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Turtle origins: *Chinlechelys tenertesta* and convergence in modern cladistic analysis †

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Abstract: The phylogenetic relationships of turtles (Testudines) challenge cladistics by demonstrating the inherent weaknesses of this non-Darwinian method of phylogeny reconstruction. Recent cladistic analyses identify sauropterygians as the closest relatives of turtles, and even identify at least one sauropterygian, *Pappochelys*, as a turtle. This is based largely on convergence of several characters associated with environmental adaptation, including relative lengths of phalanges, dense gastralia placement (assumed proto-plastron) and a well-defined intertrochanteric fossa. The lack of failure testing to identify such convergence is important in the analysis of unusual taxa because it can force a taxon into the in-group as a methodological artifact, as with cladistic placement of *Eunotosaurus* within Testudines. *Eunotosaurus* was not placed in a wider vertebrate phylogeny, which later identified it is a basal member of the Caseidae. Characteristics shared by caseids and Testudines contributed to this mistake, including relative head to body size, posterior jaw articulation and a reduced number of dorsal ribs and vertebrae. Late Triassic *Chinlechelys* provides a useful window into these varied cladistic problems due to anatomical convergence. It demonstrates an intermediate step between a carapace with neighboring ribs and a carapace fused with ribs. This earlier state lacked the organizing role of the ribs in the carapace and had multiple rows of costals (dorsal osteoderms) arranged at an angle to the ribs, a condition only known in some pareiasaurs. This fits with an evo-devo model of gradual change creating a new structure (carapace) followed by adaptive radiation filling the new niches opened by that structure.

Keywords: cladistic analysis; turtles; convergence

1. Introduction

The placement of turtles within the phylogeny of vertebrates has long puzzled both paleontologists and neontologists (see [1] for a review). Recently, molecular phylogenies have centered on the placement of turtles as sister to the archosaurs, including extant birds and crocodilians. Conversely, the placement of turtles in morphological and paleontological studies using cladistic analysis (the currently popular, but non-Darwinian, method of vertebrate phylogeny reconstruction) has varied widely from allying turtles with sauropterygians or with anapsid parareptiles, with few if any archosaur links inferred (Fig. 1).

Nevertheless, these cladistic analyses have been confounded by convergence and poor methodology. Indeed, they produced the current "consensus" on turtle origins, that they are derived from sauropterygians, that is clearly an artifact of convergence.
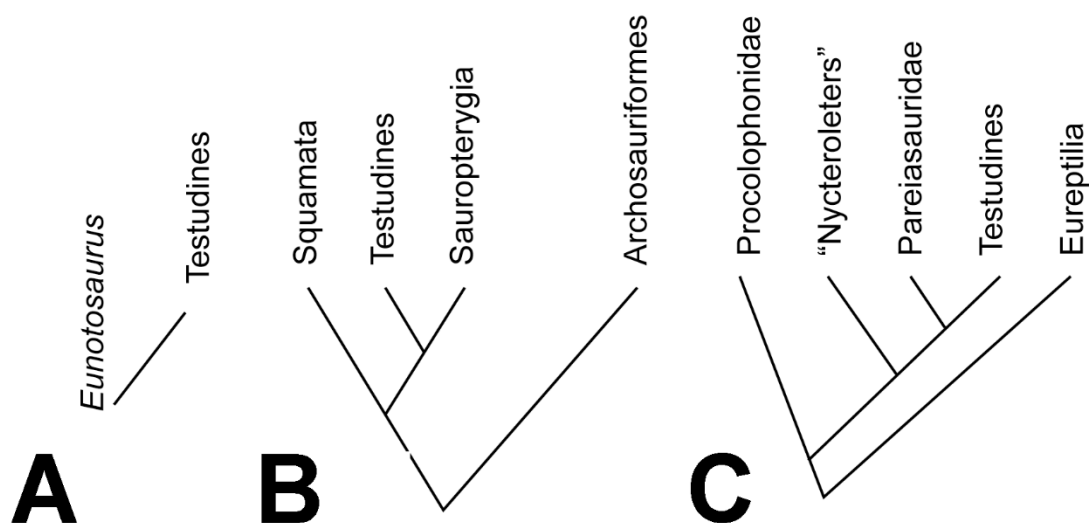
Figure 1. Cladograms showing some of the various proposed placements of turtles (Testudines) relative to other amniotes. **A.** *Eunotosaurus* as the ancestor of turtles (Watson, 1914). **B.** Turtles as the sister group to the Sauropterygia (Rieppel and Reisz, 1999). **C.** Turtles as the sister group to the Pareiasauridae (Lee, 1997).

2. Cladistic Solution 1: Turtles as Sauropterygians

Rieppel and Reisz [2] and others have argued for a diapsid origin of turtles, specifically allying them with the Triassic Sauropterygia. This group includes many previously suggested turtle ancestors that were dismissed for various reasons, including the heavily armored placodont *Henodus*. However, placodonts have in the past been argued to be a poor sister group for turtles, as their armor is formed in a manner different from that of turtles [3].

The turtle-sauropterygian relationship was given some new life with the 2015 publication of *Pappochelys rosinae*, purported to be an ancestral turtle that shared many traits with sauropterygian reptiles, particularly the placodonts. However, *Pappochelys* is a placodont and not a turtle because, among other features, it has a skull very different from any early turtle in the presence of open sutures and the pointed dorsal process of the maxilla. Furthermore, the split or merged gastralia of *Pappochelys* were interpreted as a proto-plaston despite their similarity to the gastralia of marine reptiles.

3. Cladistic Solution 2: Turtles and *Eunotosaurus*

Eunotosaurus is a basal caseid synapsid. Work by Bever et al. [4] and some papers cited there allied it with turtles, but this is a result of both taxon selection bias and the convergence of broadly phylogenetically separated taxa. *Eunotosaurus* was assumed from the outset to be a parareptile, a higher taxon of questionable validity. As such it was never cladistically compared with synapsids or even, in many analyses, eureptiles. In effect the assumption about the phylogenetic placement of *Eunotosaurus* appears to be "we need to test the phylogeny within a smaller group and we are obviously right what smaller group the animal belongs to." Thereby, either the character matrix will place unrelated taxa outside the clade or the taxon is part of the included clade, and it is assumed that the correct higher group is identified for analysis. This bias extends to the construction of the character-state matrices themselves, as such matrices are assumed effective if they output a consistent result without being checked for other biases. For example, do other animals not examined do strange things in the matrix? This may indicate that the matrix has biases dealing with outgroup taxa. This is particularly important in the case of analysis of new or unusual taxa because it can force a taxon to find a place to fit the in group just because the program is told it should be in one. It is far from true that a member of an out group placed in an analysis will always be recovered as such in the analysis.

This is highlighted in the grouping of *Eunotosaurus africanus* with Testudines. *Eunotosaurus* was always [5] considered an enigmatic taxon, but when it was later analyzed within a cladistic framework it was assumed to be a parareptile, despite the fact that some authors suggested it was a caseid synapsid (e.g. [6]). Because the assumption from the start was that *Eunotosaurus* was a parareptile, no attempt was made to place it in a wider vertebrate phylogeny. A later study [1] investigated the suggestion (never before tested) that *Eunotosaurus* is a caseid and found it likely a basal member of the group. Furthermore, other caseids entered into the reptile matrices that *Eunotosaurus* was previously entered in were found to be placed in the exact same position as *Eunotosaurus* as the outgroup to turtles and not with the caseid taxon included as an outgroup in the analysis. These few added taxa served as a failure test of the matrix previously used with *Eunotosaurus* and gave an indication that the matrix of Szczygielski [7] and, likely the previous matrices it was based on, were flawed. Given that there has been no effort to systematically study such biases it is likely there is much more to discover as far as the limitations and best ways to avoid issues with them. When the cladistic methodological problems are set aside, *Eunotosaurus* clearly is not a turtle for several reasons, including the absence of body osteoderms, the overlap of its ribs, a feature seen in no turtle and the presence of a variety of caseid and more broadly synapsid skull features.

4. Origin of the turtle carapace

Ideas about how the turtle carapace formed both anatomically and over evolutionary time have largely fallen into three categories. These are: (1) ribs broadened to form costals, (2) dermal armor formed the costals, or (3) some mix of the two. The hypotheses of a close relationship of *Eunotosaurus* and *Pappochelys* to turtles both rely on the ribs broaden to form costals hypothesis. The idea that dermal armor formed turtle costals was derisively termed the "polka dot model" by Rieppel [8] and has not seen recent support, though this model is often misconstrued as synonymous with the third model. These two models are both challenged by the anatomy of Late Triassic North American *Chinlechelys tenertesta*, which demonstrates the presence of the intermediate step between a carapace with neighboring ribs and a carapace fused with ribs (Figure 2). *Chinlechelys'* morphology fits well with the third model of both rib and osteoderm involvement in costal formation (endoskeletal and exoskeletal components). This morphology, which lacks the organizing role of the ribs in the carapace, is accompanied by multiple rows of costals (dorsal osteoderms) arranged at an angle to the ribs, a condition only known in pareiasaurs such as *Anthodon*. Furthermore, the existence of multiple rows of costals would not be expected if ribs made up the entire structure, as these have only one piece along their full length.

5. Convergence is rampant

Life is very good at finding alternate ways to make the same structure. This combined with natural selection under shared physics suggest that the same shape can arise often with a high frequency. Some notable examples include the replicated adaptive radiations of the anoles of the Caribbean Sea where the same variants arose on many islands independently but were so close anatomically it was thought several species had dispersed to each of the islands prior to the introduction of genetic testing [9, 10].

This raises the importance of the context of characters and their fine details. The atomization or simplification of characters can remove details that hint at an independent origin. For example, the costiform process of chelydrid turtles with its rib-like appearance and structure has been used to refer to any lateral projection of the nuchal bone. This kind of simplification moves cladistics toward phenetics [11] in that looking similar is all that matters, not any homology assessment. These changes are often justified based on the removal of human biases, but, in fact, simply move those biases elsewhere in the process. This can add another post hoc homology assessment at a later stage (e.g. the projection of the side of a testudinoid neural is viewed by authors as obviously not homologous, so it is coded as absent even if the feature in one specimen is very similar to a specimen in which it is coded as present).
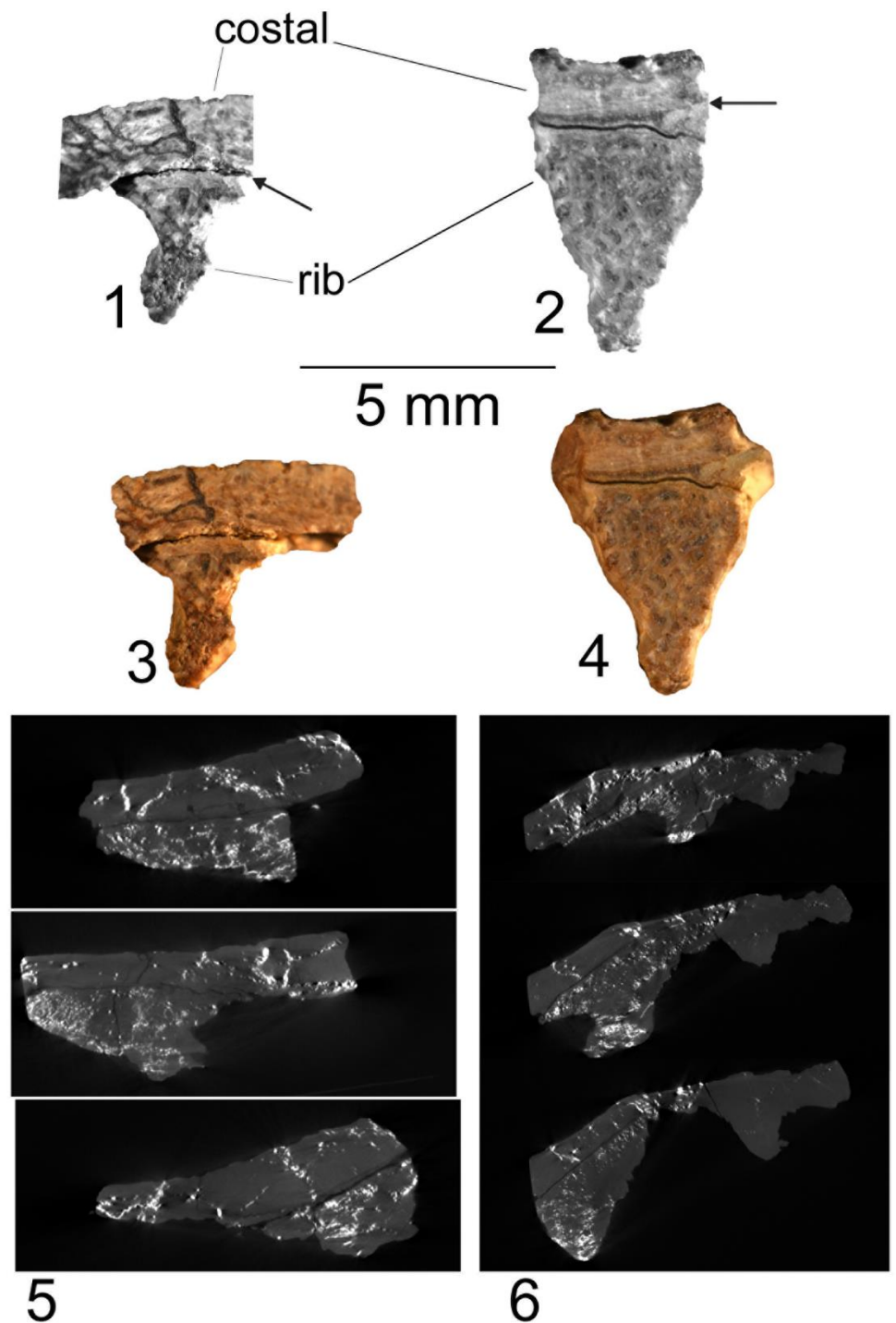
FIGURE 2. *Chinlechelys tenertesta* costal, NMMNH P-16697-3: **1,** Close up of a cross section across the rib of NMMNH P-16697-1 on the right in Figure 2.6; and **2,** cross section of rib on the left in Figure 2.6. **3,** color close up of a cross section across the same rib; **4,** color close up of a cross section; **5,** progressive ct scan slices through the rib; and **6,** progressive ct scan slices through the rib.

The atomization of characters divides the structures or functional complexes into smaller pieces, which changes the fundamental weighting of these areas in the analysis. For example, in a matrix of 100 characters you can divide 10 characters related to the forelimb into 20. You thus change the weighting from 10% forelimb to ~18%, so the 80 characters from elsewhere will carry less weight in the analysis. This may or may not cause an issue in a given case, but should be recognized as potentially biasing the results. For

example, in a turtle phylogeny with a head focus (weighted toward skull characters), what would change with a more equal weighting to the limbs and/or shell?

6. Integrating other data

It has proven challenging to integrate other sources of data with morphological cladistic analysis. The addition of a molecular backbone to some analyses has made some improvements, but this is a patch forcing one dataset to be obeyed and then asking the program to make the other dataset work in that constraint. Conversely, integrating what is known about embryology and how some changes are easier than others has been impossible thus far. Put another way, in genetic analysis programs are able to take into account the changes preferred by the underlying chemistry, but no similar constraints exist for morphological analysis. In another issue a recent study points to a gap in the set of centers of ossification in the ontogenetically early turtle skull [12]. This gap corresponds to the location of the tabular in procolophonomorphs such as pareiasaurs and might indicate a remnant of the loss of this bone (e.g., a space is still left open where the bone would have formed in early ontogeny). Should this make a sister group with an extra bone in a different place less likely?

7. Turtle Tracks

The oldest evidence of turtles is trackways in the Moenkopi Group of Utah, USA [13]. These as well as slightly younger tracks in both Utah and Germany demonstrate that the distinctive turtle method of walking was around by the late Early Triassic. A turtle's walking gait is intimately tied to its morphology, particularly its shell, and the resulting relocation of the shoulder girdle, so the trackway pattern of turtles is unique and readily recognized from that of other tetrapods (cf. [14]). This suggests that something with a more developed carapace than *Odontochelys*, the Late Triassic (Carnian) age turtle relative from China, was already present in the Early Triassic. This also suggests that the breathing modifications and other changes required for a shell were present by this point. Triassic turtle tracks are similar to those of pareiasaurs in that they have dual gait sprawling in the front and an upright gait posteriorly.

Thus, Early Triassic turtle tracks indicate that turtles and their characteristic gait had evolved by late in the Early Triassic, which is as old or older than the oldest sauropterygian fossils ([13,15,16,17]. Furthermore, the gait of turtles is quite different from the expected walking gait of sauropterygians based on their limited limb flexibility and longer bodies [18], and the length-to-width ratio of turtle trackways is inconsistent with those of a sauropterygian. Indeed, known sauropterygian track/trackways [19,20] do not even remotely resemble those of turtles.

8. Pareiasaurs and Turtles

Lichtig and Lucas [1], in a careful analysis that considered all the data, concluded that the most probable lineage to give rise to turtles is the Pareiasauridae (Fig. 3). Particularly, the dwarf pareiasaurs such as *Anthodon serriarus*, are most similar in homologous features. These similarities include the presence of ribs overlain by multiple longitudinal rows of ossifications (osteoderm or costals), dorsal ossifications oriented at a large angle to the ribs, the rigid body carapace (dorsal shell), a shared dual gait and the presence of a ventral otic notch.

9. Conclusions

In short, aspects of modern cladistic analysis, including convergence and charact atomization, have led to much confusion with regard to turtle origins. The examination of unique features gives us a more immutable standard of commonality to look to in deciphering relationships. There are no turtle features that are unique to sauropterygians, or to *Pappochelys* or *Eunotosaurus*. Instead, these taxa have been linked to turtles based on a number of widely distributed traits that happen to line up in the cladistic analysis, many of which are pleisiomorphic for the Reptilia. Furthermore, cladistic analyses that ally turtles with sauropterygians or *Eunotosaurus* have largely ignored the existence of *Chinlechelys*, which has a structure fundamentally incompatible with hypotheses relating

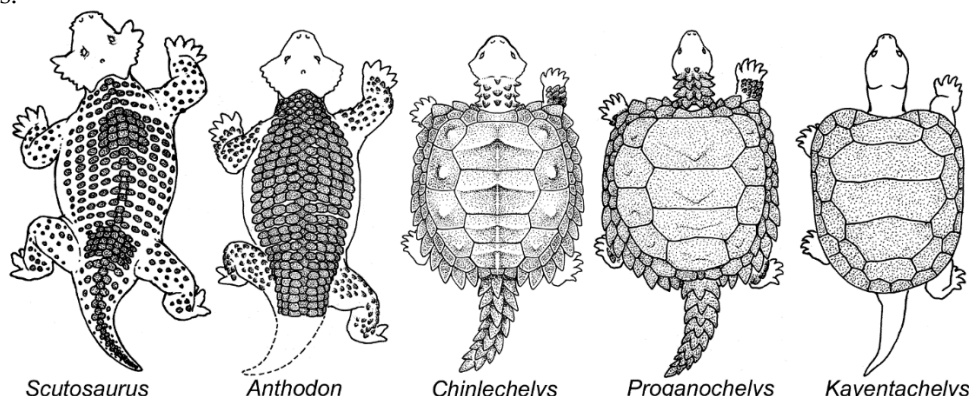it to *Pappochelys* or *Eunotosaurus*. Specifically, having both separate ribs and overlying costals.

FIGURE 3. Drawings of proposed origin of turtles from left to right: *Scutosaurus*, modified from Lee (1997), *Anthodon*, modified from Lee (1997), *Chinlechelys tenertesta*, reconstruction, *Proganochelys quenstedti*, modified from Joyce et al., (2009), *Kayentachelys*, modified from Joyce et al., (2009). Drawings by Matt Celeskey [1].

Having more than one row of costals doesn't fit with the broadened rib hypothesis. Given the unambiguous identification of *Chinlechelys* as a turtle these other two taxa cannot be turtles.

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