
Book Review

Carl Gegenbaur and evolutionary morphology

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Despite an acrimonious divorce in the late 19th century, evolutionary and experimental approaches to embryology have never been more united. This period of renaissance is enjoyed because of the arrival of new techniques providing insight into the direct and indirect genetic controls on development and therefore, an understanding of how changes in such controls can, and have, led to new developmental pathways and, ultimately, new organisms. Thus, although molecular developmental biology is experimental embryology from start to finish, with a comparative approach constrained by phylogenetic systematics, new life has been breathed into the very macroevolutionary debates that led to the demise of evolutionary embryology in the first instance, and renewed interest in the history of the scientific debates themselves. Hence, this special issue of *Theory in Biosciences* devoted to Carl Gegenbaur, his school of research, and a latter day perspective on his legacy through the eyes of molecular genetics, was published to coincide with the centenary of his death in 1903.

Over half of the contributions are dedicated to providing a fascinating overview of the development of the Gegenbaur School, from the atomistic study of morphology in pre-Gegenbaur, pre-Darwin times, through the early influences on, and stages of, Gegenbaur's career, the flowering of the School, Gegenbaur's idealistic, personal and political battles with scientific colleagues, to the attempts to maintain Gegenbaur's research programme after his death, and the eventual demise of the School as anatomy became an increasingly clinical pursuit.

In particular, Lynn Nyhart provides an assessment of the influence that the Gegenbaur School has had in the study of morphology in Germany, identifying many of the distinguishing characteristics of a distinct school of thought attempting to expand its influence within a science, facilitating the appointment of students and supporters who would in turn provide longevity, controlling the editorial policy of journals and perhaps taking a less than balanced view of work by opponents of the research framework. Thus, Gegenbaur's importance was based on his abilities not only as a scientist, but also as a manager and politician. However, with a refocusing of research objectives on more experimental, functional approaches, Gegenbaur's research programme largely petered out as it became

increasingly difficult to place new students in positions of power.

Naturally, the relationship between ontogeny and phylogeny features heavily in the history of the Gegenbaur School. Gegenbaur was instrumental in drawing Haeckel to Jena, and shared similar views on the importance of developmental data in providing polarity in attempts to understand the evolutionary relationships between taxa and the evolution of anatomy. However, Gegenbaur was immeasurably more careful, insisting on the primacy of morphological data in comparative studies, a view that evolved through time, in part guided by the influence of T. H. Huxley. Ghiselin accounts how conflict with Dohrn, although based in large part on personality and differing approaches to the dreaded 'scientific method', centred also on opposing views on the importance of developmental data.

The principles of phylogenetic systematics were formulated as an attack on the Haeckel–Gegenbaur comparative approach, which essentially followed a pre-evolutionary *scala naturae* approach to understanding phylogeny. Naef aimed to separate pattern from process, to derive an ahistorical classification scheme on the basis of shared similarities between organisms, with homologies based not on hypotheses of common ancestry, but on a common relationship of parts at the adult level. This framework could then be interpreted in the outcome of an evolutionary process, but such studies did not demonstrate phylogeny. In many ways, the differences are echoed today in the differences between evolutionary cladists and pattern cladists.

The remainder of the volume is a review of Gegenbaur's most influential hypotheses in light of molecular genetics, including head segmentation and the origin of limbs. Shigeru Kuratani provides a tour de force review of recent research into the underlying basis of metamerism in the head and how this compares to trunk segmentation where repeated myomeres and peripheral nerves are imposed by the same underlying somitomeric segmental patterns. While this may be the case in positions along the rostro-caudal axis of the amphioxus equivalent to the vertebrate head, no such mesodermal pattern exists in the vertebrate head itself. Meristic patterns in the branchial region and in the distribution of cranial nerves are instead based, respectively, on the branchiomeric and rhombomeric constraints on ectomesenchymal migration. Thus, vertebrate segmentation accords better with Romer's dual metameric model than with a modification of the singly metameric model exemplified by amphioxus.

Mike Coates provides a similarly comprehensive review of Gegenbaur's theory of the origin of vertebrate fins, as well as its rival, the fin-fold theory. This is grounded in a phylogenetic overview of the available data, both from living organisms and from fossils, providing a constraint on the pattern of acquisition of paired fin characteristics, precluding the message of characters in favour of one model or another. Paired fins with endoskeletal components emerge first at the pectoral level, and the phylogeny is robust in excluding the possibility of a common origin of pectoral and pelvic paired fins, thus the lateral fin-fold model can be rejected. Similarly, endoskeletal fin girdles never resemble gill arches and thus Gegenbaur's model of limb girdles from gill arches is precluded. Finally, Coates considers a developmental link between gill arches and limb girdles in line with Sattler's views on conceptual transformational hypotheses.

New perspectives on these theories are also provided by Grandel, and by Olsson, who explores future possibilities for modelling and understanding the underused wealth of tempo-spatial data emerging from developmental studies.

The Gegenbaur special issue of *Theory in Biosciences* is a rewarding collection of articles celebrating the integrative nature of evolutionary developmental biology. It provides a useful primer for the many young developmental biologists who are aware that they are providing the raw data long needed to make hitherto intractable debates tractable, but who lack the grounding to know exactly who, when, where and what these debates were all about. It will also provide an accessible source for historians of science who wish to gain a latter-day perspective on historical debates, to determine ultimately

who was right, and whether or not this was for the right reasons.

In the end I was inspired by Kuratani's musing over whether renewed interest in macroevolutionary problems is an end-of-century phenomenon, perhaps one best allied with other phenomena that reappear with the same cyclicity, such as extreme weather conditions and the rise of quasi-religious cults. Will the macroevolutionary renaissance be just as short-lived, perhaps ending in a mass-suicide pact? The source of the original demise for EvoDevo's forebear, experimental embryology, lay with the absence of independent phylogenetic constraint, and delay in the appearance of a successor can be attributed to an absence of tools and techniques for elucidating developmental mechanisms and their relationship to heritability. If the renaissance is to be short-lived, the source of its demise will lie elsewhere. The obligatory 'evolutionary implications' end-paragraph has long since disappeared from such bread-and-butter journals as *Development* and its kin. As regulatory networks are reconstructed in ever greater detail, it is unlikely that there will be a place for dilettantes of palaeontological, zoological, botanical and historical science background, which is perhaps both a pity and a blessing in equal measure. The appeal of evolutionary developmental biology is that everyone is welcome, even the palaeontologists, who have found new purpose, or rather, perhaps a new purpose has been found for us! Let us enjoy the renaissance while we can.

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