

# BOOK REVIEWS

## Craniology: Getting a Head

**The Skull.** JAMES HANKEN and BRIAN K. HALL, Eds. University of Chicago Press, Chicago, 1993. In three volumes. Vol. 1, Development. xiv, 587 pp., illus. \$75 or £59.95; paper, \$37.50 or £29.95. Vol. 2, Patterns of Structural and Systematic Diversity. xiv, 566 pp., illus. \$75 or £59.95; paper, \$34.50 or £27.95. Vol. 3, Functional and Evolutionary Mechanisms. x, 460 pp., illus. \$70 or £55.95; paper, \$27.50 or £21.95.

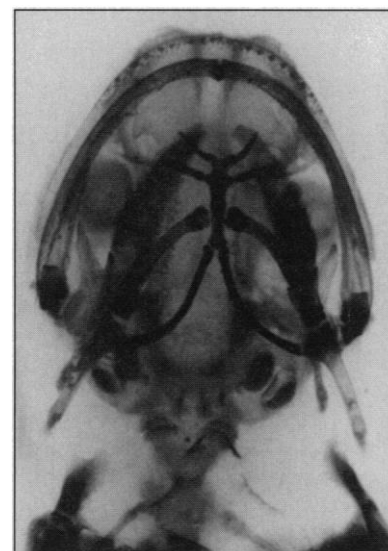
More than any other part of the body, the skull evokes the organism. Hamlet sought the essence of Yorick in his skull; vertebrate biologists seek something similar in the skulls they study. Indeed, the skull is literally as well as symbolically the essence of being vertebrate, and it is firmly at the center of the most profound issues now confronting developmental, functional, and evolutionary vertebrate biologists.

This monumental work dealing with these issues was inspired by Gavin de Beer's classic 1937 study *The Development of the Vertebrate Skull*. As Hanken and Hall are at pains to point out, however, it is not a successor to this earlier tome but rather an extension of it. De Beer himself noted that his work was hardly complete and that "if the comparative anatomy of living and fossil adult skulls had to be included the size of the work would have had to be five times what it is." Hanken and Hall have successfully undertaken just such an expansion, devoting separate volumes to structural and systematic diversity and to functional and evolutionary mechanisms. Taken together de Beer's book and these three new volumes can be considered a coherent work.

That *The Skull* comprises 29 chapters with a variety of authors, as contrasted with de Beer's single-author treatise, is an expression of late-20th-century science. It is a truism that in such compilations quality will be uneven. A few of the chapters in *The Skull* serve as little more than convenient summaries of the authors' own work and outlooks, or are rather uninspired reviews. But overall

the level of scholarship and writing is remarkably high, balanced, thoughtful, and insightful. Novacek's contribution on mammalian skull diversity, for example, enthralls with the power of its erudition. His recounting of the development and evolution of the ear and jaw complex successfully melds the old (usually German) literature with more recent findings, fine detail with broad overview, morphology with systematics and evolution. These qualities pervade many chapters in *The Skull*. Thorogood provides a wonderfully detailed rundown of morphogenesis for the uninitiated. Rose and Reiss, Sanderson and Wassersug, and Wake, dealing respectively with metamorphosis, structures for suspension feeding, and locomotor functions, masterfully harness a dispersed and often obscure literature. Lombard and Hetherington (on auditory features) and Herring (on epigenetics and growth) offer models of concision and clarity, and the diversity chapters as a whole (Janvier, Schultze, Trueb, Rieppel, Zusi, Novacek) afford lavish overviews, albeit from very different perspectives. These are just a few of many excellent contributions.

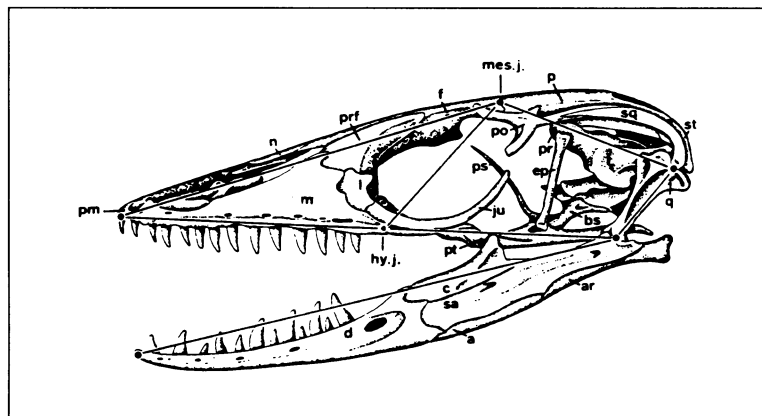
Ten years ago, Carl Gans and Glenn Northcutt argued that the head anterior to the notochord is uniquely derived in vertebrates and intimately associated with the evolution of two novel ectodermal tissue types, neural crest and epidermal placodes. Gans returns to this question in the current work and summarizes the now overwhelming support for this premise. This and many



Ventral view of the skull and hyobranchial apparatus of a salamander. The hyobranchial apparatus supports the gills in larval salamanders and the complex, projectile tongue in metamorphosed adults. [From the dust jacket of volume 3 of *The Skull*]

other chapters highlight the centrality of the neural crest in skull development and evolution. The neural crest has been examined recently in several other books and papers, but the current volumes offer an accessible review and entrée into the literature on this topic. What is frustratingly apparent is the paucity of comparative, experimental data akin to Noden's classic work on birds. This should be a rallying cry for future studies of early development in vertebrates.

Two hundred years ago, according to legend, Goethe viewed a fragmented sheep skull in a Venetian cemetery and in a flash of nonlinear comprehension formulated the vertebral theory of skull structure. Although to de Beer this theory embodied "the fantastic lengths to which speculation, unchecked by scientific evidence, can go," the ghost of Goethe lives on in the segmental theory of the skull. This theory posits that the vertebrate head is fundamentally metameric, comprising several segments comparable to (serially homologous with?) segments of the trunk, themselves most clearly evident in the mesodermal somites of early developmental stages. What answer does the "scientific evidence" hold to the question whether such cranial segmentation exists? According to *The Skull*, the answer is a resounding yes—and no. Jacobson convinc-



Skull of a monitor lizard, *Varanus salvator*, illustrating one model of intracranial mobility (cranial kinesis) in lizards. [From O. Rieppel's paper in *The Skull*, vol. 2]



## Vignettes: Identity Crises

By human standards the dog is incestuous, shameless in its excretory habits, and evil as a latent killer of sheep and among humans as a rabid brute, yet it is admired for its helping habits as herder, hunter, and protector. The dog's modern incarnation as individual personality has not reduced its ambiguity. In any issue of *The New Yorker* magazine you will find dog/man cartoons that reveal the confusion and angst incident to the fuzzy boundaries of identity among an educated elite who expiate their stress as humor.

—Paul Shepard, in *The Biophilia Hypothesis*  
(Stephen R. Kellert and Edward O. Wilson, Eds.; Island Press)

I got a cup of coffee . . . from the kitchenette and sat in my office with the door closed and wondered what was happening. . . . Was I turning into a mosquito? If so, what the hell kind of good was that supposed to do me? The company didn't have any use for a whining loner.

—Eileen Gunn, in "Stable Strategies for Middle Management" (*The Norton Book of Science Fiction*, Ursula K. Le Guin and Brian Attebery, Eds.; Norton)

ingly shows that paraxial mesoderm is segmented into somitomeres that in the trunk foreshadow somite formation but in the head do not. He argues that this "primordial segmentation" secondarily affects other systems in the head through epigenetic interaction. On the other hand, Langille and Hall illustrate how the neural crest, the single most important source of cranial tissue, is initially unsegmented, then partially segmented during migration, then again unsegmented as it fills the entire ventral portion of the head, and finally segmented in its condensation into the visceral arches. Thomson reviews the less than convincing evidence for segmentation in the adult skull. Seen in this light, the question of skull segmentation becomes almost semantic; at which hierarchical level, or at which point in time, do we consider the skull to be segmented? The more interesting question raised by these observations is, why, if the head is newly constructed from uniquely derived tissues, does it retain vestiges of the obviously ancestral morphogenetic pattern of metameric segments, at least in its mesodermal component? Does this pattern reflect plesiomorphy in the true sense, or is it merely a manifestation of underlying constraint or "rules of assembly" that delimit pathways of morphogenesis? These questions are touched upon by several authors in their discussions of epigenetic interaction, morphogenetic patterning, and the overlapping domains of HOX genes, but they remain unanswered.

Hennig wrote, "The laws of the development of form . . . are important because, following the principle of reciprocal illumina-

nation, they can help disclose the phylogenetic kinship of related groups." We read much of "reciprocal illumination" in the systematic literature these days, but sometimes the illumination is dim and it is not always reciprocal. Hence, the call to phylogenetic interpretation of form/function evolution is varyingly heeded by the contributors to *The Skull*. Views range from extreme ("Any topic of comparative biology is almost senseless without a phylogenetic goal," according to Janvier) to dubious ("The conclusion of this study seems gloomy for cladistics as presently practiced," according to Presley). Some chapters are explicitly phylogenetic, and others explicitly are not. Certainly some topics could have profited from a more phylogenetic perspective. For example, cranial kinesis in squamate reptiles is discussed in three separate chapters (Smith, Rieppel, Weishampel) from which we learn that little sense can be made of the phenomenon. Nowhere performed, however, is the simple exercise of mapping its experimentally determined occurrence onto a cladogram. Doing so reveals a striking pattern of cladistic concordance such that cranial kinesis is restricted to one of two basal squamate lineages, the other being wholly akinetic. This phylogenetic pattern exactly mirrors patterns of feeding-mode evolution and clearly suggests fruitful avenues of functional and evolutionary research.

While it is easy to criticize morphologists for phylogenetic naïveté, these volumes eloquently call attention to the other dimension of Hennig's "reciprocal illumination"—that is, the naïve approach of some systematists to morphology. As Thomson

states, "The whole matter begins and ends with homology." Individuation and codification of characters underlie every systematic analysis, and this process is based entirely on assumptions of homology. Many chapters raise alarming questions about the hierarchical nature of homology and point passionately to the need to understand fully the developmental basis of adult form before conclusions of homology can be drawn. Presley, in particular, offers a sobering view of cladistic practices; however, terrifying examples of ambiguous homology and misleading adult characters pepper the three volumes (Atchley's mouse mandible, Novacek's perforate stapes, Zusi's postorbital process, to name just a few), and each merits careful attention by systematists and anyone else interested in the vitally important issue of homology.

*The Skull* succeeds astonishingly well as a paradigm of comparative morphology and its centrality to developmental and evolutionary biology. It deals substantively with many critical issues, only a few of which are touched upon here. *The Skull* will become an essential reference to any practicing vertebrate biologist; certainly I will never teach comparative anatomy in the same way. More important, the book should act as an empirical and conceptual catalyst, stimulating and directing future work for many years to come.

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## Visual Recognition

**Selective Attention in Vision.** A. H. C. VAN DER HEIJDEN. Routledge, New York, 1992. xiv, 310 pp., illus. \$55 or £40. International Library of Psychology.

Helmholtz was the first to describe experiments demonstrating the existence of a selective process in visual perception. He found that he could set himself to "read" characters from a particular location in a visual display presented by means of an electric spark whose duration was too brief to allow eye movements to play a role. His subjective experience was that unattended characters, even when they were located near the point of fixation, were not perceived. In *Selective Attention in Vision* Van der Heijden reviews the modern work on this phenomenon, placing particular emphasis on studies done in his own laboratory.

The author provides a remarkably care-