BOOKS: PALEOBIOLOGY

Whale Origins—Conquering the Seas

John E. Heyning

Ambulocetus. A 3-m long archaeocete, which lacked tail flukes but swam by spinal undulation.

Along the now vanished shores of Tethys some 50 million years ago, a four-legged mammal ambled into the water and began one of the most dramatic morphological transformations in vertebrate evolution: the emergence of whales. Cetaceans are traditionally classified into the suborders Odontoceti, toothed whales and dolphins; Mysticeti, baleen whales; and Archaeoceti, a morphological grade of extinct whales, known only from the Eocene, that represent the transition from land dwellers to the two extant suborders. After a comprehensive overview of archaeocetes was completed by Remington Kellogg in 1936 (*1*), our knowledge of these early whales remained stagnant until the 1980s. Since then, a phenomenal proliferation of discoveries of new fossil taxa and the advances provided by new analytical tools have clarified many issues surrounding whale origins. *The Emergence of Whales*, an excellent multi-authored book edited by Hans Thewissen, offers a modern synoptic review of archaeocetes coupled with novel findings and new analyses.

The Emergence of Whales
Evolutionary Patterns in the Origin of Cetacea
J. G. M. Thewissen, Ed.
Plenum, New York, 1998. 491 pp. $115. ISBN 0-306-45853-5.

The claim that cetaceans are most closely related to ungulates (hoofed, grazing mammals) was first made over 100 years ago and has recently gained wide acceptance on the basis of molecular, morphological, and paleontological studies. The fossil record reveals numerous similarities between archaeocetes and mesonychians, a paraphyletic basal group of primarily carnivorous ungulates. This book, especially in the chapters dealing with dentition and the vascularization of the basicranium, more fully resolves the relationship between these two groups. For example, the immense mesonychian *Andrewsarchus* from Mongolia was previously thought to be closely related to cetaceans. Several phylogenetic analyses in this book suggest that *Andrewsarchus* actually falls outside the clade containing cetaceans and the mesonychids sensu stricto, and that the earlier assessment was based primarily on superficial similarities and size.

Contradicting morphology-based phylogenies, some analyses of molecular data, including two in this volume, suggest that cetaceans actually arose from within the order Artiodactyl (cows, pigs, camels) and that hippos are the living sister taxa to cetaceans. Previous experience suggests we should be cautious about wholeheartedly embracing such provocative hypotheses of relationships. More often than not, such controversial claims are found to be weakly supported or contradicted when scrutinized in more-detailed analyses (*2*) or examined using additional taxa or characters. For example, most analyses of the morphological data indicate that perissodactyls (horses, tapirs, rhinos) form the sister taxon to cetaceans (*3*), yet in all the molecular analyses this potential relationship either has not been fully explored or, in some cases, has been excluded by the designation of perissodactyls as an outgroup. Nonetheless, evaluating the most parsimonious and powerful explanation of all the observed characters warrants an analysis that includes all the available data.

One of the most dramatic morphological changes found in early cetaceans was the shift from quadruped locomotion to the axial undulation of swimming. Several chapters chronicle these changes through detailed examinations of the vertebral column, limb structure, and the presumed osteological correlates of tail flukes. In a provocative investigation, isotope ratios of oxygen and carbon within fossils are used to determine whether the Eocene cetaceans were capable of drinking seawater. One striking conclusion is how quickly these transitions occurred. Late in the Early Eocene, *Pakicetus* and its contemporaries were quadruped animals that drank freshwater. A few million years later, in the Middle Eocene, *Rodhocetus* and its kin were probably swimming with tail flukes, while feeding and drinking exclusively in the marine realm.

Without placing too much faith in the absence of fossils as evidence, the hypotheses that archaeocetes first evolved in fluvial or estuarian environments of the eastern Tethys and subsequently dispersed as the more morphologically and physiologically advanced forms conquered the oceans is certainly plausible. All of the morphologically most primitive and chronologically oldest fossil archaeocetes are found along the shores of the eastern Tethys, now India and Pakistan, whereas the more derived and fully marine protocetids and basilosaurids of the Middle and Late Eocene are found in rocks from Asia, North Africa, North America, and Antarctica.

The strength of *The Emergence of Whales* is its multi-disciplinary approach. Data from molecular genetics, functional morphology, isotopic signatures, and paleoecology are all set in a phylogenetic framework in order to provide insight into early whale evolution. Although the morphological perspective is not comprehensive, it offers important anatomical vignettes such as those relating to hearing and swimming. All told, the contributors have created an extremely data-rich volume from which scholars will glean knowledge for years to come.

References
1. R. Kellogg, *A Review of the Archaeoceti* (Carnegie Institution of Washington, Washington, DC, 1936).
2. W. P. Luckett and N. Hong, *J. Mammal. Evol.* **5**, 127 (1998).
3. D. R. Prothero *et al.*, in *The Phylogeny and Classification of the Tetrapods, Volume 2: Mammals*, M. J. Benton, Ed. (Clarendon Press, Oxford, 1988), pp. 201–234; M. J. Novacek, *Syst. Biol.* **41**, 58 (1992); J. E. Heyning, *Mar. Mammal Sci.* **13**, 596 (1997); J. G. M. Thewissen, *J. Mammal. Evol.* **2**, 157 (1994).

BOOKS: DEVELOPMENT

Heart-Making Details

Lewis Wolpert

When I was writing an introductory textbook on developmental biology, I did not discuss the heart because what was known seemed to introduce no new principles and I could not easily select details that I would want undergraduates to know. The development of the heart is, however, a process of major importance, not least because heart abnormalities are the most common congenital malformations (found in 5 to 8 of every 1000 births). Combining findings from classical embryology and modern molecu-

Heart Development
Richard P. Harvey and Nadia Rosenthal, Eds.
Academic, San Diego, 1999. 550 pp. $159.95. ISBN 0-12-329860-1.

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