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'It's a Long Way From *Amphioxus*' Anton Dohrn and Late Nineteenth Century Debates About Vertebrate Origins

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ABSTRACT – Anton Dohrn rejected the popular *Amphioxus*-ascidian theory of vertebrate origin, which saw *Amphioxus* as the most primitive vertebrate and ascidians as vertebrate ancestors. Instead he argued for the segmented annelids as the more likely candidate. Attacked for being 'unscientific' by such popular morphologists as Carl Gegenbaur and Ernst Haeckel, Dohrn countered with similar accusations. Since the debate peaked as Dohrn was establishing his Stazione Zoologica in Naples at the end of the nineteenth century, it gained him valuable attention and may have encouraged him to retain his view even in the face of new and problematic evidence. This paper explores Dohrn's contributions and the underlying commitments revealing what he regarded as important in science.

Several years ago 'Prairie Home Companion', a popular American radio show, featured songs sent in by listeners. They included one catchy and highly 'singable' song entitled 'It's a Long Way From *Amphioxus*', but the show's leader Garrison Keillor explained that they did not know its origins or precisely what the song means. They sang it anyway to the old war tune 'It's a Long Way to Tipperary':

A fish-like thing appeared among the Annelids one day.
It hadn't any parapods or setae to display.
It hadn't any eyes or jaws or central nervous cord
But it had a lot of gill slits and it had a notochord!

Chorus:
It's a long way from *Amphioxus*
It's a long way to us.
It's a long way from *Amphioxus*
To the meanest human cuss
It's good-bye fins and gill slits,
Welcome skin and hair

It's a long way from *Amphioxus*
But we came from there.
. . .
My notochord shall grow into a chain of vertebrae
As fins my metapleural folds shall agitate the sea,
This tiny dorsal nervous tube shall form a mighty brain
AND THE VERTEBRATES SHALL DOMINATE THE ANIMAL DOMAIN.[1]

This song has been familiar to students and faculty of the Marine Biological Laboratory's (MBL) course in invertebrate zoology for decades, and it was a favorite as MBL participants spread out from Woods Hole and colonized biology elsewhere. The song's refrain explains that it is a long way from *Amphioxus* to man but implies that there is a linear connection. Yet what has seemed to these generations of students as an obvious and enjoyable reflection on evolutionary history would have been highly controversial during the last quarter of the nineteenth century. Whether *Amphioxus* had any significant relation to man lay at the center of heated debate. Though a variety of theories eventually emerged to account for the evolutionary origin of vertebrates, in the 1870s two theories attracted the greatest attention: what we might call the *Amphioxus*-ascidian theory and the Annelid theory. Since Ernst Haeckel, Charles Darwin, and other luminaries held the former view, and Anton Dohrn put forth the latter as he was also trying to develop wide political and financial support for his Stazione Zoologica at Naples, much was at stake. In addition, the debate reveals underlying epistemological convictions about what questions and what sorts of evidence were to be favored.

The Russian embryologist Alexander Kowalevsky first articulated the surprising view that *Amphioxus*, ascidians, and vertebrates are all closely similar in their patterns of development.[2] Since these organisms were thought not to have been closely linked, Kowalevsky's careful demonstration of the developmental parallels captured wide attention among morphologists. His arguments that similarities in ontogenetic development revealed close ancestral connections received critical acclaim and immediate support from some researchers.

[1] 'It's A Long Way From *Amphioxus*', MBL Archives.

[2] A. Kowalevsky, 'Entwickelungsgeschichte des *Amphioxus lanceolatus*', *Mémoires de l'Académie des Sciences St. Petersbourg*, 1867 (vii), xix, No. 4. And 'Weitere Studien über die Entwickelungsgeschichte des *Amphioxus lanceolatus*', *Archiv. für mikroskopische Anatomie*, 13 (1877), 181-204.

In particular, those who stressed the importance of developmental stages found Kowalevsky's ideas compelling. As they began to look harder, they found further supporting details as well. Ernst Haeckel particularly liked the focus on development since he had elaborated in a number of works the conviction that ontogeny essentially – with some modifications – recapitulates phylogeny. Hence the study of individual development yields important insights into the otherwise hidden evolutionary or phylogenetic past. Parallels in early development revealed, for Haeckel, ancestral relations so that the more similar the ontogenetic pattern, the closer the ancestors. Darwin also held embryonic development in high regard, with optimism about its usefulness as a tool in revealing evolutionary connections.[3] The leading morphologist and Haeckel's friend Carl Gegenbaur joined the support for embryological evidence, which favored the *Amphioxus*-ascidian hypothesis of vertebrate ancestry. Thus, it seemed, ascidians were not some distant relative in the molluscan group as had been thought. Rather, ascidians were descended from *Amphioxus*, man's oldest vertebrate ancestor. Presumably, *Amphioxus* had developed the typical vertebrate type, the ascidians had evolved along the same lines, and further evolution had moved organisms along the vertebrate lineage to man.

Those who followed Haeckel and Gegenbaur remained morphologists, focused above all on developing anatomical structures. They studied adult morphology as well as the changing structural patterns exhibited in embryonic development in a variety of organisms. Identifying what they regarded as important body parts, they would compare those selected parts in several different organisms and establish in some detail the similarities and dissimilarities. They could then begin to establish which organisms were most closely related to each other. There was no need to look closely at the functions of the organs, they felt. In fact, Haeckel insisted that such a study would distract the researcher from the true relationships. Physiology would reveal details about deviations or adaptations, but could not get at the facts of central importance, which remained the anatomical relationships.

Haeckel felt, largely on theoretical rather than empirical grounds, that the various major 'higher' forms trace back to different branches from a hypothetical common ancestor, which he called the Gastraea. This gave rise to a two-layered Metazoan form, which he had decided by 1874 had branched in the distant past into the tunicates and ver-

[3] C. Darwin, *On the Origin of Species*, London: John Murray, 1859, Chapter 13, especially pp. 439-450.

tebrates. In particular, he argued that *Amphioxus* was the closest relative of vertebrates, including man.[4] Gegenbaur agreed and pointed to numerous parallels in particular between the tunicates and vertebrates. The pattern of invagination during gastrulation was closely parallel as well as revealing morphological, structural similarities. With Haeckel's and Gegenbaur's endorsement, *Amphioxus* became the prototypical form with which all vertebrate developmental and anatomical details had to be compared. In Haeckel's view, this interpretation was dogma, nearly universally accepted.[5] Kowalevsky's subsequent work which showed that ascidians were also closely related place the spotlight on this group as well as part of the *Amphioxus*-ascidian theory of vertebrate origins.[6]

Yet despite Haeckel's confidence in the theory, there were critics, Dohrn among them. At first, Dohrn remained more inclined toward the *Amphioxus* theory, but with time he changed his mind. In parallel with Carl Gottfried Semper, Dohrn developed the alternative Annelid Theory.[7] According to this view, the most primitive vertebrates actually diverged from the annelid worms, which took to swimming or crawling upside down. While this might seem far-fetched and speculative, the idea actually was attractive because that reorientation was a relatively simple change and easy to imagine. Most important, the theory accounted for the fundamentally important fact that both vertebrates and annelids are segmented – structurally and functionally – while ascidians are not. This theory placed function as the primary concern. And the functional change happened according to what Dohrn called the principle of function-change (*Functionswechsel*).

In his interpretation, each organ actually has the capacity to carry out a number of different functions in the organism. While one is primary in the current organism, secondary functions remain at the ready, in a sense waiting for their opportunity. As Dohrn explained:

[4] The details and depiction of E. Haeckel's tree of life changed significantly between his *Generelle Morphologie der Organismen*, Berlin: Georg Reimer, 1866 and *Anthropogenie: Keimes– und Stammes–Geschichte des Menschen*, Leipzig: W. Engelmann, 1874. He developed his views in, especially, 'Die Gastraea–Theorie, die phylogenetische Classification des Thierreichs und die Homologie der Keimblätter', *Jenaische Zeitschrift* 8 (1874), 1-55 and 'Die Gastrula und die Eifurchung der Thiere', *Jenaische Zeitschrift* 9 (1875), 402-508. 'Nachträge zur Gastraea-Theorie', *Jenaische Zeitschrift* 10 (1876) 55-98.

[5] E. Haeckel, *The Evolution of Man* (fifth edition, translated by Joseph McCabe), New York: Peter Eckler, 1906, p. 219.

[6] A. Kowalevsky, 'Entwickelungsgeschichte der einfachen Ascidien', *Memoires de l'Académie des Science. St. Petersbourg*, 1866 (vii), X, No. 15. Also, 'Weitere Studien und die Entwicklung der einfachen Ascidien', *Archiv für mikroskopische Anatomie*, 7 (1871), 101-130.

[7] C. Semper, 'Die Stammesverwandtschaft der Wirbelthiere und Wirbellosen', *Arbeiten aus dem Zoologischen Institut Würzburg*, 2 (1875), 25-76. For an excellent discussion of the debates see A. Kühn, *Anton Dohrn und die Zoologie seiner Zeit*, Napoli: Pubblicazioni della Stazione Zoologica di Napoli, 1950. Also, C. Groeben, (ed.), *Karl Ernst von Baer – Anton Dohrn Correspondence*, Philadelphia: The American Philosophical Society, 1993, p. 93, points out that Semper insisted that the focus on annelids had been his idea before Dohrn's.

> The transformation of an organ takes place by reason of the succession of the functions which one and the same organ possesses. Each function is a resultant of several components, of which one is the principal or primary function, while the others are the subsidiary or secondary functions. The weakening of the principal function and the strengthening of a subsidiary function alters the total function; the subsidiary function gradually becomes the chief function, the total function becomes quite different, and the consequence of the whole process is the transformation of the organ.[8]

He showed, for example, how the gill slits could have been transformed into a new functioning mouth in the appropriate ventral location on the upside-down annelid, how the gills could have become fins in fishes or limbs, the annelid segments could have been developed into various body organs, and so on.

The important point here is Dohrn's emphasis on function and changes in function as a source of evolutionary change. In taking up this physiological perspective, Dohrn was implicitly criticizing the limitations of the morphological program which relied exclusively on comparative studies of anatomical and embryological structure. He felt that such study, which tended to focus on one or another individual part, lost sight of the whole functioning and interactive organism. The study of evolutionary history must rely on both morphology and physiology, Dohrn felt, and not on either alone.

Unfortunately, at least one major problem confronted the Annelid Theory. If the annelids were the ancestors of the vertebrates, then why did *Amphioxus* appear so similar to vertebrates and yet so different from annelids? Dohrn suggested that the resemblance was secondary. Instead, *Amphioxus* actually represents a degenerate form of fish. Rather than a primitive vertebrate, it had actually descended later from a larval form of fish, possibly the Ammocoetes. It could have gone through a change in function as the larval form had become sexually active and then lost some of its functions.[9] Thus, degeneration could prove a powerful force of change. Again, understanding of the physiological processes was crucial to understanding the phylogenetic relationships. Anyone who looked only at morphological similarities might well mistake mere appearances, or analogies, for true functional homologies.

[8] A. Dohrn, *Der Ursprung der Wirbelthiere und das Princip des Functionswechsels*, Leipzig: Wilhelm Engelmann, 1875, p. 60. (Quotation translated in E.S. Russell, *Form and Function*, London: John Murray, 1916, p. 276). See Russell's chapter 14 for further discussion. Also see the series of other papers by A. Dohrn which appeared as 'Studien zur Urgeschichte des Wirbelthierkörpers', *Mittheilungen aus der Zoologischen Station zu Neapel*, 1882-1907; and M.T. Ghiselin, 'The Origin of Vertebrates and the Principle of Succession of Functions. Genealogical Sketches by Anton Dohrn, 1875, *History and Philosophy of the Life Sciences*, 16 (1994), 3-96.

[9] Also see E.R. Lankester, *Degeneration*, New York: Humboldt Publishing Company, 1891, especially pp. 17-18.

So, two theories co-existed: one maintaining that vertebrates had arisen from the ascidians and with *Amphioxus* as a close relative, and the other that the vertebrates had arisen from annelids. But they did not co-exist peacefully. This debate in itself raised numerous questions about how to decide between two alternative theories when the data remained insufficient to determine the case. More important, the debate also raised the question about what sorts of evidence would count as properly scientific, and about other more social factors that influenced the debates. Dohrn was, in effect, arguing for including a greater range of data and for relying on detailed physiological study and not just on comparative anatomy and embryology. This inclusiveness proved problematic for many. He was suggesting that his opponents had failed to consider all the facts and were thus doing less than good science when they looked at morphology alone. He also felt that they were looking at the wrong guidelines.

Among others, Gegenbaur attacked this view. In his introduction to the first volume of his *Morphologisches Jahrbuch* in 1875, he criticized Dohrn's view as 'uncritical and thus unscientific'. Though Gegenbaur did not name Dohrn, the reference was obvious. In 1875, Dohrn wrote to Darwin about the dispute. He reported that Gegenbaur had 'abused' his theory and called it 'the very extract of uncritical and unscientific method and view'.[10] He continued:

> We have been quarrelling on that chapter for many years, and his opposition cannot teach anything new to me. To call opponents ignorant, uncritical, unscientific is a matter of taste rather than a serious refutation; should Prof. Haeckel wish to come down upon me, I am prepared to read quite other things, to be more or less declared a lunatic. All this may be a great satisfaction to its authors but can hardly increase the authority of their position, and I am very satisfied, that already among the younger Zoologists there is a strong disposition to accept my views. All I could possibly expect by the publication of my pamphlet was to put a stop to the dogmatical treatment of the *Amphioxus*-Ascidian affair, and to open new roads for speculation and investigation of the sides of the Annelid-homology. I think, this has already been achieved, and I am now busy to take up a special question and to work it into a more complete form.[11]

[10] C. Gegenbaur, 'Die Stellung und Bedeutung der Morphologie', *Morphologisches Jahrbuch*, 1 (1876), 1-19. Part I first appeared in 1875, including Gegenbaur's introduction to the new journal which he edited. Translated by W. Coleman as 'The Condition and Significance of Morphology', in W. Coleman, (ed.), *The Interpretation of Animal Form*, New York: Johnson Reprint Corporation, 1967: 39-54. As C. Groeben points out in *Darwin-Dohrn Correspondence*, p. 104, fn 119, Gegenbaur clearly referred to Dohrn though he did not name him.

[11] A. Dohrn to C. Darwin. Letter 31 May 1875. In C. Groeben, (ed.), *Charles Darwin – Anton Dohrn Correspondence*, Napoli: Macchiaroli, 1982: 64-65. Also see C. Groeben, (ed.), *Emil du Bois-Reymond/Anton Dohrn Briefwechsel*, Berlin: Springer-Verlag, 1985. I would like to thank Erika Krausse and Klaus Wenig for their important contributions during the discussions of this paper at the Dohrn conference in Naples in 1991.

Dohrn wrote to Darwin several years later that he was continuing his study of vertebrate origins and was making significant progress with the fishes, though he admitted that in the meantime he had become rather occupied with other matters. In particular, running the Stazione Zoologica consumed his energies and kept him from carrying out as much research as he might have preferred.[12]

Haeckel also attacked Dohrn rather violently and continued to attack for some time. He especially ridiculed Dohrn's degeneration theory, which he said might have been respectable at one time but which he regarded as 'failing' and 'almost forgotten'. Seeing all but man as degenerate forms could be a nice theory, Haeckel acknowledged as he somewhat misrepresented Dohrn's ideas, but 'this trustful theory is in such flagrant contradiction to all the known facts of paleontology and embryology that it is no longer worth serious scientific consideration'. In fact, Haeckel claimed that Dohrn's annelid theory had been 'entirely abandoned by most competent zoologists', that while it had attracted attention for a while by 1890 it was 'dead and buried'. In increasingly vitriolic and sarcastic terms, Haeckel ridiculed Dohrn's views in subsequent editions of *The Evolution of Man*. By 1906 he was saying that:

> Unfortunately, this trustful theory is in such flagrant contradiction to all the known facts of paleontology and embryology that it is no longer worth serious scientific consideration.
>
> But the case is no better for the much-discussed descent of the Vertebrates from the Annelids, which Dohrn afterwards maintained with great zeal. Of late years this hypothesis, which raised so much dust and controversy, has been entirely abandoned by most competent zoologists, even those who once supported it. Its chief supporter, Dohrn, admitted in 1890 that it is 'dead and buried', and made a blushing retraction at the end of his *Studies of the Early History of the Vertebrate*.
>
> Now that the annelid-hypothesis is 'dead and buried', and other attempts to derive the Vertebrates from Medusae, Echinoderms, or Molluscs, have been equally unsuccessful, there is only one hypothesis left to answer the question of the origin of the Vertebrates – the hypothesis that I advanced thirty-six years ago.[13]

Yet Dohrn had not, in fact, abandoned his ideas or his approach. Rather he continued to explore both through 1906 with publications detailing yet more parts of the story and producing more data and more detail about the development of function in various organisms.

[12] A. Dohrn to C. Darwin. Letter 9 February 1882. In C. Groeben, (ed.), *Darwin-Dohrn Correspondence*, pp. 78-79.

[13] E. Haeckel, *Evolution of Man*, pp. 219-220. This view appears elsewhere as well in less drastic form.

Both Gegenbaur and Haeckel attacked Dohrn's work as 'unscientific'. Why? Not simply because it disagreed with their interpretive conclusions, but in large part because Dohrn claimed to have a better way to do evolutionary research and because he had an institution to which he could attract researchers to pursue his perspective. Dohrn's insistence on stressing adult function as well as structure violated their emphasis on morphology. But beyond that they were distressed by Dohrn's focus on different problems because, unlike Haeckel and Gegenbaur, Dohrn insisted that while they were primarily constructing phylogenies, he was doing something more. For Dohrn it was less interesting to identify the most primitive vertebrate than to discover the principles which direct evolutionary change. He argued that tracing phylogenies and lineages therefore would serve mainly to illuminate how the principle of change in function works, for example. Furthermore, such work would serve to underscore the fundamental – and to Dohrn extremely interesting – unity of nature. Thus, Dohrn saw himself as having a different focus and looking to different types of evidence for support. He seemed to suggest that his work was more important than his old teacher Haeckel's or that of Haeckel's friend Gegenbaur. This was a struggle, in part, over whose research program would reign as preeminent and over the status of the proponent.

As Dohrn explained to the aging eminent embryologist Karl Ernst von Baer, more important than the specifics of vertebrate ancestry was the basic principles guiding evolution:

> Whether *Amphioxus* is an original or degenerated fish, whether the ascidians should be understood in this way or another, this may be the major issue at the moment for the great mass of naturalists and they may tear one another's hair out about that – but if I should have succeeded in finding, with the definition of the shift of function, a truth that necessarily will produce other truths, then I shall happily be mistaken in many details.[14]

It is, as E.S. Russell noted, important that Dohrn did not become a committed materialist as Haeckel avowedly was. As Russell put it, Dohrn 'upheld the commonsense view that vital phenomena must, in the first instance at least, be accepted as they are. "It is for the time being irrelevant", [Dohrn] writes, "to squabble over the question as to whether life is a result of physio-chemical processes or an original

[14] A. Dohrn to K.E. von Baer in *Correspondence*, p. 74. It is fortunate that he did not mind being mistaken about details, since he assuredly was, and biologists have long since abandoned his particular theory, though not the larger questions about function or the evolutionary process.

property (*Urqualität*) of all being ... Let us take it as given"'.[15] In stressing the efficacy of functional development, then, Dohrn was providing a way for living processes to act – and to effect change.

Similarly, Dohrn embraced Darwinian evolution but felt that more than the forces of random variation and natural selection might be at work. As he wrote to von Baer in early 1875, he hoped that von Baer would like his theory about vertebrate origins because he saw it as similar to von Baer's views in some respects. Though disagreeing with the non-Darwinian von Baer on various important points, Dohrn wrote that he 'wanted to consider [him]self close to you and not among the orthodox Darwinians only in the sense that I am far from admitting that the range of principles that the development of life urges us to seek is exhausted with natural selection; that therefore the metaphysical needs may not be denied their rights as long as the physical explanations are so insufficient'.[16] The transformation of functions could contribute to what von Baer saw as teleological purpose or what Dohrn included as 'perfectability'.

As Theodor Boveri put it, Dohrn had a different temperament: he was more a romantic than a classic type. His work reflected his feelings as well as his intellect, and it led the reader step by step through his ideas to his conclusions. As Boveri put it, 'His writings faithfully reflected the witty, highly cultured, pugnacious man'.[17] Though a convinced Darwinian, Dohrn promoted an image of himself as retaining a larger view than either Haeckel or Gegenbaur did. He applauded careful detailed research but allowed theoretical speculation based upon the results. For Dohrn, knowledge consisted not just in tiny bits of information which might suggest structural similarities in one organ or another between different species, for example. Nor could knowledge lie in generation of wild speculative phylogenies which ran far beyond the data and which built upon unfounded metaphysical assumptions. Thus, a theory like Haeckel's which was based on assumptions that grew out of his materialistic ontology was too narrow in topic and methods and built too much on the weak observational foundations. Instead, a good biological researcher must take life as it is and study its complex manifestations.[18] Dohrn suggested that

[15] E.S. Russell, *Form and Function*, p. 278.

[16] A. Dohrn to K.E. von Baer, *Correspondence*, pp. 73-74. As C. Groeben notes in *Dohrn-von Baer Correspondence*, p. 93, von Baer commented on Dohrn's views publicly in his *Studien aus dem Gebiete der Naturwissenschaften*, St. Petersburg: H. Schmitzdorff, 1876: 476-479.

[17] T. Boveri, *Anton Dohrn Gedächtnisrede*, Leipzig: Verlag von S. Hirzel, 1910. Reprinted in H.R. Simon, (ed.), *Anton Dohrn und die Zoologische Station Neapel*, Frankfurt-am-Main: Verlag, Edition Erbrich, 1980: 106-152, reference p. 136.

[18] A. Dohrn, *Der Ursprung der Wirbelthiere*, 1875, p. 75.

speculation was acceptable if – but only if – it built upon a thorough familiarity with the way that living organisms really work. As Dohrn wrote to Robert von Keudell, the German ambassador to Rome, this debate was

> a struggle between life and death... If I were to try to explain with a metaphor what it is all about, I would say that Darwin has erected a monumental edifice, with powerful foundations and immense walls. But he has left it to the research of the century that followed him to enlarge and to furnish the house. I have taken charge of furnishing the corridors, all staircases, and the largest hall. But my former teachers Haeckel and Gegenbaur wanted to do the same thing at the same time. I reproach them, however, for having built the backstairs instead of the stately front staircases, and their corridors are nothing but blind alleys. They denounce my staircases for being fantastic products which will break down; up to now, the scientific henchmen run after them, with a few talented exceptions, but I have arrived already at the hall, with some secret constructions. And in one or two years it will become apparent who will kick whom downstairs. As for the danger, your Excellency, that you consider me a Don Quixote or a searcher for the perpetuum mobile, I promise you that I will stay in the hall and Haeckel will be thrown down the stairs...[19]

His strong stance and insistence that he should be the one to control the house of science may have helped make it possible for Dohrn to create the great international biological center that the Stazione quickly became. It separated him from Haeckel, who was committed to a radical materialistic monism, and from Gegenbaur, who was committed to comparative anatomy as the key to research in evolution. It allowed him to stress his higher purpose in seeking 'truths' about evolutionary processes rather than phylogenetic details. Younger zoologists could learn from and admire Dohrn's approach in his 'house of science' even while disagreeing with his particular theoretical conclusions or even with his precise program of research. Dohrn could learn from and encourage them even when they disagreed, as long as they remained committed to the larger questions and as long as they remained in his sphere of influence. As a result, he created a stimulating climate of intellectual exchange which excited many of the visitors.

It is therefore probably not coincidental that Dohrn fired the first shot at the dominant *Amphioxus*-ascidian theory while he was building support for his zoological station. Nor is it accidental that he dedicated his original short book outlining his alternative theory and explaining his emphasis on function to von Baer. He wanted – and needed – the great embryologist's support for the Naples Stazione.

[19] T. Heuss, *Anton Dohrn. A Life for Science*, Springer-Verlag: Berlin, 1991: 179-180.

And he obviously admired von Baer and his work. As an embryologist, it might seem that von Baer would have sided with those who invoked ontogenetic similarities to argue for the ascidian theory. Yet von Baer's embryology had shown him that early developmental stages are generally very similar and should not be over-interpreted. Von Baer also rejected the all-importance of natural selection for effecting evolutionary change and therefore could not accept Haeckel's materialist selectionist enthusiasms. Thus, in challenging these assumptions and in calling for attention to function as well as structure, Dohrn found a supporter in von Baer.

The 83-year-old von Baer did not accept Dohrn's explanations, nor his emphasis on changing functions. He wrote to Dohrn in a friendly letter: 'Are animals then supposed not to be able any longer to form anything from their own needs, but only to modulate what they inherited? . . . But I see well that the new way of viewing the world is completely different from the one to which I have become accustomed'.[20] After Dohrn's response in which he expressed his disappointment that von Baer had not found Dohrn's book more agreeable, von Baer responded that he must have been too harsh. In fact, he far preferred allying vertebrates with the segmented annelids than with the unsegmented ascidians. Likewise he liked the idea that degeneration could prove important, and the principle of shifting function. Yet von Baer did not see the need to assume that animals can have only parts that are inherited. Instead he thought that developmental regulation in the face of need would make more sense. But, von Baer concluded, those details were not all-important. Rather, 'let us not quarrel about Darwinism etc.; in any case by founding an establishment where development can be carefully studied because of the possibility of maintaining embryos alive, you have taken a step that will provide bridle and reins for Darwin's speculation if bridle and reins are needed. If you do not find the reins in Naples, then they are probably not needed at all'.[21]

Here is the crux of Dohrn's influence and the difference in his approach, as well as the key to his success. As a student of Haeckel's who now had begun what was to be a decades-long development of his own theory, Dohrn had academic credibility. With his emphasis on the search for evolutionary process by stressing function as well as structure and adults as well as embryos, he had an epistemological approach which he could invite others to share. Knowledge would consist in carefully observed and comparative details in aid of larger

[20] K.E. von Baer to A. Dohrn, *Correspondence*, pp. 76-77.
[21] K.E. von Baer to A. Dohrn, *Correspondence*, p. 81.

questions. With the Stazione Zoologica at Naples, he also had a place to share his approach and his ideas with others.

This impact is clear among the American visitors at the Stazione, for example. Charles Otis Whitman came first, in 1881. Whitman visited Naples in large part because he wanted to learn the newest techniques and use the latest equipment.[22] He had been visiting Rudolf Leuckart in Leipzig and had heard much about the Stazione and accepted the view that there was no place better for techniques. What he learned once he arrived was that Anton Dohrn and his supportive research climate was an inspiration more generally. Whitman's study of the embryology of leeches clearly shifted its focus under Dohrn's influence. He looked more closely at the details of early developmental stages, at the interactions of structure and the physiological ways that the structures were used, and at what he could learn by exploring the relationships between leeches and apparently similar organisms.[23]

A few years later the young cytologist Edmund Beecher Wilson underwent similar changes. Wilson had already demonstrated an inclination toward the Annelid theory in several short works done while he was a graduate student at Johns Hopkins. In one of these, a study of early developmental stages in several polychaetes, he reported at the end that he had just learned of a work done at Naples on *Nereis* which showed some parallels and some important differences from Wilson's organisms.[24] This proved pivotal in his career since it evidently reinforced his desire to visit Naples and presumably also to begin what became his classic study of cell lineage in *Nereis*.

When Wilson did visit Europe the next year, he intended to spend some time in Jena with Haeckel. Unfortunately, Haeckel's new laboratory was not ready and he worked in Oskar Hertwig's lab instead. Wilson reported that 'Haeckel is a most friendly and agreeable man, of perfect simplicity and kindness, but he somehow impressed me strongly with a sense of his *power*'.[25] He then continued to Naples and Dohrn, where he primarily expanded his study of the sea polyp *Renilla*. His paper published on sea polyp development in the Stazione's *Mittheilungen* reflects Dohrn's influence.[26] The paper begins with an

[22] F.R. Lillie, 'Charles Otis Whitman', *Journal of Morphology*, 22 (1911), xv-lxxvii, reference p. xxiv.

[23] C.O. Whitman, 'A Contribution to the History of the Germ-Layers of Clepsine', *Journal of Morphology*, 1 (1987), 105-182.

[24] E.B. Wilson, 'Observations on the Early Developmental Stages of Some Polychaetous Annelids', *Studies at the Biological Lab of Johns Hopkins University*, 1882: 271-299, note pp. 295-296. And E.B. Wilson. 'The Cell-Lineage of *Nereis*', *Journal of Morphology*, 6 (1892), 361-480.

[25] J. Maienschein, *Transforming Traditions in American Biology, 1880-1915*, Baltimore: Johns Hopkins University Press, 1991, p. 74.

[26] E.B. Wilson, 'The Mesenterial Filaments of the Alyconaria', *Mittheilungen aus der Zoologischen Station zu Neapel*, 1884: 1-27.

introductory section on background and methods. In each of the subsequent sections, he included a subsection on structure, another on development, and another on function. This emphasis on development and on function as equally important with structure was typical of Dohrn's approach, and Dohrn urged Wilson to stay on and pursue his researches, but Wilson could not.[27]

Furthermore, continually keeping in mind the larger questions fit with Dohrn's approach as well. In a paper a few years later, just before his second visit to Naples, Wilson surveyed 'Some Problems of Annelid Morphology'. There he discussed ideas about various details of annelid embryology and also explained why the annelids seemed particularly interesting. Yet at the end, he concluded that surprisingly – and disappointingly – little was known about the ancestral history of the segmented animals. 'It must be admitted', he wrote

> that in some respects the fundamental problems of annelid and vertebrate morphology seem to be as far from a solution as in the time of von Baer. To the investigator, however, it is the unsolved problems that call forth the deepest interest. It is the very vagueness and uncertainty of the subject that impress upon us how much remains to be done in the embryology of annelids, and arouse the interest with which we look forward to the results of future investigation in this field of study. That the problems of metamerism and apical growth will ultimately be solved, there can be little doubt; but the present need is for new facts, not for new theories. When the facts are forthcoming, the theories will take care of themselves.[28]

I do not mean to suggest that Dohrn would have said something just like this, for he surely would not have done so. Wilson reveals his roots in American biology's more pragmatic tradition in his insistence on the primacy of gathering more facts over developing theories. Yet rather than running away from a complex or vague set of problems surrounding annelid and vertebrate embryology, Wilson was inspired to look further. Where Dohrn might have generated a speculative theory to guide the research, Wilson might have insisted on sticking closer to the empirical facts and to inductive generalizations from those facts. But in saying that, Wilson would be pushing even further in the very direction of changing function to which Dohrn had pointed in his conflict with Haeckel. In any case, both Dohrn and Wilson would still have agreed that what is important is the big picture and the larger questions, toward which each researcher must work in his own way. Haeckel had emphasized the value of providing the larger theory

[27] J. Maienschein, *Transforming Traditions*, p. 104.

[28] E.B. Wilson, 'Some Problems of Annelid Morphology', *Biological Lectures Delivered at the Marine Biological Laboratory, Woods Hole*, 1890: 53-78, reference p. 78.

from the beginning and even saw a virtue in hypothesizing whatever is needed to fill in any gaps in the evidence. In contrast, for both Dohrn and Wilson only data drawn from careful study of embryological details of both structure and function could count as legitimate scientific evidence.

In addition, Dohrn's emphasis on function as well as structure meant that a variety of researchers could feel comfortable at the Stazione whether they agreed with his theoretical interpretations or not. If they shared the basic conviction that good science lay in gathering good evidence – and accepting that there was a variety of such evidence and ways to gather it – and using that to generate solidly-based theories, then they shared an ideology and an epistemology.

In contrast to Dohrn, both Haeckel and Gegenbaur insisted on allegiance to their particular theoretical interpretations as well as to their particular version of the general phylogenetic research program. Otherwise researchers could not be part of their community since, as Gegenbaur had said of Dohrn, they simply could not be good scientists.

Dohrn embraced this young talent – even when it carried the researchers in directions far different from his own work.[29] As a result, Dohrn made the Stazione into an exciting place for fertile exchange of ideas and approaches and a place for rigorous empirical methods. There Dohrn inspired the next generation. He refocused research, broadened the range of topics and techniques, and inspired ever more careful attention to observation for an expanding group of scholars. Thus it was Dohrn who helped to define what good biology would be like in the early decades of the twentieth century for a wide range of visitors. This despite his purportedly 'dead and buried' interpretation of vertebrate ancestry.

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[29] I. Müller, 'Die Wandlung embryologischer Forschung, von der deskriptiven zur experimentellen Phase unter dem Einfluss der Zoologischen Station in Neapel', *Medezinhistorisches Journal*, 10 (1975), 191-218. Her excellent paper at the Dohrn conference summarized and reinforced many of the points made in this *longer study*.