



REVIEW ARTICLE

THE ORIGIN OF THE TURTLE BODY PLAN:
EVIDENCE FROM FOSSILS AND EMBRYOSby RAINER R. SCHOCH¹  and HANS-DIETER SUES² ¹Staatliches Museum für Naturkunde, Rosenstein 1, D-70191, Stuttgart, Germany; rainer.schoch@smns-bw.de²Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, DC 20560, USA; sues@si.edu

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Abstract: The origin of the unique body plan of turtles has long been one of the most intriguing mysteries in evolutionary morphology. Discoveries of several new stem-turtles, together with insights from recent studies on the development of the shell in extant turtles, have provided crucial new information concerning this subject. It is now possible to develop a comprehensive scenario for the sequence of evolutionary changes leading to the formation of the turtle body

plan within a phylogenetic framework and evaluate it in light of the ontogenetic development of the shell in extant turtles. The fossil record demonstrates that the evolution of the turtle shell took place over millions of years and involved a number of steps.

Key words: turtle, carapace, plastron, development, phylogeny.

TURTLES are unique among known extant and extinct tetrapods, including other forms with armour formed by bony plates (e.g. armadillos), in their possession of a bony shell that incorporates much of the vertebral column and encases the trunk (Zangerl 1969; Fig. 1). This shell consists of a dorsal carapace and a ventral plastron, which are typically linked by a bony bridge on either side. It is open anteriorly for the head, neck and forelimbs, and posteriorly for the hind limbs and tail. The carapace and plastron each consist of typically suturally interconnected bony plates, which bear keratinous scutes in most turtles. In derived-stem and crown turtles the scapula lies inside the carapace, which is partially formed by the ribs, unlike the condition in all other tetrapods where the scapula lies outside the rib cage.

A midline row of plates of the carapace (neurals) is firmly attached to the underlying apices of the neural spines of the dorsal vertebrae. Most of the carapace is formed by costal plates, which incorporate the trunk ribs (Fig. 2) and extend on either side of the neural series.

Joyce *et al.* (2004) cited the presence of a complete bony shell (using the green turtle, *Chelonia mydas*, as a specifier) as the key diagnostic feature for the clade Testudinata (from Latin *testudo*, turtle), which includes crown-group turtles (Testudines) and several stem-turtles. All known testudinatans lack marginal teeth in the upper and lower jaws. Joyce *et al.* (2004) restricted the use of the

name Testudines to the clade comprising the most recent common ancestor of *Chelonia mydas* and *Chelus fimbriatus* (matamata) and all descendants of that ancestor.

The origin of the turtle body plan has long been one of most intriguing mysteries in evolutionary morphology (Lee 1993, 1996; Rieppel & Reisz 1999; Rieppel 2000, 2013, 2017; Lyson *et al.* 2010, 2013, 2016; Carroll 2013; Joyce 2015; Schoch & Sues 2015, 2018). As various authors (Rieppel 2017) have noted, the evolution of the turtle body plan was difficult to understand as the result of stepwise, gradual acquisition of features, each of which would have to confer some adaptive value.

Until recently, the geologically oldest undisputed stem-turtles dated from the Late Triassic (Norian; c. 205–215 Ma). They include *Proganochelys quenstedti*, *Proterochersis robusta* and *Keuperotesta limendorsa* from Germany (Baur 1887; Fraas 1913; Jaekel 1913–14, 1915–16; Gaffney 1985, 1990; Szczygielski & Sulej 2016, 2019), *Proterochersis porebensis* from Poland (Szczygielski & Sulej 2016) and *Palaeochersis talampayensis* from Argentina (Rougier *et al.* 1995; Sterli *et al.* 2007). These stem-turtles already have complete bony shells and thus shed little light on the early evolution of the turtle body plan. Hugall *et al.* (2007) hypothesized that turtles had probably already diverged from other reptilian lineages during the Permian Period.

The body plan of shelled turtles is so distinctive that some researchers have wondered whether it would ever be

possible to identify a turtle precursor in the fossil record. For example, Carroll (1988, p. 210) wrote that the early development of the carapace in extant turtles ‘does not provide any hint as to the way in which this pattern evolved phylogenetically.’ During the last decade, several new stem-turtle taxa have been discovered and a putative stem-turtle from the Permian has been re-evaluated. Together with modern studies on the ontogenetic development of the shell in extant turtles, they elucidate the evolutionary changes that led to the turtle body plan.

We present here a review of these diverse lines of evidence and their bearing on the origin and early evolution of the turtle body plan. Specifically, we consider four interconnected issues: (1) what are the closest relatives of turtles among *extant* reptiles: lepidosaurs (squamates and rhynchocephalians) or archosaurs (crocodylans and birds); (2) what are the closest relatives of turtles among *extinct* amniotes; (3) how does the bony shell *develop* in extant turtles; and (4) how did the bony shell *evolve* in stem-turtles. The first two issues, relating to the phylogenetic position of turtles, can be addressed through phylogenetic analysis. The third issue, the morphological transformation leading to a complete turtle shell based on the fossil record, involves the development of an evolutionary scenario within the historical framework provided by phylogenetic analysis (transformational approach; Rieppel & Kearney 2007). Finally, this scenario (Figs 3, 4) can be compared to what is known about the formation of individual features during ontogenetic development of the shell in extant turtles (generative approach; Rieppel & Kearney 2007).

This review draws on anatomical data for *Eunotosaurus* (Cox 1969; Lyson *et al.* 2013, 2014, 2016; Bever *et al.* 2015; pers. obs.), *Eorhynchochelys* (Li *et al.* 2018), *Odontochelys* (Li *et al.* 2008), *Pappochelys* (Schoch & Sues 2015, 2018), *Proganochelys* (Gaffney 1990; pers. obs.) and *Proterochersis* (Szczygielski & Sulej 2016, 2019; pers. obs.) Absolute ages for stages are based on the International Chronostratigraphic Chart v. 2018/08 (Cohen *et al.* 2013, updated)

PHYLOGENETIC POSITION OF TURTLES

The phylogenetic relationships of Testudinata to other tetrapods have long been contentious. Turtles are usually considered the sister-taxon of Diapsida, which are represented today by lepidosaurs (squamates and the tuatara)

and archosaurs (crocodylans and birds) (Werneburg & Sánchez-Villagra 2009).

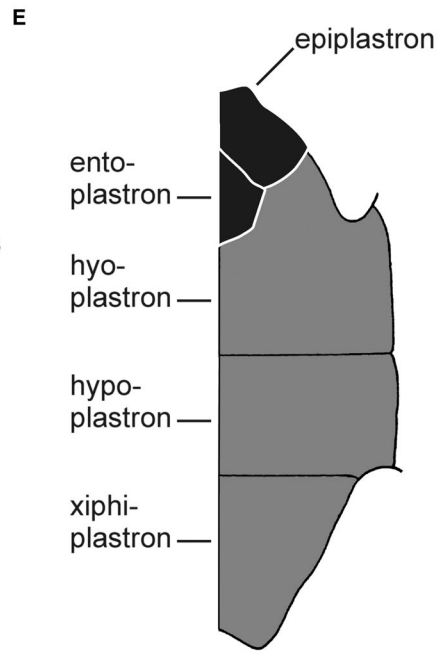
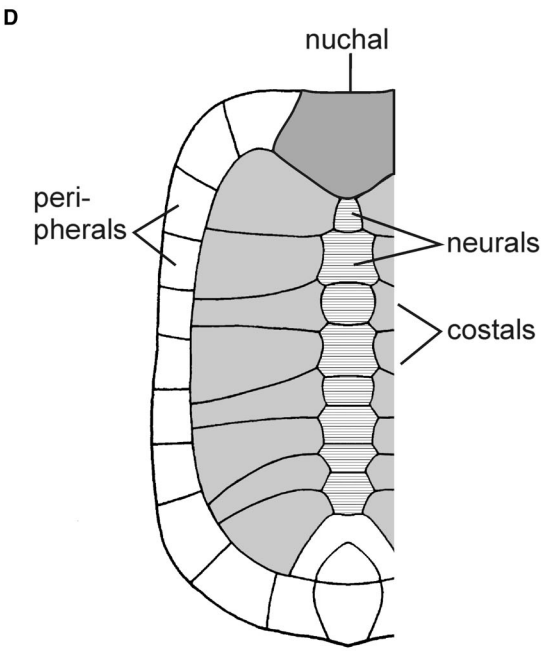
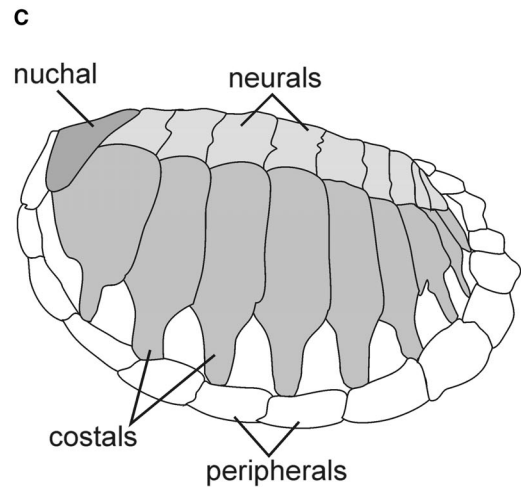
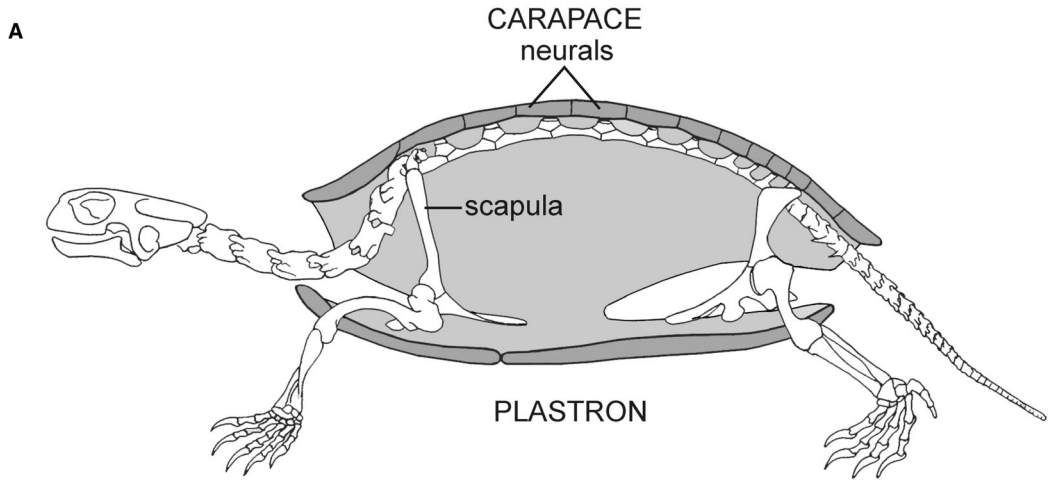
Since the pioneering work by Hedges & Poling (1999) and Zardoya & Meyer (1998, 2001) molecular-based analyses have recovered turtles either as the sister-group of archosaurs or even nested among archosaurs. An analysis using a large dataset for the absence or presence of micro RNAs (miRNA) supports a relationship between turtles and archosaurs (Field *et al.* 2014). This is consistent with other studies that were based on mitochondrial and nuclear DNA and recovered turtles with archosaurs (Iwabe *et al.* 2005; Tzika *et al.* 2011). Chiari *et al.* (2012) published an analysis of DNA sequence data from 248 genes in 14 amniote taxa and supported grouping turtles with archosaurs. A study of over 1100 ultraconserved elements and the flanking DNA sequences in the genomes of a range of reptilian taxa also supported this hypothesis (Crawford *et al.* 2012).

Most analyses of sequence data treat individual nucleotide sites as characters. Lu *et al.* (2013) attempted a different approach by using genes as characters, each with multiple states. Their study was based on a dataset comprising 4584 orthologous genes. (‘Orthologous’ denotes homologous genes that diverged after a speciation event. Orthologous genes usually have a function similar to that of the ancestral gene from which they evolved.) The authors unexpectedly generated three conflicting hypotheses: turtles were found with archosaurs, with lepidosaurs, or even as the sister-group to both. None of these results had particularly strong statistical support. Lu *et al.* (2013) interpreted this as possible evidence that turtles, lepidosaurs and archosaurs rapidly diverged from each other early and then diversified.

Many biologists consider molecular data inherently superior to morphological information for reconstructing phylogenetic relationships. In a large dataset, however, data for nucleotide sites (or amino-acid residues) can be heterogeneous. Another important issue, long-branch attraction, emerges when evolutionary divergence between lineages occurred far back in time. If some of these lineages have much greater temporal ranges than others, it is possible that these lineages evolved the same nucleotide at the same site because there are only four possible nucleotides for substitution.

Molecular studies on extant amniote tetrapods sample only a small set of tetrapod lineages: mammals, turtles, lepidosaurs, crocodylans and birds. All of these groups diversified within the last 100 million years but are linked

FIG. 1. Features of the turtle shell. A, sagittal section through the skeleton of a pod turtle (*Emys orbicularis*) (modified from Bojanus 1819–21). B–C, bony carapace of *Chelydra serpentina* in: B, oblique dorsolateral view; C, as an outline drawing with different bony components indicated by different shadings. D, carapace (in dorsal view); E, plastron (in ventral view); of a tortoise (*Testudo*) with different patterns indicating the ontogenetically distinct bony elements. Light grey, costals; medium grey, nuchals; dark grey, posterior plastral bones; black, entoplastron and epiplastra; line pattern, neurals.



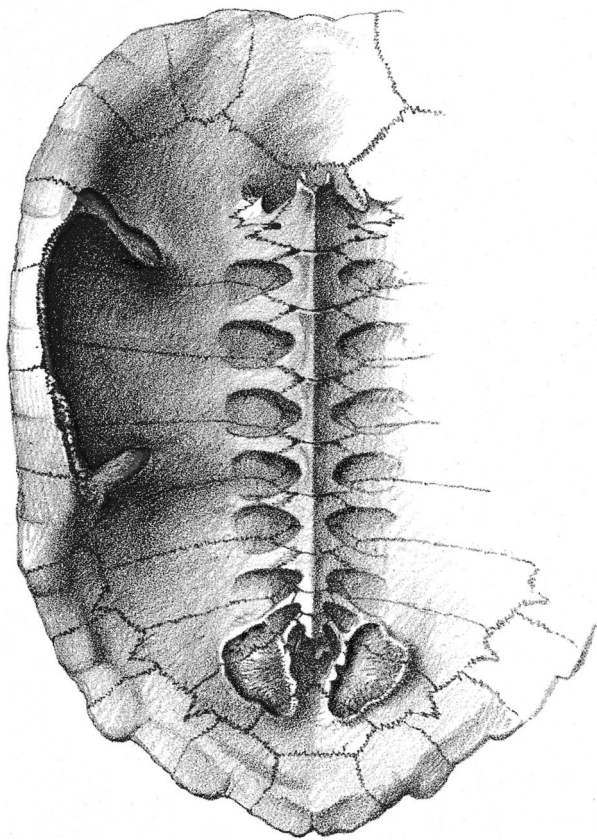


FIG. 2. Full integration of the dorsal axial skeleton into the carapace of a matamata (*Chelus fimbriatus*). Carapace shown in ventral (visceral) view. The bony ridge between the carapace and plastron has been cut. The paired posterior facets are for the attachment of the pelvic girdle. Digitally modified from an illustration in Rüttimeyer (1873).

to each other by lineages that ranged over hundreds of millions of years (Wang *et al.* 2013).

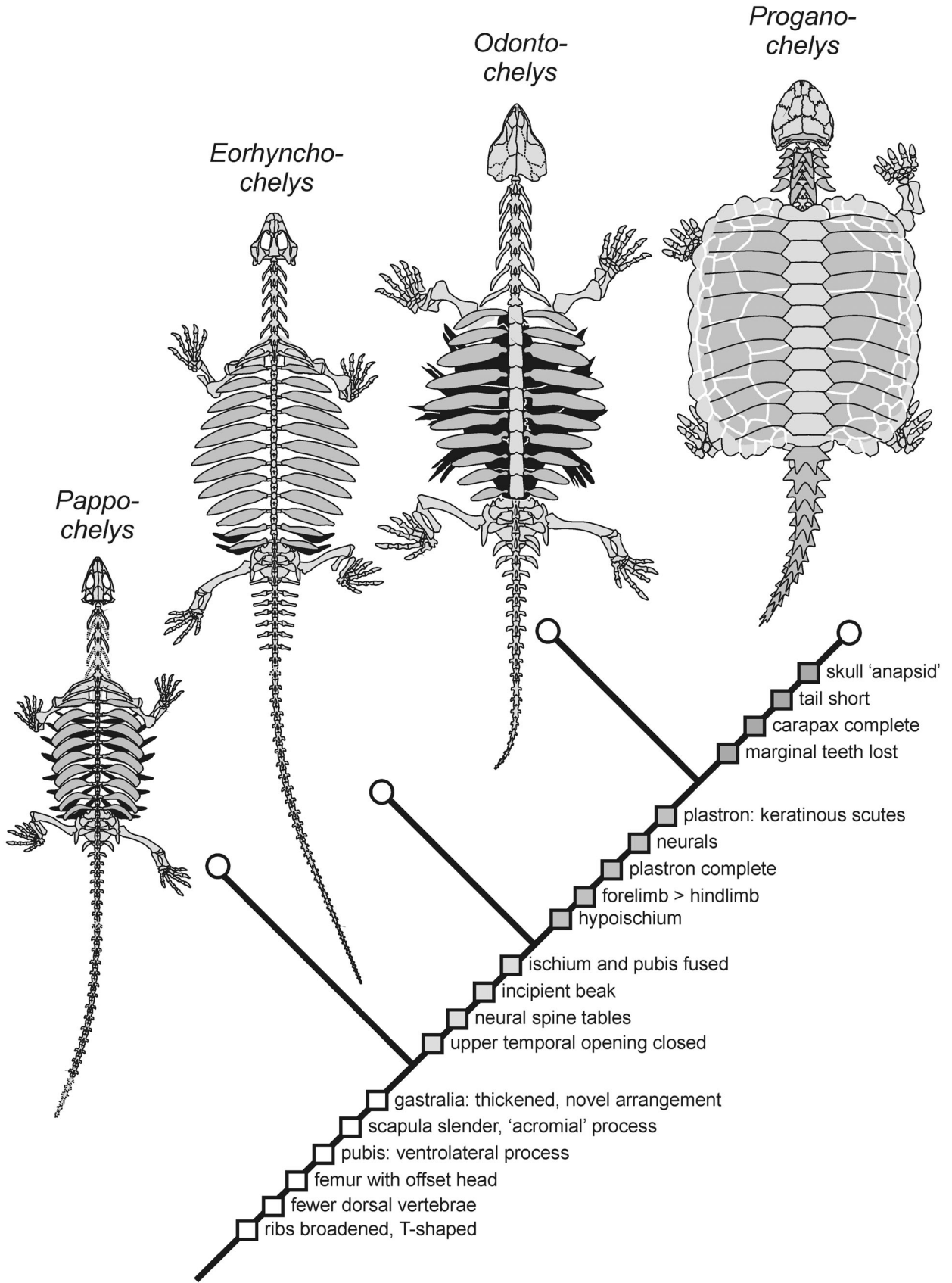
Philippe *et al.* (2011) noted that molecular methods for reconstructing phylogenies assume to at least some degree that rates of molecular change are broadly comparable across lineages. However, among extant tetrapods, crocodylians and turtles show the slowest rates of molecular change reported and snakes some of the fastest (Hugall *et al.* 2007). Averaging rates of change across lineages can pull slowly evolving groups towards one another and pushes rapidly evolving groups towards the base of the

phylogenetic tree. It is still difficult to reconstruct the deep history of evolutionary lineages using molecular methods but, in recent years, researchers have formulated probabilistic inference methods that are more robust to long-branch attraction than parsimony approaches. Variable-rates models in a Bayesian framework also hold promise for overcoming some limitations of traditional whole-tree-rate methods.

Surprisingly, there is scant morphological support for a sister-group relationship between turtles and archosaurs (Rieppel 2000). Hill (2005) noted that turtles and lepidosaurs shared several derived skeletal features such as the presence of a large opening (thyroid fenestra) between the ischium and pubis and the presence of a 'hooked' fifth metatarsal. However, the former feature is also present in various archosauromorph reptiles (Pritchard & Sues 2019) and the ontogenetic development of the latter bone (which involves the fifth distal tarsal) differs in detail not only between squamates and turtles but even among turtles (Joyce *et al.* 2013a). In a detailed assessment of the features cited in support of a close relationship between (extant) turtles and archosaurs, Rieppel (2000) only accepted the connection of the nictitating membrane of the eye to a pyramidalis muscle (derived from the retractor bulbi muscle) and the shift of the origin of the subclavian arteries from the aortic to the carotid arch as potential synapomorphies. Bhullar & Bever (2009) listed the presence of an ossified laterosphenoid element in the braincase and the presence of a row or rows of mid-dorsal armour elements as shared derived features for turtles and archosauriform reptiles. The homology of the laterosphenoid in both clades is contentious and the latter character is invalidated by the fact that the mid-dorsal plates in turtles are not dermal in origin, unlike those in crocodylians (Vickaryous & Hall 2008).

Expanding the consideration of turtle relationships to extinct clades of amniote tetrapods did not initially resolve this situation. Phylogenetic analyses by deBraga & Rieppel (1997) and Rieppel & Reisz (1999) recovered turtles as the sister-group to Sauropterygia, a major clade of Mesozoic marine diapsid reptiles, and, in turn, this sister-pair as most closely related to lepidosaurs and their close relatives (Lepidosauriformes). Further increasing the scope of the character–taxon matrix, Bever *et al.* (2015) and Schoch & Sues (2018) supported the phylogenetic

FIG. 3. Morphological transformation series for Triassic stem-turtles leading up to the presence of a fully developed bony shell in *Proganochelys*. Modified from Schoch & Sues (2015). Note that the scute arrangement on the carapace of *Proganochelys* is shown because the configuration of the bony components is not evident on any of the known specimens; the inferred extent of the neurals and costals is highlighted. If included, the equivocally positioned taxon *Eunotosaurus* would be placed at the base of the tree and change the character optimization of the dorsal vertebral count, increasing it from from 9 to the autapomorphic 12 in *Eorhynchochelys*.



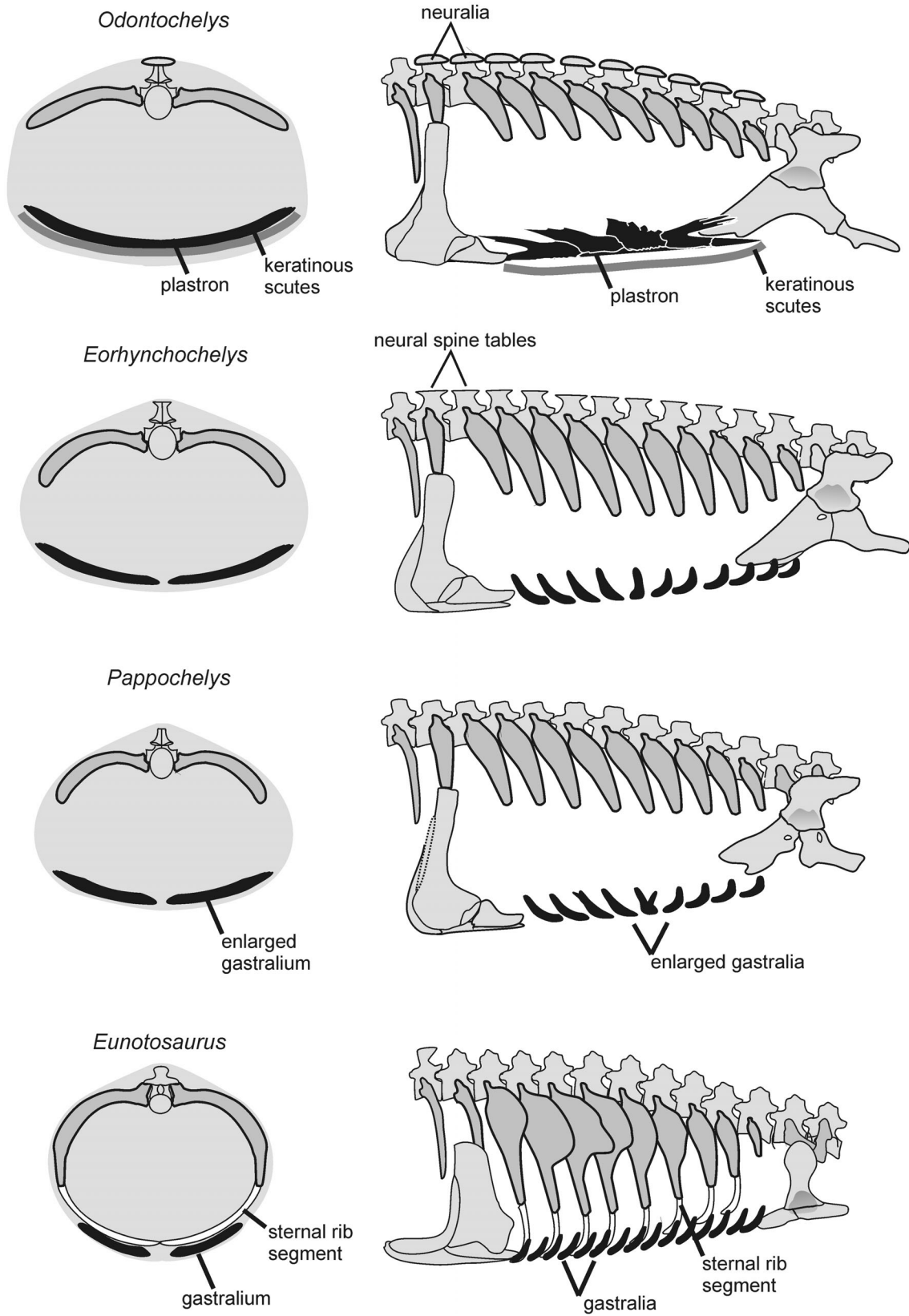


FIG. 4. Diagrams of early stages in the development of the shell in stem-turtles. For each taxon, a transverse section at mid-trunk (left) and lateral view of trunk skeleton (right) is shown.

position of turtles among diapsid reptiles but could not resolve their affinities more precisely.

The absence of temporal openings behind the orbit on either side of the cranium sets turtles apart among extant amniotes. Osborn (1903) used the different configuration of openings in the temporal region to divide Amniota into two major groups, Synapsida (mammals and their close relatives) with a single opening on each side of the cranium, and Diapsida (most reptiles and birds) with two openings on each side (although this condition is frequently greatly modified among many diapsids such as birds and snakes). A number of early reptiles (including various taxa now considered to be stem-diapsids) share with Testudinata the absence of temporal openings. Inexplicably, Osborn (1903) placed these groups among Synapsida even though they lacked the key diagnostic feature of this group. Williston (1917) proposed a third major group, Anapsida, for the reception of reptiles without temporal openings. He and later authors posited that the anapsid configuration of the temporal region represented the ancestral condition for amniotes and relegated turtles to a basal position relative to other reptiles. With a few minor modifications, the Osborn–Williston classification remained in general use until quite recently.

Goodrich (1916) already considered it likely that the absence of temporal openings in turtles represented a secondary condition. His hypothesis has received strong support from the discovery of the Middle Triassic stem-turtle *Pappochelys*, which has two clearly defined temporal openings on either side of the cranium (Schoch & Sues 2015, 2018). Werneburg (2015) suggested that the neck musculature possibly led to the loss of temporal fenestration in turtles. The tensile forces exerted by the neck muscles could have been more evenly distributed on the cranium without temporal regions than on a cranium with large temporal fenestrae and narrow bony bars bounding these openings.

THE FOSSIL RECORD OF EARLY STEM-TURTLES

In this section, we review the fossil record of early stem-turtles, proceeding from the putative Permian stem-turtle *Eunotosaurus* to various Triassic taxa that are increasingly more closely related to the crown-group Testudines (Joyce *et al.* 2004; Lyson *et al.* 2010; Joyce 2017; Schoch & Sues 2018). Phylogenetic analyses found *Eunotosaurus*, *Pappochelys*, *Eorhynchochelys* and *Odontochelys* as successive sister-taxa to Testudinata as defined by Joyce *et al.* (2004).

Eunotosaurus

Eunotosaurus africanus is an up to 30 cm long reptile from the middle Permian (Capitanian; c. 259–265 Ma)

Tapinocephalus Assemblage Zone of South Africa and probably correlative strata in Malawi. It has a proportionately small, short-snouted skull and a foreshortened, transversely broad trunk encased by anteroposteriorly broadened, slightly overlapping ribs. In his original description of *Eunotosaurus*, Seeley (1892) already compared the elongation of its dorsal vertebrae and its broad trunk ribs in to the corresponding features in turtles but hesitated to infer a close relationship. Watson (1914) first explicitly hypothesized *Eunotosaurus* as a turtle precursor. He cited the low number (nine) of dorsal vertebrae, the elongation of their centra, and especially the distinctive trunk ribs, which he compared to the broadened ribs in the embryos of extant turtles. Cox (1969) restudied all material then referred to *Eunotosaurus* and dismissed the skeletal similarities to turtles as ‘merely convergent.’ Gow (1997) reported additional specimens that provided important new anatomical data, especially on the skull. He hypothesized parareptilian affinities for *Eunotosaurus*. Later studies more specifically placed *Eunotosaurus* either in Millerettidae (Cisneros *et al.* 2004) or as the sister-taxon of that clade (Gow 1997; Tsuji & Müller 2009). Lyson *et al.* (2010, 2013, 2014, 2016) and Bever *et al.* (2015) restudied the skull and postcranial axial skeleton of *Eunotosaurus* using microCT scanning and histological analysis of postcranial bones.

The following apomorphies of Testudinata are present in *Eunotosaurus* and shared with *Pappochelys*, *Odontochelys* and *Proganochelys*:

1. Nine dorsal vertebrae. Apart from undisputed stem-turtles and crown-turtles, *Eunotosaurus* is the only reptile known to date with a comparable low number of dorsal vertebrae. (The number of dorsals in *Pappochelys* remains unknown.)
2. Centra of dorsal vertebrae more than twice as long as tall.
3. Trunk ribs broadened anteroposteriorly, with flange-like anterior and posterior extensions of the rib-shaft, which is T-shaped in transverse section.

In contrast to these shared derived characters in the postcranial axial skeleton, the cranial structure of *Eunotosaurus* differs considerably from that of other known Triassic stem-turtles as well as most diapsids. Although there is a large ventral emargination of the cheek that likely represents a lower temporal opening (Gow 1997), it is bordered posteriorly by the quadratojugal rather than the squamosal (Bever *et al.* 2015, fig. 2). This derived condition, in which squamosal and quadratojugal have changed positions, is elsewhere present only in some parareptiles such as owenettids (Reisz & Scott 2002; Cisneros *et al.* 2004; MacDougall & Reisz 2014). In *Eunotosaurus*, the squamosal is a strut rather than a four-rayed element as in *Pappochelys*, *Odontochelys* and most saurians, and the jugal is wedge-shaped, lacking the posterior (quadratojugal) process

present in many diapsids and stem-turtles (*Pappochelys*, *Eorhynchochelys*). Bever *et al.* (2015, 2016) reported upper temporal openings in a juvenile of *Eunotosaurus* and interpreted an irregular small gap between the parietal, postorbital and squamosal bones of the skull roof in an adult individual as the same opening. However, the opening is covered by a large supratemporal in the adult and closely resembles irregular gaps between bones in the temporal region of some growth stages of millerettid parareptiles (Gow 1972). In the palate, a large suborbital fenestra between the ectopterygoid and palatine characterizes all saurians, including turtles and their Triassic stem-taxa. In *Eunotosaurus*, these palatal elements are in broad contact, with the equivocal evidence of a tiny slit on the left side of the cranium, which was identified by Bever *et al.* (2015) as a suborbital fenestra.

To sum up, the skull of *Eunotosaurus*, as well as certain postcranial bones such as the ilium, more closely resemble those in parareptiles than those in stem-turtles or basal diapsids. Even if *Eunotosaurus* is found to be a stem-turtle, its cranial structure could not be considered ancestral to the turtle condition in many respects (temporal region, broad medial roof).

The phylogenetic analysis by Bever *et al.* (2015) found *Eunotosaurus* at the base of Pan-Testudines, the total clade comprising turtles and their stem-taxa (Joyce *et al.* 2004). In the analyses by Lyson *et al.* (2013) and Schoch & Sues (2015), Pan-Testudines was placed closest to sauropterygians and lepidosauromorphs. Later analyses by Bever *et al.* (2015) and Schoch & Sues (2018) recovered Pan-Testudines in an unresolved polytomy with other major clades of diapsid reptiles.

The uncertainty regarding the phylogenetic position of *Eunotosaurus* results from the still incomplete documentation of its skeletal structure and from possibly autapomorphic features such as the partially overlapping trunk ribs (Lyson *et al.* 2016). Even if it is ultimately found to be not closely related to turtles, *Eunotosaurus* provides a useful morphological model for the initial phase in the evolution of a stiffened and foreshortened trunk with ribs expanding into the dermis, a transformation that evidently occurred during the evolution of the turtle shell (Lyson *et al.* 2013, 2014; Joyce 2015).

Pappochelys

Pappochelys rosinae is a 25–30 cm long reptile from the upper Middle Triassic (Ladinian; *c.* 237–247 Ma) Erfurt Formation (Lettenkeuper) of Baden-Württemberg (Germany) (Schoch & Sues 2015, 2018). It is known from several partial skeletons and a number of isolated bones. *Pappochelys* shares various derived features with testudinans including:

1. Vomer anteriorly concave, framing large anterior fenestra and posterolaterally constricted, resulting in a medially expanded choana (as in *Proganochelys*).
2. Vomeres fused along the midline (shared with crown-group turtles but absent in *Proganochelys*).
3. Scapula tall and strut-like (as in *Odontochelys* and *Proganochelys*), with rounded acromial ‘process’ less prominently developed than in *Odontochelys* and more derived turtles.
4. Humerus with raised proximal head.
5. Reduced number of dorsal vertebrae. *Pappochelys* probably had eight to ten dorsal vertebrae, comparable to the condition in *Eunotosaurus* and in *Odontochelys* and more derived turtles.
6. Dorsal vertebral centra elongated. The centra are comparable in relative length to those of *Odontochelys*.
7. Synapophyses vertically aligned. The confluent rib facets (synapophyses) on the dorsal vertebrae are vertically aligned, probably restricting rib motion. This feature is shared by *Odontochelys* but differs from the anterodorsally inclined synapophyses in *Eunotosaurus* (Cox 1969).
8. Trunk ribs T-shaped in transverse section due to sheet-like extensions anterior and posterior to the rib-shaft, resulting in a slightly asymmetrical outline in dorsal view (shared with *Odontochelys*). Unlike in *Eunotosaurus*, the ribs do not imbricate.
9. Trunk ribs shorter and less strongly curved ventrolaterally than in basal amniotes and *Eunotosaurus*, but more so than in *Odontochelys* and more derived turtles.
10. Gastralia robust and arranged in pairs, one per vertebra and lacking a medial element. They are boomerang-shaped, slightly asymmetrical, and robust. Their distal ends lack facets for cartilaginous rib segments, unlike in *Eunotosaurus*. The external surfaces of the gastralia bear sculpturing composed of parallel grooves and ridges that terminate in bony spines distally.
11. Pubis with anteromedial process (also in *Odontochelys* and *Proganochelys*).
12. Pubis with distinct lateral process. This process contacted the plastron in *Odontochelys*, *Proganochelys* and more derived turtles; it presumably contacted the gastralia basket in *Pappochelys* anteriorly.

The diapsid configuration of the cranium of *Pappochelys* resembles the condition in saurians but differs from that in more basal diapsid reptiles such as *Petrolacosaurus* and *Youngina*. The tetradial configuration of the possible squamosal is derived relative to the condition in basal diapsids, as are its presumed contact with the quadratojugal, the shape of the jugal, and the absence of a supratemporal bone. These features are also inconsistent with previously hypothesized relationships between turtles and parareptiles (Lee 1993; Laurin & Reisz 1997) or between turtles and captorhinid reptiles (Gaffney &

Meylan 1988; Gauthier *et al.* 1988). As in *Eunotosaurus*, all jaw elements bear teeth. The following diapsid features are present in *Pappochelys*:

1. Squamosal tetra- or radiate, with long slender ventral process, rather than plate-like like the squamosal in Captorhinidae or *Petrolacosaurus*.
2. Parietal bounding anteroposteriorly short, oval upper temporal fenestra medially.
3. Suborbital fenestra well-developed.
4. Interclavicle cruciform, with large anterior process with rounded anterior margin (shared by several clades of diapsid reptiles).
5. Femur with distinct fossa between the tibial condyle and the crista tibiofemoralis (shared by turtles).
6. Iliac blade with a long posterior process and straight dorsal margin (as in *Odontochelys* and *Proganochelys*).
7. Metatarsal V distinctly hooked, with a robust medial process and a small lateral projection (although this feature has different ontogenetic histories in saurians and turtles; Joyce *et al.* 2013a).
8. Astragalus and calcaneum fused (as in pareiasaurian parareptiles, lepidosauromorph diapsids, some specimens of *Odontochelys*, and *Proganochelys*).

Various authors have interpreted gastralia as precursors of the more posterior plastral bones (Jaekel 1915; Goodrich 1930; Romer 1956; Zangerl 1969) but, until recently, there was little evidence to support this hypothesis. *Eunotosaurus* has pairs of slender gastralia lacking lateral and median elements (Lyson *et al.* 2013). The cuirass of robust gastralia in *Pappochelys* can be interpreted as structurally intermediate between the paired gastralia in *Eunotosaurus* and the fully formed bony plastron in *Odontochelys* and more derived turtles.

Eorhynchochelys

The stem-turtle, *Eorhynchochelys yuantouzhensis*, from the Upper Triassic (Carnian; *c.* 227–237 Ma) Wayao Member of the Falang Formation of Guizhou (China), differs from other Triassic stem-turtles in its much larger body size, attaining a total length of 1.8 m (Li *et al.* 2018). It resembles *Pappochelys* in the possession of a long tail, anteroposteriorly broadened but non-overlapping trunk ribs, the retention of gastralia, and the outline of the lower temporal fenestra. As in *Eunotosaurus* and *Pappochelys*, the maxilla and dentary bear small teeth. Presumably at least in part related to its much greater body size, *Eorhynchochelys* has proportionately more robust limb bones than *Pappochelys*, including a humerus with expanded articular ends. It lacks osteoderms on the limbs, neck, trunk and tail.

Eorhynchochelys shares some apomorphies with more derived turtles that are absent in *Eunotosaurus* and *Pappochelys*:

1. Premaxilla and anterior end of dentary edentulous, probably covered by a keratinous beak in life (as in derived-stem and crown turtles).
2. Upper temporal fenestra absent.
3. Neural arches of the trunk vertebrae with distinctly expanded apices.
4. Trunk ribs extending laterally with only slight ventral curvature.
5. Ischium with a posterior extension, resembling the structure where the ischium contacts the hypoischium in *Odontochelys* and more derived turtles.
6. Puboischiadic plate with the ischium and pubis firmly sutured together rather than loosely attached to each other as in *Pappochelys*.
7. Acromion on scapula more prominent than in *Pappochelys* but not as distinct as in *Odontochelys*.

The presence of 12 dorsal vertebrae in *Eorhynchochelys* differs from the condition in *Eunotosaurus*, *Odontochelys* and the fully-shelled Late Triassic stem-turtles, all of which have fewer than 10 dorsals. The number of dorsal vertebrae in *Pappochelys* cannot be established in the absence of articulated column but was probably between 8 and 10 (Schoch & Sues 2018). In addition to the absence of an upper temporal fenestra, derived features of the cranium of *Eorhynchochelys* include the fusion of the frontals, the proportionately short posterior region of the skull table, and the absence of a ventral process on the squamosal. The distinctly expanded apices of the dorsal neural spines possibly supported neural elements in life but these are not preserved in the only known specimen. An alternative interpretation of these expansions is that they served as points of attachment for well-developed epaxial muscles and ligaments between the neural spines.

The temporal region of the cranium of *Eorhynchochelys* resembles that of *Pappochelys* in the presence of a triradiate jugal with a short posterior process, a large, ventrally open lower temporal fenestra, and a triradiate postorbital. *Eorhynchochelys* also shares with *Pappochelys* dorsal ribs that terminate distally in gently tapered ends, unlike *Odontochelys*, which has ribs with blunt distal ends. As in *Eunotosaurus*, its trunk attains its greatest width at mid-length, whereas the trunk of *Pappochelys* appears to have been more or less parallel-sided. The pubis of *Eorhynchochelys* lacks the anterior (epipubic) process present in *Pappochelys* and more derived stem-turtles. Both *Pappochelys* and *Eorhynchochelys* lack an ossified hypoischium.

Odontochelys

Odontochelys semitestacea is also from the Upper Triassic (Carnian; *c.* 227–237 Ma) Wayao Member of the Falang Formation of Guizhou (China) but was recovered from a horizon about 7.5 m above the layer yielding

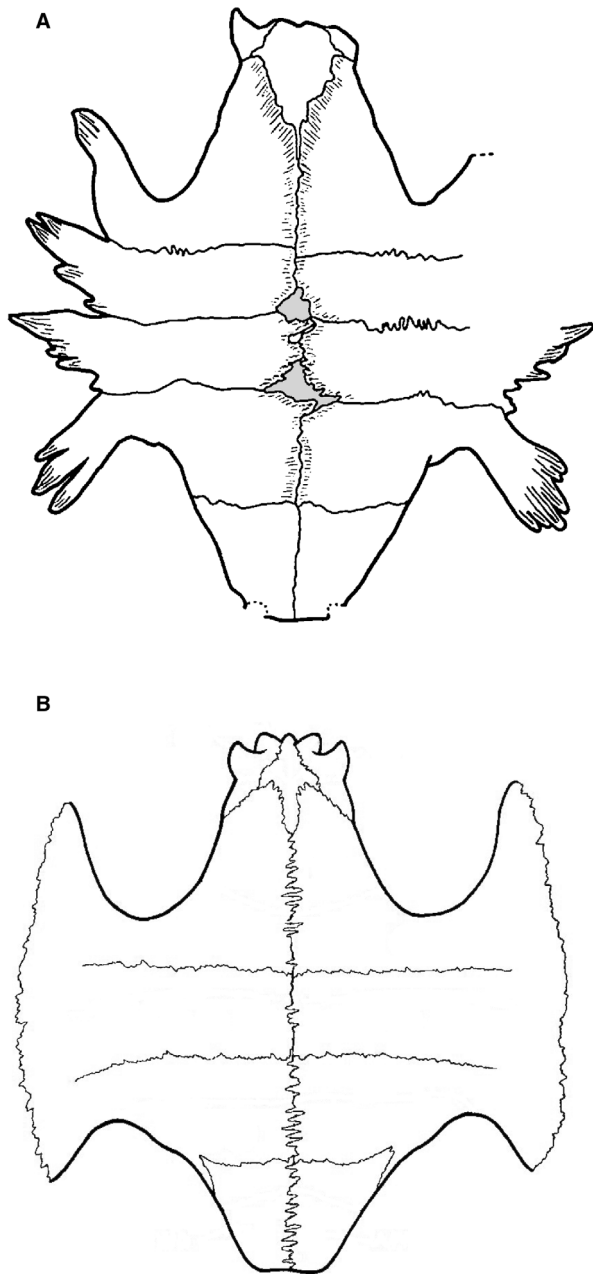


FIG. 5. The bony plastron in two derived stem-turtles. A, *Odontochelys semitestacea* (modified from Lyson *et al.* 2014), the earliest record of a fully developed plastron; light grey shading indicates unossified areas. B, *Proganochelys quenstedti* (modified from Gaffney 1990). Not to scale.

Eorhynchochelys. The published material comprises three excellently preserved specimens that together document most of the skeleton (Li *et al.* 2008). Unfortunately, these important fossils have yet to be described in detail.

Odontochelys has a fully developed plastron (except for a narrow median fontanelle in the holotype of *O. semitestacea*; Fig. 5A) but lacks a carapace. Grooves on the

plastral elements show that these bones bore keratinous scutes. The hyoplastra, hypoplastra and mesoplastra all have laterally projecting, spine-like processes. The pelvis includes an ossified hypoischium. The dorsal ribs of *Odontochelys* are broadened anteroposteriorly and T-shaped in transverse section. They extend laterally and dorsally rather than laterally and ventrally as in more basal stem-turtles. Although resembling those of *Eunotosaurus*, the ribs do not overlap, leaving gaps between successive elements, as in *Pappochelys* and *Eorhynchochelys*. *Contra* Hirasawa *et al.* (2013), they are not fused to the vertebrae, based on the photographs published by Li *et al.* (2008). *Odontochelys* has narrow, rectangular bony plates supported by its dorsal neural spines. Although probably homologous to the neurals in turtles, these elements were not fused to the neural spines and became displaced after death (Li *et al.* 2008).

Odontochelys shares various features with *Pappochelys* and *Eorhynchochelys*. In all three taxa, the shoulder girdle is situated anterior to the rib cage, unlike in more derived turtles. The humerus and femur are less robust than in *Proganochelys*, and various turtle-like features of the latter are less prominently developed (e.g. raised proximal head of humerus). The pre-ungual phalanges of the manus and pes are proportionately shorter than those in most saurians and the unguis phalanges are long. Digits III and IV of the manus and pes each have four phalanges, rather than two or three. The sacral ribs are not fused to the sacral vertebrae and the caudal ‘ribs’ are not fused to the caudal vertebrae. As in *Pappochelys* and *Eorhynchochelys*, the long tail of *Odontochelys* comprises at least 20 vertebrae. The skull of *Odontochelys* has a proportionately longer and more tapered snout than in *Proganochelys*. Marginal teeth are present in the premaxilla, maxilla, and dentary. The pterygoid has a distinct transverse process as in more basal reptiles.

Odontochelys is clearly more derived than *Pappochelys*, and it shares the following derived features with Testudinata:

1. Plastron fully developed, comprising five pairs of plate-like elements (hyoplastra, hypoplastra, xiphiplastra and two pairs of mesoplastra) as well as the fully integrated interclavicle (entoplastron) and clavicles (epiplastra). Its bones are thick, flat and firmly sutured to each other. The presence of two pairs of mesoplastra has elsewhere been documented only in the basal testudinatan *Proterochersis* (Szczygielski & Sulej 2016).
2. The entoplastron has well-developed anterolateral facets for the contact with the epiplastra, which are aligned vertically as in the basal testudinatan *Proganochelys*.
3. Forelimb markedly longer and more robust than the hind limb. The fore and hind limbs in *Eorhynchochelys* are more or less equal in length.
4. An ossified hypoischium is attached to the posterior ends of the ischia, as in *Proganochelys* and more derived turtles.

5. Pubis and ischium form a rigid bony plate.

Proterochersis

Proterochersis robusta, from the lower portion of the Upper Triassic (Norian; c. 208–227 Ma) Löwenstein Formation of Baden-Württemberg (Germany) (Fraas 1913), is the oldest known and most basal testudinatan. Szczygielski & Sulej (2016) identified two additional taxa, *Proterochersis porebensis* from the Upper Triassic (Norian) Zbaszynek Beds of Poland and *Keuperotesta limendorsa* from the lower part of the Upper Triassic (Norian) Löwenstein Formation of Baden-Württemberg. Both differ from *P. robusta* in features of the carapace. Joyce (2017) synonymized *Keuperotesta* with *Proterochersis* but retained its type species as valid.

Proterochersis is currently known only from its bony shell and pelvic girdle. The shell attained a length of about 40 cm and is highly domed, unlike the dorsoventrally somewhat flattened shell of *Proganochelys* and comparable to the condition in extant turtles with predominantly terrestrial habits. The epiplastral processes do not contact the nuchal bone of the carapace dorsally. The carapace of *Proterochersis* includes a nuchal bone and peripheral elements. Its plastron has two pairs of mesoplastra, as in *Odontochelys* but unlike in *Proganochelys*. The pelvic bones are suturally attached to the shell, a condition that evolved independently in pleurodiran turtles (Joyce *et al.* 2013b).

Proganochelys

Baur (1887) first named *Proganochelys quenstedti* in a footnote on the basis of a natural mould of the internal surface of a shell from the Upper Triassic (Norian) Löwenstein Formation (Stubensandstein) of Baden-Württemberg (Germany). Quenstedt (1889) later described the same specimen under the name *Psammochelys keuperina*. Jaekel (1914, 1915–16) described much more complete skeletal remains from the correlative Arnstadt Formation near Halberstadt in Saxony-Anhalt (Germany) under the name ‘*Stegochelys*’ (preoccupied and later renamed *Triassochelys*) *dux*. Furthermore, additional specimens of *Proganochelys quenstedti* were recovered from the Löwenstein and Trossingen formations of Baden-Württemberg. Based on a monographic revision of all available fossils, Gaffney (1990) referred the entire material to a single taxon, *Proganochelys quenstedti*. Skeletal remains of closely related stem-turtles from the Upper Triassic (Norian) Huai Hin Lat Formation of Thailand (*P. rucha*; de Broin 1984) and the Upper Triassic (Norian) Fleming Fjord Formation of East Greenland have also been referred to *Proganochelys* (Joyce 2017).

Fragmentary bones of a stem-turtle, *Chinlechelys tenertesta*, were reported from the Upper Triassic (Norian) Bull Canyon Formation of New Mexico (Joyce *et al.* 2009). Later Joyce (2017) synonymized *Chinlechelys* with *Proganochelys* but retained its type species as valid.

Proganochelys has a fully developed bony shell with the carapace and plastron connected by a bony bridge on either side. Its shell is more flattened dorsoventrally than that of *Proterochersis*, and the pelvic girdle is not sutured to it. *Proganochelys* lacks marginal teeth but its vomer and palatine bear denticles. It retains a lacrimal bone. The pterygoid lacks a transverse flange, unlike in *Odontochelys*. The basicranial joint between the basisphenoid and pterygoid is open, as in more basal stem-turtles and most other reptiles but unlike in more derived testudinatanans. The trunk ribs articulate between centra rather than on them as in more basal stem-turtles and other amniotes. The plastron of *Proganochelys* has well-developed gular and extragular projections and a pair of mesoplastra (Gaffney 1985; Fig. 5B). Unlike in *Proterochersis*, its epiplastral processes broadly contact the carapace dorsally. The carapace bore more scutes than do more derived testudinatanans. The dorsal portion of the ilium is greatly expanded. Both manus and pes have a reduced phalangeal formula of 2-2-2-2-2. Osteoderms cover the neck, limbs, and tail in *Proganochelys*. The distal tail elements form a club-like structure.

Palaeochersis

Palaeochersis talampayensis is known from one fairly complete skeleton and other skeletal remains from the Upper Triassic (Norian; 213–227 Ma) Los Colorados Formation of La Rioja province (Argentina) (Rougier *et al.* 1995; Sterli *et al.* 2007; Joyce 2017). It has a fully developed bony shell, which attained a length of 50 cm. The epiplastral processes probably broadly contacted the carapace. Although the skull of *Palaeochersis* resembles that of *Proganochelys* in the retention of lacrimal and supratemporal bones, it differs from that of the former in various derived features such as the absence of denticles on the vomer, the fusion of the basispterygoid joint, and the tight contact between the paroccipital process and the quadrate and squamosal. The shell of *Palaeochersis* differs from that of *Proterochersis* in the presence of anterior supramarginals and the absence of postanal scutes. The number of mesoplastra in *Palaeochersis* is uncertain.

EVOLUTION OF THE TURTLE BODY PLAN

During the last decade, the discoveries of the Triassic stem-turtles *Pappochelys*, *Eorhynchochelys* and

Odontochelys, along with re-examination of the middle Permian *Eunotosaurus*, have documented various morphological stages in the formation of the turtle body plan. Following Lyson *et al.* (2013, 2014), *Eunotosaurus* is used as the initial stage in this transformational sequence. In recent decades, evolutionary scenarios have received much criticism for their lack of empirical rigour. Historically, researchers often failed to make a clear distinction between reconstructing the evolutionary history of a group of organisms and generating adaptationist narratives to explain the morphological transformations observed within that group. However, Gans (1989) argued that carefully designed scenarios are helpful for understanding the evolutionary history of biological phenomena. He noted that scenarios must complement cladograms, which provide a testable historical framework and thus must be developed first. Fossils are inherently incomplete documents of extinct life-forms and must be interpreted in light of extant organisms. Developmental data on the latter provide a powerful tool for evaluating evolutionary scenarios. In this section, we compare features of the body plan of extinct stem-turtles with embryological information on the formation of homologous structures in extant turtles.

CARAPACE

Embryological evidence

The carapace of turtles is unique among amniotes in both its structure and development. It differs even from the remarkably turtle-like dermal trunk armour in the Late Triassic placodont reptile *Henodus* where the vertebrae, ribs and gastralia were presumably ligamentously attached to but are not integrated into the carapace (Westphal 1975).

The prevailing scenario involved the formation of the carapace in turtles through fusion of dermal bony plates (osteoderms) to the underlying ribs (Versluys 1914; Lee 1993, 1996; Joyce *et al.* 2009; see Rieppel (2017) for an excellent historical survey). It invoked a turtle precursor with a dense cover of dorsal armour elements, which ossified in the dermis (termed 'Polka Dot Ancestor' by Rieppel). Lee (1993, 1996, 1997) argued that such a precursor could be found among the middle to late Permian pareiasaurian parareptiles, which he considered to be the clade containing turtles. The dorsal osteoderms of the 'Polka Dot Ancestor' would eventually fuse into larger plates that in turn became fused to the underlying ribs. The phylogenetic analyses by Lee (1997) and Tsuji (2013) indeed suggest an increase in the complexity and extent of the dorsal dermal armour from basal pareiasaurs such as *Bradysaurus* to derived ones such as *Anthodon*.

However, this hypothesis does not explain how the dermal armour became fused to the underlying ribs. It also does not account for the position of the shoulder girdle inside the shell in turtles rather than outside the rib cage as in other amniotes. This led Watson (1914) and others to postulate a backward shift of the shoulder girdle during ontogeny. However, Ruckes (1929) and Burke (1991) noted that the relative position of the shoulder girdle does not actually change during ontogeny but that the developing trunk ribs grow over the shoulder girdle.

In most amniotes, the ribs develop from the somites and grow laterally and ventrally into the lateral body wall, eventually enclosing much of the thorax. In turtles, by contrast, the ribs grow mainly laterally into the carapacial disc. The carapace develops from this disc of connective tissue under the dermis on the back of the embryo (Hirasawa *et al.* 2013). Ruckes (1929) noted that the ribs become ensnared in the carapacial ridge, a distinct bulge along the periphery of the carapacial disc, and continue to grow laterally within this bulge. This ridge develops between the limb buds and subsequently extends anteriorly and posteriorly beyond these buds. The developmental processes underlying this unusual condition have been carefully analysed in recent decades. Burke (1989, 1991) first argued that the carapacial ridge generates an inductive signal that guides the lateral rather than ventral growth of the developing ribs (axial arrest). Screening for genes specifically expressed in the carapacial ridge of the Chinese soft-shelled turtle (*Pelodiscus sinensis*), Kuraku *et al.* (2005) demonstrated that this signal is triggered by the expression of certain genes that, although conserved throughout the major evolutionary lineages of vertebrates, acquired novel expression in the carapacial ridge.

Once fully developed, ossification of the cartilaginous rib precursors commences with the deposition of a sleeve of periosteal bone. Anterior and posterior extensions expand from, and remain continuous with, the periosteal sleeves of the ribs. Thus, the costal plates develop as extensions of the perichondral ossification of the ribs, not dermal bones. Similarly, the neural plates grow from the perichondral bone surrounding the dorsal neural arches. Thus, the neurals and costals are entirely endoskeletal in origin (Hirasawa *et al.* 2013).

In the stem-turtle *Odontochelys*, the trunk ribs do not fan out anteroposteriorly (as they do in many derived turtles) but converge slightly toward the mid-trunk region (Li *et al.* 2008). Nagashima *et al.* (2007) observed that experimental destruction of the carapacial ridge in embryos of extant soft-shelled turtles suppresses the fanning of the ribs. However, this procedure did not affect the lateral growth of the ribs. Based on these data, the authors argued that the carapacial ridge induces the fanning of the trunk ribs (flabellate pattern) only late in

ontogeny and that this developmental step was not yet present in *Odontochelys*.

This work, along with new data on muscle development, led Kuratani *et al.* (2011) to propose the ‘folding theory’ for the origin of the carapace in turtles. The first developmental step is the axial arrest of the trunk ribs in which the carapacial ridge suppresses the growth of the ribs into the lateral plate domain. As a result, the ribs are proportionately shorter than in other reptiles. The carapacial disc grows independent of the ribs while the body wall is folded underneath it. This infolding of the body wall leads to the ribs extending anteriorly over the shoulder girdle and results in changes in the arrangement of muscles attached to the scapula, which acquire new sites of attachment (Nagashima *et al.* 2009; Kuratani & Nagashima 2012).

Rice *et al.* (2015) demonstrated that the processes of carapace development and costal formation differ considerably between extant hard- and soft-shelled turtles. In both groups, however, the carapacial ridge prevents the ribs from extending ventrolaterally into the body wall. Rice and her colleagues underscored the role of this ridge as a signaling centre as a key evolutionary innovation of turtles.

The nuchal, the anteromedian bone of the carapace, develops separately in a two-stage ossification process from all other carapacial elements in extant turtles (Gilbert *et al.* 2007). It is now considered homologous to the paired cleithra in more basal amniotes (Lyson *et al.* 2013), after Vallén (1942) had originally homologized the nuchal with supracleithra, which, however, are elements of osteichthyans that are not present in tetrapods. The nuchal is never lost in turtles; it is even present in the leatherback sea turtle (*Dermochelys coriacea*), which otherwise lacks carapacial elements (Völker 1913). The trapezius muscle originates along the anteroventral surface of the nuchal, providing additional anatomical evidence for homologizing this shell element with the cleithra in other amniotes (Lyson *et al.* 2013).

Ossification centres of peripherals first occur along the anterior margin of the carapace and, during further growth, appear more posteriorly. These bones form the periphery of the carapace and expand laterally and internally during their growth (Gilbert *et al.* 2001). The pygal forms as the last peripheral and thus last bony element of the carapace.

Fossil evidence

Unlike *Eunotosaurus*, the stem-turtles *Pappochelys*, *Eorhynchochelys* and *Odontochelys* probably retained limited mobility of the trunk ribs based on the position and structure of the synapophyses and the presence of

intercostal spaces. The intervertebral position of the synapophyses typical of turtles is first observed in the basal testudinates *Proganochelys* and *Proterochersis*, in which the costal plates are already fully sutured to each other.

The costal plates of the carapace in *Proganochelys* and more derived turtles have a layer of cancellous bone sandwiched between an external and an internal layer of cortical bone (Scheyer & Sander 2007). This structural pattern is absent in the broadened ribs of *Pappochelys*; the conditions in *Odontochelys* and *Eorhynchochelys* are still unknown.

A nuchal is first identifiable in *Proterochersis* and *Proganochelys*. Lyson *et al.* (2013) noted that the dorsal migration of the cleithra and their eventual fusion into the nuchal, along with the loss of the scapular rami of the clavicles, led to a wide separation of these originally closely associated bones and reconfiguration of the shoulder girdle in turtles. Finally, Szczygielski & Sulej (2019) hypothesized that the peripherals, suprapygals and the pygal are most likely to be osteodermal in origin.

PLASTRON

Embryological evidence

Like the carapace, the plastron is a uniquely derived feature of turtles. The presence of a fully formed bony plastron in *Odontochelys* demonstrates that the development of the plastron preceded that of the carapace in turtles (Li *et al.* 2008). It is interesting to note that ossification of the carapace lags behind that of the plastron in extant turtles (Rieppel 1993) even though the onset of the ontogenetic development of both halves of the turtle shell coincides (Rice *et al.* 2016). Clark *et al.* (2001) demonstrated that the plastral bones are formed by intramembranous ossification of cells derived from the neural crest.

The anterior portion of the plastron consists of a pair of anterolaterally situated epiplastra and the anteromedial entoplastron (Fig. 6). Following Parker (1868), most authors have homologized the epiplastra with the clavicles in other tetrapods and the entoplastron with the interclavicle in the latter. Lyson *et al.* (2013) provided compelling support for this hypothesis by noting that the sternocleidomastoideus muscles attach to the epiplastra and entoplastron, just as they attach to the clavicles and interclavicle in other extant tetrapods. The entoplastron and epiplastra are the first to ossify during the ontogenetic development of the plastron (Rieppel 1993; Gilbert *et al.* 2001). Bone condensations with numerous bony spicules form along the lateral edges of the ventral mesenchyme and grow medially, eventually forming bony plates. Cuvier (1817) suggested that the plastron of turtles

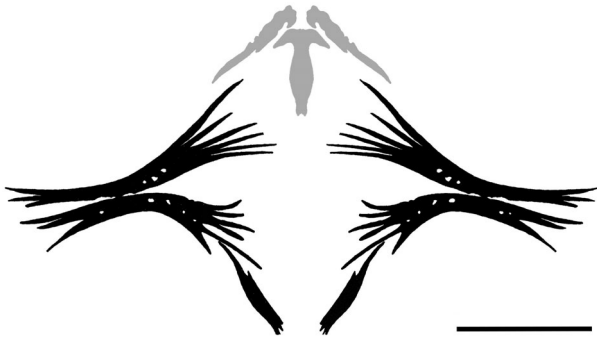


FIG. 6. The plastron of crown turtles integrates components of the dermal pectoral girdle (clavicles and interclavicle, grey) and fused gastralia (black), which can still be traced in the embryo of *Chelydra serpentina* shown here. Figure modified from Rieppel (1993). Scale bar represents 2 mm.

corresponds to the sternum in other tetrapods. Rice *et al.* (2016) demonstrated that the relative position and timing of the plastral condensations indeed matches those of the precursors of the sternal cartilages in birds and mice. However, the condensations in the ventral mesenchyme of turtle embryos commit to bone formation and hence suppress the development of sternal cartilages.

The more posterior bones of the plastron have long been considered homologous to the gastralia in other amniotes (Zangerl 1939). Early in development, these plastral elements are represented by clusters of bony spicules. Gilbert *et al.* (2007) provided histochemical evidence suggesting that the gastralia in the American alligator (*Alligator mississippiensis*) are derived from neural crest cells, much like the posterior plastral bones in turtles. However, the gastralia of the alligator develop within mesenchyme externally adjacent to the abdominal musculature (Vickaryous & Hall 2008).

Fossil evidence

Pappochelys has a ventral set of closely packed pairs of gastralia. These gastralia are robust, proportionately much longer than in other amniotes and there are no medial elements, unlike in other reptiles. Their distal ends are frequently bifurcated or brush-like. Histological examination demonstrated that the gastralia in *Pappochelys* are single elements rather than the result of fusion of smaller, more slender bones (Schoch *et al.* 2019). Individual gastralia vary considerably in shape. In addition, there is regional differentiation of these bones, with simple rod-like gastralia in the anterior region of the trunk and more posterior ones that are twisted along their long axes.

Li *et al.* (2018) illustrated a few gastralia in *Eorhynchochelys* that resemble those in *Pappochelys*, but the

arrangement of these bones is not clear as the only known skeleton of this stem-turtle is exposed in dorsal view.

Odontochelys documents the earliest appearance of a complete bony plastron in the turtle lineage. It has the full complement of plastral bones present in more derived turtles with the addition of two pairs of mesoplastra. The plastral elements form laterally extending projections that terminate in bony spikes.

STABILIZATION OF THE TRUNK

In *Eunotosaurus* (Cox 1969; Lyson *et al.* 2013, 2014; Joyce 2015) and the Triassic stem-turtles lacking a complete bony shell, the foreshortening of the trunk is associated with broadened ribs and elongated vertebral centra. The ribs are not as broad anteroposteriorly as the costal plates in the carapace of more derived turtles with fully formed bony shells but they already occupy a more dorsal position than in other amniotes.

Eunotosaurus has 10 dorsal vertebrae (Lyson *et al.* 2013), unlike the higher number (14–30) in most other reptiles (Müller *et al.* 2010). *Pappochelys* probably has no more than 10 dorsals but the exact number of its cervical vertebrae is still unknown. *Odontochelys*, *Proganochelys*, and most more derived turtles have 8 cervical and 9 dorsal vertebrae. Only *Eorhynchochelys* is unusual in the possession of 9 cervicals and 12 dorsals.

Odontochelys differs from *Pappochelys* in having ventrolaterally less curved ribs, resulting in a dorsoventrally more flattened trunk. In *Eunotosaurus*, the ribs are much longer than in any of the Triassic stem-turtles and strongly curve ventrolaterally (Cox 1969; Lyson *et al.* 2014). They are also more expanded anteroposteriorly than in *Pappochelys*, *Eorhynchochelys* and *Odontochelys*, and, unlike in the latter taxa, posteriorly overlap successive ribs for much of their length, leaving no space for intercostal muscles. The distal ends of the ribs in *Eunotosaurus* are blunt and bear facets for the attachment of cartilaginous costosternal segments as in other reptiles (Lyson *et al.* 2014), suggesting the presence of a presumably cartilaginous sternum.

In most amniotes, the ribs and abdominal muscles act in concert to facilitate respiration and stabilize the trunk (Brainerd & Owerkowicz 2006). The broadening of the trunk ribs and concomitant loss of intercostal muscles in the turtle lineage eliminated expansion and contraction of the rib cage for breathing. Instead, turtles evolved a unique respiratory system that involves two pairs of antagonistic muscles, the transversus abdominis muscle and the obliquus abdominis muscle (Gans & Hughes 1967; Landberg *et al.* 2003). In most amniotes, these muscles insert on the internal (visceral) surfaces of all dorsal ribs. In turtles, however, they insert only on the

anterior and posterior dorsal ribs and not on the mid-dorsal ribs. Lyson *et al.* (2014) demonstrated that this distinctive pattern of insertion was already present in *Eunotosaurus*.

In *Pappochelys*, stabilization of the trunk also involved its ventral basket of closely packed pairs of robust gastralia, not unlike the condition in sauropterygian reptiles (Robinson 1975). Its gastralia are proportionately much longer than in other amniotes. It is likely that the gastralia basket in *Pappochelys*, together with the foreshortening of the trunk region, would have greatly restricted abdominal flexibility and protected the underside.

PALAEOBIOLOGY OF STEM-TURTLES

The shell in extant turtles serves predominantly as protection for the animal (Zangerl 1969; Magwene & Socha 2012). Rieppel & Reisz (1999) argued that it evolved initially in water-dwelling stem-turtles because aquatic predators would probably attack their prey from below. Furthermore, Rieppel (2013) suggested that the plastron in *Odontochelys* could have served as bone ballast for buoyancy control and that the ventral position of this ballast in the trunk region would be hydrodynamically advantageous for this purpose. The occurrence of *Eorhynchochelys* and *Odontochelys* in marine strata appears to be consistent with an aquatic origin of the turtle shell. The limb proportions of *Odontochelys* correspond to those of present-day turtles that live in stagnant or small bodies of water (Rieppel 2017). However, Joyce (2015) argued that the short proximal phalanges of *Odontochelys* suggest that this stem-turtle was more terrestrial, perhaps mainly living in swampy areas. The presence of remains of land plants in the strata from which *Eorhynchochelys* and *Odontochelys* were recovered indicates that these deposits probably did not form far from land. Thus, it is likely that these stem-turtles lived along the coast rather than in the open sea (Li *et al.* 2008, 2018).

The occurrence of *Pappochelys* in lacustrine sedimentary strata could be interpreted as additional evidence for an aquatic origin of the turtle body plan. However, histological work demonstrated that bones of this stem-turtle lack the modifications (e.g. pachyostosis) commonly associated with a predominantly aquatic mode of life (Schoch *et al.* 2019). Furthermore, fossils of this stem-turtle are found together with the skeletal remains of a considerable diversity of terrestrial tetrapods (Schoch & Seegis 2016). Most specimens of *Eunotosaurus* have been recovered from strata deposited on continental floodplains with ephemeral bodies of water (Lyson *et al.* 2016).

Gaffney (1990) reconstructed *Proganochelys* as semi-aquatic based particularly on the depositional environment in which its remains were preserved. However,

Joyce & Gauthier (2004) argued that this basal testudinatan was probably terrestrial based on the relative proportions of its forelimbs. The presence of osteoderms on the neck, tail and limbs and the reduced phalangeal counts in the manus and pes of *Proganochelys* provide additional support for their interpretation. Scheyer & Sander (2007) investigated the microstructure of shell elements of *Proganochelys* and *Proterochersis*. They found that these weakly vascularized bones have well-developed external and internal cortical layers, much as in extant terrestrial turtles. This histological picture differs from that for shell elements in aquatic turtles, which typically are more vascularized and have reduced cortical layers. Scheyer & Sander (2007) agreed with Joyce & Gauthier (2004) that *Proganochelys* and *Proterochersis* were terrestrial animals.

Lyson *et al.* (2016) made a compelling case that *Eunotosaurus* was fossorial. The shoulder girdle and forelimb show features consistent with this inferred activity, including the presence of a large deltopectoral crest on the humerus, the presence of a prominent olecranon process on the robust ulna, and the large, spatulate ungual phalanges of the manus. Lyson *et al.* (2016) interpreted the broadened, overlapping ribs of *Eunotosaurus* as providing rigidity to the foreshortened trunk, which would provide a stable basis for employing the forelimbs for scratch-digging. In his analysis of broadened ribs in certain extant species of mammals, Jenkins (1970) argued that stabilization of the trunk is important for the effectiveness of forelimb use during digging and other activities. The ribs and thick intercostal muscles help provide the requisite stability.

Lyson *et al.* (2016) reconstructed *Eunotosaurus* as burrowing to create shelter but mainly foraging above ground, comparable to the habits of extant gopher tortoises. Furthermore, the authors surmised that fossoriality was an important factor in the early evolution of the turtle body plan. Based on histological data, Schoch *et al.* (2019) posited that the Middle Triassic *Pappochelys* had an amphibious and possibly fossorial mode of life. The currently available information suggests that the oldest fully-shelled stem-turtles had predominantly terrestrial habits.

CONCLUSIONS

New discoveries of early stem-turtles and recent studies of the ontogenetic development of the shell in extant turtles have led to reconsideration of the origin of the turtle shell, the key diagnostic feature of Testudinata. The earliest stem-turtles still lack a carapace and plastron but already have foreshortened trunks with broadened ribs and elongate dorsal vertebrae. The Middle Triassic

Pappochelys has a ventral basket comprising pairs of robust gastralia. The early Late Triassic *Odontochelys* is the oldest known stem-turtle with a fully developed plastron but lacks a complete carapace. The late Late Triassic basal testudinians, best documented by *Proganochelys*, have fully developed bony shells with carapace and plastron. The evolutionary trajectories in the formation of the shell in stem-turtles closely track the ontogenetic trajectories in extant turtles. Recent embryological research has demonstrated that the costal and neural plates of the carapace are exclusively endoskeletal in origin. The carapacial ridge in turtle embryos guides the lateral rather than ventrolateral growth of the trunk ribs as well as their typically fan-shaped arrangement. The latter results in the position of the shoulder girdle inside the carapace in turtles. The nuchal element of the carapace is homologous to the cleithra in other tetrapods. The plastron comprises the homologues of the clavicles and interclavicle in other tetrapods anteriorly and plates that are probably homologous to the gastralia more posteriorly. The fossil record demonstrates that the development of the turtle shell took place in multiple steps over millions of years. It is most likely that this transformation occurred in non-aquatic stem-turtles. The diapsid affinities of turtles, long hypothesized on the basis of molecular data, have received morphological support from the unambiguously diapsid cranial configuration in the stem-turtle *Pappochelys*.

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