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**Biology of Turtles:** 1-389; color photographs 24; CRC Press, Boca Raton, Florida.

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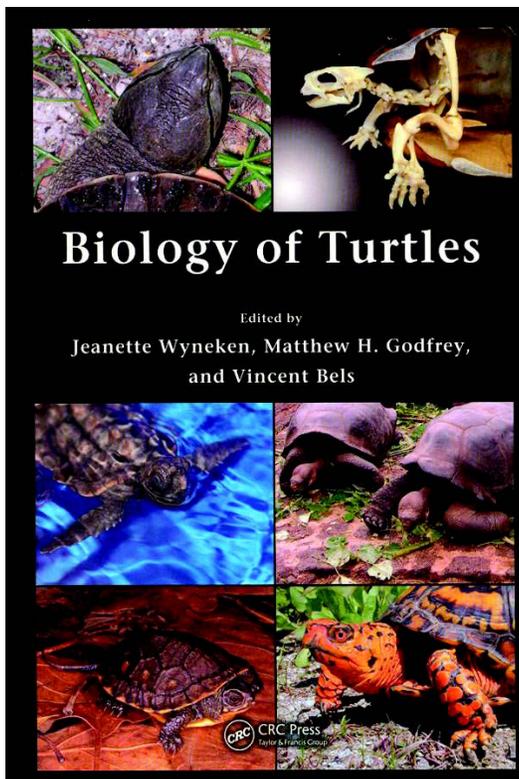
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This new turtle book joins a long list of recent titles on this most remarkable group of living amniotes. It is reminiscent of the *Biology of the Reptilia* series by Academic Press in which each volume had a different biological focus, but contains more of an admixture of topics than the volumes in that series. It is the product of a symposium on turtles held at the Sixth Congress of Vertebrate Morphology (in Jena, 2001), so it is clear why the major focus of this volume is the morphology of turtles. The volume consists of thirteen chapters ranging from reproductive structures and strategies to a review of turtle origins to a review of the neurophysiological adaptations that allow turtles to withstand anoxia. The core of the volume is the functional morphology of limbs, cervical vertebrae, feeding apparatus, and cardiopulmonary systems.

The volume covers a remarkable range of topics at very different levels. As is frequently the case with this type of volume, the chapters differ greatly in scope and depth. Some reviews are brief, others extensive; some chapters present new data, others do not. Generally, the chapters are well written and well illustrated.

For this author, the first chapter was the most interesting as it reviews the latest observations on the development of the turtle shell. The role of the carapacial ridge of Burke (1989) is confirmed. The carapace is described as developing by ensnarement of the ribs by the dermis. A summary of the role of bone morphogenetic proteins (BMP's) from the endochondral component (ribs) in inducing



ossification in the adjacent dermis provides a better understanding of the dual development of the carapace. Similarly, discussion of deep or primary and superficial or secondary dermal components provides an excellent explanation of elements that develop entirely from dermal contributions (nuchal, plastron) but in two horizons. There is also a very useful review of evidence that the plastron is derived from trunk neural crest cells. It appears that developmental biologists are getting close to giving us a molecular mechanism to explain the heterotopy of ribs and girdles that make the turtle what it is. This heterotopy of girdles inside the rib cage is a unifying consideration for nearly all of the authors in this volume.

Chapter 2 is mostly a review of Rhodin's previous work on the remarkable chondro-osseous system of *Dermochelys* and its relation to rapid growth in this species. There is a

review of skeletochronology in turtles and a summary of two modes of bone growth. This chapter adds to previous work on the topic by illustrating in detail the penetration of epiphyseal cartilages by vascular canal systems that make *Dermochelys* bone growth so different from all other living turtles. The authors review the evidence that this is an adaptation for rapid growth and suggest that although we do not yet know exactly how fast leatherbacks grow, it appears to be several times faster than humans on a gm/day basis.

Chapter 3 is a review of turtle shell morphology based largely on the author's extensive experience with material of essentially every living species. There is a short section on origins that would have benefited from a read of the first chapter in the volume. Most of this contribution is an overview of the shell, both bones and scutes, and then discussions of variation due to kinesis, sexual dimorphism, ankylosis, fontanelles, plastron reduction, and deformities. In addition, three families are picked out for special attention: the Cheloniidae, Dermochelyidae and Trionychidae. Although there is mention of fossils, the view is that of a neontologist and primitive features of the turtle shell (mesoplastra, inframarginals) are treated as "unusual". A single figure giving the standardized names for the bones and scutes of the turtle shell would have been a useful addition. As it is, the author is inconsistent with these names using the term peripherals for both the scales and the bones at the edge of the shell. At this time it seems that most authors are using neurals, costals and peripherals for the bones, and vertebrals, pleurals and marginals for the overlying scales. Many authors have also adopted the term cervical scale (for nuchal scale) and reserve the term nuchal for the anterior-most midline bone of the typical turtle shell. Many of the patterns of shell variation covered in this chapter have been discussed in the literature and it would have been useful to have references to more of that literature.

Chapter 4 provides new data on the allometry of the long bones of turtles. The authors examine scaling in the major limb elements. They come to the conclusion that the greatest locomotor specializations occur in the hand and/or foot (metapodials) rather than in the long bones themselves.

Chapter 5 examines the evolution of locomotory patterns in turtles. The authors posit that turtles are basically terrestrial animals and cite evidence that the archetypal turtle (*Proganochelys*) was terrestrial (but see chapter 13). This chapter includes a concise review of turtle paleontology and an incompletely resolved chart that summarizes much of turtle phylogenetic history. The literature on locomotory patterns of turtles is reviewed and considered in relationship to shell shape. Special attention is paid to forms with flippers and flapping or flying locomotion (sea turtles and carettochelyids). The potential for *Carettochelys* to clarify the evolution of "flying" locomotion is apparent from reading this chapter. Missing from the discussions of shell shape and locomotion is a consideration of the need to counter the compressive strength of predators, especially crocodylians, with which turtles have evolved.

Chapter 6 is a functional and kinematic study of the hindlimb of turtles that uses *Trachemys* and *Apalone* as models. It examines changes in limb function required by different functions (swimming vs. walking), complementing a similar study on the forelimb in these species (Pace et al., 2001). The authors argue that turtles are particularly useful for this kind of study because complications added by an axial contribution to locomotion are eliminated by using members of the Testudines.

Chapter 7 is a useful and succinct review of turtle cervical anatomy and function that uses a pleurodire (*Chelodina*) and a cryptodire (*Apalone*) as models. There are descriptions of osteology and musculature in these two taxa and new data on the kinematics of snorkeling are presented.

Chapter 8 examines the functional evolution of feeding in turtles. It compares the mechanisms involved in feeding on land versus water. The kinematics of ingestion, manipulation and swallowing are described for both media. Data from multiple species are provided and the evolution of feeding behavior in turtles is discussed. The importance of the hyoid apparatus in prey capture and manipulation for aquatic forms is emphasized. The introduction includes an unfortunate line that states that members of the Testudinidae “are the only species able to ingest and swallow food on land” when there is much discussion in the chapter of terrestrial feeding by *Terrapene*, an emydid. A cladogram of turtles with the ability to feed terrestrially mapped over it would have been a useful addition to the discussion of the evolution of feeding in turtles. Is it only members of the superfamily Testudinoidea that have this secondary return to terrestrial feeding? How many times has it occurred? Data on the ability of *Trachemys scripta* to feed at a variety of temperatures provide additional insight into its success as an invasive species.

Chapter 9 is a review of the morphology and function of the cardiopulmonary systems. It includes a useful review of shunting mechanisms in turtles which have a remarkable ability for breath holding.

Chapter 10 is one of the longer chapters. It is a review of the reproductive biology of turtles in 35 pages (with 18 pages of citations). It begins with reviews of the morphology of reproductive structures (including the egg) and their changes during reproductive cycles. In the section on reproductive strategies, the authors review such subjects as dimorphism, mating behavior, sperm storage, reproductive output and several aspects of nesting and development including sex determination and developmental diapause. The bibliography with this chapter is particularly useful.

Chapter 11 diverges most from the general theme of morphology. It explores the utility of uniform vs. mixed gender broods in explaining

the evolutionary value of temperature dependent sex determination (TSD) in turtles. Uniform broods are shown to be remarkably frequent and 72% are all female, raising the possibility that turtles have already been impacted by global warming. Possible responses by species with TSD to potential feminization are enumerated and the role of unisex and mixed broods for the identification of heritable traits that could compensate for feminization is explored.

Chapter 12 is a detailed examination of the ability for the turtle brain to survive anoxic conditions. It includes an excellent introduction to the remarkable ability of turtles to withstand extended periods without oxygen and a useful description for the non-physiologist of the impacts of anoxia on the brain. The capacity of turtles to survive anoxia “is not merely a side effect of ectothermy but the result of specific adaptations of the turtle brain at the physiological and molecular level that do not occur in other reptiles.” The bulk of the chapter reviews the evidence for these adaptations.

Chapter 13 is a succinct summary of the history of ideas about turtle origins with particular emphasis on recent work. It includes a very brief but useful review of recent morphological, molecular and combined analyses of the phylogenetic position of turtles among amniotes. The author settles on turtles as diapsids but suggests that we can expect ideas about the origin of turtles to remain in flux. He emphasizes the need for future studies to include additional interdisciplinary work including morphological, paleontological and molecular data.

This call for interdisciplinary work, that we hear so often today, has been met by the contributors to this volume. Functional morphologists have joined forces with paleontologists, physiologists, developmental biologists, modelers and ecologists to provide excellent new perspectives on the biology of turtles. Although it is not “the first comprehensive review of the Testudinata” as

advertised by the publisher (Harless and Morelock, 1979, was more comprehensive at the time it was published), the volume will be of great value to herpetologists of all kinds but especially to those interested in functional morphology and the evolution of turtles.

There are a few unfortunate editorial glitches, mostly related to turtle taxonomy. Chapter 1 mentions “the *Emys* and Chelydae families” (Emydidae and Chelidae?) and Chapter 10 uses the name Chelydidae for Chelydridae in two places. In chapter three *Podocnemis* is mentioned as a member of the family Pelomedusidae when most authors now recognize a separate Podocnemididae; and there is inconsistent treatment of species that are no longer included in the Emydidae but rather in the Geoemydidae (or Bataguridae). In chapter 10, the authors erroneously state that no pleurodires have TSD but then list the Pelomedusidae among the families with this trait (present in Pelomedusidae and Podocnemididae); in the same chapter the Seychelles tortoise *Aldabrachelys* is discussed under two different names: *Geochelone gigantea* and *Dipsochelys elephantina*. These may seem like minor points but if readers are considering reported observations in an evolutionary context, knowing where taxa fit in the phylogeny of turtles is facilitated by using revised taxonomies.

The quality of the color figures is excellent and adds greatly to the value of chapters one and two. But more attention should have been

given to the production of the black and white figures. Several were reproduced at too small a size or with too little contrast. The numerous figures in chapter three should have included specimen numbers and scales.

In summary, this is an excellent addition to our knowledge of evolutionary, developmental and functional aspects of turtle morphology. The volume of literature that is reviewed and the resulting bibliographies are extensive and will make the volume useful for biologists from a wide range of disciplines. It seems likely that chapters in this volume will become standard references for the current and future generations of turtle biologists. 

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## References

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