# Book Review

***Biology of Turtles: from structure to strategies of life***

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'Were there no turtles living, we would look upon the fossil turtles as the strangest of all vertebrates-animals which had developed the strange habit of concealing themselves inside their ribs, for that is literally what turtles do.'

*Samuel Williston, 1914*

The quote by Williston is a fitting synopsis of the Biology of Turtles - a book about chelonian anatomy. To be precise, this book is about how the distinct anatomy of turtles influences every aspect of their biology, including feeding, growth, locomotion, physiology, and reproduction. This novel approach was the result of the Sixth International Congress of Vertebrate Morphology held in Jena, Germany in 2001. Fittingly, the symposium occurred precisely where Ludwig Heinrich Bojanus compiled Anatome Testudinis Europaeae, an incredibly detailed atlas of the morphology of the European Pond Turtle (*Emys orbicularis*) some 180 years prior (Bojanus, 1819).

Chapters one and three of the Biology of Turtles provide an in-depth treatise of the single most important morphological adaptation of the chelonian condition: the shell. In Chapter 1, authors Gilbert *et al.* discuss the anatomy of the turtle shell. From colour photos of early embryological stages to the formation and ossification of the carapace, plastron, and nuchal bones, the authors provide a tentative outline of how the shell is formed. Much remains to be discovered, however. For instance, what causes plastral concavity in the males of certain species or how the hinge develops to permit plastral kinesis is still unknown. Nevertheless, in Chapter 3, Pritchard draws upon his extensive osteological collection at the Chelonian Research Institute in Florida to delve not only into the standard configuration of the shell but also into known deformities such as 'pyramiding' and other scute abnormalities. Clear black and white photographs are used to compare and contrast various morphological adaptations such as hinges, fontanels, and buttresses. The degree of morphological variability within the Chelonia is truly astounding and the reader will get a true sense of it in this chapter.

Chapters two and four describe how turtle long bones grow. In Chapter 2, Snover and Rhodin discuss how annuli within these bones, termed 'lines of arrested growth', can be used to estimate age and growth, a technique known as skeletochronology. Most interesting, however, is the pattern of accelerated skeletal growth in the Leatherback (*Dermochelys coriacea*). The presence of unique vascularised cartilage canals permits the Leatherback to grow at an astounding rate, an 8000-fold increase in mass from hatching to sexual maturity. Until reading this chapter, one really has no idea just how unique a life form the Leatherback is. Indeed, as the authors stated, 'it is the most remarkably specialized turtle in the world.' In Chapter 4, Llorente *et al.* investigate limb bone allometry; that is, they analysed turtle limb bone diameters and lengths and then compared and contrasted the proportions of these bones in 11 chelonian families. Based on their results, the authors concluded that turtle long bones have less in common with the proportions of quadrupedal mammal long bones than they do with those of avian hind limbs.

Chapters five and six build upon the previous chapters by providing an in-depth exploration of locomotion in turtles. In Chapter 5, Renous *et al.* begin by examining the fossil record; what do the sediments that the fossils were found in tell us about a given fossil species? Can we infer that a species was terrestrial or an aquatic bottom-walker based on a combination of anatomy and geology? On occasion, the scientific community is favoured with outstanding discoveries. For instance, Fig. 5.21 illustrates the fossilized tracks

of two Jurassic turtles. In extant chelonians, the authors explore the morphological adaptations of the shell and limbs based on a continuum ranging from terrestrial tortoises to highly aquatic sea turtles. The rest of the chapter examines the motions involved in the propulsion and limb coordination of representative aquatic species such as *D. coriacea*, *Trachemys scripta*, *Chelydra serpentina*, and *Carettochelys insculpta*. From these, one discovers that alternating limb movements are the norm in all but the most highly aquatic species - those with foreflippers. Chapter 6 focuses more on the function of hindlimbs in locomotion. Blob *et al.* compare and contrast the movements of adult and juvenile *T. scripta* and *Apalone spinifera* using high-speed video and electromyographic signals from muscles. Interestingly, the authors observed that interspecific differences observed between adults were not evident in the juveniles. The research in Chapters five and six provide the reader with a better understanding of how morphologically diverse genera are adapted to survive in a wide variety of habitats.

Chapters seven and eight delve into the anatomy of the chelonian neck, particularly with regards to extension and retraction during such necessary activities as snorkelling and foraging. In Chapter 7, Herrel *et al.* chose two genera to represent both primary modes of neck retraction. The genus *Apalone* represented the Cryptodira (turtles that retract their neck straight back like a tortoise) and Chelodina represented the Pleurodira (turtles that fold their neck to the side). Of particular interest is that the authors conclude that the neck morphology of *Apalone* is highly specialized and may not be representative of the general Cryptodiran condition. Chapter 8 examines the ingestion of food items in both terrestrial and aquatic environments. Bels *et al.* used series of photographs and x-rays to break down foraging episodes in millisecond increments for *Geochelone radiata*, *Kinixys belliana*, and *Malaclemys terrapin*. The chapter concludes with an examination of feeding in young *D. coriacea*.

Chapter nine discusses several novel characteristics of the chelonian circulatory system. Wyneken reveals that the turtle heart, for instance, is not simply three-chambered as commonly held; the ventricle is subdivided functionally into three compartments. Although it comes as no surprise that freshwater and sea turtles are particularly adept at holding their breath, what is surprising is that, in contrast to mammalian lungs, turtles have no bronchial tree or alveoli in their lungs. Moreover, the lungs of deep-diving migratory sea turtles are more complex than those of more sedentary hunters, such as *C. serpentina*. Here, as throughout this book, anatomy informs ecology.

Chapters ten and eleven provide a comprehensive review of turtle reproductive structures and strategies. In Chapter 10, Miller and Dinkelacker discuss several rarely covered topics such as cloacal and urinary bladder morphology. As to strategies, the implications of egg morphology are particularly interesting. Typically, turtles that incubate their eggs in moist environments have pliable eggs that absorb water; whereas, those that incubate them in arid or semi-arid environments produce non-porous or 'hard-shelled' eggs, presumably to limit water loss. In addition, spherical eggs are typically produced by large turtles and oblong eggs by small turtles. Thus, even egg morphology can inform ecology. In Chapter 11, Hulin *et al.* examine the implications of temperature-dependent sex determination (TSD) in 64 of the 79 species of turtles examined thus far. If offspring sex ratio is dependent upon incubation temperature, what effects might rapid climate change have? Likely scenarios are discussed at length.

Chapter twelve discusses the complex anatomical and physiological adaptations necessary for the turtle brain to tolerate hypoxic (low oxygen) and anoxic (no oxygen) conditions during brumation. At 3 ºC, Common Musk (*Sternotherus odoratus*), Northern Map (*Graptemys geographica*), and Eastern Painted Turtles (*Chrysemys picta picta*) can survive anoxic waters for 22, 45, and 150 days, respectively. This ability is a result of specific brain adaptations at both the molecular and physiological level.

In the final chapter, Rieppel examines the relationship of turtles within amniotes. Chapter 13 explores such questions as; did turtles begin as aquatic or terrestrial organisms? Ultimately, the