Heads and Tails

Before the Backbone. Views on the Origin of the Vertebrates. HENRY GEE. Chapman and Hall, New York, 1996. xx, 346 pp., illus. \$45.95 or £35. ISBN 0-412-48300-9.

Developmental and molecular biology have provided startling insights into the organization of the vertebrate head, renewing interest in vertebrate origins: These topics have a long and complex history, rich in ideas that are unfamiliar to many biologists, and Henry Gee's new book on these ideas and their history is welcome.

The author is at his best when introducing such complex topics as the general biology of deuterostomes, which provides the basis for all theories of vertebrate origins, and in reviewing current ideas of phylogenetic comparison that form the basis for evaluating these theories. This section of the book could have been improved, however, by less reliance on dated drawings and quaint photographs.

Gee's scholarly treatment of all theories of vertebrate origins is admirable. The central themes of each theory are clearly and simply outlined and placed within a historical context that allows a naïve reader to trace the genesis of these ideas and to appreciate how they still constrain our thinking. The treatment is sufficiently rich, however, to delight even veteran readers of the literature and to provide new insights into the complexities of vertebrate origins and theories of same.

As the author notes, any theory purporting to account for vertebrate origins must explain the segmentation of vertebrate bodies. The problem of head segmentation has been a stumbling block in all theoretical considerations, and Gee's discussion is no exception. He begins well enough by contrasting two important views: the Balfourian view that vertebrate heads comprise segments, composed of derivatives of both paraxial and lateral plate mesoderm, comparable to trunk segments, and the Romerian view that vertebrates arose from an ancestor that was primarily a sessile pharynx, augmented by a segmented tail.

In an unfortunate oversight, Gee fails to describe the elegant chick-quail studies of Drew Noden demonstrating that the pharyngeal muscles of vertebrates derive from paraxial mesoderm, rather than lateral plate mesoderm as Balfour believed. This was a seminal observation that, even more than the rediscovery of hindbrain neuromeres and the chaotic origin of somatic motor nuclei, sounded the death knell of Balfourian head segmentation.

Noden's discovery also forces us to rethink Romer's view of vertebrate origins, which cannot be envisioned simply as the addition of a segmented muscular tail to a pharynx. At some level, the origin of vertebrates must be viewed as the reorganization of the segmented paraxial mesoderm in the head of an amphioxus-like ancestor. Contrary to Gee's contention, molecular genetics has not solved the problem of head segmentation. We still do not understand whether pharyngeal pouches, head muscles derived from paraxial mesoderm, neural crest-derived pharyngeal arches, and hindbrain segmentation are all parts of a single segmental pattern or the result of two or more processes whose iterative units are aligned by chance. Only in this sense may Romer's theory still have validity.

After rejecting Balfour's theory, Gee attempts to salvage Romer's. As part of that effort, he rejects the "new head" hypothesis, primarily on the ground that an amphioxus homolog (AmphiHox3) of the Hox-b3 gene of vertebrates, which is expressed in a portion of the hindbrain, is also expressed in a portion of the cephalic neural tube of amphioxus that has been interpreted as part of a hindbrain. This observation does not refute the "new head" hypothesis; it merely corroborates the 50-year-old consensus that the cephalic neural tube of amphioxus consists of at least a hindbrain and some part of the diencephalon. The central premise of the "new head" hypothesis is that the unique (new) features of a vertebrate head, that is, an extensive series of neural and musculoskeletal traits, are due to the embryonic origin of neural crest and neurogenic placodes, as well as to the reorganization of cephalic paraxial mesoderm. Therefore this hypothesis can be rejected only by showing that these embryonic tissues are not unique to vertebrates.

In contrast to the author's difficulties with head segmentation, his exploration of Jefferies's calcichordate theory is masterful. The morphology and taxonomic affinities of calcichordates—an extinct group of early Paleozoic deuterostomes—has been hotly disputed. In an extensive series of publications, Jefferies has proposed that they occupy a central position in the origin of both echinoderms and chordates, and his interpretations have inspired passionate rebuttals. The history of this debate is carefully and objectively documented by Gee.

In an equally eloquent conclusions section, Gee reiterates his intent to stimulate discussion rather than present a new theory in this period of rapid discovery unparalleled since the turn of the century. He performs one final service, however, by noting that any new synthesis requires resolution of how the living chordates are interrelated. It is here that molecular approaches also hold great promise.

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Canyons of the Colorado. Joseph Holmes. Chronicle, San Francisco, 1996. 136 pp., illus. Paper, \$22.95. Includes text excerpted from John Wesley Powell, *The Exploration of the Colorado River and Its Canyons* (1895).

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