

THE DIAPSID ORIGIN OF TURTLES

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A B S T R A C T

*The origin of turtles has been a persistent unresolved problem involving unsettled questions in embryology, morphology, and paleontology. New fossil taxa from the early Late Triassic of China (*Odontochelys*) and the Late Middle Triassic of Germany (*Pappochelys*) now add to the understanding of (i) the evolutionary origin of the turtle shell, (ii) the ancestral structural pattern of the turtle skull, and (iii) the phylogenetic position of Testudines. As has long been postulated on the basis of molecular data, turtles evolved from diapsid reptiles and are more closely related to extant diapsids than to parareptiles, which had been suggested as stem group by some paleontologists. The turtle cranium with its secondarily closed temporal region represents a derived rather than a primitive condition and the plastron partially evolved through the fusion of gastralalia*

Key word –*Carapace, Plastron, Reptiles, Turtle origins*

I.INTRODUCTION

The origin and early evolution of turtles has been a longstanding problem in vertebrate morphology and phylogeny (Rieppel and Reisz, 1999). The unique composition of the turtle shell as well as the closed (anapsid) architecture of the skull had been controversially debated issues for more than a century. The lack of fossils documenting plausible stem taxa predating the Late Triassic had long formed a major obstacle in this context. Until recently, the geologically oldest and most primitive stem turtles reached back only to the later part of the Late Triassic, whereas it was long thought that the turtle clade likely diverged from other reptiles already during the Permian. Even more problematic was the fact that the oldest known stem turtles (*Proganochelys*, *Proterochersis*, *Palaeochersis*) already had fully formed shells and anapsid skulls with completely closed cheeks. This situation changed when Li et al.(2008) reported the discovery of a stem turtle from the early Late Triassic of southern China in which the plastron was fully developed, whereas what would become the carapace resembled structures in early developmental stages of crown-group turtles. The new taxon, the 220 myr old *Odontochelys semitestacea*, retained teeth in the upper and lower jaws along with numerous other plesiomorphic character states that clearly made it the oldest and most primitive undisputed stem turtle. Its carapace consisted of a single median series of bony plates on the neural arches of the trunk vertebrae and broadened ribs with T-shaped cross-sections. From embryological studies, these elements were known to form the neural and costal plates of the carapace in extant turtles (Lyson et al., 2013). Although the discovery of *Odontochelys* represented a major step in advancing our understanding of the evolution of the turtle body plan, tantalizing open questions remained, especially (i) how and from which elements much of the plastron evolved and (ii) what the original structure of the skull was like in the turtle stem line. These are not trivial questions because widely divergent views existed concerning the origin and phylogenetic relationships of turtles, highlighted by the discrepancy between the long-favored paleontological hypothesis according to which turtles evolved from parareptiles and

the persistent finding of molecular biologists that turtles are closely related to diapsid reptiles, specifically archosaurs (Hedges and Poling, 1999). In recent years, paleontologists either supported the parareptile hypothesis or the placement of turtles with lepidosaurs and a diverse clade of marine diapsid reptiles that dominated the Mesozoic seas, Sauroptrygia (Rieppel and Reisz, 1999). New detailed insight into turtle origins has now been achieved by paleontological excavations in southern Germany. In the last decade, collecting efforts near Schwäbisch Hall have yielded rich material of a range of tetrapods in late Middle Triassic sedimentary rocks (240 myr old). These collections include skeletal remains of a stem turtle even more primitive than *Odontochelys*. The new taxon, *Pappochelys rosinae*, is based on more than a dozen skeletons from a lake deposit dominated by large amphibians and a variety of diapsid reptiles (Schoch and Sues, 2015). *Pappochelys* has trunk ribs that are T-shaped in cross-section and a tall cylindrical scapula similar to that of *Odontochelys*, but retains a series of massive.

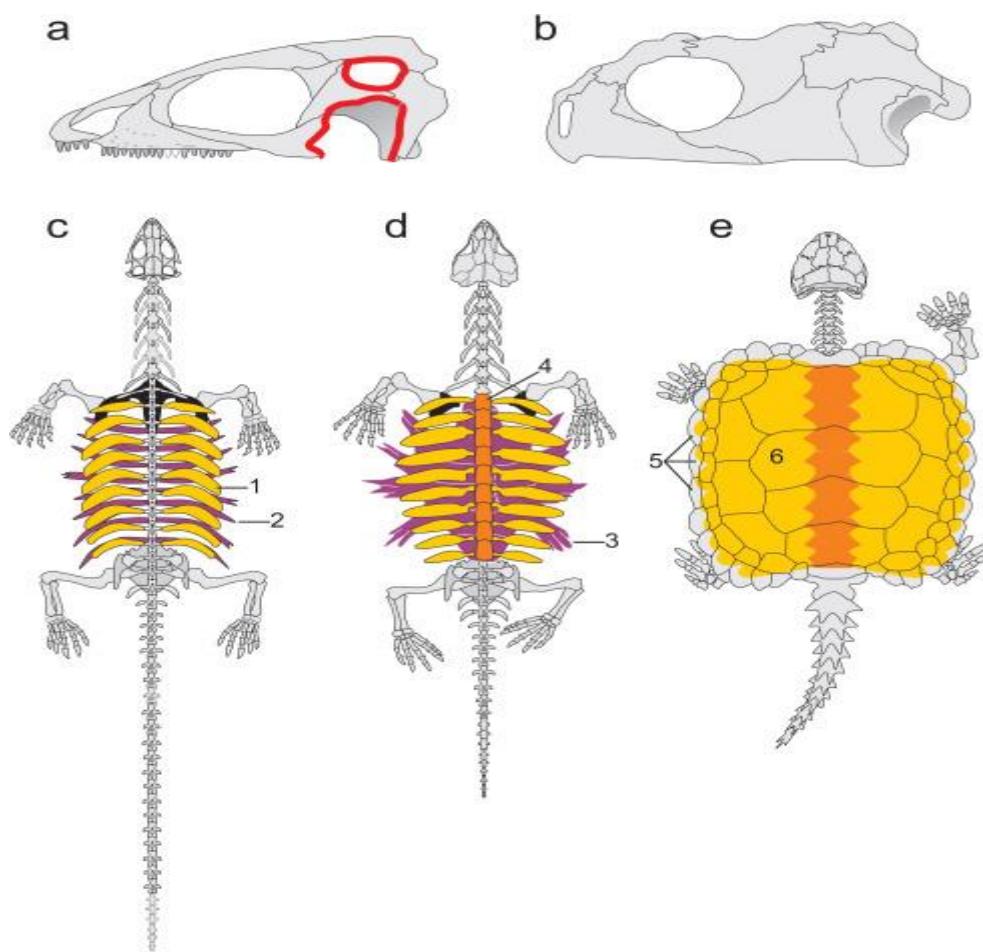


Fig. 1.

As revealed by new fossil evidence, the **anapsid**, closed turtle skull (b, *Proganochelys*) evolved from a diapsid condition, in which the cheek housed an upper and a lower temporal opening (a, *Pappochelys*). The evolutionary

sequence from *Pappochelys* (c) to *Odontochelys* (d) to *Proganochelys* (e) includes the broadening of ribs (1) and gastralia (2), the fusion of gastralia to form part of the plastron (3), the formation of **neural plates** on top of the **vertebrae** (4), and the addition of marginal elements (5) along with a suturing of all plates in the **carapace** (6)

gastralia (rod-like bones in the abdominal region common in other reptiles) instead of a shield-like plastron. Some of these gastralia have forked distal ends, closely resembling the spiky margins of the plastron in *Odontochelys*. The skull of *Pappochelys* is more delicate than that of turtles, with two large openings on either side of the temporal region – regular temporal fenestrae just like in lizards, tuatara, crocodylians and birds. Along with other rather lizard-like features (long tail, slender limb bones, separate pelvis elements, jaws with teeth), the morphology of *Pappochelys* forms a near-perfect structural intermediate between basal diapsid reptiles and turtles (Fig. 1). This discovery is also consistent with recent findings in a longknown Middle Permian reptile from South Africa, *Eunotosaurus africanus*, whose broadened, T-shaped trunk ribs and elongate dorsal vertebrae have long puzzled paleontologists (Joyce, 2015). Although lacking all other apomorphies shared by *Pappochelys* and more derived stem turtles (rod-like scapula, pubis with anteroventral process, raised heads of humerus and femur), *Eunotosaurus* appears to have had a modified diapsid skull as well (Bever et al., 2015), shedding additional light on the early stages of the evolution of the turtle body plan

II.CONCLUSION

The focus of future research is now likely to shift towards the questions of (i) which group among extant reptiles represents the closest relatives of turtles and (ii) how and why did stem turtles evolve the shell, a problem related to the unresolved question of whether early stem turtles lived in water or on land (Scheyer et al., 2013). Without doubt, paleontology will continue to play a key role in this investigation.

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