

Turtle Origins: *Chinlechelys tenertesta* and Convergence in Modern Cladistic Analysis †

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† Presented at the 4th International Electronic Conference on Geosciences, 1–15 December 2022; Available online: <https://sciforum.net/event/IECG2022>.

Abstract: The phylogenetic relationships of turtles (Testudines) challenge cladistics by demonstrating the inherent weaknesses of this non-Darwinian method of phylogenetic reconstruction. Recent cladistic analyses have identified sauropterygians as the closest relatives of turtles and even at least one sauropterygian, *Pappochelys*, as a turtle. These findings are largely based on the convergence of several characteristics associated with environmental adaptation, including the relative lengths of phalanges, dense gastralia placement (assumed proto-plastron), and a well-defined intertrochanteric fossa. A 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 the cladistic placement of *Eunotosaurus* within Testudines. *Eunotosaurus* was not placed in a wider vertebrate phylogeny, which led to its identification as a basal member of Caseidae. The characteristics shared by caseids and Testudines, including their relative head-to-body size, posterior jaw articulation, and reduced number of dorsal ribs and vertebrae, contributed to this mistake. 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, which is a condition only known in some pareiasaurs. This fits with an evo-devo model of gradual change creating a new structure (a carapace), which was followed by adaptive radiation filling the new niches opened by that structure.

Keywords: cladistic analysis; turtles; convergence



Citation: Lichtig, A.J.; Lucas, S.G. Turtle Origins: *Chinlechelys tenertesta* and Convergence in Modern Cladistic Analysis. *Proceedings* **2023**, *87*, 4. <https://doi.org/10.3390/IECG2022-14068>

Academic Editor: Angelos G. Maravelis

Published: 22 February 2023



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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 sisters to archosaurs, including extant birds and crocodylians. 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 anapsid parareptiles, with few if any archosaur links inferred (Figure 1).

Nevertheless, these cladistic analyses have been confounded by convergence and poor methodology. Indeed, they produced the current “consensus” on turtle origins, namely, that they are derived from sauropterygians, which is clearly an artifact of convergence.

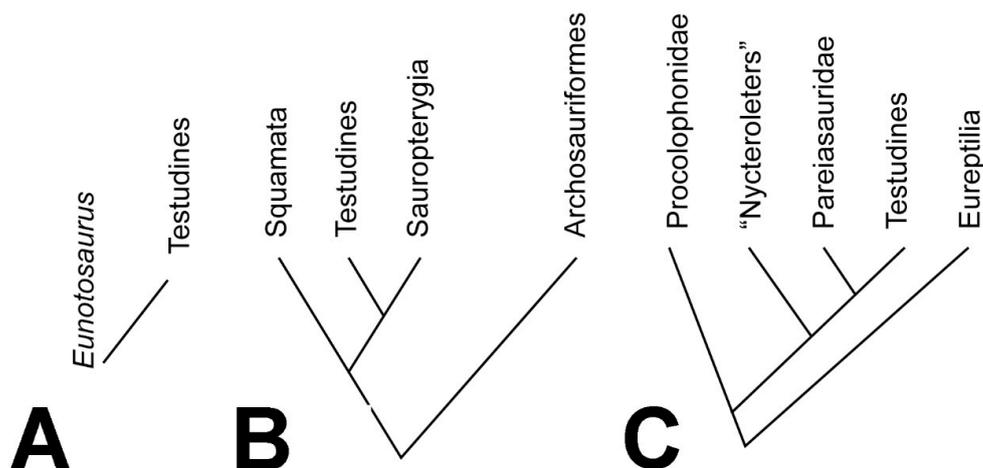


Figure 1. Cladograms showing some of the various proposed placements of turtles (Testudines) relative to other amniotes. (A) *Eumotosaurus* as the ancestor of turtles. (B) Turtles as the sister group to Sauropterygia. (C) Turtles as the sister group to Pareiasauridae.

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 previously 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*, which was 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 that is very different from any early turtle, presenting open sutures and a pointed dorsal process of the maxilla. Furthermore, the split or merged gastralia of *Pappochelys* were interpreted as a proto-plastron despite their similarity to the gastralia of marine reptiles.

3. Cladistic Solution 2: Turtles and *Eumotosaurus*

Eumotosaurus is a basal caseid synapsid. The work by Bever et al. [4] and some papers cited therein allied it with turtles, but this is a result of both taxonomical selection bias and the convergence of broadly phylogenetically separated taxa. From the outset, *Eumotosaurus* was assumed to be a parareptile, which is 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 *Eumotosaurus* 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.” Therefore, 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 to be effective if they output a consistent result without being checked for other biases. For example, do other animals not examined have strange effects on the matrix? This may indicate that the matrix has biases when dealing with outgroup taxa. This is particularly important in the case of the analysis of new or unusual taxa because it can force a taxon to find a place to fit the in-group simply because the program is told that it should be in one. It is far from true that a member of an outgroup 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]). Since the initial assumption 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 (which had never been tested) that *Eunotosaurus* is a caseid and found that it was likely a basal member of the group. Furthermore, other caseids that were entered into the reptile matrices in which *Eunotosaurus* was previously entered were found to be placed in the same position as *Eunotosaurus*, i.e., 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 developed by 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, there is likely 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, there are several reasons why *Eunotosaurus* is clearly not a turtle, including the absence of body osteoderms; the overlap of its ribs, which is a feature that has not been identified in any turtles; and the presence of a variety of caseid and more broadly synapsid skull features.

4. Origin of the Turtle Carapace

Ideas regarding how the turtle carapace formed both anatomically and over evolutionary time have largely fallen into three categories. These categories are as follows: (1) the ribs broadened to form costals, (2) dermal armor formed the costals, or (3) a combination of the previous two. The hypotheses suggesting that *Eunotosaurus* and *Pappochelys* are closely related to turtles both rely on the hypothesis that the ribs have broadened to form costals. The idea that dermal armor formed turtle costals was derisively termed the “polka dot model” by Rieppel [8] and has not seen recent support, although 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 an 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 the involvement of both ribs and an osteoderm 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, which is a condition only known in pareiasaurs such as *Anthodon*. Furthermore, the existence of multiple rows of costals would not be expected if ribs constituted the entire structure, as these have only one piece along their full length.

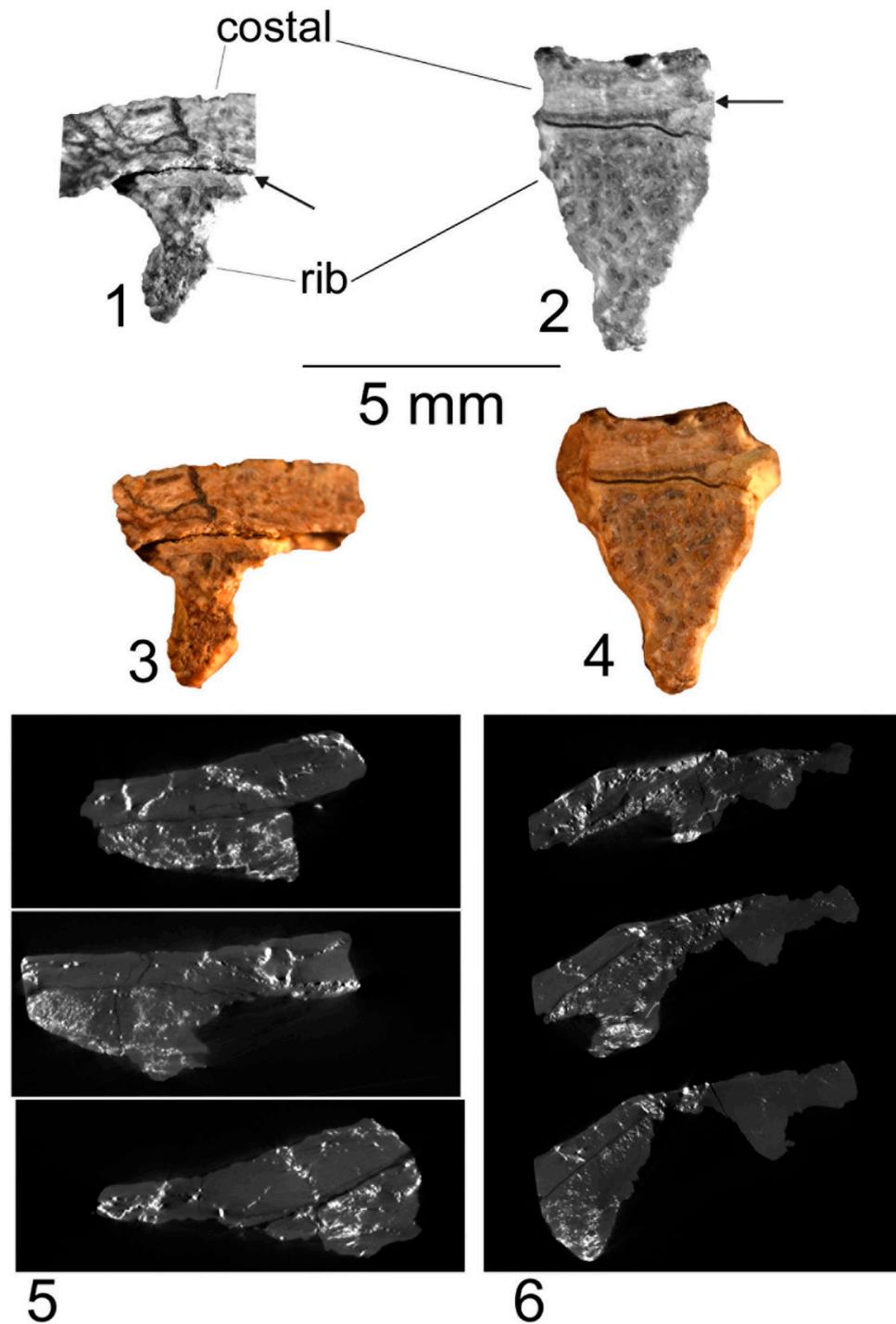


Figure 2. *Chinlechelys tenertesta* costal, NMMNH P-16697-3: (1) Close up of a cross-section across the rib of NMMNH P-16697-1 on the right in (2,6) cross section of rib on the left in (6). (3) Colorized magnified image of a cross section across the same rib; (4) colorized magnified image of a cross section; (5) progressive CT scan slices through the rib; and (6) progressive CT scan slices through the rib.

5. Convergence Is Rampant

Life is very good at finding alternate ways to form the same structure. This, combined with natural selection under shared physics, suggests that the same shape can often arise 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 that it was thought several species had dispersed to each of the islands prior to the introduction of genetic testing [9,10].

This raises the question of the importance of the context of characters and their fine details. The atomization or simplification of characteristics 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] as it suggests that looking similar is all that matters, thereby precluding homology assessment. These changes are often justified based on the removal of human biases, but they simply move those biases elsewhere in the process. This can lead to another post hoc homology assessment at a later stage (e.g., the projection of the side of a testudinoid neural plate is viewed by authors as being 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).

The atomization of characteristics divides structures or functional complexes into smaller pieces, which changes the fundamental weighting of these areas in an analysis. For example, in a matrix of 100 characters, one can divide 10 characters related to the forelimb into 20. One can thus change the weighting of the forelimb from 10% 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 a process that potentially biases the results. For example, in a turtle phylogeny focusing on the head (weighted toward skull characteristics), what would change when a more equal weighting is given 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 led to some improvements, but this is a patch forcing one dataset to be obeyed and then asking the program to make the other dataset operate within the boundaries of that constraint. Conversely, integrating what is known about embryology and how some changes occur more easily than others has been impossible thus far. Put another way, in genetic analysis, programs can account for the changes preferred by the underlying chemistry, but no similar constraints exist for morphological analysis. Regarding another issue, a recent study has indicated 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 consists of trackways in the Moenkopi Group of Utah, USA [13]. These and 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 distinguishable 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 present 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 [13,15–17]. Furthermore, the gait of turtles is quite different from the expected walk-

ing 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 that 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 relevant data, concluded that the lineage that most probably gave rise to turtles is Pareiasauridae (Figure 3). Particularly, the dwarf pareiasaurs such as *Anthodon serriarius* are the most similar in terms of their homologous features. These similarities include the presence of ribs overlain by multiple longitudinal rows of ossifications (osteoderm or costals), dorsal ossifications orienting at a large angle to the ribs, a rigid body carapace (dorsal shell), a shared dual gait, and the presence of a ventral otic notch.

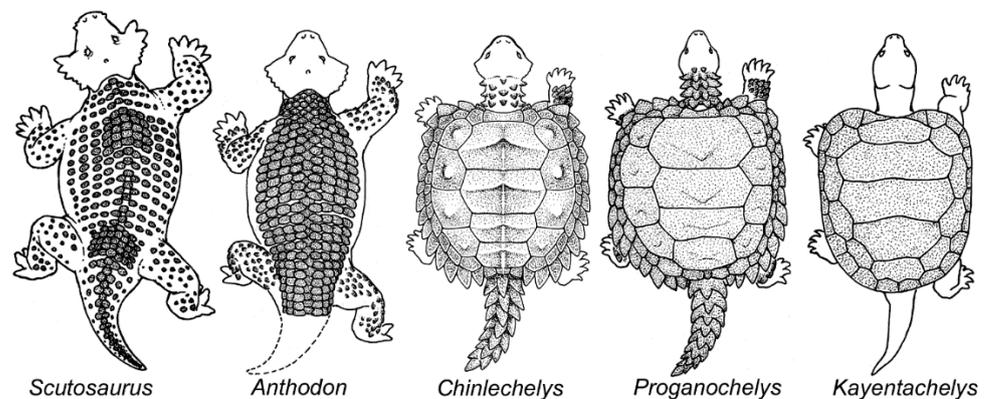


Figure 3. Drawings of proposed origin of turtles from left to right: *Scutosaurus*, modified from Lee (1997); *Anthodon*, modified from Lee (1997); *Chinlechelys tenertesta*, reconstruction; *Proganochelys quenstedti*, modified from Joyce et al. (2009); and *Kayentachelys*, modified from Joyce et al.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

9. Conclusions

In short, aspects of modern cladistic analysis, including convergence and character 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, *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 cladistic analysis, many of which are plesiomorphic for Reptilia. Furthermore, cladistic analyses that ally turtles with sauropterygians or *Eunotosaurus* have largely ignored the existence of *Chinlechelys*, which has a structure that is fundamentally incompatible with the hypotheses relating it to *Pappochelys* or *Eunotosaurus*, specifically with respect to the possession of both separate ribs and overlying costals.

The presence of more than one row of costals is incongruous with the broadened rib hypothesis. Given the unambiguous identification of *Chinlechelys* as turtles these other two taxa cannot be turtles.

Author Contributions: Conceptualization, A.J.L. and S.G.L.; methodology, A.J.L. and S.G.L.; investigation, A.J.L.; resources, S.G.L.; writing—original draft preparation, A.J.L. and S.G.L.; writing—review and editing, A.J.L. and S.G.L. All authors have read and agreed to the published version of the manuscript.

Funding: This research received no external funding.

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: Not applicable.

Conflicts of Interest: The authors declare no conflict of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript, or in the decision to publish the results.

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