Königsberg when he published some small articles, from which information about deformed swine embryos has been mentioned.

In 1827 Baer published an article on a double chicken embryo at the beginning of the third day of incubation.¹ The purpose of this work was to solve the disputed question of the origin of double monsters. "I never could bring myself to accept the idea," Baer wrote, "that double monsters arise from the union of two individuals, although previously many physiologists insisted on this opinion. It seems to me that here one difficulty has replaced another" (p. 576). The arguments proposed by Baer against the theory of union were very close to those used by Wolff in his "Description of Two-Headed Calf, accompanied by general illustrations on the origin of monsters."² In order for two embryos to unite in an earlier stage of development, it would be necessary for them to be completely movable and for there to be pressure upon them from two sides, pressing them together. But the main difficulty lay in the fact that it is impossible to imagine how the corresponding parts of the two individuals meet and why the union takes place without disturbing the topography of the parts. More naturally, Baer supposed this case to represent the splitting of a formerly unified rudiment. This explanation did not eliminate all the difficulties; it was suitable for the interpretation of lateral splitting, but left unexplained the cases of divergence of surfaces and union of twins by the ventral sides.

Baer thought that the solution to this interesting question could be achieved only through the study of the early stages of development of double monsters. He described one of these cases, in a developing chick at the beginning of

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1. Baer, "Über einen Doppel-Embryo vom Huhne aus dem Anfange des dritten Tages der Bebrutung," ARCH. ANAT. PHYSIOL. (1827), pp. 576-586.
 2. K. F. Wolff, "Descriptio vituli bicipitis . . . ," NOVI COMMENT. ACAD. SCIENT., PETROPOL., 32 (1773), pp. 504-573 (see Chapter 5). Baer did not refer to this work by Wolff. Baer's exceptional honesty, which appears in all his works, suggests that Wolff's paper on the double-headed calf was for some reason unknown to Baer.

the third day of incubation. The transparent zone (AREA PELLUDICA) had a cruciform shape with two long and two short ends; the embryos were situated in the long ends, the posterior ends of which moved apart and the anterior united in a general mass. Both the embryos were equally developed. The spinal plates, containing the foundation of the vertebrae (Pander's PLICAE PRIMITIVAE) were closed, enveloping the spinal cord; the abdominal plates (Wolff's LAMINAE ABDOMINALES) were situated nearly horizontally, i.e. the body of the embryo was still opened from below. The spinal plates passed without discontinuity into the common head, and the spinal cord into the common brain.

Baer thought it improbable that these partners were at first divided, and then united. In the period up to the third day of incubation, i.e. when the beginning of the process of union could be expected, the embryos cannot move nearer to each other because they are still situated in the convexity of the blastoderm. If it is assumed that the first foundation of the double embryo was single, that the foundation of the head was formed not at its end but in its center, then the formation of the double embryo becomes understandable. The dorsal region of the cephalic end of the embryo grows more quickly than its other parts; therefore in the single embryo the head is curved downwards, and in the double embryo the frontal parts moved away from each other. The cruciform embryonic structures meant that the basis of double-embryo formation occurred in the ovum very early.

To the question of the origin of double monsters Baer returned in two works published in Petersburg ten years later. The first article³ was very brief and was, in fact, a preliminary to the second, which was a vast work.⁴

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3. Baer, "Über doppelte Missgeburten," MEM. ACAD. SCIENCES ST.-PETERSB., VI Ser., v. 3, book 2; BULL. SCIENT., No. 2 (1835), pp. I-II.
 4. Baer, "Über doppelte Missgeburten oder organische Verdoppelungen in Wirbelthiern," MEM. ACAD. SCIENCES ST. PETERSB., IV Ser. Sc. nat., v. 4, Zool. et physiol. (1845), pp. 79-194.

Baer first referred to his findings in 1827 on the double chicken embryo, where only its description had been carried out. He again raised the question of how these monsters were formed, disagreement about which had long existed in the literature on this subject. Haller and Meckel in their own day stated their opinion that double monsters develop by way of union. Burdach later subscribed to this interpretation. Isidore Geoffroy Saint-Hilaire was a more active supporter of the theory of union. Baer decisively raised an objection to this point of view. So he was astonished to find that Barkov, in his thorough work, "Double Deformities among Animals," claimed that Baer's description of the embryo "proved directly the union of separate parts of the accreted embryo." How could it happen, Baer wrote, that, "considering myself a decisive opponent of accretion, I have apparently recognized the accretion of parts of different embryos?" (p. 81). From the moment of the appearance of Barkov's work, Baer collected additional data on double monsters, on the basis of which he reconfirmed the accuracy of his previous opinion.

Speaking of investigations of monsters generally, Baer stated that their development must be studied as exactly as the course of normal development. The achievements of embryology, making the controversy of spermatists and ovists meaningless, was a consequence of that. From elucidation of the primary conditions of the processes of reproduction and development we arrived at the fundamental study of the most formative processes.

Before turning to the description of many cases of double monsters, Baer outlined his order of presentation. In the beginning he investigated what was formed; later, by comparison with other cases and with normal development, he elucidated the question of how these monsters could be formed. Concerning why these double monsters originate, only suppositions are stated.

DOUBLE EMBRYOS OF FISH IN VERY EARLY STAGES OF DEVELOPMENT. Baer began with the description of two double monsters in perch which he found in 1835 in some eggs obtained from the Neva two days before the investigation. One embryo was double-headed. In the other the division was found in the

trunk region. The division of the cephalic end of the first embryo was incomplete, since there were two mouths and four eyes but only two ears (Figure 34, A). In the second embryo the posterior part of the body and tail was single and all the anteriorly situated parts were double. Both these cases, in Baer's opinion, totally excluded the possibility of regarding them as a result of the union of two individuals: from the moment of the appearance of the embryo not more than one day elapsed; thus during this short period the remaining undoubled parts could not have disappeared. In addition, the embryos were situated close to the yolk. They could not have been any closer in order to unite with each other. In an embryo with a partially doubled head, it can be assumed that the splitting occurred in a very late stage. In the second embryo the bodies were situated at an angle of 120° , indicating that the first foundation of the embryo, namely the primary streak, was divided from the front. The unusual width of the ovum supported this observation. A double embryo appeared after the division of the primary single rudiment. In connection with the description of these cases of double monsters in perch, Baer referred to examples of double embryos in fish described in the literature, beginning with Aldrovandi's *MONSTRUORUM HISTORIA* (1642) and ending with Heusner's "Double Monsters in Perch and Other Fishes".⁵

DOUBLE CHICK EMBRYO AT THE BEGINNING OF THE THIRD DAY. In this section Baer gave a more detailed description of a divided chick embryo, the investigation of which was illustrated in 1827 (Figure 34, B). Here Baer turned his attention to the reciprocal situation of the heads of the double embryo, excluding, in his view, the possibility of the union of two formerly divided embryos. He considered especially conclusive the reasons relating to the situation of dorsal and mainly ventral plates of both partners. "The ventral plate of one of them passed into the convexity of the blastoderm without interruption and without evidence of union in the ventral plate of the other. More exactly, one and the

5. Heusner, "Descriptio monstrorum avium, amphibiorum, piscium." Diss. inaug. Berol. (1824) (cited by Baer).

same continuous surface formed the future left ventral wall of one, and the future right ventral wall of the other partner If union had occurred during the first day of incubation, then the ventral walls could not unite, since they did not yet exist; hence they were isolated from the blastoderm only in the second day" (p. 110).

Later Baer described some cases of monsters in man. First he described twins which were joined at the forehead. In his opinion, this case was similar to the described in 1501 by Sebastian Münster. Baer cited an early description and illustration of a human double monster, according to data provided by Schmidt, published in the journal ISIS in 1825. He followed with general descriptions and drawings of "parasitic formations," as Burdach called them—i.e. additional parts attached to completely developed individuals, which were without an umbilicus and were nourished through its vessels. Baer referred to a similar case which he had observed in Königsberg. The case involved a living baby whose incomplete individual hands and legs were attached to its chest but who lacked a head and a large part of the trunk.

Referring to analogous examples from other authors, Baer mentioned a case been earlier studied by Zagorsky.⁶ He noted that that famous Russian anatomists's description, with the exception of some details, was completely correct. In this parasitic formation, as in other analogous specimens from the Academy's collection, the supply of blood occurred from *arteria mammaria* of the original individual. In addition to these cases, Baer saw examples of formations of additional extremities, always, however, connected with the other additional organs. This category, called "parasitic formations," also included those cases where two additional legs are present with an atrophied foetus, attached to the pubic region and situated in the normal legs (Figure 34, D). The genital organs

6. P. Zagorsky, "Foetus humani monstrosi, alii bene formato foetui adnati descriptio," MEM. ACAD. SCIENCES ST. PETERSB., VI Sér. Sc. math. et phys., v. 2, book 2 (1833), pp. 187-194.

and the internal organs of the pelvic cavity were also doubled. In a similar monster there was an additional leg without a mate; in the groin region of the extra leg were discovered an additional ovary and three elevations which undoubtedly were nipples. In this connection Baer thought the common phenomenon of supernumerary nipples in humans as being possibly inherited. He cited a case, described by Rober, in which a woman who had additional mammae on the right side of the thoracic cavity gave birth to a daughter with an additional mammae on the thigh. These additional mammae subsequently secreted so much milk that the woman could nurse, in addition to her own children, three additional babies for six years.

Besides the cases mentioned of parasitic formations in human beings, Baer described an analogous case in a live adult cow⁷ (Figure 34, C). In the middle of its neck there was an appendage resembling in form the scaled-down underdeveloped posterior parts with two deformed legs and a tail. The immediate investigation showed, however, that the additional legs were not posterior but anterior, and the tail-shaped structure contained a rudiment of skeletal parts of the branchial girdle. Baer investigated in detail the nerves of the parasitic formation from the cervical part of the spinal cord.

This thorough teratological work of Baer's remained incomplete information intended for the second part was never published. Probably Baer intended to include at the end of the work some theoretical consideration of the origin of double monsters. However, that which did appear in his published work is enough to suggest his point of view on this subject. As previously observed, Baer decisively rejected the idea that double monsters result from the union of formerly separated individuals. He concluded that double monsters can be formed only from the fission of the formerly single embryo. Baer supposed that the separation would be more pronounced the earlier the fission took place. The cases of "parasitic formation" Baer was inclined to interpret, apparently, from this point of view. It must be

7. Information about this case was obtained by Velyaminov from the Caucasus, which Baer published earlier under the title, "Bericht über eine ausgewachsene Missgeburt," BULL. SCIENT., ACAD. IMP. SCIENCES DE ST. PETERSB (1836), No. 1, p. 128.

noted that Baer's principle of explanation of double monsters was subsequently completely confirmed, especially when it was found that this kind of formation could be obtained experimentally by pretwisting the ova, turning the vegetative pole upwards, effecting temperature changes, and so on.

In subsequent years Baer from time to time returned to teratological questions, describing interesting cases he discovered. The following cases present information of this nature:

1. "A new case of twins joined at the forehead, and comparison of it with analogous cases."⁸ This concerned accreted twins, aged about eight months of uterine life, prepared for the Academy's collection. Both the foeti are female, well developed, joined to each other obliquely. Baer noted that similar kinds of union of accreted twins are seen more frequently in birds than in mammals and cited corresponding references.

2. "Notice sur un monstre double vivant "⁹ This case is that of a monster which attracted Baer's attention because the accreted double was delivered at full term and was born alive. The position of the twins was completely symmetrical, in contrast to the previous case, where they were at angles to each other.

3. "Remarks on blind fish, an example of delay of development."¹⁰ In these remarks Baer described a carp (*Cyprinus gibelio*) caught in a muddy pond in Kolomyaga. The eyes of the fish were rudimentary and sealed under the skin. In connection with this Baer posted the question, can darkness be the cause of underdevelopment of the eyes?

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8. Baer, "Neuer Fall von Zwillingen, die an Stirnen verwachsen sind, mit ähnlichen Formen verglichen. Mit einer Tafel," BULL. PHYS.-MATH. ACAD. SC. ST. PETERSB. (1845), 3, No.8, pp. 113-128.
9. Baer, "Notice sur un monstre double vivant, composé de deux enfants féminins," IBID. (1856), 14, No. 3, pp. 34-37.
10. Baer. "Ein Wort über einen blinden Fisch als Bildungshemmung," BULL. ACAD. SCIENCES (1862), 4, pp. 215-220.

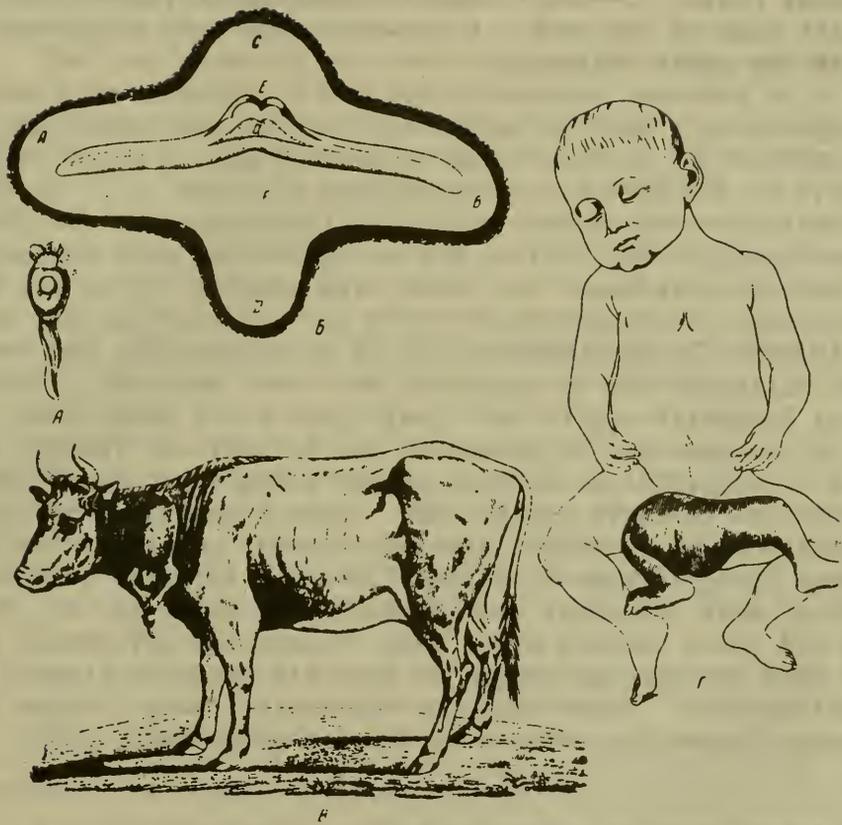


Figure 34. Illustration of Baer from "About Double Monsters"

Figure 34. Illustration from Baer, "On Double Monsters."

A--double-headed perch embryo; a--outer or upper plate of the rudiment corresponding to the abdominal wall of the embryo; b--internal or ventral plate of the rudiment or allantoic sac. B--double-bodied embryo of a chicken in the embryonic sphere, at the beginning of the third day; ABCD--transparent embryonic sphere; E--the common head; F--approximate outlines of the heart; a--thickened place on the head between the skull and thickened edge of the abdominal plate. C--adult cow with additional growth in the left side of the neck. D--newborn baby with additional legs in the pubic region.



After Baer arrived in Petersburg he ceased his systematic study of embryology. This change in his scientific interests foreign biographers explained as due to difficulties in getting embryological material. Baer himself in his autobiography supported this version of the story of how he could not organize a supply of frogs, fish eggs, and mammalian embryos. Even N. A. Kholodkovsky, the author of an excellent biography of Baer, in spite of Academician V. F. Ovsyannikov's contrasting opinion,¹¹ also cited the same strange explanation of the striking fact that this great embryologist, who was making more scientific progress than all his predecessors, suddenly left this sphere of science in which he had enthusiastically worked for more than fifteen years.

The true cause of why Baer stopped his study of embryology appears in extracts of his correspondence reported by B. E. Raikov in the commentary to his translation of Baer's autobiography.¹² Raikov cited a long portion of Baer's letter of December 30, 1845 to T. L. Bischoff (published in ALLGEMEINE ZEITUNG, 1880, No. 325, appendix). In this letter Baer explained his departure from embryology as due to the lack of consideration and the unfair attacks with which his remarkable discoveries were met in Prussia. The Minister of Education, Altenstein, after the publication of *DE OVI MAMMALIUM ET HOMINIS GENESI*, declared that "the existence of the mammalian ovum had been known for a long time," and Plagge attempted to claim for himself the fame of the discovery of the ovum in the ovary. Other German biologists showed extreme indifference to his work, which offended Baer. Not finding sympathy in their midst and not receiving from the Prussian Ministry of Education the necessary material for continuation of embryological work, Baer, in his words, "decided to tear radically from his heart all scientific ambition." Baer spoke further about his promise to himself to cease his work on embryology and not even to read any embryological literature for nine years. This decision was taken undoubtedly because of nervous exhaustion caused by

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11. F. V. Ovsyannikov, "Brief biography of Baer read in December's general meeting of the Society of Naturalists," *TR. SPB OBSHCH. ESTESTV.* (1877), 8, pp. 97-107.
 12. The materials stated below are cited with commentary 8 in Chapter 15 (pp. 519-523).

severe overwork and annoyance, and Baer himself certainly regretted it. "Generally I cannot decide," Baer wrote in the same letter, "whether I behaved correctly by making this vow, but I can confirm that I have injured myself deeply, perhaps even too deeply. Later it seemed to me that I had lost the best blood of my heart."

Discussing the contents of this truly tragic letter, B. E. Raikov correctly concluded that "there is no basis for placing responsibility for the change in Baer's scientific studies upon conditions in Russia. Not the Russian, but the Prussian conditions of his life created in him this attitude which led him to a decision so unfortunate for science."

However, in the 1840s Baer's interest in embryology reawakened, undoubtedly in connection with his professorial activity in the Petersburg Medical-Surgical Academy, where he taught comparative anatomy and physiology, in which course embryology figured significantly (114). In connection with teaching the science so near to his interest, Baer intended in 1843 to publish a Latin "essay on the history of development of men and other animals" (CONSPECTUS HISTORIAE EVOLUTIONIS HOMINIS ET RELIQUORUM ANIMALIUM) in twelve to fifteen papers with two tables of illustrations. In 1844 invited the conference of the Academy of Science to publish an atlas in Russian on this topic comprising forty papers and 150 drawings. A report by Baer on the plan of this publication was fully published in E. N. Pavlovskii's K. M. BAER AND THE MEDICAL-SURGICAL ACADEMY. The following parts of this document are interesting:

New investigations in 'developmental history' which have already been published are still little known in Russia Consequently it is reasonable now to wish for a textbook on one branch of physiology developing in recent times. This branch is not only important for physicians, and for naturalists generally, but it also illuminates other parts of physiology and anatomy. Once I dared to hope that I possessed sufficient knowledge in this subject

The first priority is to become acquainted with all current results in addition to the necessary details of the experiments on which they were based

Further, it seems important also that the application of an explanation to congenital deformities must be not only mentioned, but also investigated in order that all educated physicians can learn how to recognize and describe similar cases for the further benefit of science. The main task must be, without any doubt, the history of the formation of the human embryo, including the deformities as well. But the first stages of this formation in man are still little noted, and that includes embryos in diseased conditions (to which all abortions are related), without which we could not know the complete history, origin, or formation of any part if they were observed in mammals. The history of formation of mammals also cannot be understood at this stage if we do not have cases of observations on the formation of chicks. On this basis I find it necessary, before treating the history of human formation, to discuss as a preliminary the observations on other mammals and on the chicken in order to understand how the results are obtained and why and to what extent analogies can be drawn from them. It is necessary to discuss briefly the animals of other classes in relation to the history of formation, and especially to mention some general results

These extracts from the draft of Baer's work on the history of development of man and vertebral animals show what great educational significance Baer accorded to the field of embryology in the training of future physicians. Here also was briefly pointed out the fruitfulness of the comparative method in embryology, and also the importance of the detailed study of monstrosities, a description of which is necessary "for the future benefit of science."

The publication of Baer's projected textbook for some reason did not take place. The possibility cannot be excluded that Baer himself rejected this idea. Feeling the difficulty of the great work related to a sphere of science to which he was so close in the past, he was obliged to abandon it. Actually, it was not easy after a ten-year interval, during which Baer did not study embryology and did not follow the literature of this topic, to coordinate all that had been done by a complete galaxy of investigators—Rathke, Reichert, Kolliker, Bischoff, and others—who had followed in his footsteps, adding many new facts and raising new theoretical questions. It was also necessary to take a definite position concerning the cellular theory, which in the 1840s had spread its influence to embryology. In addition to this, and even in later years when Baer wrote his autobiography (i.e. in the 1860s), he did not consider it possible to speak decisively concerning this theory. Recognizing the importance of that wide biological generalization which the cellular theory considered, Baer could not agree with the discrete presentation of the organism which was proposed by some supporters of the cellular theory in the first period of its development, and later in the era of Virchow and Schultze.

However, Baer retained an interest in the problems of the history of animal development. In 1845-46 he made an attempt to return to research in embryology. Planning to study the embryonic development of invertebrates, Baer travelled to the Mediterranean coast and collected interesting material in Genoa, Venice, and mainly in Trieste, which consisted of fixed objects and drawings by an artist who accompanied him. In this last attempt to return to embryological investigations, misfortune pursued Baer. Part of the material was accidentally destroyed in Venice; another part of it was lost elsewhere.

But not all of the research carried out on the Mediterranean coast could be considered fruitless (115). The principal task of his trip to Genoa, Venice and Trieste, as Baer wrote in his report,¹³ was the study of the

13. "Auszug aus einem Berichte des Akademikers v. Baer aus Triest vom 1 (13) November 1845," BULL. PHYS.-MATH. ACAD. SC. ST. PETERSB. (1847), 5, No. 15, pp. 231-240.

(Contd. on next page)

possibility of artificial fertilization in different marine animals (116).

Baer noted that since the time of Spallanzani it was known that it is easy to fertilize artificially the ova of frogs. Spallanzani (and later Rossi) inseminated a bitch by the artificial introduction of sperm. Baer's contemporaries, according to him, questioned these data, although without foundation, because Bischoff's work had made it apparent that in mammals and also in other animals, the separation of the ovum is due to its maturation and not a result of copulation.

Baer thought it evident that every mature ovum introduced into contact with sperm of the same species is fertilized and, if situated in suitable conditions, develops into an embryo. Sometimes experimental difficulties arise, which can, however, be overcome. His failures in Petersburg with artificial insemination of fish ova Baer explained by unsuitable temperature conditions.

In Genoa at the end of August 1845 Baer made the first experiments in the artificial insemination of the ova of Ascidians. "In the earliest hours," Baer wrote, "the division began, and before the day had passed larvae hatched in the form of large cercariae." The experiment of artificial insemination of mature ova of the sea urchin, carried out on the same day, was also crowned with success. Within sixteen hours freely moving embryos developed. "It was a very great success for one day," Baer stated: "a researcher rarely succeeds sufficiently to exclaim VENI, VIDI, VICI! After the first glitter, I was on top of the world" (p. 233). However, it was extremely difficult to keep the ascidian larvae alive. They died within hours after hatching; the sea urchin larvae did not live more than four days.

Gaining success in the artificial fertilization of the ova of sea urchins, Baer turned to study their development. He observed the early stages of development at first in Genoa

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13. Extracts from this report were published in FRORIEP NOTITZEN (1846, No. 39, pp. 38-40) under the heading, K. E. v. Baer, "Neue Untersuchungen über die Entwicklung der Thiere."

in the ova of *Echinus brevispinosus (esculentus)*, and then in Trieste on the smaller, more transparent ova of *Echinus lividus (saxatilis)*. With the first, his attention was attracted to the fact that inside the ovum, soon after fertilization but before the beginning of division, a light radiance appeared but shortly afterwards disappeared. Applying slight pressure upon the ovum, Baer could get an extended vesicle (nucleus) or two vesicles situated side by side. Noting the direction of the longitudinal axis of this extended light region, Baer observed that after the yolk (ovum) divided into two halves, the centers of these halves were situated in the same axis. From these first observations he concluded that "the processes in the internal region of the ovum precede the division of the yolk and predicate it." The study of the subsequent stages of division led Baer to the conclusion that the externally observable phenomenon of division always precedes the division of the transparent nucleus present inside. The details of the ovum structure, using intravital observations with little magnification, Baer of course could not investigate, and discussions preserved the terminological confusion of that time, when the relations between the nucleus of the immature ovum (embryonic vesicle, or Purkinje's vesicle), the ovum nucleus, and its nucleolus (Wagner's spot) were still not established.¹⁴

For the first stage of development of the immature ovum, Baer wrote,

I consider the nucleus to be identical with that part which is usually called Wagner's spot Much later the part which is apparently considered an embryonic vesicle occupies a great part of the ovum. Because the small body shows, under pressure, a great resistance, the name "spot" is not so suitable. It seems to me very probable that the

14. It must not be forgotten that even thirty years later O. Hertwig thought that during the maturation of the ovum the embryonic vesicle disappears, and the embryonic spot becomes the nucleus of the mature ovum (O. Hertwig, "Beiträge zur Kenntniss der Bildung, Befruchtung und Teilung des tierischen Eies," MORPH. JAHRB., I (1875); III (1877); IV, (1878).

role which this nucleus (or embryonic spot) plays in the ovum of the sea urchin occurs in other animals in the embryonic vesicle. In addition to this, in the ovum of the sea urchin the part called embryonic vesicle disappears long before the end of maturation. (p. 238)

If the details of maturation remained unclear for Baer during the study of the processes of segmentation he could, despite his imperfect means of observation, see much and essentially move ahead of his contemporaries. According to Baer's description, after fertilization the ovum nucleus greatly submerges in the yolk and after some minutes it seems that it completely disappears. "However, under the microscope," Baer states, "the nucleus may be seen, although its boundaries are unclear due to uneven refraction of the surrounding granular yolk. Sometimes only a limited light radiance is seen. During the delivery of the ovum its boundaries, having the form of a circle, become more distinct" (p. 238).

Baer described the process of division itself in the following manner:

After the period of dormancy, the nucleus, having until then a spherical form, very quickly becomes elongated, and at the same time processes of protuberances appear from both of its sides. These ends of the nucleus swell, and its center becomes thin and is quickly torn off, so that two comet-shaped nuclei with tails directed towards each other are formed. The tail-shaped appendage quickly extends inside its spherical mass, and then two nuclei are apparent Just before division the nucleus increases in size; at the time of division this increase progresses, so that each of the two new nuclei is approximately equal in size to the initial one Only after that, when both of the new nuclei are separated from each other, does the retwisting of the ovum begin, in consequence of which it is divided into two halves near to each other, each surrounded by its portion of yolk. (pp. 238-239)

Here Baer referred to Kölliker's paper.¹⁵ Since Kölliker did not doubt the complete disappearance of the embryonic vesicle, Baer, referring to his authority, left his own completely accurate observations in doubt and considered it necessary to check them again. Baer noted, however, that he could never ascertain the moment when the nucleus was completely absent. And what is more, he expressed confidence that in the ova of frogs the embryonic vesicle would be detectable in this period when, as it was believed, it completely disappears.

Further on, Baer passed to the description of the following stages of segmentation. Soon after the division of the ovum into two parts, "each nucleus begins by the way previously described to form processes, and changes by dividing in the middle into two new nuclei; the mass of yolk adjacent to it also is divided, so that all the ovum disintegrates into four masses. Each quarter becomes rounded, and in the center between them an empty space¹⁶ is formed. The division of quadrants takes place completely similarly; moreover, the newly formed processes are situated at right angles to the previous ones. This continues also during the following divisions; moreover, for every new fragment of yolk a nucleus is formed by division of the earlier one.

Baer noted that the nucleus in the process of division is not always distinctly demarcated from the surrounding substance. "In the period of dormancy," Baer wrote, "a clear boundary line is seen under the microscope, but at the time of formation of the processes it cannot be observed with definition" (p. 239). Further, he drew from his observations another essential conclusion, concerning the method of formation of cells in the process of early embryonic development in the sea urchin. With great accuracy it can be established, and for subsequent divisions also, that when

15. A. Kölliker, "Beiträge zur Entwicklungsgeschichte wirbelloser Thiere. 1: Über die ersten Vorgänge im befruchteten Ei," ARCH. ANAT., PHYSIOL. (1843), pp. 68-141.

16. This rudiment of the division cavity (blastocoel) is called Baer's cavity by R. Remak.

the nuclei are surrounded with a small layer of yolk the new cells are not formed "inside the maternal ones" ("yolk bodies," in Baer's terms).

Up to the stage of thirty-two blastomeres he could note directly the appearance of new blastomeres by division. Later on when they became numerous, it did not seem to be possible to trace the appearance of each. "However, here and there," Baer wrote, "in the yolk bodies, situated in the edge, the processes of division can be seen also as earlier. Even when the embryo leaves the ovum membrane and moves by the help of the cilia, every granule or each histogenic element (cell) possesses a very distinct nucleus" (p. 240). Baer could not trace the subsequent development, due to the movement of the embryo. Nevertheless, on the basis of the observations described above he reached the conclusion that later the histogenic elements (i.e. cells) result from earlier existing ones by means of the same kind of division. The general conclusion with which he ended the report stated: "The division of the yolk is considered only the beginning of the histogenetical separation, which continues uninterruptedly to the final formation of the animal. If this presentation is correct, then the question of the pre-existence of the new individual, before fertilization, is beyond any doubt. The unfertilized ovum is an embryo having latent life. The fertilization makes its life active" (p. 240).

This short paper of Baer's, as can be seen from its summary, contains an extremely rich content. There is no doubt that Baer saw with complete clarity all these processes of maturation and division of the ovum, which can be seen by intravital observations. He surpassed, by many decades, the views of his contemporaries, showing, first, that the nucleus of the fertilized ovum does not disappear, but becomes only less distinctly visible. He saw further the appearance of the radiant achromatic figures in the mitoses of division, the change at the time of their division, the disappearance of the nuclear membrane at the time of mitosis, and its appearance in interkinesis.

Drawings were not appended to the published report. If one looks at a picture of the division of the sea urchin ovum by intravital observation performed approximately a century

later with an apochromatic objective and condenser, one will be surprised by the accuracy of Baer's observations and the insight of his discussion.

While his work on the history of development of invertebrates was not continued, Baer continued to the end of his life to be interested in the progress of the science of development and responded to every major event in this sphere.

The discovery, by N. P. Wagner of Kazan, of asexual reproduction in the larvae of diptera from the family Cecidomyidae¹⁷ evoked from Baer first a short report¹⁸ and then a long paper.¹⁹ Wagner found that from the ova laid by winged adults come large larvae, which, however, do not pupate. Inside each of these larvae a new generation of larvae develops, feeding on the fat body and other organs of the mother. Inside the larvae of the second generation the third generation originates and so on, resulting in an intermediate series of asexually formed generations. The larvae pupate and produce the dioecious winged cecidiums. The discovery of this unusual method of reproduction in dipters caused such great doubt that Siebold did not dare even to publish in the journal which he edited (ZEITSCHRIFT FÜR WISSENSCHAFTLICHE ZOOLOGIE) an article sent to him by Wagner.

17. N. P. Wagner, SPONTANEOUS REPRODUCTION OF CATERPILLARS AND INSECTS (Kazan, 1862), 50 pp.
18. Baer, "Bericht über eine neue von Prof. Wagner in Kasan an Dipteren beobachtete abweichende Propagationsform," BULL. ACAD. SC. ST. PETERSB. (1863), 6, pp. 239-241.
19. Baer, "On the discovery by Professor Wagner of the asexual reproduction of larvae, on additional observations on this subject by G. Ganin, and on paedogenesis generally," Appendix to Vol. 10 of ZAPISOK IMP. AKAD. NAUK (1866), No. 1, pp. 1-77.

Academicians Baer and Ovsyannikov personally were sure of the reliability of Wagner's observations, and he, after review by a committee that included Baer, Ovsyannikov, and Brandt, was awarded the Demidov prize.²⁰ In the same year in Denmark Meinert²¹ confirmed Wagner's discovery, and proposed for cecidia, the larvae of which kill their mother during their development, the new generic name MIASTOR (Greek for killer, villain). Meinert also agreed with Wagner that the larvae of the new generation arise from the fat body of the larva-mother. Pagenstecher²² also confirmed the fact of asexual reproduction among the larvae of cecidia, but he thought the larvae to be formed, not from the fat body, but from minute ova, but Pagenstecher could not establish the places of appearance of the ova.

The subsequent investigations of the reproduction of Miastors were performed in Leuckart's laboratory at Giessen; I. I. Mechnikov, who worked there, shared in them. In a preliminary report published in NATURALIST (No. 8, 1865), Mechnikov wrote that he, together with Leikart, found in the larvae of cecidia special organs—"small embryos, fissionable into separate compartments, swimming freely in the body cavity and producing new embryos. The development of the latter," Mechnikov continued, "I have also observed, and have found that the small embryos are formed from direct transformation of 'polar cells,' as in the genus Chironomus, as earlier blastomeres." Baer especially underlined the importance of Mechnikov's discovery, that "the small embryos or ovaries—call

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20. Spontaneous reproduction of caterpillars and insects. Prof. Wagner. Kazan (Thirty-third Award of P. N. Demidov prize, June 26, 1864, pp. 238-242) (review by Baer together with Ovsyannikov and Brandt).
 21. F. Meinert, "Weitere Erläuterungen über die von Prof. N. Wagner beschriebene Insektenlarve, welche sich durch Sprossenbildung vermehrt," ZEITSCHR. WISS. ZOOL. (1864), 14, pp. 394-399.
 22. A. Pagenstecher, "Die ungeschlechtliche Vermehrung der Fliegenlarven," ibid., pp. 400-416.

them what you will" are formed from special polar cells. "If the formation of the small embryos from these 'polar cells' is confirmed, then it will be an important increase of our expanded knowledge about the process of animal development" (p. 10).²³

Later Baer reported in detail the investigations of M. S. Ganin,²⁴ prosector at Kharkov University. His observations are "extremely careful and circumspect, representing great interest." Describing in detail the structure of larvae, Ganin turned to their embryonic development; moreover, he reached the conclusion that the development of the young larvae inside the older ones did not arise from the fat body. He found an ovary, in which ova developed, giving the beginning to the young generation. Ganin thought that the ova of viviparous diptera that he investigated are differentiated from the ova of those insects which are characterized in the imaginal stage by the absence of the nucleus (Purkinje's vesicle) (117). Leuckart soon confirmed Ganin's observations concerning the development of *Miastor* ova within special organs, but he called these organs small embryos and not ovaries as Ganin called them. The developing group of cells in these small embryos are separated and fall in the body cavity. In each of these groups one cell increases in size and serves for the formation of the embryo, while the others, as in the embryonic chambers of other insects, play the role of feeding cells.

Baer considered it correct to distinguish the embryos identical with ova which are developed from ovaries producing true ova, and approved Leuckart's suggestion of calling the early embryos of the *Miastor* false ova (PSEUDOVA) (118).

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23. In the following year Mechnikov published detailed reports on the embryonic development of *Miastor* ("Über die Entwicklung der viviparen Cecidomyidenlarve, nebst Bemerkungen über den Bau und die Fortpflanzung derselben," *ibid.* (1866), 16, p. 407). In this paper the development of small embryos from polar cells was traced in detail.
24. M. Ganin, "Neue Beobachtungen über die Fortpflanzung der viviparen Dipterenlarven," *ibid.* (1865), 15, p. 375; ZAPISKI IMP. AKADEMII NAUK, 1865, 8, pp. 36-56.

Returning to Wagner's discovery, Baer mainly emphasized the distrust with which it was first viewed. "This circumstance," he stated, "shows to what extent the aforesaid discovery was unexpected and how little prepared we were for it. Subsequently, its importance lay in its proof, and credit was given to him" (pp. 22-23). In connection with this he mentioned the words of Humboldt: "A book which, upon its appearance, immediately meets with general approval cannot be worth the publishing, because it can only conclude what already completely predominates in everyone's convictions." Illustrating this, Baer noted the discovery made by Peyssonel in 1723 that corals are animals, which "the great Réaumur rejected as an absurdity," so that Peyssonel could only publish it thirty years later. Further, Baer noted the fate of Harvey's discovery of blood circulation, which was subjected to doubt because "they did not know where air goes, it was assumed to exist in the arteries. The correctness of his discovery was recognized twenty years later, that is to say after Harvey's death. More time elapsed before the general recognition of Copernicus' discovery. The earth made its orbit around the sun many times before popes could speak of this publicly" (p. 24).

Baer remarked later that he did not mean to compare the discovery of asexual reproduction of larvae with the basis of the heliocentric theory; he wanted only to call attention to the frequently repeated historical relation of new ideas. He cited Agassiz, that each newly appearing study must pass through three phases: first they will say that it is incorrect, then that it is against religion, and finally that it had been known for a long time. "Wagner's discovery," Baer stated, "without doubt, does not need proof that it is not contrary to religion, or rather, dogma, for no dogma is concerned with fly larvae" (p. 25). This discovery had already reached the stage of general recognition, the stage of coordinating it with previous opinions, for which it was necessary to change them somewhat. The idea must be rejected that the reproduction of posterity by means of fertilization, which is characteristic of man and other vertebrates, is a rule, and that all other forms of reproduction are exceptions. This idea is the source of the usual anthropomorphism, "man always standing at the center of his mental as well as his physical horizon" (p. 26).

Sexual reproduction, which is considered a necessity for the majority of animals, especially the higher ones, is intrinsic also to the plant kingdom, but in the latter it is not so necessary and frequently is changed into different forms of vegetative reproduction.

Referring to corresponding examples (potato, weeping willow, bulbous plants, and so on), Baer turned to the invertebrates, noting that in them also (for example, in Infusoria, Bryozoa, Ascidia, and polyps) reproduction by division and budding is very usual. Other forms of reproduction without fertilization, namely parthenogenesis, is characteristic among insects. The main form of parthenogenesis was considered Wagner's discovery of the *Miastor*. Contrary to the earlier known parthenogenesis, in which the source of ova developing without fertilization was thought to be the sexually mature females, in viviparous cecidia the embryos originate in the organism of the unformed larvae incapable of fertilization. Baer considered it advisable to give this form of reproduction a special name, and by analogy with parthenogenesis he termed it *paedogenesis*.²⁵ In both terms, Baer wrote, the first half of the word shows the producing subject. In a footnote he mentioned the correctness of Leuckart's note that the word parthenogenesis actually means the genesis of a virgin, and not genesis by a virgin; however, as this term became generally used, it was impossible to avoid analogy with it in the formation of a new record.

Comparing the phenomenon of parthenogenesis in Aphidae with *paedogenesis* in cecidia, Baer reached the conclusion that, as in Aphidae, the appearance of this or that form of reproduction (with fertilization or without it) is closely related to conditions of existence, in particular to intensity or nourishment; more abundant nutrition aids parthenogenetic and *paedogenetic* reproduction. The main conclusion to be drawn from the comparison of these forms of reproduction is that they both are an example of alternation of generations, or "alternating reproduction," during which sexual generation, i.e. by means of fertilization, alternates in one or more generations with reproduction without fertilization. To

25. From the Greek PAIDES, meaning children.

substantiate this conclusion Baer extracted material from Steenstrup's ÜBER DEN GENERATIONSWECHSEL,²⁶ and other sources. He rated highly Steenstrup's work, in which the wide distribution of the phenomenon of alternation of generations is shown, which indicated its general biological significance. Baer turned his attention to the fact that Steenstrup had stated almost nothing about the alternation of generations in plants. Attempting to fill this gap, Baer cited many clear examples related to sporophytic and phanerogamous plants. These examples show that the alternation of two forms of reproduction—sexual and asexual (i.e. occurring without fertilization)—is inherent to the entire organic world. The alternation of generations, during which the ability to reproduce asexually appears (Baer related it not only to division, as in budding and other forms of vegetative reproduction, but also to development from unfertilized ova, i.e. parthenogenesis and paedogenesis), he considered not an exception but a rule. The essential difference between sexual reproduction and all forms of asexual reproduction Baer concluded from the fact that sexual reproduction takes place only in the adult condition, while asexual reproduction occurs in different stages of ontogenesis. In particular, adult individuals are capable of parthenogenesis and reproduction by means of fertilization, while the paedogenesis of dipterous insects occurs only in larvae.

The ability to reproduce in a sexually immature condition is characteristic also for other invertebrates—Coelenterata, parasitic Platyhelminthes, and Tunicata; therefore, all sexually immature forms of different animals—rediae, cercariae, brachiolariae, tornariae, strobiliae, scyphistomae, and so on—must also be called larvae.

In comparing the individual life of the organism—i.e. its development with reproduction—with the life of the species,

26. J. J. Steenstrup, ÜBER DEN GENERATIONSWECHSEL, ODER DIE FORTPFLANZUNG DURCH ABWEICHENDE GENERATIONEN, EIN EIGENTHÜMLICHE FORM DER BRUTSFLAGE IN DEN NIEDEREN THIERCLASSEN (Copenhagen, 1842), 140 pp. This edition represents the translation of Forentsen from a manuscript published at the same time in Danish.

Baer was concerned with the question of the relation of the instinct for self-preservation to the sexual instinct, and in connection with this he touched upon a question which worried him, on the possibility of including the understanding of purpose in a sphere of strict scientific investigation. His considerations are discussed below.²⁷

In the concluding chapter of his work Baer again noted the importance of the discovery of paedogenesis for understanding the idea of parthenogenesis and the alternation of generations. Understanding of these phenomena required systematic examination of different forms of reproduction. "I sought," Baer wrote, "to look through all that had been written on this subject, as in a consultation with myself—a consultation which may prompt more young investigators to attempt to make similar comparisons that would also be useful for them. During this, difficult tasks appear which we must trace more closely" (p. 70). To these tasks Baer related the experimental investigations of the external conditions upon which the parthenogenesis of Aphidae and the paedogenesis of cecidia occurs. By means of these experiments, Baer supposed, it could be elucidated why, in apparently related species of medusa, one species immediately forms sexually mature medusa from the swimming larvae and the other goes through the sessile stage which is the budded strobila.

To these facts and considerations Baer gave the following resumé:

Organic bodies possess the ability to self-develop by action intrinsic to them, as soon as they have the possibility of receiving the necessary material. In addition, they still have the ability to produce new individuals. (p. 72)

Self-development moves from absolutely simple forms and elementary parts by gradual transformations The sequence of these changes is called in scientific terms development, and in ordinary term life, growth;

27. See Chapter 24.

in addition, it means mainly the increase of body. But this increase in every separate vital process ceases early or late, although the tendency of self-preservation continues to exist, but the changes lead the organism to final dissociation. The capacity of reproduction, on the contrary, creates new individuals of this species. (p. 73)

The ability to reproduce is present in two forms. First, it may be considered a result of the necessary influence of one on the other of two materials This reproduction is called sexual, even in the case in which male and female sexual organs are present in the same individual. These individuals are called hermaphrodites. The second kind of reproduction is termed asexual reproduction. It is frequently seen in plants and the lower animals. Asexual reproduction in many organisms is found together with sexual reproduction This union of both kinds of reproduction can be called, according to Owen, metagenesis, or, according to Van Beneden, digenesis. The expression "alternation of generations". . . must be used only in those conditions when these forms of reproduction are alternated one with the other Sexual reproduction can never appear at the beginning of individual development, because the sexual organs must be formed early and secrete their products. The embryo produced by fertilization must always pass through all the stages of development intrinsic to this organism. When asexual reproduction takes place in the mature condition of the female individual, then it is called parthenogenesis. Similar reproduction in the immature condition we suggest calling paedogenesis. The latter may occur in all the different periods of development and may appear in very different forms, and also begins the course of development each time from the beginning, or may only continue it. (pp. 75-76)

From this it is clear that Baer established an orderly classification of the methods of reproduction, including all

the organic world from the lower water plants to man, showing, in fact, the form of reproduction for evolution.

N. P. Wagner's discovery of the phenomenon of paedogenesis, which served as the starting point for Baer's discussions and also M. S. Ganin's detailed investigations in this topic, attracted Baer's intense attention. Because these works were considered evidence of the successes of Russian embryology, Baer always showed great care for its development. He energetically popularized works by Russian authors in his reports, published statements and letters. He was glad of the recognition of the importance of these works by influential investigators abroad and expressed the conviction that "there is yet no single route to us via the printing press and book trades" (p. 22).

It is interesting historically, however, that Baer's other great work, in which he posed the question, "Do the larvae of simple ascidia develop initially like types of vertebrates?"²⁸ was very controversial.

The cause of his writing this paper was sensational. As Baer wrote, A. O. Kovalevsky discovered that ascidians, which in their adult condition are so strongly differentiated from vertebrates, at the beginning develop similarly to vertebrates. "If this conclusion," Baer stated, "could have been substantiated, the sensation would have been completely valid, since Darwin's bold hypothesis that the higher organisms have evolved over the course of time from the lower, the lowest form differing absolutely from the highest, received great support" (p. 1).

Outlining the content of Kovalevsky's work,²⁹ Baer again returned to the idea that "rigorous comparison of ascidian

28. Baer, "Entwickelt sich die Larve einfachen Ascidien in der ersten Zeit nach dem Typus der Wirbelthiere?" MÉM. ACAD. IMP. SCIENCES ST. PETERSB., VII Sér (1873), 19, No. 8, pp. 1-35.

29. A Kovalevsky, "Entwicklungsgeschichte der einfachen Ascidien," ibid. (1866), 10, No. 15, 16 pp.

larvae with the early stages of vertebrates . . . apparently removes the difference between the main groups of the animal kingdom and makes obvious what has been accepted by many authors subsequent to Darwin, that the transition is made from lower forms into absolutely higher forms" (p. 3). How great the attention attracted by Kovalevsky's paper was, Baer judged by London's QUARTERLY JOURNAL OF MICROSCOPICAL SCIENCE, which as a rule printed only original papers, but made an exception for Kovalevsky's paper and published a translation of it practically in full.

Baer then referred to the investigation of I. I. Mechnikov,³⁰ "also an experienced embryologist," and in particular to the data of K. Kupffer which he stated in a letter to M. Schultze and which were confirmed by the latter, and attached to Kupffer's detailed article. "Already the name itself," Baer wrote, "'the genetic relationship between Ascidiae and vertebrates,'³¹ indicates the importance of the results received. The factual data and Kovalevsky's interpretations concerning the coincidence of the development of ascidia and vertebrates, were confirmed and partially made more accurate" (pp. 4-5). Further on Baer noted this relation to Kovalevsky's discovery, which Darwin had mentioned in THE DESCENT OF MAN, and cited the following passage from this work:

Kovalevsky has lately observed that the larvae of Ascidians are related to the Vertebrata, in their manner of development, in the relative position of the nervous system, and in possessing a structure closely like the CHORDA DORSALIS of vertebrate animals . . . Thus, if we may rely on embryology, ever the safest guide classification, it seems that

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30. I. Mechnikov, "Observations on the development of some animals (Bothryllus and solitary ascidia)," IZV. PETERSB. AKAD. NAUK (1869), 13, pp. 284-300.
31. K. v. Kupffer, "Die Stammverwandschaft zwischen Ascidien und Wirbelthieren," ARCH. MIKR. ANAT. (1870), 6.

we have at last gained a clue to the source whence the Vertebrata were derived. We should then be justified in believing that at an extremely remote period a group of animals existed, resembling in many respects the larvae of our present Ascidians, which diverged into two great branches--the one retrograding in development and producing the present class of Ascidians, the other rising to the crown and summit of the animal kingdom by giving birth to the Vertebrata.³²

Baer cited after this only one negative treatment of Kovalevsky's discovery,³³ and with characteristic honesty he drew attention to its groundlessness. Baer's objectivity stands out here more clearly, since he himself did not agree with the opinions of Kovalevsky, Kupffer, and Darwin. In the next twenty pages of his article, he brought all his learning and all his authority to bear on the idea of the relationship between tunicates and vertebrates and attempted to prove their systematic nearness to the bivalves, agreeing in this with Cuvier and basing his ideas upon the situation of siphons, nervous ganglia, and so on. Baer confirmed in particular that the side of the body where the nervous ganglion of ascidians is present is not the dorsal, but the ventral; therefore the nervous system of ascidians could not be homologous to the central nervous system of vertebrates. Later he discussed the cord in the caudal part in the larvae of ascidians and also refused to recognize its homology with the spinal cord of vertebrates. All polemics were sustained in very correct tones. Of his scientific opponents Baer everywhere spoke in a tone of complete respect to their scientific services and high competence.

Afterwards Baer explained why he went into anatomical details in this article, where it might better have been limited to brief reminiscence. "I meant," Baer wrote, "to

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32. Charles Drawin, THE DESCENT OF MAN, AND SELECTION IN RELATION TO SEX. rev. ed. (New York, 1883), pp. 159-160. Russian translation edited by I. M. Sechenov, SOCH., Vol. 5 (Izd. AN SSSR, 1953), pp. 268-269.
33. ARCH. ANAT. PHYSIOL. (1870), p. 762.

show many dilettantes unconditionally believing in the possibility of transmutation and inclined to believe that the nonrecognition of ascidians as ancestors of man is attributable to sheer vanity" (p. 35).

The source of all his interpretations which were basically erroneous was Baer's view of the theory of evolution, in particular in relation to Darwinism. The discussion of Baer's views on evolution is beyond the scope of the present book. They did not appear in the literature; however, they have not been investigated sufficiently. But here it can be mentioned that Baer considered the evolutionary development of the organic world to be without doubt, but with known limits, having their sources in the theory of types established by him and Cuvier.

Stating the presence of transitional forms between the systematic groups within each of the four types, which testifies to the community of origin of all representatives of the type, Baer doubted that the signs of one type could be seen in the development of another type (119).

Proceeding from this belief, Baer could not imagine that the tunicates, not having in the adult condition the general typical signs of the vertebrates, could show at any stage of development the characteristics of this type. From here there was a persistent striving from his side to give Kovalevsky's discovery this explanation, which did not stand in conflict with the theory of types.

Being considered the founder of embryological science, Baer did not leave behind him what could be called a school. In Königsberg there were some young people who performed under his guidance dissertations on teratology, touching to some extent upon the history of development (120). One Königsberg student of Baer's, A. E. Grube (1812-1886), was later recommended by him to the Department of Zoology in Dorpat University. Grube published many works on zoology and comparative zoology; in addition he mainly studied annelids.

The influence of Baer's scientific interest is recognized first in the work Grube performed in Dorpat and published in 1844 (see Chapter 25), and also in the investigations of Majewski and Tschernow, whose dissertations were also defended at Dorpat University, in 1858. Both these dissertations illustrated the embryo-physiological problem of the chemical composition of the foetal fluids in mammals. Majewski³⁴ (121) investigated the composition of the amniotic and allantoic fluids in twenty-eight embryos of sheep (four to thirteen weeks old) and in sixteen embryos of cattle (twelve to twenty-six weeks old), adding to this data concerning some embryos of swine and man. In this work he determined the weight, the length of the embryos studied, the quantity of amniotic and allantoic fluids, their specific gravity and reaction, and also the amount of solid constituents, either organic or inorganic, namely albumin, sugar, urea, phosphoric and sulphuric acids. In the tables of this dissertation, numbers are given for separate observations and average numbers for different periods of development. Majewski established that, according to the extent of formation of the embryo, the amount of the solid constituents in amniotic fluid increases. In particular, in all stages of intra-uterine life in all investigated animals and in man, the albumin and sugar are present in the amniotic fluid; the quantity of albumin shortly before birth somewhat decreases, and the quantity of sugar in the process of development of the embryo gradually increases, reaching the maximum before birth. The quantity of fluid in the allantois, and also the content of solid matter in it, increases with the development of the embryo. The allantoic fluid always remains transparent and similar to the saturated urine, while the quantity of urea in it gradually increases; in it there are also albumin and sugar. On the basis of his investigations, Majewski reached the conclusion that the amniotic fluid does not serve to feed the embryo, but protects it from external harmful influences and that the feeding of the foetus takes place only through the placenta.

34. Adolphus Majewski, polonus, DE SUBSTANTIARUM, QUAE LIQUORIBUS AMNII ET ALLANTOIDIS INSUNT, DIVERSIS VITAE EMBRYONALIS PERIODIS (Dorpat, 1858), 44 pp.

The thesis of Tschernow³⁵ (122) is a natural continuation of the investigations of Majewski, which dealt with herbivorous animals, while Tschernow performed the study of the chemical composition of foetal fluids on carnivorous animals, mainly cats (he investigated forty-four foeti, weighing from 0.074 to 107.3 gm). In addition, in his collection there were embryos of four dogs, nine swine, and one human, and also one horse embryo, which was used for comparison with carnivorous animals. Tschernow established that in the amniotic fluid the relation of the quantity of water to the solid constituents remains constant. In the allantois, the quantity of fluid in the process of foetal development gradually decreases, and simultaneously the relative quantity of water diminishes (from 989.5 to 949.8%). The amount of solid material in the fluid of the allantois increased at the expense of the organic matter (albumin—from 1.05 to 5.59%; sugar—from 0.95 to 2.02%; urea—from 1.48 to 12.10%). The albumin of allantoic fluid, according to Tschernow, is not necessarily secreted by the capillary renal vessels, although this possibility is not excluded, as the vessels of the foetus probably possess different permeability properties than the born animals, in whose urine there are no traces of albumin. Tschernow thought that albumin passes in the fluid of the allantois from the amniotic fluid, where it is always present. The sugar in the allantoic fluid of carnivores is significantly lower than in herbivores (in sheep, according to Majewski, it averages 7.57%, and in horses, according to Tschernow's observations, it averages 11%). On the other hand, the urea in the allantoic fluid in carnivores is greater than in herbivorous animals.

The tradition of embryological investigations in Dorpat University, which is connected with the influence of Baer, remained. Thus, M. Braun, who was present from 1880 to 1886, in the beginning as a prosector of comparative anatomy and then as professor of zoology, worked on the embryology of bivalves, tapeworms, reptiles, birds, and mammals (among these works, investigations on the development of the wavy parrot

35. Nikolaus Tschernow (Estonus), DE LIQUORUM EMBRYONALIUM IN ANIMALIBUS CARNIVORIS CONSTITUTIONE CHEMICA (Dorpat, 1858), 35 pp.

were distinguished). Yu. Kennel replaced him in the department in 1887. He studied the embryology of Prototracheata and published three works on this topic.

The true successors of Baer as embryologists were, of course, A. O. Kovalevsky and I. I. Mechnikov. Not formally students of Baer, they nonetheless paid high tribute to his classical investigations. To Kovalevsky and Mechnikov belong that unquestionable service of further development of Baer's studies and the creation of the theory of embryonic membranes, making the basis for comparative and evolutionary embryology.

Therefore, it was not by chance that in connection with Baer 1864 jubilee, the Academy of Science established a prize in his name for the best works on biological sciences. The first award of Baer's prize was received by Kovalevsky and Mechnikov. Baer himself participated in the discussion of candidates for the prize and expressed a patriotic pride on the occasion of its being awarded to Russian investigators.

In the conclusion of this chapter, some words must be stated about Baer as historian of embryology. Although he was not studying systematically the history of embryology, Baer stated many profound ideas about the development of this science. His discussions on this question are scattered through many works. Besides this, Baer subjected the literature of his prominent predecessor in the field of embryology, K. F. Wolff, to special study, and published a report on this work.³⁶ Baer's research concerning Tretern has been mentioned in Chapter 11.

References to the history of embryology in the works of Baer are always intimately connected with his own works;

36. Baer, "Über den litterarischen Nachlass von C. F. Wolff, ehemaligem Mitglied der Akademie der Wissenschaften zu St. Petersburg," BULL. CL. PHYS.-MATH. AC. ST. PETERSB. (1846), 5, No. 9, 10, pp. 129-160.

however, they frequently include an unusually large number of quotations from the works of his predecessors, and represent fragments of investigations in the field of history of science, showing a deep, thorough acquaintance with the literature (always from original sources), and briefly describe the scientific epoch or direction of scientific thought.

CHAPTER 24

ON THE QUESTION OF BAER'S THEORETICAL VIEWS

For the exhaustive characteristics of Baer's views, it is necessary to consider all his papers and correspondence with regard to published and archival materials. This task is a matter for the future. Until now, discussions of Baer's theoretical views as a rule have been limited to evaluation of his scientific work. Therefore, all opinions up to the present about Baer's philosophical views have made a common mistake, for which the authors cannot always be blamed. Their errors could result in part from the fact that Baer was sometimes undoubtedly forced to present his thoughts in a form adapted to the censors' requirements of his time. As for articles published in the Russian language, the possibility must also be considered that the translation from the German original, as it was written by Baer, was misrepresented.

But regardless of these circumstances, the well-founded discussion about Baer's methodical views is difficult to dispute. The spiritual personality of the great naturalist was too complicated and multifaceted to determine the essence of his views easily and at the same time to state the changes which were made during his long years of scientific activity.

Baer did not avoid stating his opinions concerning general questions, beginning with the earliest work, such as the article "Two Words on the Recent Condition of Natural History,"¹ and ending with the general philosophical conclusions of SPEECHES AND ARTICLES (1864-1876). In striving for a description of Baer's theoretical views, one must turn to his own discussions on the general questions of philosophy

1. K. E. v. Baer, "Zwei Wörte über den jetzigen Zustand der Naturgeschichte," Vortäge bei Gelegenheit der Errichtung eines zoologischen Museums in Königsberg (1821), 48 pp.

and natural sciences. But they should not be considered satisfactory, and hence they may represent falsification (123). The latter is correct, in particular, in relation to R. Stölzle, professor of philosophy at Würzburg, who wrote a vast work in 1897 under the title *KARL-ERNST VON BAER AND HIS WORLD-VIEW*.² From the beginning Stölzle stated that in his book he would judge Baer from a theistic-Christian standpoint; he lamented that this point of view, especially in the natural-scientific and philosophical circles of his day, was generally ridiculed as being absolutely unscientific, and either regarded as an anachronism or simply disregarded.³ Stölzle praised Baer for his world-view and unconditionally set him up against evolution, teleology and idealism. However, at the same time he remarks, apparently indignantly, upon the "errors" of the great scientist concerning Baer's sharp opinions against creationism. Stölzle wrote, for example, of the "barely respectable polemics of Baer against the idea of a creator" and cited his ironical discussion of the origin of new classes of animals on the earth: "I do not want to trouble Our Lord with this 'creation of new classes,' for if he wishes to throw down from the sky a new class of animals on earth, then they must, due to the quick motion of the earth—four miles per second! and this is not a joke—shatter into dust. Our Lord, therefore, must come down to the earth and arrest its velocity; only then can he create new living creatures."⁴

Actually, in the concluding chapter of his book, Stölzle "absolved" Baer for all his "inconsistencies" and for all his "errors," assuming that Baer "at the end turned to faith in the ever-living God; probably this may confirm

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2. R. Stölzle, *KARL ERNST VON BAER UND SEINE WELTANSCHAUUNG* (Regensburg, 1897), xi + 687 pp.
 3. *Ibid.*, p. 5. Haake, in his work on Baer (W. Haake, *KARL ERNST VON BAER* (Klassiker der Naturwissenschaften) (Leipzig, 1905), 175 pp.), also extolled Baer for his supposedly high evaluation of the religious need of man.
 4. Stölzle, *KARL ERNST VON BAER*, p. 167.

also (his) faith in Christ."⁵ Stölzle took this confidence from journal articles, based on information from a Pastor Engelhardt. The later asserted that on his deathbed Baer regretted his unbelief. The foolishness of this idea was documented not long ago by B. E. Raikov.⁶

Also, contentious and groundless discussions of Baer's philosophical ideas were given by Stölzle. Their source was explained by him as Schelling's natural philosophy, which at the beginning of the nineteenth century had received very wide distribution among naturalists. About the wreck of natural philosophy, Stölzle correctly wrote. Instead of the fantastic opinions which fear experiments, come sober ideas which are based on experiments instead of intuition, on the firm and slow work of induction in place of metaphysics—either the rejection of all that is transcendent, as in the ideas of Francis Bacon, as also in the ideas of Kant and Comte, or materialism.⁷ Talking of Baer's earlier interest in Naturphilosophie and even mentioning his ironic references to the lecture of Wagner, Stölzle nevertheless remarked that

5. *Ibid.*, p. 644.

6. B. E. Raikov, "Poslednie dni Baera" (Baer's last days), TRUDY INSTITUTA ISTORII ESTESTVOZNANIYA AN SSSR, 2 (1948), pp. 575-583.

If it could not be doubted that church orthodoxy was alien to Baer throughout his life, then it would be difficult to state with confidence his relation to deistic thought. In his writings, especially in his popular scientific discussions, one finds theories of creation as first origin of all beings. See, for example, the series of articles under the common title "Man's Place in Nature," published in NATURALIST, Vol. II (1865), Nos. 2, 3, 4, 19, 20, 21, 22, 23, and 24; Vol. III (1866), Nos. 9, 18, 22, 23, and 24; Vol. IV (1867), Nos. 1, 2, and 3. These articles, according to B. E. Raikov, were strongly misrepresented by the censor.

In these articles, and also in his German-language article "On the Doctrine of Darwin" ("Über Darwin's Lehre," REDEN. . . UND KLEINERE AUFSÄTZE, II, pp. 235-480). Baer argued against Darwin and his followers (mainly against T. Huxley) on the question of the origin of man, decisively

(Footnotes continued on next page)

Baer "did not throw out the baby with the bathwater, and while discussing the false path into which Naturphilosophie had been enticed, he recognized it as a source for a deeper understanding of nature."⁸

For the proof of this statement, Stölzle referred to the following view by Baer which he stated in his earliest theoretical writing, "Zwei Wörter über den jetzigen Zustand der Naturgeschichte": "In spite of the giddiness experienced by the nature-philosophers, the world nevertheless must move with inevitability in itself, because this takes place in reality. With this, frequently and not very seriously, they made merry, exclaiming: 'We shall only hold on to the earth more strongly, then our heads will not whirl.' It seems to us, on the contrary, that all the significant progress in science is inevitably accompanied by fever, and during fever there are frequently dreams and apparitions. The experienced doctor is sometimes satisfied with the course of fever in his patient if he notices in it the preparation for a crisis."⁹

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- 6... rejecting the possibility of his development from any of the other living species of monkeys. In addition to strictly scientific reasons from the field of comparative anatomy and comparative psychology, there are also appeals to common sense, hindering, in Baer's opinion, recognition of an animal origin for man. In discussions concerning the evolution of the organic world and especially the origin of man, Baer undoubtedly did not overcome the religious faction, and was even inclined to renounce his partial recognition of the idea of evolution, which he had stated many years before this.
 7. Stölzle, KARL ERNST VON BAER, p. 36.
 8. Ibid., p. 39.
 9. Baer, "Zwei Wörter," p. 40.

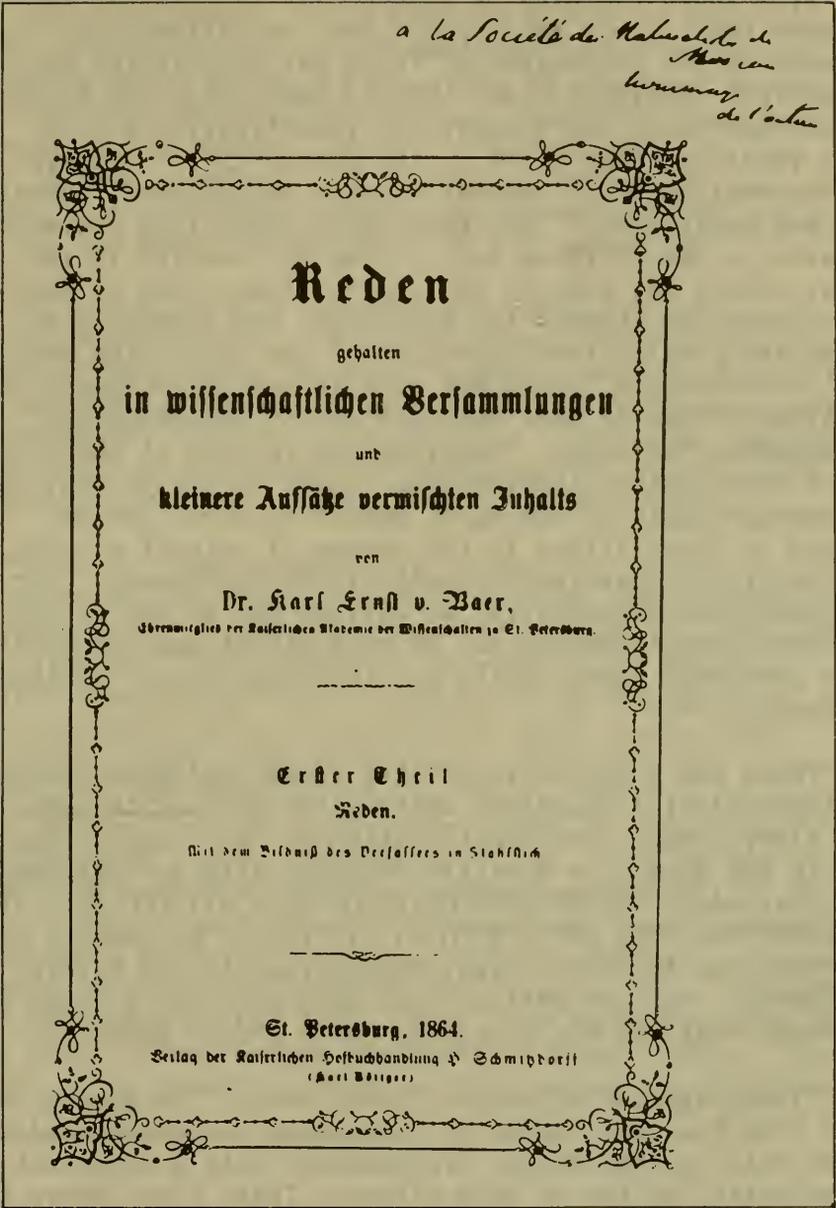


Figure 35. The title page of the collection REDEN...UND KLEINERE AUFSÄTZE by K. M. Baer, with his autograph; presented by Baer to the Moscow Society of Nature Investigators.

From these examples of speeches it is possible to conclude that in his early years Baer was already an opponent of the collection of facts not illustrated by theoretical generalization. Of the importance for science of both empirical and theoretical investigation and of their relation, Baer wrote in the same article: "There are two ways in which natural science can succeed: observation and meditation. The investigator goes into the majority of cases in one of these ways. Some of them are thirsty for facts, others for results and general laws; some of them for information, others for knowledge; the first can be called the careful investigators and the latter the serious ones. Fortunately, the human mind is rarely developed so one-sidedly that he uses only one way of investigation, disregarding the other. Despised abstraction at the time of his observations involuntarily leads to meditation, and his opponent only in the short period of fever can be engaged in speculations in the sphere of natural science, absolutely disregarding the data of the experiment. For the individual personality, as well as for an entire age of science, one tendency may be predominant and the objectives follow it consciously, but the other is not excluded completely."¹⁰

These two sides of scientific investigation—experiment and theoretical discussion, observation and meditation—were always taken into consideration by Baer, and he put them in the form of a subtitle sounding like an epigraph to his great work: ÜBER ENTWICKLUNGSGESCHICHTE DER THIERE: BEOBACHTUNG UND REFLECTION. It is not by chance, however, that here, as in other cases, observation is put before meditation. One can reflect only upon what has already been observed; Baer did not recognize any *a priori* truths.¹¹

"Investigation of nature," Baer wrote, "in general must start from the observation of individual phenomena, and the latter only in that extent are combined into a universal authenticity, as far as this allows. There also, where it

10. Ibid., p. 31.

11. In this idea he made an exception only for mathematics.

ends, ignorance begins."¹² Elsewhere he stated that the history of science is a long commentary on the situation that the material for one's knowledge of the outer world is collected by detailed observation, and that these are processed by the natural ability of meditation. No discovery is done *a priori*. "I doubt that man would have, in general, any information about the existence of the world, if he did not make certain of it by his senses."¹¹

The statement that the endlessly variable world exists independently of our consciousness, and is perceived by means of the organs of sense, was connected in Baer with confidence in the unlimited cognitive power of human intelligence and his creation, the sciences. As to the question of the importance of science, Baer repeatedly clothed his discussion either in a pathetic or a sarcastic form.

"Science," Baer stated, "is eternal in its source, not limited in its activity either by time, or by distance, immeasurable in its size, endless in its tasks, unachievable in its aims."¹⁴ This aphorism, especially its Russian translation published in the journal of the Ministry of Public Education and not re-edited by Baer, needs some explanation. Baer spoke of science "eternal in its source" (EWIG IN IHREM QUELLE),¹⁵ i.e. having its source in eternal nature, but the translator turned it into science "resulting from eternal beginnings," i.e. as if having its source in revelation. Speaking of the unachievability of aims in science, Baer undoubtedly meant the impossibility of exhausting by scientific knowledge the endless variable phenomena of the world, and not the presence in it of anything beyond the grasp of the mind. That this interpretation of Baer's ideas is correct is confirmed to other places. For example, in the speech, "View on the Development of Science,"

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12. Baer, "Über Zielstrebigkeit in den organischen Körpern insbesondere," REDEN, II, 2te Aufl. (1886), pp. 170-234.
 13. Akad. ber Vzgl'yed na razvitie nauk. Zhurn. Min. Nar. Prosv., May 1836, p. 207.
 14. *Ibid.*, p. 245.
 15. Baer, "Blicke auf die Entwicklung der Wissenschaft," REDEN, I, 2nd ed., p. 121.

Baer wrote: ". . . The limited minds cherished the hope, or rather expressed the apprehension, that the limits of human knowledge will soon be achieved. The idea is cowardly, unworthy of the endless productivity of the human intelligence."¹⁶

The attention of many authors, attempting to interpret Baer's viewpoints either from orthodox theological and idealistic positions, or from materialistic positions, was mainly attracted by his discussion concerning purpose in nature in general and in particular in the organic world. Baer illustrated these questions in two vast articles published in the second volumes of his REDEN UND KLEINERE AUFSÄTZE. In order to form a presentation of Baer's real views on the problem of purpose, especially in individual development, it is necessary to turn to the articles mentioned and look at the details of their terminology. Only then will it be possible to attempt to determine what arises from Baer's spontaneous materialism and what amid the health of his ideas must be considered idealistic slag.

The first of these articles is called "On Purpose in the Phenomena of Nature."¹⁷ It begins with the assertion that naturalists are extremely worried about the recognition of purpose in the processes and products of nature. In order to make this account completely clear, Baer considered it necessary to come first to an understanding about the application of the concept. He began with the word "nature," which means all that really exists and arises without the participation of human skill. The last is especially important to bear in mind, because all that exists was placed, was made through formation as it is presently. The solid rock as well as the changing cloud are both the results of a development process. But the correctness of this idea is especially confirmed by organic bodies, which are present in a condition change. The present condition of an organism became possible

16. Baer, "View of the Development of Science," p. 194.

17. Baer, "Über den Zweck in den Vorgängen der Natur. Erste Abtheilung: Über Zweckmässigkeit oder Zielstrebigkeit überhaupt," REDEN, II, p. 49-105.

only in connection with the previous and the future conditions, in connection with the present. The essence of life itself is considered the course of the vital process, i.e. a series of conditions following one after the other. Of the source of this change, Baer spoke with a certainty excluding all doubt.

We cannot leave without discussing the idle argument about the vital power, that matter goes only by necessity, causing all the momentary conditions of organization that follow one after the other In order to make this more obvious, we say that in organic life, each separate condition is only a momentary expression of formation, or that the settled condition is only a making visible, and that formation is essence and permanence.¹⁸

The latter condition is the consequence of the previous, not only by time, but also in relation to their internal conditions. To illustrate, Baer mentioned the example of the butterfly, whose imaginal condition is anticipated and conditioned by the pupa stage, the condition of the pupa by the caterpillar stage, the condition of the caterpillar by the stage of the ovum appearing in the mother. The source of material for all these transformations is, according to Baer, the plant food used by the caterpillar. The materials taken up as food are processed in the caterpillar into reserve products which are used in the following conditions. The vital process of the developed insect "needs food—we call this demand hunger—thus, it demands enough food to suffice it not only for the intensive growth of the caterpillar, but also for the creation of reserves for future stages."¹⁹

Baer especially underlined the connection of these conditions, processes and preparatory changes with the final condition; in their resulting "from a spherical or ellipsoidal

18. Ibid., pp. 52-53. The same idea was stated by Baer in the speech "Welche Auffassung der lebenden Natur ist richtige " delivered at the opening of the Russian Entomological Society in 1860 (REDEN, I, 1864, p. 268).

19. Ibid., pp. 53-54.

ovum through many intermediate stages the final goal (ZEIL) is reached—the fluttering butterfly."²⁰ "The more we enter into details, the more completely this special relation (ZWECKBEZIEHUNG) appears. It must be noted that for the work which must be performed in each separate condition, all necessary instruments are not only present at the necessary time, but are formed in the previous condition."²¹

"The maxillae and extremities of the caterpillar, which are adapted to its form of life, are developed in the ovum, so that from the moment of hatching everything necessary for the function of intensive feeding is already prepared. The organs of the butterfly—wings, long legs and spiral proboscis—are developed in the pupa stage, i.e. long before these organs will be used. Within the hard shell of the pupa, internal transformations take place which are completely connected with the future and not with the present."²²

Baer also discussed this question in detail in the second article, considering the continuation of the work "On Purpose in the Phenomena of Nature" and entitled "On the Trend of Processes, Especially in Organic Bodies."²³

Speaking of embryonic development, he noted that already in the earliest stages the material of the ovum is processed for the formation of organs, so that development proceeds "as if there sits in the ovum a judicious and understanding builder."²⁴ This metaphor was necessary to underline that from his point of view the vital process in particular and the development of the individual is characterized by a trend towards a definite end, although the ovum and the developed embryos, of course, do not recognize this end. Here Baer also had mentioned that the trend of development is not absolute, but adapted to surrounding conditions; thus, the eggs of birds require the effect of heat and the free flow of air. The necessity for determined conditions for development is shown also by other animals; their life, i.e.

20. Ibid., p. 54.

21. Ibid., p. 55.

22. Ibid., p. 57.

23. Baer, "Über Zielstrebigkeit."

24. Ibid., p. 228.

continuous internal preformation, can take place only during suitable external conditions. "Life," Baer wrote, "is nothing other than a movement towards a definite final self-transformation, adapted to external conditions." To illustrate, Baer described the early stages of development of the eggs of the hen, of the frog, and of the sea urchin, and also described the behavior connected with reproduction.

From the actual data cited, he concluded the following. The physico-chemical processes in the early stages of development, when their direction appears, have been studied very insufficiently. In the vertebrate embryo, two shafts ascend on the dorsal side which are then united in a tube; the results and the significance of this process is clear: the central nervous system is formed from the internal layer of the tube, and from the external layer the bones, muscles, and skin are formed. "Thus, in relation to this process, the question why is very easy to answer, and the question, by what means does it happen, remains completely open for the naturalist. Naturally, one doubts that this process is conditioned by physical necessity, since the end of any process is reached only on the basis of the laws of nature; without reference to the latter, any phenomenon must be considered magic."²⁵

"I can then repeat the question," Baer continued, "how is it possible to overemphasize that all these processes are related to future requirements? They are directed to what must originate. Philosophers who wrote in Latin called this relation *causa finalis*, or final cause (ZIEL). . . . And in all other animals the changes following one after another must serve a purpose (ZWECKSINNLICH SEIN)."²⁶ For the exact understanding of Baer's idea it is necessary to review his terminology. In the German language there are two words—ZWECK and ZIEL—which are both translated into the Russian language as "purpose"; as a matter of fact, in the normal German usage as well, these words can replace each other. However, Baer found in them this shade of meaning; he considered it possible to use them for the designation of different concepts, proceeding from the following considerations.

25. Ibid., p. 192.

26. Baer, "Über den Zweck," p. 58.

A large part of psychological terminology is based on the use of spatial, generally sensory perceptions. "We speak about deep or superficial ideas, about difficult and easy problems, about obscure and clear ideas, about strong, weak, hard-hearted and gentle characters, and so on.²⁷ If in the language a word appears to designate a psychological condition, then, of course, it concerns man. This, in particular, relates to the word ZWECK.²⁸ For the achievement of purpose by man it is necessary and advisable for him to select his means. There are people who devise excellent aims for themselves, but do not achieve them, because they use inadvisable means. On the contrary, in relation to many phenomena of nature, even if they end with a definite result, it is impossible to claim that they result from an aim determined by an intelligent being. According to Baer, the result of separate processes can be designated by the word ZIEL, which does not assume the involvement of judicious consciousness. ZIEL is the end of motion; its achievement is completely based upon necessity. "Sending the arrow or bullet into the target (ZIEL), I use mechanical powers in the necessary proportions and I orient them in a definite direction. The purpose which I am pursuing in this case I can hold in front of me and, if all is correctly calculated, an arrow must of necessity fly

27. Ibid., p. 74.

28. The Russian translation of the words ZWECK, ZIEL, and their derivatives are connected by known convention. Hereafter, ZWECK, ZWECKMASSIG, and ZWECKMASSIGKEIT will be designated by the words "purpose," "expedient," and "expediency." For the designation of the concept ZIEL, after many attempts to select a more successful word, we settled on "final end," using in many cases the words "trend," "end," "target" (followed throughout by ZIEL in brackets); ZIELSTREBIG is translated as "definitely directed," "going or acting in a definite direction"; ZIELSTREBIGKEIT is translated as "direction," "definite direction."

into the target (ZIEL), regardless of the purpose (ZWECK)."²⁹ Therefore, for natural phenomena, Baer proposed to use the expressions ZIEL, ZIELSTREBIG, ZIELSTREBIGKEIT instead of ZWECK, ZWECKMASSIG, ZWECKMASSIGKEIT, as the first expressions are free of that shade of meaning which expresses the adoption of a conscious decision.

These considerations Baer illustrated by the following example: "In saying that the new-laid egg has the purpose to be a hen, I can be asked how. Is there in it a creature possessing creative powers and will? If it is also stated that this egg is predetermined to form a chicken, then with this all will agree, because it is known that the egg is formed in a natural way and possesses an ability of necessity to form a chicken, of course given the suitable temperature."³⁰ The presence of a definite direction of development, predetermined by the structure of the egg, Baer called the final end (ZIEL), and did not mean here conscious purpose, when actually there is no sense in searching for it, neither in the yolk nor in the albumin. The purpose (ZWECK), in his opinion, must be sought in much earlier stages, in the ability of organic bodies to give rise to new individuals of the same species. Baer designated final goal (ZIEL) not only as the result of activity, the end towards which something moves (in the present case, transformation at the time of development), but he meant the forced necessity which acts in a definite direction.

In the article "Über Zieletrebigkeit in den organischen Körpern," Baer returned to definite concepts. He wrote: "ZWECK is a consciously determined task, ZIEL is the given direction of the action; ZWECK is the source of freedom, ZIEL is an outlined success which may be achieved by means of necessity. If we apply this understanding to nature, then naturally we cannot attribute to it any purpose (ZWECK); however, it is unconditionally impossible to disclaim trend or direction. Each organism in the process of formation is characterized by a direction and a final goal (ZIEL) of this process."³¹

29. Baer, "Über den Zweck," p. 186.

30. Ibid., p. 83.

31. Baer, "Über Zielstrebigkeit," p. 180.

Later, Baer asked why the mention of processes which serve purposes is met by naturalists with such distrust, and whether there is any real basis for this distrust. In order to answer this question, Baer turned to the history of natural science. Man first sought to solve the most common problems, and only later did he learn to open up questions and pose them so that he could give concrete answers. Thus, at the beginning, the ancient Greeks proposed many hypotheses about the origin and existence of the world. Only gradually did they begin to observe reality and to meditate upon the processes of nature. They established that in nature there are known powers or regularities acting. The Romans added very little to that which had been known by the Greeks, and gradually showed little inclination to present new methods in the field of science. Meanwhile, as other peoples of Europe emerged from the state of barbarism, a characteristic religion spread which for a long time devoured all spiritual inquiries. When this religion became dominant in Byzantium and Rome, a powerful priesthood worried about whether men in their scientific aspirations followed the course outlined for them by the church. As a result of this, for a long time in the natural sciences there was no noticeable progress. The discovery of America and of previously unknown living beings, the discovery of a sea route to India, the ideological interpretations of the epoch of the Reformation, and, mainly, Copernicus' proof of the earth's rotation around its axis and around the sun, regardless of the evidence of vision—all this aided the powerful increase of scientific interest and provoked the independence of ideas and their critical relation to authority.

However, the scientific struggle kept its medieval character for a long time. Many absolutely groundless statements were put forward; thus, in the structure of the organism it was desirable first of all to see the intention of the Creator. In accordance with the studies of the Christian religion, seeing a spiritual beginning in all activities, they searched for the acting power everywhere. Even in the middle of the seventeenth century, Fabricius ab Aquapendente, in a work illustrating the development of the hen's egg, declared the existence of six forces upon which the formation of the chick depends. However, in his actual observation he committed very flagrant errors. From the beginning of the sixteenth century, the study of anatomy

became animated. For a very long time students had only repeated what was known to the ancient Greeks. In the study of the structure of organisms, they everywhere collided with the manifestation of purpose, whose existence, as all else, was attributed to the omnipotent Creator. Thus, one teacher stated that he illustrated the effect of the wisdom of God, in that God, in his opinion, directed the flow of the rivers to where the big cities are. In other cases a purely mechanical necessity was attached to this idea. Spiegel,³² a seventeenth-century anatomist, speaking of the sciatic muscles in man, which develop more in connection with the direct process of walking than in other animals, stated his belief that man possesses such powerful sciatic muscles so that he may sit on soft bedding when he meditates on the greatness of God. "Another anatomist," according to Baer, "posed the question, why does man not have two backs, and answered, because that would be ridiculous."³³ The new method was established by Newton and his contemporaries, showing the application of the fall of bodies and the movement of the planets to simple laws of nature and their effect. Only then did "the powers contrived from a scarcity of knowledge, about which it was impossible to state any definite thing . . . disappear as ghosts in the light."³⁴

"At the end of the eighteenth century," Baer wrote in his article "Über Zielstrebigkeit," "man did not doubt that all physico-chemical processes are under obligation to natural necessity."³⁵

Otherwise at that time they were related to vital manifestations, the supposition being that they obeyed special regularities absolutely. In relation to living beings it was considered necessary to take into consideration "a special power which shows its activity on these bodies and all conditions which could not be explained with the help of the already known physical and chemical powers; this power

32. Adriaan van den Spiegel, Dutch anatomist and embryologist (1578-1625). He wrote DE FORMATU FOETU (Amsterdam, 1645).

33. Baer, "Über den Zweck," p. 62.

34. Ibid., p. 64.

35. Baer, "Über Zielstrebigkeit," p. 186.

was called the vital power. All different activities must be attributed to it; it must not only expediently build the body, but also must prevent the disturbance of its building by disease or injury; it must select from the substances of the surrounding world those which are necessary for building up the body and supporting life. Thus, nothing such as the activity of the mind was attributed to it, because it must act in accordance with purpose. Later this idea contrasted with another idea widely distributed in the nineteenth century. This latter stated that the vital power is only a result of fantasy, invented to cover ignorance. The vital process is a physico-chemical process so complicated that, after a long time, we still cannot break it down into its separate components; as a whole it exists by physico-chemical laws, i.e. it arises by strict necessity. The most diligent supporters of this idea added that about the purpose and trend of vital phenomena there must not be any speech."³⁶ Concerning the idea of the vital power, Baer absolutely agreed with the assertion that it must be regarded as an attempt to obscure an inability to solve a problem.

A power to which it is impossible to add measures, a power which strives for the final end which is a result of fantasy of a production of ideas The organism, undoubtedly, is considered a mechanical apparatus, a machine that builds itself. The vital process takes place by means of continuous physico-chemical processes; as a result of this the organism can be called a chemical laboratory, although at the same time it can also be considered a laboratory technician Regardless of the achievements in knowledge of individual processes in the organism, nothing remains directed and predominated on physico-chemical processes in them, namely life itself.

It is absolutely natural that now everything is investigated from the point of view of

36. Ibid., p. 187.

unconditional necessity, and I consider this direction absolutely correct The physics and chemistry of our time reap their fruits. With the help of these sciences they sought to interpret the vital phenomena of plants and animals also as a physico-chemical process which arises for each organic form by special means; by these ways many things already can be explained, and it can be hoped that present problems with time will be solved.³⁷

However, Baer considered that success in the knowledge of nature's processes, appearing as a necessary activity, must not lead to denying direction and purpose (ZIELE UND ZWECKE) in nature. Baer did not agree with the opinion of those who considered that teleological opinion in the study of nature is absolutely unsuitable and that in nature there is neither direction nor purpose (WEDER ZIELE NOCH ZWECKE). "Teleology," Baer stated, "is the study of direction (ZIEL),³⁸ and thus purpose (ZWECK) and the final end (ZIEL) are also present; then teleology is a study of the objective relations in natural phenomena. I can never be sure of the absence of all direction, or consider the question as ridiculous or shameful."³⁹

Baer discussed Haeckel's opinion from his GENERAL MORPHOLOGY that chance and purpose are absent in nature and only absolute necessity predominates (compulsion). Baer considered it erroneous to contrast necessity and purpose, because in his opinion purpose is reached by means of necessity.

The marble statue, it is known, is built by mechanical means. Absolute necessity consists in that the marble block is beaten by hammer and

37. Baer, "Über den Zweck," pp. 64-65.

38. In a footnote Baer explained that "the Greek word *τελος* (end, outcome, result—L.B.) is in German designated ZIEL.

39. Baer, "Über den Zweck," p. 65. From this extract it will be seen that Baer has confused his differentiations between ZIEL and ZWECK.

chisel as much as by necessity for its transformation into a human figure. However, when the production of art is present before us, we must recognize that all the necessities used served only for realizing the idea of the artist, and his purpose (ZWECK).⁴⁰

Baer thought that the process of formation must not be credited to the effect of powers, but that the powers must be measured in accordance with the final end (ZIEL), or they will not build anything and can only destroy.

In another instance, Baer noted that naturalists who dread purpose or direction have a confusion of ideas. The naturalist must put the question to nature: "how?" or "what?" Then, "due to what?" And finally "why, or what for?" For the answer to the questions how and what, he investigates the acting conditions and finds the necessities which he calls laws of nature. If the effect of necessity is not definitely directed (ZIELSTREBEND), then the vital process cannot be realized. The question why or for what is related to the study of this trend (ZIELSTREBIGKEIT). This question, in Baer's opinion, is absolutely lawful for the complete understanding of the phenomenon. It produces misgivings because in past centuries, when men believed in the omnipotent nature of God, above natural law, they answered the question why with reference to the direction of the process, and imagined it not as being realized by means of necessity, but as a human purpose, reached by conscious will. The investigation of animal embryology is considered that branch of nature study where the direction of processes stands out especially clearly, because the organic body is regarded in its formation. The processes of formation are definitely directed (ZIELSTREBIG), they arise from their result; they, of course, are conditioned by necessity. In Baer's opinion, however, it would have been scientific superstition to consider that one could speak about the necessity of the progressing phenomena without turning attention to their direction

40. Ibid., p. 69.

(ZIEL). It must only be remembered, Baer stated, that the final end (ZIEL) is achieved not by intelligent will, but by means of necessity.

"In the elucidation of how life in nature is formed from necessities, leading to a definite final end (ZIELSTREBIGE NOTWENDIGKEITEN), and from the directed processes conditioned by necessity (NOTWENDIG VERFOLGTEN ZIELEN), it seems to me the true task of the study of nature is concluded."⁴¹

"If the old wisdom," Baer states, "which recognizes expediency and greatness in the activities of nature, must be rejected, after it has been explained that the opinions on which it is based are too intimately connected with human behavior, this does not give one the right to assert that in nature the necessities act alone, devoid of direction (ZIEL). It is absolutely clear that nothing takes place without basis; however, indirected forces of nature cannot build any regulated thing, not even a mathematically defined form and even less a complicated organism; they can only destroy."⁴²

Mentioning many examples of expediency (corresponding to necessity) of organization of living creatures and indistinctly forming the idea of progressive evolution, whose crown is considered the wise man, Baer cited his statement of thirty-three years earlier, invested in idealistic form: "The earthly body is only a bed, on which the hereditary spiritual resplendence of man develops. The history of nature is only a history of the progressive victory of the spirit over matter."⁴³ After Baer's statement of theoretical opinions about the phenomenon of individual development, it is permissible to posit a question about the essence of his outlook.

It is decidedly necessary to mark off Baer's opinions from the reactionary idealism of Stölzle, Helmersen, and others who insisted on the identity of Baer's ideas with

41. Ibid., p. 73.

42. Ibid., p. 88.

43. Baer, "Das allgemeinste Gesetz der Natur in aller Entwicklung," REDEN, I, 2nd ed. (1886), pp. 71-72.

their own opinions. Similar evaluation of Baer's views in many cases depends upon an arbitrary interpretation of his separate discussions, sometimes pulled out of context: in addition to this, this evaluation does not reflect the contradictions within Baer's views, so natural in his era, when religious dogma and philosophical idealism resisted the tendency to interpret natural phenomena by a simplified materialism.

In the remarks on his list of works published in his autobiography, in particular in the remarks to ÜBER ENTWICKLUNGSGESCHICHTE, Baer wrote:

On the subject of my general opinions situated in both parts of this work, the reproach was made that they were too mechanical. I confess that I take this reproach for praise, because it is better to stand on solid ground than to be up in the clouds. For the naturalistic point of view the rule generally answers of talking only about what I have really seen, and concluding ideas from observations, and not basing observations on preconceived ideas. That is what I took for myself from the rule.⁴⁴

Baer's philosophical terms must not be judged by present-day standards. When Baer accepted the statement about his "mechanical" opinions as praise, it must be taken as his recognition of the materialistic character of his thought. Baer wanted to assert that his views were opposite to an idealistic "being up in the clouds." His naturalistic approach, based on observations of actually existing phenomena, free from preconceived ideas, must be regarded as a progressive outlook for a naturalist of the first third of the nineteenth century.

In this remark Baer recalled his studies of the history of embryology, in particular the work of Fabricius ab

44. Baer, NACHRICHTEN ÜBER LEBEN UND SCHRIFTEN, p. 441.

Aquapendente. Extremely uncomplimentary about the factual data,⁴⁵ Baer stated, "The study of Fabricius was for me an excellent means for recovering from philosophical theories not based on direct observation.⁴⁶ Thus, there should be no preconceived explanations, but only accurate observations and conclusions for them."

Baer's "naturalistic" outlook must stand in conflict with the materialistic ideas current in his day, especially in the second half of his career, taking the form of simplified mechanical materialism. His philippics, against naturalists who seek to bring all the vital processes under physico-chemical laws and do not see the qualitative peculiarities of these phenomena, were directed mainly towards the representatives of mechanical materialism. Thus Baer also came out sharply against the other camp—against fideism, coetionism, and anthropomorphism. Here he did not avoid sarcasm and gave a similar kind of opinion to those addressing God, examples of which were mentioned above. What outlook remained? Baer took on the task of creating his own world view. In vain did his biographers promote the idea of a close relation between his study of the direction (ZIELSTREBIGKEIT) of vital phenomena with Aristotle's study of entelechy; in vain they emphasized Baer's sympathy with Spinoza, whose materialistic philosophy they falsely described as pantheism. Baer knew Aristotle well and Spinoza also, but he went his own way as a naturalist, which, of course, could not rise to the heights achieved consequently by materialism.

Namely, this last circumstance was the reason that in the struggle against simplified materialism Baer was sometimes obliged to use ammunition from the arsenal of the fideism and anthropomorphous teleology which he had attacked.

45. "The author used many efforts," Baer wrote, "so that even absurd matters are represented as important and essential. During this he described in detail things which it is impossible to see properly in the egg and also incorrectly described what really can be observed" (NACHRICHTEN, p. 449).

46. The speech was about idealistic natural philosophy, at whose altar Baer gave tribute in his early youth.

Attempting to create his own philosophy of nature, giving it a logical basis and providing it with new terminology, Baer mobilized the differences of shades of meaning which had characterized in German the words ZWECK and ZIEL. Rejecting the understanding of purpose (ZWECK) for the organic world, in whose phenomena he did not discover the presence of a conscious intelligent activity, he strove for the words ZIEL and ZIELSTREBIGKEIT to designate expediency, i.e. adaptive to the building and function of living beings, and in particular their development either individual or historical. The development of the individual which is steadily (ZIELSTREBIG, ZIELMASSIG) producing in each generation all principal signs of the species, was for Baer an especially conclusive proof that the processes of development cannot be directed by accidental actions of the physico-chemical powers.

Baer's frequently repeated assertions that the final end (ZIEL) of development of an individual is the formation of the organism, that in development a steady movement towards this final end (ZIELSTREBIGKEIT) appears, do not have in Baer that outspokenly idealistic opinion expressed by the analogies of vitalists and antidarwinists at the end of the nineteenth and the beginning of the twentieth century. Even using the expression—which is interesting in the idealistic form—that the development of the individual is directed by the idea of the species, Baer apparently had in mind primarily an idea that the direction of ontogeny in each generation repeats the ontogeny of the previous generation, i.e. that the development of the individual is determined by specific peculiarities which may appear more distinctly in the adult condition. It can be recognized that in Baer's discussions and mainly in his terminology, the knife's edge of difference between ZIEL and ZWECK is so minute that he continuously risked sliding from the meaning of ZIEL into the meaning of ZWECK; undoubtedly this happened in many of his statements. It can be recognized that Baer was insufficiently constant in his struggle against fideism and that some of his expressions are open to deistic and pantheistic interpretations. However, neither these separate idealistic discussions nor the appearance of inconsistency should interest those who want to make for themselves a correct estimation of the views of the great naturalist.

Baer's teleological discussions were, as stated, directed against popular materialistic neglect of objectivity which existed expediently (adaptivity) in the structure and vital activity of organisms. These discussions were, however, inconsequent and sometimes invested in idealistic form because Baer, denying adaptive evolution in the animal and plant world as the result of natural selection, by the same token passed over the real source of expediency in living nature.

Skepticism toward the idea of evolution, toward Darwinism, led Baer, especially in the last years of his life, to deviate from the materialistic opinions characteristic of the period of scientific activity to which his unfading embryological works are related.

Nevertheless, in relation to Baer, we may cite the man who may correctly be called the greatest thinker of the Russian Academy of Science for a century before Baer—Mikhail Vasilevich Lomonosov: "As to people serving the Republic of Science, I shall not attack them for their errors, but I will try to put into action their good ideas."⁴⁷

47. See "267 Remarks on Physics and Corpuscular Philosophy," 16th Remark, M. V. Lomonosov, SOBR. SOCH., Vol. I (Izd. AN SSR, 1950).

CHAPTER 25

INVESTIGATIONS ON INVERTEBRATE EMBRYOLOGY:

WORK OF A. GRUBE, A. D. NORDMANN,

N. A. WARNEK, AND A. KROHN

During the first twenty to thirty years of the nineteenth century, embryology remained chiefly the study of the embryonic development of vertebrates; the comparative peculiarities of development of different animals was studied only at the limits of this most studied group. By the end of the twentieth year of that century, i.e. the period of Baer's active work in embryology, the first investigations into the development of invertebrates appeared. Baer himself, as mentioned above,¹ turned his attention to the characteristic peculiarities of development of arthropods, noting in particular that their blastoderms are situated on the abdominal side of the egg and distributed from here in the dorsal direction. Baer was not able to explain the development of arthropods more clearly. Even the investigations of his predecessor Herold, which were limited to the study of the late stages of development of butterflies and spiders,² could not give Baer material for well-grounded comparative embryological conclusions.

The aspiration to apply embryological principles to arthropod development was actualized by Baer, first in the study of embryonic layers, reflected in the works of

1. See Chapter 15.

2. J. M. D. Herold, ENTWICKELUNGSGESCHICHTE DER SCHMETTERLINGE ANATOMISCH UND PHYSIOLOGISCH BEARBEITET (Cassel u. Marburg, 1815), vi + 118 + xxxiv pp.; EXERCITATIONES DE ANIMALIUM VERTEBRIS CARENTIUM IN OVO FORMATIONE. DE GENERATIONE ARANEORUM IN OVO (Marburg, 1824), x + 63 pp.

M. H. Rathke. A native of Danzig, Rathke in 1829 arrived in Russia, where he was professor for six years at Dorpat University. Before that, he published many embryological works, including a valuable work on the development of crayfish.³ During his tenure at Dorpat, Rathke visited Moscow and Petersburg and also travelled in the Crimea to investigate the fauna of the Black Sea. On the Black Sea coastline, Rathke collected comparative embryological material which was later used in ON MORPHOLOGY: TRAVEL NOTES FROM TAURIA.⁴ In this collection, in addition to brief information about the embryonic stage of actinia, there is also an essay on the embryology of the Crimean scorpion and investigations concerning the development of nine species of crustacea of different orders (copepods, amphipods, decapods, and isopods). Rathke's work on crayfish development, and also his investigations on the development of other arthropods (124), represent a clear interest in describing the phenomenon of embryonic development in arthropods according to the ideas of Pander and Baer. Rathke spoke of the embryonic disk or blastoderm, of the primary cavity, and of the two embryonic membranes (serous and mucous) into which the blastoderm is divided. The first stages of development, the division of the ovum and the first processes of separation of the rudiments, remained untraced.

It must be borne in mind that a clear presentation about the essence of the processes which take place in the early stages of embryonic development—i.e. first of all the process of division—was not yet established in the first forty years of the last century. Thus, Reichert (125) studied the development of the frog ovum but reached an incorrect conclusion about the structure of the still-undivided ovum, supposing that it consisted of many cells (by cells he meant the round accumulations of the yolk plates). This point of view was raised by Reichert both in his DIE ENTWICKELUNGSLEBEN IM WIRBELTHIRREICH and in an article published one year before, "On the Process of Division in the Ova of Amphibia,"⁵

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3. H. Rathke, ÜBER DIE BILDUNG UND ENTWICKELUNG DES FLUSSKREBSSES (Leipzig, 1829), 97 pp.
 4. Rathke, ZUR MORPHOLOGIE. REISEBEMERKUNGEN AUS TAURIA (Riga und Leipzig, 1827), 192 pp.
 5. K. B. Reichert, DIE ENTWICKELUNGSLEBEN IM WIRBELTHIERREICH (Berlin, 1840), x + 261 pp.; "Über den Furchungsprozess der Batrachier," ARCH. ANAT. PHYSIOL. (1841), pp. 523 - 541.

in which he wrote: The process of division of the amphibian ova is nothing more than successively accomplished generic action (GEBURTSACT) of the maternal cells, repeatedly invested in each other.

T. Bischoff, working on the embryology of mammals and publishing in the period from 1842 to 1852 a monograph about the development of man, rabbit, dog and guinea pig, also did not reach a clear understanding of processes of division and did not recognize the spheres resulting from division as cells; since in his opinion, the cell must possess a cavity, but the spheres resulting from division are filled with yolk, the nuclei of the blastoderms were taken by Bischoff as fat droplets.

A. Kölliker⁶ went much further in the analysis of the process of ovum division, admitting the direct continuity of the blastoderms and those cells from which the embryo is built in later stages.

In all these cases the discussion was about the forms of development, complicated by the great quantity of yolk in the centrolecithal and telolecithal ova. The nature of the occurrence there of superficial and discoidal division was explained much later, after the introduction of sectioning in embryology.

A more distinct presentation on the phenomena of division was stated by Baer in his work on the development of amphibia,⁷ but especially in the work noticed by his contemporaries and later forgotten on the development of the ova of the sea urchin.⁸

Certain embryologists of the thirties and the forties nearly approached the correct interpretation of the phenomena of the ovum division. They include Kölliker, then Lovén,⁹

6. A. Kölliker, ENTWICKELUNGSGESCHICHTE DER CEPHALO-
PODEN (Zürich, 1844), 180 pp.

7. See Chapter 21.

8. See Chapter 23.

9. S. L. Lovén, "Bidrag til kännedomen af Molluskenas
untveckling," K. VET. AKAD. HANDLINGAR (1839),
pp. 227 - 241.

Sars,¹⁰ van Beneden,¹¹ and Quatrefages¹² and must be mentioned. The first four investigated mollusc development, and the last studied the development of annelids. They presented some stages of ovum division, but did not broach the subject of the internal processes occurring in it nor of the fate of the spheres of division.

A great part of the works of that time concerning the development of invertebrates was illustrated by the study of different types of reproduction, and also by the description of the structure and the transformation of different larval forms which sometimes did not yield to systematic determination and figured under different specific names (126). The investigations of forms of reproduction became especially popular after Steenstrup showed the wide distribution of the alternation of sexual and asexual generations of many invertebrates; the application of this empirical regularity to groups of animals not investigated before this time constituted the majority of works in the present sphere. The single base for generalization concerning early embryonic development is thought to be the cellular theory formed shortly before this. Using extremely imperfect microscopic techniques, the embryologists of the first half of the nineteenth century posed the question, can the spheres of division be called cells, and are the cells of which the embryo consists the direct descendants of the primary spheres of division? They attempted to trace the fate of those existing in the unfertilized ova "embryonic vesicle" (and "embryonic speck"), i.e. to explain whether these

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10. M. Sars, "Beitrag zur Entwicklungsgeschichte der Mollusken und Zoophyten," ARCH. NATURG., 6 (1840), pp. 196 - 219.
 11. P. J. van Beneden et Ch. Windischmann, "Recherches sur l'embryogénie des Limaces," ARCH. ANAT. PHYSIOL. (1841), pp. 176 - 195.
 12. A. de Quatrefages, "Sur l'embryogénie des Annélides," ANN. SC. NAT., 3 Sér. Zool. 8 (1847), pp. 99 - 102.

formations disappear after fertilization without a trace or whether they stand in continuous genetic connection with the nucleus (and the nucleolus) of the cells of the embryo. On the foundation of a one-sided and primitive understanding of the cellular theory, fantastic presentations sometimes grew, like the ideas of Reichert, which resurrected the long-buried theory of preformation.

For the purposeful coordination of the efforts of zoologists studying invertebrate development, the theory of embryonic layers, which still had not become a broad scientific generalization, could not serve. Its correctness was proven only for vertebrates, but the application of the theory of embryonic layers to invertebrates was believed by nearly no one. Rathke's old data concerning crayfish were known. More than a quarter of a century later Zaddach also reported on the embryonic layers of insects, admitting to his descriptions crude morphological mistakes.

The data related to the development of different types of invertebrates were accumulated relatively slowly, because a theoretical conception for which this material could be used did not exist. The study of the types of structure and development of animals, taking its beginning from the opinion of Cuvier and Baer, fell into decay. The formally opposite theory of types, that of Naturphilosophie, the idea of unity of planes, caused little enthusiasm. Only after fifty years, after the appearance of Darwin's theory, did this period of mental stagnation end. Then the naturalists were divided into two camps—the hearty supporters and the violent opponents of the theory of evolution. Practically none of the contemporaries of the great reformer of biological science could keep an olympian calm and sustain neutrality for any length of time.

The investigations preceding the publications of the *ORIGIN OF SPECIES* played, however, its historical role. Factual material was collected which Darwin and his early followers used. In this period came the important works of the Russian embryologists A. Grube, A. D. Nordmann, N. A. Warnek, and A. Krohn.

To Dorpat University professor A. Grube belonged serious investigation on the development of annelids; he studied the embryonic and partly post-embryonic development of the

Proboscidea leeches *Clepsine complanata* and *C. bioculata* (genus *Glossosiphonia*, according to the current terminology).¹³

Adolf Edward Grube¹⁴ was born in 1812 in Königsberg, where he graduated from the university. For thirteen years (1843 - 1865) he was professor of zoology and comparative anatomy in Dorpat University, and to this period of Grube's life are related his most important works in systematics, anatomy, and embryology of the annelids.

Grube's work undoubtedly possesses remarkable significance. Because it was undeservedly forgotten and not mentioned even in the detailed reports and special works on the development of leeches (127), we must dwell here on its content.

In the introduction to his work, Grube turned to memories of his years of study in Königsberg, where Baer was working. Actually the great embryologist at that time read few lectures, being engrossed in the investigations of development of fish and amphibia. He was helped by Grube's friend, the clever graphic artist Burov, who, by the way, encouraged Grube's attraction to the laboratory, where the latter acquired a taste for embryological investigations. Grube was aware of the difficulty of these observations, but he did not abandon his idea of devoting himself to embryology.

Shortly after graduation from the university, Grube left for a trip to the Mediterranean seacoast. "Baer's observations on the history of animal development," Grube wrote, "accompanied me on the trip to Italy, and along with the enjoyments of nature and art I continuously sated my

13. A. E. Grube, UNTERSUCHUNGEN ÜBER DIE ENTWICKLUNG DER ANNELIDEN. I: UNTERSUCHUNGEN ÜBER DIE ENTWICKLUNG DER CLEPSINEN (Königsberg, 1844), ii + 56 pp.

14. The author expresses heartfelt gratitude to the head of the Department of Zoology at the University of Tartu, Professor Kh. Kh. Riikoya, for the photo reprinted here of A. E. Grube.

interest in this sphere of science" (p. 1). On the coast Grube zealously collected zoological materials and made dissections, considering these studies important for his future embryological investigations. His attention was attracted mainly to annelids, the study of which became his basic zoological specialty. Only in 1839 did Grube turn to work directly on annelid development, beginning with the study of the very small ova of the *Saenuris variegata* described by Hofmeister. In addition he reported that their development differs in many relations from the corresponding phenomena in medical leeches which had been very superficially described by E. Weber. The following spring, Grube studied the embryology of the leech and confirmed the reality of the formerly discovered differences. Preparing the results of his observations for publication, Grube conscientiously studied the works of the authors whom he considered his predecessors. The work of Filippi on the anatomy and embryology of Proboscidae leeches,¹⁵ recently published, especially interested him. Grube found that in Filippi's investigations there was only scanty information about the division of the ovum, as the Italian author saw only "six lobes, situated in one and the same plane around the seventh, situated in the center." To this description he added that these spherical segments disintegrate into smaller spheres (GLOBULI ORGANICI), sharing in the formation of the embryo. Filippi apparently studied the developing ova through the membrane of a cocoon, which can explain the indistinct results of his observations. The first foundation of the embryo Filippi described with an indefinite expression—cutis (LA CUTE). He also erroneously considered, that the hatched young is nearly similar to the adult leech and at once is attached to the mother by the help of posterior suckers (in fact they are not present at this time).

Grube could trace the development of Clepsine in incomparably more detail; his success was aided by the application of concentrated reagents, in particular diluted nitric acid. In the first section of his work, Grube described the structure of the female and male sexual

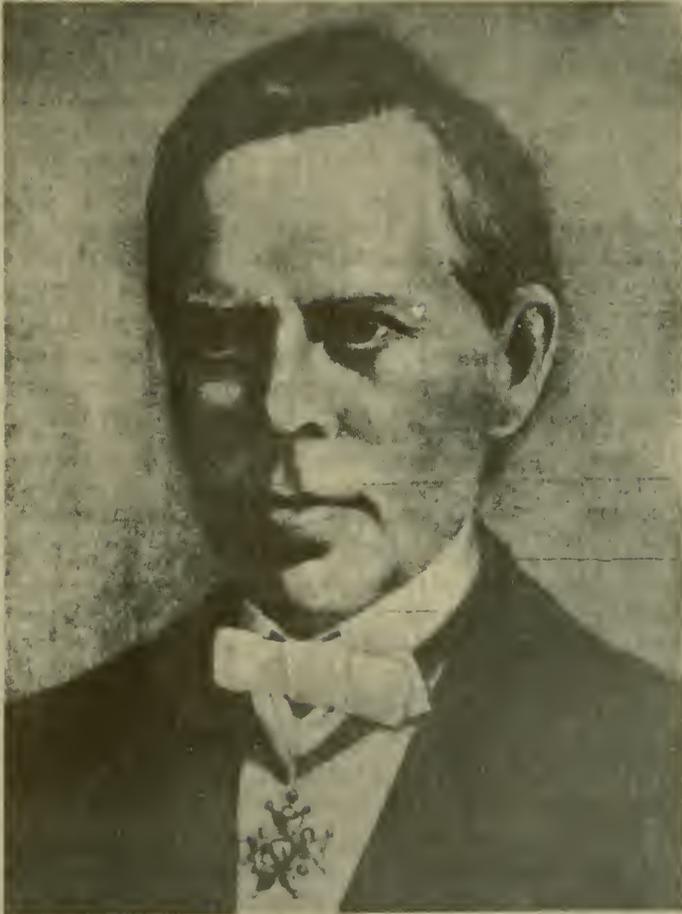
15. F. de Filippi, LETTERA AL S. DOTT. RUSCONI SOPRA L'ANATOMIA E LO SVILUPPO DELLE CLEPSINE (Pavia, 1839).

organs, copulation, the act of deposition of eggs, and also the structure of the ova at the time of maturation and directly after deposition.

The still-undeposited egg, hung in a special pocket in the oviduct, consists of a fine-grained substance (molecular bodies) and yolk (fatty bodies); it is provided with a nucleus (embryonic vesicle). Before the deposition, the ovum, which is separated from the oviduct and is freely situated in the egg-reservoir, has the same structure; the nucleus already cannot be seen in a beam of light and can be seen only during the crushing of the ovum. Later the embryonic vesicle disappears completely.

The second section of the work was devoted to the description of embryonic development. In the deposited ovum for one hour no change can be seen, and then at its poles the following phenomena can be observed. At the beginning, on one of them, a white spot appears; this increases and turns into a disk with a grey spot in the center (Figure 36,a). Then this grey center increases and a white spot appears in it, and the external white disk is transformed into a ring, which Grube called the polar ring (Figure 36,b). The field of formation of the polar ring he called the active pole, since according to his observations, it is here at the time of development of the embryo that the most noticeable changes take place. On the opposite inactive pole a white ring appears, but less distinctly delimited. The polar ring ascends over the surface of the ovum in the form of a papilla, so that after its infiltration its condensation can be prepared. Grube considered that the formation of polar rings is the result of the displacement of an internal substance, during which the "molecular bodies" are gathered in the form of rings on the poles.

Following the appearance of polar rings, or, in Grube's expression, "the process of formation of fissures (DURCHFURCHUNG) or, rather, cleft (ZERKLUFTUNG).... those fissures not only occur on the surface, but penetrate deep into the mass of the yolk, as a simple experiment shows: under careful pressure of the condensed yolk, it disintegrates into as many parts as the segments are delimited by the fissures" (p. 17). The first fissure divides the ovum into



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two unequal parts (Figure 36,c), so that the polar ring can be divided into halves, or from it a small part is separated, or the fissure occurs in direct proximity from the ring, not touching it completely. The second fissure divides the small segment approximately at a right angle to the first (Figure 36,d), and the third also divides the large segment (Figure 36,e).

Thus, the ovum passes into the stage of four blastomeres (Grube noted that the large segment in many cases is divided earlier than the smaller one). Of the four segments formed, one is larger than all the others, and it is divided by a fourth fissure which provides the beginning of the fifth segment. The following division is concerned with this last and takes place not along its length, but transversely, the result of which is that the divided fifth segment forms a region in the form of a polar field in the inactive pole of the ovum (Figure 36,f). The sixth, seventh and eighth fissures again go from the active pole to the polar field of the inactive pole. After the sixth division the polar ring on the inactive pole usually disappears. Grube did not see more than eight meridional divisions, and said that in leeches the blackberry stage characteristic for many animals is absent; in this stage the meridional divisions are replaced by transverse ones.

At the same time as the division, accomplished by means of fissures, in the ovum of Clepsine the process of separation of the small globules from the large segments of the ovum first described by Grube takes place; these globules Grube called WANDUNGSBALLEN. In his opinion, the wall of the body of the embryo is built from them; "Segments of the yolk" and Wandungsballen are nothing more than the macromeres and micromeres of the terminology of today's embryology. The first small globule, as Grube noted, appears on the active pole after the formation of the first fissure and appears to be situated in this fissure. Judging by time and place of the appearance of this globule, here the discussion does not concern the formation of the micromeres, but the separation of the first polar body. The following small globules, forming on the active pole of the ovum, undoubtedly are micromeres. Grube described their accumulation, ascertaining during this that by the increase of the number of fissures the number of micromeres increases also; however, these phenomena do not stand in an indissoluble

connection (Figure 36,e and g). The formation of micromeres, according to Grube's description, is accompanied by the replacement of substances inside the ovum segments; he described these replacements in detail, alternating the statement of facts about his observations with theoretical conjecture about the forces of attraction, points of their application, and so on.

The micromeres, accumulated on the active pole, do not exhibit equal size; the smaller they are, there are relatively larger molecular substances (protoplasm) and smaller fatty globules (yolk) in them. The smallest consist only of protoplasm and a round transparent nuclear body. These micromeres, according to Grube, never arise from macromeres; therefore, he wrote, "I must conclude that the small globules originate from those large globules already present on the pole which earlier separated from segments of yolk" (p. 22). The accumulation of micromeres forms a plate in the form of an isosceles triangle, without sharp limits passing into the other surface of the ovum. This plate, which Grube called the embryonic field, is so situated that the summit of the triangle is turned toward the active pole and corresponds to the cephalic part of the future embryo.

It consists of "mosaic pieces" which arise as a result of the multiplication of micromeres; in addition, these pieces are smallest when they are nearest to the cephalic end. In the stage described, not only the anterior and posterior ends of the embryo, but also its upper and lower sides, as the surface of the embryo, on which the embryonic fluid is situated, correspond to its abdominal side. Using the descriptive phrase "mosaic pieces", Grube resolved consciously to avoid using the term cell, not being sure that it inherits its own features, which are characteristic of typical, in particular plant, cells.

The anterior end of the embryonic field quickly expands (Figure 36, c), and by forming two summits it produces S-shaped curved shafts (Figure 36, j), which Grube called the abdominal shafts. This name is well-founded, because these shafts, appearing in the field of the active hemisphere of the ovum, i.e. the future dorsal side of the embryo, are displaced towards its ventral side, where they later accrete into a

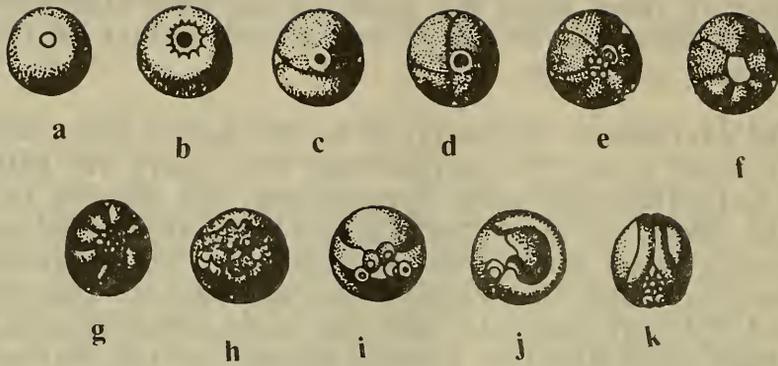


Figure 36. The development of Clepsine (by Grube).

a—fertilized ovum. b—ovum on which the white disk with grey ring appeared. c—first fissure; the white disk is present near it. d—yolk globule, divided into four parts. e—yolk globule, divided by six transverse fissures; the polar field increases as the surrounded globular segments decrease in size due to the loss of albumen (molecular) mass used for the formation of WANDUNGSBALLEN on the active pole. f—the same stage, globules of division from the lower side; on the inactive pole the polar field is seen, i.e. the surface of the seventh segment, separated from the other round fissures. g—somewhat later stage, view from, above; the number of WANDUNGSBALLEN increasing, they then form a small disk which can be regarded as a rudiment (KEIM). h—WANDUNGSBALLEN increase in number and occupy a great area, forming the embryonic field. i—the view of the abdominal shaft from behind; they move so far apart that they envelop the yolk globule by a ring. j—the abdominal shaft from the side; on the posterior end of each, three whitish globules are present. k—the abdominal shafts unite together.

single ventral embryonic region. The ventral shafts, according to Grube, on the ventral side of the leech embryo play the same role which the dorsal shafts play in the vertebrate embryos, because from them the wall of the body, in particular its muscles, is formed. The ventral shafts are composed of extremely small, closely adjacent other globules. At the posterior end of the embryonic field remain large globules which form part of its molecular (protoplasmic) content; three of these terminal globules usually are present on each side (Figure 36,k). The internal part of the yolk globule (the divided ovum) constitutes a mass containing little protoplasm. This rich yolk mass is used mainly for building organs which are present in the abdominal cavity, in particular the intestinal canal; above it a layer grows, composed from a molecular mass which takes its origin from the ventral shafts.

The rudiment of the neural cord appears in the form of two white stripes, joined to the external side by the recently formed embryonic stripes. After their closure on the ventral sides, the halves of the paired rudiment of the nervous system are united.

In this period the surface of the embryonic body is already covered with epithelium, composed of flat cells of different sizes and forms. At the same time in the body cavity dissepiments are situated, their number gradually increasing.

In the third part of Grube's work he included changes occurring after the hatching of Clepsine from the egg membrane. Contrary to Filippi, Grube found very essential differences between the just-hatched leech and the formed worms. In the short, cylindrical little worm hatching from the egg, there are still no posterior sucking discs, no eyes, no blood vessels, and the formation of the dissepiments is also unfinished. As the young larvae are also immediately fixed by the anterior end, Grube assumed the presence of the rudiment of the anterior sucker with longitudinal and circular muscles. Within one day after hatching this sucker is clearly noticeable in the form of a convex ring; after two days this ring elongates, as Grube thought, under the effect of the heaviness of the body of the leech hanging on it. Inside the elongated ring a canal appears representing, according to

Grube, the rudiment of the sheath of the still unformed proboscis. The wall of the intestinal canal, or yolk sac, consists at this time of large cells. Later, by means of a circular twist of the most anterior part of the body, the caudal disc develops and the proboscis is formed, which the larva can let out and pull in. The digestive canal is formed in this way. On the intestinal canal extensions appear, and in addition to this, it is divided into three parts. The anterior and posterior parts are significantly thinner than the middle one which composes the future stomach. In the last the more enlarged lateral pouches appear. Later on the eyes develop; at first they have the form of circular red spots. The vascular system develops, and, on the dorsal side of the body, the pulsating heart first becomes noticeable.

Grube finished the description of his observations with the following words: "The development considered here is probably spread extensively in the class ANNULATA. This is established on the basis of detailed investigations on many representatives of Naidae and Lumbricinae namely in *Saenuris variegata* Hoffm., *Euaxes acutirostris* Gr. and *Lumbriculus variegatus* Gr., and if it can be judged by an analogy with the adult animals, it will be also correct for the genus *Lumbricus*, and also for many sea worms" (p. 45). With this, Grube carefully observed that discussion of analogy without special investigations can lead to erroneous conclusions.

A discussion of Grube's work leads to the conclusion that he promoted the study of embryology of the annulated worms (annelids) and discovered phenomena the detailed study of which was done significantly later. His most important achievement in terms of recent embryology can be summarized in the following way:

1. Grube established that in the eggs of Proboscidea leeches there are polar plasmas; especially conspicuous are protoplasmic rings on the animal pole.

2. He recognized the complete, unequal division of the ovum of Proboscidea leeches, during which the animal polar plasma can go in one of the blastomeres of the four-celled stage.

3. Grube clearly saw how in the stage of the four blastomeres, from the animal side, very small globules of division began to separate; i.e. he established the fact of the formation of micromeres, which are composed mainly of protoplasm, and macromeres, which are rich in yolk.

4. Later he established that the number of micromeres increased either by separation from macromeres, or by means of multiplication of the early formed micromeres.

5. By Grube's observations, the "rudiment" which is formed on the animal pole, owing to the multiplication of micromeres, spreads over the surface of the ovum, as a result of which the macromeres appear inside the embryo. This phenomenon very nearly resembles epibolic gastrulation.

6. At the end, Grube described the embryonic stripes coming out from three pairs of terminal cells; i.e. he discovered in the annulated worms the phenomenon of teloblastic development.

7. The embryonic stripes, in Grube's observations, are displaced towards each other and are united on the ventral side. From the material of the embryonic stripes ("the abdominal shafts") the wall of the worm's body-tgments, muscles, and nervous system is formed.

Grube's excellent work was forgotten, and superiority in the study of the embryology of annulated worms, in particular the leeches, was accorded to Rathke, whose work was published eighteen years later. Rathke's work without doubt has merit, but also has many defects, so that it can be seen as a step backwards in comparison with the work of Grube. Thus in the maxillary leech *Nepheleis vulgaris* Rathke clearly saw the formation of micromeres, which in *Clepsine complanata* he did not see, and instead of the micromeres only granularity is illustrated in his drawing in the animal parts of the blastomeres. At a later stage it is shown as if the unlacing of the micromeres has begun, but he did not see whether this led them to division. Together with this, Rathke reproached Grube for seeking the source of micromeres (WANDUNGSBALLEN) in the depths of the globules of the division, while Rathke himself in general

did not see their separation. According to his description, a number of hillocks on the animal pole of the divided ovum directly turned into a thickening which is the rudiment of the embryonic stripes. The embryonic stripes of *Nephelis* are illustrated very schematically by Rathke; he did not observe the characteristic cellular rows in these stripes, neither did he recognize the connection between the only three teloblasts illustrated in his drawing which are situated as if they lie at the extreme ends opposite to the embryonic stripes and the middle one as if it lies between these ends. Rathke also represented the embryonic stripes of *Clepsine* less distinctly than Grube.

All this is mentioned not to underestimate the significance of Rathke's investigations, but only to draw attention to the more perfect work, in many aspects, of Grube, to call to mind its priority and to show the importance of his work in the history of Russian and world embryology.

In the 1830's and 1840's, the development of invertebrates also interested A. D. Nordmann (1803 - 1866). Aleksandr Davidovich Nordmann was the son of a Russian officer born in Finland. In 1821 he entered the university in Abo, and after graduation he worked for some years in Berlin with Rudolphi and Ehrenberg. During his stay in Germany he accompanied Oken, Tiedemann, and Chamisso on a trip for the study of sea fauna. In Berlin Nordmann published his first work, MICROGRAPHICAL INFORMATION, dedicated to the structure and taxonomy of parasitic worms (describing many new forms, in particular "spainika" - *Diplozoon paradoxum*), and also the structure and development of parasitic copepods.¹⁶ In 1832 Nordmann was invited to join the department of zoology

16. A. v. Nordmann, MIKROGRAPHISCHE BEITRÄGE ZUR NATURGESCHICHTE DER WIRBELLOSEN THIERE (Berlin, 1832), Vol. I, viii + 118 pp., 1: ÜBER BINNENWÜRMER IM AUGE HÖHERER THIERE; 2: BESCHREIBUNG EINIGER NEUEN HELMINTHE. Vol. II, xviii + 150 pp., 1: BESCHREIBUNG EINIGER NEUEN PARASITISCHEN ENTOMOSTRACEEN; 2: ERSTER BEITRAG ZUR NATURGESCHICHTE DER LERNÄEN.

and botany of Lyceum Rishel in Odessa, and in the following year he took the post of director of Odessa Botanic Garden (128). In 1833 Nordmann together with Rathke, S. S. Kutorgaya and Steven travelled to the Crimea. In the following years he travelled much in the south of Russia; in particular, he led excursions in the Crimea of students of the Odessa Lyceum. When he was sent with a scientific mission to Paris, Nordmann visited with Milne-Edwards the coast of Normandy. In 1849 Nordmann came to Helsingfors University, where from 1852 to the end of his life he headed the department of zoology. During the period of his scientific activity, Nordmann published fifty-seven works in Russian, Latin, German, French and Swedish on anatomy, embryology, taxonomy and zoography of different groups of vertebrates (mammals, birds, fish) and invertebrates (insects, spiders, crustaceans and worms, mainly the parasitic molluscs, bryozoans and Coelenteratae); he also studied botany and paleontology.

In the previously mentioned MICROGRAPHICAL INFORMATION, the results of Nordmann's observations on the development of parasitic copepoda *Achtheres percarum* appear, and the larval stages of other related forms (*Ergasilus Sieboldi* Nordm., *Tracheliastes polycolpus* Nordm. and *Lernaeocera cyprinacea*) are described. These investigations met the need to explain the systematic situation of parasites, which at that time were related either to molluscs or to the annulated worms, or even to coelenterates. If the relationship of some representatives of the mentioned groups (for example, Caligus) to crustaceans was to some extent only probable, then these forms, such as *Lernaeocera*, which in the adult condition are completely unlike arthropods, remained in their systematic relations mysterious.

The embryonic development of *Achtheres* was described by Nordmann rather incompletely. "On the upper surface of the yolk," he wrote, "is found at first a more transparent region, and a granular part of the yolk, having the significance of a rudiment (KEIM), turned into round or spherical forms from which the more peripheral give material for the formation of the rudiment membrane (KEIMHAUT)... The latter completely envelops the yolk and... forms later on the wall of the body of the embryo (p. 78). After referring to the separation of the head and the appearance of the

rudiments of the extremities, Nordmann turned to the characteristics of the nauplius larva, whose structure becomes complicated after moulting.

Its central point was the description of the larval stage of *Lernaeocera cyprinacea*. The adult animals of this genus were already known to Linnaeus; they are characterized by a sacculated unopened body, deprived of extremities and organs of sensations (Figure 37, A). "If naturalists," Nordmann wrote, "are astonished at the structure of the body of the mature animal of this kind, their astonishment will be more natural when an opportunity arises for them to observe the young animals. It can hardly be imagined that there is anything more striking than an offspring having absolutely nothing in common with its parent. Before my eyes the egg receptacle in the mature animal was ruptured, and the embryos set free. I saw young animals exactly the same as I represent them in the drawing (Figure 37, B); they have extremities, antennae, and even bright red eyes" (128).

Nordmann's observations met, according to him, decided distrust from Berlin zoologists to whom he demonstrated the nauplius larvae of *Lernaeocera cyprinacea*. Later the significance of this discovery was universally recognized (129).

After some years Nordmann published a small embryological work concerning the Black Sea bryozoan *Tendra zostericola*.¹⁷ In one zooid Nordmann found from four to seven eggs and saw the penetration of the spermatozoids in the female cells through an opening in their base. Later he saw the embryos hatched from the eggs swimming by means of cilia and finally settling in the seaweed *Zostera*. "As far as it is possible," Nordmann wrote, "I observed the transformation of the young animals and the development of polyps from them." Greater significance was possessed, however, by other embryological work of Nordmann's on the development of molluscs.

17. A. v. Nordmann, "Recherches microscopiques sur l'anatomie et le développement du *Tendra zostericola*, espèce de polype de la section des Bryozoaires," ANN. SC. NAT. ZOOL., 11 (1838), pp. 185 - 191.



Aleksandr Davidovich Nordmann

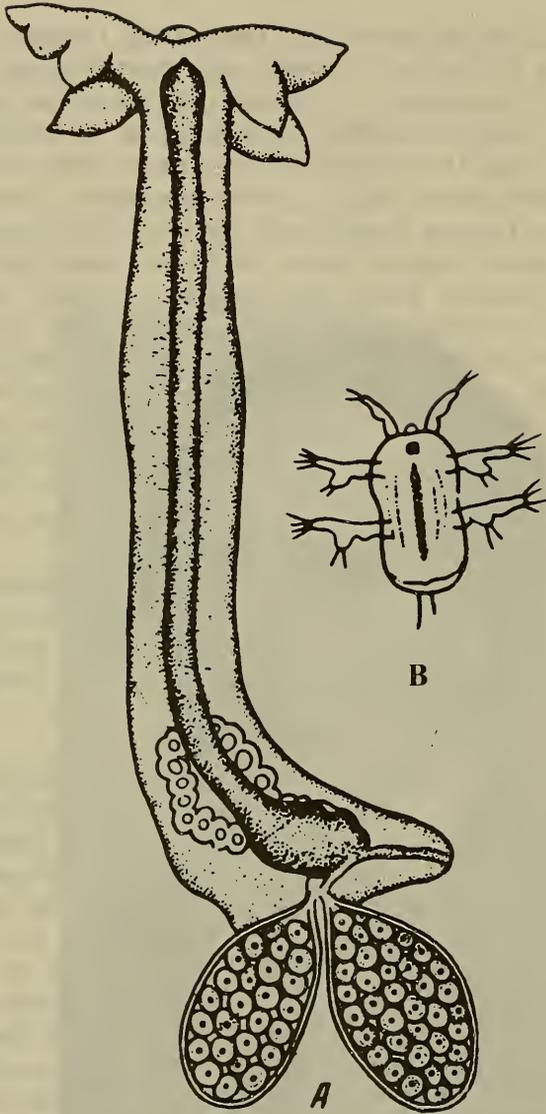


Figure 37. *Lernaecera cyprinacea* (A) and its larva (B)
(by Nordmann).

The molluscs, especially the gastropods and lamelli-branches, are considered easily available material for the study of development processes; therefore they early attracted the attention of embryologists. The division of the ova of the gastropod molluscs is described in the investigations of Van Beneden and Windischmann, and the division of the ova of the lamellibranchs—in the work of Lovén. In the ova of *Modiolaria marmorata* (*Mytilus discors*) Lovén observed a maturation division and described it, as a process of ejection of nucleolus (embryonic spot). The important result of his work was the establishment of the fact that during the division of the ovum of *Modiolaria* the separation in the vegetative hemisphere of non-nucleated lobes takes place which soon merges with one of the blastomeres. This phenomenon is repeated many times during the time of the following divisions. Lovén saw clearly the process of division itself, i.e. the deviation of the ovum into separate blastomeres, but he did not trace the changes in the nuclei, the equal and mutual distribution of blastomeres.

The separation of polar bodies in the ovum of the grey slug is sufficiently clearly described in the above-mentioned works of Van Beneden and Windischmann, although the division following the separation of the polar bodies was inaccurately described by them; they spoke about the formation of elevations on the surface of the yolk, divided by fissures. As a result of this the entire surface of the ovum becomes at the end as if embossed (BOSSÉLÉ) and resembles a raspberry. The Belgian authors did not connect the formation of "the yolk cells" with the appearance of the cuts on the surface of the yolk; according to their concept, the yolk cells originate under the superficial layer of the yolk. The drawings illustrating their work show round bulges on the surface of the developing ovum, and not its division as a whole into separate blastomeres. The internal processes in the divided ovum and blastomeres are neither described nor illustrated in the drawings. Erroneous ideas of the processes of division in the gastropodan molluscs were retained in the work of O. Schmidt appearing ten years later.¹⁸ "The

18. O. Schmidt, "Über Entwicklung von *Limax agrestis*," ARCH. ANAT., PHYSIOL. (1851), pp. 278 - 290.

description of the ovum and the processes of division inside it up to the formation of the embryo," Schmidt wrote, "was given so completely by van Beneden and Windischmann that I cannot add anything to it" (p. 278).

The subject of Nordmann's above mentioned work on the development of the gastropodan molluscs was the nudibranchiate mollusc *Tergipes Edwardsii*. The description of the phenomena of its embryonic development constitutes part of the extensive monograph,¹⁹ beginning with the presentation of anatomical data. Nordmann described in detail the development of the ovum in the ovary (§ 28 - 31), characterized the yolk elements of the ovum (§ 32), the structure of the egg ready for oviposition (§ 33) and its membranes (§ 34). The process of division (§ 39) of the ovum of *Tergipes* was described by Nordmann as the following: the first fissure of division can take place in different directions and divide the ovum either into equal, or into very unequal parts. The fissure dividing the ovum into four globules of division takes place at right angles to the first fissure, after which the ovum is divided into eight globules, and so on. The generally uneven character of division is noted in the following expression. "Although the tendency to even progressive division cannot be disputed, it also shows that the yolk, especially up to its acquisition of the mulberry form, appears to divide very unevenly" (p. 573) (Figure 38, a-g). Nordmann noted especially that the fissures cut all the mass of the yolk, i.e. that the division was complete.

All the course of development of *Tergipes* Nordmann summarized in the following statements:

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19. Nordmann, "Versuch einer Natur- und Entwicklungsgeschichte des *Tergipes Edwardsii*," MEM., prés. à l'Acad. Sc. St.-Petersb. par divers savants, 4 (1845), pp. 495 - 602. A brief translation of this work in French was published by K. Vogt ("Essai d'une monographie du *Tergipes Edwardsii*," ANN. SC. NAT., 3, ser. Zool., 5 (1846), pp. 109 - 160).

1. The chorion extend to one-fifth the diameter of the ovum and becomes oval.
2. At this time a light fluid, similar to albumin, discharges from the ovum.
3. The yolk loses its spherical form, its mass loosens, and the contours become wrinkled.
4. The embryonic vesicle and the embryonic spot disappear.
5. The upper layers of the yolk lose their reddish coloration.
6. In too many cases separate yolk cells are separated from the other mass of the yolk and give origin to the parasitic creatures.²⁰
7. The ovum is divided by a fissure into two globules.
8. The division process continues regularly.
9. The yolk acquires the form of a mulberry.
10. A bubble of air leaves the yolk (?).
11. The surface of the yolk becomes granular.
12. First establishment of the embryo. The yolk acquires an elongated form, and then the form of a roughly outlined triangle.
13. The distinct appearance of the animal system and the cutaneous system. The configuration of the embryo.
14. Twisting of the anterior part of the embryo is noted (future organs of movement).
15. On the wide anterior area folds appear, from which two lateral round growths are gradually formed. The growths are transformed into lobes and between them a third growth, the foot, appears.
17. Beginning of the formation of mantle and concha.
18. On the lobes the cilia grow.
19. The first movement of the embryo. On the foot the vibrating cilia appear.
21. The lobes of the sail become disc-shaped. The rotatory movement of the embryo.
22. Cells sharing in the formation of mantle are dissolved and disappear.
23. The concha significantly enlarges.
24. The isolated cellular rows indicate the formation of the attached muscles.
25. The formation of the internal organs, among which the intestine is distinctly differentiated.
26. The liver and other glandular bodies are clearly seen. The anus and ganglia.
27. The cells forming

20. Nordmann gave this parasite the name *Cosmella hydrachnoides* and suggested the possibility of its origin from particles of the yolk of *Tergipes*.

the attaching muscles disappear. 28. Deposition of the pigment in the eyes. 29. Between the chorion and the embryo the astonishing parasites appear to rush out. 30. The complete formation of the embryo larva; the roof of the shell opens and closes. 31. The extension of the chorion. 32. The presence of the young in the common ovum chamber. 33. The larva cuts the chorion. 34. Hatching. (pp. 565 - 567)

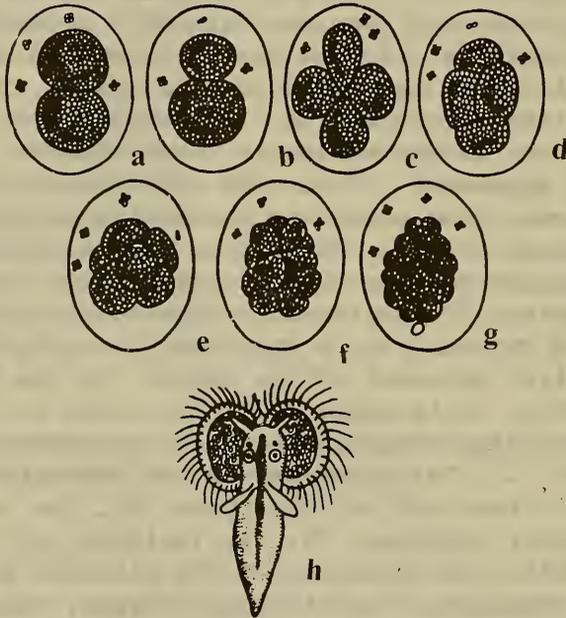


Figure 38. The development of *Tergipes Edwardsii* (by Nordmann) a-g—division of the ovum; h—larva.

From the above it can be seen that Nordmann's main attention was to the relatively late stages of embryonic development, while he investigated the process of division of *Tergipes* only extremely incompletely.

The brief discussion of the works of van Beneden, Lovén and Nordmann on the embryology of molluscs demonstrated the level of knowledge in this sphere at that time. When the development of molluscs was studied by the Russian embryologist N. A. Warnek, his work can be unconditionally called classical (131). Warnek's scientific activity, unfortunately, was brief and was cut short by external circumstances.

Nikolai Aleksandrovich Warnek was born in 1821. When he was eighteen years old he entered the faculty of law at Petersburg University, but in the same year he transferred to a department of the faculty of philosophy. During his years of study, Warnek received in 1843 the gold medal for his "Process of Moulting of External Tegmens and Formation of Millstone in the Ordinary River Crayfish." In 1846 he graduated from the university with a candidate's degree, and for three years he taught botany and zoology in Gorn Institute. Warnek received his master of science degree for his work on the structure and function of the crayfish liver²¹ and in 1849 he started reading lectures to naturalists and medical men in comparative anatomy and physiology in Moscow University, first as junior scientific assistant and then as extraordinary professor (from 1852). In 1848 Warnek wrote the vast work "On the Formation and the Development of the Embryo in the Gastropodan Molluscs," which was published two years later in the BULLETIN OF THE MOSCOW SOCIETY OF NATURALISTS;²² a summary of this work was published abroad under

21. N. A. Warnek, "On the Liver of River Crayfish in Anatomical and Physiological Relations" (SPb., 1847), 40 pp.

22. Warnek, "Über die Bildung und Entwicklung des Embryos bei Gasteropoden," BULL. SOC. NATUR. MOSCOW, 23 (1850), pp. 90 - 194.

the title "On the Process of Division and Structure of the Ovum in Gastropods."²³

In 1860 Warnek retired and departed to Tver; where for three years he was director of a secondary school, and then director of the schools of Tver Province.

Until recently it was thought that Warnek's scientific and literary activity ended in 1863 and that in 1867 he died. From recent work by T. P. Platovaya²⁴ it is now known that in 1880 and 1881 Warnek read a report to the Moscow Society of Naturalists on the biology of agricultural pests, and in 1884 a report on the microscopic structure of the fish ovum and on the morphology and taxonomy of fish. The exact date of his death remains unknown.

Concerning his retirement from Moscow University evidence has been kept which is probably not completely objective and in any case explains only incompletely the cause of his retirement from teaching and from scientific work.

In the multi-volume apologetical biography of the reactionary historian Pogodin, its author N. Barsukov²⁵ reminisced about I. A. Mitropolsky, who was in 1850 a student in the Faculty of Medicine in Moscow University. According to Mitropolsky, when Warnek was reading zoology and comparative anatomy he was noted for an extremely scornful nature; due to this he was disliked by the students and medical men. One of Warnek's clashes with the students, Mitropolsky reported, ended in a noisy scandal, in which both students and medical men participated. In order to confirm to the reader the ultimate rightness of the students, Mitropolsky declared that "the students could endure the tricks of the professor only if his lectures gave them anything useful. But they got nothing from them."

23. Warnek, "Über den Furchungsprozess und die Struktur des Eies der Gasteropoden," FRORIEP'S TAGESBERICHT, No. 280 (1851), pp. 43 - 44.

24. See (131).

25. N. Barsukov, ZHIZN'I TRUDY M. P. POGODINA (Life and Works of M. P. Pogodin), Vol. 16 (1902), pp. 116 - 117.

Another aspect of this incident is mentioned in the reminiscences of L. V. Lebedinsky, which were published in VOICE OF THE PAST in 1912.²⁶ Lebedinsky characterized Warnek as talented, but very proud and sharp in his treatment of people, who "excited against himself the students and medical men by his tactless relations with them and an unusual strictness during examinations." Handbooks in Russian in zoology and comparative anatomy were absent at that time, and Warnek suggested foreign books, which the students, due to their ignorance of the languages, found difficult to use. He did not read a systematic course, but selected works of his own, which he considered more important and interesting. In answer to the protests of students on this occasion Warnek declared that "the students of a university are not secondary school-boys, they must work independently. The professor in his lectures has only to point out a direction and a method by which the students must carry out their work." The dissatisfaction of the students and medical men was expressed in the organization of meetings in which the students of other faculties shared, students of law and philologists who did not attend the lectures of Warnek and could not judge their effects and defects. In these meetings it was decided to criticize the professor, and then oblige him to leave the department. Only some of the students and medical men, Lebedinsky continued, strongly defended the professor. "They said that Warnek was regarded differently and they loved him for his talented presentation of the subject." The planned obstruction was nonetheless carried out, mainly by students of other faculties who shared in the action, especially those of the faculty of law. This produced on Warnek a stunning effect. "Warnek went into an adjacent room," Lebedinsky wrote, "where he fainted away;

26. UZ ZHIZNI MOSKOVSKOGO UNIVERSITETA. VARNEKOVSKAYA ISTORIYA. "GOLOS MINUVSHEGO" (From the life of Moscow University. Warnek's History. "Voice of the Past") (Otd. Ottisk, pp. 210 - 218). For this source, as well as for the answer in HERZENOVSKY "KOLOKOLE" (see [132]), the author expresses deep gratitude to V. V. Sorokin.

it is even said that blood gushed from his throat." Soon after this incident Warnek retired, insisting on it despite intensive persuasion.

Already this comparison of evidence shows the impossibility of placing complete responsibility on Warnek himself for what occurred. The objective evidence of Lebedinsky about Warnek's talented lectures to the students and medical men and their good relation to him unmasks the tendentious assertion of Mitropolsky that Warnek's lectures gave nothing to the students. The impression one has of Warnek is of a serious, exacting professor who loved his subject and taught it on a high level. Certain students and medical men understood his efforts and valued his services to them, while the majority of students were interested in the applied questions and not in understanding Warnek's theoretical views, and saw him only as a strict examiner who shamed them, in addition to his ridiculing of their ignorance.

In all this sad "history of Warnek" there is still one significant side which can be read between the following lines in Lebedinsky's memoirs: "Even among the professors there were people who sympathized with the students, the professor of theology Sergievsky among them. This handsome, somewhat fanciful, young orator was sometimes present in the department. He unnoticeably and cleverly approached the evils of the day, said a few words hinting at an excellent understanding of the students, and was zealously rewarded with applause. In the time of the aforementioned event, one of his lectures, which was full of these hints, ended with the following significant words: 'Yes, this darkness does not triumph over the world!'"

It is logical to ask why Warnek was not pleasing to the professor of theology. What world of darkness and damage spreading from Warnek's department was frightening to Sergievsky? To answer this question is not difficult. Warnek was a convinced materialist, as is easy to ascertain from a study of his basic work. It is improbable that in his lectures Warnek did not touch upon questions of ideology, which, of course, was used against him by Sergievsky, who considered it his responsibility to protect the world of "religion" from the "darkness" of the natural-scientific

materialism. Sergievsky's Jesuitical activity made the best use of the dissatisfaction of the protesting group of students, who played a role obviously of considerable importance in the organization of the obstruction, which took place with the obvious support of the administration of the university, usually so vigilant when the matter is concerned with student disturbances (132).

The fault, or rather misfortune, of Warnek was his sharp and derisive character, his inability to adapt himself to his surroundings. Warnek did not want to reconcile himself with the manifestations of ignorance, even if its carriers were respectable scientists. This can be witnessed by Warnek's review of a scholarly book by A. Bogdanov.²⁷ This review shows great and extensive knowledge and unquestionable educational talent of the reviewer and his understanding of the problem of the teaching of natural sciences. In addition, the review is written in an overly particular and caustic tone; Warnek did not let pass any mistake, any slip of the tongue, or any lame expression from the author of the book. It is easy to imagine what reaction Warnek's article could produce in Bogdanov. If Warnek behaved similarly in the professional milieu of Moscow University, and used to deride the lectures of his colleagues, then he undoubtedly provoked against himself not only a certain group of students, but also some professors.

Valuable evidence of Warnek's high character as a lecturer and scientific worker is contained in the words of I. M. Sechenov:²⁸

Junior Scientific Assistant Warnek taught us zoology. He read simply and clearly, dwelling mainly on general signs applied in zoology departments, and the description of protozoa was prefaced by a long treatise on the cell in general. This last study was built, however, on unprepared ground. Moscow still did not think much at that time of the microscope; among Warnek's students it was not used successfully, and in mockery they nicknamed him "Cellular."

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27. Warnek, "Zoologiya i zoologicheskaya khrestomatiya v obieme srednykh uchebnykh zavedenii," Author Anatolii Bogdanov, OTD. Pervy Zh. MNP, ch. 118 (1863), pp. 47 - 73.
28. I. M. Sechenov, AVTOBIOGRAFICHESKIE ZAPISKI (Izd. AN SSSR, 1945), 176 pp.

In a footnote Sechenov added: "Too late, I have learned that Warnek and the famous botanist Tsenkovsky were among the first Russian biologists who worked at that time with the microscope."

On Warnek's socio-political opinions there is no information. His statement against Bogdanov's book, based on the principles of Darwin's evolutionary study, was published in a government journal; objectively, it could have played a reactionary role. The mutual relations of Warnek with the students creates the suspicion of the possibility that the rising conflict was of a political nature. Concerning Warnek's "political orientation," it can be seen that he was later assigned responsible posts in the Department of Education. A search of the archival material may throw light on this subject.

For a characterization of Warnek's scientific work and world view, it is necessary to gain acquaintance with the contents of his basic work, "On the Formation and Development of the Embryo in the Gastropodan Molluscs."²⁹ As an epigraph to this work Warnek selected the words of Reil: "The phenomena of individual life are the necessary result of formation and merging." This idea, as can be seen from the final chapter of this work, Warnek interpreted materialistically. Warnek himself also considered that only in the definite mixing of substances in definite spatial position (form) can the solution of vital phenomena be sought. Science, in his opinion, is not in need of additional idealistic assumptions.

As it is seen from the introduction of his work, Warnek considered his principal task to be the explanation of how the yolk, i.e. substances of the ovum, are transformed into tissue of the embryo and what conditions this transformation. The solution to this question, in Warnek's opinion, is possible only through a thorough investigation of the processes of development, and that is why he also outlined the following vast program. First of all, Warnek suggested, it is necessary to study the reproduction of molluscs, either hermaphrodites or separate sexes. For this aim the following must be studied: 1) structure of male and female sexual organs; 2) origin of

29. See footnote 22 of this chapter.



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embryo, i.e. development of yolk (ovum) and semen;
3) processes occurring during copulation, i.e. the influence of sperm upon the yolk, and finally 4) formation of the additional parts of the ovum—albumin, membranes and ovum cocoons.

Only after this it is possible to begin the study of embryonic development, which Warnek divided into two periods. The first period includes the development of the fertilized ovum, i.e. the process of division and preparation of the development of organs, and the second, the period of development of all systems of organs of the developing animal.

In his investigations Warnek proceeded from the following situations established by the embryologists: 1) for the transformation of yolk into an embryo fertilization is absolutely necessary; 2) this last consists of the material influence of semen on the yolk; 3) this influence takes place only in an infinitely small space, therefore the spermatozoa of the semen must come in direct contact with the mass of yolk; 4) the result of fertilization is the formation of the elementary organs of the embryo (cells); 5) the cells acquire different forms, grouped in complicated organs of the embryo, and thus form its body.

Warnek expressed regret that embryologists could not completely solve the following important questions related to the development of animals: 1) how the yolk, i.e. substance of the ovum is transformed into tissue of the embryo; 2) how its transformation at the time of development occurs; 3) in what does the secret influence of the semen on the yolk consist.

The first question Warnek considered to be solvable, and he expressed the hope that in a short while the other two questions would also be explained.

The solution of the principal questions of embryology, in Warnek's opinion, could take place on the basis of the following presentations:

The cause of the phenomena conditioning the beginning and the subsequent development of the embryo is ordinarily attributed to the vital power, which

absolutely clearly shows that the beginning of life must be sought in the formation of the ovum in the ovary, and the beginning of its development in fertilization, namely in the influence of semen on the yolk. And, of course, the essence of the powers which condition all phenomena of nature remains unknown. If all this can reduce the different phenomena to one cause, this will make a great step toward the goal we have established. (pp. 94 - 95)

During the last four years, aspiration to a solution of the aforementioned general questions was my dearest hope. Devoting myself year after year to the study of the formation, development, and functions of cells, I have stuck to the idea that elucidation of the ideas of development and activity of the cells is the only way to select from the labyrinth of recent presentations about the organic world. The explanation of the causes of the vital activity in the cells leads to a clear presentation about life in general and about causes directing it throughout the organic world. (p. 95)

The following work of Warnek represents the first part of investigations of his planned program; it is concerned with ovum structure and processes of its division in the gastropodan molluscs.

Warnek began with the description of the form of oviposition of the different fresh-water snails; he detailed the periods of oviposition in the region of Petersburg and the structure of gelatinous mass surrounding the ovum. Later he described the structure of the laid ova, especially in the species used in this work: *Lymnaeus stagnalis* and the slug *Limax agrestis*. Transferring to the principal part of the work, throwing light on the study of division, Warnek paused at the characteristics of the yolk granules filling the fertilized ovum. Among these granules Warnek saw a light spot which was not delimited from the yolk membrane and was always situated in the center of the ovum. All the process of division of the ova of the molluscs which he studied Warnek divided into stages, described in succession.

FIRST STAGE: For this stage, characteristic phenomena are taking place in the above mentioned light spot, which, in Warnek's words, occupies the place of the rudimentary (embryonic) vesicle. This spot is in the beginning completely round (Figure 39, 3), then becomes elongated and subsequently takes the form of a biscuit and the shape of a figure eight (Figure 39, 4 and 5). After that when the spot (i.e. nucleus) is twisted by the means just described, it comes nearer to a certain region of the periphery of the yolk (ovum). The end of the spot which is turned to the surface of the yolk widens, and it acquires the form of a blunt rounded cone, in addition between the outer area of this cone and the membrane of the yolk a transparent crescent-shaped region appears (Figure 39, 7). From this crescent-shaped region two small vesicles become separated, which, being isolated from the ovum, remain near it throughout the following development. The place of deviation of these vesicles becomes the center of formation of fissures, later dividing the yolk into two, then into four parts.

The separation of the vesicles Warnek described as follows: on the external surface of the crescent-shaped region a small elevation appears under the yolk membrane. It gradually enlarges, acquiring the form of a spherical segment, a hemisphere, then a complete globule, which is set on a sufficiently thick stalk. Then this stalk becomes unlaced, and the globule becomes free (Figure 39, 9). After the formation of one vesicle the second one appears exactly as the first (Figure 39, 9 and 10). Thus, in Warnek's observations, the crescent-shaped region separates the forming vesicles from the light spot (i.e. from both nuclei of the ovum). He concluded that the nucleus does not share in the formation, at least, of the external vesicles. He made this erroneous conclusion because the intravital observations which Warnek used did not suggest tracing the processes taking place in the nucleus. From this came the further erroneous claim that the separating vesicles could not be regarded as the vesicles of Purkinje or its remnants. In accordance with this assertion Warnek refused to recognize for the vesicles separated from the ovum that important role claimed for them by many authors, and he objected to the name "directing vesicle" (*vesicula directrix*). Warnek did not like this name as it returned embryologists to the time when they believed in an Archean spirit directing vital phenomena.

The presence of vesicles where the formation of fissures of division begins did not prove, in Warnek's opinion, that the topographical position of the fissures was determined by the vesicles. Preferably, as he thought, the matter was the contrary: the vesicles are separated where the center of division is present. In later stages of division many fissures appear without preliminary separation of the vesicles.

After the separation of both vesicles the transparent crescent-shaped region also disappears. In the ova of the slug there appear two nuclei distinctly separated from each other. At this time the nuclei each acquire distinct contour and a large nucleolus.

THE SECOND STAGE begins with the loss of the membranes of the nuclei and their merging into one common mass. This mass acquires an extended form, situated on the longitudinal diameter of the yolk, i.e. at right angle to the position which is characteristic for the first stage (Figure 40, 11). Then the nucleus becomes biscuit-shaped (Figure 40, 12) and at the same time the division of the yolk begins. In the last description Warnek used topographical terms, and their significance is explained in the literal remark. The transverse diameter he called the diameter; passing through the vesicles from the yolk at right angle to it the longitudinal diameter is situated. The terminal points of these diameters he called poles: the dorsal pole in the place where the external vesicles were present; the ventral pole situated against the dorsal one; the poles of the longitudinal diameter designated as right and left.

The division of the yolk is preceded by a thickening of the dorsal pole, in its field; then a fissure in the form of a cut appears. Due to its deepening the ovum becomes in form more like the kidney (Figure 40, 13). The direction of the fissure does not coincide with the transverse diameter; it is inclined to it at a 45-degree angle. The light spot decreases and becomes less noticeable even in the ova of the slug, and in (*Lymnaeus stagnalis*) it is not seen in the majority of cases from the very beginning of the division.

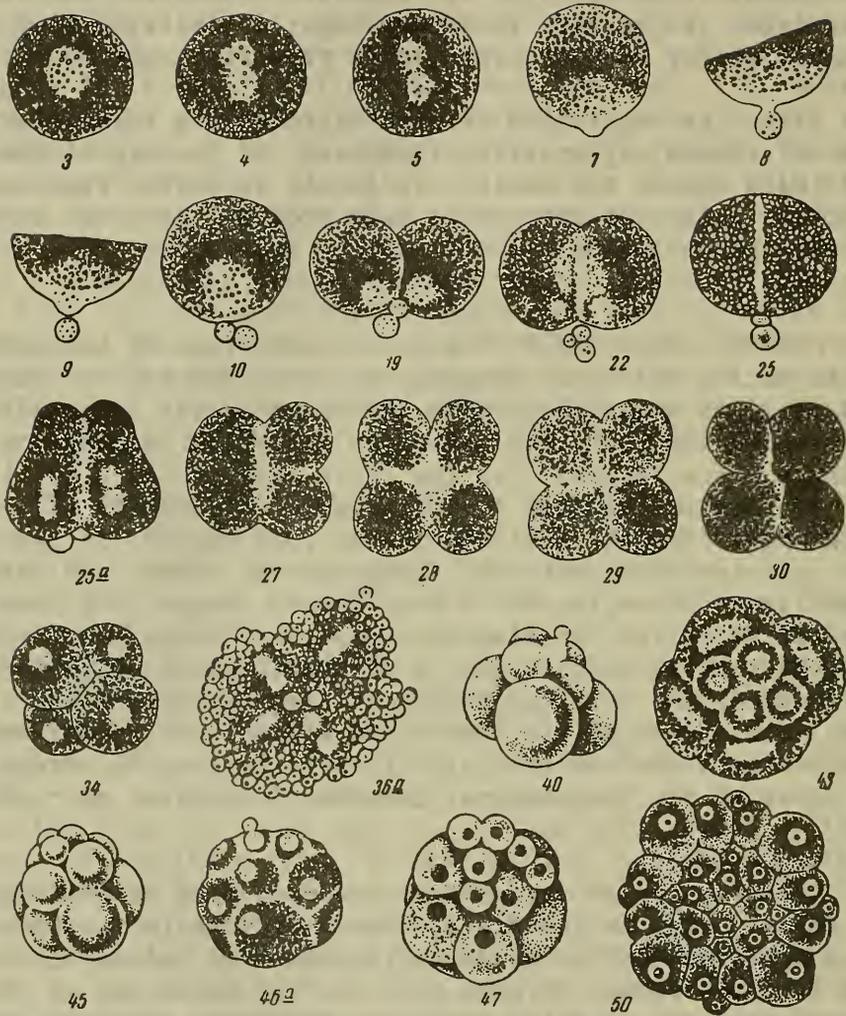


Figure 39. Warnek's drawings for his work on the development of gastropodan molluscs (development of *Lymnaeus stagnalis*)

Figure 39. Warnek's drawings for his work on the development of gastropodan molluscs (development of *Lymnaeus stagnalis*).

- 3-5—the division of the light spot in the fertilized ovum;
- 7—at the external area, light spot coming near the surface; a light crescent-shaped formation appears; the beginning of the formation of elevation;
- 8—the elevation acquires the form of a club-head;
- 9—the second elevation begins to form;
- 10—the second vesicle separates; the light spot becomes spherical; the crescent-shaped region disappears;
- 19—completely separated yolk globules;
- 22—the beginning of secondary nearness of the yolk globules; between them a light space;
- 25—the greatest nearness of the yolk globules; the nuclei are not seen;
- 25a—non-simultaneous division of nuclei into two primary yolk globules;
- 27—non-simultaneous division of yolk globules;
- 28-30—gradual distortion of first fissure of division;
- 34—cross-shaped position of the globules of division;
- 36a—non-simultaneous division of the nucleus into four yolk globules;
- 40—globules of division of the fourth stage (1a-1d) are situated in the space between globules of the third stage (1A-1D);
- 43—extension of nuclei in the yolk globules of the third stage (1A-1D);
- 45—the yolk globules of the fifth stage (2a-2d) separated from the globules of the third stage (2A-2D) and situated between the latter;
- 46a—adjacent situation of nuclei, showing the origin of the yolk globules of the fifth stage from the globules of the third stage;
- 47—the yolk globules of the sixth stage (1a²-1d²) separated from globules of the fourth stage (1a²-1d²);
- 50—the ninth stage of division.

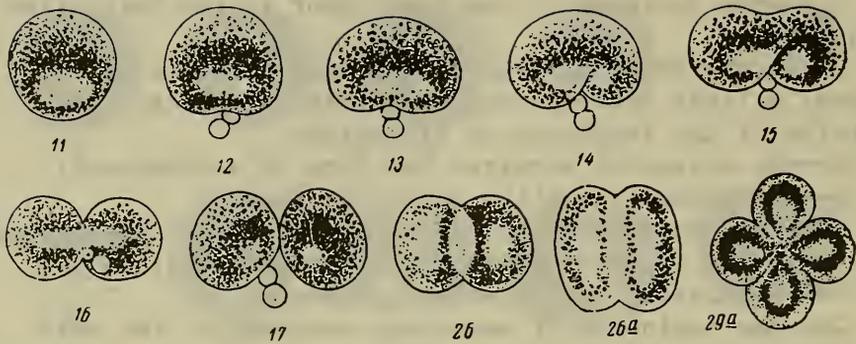


Figure 40. Warnek's drawings for his work on the development of gastropodan molluscs (development of a slug)

11—in the place of the lost membrane of the nucleus, the oval light spot is seen;

12—the yolk has the form of a globule thickened from one side; the light spot is elongated;

13—in the thickened side of the yolk the beginning of the formation of a fissure is seen; the light spot becomes more elongated;

14—the fissure twists the yolk diagonally; the light spot is extended;

15—the fissure envelops half of the periphery of the yolk; at the ventral pole is the beginning of the formation of a fissure in the form of a deepening;

16—deeper twisting of the yolk, viewed from the dorsal pole;

17—the yolk globules are completely separated from each other; the light spot is hardly noticeable;

26—the nuclei are deprived of membranes and begin to extend in a direction perpendicular to the longitudinal pole;

26a—still more distinct changes, the beginning of which is illustrated in Drawing 26;

29a—the stage of four yolk globules.

On the basis of experiments on ova which had been pressed in water, Warnek concluded that the structural changes in the nuclei depend upon the change of their chemical composition. The chemical changes that appear, in Warnek's opinion, condition also the further transformations in the developing ova. After that when the fissure begins in the dorsal side (Figure 40, 14), it passes around half the periphery of the yolk; also in the ventral side, a deepening appears (Figure 40, 15) and the yolk is twisted by the meeting fissures. It acquires first the form of a biscuit, and then two united or even completely isolated globules (Figure 40, 17). At the time of division of the yolk the light spot (nucleus) divides into two parts, each of which at first have caudiform processes, directed to the point of contact of the yolk globules (Figure 40, 16). The processes quickly disappear, and the spot becomes spherical.

These phenomena, according to Warnek, characterize the first half of the second stage of division. At this time it is not possible to isolate the nuclei by (pressing) the yolk globules; from which it must be concluded that the nuclei are still deprived of membranes.

The second half of the second stage begins with the dividing globules moving nearer. Between them a noticeable cavity, formed from a transparent substance, emerges. Warnek considered this transparent substance the product of separation of the yolk globules. At the time the dividing globules are moving closer, the contours of the nuclei in them again become clear, i.e. the membrane appears (it is clearly noticeable in *Limax*) by strongly refracting the color of the nucleolus. In *Lymnaeus stagnalis* the nuclei, at first, are situated near each other (Figure 39, 22), then separate, sink in the depth of the yolk globules, and at the end become invisible (Figure 39, 25). Following the described phenomena each of the two yolk globules become pear-shaped. This outlines the passage to the third stage of division, during which the yolk is divided into four parts.

THE THIRD STAGE begins with changes in the nuclei, acquiring a biscuit or figure-eight shape (Figure 39, 25a); in the drawing it is seen that their division is not accomplished simultaneously: when one divides, the other

keeps the form of a quadrant. The details of these changes can be traced only in the transparent ova of slugs. When the yolk takes the biscuit form, the nuclei are elongated (Figure 40, 26); following this the elongation and twisting of the yolk globules themselves takes place (Figure 40, 26a). The twisting in *Lymnaeus stagnalis* and slugs begins in one globule earlier than in the other (Figure 39, 27), however, soon after this difference smoothes out. The boundary between the globules of division, corresponding to the first fissure, is at first straight (Figure 39, 27), and then becomes curved (Figure 39, 29, 30), and the yolk globules are situated crosswise in two planes.

The processes taking place in the nuclei were described by Warnek as follows: "The membranes of the nuclei disappear, the nuclei elongate, take an oval biscuit-shaped form, then bulge out, and finally each nucleus from the beginning of the division of the yolk globules is divided into three parts. From these parts of the nuclei only four are present in the globules of the division, and two gradually disappear in the fissures between the globules. The four nuclei at first have the form of a comet. When the division of the yolk globules is finished, the CAUDIFORM processes of the nuclei extend and the nuclei again acquire the rounded form" (pp. 146 - 147). The three parts into which, according to Warnek, each nucleus is divided correspond to the two daughter nuclei and to the achromatic figure of mitosis situated between them.

The final step of the third stage is the formation of the membranes around the nuclei and subsequent turning of the cross-shaped globules of division. Two of them are in contact with each other on the dorsal side, and the other two on the ventral (Figure 39, 34). Between the yolk globules a rhomboid space appears during which this is especially clear in *Limax*.

THE FOURTH STAGE. At the beginning of the fourth stage the nuclei in the yolk globules of *Lymnaeus stagnalis* again become unnoticeable from outside. During the crushing out of ova it is possible, however, to see the changes occurring in the nuclei, which, as in the previous stage do not take place at the same time. In Figure 39, 36a it is

seen that in the two globules of division which have the longitudinal form, one nucleus is biscuit-shaped, and the other consists of two isolated parts. After that, when the nuclei become elongated (in slugs this is seen also in the intact globules of division), each yolk globule stretches and becomes pear-shaped. Then the twisting occurs in this form so that the newly forming globules are of unequal size, each separating a region of one third the size. The four smaller globules become displaced and are situated in the spaces between the larger two (Figure 39, 40). "The remarkable reciprocal situation of the yolk globules," Warnek wrote, "is kept and is repeated in all the following stages; this allows one, without ever noticing the further formation of the yolk globules, to solve the question, what globules of division result from each present globule. During this it is necessary to keep in mind the position of the nuclei and the relative size of the yolk globules" (p. 153).

These accurate observations surpassed those investigations of nearly a quarter of a century afterwards. By the initiative of A. O. Kovalevsky, the blastomeres of the dividing ova were given individual designations (in letters and numbers), tracing during the process of development the fate of each blastomere and its derivatives. Warnek formally applied a less suitable and obvious method of designation of the globules of division and their descendants. He named the blastomeres arising in one or the other stage by the number of this stage, keeping for them the same designation also in the following stages of division. During this he mentioned that the yolk globules changed from stage to stage, so that, for example, during the transfer to the fifth stage the globules of the fourth stage were already unequal to the globules of the fourth stage at the moment of their formation. They decrease in size and are changed by chemical properties and internal structure.

THE FIFTH STAGE. In this stage the formation of the new globules of division follows the rules which also hold for the following stages of division. Instead of the sixteen yolk globules which must be present if each of the eight globules of the fourth stage is divided, here only twelve globules are found. This can be explained by the fact that during the fourth stage only four large globules are

divided, and the other four small globules remain unchanged. Before the division itself the nucleus of the ventral (large) yolk globules become invisible, although on crushing out of the ova, it is seen that they elongate, i.e. they are present in a condition of division, while the nuclei or the dorsal (small) globules are not divided and remain round (Figure 39, 43). The dividing yolk globules are stretched and twisted in the diagonal direction (Figure 39, 45). The newly arising yolk globules (again smaller in size than those which gave them the origin) are generally situated by the general rule, in the spaces between the large vegetative globules. The twelve globules of division present in the fifth stage are situated in three rows. The ventral row consists of four globules of the third stage, in the dorsal side four yolk globules of the fourth stage are present, and between the ventral and dorsal globules four newly arising yolk globules of the fifth stage are situated. The globules of the upper and lower rows stand against each other, and in the spaces between the globules of these rows the globules of the middle row are present. Concerning the origin of globules of the fifth stage from the globules of the third stage it is judged by the neighboring situation of their nuclei (Figure 39, 46a). In the second half of the fifth stage, as in the previous one, the smoothing of the surface of all globules of division and their nuclei becomes more distinct. Between the yolk globules a vesicular light space appears.

THE SIXTH STAGE. At the beginning of this stage four yolk globules of the fourth stage become more convex and the globules of the sixth stage separate from them. The yolk globules of the fifth stage remain the spaces between the globules of the third stage (Figure 39, 47). The total number of globules of division in this stage is sixteen.

THE SEVENTH STAGE is characterized by the three divisions of the globules of the third stage, giving rise to the four yolk globules of the seventh stage. The total number of globules of division is twenty.

THE EIGHTH STAGE. In this stage the four globules of the eighth stage are separated from the yolk globules of the

fourth stage. The total number of yolk globules grows to twenty-four.

SUBSEQUENT DIVISION. In each of the following stages four yolk globules are formed. As an example the ninth stage can be employed. In the given drawing (Figure 39, 50) the dividing ovum is pressed, so it is possible to see a great number of globules of division. In the middle the yolk globules of the fourth stage are situated. To these last the oldest and large globules of the fourth stage are adjoined, moving far aside from each other by pressure. To the left of the globules of the third stage the globules of the fifth stage are present, obliquely from which the youngest globules of the ninth stage are twisted; they are situated in the spaces between the globules of the fifth and seventh stages. The globules of the seventh stage originate also from the globules of the third stage and are situated to the right of the last globules. Finally between the yolk globules of the fifth, seventh and fourth stages the globules of the eighth stage are present, arising as a result of a second division of the globules of the fourth stage.

Further Warnek carried out an analogical analysis of the fifteenth stage and established the origin of all globules present at this moment of division.

It is instructive to compare the genealogy of blastomeres, established by Warnek, in gastropodan molluscs with recent data. This comparison shows the complete agreement of Warnek's results with recent data, as seen from the table. In it the designations applied by Warnek and the presently applied literal numerical designations are given.

The same comparison is given in Figure 41, where the contours of drawings 40, 45, 47 and 50 of Warnek are repeated and the data of the recent designations of blastomeres and their designations by Warnek are compared.

There is no doubt that Warnek completely and distinctly chose to follow the fate of the separated blastomeres ("yolk globules") and the participation of their descendants in the formation of organs of the developing animal. Selecting an

irreproachable method by which this problem can be solved, Warnek in the first published investigations on the embryology of gastropodan molluscs described the first period of development up to the formation of the spherical multicellular stage, i.e. the blastula. Only at the end did he briefly mention the following period, when "some yolk globules share in the formation of first internal organ—the yolk sac." This first internal organ, the yolk sac, is of course nothing other than the endoderm of the embryo.

Concerning some details of division, Warnek noted that during the division of the nuclei of the yolk globules the nucleolus appears earlier than the nucleus when divided into two parts, therefore it is possible to find nuclei with two nucleoli. Warnek never saw the process of division of the nucleolus itself. The division of the nucleus in his experience was always accomplished by one plan, which in the early stages of divisions was the same as in the subsequent development of the embryo. This division in all conditions takes place after the stage of stretching of the nucleus, which then acquires the shape of a biscuit and a figure eight and is finally transformed into two separate nuclei.

The globules of division Warnek identified as the elementary organs, i.e. cells, and considered that their multiplication, beginning at the time of division, continued throughout the period of development and even through the entire life of the animal.

All the activity of the developing embryo and the animal forming from it is, in Warnek's opinion, the result of that primary influence which the ovum ("yolk mass") is subjected to by the semen. "This influence," Warnek wrote, "has a purely chemical nature; therefore the explanation for this is still obscure for us; the vital phenomena must be given by physicists and chemists" (p. 168). "The effective element in the organism," Warnek continued,

is the material; this same material influences also outside the organism. If we explain this activity by chemical and physical powers, then there is no reason to deny the activity of these powers in the organism as well. Although these powers still cannot be

completely explained, we do not possess the right to discard them and resort to the help of this power, which exists only in the imagination. Can we explain the phenomenon of crystallization? Why does sodium chloride always crystallize in the form of a cube, and pure carbon in the form of an octahedron? Is not the formation of globules of division, from the point of view of form, a kind of crystallization of organic matter? The successes of organic chemistry belong to us, because the processes accomplished during nutrition, respiration, and excretion are more satisfactorily explained by means of physics and chemistry than by means of a special vital power. This power has retreated into the dark field of our knowledge about the functions of brain and nerves and still dominates in the sphere of embryology. However, new histological directions make the study of the vital power even more unsteady in this sphere, so we are not far from the time when chemistry will completely exclude it from there as well. The concept of vital power must remain as a reminder of our previous ignorance. Only quite recently the influence of semen on the yolk was called dynamical; this expression shows only that the phenomena of fertilization could not be explained. (p. 170)

In these words Warnek exhibited the materialistic world view with complete clarity. He decisively objected against the dull idea of the vital power for the explanation of phenomena of organic life. The only way in which this explanation could be achieved Warnek considered to be the physico-chemical investigations of vital phenomena. Regarding fertilization as a chemical process, Warnek thought that the subsequent transformations of the dividing ovum have as their source continuous chemical changes. Of course, Warnek's materialism has a mechanical character, but it is not excessively simplified vulgar materialism.

Warnek's embryological opinions are expressed in his theses, the most important being:

The yolk mass after fertilization undergoes chemical changes, therefore the fertilization itself must be regarded as a chemical process. It causes changes in the unfertilized ovum which are necessary for further development of the embryo.

The Genealogy of Blastomeres

Comparison of Warnek's designations—stage numbers (in parentheses) in comparison with the recent literal-numerical. (In the square brackets the designation of the resulting blastomeres of the previous stage are repeated.)

- | | |
|-------------------------------------|----------------|
| Key: 1. Stage of division by Warnek | 5. The sixth |
| 2. The third | 6. The seventh |
| 3. The fourth | 7. The eighth. |
| 4. The fifth | |

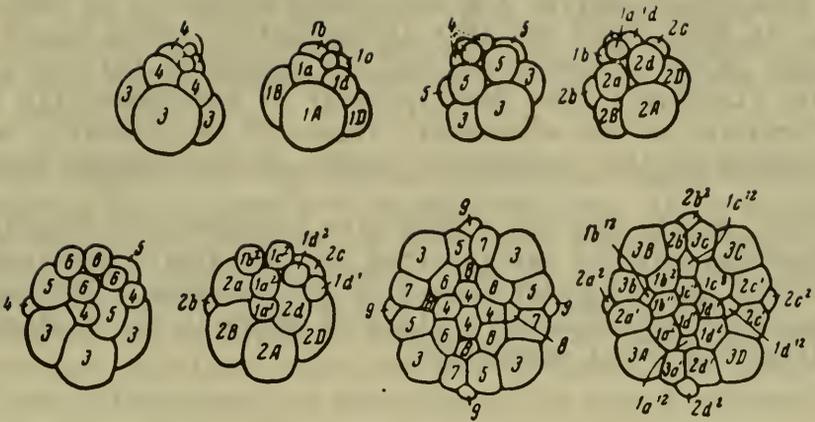


Figure 41. Comparison of Warnek's designations of blastomeres (stage numbers) with the recent literal-numerical designations of blastomeres. These and the other designations are put in the contours of Warnek's drawings.

During the development of the embryo, further changes of chemical processes take place.

The gastropodan molluscs are characterized by complete division.

The globules of division may be considered true cells.

In each stage of a division process four yolk globules are formed, i.e. the division proceeds not in geometrical, but in arithmetical progression.

Beginning with the third stage, the globules of division have unlike sizes.

Warnek's work produced a new page in embryology, directing the investigations of the history of individual development towards the study of subsequent changes of the fertilized ovum and the forming from it of blastomeres, and towards a study of the fate of the separate blastomeres and their descendants during the subsequent formation of the embryo. In this sense Warnek's investigation foreshadowed the works of A. O. Kovalevsky and his countless followers who were studying either descriptively or experimentally the transformation of the elementary organs of the dividing ovum the blastomeres into systems of organs of the forming organism.

N. A. Warnek was for a long time undeservedly forgotten. His classical work is rarely cited and not always mentioned even in the embryological summaries and textbooks, although he unquestionably deserved a place of honor in the history of Russian and world embryology.

The investigations of Grube, Nordmann and Warnek were monographical descriptions of the embryological development of certain representatives of the invertebrates. These works, with all their significance, did not answer, however, the requirements of comparison of the phenomena of development in different types of animals. The first attempt to include a wide number of invertebrates in embryological investigations was done by A. Krohn, whose services in this sphere are much undervalued. Krohn was so thoroughly forgotten that his name was not mentioned either in the encyclopaedias or in the biographical reference books.³⁰ The following circumstance is sufficient to attract the attention of historians of Russian science to Krohn.

During the first committee discussion of Baer's prize of the Russian Academy of Science in 1867, considering possible

30. For help given in researching biographical and bibliographical data about Krohn, the author thanks the biological section of Saltykov-Sedrin Gos. Publichnaya library in Leningrad, especially librarian V. L. Levin.

candidates for the prize, the following was stated: "If the matter concerned the crowning of previous scientific works, then the committee does not doubt that the prize belongs to one of our compatriots, Krohn, who was born in Petersburg. For many years from the fertile shores of the southern seas he collected a rich material which he investigated for the development of different animal forms. His investigation resulted in many excellent works which deserve respect from the scientists of all countries. However, the competition was to take under consideration only the works of the last three years."³¹

The absence of biographical information about Krohn is compensated for by some bibliographical data. It is established that Krohn published no less than eighty works,³² including some small monographs. Many of his publications were accompanied by indications of the time and place of performance of the corresponding work. With these indications one can form opinions about the life of Krohn, who spent no less than thirty years in travel with the aim of scientific investigations, zoological and embryological.

August David Krohn was born in Petersburg in 1803.³³ Concerning his birth and student years of study of Krohn we

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31. "Extract from the report of the committee on the discussion of the prize of secret adviser K. M. Baer, read in public meeting of the Academy of Science on February 17, 1867 by Academician Ovsyannikov," *NATURALIST* (1867), vol. 4, No. 7 - 9, pp. 98 - 104; No. 10 - 12, pp. 146 - 148. The extract cited is on p. 99.
32. The list of publications by A. Krohn is presented in the following:
1. *CATALOGUE OF SCIENTIFIC PAPERS*, compiled by the Royal Society of London (Vol. III, 1869. Vol. VIII, 1879);
 2. W. Engelmann, *BIBLIOTHECA HISTORICO-NATURALIS*, Suppl. Band: J. V. Carus und W. Engelmann, *BIBLIOTHECA ZOOLOGICA: VERZEICHNIS DER SCHRIFTEN ÜBER ZOOLOGIE, WELCHE IN DEN PERIODISCHEN WERKEN ENTHALTEN VOR JAHR 1846 - 1860 SELBSTANDIG ERSCHIENEN SIND*, Bd. I - II (Leipzig, 1861), 2144 pp.
33. Information on the dates of Krohn's birth and death are taken from the brief bibliographical catalogue published by the Library of Congress in Washington.

could not discover any information. One of his early works was produced in Vienna (1836); of the next work there is a memorandum, Petersburg (1837). Later on Krohn was in Heidelberg (1839), and from 1840 he worked nearly continuously on the shores of the Mediterranean Sea and the islands of the Atlantic Ocean. In 1840 and later he was in Naples; from the autumn of 1844 to the spring of 1845 in Messina; 1848 in Nice; 1850 in Naples. In the beginning of 1835 and the winters of 1853/54 and 1856/57 he again was in Messina; in the winter 1855/56 and the spring and summer of 1865 he worked in Funchal (in Madeira) and in Santa Cruz (Tenerife). In December 1860, in May 1861 and in 1867 Krohn was in Nice, and in the first half of the year 1869 he was in Naples. In the intervals between travelling he lived in Paris (winter of 1851/52, spring of 1857) and in Bonn (summer months of 1851, 1853, 1855, 1857 and 1859, winters of 1859/60, 1864/65 and 1856/66, and also the second half of the year 1869).

Concerning the last twenty years of Krohn's long life of eighty-eight years there is again no information.

During his travels Krohn maintained contact with his country, as seen by the report of the conference of the Academy of Science in Petersburg, which presents the following records:

"Mr. August Krohn is a doctor who is famous for his works on anatomy and physiology. He has sent the Academy a significant collection of invertebrate sea animals which was collected by him near Naples, which, in quantity and quality, deserve the thanks of the Academy" (Report from December 16, 1842).

"Dr. Krohn sent again, as a gift to the Academy Museum, two new collections, about one hundred species of fish, crustaceans and others" (Report of September 13, 1844).

On the 7th of November 1855 Krohn was recommended as candidate for corresponding member of the Academy of Science in Petersburg, but was not elected. The biographical data given during this presentation shows only that he was born in Petersburg, lived abroad, and wrote about thirty valuable works dedicated to molluscs (*Paludina*, *Phyllirhoe* and *cephalopoda*),

worms (*Sipunculus*, *Syllis*, *Alciopa*), and tunicates (*Doliolum*).³⁴

During his travels Krohn entered into friendly relations with many great zoologists of the time, such as Johannes Müller, M. Sars, and Delle-Kyaie, and also the young investigators A. Kölliker,³⁵ K. Gegenbaur,³⁶ and A. Schneider. Johannes Müller (1801 - 1851) was a great German zoologist, embryologist and physiologist. For a long time he was the editor of the widely distributed journal ARCHIV FÜR ANATOMIE, PHYSIOLOGIE UND WISSENSCHAFTLICHE MEDIZIN, in which Krohn published about thirty articles. Part of this information Krohn sent to the editor of the journal in the form of letters, containing information about his last works, and Müller published them in his ARCHIV which he sometimes accompanied by remarks and additions, always with a friendly and positive tone. In those remarks of Müller's, discussions can frequently be found revealing his high regard of Krohn's scientific activity.

Krohn willingly related his observations to the zoologists who were working at the same time with him along the sea coast (133). His objective was to verify his data and to confirm their authenticity, and equally to help also the beginning investigators. His description of the planula hydromedusa *Cladonema*, Krohn accompanied with the remark that he showed them to Sars and Gegenbaur, thus certifying the accuracy of his observations.

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34. Archives AN SSSR, fund 2, inventory 17, No. 6. The author is deeply grateful to B. E. Raikov. On a commission from him, extracts of reports of conferences of the Academy of Science were carried out here and an Archives Certificate received.
35. "For accurate information about the structure of marginal bodies in medusa," Krohn wrote, "I am grateful to my young friend Kölliker from Zurich" (A. Krohn, "Einige Bemerkungen und Beobachtungen über die Geschlechtsverhältnisse bei den Sertularinen," ARCH. ANAT., PHYSIOL. (1843), pp. 174 - 181). Albert Kölliker was a well-known histologist and embryologist.
36. Karl Gegenbaur (1826 - 1903) later became a famous comparative anatomist and embryologist.

Anton Schneider (1831 - 1890) was a famous German zoologist, who in a work on the development of the mollusc *Phyllirhoe bucephalum*³⁷ warmly mentioned "the repeated friendly directions" which he received from Krohn not only during the observations taken for that work, but also throughout the time of their presence together in Messina in the spring of 1858. Significantly later, in 1867, Krohn met with Schneider in Nice; Schneider was interested there in larvae of any polychaetes which were covered with peculiar porous membrane. Schneider found that these larvae were well known to Krohn. In addition, as Schneider wrote, "Krohn, with his characteristic generosity, gave me the relevant pages of his journal that I might use the information contained in it at my discretion, expressing the hope that I could trace the further development of these larvae" (p. 498, footnote).

Other works reveal that Krohn did not intend to publish his materials on the development of this polychaete, and agreed that Schneider would do this himself. Schneider wrote the work, its first part (description of the early stages) containing his own materials, and the second the results of Krohn's observations on subsequent development. The work was published under the names of both authors, Krohn's name in first place.³⁸

Helping to increase his material, Krohn showed at the same time extreme punctiliousness in relation to the strange data. This is illustrated by Krohn's following remark on one of the early works about the structure of the nervous system in the echinoderms,³⁹ as he sought to eliminate all shades of suspicion of incorrectness in relation to the published data of other investigators:

37. A. Schneider, "Über die Entwicklung der PHYLLIRHOE BUCEPHALUM," ARCH. ANAT., PHYSIOL. (1859), pp. 35 - 37.

38. A. Krohn und A. Schneider, "Über Annelidlarven mit porösen Hüllen," ARCH. ANAT., PHYSIOL. (1867), pp. 498 - 508.

39. A. Krohn, "Über die Anordnung des Nervensystems der Echiniden und Holothurien im Allgemeinen," ARCH. ANAT., PHYSIOL. (1841), pp. 1 - 13.

After I finished my observations on the nervous system of echinoderms and reported all the existed to Mr. Delle-Kyaie, I learned from this scientist that Mr. Van Beneden, a year before, had already discovered traces of the nervous system in echinus, information about which had appeared in L'INSTITUT. Because I could never get the proper issue of this journal, I should not be blamed for not mentioning Van Beneden's observations. (p. 7)

In all his works Krohn, with exceptional honesty and modesty, mentioned the results of the work of his predecessors, not fearing to recognize the superiority of foreign observations over his own.⁴⁰

No information was kept on personal events in Krohn's life. He was not connected in his work either with scientific institutions or with universities. His life as a traveller-naturalist hardly assisted the acquisition of a family of his own. To his relatives Krohn superficially referred in a letter to Johannes Müller:⁴¹ "After eight months absence, during which I spent April and May in Santa Cruz in Tenerife, I returned to Europe. The immediate cause for this was a forthcoming meeting with close relatives, whom I had not seen for some years" (p. 515).

In the first period of scientific activity (up to 1846) Krohn's scientific interests were concentrated in the anatomy of vertebrates (fish, amphibia, birds) and invertebrates (coelenterates, annelids, arachnids, chaetognatha, molluscs, bryozoa, crustaceans, echinoderms, tunicates). Incidentally to his morphological investigation, Krohn found parasites in the venous sinuses of cuttlefish (apparently diciemid) and described new species of pteropod and cephalopod molluscs.

Zootomical and zoological investigations were continued by Krohn, investigating the structure of protozoa, siphonophora,

40. Concerning the budding of the complex ascidian, Krohn wrote: "Mechnikov, with greater success than I, has traced the gradual development of buds" (Krohn, "Über die Fortpflanzungsverhältnisse bei den Botrylliden," ARCH. NATURGESCH., 35 (1869), pp. 190 - 196).

41. ARCH. ANAT., PHYSIOL. (1856), pp. 515 - 522.

annelids, sea spiders, and arachnids, and describing new species of annelids, chaetopods, and gastropodan molluscs.

There is much authoritative evidence on the accuracy of Krohn's observations and morphological descriptions. These are sufficient to justify the opinion of Kovalevsky,⁴² who was shared in the discussion of the nature of the so-called "ventral saddle" of sagitta. Krohn in 1844⁴³ considered this formation to be due to the nervous ganglion. Later, W. Busch⁴⁴ corrected Krohn's opinion, and, in spite of the latter's objection, Busch shared this point of view with Keferstein, R. Leuckart, Pagenstecher, and K. Gegenbaur. Keferstein did not agree with Krohn, but he gave credit to his anatomical investigations: "Krohn, as it is known, related this saddle's very great size to the nervous ganglion. I, together with Busch, do not doubt in that this excellent investigator was in the present question mistaken."⁴⁵

Kovalevsky, again investigating the anatomical structure of sagitta, strongly supported Krohn against the above mentioned authoritative zoologists. "I am against the new investigators," Kovalevsky wrote, "in considering Krohn correct concerning the ventral ganglion, and I hope to convince my readers of this also" (p. 135). "The ventral ganglion," he continued, "has the form of a long oval or quadrangular body with four large nervous trunks, from which two on the anterior end continue to the brain or the cephalic ganglion, connecting, as Krohn showed correctly, with the lateral nerves of the cephalic ganglion" (p. 136).

42. A. O. Kovalevsky, "Embryologicheskie issledovaniya chervei i chlenistonogikh" (Embryological investigations of worms and arthropods) (1871), IZBRANNYE RABOTY (Izd. AN SSSR, 1951), pp. 123 - 266.

43. A. Krohn, ANATOMISCH-PHYSIOLOGISCHE BEOBACHTUNGEN ÜBER DIE SAGITTA BIPUNCTATA (Hamburg, 1844), 16 pp. This work was published a year later in French (ANN. SC. NAT., 3 Sér., Zool., 3 (1845), pp. 102 - 116) and in English (ANN. NAT. HIST. 16 (1845), pp. 289 - 304).

44. W. Busch, BEOBACHTUNGEN ÜBER ANATOMIE UND ENTWICKELUNG EINIGER WIRBELLOSEN SEETHIERE (Berlin, 1851), viii + 143 pp.

45. Cited in the article by A. O. Kovalevsky.

From 1846, Krohn frequently turned to the study of the phenomena of reproduction and development of different invertebrates - coelenterates, worms, molluscs, crustaceans, and mainly the echinoderms and tunicates.

The development of coelenterates is described in the following words—first, concerning the hydromedusa *Cladonema* and its development from the polyp *Stauridium*⁴⁶: the polyp forms buds from which the medusae are formed. Similar to oceanids, in these medusae, as in *Oceanidae*, in the walls of the stomach the sexual products develop. If mature males and females are situated in separate vessels, then after a short time on the bottom and walls of the latter ova can be seen, covered by a closely adjacent yolk membrane. That these ova are fertilized, Krohn judged by the absence of any embryonic vesicle and embryonic spot (nucleus and nucleolus). Krohn mentioned later the process of ovum division, though not describing it in detail, and referring to the fact that this process was observed already by Dujardin, who did not, however, evaluate its significance. Within two days after fertilization the formed larva is seen in the egg, which later on leaves the ovum membrane and swims with the help of cilia. The larva was characterized by a light superficial layer and included a dark, probably hollow nucleus (Figure 42, A). By its structure the larvae of *Cladonema* are similar with the young of higher organisms such as planulae (*Aurelia*, *Cyanea*, *Cephea*). After two to five days the planula *Cladonema* becomes rounded, situated on the bottom, loses its cilia, and is transformed into a disk, not changing its internal structure. In the middle of the disk appears a round, hollow hillock, which grows later into a cylindrical process, composed of two layers present in planulae. On the upper end of the cylinder (rudiment of the polyp) four hillocks form, corresponding to the external ends of the future antennae. Already at this stage the first stinging capsules are seen (Figure 42, B). Thus, Krohn concluded that "*Stauridium* resulted from the budding of the medusa *Cladonema*, which reproduced by ova; the young developing from the ovum is again transformed into the form

46. A. Krohn, "Über die Brut des *Cladonema radium* und deren Entwicklung zum *Stauridium*," ARCH. ANAT., PHYSIOL. 1853, pp. 420 - 426.

of a polyp. The subsequent change of heteromorphic generation, from which more highly organized medusa develop must be regarded as a generic form and is considered, consequently, "factually proved" (pp. 425 - 426).

A preliminary report on these observations Krohn included in a letter addressed to Müller.⁴⁷

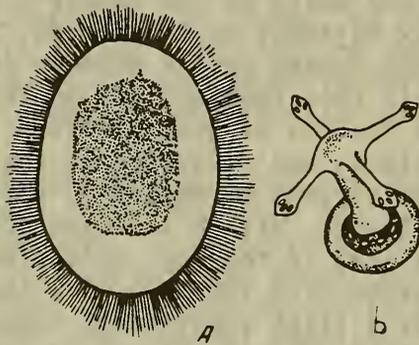


Figure 42. Planula hydromedusa *Cladonema* (A) and the polyp developed from it *Stauridium* (B) by Krohn.

Two years later Krohn published a report about the structure of the early stages of development of the medusa *Pelagia noctiluca*.⁴⁸ At first he found near Messina invertebrate medusae similar to ephyra scyphomedusa, separating from "polyp-form helminths" (scyphistoma), and he found also earlier larvae.

47. A. Krohn, "Über einige niedere. Thiere. Briefliche Mitteilung a. d. Herausgeber," ARCH. ANAT., PHYSIOL. (1853), pp. 137 - 141.

48. A. Krohn, "Über die frühesten Entwicklungsstufen der *Pelagia noctiluca*," ARCH. ANAT., PHYSIOL. (1855), pp. 491 - 497.

The supposition that they were stages of development of *Pelagia noctiluca* was completely confirmed. After many unsuccessful attempts, Krohn could carry out artificial insemination. As a result of division, larvae formed having a cylindrical, usually stretched form (Figure 43, A). The end of the larvae (a) which is directed forward while swimming is rounded, and the other (b) is chipped off. The surface of the larva is covered by short cilia. In the blunt end occurs a depression with an extremely small, round orifice is seen. This orifice is the mouth, which leads to the round, clearly outlined cavity of the stomach (c), occupying the posterior third of the body. The mouth and stomach, in Krohn's words, are already clearly differentiated already in the natural forms, but it is still a non-hatched embryo. However in the present stage the stomach is shorter and more rounded than in the free larvae.

Mechnikov rated highly this discovery by Krohn. In his monograph EMBRYOLOGICAL INVESTIGATIONS ON MEDUSA (1866),⁴⁹ he noticed the weak interest in embryology by the zoologists of the mid-nineteenth century. He wrote:

Even important generalizations, such as the similarity between the two layers of coelenterates and the embryonic layers of the higher animals, emphasized by Huxley, and significant facts, such as Krohn's discovery of the formation of a stomach in *pelagia* by a stretching of the blastomeres, remained without attention and in a lower plane. (p. 284)

The correctness of these observations by Krohn was later confirmed by Kovalevsky and Mechnikov. In this work also, Krohn reported one important discovery: "On the contrary to *Medusa aurita* and other above-named medusae,"⁵⁰ he wrote, "*Pelagia noctiluca* develops without the generation of helminths" (p. 469). Krohn could trace how the swimming

49. Cited in I. I. Mechnikov, IZBRANNYE BIOLOGICHESKIE PROIZVEDENIYA (1950), pp. 271 - 472.

50. Krohn compared the development of *Pelagia* with the development of *Medusa*, *Cyanea*, *Chrysaora*, *Cephea*, and *Cassiopea*.

planula *Pelagia*, while not settling on the bottom and not transformed into scyphistomae, forms on the edges of the mouth orifice processes, later becoming part of *Ephyra* (Figure 43, B and C) with marginal sensory bodies. The citation of this discovery can be found either in later investigators of the embryology of medusae (for example, Kovalevsky⁵¹ and Mechnikov (134)), or in textbooks.⁵²

In 1861, during his residence in Nice, Krohn observed the reproduction and development of hydromedusa *Eleutheria*.⁵³ The ova arise between ecto- and endoderm and there they develop into the larval stage of larva. Ectoderm, covering the embryonic chambers, swells into hillocks, which subsequently break and release young. The larvae are considered typical planulae and are subjected to the same transformation as in the planula *Cladonema*.

The budding occurs not only in asexual, but also in completely differentiated bisexually related individuals. Krohn described the process of budding, and noticed that the budding begins in very young individuals, which are still not completely separated from the maternal individual.

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51. A. O. Kovalevsky, "Observations on the development of Coelenterata," IZV. OBSHCH. LYUBIT. ESTESTV. ANTROP. I ETNOGRAFII, 10 (1874), vyp. 2, pp. 1 - pp. 1 - 36. To the work of Krohn there is reference on p. 7.
 52. K. N. Davydov, TRAITÉ D'EMBRYOLOGIE COMPARÉE DES INVERTÉBRÉS (1928), p. 78. The drawings given by Davydov (Figure 36) illustrating the development of *Pelagia* were taken by him from the work of Delap, published more than fifty years after Krohn's. They are not a bit better than Krohn's drawings.
 53. A. Krohn, "Beobachtungen über den Bau und die Fortpflanzung der *Eleutheria Quatref.*," ARCH. NATURG., 27 (1861), 1, pp. 157 - 170.

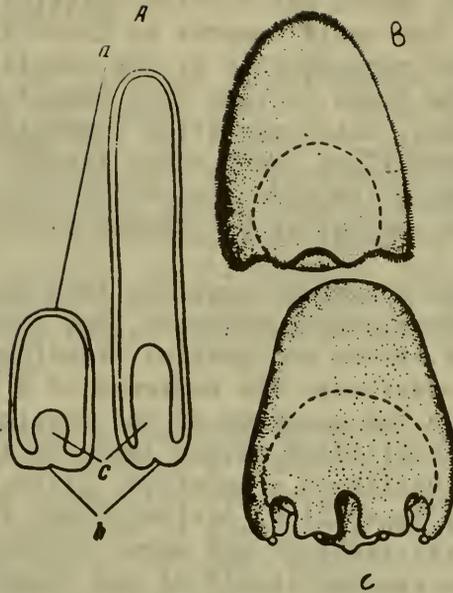


Figure 43. Later stages of development of medusa *Pelagia noctiluca* (by Krohn).

a—anterior; b—posterior end of the body;
c—stomach.

The development of worms⁵⁴ Krohn described in many separate reports. In 1851 he wrote an article on the

54. Of the types of worms known in the mid-nineteenth century, many were distinguished later on in independent groups of forms, including phoronids and chaetognaths, and are so listed.

reproduction and larval stages of "gefirei."⁵⁵ He established the fact of dioecious *Phascolosoma* and described the structure of mature ova of *Sipunculus nudus*. Attempts at artificial insemination of these ova were unsuccessful, and Krohn had to be satisfied with the study of the larvae of *Sipunculus* caught in plankton, whose description constituted the final part of the work. Two small remarks by Krohn are concerned with the vegetative reproduction of the annulated worm *Syllis* and *Autolytus*.⁵⁶ He found in them this change of sexual and asexual reproduction, which permitted comparison with true alternation of generations. Many years later⁵⁷ Krohn again turned to the study of reproduction in sillids, describing the new viviparous species of polychaeta of this genus.

Other of Krohn's reports separate information about the development of nemertineans, phronids, and chaetognaths. The description of larvae and partial transformation of the first two forms constitute the contents of a special article⁵⁸ (135). On the question of the development of nemertineans inside pilidium, Krohn inclined to the opinion that pilidium is considered a helminth, giving origin to worm-shaped sexual generation. Actinotrocha, in Krohn's opinion, is a larval stage of any worm, tentatively relating to echiuroids. The process itself of the transformation of actinotrocha he did not observe and noted only the disappearance of the larval organs and the concentration of antennae in the circumoral corona.

In his excellent investigations on the structure of chaetognaths, Krohn added the study of their development.

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55. A. Krohn, "Über die Larve des *Sipunculus nudus* nebst vorausgeschickten Bemerkungen über die Sexualverhältnisse der Sipunculiden," ARCH. ANAT., PHYSIOL. (1851), pp. 368 - 379.
56. A. Krohn, "Über die Erscheinungen bei der Fortpflanzung von *Syllis prolifera* und *Autolytus prolifer*," ARCH. NATURG., 18, 1 (1852), pp. 66 - 76; "Über die Sprossling von *Autolytus prolifer* Gr.," ARCH. ANAT., PHYSIOL. (1855), pp. 489 - 490.
57. A. Krohn, "Über eine lebendiggebarende Syllisart," ARCH. NATURG., 35 (1869), pp. 197 - 200.
58. A. Krohn, "Über Pilidium und Actinotrocha," ARCH. ANAT., PHYSIOL. (1858), pp. 289 - 301.

In a letter to Johannes Müller sent on February 2, 1853 from Messina,⁵⁹ he reported: "I have at the same time studied the development of sagitta. What Darwin has said about it relates to the development of any fish" (p. 141) (136). Krohn did not publish any further special work on the development of sagitta.

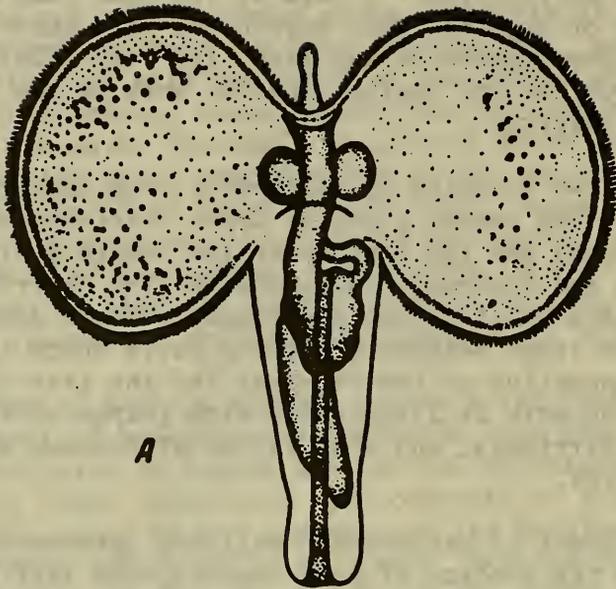
Of Krohn's two articles on Cirripedia, one concerns the structure of the cement gland of *Lepas anatifera* and *Conchoderma virgata* and the anatomy of the female genital system of *Lepas* and *Balanus trintennabulum*. The other⁶⁰ includes some data about larval development. Krohn described the intermediate stage between the young larva which is similar to the nauplius of the copepods and the late cirripes-shaped larva. The work is illustrated with graphs of very young larva of cirripeds, and also larvae of *Balanus* species and *Lepas anatifera*.

The development of gastropodan molluscs (pteropods and heteropods) was the subject of four reports, the last with the character of a detailed monograph.⁶¹ In these investigations his main attention is given to a detailed description of larvae of pteropods (subclass opisthobranchia): *Cymbulia Peronii*, *Tiedemannia neapolitana*, *Gastropteron Meckelii*, and also the larvae of carinate molluscs (subclass prosobranchia): *Pterotrachea* (two species), *Carinaria mediterranea*, and *Firiolides* (Figure 44).

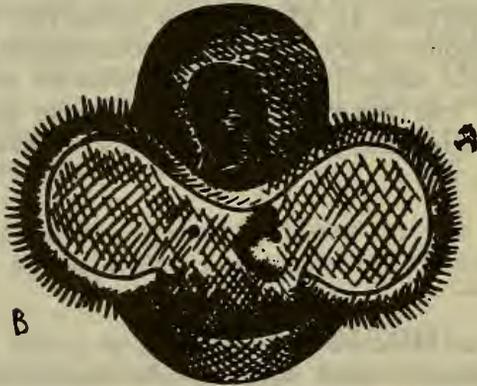
59. ARCH. ANAT., PHYSIOL. (1853), p. 137.

60. A. Krohn, "Beobachtungen über die Entwicklung der Cirripedien," ARCH. NATURG., 26, 1 (1860), pp. 1 - 8.

61. A. Krohn, "Beobachtungen aus der Entwicklungsgeschichte der Pteropoden, Heteropoden, und Echinodermen. Briefl. Mitt. a. d. Herausgeb.," ARCH. ANAT., PHYSIOL. (1856), pp. 515 - 522; "Beiträge zur Entwicklungsgeschichte der Pteropoden und Heteropoden," *ibid.* (1857), pp. 459 - 468; "Über die Schale und die Larven des *Gastropteron Meckelii*," ARCH. NATURG., 26, 1 (1860), pp. 64 - 68; BEITRÄGE ZUR ENTWICKELUNGSGESCHICHTE DER PTEROPODEN UND HETEROPODEN (Lepizig, 1860), 46 pp.



A



B

Figure 44. A-Larva *Clio* from the dorsal side with not completely straightened fans of sailing; B—extracted from ovum larva *Firiolides*, view from above (by Krohn).

The accuracy of Krohn's observations concerning the structure of the larvae of gastropodan molluscs is noted in recent books on comparative embryology. For example, K. N. Davydov wrote that "Already, long ago, zoologists turned their attention to the development of gastropodan molluscs, and Krohn and Nordmann left for us memoirs which even at present do not lose their significance" (p. 625).⁶² And elsewhere: "It is known that the classical case of heteropods (*Firiolides*) was described by Krohn in 1860" (p. 651).

A significant place in Krohn's scientific heritage is occupied by his investigations on the development of echinoderms; they were described in no less than ten special reports and transitional notes in works describing other subjects. His systematic study of the embryology of echinoderms Krohn began in 1848 at the time of his three-month stay in Nice. In February-April he experimented with the artificial insemination of the ova of the echinoid *Echinus lividus*. His observations were compared with data published shortly before by Derbès,⁶³ who also studied the development of *Echinus brevispinosus*.

The mature ovum of *Echinus lividus*, according to Krohn, is covered by membrane (chorion) and composed of yolk (this term Krohn called the ooplasm with nutritional inclusions), with an embryonic vesicle (nucleus) and embryonic spot (nucleolus). Derbès' assertion that the embryonic vesicle disappears in the mature ova up to fertilization, Krohn considered the result of Derbès' insufficiently thorough investigation. Within approximately half an hour after fertilization of the ova, the membrane is separated from the yolk, a phenomenon, which Krohn explained by processes of endosmosis and exosmosis: "the ovum membrane absorbs the fluid from the surroundings and again gives it, to its internal surface" (p. 6). After fertilization the embryonic vesicle and the embryonic spot are no longer seen. In the place of the ovum nucleus, not far from the surface of the ovum, Krohn saw an

62. Davydov, TRAITE D'EMBRYOLOGIE.

63. Derbès, "Observations sur le mécanisme et les phénomènes qui accompagnent la formation de l'embryon chez l'Oursin comestible," ANN. SC. NAT., 3 Sér., 8 (1847), pp. 80 - 98.

64. A. Krohn, BEITRAG ZUR ENTWICKELUNGSGESCHICHTE DER SEEIGELLARVEN (Heidelberg, 1849), 36 pp.

empty vesicle. With Baer and Derbès, he considered this vesicle the nucleus of the fertilized ovum and suggested that the process of yolk division can begin only after the appearance of this nucleus. Within three to four hours after fertilization the division of the nucleus begins. Referring to Baer's excellent observations, Krohn left out the description of the initial processes of the division. In the conclusion of the monograph he noted that the result of the yolk division is the formation of cells, from which the body of the embryo is formed, because the globules of division are unnoticeably transformed into cells of the developing larva. The evidence of this transformation is found in the contents of the cells; "numerous molecules inside the last substance are nothing but yolk granules, from which the division globules are previously formed" (p. 29). "In the same genetic relation, the nuclei of the cells are related to the vesicular nuclei of the division globules" (p. 30).

Krohn prefaced the characteristic of the fully formed echinus larva with the development of the larva, suggesting that knowledge about the final development must help the understanding of the phenomena leading to it. The external form of the pluteus, the structure of its skeleton and the digestive system are represented in the drawings and are described as follows. The formed larva, within eleven days after the fertilization, is pear-shaped (Figure 45, F); it possesses two pairs of limbs: the short ee and the long dd. On the convex side, facing the mouth f, and situated between the limbs, the anal opening q is present, although frequently closed, which is why Johannes Müller missed it in the larvae of ophiuroids and echinus. The bilateral symmetry of the larva is absolutely clear and is expressed in the pairing of limbs and the calciferous skeleton carrying their branches, in the situation of the mouth and the anus in the plane of symmetry. Inside the larva is a cavity extending to the end of the limbs; the digestive tract lies in this cavity, surrounded by loose fibrous tissue. The larval surface is covered with skin; the last is formed from twinkling cells, in each of which there is a nucleus with nucleolus. The calciferous skeleton consists of four pairs of toothed branches (Figure 45, G), the longest branches gg are club-shaped, the next pair is found in the long limbs hh, another pair in the short limbs kk, and the last pair ll is situated across the longitudinal axis of the larva.

The digestive canal consists of three parts, the anterior (the pharynx), the middle (stomach) and the posterior (intestines), all covered by cells with cilia, similar to the cells of the skin. The digestive canal is attached to the body cavity by fibrous tissue; it forms a network united with the internal surface of the skin. In the junctions of the network, nucleus-like formations are situated; they are numerous also under the skin, in the neighborhood of the calciferous skeleton. Krohn noted Johannes Müller's error when he assumed them to be strong fibers instead of nerves, and the nuclei of fibrous tissue instead of nerve ganglia. The larva swims with its limbs, mouth opening forward; its movement is carried out by the activity of the cutaneous twinkling cilia, which also drive into the mouth food particles suspended in the water.

The formation of the larva described here takes place as follows. After the division is completed, the young spherical larva rotates in the ovum membranes with the help of the long cilia which cover all the surface of its body. In the larva at this time can be observed a closed central cavity and cover, which can be differentiated, forming the wall of the latter. Krohn erroneously considered that the wall of the body consists of many layers of cells. Within a day after fertilization, when the number of the cover cells becomes sufficiently large, the ovum membrane is torn and the larva begin to swim. Soon after hatching it acquires its ovoid form (Figure 45, A); during swimming its narrow end is directed forward.

In the body cavity of the larva, from the side of the blunt end, an accumulation of closely situated dark bodies, similar to the nuclei, is seen. The number of these nuclei at first is small, but it quickly increases so that they are found filling half of the body cavity of the larva, toward its blunt end (Figure 45, A,e). Later, nuclei are separated from each other and distributed evenly in the body cavity, and then partially accumulate not far from the rudiments of the calciferous skeleton. After this, the nuclei become angular or fusiform and begin their transformation into the fiber of the reticular tissue which strings the body cavity and holds the digestive tract.

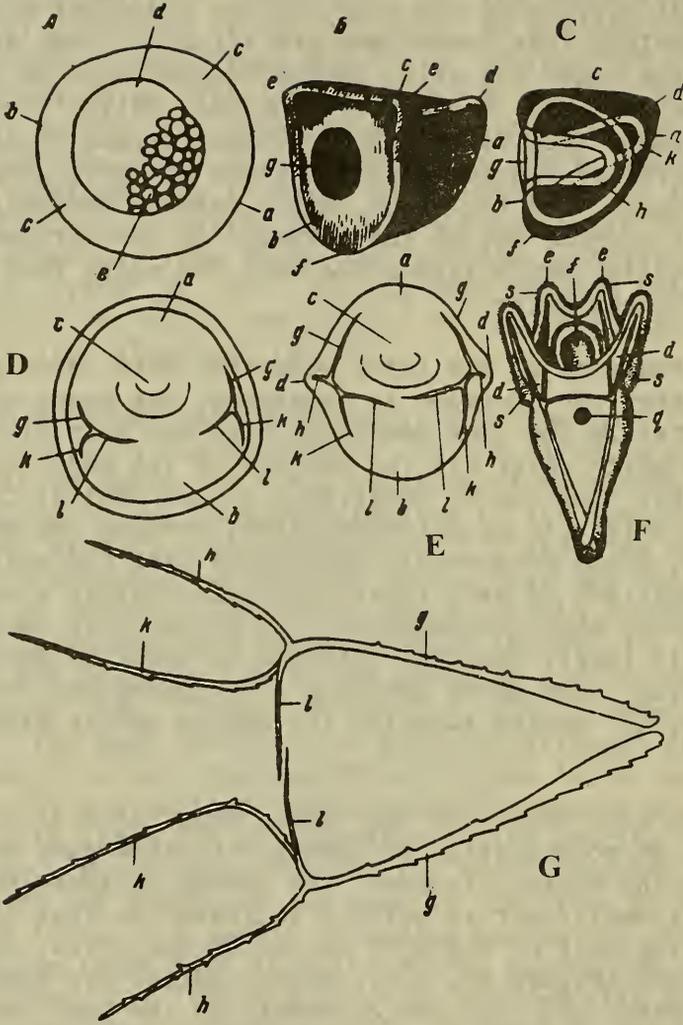


Figure 45. Development of echinus, *Echinus lividus* (by Krohn).

Figure 45. Development of echinus, *Echinus lividus* (by Krohn).

- A—larva shortly after hatching: a—blunt pole; b—sharp pole; c, c—cover; d—central cavity; e—accumulation of "nucleus-like formations" from which the fibrous tissue is later formed.
- B—"ideal sketch" of the larva, already having the form of the body with three surfaces: a, b, c—anterior, posterior, and upper surfaces; d—anterior angle; e, e—posterior angles; f—lower angle; g—anus.
- C—cross-section of this same stage of development, in which for elucidation of the passage the previous apple-shaped form was drawn: a, b, c, d, e, f, g—as in figure B; h—rudiment of the digestive tract in immature form; k—its rudiment in later form.
- D—larva of the following form, back view: a, b—posterior and upper surfaces; c—anus (back passage); gg, ll, kk—rudiments of club-shaped, arch-shaped, and transverse branches of calcareous skeleton.
- E—later larva: a, b, c, g, k, l—as in figure D; dd—rudiment of posterior limbs; hh—first traces of hydrants in it.
- F—larva of pear-shaped form, back view: dd—posterior limbs; ee—anterior limbs; f—mouth; q—anus; ssss—cilia apparatus.
- G—calcareous skeleton of the formed larva, represented in an islated view: gg—club-shaped hydrants; hh—hydrants of anterior limbs; kk—arch-shaped hydrants; ll—transverse hydrants.

From Krohn's description it is clear that he saw, for the first time, in the cavity of echinus division that accumulation of cells, which was called by the latest embryologists the primary mesenchyma. He correctly determined the fate of these cells in larval development. This discovery of Krohn's was so thoroughly forgotten that Mechnikov, who was well acquainted with the old embryological literature, attributed it to Selenka, whose work was published exactly thirty years later after Krohn's monograph.⁶⁵

"The development of *Echinus microtuberculatus*," Mechnikov wrote, "was studied by Selenka. The first differentiation of the embryonic layers begins with the bulging of the lower cells of the blastoderm. Until the beginning of their protrusion they form a number of wandering cells, which later develop into the cutis and are considered mesodermal or mesenchymal cells."⁶⁶

Krohn observed that after nearly thirty hours after fertilization the following important changes take place in the larva of *Echinus lividus*. In the center of the blunt pole a small hole-like deepening appears. The blunt pole widens and thickens; the hole in its center becomes deeper and wider, so that the body of the larva becomes similar in form of an apple. The more enlarged hole "formed as a result of that," Krohn wrote,

caused the skin in this area gradually to protrude (EINSACKT ODER EINWARTSSTULPT) into the cavity of the body. The protrusion (EINSACKUNG) submerged deeper in the body cavity and extended into a canal which finally reached the walls of the body cavity toward the blunt pole. The sac which appeared by this means stretched through the body cavity (Figure 45, C, h, k) and is the rudiment of the digestive cavity. The edge or circumference of the primary hole becomes a leading opening in the canal, which is the anus. In

65. E. Selenka, "Keimblätter und Organanlage bei Echiniiden," ZTS. WISS. ZOOL., 33 (1879).

66. I. I. Mechnikov, "Vergleichend-embryologische Studien. 3: Über die Gastrula einiger Metazoen," ZTS. WISS. ZOOL., 37 (1882), pp. 286 - 313.

this view's favor—on the manner of appearance of the digestive tract—is the fact that it also indicates that the wall of the canal is absolutely equivalent to the skin in thickness and structure. (p. 18)

Krohn's discovery of the nature of the formation of the larval intestine of echinus undoubtedly possesses outstanding significance. This, unquestionably, is the first description of the invaginated gastrulation phenomenon. Its study subsequently played a great role in the progress of comparative embryology. Comparative analysis of methods of separation of the endoderm is included in the basis of Kovalevsky's evolutionary concept about the formation of the embryonic layers, and also in the basis of Haeckel's gastrula theory. Krohn's priority in this question was not definitively underlined. Mechnikov, in the article just cited, wrote the following.

Derbès (1847) described the formation of the larva of *Echinus esculentus* and mentioned a stage in the form of a double sac with skin layer in which the caecum opened to the outside. Twenty-five years later, Haeckel gave this the name gastrula, which was accepted by scientists all over the world. Derbès thought that the opening of the rudiment of the intestine was the mouth, but August Krohn (1849) showed that it corresponded to the anus of the pluteus. He described the process of protrusion itself.

Krohn referred to Derbès' observations: "The reader can form an excellent concept of the gradual formation of the digestive tract just described by looking at Figures 13 and 14 in Derbès' article; however, the author apparently did not pay attention to the process of formation itself" (p. 19). The following is written by Derbès: "The spherical form of the larva is changed by pressure at one point of the surface. Gradually this pressure becomes more pronounced, and its center is penetrated by an opening which leads to a rudiment of the intestinal cavity. Beginning from this moment, the movement of this opening is always directed forward and, later, upwards. . . that is, the mouth looks towards the zenith" (pp. 91 - 92). It is clear that Derbès did not put the deepening on the surface of the spherical larva in genetic relation with the formed intestine. According to his opinion, the opening formed in the center of the deepening united in an unknown way

the developed rudiment of the digestive tract with the external world. Krohn pointed also to Derbès' mistaken assumption that this opening was the mouth. He established that the opening in the area of protrusion is the anal opening, and the mouth is formed in another place significantly later (on the fourth day after fertilization).

Further observations of Krohn are concerned with the changes in the larval form as it becomes bilaterally symmetrical (Figure 45, B and C). He described the formation of limbs and the calciferous skeleton (Figure 45, D and E), which gradually acquires a different configuration.

In the following year, Krohn repeatedly returned to the study of development of the different echinoderms and published many reports on this subject, One of these reports considered the development of the holothurian and echinus.⁶⁷ The larvae of holothurians (*Holothuria tubulosa*) were obtained from plankton, because attempts at artificial insemination proved unsuccessful. The youngest larva observed by Krohn "is similar to an elongated egg (Figure 46, A); in its sharp pole there is an opening leading to a sac-like protrusion in the body and an ampulla-shaped canal widening at the end b. This sac is the rudiment of the digestive tract, the opening doubtlessly is the anus" (p. 345). Krohn noticed that the larva of *Holothuria tubulosa*, at this stage, is very similar to the larva of *Echinus lividus* described earlier by him (1849). Similar to the latter, the larva of *Holothuria tubulosa* is covered by cilia, and with their help it swims with the imperforate pole forward. The surface of the body and the digestive tract consist of cells which, with their nuclei, become noticeable with the addition of fresh water. In the body cavity, as in the larvae of *Echinus lividus*, fibrous tissue with fusiform cells is found. Later (Figure 46, B) on the abdominal side of the larva a depression appears—which is the future transverse fissure of ausicularia; in this fissure the mouth opening later appears. Later the body acquires a kidney-shaped configuration (Figure 46, C). The digestive tract, at this time, forms the rudiments of the three

67. A. Krohn, "Beobachtungen aus der Entwicklungsgeschichte der Holothurien und Seeigel," ARCH. ANAT., PHYSIOL. (1851), pp. 344 - 352.

parts, pharynx e, stomach d and intestines c. The appearance of the mouth opening coincides with the beginning formation of the ciliary strings in the auricularia. At this stage there is some data about the transformation of the *Echinus lividus*.

Krohn's other reports on the development of echinoderms briefly designate some representatives of the type⁶⁸ or species.⁶⁹

Special attention must be given to Krohn's investigations on the development of tunicates. Originally his interest was attracted by Salpa, in which the wonderful phenomenon of the alternation of sexual and asexual generations had already been recognized. This discovery belongs to the poet Adalbert Chamisso (1781 - 1838). With the Dorpat-born zoologist J. F. Eschscholtz, he traveled around the world on the Russian ship RURICK. Chamisso published the results of his investigations in "On Some Animals of the Linnean Class of Worms, noted during a world tour, performed by Count N. Romanzoff, under the command of Otto von Kotzebue, from 1815 to 1818, Part I: On Salpa."⁷⁰

68. A. Krohn, "Bemerkungen über einige Echinodermenlarven," ARCH. ANAT., PHYSIOL. (1851), pp. 353 - 357; "Über die Entwicklung der Seesterne und Holothurien (Briefl. Mitt. a. d. Herausgeb.)," ibid. (1853), pp. 317 - 321; "Beobachtungen über Echinodermenlarven (Briefl. Mitt. a. d. Herausgeb.)," ibid. (1854), pp. 208 - 213; "Über neuen Entwicklungsmodus der Ophiuren," ibid. (1857), pp. 369 - 375.

69. A Krohn, "Über die Entwicklung einer lebendiggebärenden Ophiure (Briefl. Mitt. a. d. Herausgeb.)," ARCH. ANAT., PHYSIOL. (1851), pp. 338 - 343; "Über die Larve von *Spatangus purpureus* (Briefl. Mitt. a. d. Herausgeb.)," ibid. (1853), pp. 255 - 259; "Über die Larve des *Echinus brevispinosus*," ibid. (1853), pp. 361 - 364.

70. DE ANIMALIBUS E CLASSE VERMIUM LINNEANA IN CIRCUMNAVIGATIONE TERRAE AUSPICANTE COMITE N. ROMANZOFF DUCE OTTONE DE KOTZEBUE ANNIS 1815, 1816, 1817, 1818 PERACTA OBSERVATIS ADELBERTUS DE CHAMISSO, Fasc. primus: DE SALPA (Berlin, 1819), iv + 24 pp.

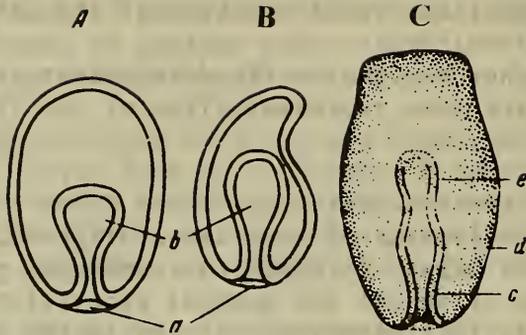


Figure 46. Three stages of the development of the sea cucumber *Holothuria tubulosa* (by Krohn).

A and B: a—anus; b—digestive cavity.
 C: b—anus; c, d, e—rudiments of the intestine, stomach and pharynx.

The alternation of sexual and asexual generations in Salpa was described by Chamisso as follows:

The species of Salpa is found in double form: each generation of the species is dissimilar to its parents, but through birth posterity is similar to the last, so that any Salpa differs from its parent but is identical with its grandparents. Both forms are similar to headless molluscs, hermaphrodites or the female sex. Both of them are viviparous, but one of them is a solitary animal, the originator of many descendants. The other represents a complicated branch consisting of animals, each united with the others by the necessary connection which gives birth to one descendant. These changed forms of the unchanged species are called solitary (*Proles solitaria*) and aggregated or colonial (*Proles gregata*) generations.
 (p. 2)

After the discovery by M. Sars⁷¹ of the analogical change of generations in scyphomedusa, Steenstrup united these facts to produce one biological regularity. Steenstrup's general conclusion was highly regarded by his contemporaries, in particular by Baer.⁷² Krohn also gave great significance to Chamisso's discovery and Steenstrup's ideas. He made it his task to study in detail the reproduction and development of Salpa. To do this, he settled for many months on the coast of Sicily, where the sea provided him the necessary material. Krohn put the results of his observations into a special work,⁷³ in which, first of all, he completely confirmed Chamisso's observations, by distributing them over seven species of Salpa which were, for the first time, partly described by him. The comparison of the solitary and colonial forms (*Proles solitaria* and *Proles gregata*, in Chamisso's terminology) allowed Krohn to regulate the taxonomy of this group of tunicates. He showed that salpae described under different names frequently proved to be different stages of the development of one and the same species (137). Later, Krohn gave the characteristics of the structure of the heteromorphic generation, and also described the ovum, the seminal glands, and the process of fertilization in the sexual generation.

Within the present book, the greatest significance is placed on the section in Krohn's article (111) in which he discussed development of the embryo in the maternal organism. After fertilization, the embryonic vesicle and the embryonic spot disappear, after which the ovum enlarges in size and acquires a regular spherical form. This was according to Krohn, who was not completely convinced of its authenticity. Sometimes the ovum is not seen like that, and in its place a round body appears, raising a region of tunica of the mother and jutting into its cavity in the form of papilla. This body, Krohn wrote, is nothing other than the rudiment of the placenta which, by deepening in the cavity of the body of the maternal organism, enters in connection with two of its blood vessels. Only after the formation of the placenta does the embryo begin to develop, at first in the form of a very small body appearing

71. M. Sars, "Über die Entwicklung der *Medusa aurita* und *Cyanea capillata*," ARCH. NATURG., 7 (1841), pp. 9 - 34.

72. See Chapter 23.

73. A. Krohn, "Observations sur la génération et le développement des Biphores (*Salpa*)," ANN. SC. NAT., 3 Sér., Zool., 6 (1846), pp. 110 - 131.

on the summit of the placenta under its cover (138). In this rudiment of the embryo all organs of the last are developed; "however," Krohn wrote, "all that concerned its development during the first period remained for me almost completely unknown" (p. 123). He could only establish that one of the first organs of the embryo by the time of appearance is "the respiratory cavity." The embryo changes from compact to hollow, following which the rudiments of the branchae and nervous ganglion are already seen, while the organs "visceral nucleus" and heart become noticeable only later. Only after that does the embryo acquire a definite form; the anterior and posterior openings appear in it. At the end the embryo becomes more voluminous than the placenta, and all its organs intensively enlarge, especially the nervous ganglion, from which numerous nervous branches grow. At the same time muscular strips and blood vessels appear, which are not completely formed.

Krohn's concluding paragraph of the work is dedicated to the processes of budding in the asexual regeneration of Salpa, and to the formation of colonies; the character of the last varies in different species. Here the description of the stolon and the embryos is given, situated along it so that their axes cross the stolon at a right angle. These embryos develop in definite succession, depending on their situation on the stolon.

The development of salpa, especially the formation of their embryos from fertilized ova, represents one of the most difficult principles of embryology. Krohn's investigations began this study and recent opinions are credited to many Russian embryologists at the end of the nineteenth and the beginning of the twentieth century, including A. O. Kovalevsky, M. M. Davydov, A. A. Korotnev, and V. V. Zalensky.⁷⁴

Six years after the publication of the above-mentioned work, Krohn published an article presenting the results of his investigations of the little-studied group of tunicates, the doliolum.⁷⁵ Quoy and Gaimard made a voyage on the

74. "The first investigations of the development of Salpa go back to Krohn," K. N. Davydov wrote in his handbook (TRAITÉ, p. 867).

75. A. Krohn, "Über die Gattung Doliolum und ihre Arten," ARCHIV. NATURG., 18 (1852), pp. 53 - 65.

ASTROLABE⁷⁶ to Road Island, Ambon (in the Moluccas), and to the coast of the Vanikoro Islands (between the New Hebrides and the Solomon Islands). During this time they discovered this small transparent tunicate, which they described and presented only incompletely, and for which they suggested the generic name *Doliolum*.

Later T. Huxley, on a tour around the world aboard the ship RATTLESNAKE, saw doliola in the southern part of the Pacific Ocean and described their structure more exactly and in more detail than Quoy and Gaimard,⁷⁷ but in his notes the male genital glands were given for individuals of sexual regeneration.

Krohn, for the first time, discovered the presence of doliola in the Mediterranean Sea (near Messina and Naples), studied the structure and described three new species. According to Krohn, doliola "are free living ascidians, but in many respects are similar to salpa and form, therefore, an interesting intermediate link between both these orders of tunicates" (p. 53). From Krohn's description, the structure and reproduction of doliolum, according to the majority of the features, must be related to salpa; this applies also in the present taxonomy.

Krohn observed that from the ova of doliola cercaria-like larvae develop which later undergo metamorphosis. The peculiarities of the larvae are connected, according to Krohn, with the mode of life of the tunicates more than to ascidians, which are in their adult condition fastened motionless to the substrate. In accordance with this, in the ascidian larvae the tail disappears early, but in the larvae of doliola it remains throughout metamorphosis and serves as an organ of movement. The process of reduction of the tail in the larvae

76. VOYAGE DE DECOUVERTE DE L'ASTROLABE EXECUTE PAR ORDRE DU ROI PENDANT LES ANNÉES 1826 - 29 SOUS LE COMMANDEMENT DE M. J. DUMONT D'URVILLE. ZOOLOGIE PAR MM QUOY ET GAIMARD, vol. 3 (1834).

77. T. Huxley, "Remarks upon Appendicularia and Doliolum, Two Genera of Tunicates," PHIL. TRANS. ROY. SOC. LONDON (1851), pp. 599 - 602.

of doliola takes place as in the larvae of ascidians. In the latter the disappearance of the tail was noticed for the first time by Milne-Edwards in an example of the colonial ascidian *Amourucium proliferum*, and was described in more detail by Krohn for *Phallusia mammillata*.

The metamorphosis of doliola was again studied by Krohn on the species *Doliolum Nordmanni*. Krohn represented two stages of transformation; Figure 47, A represents the stage when the tail of the larva has not begun reduction; and Figure 47, B, the larva with shortened tail. Until metamorphosis the tail of the larva is tapered, with the two ends covered with gelatinous membrane a; its axis d is composed of cuboidal cells situated in one row, so that it seems to be segmented. The root of this axial shaft penetrates into "the vesicular appendix" c, lying under the digestive tract of the larva. This vesicle decreased simultaneously with the reduction of the tail and at the end it disappears (139). In the stage represented in Figure 47, B, all organs in the larva are already differentiated; on its dorsal side there is the placing of the stolon q.

Krohn's description of the structure of the larva of doliolum and its transformation distinctly shows that he saw in it all the principal features of organization, on the basis of which the doliolum was later counted as a type of chordate (subtype tunicate, class salpa): the presence of the reduced cord at the time of metamorphosis ("axis of tail"), the situation of the nervous ganglion o on the dorsal side and the heart m on the ventral side.

Correct evaluation of Krohn's investigations was given by V. N. Ulianin in the classic monograph on doliola, first published in Russian, and two years later in German.⁷⁸ Ulianin wrote the following: "Soon after the appearance of Huxley's article the doliolum was found in the Mediterranean by Krohn.

78. v. Ulianin, ON THE DEVELOPMENT AND REPRODUCTION OF DOLIOLUM (Moscow, 1882), 100 pp. B. Uljanin, DIE ARTEN DER GATTUNG DOLIOLUM IM GOLFE VON NEAPEL UND DEN ANGRENZENDEN MEERABSCHNITTEN, FAUNA UND FLORA D. GOLFES V. NEAPEL, x. Monographie (1884), 140 pp.

The article in which this discovery was published possesses important significance in the history of doliolum, as it contains the first observations on the development of this animal. Krohn not only described the tailed larva of doliolum, but he also pointed out the alternation of generations in the reproduction of this animal.... On the basis of his observations Krohn concluded that from the ovum of doliolum is formed the tailed, freely swimming larva, which after the loss of the tail is transformed into an asexual doliolum" (p. 2). Later on Ulianin noticed Krohn's mistake in dividing doliolum according to the number of muscular strips. In all species of sexual generation there are eight, but in asexual species there are nine strips. Therefore the species described by Krohn, *Doliolum Troscheli*, is in fact an asexual individual *D. denticulatum* Q. and G., and *D. Nordmanni* Krohn is the asexual generation of *D. Mulleri* Krohn. Particular significance was given by Ulianin to Krohn's embryological observations. "All that is known presently about the embryological development of Doliolum," Ulianin wrote, "comes exclusively from Krohn, who for the first time described the free larva. All later authors.... only redescribed it, not adding anything essential to Krohn's description (p. 47).

The central place among Krohn's investigations of the development of tunicates is occupied by his work concerning the solitary ascidians.⁷⁹ The artificial insemination in ascidians which was used successfully for the first time by Baer, Krohn also used, observing the development of *Phallusia mammillata* step by step for three months. He described the mature ovum of this ascidian in the following way. The ovum present in the ovum-fluid is supplied by papillae and covered by a cover membrane under which the proper ovum membrane is present. Somewhat deeper lies a hyaline membrane containing inclusions which is green in color. The yolk itself is colorless, the embryonic vesicle and the embryonic spot in the mature ova are unnoticeable. The above mentioned green hyaline membrane was considered by Krohn, following Milne-Edwards, a source of formation of tunica. The error of this view was later established, but it was repeated in many

79. A. Krohn, "Über die Entwicklung der Ascidien," ARCH. ANAT., PHYSIOL. (1852), pp. 312 - 333. In the following year this work was published in English as "On the Development of the Ascidians," SC. MEM. NAT. HIST. (1853), pp. 312 - 329.

subsequent embryological works. The division of the ovum begins two to three hours after contact with the sperm. Krohn considered that the division, at least in the first stages, follows the rule of progress. The vesicular nuclei of the globules of division disappear before every division and then again become visible. "Instead of nuclei," Krohn wrote,

in every divided globule an absolutely peculiar distribution of yolk molecules is noticed. Namely, they are distributed in the form of strands, which are directed from the depth, from the medial point by radius in all directions to the lighter periphery of the ovum and, apparently, come out from two centers of irradiation. After the end of division, inside the new globules the nuclei again become noticeable, then these radiant figures disappear and the yolk granules are found to be situated close to each other. (p. 315)

These observations show that Krohn exactly described many details of mitotic division in blastomeres.

Embryonic development goes quickly, and a day after fertilization a cercaria-like embryo with a more or less developed tail is already present in the ovum membrane. The body and the tail of the embryo are composed of cells which are especially noticeable on the surface. The cells have a polygonal form, and contain granules and nuclei in the center. The axis of the tail, according to Krohn's description, is composed of larger rectangular cells with nuclei situated in a row, one following the other, and therefore they have a striated or a disjointed form (Figure 48, A, b).

Shortly before the final formation of the larva the tail undergoes remarkable transformations. According to Krohn's observations, they amount to the following. The axis is transformed into a canal, as its cellular structure gradually disappears due to the destruction of the partitions between the neighboring cells and the liquefaction of their contents. The small cells surrounding the central tail strand are transformed into longitudinal muscular fibers. On the dorsal side of the larva at first appears one, and then behind it another, pigmented spot of granular origin (Figure 48, A, d, e and B, e, f). At the time of transformation this formation is

destroyed, and the pigment passes into the blood channel. The formed larva is set free from the membrane by the tail movement. The body of the larva (Figure 48, B) in the anterior end is supplied by three similar processes on the sucker. The larva is soon attached at the anterior end and undergoes transformation, one of its marks being the disappearance of the tail. Milne-Edwards saw only that the axial part of the tail is set free from its covered sheath and extends into the body of the larva, but he did not elucidate the subsequent fate of this formation. "By my observations," Krohn noted,

the setting free and the extension of the tail axis, the deep immersion by the tail in the body of the larva only precedes the processes of reduction which it soon undergoes. Directly after the extension, the tail axis remains undamaged at the posterior part of the body. It is situated here convoluted into a spiral coil With the beginning of the development of the young ascidian, this coil first disintegrates into a large number of strips situated close to each other, which then are gradually destroyed; the number and size of the strips decrease, but the insignificant remnant does not disappear entirely. (Figure 48, C) (pp. 318 - 319)

Krohn himself considered his observations on the development of ascidians incomplete, and he acknowledged only the most essential changes. He described in particular the formation of the vessels of the tunica and the development of the respiratory cavity, or gill cleft, and behind it the rudiment of the digestive canal in the form of a loop-shaped canal. Somewhat later three openings on the spinal side of the body appear: the most anterior, the inlet into the respiratory cavity and digestive canal, and two posterior which later merge together in a common excretory opening. Simultaneously, the nerve ganglia develop in an elongated formation in the middle of the back near both pigmentation spots. Near the nerve ganglia the rudiment of the muscular strands form and the dorsal fissure appears. The digestive canal is differentiated into three parts: a canal which opens into the respiratory cavity, stomach, and intestine. In the walls of the respiratory cavity there develop near the stomach the first branchial clefts with cilia at the edges, and at the ventral fissure the heart develops, possessing the form of a short duct. The metamorphosis is completed by the specialization of the gill-clefts and the development of siphons.

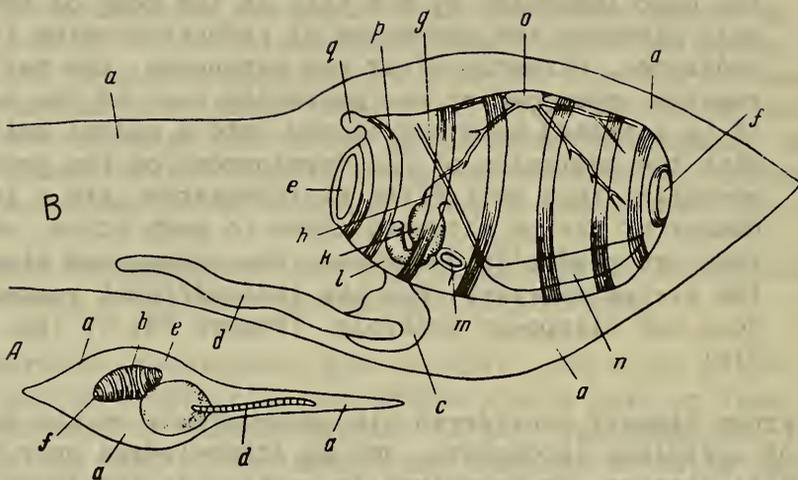


Figure 47. Larvae of *Doliolum Nordmanni*.

A—Larva up to transformation: a—larval membrane; b—young doliolum; e, f—posterior and anterior openings; d—axis of the tail;
 B—larva of doliolum in the beginning of transformation: a, d, e, f—as in A; c—"vesicular appendix; g—wall of the respiratory cavity; h—digestive tract; k—stomach; l—intestine; m—heart; n—ventral fissure; o—nervous ganglion with outgoing nerves; p—the third from back muscular strand, penetrating the rudiment of the stolon (q) (by Krohn).

Krohn's work represents the first systematic description of ascidian development in world literature; it remains incomplete and not free from mistakes, which, of course, does not reduce the historical significance of this undoubtedly remarkable investigation. But the exact and detailed study of the embryology of ascidians belongs to A. O. Kovalevsky. In his work, their relationship to the vertebrates was proved, delivering a fatal blow to the metaphysical theory of types in the animal kingdom. It formed the basis of comparative evolutionary embryology, first advanced by Krohn. In the work dedicated to the development of ascidians,⁸⁰ Kovalevsky wrote the following:

Leaving aside the investigations of earlier authors, whose results either are already completely reworked by present scientists, or, to a lesser extent, are partially expanded, we must mention Milne-Edwards, Van Beneden, Kölliker, and, in particular, Krohn. Of all these investigations the results of Krohn's investigations are in closest agreement with our own results. Although he described the accumulation of pigments, which completely coincides with our observations, he did not discover the walls of the saccule in which these organs of sensation are situated, and generally he traced the development step by step. The formation of the axial strand in the tail of the ascidian larva was observed by Krohn, although he explained it as a formation of emptiness in the cells. Although the transformation of the larva into the sessile form was described by him in detail, he had only a slight understanding of the anatomy of the larva and therefore he could not observe the particular features. (p. 41)

At the end of the 1860s, in Naples, Krohn studied budding in the complex ascidian *Botryllus*, and he presented the results of his observations in two reports.⁸¹ In the first of these

80. A. O. Kovalevsky, "Istoriya razvitiga prostykh astsidii" (The history of development of the simple ascidia) (1886), SELECTED WORKS (Izd. AN SSSR, 1951), pp. 41 - 78.

81. A. Krohn, "Über die früheste Bildung der Botryllusstöcke," ARCH. NATURG., 35 (1869), pp. 190 - 196; "Über die Fortpflanzungsverhältnisse bei den Botrylliden," ibid., pp. 326 - 333.

articles Krohn disproved the erroneous data of Milne-Edwards and Sars and confirmed the observations of Mechnikov that the larva of *Botryllus* possesses the same simple structure as that of the solitary ascidian and undergoes analogical metamorphosis. After settling on the bottom, the young *Botryllus*, already in the process of transformation, produces a bud from which a second individual originates, which in turn begins to bud. As a result a stellate colony is obtained. The budding of the colonial ascidian is represented in the second article, in which Krohn compared its details with the corresponding phenomena in salpa.

With these fragmentary investigations of vegetative multiplication, Krohn's scientific activity apparently came to an end. In the following years (1870 to 1880) his reports were regularly placed in journals, but no works appeared after this time.

For thirty-five years he collected facts from the field of anatomy and embryology, mainly of invertebrates, covering a very great number of systematic groups (140). His embryological works (including descriptions of larvae and means of reproduction) concerned coelenterates, nemerteans, annelids, molluscs, crustaceans, echinoderms, and tunicates.

Krohn did not belong to those investigators paving new roads in science. All his comparative-anatomical and comparative-embryological remarks are concerned with the comparison of closely related forms. Comparing, for example, representatives of different classes of echinoderms and establishing the features of similarity and difference between salpa and ascidians, Krohn did not offer sympathy either to the theory of types, nor to the idea of unity of planes, nor to evolutionary study. Krohn cited Darwin only in his works on the structure and development of cirripedes, highly rating his monograph dedicated to this order of crustacean.

Besides this, evidence exists about Krohn's deep interest in the investigations of A. O. Kovalevsky, who established the similarity of the embryonic development of ascidians and vertebrates. The first report by Kovalevsky dedicated to the development of ascidians was published in 1866 in ZAPISKAKH PETERBURGSKOI AKADEMII NAUK (Notes of the Petersburg

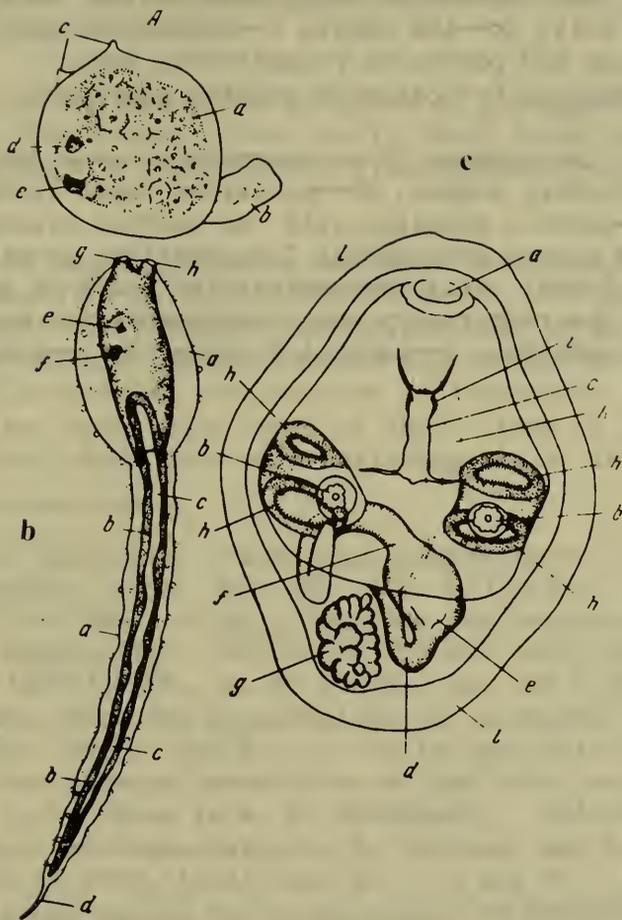


Figure 48. The development of the ascidian *Phallusia mammillata* (by Krohn).

Figure 48. The development of the ascidian *Phallusia mammillata* (by Krohn).

A—late embryo with two pigmentation spots: a—body; b—beginning of the tail; c—rudiment of upper sucking processes; d, e—anterior and posterior pigmentation spots.

B—larva, side view: a—tunica with green bodies; bb—the axis of the tail; cc—its canal; d—horizontal half; e, f—anterior and posterior pigmentation spots; g—right anterior; h—posterior sucking processes.

C—*Phallusia* in the process of metamorphosis: a—widely opened respiratory siphon; bb—posterior (constrictor) siphons; c—nervous ganglion with the nervous branches; d—digestive tract; e—stomach; f—intestine; g—situating coil of the larval tail; hhhh—first two pairs of gill openings of the respiratory sac; i—pigmentation mass over the nervous ganglion; k—ventral fissure; l, l—tunica.

Academy of Science); two years later an article followed in NACHRICHTEN VON DER GESELLSCHAFT ZU GÖTTINGEN. The data mentioned there, apparently, did not convince Krohn. In 1871 in ARCHIV FÜR MIKROSKOPISCHE ANATOMIE, edited by Max Schultze, a new work by Kovalevsky was published,⁸² at which time Schultze added the following postscript to a letter directed to Kovalevsky on January 18, 1871: "Krohn, who read your article in proof and made minor corrections, sends you heartfelt regards. At first he was, as you can imagine, very much against the relationship with vertebrates;⁸³ but then he began to hesitate."⁸⁴

Krohn was one of the pioneers of zoological investigations on the Mediterranean coast, which later became a place of pilgrimage for naturalists from different countries of Europe.

It is highly probable that Kovalevsky and Mechnikov were well acquainted with the works of Krohn. His remarkable comparative embryological investigations, of which they became aware in the mid-1860s, revealed the nature of Krohn's scientific activity and produced an impression on them. Like Krohn, they spent many years of their lives as travelling naturalists, more than once following him to those localities

82. A. O. Kovalevsky, "Entwicklungsgeschichte der einfachen Ascidien," MEM. AC. SC. ST. PETERSB., VII Sér., 10, No. 15 (1866), 16 pp.; "Beitrag zur Entwicklungsgeschichte der Tunicaten," NACHRICHTEN VON DER GESELLSCHAFT ZU GÖTTINGEN, No. 19 (1868), pp. 401 - 415; "Weitere Studien über die Entwicklung der einfachen Ascidien," ARCH. MIKR. ANAT., 7 (1871), pp. 101 - 130.

The Russian translation of the first and third articles are to be found in A. O. Kovalevsky, SELECTED WORKS, editor and commentator A. D. Nekrasov and N. M. Artemov (Izd. AN SSSR, 1951), pp. 41 - 78 and 79 - 122.

83. The paper was on the relationship of ascidians to vertebrates.

84. Schultze's letter is included in the book PEREPISKA A. O. I V. O. KOVALEVSKY (Postscripts of A. O. and V. O. Kovalevsky), edited by A. A. Borisiak and S. Ya. Streich. The extract of this letter is published here with the permission of S. Ya. Streich.

rich in the zoological material of the sea—Naples, Messina, Nice, Madeira—and using, in particular, those subjects on which Krohn made many important observations leading to serious theoretical meditation. Kovalevsky later cited with respect the works of Krohn on the structure of sagitta and the development of tunicates, and Mechnikov cited his works on the development of coelenterates and echinoderms.

In the preparation of that revolution in embryology which was accomplished by Kovalevsky and Mechnikov, converting the comparative-descriptive embryology into comparative evolutionary embryology, Krohn's modest investigations played their role, and therefore his name must not be forgotten in the history of Russian science.

COMMENTS

(1) Needham arbitrarily limited the contents of his book absolutely to the history of chemical embryology. In addition, his extreme unobjectivity drew attention, as he dwelt mainly on the works of English authors, while, according to his opinion, the book should have represented the history of embryology of all times and peoples. In the chronological table of scientists of the world embryology, covering up to the beginning of the 20th century (p. 266 of Russian translation), Needham did not find places for the names of N. A. Warnek, A. O. Kovalevsky, I. I. Mechnikov and their numerous Russian followers in contrast to Fr. Balfur, who published more than 70 years ago the first (and for that time excellent) manual book on comparative embryology, in which the Russian works were given proper places (14).

(2) Samples of these "compositions" are pictured on the prints of that time, reprinted in the book "Kunstkamera Peterbergskoi Akademii Nauk", 1853, 293 p. (see Fig. 6.10 and 11 of the mentioned book). Description of anatomical and embryological "compositions of Ryuish and texts of the poetical Latin inscriptions which accompanied them much earlier were mentioned by Baer in 'Memories about anatomical cabinet' ('Mémoire uber das Anatomische Kabinet, gelesen in den Sitzungen der Phys.-math. Kl. d, Sep. 20, 4 u. Oct. 18, 1850; Collection the museum of anthropology and ethnography in Imp. Ac. Sc., 1900, p. 111-152) (21).

Here and below figures in round brackets show the number of text page, to which the comment is related.

(3) Doctor van der Hulst, (see below for data about him) on April 14, 1724 "sent organs which belonged to a girl, who died of smallpox, in Kunstkamera. Caesar honored him due to the hermaphrodite (Materials for history of Imp. Ac. Sc., V. 1 Spb, 1855, p. 38) in the other place of these "Materials" wrote due to bringing to the Academy of Science a monster, who was born with two heads, determined by Doctor Stepan Gaokantsk, ...8 roubles were given" (V. II, on March 9, 1732, p. 119) (23).

(4) In "Materials for history of Imp. Ac. Sc." there are many documents about the obtaining of teratological objects into Kunstkamera.

A letter from Vyborgkh by colonel general Karnov says "his major Beshentsev Fedor Fedrov in the Vyborgskaya office found a monster of a lamb having four legs and one neck, and the head had the view of a double one. This head had two mouths with tongues and two eyes: they were in the middle where the forehead must have been..." ("Materials..." V. I, Spb., 1855 No. 165, March 9, 1725, pp. 9-97).

Inventory of objects, obtained on March 8, 1725
"Number 1: lamb, with 8 legs, another with three eyes, two trunks, 6 limbs were sent from Tobol'sk by Kozlovsky. Number 2: baby, with 3 legs: from Lower Novgorod from Governor Rzhevsky. Number 3: calf with 2 deformed legs: from Ufa from commandant Bakhmetov. Number 4: baby with two heads also from Bakhmetov. Number 5: one baby, with eyes under the nose and ears under neck: from Nezhin. Number 6 - two babies - breasts and abdomens were joined - from Akhtyrok from prince Mikhail Golitsyn; hands, legs and head were normal. Number 7 - baby, with a fish tail, born in Moscow in Tverskaya. Number 8: two puppies, born from a 60-year-old woman, from Akhtyrok from prince Golitsyn. Number 9: baby with 2 heads, 4 hands, 3 legs: from Ufa from commandant Bakhmetov" ("Materials...", V. I, No. 193, March 18, 1725, p. 99).

Grigorii Ivanov found a monstrous head puppy with 8 legs ("Materials, V. I, No. 291, September 21, 1725, p. 145).

"...Dead body of an infant, with 6 fingers, born by a daughter of Tikhanov who was working on a marine ship Astrakhan...given in Kunstkamera" ("Materials..." V. II, 1886, No. 99, November 29, 1731, p. 83).

"On January 17 of this same year, my brother sent a monster which had 2 mouths, the daughter of Ulita Kiryanova the wife of sergeant Nikivor Kosharov gave birth to it: this monster had four hands, four legs and two faces, one had normal view and the other had one eye" ("Materials...", V. III, 1886, No. 13, January 20, 1736, p. 14).

"This monster was accepted for preservation in Kunstkamera and Kosharov was given 4 roubles as a reward" (there is also, No. 41, February 17, p. 36) (23).

(5) Iogani-Georg Dyuvernuia (1691-1759)..... a Russian academician in the department of zoology and anatomy, was invited to the academy during its foundation. In 1741, by efforts of Shumakher, he was compelled to leave work and travel to his homeland, in Germany. Following him, up to 1758 Abraham Kaau-Boerhave (1715-1758) had been in charge the department of anatomy and physiology in the Academy of Science. In his era, the anatomical and embryological collections of the academy came into being, but he practically did not use them. He published one of them in detail (Abraham Kaau-Boerhave was related to those foreigners, living in Russia, who did not make anything for promoting its sciences and for preparing the young Russian scientists (23).

(6) Family of van der Hulst was repeatedly mentioned in the documents of Petrovskaya epoch. Doctor Zakharii van der Hulst arrived in Moscow from Holland, apparently in the 70s of the 17th century, and for a long time he was the physician of Aptekarsky department and court physician at tsars Ivan and Petr. Then after the death of Ivan, he became the physician of Petr I. He accompanied him on both journeys to Arkhangelsk (1693 and 1694). On the second Journey, he died suddenly¹. Another van der Hulst

1. V. Rikhter. "Istoriya meditsiny v Rossii" (History of Medicine in Russia), p. 2, Moscow, 1820, p. 313, M. M. Bogoslovskii, Petr I, V. I, p. 181= V. II, 1941, pp. 123-124.

participated in 1691 in Poteshny battles" in the army "generalissimusa" of I. I. Buturlin². In 1695 in "Rospisi nachalnym lyudam Semenovskogo polky" captain Andrei Yakovlevich van der Hulst was mentioned³. On the first journey of Petr to Holland, at the Russian Embassy, lieutenant (or captain) Andrei (Yakovlevich) van der Hulst⁴ became the translator. One year later, he was sent by the Dutch government to Moscow as resident⁵. Later on, the son of the above mentioned "doctor" Zakharii van der Hulst—Zakhar Zakharovich—was known. By the order of Peter I, he received "traveller sheet" via Mozhaisk, Vyazm, Dorogobuzh and Smolensk in foreign lands for studying science. Although it was impossible to detect exactly the time of his return to Russia but there was no doubt about it. He was a teacher of surgery at Peterburgsky Hospital 1723⁶. Ya. Chistovich informed, that "Z. Z. van der Hulst passed the Doctorate degree examination in Leiden and after returning to Russia he was the senior doctor in Petersburg Admiral Hospital and, in addition, a teacher for medical students and pupils of this hospital. Later on, he lived in Moscow and when a "Doctor's committee"⁷ (1730) which comprised five doctors was established, he was one of its members. It is most

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2. There also, V. I, p. 127.
 3. "Sb. vypisok iz arkhivnykh bumag O petre Velikom" (Collection from archives papers about Petr the Great), VI, Moscow, 1872, p. 148.
 4. M. M. Bogoslovskii. Petr I, V. II, p. 155, 182, 421.
 5. There also, V. II, p. 432; V: IV, 1948, p. 252, 339, 340, 344, 346.. M. A. Venevitinov. "Russkie v Gollandii. Velikoe posol'stvo 1691-1690 godov" (Russians in Holland. The great embassy 1697-1698) Moscow, 1897, p. 79.
 6. V. Rikhter, Istoriya meditsiny v Rossii, p. 3, 1820, p. 149.
 7. Ya. Chistovich. "Istoriya pervykh meditsinskikh shkol v Rossii" (History of first medical schools in Russia). Appendix X. Alphabetical list of doctors of medicine, working in Russia in the 18th century.

probable, that Zakhar Zakharovich van der Hulst is the author of a dissertation cited in the text on page 7: the difference of names (Zakharii and Arnold) does not speak against this supposition, as both names could belong to the same person. Anyhow there is no doubt about the belonging of the author of dissertation to the Moscow family of van der Hulst (25).

(7) Speaking about the collection of anatomical preparations, present in Kunstkamera N. G. Kurganov noticed, that "the greatest attention was given to these parts, which explained parturition. A number of the foeti exceeded more than one hundred and composed a gradualness from an embryo having the size of an anisic grain to a completely formed baby. The collection of monsters was extremely big. These anatomical descriptions with sketches, reprinted on copper, had a scientific significance" ("Pismovnik", the second part, p. 196) (32).

(8) In chapter 26, "Gippokratovskoi sbornik" it is possible to read the following: "All organs are distinguished simultaneously and they grow, and not one is distinguished earlier than the other. But the larger ones in nature are distinguished before the smaller ones, not originating in any case earlier. However not all receive the final structure in equal time, but some are quicker, others are slower, since each meets sufficient nutrition. In some, all become distinct within 40 days in others—within 2 months, in others—within 3 months, and in others—within 4 months" (See V. I. Karnov. Aristotle i antichnaya embriologiya. Introductory article in the translation of Aristotle" "O voznikovenii zhivotnykh" Izd. AN SSSR, 1949, p. 23 (35).

(9) The embryological opinions of Dekart are stated in the treatise "Opisanie chelovecheskogo telo" (Description of human body), where they compose its fourth part—"About the development of the embryo. Parts, formed in semen" and the fifth part "the formation of hard parts". The treatise was published two years before the death of the philosopher, in 1648. In addition, with the birth conception of living substances, "which are produced by semen", Dekart also

assumed the possibility of spontaneous conception (without semen and uterus").¹

In case of conception from parents, their semen is mixed and forms cloudy liquid which undergoes a kind of fermentation, what is formed during this heat widens the particles of semen, they "press on other particles subsequently locating them gradually. This is the way of forming the body organs... Heat compels some of the particles of semen to be collected near definite points of the space... Thus the heart begins to be formed"². The movement of blood from heart makes a way through semen particles, that is why the blood again returns to the heart, and by this way the vascular system is formed. After this, the movement of particles of different kinds leads to the subsequent formation of the organs - vertebrates with spinal cord, brain, paired organs of sensation and so on. The energetic character of these embryological presentations is completely obvious. However, Dekart considered that it is necessary to underline this. "In order to get acquainted with the figure of the already formed animal, it should be understood what it represents at the beginning of its formation and it is necessary to imagine semen, as some mass, from which, the heart is first formed, around it the hollow vein is located on one side while on the other the large artery, united by two tips. The tips of these vessels, to which the openings of the heart are directed, indicate the side, where the head must be present, others also indicate that side, where the lower parts of the body must be present"³ (36).

(10) The idea of preformation may be traced back to remote ancient times. Anaksagor taught that "hairs cannot be formed from no hairs and raft from no raft" similar ideas were stated by several authors especially Senekoi, who in "Questions of nature" wrote: "In semen all future

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1. See S. F. Vasilev. "Evolution ideas in Dekart philosophy (Introductory article in book" Rene Dekart. Kosmogoniya. Two treatises. GTTI. 1934, p. 121).
 2. R. Dekart. Description of human body. In book: Kosmogoniya, p. 286-287.
 3. See also pp. 298-299.

parts of the human body are contained. The baby in the uterus of the mother has already roots of beard and hair, which he will carry. In a similar way, in this small mass, are contained all features of the body as well as all those, which will be present in his posterity" (see Dzh. Needham, History of Embryology, page 76) (37).

(11) The theory of "investment", conformable to plants and animals, was stated by Mal'bransh in the following expressions: "It seems, although it may be a hardly-accepted idea, that in one embryo a countless number of trees is included, because this embryo does not include only a tree, serving as its seed, but also, great number of seeds, which can include new trees and new seeds of trees, containing, in turn, probably in an incomprehensible little form, other trees and other seeds, are fruit bearing as the first and so on till infinity. All what is mentioned about plants and embryos can be also applied on animals and their embryos, from which they were produced. In the embryo of a bulb of tulip, it is possible to distinguish all tulips. Thus in the embryo of a fresh non-hatching egg as well, it is possible to see a chick, which may be nearly completely formed. In the eggs of frogs, it is easy to recognize frogs, we will also find other animals in their embryo when we become so experienced and skilful, that we can open them (N. Mal'bransh. "seeking out truth" translated by E. B. Smelovaya, V. I, 1903, p. 51-52) (38).

(12). Speaking of the influence of the mother's impression on the formation of fetus, Mal'bransh, among other examples, mentions the following: "One year did not elapse still from that time, when a woman, looking with great zeal on the picture of Saint Pia at the time of the celebration of his canonization, delivered a child, absolutely like the Saint. He had senile face, which was impossible for a child, but did not possess a beard. His hands were put together as cross on the chest, his eyes were directed to the sky. He had a very small forehead, because on the picture, the image of this Saint was raised to the dome of the church, directed to the sky, so that his forehead was nearly unnoticed. On his shoulders, he had something like overturned mitre with some round birth marks, at these places where mitres were decorated with precious stones. In short, this infant extremely

resembled the picture, but his form was made by the strong imagination of his mother. All Paris could see him, as I could, because this infant was preserved for a long time in spirits of wine" (N. Mal'bransh. Seeking out truth, V. I, p. 173).

The description of deformity was so expressive and exact, that confidently it was sufficiently possible to characterize it in terms of recent teratology. Probably, the matter was a case of amencephaly or, may be, cerebral hernia of occipital region. It is not wonderful that the baby, resembling Saint Pia, was shown in a jar with spirit directly after birth (38).

(13) Philosophy, Leibnits spoke, - gave itself much work about the origin of forms, entelechy and soul. Meanwhile, different accurate investigations, performed on plants, insects and animals, led to this conclusion: that the organic bodies of nature never originated from chaos or not, but always from semen, in which, undoubtedly, preformation was already present... We see something similar, when, for example, worms become flies and caterpillars become butterflies" (Monadologiya, No. 74), (38).

(14) "Thus, I suppose that souls which once must become human souls, as well as souls of other kinds, existed in semen, in ancestors up to Adam, i.e. from the very beginning of things they existed in the form of organic bodies—a view, which was apparently approved by Swammerdam, Mal'bransh, Beil', Pitkari, Gartsuker and many other learned men. This view is also sufficiently confirmed by microscopic observations of Leeuwenhoek and other fairly prominent naturalists "(Teoditsey, I, No. 91) (38).

(15) Leibnits considered that monads are alive and animated, characterized by incessant change which is accomplished continuously without leaps. "I confirm, as an indisputable truth—he wrote—that all things were exposed to change, and became monads and that in each monad this change was accomplished continuously" (Monadologiya, No. 10). From continuous change, the developing monad natural passage of Leibnits to gradation of monads, forming continuous eternal ascending series of substances, progressing from

unaccomplished to accomplished. By his investigations "Swammerdam showed that insects, by their respiratory organs, are similar to plants, and that in nature, an order of gradualness, descending from animals to plants, exists. However, there may be, in addition, intermediate substances between these and others" (Letter of Leibnitz to Bung). And in another letter: "I am sure, that these substances must be present, and natural science may discover them. Nature never disturbs continuity anywhere. It does not make leaps. All categories of substances of nature form one sole chain, where different classes, like links, so closely join to each other that for sensual presentation it is impossible to determine the point, where each of them begins or ends" (cited by Kuno Fisher) ("History of new philosophy, V. Lebnitz", p. 460) (38).

(16) About this change of his opinions, Haller wrote the following: "In the body of animal, there is no part which can originate earlier than the other: all of them are formed at the same time... If Harvey supposed that he discovered the epigenetical development, it is because from the beginning he only saw small haziness and then the rudiments of the head and eyes, exceeding in size all other bodies, and finally gradually—the internal organs. More than 20 years ago, i.e. before my numerous observations on eggs and females of *Tetrapoda*, I used this argument to prove that embryo strongly differed from the formed animal, while I confirmed, that in animals at the moment of conception parts which were present in completely formed animal were absent. From this time, I had the complete possibility to confirm that all that was deduced by me against preformation theory, in fact speaks in its favor" (cited by Dzh. Needham, History of Embryology, p. 226-227) (39).

(17) On the basis of the confirmation of the Bible, that earth and mankind populating it, have existed about 6000 years and from that the average duration of life of man is equal to 30 years, Haller calculated, that God created at the same time a minimum of 2000,000,000,000 people (cited by article of Kirchhoff on Wolff, p. 204) (39).

(18) Speaking about the impression produced on contemporaries by the discovery of Bonnet (about the development of

bodies from unfertilized ovum), A. E. Gaisinovich noticed that the scientists of that time...lost sight of that it proved in the best case only ovism but not preformation (Cited article in the edition of translation "Theory of conception" of Wolff, 1950, p. 379). With the latter confirmation, it is difficult to agree: ovism is one of two forms of the preformation theory and is principally identical with its other form—animalculism. (40)

(19) After that the chapters of this book, dedicated by Wolff, were written, he mentioned in the preface "Theory of conception" of Wolff (Publisher House Ac. Sc. USSR, 1950) which was published with the supplement of article A. E. Gaisinovich "K. F. Wolff and studies on development" (pp. 363-477) Tasks, which the author of this interesting article put before himself, did not allow him, apparently, to stop and dwell in more detail on embryological and teratological works of Wolff.

Here it is also necessary to notice that the translation replaced in the Russian edition of Wolff the term "generation" by the word "conception", which could not be considered felicitous. The term "conception" meant the beginning stage of development, appearance of a new individual, while Wolff did not mean only this stage, but also all subsequent individual development. It is completely accurate to translate "generation" by the word "development". Wolff himself used in his German book neither the term "conception" (Entstehung) nor the term "development" (Entwicklung), and kept the Latin root in the German word "die Generation". In accordance with this, upon the examination of Wolff's dissertation and its popular summary in German below the original Wolff term "generation" is preserved (43).

(20) In the first volume of "Zur Morphologie" Gete mentioned Wolff in four places. He gave a brief account of biography of Wolff (p. 80-83), mentioned in the notes of Murzinitsa on Wolff (p. 252-256), then dwelt on studies of Wolff about metamorphosis of plants (p. 83-87). At last he tackled the understanding of educational yearning, using the terms of Blumenbakh (pp. 114-116).

In the last extract Gete writes the following "In criticism of ability to reach an opinion" Kant states "In

relation to the theory of epigenesis no one worked either for its proof and for substantiation of true principles of its application, or partly for the restriction of its extremely wide application, as Mr. Buildings advisor Blumenbakh". This evidence of honest Kant encouraged me again to scrutinize work of Blumenbakh, which I truly read before, but did not imbue it. Here I found my Christof (1-L.B.) Friedrich Wolff as an intermediate link between Haller and Bonnet, on the one hand, and Blumenbakh, on the other. For his epigenesis, Wolff must suppose the presence of an organic element, on which creatures feed, which is intended for organic life, and supplied this material by an essential force". The mentioned words of Gete witness to the superficial acquaintance of the great poet with the views of Wolff (Even Wolff's name was written incorrectly by Gete (44).

(21) A. E. Gaisinovich (1950, p. 462-463) mentioned information, that Wolff at the beginning of the 70th year taught in the academic high school—chemistry, anatomy and botany, and he also directed the preparation of the scientific activity of student Fedor Galchenkov (48).

(22) This place in the translation of Meckel tendentiously stated: instead of "the Highest Creator" was put "The creating nature". Wolff disputed the preformation of formulated parts; in the German translation, his skepticism is not related to the Creator for the authority is untouched, but to nature. This "liberty of translation" bars the radicality of scientific and philosophical view of Wolff (76).

(23) Here the phrase made by Wolff, has no connection with other discussions and clearly intended for not blaming atheism: *eiusmodi vero materia, talibus, viribus instructa immediate a Deo ex nihilo creata sit* (it is also true that material, supplied by these forces, is directly created by God from nothingness) (76).

(24) A. E. Gaisinovich (1950, p. 455) repeated the mentioned statement of K. M. Baer nearly literally: "This remarkable work of Wolff...did not draw the attention of all the scientific world up to 1812, when Meckel translated it from the Latin language". It is necessary to notice, however, that the work of Wolff was given due attention and

it was evaluated as a remarkable work in the book of I. Bezeke, published in 1797 (see p. 114) and in the dissertation L. Tredern (1808) (see Chapter 11) (87).

(25) Apparently, in the declaration of biological works by the Academy of Science for a prize, Wolff showed initiatives also early. Thus, in 1779 the academy declared a competition for a prize on the question about reproduction of cryptogamous plants. This theme of competitive work was written in expressions which a great probability impel to consider Wolff the author of this question: "Theoriam generationis et fructificationis plantarum cryptogamicarum Linnaei dare etc...." (gives the theory of development and fruiting of cryptogamous plants, by system of Linnae, plants and so on).

In 1783, this prize was awarded to a professor in Leipzig, Iog. Gedvig for the work under the title "Theoria generationis et fructificationis plantarum cryptogamicarum Lennaei, mere propriis observationibus et experimentis superstructa dissertatio, quae praemio ab. Academia imp. Petropol. pro Anno MDCCLXXXIII proposito ornata est" (105).

(26) It is necessary to notice, that the embryological problems have interested Petersburg Academy of Science before the arrival of Wolff. It is possible to judge this, in particular, by the published collection in 1756, which is composed of two works (dissertations), and sent to the competition announced by the academy. The question, put by the academy, touched upon the possible influence of the impression, felt by the pregnant woman, on the developing fetus. One of the mentioned works belonged to a professor at Leipzig University C. Ch. Krauze¹, and another—to a member of Petersburg Academy of Science, I. G. Rederer. In lively controversy on this theme Byuffon participated. He energetically objected to preformists, who according to their views, the embryo is proved to be similar with the parents under the influence of imagination of the mother.

1. Caroli Christiani Krauze. Dissertatio de questione ab Academia imp. scientianim petropolitana pro praemis in annum MOCCLVI proposita. Quaenam sit causa proxima mutans, corpus foetus etc... There also, J. D. Roederer Dessertatis Petropoli 1956.

In the controversy Turner also participated. He objected to Blondel, denying the influence of mother imagination on the embryos. Argument of Turner was confirmed by the fact that the blood vessels of the mother directly passes in the vessels of the fetus. Ens subscribed to Turner's opinion. Apparently, the difference, existing on this question in literature, induced Petersburg Academy of Science to announce competition on works which would comprehensively answer it. The scientific committee of the Academy, examining the competitive works, revealed scientific impartiality, and the Academy published two works, each one of them represented a contradictory opinion. Krauze was a supporter, and Rederer was an opponent of the influence of maternal imagination on the fetus.

Krauze considered that the question raised was very difficult, nearly hopeless to solve. However, he noticed, that many examples were present, when the fetus was changed in a way, that not only simple people and the mother herself, but even sharply sensitive scientific people in medical practice related it, although partially, to the strong emotional shock of the mother. Enumerating the opinions of authors, discussing this question (Sennert, Morisso, Ludvig, Hofman, Abraham Kau-burgav, Takhoni and others), Krauze suggested, that the reader can make for himself the most classical ironical defiance: "Hic Rhodus, hic salta!" (literally: "Here Rodos also jump!") and all the following statements attempt to answer this call. As also the majority of his predecessors, Krauze paid attention mainly to cases of appearance of pigmental birth marks, where their forms and situation compel to suggest the influence of pregnant women. He began with these sharp effects, as terror, fear, anger and so on, showing strong physiological influence expressed first of all in the reaction from the side of vascular and nervous systems. From this Krauze made the conclusion, that "if the brain was strongly alarmed, then small changes took place in the body". Referring to known cases of adult people suddenly growing grey under the effect of deep feelings, Krauze suggested that, there were more bases to expect changes of skin color of the fetus under the effect of maternal imagination. If terror or fear can cause small ulcers on lips or erysipelas, then why does it seem incredible to you, that the same phenomena can take place in the body of the fetus, whose structure is so weak and delicate, and its vessels are so numerous and full of juices?"

In order to imagine the possibility of this phenomenon, which is shown by the influence of changes in the organism of the mother on the fetus, it is necessary to prove their close relation. On his side Krauze confirmed, "fetus with the uterus represents a single continuous whole". According to this opinion, this is especially related to the nervous system, so that "stimulation of the nerves of the uterus may and must be passed to all the nervous system of the fetus. Distributing this confirmation on psychics, as well as suggesting, that the fetus was capable of psychological manifestations, Krauze deduced the following conclusion: "In the brain of the fetus exists the same condition, which exists in the brain of the mother". All these views are summarized in the concluding paragraph of the dissertation". What was stated so far may be added to all these examples, which instruct, that the fetus body is changed from the mother, if her soul is strongly shocked. Ideas, originating in the mother's brain are "united with fetus brain"; they are stimulated in it more quickly and energetically, than in the soul of the mother herself, as the pulse of arteries and effect of nervous and generally all responses in babies are quicker than in adults. Under the influence of these ideas, the fetus brain gives effect on its body and namely in this way, which corresponds to perceived ideas. Therefore, the fetus's brain produces in the corresponding parts of his body the same things which he himself undergoes".

Directly after the considered work of Krauze, it is necessary to examine the work of Rederer, which is simply entitled "Dissertatis" and also begins with the formulation of the question raised by the Academy: "What is the direct cause for changing the fetus body?..."

In order to possibly answer this stated question, Rederer considered that it is necessary to study thoroughly, how the mother's body unites with the embryo, taking into consideration, that the only connection between them is carried out through the placenta. The investigation of this connection led him to the following conclusion. The lumens of the blood vessels of the placenta, directed to the uterus, up till this stage, are so narrow. They do not admit turpentine oil or any other liquid to pass. True anastomoses, connecting the vessels of the uterus

and vessels of placenta, do not exist; Vasa hypogastrica which is full, by all means of a waxen mass or any other fluid, does not pass its contents to the umbilical vessels. This was established either in human carcass, or in living cows, ewes, bitches and other animals. If the pregnant animal is fed on roots of *Rabiae tinctorum*, then the fetus bones will not be stained with the red color. The blood of the fetus differs from the mother's blood in that it is more liquid. Finally, the fetus pulse also differs from the mother's rate.

Subsequently, the fetus lives its independent life, moving its own blood by its forces, beating of its heart, by blood circulation and through placenta, without the help of the maternal blood. Therefore, rest, movement, sleeping, awakening and even life and death of the mother and fetus are not obligatory present in harmony. Later on, Rederer categorically denied the existence of a nervous connection between the placenta and the mother. The comparison of the positions of the birth marks as well as their presence or absence in the mother and baby does not give, according to his opinion, basis to suggest the influence through blood or nervous system. Rederer discussed in detail the question about "mind" of the fetus and passed to the conclusion, that this mind cannot adequately respond to the feeling of the mother. This is stated by the examples of strong shocks in the mother, not accompanied by the appearance of birth marks in the baby, and examples of appearance of birth marks and warts without any connection with the mother's feeling. In the following pages the various deformities of human beings are mentioned, and Rederer reached the conclusion that the birth marks differ from true deformities only quantitatively. They are also disturbances of the normal development. As the deformities frequently affect the internal organs, then in relation to them, the usual supposition about maternal influence loses its significance. The general conclusion of Rederer comes to that the confirmations about the influence of the mother's feeling on the baby are not supported by verified facts, and are but the product of fantasy (105).

(27) The effect of vitalistic views of Blumenbackh on some Russian physicians-biologists can be traced up till the 20's of the 19th century. Thus, in 1825 at Moscow

University, the surgeon Nikifor Dmitrievich Lebedev discussed a thesis for the degree of Doctor of Medicine. He later on read at the university "history and literature of medicine". Lebedev dissertation was entitled "About the nature of weightless substances in general and vital powers in particular" (*Dissertatio inauguralis physisologica de natura imponderabilium in genere et de viribus vitalibus in specie, quam...in Universitate caesarea Mosquensi, pro gradu doctoris medicinae...elaboravit publiceque defendet chirurgus I-mae classis Nicephorus Lebedev, Mosquae, 1825. 28 p.*). Lebedev, referring to Blumenbakh, dwelt on the idea that all vital processes—organic formation and growth as well as movement of already formed parts—possess their own source of a special vital power (55). The vital power, according to his opinion, is an internal, inherent character in the organic body, which is the cause of life and at the same time seems to be its product (*Vis vitalis est interna et propria organici corpori qualitis, quae vitae causam constituit et simul ejusdem est quasi productum, thesis 9*). Works of similar kind are not characteristic of the common materialistic trend of Russian biological and medical sciences. Therefore, the dissertation of Lebedev served as a reference and mainly as an illustration of this negative influence, which was shown by the idealistic German philosophy and some representatives of Russian sciences especially the naturalists who worked under its direct influence (106).

(28) Izef Gotlib Kelreiter (1733-1806), botanist and zoologist, worked from 1756 to 1761 as a junior scientific assistant at Petersburg Academy of Sciences, with which he kept in close contact after returning back to Germany and till the end of his life. In the period, from 1758 to 1811, 15 botanical and more than 20 zoological works of Kelreiter were published in Russian scientific and scientific popular editions (*Novi Commentarii Acad. Scient. petropolitanae, Acta Acad. Scient. petropol. Nova Acta Ac. Sc. Petropl., Trudy Volnogo Ekonomicheskogo Obshestva* and in the journal "Sochineniya, K polze i uvecheniyu sluzhashchie"). His scientific fame is connected mainly with the study of reproduction and hybridization in plants (see *Ioz. Kelreiter* "Study about sex and hybridization in the plant", the editor with a biological essay was prof. E. V. Wolff, 1840).

The work of Kelreiter about the irritability in the plant, to which Wolff referred, was called: "Nouvelles observations et expériences sur l'irritabilité des etamines de l'épine vinette (*Berberis vulgaris*)", Traduit de l'allemand par M. l'adjoin Sewergin, Nova Acta Acad. Scient. Petropol., 4, 1790 (German original was received in Petersburg in 1788) (112).

(29) The point of view of A. E. Gaisinovich is similar to the presentation mentioned here about the outlook of Wolff (see Wolff "Theory of conception"). It is possible to combine with it the confirmation, that the studies on preformation and epigenesis do not always correspond to the demarcation between idealism and materialism in biology. The following serves as an evidence, that preformists were also idealists (Leibnitz, Haller, Bonnet) and mechanical materialists (for example, Lamettri); equally as epigenetics, were either idealists (Aristotle Harvei), or mechanical materialists (Dekart, Maupertuis, Byuffon and Diderot). A. E. Gaisinovich included Wolff as well in the latter category. His "absolute epigenesis" was grouped together with Gaisinovich in the mechanical materialism. For its complete verification, this statement could be desired as only a less categorical expression. In the evaluation of Wolff's outlook, it is impossible, apparently, to deny absolutely his fluctuations between materialism and idealism; these fluctuations were an unavoidable originality even by the most prominent thinkers of all historical epochs, preceding the formation of successive system, i.e. dialectic system and materialism (119).

(30) Semen Gerasimovich Zybelin (1735-1802), after finishing the study in Moscow Ecclesiastical Academy, joined Moscow University till the opening there of a medical faculty. After he finished the course, he was sent to study medicine abroad. At Leiden, Zybelin defended a doctor's dissertation in 1764. After returning back to Moscow he read courses of anatomy, physiology, chemistry, pharmacology and therapy as a professor in the medical faculty. In 1784, he was elected member of the Academy of Science (121).

(31) Prince Dmitrii Alekseevich Golitsyn (1731-1803), a prominent Russian diplomat, was a former ambassador in

Holland and France, friend of Diderot and Galvetsy, known as author of many physical works (122).

(32) Dzh. Needham in his "History of Embryology" prefaced the list of the literature sources used by him with a list of works, which he could not obtain. As "less important works on the history of embryology" Needham also mentioned Bezeke's book. It is difficult to decide, on which basis the English historian of embryology considered Bezeke's book less important, if we take into consideration that according to his confession, he never saw it (122).

(33) Two extracts compose the contents of the already mentioned book of 1797 (in it, as stated, were present an essay on the history of a hypothesis about the conception and development of animals and in addition, "History of the origin of division of the natural bodies into three kingdoms"). The third extract appeared in the form of a separate small volume in the year of the author's death (J. M. G. Bezeke. Allgemeine Geschichte der Naturgeschichte in dem Zeitraume von Erschaffung der Welt bis auf das Jahr N. C. G. 1791. Mitau, 1802, XXXII±154S).

For more details about the works of Bezeke see the article by the author of the present book in "Trudy instituta istoriit estestvoznaniya i tekhniki, V.IV, 1955" (Works of the Institute of History of Natural Sciences and Technique) (123).

(34) Matvei Khristianovich Pekén was born in Petersburg, he studied medicine in Ien, where he obtained the degree of Doctor of Medicine (according to other data-- in Gettingen). When he returned back to Russia he worked as the admiralty doctor, read a course of obstetrics in Petersburg hospitals. From 1793, he travelled to Moscow, where he read pathology and organized the first therapeutic clinic with ten beds (124).

(35) Nestor Maksimovich Maksimovich-Ambodic (1744-1812) finished Kiev Ecclesiastical Academy, studied medicine in Strasburg, where he defended a doctor dissertation about "human liver" (1755). At Petersburg admiralty hospital, he read obstetrics and wrote a lot of works and manual books. The second part of the family (Ambodic) was written by himself in connection with accord of patronymic and family (127).

(36) "Dictionary" of Maksimovich Ambodic is composed of two parts: Russian-Latin-French and Latin-Russian, which was prefaced with 65 pages of the text, explaining the significance of this first Russian terminological dictionary, contents of anatomy and physiology and even some information about these sciences.

In "the foreward to the dictionary in general", Maksimovich-Ambodic writes: "During collection of the words, related to my subject of practice, I have been collecting bees for more than 10 years. The major reason was that the Russian words had been collected from various ancient and recent manuscripts belonging to church and civics."

It is difficult to overestimate the significance of this work as a result of the great quantity of terms created, which were absent in the Russian language. This significance is not diminished by the bulkness of some terms which are not contained in scientific language together with others which are archaic and have disappeared from the language in the process of its evolution.

The historian of national medicine Ya. A. Chistovich drew a special attention to the significance of "the dictionary" of Maksimovich-Ambodic. He noted the unfair relation to Maksimovich on the part of V. M. Richter, who "did not offer him a single line in his biographical History of Medicine in Russia". Fortunately, the voice of this light word was fair and, in defiance of the partial historian, preserved the name of Maksimovich from undeserved oblivion" (Ya. Chistovich. First obstetrician schools in Russia (1754-1785. Essays from history of Russian medical institutions of the 18th century. SPb., 1870, p. 199) (131).

(37) Khristian Elias Genrikh Knakshtedt was born in Braunschweig in 1749, studied surgery in Bryunn and in 1786 travelled to Petersburg, where he was professor of anatomy and surgery at Kalinkinsky hospital. In 1790, due to the work "Beschreibung der trockenen Knochen des menschlichen Körpers" (SPb., 1791) the medical college awarded him the degree of Doctor of Medicine. Knakshtedt died in 1799. In addition to the mentioned works, he also published "Descriptio praeparatorum maximam partem osteologicorum rarissimorum"

(Braunschweig, 1785) and Latin-German terminological medical dictionary "Erklärung lateinischen Wörter, welche zur Gliederungslehre Physiologie; Wundarzneywissenschaft und... Ordnung" (Braunsch., 1784, 2nd edition, SPb., 1788). In the title page of the latter he called himself Russian surgeon and ordinary teacher of studies about bones and all their diseases at the imperial surgical school in Petersburg.

To the work of Knakshtedt mentioned in the text "Anatomical description of the monster" an invitation to Medico-surgical school is addressed to "all famous persons and members of medico-surgical sciences" to attend the meeting "near Kalinkinsky bridge at Ekateringofskaya and listen to "some works and speeches by some teachers and students. The meeting was proposed to take place on January 7 at 10 a.m. (131).

(38) Petr Andreievich Zagorskii (1761-1845) is the one who founded the first Russian anatomical school. After teaching at the Cheringovsky college he went to the hospital school in Petersburg. After he finished there, he worked for three years as prosecutor Petersburg medico-surgical school with professor N. P. Karpinsky. From 1799 to 1833, he was junior assistant, and then professor in medico-surgical school, and from 1805 up to the end of his life he was a member of the Academy of Sciences. Zagorskii organized excellent anatomical museums at the medico-surgical school and Academy of Sciences, published the first Russian manual book on anatomy and a great number of works on anatomy, teratology and different medical topics.

(38a) The same opinion on the origin of monsters was also supported by the academician N. Ya. Ozeretskovskii, who informed the Academy on April 25, 1799¹ about two cases of double monsters in the preparations of the academic museum of natural history. One of these cases was united twins (union in the region of the upper part of the chest, both partners

1. N. Ozeretskovskii. De doubus foetibus humanis, monstrosus. Nova Acta Acad. Sc. imp. Petropol., 14. 1805, p. 367-372. The article of Ozeretskovskii was published in the same volume of Nova Acta Academiae Petropolitanae, where the above mentioned report of Zagorskii was also published.

were completely formulated). The second case was the doubling of the head end, beginning from the girdle region; the monster had three correctly-formulated hands, two normal and one underdeveloped legs. The description of the monsters (the first case was illustrated by two excellently-engraved figures, representing the twins from the front and from behind) was concluded with a brief account about the reason for the monsters appearance. By comparison of the described cases, Ozeretskovskii made the conclusion that monsters can be very variable and that each monster, must possess its natural cause. "The physiologists—Ozeretskovskii wrote—must explain these causes and find the specific original source of these monsters—whether their origin is due to the union of two embryos, or from strengthened, weakened or incomplete development of parts of the body" (p. 371).

In another article, whose contents were received by the Academy one year before (on October 25, 1798)¹, a description was given for non-hatched hen's egg with an opening in the shell; through this opening the end of a blood vessel passed. When the egg was opened, in addition to yolk and egg white, a pear-shaped body was found in it, which was full of clotted blood. Ozeretskovskii considered the described content in the egg as a polyp of the oviduct, torn at the time of yolk passing, falling in the egg together with the white. In connection with this, he assumed, that the presence of similar kinds of strange bodies in the eggs of birds may be the cause of appearance of monsters, as the mechanical pressure on the delicate parts of the developed embryo inevitably leads to their deformation. During this, Ozeretskovskii referred to cases of development in double-yolk eggs of doubled embryos which—as a rule—are monsters. During more or less normal development of these twins, they can unite with each other. "Some years before" Ozeretskovskii wrote "we saw here, in Petersburg, doubled chickens, hatched from one egg, provided with all organs and united at the backs; when one of them stood on the legs, the other lied on it on the back with legs upwards in the most unnatural position. It is clear that,

1. N. Ozeretskovskii. De ovo perforata. There also, 12.1801, pp. 364-368.

only the narrowness of the shell was the cause that the twin chickens, which were pressed to each other, united by the backs, similar to the united apples, which, beginning from the moment of flowering, closely adjoined each other".

Both mentioned articles of Ozeretskovskii witness that the Russian academician considered the deformity a result of the caused changes of normal development by external influences, i.e. explained their appearance epigenetically (134).

(39) K. Fr. Kielmeyer (1765-1844), is a famous German naturalist, held in great respect by the contemporaries although he hardly left published works. The most famous work of Kielmeyer was his speech "About the relation of organic powers between each other" (1793). Kielmeyer particularly suggested the idea of powers, inherent within the living beings—irritability, sensibility and reproduction. Their combination in the form of ascending and descending rows corresponds to the stage of the individual development as well as the stage of development of all the organic world, in which, according to Kielmeyer, "the plan of nature" is found. By comparison of the stages of development with these rows, in which adult forms may exist, Kielmeyer made a conclusion, stated by him in a conversation with Gete (1797), that the higher organisms pass many stages in the process of embryonic development, in which they become lower. Shelling attached a very great importance to the ideas of Kielmeyer considering, that they usher in a new epoch in science. In fact, he found later on that before Kielmeyer a similar idea was stated by I. G. Gerder (1744-1863), who was a publicist, poet and philosopher. The works of Gerder, in particular, had a relation to the question discussed—"The ideas of the philosophy of the humanity history", were highly evaluated by Gete. They were popular in Russia as well and had a known effect on Karamzin, Shevryev and Maksimovich (143).

(40) Prince A. P. Baryatinskii a personality of the Southern Secret Society and active propagandist became, towards the end of 1825, the chief of Kilchinskaya board (in Tul'chin the staff of the 2nd army was present, in which Pestel and some other members of Southern Secret Society served) (148).

(41) Efrem Osipovich Mukhin (1766-1850) studied at the Kharkovsky College and Elisavetgradskaya Hospital School, and then at Moscow University. He was a junior assistant at the department of pathology and therapy at Moscow Medical School, and later on a professor at the university. He wrote a great number of manual books and special works (162).

(42) Vilglin Michailovich Rikhter (1767-1822) was born in Moscow, finished Moscow University and published a doctor's dissertation in Erlangen. From 1790 he was a professor of obstetrics at Moscow University. Rikhter is the author of project "Practical obstetrical institute" and many manual books (162).

(43) Ivan Fedorovich Wenssowitsch (1769-1811) studied at the Kharkovsky college and Moscow University secondary school, from where he joined the university, where he successively joined the faculties of philosophy, law and medicine. He finished the university and became a candidate of medicine. In 1803, he defended a doctor's dissertation in Moscow. From 1805 he was a professor of anatomy, physiology and forensic medicine. He published "journal medico-physical. He died from tuberculosis at the age of 42 (163).

(44) Yakov Kuzmich Kaidanov (1779-1885), from Kiev Ecclesiastical Academy, studied in the Petersburg medico-surgical school. After finishing there, he was sent to Vienna to study veterinary medicine. After his return back, he became a junior assistant at the Medico-surgical Academy. From 1809, he became an ordinary professor of veterinary sciences. In 1812, he defended a doctor's dissertation "Quaternary of life".

The contents of the work of Ya. K. Kaidanov were elucidated in B. E. Raikov's book "Ocherki po istorii évol'yutsionnoi idei v Rossii do Darvina" (Essays on history of the evolution concept in Russia before Darwin). Evaluating the outlook of Kaidanov, Raikov, as it seems, insufficiently set off the nature-philosophical, mystical element of "Quaternary of life". M. G. Pavlov could not be called a follower of Kaidanov; his ideas, except for the above-mentioned place in the dissertation of Pavlov, did not find any reflection (168).

(45) Ivan Mikhailovich Boldyrev (?-1819) finished Moscow Medico-Surgical Academy (in the staff of its first graduates). From 1815, he was a junior assistant there, and from 1817 he was an ordinary professor of anatomy and surgery. In 1815, he defended a doctor's dissertation. He died when he was still young (168).

(46) From the comment of Gertsen, it is possible to make the conclusion that the services of M. G. Pavlov in the fields of physics, chemistry and agriculture sciences are extremely insignificant. This conclusion is contradicted, however, by the opinions of either the contemporaries of Pavlov, or the historians of sciences. His scientific and social activities especially in the field of scientific agriculture in Russia were highly estimated. See, for example, the articles of G. Kolosov "Mikhail Grigorevich Pavlov" (1793-1839) ("Vrachebnoe delo", 1927, No. 17, pp. 1217-1220) (173).

(47) In the book of Evg. Bobrov "Filosofiya v Rossii" (Philosophy in Russia) (part 2, Kazan, 1899, pp. 115-118 and part 4, Kazan, 1901, pp. 20-35 and 228-233) in addition to the characteristics of Gertsen, the comments of Linovsky, Amekov Rozanov, Galakhov, Pogodin and others were also mentioned.

Professor of Kazan University, Bobrov, collected in his book sufficiently vast unworked out material, composed mainly of citations, which could be used. Bobrov's own discussions are also considered the idealistic falsification of the history of Russian philosophy (173).

(48) P. N. Sakulin¹ supposed, that under the names of interlocutors of Menon are implied the brothers of Polevye-Nikolai (Polist), their speeches were parodied by the lectures of I. I. Davydov and Ksenofont (Kenofon). In favor of this, the sound coincidence of Pol-ist-Pol-evye stated, by the way hinting at mercenary tendencies of

1. P. N. Sakulin. Iz istorii russkogo idealizma Knyaz'V.F. Odoevskii, V. I, 1913, p. 123.

Nik. Polevoi (πωλητης - merchant) and nearly an exact origin of name of Ks. Polevoi (by the way, $\times\epsilon\nu\omicron\text{-}\phi\omega\nu\iota\alpha$ means idle talk). The articles of M. G. Pavlov in "Atenee" opened polemics. N. Polevoi (under the pen-name $\Theta\cdot\Theta\cdot\Theta\cdot$) in "Moskovsky telegraf"² in an ironical way discussed the opinions of Pavlov and advocated the views of Davydov. The article of Polevoi represents a dialogue between Davydov (Alkin) and Pavlov, who was called Kassy Feliks Iatrosolist, and his philosophy was named "Al'fomegalogy". Pavlov again answered in "Atenee" (part III, No. 11, 1828, pp. 333-348) under the signature "-lv-". (174)

(49) I. Bremser dwelt on the constructive opinions about the origin of the animal kingdom joining the imitation of Kyuve, who completed his theory of the catastrophe of ideas of repeated creations.

The opinion of Bremser about the origin of parasitic worms is also an expression of his idealistic views on the plastic power, which was given by the Creator to the living nature.

2. Magazine "Moskovsky telegraf" was organized by N. A. Polevoi in 1825. He directed it during 10 years. This magazine had a notable influence on the history of Russian journalism. The initial periods of the activities of Polevoi, as the editor of "Moskovsky telegraf" were highly estimated by Belinskii and Gertsen, giving credit to Polevoi for his passionate propagation of progress, but not hiding the contradictions and faults in the trend of his journal. Later on, Polevoi passed to more reactionary positions, which did not, however, save "Moskovsky telegraf", which was closed in 1834 by the order of Ministry of Education. After this, from 1835 to 1844 Polevoi published (under a strange name) popular scientific journal "zhivopiance obozrenie", in which as B. E. Raikov stated, actively (although also anonymously) K. F. Rulé participated (see B. E. Raikov. Russkie biologi - évol'yutsionisty do Darvina, V. III, 1955). At the same time, with the scientific—popular articles for "Zhivopisnoe obozrenie" N. Polevoi wrote hurrah-patriotic plays, as "Dedushki russkogo flota" (Grand-dad of Russian fleet), owing to this he was in 1839 given a brilliant ring (see V. Veresaev. Sputniki Pushkina, V2. Izd. "Sov. pisatel", 1937, pp. 352-357).

The anonymous translator referred in the preface to the advice of prof. I. T. Spassky to translate this book, which was highly estimated by Spassky. The small paragraph of Spassky "About the spontaneous or indefinite generation of the organic bodies (*generatio aequivoca spontanea*) is added to the translation of Bremser's book on the initiative of the translator (177).

(50) For the characteristics of the outlooks of Aleksey Leont'vich Lovetskii, who, together with I. E. Diadkovskii, stayed at the Moscow Medico-Surgical Academy, it is possible to cite the evidence of this "loyal" personality, as D. K. Tarasov. Later on, the surgeon Aleksander I. Tarasov wrote in his memoirs, that in January 1815, after finishing Ryaznskaya ecclesiastical seminar, he, together with V. V. Markov, travelled to Moscow to join the Medico-Surgical Academy. "We did not hesitate to go to the academy, where we found 8 men from Ryazan, the most remarkable amongst them Diadkovskii and Lovetskii who had already finished the course and were appointed as coaches or professors. As fellow-townmen we got acquainted with them. The system in the academy, the accommodation of students, their treatment and the study itself pleased us. However, only one circumstance, unexpectedly encountered us, and strongly affected me in particular, and we decided that it was better for us to travel to Petersburg. This circumstance was as follows: As a native of Ryazan G. Lovetskii quickly gained my admiration by his frankness. Discussing once with me the different scientific subjects, he asked me some questions related to religion. As to my answers, which were characterized by faith and persuasion, he presented these refutations, which stimulated in me a strong indignation, that I, on informing my friend Markov of this decidedly told him, that I was absolutely sure, that we must travel to Petersburg and do not have by any means such a company against which I had the most disagreeable prejudice" ("*Vospominaniya moei zhizni. Zapiski pochetnogo leib-khirusga D. K. Tarasova*", 1792-1866, *Russkaya Starina*", 4, 1871. The author is grateful to prof. I. D. Strashun for the indication of this source).

From what is stated, it is clear, that Lovetskii adhered to atheistic opinions, from which the Godfearing

Ryazan's students became frightened, and were the cause of their running away from Moscow (183).

(51) In the footnote Diadkovskii made a reservation, that he did not want to associate himself with the existing materialistic opinions, obviously, distinctly confessing the dissatisfaction of the mechanical materialism. He wrote: "I request not to conclude that I follow, in relation to the opinion about materials, the atomistic or mechanistic system. I accept material as material, as the atomists make this. However, I do not assume any powers inside material, as dyanmists (although I do not want, as it is clear, to regard the material according to their custom, as a phenomenon of power aggregates). Briefly: for me personally the material is a functioning and searching action". Lebedev has also omitted tendentiously this footnote in his translation.

Lebedev interpreted the materialistic ideas of his teacher I. E. Diad'kovskii and in the years of scientific and teaching activities (1831-1843) publicized them in his published articles (see for example, article A. V. Lebedev "About life" in "Uchenya Zapiski" of Moscow University, XII, 1834). Ten years later, when successively dismissed from university and Moscow Medico-Surgical Academy, Lebedev did not decide to represent him in censorship without alleviated comments and notes (197) on the publication of the translation of Diad'kovskii's dissertation.

(52) Oken referred twice to Tredern's dissertation. In the discussion of Pander's dissertation ("Isis, No. 192-193, 1817), he enumerated the most important investigations of chicken development by Malpighi, Haller, Wolff and Spallantsani. Oken continued: "To this must be added the dissertation of Tredern just conducted here. (Why doesn't Tredern give any information about himself?)". One year later Oken published the summary of Dyutrochet's article under the title "Investigations of Zh. Kyuve on fetal membranes" ("Isis", 1818, I, pp. 114-126). Dyutrochet wrote the following: "In his thesis about the history of egg and incubation, which he defended in Ien in 1808, Tredern called the allantoic sac the chorion". Oken made this note about this phrase: "We must notice here that all which was mentioned by Tredern in his dissertation was but a result of his own, and constituted the service he had rendered (210).

(53) A. V. Haller (Sur la formation du coeur dans le poulet, 1758) observed within 70 hours of age, a sac that was not the rudiment of the beak and nothing more than the forehead (bullam dicit auctor, quae nihil aliud est, quam frons).

Wolff in the dissertation "Theoria generationis" distinctly distinguished both these parts after five days of incubation.

Malpighi ("De formations pulli in ovo", 1867) also considered this formation as the forehead. In Fig. 20 of his work, relative to which Tredearn stated that it was less thoroughly performed, than many others, the first appearance of the beak was shown on the 7th day of incubation (222).

(54) J. Koiter (De ovorum gallinaceorum primo exordio progressusque et pulli gallinacei creationis ordine, 1572) said that he found something similar to the beak after six days.

J. Vesling (Syntagma anatomicum, 1666) confirmed, that the formation of the beak begins after the 8th day. N. Stenon (Observationes anatomicae, 1662) indicated nearly the same period (222).

(55) Maître-Jean (Observations sur la formation du poulet ou les divers changements qui arrivent a l'oeuf à mesure qu'il est couvé son exactement expliqués etc., 1772) said, that at about the 164th hour of incubation, he found still a soft beak. Tredearn later on noticed that the description of the beak development by this author was not accurate and incomplete (auctor de rostro nec accurate nec plane loquitur) (222).

(56) Haller confirmed that the hard beak was present after 214 hours of incubation. According to Malpighi the cartilagenous beak existed on the 10th day. Tredearn assumed, that a very early period was indicated here (222).

(57) This white point on the apex of the beak was also seen by Stenon on the 10th day of incubation (223).

(58) Aristotle, who was cited by Treder in the French translation of Kamyus (1783) said: "umbilical cord, united with the yolk, is attached to the small intestine" (223).

(59) For example, J. B. L veill  (Dissertation physiologique sur la nutrition des foetus etc., J. de Physique, 1999) could not make certain that the chord, supporting the yolk, was a flap (223).

(60) Blumenbakh in his "Comparative anatomy" related the beginning of the existence of intestines to the 4th day. Vesling saw the intestines on the 5th day, and Stenonus saw them on the 7th day. According to Vicqd'Azyr, the intestines appear after 90 hours of incubation; this is the earliest period, but usually after 120 hours. Treder noted that the latter data corresponded to his own observations. (223)

(61) In this connection Treder said in the commentary on the literature reference to Wolff: "On the 3rd day, both plate and mesentery are present, from which the formation of the middle intestines takes place" (Die III adsunt ambae lamellae atque mesenterium, ex quo formatio intestini medii progreditur). (224)

(62) Malpighi, and equally Koiter also wrote that on the 10th day the intestine hangs down from the abdominal cavity. Harvey said, that on the 14th day the intestine and the stomach are still not included in the abdominal cavity; the stomach is rarely present outside it. Treder added that seeing something similar, he considered this phenomenon as a deviation from norm (224).

(63) Malpighi mentioned the rudiments of the wings already at the stage of 24 hours of incubation. Haller fairly pointed to the erroneousness of this confirmation. According to Stenonus, on the 5th day the upper part of the thigh as well as the feet and wings are formed. According to Vesling, the rudiments of legs appear on the 4th day while according to Harvey on the 5th day. Ma tre-Jean, Vicq d'Azyr as well as Haller mentioned much earlier periods of appearance of extremity rudiments (after 60-70 hours of incubation) (224).

(64) According to Maître-Jean, the fingers appear for the first time, within 164 hours after the start of incubation. Malpighi gave quite contradictory data: on his four figures the first appearance of fingers is manifested on the 9th, 11th, 12th and 15th day. According to Vesling, the feet and fingers are already clearly distinguished on the 7th day. (224)

(65) In the book of B. E. Raikov (Russkie biologi-évoluytsionisty do Darvina, (Russian biologists-evolutionists before Darwin), V. I) is given a clear essay of the life and activities of Bojanus—comparative anatomists and evolutionist. About his embryological investigations, what is stated there is casual and moreover incompletely accurate information. Thus, on page 375 it is said "Bojanus, long before the researches of Baer showed, that allantois was an independent formation in the form of a sac, which was present inside the amnion and sided with it". In fact, Bojanus confirmed that the allantois surrounded the amnion from outside and sided from the inside with the chorion. (228)

(66) Pander enumerated the different opinions about "paunch". "Emil Parizan considered it the semen of the cock, Harvey, Lengli and Maître-Jean called it paunch, Malpighi—follicule, Coiter—dot or circle, Vesling—while spot, Vicq d'Azyr—paunch or embryo, Tideman—paunch or spot, Illiger—embryonic or jumping dot" (Pander. Dissert., p. 18, footnote). (245)

(67) In the footnote Pander (Dissertatio, p. 22) noted that before Wolff no author even mentioned the blastoderm. Wolff in the article "About the formation of intestine" (Novi Comment. Acad. Petrop. V. 13, p. 431) wrote about a zone, surrounding the embryo, in which the embryo cannot be also developed. "All other writers,—Pander said,—strongly deviated from that fact and called the blastoderm sometimes paunch (many authors), sometimes clot (Malpighi, Lengli, Harvey), sometimes the sac of the clot (Malpighi), sometimes the eye of the egg (Harvey), sometimes bed of the hen (le lit de la poule) Maître-Jean, sometimes yolk sac (Haller), which is already absolutely incorrect—all authors, discussing, after Wolff, the formation of the chicken in the egg, did not mention the blastoderm and called it widening of a spot (Tideman) or bulging of yolk membrane (Oken)" (246).

(68) To the title of the paragraph, Pander made a footnote, in which he indicated that Malpighi saw the rudiment of the embryo in a still non-incubated egg, and at six hours of incubation-embryo with head. Pander did not suspect the reliability of these observations, although he presumed that there was erroneous determination of the time of incubation here, because development could begin before incubation (246).

(69) Haller had already described this transparent field, as Pander noted in the footnote, and called it nidus of the chicken (nidus pulli). He indicated that it could assume different forms (246).

(70) Pander considered that from the two layers, described by Wolff, the external one was the yolk membrane, and is referred to in the article "About development of intestine" (Novi Comm. Acad. Petropol., V. 12, p. 415): "There is no basis to consider, that it is related to the self-cover of the embryo; it forms the common membrane of the yolk, in which the embryo and the amnion are also included". Pander, apparently, made a mistake, because in many places of the Wolff's article cited by him, Wolff spoke sufficiently clearly about two layers, which were related to the embryo itself and were present under the yolk membrane (246).

(71) Pander referred here to the description of the early embryos by Tideman and Oken. The two latter authors saw only a thread-like body of the embryo with a swollen head end. Only Haller noticed "the split tail, widening at the start and assuming the form of lancet at the end. These halves of tail, obviously, correspond to the posterior ends of Pander's primary folds (251).

(72) Concerning the distribution of this legend, it is possible to judge, in particular, by the mentioned course of physiology of Burdach. He spoke about the stages of the study of the embryonic development and characterized the two first epochs of history of embryology—the epoch from Aristotle to Harvey and the epoch of Wolff. He wrote later on: "The third epoch consisted of the works of Döllinger and Pander, who, in many years, compiled investigations

which dealt more profoundly with the essence of development, namely, when they studied the development of embryonic membranes in a structure of three plates and the development of the different organs of them" (K. F. Burdach. Die Physiologie als Erfahrungswissenschaft, 2 te Aufl, Leipzig, 1837, 2-ter Bd., S. 160).

This is also witnessed by the incorrect bibliographical reference to the German variant of Pander's dissertation, given at a significantly later time (1884) by Ya. A. Barzenkov in "Chteniyakh po sravnitel'noi anatomii" (Readings in Comparative Anatomy). Barzenkov referred there to the non-existent article. Pander, Döllinger und D'Alton Beiträge zur Entwicklungsgeschichte des Hühnchens im Eie (260).

(73) Oken was not completely right. In the German variant of Pander's dissertation there is a special "table of sections", in which schematical presentations of the early stage of development of the hen's embryo were given. From these figures, particularly represented above (p. 247), it appears that the formation of intestines and especially the allantois ("chorion") was obscurely imagined by Pander. In return, the figures of amniotic fold and the serosa formed of it ("false amnion") and amnion ("true or proper amnion") were represented very well. From the recent figures, these schemes of Pander differed only in that, he did not take into consideration the participation of mesoderm in the formation of the embryonic membranes (261).

(74) In his autobiography, Baer stated (p. 300) that in the "Medico-surgical Newspaper" (1818, No. 14) the review of F. Gruitguzen appeared, in which there were some excerpts of both works of Pander. The author of the review stated as if he completely understood and knew the description.

Reference to the written comment on the dissertation of Pander which was given by the academician P. A. Zagorskii was cited in the book of M. A. Tikotin "P. A. Zagorskii i pervaya russkaya shkola" (P. A. Zagorskii and first Russian anatomical school) (Medgiz, 1950), based, apparently, on misunderstanding. In the mentioned book, on page 143, Tikotin wrote: "In the archives of the Academy of Sciences of USSR....we found the review by academician P. A. Zagorskii

on Pander's article "Beitrage zur Entwicklungsgeschichte des Hühnchens in Eie" (Archives of Academy of Sciences of USSR, funds I, inventory 2, § 128, 1820)". In the reply to the request to send a photocopy of this review in the Archives of the Academy of Sciences of USSR on April 3, 1951 (No. 783) it was informed, that "in funds 1, inventory 2, 1820, § 128 there was the comment of the academicians P. A. Zagorskii and A. F. Sevastyanov on the article of Pander "Das Skelett der Knochenfische". The comment on the article of Pander which is of interest to you, is not found in the Archives of the Academy of Sciences of USSR. There is only a mention in the proceedings of sessions of the conference of the Academy of Science on March 15, 1820 (§ 76) about the representation by Pander concerning his published work "Beitrage zur Entwicklungsgeschichte des Hühnchens im Eie" (264).

(75) Oken widely used the right given to him as an editor to put his remarks and polemical discussions in the strange articles which were published in "Izid". Thus, publishing the major article of Döllinger, he combined it with similar remarks, sometimes very unceremonious, as exclamations: "Oho" and so on.

In the stated article of Pander, many remarks of Oken were mentioned (264).

(76) Aristotle arches, passing in the visceral arches between branchiate slits, were not known to Pander, they were discovered and described in detail later on. The main merit in their study belongs to Baer (see Chapter 16) (266).

(77) Here Oken noted "It is absolutely clear, that they were also formed of segments, he and ei?". Thus, the idea about the non-embryonic blastoderm, as distinctly developed by Pander, remained nevertheless obscure for Oken (268).

(78) In the same place Oken again made a note in which, in spite of obviousness, with amazing persistence, he repeated his idea about bladders as the primary formations in the development of the embryo (268).

(79) In this place, Oken made a funny remark: As we have always confirmed, this was studied and represented in

our reports. What do we argue about? Therefore, in fact, what was said by Wolff (and also the authors in their Latin dissertation) is incorrect, namely, that the intestine by length is split, and that the rectum and small intestine grow opposite to each other. We now are liable to be annoyed by that zeal, with which we attempt to show that the studies of Wolff are worthless, or at least are false interpretation and understanding. Good friends, all this, however, could be avoided, if in the Latin dissertation, instead of the defending (Wolffina) and rising against us, stated his present opinion. From now on, there will be peace between us!" (p. 269).

Nearly it is impossible to imagine, how Oken could, by a similar way, misinterpret Pander's data, which absolutely and undoubtedly confirmed the principal idea of Wolff about the system of the intestine formation (269).

(80) Edward Ivanovich Eichwald was born in Mitav in 1795. In 1819, he defended at Vilensky University dissertation for the degree of doctor. From 1821 to 1823, he was an assistant professor for the course of zoology, and from 1823 to 1827 he became professor of midwifery at Kazan University, where, in addition, he read lectures on zoology and comparative anatomy. In Kazan, Eichwald published the article mentioned on page 155 about the human ovum. For the following ten years Eichwald was the head of zoology and comparative anatomy department at the Vilensky University. He died in Petersburg in 1878 when he was honored as professor and academician. Eichwald left a great number of articles in different branches of natural sciences and archaeology, having on the whole only an historical interest (271).

(81) It is possible to have a look into the life and works of K. M. Baer through the biographical essays of L. Stieda¹, N. A. Kholodkovskii² and B. E. Raikov³. Some

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1. L. Stieda. Karl Ernst von Baer, eine biographische Skizze, Braunsch., 1886.
 2. N. A. Kholodkovskii. "Karl Bér. Ego zhizn i nauchnaya deyatel'nosti" (Karl Baer. His life and scientific activities). 1923, 110 pages.
 3. B. E. Raikov "O zhizni i nauchnoi deyatelnosti K. M. Bér" (About the life and scientific activities of K. M. Baer. In the book: K. M. Bér. Istoriya razvitiya zhyvotnykh (History of animal development). Izd AN SSSR, 1950, p. 383-438.

trips of Baer and his works in the field of geography and applied zoology are elucidated in the works of I. D. Kuznetsov¹ and M. M. Colovev². The activities of Baer as professor in the Petersburg Medico-Surgical Academy were studied by E. N. Pavlovskii³ (275).

(82) Baer in his "Autobiography" (p. 196) said the following about Döllinger: "He has comprehended by philosophical views the gaps in the accurate knowledge, without having possessed the possibility to fill them. Döllinger never attempted to bridge these gaps by means of philosophical deductions which was, moreover, astonishing, because he undoubtedly had a philosophical mind. Early, he studied keenly Kant's philosophy. Then, he was attracted by Schelling, with whom he was intimate, but due to the critical discussion and systematic imagination he quickly understood, that Schelling rendered difficult the tasks of philosophy by the pedestal of his natural-philosophical teachings. Later on Döllinger reluctantly spoke about this period and expected the successes of physiology from special observations, which must only then philosophically be generalized" (278).

(83) In connection with the opening of zoological museum, Baer published the article "Two words about the present condition of the natural history" (Zwei Worte über jetzigen Zustand der Naturgeschichte. Königsb., 1821, 48S. The title is extremely moderate (in the Russian edition of "Autobiography" of Baer (1950, p. 260) the title of this work was incorrectly translated), although this article included many profound ideas which will be dealt with hereinafter (see Chapter 24) (279).

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1. I. D. Kuznetsov. "Akad. Karl Ernst (Karl Maksimovich) von Bér. Ego zhizn i deyatelnost." (Acad. Karl Ernst (Karl Maksimovich) von Baer. His life and activities).... Vestnik rybopromyshlennosti, 1892, No. 12.
 2. M. M. Colovév. "Bér na Novoi Zemle" (Baer in the New World). Izd. AN SSSR, 1934, 51 pages, the same author also "Baer na Kaspii" Baer in Caspii). Izd. AN, 1941.
 3. E. N. Pavlovskii. "K. M. Bér i Mediko-khirurgicheskaya akademiya" (K. M. Baer and the Medico-Surgical Academy). Izd. AN. SSSR, 1948, 215 pages.

(84) From the works of Baer, based on his opinions about the system of animals and carried out in connection with much later embryological investigations to the creation theory of types, it is necessary to mention the major article which is composed of seven independent reports: Beiträge zur Kenntniss der niedern Thiere (Nova Acta phys. med. Acad. Caes. Leopoldino Carolinae naturae curiosorum, T. 13, p. 2, 1827, S. 525-762). This work elucidated the description of different worms, parasitizing on molluscs, amphibiae and some planarie and ended with the article "About congeneric relations of lower animals between themselves".

In addition, Baer published some special zoological and zootomical works, also connected in one way or another with his subsequent embryological works. The following works are from them:

1. Ueber den Weg, den die Eier unserer Süßwassermuscheln nehmen, um in die Kiemen zu gelangen, nebst allgemeinen Bemerkungen über den Bau der Muscheln, Arch. Anat., Physiol., 1830, S. 313-352.

Concerning the vexed question about the presence of orifice in the ovary of the bivalve (or, by that time terminology, headless) molluscs, Baer reported his observations, according to which in many species of freshwater mussels these openings are closed, although the way of transference of the ova to the branchiate cavity in them is the same as in other Lamellibranchiata.

2. Bemerkungen über die Erzeugung der Perlen, Arch. Anat., Physiol., 1830, pp. 352-357). In this paragraph, Baer objected to Gom, who considered, that pearl-oysters are the covers of the eggs of mussels. Baer found pearl-oysters only in mantle and considered them as a manifestation of pathological process. (280).

(85) Both these editions represent at the present time great rarity. In 1829, extracts of an inaccurate French translation of both these works, performed by Breschet, appeared ("Lettres sur la formation de l'oeuf dans l'espèce humaine et dans les mamifères" "Commentaire de mémoire précédent", publiés par Breschet, Paris). This edition was, apparently, published in very few editions, that even Baer

himself, as he noted this in his "Autobiography", never saw it. In the German language, the classical work of Baer was published in the translation of B. Ottov in 1927, in the centennial anniversary of the publication of the Latin original. This work of Baer is still not published in Russian translation.

In 1931, the work of Sarton appeared "The discovery of mammalian egg and the foundation of modern embryology", *Isis*, 16, pp. 15-330, to which the Baer's facsimile "De ovi mammalium et hominis genesi" (pp. 331-377). (Cited in the book, O. W. Meyer. *The rise of embryology*, 1939) (286).

(86) G. Prokhaska in the: "Physiology, or science about the nature of humanity", published in 1820, which in 1822 was translated into the Russian language by D. Vellanskii who wrote: "Uterine tubes have in their ends the ovaries, from which the female fertile material raises and conduct it to the uterus for mixing with the male semen. The female fertile material, similar to the embryo of the ova-bearing animals, must be located in the Graafian follicles. But these follicles are attached to the ovaries, so they can separate from them with difficulty, and the uterine tubes are narrow for the passage of the follicle. Therefore, I think it explodes, and the fluid present in it passes through the tube to the uterus. May be at the time of copulation the follicle by self-power separates from the ovary, and the tube is widened from conducting it. This is, however, necessary to be proved by more experiments" (§ 352 "About the reproduction and conception of the embryo", p. 543) (288).

(87) William Cruikshank (1745-1800) was a professor of anatomy and surgery in London. He published many works on anatomy, medical problems as well as physics and chemistry (288).

(88) Jean Luis Prévost (1790-1850)—Swiss physician, physiologist and chemist. His investigations on embryology were partially performed in collaboration with Jean Batist Dumas (1800-1884), who was later on a famous chemist (288).

(89) The complete title of Purkinje, in which the description of the ovum nucleus was included, is: "Ioan. Fried. Blumenbachio, ...etc. summorum in medicina honorum semisaecularia

gratulatur ordo medicorum Vratislaviensium interprete Joanne Ev. Purkinje P. P. O. Subjectae sunt symbolae ad ovi avium historiam ante incubationem; cum duobus lithographiis. Vratislaviae, typis universitatis (anno 1825, mense sept. (edit.)). (Iog. Frid. Blumenbach from the name of Bratislava physicians Iog. Ev. Purkinje was congratulated on the occasion of being awarded a higher honor in the field of medicine. The enclosed article is about the history of birds' eggs till hatching with two lithographs (Bratislava Published in September 1825 at the university printing-house) (298).

(90) Studying the embryological works of Baer, the author of the present book did not possess at hand the translation of "History of animals development" existing now and he used the German text of both volumes in the copy, preserved at the library of Moscow Society of naturalists, as well as the text of the concluding part—in the copy from governmental library of USSR named V. I. Lenin (302).

(91) Burdach published these materials in the second volume of his "Physiology" (Die Physiologie als Erfahrungswissenschaft, herausgegeben von Prof. Dr. K. Burdach, Leipzig, 1828—Geschichte des Froschembryo, S. 297-312 and Geschichte des Hühnerembryo, S. 335-466).

Unwarranted notes and rearrangement in the Baer's text, which was done by Burdach, caused the indignation of Baer who, due to this, considered it necessary to publish his embryological article in a separate edition. This in turn led to the displeasure of Burdach. Baer stated in his "Autography" in detail the history of his disagreement with Burdach (see p. 393 and the Russian edition) (303).

(92) Rudiment (Keim) as called by Baer is the formation, which gives later on either the embryo (Embryo), or the non-embryonic blastoderm, which he called "rudiment membrane" (Keimhaut). In the commentary on the Russian translation (edition of 1950) there was a suggestion to translate the Baer's terms as follows: Keim-embryo, Embryo-embryon. In fact, this removes the confusion in the understanding, but allows a certain mistake against the accuracy of the translation and purity of Russian embryological terminology.

In fact, in the recent Russian literatures, the understanding of "embryon" and "embryo" is a synonym, and mostly reveals the tendency to use Russian and not Greek words. (Russian physiologist of the 18th century N. M. Maksimovich-Ambodik in his "Dictionary" (see Chapter 10) was one of the early scientists who apparently changed the word "embryon" to the Russian words "Zarod", "Zarodok", "Zarodish (embryo)"). In accordance with this, the German term "Keim" (Greek is blastos) is more suitable to be translated into the word "Rudiment", as this, for example, was made by L. F. Zmeev, who translated Ratke's book (History of vertebrates, with the preface of K. A. Kölliker, translated from German language by L. Zmeev, number 1. Stavropol, Izd. Gub. Pravleniya, 1866, pp. 1-45) (310).

(93) Establishing that the long axis of the embryo is perpendicular to the longitudinal axis of the egg and the left side of the embryo is directed to the blunt end of the egg, Baer stated an evoked assumption by the natural-philosophical principles, that this position depends on polarity of the egg. The latter, according to his opinion, arises in the maternal organism and is expressed by the movements of substances from a blunt pole to a sharp one probably under the influence of electromagnetic powers (311).

(94) One year before the publication of the first volume of "History of animal development", Baer published a special article, dedicated to the development of branchiate slits, arch and blood vessels in the embryo of vertebrates, in which he showed, that the branchiate slits discovered by Ratke in the birds' embryo, were also present in other vertebrates (K. E. V. Baer. Über die Kiemen und Kiemengefäße in den Embryomen der Wirbelthiere. Arch. Anat., Physiol., 1827, S. 556-568).

Later on the article of Baer appeared also in French in the form of one whole report (Des branchies et des vaisseaux branchiaux dans les embryons des animaux vertébrés. Ann. Sc. nat., 15, 1828, pp. 266-284; Ann. Sc. d'observ., 2, 1828, pp. 116-123) (323).

(95) At first the term "scholni" meant the notes on the fields of the manuscript texts of the antique writers. It does not, however, constitute systematized commentaries. In the

middle-centuries philosophical and theological treatises, the scholni meant, in general, addition and remarks.

Corollarium are interpreted comments (339).

(96) The priority of the correct interpretation of Baer's teaching about the embryonic plates and criticism of erroneous opinions at the expense of Bischoff and Filipchenko is belonging to T. A. Detlaf. Her opinions are included in a doctor dissertation "Comparative-experimental study of evolution of the ectoderm, chordomesoderm and their products in Anamnia" (M., 1948) and later on in the article "Discovery of the embryonic plates by K. F. Wolff and Kh. Pander and the study on the embryonic plates of K. M. Baer" (Trudy In-ta ist. estestovzi., V., 1953, pp. 281-316) (343).

(97) The theory of the embryonic plates which is found as a comparative-embryonic principle and expressed in the works of Baer, met sympathy by the majority of his contemporaries—Rathke, Kost, Valentin, Remark and others—and determined the trend of their works. Among the few opponents of the embryonic plates theory, it is necessary to mention Reichert. The latter suggested an opinion, according to which "temporary covering membrane" first exfoliates in the egg of the frog and under its protection, the development of the embryo takes place. The latter is concluded, according to opinion of Reichert, in the gradual formation of the animal system of the organs:—central nervous system, intestinal system and, at last, the mucous membrane of the digestive tract. In the embryo of the chicken, according to Reichert, up to incubation there is only one-layered rudiment thin skin, which gives the origin of integuments, and at the time of incubation from the yolk subsequently develops the central nervous system, intermediate membrane, containing the chord and, at last, during the appearance of the head part of the visceral tract,—a last membrane-like cellular cell for the formation of the mucous membrane of the intestines. Remak perspecaciously considered these opinions as containing a progressive idea, because from Reichert's point of view it was possible to introduce amendments in these ideas of Baer, as the separation of the central nervous system from the semi-fluid contents of the spinal plate. At the same time, Remak decidedly raised an objection against the opinion of Reichert on the development in a layered appearance of

layers of organs, as "the rudiment already before incubation, is composed of two plates or layers, which constitute the layers of all the embryo". The opinion of Reichert was a step backwards, because the refusal of the theory of embryonic plates is at the same time a negative step in the development of lower and higher vertebrates (344).

(98) In one of the theses (2), enclosed in this dissertation and not connected with its contents, Baer wrote: "Legem a nature scrutatoribus proclamatum evolutionem, quam prima aetate quoque subit animal, evolutioni, quam in animalium serie observandam putant, respondere", a natura alienam esse contendo" (I decidedly confirm that the law, proclaimed by the naturalists, "development, inherent from the beginning in a separate animal, corresponds, as it is supposed, to the development, observed in animal series", is alien to nature). In the commentary on the list of his works ("Autobiography", German edition, p. 607) Baer himself noted that the contents of this thesis is an indication to the beginning of his investigations on the history of animal development (350).

(99) Baer cited with bewilderment Erman, who confirmed that the birds eggs could develop in the absence of oxygen (in an atmosphere of hydrogen, nitrogen or carbon dioxide gases). The importance of atmospheric air for the development of chicken embryo was demonstrated for the first time by Geoffroy St. Hilaire in experiments of varnishing the egg shell (E. Geoffroy St. Hilaire *Mémoire sur les différents états de pesanteur des oeufs au commencement et à la fin de l'incubation*, "Isis", 1820, pp. 918-925).

It was not longer before spectacular results of Erman were disapproved. T. Shvani, under the advice of his teacher Iog. Müller, was dedicated to investigate this question through a doctor dissertation "De necessitate aeris atmosphaerici ad evolutionem pulli in ovo incubato" (Berolini, 1834, 4^o). From which extracts were published in the same year in German: T. Shvani. *Über die Nothwendigkeit der atmöspharischen Luft zur Entwicklung des Hühnchens in Ei*, *Frör. Not.*, 41, No. 896, 1834, pp. 241-245.

At the time of the publication of the second volume of "History of animals development" Baer had stopped his work on

tracing the embryological literatures. Therefore, the investigations of Shvani were unknown to him (376).

(100) In the footnote, Baer proved his suggestion to replace the name "allantois" by the term "urine sac". It is necessary to admit that both the old name—allantois and that of Baer—"allantoid" which corresponds to the form of embryonic organ only in hoofed mammals, or Baer's name—urine sac were successful. The urine sac, i.e. the reservoir of products of excretion, as allantois is in *Sauropsida* and in a few mammals (namely in hoofed), while in other mammals it possesses an underdeveloped cavity or even, is quite absent.

(101) In the note to the place of the Russian work of Baer, P. G. Svetlov drew attention to the importance of the mentioned idea of Baer. It was totally fair to regard it as containing the rudiment of the theory of embryonic plates as parts of general vertebrates. Moreover, this generalization arises in the process of embryonic development and can be established only during the study of the latter one. In the same note, it was stated, that layers, noticed by Baer in the body of vertebrates, did not, strictly speaking, correspond to embryonic plates and that Baer was not in situation "to complete his outstanding retrospective analysis of organs of the formulated animal up to the stage of "primary separation", i.e. to the embryonic plates" (Note 34, p. 459) (381).

(102) This place of the Baer article is difficult to understand, as the translators of the second volume of "History of animal development remarked. P. G. Svetlov, made an attempt to interpret the very laconic stated ideas of Baer. The interpretation suggested by him (note 63, page 464) is extremely probable, but cannot withstand a complete proof (390).

(103) The aspiration for widening the field of the comparative-embryological investigations prompted Baer to use the necessary materials so as to strengthen the researches. In the work about the development of tortoise (see footnote on page 405), Baer described the difficulties to which the obtaining of their eggs was connected. In environs of Kenigsberg, tortoises were absent. He asked for tortoise eggs from Litva. "If the eggs died on the way, or females carried infertile eggs, I did not obtain, in all cases, desirable results.

Finally, during last summer, one tortoise, which was offered to me for sale, was so helpful, that it gave me eggs directly in my hand, just when I raised it. I appreciated this considerable deposit and made the tortoise my house friend". This tortoise deposited many eggs from the ovary and began to develop. However, the development continued only till the 10th day, then the embryos died. Concerning the causes of the embryos' death, Baer stated different suppositions (deficiency of humidity, heat, oxygen). In all cases, the early death of embryos is an indication that the course of their development, in many cases, could deviate from norm. Therefore, Baer did not get authentic data about the tortoise development (405).

(104) In the figure given in text (p. 407) (Fig. 30), and taken from this work, Baer selected the embryonic thorax (Fig. 17) and its transverse section under 10 times of magnification (Fig. 18). According to Baer's opinion, the tortoises are characterized by immersed spinal plates inside the fissure (ab) and by abdominal plates coming forward (bc). This peculiarity of early embryonic development of tortoises is referred to by Baer to explain the peculiarity of the formation of axial skeleton and ribs in the formulated animals. This conclusion is undoubtedly erroneous, because the region ab in Fig. 18 is the spinal canal, and the region bc—is what is called spinal plates by Baer. The confirmation of Baer that the extremities in the tortoises are formed in a way different from other animals, is also incorrect. The deficiency of materials and disturbances of development, connected with the unsuitable conditions of egg maintenance, were the sources of the erroneous conclusions (405).

(105) Baer's investigations on the embryology of man were known in Russia. Brief popular statements of the phenomenon of conception and embryonic development of man were given by P. F. Goryaninov in the article "Development of human embryo in the uterus", which was published in 1887 ("Drug zdraviya" (public medical journal), No. 32, pp. 241-243, 4^o). In this article, Goryaninov talked only about two layers—external and internal. "From internal, he wrote, the intestinal canal, lungs, mesentery and other vegetative organs are formed, and from the external—animal region skeleton, muscles and skin. Obviously, Goryaninov, not wishing to go into details, distinguished only the regions of the embryo, which were called by

Baer the animal and plastic parts, and did not touch the subdivision of these layers into embryonic plates (418).

(106) Baer made a mistake, suggesting that Swammerdam did not see the division of the ovum. In *Bibia naturae*, Swammerdam gave a figure of the dividing ovum of frog (stage of two blastomeres). Reference to Swammerdam by Baer was not accidental, Baer highly estimated the unusual accuracy of Swammerdam's observations, contained in his interesting speech, made at the opening of the anatomical institute in Kenigsberg in 1817). (*Iohann Swammerdam's Leben und Verdienste um die Wissenschaft* (K. E. v. Baer. Reden. 2-te Aufl., Braunsch., 1886. 5.3-34) (420).

(107) Later on ("Autobiography", p. 383 and the following pages) Baer decidedly raised an objection to the term "process of fissure formation" (Furchungsprozess), which at that time in particular was used by Kolliker and Reichert. The use of this word, according to Baer's opinion, could be a source of incorrect interpretation of the phenomenon. In spite of this fair note, in German literature and later on, the division was designated as "fissure formation", although, of course, no one thought that the matter was the appearance of only a fissure on the yolk surface. (421)

(108) The discovery of the division process by Baer was not completely unexpected by the embryologists. The observations of Prévost and Dumas, as well as Rusconi, constituted the preparation for this discovery. As already stated, the French embryologists did not consider the appearance of the fissure on the ovum surface as a sign of its division into parts. Rusconi considered that the splitting leads to this division, but the terminological disagreement caused discussion between Baer and Rusconi which was based on misunderstanding. It is necessary to admit that Baer, in his observations on splitting and in the analysis of this phenomenon, has significantly gone beyond the Italian author. Baer, much more correctly than many of his contemporaries, looked for the process of splitting itself, comparing it to the division of cells in the organism of the multicellular animals. Thus, Shvani in his "Microscopical investigations" wrote, that during the splitting of ovum "inside the yolk two cells develop, in each of them two are formed again and so on",

i.e. he did not accept the division of the ovum into blastomeres, but their endogenous formation in the ovum. Bergman raised an objection to Shvani and compared the blastomeres formation to the division of plant cells. Reichert, on the contrary, confirmed that he could observe in the frog's egg, up to splitting, sphere-like accumulations of granules of nutritive substances, which were equated by him to cells. Kölliker suggested that, turned into the cells of the embryonic tissues were not the spheres of splitting themselves, but vesicles, noticed in the eggs of frogs which, later on, were identified as cellular nuclei. At the same time, the surrounding yolk substances of spheres of splitting are dissolved. In fact, Kölliker shortly afterwards retracted these opinions.

The Baer presentation that each step of splitting is forewarded by a nucleus division was confirmed in the investigations of N. A. Warnek (1850) on the eggs of gastropod molluscs (see chapter 25) and I. Müller, who studied the development of ova of *Entoconcha mirabilis*, a mollusc which parasitizes on sea cucumbers. Warnek and Müller's works on eggs of molluscs and Remak's work on frogs' eggs showed, that the embryonic vesicle of the egg was divided into light spots (nuclei) of cells of splitting (426).

(109) Martin Henrich Rathke (1793-1860) after finishing the Gettingsky University, where he studied natural sciences and medicine, worked as school teacher and practical physician in Dantsig for over 16 years. During this time, Rathke gained fame due to many valuable works in the field of comparative anatomy and embryology. In view of this he was invited to Derptsy University, where he lectured on physiology and general pathology as well as zoology and comparative anatomy (1829-1835). S. S. Kutorgaya was among his students, later on he worked as professor at Petersburg University. Rathke is the author of a great number (more than 125) of works, mainly of embryological contents. His name is connected with the discovery of embryonic plates in crayfish and branchiate slits in the mammalian embryos as well as provisory kidneys in all vertebrates. At first, the primary bundle was described by K. F. Wolff in chicken embryo, therefore, Rathke suggested for this organ the name Wolff's body, which is maintained in recent embryology.

The branchiate slits in the embryos of higher vertebrates were discovered by Rathke (H. Rathke, Kiemen bei Saugethieren, "Isis", 1825, S. 474-749; Kiemen bei Vögeln, Ibidem, S. 1100-1101). In the letter cited by Baer, Rathke reported the discovery of these structures in human embryos too. At the time of his work in Russia, Rathke published a special monograph on this subject (H. Rathke. Anatomisch-physiologische Untersuchungen über den Kiemenapparat und das Zungenbein der Wirbeltiere, 1832, Riga) (435).

(110) In relation to this, Baer noted that in all oviparous lizards and snakes the eggs are laid only, when the urinary sac is so developed, that it can perform the respiratory function; Baer referred to his article about duck-bill. Noch eine Bemerkung über die Zweifel, welche... (p. 362 (text)) (Arch. Anat., physiol., 1827, S. 568-576), in which he joined the opinion of Meckel (against Zhoeffru Sent Iler) about the true existence of lactation glands in duck-bill. The existence of lactation glands, according to Baer's opinion, does not exclude oviparity, as between oviparity and viviparity there is no principal difference, as he showed in lizards and snakes (437).

(111) Baer was interested in the embryology of invertebrates in the period of his work as assistant of Burdach. Later on they together discovered that in *Crustacea* the laying of the embryo takes place on the ventral side and grows in the dorsal side. This discovery was not published in the proper time, thus its priority is usually ascribed to Rathke, who studied *Crustacea* in more detail. Two small paragraphs by Baer were dedicated to the phenomenon of moulting. One was concerned with the so-called renovation of stomach in river crayfish, which was nothing other than moulting ("Über die sogenannte Erneuerung des Magens der Krebse und die Bedeutung der Krebssteine" Arch. Anat., Physiol., 1834, S. 510-527). In the other paragraph ("Beobachtungen über die Häutungen des Embryos und die Anwendung derselben auf die Erkenntniss der Insecten-Metamorphose" Froriep Notizien, 31, No. 10, 1831, S. 145-154) speech goes about the calf embryo, in which under the skin Baer discovered a second layer of skin; he tried to compare this observation (erroneous by all probabilities) to the phenomenon of moulting in metamorphosis in insects (442).

(112) Baer referred to Pokels' article in the journal "Isis" (13, 1825). Baer himself also published a small article on a case of the underdevelopment of swine embryos "Schädel und Kopfmangel an Embryonen von Schweinen aus der frühesten Zeit der Entwicklung beobachtet" (Nova Acta Acad. caes. Leopold. Carol. Nat. Curios., 13, S. 829-835, 40). This report is interesting not because of its factual side as it is based on the description of badly preserved fetus, but because Baer passed through it to an important conclusion: that acephilia can arise not due to the damage of already-formed head, but as a result of the absence of its primary rudiment (450).

(113) This anatomical article cannot be elucidated here in detail. It is sufficient to point out its most important conclusions. The comparative investigation of structure of placentae in different mammals, including man as well, led to the following classification of these organs. Baer distinguished four types of placentae: 1) placentae, only adjacent to the maternal placenta,—a) continuous, belt-like (in swine) and b) placenta divided into many parts—cotyledons (in ruminants); 2) placentae, combined with the maternal,—a) surrounding the fertilized ovum by a belt (in Carnivora) and b) occupied one of its ends (in man). On the basis of a thorough study of the way of blood vessels, Baer confirmed, that he never found passage of vessels of mother to the ovum. In the adjacent combined placentae, the vessels go beside each other, so that the maternal vessels are distributed in that part of placenta, which is directly connected with the chorion, and the vessels of the fetus, on the contrary, only enter the mass adjacent to the placenta.

About the mechanism of gas exchange and nutritional substances between blood, flowing in maternal vessels, and blood, moving in the vessels of the fetus, Baer,—as he put it—"could not form any opinion" (450).

(114) The influence of Baer affected the university programs of that time. At Petersburg University, the history of development of animals within 30 and 40 years was read by Stevan Semenovich Kutorgaya (1808-1861), the brilliant lecturer, who attracted in his lecture room students

from different faculties. He was characterized by unusual breadth of erudition. From 1836 to 1861, he read a great number of general and special courses: zootomy, system of animal palaeotology (or as he called it, zoology of first-living world), comparative anatomy, anatomy of man, natural history of man, natural history of echinodermata (polyyps); polyyps and corals, natural history of insects and, at last, embryology (history of development). The latter subject was stated at first by Kutorgaya (1836/37) according to Burdach (it is necessary to remember, that the corresponding chapters of "Physiology" of Burdach were written by Baer), and then (in 1843 and 1844/45)—by the observations of Rathke, Baer, Purkinje and Valentin. (Imperatorskii Sanktpeterburgskii Universitet v techenie pervykh pyatidesyati let ego sushchstvovaniya) (Imperial Sanktpeterburg University during the first years of the existence) Historical reprint, composed by V. V. Grigorev. SPb, 1870, 432 pages) (464).

(115) The biographers of Baer overlooked these investigations or did not evaluate them as they should be. Informing about the trip of Baer to the coasts of the Mediterranean Sea in 1845 and 1846 for embryological investigations, B. E. Raikov wrote: "As to his purposes, nothing was fulfilled. Material, collected in the Mediterranean Sea, remained unworked out, and the trials to return back to the study of embryology within a ten-year interval did not achieve any results." ("Russian biologists-evolutionists before Darwin", V. II, 1951, p. 68). The only exception in the evaluation of the mentioned investigations of Baer is their statement in T. P. Platova article "Development of the study about the cell in Russia within 40-50 years of the 19th Century" (Tr. In-ta istorii estestvozn. V. IV, 1952, pp. 332-372). The negligence of the last embryological work of Baer, can be explained only, by that in the vast literature legacy of Baer (his works, concerning embryological questions, occupy no less than 125 printed pages) it is easy to lose a paragraph in 10 columns under a modest title "Extract from the report of academician Baer from Trieste". However, in this article incomplete observations were stated which, later on, were discontinued, although their significance was so great, that the contents of the article served as sufficient detailed statement. This is necessary in order to bring to light the observations and ideas of Baer and to call to mind the priority of the Russian

investigator in the questions, their decisions later on were registered by foreign authors (466).

(116) The reproduction phenomena, closely connected with the embryonic development, already attracted Baer's attention for a long time. He followed the corresponding literatures and performed some small investigations, concerning reproduction of different organisms. He published on this subject the following reports:

- 1) Selbstbefruchtung an einer hermaphroditischen Schnecke beobachtet, Arch. Anat., Physiol., 1825, S. 224;
- 2) Doppelter Muttermund des einfachen Fruchthalters vom Ameisenfresser, Ibid., 1836, S. 384;
- 3) Über mehrfache Formen von Spermatozoen in denselben Thiere, Bull. phys. math. Ac. Sc. st. Péterb. 5, No. 15, 1847, S. 230;
- 4) Zusatz. zu Dr. J. F. Weisse's Aufsatz: Ueber die Vermehrungsweise des Chlorogonium euchlorum, Ibid., 6, No. 20, 1847, S. 315-317;
- 5) Ueber Herrn Steenstrup's Untersuchungen betreffend das Vorkommen des Hermaphroditismus in der Natur, Froriep Notizen, III Reihe, 1, 1847, S. 129-135 (467).

(117) Between I. I. Mechnikov and M. S. Ganin a lively discussion took place. In its course, they both approved of Baer's authority, turned to him by letters, also published at that time. Recently A. D. Nekrasov touched the argument of Mechnikov with Ganin in the article "First embryological work of I. I. Mechnikov and the discovery of pedogenesis in cecidomie by Nikolay Wagner" (Trudy In-ta istorii estestvozn. V. IV, 1952, pp. 315-324) (474).

(118) This name was suggested by Hexly before Leikart, although he could not give signs, which essentially differentiate the true ova from false ones. Later on, Zalenskii with certainty showed, that between "false ova" of cecidomie and ova of other insects, there was no principal difference (Trudy 3-go S'ezda Russkikh Estestvoispytatelei v Kiev. 1872) (474).

(119) Baer, however, held a similar point of view but not completely successful. In this connection, it is possible to have an assurance if you remember that he has assumed the existence of an intermediate form between types (see, for

example, p. 352, where contents of corresponding place were indicated "History of animal development"—Part II, Scholi V, § 3) (483).

(120) In "Autobiograph" Baer gave, from memory probably an incomplete list of these works: 1) Littsau. History of three monsters (*Historia trium monstrorum*), 1825; 2) Blyumental; about the deformed skeleton of a calf "*De monstroso vituli sceleto*", 1826 and 3) Rozenbaum; about the monstrosity of human fetus (*De singulari cujusdam foetus monstrositate*), 1828 (483).

(121) Adolf Ivanovich Majewski was born in 1826 in the Kovenskaya province (now the Lithuanian Soviet Socialist Republic). From 1853 to 1858, he studied at a medical faculty in the Derptsy University, where he defended a dissertation "About contents of substances, inherent in fluids of amnion, allantois, in various periods of the embryonic life". After finishing the university, Majewski worked in Viln (now Vilnius, the capital of Lithuanian SSR) as a teacher, then a director of obstetrics institute (484).

(122) Nikolai Invanovich Tchernow was born in 1834 in the Estlyanskaya province (now the Estonian SSR); he finished the faculty of medicine in Derptsy University as public grant-assisted student in 1859, obtained the degree of a doctor of medicine by a dissertation "About chemical composition of the fetal fluids in carnivorous animals". Later on, Tchernow worked in Orl as obstetrician at the province medical council. He was an extremely popular physician, characterized by exceptional sympathy and he did not only treat the patients free of charge, but also offered material help to his poor patients, who called him (our Nikolai miracle man" (Russian biological dictionary, editor A. A. Polovtsev, 1905, V. 22, p. 276 (485).

(123) See, for example, G. P. Helmersen, K. M. Baer (Speech, delivered at the general meeting of Academy of Science on December 3, 1876. *Jurn. Min. Nar. Prosv.*, 1877, February, p. 115-117) or (E. Nordenskjold. *Geschichte der biologie* S. 491) (490).

(124) Materials on the development of Crustacea are also present in the collection of works of Rathke "Aband.

bengen zur Bildungs—und Entwicklungsgeschichte des Menschen und der Thiere" (2-ter Theil, Leipzig, 1833, 102, S). This collection, denoted by Baer to the materials on the development of wood-louse and other Crustacea (*Daphnia pulex*, *Lynceus spaericus*, *Cyclops quadricornis*). See also H. Rathke. Über die Bildung und Entwicklung des Wasserassels, Leipz., 20 S in., 4^o, Zur Entwicklungsgeschichte der *Blatta germanica*. Arch. Anat., Physiol., 1832, pp. 371-379 (514).

(125) Karl Boguslav Reichert (1811-1884)—the disciple of K. M. Baer and Iog. Müller. From 1843 to 1853, was a professor of human anatomy and comparative anatomy at the Derptsy University (now Tartu, Estorian SSR), after this he respectively headed the department after Zibold in Breslavi and Müller in Berlin. Under the supervision of Reichert, the dissertation of E. Reisner about the development of internal ear was conducted.

It is necessary to mention the investigations of Reichert on the development of the head and branchite arches of the vertebrates and on the embryology of the guinea pigs. He interpreted the cellular theory in the form which was formulated by Skleidon and Shvani, Reichert rejecting all trials to introduce in it amendments, that resulted from later works. The characteristics of Reichert was given by Baldeier in the biography, published in "Biographisches Lexikon der hervorragenden Ärzte, 2-te Aufl., IV, 1932, S. 752-753). "The peculiarity of Reichert was the doubtful relation to the new scientific views and the persistent defence of the previous positions, in which he reached the extremes. Reichert especially revealed his peculiarity in the speeches against the reformation of the cellular theory, against Darwinism and even against studies on transmutation. Owing to this, Reichert in the last years of his life found himself isolated, so that he went in oblivion. This was the significant and good thing which he made for science" (514).

(126) These are the contents of reports of L. Agassits (*Echinodermata*, tunicates), P. van Beneden (hydroids, Bryozoa, parasitic warms, annelidae, tunicates), K. Gegenbaur (hydroids, molluscs, echinodermata), L. Dyufur, N. Joly and E. Perri (insects), A. Katfahz (annelidae, molluscs), K. Klaus (Crustacea), I. Kren and D. Danielsen (hydroids, crustacea, molluscs),

A. Lakaz-Dyutbe (molluscs), P. Leikart (parasitic worms, insects), S. Loven (hydroids, annelidae, molluscs), A. Miln-Edwards (parasitic worms, annelidae, crustacea, arachnida), I. Müller (planariums, eckinodermata), M. Sars (medusa, annelidae, molluscs, echinodermata), J. Tomson (Crustacea), K. Fogt (molluscs) M. Shultse (annelidae, molluscs, echinodermata) and many others (516).

(127) In the manual of Balfour (F. M. Balfour. A treatise on comparative embryology, London, 1880), there are extremely honest works, in which the embryologists were given places in accordance to their services. The work of Grube was mentioned twice in the list of literature, but in the text there was no reference to it. K. N. Davydov in both editions of his "Course of invertebrates embryology" (1914 and 1928) completely forgot about Grube and the chapter about the development of leeches started by the words: "Systematical study of leeches embryology started at the beginning of the 60s (Rathke, 1882, p. 162)". Rathke himself in the article, which was mentioned by Davydov (H. Rathke, Beiträge zur Entwicklungsgeschichte der Hirudineen. Leipzig, 1862, IV + 116 S., 4^o), only causally cited Grube's work. His reader did not try to go deep into the origin of the investigations of Grube; therefore, it was possible to form an impression, that Rathke namely was the pioneer of the study of the ring worms embryology. The same relation to the scientific services of Grube was also maintained by many late investigators for example, B. V. Sukachev (Beiträge zur Entwicklungsgeschichte der Hirudineen. II. Über die Furchung und Bildung der embryonalen Anlagen bei *Nephelis vulgaris*, Zts. wiss. Zool., 73, 1903, S. 321-367). G. A. Schmidt was an exception. He referred more than once to the works of Grube (for example, in article "Development of endoderm in *Protoclepsia tessellata*". Dnevn. Zool. otd, obshchva lyub. est. antr. i eti., IV, No. 1, 1917, pp. 1-22), although he did not reveal in these references the whole significance of investigations of Derptsyky embryologist (518).

(128) This aspect of the activities of Nordmann was reflected in his booklet "Description of imp. Odessa botanical gardens and his view on vegetation and climatic relations of the environs of Odessa". Odessa, 1847, 43 pages (530).

(129) Comparison of the data of Nordmann to the observations of Tomson, published one year before, showed that cirripedes, on the basis of structure of their larvae, must not be related to molluscs, but to Crustacea, Davydov wrote: "Naturally, discoveries of Tomson and Nordmann had a very great significance. They showed this role, which could be played by embryological science in the study of congeneric relations of organisms" (C. Davydoff. *Traité d'embryologie comparée des invertébrés*. Paris, 1928, p. 403) (530).

((130) Monograph of Nordmann was highly evaluated by competent zoologists of that time. On August 23, 1844, K. M. Baer, at the meeting of physico-mathematical department of Petersburg Academy of Science read the report written by him together with F. F. Brandt (Bericht über Nordmann's Monographie des *Tergipes Edwardsii*. Bull. Cl. phys. math. Acad. Sc. St. Petersburg, 3, No. 16-17, 1844, S. 269-272), in which it was noted that the reviewers considered this work on *Tergipes Edwardsii* "model anatomy—physiological investigations of the structure and development of the named species of molluscs" (p. 270). Voicing doubt about the possibility of the spontaneous conception of parasites *Cosmella* in eggs, Baer and Brandt continued "Other remarkable peculiarities of development—division of yolk sphere, presence of shell with cover and two ciliary organs (vibracula of Loven) on the early larval stages already were observed in the related forms, although the confirmation of the similar data is always desirable..." (p. 277). In conclusion, the authors of the report expressed satisfaction, that Nordmann with a great circumspection, in his work on the terminology of cellular theory, distinctly differentiated the really-observed facts from the theoretical assumption. In addition, they considered it extremely important, that Nordmann could trace the formation of muscular fibers from the primary cells of the embryo. Later on, historical importance of the work of Nordmann was recognized without reservations. The famous investigators of the Molluscs—the Danish embryologists Koren and Danielsen—counting their predecessors, mentioned first of all Nordmann (J. Koren und D. C. Danielsen. *Beiträge zur Entwicklungsgeschichte der Kammkiemer*, translated from Danish language by Troshel, "Arch. Naturgesch", 19, 1, 1853, pp. 173-206 (534)).

(131) Till recently the investigations of Warnek were seriously forgotten. In spite of that, his contemporaries evaluated them highly. It is sufficient to refer to reviews of authors, working on embryology of molluscs (H. Fol. Sur le developpement des Pteropodes. Arch. Zool. exp. gen., 4, 1875 and Vl. Wolfson. Embryological development of *Lymnaeus stagnalis*. Appendix to the 36th volume of Zap. Peterb. Akad. nauk, 1879, No. 2, 111 pages). About the observations of Warnek, concerning phenomenon of fertilization in molluscs, A. D. Nekrasove wrote (fertilization in animal kingdom, History of the problem" 1930, pp. 105-106). In recent years, detailed information about the scientific and teaching activities of Warnek were published by T. P. Platova ("Development of studies on cell in Russia in the 405 to the 505 of the 19th century", Fr. In-ta istorii estestvozn., 4, 1952, pp. 332-372 and "N. A. Warnek and Moscow University in the middle of the 19th century", here also, 5, 1953, pp. 317-362) (537).

(132) "Warnek's history" found response on the pages of "Kolokol" published by Hertsen, where the following was present "Historical notes, composed by University committee on the occasion of confusions occurred among students of the Moscow University in September 1861". These "notes", or, as these directly called in No. 127 of "Kolokol",—denunciation of Moscow professors—signed by the most reactionary professors—Solovev, Bodyanskii, Leontev, Eshevskii and Chickerij and published as confidential document only in five copies, contains lamentation on inaction of university police and abolition of punishment room, which, according to the authors of "the notes", explains the impunity of the organized student speeches. The clash between the students and professor Warnek, is also mentioned among other analogical events. It is significant that the authors of "the notes" did not express even by one word their sympathy with the professor who suffered from "excess" of students. This is a personal proof of the unfavorable relation of the reactionary professors to Warnek (541).

(133) In turn, the colleagues of Krohn, interested in his opinions on their works, demonstrated to him the results of their observations. Thus, the famous Norwegian zoologist M. Sars (1808-1869), describing the phenomenon of protection

of posterity of starfish (*Asterias sanguinolenta* and *A. angulosa*), mentioned that he turned for advice to Krohn because he wished to confirm the authenticity of his discovery (M. Sars. *Über die Entwicklung der Seesterne*, Arch. Anat., Physiol., 1842, S. 328) (563).

(134) In the monograph "Embryological investigations on medusa" I. I. Mechnikov wrote, that the situation about the development of the hydroidal polyps without alternation of generations "could be also distributed on akalef after that, Krohn obtained young medusae of *Pelagia* directly from the eggs. This observation proved to be mainly astonishing, because *Pelagia noctiluca* was very similar to *Chrysoara*; alternation of its generations was established by works of Dalziel and Bush" (p. 283). In another place, Mechnikov wrote: "On *Pelagia noctiluca*, it was proved for the first time that there were medusae which developed directly from eggs. Later on, this discovery was confirmed by Agassiz (on *P. cyanella*), Kovalevsky (on *P. noctiluca*) and Meckel (on *P. perla*)" (p. 388) (570).

(135) One year before this, in the work, dedicated to the larvae of molluscs, Krohn also mentioned pilidium which he considered "larva of *Nemertes* in the broader sense of the word" (p. 468), and actinotroch as larva of this worm living in the duct of Polychaeta (572).

(136) In the work of Darwin "Observations on the structure and propagation of the genus *Sagitta*" (Ann. nat. hist., 13, 1844, p. 1-6).

The Russian translation of this article, see: Charles Darwin. Works, V. 2, idz. AN. SSSR, 1936, pp. 95-102). As Krohn noticed fairly—for the eggs of *Sagitta*, Darwin has truly assumed the pelagic span of this fish (573).

(137) Krohn stated the list of the seven species of *Salpa*, from which it is clear, that forms, described by different authors under different specific names, in many cases are, indeed, sexual and asexual generations of the same species.

Individual, sexual generation (Proles solitaria (by Chamisso))	Colonial, asexual general (Proles gregata (by Chamisso))
I. (<i>S. democratica</i> Forskal <i>(S. spinosa</i> Otto	<i>(S. mucronata</i> Forsk. <i>(S. pyramidalis</i> Quoy and Gaimard
II. <i>S. africana</i> Forsk.	<i>(S. maxima</i> Forsk. <i>(S. Forskalii</i> Lesson
III. <i>S. runcinata</i> Chamisso	<i>(S. fusiformis</i> Cuvier <i>(S. maxima</i> var. <i>prima</i> Forsk. <i>(S. runcinata gregata</i> Cham
IV. <i>S.*</i> <i>(S. scutigera</i> Cuv	<i>S. punctata</i> Forsk.
V. <i>(S. vivipara</i> Peronet & Lesueur <i>(S. gibta</i> Bosc. <i>(S. dolium</i> Q. and G.	<i>(S. bicaudata</i> Q. and G. <i>(S. nephodea</i> Less.
VI. <i>S.*</i> (like <i>S. pinnata</i> Cham.)	<i>S. proboscidalis</i> Less. <i>(S. zonaria</i> Cham.
VII. <i>S. cordiformis</i> Q. and G.	<i>(S. polyeratica</i> Forsk.

By the mark* in Krohn's table is meant new, discovered species, to which he did not give names.

Later on, on the basis of these data of Krohn, in systematics of Salpa, double specific designations were established, for example, *Salpa democratica mucronata*, *S. maxima-africana*, *S. runcinata-fusiformis* and so on (585).

(138) About the same succession of development (at the beginning placenta, and then the embryo itself), referring to Krohn's data, V. V. Zalenskii, the famous investigator of Salpa embryology spoke later on. (Ueber die embryonale Entwicklungsgeschichte der Salpen. Zts. wiss. Zool., 27, 1878, S. 179-237) (586).

(139) V. N. Ulianin, to whom science is indebted due to recent ideas about the structure and development of these organisms, in the work, published 30 years after Krohn, gave, of course, detailed data but very similar to Krohn representation of their larvae. In particular, he remarked on the development and reduction of this ectodermal swelling on the boundary of the trunk and caudal part, which Krohn called "vesicle-like appendix" (588).

(140) The printed works of Krohn are distributed between the subjects of his investigations in the following way (in brackets the number of publications is indicated): Protozoa (1), Dociemids (?), Coelenterata (6), Nemertinea (1), ring worms and forms, which were appointed to the latter by him (Sepunculidae, Phoronidae, Chaetoganthae) (16), (Bryozoa (1), Molluscs (22), Arthropoda (10), Echinodermata (11), Tunicatae (7) and vertebrates (4) (594).

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