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.

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CREDITS: AFTER FIG. 29, *COUR. FORSCH.-INST. SENKENBERG* **191**, 1 (1996)

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.

lar techniques, the 65 contributors to *Heart Development* describe our current knowledge of the processes shaping normal and abnormal hearts. Their studies also suggest why cardiovascular development has proved so hard to understand.

The vertebrate heart, the main system covered in the book, is indeed a complex organ. Study of its development is made difficult partly because its preliminary structures are neither obvious nor easily identified and measured, unlike the cartilage elements that are the beginnings of the embryonic limb. There are also no simple distinctions between either the vascular or electrical conduction systems and the contractile structures. Early on, the cellular precursors, in the chick embryo for example, are present in the primitive streak just behind Hensen's node. A little later the cardiogenic mesoderm lies on each side of the primitive streak and will soon fuse along the midline to form a tubular heart. The anterior region of this tube gives rise to the ventricles, while the atria originate in posterior tissue. Thus the early patterning is along the antero-posterior axis. The movements associated with looping then reverse the positions of atria and ventricles, and also instigate septation and the formation of the four heart chambers. These morphogenetic rearrangements of tissue are poorly understood, and even the formation of the initial heart tube receives scant attention in this book.

Several chapters summarize numerous studies on the induction of the heart mesoderm. Because these studies do not rely on the observation of heart formation but rather document the differentiation of heart muscle cells, they could be quite misleading. It seems that these cells follow a fairly common pathway for differentiation in embryonic stem cell cultures. Other cells important in heart formation include precursors to the endocardium and the conduction system, cells of the vascular system such as endothelial and smooth muscle cells, and cells that form the valves, though these latter structures are barely touched upon. Neural crest cells, primarily responsible for forming the neural tube, also contribute to the formation of the cardiac outflow tracts and great arteries.

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The volume emphasizes results from the mouse, frog, chick, and zebrafish, which have become model organisms for studies of heart development. The zebrafish provides an interesting set of mutations affecting the heart, particularly the looping of the tube. Although some of these mutations eliminate the ventricle, none that have been found eliminate the heart completely. This pattern fits with a widely held view that each cardiac chamber and its vascular connections have their own independent control systems.

There are also valuable contributions from *Drosophila*. Although a much simpler structure than vertebrate hearts, the fruit fly's heart also develops from a tube formed by the fusion of two bilateral primordia. And it is striking that the gene *tinman*, which is required for heart formation in *Drosophila*, is related to the *Nkx2* genes, which play a key role in vertebrate heart formation. Vertebrate genes of the *Nkx2* family can rescue some *Drosophila* abnormalities associated with mutations in *tinman*. Surprisingly, there is no evidence that the patterning of the heart tube in vertebrates along the antero-posterior axis is linked to homeobox (*Hox*) gene expression. Instead, members of the *Nkx2* family may provide the positional code, though what specifies the pattern of these genes is not known.

Other questions addressed by the contributors concern the cell lineages that give rise to the heart and the patterns of gene expression, which tell one rather little about mechanisms but are essential molecular descriptions. For example, members of myocyte enhancer family–2 (MEF-2) play several roles in heart development and are important in the activation of many cardiac and skeletal muscle genes. And one of the chamber-specific isoforms of the myosin light chain–2 (MLC-2) protein is the earliest specific marker of the ventricles. In the mouse, knocking out this gene results in failure of the embryo to develop beyond day 12.5. But these are genes involved in the differentiation of only one cell type.

One of the most intriguing aspects of cardiac development is the breaking of bilateral symmetry by the looping of the heart tube to the right of the embryo. Recent studies have dramatically revealed the earliest molecular events in the cell-to-cell signaling that determines this asymmetry and that this signaling occurs in noncardiac mesoderm. The pertinent genes include *activin* and *sonic hedgehog*, which also control patterns in many other systems. Perturbation of development, for example, by insertion of beads containing activin can lead to the randomization of heart asymmetry. With the cloning of several of the genes that can randomize asymmetry and the discovery that the *inversus viscerum* gene codes for axonemal dynein, researchers are getting close to determining how this bilateral asymmetry is established.

The 28 chapters in *Heart Development* are very well written. The book is beautifully produced and contains many excellent diagrams, but suffers from repetitions of both text and figures (one figure appears twice within 12 pages). It might have been better with fewer chapters and tighter summaries. The volume is indispensable for those who work on the heart, but it may be an expensive luxury for others. Hopefully, with additional progress in our understanding it will be soon out of date.

BROWSINGS

Galapagos. Islands Born of Fire. *Tui De Roy.* Warwick, Toronto, 1998. 160 pp. $39.95, C$45. ISBN 1-894020-39-1.

Fiery eruptions, cold waters, finches, and sperm whales are among the habitats and fauna photographer De Roy portrays in a series of short essays and enchanting images. The giant tortoises of Alcedo Volcano (left) include individuals that may have been present when the young Charles Darwin visited these islands in the 1830s.

CREDIT: TUI DE ROY/*GALAPAGOS*