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what you amateur psychoanalysts are thinking. When you are in science, you tend to meet other scientists. It is just like any other field in that you socialize with the people that are around you. When I met my husband, Ed Connor, I thought he was a snob because he seemed really standoffish. It turned out that he thought the same thing about me. Once Ed and I got a chance to really talk at a bar with other friends, we realized that we got along really well (even after the gin wore off). Over the years it has been terrific to be married to another neuroscientist because we help each other with papers and grants. It is particularly nice because we truly understand the highs and lows of the job: the joy of finally getting a paper published after many revisions and the agony of rejection. We now have an 11-year old son named Malcolm who seems to like science almost as much as video games, and a bad dog named Ollie.

Do you ever wish that you did something else? Of course, who doesn't? It is usually when I am revising a grant for the umpteenth time or reviewing a badly written paper. When I fantasize about another job, it is almost always as some kind of field biologist. I am fascinated by the intelligence of animals and would have enjoyed studying them. For example, I get pretty envious when I read articles from people who study octopus behavior or the social structure in elephants. These animals have such interesting flavors of intelligence and they seem bizarre and magical to me. The only animal that I get to 'study' behaviorally is our dog Ollie, who finds new and exciting ways to destroy things in the house.

What advice would you give to younger scientists? I tell all my students and postdocs that they should do their damnedest to have fun doing science. If you are not having a good time, it is the wrong job. Don't get me wrong, science won't always be fun, but you should feel some sense of joy and happiness most days. And, of course it helps to have a sense of humor.

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Quick guide

The turtle's shell

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What makes a turtle a turtle, and what makes their shell unique? Turtles, as defined by their shells, are perhaps one of the most easily recognizable and enigmatic creatures on Earth. The shell provides shelter from the environment, enhances thermoregulation, protects from predator attacks and even acts a rich reservoir of fats, minerals and water. Thus, the shell is considered an anatomical innovation that has set turtles off along a unique evolutionary trajectory. Among animals, turtles are most closely related to crocodilians and birds. However, early doubts about this classification stimulated a great deal of scientific interest in turtles, particularly with respect to clarifying major evolutionary transitions in the history of tetrapod animals. Although this pursuit continues to motivate intense examination of living and extinct turtles, many questions concerning the origins of these shelled reptiles remain unanswered.

What are the evolutionary origins of the turtle's shell? For many years a remarkable fossil from Germany, *Proganochelys quenstedti*, was the oldest known turtle, dated to 210 million before the present. Thus, the age of modern turtles could be estimated but evolutionary relationships to other ancient fossil lineages could not be determined. Recently, extraordinary fossil discoveries indicate that terrestrial 'proto-turtles' or stem lineages that diverged from the ancestor of birds and crocodilians arose around 220–260 million years ago. These early turtle-like reptiles included transitional features that eventually gave rise to the fully shelled *Proganochelys.* Turtle-like fossils, such as *Eunotosaurus* (260 million years old), *Pappochelys* (240 million years old) and *Odontochelys* (220 million years old) suggest that the ventral shell elements evolved first, followed by broadened ribs that eventually morphed into the fully hardened dorsal shell. This has recently led to the intriguing hypothesis that the incipient shell might have evolved as an adaptation to life underground, rather than, as traditionally thought, an anti-predator defense. Moreover, other distinctive turtle skull and limb traits were apparent in these fossils. Notably, many armored living and extant tetrapods are known, but none with the extraordinary characteristics of shell formation in turtle embryos.

What is the evolutionary potential of the turtle's shell? Today, turtles live in freshwater, marine, and terrestrial environments, comprising more than 330 described species found all across the planet (Figure 1). This diversification is reflected in the remarkable variation in shells, suggesting that form and function of the turtle body plan had much potential to evolve. Indeed, the last 210 years of turtle evolution have yielded a bewildering array of forms, including: hard- and soft-shelled varieties; side-necked and hidden-necked turtles; extremely flattened pancake-like shells; shells with flexible hinges that permit shell-closure (shell kinesis); adult-sized shells ranging from the size of a Volkswagen beetle to that of a hamster; shells with an unimaginable number of color combinations and tones; and highly reduced shells that leave much of the skin exposed. Intriguingly, other structural components of the turtle body plan have evolved in concert with the shell. For instance, internal muscle connections and limb articulations were modified during the repeated evolution of shell kinesis in small-bodied terrestrial or semi-aquatic turtles. Moreover, the evolution of jumbo-sized shells was accompanied by modifications of the limbs in terrestrial species (tortoises). Also, change in the muscles that enable lung function was necessary to accommodate early steps in the evolution of the shell. Subsequently, the heart was repositioned during the evolution of soft-shelled turtles with extremely flattened shells.

How does the turtle get its shell? The shell is a composite of several skeletal structures that develop, to some degree, independently from one another. Specifically, dorsal (carapace) and ventral (plastron) shell components arise via the activity of distinct gene regulatory networks that pattern the thoracic region in a manner that is highly specific to turtle embryos. In fact, early turtle embryos display a unique transient

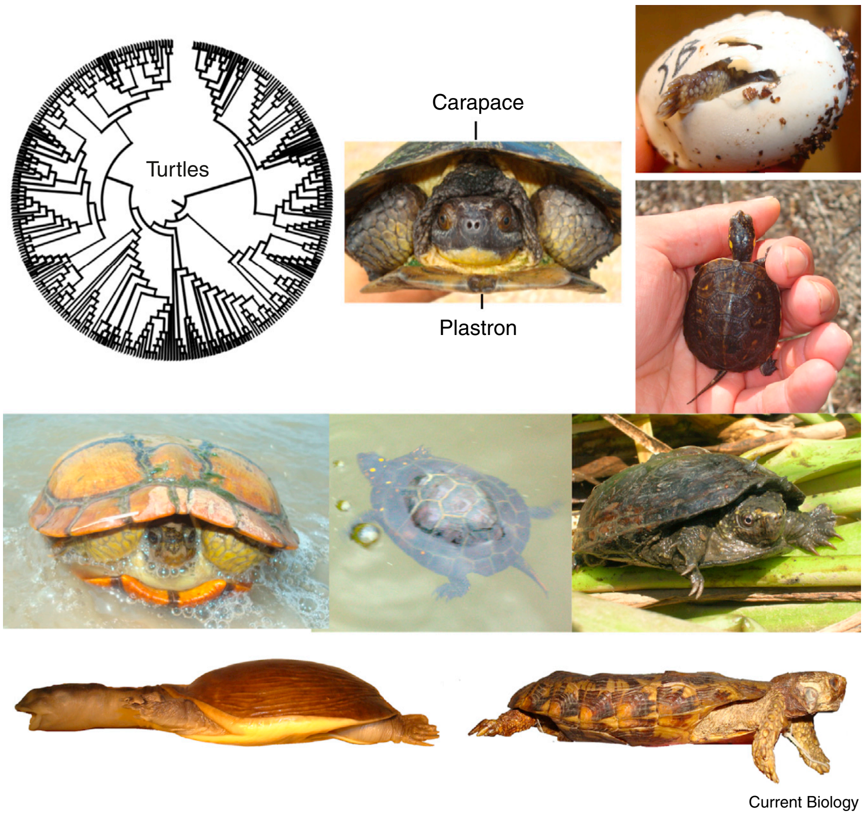

Figure 1. Diversity of turtle shells.
The turtle tree of life (upper left) contains more than 330 living species, all of which feature two major shell components: the carapace and plastron as displayed in an adult blanding's turtle (*Emys blandingii*). Turtles lay eggs in which most of the major components of the shell form (upper right; *E. blandingii*). In the middle panel, a sample of shell diversity is displayed (from left to right) by the chicken turtle (*Deirochelys reticularia*), spotted turtle (*Clemmys guttata*), and eastern mud turtle (*Kinosternon subrubrum*). Some of the most remarkable shell forms are exemplified by soft-shelled turtles with shell kinesis (i.e. mobility: *Lyssemys scutata*; lower left) and the pancake tortoise (i.e. *Malacochersus tornieri*; lower right) (specimens from the Smithsonian herpetological collection). All photos by G.A. Cordero.

structure, known as the carapacial ridge, that appears to govern the positioning of dorsal ribs such that they do not grow and meet on the ventral surface of the thoracic region, unlike in other vertebrates. The plastron forms via calcification of bony breastbone tissue that does not originate from a cartilage precursor. In addition, similarly structured bony belly plates often referred to as 'floating ribs' or gastralia in reptiles contribute to plastron formation. Although the proper rib cage arises from a cartilage template, they also instruct surrounding dermal tissue to calcify such that they contribute to the hardening and shaping of the carapace. With the exception of the short-lived carapacial ridge, no new structures form during shell development. Instead, skeletal elements that were otherwise present and common among ancient reptiles were developmentally co-opted to form the turtle's shell. Even so, shell formation has led to unprecedented spatial reconfiguration of skeletal structures such as the shoulder blade, which is encapsulated by the shell. The turtles's shell poses a major challenge to what we currently know about the limits of organismal architecture, as its formation entails a series of complex processes: altered growth of the rib cage; rearrangement of muscles enabling the subsequent encapsulation of the shoulder blade by the shell; recruitment of dermal bones to assist in calcification of the carapace and plastron. Last but not least, keratinous ectodermal appendages analogous to our fingernails and that provide a protective coating to underlying bones must differentiate in conjunction with the shell. The fascinating book of turtle shell development and evolution continues to be written and awaits revision pending future discoveries.

What does the future hold for turtles?

These ancient reptiles have survived for hundreds of millions of years but their spectacular morphology may put them at a disadvantage in the modern world. Their slow demeanor coupled with their close relationship with humans has contributed to the decline of many turtle populations. Diverse species across the world are currently on the brink of extinction. Nonetheless, many species continue to inhabit freshwater, marine, and terrestrial ecosystems worldwide where they increasingly depend on conservation efforts to maintain viable populations. Future research efforts must continue to combine anatomical, genetic, embryological, and paleontological approaches to address, for instance, whether shell evolution may be rapid, gradual, modular, repeatable or reversible. Does early shell formation vary among species? Also, how do other skeletal structures and internal organs change in conjunction with novel shell traits? Do correlated structures constrain shell evolution? These topics are key to deciphering the origins and diversification of the iconic turtle's shell.

Where can I find out more?

Burke, A.C. (2015). Origin of the turtle body plan. In Great Transformations in Vertebrate Evolution, E.L. Brainerd, N. Shubin and K.P. Dial, eds. (Chicago: University of Chicago Press), pp. 77–90.
Cordero, G.A., and Quinteros, K. (2015). Skeletal remodelling suggests the turtle's shell is not an evolutionary straitjacket. Biol. Lett. *11*, 20150022.
Gilbert, S.F., Cebra-Thomas, J.A., and Burke, A.C. (2008). How the turtle gets its shell. In Biology of Turtles, J. Wyneken, M.H. Godfrey and V. Bels, eds. (Boca Raton: CRC Press), pp. 1–16.
Lyson, T.R., Rubidge, B.S., Scheyer, T.M., de Queiroz, K., Schachner, E.R., Smith, R.M., Botha-Brink, J., and Bever, G.S. (2016). Fossorial origin of the turtle shell. Curr. Biol. *26*, 1887–1894.
Pritchard, P.C.H. (2008). Evolution and structure of the turtle shell. In Biology of Turtles, J. Wyneken, M.H. Godfrey and V. Bels, eds. (Boca Raton: CRC Press), pp. 45–138.
Rice, R., Riccio, P., Gilbert, S.F., and Cebra-Thomas, J. (2015). Emerging from the rib: resolving the turtle controversies. J. Exp. Zool. B. Mol. Dev. Evol. *324*, 208–220.
Schoch, R.R., and Sues, H.D. (2015). A Middle Triassic stem-turtle and the evolution of the turtle body plan. Nature *523*, 584–587.

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