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LETTER

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Evolutionary origin of the turtle skull

G. S. Bever[1,2,3], Tyler R. Lyson[3,4], Daniel J. Field[5] & Bhart-Anjan S. Bhullar[5,6]

Transitional fossils informing the origin of turtles are among the most sought-after discoveries in palaeontology[1–5]. Despite strong genomic evidence indicating that turtles evolved from within the diapsid radiation (which includes all other living reptiles[6,7]), evidence of the inferred transformation between an ancestral turtle with an open, diapsid skull to the closed, anapsid condition of modern turtles remains elusive. Here we use high-resolution computed tomography and a novel character/taxon matrix to study the skull of *Eunotosaurus africanus*, a 260-million-year-old fossil reptile from the Karoo Basin of South Africa, whose distinctive postcranial skeleton shares many unique features with the shelled body plan of turtles[2–4]. Scepticism regarding the status of *Eunotosaurus* as the earliest stem turtle arises from the possibility that these shell-related features are the products of evolutionary convergence. Our phylogenetic analyses indicate strong cranial support for *Eunotosaurus* as a critical transitional form in turtle evolution, thus fortifying a 40-million-year extension to the turtle stem and moving the ecological context of its origin back onto land[8,9]. Furthermore, we find unexpected evidence that *Eunotosaurus* is a diapsid reptile in the process of becoming secondarily anapsid. This is important because categorizing the skull based on the number of openings in the complex of dermal bone covering the adductor chamber has long held sway in amniote systematics[10], and still represents a common organizational scheme for teaching the evolutionary history of the group. These discoveries allow us to articulate a detailed and testable hypothesis of fenestral closure along the turtle stem. Our results suggest that *Eunotosaurus* represents a crucially important link in a chain that will eventually lead to consilience in reptile systematics, paving the way for synthetic studies of amniote evolution and development.

At least 270 million years[6] of evolution within the reptile crown clade has produced a panoply of cranial forms. From the hyperkinetic anatomy of snakes to the encephalized and highly visual architecture of birds, the reptile skull is an increasingly popular model for understanding the evolution and development of vertebrate adaptation[11,12]. Turtles are an important yet enigmatic piece of this evolutionary puzzle. The earliest uncontroversial stem turtles[1,13] exhibit an anapsid skull with an adductor chamber concealed by bone (Fig. 1). Although emargination has modified this dermal covering in the vast majority of crown-group turtles[14], the absence of temporal fenestration is a feature shared by currently recognized crown- and stem-group turtles, the immediate fossil outgroups of the amniote crown clade, and many early reptiles (sauropsids)[10]. If this absence reflects conservation of the ancestral amniote condition, then turtles are an extant remnant of an early reptile radiation that excludes the other living forms (tuatara, lizards, snakes, crocodilians, birds). If, however, turtles are nested within the radiation of anatomically diapsid reptiles, which includes both the diapsid crown group and a majority of its stem lineage[15], then the anapsid skull of turtles is a secondary configuration built on an ancestrally diapsid structural plan. Despite the strong support that a diapsid origin of turtles enjoys from genomic data sets[6,7], no direct palaeontological evidence yet exists for the loss of a diapsid skull along the turtle stem. This situation epitomizes a general discord between the fossil record and the molecular signature of living taxa that

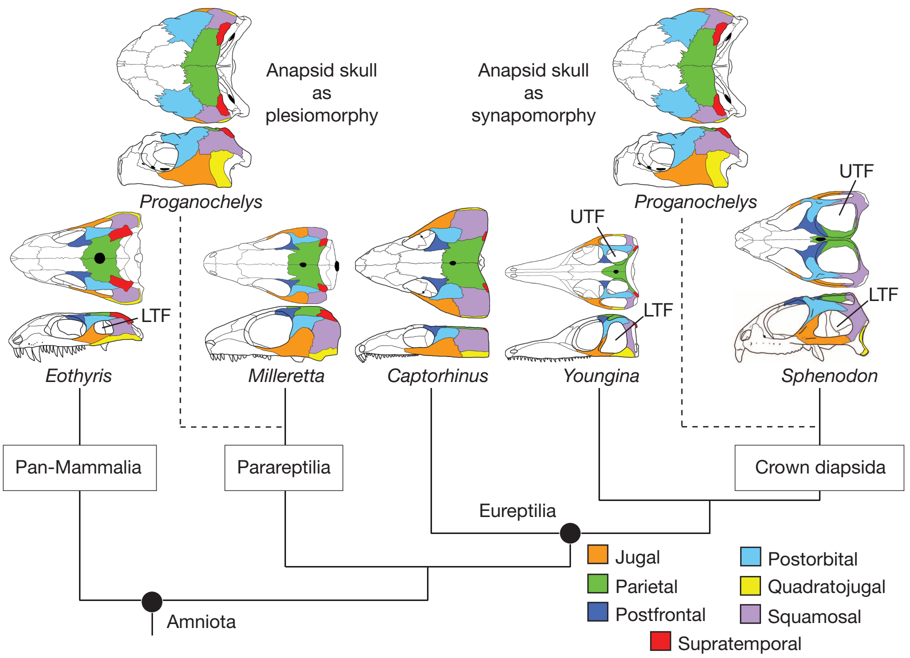

Figure 1 | Competing hypotheses for the origin of the anapsid skull of modern turtles. Historically, this closed condition was accepted as the conservation of the ancestral amniote state with turtles originating among early, long-extinct forms[10,15]. More recent analyses largely reject this hypothesis for a turtle origin within crown-group Diapsida[16,17]—a radiation that includes modern lizards, snakes, tuatara, crocodilians, and birds, and that is generally characterized by a skull with upper and lower temporal fenestrae (UTF and LTF, respectively).

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currently obfuscates attempts to synthesize broad evolutionary patterns across Reptilia[16].

Eunotosaurus africanus Seeley is an approximately 260-million-year-old fossil reptile from South Africa[17] that shares a number of uniquely derived postcranial features with turtles—features that appear to inform the evolutionary origin of the iconic turtle shell and the highly derived mechanism by which turtles ventilate their lungs[2–4]. The character-rich skull is an obvious source for testing these homology claims, but cranial details for *Eunotosaurus* remain scant. Existing studies stress the lack of cranial support for a privileged *Eunotosaurus*–turtle relationship[18–20], thus establishing a cranial–postcranial conflict that parallels the ongoing genotypic–phenotypic phylogenetic dispute. Here we use high-resolution computed tomography and phylogenetic analyses to: (1) examine the skull of *Eunotosaurus*; (2) test the current hypothesis that cranial data do not support this taxon as an early stem turtle; and (3) formulate an evolutionary model (predictive series of evolutionary steps) for the origin of the anapsid skull of modern turtles.

The skull of *Eunotosaurus* is relatively short and wide (Figs 2, 3 and Extended Data Figs 1–3). Its compact snout bears approximately 23 robust, subthecodont marginal teeth and nasals that are longer than the frontals. The palate includes an unfused basicranial articulation, an absence of basioccipital tubera, a laterally angled transverse process of the pterygoid, an edentulous ectopterygoid, a long interpterygoid vacuity, and a moderately sized suborbital fenestra. The gracile lower jaw exhibits a prominent coronoid process, a surangular that contributes to the articular surface, a splenial that does not participate in the mandibular symphysis, and 18 teeth.

The cheek is open with a single, large fenestra. The fenestra is defined anteriorly by an expanded postorbital and tall, comma-shaped jugal. Its posterior margin is formed by an elongate, vertically oriented squamosal and quadratojugal. The quadratojugal is especially tall, spanning the full height of the cheek. A lower temporal arcade is not present, leaving the cheek open ventrally. The roof of the adductor chamber in a juvenile skull is marked by a distinct upper temporal fenestra (on both sides; Extended Data Fig. 2), previously unrecognized and identical to the unique upper temporal fenestra in uncontroversial diapsid reptiles, which is separated from the lower fenestra by a completed upper temporal arcade (Fig. 3). In the adult, the upper fenestra is covered by a distinctly elongate supratemporal that contacts the postorbital and postfrontal anteriorly (Fig. 2). Digital removal of the supratemporal reveals the upper fenestra is retained in the adult, though its diameter is reduced through expansion of the surrounding elements—most notably the postorbital and squamosal (Fig. 3). The relatively late ontogenetic expansion of these bones also reduces the circumference of the lower temporal fenestra and modifies its rounded shape. The adductor chamber is closed posteriorly by what appears to be an expanded tabular, though this bony plate may represent a posterolateral flange of the parietal. The putative tabular fills a space corresponding to what would otherwise be a moderately sized post-temporal fenestra (Extended Data Fig. 3).

Phylogenetic analyses, employing maximum parsimony and Bayesian optimality criteria were performed on both the complete character matrix and one restricted to cranial features, all of which strongly support an exclusive *Eunotosaurus*–turtle clade (Extended Data Figs 4–7). Examples of turtle features expressed in the skull of *Eunotosaurus* include marked preorbital shortening, relative shortening of the frontals, prootic-quadrate contact, and an anteriorly placed craniomandibular joint[13]. The prootic also has an anterior contact with a plate-like ossification of the primary braincase wall (Extended Data

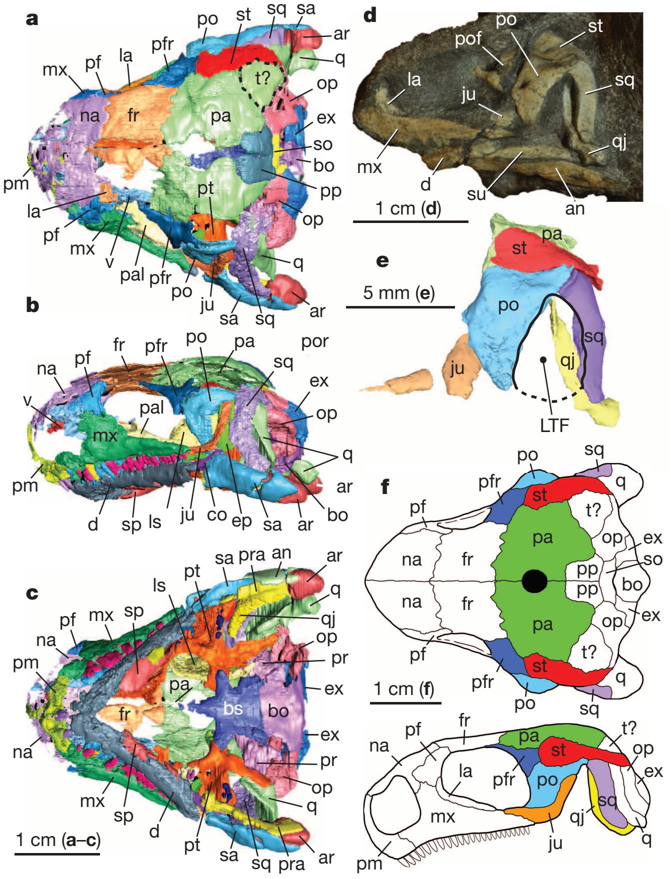

Figure 2 | The adult skull of the early stem turtle *Eunotosaurus africanus*. **a**–**c**, Dorsal (**a**), left lateral (**b**), and ventral (**c**) views of the digitally segmented skull of CM777. **d**, Reflected right lateral view of CM 86-341. **e**, Digitally rendered and reflected right lateral view of the temporal region of CM 86-341. **f**, Composite reconstruction of dorsal (top) and left lateral (bottom) views. an, angular; ar, articular; bo, basioccipital; bs, parabasisphenoid; co, coronoid; d, dentary; ep, epipterygoid; ex, exoccipital; fr, frontal; ju, jugal; la, lacrimal; ls, laterosphenoid; mx, maxilla; na, nasal; op, opisthotic; pa, parietal; pra, prearticular; pf, prefrontal; pfr, postfrontal; po, postorbital; pp, postparietal; pr, prootic; pt, pterygoid; q, quadrate; qj, quadratojugal; sa, surangular; so, supraoccipital; sp., splenial; sq, squamosal; st, supratemporal; t?, putative tabular; v, vomer.

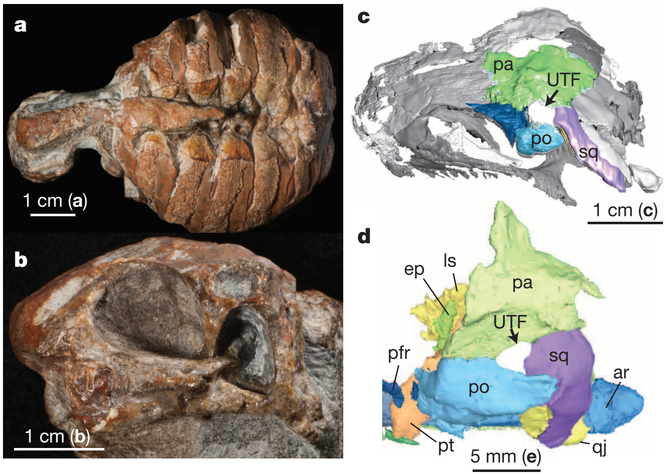

Figure 3 | The body plan of the early stem turtle *Eunotosaurus africanus*. **a**, **b**, The postcranium (**a**) and skull (**b**) of a juvenile *Eunotosaurus africanus* (SAM-PK-K7909) in dorsal and right lateral (reflected) views, respectively. **c**, **d**, The digitally rendered adult skull of *Eunotosaurus* in dorsolateral (CM777; **c**) and dorsal (CM86-341; **d**) views, with the supratemporal bone digitally removed in each. The UTF, clearly expressed in the juvenile, is retained in the adult but covered by the postnatal development of an elongate supratemporal bone. The size of the UTF and LTF of adult *Eunotosaurus* is reduced through late-stage ontogenetic expansion of the surrounding dermal elements. Abbreviations as in Figs 1 and 2. Scale bars: **a**–**c**, 1 cm; **d**, 5 mm.

Figs 1 and 3) that corresponds to a rare combination of ossified orbital cartilages present at least in *Proganochelys quenstedti* among stem turtles[21].

These data resolve the cranial–postcranial conflict in that both modules now support *Eunotosaurus* as an early stem turtle, thus bolstering evidence for the turtle stem in the terrestrial ecosystem of Gondwana approximately 260 million years ago (Supplementary Tables 1–3). Considering that *Eunotosaurus* is widely accepted as lying outside the pandiapsid radiation, this shared signal seems only to exacerbate the phylogenetic gap between the phenotypic and genotypic explanations of turtle origins. Although it is the case that neither our parsimony nor Bayesian analyses recover the dominant molecular solution of a unique turtle–archosaur relationship, both approaches do agree that turtles arose somewhere within the greater diapsid radiation (Extended Data Figs 4 and 5). Our morphological results remain ambiguous as to whether that origin is nested within the diapsid crown clade or among those stem forms expressing a morphologically diapsid skull. The lack of clear morphological support for the refined position of turtles within Eureptilia probably reflects some combination of the rate at which these stem lineages diversified and our poor understanding of their respective fossil records[22]. For example, the early lepidosaur stem comprises comparatively few taxa, and the most conservative stem archosaurs bear a striking resemblance to apparent proximal stem diapsids, throwing into question the sequence of acquisition and degree of variability of crown diapsid autapomorphies[23].

The presence of a lower temporal fenestra in *Eunotosaurus* supports the hypothesis that the characteristically closed cheek of modern turtles is a secondary condition that evolved through expansion of the jugal, quadratojugal, and squamosal[24]. Singular expression of a lower temporal fenestra once unambiguously diagnosed mammals and their stem lineage[10] but is now recognized in a number of phylogenetically disparate 'anapsid' parareptiles[25], and may represent the ancestral condition for the amniote crown[26]. This observed pattern of concentrated homoplasy near the evolutionary origin of a character state is congruent with the concept of a protracted zone of variability that may commonly confound attempts to resolve the early history of clades and character systems[27].

The amniote upper temporal fenestra has enjoyed a famously uncomplicated history, being a nearly consistent fixture of the diapsid body plan since its first appearance in the Carboniferous[28]. The combined morphologies expressed in the juvenile and adult specimens of *Eunotosaurus* provide not only the earliest direct evidence of an upper temporal fenestra in a putative stem turtle, but the first evidence for how that fenestra may have closed before the origin of the turtle crown clade. This evidence supports a model of temporal closure whose initial steps include a significant expansion of the dermal roof (postorbital, squamosal, and probably parietal) that first constricts and then closes the upper temporal fenestra (Fig. 4). Such steps are expected components of any hypothesis where turtles evolve from a diapsid ancestor. The addition of *Eunotosaurus* to this model is significant because it provides the first empirical evidence of these transitional expansions, which in turn allows the timing of these transformations to be anchored within the geological history of diapsids. *Eunotosaurus* also provides insight into the possible role of developmental timing in producing the modern anapsid condition. Phylogenetic acceleration (peramorphosis) of the inferred postnatal trajectory of dermal expansion around the temporal fenestrae of *Eunotosaurus* may explain the transition from a *Eunotosaurus*-like morphology to that expressed in *Odontochelys*, *Proganochelys*, and more crown-ward turtles.

The role of the supratemporal is an aspect of the *Eunotosaurus* model of temporal closure that would not have been predicted based on earlier studies. An anteriorly expanded supratemporal that develops late in postnatal development to cover the upper temporal fenestra must currently be considered an autapomorphy of *Eunotosaurus*. Future fossil discoveries will determine whether an expanded supratemporal was ancestral to crown-ward turtles, but it is important to stress that an expanded supratemporal is not a necessary component of an evolutionary model of fenestral closure in turtles that has *Eunotosaurus* as a central figure. For example, an analogous secondary expansion of the supratemporal partially or completely covers the upper temporal fenestra of the marine thalattosaurs[29]. Moreover, the construction of the modern turtle skull played out over a time span of tens of millions of years, and it is well attested that dermal bones in major vertebrate lineages can shift back and forth considerably relative to the underlying tissues on these timescales; for instance in the complex history of the synapsid skull and the shoulder girdle of sarcopterygians (and tetrapods, most notably turtles themselves[30]).

It is thus evident that the turtle skull, like the turtle postcranium, underwent profound modifications during its history that similarly obscured anatomical evidence for phylogenetic affinities by the time the crown-group condition was reached. The ecological context in which the earliest stem turtles lost their upper temporal fenestra is

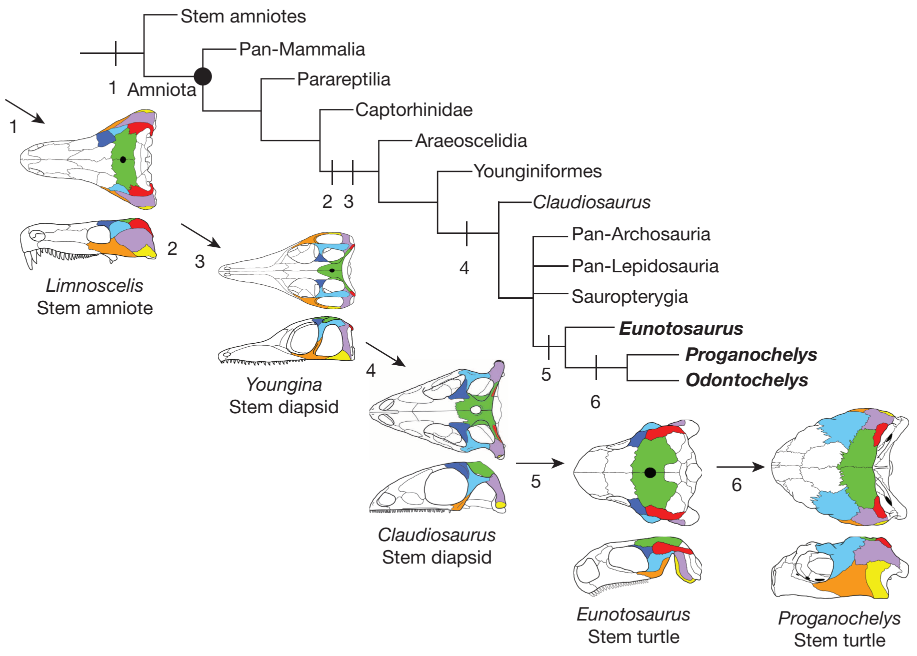

Figure 4 | Generalized amniote phylogeny showing sequence of major transformations in the origin of the turtle skull. (**1**) Ancestral crown amniote retains anapsid condition of amniote stem. (**2**) and (**3**) LTF and UTF appear, producing a fully diapsid skull. (**4**) Loss of lower temporal bar results in ventrally open LTF. (**5**) Size of UTF and LTF constricted through postnatal expansion of surrounding dermal elements (most notably postorbital and squamosal). Superficial covering of the UTF by the supratemporal, as expressed in *Eunotosaurus*, may or may not be ancestral to modern turtles. (**6**) Closure of LTF and UTF, perhaps involving a peramorphic shift in dermal bone growth. A secondary reduction of the supratemporal also may have occurred at this point.

unclear, although the upper fenestra in extant diapsids relates to the bulging of the pseudotemporalis muscle mass. It is thus likely that fenestral closure along the turtle stem had implications for the masticatory apparatus, and these implications may be reflected in the various modifications of the rostral portion of the skull.

Online Content Methods, along with any additional Extended Data display items and Source Data, are available in the online version of the paper; references unique to these sections appear only in the online paper.

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Supplementary Information is available in the online version of the paper.

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Author Contributions G.S.B. designed the study, processed the CT data, performed the analytical work, constructed the figures, and wrote the paper. T.R.L. performed analytical work, assisted writing the paper, and assisted with figures. D.J.F. and B.-A.S.B. performed analytical work and assisted writing the paper.

Author Information Reprints and permissions information is available at www.nature.com/reprints. The authors declare no competing financial interests. Readers are welcome to comment on the online version of the paper. Correspondence and requests for materials should be addressed to G.S.B. (gbever@nyit.edu).

METHODS

No statistical methods were used to predetermine sample size. The experiments were not randomized and the investigators were not blinded to allocation during experiments and outcome assessment.

Specimens and CT scanning. Although *Eunotosaurus africanus* is known from a surprisingly large number of specimens ($n > 44$), relatively few of these include cranial material (see below). Our study was built largely around the adult morphology of CM777 and CM86-341, and the juvenile features of SAM-PK-K7909. NMQR3299 was also examined, but relatively poor preservation restricted its contribution to our cranial assessments. The skull of CM 777 was scanned at the University of Texas High-Resolution X-ray CT Facility (UTCT). Scanning was performed using no filter, an air wedge, a voltage of 200 kV and a current of 0.17 mA. The resulting images were then processed for the removal of ring artefacts. The specimen was scanned along the coronal axis for a total of 1,003 slices with an image resolution of 1024 × 1024 pixels and a reconstructed field of view of 34 mm. Voxel size (mm) is 0.03657 × 0.03320 × 0.03320. Each image has a reconstructed field of view of 34 mm. Additional images are available at DigiMorph (http://www.digimorph.org/specimens/Eunotosaurus_africanus). Original slice data are available on request.

NMQR3299 (skull and postcranial skeleton) was scanned at UTCT with no filter, an air wedge, a voltage of 200 kV, and a current of 0.19 mA. Ring artefacts were removed. Scanning was performed along the coronal axis for a total of 1,764 slices with a resolution of 1024 × 1024 pixels and a reconstructed field of view of 62 mm. Voxel size (mm) is 0.06065 × 0.06065 × 0.06618. No digital segmentation of this data set was performed.

CM86-341 was scanned at the American Museum of Natural History Microscopy and Imaging Facility (AMNH MIF) using a copper filter, an air wedge, a voltage of 150 kV, and a current of 124 mA. The specimen was scanned along the coronal axis for a total of 950 slices with a resolution of 1024 × 1024 pixels and a reconstructed field of view of 35 mm. Voxel size (mm) is 0.03403 × 0.03403 × 0.03403. Digital segmentation of the recognizable cranial elements was performed using VGStudioMax2.1.

This study also includes novel morphological data derived from the recent physical preparation of two specimens of *Eunotosaurus* (using small PaleoTools microjack and microscope). CM86-341 was prepared in 2010–2012 by M. Fox (Peabody Museum, Yale University) under the direction of J. Gauthier. SAM-PK-K7670 was prepared in 2014–2015 by Z. Erasmus (Iziko Museums of South Africa) under the direction of R. Smith.

List of examined cranial specimens of *Eunotosaurus africanus*. CM86-341: beautifully preserved partial skull, completely articulated neck with a few cervical ribs, and complete carapace (nine dorsal vertebrae and nine pairs of dorsal ribs) (Fig. 2 and Extended Data Fig. 1). CM777: articulated skull, neck, elongate cervical ribs, shoulder girdle, limb elements, and cranial half of carapace including dorsal vertebrae and ribs (Fig. 2 and Extended Data Figs 2 and 3). Unnumbered CM specimen figured in ref. 19. NMQR3299: mostly complete skeleton including articulated skull (Fig. 2). NMQR3474: impression of a mostly articulated skeleton, including the skull. SAM-PK-K7670: highly weathered nodule with mostly complete skeleton including cranial two-thirds dorsal ribs and vertebrae, impressions of the cervical vertebrae, and an impression of the skull. SAM-PK-K7909: weathered nodule with complete shell and shoulder girdle, articulated neck, and essentially complete and articulated skull (Fig. 3). Juvenile based on its small size and expression of numerous features indicative of skeletal immaturity in reptiles (that is, unfused scapula and coracoid)[31,32].

Institutional abbreviations used are as follows: CM, Council for Geosciences, Pretoria; NMQR, National Museum, Bloemfontein; RC, Rubidge Collection, Graaff-Reinet; SAM-PK, Iziko Museums of South Africa, Cape Town; YPM, Peabody Museum, Yale University, New Haven.

Phylogenetic analysis. The phylogenetic relationships of *Eunotosaurus africanus* were assessed using a novel character/taxon matrix consisting of 268 characters (174 cranial, 94 postcranial) scored for 47 taxa distributed broadly across amniotes with emphasis on Pan-Reptilia. Our primary purpose was to determine how an enhanced understanding of the cranial anatomy of *Eunotosaurus* affects its phylogenetic status as an early stem turtle and the topological position of turtles in general. This is especially important considering that many of the more compelling *Eunotosaurus*–turtle synapomorphies are features associated with the iconic, shelled body plan[2–4]. While of considerable interest, the shared expression of these features also raises the question of convergence—perhaps there are only so many ways to build a shell. The skull serves as a relatively independent module on which to test the *Eunotosaurus*–turtle hypothesis.

Tree topologies were inferred using both maximum parsimony and Bayesian optimality criteria. To specifically assess the dominant phylogenetic signal within the cranial data, separate analyses were performed on the complete matrix and a matrix restricted to cranial characters. The maximum parsimony tree was generated using TNT1.1[33]. *Seymouria spp.* was specified as the outgroup, and heuristic searches were conducted using tree-bisection-reconnection (TBR) branch swapping with 1,000 replicates of random stepwise sequence addition. Minimum branch lengths were set to collapse. Support for each node was measured by calculating Bremer support and bootstrap frequencies, with 1,000 bootstrap replicates and 1,000 random sequence addition replicates. Characters 34, 62, 67, 85, 107, 118, 148, 155, 193 and 220 (Supplementary Table 1) were treated as ordered as their derived states were interpreted as non-mutually exclusive (that is, the possession of either derived state reflects shared information that should be considered in the analysis). The implications of this approach were tested by comparing the results with iterations where all characters were analysed as unordered.

Bayesian phylogenetic analyses were run using MrBayes (v3.2.2)[34] on the CIPRES Science Gateway[35]. The Mk model[36] was used to analyse the full and cranial-only character matrices with gamma-distributed rate variation and variable coding. All analyses were performed with a sampling frequency of 1,000, two concurrent runs, and four Metropolis-coupled chains ($T = 0.1$) for 30,000,000 generations. Characters 34, 62, 67, 85, 107, 118, 148, 155, 193 and 220 were again treated as ordered. All analyses were checked for convergence using standard MrBayes diagnostics (for example, PRSF < 0.01, mixing between chains $> 20\%$) and Tracer (v1.5)[37] (for example, ESS > 200). A 25% relative burn-in was implemented for all summary statistics.

A list of the cranial characters and their definitions is provided as Supplementary Table 1. Postcranial characters are taken directly from ref. 3. Supplementary Table 2 provides character scores and Supplementary Table 3 provides a list of synapomorphies for each of the reptile clades within which *Eunotosaurus* is nested. Supplementary Table 4 lists the observed specimens and primary references from which we compiled our character matrix.

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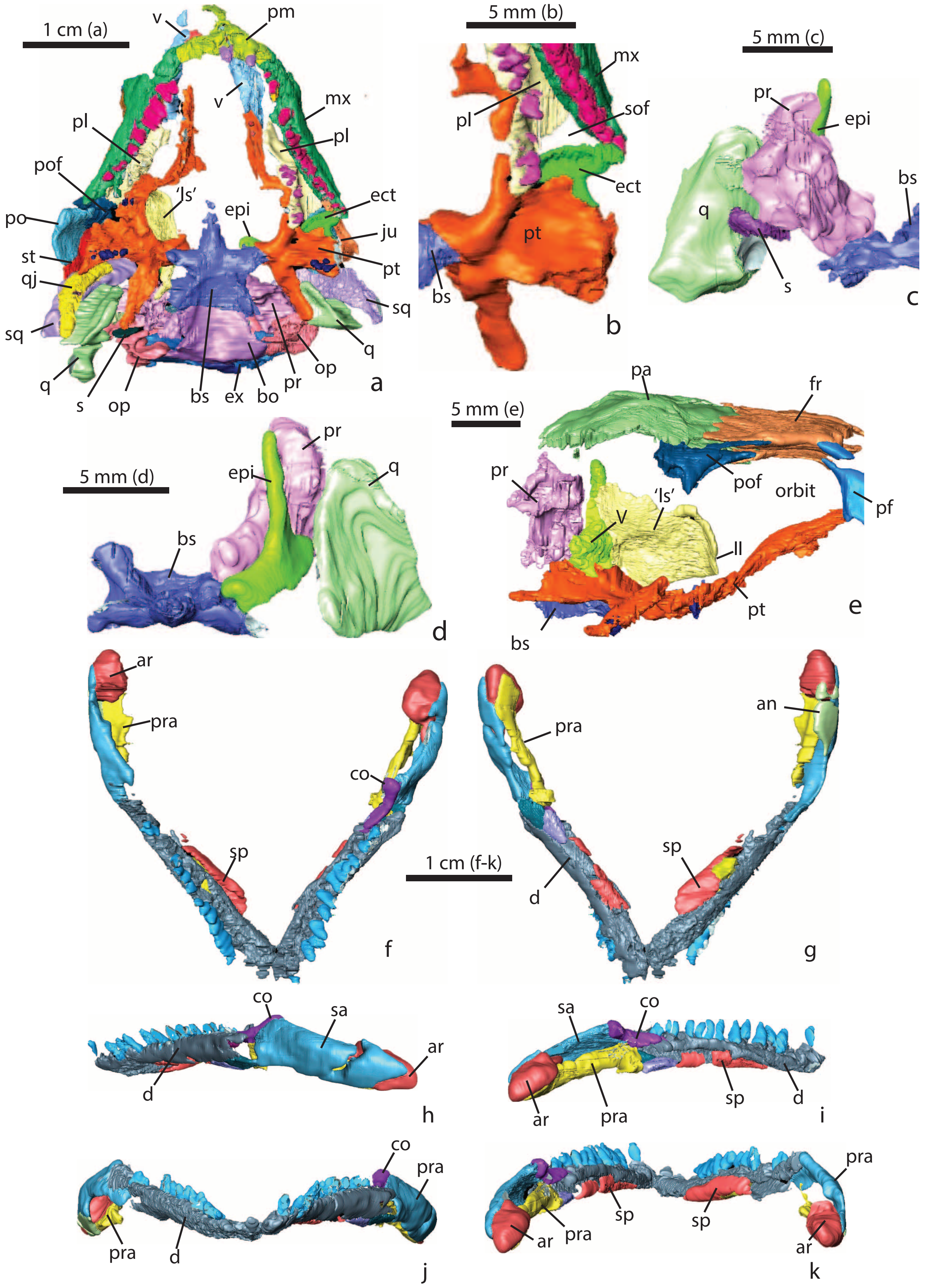
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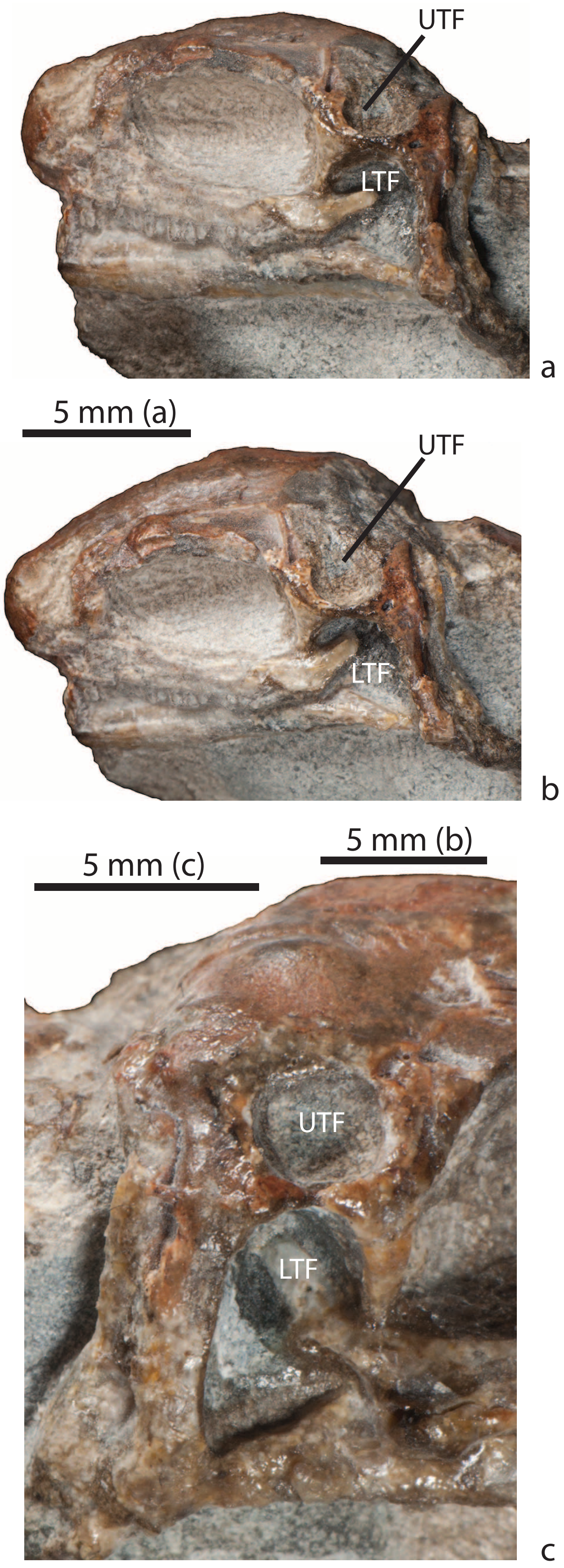
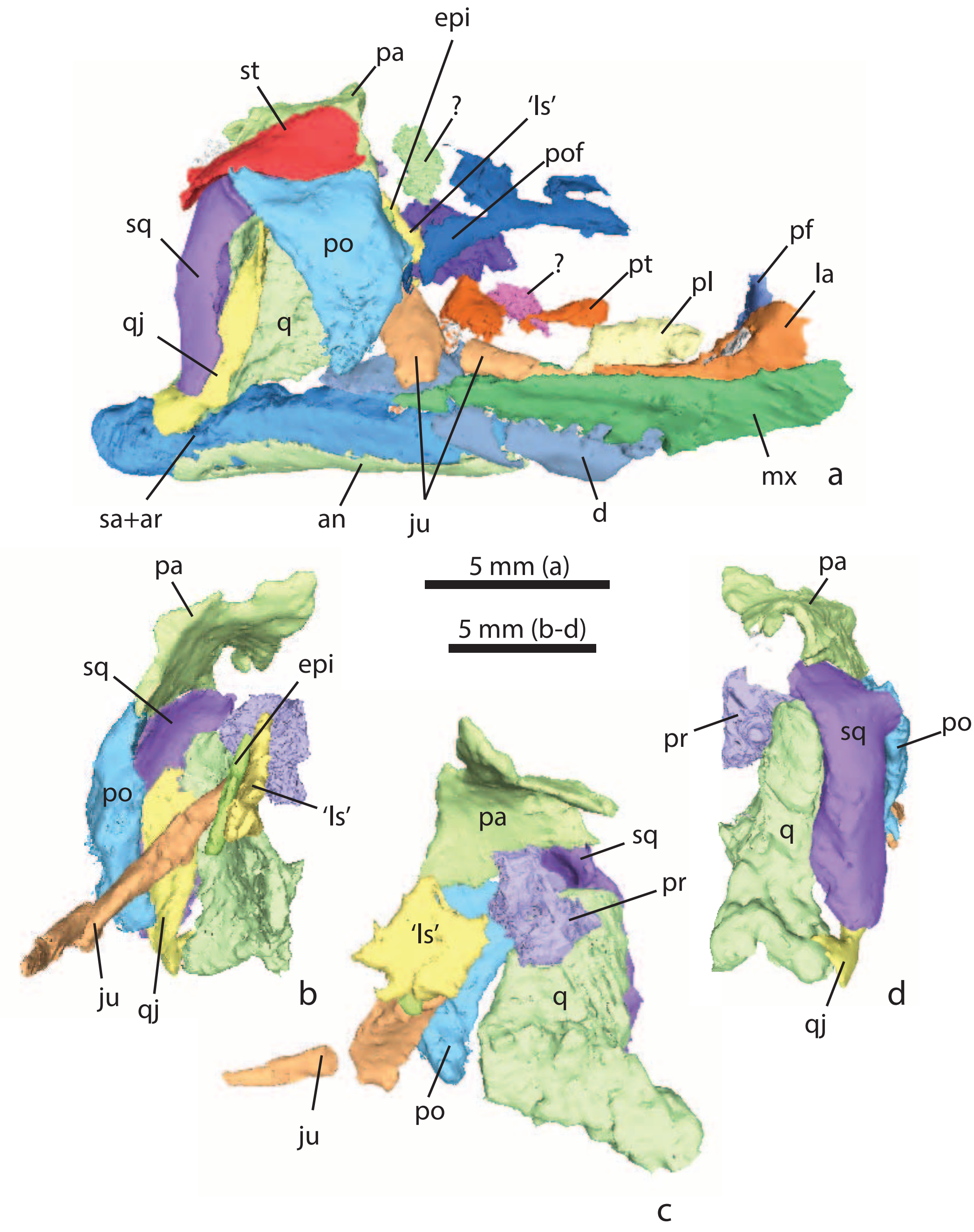
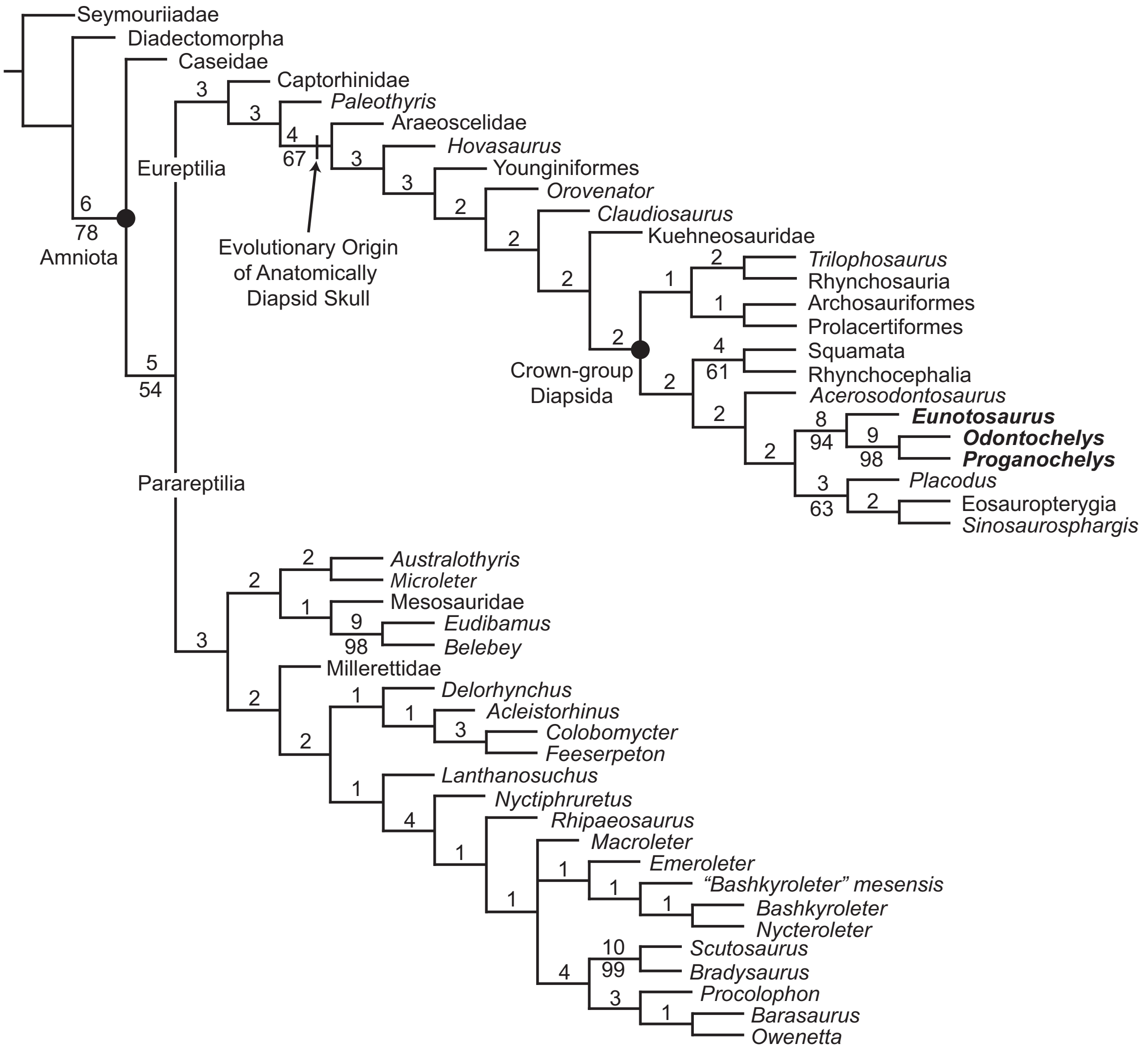
Extended Data Figure 1 | Digital reconstruction of segmented cranial elements of *Eunotosaurus africanus* CM 777. **a**, Palatal view with the lower jaws digitally removed and major roofing elements not rendered. **b**, Anteromedial view of left palate showing moderately sized suborbital fenestra. **c**, **d**, Posteromedial (**c**) and anterolateral (**d**) views of left quadrate, prootic, stapes, epipterygoid and midline parabasisphenoid. **e**, Right lateral view of anterior braincase wall and surrounding elements. Note sutural contact of prootic and quadrate. **f**–**k**, Lower jaws in dorsal (**f**), ventral (**g**), left lateral (**h**), medial (left jaw) (**i**), anterior (**j**), and posterior (**k**) views. an, angular; ar, articular; bs, parabasisphenoid; co, coronoid; d, dentary; ect, ectopterygoid; epi, epipterygoid; fr, frontal; ju, jugal; la, lacrimal; ls, laterosphenoid; mx, maxilla; op, opisthotic; pa, parietal; pf, prefrontal; pl, palatine; pm, premaxilla; po, postorbital; pof, postfrontal; pr, prootic; pra, prearticular; pt, pterygoid; q, quadrate; qj, quadratojugal; s, stapes; sq, squamosal; sof, suborbital fenestra; sp., splenial; st, supratemporal; sa, surangular; v, vomer; II, inferred exit point for orbital nerve; V, prootic incisure, exit point for trigeminal nerve.



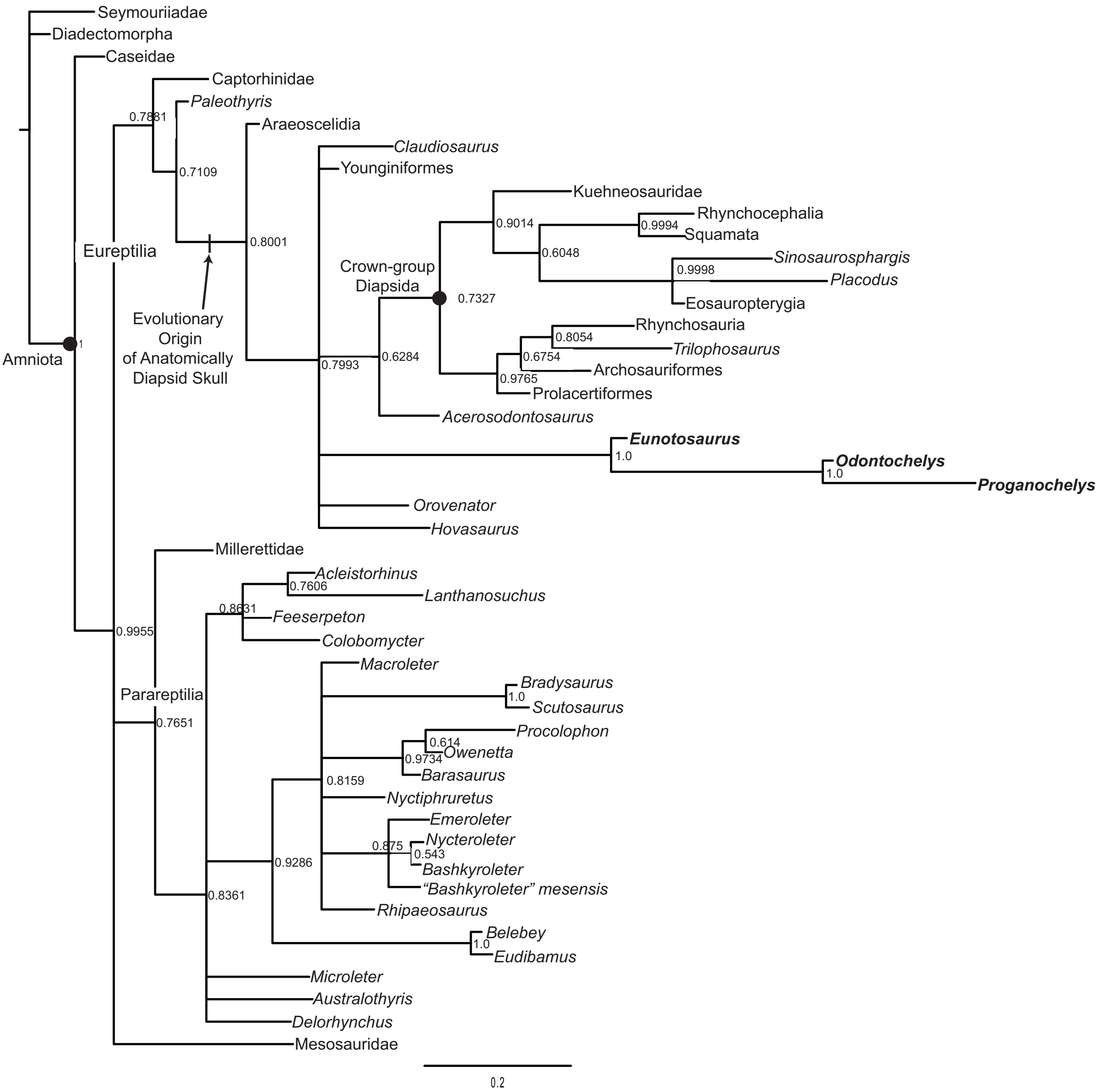
Extended Data Figure 2 | The juvenile skull of *Eunotosaurus africanus* (SAM-PK-K7909) showing clear expression of both LTF and UTF. **a**, **b**, Left lateral view with the rostrum held horizontally (**a**) and slightly downturned (**b**). **c**, Close-up view of fenestrated cheek in right lateral view. The size of the fenestrae decreases in the late stages of postnatal ontogeny through expansion of the surrounding dermal bones. The upper temporal fenestra is eventually obscured by the late-stage ontogenetic development of an elongate supratemporal.



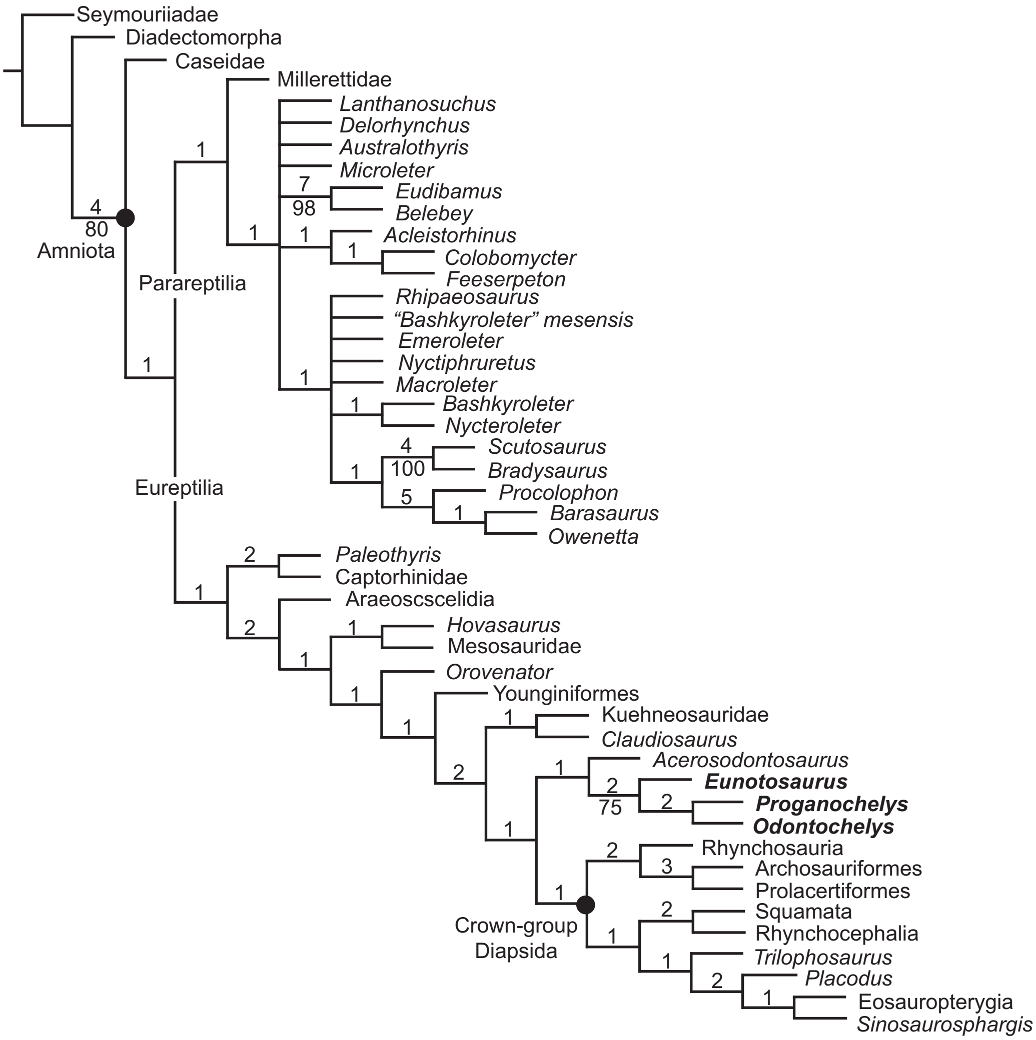
Extended Data Figure 3 | Digitally segmented and reconstructed cranial elements of *Eunotosaurus africanus* (CM86-341). a–d, Right lateral view (**a**), anterior (**b**), posterior (**c**), and right medial (**d**) views. an, angular; d, dentary; epi, epipterygoid; ju, jugal; la, lacrimal; 'ls', 'laterosphenoid'; mx, maxilla; pa, parietal; pf, prefrontal; pl, palatine; po, postorbital; pof, postfrontal; pt, pterygoid; q, quadrate; qj, quadratojugal; sa + ar, surangular and articular; sq, squamosal; st, supratemporal; UTF, upper temporal fenestra; ?, unclear identity.



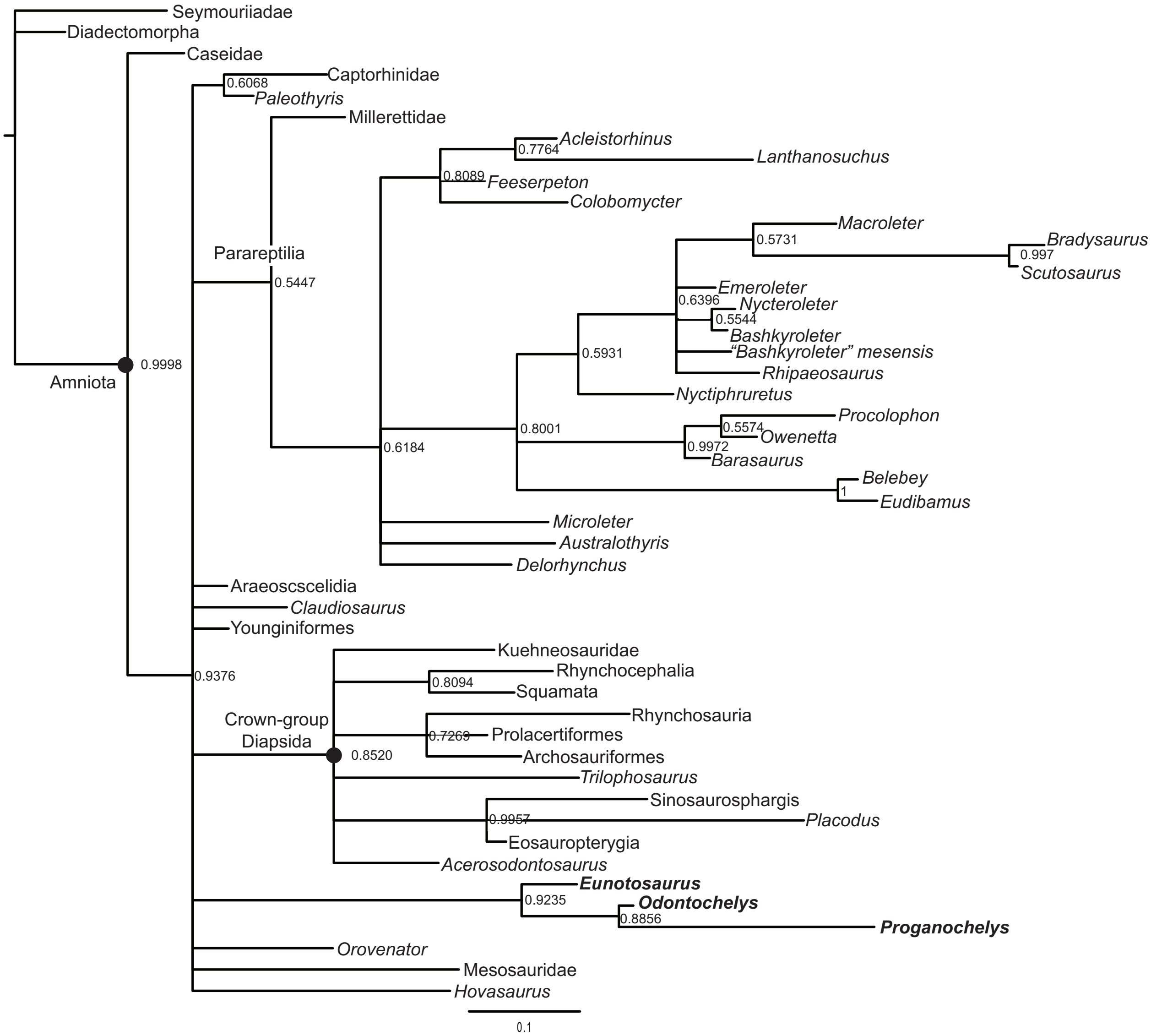
Extended Data Figure 4 | Strict consensus of two most parsimonious recovered from total character matrix. Bremer support values are provided for each clade (above line). Bootstrap values exceeding 50% are provided (below line). A *Eunotosaurus*–turtle clade is extremely well supported. That this pan-turtle lineage originated somewhere within the radiation of anatomically diapsid reptiles is well supported, although a refined phylogenetic position remains morphologically elusive. Tree length = 1,087; consistency index = 0.4013; retention index = 0.590.



Extended Data Figure 5 | Bayesian tree topology derived from total matrix (50% majority rule consensus). An exclusive *Eunotosaurus*–turtle clade is recovered with 100% posterior probability. This pan-turtle lineage is nested within the radiation of anatomically diapsid reptiles; however, in contrast to the parsimony solution, turtles are excluded from crown-group Diapsida. The Bayesian results agree with the parsimony in revealing strong support that: (1) *Eunotosaurus* is an early stem-group turtle; and (2) the ancestral stem turtle expressed a fully diapsid skull. The two analyses also agree that there is currently poor morphological support for a refined position of turtles within the greater diapsid radiation.



Extended Data Figure 6 | Strict consensus of 13 most parsimonious trees recovered from cranial-only matrix. The *Eunotosaurus*–turtle clade is recovered, which supports the hypothesis that the postcranial synapomorphies of *Eunotosaurus* and turtles are homologous and not the products of convergence. Tree length = 777; consistency index = 0.3956; retention index = 0.4743.



Extended Data Figure 7 | Bayesian tree topology derived from cranial-only matrix (50% majority rule consensus). When studied in isolation, cranial anatomy provides poor resolution of the deep divergences within Pan-Reptilia, but a *Eunotosaurus*–turtle signal is clearly present.

Supplementary Discussion

Expanded Cranial Description

The purpose here is not an exhaustive description or history of the cranial observations on *Eunotosaurus africanus*, but rather an overview of the cranial details for the adult morphology of this taxon as observed in the two best cranial specimens CM777 and CM86-341. Some supplementary observations from the juvenile skull of SAM-PK-K7909 also are included. Emphasis is placed on the most phylogenetically relevant features. A detailed bone-by-bone description with more comprehensive phylogenetic and ontogenetic comparisons, figures, and phylogenetic analysis will be published elsewhere.

CM777 is a largely articulated, three-dimensionally preserved skull with lower jaws (Figs.2, 3; Extended Data Fig. 1). It exhibits some degree of post-mortem distortion but represents the most complete of the known cranial material. Initially described by Keyser and Gow[1] and then redescribed by Gow[2], CM777 is the largest known specimen of *Eunotosaurus* and expresses no indication of skeletal immaturity (e.g., its scapula and coracoid are fully fused[2]). Its preserved dermal elements include the left and right nasal, prefrontal, frontal, postfrontal, parietal, postorbital, jugal, squamosal, postparietal, premaxilla, maxilla, vomer, palatine, pterygoid, dentary, splenial, prearticular, and surangular. The lacrimal, quadratojugal, supratemporal, putative tabular (see below), and angular are present only on the right side, whereas only the left ectopterygoid and coronoid are preserved. The splanchnocranium is represented by the left and right quadrate, epipterygoid, and articular, as well as the left stapes. The preserved braincase elements include the left and right prootic, opisthotic, and exoccipital and the midline basioccipital and parabasisphenoid. The primary wall of the braincase anteriorly is ossified between cranial nerves V (trigeminal) and II (optic), but there is no evidence of the more anterior sphenethmoid or septomaxilla. The high-preservational quality of the orbital region and rostrum suggests the absence of these elements reflects anatomical reality rather than a post-mortem artifact. The original physical preparation damaged the external surface of CM777, especially on the left side (e.g., note dermal roofing elements; Fig. 2), and removed much of the dermal sculpturing evident in NMQR3299. It is unclear to what degree, if any, preparation was responsible for the asymmetric expression of individual elements.

The surface details of the previously undescribed skull of CM86-341 are well preserved (Figs. 2, 3; Extended Data Fig. 3), though the clarity of the resultant CT data is somewhat lower than for those of CM777. While smaller than CM777, this specimen also appears to be skeletally mature. The CT data do reveal that the preserved elements of this skull are largely restricted to the right side and that some degree of mediolateral compression has left many of the elements slightly out of place. This is less true for the especially well-preserved temporal region, with jugal, postorbital, squamosal, quadratojugal, and supratemporal all complete and in basic articulation (the jugal and quadratojugal are somewhat displaced). The posterolateral margin of the right parietal is present, as is what may either be a posterolateral fragment of the parietal or a portion of the tabular. The postfrontal is present but slightly displaced. The maxilla, lacrimal, and what are likely fragments of the frontal, prefrontal, palatine, and pterygoid are preserved anteriorly. The vertical component of the epipterygoid and laterosphenoid are present and appear to be in place. A large number of elements are preserved in the posterior braincase region but are difficult to identify with confidence at this time.

As in *Odontochelys*[3] and *Proganochelys*[4], the skull of *Eunotosaurus* overall is relatively short, broad, and deep, with a postorbital length exceeding that of the rostrum (preorbital length). The rostrum forms a distinctive downward arc (in both juvenile and adult) that is especially prominent anterior to the frontal-nasal suture, much like *Proganochelys* (see [4, fig. 43]). The nasals are longer than the short and wide frontals and sweep forward to meet the thin ascending processes of the premaxillae. As in *Odontochelys*, these structures only narrowly separate the ovoid external nares at the midline. Nasal elongation is uncommon outside of Eureptilia (but see, e.g., mesosaurs[5]; *Bradysaurus*[6]) and is not expressed in either *Odontochelys* or *Proganochelys*.

The prefrontal reaches the palate ventrally, with the contact being obscured externally by the tall, ascending process of the maxilla. Such a prominent ascending process is shared with crownward and modern turtles and appears to be a feature that evolved independently in parareptiles and eureptiles[7-10]. The maxilla houses approximately 23 relatively long, conical teeth set in shallow sockets (similar to the marginal teeth of *Odontochelys*). Its lateral surface lacks the distinctive anterior foramen common among parareptiles (e.g., *Acleistorhinus*[11], *Macroleter*[12]). As in *Proganochelys*, the maxilla makes a small contribution to the ventral orbital margin.

Unlike *Odontochelys* and *Proganochelys*, the frontal retains its contribution to the dorsal orbital margin. This contribution is highly variable within crown Testudines[13, 14].

The postorbital is large and clearly distinct from the postfrontal, in contrast to the fusion that likely characterizes *Proganochelys* and crownward turtles[4, 13]. The dorsal margin of the postorbital is marked by a distinct groove that accepted the lateral borders of the postfrontal anteriorly and supratemporal posteriorly. Its posterior margin is distinctly concave with a posterodorsal terminus that reaches the upper margin of the squamosal. The postorbital likely made at least a small contribution to the anterior margin of the lower temporal fenestra in the adult skull, but this cannot be established empirically as none of the preserved jugals are exactly in place. The jugal is a gracile, comma-shaped element that lacks a subtemporal process. Its rostral process runs over the caudal end of the maxilla and along the ventral orbital margin where it contacts the distal extent of the lacrimal (as in *Proganochelys*). The tall ascending process extends along the posterior margin of the postorbital but likely does not reach the squamosal/quadratojugal contact above the lower temporal fenestra. A comma-shaped jugal, or at least one lacking a distinct posterior process, also characterizes embryonic crown-group turtles[15-18].

The posterior margin of the lower temporal fenestra is formed by the vertical components of the quadratojugal and squamosal. The squamosal is a tall element with a slightly concave rostral and caudal margin (distinctly so in CM86-341; Fig. 2, Extended Data Fig. 3). Its ventral length approximates the inferior cranial margin, which is the ancestral condition for amniotes and likely a reversal if *Eunotosaurus* is a diapsid (though this reversal is common in crownward and crown-group diapsids (e.g., *Hupehsuchus*[19], *Sphenodon*[20], *Sophineta*[21], *Marmoretta*[22], *Prolacerta*[23]; *Protorosaurus*[24]; sauropterygians[25-28]). Ventrally, the quadratojugal forms a short horizontal process that runs ventral to the squamosal. There is no subtemporal process of the quadratojugal, but a tall ascending process lies deep to the squamosal and may have reached the squamosal-postorbital contact. A vertically oriented and tall quadratojugal is known from a number of crown-group diapsids (e.g., *Euparkeria*[29], *Mesosuchus*[30]) and parareptiles (e.g., *Nyctiphruretus*[31]). In none of these taxa, however, does the quadratojugal traverse the entire height of the cheek as it does in *Eunotosaurus*, *Proganochelys*, modern turtles[13], and *Milleretta* (see [32], fig.8). The anterior margin of the quadratojugal likely had an extremely narrow exposure rostral to the squamosal.

The upper temporal fenestra is defined by the parietal medially, postorbital and quadratojugal laterally, and postfrontal anteriorly. The juvenile upper temporal arcade is thin and thus compares closely with the same structure in the majority of diapsids. Ontogenetic expansion of the postorbital and squamosal broadens the arcade and constricts the diameter of both the upper and lower temporal fenestrae. The elongate supratemporal, which covers the upper temporal fenestra in the adult skull, is not expressed in SAM-PK-K7909 though some amount of ossified supratemporal may be present posteriorly. This morphological disparity indicates that the full, adult expression of the supratemporal appears relatively late in postnatal ontogeny.

The third major window into the amniote adductor chamber is the post-temporal fenestra, which may be completely absent in *Eunotosaurus*. The area expected to house the fenestra is instead occupied by a flat bone, fully preserved only on the right side of CM777 (Fig. 2), historically considered to be a large tabular (e.g., 2). This interpretation may be correct; but, its upper margin with the parietal in CM777, even with CT data, is difficult to differentiate as a suture or a break. A tabular seems to be present in NMQR3299 based on an external examination (CT data inconclusive) and the posterolateral margin of the parietal in CM86-341 lies approximately at the position of the suture/break in CM777—both observations support the conclusion that a tabular was present. This parietal margin, however, is also distinctively rounded to a shape suggestive of a post-temporal fenestra—one that was bounded by the squamosal laterally and secondarily covered by either the reappearance or apomorphic expansion of the tabular. We conservatively accept that a tabular is present and a post-temporal fenestra is not (reflecting both as such in the matrix). Alternatively, it is a posterolateral flange of the parietal that secondarily closed the post-temporal fenestra. The latter interpretation is more congruent with a diapsid status of *Eunotosaurus*, as the tabular is lost relatively early in diapsid radiation (crownward of the *Youngina*-Diapsida node). It should be noted that a tabular was reported for the putative crown diapsid *Paliguana*[33, 34]. Under either scenario, the loss or extreme reduction of the post-temporal fenestra is likely an autapomorphic feature of *Eunotosaurus*, especially if *Eunotosaurus* is a diapsid.

The putative tabular is bounded medially by a parietal-opisthotic contact, which is present otherwise only in a small number of crown amniotes including *Proganochelys* (also *Claudiosaurus*[35]). This contact separates the tabular from a paired postparietal. As with the tabular, postparietals are often lost in crownward stem diapsids (e.g., *Askeptosaurus*[36], *Clarazia*[37], *Thalattosaurus*[38], *Hupehsuchus*[19]). There are numerous examples of postparietals in advanced diapsids, including crown forms (e.g., *Palaeagama* and *Paliguana*[33], *Euparkeria*[29]; *Chanaresuchus*[39], *Czatkowiella*[40]) and even the crown-group archosaur *Gracilisuchus*[41]. These records support the conclusion that the pathways responsible for postparietal development are highly conserved even if their expression as independent ossifications is variable[42].

The palate of *Eunotosaurus*—as in *Odontochelys* and most diapsids, but unlike most parareptiles (e.g., *Procolophon*[43], *Belebey*[44], pareiasaurs[6, 45])—is relatively open with an extensive interpterygoid vacuity whose acute rostral apex extended beyond the posterior margin of the palatines. The palate overall is oriented at an acute anterodorsal angle that also characterizes the palate of at least some stem-group turtles (e.g., *Meiolania*[46], *Proganochelys*[4]). The pterygoid is plesiomorphically tetraradiate with a prominent palatal process that contains a series of small teeth. This ramus extends rostral to the palatines (in contrast to *Proganochelys*, unknown in *Odontochelys*) but is unusual in that it is separated from the palatine for most of their shared length (Extended Data Fig. 1). As in *Odontochelys*, the transverse ramus is strongly developed and laterally oriented with prominent teeth arranged largely along its posterior margin. The ventral extent of the ramus' distal end may slightly exceed that of *Proganochelys* and *Odontochelys* but is reduced relative to the plesiomorphic amniote condition[8]—it certainly extends no further ventrally than in some crown-group diapsids, such as the stem-group archosaurs *Mesosuchus*[30] and *Trilophosaurus*[47].

The transverse process extends along the posterior margin of a moderately elongate ectopterygoid (lost in *Proganochelys* and other crownward stem turtles). With the palatine and maxilla, this element defines a communication between the posterior palate and orbital cavity (Extended Data Fig. 1). The opening is positionally homologous with the amniote suborbital fenestra, and comparable in size to the opening in *Proganochelys* (foramen palatinum posterius[6]) and distinctly larger than the foramen-sized opening characterizing parareptiles[10, 48]. It differs from *Proganochelys* and the typical diapsid condition in its more triangular shape and lack of an obviously finished rim. In these atypical qualities, it compares closely with the post-temporal fenestra of the stem archosaur *Mesosuchus*[30] and we score it as homologous to that structure.

The quadrate has a thin exposure behind the squamosal-quadratojugal complex. Its anterior contact with the quadrate process of the pterygoid is completely vertical as in other stem turtles (e.g., *Proganochelys*[4], *Condorchelys*[49]). Its posterior margin is slightly concave but likely did not support a tympanic membrane and an impedance-matching ear[10, 50]. This plesiomorphic condition is shared with *Odontochelys*[3] suggesting that the advanced ear of modern turtles is secondary regardless of where turtles originated on the tree. The stapes (Extended Data Fig. 1) is shorter than that of *Proganochelys* but more elongate and gracile than that of the early parareptile *Milleretta*[32]. A strong sutural contact between quadrate and prootic closes the caudal length of the cranioquadrate space dorsally (Extended Data Fig. 1) as it does in all known panturtles, including *Proganochelys*. The posteromedial margin of the quadrate receives the distal end of a triangle-shaped paroccipital process formed by the opisthotic.

The occipital condyle is not preserved and/or observable in any of the known specimens (but the floor of the foramen magnum appears to have been formed by the basioccipital and not by a medial contact of the exoccipitals as in *Proganochelys* and all crown-group turtles[13]). The basioccipital and parabasisphenoid form a completed suture, with a combined ventral surface marked by a distinctive pocket for the insertion of the deep, prevertebral muscles of the neck. As in *Odontochelys* but in contrast to *Proganochelys*, the basipterygoid processes enter the basicranial joint at a largely transverse orientation.

The dorsal surface of the basisphenoid accepts the prootic anteriorly, which is complete and appears to have included an ossified medial wall. More specific details of the internal prootic anatomy are currently difficult to interpret. Anteriorly, the prootic contacts a large plate-like ossification positioned medial to the columnar epipterygoid and extending forward to a point approximating the posterior orbital margin (Extended Data Fig. 1, 3). In CM777, the epipterygoid has been displaced medially across the cavum epitericum where it disrupts the contact between the prootic and this element. We interpret the element as an ossification of those orbital cartilages forming the primary wall of the anterior braincase between the points where the neurovascular bundles associated with the optic and trigeminal (CN II and V, respectively) exit the cranial cavity. The ventromedial orientation of this element in CM777 likely reflects the original angle of the cartilaginous wall and supports the conclusion that it is a bilateral element (it is not preserved on the left side of CM777).

Variable degrees of ossification of this general region are not uncommon within crown diapsids[51], being most commonly found anteriorly around the optic nerve and the corresponding portions of the chondrocranial pila metoptica and taenia medialis[52, 53]. These ossifications typically are referred to as orbitosphenoids in both pan-archosaurs (Archosauromorpha)[54, 55] and lepidosaurs[56-58]. The shared name minimally reflects the primary homology of these structures (*sensu*[59]) though their secondary homology is difficult to establish as neither stem-group lepidosaurs nor the earliest stem-group archosaurs are known to preserve these elusive elements. *Proganochelys* and Archosauriformes appear to be unique among panreptiles in combining an extensive ossification of the pila metoptica and taenia medialis with ossification of the dorsal length of the pila antotica[61]. Ossification of this more posterior cartilage forms a bony anterior wall of the prootic incisure, and produces a contact with the prootic. It is the prootic that completes the enclosure of the trigeminal nerve by forming the posterior wall of the prootic incisure, in contrast to the development of the althenophidian condition[51]. Bhullar and Bever[60] recognized this derived information with the name laterosphenoid—a term that previously had been restricted to the archosauriform radiation[61]. Phylogenetic analysis, however, did not recover turtles as the sister taxon to Archosauriformes even when turtles were constrained to a privileged relationship within Pan-Archosauria[60], meaning that the ‘laterosphenoid’ of stem turtles and archosauriforms currently fails the test of secondary homology[59].

The bony element forming the anterior wall of the braincase in *Eunotosaurus* also exhibits a prootic contact and clearly defines an opening topologically homologous to the prootic incisure (housing CN V) in reptile crown clades[54]. The element in *Eunotosaurus* differs from that of *Proganochelys* and Archosauriformes in lacking a deeply excavated fenestra metoptica and ossifying the taenia medialis to a lesser degree (the plate in *Eunotosaurus* remains well below the overlying dermal roof). Instead of adopting the more generalized term pleurosphenoid (see [51, 61]) for the structure in stem turtles, we utilize ‘laterosphenoid’ to convey the uniquely derived information present in these stem-group turtles and archosauriforms—information that should be reflected in character matrices even if the resultant tree topology dictates separate origins (certainly until the origin of turtles is satisfactorily resolved). The issue of secondary homology is not avoided by calling the turtle structure a pleurosphenoid, as this term is also applied to the structure within althenophidian snakes that lacks the apomorphic features that make the turtle-archosauriform structure unique[51, 61].

The lower jaw is gracile overall with approximately 18 teeth set in shallow sockets (Extended Data Fig. 1). Its articulation with the quadrate closely resembles that of *Odontochelys* in lying just in front of the craniovertebral joint (maybe slightly posterior of the condition in *Odontochelys*)—a position exaggerated in crownward and crown-group turtles[4, 13]. The coronoid process includes a single coronoid bone with a prominence that corresponds roughly to that of *Proganochelys*. A tall coronoid process appears to have evolved independently within parareptiles and pandiapsids[23, 25]. As in *Proganochelys*, pareiasaurs[6], and a small number of diapsids (e.g., *Huehuequetzpalli*[62], *Mesosuchus*[30], some sauropterygians[63]), the surangular provides a thin contribution to the articular surface. The splenials are present but clearly do not contribute to the thin mandibular symphysis. The anterior tip of the symphysis remains well behind the forward projection of the overlying rostrum resulting in an exaggerated overbite.

Phylogenetic Analysis

Maximum parsimony analysis of the total character matrix (with selected characters ordered) recovers two shortest trees, both of which indicate *Eunotosaurus* is the sister taxon to the unequivocal stem-group turtles *Odontochelys* and *Proganochelys* with strong Bremer and bootstrap support values (Extended Data Fig. 4). An exclusive *Eunotosaurus*-turtle clade is also recovered when the total character matrix is analyzed using Bayesian optimality criteria (100% posterior probability; Extended Data Fig. 5), and when the cranial-only matrix is analyzed with maximum parsimony and Bayesian approaches (Extended Data Figs. 6 and 7). Recovery of a *Eunotosaurus*-turtle clade from a cranial-only matrix suggests that the postcranial synapomorphies shared by *Eunotosaurus* and turtles are homologous and thus cannot be dismissed *a priori* as simple convergence towards a shelled body plan. The support values certainly decrease when the skull is considered in isolation, but this is not surprising and is true for almost all relationships within the topology (presumably reflecting the decreased number of total characters in the cranial-only matrix). A second iteration with all characters left unordered resulted in a single most-parsimonious tree with an almost identical tree topology as the ordered analysis. The only difference is that leaving the characters unordered resolves the polytomy, deeply nested within Parareptilia, between *Macroleter*, the *Emeroleter-Bashkyroleter-Nycteroleter* clade, and the pareiasaur-*Procolophon*-owenettid clade.

Cranial characters supporting the monophyly of a *Eunotosaurus* + turtle clade include an extreme dorsal expansion of the quadratojugal, sutural contact between the prootic and quadrate, ossification of the primary wall of the anterior braincase, an anterior repositioning of the craniomandibular joint, and a reduction of the retroarticular process. As diapsids, *Eunotosaurus* and turtles also share an apomorphic expansion of the postorbital and squamosal that in *Eunotosaurus* reduces the size of the temporal fenestrae, and in crown-ward turtles, closes those fenestrae completely. The level of support for a *Eunotosaurus*-turtle clade is remarkable considering the theoretical expectation that as a stem lineage is sampled closer to its evolutionary origin the number of characters diagnosing that lineage will diminish.

Maximum parsimony and Bayesian analyses agree that Pan-Testudines (including *Eunotosaurus*) did not arise from within parareptiles (contra [64, 65] and numerous earlier studies), but rather evolved as part of the radiation of anatomically diapsid reptiles. The hypothetical ancestral stem turtle can thus be inferred as having expressed a fully diapsid skull, and *Eunotosaurus* provides the first direct evidence of this widely accepted conclusion. Our parsimony and Bayesian topologies do differ as to whether or not PanTestudines is part of the diapsid crown group. The close relationship that parsimony indicates between panturtles, sauropterygians, and lepidosaurs is poorly supported, as is a crown-group Diapsida that includes panturtles. Higher support values characterize the deeper nodes of the diapsid stem lineage, most notably the node defined by the divergence of Araeoscelidae, which marks the origin of the anatomically diapsid skull. In addition to fenestral characters, the *Eunotosaurus*-turtle lineage is supported as diapsid by such features as reduction of the splenial, loss of the jugal-squamosal contact (reversed in crownward stem turtles), loss of parasphenoid teeth, prominent ascending process of the maxilla, medially positioned external nares, loss of a caniniform region, and loss of the sphenethmoid. All but the last of these features transform independently within Parareptilia, reinforcing the potential for long-branch attraction (to either lineage).

The generally poor parsimony support for a refined position of turtles within the greater diapsid lineage is reflected in the topology and posterior probabilities of the Bayesian analysis where the *Eunotosaurus*-turtle clade lies outside the diapsid crown group in a largely unresolved relationship with taxa of the diapsid stem. Thus, neither parsimony nor Bayesian optimality criteria as applied to this morphological dataset recover the dominant genomic signal of a turtle-archosaur clade ([66-77], but see [78]). Our results suggest that a better understanding of the individual and collective stem lineages of archosaurs and lepidosaurs will be necessary before a well-supported morphological hypothesis for the position of turtles among diapsids can be articulated.

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Table S1. Descriptions of the cranial characters used in the phylogenetic analysis. Although not meant as an exhaustive history of the characters, some citations and their corresponding character numbers are provided. Cranial scores are provided in Supplementary Tables (1 and 2). Descriptions of individual postcranial characters (175-268) are not provided here as they reflect the definitions and scorings of characters 97-190 of Lyson *et al.*[65].

1. *Skull proportions* (Rieppel[25], 9; modified from Laurin & Reisz[8], 32; deBraga & Rieppel[9], 19; Müller & Tsuji[10], 32): preorbital skull length equal to postorbital length [0]; preorbital length exceeds postorbital skull length [1]; postorbital length exceeds preorbital skull length [2].
2. *Snout, shape* (Müller[7], 3): unconstricted [0]; constricted [1].
3. *Premaxilla, size* (Müller[7], 1): small [0]; large, forming most of snout in front of external nares [1].
4. *Premaxilla, shape* (Dilkes[30], 6; Müller[7], 83): horizontal ventral margin [0]; down-turned ventral margin [1].
5. *Premaxilla, postnarial process* (Müller[7], 2): absent [0]; present, restricting contact of the maxilla to the external nares or even excluding maxilla [1].
6. *External nares, location I* (Dilkes[30], 11; Müller[7], 85): marginal [0]; close to midline [1].
7. *External nares, location II* (Müller[7], 180)*:* positioned anteriorly [0]; situated in central or posterior area of the antorbital skull portion [1].
8. *External nares, internarial bar* (Dilkes[30], 10; Müller[7], 84): separated by internarial bar of premaxilla (0); confluent [1].
9. *External nares, shape* (Dilkes[30], 12; Müller[7], 86): rounded [0], elongate [1].
10. *Premaxilla, contribution to internal naris* (Müller[7], 33): present [0]; absent, excluded [1].
11. *Premaxilla-maxilla suture* (Dilkes[30], 17; Müller[7], 88): simple vertical or diagonal [0]; notch present in maxilla [1].
12. *Premaxilla, dentition* (deBraga & Rieppel[9], 3; Müller[7], 152): present [0]; absent [1].
13. *Premaxillary/maxillary teeth, separated by diastema* (Müller[36], 28; Müller[7], 116): absent [0]; present [1].
14. *Anterior (premaxillary/maxillary) teeth, orientation* (Müller[7], 117): upright [0]; strongly

procumbent [1].

15. *Premaxilla-frontal contact* (Müller[7], 5): absent, nasals meet in dorsomedial suture [0]; present, nasals separated [1].
16. *Septomaxilla* (Dilkes[30], 14; Müller[7], 87): present [0]; absent [1].
17. *Nasals* (modified from Müller[7], 153): present [0]; absent [1].
18. *Nasals, fusion* (modified from Müller[7], 153): paired [0]; fused [1].
19. *Narial shelf* (Laurin & Reisz[8], 1; Tsuji *et al.* [79], 1): absent [0]; present [1].
20. *Nasal/frontal ratio* (deBraga & Rieppel[9], 9; modified from Müller[7], 4): nasal equal to or shorter than frontal [0]; nasal at least one-third longer, or better [1].
21. *Maxilla, ascending process* (Laurin & Reisz[8], 19; deBraga & Rieppel[9], 11; Müller[7], 126; Müller & Tsuji[12], 19; Tsuji *et al.*[79], 19): absent [0]; present between orbit and external nares [1].
22. *Maxilla-prefrontal contact, anterior to lacrimal* (Müller[7], 179): absent due to nasal-lacrimal contact [0]; present, separating nasal and lacrimal [1].
23. *Maxilla-frontal contact* (Reynoso[62]): absent [0]; present, separates prefrontal and nasal [1].
24. *Maxilla length* (deBraga & Rieppel[9], 14; Müller[7] 127); extends to posterior orbital margin (0); does not reach posterior margin of orbit [1].
25. *Maxilla, orbital exposure* (deBraga & Rieppel[9], 15; Müller[7], 128): absent [0]; present [1].
26. *Maxilla-quadratojugal contact* (Laurin & Reisz[8], 22; deBraga & Rieppel[9], 16; Müller & Tsuji[10], 21; Tsuji *et al.* [79], 21): absent [0]; present [1].
27. *Maxilla-vomer contact* (Dilkes[30], 38; Müller[7], 92): absent [0]; present [1].
28. *Maxilla-ectopterygoid contact* (Dilkes[30], 40; Müller[7], 94): present [0]; absent [1].
29. *Maxilla-pterygoid contact* (Gaffney[4]): absent [0]; present [1].
30. *Maxilla, anterolateral foramen* (Laurin & Reisz[8], 20; deBraga & Rieppel[9], 13; modified from Müller & Tsuji[10], 20; Tsuji *et al.* [79], 20): absent or if present equal in size to all other foramina [0]; present at least twice the diameter of all other foramina [1].
31. *Maxilla, tooth row* (Rieppel[25], 46; Müller[7], 118): restricted to level in front of the posterior margin of the orbit [0]; extends behind posterior margin of orbit [1].
32. *Teeth, button-like durophagous* (Müller[36], 32; Müller[7], 122): absent [0]; present [1].

33. *Antorbital fenestra* (Dilkes[30], 5): absent [0]; present [1].

34. *Lacrimal, morphology* (deBraga & Rieppel[9], 17; Müller & Tsuji[10], 10): present and contributing to external nares [0]; present at least as long as tall, but excluded from external nares [1]; if present small, restricted to orbital margin, or absent entirely [2].

35. *Lacrimal, orbital margin* (Müller[7], 181): lacrimal enters orbital margin [0]; excluded from margin due to external contact between posteroventral part of prefrontal and posterodorsal margin of maxilla [1].

36. *Lacrimal duct* (deBraga & Rieppel[9], 18; Müller[7], 129): enclosed by lacrimal only (0); lateral border formed by maxilla [1].

37. *Lacrimal, suture with jugal* (Gaffney[4]): present (0); absent (1).

38. *Prefrontal, bulbous medial process* (Laurin & Reisz[8], 8): absent [0]; present [1].

39. *Prefrontal, contact with palate* (Laurin & Reisz[8], 6): absent [0]; present [1].

40. *Prefrontal, medial flange* (Laurin & Reisz[8], 7): narrow [0]; wide [1].

41. *Foramen orbitonasale* (Laurin & Reisz[8], 10): absent [0]; represented by a medial indentation on the lacrimal and a dorsal indentation on the palatine [1]; enclosed between prefrontal, lacrimal and palatine [2].

42. *Frontal, overall shape* (deBraga & Rieppel[9], 27): parallelogram [0]; hour-glass [1].

43. *Frontal, proportions* (Lee[88], 24; deBraga & Rieppel[9], 26; Müller[7], 155): length exceeds width by at least four times [0]; length no greater than twice width [1].

44. *Frontal-parietal length ratio* (Dilkes[30], 19): >1 [0]; < or = 1 [1].

45. *Frontal-nasal suture* (deBraga & Rieppel[9], 23; Müller[7], 154): transverse [0]; oblique, forming an angle of at least 30º with long axis of the skull [1].

46. *Frontals, fusion* (Rieppel[25], 11): absent, paired [0]; present, fused [1].

47. *Frontal, contribution to orbit* (Laurin & Reisz[8], 2; deBraga & Rieppel[9], 22; Müller[7], 7): absent, due to prefrontal-postfrontal contact along orbital margin [0]; present [1].

48. *Frontal, lateral lappet* (deBraga & Rieppel[9], 24; Tsuji *et al.*, 5): absent [0]; present [1].

49. *Frontal, posterolateral processes* (Rieppel[25], 12; deBraga & Rieppel[9], 25; Müller[7], 10): absent [0]; present [1].

50. *Orbit, shape* (deBraga & Rieppel[9], 28; Laurin & Reisz[8], 36; Müller & Tsuji[10], 37): generally circular [0]; anteroposteriorly elongate so that the length exceeds the height by

at least 30% [1].

51. *Dermal sculpturing* (modified from Laurin & Reisz[8], 38): absent [0]; present [1].
52. *Dermal sculpturing, morphology* (modified from Laurin & Reisz[8], 38): tuberosities [0]; tuberosities and pits [1]; honeycomb pattern of ridges and pits [2].
53. *Circumorbital bumps* (Tsuji[12], 45; Müller & Tsuji[10], 39): absent [0]; present [1].
54. *Postfrontal* (Gaffney[4]): present [0]; absent, probably through fusion with postorbital [1].
55. *Intertemporal* (deBraga & Rieppel[9], 54): present [0]; absent [1].
56. *Postorbital-parietal contact* (deBraga & Rieppel[9], 31; Dilkes[30], 22; Müller[7], 89): absent [0]; present [1].
57. *Postorbital, posterior extent* (Laurin and Reisz[8], 13; deBraga & Rieppel[9], 32; Müller[7], 131): terminates prior to reaching posterior limit of parietal [0]; reaches nearly the posterior extent of the skull [1].
58. *Postorbital, shape of posterior process* (Müller & Tsuji[10], 13): slender, half as wide as it is long [0]; increased width, parallelogram outline in lateral aspect [1].
59. *Supratemporal* (Müller[7], 21): present [0]; absent [1].
60. *Supratemporal, size* (modified from Laurin & Reisz[8], 18): large [0]; small [1].
61. *Postorbital-supratemporal contact* (Laurin & Reisz[8], 12; Müller[7], 184): present [0]; absent [1].
62. *Parietal, skull table proportions* (modified from deBraga & Rieppel[9], 47; Müller[7], 13): broad, width not less than half of the length measured along the element's midline [0]; weakly constricted [1]; strongly constricted with the length exceeding the width by at least three times [2]; forming sagittal crest [3].
63. *Parietal, shelf for adductor musculature* (deBraga & Rieppel[9], 48; Müller[7], 157): absent [0]; present as shallow excavations on the lateral margins of the parietal [1].
64. *Parietal-prootic contact* (deBraga & Rieppel[9], 67; Müller[7], 160): absent [0]; present [1].
65. *Parietal-opisthotic contact* (Gaffney[4]): absent [0]; present [1].
66. *Pineal foramen* (modified from Rieppel[25], 15; Laurin & Reisz[8], 3; deBraga & Rieppel[10], 49; Müller[7], 12): present [0]; absent [1].
67. *Pineal foramen, position* (modified from Rieppel[25], 15; Laurin & Reisz[8], 3; deBraga & Rieppel[9], 49; Müller[7], 12): present, located near the middle of the parietal body [0];

present, displaced anteriorly [1]; present, displaced posteriorly [2].

68. *Parietal-squamosal contact* (Müller & Tsuji[10], 12): absent [0]; present [1].

69. *Parietal, fusion* (modified from Müller[7], 11): absent [0]; fully or partially fused in adult [1].

70. *Postparietal* (Müller[7], 14;): present [0]; absent [1].

71. *Postparietal, fusion* (modified from Laurin & Reisz[8], 4; deBraga & Rieppel[9], 52): paired [0]; fused [1].

72. *Postparietal, position* (Laurin & Reisz[8], 5): dorsally exposed, integrated into skull table [0]; restricted to occipital plate [1].

73. *Posterolateral skull roof, composition* (Tsuji *et al.* [79], 15): formed by tabular [0]; formed mostly by supratemporal [1]; formed by parietal and small supratemporal or parietal along [2].

74. *Tabular* (modified from Laurin & Reisz[8], 17; Müller & Tsuji[10], 16): present [0]; absent [1].

75. *Tabular, position* (modified from Laurin & Reisz[8], 17; Müller & Tsuji[10], 16): part of skull table [0]; restricted to occiput [1].

76. *Jugal, anterior process* (Laurin & Reisz[8], 11; Müller & Tsuji[10], 12): does not extend to anterior orbital rim but reaches posterior margin of orbit [0]; extends at least to level of anterior orbital rim [1]; fails to reach posterior margin of orbit [2].

77. *Jugal, subtemporal process* (modified from Dilkes[30], 32; Müller[7], 91: present [0]; absent [1].

78. *Jugal, subtemporal process extent* (deBraga & Rieppel[9], 33; Müller[7], 16): extends posteriorly no further than the middle of the cheek [0]; reaches nearly the posterior limit of the skull [1].

79. *Jugal, subtemporal process morphology* (modified from Dilkes[30], 32; Müller[7], 91): robust, with height >50% of length [0]; slender, height <50% of length [1].

80. *Squamosal, ventral extent* (Müller[7], 18): descends to ventral margin of skull [0]; reaches only the approximate midlevel of the lower temporal fossa [1]; remains distinctly restricted to the dorsal region of the cheek [2].

81. *Squamosal, contribution to post-temporal fenestra* (Laurin & Reisz[8], 26; deBraga &

Rieppel[9], 36; Müller & Tsuji[10], 25): absent, elements separated [0]; present [1].

82. *Squamosal, occipital flange* (modified from Laurin & Reisz[8], 27; deBraga & Rieppel[9], 37; Müller[7], 132): absent or poorly developed forming only a thin ridge [0]; flange developed forming a broadly exposed lappet [1].
83. *Quadratojugal* (Müller[7], 19): present [0]; absent [1].
84. *Quadratojugal, anterior process* (Müller[7], 20): present [0]; absent [1].
85. *Quadratojugal, vertical process* (modified from Laurin & Reisz[8], 28; Müller[7], 182): absent, restricted to ventral margin of cheek [0]; present, distinct dorsal extension that does not extend above the dorsoventral midline of the orbit [1]; present, process extends to a point above the dorsoventral midline of the orbit [2].
86. *Quadratojugal, anterior extent* (Laurin & Reisz[8], 23; Müller & Tsuji[10], 22): reaches level of posterior border of orbit [0]; does not reach level of posterior border of orbit [1].
87. *Quadratojugal, ornamentation* (deBraga & Rieppel[9], 43; Müller & Tsuji[10], 27): absent [0]; present [1].
88. *Postorbital region, ventrolateral expansion* (modified from Laurin & Reisz[8], 33; Müller & Tsuji[10], 33): rectilinear or emarginated [0]; expanded below level of maxilla [1].
89. *Jugal-squamosal contact*: present [0]; absent [1].
90. *Upper temporal fenestra* (Laurin & Reisz[8], 29; deBraga & Rieppel[9], 50; Müller & Tsuji[10], 28): absent [0]; present [1].
91. *Upper temporal fenestra, size* (Rieppel[25], 10; modified from Müller[7], 9): comparable to orbit size or smaller [0]; distinctly larger than orbit [1].
92. *Upper temporal fenestra, contribution from frontal* (Rieppel[25], 13; Müller[7], 178): frontal widely separated from upper temporal fenestra [0]; narrowly approaches or enters the anteromedial margin of the upper temporal fossa [1].
93. *Upper temporal fenestra, contribution from postfrontal* (modified from Rieppel[25], 13; deBraga & Rieppel[9], 29; Müller[7], 90): absent due to postorbital-parietal contact [0]; present [1].
94. *Lower temporal fenestra* (Laurin & Reisz[8]; 30): absent [0]; present [1].
95. *Lower temporal fenestra, ventral margin* (modified from deBraga & Rieppel[9], 51; Müller[7], 17): bounded ventrally by bone [0]; open ventrally, subtemporal processes of

jugal and quadratojugal not in contact [1].

96. *Lower temporal fenestra, postorbital contribution* (Müller & Tsuji[10], 30): present [0]; absent [1].

97. *Lower temporal fenestra, quadratojugal contribution* (Müller & Tsuji[10], 31): absent [0]; present [1].

98. *Post-temporal fenestra* (modified from Laurin & Reisz[8], 60; deBraga & Rieppel[9], 59; Müller & Tsuji[10], 66): absent [0]; present [1].

99. *Post-temporal fenestra* (modified from Laurin & Reisz[8], 60; deBraga & Rieppel[9], 59; Müller & Tsuji[10], 66): small, diameter less than half of the diameter of the foramen magnum [0]; large, diameter at least equal to that of the foramen magnum [1].

100. *Interpterygoid vacuity, presence* (modified from Laurin & Reisz[8], 39; Müller & Tsuji[10], 41): vacuity absent [0]; present [1].

101. *Interpterygoid vacuity, anterior extent* (modified from Laurin & Reisz[8], 39; Müller & Tsuji[10], 41): extends beyond posterior margin of palatine [0]; does not reach posterior margin of palatine [1].

102. *Interpterygoid vacuity, shape* (deBraga & Rieppel[9], 73; Müller[7], 162): anterior end tapers sharply [0]; anterior border crescent-shaped [1].

103. *Pterygoid, palatal process* (deBraga & Rieppel[9], 76; Müller[7], 139): extends anterior to the anterior limit of the palatine [0]; forms oblique suture with palatine but process ends before reaching anterior limit of palatine [1]; forms transverse suture with palatine [2].

104. *Pterygoid, anterior extent* (Laurin & Reisz[8], 44; Müller & Tsuji[10], 46): reaches level of posterior end of choana [0]; remains posterior to choana [1].

105. *Pterygoid, teeth on palatine ramus* (Müller[7], 100): present [0]; absent [1].

106. *Pterygoid, transverse flange development* (Rieppel[25], 35): well developed [0]; strongly reduced [1].

107. *Pterygoid, orientation of transverse flange* (Laurin & Reisz[8], 45; deBraga & Rieppel[9], 77; Müller[7], 140; Müller & Tsuji[10], 48): directed predominantly laterally [0]; oriented in an anterolateral direction [1].

108. *Pterygoid, dentition on transverse flange* (modified from Laurin & Reisz[8], 46; deBraga & Rieppel[9], 78; Müller[7], 163; Müller & Tsuji[10], 49): present [0]; edentulous [1].

109. *Pterygoid, tooth morphology on the transverse flange* (modified from Laurin & Reisz[8], 46; deBraga & Rieppel[9], 78; Müller[7], 163; Müller & Tsuji[10], 49): present as a shagreen of teeth [0]; present but with one large distinct row of teeth along the posterior edge of the transverse flange [1].
110. *Pterygoid, ventral extent of transverse flange* (Lee[88], 14; deBraga & Rieppel[9], 79; Müller[7], 142): extends below maxillary tooth row [0]; terminates at or above maxillary tooth row [1].
111. *Pterygoid, quadrate ramus* (Tsuji *et al.* [79], 50): merges smoothly into transverse flange without distinctive excavation [0]; deep excavation on posterolateral surface [2].
112. *Ptergyoid, aruate flange* (Laurin & Reisz[8], 42): present [0]; absent [1].
113. *Basipterygoid processes, orientation* (Dilkes[30], 43; Müller[7], 96): lateral [0]; anterolateral [1].
114. *Palate, basicranial articulation* (Gaffney[4]; Lee[90], 2; Rieppel[25], 32; deBraga & Rieppel[9], 72; Müller[7], 30; Müller & Tsuji[10], 54): kinetic [0]; akinetic [1].
115. *Basicranial articulation, length* (Tsuji *et al.*, 55): restricted to lateral margin of the parasphenoid [0]; extends over much of the length of the main body of the parasphenoid [1].
116. *Ectopterygoid* (Rieppel[25], 37; Müller[7], 34): present [0]; absent [1].
117. *Ectopterygoid, teeth* (Laurin & Reisz[8], 48; modified from deBraga & Rieppel[9], 81; Müller[7], 51): present [0]; absent [1].
118. *Ectopterygoid-pterygoid suture* (modified from Müller[7], 95): transverse process extends along posterior margin of ectopterygoid and reaches its posterolateral corner [0]; extends along posterior margin but does not reach its posterolateral corner [1]; contact restricted to medial surface of ectopterygoid [2].
119. *Choana, palatal exposure* (Laurin & Reisz[8], 40; modified from deBraga & Rieppel[9], 8; Müller[7], 125; Müller & Tsuji[10], 42): parallel medial border of maxilla, palatine forms posterior margin only [0]; deflected posteromedially, palatine forms posterior and part of its lateral margin [1].
120. *Suborbital foramen* (modified from Laurin & Reisz[8], 49; Müller[7], 31; Müller & Tsuji[10], 53): absent [0]; present [1].

121. *Suborbital foramen, size* (Rieppel[25], 34; modified from Laurin & Reisz[8], 49; Müller & Tsuji[10], 53): small [0]; enlarged as fenestra [1].
122. *Suborbital foramen, lateral border* (modified from Laurin & Reisz[8], 41, 49; deBraga & Rieppel[9], 74) formed by dermal cheek—maxilla and/or jugal [0]; dermal cheek excluded by palatine contact with transverse process of pterygoid or ectopterygoid [1].
123. *Palatine, teeth* (Dilkes[30], 67; Müller[7], 99): present [0]; absent [1].
124. *Vomer, teeth* (modified from Müller[7], 121): edentulous [0]; present [1].
125. *Vomer, distribution of teeth* (modified from Müller[7], 121): extend along a majority of the vomer's rostrocaudal length, not restricted to anterior end [0]; restricted to the rostral end of the vomer [1].
126. *Vomer, alar flange* (Tsuji[12], 50; Müller & Tsuji[10], 43): absent [0]; present, mediolateral expansion positioned just behind contact with premaxilla [1].
127. *Quadrate, posterior excavation* (Rieppel[25], 29; modified from deBraga & Rieppel[9], 38; Müller[7], 26): straight posterior edge [0]; posterior edge deeply excavated forming a concave region [1].
128. *Quadrate, lateral exposure* (Rieppel[25], 30; Laurin & Reisz[8], 34; deBraga & Rieppel[9], 39; Müller[7], 27; Müller & Tsuji[10], 34): absent, covered by squamosal and quadratojugal [0]; present [1].
129. *Quadrate, lateral conch* (Rieppel[25], 31; deBraga & Rieppel[9], 40; Müller[7], 29): absent [0], present [1].
130. *Quadrate, anterior process* (modified from Laurin & Reisz[8], 35; deBraga & Rieppel[9], 41; Müller[7], 156; Müller & Tsuji[10], 35): long, extending forward along its sutural contact with the quadrate process of the pterygoid to nearly reach the level of the transverse flange [0]; short, not extending anteriorly beyond half the length of the quadrate process of the pterygoid [1].
131. *Quadrate-prootic contact* (Gaffney[4]): absent [0]; present [1].
132. *Quadrate, articular surface of condyle* (Laurin & Reisz[8], 65; Müller & Tsuji[10], 72): strongly convex, antero-posteriorly long [0]; nearly flat, anteroposteriorly shorter than they are wide [1].
133. *Temporal notch* (modified from Laurin & Reisz[8], 31; MacDougall and Reisz[80], 59):

absent [0]; present [1].

134. *Temporal depression* (MacDougall & Reisz[80], 60): absent [0]; present [1].

135. *Stapes, shape* (modified from Laurin & Reisz[8], 66; deBraga & Rieppel[9], 45; Müller[7], 133; Müller & Tsuji[10], 73): robust, greatest depth exceeding one-third total length [0]; slender, length at least four times depth [1]; slender but short [2].

136. *Stapes, dorsal process* (Laurin & Reisz[8], 67; deBraga & Rieppel[9], 46; Müller[7], 134; Müller & Tsuji[10], 74): ossified [0]; unossified or absent [1].

137. *Epipterygoid, dorsal wing* (Müller[7], 28): broad [0]; narrow [1].

138. *Cranioquadrate space* (Laurin & Reisz[8], 43): small, quadrate ramus of pterygoid and paroccipital process of opisthotic converge posterolaterally [0]; large, quadrate ramus of pterygoid and paroccipital process of opisthotic are parallel to each other [1].

139. *Supraoccipital, occipital crest* (modified from Laurin & Reisz[8], 55; deBraga & Rieppel[9], 56; Müller[7], 25; Müller & Tsuji[10], 60): plate-like, no sagittal crest [0]; body constricted at midline forming sagittal crest [1].

140. *Medial wall of inner ear as formed by the prootic* (Lee[88], A6; Laurin & Reisz[8], 59; deBraga & Rieppel[9], 68; Müller[7], 161): unossified [0]; ossified with acoustic nerve foramina [1].

141. *Paroccipital process*, *orientation* (deBraga & Rieppel[9], 60; Müller[7], 158; Müller & Tsuji[10], 62): directed primarily laterally, approximately perpendicular to the parasagittal plane [0]; paroccipital process deflected posterolaterally at an angle of about 20º from the transverse width of the skull [1]; paroccipital process deflected dorsolaterally at an angle of nearly 45º [2].

142. *Paroccipital process, distal end* (Müller[7], 98): ends freely or contacts skull table [0]; contacts suspensorium, including quadrate, squamosal, and/or supratemporal on the occiput [1].

143. *Exoccipitals, contact each other below foramen magnum* (Rieppel[25], 28; modified from Müller[9], 23): present [0]; absent [1].

144. *Exoccipital, lateral process* (Laurin & Reisz[8], 64; Müller & Tsuji[10], 71): absent [0]; present, lateral flange extending deep to paroccipital process [1].

145. *Occipital condyle, shape* (Laurin & Reisz[8], 62; Müller & Tsuji[10], 68): transversely broad

[0]; reniform to circular [1].

146. *Basioccipital/basisphenoid relationship* (Lee[88], A5; modified from Laurin & Reisz[8], 61; deBraga & Rieppel[9], 63; Müller[7], 137; Müller & Tsuji[10], 67): elements separated by unossified gap [0]; elements with ossified suture [1].
147. *Parasphenoid, pocket for cervical musculature* (Laurin & Reisz[8], 50; Müller & Tsuji[10], 56): present [0]; absent [1].
148. *Parasphenoid, cultriform process* (modified from Laurin & Reisz[8], 52; deBraga & Rieppel[9], 75; Müller[7], 141; Müller & Tsuji[10], 58): long, exceeding length of parasphenoid body and reaching forward to the level of the posterior limit of the internal nares [0]; short, not reaching the level of the internal nares [1]; absent [2].
149. *Parasphenoid, teeth* (Laurin & Reisz[8], 53; Müller[7], 97; Müller & Tsuji[10], 59): present [0]; absent [1].
150. *Parasphenoid wings* (Laurin & Reisz[8], 51): present, parasphenoid broad posteriorly (0); absent, parasphenoid narrow posteriorly (1).
151. *Ventral braincase tubera*: (modified from Lee[90], 13; modified from Laurin & Reisz[8], 63; deBraga & Rieppel[9], 65; Müller[7], 136; Müller & Tsuji[10], 70): absent [0]; present [1].
152. *Sphenethmoid* (deBraga & Rieppel[9], 70; Müller[7], 138): present [0]; absent [1].
153. *"Laterosphenoid"* (modified from deBraga & Rieppel[9], 71): absent [0]; present [1].
154. *"Laterosphenoid", extent* (Bhullar & Bever[60]): not in contact with parietal [0]; forms osseous bridge between basisphenoid and dermal roof [1].
155. *Mandibular joint, position relative to occipital condyle* (Rieppel[25], 27; Laurin & Reisz[8], 36; deBraga & Rieppel[9], 82; Müller[7], 22; Müller & Tsuji[10], 36): even with [0]; posterior to [1]; anterior to [2].
156. *Coronoid process* (modified from Laurin & Reisz[8], 79; deBraga & Rieppel[9], 83; Müller[7], 36; Müller & Tsuji[10], 87): absent or small and formed by multiple elements [0]; tall, formed by coronoid [1]; tall, formed by dentary [2].
157. *Coronoid, number* (Laurin & Reisz[8], 74; deBraga & Rieppel[9], 84; Müller[7], 183; Müller & Tsuji[10], 82): more than one [0]; only one coronoid [1].
158. *Meckelian fossa, orientation* (Laurin & Reisz[8], 70; deBraga & Rieppel[9], 85; Müller[7], 165): faces mediodorsally, prearticular narrow [0]; faces dorsally, prearticular broad [1].

159. *Meckelian fossa, length* (Laurin & Reisz[10], 71; Müller & Tsuji[12], 79): long, occupies at least 25% of lower jaw length [0]; short, occupies less than 25% of lower jaw length [1].

160. *Surangular, length* (Laurin & Reisz[8], 72; deBraga & Rieppel[9], 86; Müller[7], 143): extends anterior to coronoid eminence [0]; does not extend anterior to coronoid eminence [1].

161. *Surangular, lateral shelf* (modified from Laurin & Reisz[8], 78; deBraga & Rieppel[9], 87; Müller[7], 166; Müller & Tsuji[10], 81): absent [0]; present [1].

162. *Surangular, contribution to articular facet* (Lee[6], W10): absent [0]; present [1].

163. *Splenial* (modified from Laurin & Reisz[8], 80; deBraga & Rieppel[9], 88; Rieppel[25], 41; Müller[7], 37; Müller & Tsuji[10], 88): present [0]; absent [1].

164. *Splenial, mandibular symphysis* (modified from Laurin & Reisz[8], 80; deBraga & Rieppel[9], 88; Rieppel[25], 41; Müller[7], 37; Müller & Tsuji[10], 88): contributes to mandibular symphysis [0]; reduced, excluded from mandibular symphysis [1].

165. *Mandibular symphysis, length* (Rieppel[25], 40): short [0]; elongated [1].

166. *Angular, lateral exposure* (deBraga & Rieppel[9], 89; Müller[7], 167): exposed along 1/3 the lateral face of the mandible [0]; exposed only as a small sliver along the lateral face [1]; absent from lateral aspect [2].

167. *Prearticular, extent* (Laurin & Reisz[8], 75; deBraga & Rieppel[9], 91; Müller[7], 168): extends anterior to coronoid eminence [0]; terminates prior to reaching coronoid eminence [1].

168. *Retroarticular process, morphology* (Rieppel[25], 38; modified from Laurin & Reisz[8], 76; deBraga & Rieppel[9], 92; Müller[7], 35; Müller & Tsuji[10], 84): absent, small or narrow [0]; transversely broad, dorsally concave [1].

169. *Retroarticular process, upturned* (Müller[7], 101): absent [0]; present [1].

170. *Caniniform region* (Laurin & Reisz[8], 24; Müller & Tsuji[10], 23): present [0]; absent [1].

171. *Single caniniform tooth* (Laurin & Reisz[8], 25): absent [0]; present [1].

172. *Tooth implantation* (modified from Rieppel[25], 42; deBraga & Rieppel[10], 94; Müller[7], 38): subthecodont [0]; thecodont [1]; ankylothecodont [2], superfically attached to bone [3].

173. *Marginal dentition, morphology* (modified from Tsuji[12], 71; Müller & Tsuji[10], 76): single cusp [0]; multiple cusps [1]; leaf-shaped w/denticles [2].

174. *Labryrinthodont infolding* (Laurin & Reisz[8], 68): present [0]; absent [1].

Table S2. Scores for the 268 phylogenetically informative characters considered in this study. Definitions for the cranial characters (1-174) are provided in Table S1. Nexus files are available on request from the corresponding author.

Acerosodontosaurus piveteaui

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Acleistorhinus pteroticus

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??????????	??????????	??????????	??????????
??????????	??????????	????????	

Araeoscelidae

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0001000000	1001000000	1001000000	0011000100
010[12]000000	0000001000	0010110000	0000110101
100?000000	000000000?	00???0?0	

Archosauriformes

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01[01]1110111 000110103[12] [01]11011201[01] 1110010101
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Australothyris smithi

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Barasaurus besairiei

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0?0???000? ?01???00? 0???????

“Bashkyroleter” mesensis

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Bashkyroleter bashykyricus

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??????10??	0?01??????	??????????	??????????
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Belebey vegrandis

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Bradysaurus spp.

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Captorhinidae
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0002000000 0000000000 0000010000 0000010000
000?000000 000000000? 00???000

Caseidae
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Claudiosaurus germaini
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Colobomycter phloleter

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Delorhynchus cifelli

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Emeroleter levis

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Feeserpeton oklahomensis

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Hovasaurus boulei

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Kuehneosauridae

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Lanthanosuchus watsoni

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Macroleter poezicus

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Mesosaurus

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Millerettidae
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Nycteroleter ineptus
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Odontochelys semitestacea

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Orovenator mayorum

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Owenetta spp.

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Paleothyris acadiana

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0?0000?000 1001000000 1001000000 0000000100
0101000000 0000001000 0000010000 0000010101
100?000000 000000000? 00???000

Placodus spp.

2110011001 00110?0101 11000?1001 0102?1?0?0
?011000010 0?00100111 1111?001[01]1 ??21?10000
1100110001 1010???101 ?121101?0 0111001211
0[01]00?01101 011???1001 011?1?1111 110?111111
0?00101101 01?100000? 1111111?11 1110001011
11110121?? 1?00101101 111?010001 10000?0100
0010?00000 010000000? 00101001

Procolophon spp.

0000010000 0000000010 1001000101 0001000121
?100001011 0?00110100 0000000001 ??10111??1
0101101010 ???1011111 01110011?0 1010001001
0001001000 0100110110 0110111110 100?011111
0001001101 00010[01]0000 1002001100 101010?100
[01]002100100 0100110000 0100011100 1000020110
01[01]0000000 001000000? 0020?000

Proganochelys quenstedti

2000010101	01??010000	1100101?10	??02000021
?010000000	10011?0101	100111?101	??21?00002
1000210000	???0???111	0011001001	011001??11
1101001110	111?211011	0100111111	0111011011
110100100?	????111001	1101100111	0000221010
1002210010	1000011110	1111111100	1110100120
0110101111	1101211111	1121?110	

Prolacerta broomi

1001[01][01]00[01][01]		[01]000010001	[01]001[01]0[01]001
000[12]0000?0	?[01]01[01]01000	0?00110001	1[12]1[01]01100[01]
1?21?[01][01][01]10	0000[01]10011	0001101111	000[01]000[01]11
0110001001	10010[01]11[01]1	011?11?000	[12]1101[01]1011
110?1010?1	0001001[01]11	0001001[02]0?	1[01]11[01]00110
1101001000	001201[12]111	[01]001101?01	01100120[01][01]
11[01]0[01]10101	100?000000	000000000?	00???0?0

Rhipaeosaurus spp.

??????????	??????????	??????????	??????????
??????????	??????????	??????????	??????????
?????????0	??????????	?????000??	0???0????1
0?????????	??????????	??????1?11	0????????1
???????0??	??110?????	???2??0???	????10????
?0?1?0?0??	?1???11?0?	????011???	????00?00?
0?????????	??1???????	????????	

Rhynchocephalia

2000000000	0000000000	1100100000	0002?1?0?0
?101101000	0?00111011	1211000111	??21?00110
1100110001	0011001111	00111001?1	0100001001

100[01]101111 011?111010 1110110111 110?111011
0001011001 030100[01]01? 1001[01]00110 1121001000
01[01]1200011 1000101[01]01 010111110[01] 1111120101
100?000000 000000000? 0010?000

Rhynchosauria
0001110111 1010010000 1101001001 00010000?0
?001001000 0?00110011 1310000111 ??21?10111
1000110011 1111101110 ??000001?0 0110001101
1001001101 011??11001 1100111111 010?111001
1101011111 02?1001001 1001000110 111?0010[01]0
0011010110 0001101101 0111112010 1110110101
110?000000 000000000? 0010?000

Scutosaurus spp.
2000010000 0000000000 1001010001 00000?0010
?011000000 1110110100 0000000000 1010111??0
0102001100 ???0???111 1111001010 1011001111
0101010000 ?11001?11? 0101101111 000?011111
0100?01101 002111000? 0002001111 101011?100
0002200100 0110110010 0000011000 1000021020
0112110000 001000000? 00??00??

Seymouriiadae
0000000000 0000000000 0001010000 0000000010
0000001000 1200000100 0000001000 00000[01]0001
0001000000 ???00??0?0 ??001001?0 0100000000
??01001000 0000100?0 2010001010 000?200000
00000000?0 0000000000 0000000000 0000000000
0000000100 0000000000 0000000000 0000000000

000?000000 000000000? 0000?000

Sinosaurosphargis yunguiensis

1110011010 ?0000?0100 11010?000? 1002???0??
?011101010 ??011?0011 111??00111 ??21?10010
??1????00 ???11????1 0111011?1 ??11?012?0
??1????0?1 ?11??????? 1???11111? 0???201???
??010??0?1 000??????? ?????????? ??????????
?????????? ?????????? ?????????? ??????????
?????????? ?????????? ????????

Squamata

[01]0[01]00[01]00[01][01] 0000000000 1101001000
00020100?0 ?10[01]11100[01] 0?0011[01]0[01]1 1211000111
??21?1[01]012 001????011 000110?111 00110011?0
0100001201 1010?01111 011?111011 1110110111
110?111011 1[01]01011101 0[03][01]1001[02][01]1
100110011[01] 1[01]21001000 1111[02]10[01]11 1000101[01]01
01[01]1111101 1111[01]20101 100?010000 0000000000
00???0?0

Trilophosaurus buettneri

1000100010 01??010000 ??0???0??1 000???????
?001101000 0?0??0??11 1311?1??01 ??21??001?
???????0?1 1110???111 ?00?101110 0111001??1
1010??110? ?11??10??1 11??01?111 110?011100
00010?1101 00010?1[1 2]01 1011000?10 111?101000
0012010000 0001101101 0110012010 1110110101
100?000000 000000000? 00???0?0

Youngina capensis

1000000000 0000000000 1100010100 0001000000
0001001010 0?00111001 1010001100 0120110010
1100010011 0001001111 0000000011 0110001001
1001000101 001?11?001 0110101001 000?101001
000000?001 1001000001 10010001?0 [01]1[01]1?01000
0011[02]0[01]101 0100111?01 0110110000 0100110101
100?000000 000000000? 00???0?0

Table S3. Synapomorphy list for those reptile clades within which *Eunotosaurus africanus* is nested based on the maximium parsimony analysis of the total character matrix. Also included are the transformations supporting the monophyly of *Odontochelys* + *Proganochelys* exclusive of *Eunotosaurus*. Character numbers refer to Table S1.

Odontochelys + *Proganochelys*

47: 1 to 0
66: 0 to 1
90: 1 to 0
94: 1 to 0
220: 1 to 0
225: 0 to 1
242: 0 to 1
243: 0 to 1
247: 0 to 1
257: 0 to 1
258: 0 to 1
261: 0 to 1
262: 0 to 1
264: 0 to 1

Eunotosaurus + *Odontochelys*, *Proganochelys*

25: 0 to 1
51: 0 to 1
59: 1 to 0
62: 1 to 0
63: 1 to 0
85: 1 to 2
108: 1 to 0
130: 1 to 0

131: 0 to 1
151: 1 to 0
153: 0 to 1
155: 1 to 0
168: 1 to 0
192: 1 to 0
193: 1 to 0
202: 1 to 0
204: 1 to 2
205: 0 to 2
215: 1 to 0
248: 0 to 1
249: 0 to 1
250: 0 to 1
251: 0 to 1
254: 0 to 1
255: 0 to 2
256: 0 to 1
263: 1 to 2
267: 0 to 1

+ Sauropterygia
24: 1 to 0
43: 0 to 1
25: 1 to 0

+ *Acerodontosaurus*
120: 1 to 0
123: 0 to 1
156: 1 to 0

+ Lepidosauria
34: 1 to 2
103: 0 to 1
104: 0 to 1
159: 0 to 1
224: 0 to 1
236: 1 to 2

+ PanArchosauria (crown-group Diapsida)
25: 1 to 0
28: 1 to 0
37: 1 to 0
44: 0 to 1
49: 1 to 0
108: 0 to 1
148: 0 to 1

+ Kuehneosauridae
59: 0 to 1
62: 0 to 1
67: 1 to 0
70: 0 to 1
82: 1 to 0
151: 0 to 1
168: 0 to 1
206: 0 to 1
209: 0 to 1

+ *Claudiosaurus*

24: 0 to 1
93: 0 to 1
95: 0 to 1
127: 0 to 1

+ *Orovenator*
6: 0 to 1
25: 0 to 1
26: 1 to 0
37: 0 to 1
44: 1 to 0
171: 1 to 0

+ Youngina
57: 0 to 1
142: 0 to 1
215: 0 to 1
220: 0 to 1

+ *Hovasaurus*
128: 0 to 1
136: 0 to 1
188: 0 to 1
189: 0 to 1
192: 0 to 1
197: 0 to 1
198: 1 to 0
203: 0 to 1
208: 0 to 1
210: 0 to 1

+ Araeoscelidae
1: 0 to 1
44: 0 to 1
49: 0 to 1
89: 0 to 1
90: 0 to 1
113: 0 to 1
124: 0 to 1
193: 0 to 1
194: 0 to 1
223: 0 to 1
225: 0 to 1
235: 0 to 1

+ *Paleothyris*
39: 1 to 0
51: 1 to 0
181: 0 to 1
238: 0 to 1
240: 0 to 1
241: 0 to 1

+ Captorhinidae
60: 0 to 1
61: 0 to 1
68: 0 to 1
73: 1 to 2
112: 0 to 1
120: 0 to 1

130: 0 to 1
198: 0 to 1

+ Parareptilia
75: 0 to 1
81: 0 to 1
133: 0 to 1
157: 0 to 1
204: 0 to 1
236: 0 to 1

+ Caseidae (crown-group Amniota)
73: 0 to 1
80: 1 to 0
82: 0 to 1
98: 0 to 1
105: 1 to 0
145: 0 to 1
174: 0 to 1

Table S4. Observed specimens and primary references for the fossils on which the data matrix (Table S2) was constructed. Institutional abbreviations: **AMNH** = American Museum of Natural History, New York; **CG, GC, GC/K, GM, GSC, GSC-CGP** = Council for Geosciences, Pretoria; **BMNH** = Natural History Museum, London; **BPI** = Evolutionary Studies Institute, University of the Witswatersrand, Johannesburg; **FMNH-UR** = Field Museum of Natural History, Chicago; **KUVP** = University of Kansas Natural History Museum, Lawrence; **MCZ** = Museum of Comparative Zoology, Harvard University, Cambridge, MA; **RC** = Rubidge Collection, Graaff-Reinet; **SAM-PK** = Iziko Museums of South Africa, Cape Town; **SMNS** = Staatliches Museum für Naturkunde, Stuttgart; **TMM** = Texas Memorial Museum, Vertebrate Paleontology Laboratory, University of Texas, Austin; **UCMP** = University of California Museum of Paleontology, Berkeley; **YPM** = Peabody Museum of Natural History, Yale University, New Haven.

Acerosodontosaurus piveteaui: Currie[81], Bickelman *et al.*[82].

Acleistorhinus pteroticus: FMNH-UR1038; Daly[83], debraga & Reisz[11].

Archosauriformes

- *Erythrosuchus*: BP/1/383, RC 59; Parrish[84], Gower[85,86].
- *Euparkeria*: SAM-PK-K6047, K7696; Ewer[29], Gower & Weber[87], Senter[88].
- *Proterosuchus*: RC96, SAM-PK-K591, K10603; Welman[89], Klembara & Welman[90].
- Other references: Borsuk-Białynicka & Evans[40], Nesbitt[91].

Araeoscelidae

- *Araeoscelis gracilis*: MCZ 4380, 8828; Reisz *et al.*[92].
- *Petrolacosaurus kansensis*: KUVP 1423, 1424, 1426, 1427, 8351, 9951, 9952, 33606, 33607: Reisz et al.[93].

Australothyris smithi: SAM-PK-K8302; Modesto *et al.*[94].

Barasaurus besairiei: SAM-PK-K8275, K8276, K8571, K8574; Meckert[95], Ketchum & Barrett[96].

Bashkyroleter bashykyricus: Müller & Tsuji[10], Tsuji *et al.*[79].

“Bashkyroleter” mesensis: Müller & Tsuji[10], Tsuji *et al.*[79].

Belebey vegrandis: Reisz *et al.* 2007[44].

Bradysaurus spp.: AMNH 2452, 3897, 4410, 4457, 4877, 5323, 5324, 5367, 5604, 5668, GM uncatalogued specimens; Lee[6].

Captorhinidae:

Captorhinus spp.: AMNH 4333, 4425, 4760, 5494, 19370-19402, 25401-25550, 25576-25619; Fox and Bowman[97], Heaton[98], Heaton & Reisz[99], Modesto 1998[100].

Protocaptorhinus spp.: AMNH 11539, 20890, 20891; Fox and Bowman[97], Heaton[98], Heaton & Reisz[99].

Other references: Müller & Reisz[101].

Casesauria:

Cotylorhynchus romeri: AMNH 7516; Stovall *et al*.[102].

Eothyris parkeyi: MCZ 1161; Reisz *et al.*[103]

Mycterosaurus longiceps: AMNH 7002

Oedaleops campi: UCMP 35758; Langston[104], Reisz *et al*.[103], Sumida *et al*.[105].

Other references: Romer and Price[106], Reisz et al.[107], Reisz & Dilkes[108].

Claudiosaurus germaini: SAM-PK-K8263; Carroll[35].

Colobomycter phloleter: Laurin and Reisz[109], Modesto[110], Modesto and Reisz[111].

Delorhynchus cifelli: Reisz *et al.*[112].

Diadectomorpha

Limnoscelis paludis: YPM 811; Romer[113], Fracasso[114], Reisz[115].

Diadectes spp: AMNH 2126, 4350, 4352, 4357, 4375, 4839; Berman *et al*.[116], Reisz[115].

Other references: Berman *et al*.[117], Kissel and Reisz[118], Kissel[119].

Emeroleter levis: Müller & Tsuji[10], Tsuji *et al.*[79].

Eosauropterygia: Rieppel[25], Rieppel & Wild[63], Rieppel et al.[28], Merck[120]

Eudibamus cursoris: Berman *et al.*[121].

Feeserpeton oklahomensis: MacDougall and Reisz[80].

Hovasaurus boulei: Currie[122], Bickelman *et al.*[82].

Kuehneosauridae
- *Icarasaurus siefkeri*: AMNH 2101; Colbert[123].
- *Kuehneosaurus latus*: Robinson[124], Colbert[123].

Lanthanosuchus watsoni: deBraga and Reisz[11].

Macroleter poezicus: Tsuji[12], Müller & Tsuji[10].

Mesosauridae:
- *Mesosaurus spp*.: AMNH 2440, 6988, 23800-23876, SAM-PK-K8367, K8381; Modesto[5,125].
- *Stereosternum* spp: AMNH 6993, 11003.
- Other references: Piñeiro *et al*.[126].

Microleter mckinzieorum: Tsuji *et al.*[127].

Millerettidae
- *Milleretta spp*: BPI/1/7, 720, 2610, 2612, 2614, 2876, 2886, 3818, 3822; RC14, 14b, 15, 70, 71, 78, 226, SAM-PK-K7751, K8609, K10082; Gow[32]; Gow[2,128].
- *Millerosaurus*: SAM-PK-K5212 Gow[32].
- Milleretid: BPI/1/2885.
- Other references: Cisneros *et al*.[129].

Nycteroleter ineptus: Tverdokhlebova and Ivakhnenko[131], Müller and Tsuji[10], Tsuji *et al.*[79].

Nyctiphruretus acudens: Müller & Tsuji[10], Säilä[31].

Odontochelys semitestacea: IVPP V13240, V15653, V15639; Li *et al*.[3].

Orovenator mayorum: Reisz *et al.*[131].

Owenetta spp: BPI/1/1395, 1396, 13819, 5398; RC50, 125, 126-128; SAM-PK-K5226, K7581, K10216, K10680; Reisz & Scott[48].

Paleothyris acadiana: MCZ 3472, 3481-3492; Carroll[132].

Placodus spp: Sues[133]; Rieppel[26]; Rieppel and Zanon[27].

Procolophon spp.: AMNH 5693, 9501, 9506-9509, 9511, 9512, 9533; BPI/1/4246, BPI/1/5927, GC 423, GSC_1.127, GSC_CGP_1.1; Carroll & Lindsay[43].

Proganochelys quenstedti: SMNS 16980; Gaffney[4].

Prolacerta broomi: BPI/1/471, 4504a, 5066, 5375, 15880, GC431; Evans[134], Modesto & Sues[23].

Rhipaeosaurus spp: Chudinov[136]; Tsuji *et al.*[79].

Rhynchosauria
    Mesosuchus browni: SAM-PK-K6536: Dilkes[30]; Müller[7].

Scutosaurus spp: Lee[6].

Seymouria spp.: AMNH 1843, 34342: Laurin[136, 138], Berman et al.[139].

Sinosaurosphargis yunguiensis: Li *et al*.[139].

Trilophosaurus buettneri: TMM 31025; Gregory[47]; Merck[120]; Nesbitt[91].

Youngina capensis: AMNH 5561; BMNH R5481, BPI/1/3859, GC/K/106, RC90, RC625, SAM-PK-K7578, K8655, K7710; Carroll[31], Gardner *et al*.[140], Smith and Evans[141].