



A Thin-Shelled Reptile from The Late Triassic of North America and the Origin of the Turtle Shell

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Abstract

A new, thin-shelled fossil from the Upper Triassic (Revueltian: Norian) Chinle Group of New Mexico, *Chinlechelys tenertesta*, is one of the most primitive known unambiguous members of the turtle stem lineage. The thin-shelled nature of the new turtle combined with its likely terrestrial habitat preference hint at taphonomic filters that basal turtles had to overcome before entering the fossil record.

Chinlechelys tenertesta possesses neck spines formed by multiple osteoderms, indicating that the earliest known turtles were covered with rows of dermal armour. More importantly, the primitive, vertically oriented dorsal ribs of the new turtle are only poorly associated with the overlying costal bones, indicating that these two structures are independent ossifications in basal turtles. These novel observations lend support to the hypothesis that the turtle shell was originally a complex composite in which dermal armour fused with the endoskeletal ribs and vertebrae of an ancestral lineage instead of forming de novo. The critical shell elements (i.e. costals and neurals) are thus not simple outgrowths of the bone of the endoskeletal elements as has been hypothesized from some embryological observations.

1. INTRODUCTION

Phylogenetically placing turtles within the tree of life and understanding the origin of the unique turtle shell have proved to be difficult, because testudinales are molecularly, morphologically and developmentally distinct from all other groups of amniotes (Burke 1989; Rieppel & Reisz 1999; Zardoya & Meyer 2001). An extremely poor pre-Jurassic fossil record (Lucas *et al.* 2000) only exacerbates this situation. Here, we document a new fossil taxon, *Chinlechelys tenertesta*, from the Upper Triassic of New Mexico, USA, which is the oldest known turtle from the North American main continent and comprises one of the most basal unambiguous representatives of the turtle stem lineage known to date. It is unique among basal turtles in its markedly thin shell, dorsal ribs that are not fully integrated with the overlying dermal bone and neck spines that consist of multiple osteoderms. *Chinlechelys tenertesta* provides data that are important in explaining the scarcity of basal turtles in the fossil record and constitutes significant palaeontological evidence that, concerning the debate on the origin of the turtle shell, favours a composite between the endoskeletal and dermal elements.

2. SYSTEMATIC PALAEONTOLOGY

Reptilia Linnaeus, 1758

Testudinata Klein, 1760 (*sensu* Joyce *et al.* 2004)

Chinlechelys tenertesta gen. et sp. nov.

(a) *Etymology*

'Chinle' in reference to the Upper Triassic type horizon and 'chelys' from the Greek for turtle. 'Tener' and 'testa' are Latin for delicate and shell, respectively, in reference to the thin-shelled nature of this taxon.

(b) *Holotype*

Partial skeleton including the central portion of the carapace, left hypoplastron, a posterior costal with ribs, portions of the bridge, a neck spine and isolated osteoderms (New Mexico Museum of Natural History and Science (NMMNH) collection number P-16697; figures 1*a-j* and 2*a-j*).

(c) *Horizon and locality*

NMMNH locality 001, Bull Canyon Formation, Chinle Group, Late Triassic (Revueltian: Norian) of Revuelto Creek, Quay County, New Mexico, USA (Hunt 2001).

(d) *Diagnosis*

Characters that are derived relative to non-testudinate amniotes: presence of a plastron, carapace and multi-element neck and tail armour; dorsal centra hourglass-shaped, platycoelous, with distinct ventral keel; and dorsal ribs contact two dorsal vertebrae. Derived and/or autapomorphic characters: dorsal ribs compressed, oriented vertically and only lightly associated with overlying dermal armour; double contact between dorsal vertebrae and dorsal ribs only incipient; carapace and most of plastron laminar in thickness; carapace with distinct medial ridge that widens towards posterior; plastron with sloping inguinal notch; and neck armour prongs form angular cones.

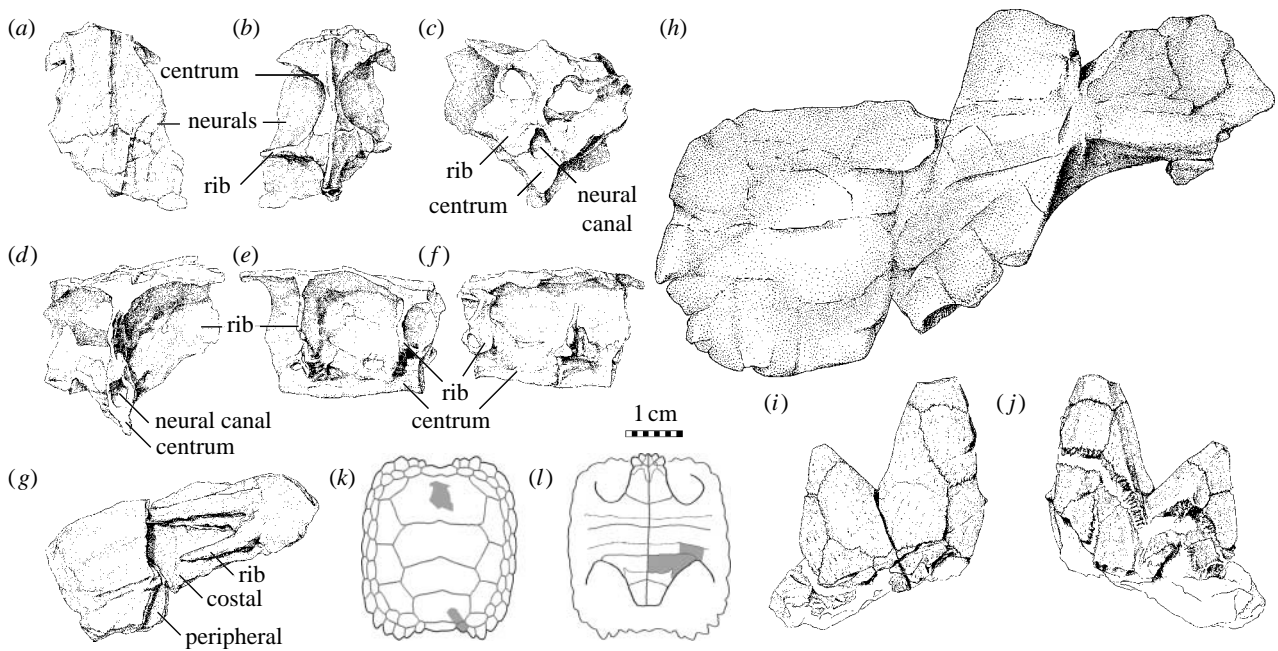


Figure 1. Illustrations of *C. tenertesta*, NMMNH P-16697. (a) Dorsal, (b) ventral, (c) anterior, (d) posterior, (e) right lateral and (f) left lateral views of a portion of the central carapace with the associated dorsal vertebrae and ribs. (g) Ventral view of a posterior carapacial fragment, consisting of two right costals, two ribs and some peripherals. Note how the ribs run superficially along the visceral surface of the overlying osteoderms. (h) Ventral view of partial left hypoplastron. (i) Anterior and (j) posterior views, respectively, of the neck spine consisting of multiple osteoderms. Approximate location of illustrated shell fragments within the (k) carapace and (l) plastron of the better known basal turtle *Proganochelys quenstedti* (redrawn from Gaffney (1990) and Joyce (2007)).

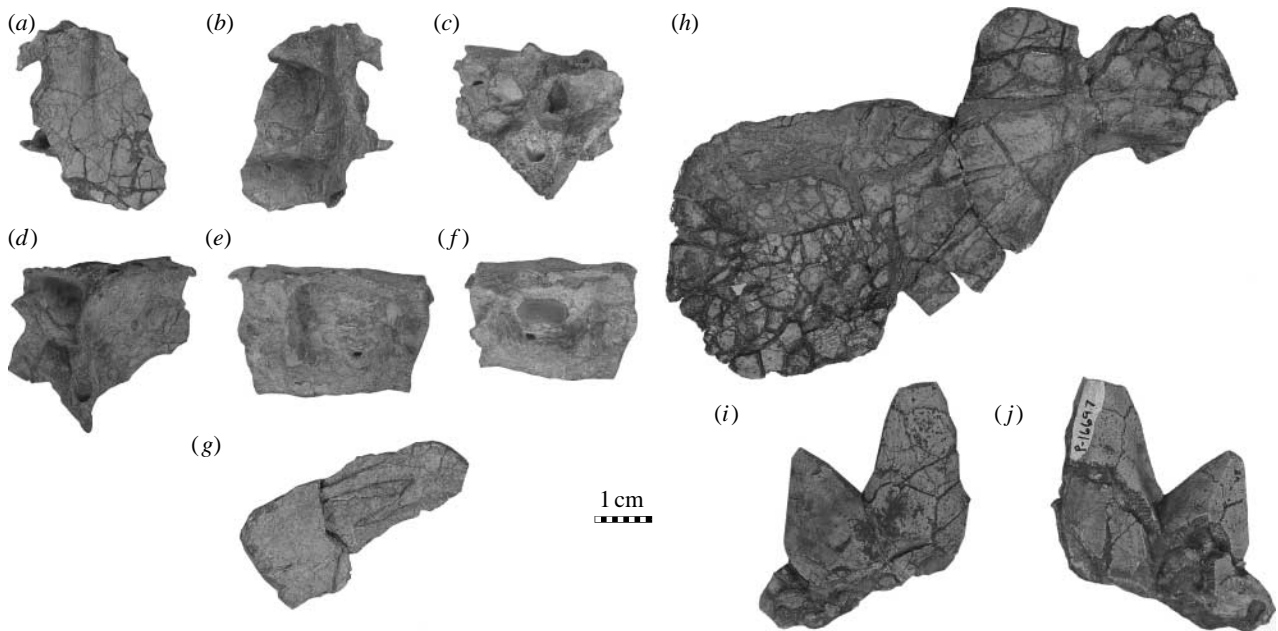


Figure 2. Photographs of *C. tenertesta*, NMMNH P-16697. (a) Dorsal, (b) ventral, (c) anterior, (d) posterior, (e) right lateral and (f) left lateral views of a portion of the central carapace with the associated dorsal vertebrae and ribs. (g) Ventral view of a posterior carapacial fragment, consisting of two right costals, two ribs and some peripherals. Note how the ribs run superficially along the visceral surface of the overlying osteoderms. (h) Ventral view of partial left hypoplastron. (i) Anterior and (j) posterior views, respectively, of the neck spine consisting of multiple osteoderms.

3. DESCRIPTION

The type specimen consists of multiple disconnected remains that were collected over the course of several field seasons. However, given that all fragments were collected from the same lithofacies and stratigraphic interval within less than 10 m², are diagnostic of Testudinata (*sensu* Joyce *et al.* 2004), exhibit the same

type of preservation and do not replicate each other anatomically, all are confidently assigned to a single species and one individual. The alternative would be the occurrence of either at least two individuals or possibly at least two sympatric Triassic basal turtle species in a small localized area that, in comparison with other localities from that time period and given

the extreme scarcity of turtle material therein, is not to be expected.

The material that most closely diagnoses *C. tenertesta* as a turtle is a portion of the carapace consisting of one and a half dorsal vertebrae, the proximal portions of the associated ribs and the overlying dermal bone (figures 1a–f and 2a–f). Although the exact location of this fragment within the dorsal column is uncertain, we speculate that it originates from the anterior portion of the column, because the neural arches increase in height posteriorly as they do in *Proganochelys quenstedti*. The central articulations of the dorsals are triangular, fully platycoelous and notably small, roughly the size of the neural canal. As in modern turtles, the main body of each dorsal centrum is hourglass-shaped in ventral view and exhibits a well-developed ventral ridge. Although the contacts are not fully clear, it appears that the dorsal rib heads only incipiently contact two dorsal centra, an unambiguous synapomorphy of Testudinata. The ribs are unique among turtles, in that they are near laminar in thickness and stand upright (i.e. are oriented dorsoventrally), the basal condition seen in most amniotes. The chamber that is formed between the ribs and the overlying carapacial bones are thus reduced in size. The neural canal is clearly discernable at the ends of the specimen and highly ovoid in shape. The narrow bridge that connects the vertebral centra with the carapace is formed by the neural arches and increases in height from anterior to posterior in the preserved portion of the specimen. The overlying carapacial bone exhibits a low sagittal keel that fades posteriorly. A single cross-running suture is present, presumably subdividing what is preserved into two wide neurals, but the lateral portions are too damaged to assess the actual shape of these elements.

The carapace is furthermore represented by a crushed portion of the bridge, various costal portions with vertical rib parts (not shown) and a fragment from the posterior region of the shell that consists of one or two peripherals, two partial costals, possible portions of the neurals and two dorsal ribs (figures 1g and 2g). Interestingly, in all elements, the dorsal ribs run elevated across the visceral surface of the costals instead of being tightly integrated into them. Thus, the dorsal ribs and costals appear to be independent osteological elements. The costals exhibit no evidence of fontanelles, indicating that the carapace was fully ossified. Sulci are not apparent, but we do not conclude that scutes were absent, as sulci are often faintly preserved in fossil turtles. The most striking feature of the carapace is its laminar thickness. Although the carapace reaches approximately 3 mm in thickness where the median keel runs the highest on the putative neurals, it quickly thins to less than approximately 1 mm in the remaining carapace. We estimate *C. tenertesta* to have had a carapace length of 35 cm by comparison of the available material with the larger but approximately coeval turtle *P. quenstedti* (Gaffney 1990), so *C. tenertesta* is the thinnest shelled turtle taxon known with a fully ossified shell.

The plastron is represented by the well-preserved left hypoplastron (figures 1h and 2h). Unfortunately, scute sulci cannot be traced, thus rendering this identification somewhat tenuous. However, the transverse orientation of the posterior suture with the xiphiplastron and the shortness of the xiphiplastral branch of the hypoplastron allow us to conclude that this must indeed be a hypoplastron. By

contrast, the anterior hyoplastral suture with the epiplastra is oblique in all basal turtles and the epiplastron branch of the hyoplastra is relatively longer. Unlike all preserved portions of the carapace, the hypoplastron is notably thick along the inguinal notch (approx. 10 mm at its deepest point), exhibits a thickened ridge that runs anteriorly towards the axillary notch (approx. 7 mm), but thins rapidly in all other directions, down to 2 mm. The inguinal notch is unique in not forming a sharp rim, but rather a sloping plate. Another fragment (not shown) is available which we interpret as the central portion of the left hypoplastron due to the presence of what appears to be the rim of the axillary notch, but this identification is tentative.

The available material of *C. tenertesta* includes various remains of non-shell-related dermal armour, the most prominent of which is a well-preserved partial neck spine of which two prongs are preserved (figures 1i,j, and 2i,j). The possibility that this element represents the serrated posterior rim of the shell is excluded, given that sufficient amounts of this region are preserved otherwise (see costal element above) and that the interpretation of this element as being the posterior rim of the carapace would imply the unparsimonious conclusion that this taxon not only possessed supernumerary bones within the tip of every marginal scute, but also additional bones along the ventral margin of the carapace. Finally, by comparison with *P. quenstedti*, the element is too large to be considered a tail spike. Despite its massive appearance, the element is hollow (Lucas *et al.* 2000), and the thickness of the preserved dermal bone is similar to that of the carapace. In comparison with the neck spines of the coeval turtle *P. quenstedti* (Gaffney 1990), the surface is smooth, and each prong forms an angular cone that is delimited from neighbouring cones by the development of a sulcus, indicating that the neck spines were covered in the living animal by keratinous scutes, much similar to the shell. Finally, unlike the previously available material of *P. quenstedti*, the new element is clearly formed by multiple osteoderms.

Prior to the discovery of more diagnostic material, the fragmentary neck spine was the only known remain of *C. tenertesta*. Lucas *et al.* (2000) noted the great resemblance of this bone to the neck spines of the Triassic turtle *P. quenstedti* (Gaffney 1990) and tentatively assigned it to Testudinata. However, this identification always appeared questionable (Gaffney *et al.* 2006), because the composite nature of this element contrasts with the apparently single and fused morphology seen in *P. quenstedti*. The recovery of the only known bona fide turtle material from the Triassic of the entire North American main continent from the same locality that produced the turtle-like neck spine leads us to firmly conclude that this spine indeed belongs to a turtle. Conversely, considering that the sutures of the shell (Gaffney 1990) or between the cleithrum and the plastron (Joyce *et al.* 2006) are obscured in the available material of *P. quenstedti*, we suggest that this taxon probably possessed multipart neck spines as well, and that the sutures were obscured during ontogeny as were those of the remaining dermal armour.

As with any species known from a single individual, assessing the relative ontogenetic age of NMMNH P-16697 is difficult. Furthermore, given that the ontogeny of basal turtles is only poorly known, comparisons with extant turtles may perhaps lead to unjustified inferences

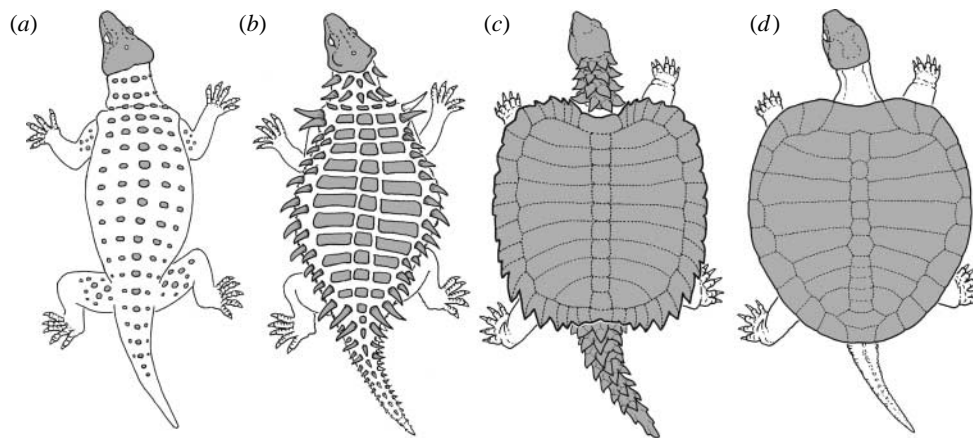


Figure 4. The composite ('gradual') origin of the turtle shell with two hypothetical ancestors. All dermal armour is highlighted in grey. Two hypothetical turtle ancestors that exhibit (a) incipient and (b) enlarged amounts of isolated, knobby dermal armour that is organized in rows. The idea of an ancestral turtle with isolated dermal armour in the skin is not new (e.g. Versluys 1914; Deraniyagala 1930; Lee 1997a), but, as with all previous authors, it serves only to illustrate the composite origin of the turtle shell. The development of dermal armour as seen in (c) the well-preserved Late Triassic turtles, *P. quenstedti*, and as was probably present in *C. tenertesta*. The dermal armour has consolidated into spikes and the turtle shell and the association of the dermal and endoskeletal component is near complete. For simplicity, the sulcus pattern is removed, thus revealing the pattern of bones only. However, given that the exact arrangement of elements is uncertain for the shell of *P. quenstedti*, the arrangement presented herein is somewhat speculative, although it appears safe to presume that this taxon has a central series of neurals, more than 10 pairs of costals and more than 11 pairs of peripherals. The modern turtle shell, as first seen in (d) the Early Jurassic turtle *Kayentachelys aprix*. At this stage, no dermal armour is present on the limbs, neck and tail, and the number of elements composing the shell and its integration are essentially at the level seen in extant turtles.

the dorsal ribs with the overlying dermal armour, the hyper thin-shelled nature of the shell and the incipient double contact of the dorsal ribs with the vertebral centra. Somewhat vertically oriented ribs are also present in *P. quenstedti* and *Palaeochersis talampayensis*, but they are significantly more massive than in *C. tenertesta* (Gaffney 1990; Sterli *et al.* 2007). Although the thin development of the ribs may again hint at a basal placement, we do not see this character as direct evidence of a basal placement, given that all remaining amniotes have well-developed ribs again. All in all, it appears most conservative to place *C. tenertesta* in a polytomy with *P. quenstedti* at the base of the turtle tree (figure 3).

(d) Turtle shell origins

The origin of the turtle shell has fascinated naturalists for more than 200 years (Cuvier 1800–1805; Vallén 1942) and the recent search for evolutionary novelty has rekindled interest in this topic. Two primary hypotheses characterize the debate. According to the composite model, the turtle shell is thought to have derived from a series of intermediate forms that possessed ever-increasing amounts of dermal armour that eventually fused with the underlying internal skeleton to form the carapace and plastron (Lee 1996; Cebra-Thomas *et al.* 2005). The de novo model, by contrast, sees the turtle shell as an evolutionary novelty that developed through outgrowths of the ribs from non-shelled forms and with no significant intermediates (Gilbert *et al.* 2001; Rieppel 2001). The terms 'gradual' and 'saltatorial' commonly used to label these hypotheses are not used herein, as they incorrectly imply that one evolutionary scenario must have occurred in less time than the other. The various highly contrasting phylogenetic hypotheses of turtle origins often directly favour one model over the other. In particular, testudinate affinities with armoured groups of reptiles (Gauthier 1994; Laurin & Reisz 1995; Lee 1996, 1997a,b) provide

phylogenetic support for the composite evolution of the turtle shell, whereas an affiliation with non-armoured amniotes (deBraga & Rieppel 1997; Rieppel & Reisz 1999; Hill 2005) favours a de novo mode.

With the apparent lack of true intermediate fossil forms that could elucidate this problem, most studies had to rely on neontological data. Embryological observations of extant turtles have repeatedly confirmed that the costal and neural bones of the carapace do not form independently from the ribs and vertebrae to recapitulate a composite phylogeny, but rather grow directly from these elements within the confines of their periosteum (Gilbert *et al.* 2001; Cherepanov 2005), hinting at an endoskeletal identity of these elements and the de novo origin of the turtle shell (Rieppel 2001). However, given that morphogenetic studies of the turtle shell focus on the early phases of development, data are typically disregarded from later stages of ontogeny. In particular, histological analyses of costal and neural bones clearly confirm an endoskeletal mode of growth for the ribs and vertebrae, but the overlying portions of the costals and neurals show residual structures of the dermis (Scheyer & Sander 2007; Scheyer *et al.* 2007), thus demonstrating that these bones are the result of ossification to the dermis *per se* (i.e. metaplastic ossification of the dermis; *sensu* Haines & Mohuiddin 1968; Main *et al.* 2005). Thus, histology supports the notion that these elements are true composites. We thus argue that neontological data alone do not conclusively identify the process by which the turtle shell originated.

Chinlechelys tenertesta is the first fossil to document directly the later phases in the development of the turtle shell by being either the most basal turtle or the least sutured basal turtle known to date. One of the most notable aspects of this taxon are the thoracic ribs that connect only poorly with the overlying costal bones. This observation supports a composite origin of the turtle shell, because basal stem turtles in this model are hypothesized to possess

shells with less strongly associated ribs and costal bones. By contrast, given that the costals are interpreted as outgrowths of the ribs, the de novo model predicts that basal turtles should have less ossified costal bones and, more importantly, that the ribs should be as tightly associated with the costals, as they are in extant turtles. Furthermore, the presence of multi-element osteoderms in the neck and tail regions indicates that *C. tenertesta* was systematically covered with rows of osteoderms along the entire length of the vertebral column and that the modern turtle shell ultimately represents a remnant population of osteoderms that consolidated in the thoracic region to form a disc and fused with the underlying endoskeletal elements (figure 4).

Given that fossil data now unambiguously reveal that the costal and neural bones are dermal in nature, we hypothesize that only minor adjustments in later portions of the developmental pathway were necessary to create the appearance that these elements are only perichondral outgrowths. Embryological observations ultimately reveal how this feat was accomplished during phylogeny. In particular, during early phases of embryology, the ribs of extant turtles grow mediolaterally into the dermis towards the carapacial ridge (e.g. Burke 1989; Kuraku *et al.* 2005). The elements now understood to be osteoderms (i.e. costals) then directly precipitate during the adjusted, later phase of development onto the rib, instead of having to form independent ossification centres within the nearby dermis. The fusion of dermal and endoskeletal anlagen in the neural and costal bones is, although not easily verifiable during development (Scheyer *et al.* 2008), interpreted as an example of Patterson's (1977) concept of 'phylogenetic fusion between a dermal bone and a cartilage bone'. It is apparent that, during phylogeny, dermal ossifications generally do not discriminate onto what former germ layer they precipitate. Thus, the tale of the origin of the turtle shell is ultimately one of simplification, where, through time, endoskeletal bone established itself as the precipitation surface of dermal bone and fully armoured forms gave rise to less armoured forms.

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