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Invited Perspectives

The amniote temporal roof and the diapsid origin of the turtle skull

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ABSTRACT

Fossils provide a glimpse into the architecturally complex origins of modern vertebrate body plans. One such origin that has been long debated is that of turtles. Although much attention has been directed toward the origin of the shell, the enigmatic evolution of the turtle skull and its anapsid temporal region has long clouded our understanding of reptile phylogeny. Two taxa, *Eunotosaurus africanus* and *Pappochelys rosinae*, were recently and independently described as long-anticipated stem turtles whose diapsid skulls would cement the evolutionary link between turtles and other modern reptile lineages. Detailed μ CT analysis of the stratigraphically older and phylogenetically stemward of the two, *Eunotosaurus*, provides empirical insight into changing developmental trajectories that may have produced the anapsid cranial form of modern turtles and sets the stage for more comprehensive studies of early amniote cranial evolution.

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The vertebrate skull is an exceedingly complex structure (Goodrich, 1930). Comprised of tissues derived from multiple embryonic sources, the skull reflects the interplay of developmental innovations and constraints that evolve within the context of multitudinous functional demands. These competing influences range from food acquisition and processing, to sexual selection and defense, to the support and protection of the brain and sensory organs. The remarkable disparity of cranial forms exhibited by extant vertebrates provides a compelling illustration of the evolutionary potential of cranial tissues. The major vertebrate crown clades, however, are generally separated by long phylogenetic stem lineages whose frequently enigmatic histories may obfuscate the evolutionary origin of distinctive vertebrate body plans and their unique cranial signatures.

Because phylogenetic stem lineages, by definition, lack extant representatives, the nature, timing, and sequence of the character transformations they encompass are empirically accessible only through fossils. Unfortunately, important transitional fossil taxa are often known from limited numbers of specimens making it impossible to subject them to the invasive techniques historically required for detailed anatomical study. This leaves us to draw insight from external surfaces alone. Advances in imaging technol-

ogy are helping to lift these logistical constraints, and computed tomography (CT) is nearing standard practice in vertebrate paleontology. That stated, CT-based approaches have yet to be widely applied to early amniote fossils and the evolutionary problems they present—including the origin of turtles.

Conventional wisdom long held that turtles are survivors of an early reptile lineage that diverged prior to the radiation of the other modern reptile clades (lepidosaurs and archosaurs) (see Joyce, 2015). This conclusion was influenced by the observation that early reptiles and turtles both express an anapsid skull—with an adductor chamber covered dorsally and laterally in dermal bone. Recent analyses of both molecules and morphology (e.g., Field et al., 2014) recover turtles among the other extant reptiles whose adductor chamber is exposed through dorsal and lateral temporal windows (diapsid condition). If this hypothesis is correct, then the anapsid skull of turtles is secondarily derived, and the fossil record can be predicted to one day produce an early turtle relative with a diapsid skull.

That day has apparently come: 2015 witnessed the independent publication of two stem turtles expressing diapsid skulls (Bever et al., 2015; Schoch and Sues, 2015). The stratigraphically oldest and phylogenetically stemward of the two is *Eunotosaurus africanus* from the Middle Permian of South Africa (~260 mya). First described in 1892, *Eunotosaurus* is now represented by ~50 specimens of varying ontogenetic stage. Its recent emergence as an important stem turtle was largely a function of how its post-cranial skeleton informs the origin of the shelled body plan and

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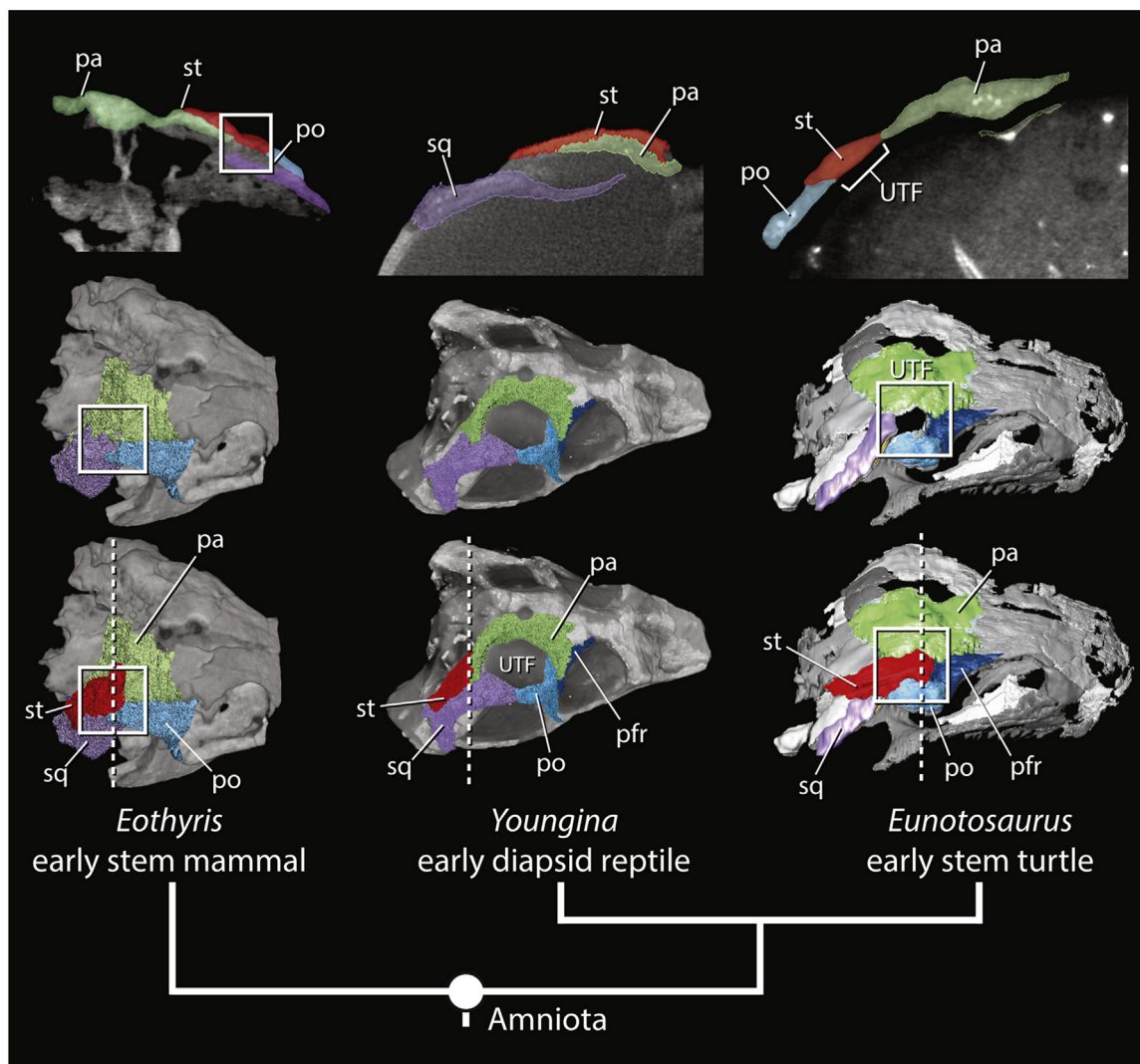


Fig. 1. Temporal region of the early stem mammal *Eothyris parkeyi* (MCZ 1161), the early diapsid reptile *Youngina capensis* (AMNH 5561), and the early stem turtle *Eunotosaurus africanus* (CM 777) (not to scale). The skulls of *Eothyris* and *Youngina* are presented as volume renderings whereas that of *Eunotosaurus* is a surface rendering of the fully segmented skull. Digital removal of the supratemporal in *Eunotosaurus*, unlike in *Eothyris*, reveals a circular opening spatially congruous with the diapsid upper temporal fenestra (UTF). The supratemporal (st) in each of these taxa is a superficial element that does not contribute to the primary temporal roof, which is formed through variable contact of the parietal (pa), squamosal (sq), and postorbital (po). Increased sampling using CT will determine the phylogenetic extent of this configuration and whether it represents the ancestral amniote condition. Abbreviations: AMNH, American Museum of Natural History, New York; CM, Council for Geosciences, Pretoria; MCZ, Museum of Comparative Zoology, Harvard; pfr, postfrontal.

highly derived breathing mechanism of modern turtles (Lyson et al., 2013, 2014), whereas its skull remained enigmatic. One of the few cranial details that seemed clear was that *Eunotosaurus* lacked the diapsid upper temporal fenestra (Gow, 1997).

To better understand *Eunotosaurus* and how its skull might inform turtle origins, we digitally dissected the best-preserved skulls into their component elements using μ CT and studied them in light of an expanded early reptile dataset (Bever et al., 2015). This represented the first such attempt for a Permian amniote, and the results were unexpected. Cranial synapomorphies were discovered that further support *Eunotosaurus* as the earliest stem turtle, but we also found that a dermal roofing element – the supratemporal – stretches across the adductor chamber to overlap the postorbital bone. Digitally removing the supratemporal unexpectedly revealed a circular window whose position suggests homology with the diapsid upper fenestra (Fig. 1).

To begin testing whether *Eunotosaurus* has a diapsid architecture that is concealed superficially by the expanded supratemporal, we used μ CT to examine temporal construction in the early stem

mammal *Eothyris parkeyi* (Fig. 1). This early amniote bears a completed primary roof deep to the superficial supratemporal with squamosal, parietal, and postorbital in full contact. There is no evidence of a circular opening beneath the supratemporal. Although we predict that with increased taxonomic sampling significant variation in amniote dermal architecture will be recovered, this observation supports the hypothesis that the *Eunotosaurus* opening is not plesiomorphic, but rather is a derived feature shared with diapsid reptiles.

This hypothesis is further supported by a juvenile *Eunotosaurus* specimen whose skull clearly expresses upper and lower fenestrae (Fig. 3 in Bever et al., 2015). The lack of an extensive supratemporal in this specimen, and the gracile nature of its other temporal bones, indicates that significant late-stage skeletal growth closed the *Eunotosaurus* adductor roof and that a peramorphic shift in these developmental events may well explain the anapsid nature of more crownward turtles. The disarticulated skull of *Pappochelys* (~240 mya) appears to house fenestrae intermediate in size between those of juvenile and adult *Eunotosaurus*. The

overall size of *Pappochelys* and the unfused nature of its scapula-coracoid (Schoch and Sues, 2015) compare closely only to the youngest specimen of *Eunotosaurus*, suggesting the *Pappochelys* material is skeletally immature. If so, its fenestral morphology and apparent lack of supratemporal may reflect its ontogenetic stage.

Regardless of what model of temporal closure is ultimately supported for turtles, it seems clear that advanced imaging will continue to reveal exciting and unforeseen morphology that forces us to rethink long-held perceptions of cranial evolution in amniotes and across vertebrates.

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