ANNUAL REVIEWS

Annual Review of Ecology, Evolution, and Systematics

Origin and Evolution of the Turtle Body Plan

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Annu. Rev. Ecol. Evol. Syst. 2020. 51:143–66

First published as a Review in Advance on July 31, 2020

The *Annual Review of Ecology, Evolution, and Systematics* is online at ecolsys.annualreviews.org

https://doi.org/10.1146/annurev-ecolsys-110218-024746

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Keywords

turtle shell, anapsid, diapsid, amniote, innovation

Abstract

The origin of turtles and their uniquely shelled body plan is one of the longest standing problems in vertebrate biology. The unfulfilled need for a hypothesis that both explains the derived nature of turtle anatomy and resolves their unclear phylogenetic position among reptiles largely reflects the absence of a transitional fossil record. Recent discoveries have dramatically improved this situation, providing an integrated, time-calibrated model of the morphological, developmental, and ecological transformations responsible for the modern turtle body plan. This evolutionary trajectory was initiated in the Permian (>260 million years ago) when a turtle ancestor with a diapsid skull evolved a novel mechanism for lung ventilation. This key innovation permitted the torso to become apomorphically stiff, most likely as an adaption for digging and a fossorial ecology. The construction of the modern turtle body plan then proceeded over the next 100 million years following a largely stepwise model of osteological innovation.

1. INTRODUCTION

Twenty-one years ago this journal published an influential contribution to a long-standing debate. The debate itself concerns the origin of the structurally unique and in many ways bizarre body plan of turtles (**Figure 1**), a problem whose constitution we recognize today as evolutionary but whose earliest exchanges predate Darwinian theory. The historical, and often heated, unfolding of this dialogue attests to its perceived scientific importance as it successfully engaged some of the greatest minds in the annals of comparative biology—names such as Georges Cuvier, Geoffroy St. Hilaire, Richard Owen, Martin Rathke, and Georg Baur among many others (see MacCord et al. 2014). Even Karl Ernst von Baer (1828) claimed that the embryonic modifications permitting the development of the turtle would be fascinating to know. This trend clearly continued after 1859 with turtles widely recognized as a natural evolutionary experiment whose resultant structural organization presses firmly against the known boundaries for vertebrate tissues and their development networks. The review was that of Rieppel & Reisz (1999), and its publication marks a watershed period in the study of turtle origins.

The primary focus of Rieppel & Reisz (1999) was the phylogenetic position of turtles among living and extinct amniotes. The unclear nature of turtle relationships was, and is, a serious impediment to resolving the origin of their body plan as the tempo, mode, and polarity of the involved transformations are, of course, dependent on the phylogenetic position one ascribes to turtles. The spread of phylogenetic systematics in the latter decades of the 20th century established a critical framework for studying turtle origins but did little to actually resolve the topological details of their evolutionary appearance (**Figure 1**). Differences in the character and taxonomic makeup of these competing morphology- and fossil-based matrices resulted in a series of competing phylogenetic solutions. These hypotheses included turtles as the sister group to other living amniotes (Gaffney 1980), turtles as part of an early and otherwise extinct radiation of reptiles known as Parareptilia (but at an unclear position within that radiation) (Gauthier et al. 1988; Laurin & Reisz 1995; Lee 1997a,b), and turtles as closely related to the other living reptile lineages (Lepidosauria and Archosauria) but still outside their collective crown clade (Sauria) (Gaffney & Meylan 1988). The exclusion of turtles from Sauria is really the one ringing consensus these early cladistic studies managed to achieve (**Figure 1**).

The late 1990s, however, witnessed vigorous research on turtle origins that seriously eroded confidence in their non-saurian status. It was during these years that the initial pulse of broadly comparative molecular sequence data became available. These early sequences were mostly derived from mitochondrial genes, and their analysis recovered a surprisingly clear and consistent signal—turtles are indeed nested inside Sauria, as the extant sister taxon to Archosauria (Zardoya & Meyer 1998, Hedges & Poling 1999, Kumazawa & Nishida 1999) (**Figure 1**). The nature of the morphological signal during this period also began to shift toward a saurian origin, although without the clarity or consistency apparent in the molecular data. There continued to be serious studies that recovered turtles among parareptiles (Reisz & Laurin 1991, Laurin & Reisz 1995, Lee 1997a,b), and the emerging saurian signal in the morphology seemed to contradict the molecular data by allying turtles with a Mesozoic clade of marine reptiles (Sauropterygia) on the lepidosaur rather than the archosaur side of the saurian radiation (Rieppel & deBraga 1996, deBraga & Rieppel 1997, Rieppel & Reisz 1999). Nevertheless, the real possibility that some semblance of a molecular-morphological consensus might be achieved and that this consensus would rearrange long-accepted patterns of amniote phylogeny generated considerable excitement. It was this excitement that prompted the review of Rieppel & Reisz (1999).

Our review picks up where that of Rieppel & Reisz (1999) left off. We discuss the research cycle of the past 20 years, emphasizing the wealth of paleontological discoveries and the unprecedented

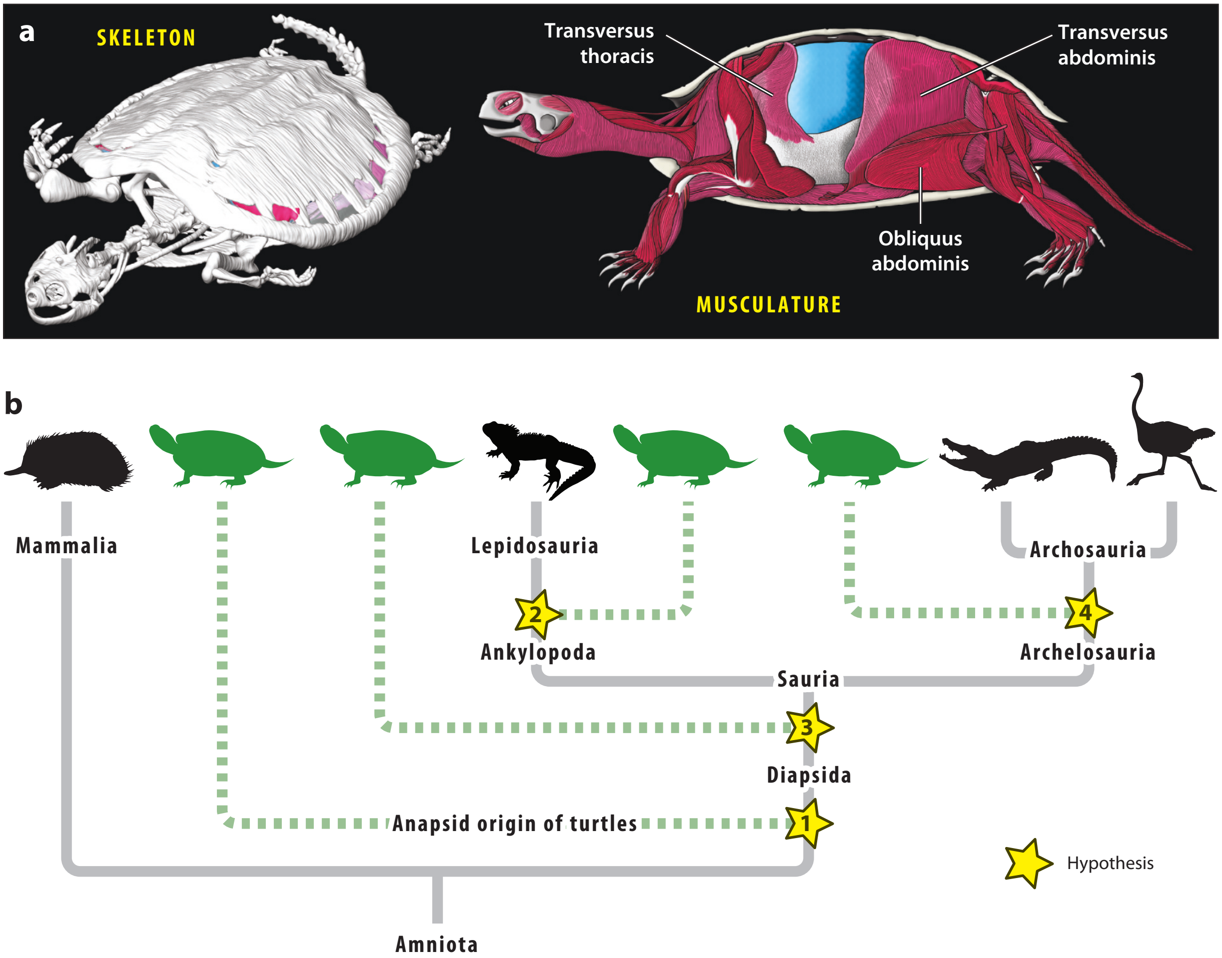


Figure 1

(*a*) The enigmatic nature of the turtle body plan, including ensnarement of the ribs, vertebrae, and dermal elements of the shoulder girdle into the shell; anapsid skull; and novel breathing mechanism driven by abdominal muscles, has long contributed to the group's phylogenetic instability among amniotes, both living and extinct. (*b*) Most of the early morphology-based phylogenies (Gauthier et al. 1988; Reisz & Laurin 1991; Laurin & Reisz 1995; Lee 1997a,b) recovered turtles with early anapsid reptiles, placing them well outside crown group Sauria (birds, crocodilians, lizards, and tuatara) and Diapsida (hypothesis 1). Some contemporary studies (Rieppel & deBraga 1996, deBraga & Rieppel 1997), however, found turtles to be diapsid reptiles, positioned inside the saurian crown as the extant sister to lepidosaurs (lizards + tuatara) (Ankylopoda; hypothesis 2)—a phylogenetic hypothesis that remains viable and is still much discussed among paleontologists (Hill 2005; Li et al. 2008, 2018; Lyson et al. 2012; Bever et al. 2015; Schoch & Sues 2015). A third morphology-based hypothesis is that turtles are diapsid reptiles but are positioned outside crown Sauria (hypothesis 3) (see Bever et al. 2015, Laurin & Piñeiro 2017). Molecular data are remarkably consistent in recovering turtles inside Sauria as the extant sister to Archosauria (birds and crocodilians) (Archelosauria; hypothesis 4) (Zardoya & Meyer 2001; Iwabe et al. 2005; Matsuda et al. 2005; Hugall et al. 2007; Shen et al. 2011; Tzika et al. 2011; Chiari et al. 2012; Crawford et al. 2012, 2015; Fong et al. 2012; Lu et al. 2013; Shaffer et al. 2013; Wang et al. 2013; Field et al. 2014). Skeletal illustration provided by E. Schachner. Musculature illustration adapted with permission from Lyson et al. (2014) and originally redrawn from Bojanus (1819–1821). Tuatara silhouette adapted from **http://phylopic.org/** (public domain).

light they are shedding on the timing, tempo, and structural nature of fundamental transformations in the turtle body plan. These topics include the homology of the bones that make up the shell, the incorporation of the ribs into the dorsal dermis, the contributions of the pectoral girdle to the front end of the shell, the exaptive emergence of the turtle respiratory apparatus, the status and deep history of the anapsid turtle skull, and the potential roles that behavioral ecology played in driving these changes.

What is perhaps most exciting about this particular moment in the long history of research on turtle origins, and what we most want to drive home with this review, is the fact that the feedback loop between fossil, developmental, and phylogenetic data on turtle origins has entered a more mature phase. Turtles and their body plan have emerged as a highly informative system for exploring baseline mechanisms and patterns in the evolution of morphogenesis—one that rivals more established models in its potential for revealing how the evolution of developmental networks over deep time can produce major changes in the structural and functional organization of the vertebrate form.

2. THE MODERN TURTLE BODY PLAN

Turtles are easily among the most recognizable of all modern vertebrate clades. Their distinctiveness derives directly from their shelled body plan, whose detailed architectural and developmental construction is wholly unique in the known history of vertebrates (**Figures 1** and **2**). The modern shell conveys benefits ranging from predator defense, thermoregulation, and shelter to a repository for fat, minerals, and water (Zangerl 1969, Jackson 2011). It is divided into an upper carapace and lower plastron, connected laterally by a bony bridge (Zangerl 1969). The carapace represents the integration of approximately 50 individual bones, divisible into a number of distinct series (**Figure 2**). The neural and costal series are similarly structured with a core of chondral bone (contributed by the dorsal vertebrae and ribs, respectively) set within a horizontal plate of membranous (i.e., dermal) bone (for an extensive historical discussion regarding the homology of these and other bones of the shell, see Szczygielski & Sulej 2019). In both series, the membranous plate forms an upper cap, which in the neurals extends from the distal end of the vertebral neural process and in the costals results in a T-shaped, cross-sectional form (Scheyer et al. 2008, Lima et al. 2011, Hirasawa et al. 2013). Numerous tetrapod lineages exhibit broadened ribs, but only those of turtles bear this distinctive T shape (Lyson et al. 2013a). The periphery of the carapace is formed of membranous bone only and is dominated by the aptly named peripheral series (usually 11 per side). The peripherals fail to fully circumscribe the carapace only because they are interrupted by the midline nuchal (anteriorly) and from one to three midline pygals (posteriorly). The plastron is a composite structure formed through the sutural integration of 9 to 11 membrane bones: the entoplastron, and the paired epi-, hyo-, hypo-, xiphi-, and, in some taxa, mesoplastra (**Figure 2**). In hard-shelled turtles, the carapace and plastron are covered by a complex network of keratinized epidermal scutes whose patterning is conserved to such a degree as to be phylogenetically informative (Moustakas-Verho & Cherepanov 2015).

The shell is a dominating structure, and its influence extends to a wide array of features. This connection ranges from the direct and obvious to the indirect and unclear, but each contributes to the highly derived nature of turtle anatomy and physiology. The number of dorsal vertebrae ($N = 10$) is fewer in turtles than in other amniote lineages, suggesting that the emergence of the shell was related to a shortening of the trunk (Müller et al. 2010). The completed shell fully encapsulates the scapula/coracoid and bony pelvis, leaving the functional shoulder and pelvic girdles in an internal (deep) position relative to the ribcage (Ogushi 1911, Ruckes 1929, Burke 1991, Nagashima et al. 2009). This deep position does not mean the girdles lie inside the ribcage, as

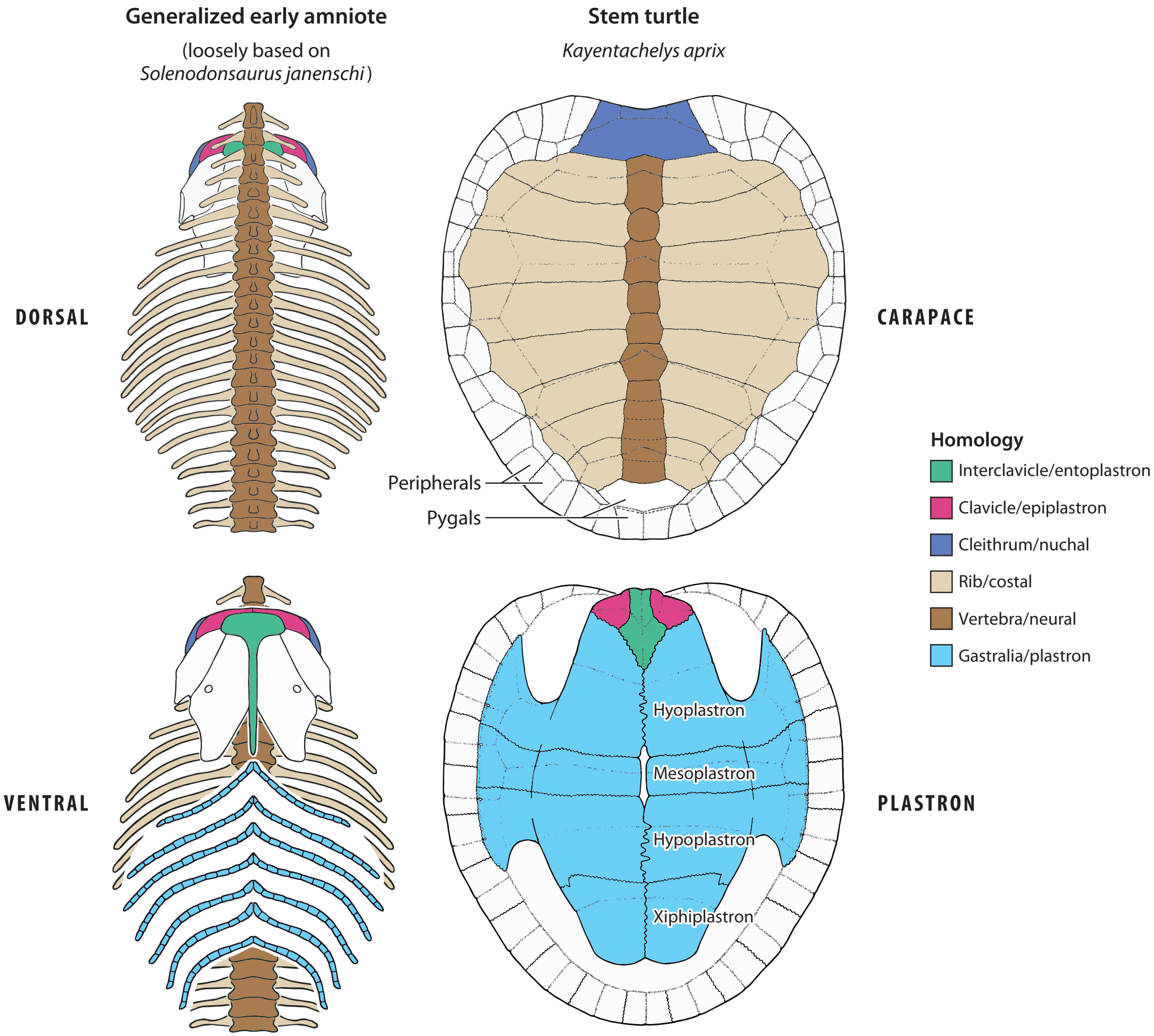


Figure 2

Proposed homology for the ~60 bones that make up the turtle shell. Compared are the dorsal/carapace (*upper* images) and ventral/plastron (*lower* images) views of the stem turtle *Kayentachelys aprix* and the shoulder girdle and trunk skeleton of a generalized early amniote. All bones of the shell have homologs outside turtles with the exception of the peripheral and pygal bones. These are widely regarded as neomorphs. Figure adapted with permission from Lyson et al. (2013b).

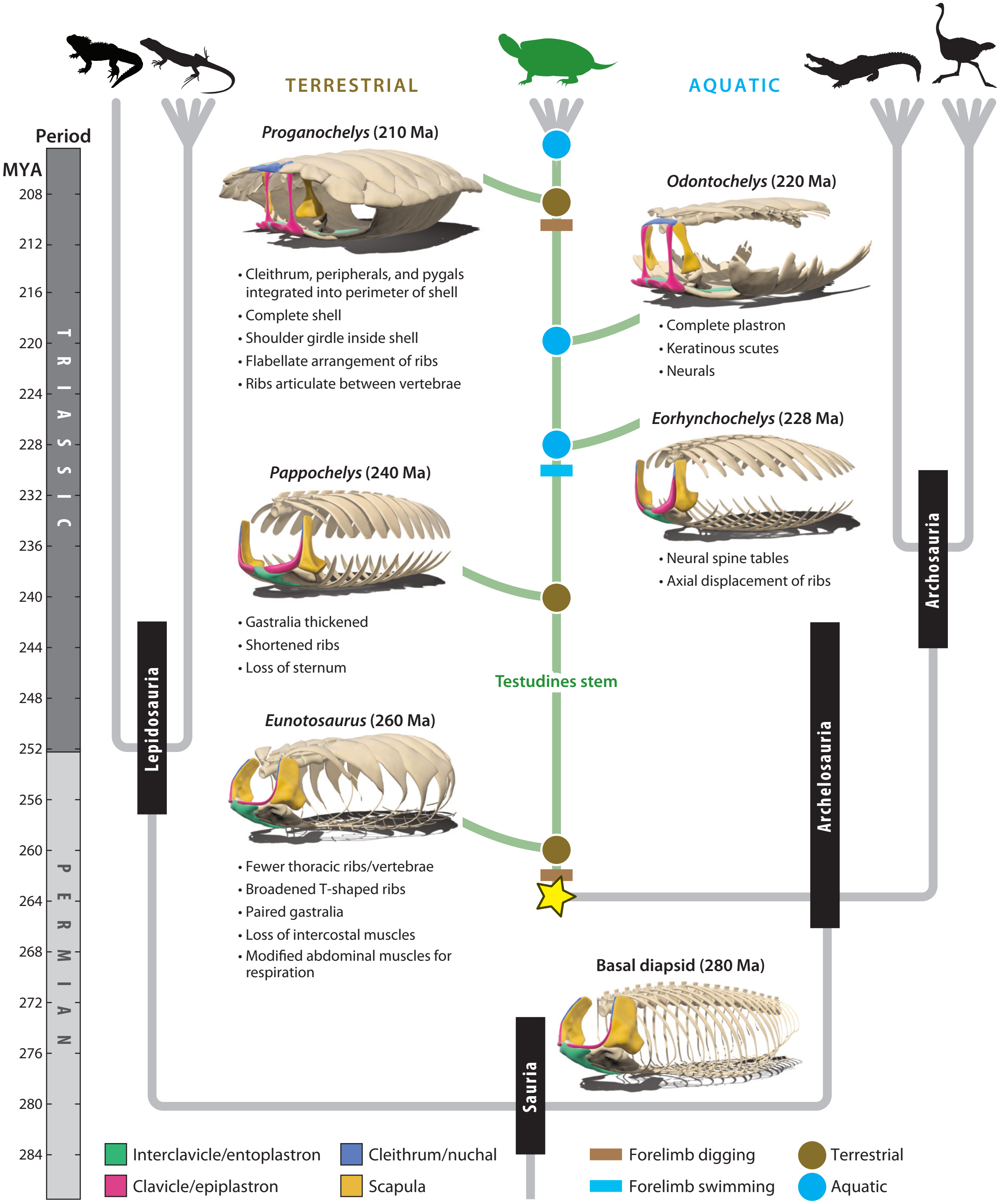
they are often described (Bonin et al. 2006). This misconception derives from a dramatic morphogenetic transformation in which the upper- and lowermost elements of the primitive tetrapod shoulder girdle are actually incorporated into the shell (Ogushi 1911, Ruckes 1929, Lyson & Joyce 2012) (see Section 6). Regardless, the position of the girdles inside the rigid shell limits the range of motion in the limbs (Walker 1979) and has led to a number of secondary modifications (Cordero & Quinteros 2015) that circumvent these constraints in order to maintain functionality (Mayerl et al. 2019).

The sutural connection between the successive neurals and costals is correlated with a significant alteration of thoracic function traceable through the derived state of the trunk musculature. The epaxial muscles responsible for stabilizing and bending the trunk in other vertebrates are lost, as are the hypaxial intercostal muscles (Bojanus 1819–1821; Gaunt & Gans 1969; Hirasawa et al. 2013, 2015). Both losses reflect a stiffening of the trunk, which begs the question of how turtles manage to ventilate their lungs without the ability to alter the size and shape of their trunk skeleton. We address the evolutionary history of this transformation below (Section 7), but the answer lies in an extreme modification of the abdominal muscles (Musculus obliquus abdominis, M. transversus abdominis, and M. transversus thoracis) producing a dynamic sling that hangs between the anterior and posterior ribs of the carapace and passes above the plastron but below the thoracoabdominal viscera (**Figure 1**). Contraction of this sling elevates these viscera away from the plastron, resulting in a compression of the dorsally placed lungs against the deep surface of the carapace. This action and its associated release produce the volumetric changes necessary for lung ventilation and pulmonary breathing (Mitchell & Morehouse 1863, Gans & Hughes 1967, Gaunt & Gans 1969).

The head and neck of modern turtles also exhibit significant modification. The cervical vertebrae are notable for the range of their morphology, which reflects the two ways in which crown group turtles draw their head into the shell for protection; pleurodires retract their head through a lateral bending of the neck, whereas cryptodires pull their head back directly through S-shaped cervical folding (Williams 1950, Werneburg et al. 2015a). The skull is famously akinetic and anapsid, without the upper and lower temporal fenestrae that mark the skulls of other living reptiles (Romer 1956). In most crown species, the anapsid skull is secondarily opened through an upper (temporal) and lower (cheek) emargination, which permits the chewing muscles to extend beyond the limits of the primitive adductor chamber (Gaffney & Meylan 1988). The path these muscles take en route to the lower jaw also bears a uniquely turtle quality, with the fibers bending over a synovial capsule formed on either the quadrate/prootic (cryptodires) or pterygoid (pleurodires) (Gaffney & Meylan 1988, Joyce 2007). Modern turtles lack both palatal and marginal teeth, the latter being replaced by a keratinous rhamphotheca that covers the feeding surfaces.

3. CHALLENGES TO RESOLVING THE TURTLE STEM LINEAGE

The above summary details some, but certainly not all, of the differences that constitute the modern turtle body plan and that distinguish turtles from all other extant vertebrates. Because we can infer that each of these distinctive features was in place by the origin of the turtle crown clade (currently estimated at ∼180 MYA) (Kumar et al. 2017), the challenge of understanding the origin of the turtle body plan is establishing the tempo, mode, functional/ecologic context, and developmental mechanisms through which these features arose and became integrated along the turtle stem lineage. Stem lineages, by definition, lack extant representatives, which means their histories must largely be inferred from observations made within the adjacent crown clades. But as these stems circumscribe more and more evolutionary time, the explanatory power of crown-based inferences weakens. This is why fossils, as the only empirical window into this history, play such a crucial role in exposing the major morphologic and ecologic transitions that especially long stem lineages tend to conceal (Gauthier et al. 1988). Based on a tree topology wherein turtles are the sister taxon to archosaurs, the turtle total group originated ∼265 MYA (Kumar et al. 2017) (**Figure 3**), indicating the turtle stem is roughly 80 Ma in length. If one were forced to choose why the origin of turtles has perplexed comparative biologists for so long, it would be the sustained absence of a transitional fossil record across this immense time interval. Relief on this front has begun in earnest only recently. But before we detail how these new fossil discoveries can be



(*Caption appears on following page*)

Figure 3 (*Figure appears on preceding page*)

Evolutionary origin of the turtle shell based on recent discoveries in the fossil record of the turtle stem lineage. Recent molecular analyses estimate the turtle/archosaur split at 265–242 MYA (Kumar et al. 2017). *Eunotosaurus* is dated to within this estimated interval but already exhibits a range of synapomorphies representing fundamental features of the turtle body plan. The 50-Ma interval separating *Eunotosaurus* from the earliest fully formed turtle shell is now sampled with a series of Triassic stem turtles that further demonstrate the step-wise nature of this evolutionary history. Also included are inferred ecologies (*colored horizontal bars*) at different points along the turtle stem lineage based on the anatomy and geological setting of the relevant stem fossils. The yellow star at the base of the turtle stem denotes a key transformation in the abdominal muscles and dorsal ribs from an ancestral dual function of breathing and torsional control during locomotion (Carrier 1987) to a division of function with the abdominal muscles (see Musculus obliquus abdominis, M. transversus abdominis, and M. transversus thoracis in **Figure 1**) forming a specialized mechanism for lung ventilation, whereas the ribs, which are incorporated into the shell ∼50 Ma later, serve to prevent torsion during locomotion. Nodes are coupled with heavy vertical black bars representing confidence intervals of divergence estimates (Kumar et al. 2017). Geologic timescale adapted from Cohen et al. (2013). Basal diapsid, *Eunotosaurus*, *Odontochelys*, and *Proganochelys* images adapted with permission from Lyson et al. (2014). Tuatara silhouette adapted from **http://phylopic.org/** (public domain).

integrated with emerging developmental data to articulate a detailed evolutionary developmental model of turtle origins, it is worth describing a bit of the historical dialectic between these two data sets and how we got to where we are today.

For more than a century, the earliest clear view we had of the turtle stem lineage was through the late Triassic (∼210 Ma) *Proganochelys quenstedti* (Baur 1887, Gaffney 1990). This form is roughly 30 Ma older than the crown and exhibits many plesiomorphic features that inform the timing of apomorphy accrual along the stem—e.g., retention of palatal (but not marginal) teeth and absence of a mechanism for either full head retraction (but see Werneburg et al. 2015b) or redirecting the vector of the primary jaw adductors (Gaffney 1990, Joyce 2007). The problem is that *Proganochelys* is already in possession of a completed shell, compromising its ability to inform the earliest transformations in this body plan and thus to serve as that critical morphologic and phylogenetic bridge between modern turtles and other reptile groups. The absence of other fossil taxa that might better fill this role prompted considerable speculation among both paleontologists (Lee 1997a,b; Joyce et al. 2009) and developmental biologists (Gilbert et al. 2001, Cebra-Thomas et al. 2005) and suggested to some that the turtle body plan must have evolved rapidly, under a macromutational so-called hopeful monster scenario (Rieppel 2001, 2013, 2017). There were no transitional turtles because either the transitional period never actually existed or it was opened and closed with such rapidity that the probability of sampling fossils from within the transitional period approaches zero.

One feature of special interest that *Proganochelys* does possess is its osteoderms: individuated ossifications within the dorsal dermis that in *Proganochelys* cover the limbs, neck, and tail (Gaffney 1990). Their presence in what again was the earliest known stem turtle was congruent with, and served to support, a widely accepted origin model in which the turtle shell formed through a developmental melding of the underlying (chondral) vertebrae and ribs with the overlying (membranous) osteoderms. This composite hypothesis (Lyson & Gilbert 2009; or polka dot ancestor, see Rieppel 2017) was so influential during the second half of the twentieth century that an absence of osteoderms became an implicitly acceptable criterion for rejecting a fossil from the turtle stem lineage a priori (e.g., Romer 1956, Cox 1969). This point could be made by simply considering all the different osteoderm-bearing lineages that were promoted during this period as the extinct sister group to turtles, from terrestrial pareiasaurs (Lee 1997a,b) to various marine sauropterygians (Rieppel & deBraga 1996, deBraga & Rieppel 1997). But the influence of the composite hypothesis, which persisted into the 2000s (Scheyer et al. 2008, Joyce et al. 2009), is probably more clearly conveyed by considering which osteoderm-free lineages were denied serious analytical consideration—a prime example being a middle Permian reptile from southern Africa named *Eunotosaurus africanus*. We discuss *Eunotosaurus* in greater detail below (Sections 5 and 6). For now, it is important to note only that despite being described in the late nineteenth century as a potential turtle ancestor (Seeley 1892), and despite the intense research interest and activity surrounding turtle origins in the decades following the widespread adoption of cladistic techniques for phylogenetic reconstruction (**Figure 1**), *Eunotosaurus* was never included in a phylogenetic analysis with turtles until 2010 (Lyson et al. 2010). What changed in the years leading up to that 2010 study that permitted *Eunotosaurus* to once again be considered as a potential player in the enigmatic early history of turtles? The answer is twofold, with complementary insights arising out of both developmental biology and paleontology.

4. DEVELOPMENTAL ORIGINS OF THE DE NOVO HYPOTHESIS

The end of the last millennium marked the beginning of a spirited research cycle on the development of the turtle body plan. This work found its modern footing in the experiments and observations of Ann Burke (Burke 1989, 1991), which identified a longitudinal thickening of the embryonic trunk as a critical structure in turtle-shell development. The lateral emergence of this carapacial ridge (CR) between the fore and aft limb buds is the first morphologic indication that a tetrapod embryo is a turtle (Burke 1989, 1991; Rice et al. 2016). Eventually the CR fully circumscribes the embryonic trunk to form the peripheral edge of the developing carapace. Its cellular profile of superficial ectoderm underlain by a condensation of somite-derived mesenchyme typifies the epithelial-mesenchymal interactions that perform essential patterning roles in more thoroughly studied developmental systems (e.g., apical ectodermal ridge of the tetrapod limb) (Burke 1989, 1991; Gilbert et al. 2001; Cebra-Thomas et al. 2005; Kuraku et al. 2005; Nagashima et al. 2007; Moustakas 2008; Pascual-Anaya et al. 2014).

Initial efforts to establish detailed, gene-based mechanisms for turtle-specific features focused on the role of the CR in directing what is known as the axial remodeling of turtle ribs (Burke 1989, 1991; Gilbert et al. 2001; Cebra-Thomas et al. 2005; Nagashima et al. 2007; Rice et al. 2015). In nonturtle vertebrates, the sclerotomal cells that differentiate as dorsal ribs enter the somatopleure (a tissue formed of lateral plate mesoderm and overlying ectoderm) of the lateral and ventral body wall so that the mature ribs extend down and around the trunk cavity (Shearman & Burke 2009). These cells in turtles never cross the critical morphogenetic boundary (i.e., the lateral somatic frontier) (Shearman & Burke 2009) but are instead deflected into the rapidly expanding dorsal dermis (Ruckes 1929, Burke 1991, Gilbert et al. 2001, Nagashima et al. 2007, Shearman & Burke 2009, Hirasawa et al. 2015). There are two major ways that the turtle ribs are remodeled so that they remain in a dorsal position (Rice et al. 2015). In hard-shelled turtles, the leading (distal) margin of the turtle proto-rib eventually reaches the CR and embeds itself into the structure's mesenchymal core. This axial displacement allows the ribs to grow in the dorsal dermis and curve with the CR. Here, the CR is proposed to be a signaling center with a primary role in patterning the migration of the rib. Early experiments where CR was removed appear to support this inductive role, with ribs of perturbed embryos growing either in the downward plesiomorphic trajectory or toward an adjacent segment where CR remained intact (Burke 1989, 1991). Subsequent gene-expression and bead-implantation experiments revealed a potential mechanism for this induction, with CR fibroblast growth factor (FGF) 10 synthesis entering into a positive feedback loop with rib FGF8 (Loredo et al. 2001, Cebra-Thomas et al. 2005). The chemotactic product of this dynamic is that the ribs enter the dorsal dermis as a function of their apical growth toward the CR. This co-optation of a signaling pathway utilized by the developing limb, if correct, represents a textbook example of heterotopy at both the molecular and morphological levels (Gilbert et al. 2008).

The second model, which is based on soft-shelled turtles, indicates instead that the ribs enter the dorsal dermis under the influence of a canonical Wnt pathway, although the details of the involved mechanism and the cellular source of the signaling proteins remain unclear (Kuraku et al. 2005, Wang et al. 2013, Nagashima et al. 2014). However, once in the dorsal dermis, the ribs do not migrate to the CR, allowing the CR to migrate without incorporating the rib. The immediate product of this derived connectivity is that turtle ribs are shorter, are less curved, and project more laterally than ribs of other vertebrates (Nagashima et al. 2007, Hirasawa et al. 2015). They also exhibit a specific radiating pattern referred to as flabellate (Nagashima et al. 2007, Kuratani et al. 2011, Kuratani & Nagashima 2012). Thus, the CR still plays an important role in this second model, serving to draw the ribs into the characteristic flabellate pattern. The structural consequences of this pattern are especially significant anteriorly where the M. serratus anterior, whose connections are established early, rotates under the carapace as the body wall folds inward. This inhibits the invasion of the later-developing dorsal muscles of the limb bud, such as the M. latissimus dorsi and M. pectoralis. These muscles circumvent the CR and establish attachments on the nuchal and ventral portions of the clavicle (Nagashima et al. 2009, Kuratani & Nagashima 2012).

Regardless of the CR's ultimate signaling role, the morphogenetic products that lie downstream from axial modification are profound, which is why such axial modification is widely accepted as a key innovation of the lineage (Burke 1989, 1991; Gilbert et al. 2001; Cebra-Thomas et al. 2005; Kuraku et al. 2005; Nagashima et al. 2007; Kuratani et al. 2011; Pascual-Anaya et al. 2014). For example, it was noted above (Section 2) that the costal series of the carapace bones is the product of biphasic ossification with endochondral ribs set within an orthogonally oriented plate of dermal bone (Scheyer et al. 2008, Lima et al. 2011, Hirasawa et al. 2013). The working developmental explanation is that after the ribs enter the dermis, bone morphogenetic proteins (BMPs) secreted by rib cartilage during the normal process of endochondral ossification induce BMPs in adjacent connective tissue (Cebra-Thomas et al. 2005). This dermal ossification predictably begins along the periosteum—the dense connective tissue along the perimeter of the rib (Gilbert et al. 2001). In the early stages of costal bone formation, this perichondral collar begins to expand laterally and dorsally, encroaching on the intercostal dermis and subdermis. BMPs from the rib and this expanded periosteum are considered capable of converting the adjacent dermal cells into osteoblasts, producing what is known as metaplastic ossification (Chen et al. 2012, Salazar et al. 2016). In hard-shelled turtles, the periosteum may propagate BMP expression, producing a leading edge of ossification that moves away from the rib proper. This metaplastic wave conveys the T-shaped cross-sectional morphology to the early postnatal rib before eventually meeting its counterpart from a neighboring segment. At that point, a sutural connection is formed, and the architectural framework of the costal series and carapace is established. In soft-shelled turtles, only the first stage of this ossification is seen to occur (Hirasawa et al. 2013). This paracrine theory of turtle shell development (where the CR induces the ribs to enter into the dorsal dermis and the ribs subsequently act as the center to promote costal bone development) is known as the de novo model of shell formation (Lyson & Gilbert 2009). In contrast to the composite model, it does not require the presence of osteoderms in the earliest history of the turtle stem lineage (Lyson & Gilbert 2009, Rice et al. 2015, Rieppel 2017).

5. *ODONTOCHELYS* AND THE LIBERATION OF THE TURTLE STEM LINEAGE

Paleontological support for the de novo hypothesis came with an astounding discovery from late Triassic, near-shore marine sediments in China. *Odontochelys semitestacea* (220 Ma) is approximately 10 Ma older than *Proganochelys* and hosts a surprising mixture of primitive and derived features that do not include osteoderms (Li et al. 2008) (**Figure 3**). The *Odontochelys* skull, like that of *Proganochelys*, is fully anapsid, but with both palatal and marginal teeth. The plastron is complete, whereas the carapace is present only in the form of broadened, T-shaped ribs whose resemblance to the ribs of early postnatal, extant turtles (before the metaplastic wave between adjacent ribs coalesces into a unified costal plate) is striking (Li et al. 2008). The discovery of *Odontochelys* cast serious doubts on the need to invoke markedly high rates of phenotypic evolution (a modified form of a hopeful monster scenario) for turtle origins. It also served as a critical guide to the features likely to populate the even deeper recesses of the turtle stem lineage. This combination, in effect, opened a paleontological floodgate that had been securely fastened for well over a century.

The next major contribution was a series of studies re-examining the anatomy of *Eunotosaurus africanus* and its implications for the morphologic, phylogenetic, and ecologic makeup of the early turtle stem (Lyson et al. 2010, 2013a,b, 2014, 2016; Carroll 2013; Lee 2013; Bever et al. 2016, 2015). *Eunotosaurus* is old (260 Ma), approximately 40 Ma older than *Odontochelys*, 80 Ma older than the turtle crown clade, and within roughly 10 Ma of recent molecular estimates for the origin of the turtle stem (**Figure 3**). Such antiquity brings with it a particular relevance for the origin and early evolution of the turtle body plan. The most notable feature of *Eunotosaurus* is its series of T-shaped ribs—set within a shortened, circular trunk and histologically indistinct from developing extant turtle costals (Lyson et al. 2010, 2013a). This similarity includes a histological signature indicating the intercostal muscles were lost and that an early form of the abdominal sling was present (Lyson et al. 2014). The implication here is that the derived mechanism through which modern turtles breathe is one of the earliest transformations in the turtle body plan and was in place prior to the locking of the ribs in a completed carapace (**Figure 3**). This sequence is not terribly surprising given that a new way of breathing could not have waited until after the plesiomorphic mechanism was lost. Still, evidence of these transformations in a Permian reptile was both surprising and exciting. *Eunotosaurus* shows no evidence of a plastron, although it does contain the paired abdominal gastralia from which much of the plastron is thought to have evolved (see Section 6).

Additional surprises were revealed in a computed tomography study of the *Eunotosaurus* skull. Most notable here was a small fenestra in the posterior dermal roof, hidden beneath a forward extension of the supratemporal bone, whose topology and connectivity support homology with the upper temporal fenestra of diapsid reptiles (Bever et al. 2015, 2016). The phylogenetic hypothesis that turtles evolved within the saurian crown clade necessitates that the anapsid skull of *Odontochelys*, *Proganochelys*, and more crown-ward turtles is secondary and that the early turtle stem should include forms with the upper and lower fenestra indicative of this diapsid ancestry (Müller 2003). The lower temporal fenestra of *Eunotosaurus* is clear, but this opening is of questionable phylogenetic relevance given that its distribution extends outside diapsid saurians (Piñeiro et al. 2012, Ford & Benson 2020). The upper fenestra, in contrast, is an unambiguous apomorphy of the diapsid radiation and thus the key feature of this unique architecture. The diapsid nature of the adult *Eunotosaurus* skull is clearly confirmed by a juvenile skull whose supratemporal had yet to fully ossify. Here, the fenestrae are relatively large and conform closely to the morphology of other diapsid reptiles (Bever et al. 2015).

In the time since the new studies of *Eunotosaurus* began to be published, two new critically important stem turtles were recovered from the stratigraphic and phylogenetic space separating *Eunotosaurus* from *Odontochelys*. The first of these is *Pappochelys rosinae*, which was discovered in middle Triassic rocks in Germany estimated at ∼240 Ma (Schoch & Sues 2015, 2016, 2017, 2020; Schoch et al. 2019). *Pappochelys* bears the same T-shaped ribs as *Eunotosaurus* and *Odontochelys*, but unlike *Eunotosaurus*, its gastralia are thickened in a manner that suggests the transformation into a plastron had begun. The skull of *Pappochelys* also exhibits a relatively small upper temporal fenestra. Its apparent lack of a supratemporal indicates the secondary covering of the *Eunotosaurus* fenestra may well be an autapomorphy of that taxon. The second of the recently discovered early stem turtles, *Eorhynchochelys sinensis*, is from the same formation that produced *Odontochelys*, although from a slightly lower horizon (~7.5 meters below *Odontochelys*) (Li et al. 2018). Estimated at 228 Ma, *Eorhynchochelys* is most notable as the earliest form with the secondary anapsid skull (Li et al. 2018, Schoch & Sues 2020). It also exhibits a loss of the anterior-most marginal teeth, hinting that the developmental pathways responsible for the loss of marginal teeth in *Proganochelys* and more crown-ward forms had begun to be assembled. The basal position of *Eorhynchochelys* relative to *Odontochelys*, however, indicates the marginal tooth row of stem turtles was reduced at least twice (i.e., the *Eorhynchochelys* reduction is nonhomologous with that of the crown).

This wealth of long-awaited data from the turtle stem deep to *Proganochelys* is also being supplemented with important new specimens and discoveries from late Triassic rocks from around the world that are roughly contemporaneous with those producing *Proganochelys* (Joyce 2017). These include *Proterochersis* spp. from Europe (Szczygielski & Sulej 2016, 2019), *Palaeochersis talampayensis* from South America (Sterli et al. 2007), and *Chinlechelys tenertesta* from North America (Joyce et al. 2009). These fossils emphasize the enormous strides that paleontology, developmental biology, and phylogenetics have made over the past 20 years toward a meaningful understanding of the origin and early evolution of the turtle body plan. These collective advances support a detailed and integrated model of developmental evolution that both highlights the empirical achievements of this work and points to the questions that should serve as a rich substrate for future work.

6. A STEPWISE MODEL FOR THE ORIGIN OF THE TURTLE BODY PLAN

The population of the turtle stem lineage with these new fossil discoveries, along with the detailed developmental data, has allowed for the advancement of evolutionary developmental models that document key transformations in both the turtle shell and skull (Kuratani et al. 2011; Nagashima et al. 2012; Lyson et al. 2013a; Bever et al. 2015; Schoch & Sues 2015, 2020). The following hypothesis is partitioned according to the crown-ward order of stem turtles as recovered in recent phylogenetic analyses (Bever et al. 2015; Schoch & Sues 2015, 2017; Li et al. 2018). It builds on previous recent efforts to articulate this integrated history (Kuratani et al. 2011; Nagashima et al. 2012; Lyson et al. 2013a; Schoch & Sues 2015, 2020) and is remarkable in the degree to which the ontogenetic and phylogenetic histories parallel each other (Lyson et al. 2013a) (**Figure 3**). The evolutionary transformations inferred along the phylogenetic backbone of turtles are placed within a temporal framework based on the estimated absolute ages of the appropriate stem fossils (**Figure 3**). These are minimum ages for the actual transformations, as the disparity between the age of the fossils and the absolute timing of their divergence from the primary turtle lineage is unknown.

6.1. Prior to *Eunotosaurus* (>260 Ma)

The broadened T-shaped ribs, representing a derived outgrowth of membranous bone from the perichondral/periosteal collar of the developing rib shaft (Gilbert et al. 2001, Scheyer et al. 2008), appear to be the earliest skeletal transformation that clearly marks the turtle body plan (Lyson et al. 2013a). Its early phylogenetic appearance is mirrored in its precocial ossification (Sheil 2005, Sheil & Greenbaum 2005, Smith-Paredes et al. 2020) and reflects an overall stiffening of the trunk. These changes are phylogenetically congruent with a reduction in trunk segments (>18 to 9 dorsal vertebrae) (Müller et al. 2010, Lyson et al. 2013a), loss of intercostal muscles, and modification of the abdominal muscles into a derived sling-like mechanism for ventilating the lungs (Lyson et al. 2014).

The phylogenetic timing of the CR is an important, unresolved question. Ontogenetically, the CR precedes the formation of T-shaped ribs, and there is often an implicit, but untested, assumption that axial modification and its associated rib-CR contact is a necessary first step for inducing the T-shaped morphology. The ventrolateral curvature of the *Eunotosaurus* ribs, however, suggests that axial remodeling was not yet in place and that perhaps the CR evolved later, insinuating itself into an early stage of morphogenesis. This is potentially more in line with those studies that argue for an exclusive, inductive relationship between the CR and flabellate ribs (e.g., Nagashima et al. 2009, 2012, 2014; Kuratani & Nagashima 2012), which do not appear until later on the tree (**Figure 3**) (see Section 6.3). More work is needed to resolve these issues, but a sobering point that must be kept in mind is that the detailed inductive relationships in place within the crown clade may not reflect the developmental pathways as they existed in the earliest stem history of the associated phenotypes.

The skull at this early stage exhibits a relatively small list of derived turtle features that includes, for example, a somewhat shortened rostrum and a structural connection between the otic capsule (specifically the prootic and opisthotic and suspensorium (quadrate) (Bever et al. 2015). It is important to note, however, that the collective expression of these few apomorphies supports *Eunotosaurus* as an early stem turtle even when analyzed independent of the postcranial skeleton (Bever et al. 2015). More noteworthy is the retention of clear diapsid features, highlighted by the two temporal and suborbital fenestrae (Bever et al. 2015, 2016) (**Figure 4**). Direct evidence that the turtle skull is built on a diapsid structural framework represents a significant breakthrough in reconciling the historic disparity between morphology and molecules and their placement of turtles within the larger reptile tree. Evidence that this consilience might soon extend beyond a general diapsid origin to include the more exclusive turtle-archosaur clade (**Figure 1**) is perhaps found in a posterior ossification of the orbital cartilages in *Eunotosaurus* and *Proganochelys* (Bever et al. 2015), which may prove homologous with the archosaur laterosphenoid (Bhullar & Bever 2009). Comparing the juvenile and adult skulls of *Eunotosaurus* indicates the temporal fenestrae of early stem turtles became constricted through the sustained postnatal growth of the surrounding membrane bones. The crown-ward extension and/or acceleration of this derived trajectory membrane is a viable hypothesis explaining the secondarily anapsid character of later forms (Bever et al. 2015) (see Section 6.3).

6.2. Between *Eunotosaurus* and *Pappochelys* (260–240 Ma)

A notable transformation here is a distinct broadening and lengthening of the abdominal gastralia (Schoch & Sues 2015, 2017; Schoch et al. 2019). The hyo-, hypo-, and xiphiplastra are hypothesized to be derived from trunk neural crest (Clark et al. 2001; Cebra-Thomas et al. 2007, 2013; Gilbert et al. 2007; Rice et al. 2016; but see Nagashima et al. 2014) and are accepted as the product of the thickening/fusion of the abdominal gastralia initiated deeper on the tree (**Figure 2**). Ontogenetically, the posterior plastral bones ossify early (around the same time as the costals) (Sheil 2005, Sheil & Greenbaum 2005, Smith-Paredes et al. 2020), making their early stratigraphic and phylogenetic appearance perhaps unsurprising. The broadened dorsal ribs of *Pappochelys* are somewhat short and straight (Schoch & Sues 2020) but not to the degree of more crown-ward turtles (**Figure 3**). In addition, the finished apices on the dorsal ribs suggest loss of the sternum (Schoch & Sues 2015, 2017, 2020). The shoulder girdle resembles that of earlier stem turtles, but with a slight lengthening of the acromion process of the scapula (Schoch & Sues 2015, 2017) (**Figure 3**).

The skull of *Pappochelys* is known from various disarticulated elements, some of which, based on size and the unfused nature of the scapula-coracoid, are from subadults (Schoch & Sues 2015, 2017). Its temporal fenestrae are slightly larger than in the adult of *Eunotosaurus* but are still

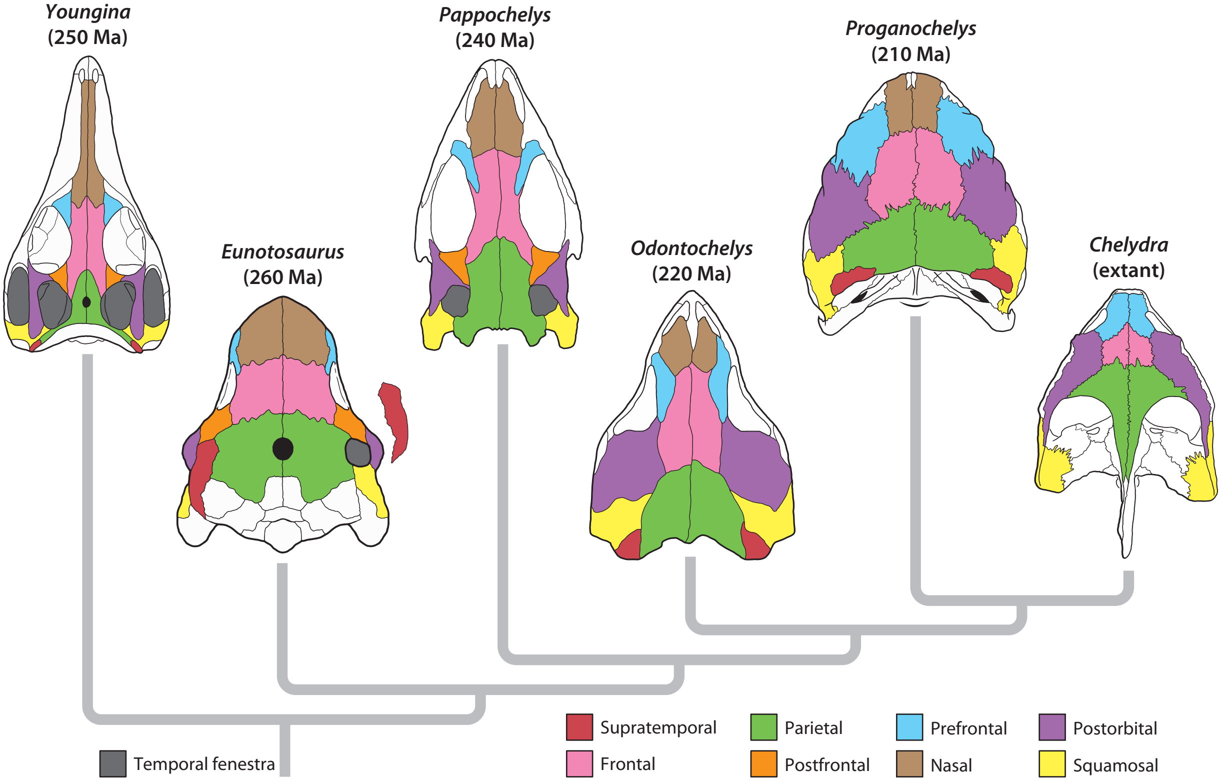


Figure 4

Evolutionary origin of the turtle skull based on recent fossil discoveries from the turtle stem lineage. Both *Eunotosaurus* and *Pappochelys* have diapsid skulls, with small upper (*gray*) and open lower fenestrae. *Eunotosaurus* illustration shows the right supratemporal bone removed to reveal underlying fenestra. *Odontochelys* (and likely *Eorhynchochelys*) exhibit the anapsid condition found in all crown-ward turtles. Modern turtles modify this anapsid condition through a wide degree of emargination to the lateral cheek region and posterodorsal skull roof. All drawings are dorsal views. Images adapted with permission from Gaffney (1990), Bever et al. (2015), and Schoch & Sues (2017).

apomorphically small relative to classic diapsid forms (e.g., *Sphenodon*, *Youngina*) (**Figure 4**). The size disparity may reflect the skeletal immaturity of the *Pappochelys* specimens or the nonlinear nature of the turtle stem with regard to fenestral closure (Bever et al. 2015, 2016).

6.3. Between *Pappochelys* and *Eorhynchochelys* (240–228 Ma)

A broadening of the neural processes of the dorsal vertebrae in *Eorhynchochelys* (Li et al. 2018) was initiated during this interval. There is little descriptive embryological and no directed experimental work on neural formation, but it may be induced by a penetration of the dorsal dermis by the vertebral neural processes (similar to the biphasic ossification of the costals) (Scheyer et al. 2008). Ontogenetically, the neurals ossify after the costals and plastral elements (Sheil 2005, Sheil & Greenbaum 2005, Smith-Paredes et al. 2020). The ontogenetic and stratigraphic lag between neural and costal formation indicates the two features enjoyed some measure of early independence. This interval was witness to the full axial remodeling of the ribs, as indicated by the short, straight dorsal ribs of *Eorhynchochelys* (Li et al. 2018) (**Figure 3**).

The temporal region completes its secondary covering and is fully anapsid (**Figure 4**). The anterior-most marginal teeth of *Eorhynchochelys* are lost, producing a partially edentulous beak

(Li et al. 2018). Tree topology necessitates that this tooth reduction is nonhomologous (secondary homology) with the complete loss of marginal teeth in *Proganochelys* and more crown-ward forms. It may also, however, reflect the acquisition of a homologous, but still variable, developmental mechanism for tooth loss. If so, a parallel, stepwise pattern of tooth loss in the more crown-ward part of the tree might be expected.

6.4. Between *Eorhynchochelys* and *Odontochelys* (228–220 Ma)

This interval witnessed a further expansion of the neurals, a completion of the plastron, and the first appearance of scutes (Li et al. 2008, Lyson et al. 2014). Here, the strap-like clavicles and interclavicles found in the primitive tetrapod shoulder girdle and retained in *Eunotosaurus*, *Pappochelys*, and *Eorhynchochelys* become fully integrated into the anterior portion of the plastron as the epiplastra and entoplastron, respectively (**Figures 2** and **3**). The broadened gastralia ossify to such a degree that they meet one another laterally and medially to complete the bony plastron. Keratinous scutes appear on the plastron and might presume that some form of dorsal keratinization was also underway given that no known turtle (crown or stem) has plastral but not carapacial scutes (or vice versa) (Lyson et al. 2014).

6.5. Between *Odontochelys* and *Proganochelys* (and Other Rhaetian/Norian Late Triassic Forms)

This interval is populated with the first appearance of a completed carapacial margin formed of membrane bone (**Figure 3**). This bilateral series of peripherals and the midline pygals ossify late in extant turtles (Sheil 2005, Sheil & Greenbaum 2005, Lima et al. 2011) and are considered modified osteoderms unique to turtles (Szczygielski & Sulej 2019) (**Figure 2**). It should be noted that the shells of *Proterochersis* spp., which are the oldest fully formed shells known (Middle Norian) (Szczygielski & Sulej 2019), deviate somewhat from the constructional pattern described here. Instead of a clear pygal(s) and posterior peripherals, these forms express a mosaic of posterior ossifications that may not be ancestral to crown turtles but rather reflect an autapomorphy for this particular group (Szczygielski & Sulej 2019). In addition, this interval is marked by the flabellate arrangement of the ribs and their anterior shift to articulate between the vertebrae, rather than along the body of the vertebrae (**Figure 3**).

The carapacial margin is completed anteriorly with the appearance of the nuchal whose developmental and evolutionary origins are more complicated than those of earlier stem turtles (**Figure 3**). This midline element is hypothesized to represent the fusion of the paired cleithra—neural crest-derived, dorsal elements of the primitive tetrapod shoulder girdle (Vallén 1942, Lyson et al. 2013b). Support for this conclusion is drawn from a number of observations made within the crown, including the nuchal's conserved connectivity as a point of origin for the dorsal fibers of the cucullaris muscle group (i.e., M. trapezius) (Lyson et al. 2013b), its developmental origin from paired anlage (Sánchez-Villagra et al. 2009, Smith-Paredes et al. 2020), and the positive staining of these anlage for multiple neural crest cell markers (Clark et al. 2001, Gilbert et al. 2007). Supporting evidence from the fossil record includes its conserved topology dorsal to the scapulae. A slender cleithrum is present in its plesiomorphic orientation in *Eunotosaurus* (Lyson et al. 2013b). The presence and similar orientation for the cleithrum is hypothesized for both *Pappochelys* and *Eorhynchochelys*. These elements likely moved into an even more dorsal position, with a derived, horizontal orientation, prior to their midline fusion (following their ontogenetic progression), and this condition may characterize the *Odontochelys* grade of evolution. The paired elements are integrated with the peripherals and costals along the perimeter of the shell by the Middle Norian (late Triassic), in the oldest known fully formed turtle shell (*Proterochersis robusta*) (Szczygielski &

Sulej 2019). The fusion of the paired cleithra into the nuchal and the final separation of the turtle cleithra from the clavicles/interclavicle, which is unique among tetrapods, occurs crown-ward of *Proganochelys*. Here, the dorsal process of the clavicles is reduced, as in the middle Jurassic stem turtle *Kayentachelys aprix*, and finally lost (Joyce 2007, Lyson et al. 2013b). The vertical scapula is more rod-like, and the acromion process of the scapula lengthens, giving the shoulder girdle its characteristic tripartite morphology (Joyce et al. 2013).

Under this hypothesis, the entire anterior end of the turtle shell is formed completely by the neural crest-derived elements of the primitive tetrapod shoulder girdle (**Figure 2**). The chondral elements of that girdle, the scapula and coracoid, are maintained in turtles with their plesiomorphic connectivity. The split nature of these elements in turtles represents a reorganization of the functionally integrated shoulder girdle and is a foundational component of the turtle shell and thus the modern turtle body plan (Lyson et al. 2013b).

This area of the tree is marked by surprisingly few changes in the skull that are especially noteworthy. The marginal teeth are lost, as is the transverse flange of the pterygoid. Other features expressed in the modern turtle skull all transform in a more crown-ward position; a few examples include loss of palatal teeth, loss of the supratemporal, loss of the lacrimal bone and duct, loss of the basicranial joint, a wide range of upper temporal and cheek emargination morphologies, the derived system for adducting the lower jaw, and the derived retraction system for retracting the head (**Figure 4**). It is important to note that although the derived head-retraction mechanisms of the crown are lacking in *Proganochelys*-grade turtles, these stem forms were able to protect their heads to some degree by tucking them laterally under the carapacial margin (Werneburg et al. 2015b).

7. FUNCTIONAL MORPHOLOGY AND THE PALEOECOLOGY OF TURTLE ORIGINS

As mentioned above (Section 3) the dorsal ribs and hypaxial trunk muscles of most amniotes work together in the shared responsibility of stabilizing the trunk against the torsional forces generated during locomotion and facilitating the volumetric changes necessary to ventilate the lungs (Carrier 1987). These responsibilities in turtles are anatomically partitioned—liberating both sets of structures from the constraints of serving a second functional role and in turn promoting specialization (Mitchell & Morehouse 1863, Gans & Hughes 1967, Lyson et al. 2014). The freeing of the ribs from their plesiomorphic role in lung ventilation permitted them to become distinctively broad and increasingly effective at stiffening the trunk. The freeing of the hypaxial trunk muscles from any meaningful supportive role resulted in the complete loss of the intercostals and a dramatic rearrangement of the abdominal muscles into an elongate sling (**Figure 1**), one highly specialized for compressing the lungs against the deep surface of the carapace. Such an evolutionary scenario is viable only if the division of function and derived breathing mechanism were already in place when the ribs lost their ability to effectively expand and contract. The anatomy and histology of *Eunotosaurus* confirms these changes are indeed some of the earliest apomorphies in the turtle body plan (well within the Paleozoic and at least 50 Ma before the oldest fully formed shell) (Lyson et al. 2014) (**Figure 3**).

This raises the question, however, of what evolutionary pressures might have promoted these foundational changes. The protective function (Zangerl 1969, Jackson 2011) conferred by the shell in extant turtles fails to adequately explain the initial broadening of the ribs as seen in the earliest partially shelled stem turtles *Eunotosaurus*, *Pappochelys*, *Eorhynchochelys*, and *Odontochelys*. The head, neck, and whatever epaxial musculature was still present in these animals would have remained unprotected, as it is in extant mammals with broadened ribs (Jenkins 1970). Not until *Eorhynchochelys* do we find expanded neural spines with limited protective value for these muscles

(Li et al. 2018). In addition, osteoderms are a much less costly strategy for external protection. They do not constrain breathing or locomotion (Jenkins 1970) and are prominent features of numerous amniote lineages—from pareiasaurs to anklyosaurian dinosaurs, from crocodylians to armadillos (Hill 2005).

The increasing rigidity of a body wall characterized by broadened ribs and reduced numbers of segments (vertebrae and ribs) certainly affected the ability of early stem turtles to bend their trunk laterally as a means to increase stride length and speed (as seen in other saurians with a sprawling gait) (Sumida & Modesto 2001, Lyson et al. 2016). For this specialized morphology to have evolved via natural selection, with its associated shortened stride length and decreased speed, an adaptive advantage that outweighs these costs was required. That advantage may be the increased power that a stiffened body wall conveys to the limbs during forelimb digging (Jenkins 1970, Lyson et al. 2016). Here the broadened ribs found in the earliest stem turtles *Eunotosaurus* and *Pappochelys* provided a stable base on which to operate a powerful forelimb digging mechanism (Lyson et al. 2016, Schoch et al. 2019). The functional advantages conferred by broadened ribs thus provided the initial impetus for the earliest history of the shelled turtle body plan (Lyson et al. 2016). Modifications to the thoracic cavity and early origin of the shell thus appear to have a terrestrial origin, supported by the fact that the earliest stem turtles, *Eunotosaurus* and *Pappochelys*, are found in fully terrestrial environments (Lyson et al. 2013a, 2016; Schoch & Sues 2015, 2017; Schoch et al. 2019) (**Figure 3**).

Adaptations related to a powerful shoulder and forelimb digging overlap with those for forelimb-powered swimming, as both activities use the forelimb to propel the body forward by the displacement of surrounding mediums (soil versus water), and may have helped facilitate the movement of early stem turtles into aquatic environments (Lyson et al. 2016). The crown-ward stem turtles *Eorhynchochelys* and *Odontochelys* both have forelimbs that are larger than their hindlimbs, are found in marine environments, and are inferred as aquatic animals that inhabited near shore marine or lagoonal environments (Li et al. 2008, 2018; Rieppel 2017). Interestingly, the first appearance of a full plastron appears in aquatic environments, suggesting it may have arisen as an adaptation for swimming, acting as a ballast (Rieppel 2017) (**Figure 3**).

Unique developmental histories and staggered appearances in the fossil record for the carapace and plastron support the idea that different evolutionary pressures are responsible for their origins. Here, broadened ribs and a stiffened body wall that form the base of a powerful forelimb digging mechanism in a terrestrial environment provide the initial evolutionary pressure in the earliest origins of the carapace. Once turtles moved into an aquatic environment, adaptations related to buoyancy control and diving may have accelerated the evolution of those developmental pathways responsible for constructing the plastron. Finally, the appearance of neomorphic osteoderms along the perimeter and the first appearance of a full shell occur in taxa (*Proterochersis* spp., *Proganochelys*, *Palaeochersis*) that are found, and have adaptations for living, in terrestrial environments (Gaffney 1990; Joyce & Gauthier 2004; Scheyer & Sander 2007; Sterli et al. 2007; Szczygielski & Sulej 2016, 2019; Lautenschlager et al. 2018) and more likely arose for protection as in other osteoderm-laden taxa. Under this scenario, the initial two steps (broadened ribs and plastron) are regarded as exaptations, whereas the last step confers to the shell the full extent of its modern protective function.

SUMMARY POINTS

1. The past decade witnessed a bounty of fossil discoveries that provide unprecedented insight into the identity, sequence, and timing of the structural changes constituting the

long-enigmatic body plan of modern turtles. This period of discovery was initiated by the recovery of the late Triassic *Odontochelys semitestacea*, whose T-shaped ribs and lack of osteoderms served as an important guide for what morphologies could be expected in the deeper reaches of the turtle stem lineage.

2. An important example of this sequence is the re-examination of the middle Permian reptile *Eunotosaurus africanus*, whose unusual morphologies can now be recognized as key early features in the evolutionary construction of the turtle body plan.
3. Insights from the fossil record can now be integrated with critical developmental data from the turtle crown clade to articulate a temporally constrained evolutionary and morphogenetic model for the origin of the turtle body plan.
4. This integrated model demonstrates a stark parallelism between the phylogenetic and ontogenetic acquisition of many turtle apomorphies.
5. The origin of the shelled body plan appears grounded in a division of labor between the ribs and abdominal musculature that resulted in a stiffened trunk and novel mechanism for ventilating the lungs.
6. These foundational changes may well be related to an initial fossorial ecology, whose specialized morphologies can also be employed for increased efficiency in swimming and may explain the seeming ease with which turtle lineages can move back and forth between the land and water.
7. The fossil record of stem turtles now includes direct evidence of a diapsid skull (*Eunotosaurus* and *Pappochelys*), effectively ending the long debate of whether turtles arose from an early, anapsid amniote lineage.
8. Evolutionary studies are greatly facilitated by the integration of developmental, physiological, and paleontological perspectives. Together, these can give new insights into the mechanisms whereby new structures are formed.

FUTURE ISSUES

1. Recent fossil discoveries provide long-awaited and much-needed resolution to the deep history of turtles but also highlight where further discoveries are most needed, two examples being the stratigraphic space on either side of the Permian–Triassic mass extinction event and the tree deep to *Eunotosaurus*.
2. The search for even earlier stem turtles is hindered by the phylogenetic reality that as a stem lineage is sampled increasingly close to its basal node, relevant apomorphies will be progressively lost (making these fossils increasingly difficult to accurately diagnose).
3. Earlier stem lepidosaur, archosaur, and turtle fossils would also be increasingly likely to retain features informing the enigmatic phylogenetic position of turtles among reptiles, potentially bringing consilience to the phylogenetic incongruence that still exists between morphological and molecular data sets.
4. The largest morphologic obstacle to phylogenetic consilience may no longer be the earliest stem history of turtles but rather the still-problematic early history of the archosaur and especially the lepidosaur stem lineages.

5. The consistent turtle-archosaur clade recovered by multigene and now genomic analyses constitutes strong evidence, but these matrices still need critical evaluation to ensure that genes of inappropriate evolutionary rates or the misapplication of nonstationary models to sequences with dynamic histories are not conveying a false sense of phylogenetic stability (e.g., Hsiang 2015).
6. The inductive relationship between the carapacial ridge, the axial remodeling of the ribs, and the flabellate patterning of the ribs needs resolution. It may be that the disparate signals based on hard- and soft-shelled cryptodires are both correct and that parallel studies of pleurodires are needed to resolve which condition is ancestral and which is derived for the turtle crown.
7. Full integration of the fossil record with developmental data requires clear correlations between developmental interactions and morphologic expression; however, these morphogenetic relationships must also be interpreted with the recognition that they too can evolve and thus differ to some extent between stem and crown.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

We thank our many collaborators for their important contributions and wealth of fruitful discussions. We extend special thanks to our South African colleagues and their institutions who made much of this work possible. We thank G. Hunt and S. Gilbert for reviewing earlier drafts of our manuscript. We thank A. Atuchin, B. Lyons (Stroma Studios), and E. Schachner for the artwork used in **Figures 1** and **3**. This material is based upon work supported by the National Science Foundation under grant NSF-DEB-1947025 to G.S.B. and T.R.L.

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RELATED RESOURCES LIST:

1. Evolutionary Origin of the Turtle Shell: **https://www.youtube.com/watch?v=G6HvmOyKYRo**. A 7-minute lecture by Dr. Tyler Lyson as part of the Smithsonian Institution's National Museum of Natural History *Lightning Talks*
2. Evolution of the Turtle Shell (Illustrated): **https://www.youtube.com/watch?v=NphNApmSZ0U**. Includes illustrations of fossil taxa, based on developmental and fossil data
3. Evolution of the Turtle Shell: **https://www.youtube.com/watch?v=qIOPDysP74g**. Based on developmental and fossil data
4. Evolution of the Turtle Shoulder Girdle: **https://www.youtube.com/watch?v=fHVlEUgF_nw**. Based on developmental and fossil data
5. How Turtle Shells Evolved. . .Twice: **https://www.ted.com/talks/judy_cebra_thomas_how_turtle_shells_evolved_twice?language=en**. TED-Ed talk
6. How the Turtle Got Its Shell: **https://www.youtube.com/watch?v=fLjXIFvafSE**. *PBS Eons*

Annual Review of
Ecology, Evolution,
and Systematics

Volume 51, 2020

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