Mesozoic 002 (2): 143–154
https://www.mapress.com/mz/

Article

ISSN 3021-1859 (print edition)
MESOZOIC
ISSN 3021-1867 (online edition)

https://doi.org/10.11646/mesozoic.2.2.4

http://zoobank.org/urn:lsid:zoobank.org:pub:1B615A91-6EDB-4A95-84BE-DF021A4E9325

New insight into the paleobiology and systematics of the Mesozoic turtles of Central Europe (*Chelonipus triunguis* Karl & Tichy, 2000; *Priscochelys hegnabrunnensis* Karl, 2005) and their morphological relationship with the toothed turtle (*Odontochelys semitestacea* Li *et al*., 2008) of China

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Abstract

The origin of the turtle body plan remains one of the great mysteries of reptile evolution. To establish the relationships between turtles of different clades in palaeobiological aspects is highly difficult. Here we describe a review of the oldest Mesozoic turtles of Central Europe (*Chelonipus triunguis*; *Priscochelys hegnabrunnensis*) and their morphological relationship with the toothed turtle (*Odontochelys semitestacea*) of China. *P. hegnabrunnensis* is a fossil turtle from the Middle Triassic (lower Ladinian) of Hegnabrunn, Germany. It is known from a single, fragmentary shell plate and is considered a very early turtle, potentially the oldest known stem turtle. The fossil provides insights into the early evolution of turtle shells and their transition from a more primitive state. The habitat preferences of *Priscochelys hegnabrunnensis* remain uncertain. However, given the informative nature of the material available and, since that it was found mixed with marine and terrestrial faunas, it was probably allochthonous. The other older known turtle record is a trackway from the Bunter Sandstone of Thuringia (Germany) and represents the autochthonous ichno-taxon *Chelonipus triunguis*. *Odontochelys semitestacea* was a 220-million-year-old specimen excavated in Triassic deposits in Guizhou, China. *Odontochelys* only possessed the bottom portion of a turtle‘s armour, the plastron. It did not yet have a solid carapace as most other turtles do. Instead of a solid carapace, *Odontochelys* possessed broadened ribs like those of modern turtle embryos that still have not started developing the ossified plates of a carapace.

Keywords: *Chelonipus triunguis*, *Priscochelys hegnabrunnensis*, *Odontochelys semitestacea*, Early and Middle Triassic, Central Europe

Introduction

Reptilian fauna was dominant throughout the Mesozoic. In addition to the occurrence of large profound changes, climatic upheavals also resulted in extinction, accompanied by a significant period of evolution for terrestrial biota (Rögl, 1999; Karl *et al*., 2021, 2024a, 2025). Equivocal reconstructions of turtle evolution and biogeographic or palaeo-climatic data with phylogenetic hypotheses and new images of the holotype reconstructions of fossil turtles are important for prehistoric turtle fossil remains (Karl *et al*., 2024b). Although the science of vertebrate palaeontology is primarily concerned with the anatomy, phylogenetic relationships, function, and ecology of extinct vertebrates, much public attention is devoted to the discovery of the first and oldest fossil occurrences (Joyce & Karl, 2006). *Priscochelys hegnabrunnensis*, a fragmentary piece of armour shell from the Muschelkalk of Germany (Upper Triassic) with few diagnostic features, was proposed to represent the oldest known stem turtle (Scheyer, 2008). This contribution is concerned with a single, fragmentary vertebrate fossil (SMNS80141) from the Middle Triassic of Germany that was reported as the oldest fossil turtle occurrence (Wild, 1972). It was claimed that it might represent the oldest turtle (*e.g*., Młynarski, 1976; Rieppel & Reisz, 1999; Lucas *et al*., 2000) until it was formally described as a new species of fossil turtle, *Priscochelys hegnabrunnensis*, by Karl (2005). Although the formalities associated with the naming of *Priscochelys hegnabrunnensis* are sufficient to establish an available taxon name, those who doubt its identity as a basal turtle may consider the accompanying description and discussion

Submitted: 24 Mar. 2025; accepted by D.-Y. Huang: 23 Jun. 2025; published: 30 Jun. 2025

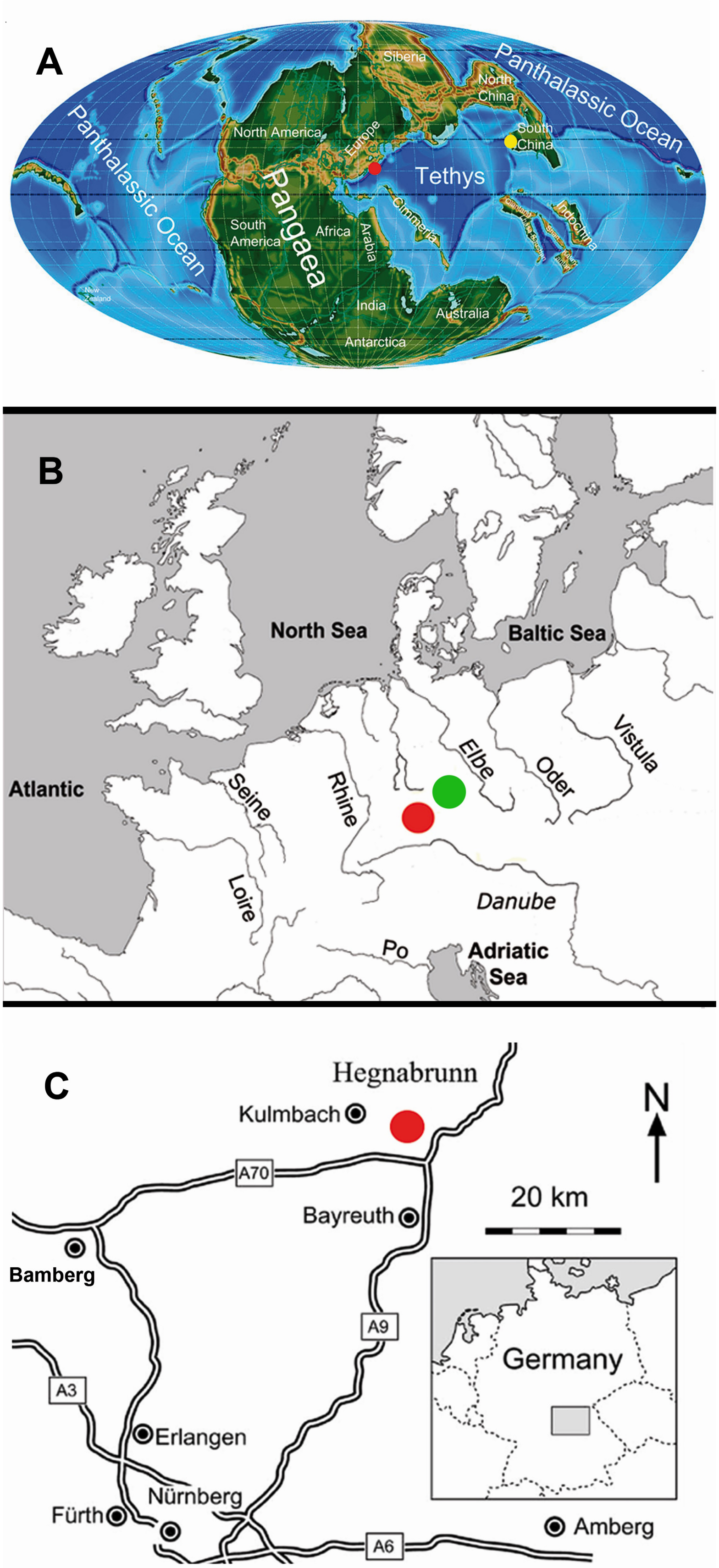

FIGURE 1. A, Schematic world map at the Lower Triassic with markings of Central Europe (red) and China (yellow). **B**, Schematic map of Central Europe with markings of Upper Franconia, Bavaria (red) and the Thuringian Basin (green). **C**, Schematic map of Upper Franconia, Bavaria with marking of *Priscochelys* (red). Palaeomap (1), Joyce & Karl, 2006 (3).

insufficient. To assuage critics, it should be noted that Joyce & Karl (2006) described SMNS 80141, and its identity as a basal turtle was argued in detail. The nomenclature of the turtle shell used herein follows that of Zangerl (1969). All names used throughout the text are clade names and follow the definitions of Joyce & Gaultier (2004). To distinguish them from traditional ranked-based taxon names, they are placed throughout the text in small caps.

Institutional Abbreviation: SMNS = Staatliches Museum für Naturkunde Stuttgart, Germany; PLUS = Paris-Lodron-University Salzburg, Geology and Physical Geography, Austria.

Geological setting

The putative fossil turtle fragment (SMNS80141) was acquired by the "Staatliches Museum für Naturkunde Stuttgart", Germany, in 1988 as part of the private Muschelkalk fossil collection of M. Wild of Kulmbach, Germany. The specimen was found on March 6th, 1969 in the since-abandoned Schmidt Quarry, which is located halfway along the road that connects the villages of Hegnabrunn and Feuln near the Upper Franconian town of Kulmbach, Germany (Fig. 1). The Gauss-Krüger Coordinates of the quarry are R4468125/H5550075. Sixteen meters of Upper Muschelkalk sediments are exposed in the Schmidt Quarry that can be attributed to the lower spinosus to the upper nodosus ammonoid biozones. The fossil was found embedded in a fist-sized clay-rich geode that was located in a limestone bench of the central section of the *enodis/laevigatus* ammonoid Biozone. The find can thus be placed into the Lower Ladinian (Middle Triassic). The fossil fragment was found shattered and minor bits were thus invariably lost. The vast majority of parts, however, could be recovered from the geode, were cleaned with water, and later reassembled. Minor sections, nevertheless, needed restoration. All details regarding the circumstances of this find and stratigraphy are based on personal communication of R. Wild (SMNS), summarized in Karl (2005). During the Middle Triassic, a particularly shallow epicontinental sea covered much of central Europe (Germanic facies) that was incompletely connected towards the south with the open sea (Alpine facies) and thus almost fully surrounded by land. Additional vertebrate fossils found from the Germanic facies of Upper Franconia include numerous shallow marine taxa, in particular sharks, teleosts, placodonts, nothosaurs, pistosaurs, and proterosaurs. Numerous finds of temnospondyls and lungfish, however, indicate a clear terrestrial influence to this region as well. Given the proximity of land, is appears plausible that terrestrial faunas were occasionally washed into the basin, in particular from the Bohemian Massif to the east (Wild, 1972) (Fig. 2).

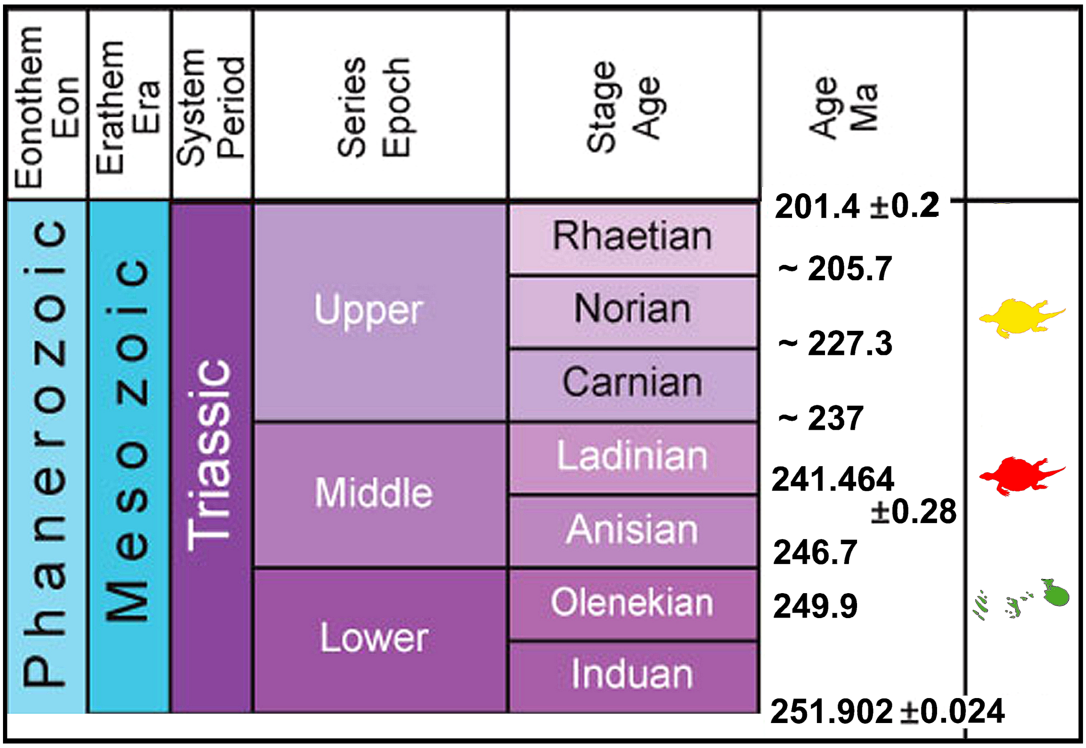

FIGURE 2. Section from the Stratigraphic Table of Germany with Triassic, with a marking of the stratigraphic position of *Chelonipus triunguis* (green), *Priscochelys hegnabrunnensis* (red), and *Odontochelys semitestacea* (yellow). ICS-International Commission on Stratigraphy (2024): International Chronostratigraphical Chart. https://stratigraphy.org/ICSchart/ChronostratChart2024-12.pdf

Results

Key details about Priscochelys hegnabrunnensis

Type Specimen: A single, fragmentary bony plate with sulci (grooves) on the external surface.

Fossil location and age: Found in Hegnabrunn, Germany (Fig. 2); Middle Triassic (lower Ladinian).

Significance: The specimen is important because it pushes back the date of the first appearance of turtles by about 20 million years.

Morphology: The shell exhibits features like irregularly sized, conical scutes and distinct sulci, confirming its turtle identity.

Supramarginals: It appears to have more supramarginal bones than *Proganochelys quenstedti*, another early turtle. This might suggest Priscochelys is more basal (closer to the origin of turtles).

Description of holotype SMNS 80141

SMNS80141 (Fig. 3) is a bone fragment with a maximum width of 84 mm, a maximum height of 73 mm, and a maximum thickness of 12 mm. Because we ultimately conclude the specimen to be a carapacial fragment of a stem representative of the turtle crown, we refer to the more heavily sculptured side as the dorsal surface and the smooth side as the ventral or visceral surface. For simplicity, the edge with the numerous smaller dorsal fields is referred to as the posterior. All figures of the specimens follow this convention as well. The specimen generally appears weathered, primarily along the dorsal surface, which is sculptured by numerous pockmarks. Postmortem processes that occurred while the specimen was lying on the seafloor probably created these. The ventral side, in contrast, is rather smooth, perhaps because it was protected from scavenging. All edges

FIGURE 3. Cast of the holotype of *Priscochelys hegnabrunnensis*, Karl, 2005, for comparison with the original in Karl (2005), plate 1. **A**, Dorsal. **B**, Visceral, original.

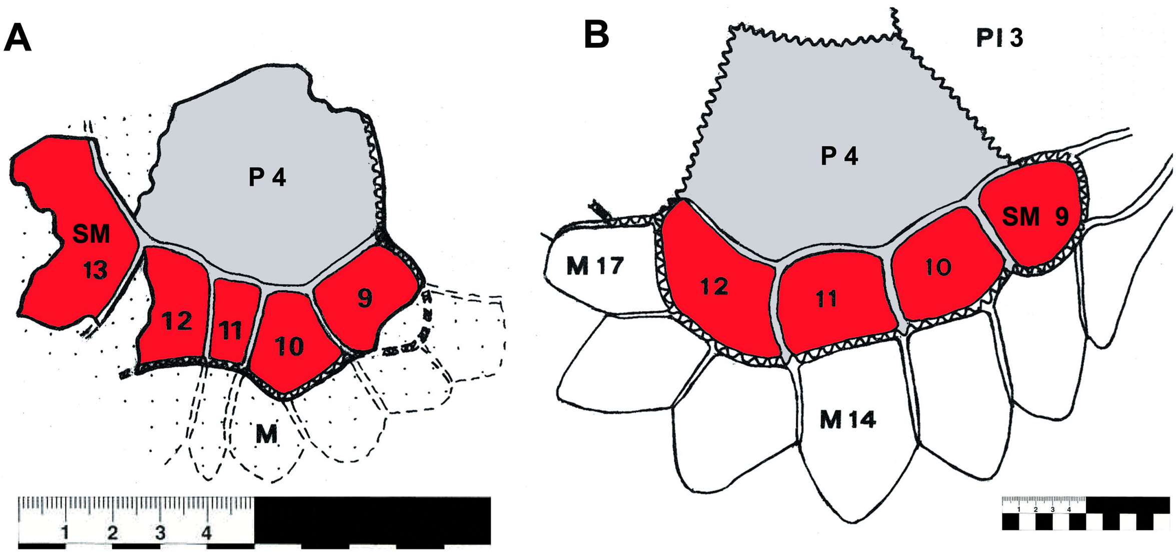

FIGURE 4. A, Schematic representation of the position of the supramarginalia on the pleural 4 of *Priscochelys hegnabrunnensis* for comparison with **B**, *Proganochelys quenstedti*. (After Karl, 2005, figure 2, modified).

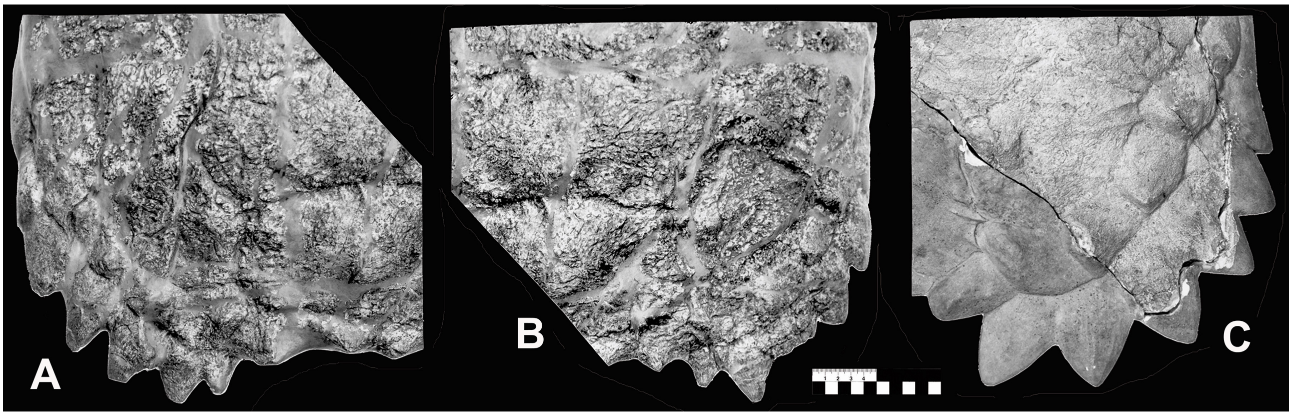

FIGURE 5. *Proganochelys quenstedti* Baur, 1887; posteriory peripheral margins according to Karl (2005), plate 2. **A**, SMNS15759. **B**, SMNS16980. **C**, Posterior peripheral margin dex., reconstruction. Photos: Archive SMNS. Scale = 10 cm.

of SMNS80141 show signs of mechanical breakage or weathering. SMNS80141 appears to be a postero-lateral carapace element and thus conclude all edges to be not broken. Clear sutures are visible on the entire specimen. In lateral view, the specimen can be subdivided into an anterior and posterior section of subequal size that stands at an angle of 20 degrees relative to the other. A slight thickening accompanies the area where the two sections meet, like the caudal edge in other turtles.

The visceral surface of SMNS80141 is rather smooth and lacks any notable features. The dorsal surface, in contrast, is characterized by numerous deep sulci that subdivide the surface into six fields, which will be referred to as supramarginals 1 through 6 as homology to the same in *Proganochelys* (Figs 4, 5). The sulci generally resemble those of turtles, by being u-shaped in cross section and by gently melting together at intersections, but they are significantly deeper than those of any previously described representative of Testudinata.

Discussion

Taxonomic identity

Numerous Triassic vertebrate groups are characterized by the presence of osteoderms. These include temnospondyls, placodonts, turtles, and numerous basal archosaurs such as aetosaurs and phytosaurs. To date, however, only two taxa are known from any time to exhibit scutes with

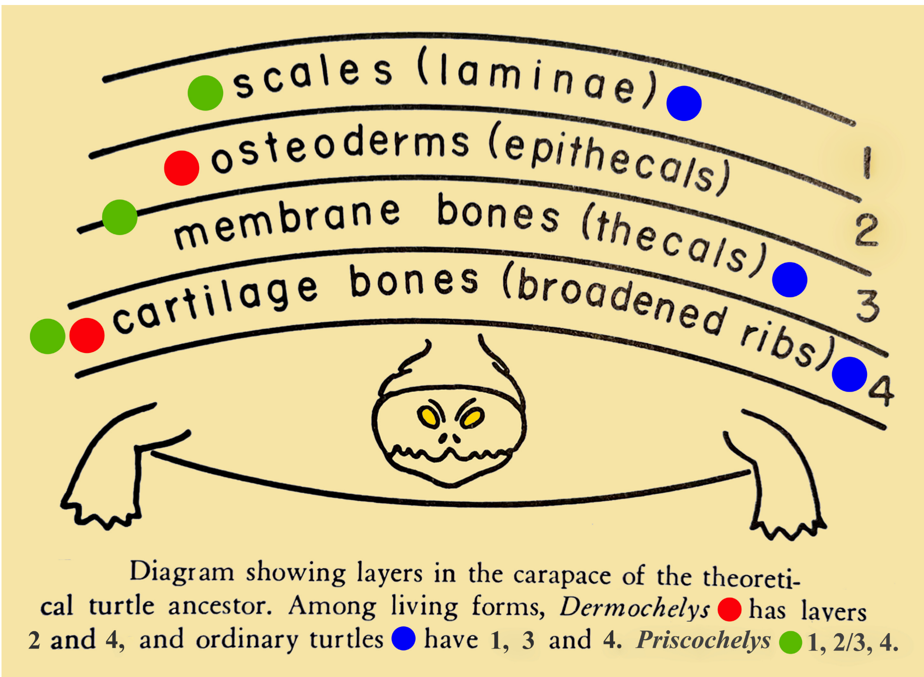

FIGURE 6. Schematic representation of the tissue layers of the turtle shell with the epithecal and thecal structure according to Carr (1955), modified and supplemented.

sulci: placodonts and turtles (Carroll, 1988). Although the possibility remains that SMNS80141 represents an unknown group with these features, we avoid such ad hoc arguments herein, focus on the positive evidence that is available, and discuss similarities and differences of SMNS80141 with representatives of placodonts and testudinates.

The bony shell of those placodonts that possess a more or less enclosed theca is comprised of bony elements of significant thickness that are overlain by epidermal scutes. Although the actual scutes are not preserved, some taxa exhibit sulci making an analogy with the turtle shell almost perfect. However, noteworthy differences exist between the shells of placodonts and those of turtles. In general, placodont thecae are comprised of a multitude of small bony elements that generally form a mosaic of regular, hexagonal plates. In contrast, the shell of turtles is generally comprised of a limited set of larger elements that correspond in their numbers somewhat to that of the underlying endochondral skeleton (Zangerl, 1969; Westphal, 1975) (Fig. 6). A placodont-like pattern can also be observed in representatives of Cenozoic dermochelyids (Fig. 7), but phylogenetic and stratigraphic considerations demonstrated this to be homoplastic (*e.g*., Völker, 1913;

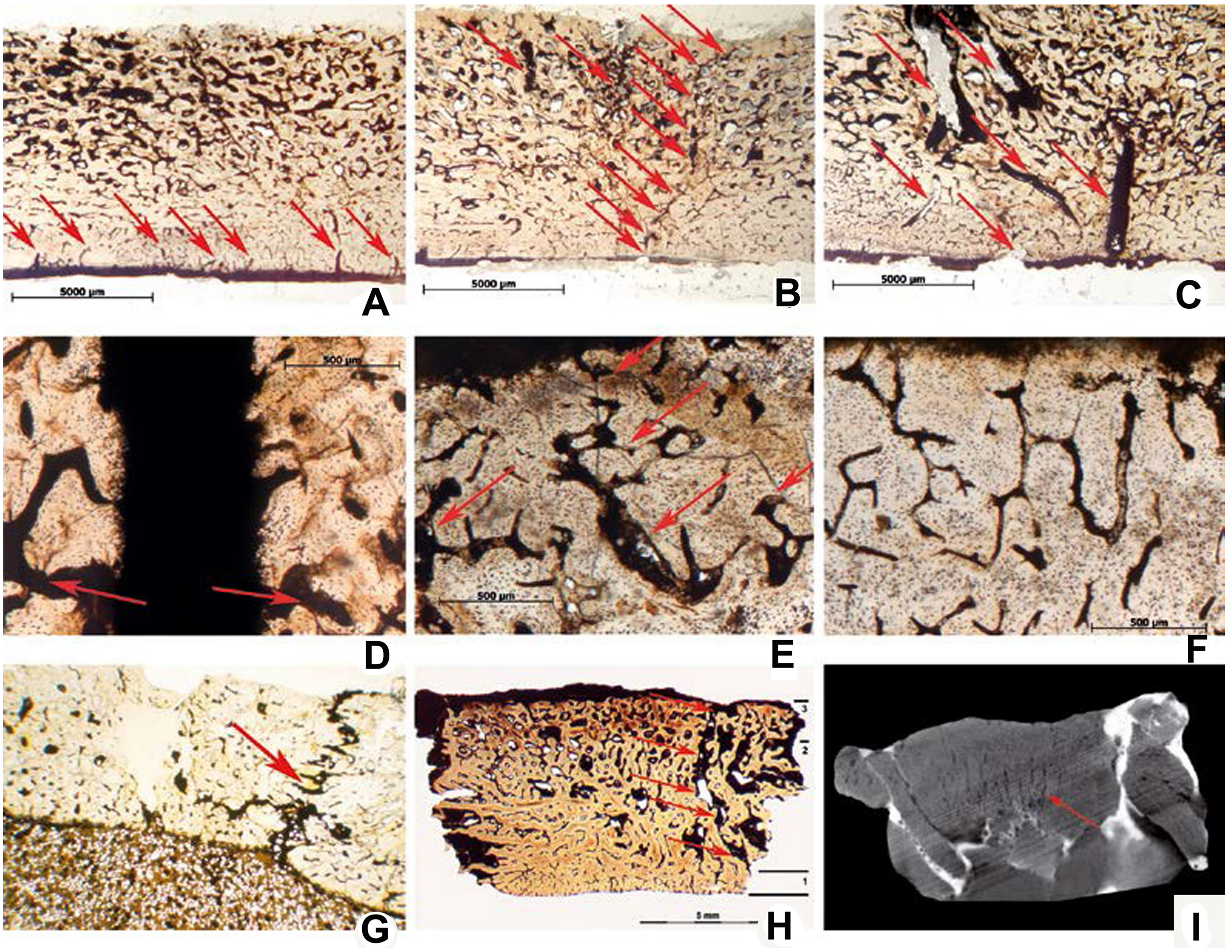

FIGURE 7. Thin sections of dermal placoids of *Pseudosphargis* and *Psephophorus* and the armour plate of *Priscochelys*. **A**, *Pseudosphargis rupeliensis* from Doberg. In contrast to *Psephophorus* (Karl, 2014; fig. 79), only a dizonation into a visceral compact and a dorsal spongy layer can be seen here. Note the massive foramina nutricius at the base. **B**, *Pseudosphargis rupeliensis* from Doberg. Course of a canalis nutricius of the Haversian system from the visceral to the dorsal surface and its radial arrangement. **C**, *Pseudosphargis rupeliensis* from Doberg. Several main ducts in the visceral area. **D**, *Pseudosphargis rupeliensis* from Doberg. One of the main ducts for the introduction into the canalis nutricius of the Haversian system runs through the entire plate and opens into the dorsal and visceral foramina nutricia. **E**, *Pseudosphargis rupeliensis* from Doberg. Stronger canalis nutricius of the Haversian system above the layer in g. **F**, *Pseudosphargis* rupeliensis from Doberg. Visceral, compact layer comparable to layer 3 in **H** with brain-like structure. **G**, *Psephophorus polygonus* from Süchteln from Rothausen. Note the clear amplitude of the suture teeth. **H**, *Psephophorus polygonus* from Karl *et al*. (2012: fig. 3). Note the clear trizonation. **I**, CT scan of the armour plate of *Priscochelys hegnabrunnensis* from Scheyer (2008: fig. 1b) with permission of Torsten Scheyer. The characteristic radially arranged main supply channels are features of the epithecal armour of Placodontia, *Priscochelys*, *Egyptemys*, *Pseudosphargis*, and *Psephophorus* and indicate a marine adaptation. a-g from Karl (2014: fig. 92), **H** from Karl *et al*. (2012: fig.3), **I** from Scheyer (2008: fig. 1 b).

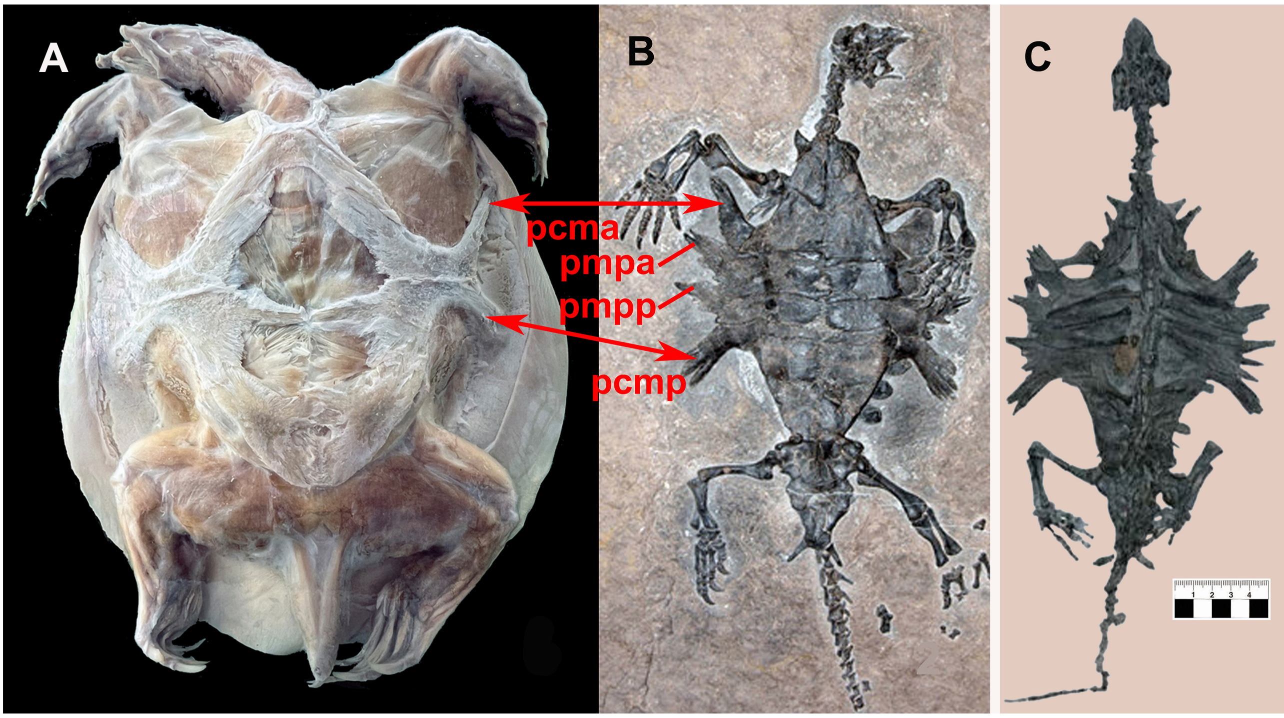

FIGURE 8. Morphology of distinct masculine cardinal processes in Odontochelys and Trionychidae. **A**, *Apalone muticus*, anatomical preparation showing the armour elements in situ from visceral, original. **B**, *Odontochelys semitestacea* after Li *et al*., 2008 visceral view. **C**, As 2 dorsal view. pcma: Processus cardinus masculi anterior; pmpa: Processus mesoplastralis anterior; pmpp: Processus mesoplastralis posterior; pcmp: Processus cardinus masculi posterior.

Versluys, 1914; Dziomber *et al*., 2020). Similarly, when present, the scutes of placodonts display a highly regular pattern of subequally sized elements that systematically correspond to the underlying bony pattern. Turtles, in contrast, display a pattern of highly variably-sized scutes. To achieve greater strength, the shells of all known basal turtles tend to fuse at maturity, in contrast to placodonts, which always display distinct sutures regardless of size (Joyce & Karl, 2006; Scheyer & Sander, 2007). Finally, the scutes of all placodonts are flat, whereas the scutes of primitive turtles are somewhat conical. In conclusion, based on the lack of distinct sutures, the presence of irregularity-sized scutes, and the conical shape of the scutes, the interpretation of SMNS80141, and as such *Priscochelys hegnabrunnensis*, as a primitive turtle is consistent by the available data and not contradicted by any morphological evidence (Joyce & Karl, 2006).

Anatomical identity

The carapace of all known turtles consists of a series of large, bilaterally symmetric scutes and can thus quickly be excluded from considerations of scutes of varying sizes arranged in four rows: a medial row of larger scutes including a nuchal, multiple vertebrals, and a pygal; a row of intermediate-sized pleurals, a row of numerous smaller supramarginals; and finally, a lateral row of smaller marginals (Gaffney, 1990).

More advanced turtles generally retain this pattern, although the row of supramarginals is quickly lost, because they appear to be functionally dispensable (Hutchison & Bramble, 1981). The scutes observable on SMNS80141 display a pattern of at least one larger scute contacting a series of at least four smaller scutes. The original size of the final scute (field 5 of the description above) is unclear, so it may be interpreted as another large scute or another small scute. The possibility that the smaller scutes represent marginals is dismissed because the hypothesized marginal scutes do not extend to the visceral surface, as is seen in all other known turtles. SMNS80141 is thus interpreted as possessing at least one pleural scute that contacts a series of at least four supramarginal scutes. A similar arrangement of scutes is otherwise only known from *Proganochelys quenstedti*, although differences exist in the shape and size of the putative supramarginals. Karl's (2005) interpretation of SMNS80141 as representing the most posterior pleural and supramarginals is primarily based on the curved suture that exists between the putative Pleural and supramarginals, as seen *P. quenstedt*i (Joyce & Karl, 2006).

Histological identity

A main argument of Scheyer (2008) was the existence of supply channels inside the armour plate of *Priscochelys hegnabrunnensis* (Fig. 7I), Karl (2014) also demonstrates thin sections of epidermal placoids of dermochelyidae (Fig. 7A–G) which also have a canal system in the dermalplacoids. Scheyer (2008) worked on *Priscochelys hegnabrunnensis*, and challenged the previous interpretations of its placement within the turtle lineage as he argued that features like conical scutes and the presence of foramina, previously considered key indicators of its turtle identity, were more characteristic of placodonts (specifically, cyamodontoid placodonts). His analysis suggested *P. hegnabrunnensis* is not a stem turtle, but rather a piece of cyamodontoid armour.

Phylogenetic relationships

The presence of distinct masculine cardinal processes in *Odontochelys semitestacea* and the corresponding relationships between the plastral bridges to the carapace and the comparable elements in Trionychidae (*Apalone muticus*) (Figs 8A, 2) as well as the flattened ribs (Fig. 8C) suggest a postmortem lost epithecal armour as in *Priscochelys*, which is assumed here (Karl, 2012) (Fig. 9). Based on the presence of a turtle shell consisting of dermal bone and scutes and the presence of a complete row of supramarginals, SMNS80141 can be phylogenetically within the clade Testudinata but must be considered more primitive than *Proterochersis robusta*. Only three other turtles are currently hypothesized to be more primitive than *Proterochersis robusta*, namely *Proganochelys quenstedti* from the Late Triassic of Germany, *Palaeochersis talampayensis* from the Late Triassic of Argentina, and *Australochelys africanus* from the Late Triassic/Early Jurassic of South Africa. The latter two taxa are currently only known from insufficient carapacial material and therefore cannot be compared to SMNS80141. The question thus remains whether SMNS is the sister to or whether it is more primitive or derived than *P. quenstedti* relative to the turtle crown (Joyce & Karl, 2006). SMNS80141 and *Proganochelys quenstedti* are currently the only turtles known to possess a complete row of supramarginals, but it ultimately unclear if this is the symplesiomorphic condition (thus indicating a basal grade of turtles) or the synapomorphic condition (thus uniting *Proganochelys quenstedti* and *Priscochelys hegnabrunnensis* as a clade). If field V is interpreted as a supramarginal, then *Priscochelys hegnabrunnensis* differs from *Proganochelys quenstedti* by having five supramarginals contact a lateral scute, instead of just four. Given the general trend in chelonion evolution towards the reduction of scutes in general (Hutchison & Bramble, 1981) and the supramarginals in particular (*e.g.*, Joyce, in Review), the presence of an additional supramarginal

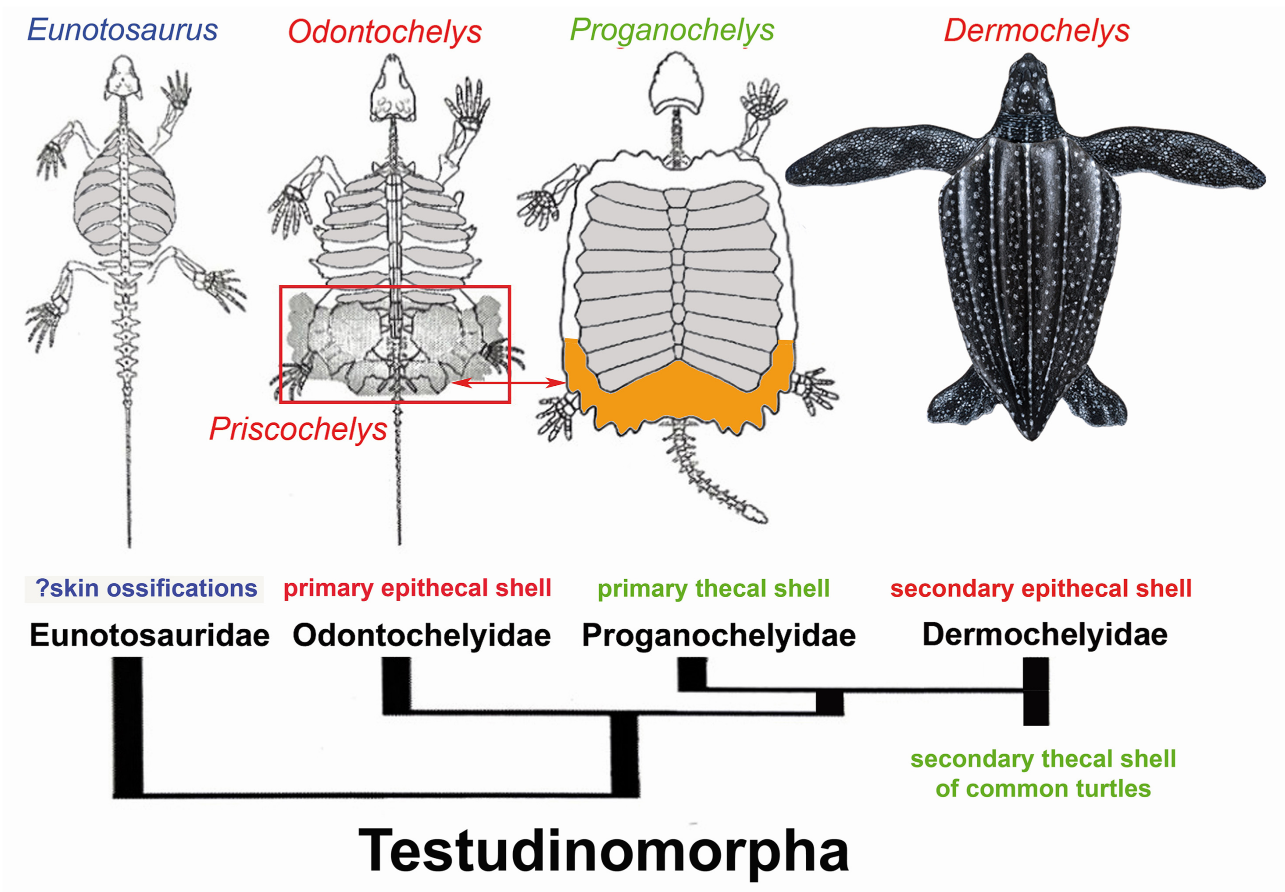

FIGURE 9. Overview of Testudinomorpha to illustrate the multiple occurrences of epithecal armour formations after Karl, 2012, 2013: figure 15, added.

scute may be taken as weak evidence in support of a basal position of *Priscochelys hegnabrunnensis* relative to *Proganochelys quenstedti*. Such a hypothesis is generally consistent with its stratigraphically older age as well (Joyce & Karl, 2006). According to our hypothesis, five stages in the major processes of shell development in the Testudinata can now be represented (Fig. 9): 1) stage with broadened ribs and probably no dermal shell (*Eunotosaurus*); 2) stage with broadened ribs and processus carnus masculi (*Odontochelone*) and epithecal shell with supply channels and visceral bone fibers *(Priscochelys*); 3) stage with primary thecal shell with connection of the skeleton and the shell (Proganochelyidae); 4) stage with secondary thecal shell (common turtles, derived from Triochychidae) and the 5) stage with secondary epidermal shell (Dermochelyidae).

Ecological Settings of Turtle Origins

A recent review of basal turtle ecology revealed that the entire phylogenetic stem of turtles must be optimized to have been terrestrial in its habitat preferences and that the origin of turtles must have occurred on land and not in water (Joyce & Gauthier, 2004; Joyce & Karl, 2006; Lepper *et al*., 2013). This is also shown by the sedimentation conditions in the Buntsandstein around the turtle track species *Chelonipus triunguis* Karl & Tichy, 2000 (Fig. 10). The ichnotaxon was described in a classic work by Lilienstern (1939). Recently, there have been increasing reports of this ichnotaxon (Lichtig *et al*., 2017; Lovelace & Lovelace, 2012; Xing *et al*., 2024a, 2024b, 2025).

For theoretical reasons, Rieppel & Reisz (1999) previously argued that the origin of turtles must have been aquatic, citing the marine provenance of SMNS80141 from Muschelkalk as positive evidence in support of their hypothesis. Although the vast majority of Muschelkalk localities indeed contain only marine fauna, the SMNS80141 locality is unique in also containing distinct terrestrial elements, notably temnospondyls and lungfishes (see "Geological Settings" above). Although it is impossible to definitively assess the ecology of *Priscochelys hegnabrunnensis* based on the morphology of a single fragment or the taphonomic conditions in which it was found, it is important to note that this lack of positive knowledge regarding its habitat preferences does not support or refute any of these hypotheses. According to the person who recovered the fossil, it was found in a geode in which the slab remnant is embedded in a reddish-brown clayey silt. We therefore assume allochthonous conditions (Fig. 11). Because it is based on a single, fragmentary specimen, *P. hegnabrunnensis* provides limited information about the turtle's overall anatomy and evolution; however, the detailed analysis of its shell morphology has contributed to our understanding of early turtle evolution and the development of the turtle shell.

The morphology of this single fragment, specifically the presence of a bony plate with visible sulci on its outer surface and the arrangement of bony sutures, confirms its identity as a turtle, not a placodont. The other key features that identify it as a turtle are:

1) Absence of distinct bony sutures: This indicates a fused shell structure characteristic of turtles.

2) Conical scutes with sulci: The presence of irregularly sized, conical scutes (bony plates) with distinct sulci (grooves) is a turtle-specific feature.

3) Supramarginals: The apparent presence of more supramarginal bones than in *Proganochelys quenstedti*

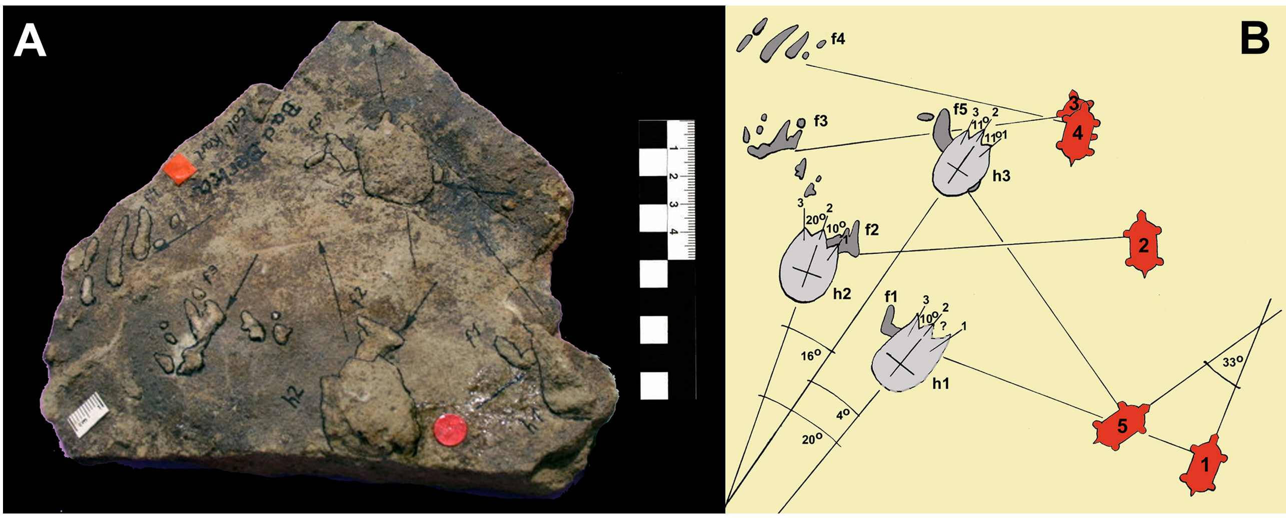

FIGURE 10. The most oldest evidence of Testudinomorphs to date. **A**, Holotype of the ichnospecies *Chelonipus triunguis* Karl & Tichy, 2000 (PLUS). **B**, Schematic representation with angular relationships to illustrate the turning movement of a turtle after Karl, 2012, modified.

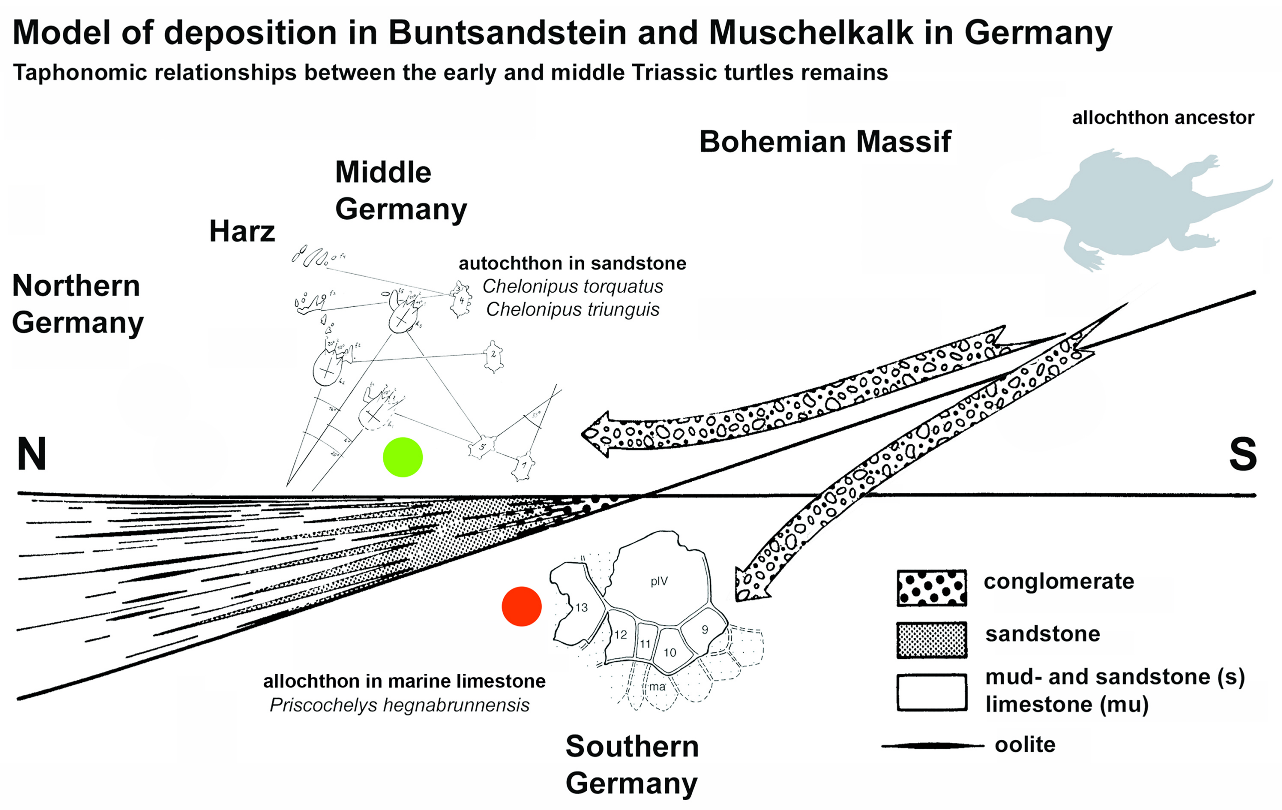

FIGURE 11. Mode of deposition in Buntsandstein and Muschelkalk in Germany with position of *Chelonipus triunguis* (green) and *Priscochelys hegnabrunnensis* (red). Adapted according to Karl, 2012.

FIGURE 12. Sections of the holotype of *Priscochelys hegnabrunnensis* SMNS80141, according to Scheyer, 2008, adapted. **A**, The lateral view shows distinct toothed suture areas of the turtle shell. **B**, The visceral view shows distinct ossified collagen fibres that serve to anchor connective tissue structures to the epithelial shell.

(an early turtle) suggests *P. hegnabrunnensis* might be one of the most basal turtle species known.

4) Placement within the Turtle Lineage: The features of *P. hegnabrunnensis* suggest it is a stem turtle, meaning it represents an early evolutionary branch of turtles. Its morphology bridges the gap between more basal turtles like *Proganochelys* and more derived forms.

Conclusion

A close review of SMNS80141, the holotype of the putative fossil turtle *Priscochelys hegnabrunnensis*, confirms its identity as a carapacial fragment of a fossil turtle. Although the type specimen is highly fragmentary, *Priscochelys hegnabrunnensis* is placed along the phylogenetic stem of turtles and speculated to be positioned basal to *Proganochelys quenstedti* relative to the crown. This assessment not only renders *Priscochelys hegnabrunensis* the oldest known, but also the most primitive unambiguous stem representative of the turtle clade. Olivier Rieppel (2017) notes in his book that the German Muschelkalk also contains placodonts, including armoured placodonts of the genus *Cyamodus*. This led to a controversy regarding whether the carapace fragment known as *Priscochelys* truly represents a turtle (which would make it the oldest known turtle) or if it instead belongs to an armoured placodont. One expert opinion, based on anatomical considerations, confirmed the chelonian nature of the fossil, while another, based on microstructural analysis of the bone, identified the carapace fragment as belonging to a cyamodontoid placodont (Joyce & Karl, 2006; Scheyer, 2008, 2009). The surprisingly rare carapace fragments from the Muschelkalk of Germany which have been definitively attributed to cyamodontoid placodonts, differ from *Priscochelys*, making the latter‘s chelonian nature more plausible. Ultimately, the specimen is too incomplete to significantly influence discussions about the origin of turtles; its importance lies more in establishing the timing of the first appearance of turtles in the fossil record, if it indeed does. Nevertheless, the debate surrounding this carapace fragment highlights how similar the body armor of turtles and camodontid placodonts can appear—an issue that will need to be revisited in discussions about the evolution of the turtle shell. This is the primary focus of this study. The oldest evidence of turtles in the Buntsandstein is *Chelonipus triunguis*.

Acknowledgements

We thank all staff members of the Staatliches Museum für Naturkunde Stuttgart, Germany, as part of the private Muschelkalk fossil collection of M. Wild of Kulmbach, for access to the important specimen SMNS80141 for examination and photographs and two reviewers for helpfull comments.

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