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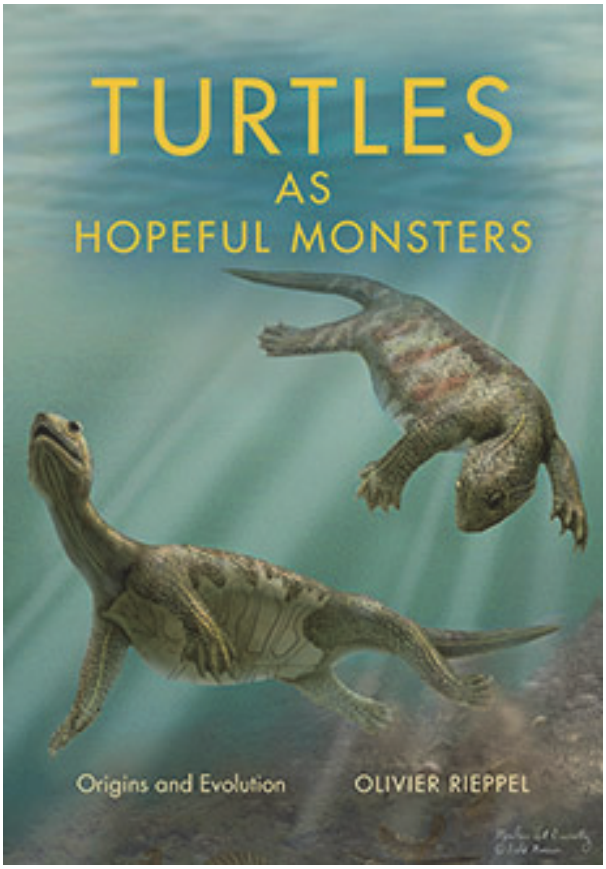
Turtles as Hopeful Monsters: Origins and Evolution

Book reviewed by Darren Naish

Turtles as Hopeful Monsters: Origins and Evolution, by Olivier Rieppel. 2017 Indiana University Press, Bloomington and Indianapolis. $45.00 ISBN 978-0-253-02475-6

It is cliché today to describe turtles as among the greatest of enigmas in the world of tetrapod evolutionary history. Turtles – Testudinata or Testudines, according to your preference (don't use Chelonia, please) – are anatomically ridiculous (limbs and limb girdles *inside* the ribcage?), their unique Bauplan obscuring efforts to determine their affinities within Reptilia. Olivier Rieppel's *Turtles as Hopeful Monsters: Origins and Evolution* discusses, over six chapters, what we know of the turtle fossil record and what we think and have thought about turtle origins and evolution, though note that this work only discusses the earliest stages of turtle evolution and is not concerned with the clade's in-group relations. More specifically, this most attractive book is devoted first and foremost to Rieppel's coverage of competing models of turtle origins and evolutionary history and the scientists involved, though it's rather more complicated than that.

Rieppel is one of the world's foremost authorities on reptile anatomy and evolution and it turns out that he is not just a formidably qualified, highly experienced and respected scientist and science historian but an excellent and engaging popular writer as well. The volume is as much about the history and philosophy of evolutionary biology and those who have studied it as it is about the science itself. In fact, turtle evolution effectively forms the backstory to the book; ideas and arguments about turtles often being used more to connect the main themes of discussion than be the focus of attention themselves.



Indeed an argument might be made that the book's title is a bit of a cheat: *Turtles as Hopeful Monsters* isn't as much about turtles as I hoped it would be, nor is it especially about hopeful mon-

Darren Naish. Ocean and Earth Science, National Oceanography Centre, Southampton, University of Southampton, Southampton, UK. eotyrannus@gmail.com

Naish, Darren. 2017. [Review of *Turtles as Hopeful Monsters: Origins and Evolution*]. *Palaeontologia Electronica* Vol. 20, Issue 2; 1R:3p;
palaeo-electronica.org/content/2017/1975-review-turtles

sters or about turtles as hopeful monsters; it is instead a discussion of thoughts pertaining to evolutionary processes, focusing on saltation, macroevolutionary transformations and the appearance of novelty; turtles and their fossil record do not become the area of focus until the last two of the book's six chapters, a sensible conclusion I only realised while writing this review being that one requires that extensive background information on saltation and so on before understanding Rieppel's take on turtles. Do fossils reveal incremental changes of the sort imagined by palaeontologists to lead to novel anatomical conditions (as per the transformationist paradigm), or are fossils not especially helpful when changes as radical as the evolution of the turtle shell are the focus of interest? That is, do turtles illustrate the emergentist paradigm?

Most if not all readers of this book will understand how the title references Richard Goldschmidt's 1933 concept of 'hopeful monsters'. I was always taught that Goldschmidt meant this term to mean that seemingly 'impossible' transitional organisms simply must have existed at some point in the evolutionary history of a lineage (cue a reference to Thomas Frazzetta's famous 1970 paper on bolyerine snakes). But a better interpretation is that Goldschmidt – very much interested in genetics and a student of Carl Gegenbaur and Haeckel protégé Richard Hertwig – took embryonic remodelling to result in the appearance of a body plan quite distinct from that of the ancestor.

This theme – the exploration of the hopeful monster paradigm – is central to the book and never has such an amount of analysis and discussion on the matter been gathered together before, nor has all that much been written on the idea that turtles themselves might have originated as hopeful monsters. Having read Rieppel's technical papers on turtles and been somewhat confused as to what he was driving at (the works concerned have involved objections to the transformationist model of correlated progression proposed by Michael Lee), I finally feel as if all is revealed. It is certainly a compelling, exciting and illuminating view. But if embryological repatterning and profound developmental novelty explain turtle origins, have palaeontologists been over-reliant on the idea that fossils will provide the answers they seek?

Claims that fossils might never supply those answers and, potentially, are not that useful when it comes to determining the affinities and origins of controversial animal groups – a soundbite, to be clear, never stated outright by Rieppel but hinted throughout his critiques of transformationism – can be encountered elsewhere in the evolutionary literature, albeit sparingly. Rieppel recounts an argument at a 1950 seminar in Berlin where Willi Hennig denounced fossils as of "no interest" with regard to phylogenetic relationships, Walter Gross' retort being that theories of phylogeny were of no interest to him either if fossils were not part and parcel; I am aware of similar exchanges involving contemporary advocates of phylogenetic philosophy and palaeontology, and am reminded also of the late Brad Livezey's arguments about neornithine bird phylogeny.

All of this often seems unsatisfying in requiring that we all but ignore those wonderful models invoking incremental change devised and cherished by palaeontologists. Even worse is the annoying charge that we must look for answers in non-palaeontological disciplines, developmental embryology and genetics in particular. Of course, it is in reality hard not to conclude that palaeontology benefits from increased integration with genetics, embryology and comparative anatomy, and one might argue that this is all part of that trend whereby palaeontology is 'welcomed to the high table', forever relevant, and no longer deemed esoteric or potentially irrelevant to biology as a whole. But… is it right? Does the development of hopeful monsters tell us more about turtle origins than Permian and Triassic fossils identified as early members of the turtle lineage? I find this hard to answer given *Odontochelys, Pappochelys* and, now, *Eunotosaurus* – Rieppel seems to indicate likewise – but it might be that it solves the final hurdle of turtle origins (those profound modifications involving the 'completion' of the shell), not the development of the turtle body plan right from its origin.

Relevant (but perhaps not essential) to this argument is the debate over turtle affinities, covered by Rieppel early on in the book and in part inspirational for the entire line of inquiry. Those familiar with the recent literature will be aware of proposals that turtles emerged from pareiasaurs or procolophonids, archaic reptiles conventionally regarded as well outside Diapsida and grouped together within Parareptilia. Molecular data has presented the primary challenge to these models, it being repeatedly shown via DNA analysis that turtles are diapsids and deeply nested within the clade, most likely belonging to the archosaur lineage. Even if this debate did not exist, however, we

would still be pursuing the origins of the turtle body plan, such is its novelty.

Also early in the book, Rieppel states how he aims to show how a group of authors used clever language and wording in order to push a particular transformationist agenda on turtle origins and evolution. On this front, I felt that the book did not deliver. Rieppel's argument with Lee about the position of turtles within Reptilia has parallels with a debate the same authors (and their colleagues) have engaged in regarding snake affinities; there too, the argument can be made that particular wording has been used to denigrate one model and promote another, but it is somewhat ironic that, in *Turtles as Hopeful Monsters*, it is Rieppel who uses word-tricks to downplay a model he disagrees with. I refer to his use of the term 'Polka Dot Turtle Ancestor' to describe the hypothetical turtle ancestor scattered with osteoderms. Ok, 'Polka Dot Turtle Ancestor' might be accurate as physical descriptions go, but it's a term tinged with comedy.

Some diagrams, high-quality photographs and pieces of art appear throughout this work; the editing is immaculate. A few footnotes appear in several chapters and citations appear throughout. The book includes a substantial quantity of biographical information concerning both Rieppel's own adventures in the world of palaeoherpetology, his meetings with contemporaries and recollections of various conferences and meetings, and much on the many scientists whose work he reviews. Biographical information on continental European scientists is often scarce in English language sources, so all of this is most welcome.

Despite my statement earlier about there not being enough turtles in this ostensibly turtle-themed book, turtles do appear throughout and a goodly number of interesting nuggets about the history of ideas on turtle origins, evolution and anatomy are covered. *Turtles as Hopeful Monsters* is extremely well written and designed, even though I do find the IUP style of leaving great blank margins on every page rather irksome. Ultimately, the book should be read by anyone interested in the history of evolutionary biology, in herpetology and palaeoherpetology, or in turtles specifically. Maybe I would have liked something that focused on turtles a whole lot more, but, then, if the title were different I may well not have read a book that I certainly will not forget or hide in an obscure corner. And now that we know that Rieppel can produce volumes of this quality and readability, I say: more please.

REFERENCES

Frazzetta, T. H. 1970. From hopeful monsters to bolyerine snakes. *The American Naturalist* 104, 55-72.

Goldschmidt, R. 1933. Some aspects of evolution. *Science* 78, 539-547.

Livezey, B. C. 2011. Progress and obstacles in the phylogenetics of modern birds. In Dyke, G. and Kaiser, G. (eds) *Living Dinosaurs: the Evolutionary History of Modern Birds.* John Wiley & Sons (Chichester, UK), pp. 117-145.