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Ontogeny, Anatomy, and the Problem of Homology: Carl Gegenbaur and the American Tradition of Cell Lineage Studies

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Summary: In this paper we analyze Carl Gegenbaur's conception of the relationship between embryology ("Ontogenie") and comparative anatomy and his related ideas about homology. We argue that Gegenbaur's conviction of the primacy of comparative anatomy and his careful consideration of caenogenesis led him to a more balanced view about the relationship between ontogeny and phylogeny than his good friend Ernst Haeckel. We also argue that Gegenbaur's ideas about the centrality of comparative anatomy and his definitions of homology actually laid the conceptual foundations for Hans Spemann's (1915) later analysis of homology.
We also analyze Gegenbaur's reception in the United States and how the discussions between E.B. Wilson and Edwin Conklin about the role of the "embryological criterion of homology" and the latter's argument for an even earlier concept of cellular homology reflect the recurring theme of preformism in ontogeny, a theme that finds its modern equivalent in various genetic definitions of homology, only recently challenged by the emerging synthesis of evolutionary developmental biology. Finally, we conclude that Gegenbaur's own careful methodological principles can serve as an important model for proponents of present day "evo-devo", especially with respect to the integration of ontogeny with phylogeny embedded in comparative anatomy.

Introduction

Towards the end of his appreciation of the life and work of his mentor Carl Gegenbaur, Heidelberg anatomist Max Fürbringer applied Gegenbaur's very own methodological principles and compared his teacher to other giants in the field. He praised Cuvier, Johannes Müller, and Darwin for the range of their contributions, Haeckel for his introduction of far-reaching principles and productive speculations, Huxley for his wit and

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ability to explain difficult facts in eloquent prose. Yet, Fürbringer said, no one equaled Gegenbaur's "depth and concentration in comparative morphology" nor "rivals his contributions to the methodology of comparative anatomy." (Fürbringer 1903, pp. 58–59)

In this paper we sketch briefly how one of Gegenbaur's methodological concerns – the integration of ontogeny, or *Entwicklungsgeschichte*, with comparative anatomy – was received and further developed by American embryologists around the turn of the 20th century. The central issue was the explanatory power of ontogeny for phylogeny and the related question of homology. These questions are often seen as just two sides of the same coin, especially in the context of late 19th century evolutionary morphology. Here we argue that Gegenbaur's emphasis of the primacy of comparative anatomy and his definitions of homology actually laid the conceptual foundations for Hans Spemann's (1915) later analysis of homology.

We also analyze how the discussions between E. B. Wilson and Edwin Conklin about the role of the "embryological criterion of homology" and the latter's argument for an even earlier concept of cellular homology reflect the recurring theme of preformism in ontogeny, a theme that finds its modern equivalent in various genetic definitions of homology, only recently challenged by the emerging synthesis of evolutionary developmental biology. And we conclude that Gegenbaur's own careful methodological principles can serve as a important model for proponents of present day "evo-devo," especially with respect to the integration of ontogeny with phylogeny embedded in comparative anatomy.

The Homology Problem after Darwin

The concept of homology originated in pre-evolutionary times (e.g. Goethe 1784; Geoffroy de Saint-Hilaire 1818; Meckel 1821) in the context of comparative anatomy and morphology. It found its canonical definition with Owen (1848), at the apex of what has been called the idealistic period of comparative anatomy (Spemann 1915; Russell 1916). From its beginnings homology (analogy for Geoffroy) referred to a relation of "sameness" between individual structures in different organisms. There have always been two different problems associated with homology: one related to the question of how one could establish the "sameness" between structures and the other related to how one could explain the existence of such "sameness" between structures of different species.

The latter question was answered radically differently after the publication of the "Origin of Species" when the idea of an ancestor replaced any reference to an ideal type, or archetype, as the ultimate explanation for the "sameness" of organs. This, however, did not solve the problem of how homology between two organs could be detected, nor did it really explain in a mechanistic or verifiable fashion how organs in different species came to be the same (a criticism that was at the heart of the newly emerging program of *Entwicklungsmechanik*).

The one proposal that claimed to give a comprehensive answer to all these questions (except for how one actually would detect homologies) was Haeckel's formulation of the biogenetic law, which shifted the explanatory reference frame for homologies towards ontogeny as the observable record of phylogeny. In practice, the biogenetic law, even in its most radical formulation as more or less strict recapitulation, produced a variety of methodological problems for researchers interested in detecting homologies. As Haeckel already realized, ontogeny is not an unequivocal record of phylogeny, rather it is the product of both environmental and intrinsic conditions. "True" or palingenetic development is thus masked by "false" or caenogenetic processes. These processes are a formidable challenge for the researcher who attempts to use ontogeny in order to establish homology between different structures. (Haeckel 1866) By the mid-1880s disregard of these complications was seen as the major contributor to the rampant speculations and dead-ends ("Irrwege") in attempts to reconstruct phylogeny. (Gegenbaur 1888) Solving these problems, however, required the integration of ontogeny with comparative anatomy.

Gegenbaur's synthesis of Entwicklungsgeschichte and Comparative Anatomy

Throughout his career Gegenbaur refined his conception of the relationship between comparative anatomy and ontogeny (*Entwicklungsgeschichte*). The clearest expression of this conceptual development can be found in the general and introductory parts of his textbooks (*Grundzüge der vergleichenden Anatomie*, 1859, second edition 1870; *Grundriss der vergleichenden Anatomie*, 1874, second edition 1878; and *Vergleichende Anatomie der Wirbeltiere mit Berücksichtigung der Wirbellosen,* Volume I, 1898) and in the occasional programmatic paper, such as his introduction to the first issue of the *Morphologisches Jahrbuch*, "*Die Stellung und Bedeutung der Morphologie*" (1875) and his programmatic synthesis "*Ontogenie und Anatomie in ihren Wechselbeziehungen betrachtet*" (1889), as well as in his rare public speeches, such as in his address to the Anatomical Society in Würzburg, "*Über Cänogenese*" (1888).

In his 1889 paper on the relationship between embryology ("Ontogenie") and anatomy, fifteen years after he had left Jena for Heidelberg and with enough critical distance from his close friend Ernst Haeckel's campaign for the biogenetic law, Gegenbaur identified two types of relations between embryology and anatomy. Analysis of individual developmental stages of an organism's ontogeny completes the task of descriptive anatomy in that it describes the origin of anatomical structures from embryological anlagen. Ontogeny also further clarifies the connections and correlations between individual organs and explains, at least proximately, the origin of animal forms. But at the same time descriptive embryology relies on anatomical methodology and concepts, such as the location, relative position, and structure of organs and their developmental stages. Descriptive anatomy and embryology are thus mutually dependent.

The second relation, according to Gegenbaur's analysis, exists between embryology ("Ontogenie") and comparative anatomy. The goal of comparative anatomy is the discovery of the intrinsic connections between different types of (animal) organizations. Connections are established by means of comparison and the result is a hierarchical system of relations between different forms. In the context of the theory of descent these relations are interpreted as genealogies. Establishing phylogenies thus becomes the new goal of comparative anatomy. The genealogical arrangement of different types of organization adds a temporal dimension to comparative anatomy and allows for the study of differentiation (progression) as well as of regression of individual organs as an ordered series of events. Ontogeny also leads to a temporal series of states that show the gradual differentiation of individual organs. However, the relationship between these two temporal series is not straightforward. Ontogeny, and here Gegenbaur is quite adamant, is not a strict recapitulation of phylogeny.

This raises two important questions: (1) in what way can ontogeny provide an explanations for the patterns of phylogeny; and (2) how should embryological observations be ordered and integrated into the more advanced body of knowledge in comparative anatomy. In the first edition of the *Grundriss* (1874) Gegenbaur clearly stated his conviction that "Comparative anatomy explains the phenomena of ontogeny." (p. 7) This means that as long as ontogeny is embedded within the framework of comparative anatomy and its principles of localization (how can one identify individual characters), correlation (how is the variation of individual characters constrained by their mutual interdependencies), differentiation (how can the differentiation and regression of individual organs in different species relative to each other be established), homology (how can the "sameness" of organs in different species be established), and comparison (a hermeneutical principle that refines the system of hypotheses by weighing existing and new information), it is an important source of information for phylogeny. However, due to the complications brought by caenogenetic modifications in development, any developmental sequence needs to be critically evaluated by comparison with other such series and adult anatomy before it can become evidence for phylogenetic reconstructions. (see also Gegenbaur 1888)

As a comparative anatomist Gegenbaur was keenly aware of the central role of the homology concept for his discipline and the crucial role that homologies played in the integration of ontogeny with anatomy. A detailed definition of homology is thus part of all his textbooks. Indeed Gegenbaur provided his very own definition of homology and followed Owen in his distinction between analogy, based on physiological "sameness," and homology, based on morphological "sameness."

At the heart of Gegenbaur's homology definition is a distinction between general (*allgemeine*) and special (*spezielle*) homology that is different from Owen's earlier account. General homology implies the comparison of an organ with a category of organs or it exists when an individual organ is seen as a representative of such an organ category. General homology always refers to the "same" organs within the same organism; its three main categories are *Homotypie* (between organs of the right and the left side of the body, such as the right and the left kidney), *Homodynamie* (between organs that are arranged along the anterior – posterior axis or metameric organs, such as vertebrae), and *Homonomie* (between organs that are arranged along a secondary axis or only take up a small section of a primary body axis, such as fin rays or digits). (See Gegenbaur (1870, 1874, 1878, and 1898) for essentially the same definition with only minor changes in wording.)

Special homology, or homology in the narrow sense, on the other hand refers to the "sameness" between two organs of similar descent that developed from the "same" anlage.[1] Gegenbaur further distinguishes complete special homology (when all parts of the organ are present albeit functionally modified, such as the humerus of all tetrapods) from incomplete special homology (when one organ either has additional or missing parts compared to the same organ in another species, as is the case in the vertebrate heart). This definition of special homology, the kind of homology that is of primary interest for the comparative anatomist, thus connects phylogeny with ontogeny in that it emphasizes the ontogenetic criterion for the recognition as well as the explanation of sameness.

Gegenbaur was well aware of the problems hidden in that deceptively simple definition of special homology, especially complications related to caenogenesis, and he was extremely careful in the practical application of his definition, always emphasizing the primacy of the comparative method. Yet the allure of evolutionary morphology led researchers to produce a number of speculative trees and equally fantastic reconstructed ancestors. This initial emphasis on phylogeny reconstructions was, however, shortlived, as has recently been shown by Lynn Nyhart (1995). As part of the reorientation of morphology during the 1880 and the advent of *Entwicklungsmechanik* the interpretation of homology also experienced several transformations.

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[1] Gegenbaur wrote: „Specielle Homologie, Homologie im engeren Sinne. Wir bezeichnen damit das Verhältniss zwischen zwei Organen gleicher Abstammung, die somit aus der gleichen Anlage hervorgegangen sind.“ (Gegenbaur, 1870, 1874, 1878)

In his seminal essay "*Zur Geschichte und Kritik des Begriffs der Homologie*" Hans Spemann (1915) analyzed the implicit changes of the homology concept as well as the conceptual problems of this "genetic homology concept" during what he calls the "historical period of comparative anatomy". Spemann's main criticism of the "genetic homology concept" was that it is essentially preformistic and does not take the complications of the developmental process into account. While he cites Gegenbaur's definition as a prime example of this period, he nevertheless praises Gegenbaur's scientific work as that of the "most conscientious morphologist of the post Darwinian era." (p. 76) Gegenbaur earned this praise largely because he was keenly aware of the limitations of his own homology definition.

In what can be seen as his scientific testament, the two-volume *Vergleichende Anatomie der Wirbeltiere mit Berücksichtigung der Wirbellosen* (volume I 1898, volume II 1902), Gegenbaur again expresses his reservations about the historical homology concept: "If homology is explained solely by means of ontogeny we are caught in a dead end far away from our original goal. The reason for this lies in the caenogenetic elements of development, which are interspersed with palingenetic stages. Therefore, we have to clearly distinguish between caenogenesis and palingenesis."[2] He also changes for the first time in more than 30 years his definition of special homology: "Special homology, homology in the narrow sense, refers to the "sameness" between two organs of similar descent, which, originating from the "same" anlage, exhibit similar morphological behavior."[3]

This change is crucial in that Gegenbaur now emphasizes the similarity of morphological behavior ("morphologisches Verhalten"), which on the one hand asserts the primacy of comparative anatomy for any assessment of homology as an integral part of its definition and, on the other hand, opens his definition of homology to a more detailed understanding of the developmental mechanisms that generate adult structures. Spemann's own adaptation of Lankester's (1870) distinction between homogeny and homoplasy, motivated largely by empirical studies of development and regeneration, as well as the American debates about the importance of cell lineages for homology assessment, all address the question of what similar morphological behavior can mean in a developmental context.

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[2] German original: „Dagegen eröffnet sich bei der ausschließlichen Begründung der Homologie auf die Ontogenese ein bedeutender Irrweg, der weit vom Ziele abführt. Das wird verständlich durch die cänogenetischen Vorgänge, welche die palingenetischen Momente durchsetzen, so dass das strenge Auseinanderhalten beider zu einer unerläßlichen Aufgabe wird" (Gegenbaur 1898 p. 25).

[3] German original: „Specielle Homologie, Homologie im engeren Sinne bezeichnet das Verhältnis zwischen zwei Organen gleicher Abstammung, die somit aus der gleichen Anlage hervorgegangen, gleiches morphologisches Verhalten darbieten." (Gegenbaur 1898 p. 24).

The American Reception of Gegenbaur: Cell Lineage Studies and the Problem of Homology

This is where the American embryologists had something different to say. Like Gegenbaur, they rejected Haeckel's proposal that phylogenies cause ontogenetic development in any serious way. Also like Gegenbaur, they looked to anatomy and comparative studies to understand morphological relationships. Yet they drew different conclusions. And the embryological and cell studies became more important to them than the comparative anatomy that initially connected them to Gegenbaur's approach.

By the 1890s, a group of Americans had begun to examine cell lineages. Their assumption, inspired by Charles Otis Whitman and Edmund Beecher Wilson, was that the details of development from the very earliest stages would reveal similarities and differences that would illuminate the nature of core biological phenomena. What do cells do during development? What patterns of cell division do they exhibit? To what extent are these patterns the same or different in different organisms, and does it matter how closely those organisms are related? To what extent do the early developmental patterns reveal other relationships? To answer these questions, cell lineage studies became very fashionable in particular at the Marine Biological Laboratory in Woods Hole, Massachusetts, and at the University of Chicago during the 1890s.

In 1894, Wilson presented one of the MBL's Friday Evening Lectures, considering "The Embryological Criterion of Homology." He pointed out that the term "homology" was used in different ways but that the historical, or descent relationship, was the meaning of interest. Such genetic homology had initially referred only to anatomical data, Wilson explained. He continued, emphasizing that the recapitulation idea had led to a replacement of the anatomical with embryological criteria for descent.

Wilson noted that this was remarkable. Why should the embryological criterion have gained such hegemony when "no one believes that ontogeny is actually a true and complete record of phylogeny." (Wilson 1894, p. 102) Darwin himself had let such thinking into his work, and current dictionaries made the same mistake, Wilson noted. He pointed to the *Century Dictionary* as holding that "Homology is 'that relation of parts which results from their development from corresponding embryonic parts." Homology in this sense implies genetic relationship, and consequently morphological likeness or affinity' – i. e., the morphological likeness is an inference from the mode of ontogeny!" (Wilson 1894, p. 102)

Yet we, like Wilson's contemporaries, can easily be blinded by the impact of Haeckel and his ideas that we fail to see the problem. Wilson's point was that homology had become so tied together with embryological thinking that it was difficult to untangle the two concepts. "And, yet, it must be evident to any candid observer not only that the embryological method is open to criticism but that the whole fabric of morphology, so far as it rests upon embryological evidence, stands in urgent need of reconstruction." (Wilson 1894, p. 103) Alas, this embryological focus had also led to excessive, and often "wild", speculation and a resulting distortion of biology, as Gegenbaur had already remarked five years earlier.

The "embryological method" might seem safe enough if it referred existing structures back to their origins in the germ layers. The assumption was that the developmental steps were sufficiently conservative that similar patterns of development and similar origins must reflect parallel origins. But, no. The germ layers are not, in fact, primary or fixed, but rather arise in response to a complexity of environmental (or "surrounding conditions") as well as hereditary conditions. We must have some alternative grounds for homology, and Wilson urged that there was none yet. He did not emphasize the value of cell lineage studies, though others soon did. In the meantime, Wilson held the same view as Gegenbaur, that comparative anatomy must remain the primary standard for assessing homologies. He saw value in the comparative studies, for "I do not belong to those who, impressed by the rich fruits and still greater promise of the experimental method, regard the past achievements of comparative morphology as labor lost, and look forward with indifference to its future. If its present methods are defective, they must be reformed; but the great body of facts it has accumulated, and will accumulate hereafter, will always form the very framework of biological science." (Wilson 1894, p. 124)

Two years later, Wilson's friend and colleague Edwin Grant Conklin pointed to cell homology as a likely new source of information about development and about genealogical relationships. Germ layers are not the place to start looking for meaningful similarities, Conklin concluded. It is easy to see why researchers would look to the germ layers rather than earlier stages, since those earlier cell divisions exhibit a messy abundance of different patterns. There are so many different forms of cleavage, so many different responses to changing conditions, that it is difficult to discern patterns and parallels. And yet, though these early stages may not easily reveal evolutionary relationships, they do tell us much about comparative anatomy and development of form and function. Cleavage patterns fall into various groupings, with considerable similarities in some cases.

Conklin was sure that the causes of such similarities in developmental pattern must be due to similar protoplasmic structures. "Whatever criterion of homology one may adopt – whether similarity of origin, position, history, or destiny, or all of these combined – certain of these resemblances in cleavage bear all the marks of true homologies." (Conklin 1897, p. 173) Yet if these blastomeres are homologies, then what follows from this? First that cleavage does have phylogenetic significance and preserve ancestral conditions and relationships through a sort of reminiscence. Second that early cleavages would be more important than later ones since so many different additional factors affect each stage as development progresses. This seems odd, Conklin admitted, since we generally assume that later stages are more important, but these later differences are dependent on the earlier ones, which would therefore be more important.

It remained an open question how important early cleavages might be. While Conklin continued to see the similarities and the prospects for establishing relationships, others saw differences and undercut the very notion of homologies. If later similar parts arise from very different beginnings, can they be truly homologous? Can they be homologous in ways that reflect their ancestral evolutionary past, or do they just have the same forces and protoplasmic factors at work, as Wilson had suggested?

The next decade involved generating considerably more data about cell lineages and cell fates. The data was confusing, and without adequate database storage or ability to process the data, the information largely piled up in journals. It proved expensive even to publish the results, since publication entailed mainly plates to illustrate patterns of cell division. Therefore, the research program largely languished by 1910. Yet the promise remained. Clearly there are some cell homologies, and that is a reasonable place to look for homologous relationships. And since the cellular environment also plays a powerful role in shaping details of development, not all similarities and differences represent homologies. The program of cell lineage studies thus encapsulates the fundamental tension of preformistic and epigenetic interpretations of development. It remained for new tools and techniques of data processing almost exactly a full century after this research began for scientists to return to the promise of cell homology studies, now mostly re-conceptualized as the study of gene expression patterns.

Because of the difficulties of interpretation, and despite the fact that the cell lineage studies of the 1890s and first years of the twentieth century brought considerable focus on these earliest stages and with them on what we mean by homology, anatomists largely ignored this discussion, which did not seem relevant to them. Even decades later when evolutionary biologists began to realize that early development is important, they first looked to genetics and correlations of genes for information.

Conclusion

Gegenbaur's assertion of the primacy of comparative anatomy and his later modification of his definition of special homology strike remarkably near the core of current debates within the "Evo-Devo" community about the nature of homology, evolutionary relationships, and the significance of embryological criteria. Despite Spemann's emphasis that Lankester's (1870) definition of homoplasy as similarity that is produced "when identical or nearly similar forces, or environments, act on two or more parts of an organism which are exactly or nearly alike" more adequately reflects the mechanistic understanding of similar morphological behavior[4] and therefore provides a better explanation for homology, preformistic notions of homology continued to have a wider appeal. Only gradually are "evo-devo" researchers returning to the fundamental questions raised by these American cell lineagists, the comparative anatomical focus of Gegenbaur, and to the causal-analytical approach of Spemann.

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[4] German original: „gleiches morphologisches Verhalten".