STEPWISE ASSEMBLY OF CROWN REPTILE ANATOMY CLARIFIED BY LATE PALEOZOIC OUTGROUPS OF NEODIAPSIDA

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Abstract

Living reptiles include more than 20,000 species with disparate ecologies. Direct anatomical evidence from Neodiapsida, which includes the reptile crown-group Sauria and its closest extinct relatives, shows that this diversity originates from a single common reptilian ancestor that lived some 255 million years ago in the Paleozoic. However, the evolutionary assembly of crown reptile traits is poorly understood due to the lack of anatomically close outgroups to Neodiapsida[1-7]. We present a substantially revised phylogenetic hypothesis, informed by new anatomical data derived from high-resolution synchrotron tomography of Paleozoic reptiles[8-12]. We find strong evidence placing the clade Millerettidae as a close sister to Neodiapsida, which uniquely share a suite of derived features among Paleozoic stem reptiles. This grouping, for which we name the new clade Parapleurota, replaces previous phylogenetic paradigms by rendering the group Parareptilia as a polyphyletic assemblage of stem reptiles, of which millerettids are the most crownward. Our analysis presents hypotheses that resolve long-standing issues in Paleozoic reptile evolution, including the placement of captorhinids on the amniote stem lineage and firm support for varanopids as synapsids, which taken together provide a greatly improved fit to the observed stratigraphic record. Optimizations of character evolution on our phylogenetic hypothesis reveals gradual assembly of crown reptile anatomy, including a Permian origin of tympanic hearing, the presence of a lower temporal fenestra in the amniote common ancestor, with subsequent modifications on the reptile stem lineage, leading to the loss of the lower temporal bar. This evolutionary framework provides a platform for investigating the subsequent radiations of the reptile crown group in the Early Triassic, including the lines leading to dinosaurs (including birds), crocodilians, lepidosaurs, and extinct marine reptiles.

Introduction

Living reptiles include lepidosaurs, turtles, crocodilians, and birds[13] within the reptile crown group Sauria, which exploded in diversity ~250 million years ago in the Triassic Period. Early saurian diversification involved transformation of key anatomical traits that have long been debated, including impedance-matching hearing[14-15], temporal fenestration[16-17], and the reorganization of the hindlimb musculature for tail-driven locomotion[18]. Relevant taxa informing the origins of these traits include the late Permian non-saurian Neodiapsida such as terrestrial younginids[19], semiaquatic tangasaurids[20], and gliding weigeltisaurids[21]. Close neodiapsid outgroups have great leverage for understanding these anatomical transformations but remain almost completely unknown for much of the Permian[2].

Prevailing hypotheses of Paleozoic reptile evolution[5-7] generally posit a deep phylogenetic split prior to the origin of Neodiapsida between 'near reptiles' (Parareptilia), an ecomorphologically diverse group that is thought to be only distantly related to Sauria, and 'true reptiles' (Eureptilia), a clade that includes the Late Carboniferous *Hylonomus* (~318 MA) and various Permian taxa interpreted as successively closer sister-groups to Sauria (Fig. 1). The origins of this dichotomy lie in the foundational work of Olson[22], who

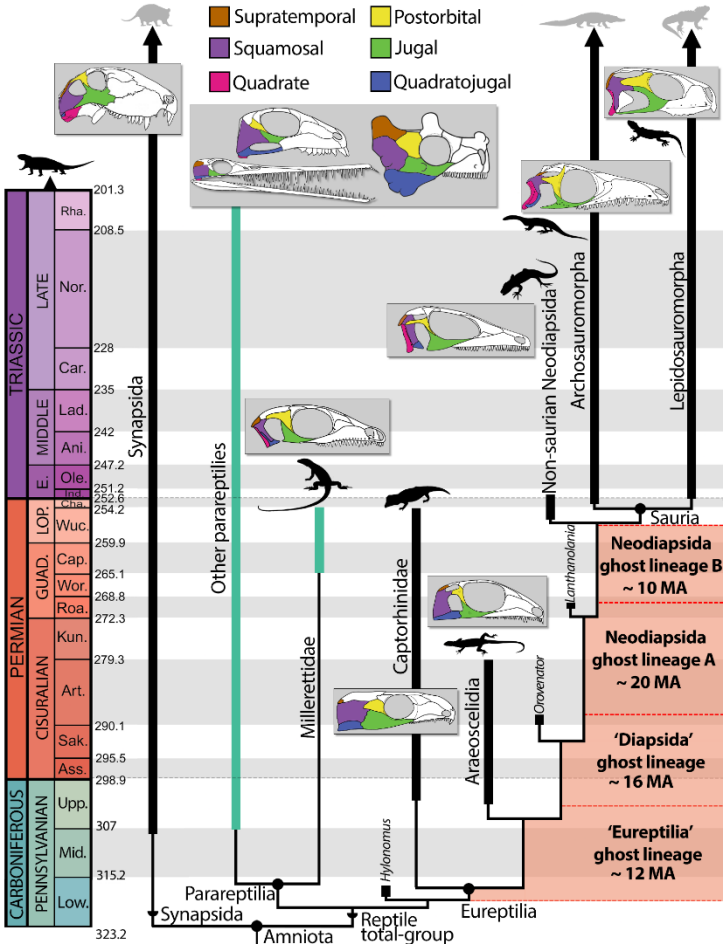

Figure 1. Traditional phylogenetic hypothesis of Late Carboniferous-Triassic amniote relationships, highlighting the longstanding stem-reptile ghost lineages from the Late Carboniferous through late Permian. Green branches represent 'Parareptilia'. Diagrams of amniote fenestration are not to scale and have been redrawn based on the following reconstructions (left to right): *Dimetrodon*[62], *Mesosaurus*[87], *Belebey*[10], *Milleropsis* (this study), *Bunostegos*[88], *Captorhinus*[89], EAZ younginiform (this study), *Petrolacosaurus*[34], *Prolacerta*[90], and *Clevosaurus*[91]. Silhouettes are available from Phylopic (www.phylopic.org) under CC BY 3.0 licenses or within public domain.

allied the Seymouriamorpha and Diadectomorpha with Procolophonia and Chelonia (turtles) in the class ‘Parareptilia’; and the Captorhinomorpha, Synapsida (mammal-line amniotes), and fenestrated reptiles in the class ‘Eureptilia’. This hypothesis was largely ignored by Watson[8] and Romer[12] who considered seymouriamorphs, diadectomorphs, and captorhinomorphs as earlier-diverging tetrapods more distantly related to amniotes. Although Olson’s original hypothesis for a monophyletic Parareptilia and Eureptilia has not found support since the advent of cladistics1-7,23-28, the concept of a parareptilian clade that includes Procolophonia with other taxa has nevertheless persisted.

Early cladistic analyses on amniote origins opted to use ‘Parareptilia’ for a clade consisting of Procolophonia, Mesosauridae, and Millerettidae and ‘Eureptilia’ for a clade containing captorhinids, protorothyridids, and diapsid (two temporal fenestrae) reptiles[5]. Soon after, the late Carboniferous and Permian clades Acleistorhinidae[6] and Bolosauridae[10] were also placed within Parareptilia, based on observations of the temporal and palatal regions[10]. Tsuji and Müller[29] proposed the following definition for Eureptilia “as the most inclusive clade containing *Captorhinus aguti* and *Petrolacosaurus kansensis* but not *Procolophon trigoniceps*” and Parareptilia “the most inclusive clade containing *Milleretta rubidgei* and *Procolophon trigoniceps* but not *Captorhinus aguti*”. This framework set the stage for the understanding of early reptile evolution since the early 2000s.

The validity of Parareptilia and Eureptilia under these definitions has been questioned by recent phylogenetic analyses, with the most comprehensive studies finding a polyphyletic Eureptilia either as a grade of stem-amniotes[25,26] or earliest-branching reptiles and Parareptilia as a paraphyletic grade of stem reptiles closer to the reptile crown group Sauria[4,25,27]. However, substantial uncertainties remain regarding the affinities of some groups to the reptile or even the mammal stem-lineage[4] and whether some taxa long-regarded as stem

reptiles instead belong to the amniote stem-lineage[25-26]. For example, the Varanopidae and Recumbirostra - two clades traditionally placed on the mammal and amniote stem-lineages, respectively, have recently been interpreted as stem reptiles[4,30]. Similarly, the Captorhinidae, a group interpreted as stem-reptiles for much of the latter half of the 20th century (but see[8,12,16-17]), have been recently posited as stem-amniotes[25]. Challenges to this phylogenetic paradigm of Eureptilia and Parareptilia have yet to achieve consensus, but these two clades are still assumed to be monophyletic in literature on early reptile origins through the past four decades.

The paradigm of a deep phylogenetic split between Parareptilia and Eureptilia imply extensive ghost lineages along the reptile stem lineage[31], particularly for neodiapsid origins[2] (Fig. 1). These include a ghost lineage for Eureptilia between the appearance of the earliest candidate eureptile *Hylonomus*[32] (~318 MA) and the next unambiguous early reptiles towards the end of the Carboniferous[33-34] (~302 MA) (Fig.1, Eureptilia Ghost lineage). More central to the question of the crown reptile origins, however, are several ghost lineages in the sporadic fossil record of non-saurian neodiapsids, which are only partially closed by the putative neodiapsids *Orovenator mayorum* (early Permian, ~288 MA[35]) and *Lanthanolania ivakhnenkoi* (middle Permian, ~265 MA[36]), both genera represented only by partial skulls (Fig. 1A, B; “Diapsida”, and “Neodiapsida ghost lineages”). Within Parareptilia, the phylogenetic position of Millerettidae[9] in an early branching position among parareptiles further exemplifies the poor stratigraphic fit as this group is the geologically youngest to appear among them, leading to an expansive ghost lineage spanning nearly the entire Permian[31] (Fig. 1).

The poor stratigraphic fit of these prevailing hypotheses of early reptiles makes it difficult to reconstruct the series of anatomical transformations involved in the origins of crown reptile anatomy, particularly the dearth of fossil stem reptiles bridging the morphological gap between primitive araeoscelidians in the late Carboniferous[33] and the first adequately known neodiapsids in the later Permian[19] (Fig. 1). For instance, key

neodiapsid postcranial traits such as an ossified sternum, the appearance of an outer process on the fifth metatarsal suggesting a restructuring of m. gastrocnemius femoralis, and laterally-directed caudal ribs supporting the caudofemoralis musculature are first documented in late Permian non-saurian neodiapsids such as *Youngina*[18]. Late Permian neodiapsids also contrast with araeoscelidians in the loss of amniote plesiomorphies such as a trough on the dorsal surface of the iliac blade, asymmetrical femoral condyles and the cnemial crest of the tibia[4]; features which are also lost among some groups of middle and late Permian parareptiles, such as millerettids[9].

Early Permian reptiles relevant to this issue remain stubbornly absent from the fossil record, but their anatomical features can be inferred from geologically younger taxa given robust hypotheses for their phylogenetic relationships. One group of saurian-like reptiles in particular hold latent information that could potentially inform early reptile relationships: millerettid parareptiles (Figs. 2-3). Prior to the advent of cladistic methodologies both Watson[8] and Romer[12] interpreted millerettids as close relatives of the 'Eosuchia', a now paraphyletic grade loosely equivalent to early Neodiapsida. These historical observations were based on anatomical features suggesting the secondary loss of an upper temporal fenestra and the presence of a tympanic emargination located posteriorly on the skull. Other studies even hypothesized that these derived anatomical features of millerettids were indicative of their placement within the reptile crown, either as stem archosaurs[37] or lepidosaurs[9]. However, current phylogenetic hypotheses[4,25] usually interpret these similarities as homoplasies. New data on Permian stem reptiles such as millerettids therefore has the potential to influence phylogenetic

hypotheses, with implications for stem reptile relationships and the evolutionary assembly of crown reptile adaptations.

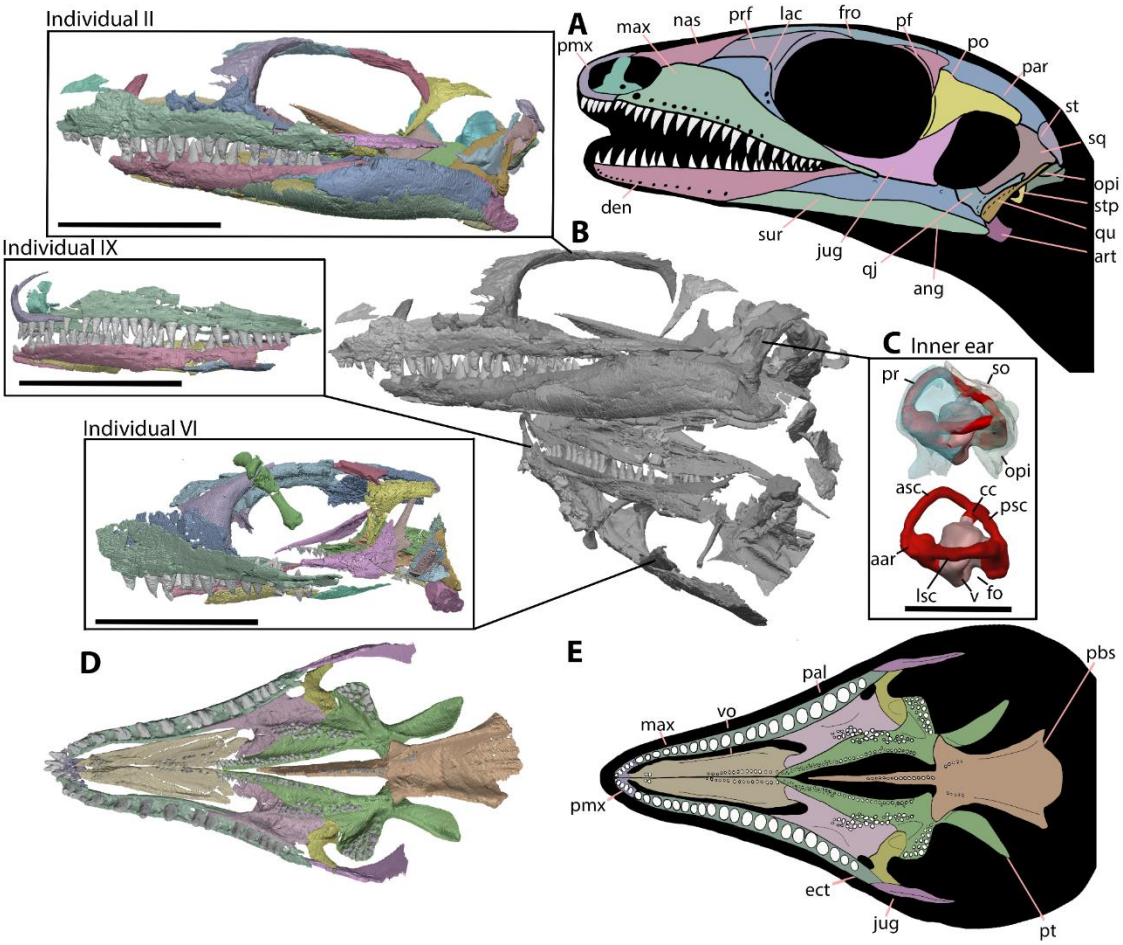

Figure 2. New information and individuals of *Milleropsis* presented here. **A**, line reconstruction of the cranial anatomy of *Milleropsis pricei* BP/1/720. **B**, segmentation of all three individuals (following that of [7]) of *Milleropsis* present in BP/1/720, individual II, IX (mirrored), and VII (mirrored), in left lateral views **C,** segmented endosseous labyrinth of *Milleropsis* BP/1/720 individual II in left lateral view with bones of the otic capsules opaque and removed (lagena not reconstructed), **D**, virtual reconstruction of the palate of Individual II (left ectopterygoid mirrored), and **E**, line reconstruction of Individual II in palatal view. Scale bars for skulls are 10 mm whereas inner ear scale bar is 5mm. Abbreviations: aar, anterior ampullary recess; asc anterior semicircular canal; ang, angular; art, articular; cc, common crus; den, dentary; ect, ectopterygoid; fro, frontal; fo, fenestra ovalis; jug, jugal; lac, lacrimal; lsc, lateral semicircular canal; max, maxilla; nas, nasal; opi, opisthotic; pal, palatine; par, parietal; pbs, parabasiphenoid; pf, postfrontal; pmx, premaxilla; po, postorbital; pr, prootic; prf, prefrontal; psc, posterior semicircular canal; pt, pterygoid; qj, quadratojugal; qu, quadrate; so, supraoccipital; sq, squamosal; st, supratemporal; stp, stapes; sur, surangular; v, vestibule; and vo, vomer.

We reevaluate the evolutionary relationships of early reptiles by conducting an extensive phylogenetic revision of Paleozoic reptiles, informed by new X-ray micro-computed tomography (µCT) data, including high-resolution synchrotron phase-contrast µCT that enable us to collect and analyze previously unobservable character information. Our phylogenetic dataset improves on previous datasets by broadly sampling all putative stem-reptiles from the Late Carboniferous (Pennsylvanian) through the explosive radiation of the reptile crown

in the Triassic, and by incorporating unsampled character-rich systems (e.g., neurocranium and palatoquadrate) in key taxa. Our new tomography data includes putative stem reptiles such as the varanopid *Heleosaurus*[38], the araeoscelidian *Araeoscelis*[39], the millerettids *Milleropsis*[8] and *Milleretta*[9], and neodiapsids, including *Youngina*[40] and the EAZ younginiform[41] SAM-PK-K7710, as well as other taxa across early amniote phylogeny (Table 1). We placed a special focus on millerettids, which share previously underappreciated similarities with Sauria[42-43] (in modern cladistic frameworks) and which substantiate our understanding of anatomical transformations along the reptile stem lineage (Figs. 2-3, Videos S1-3).

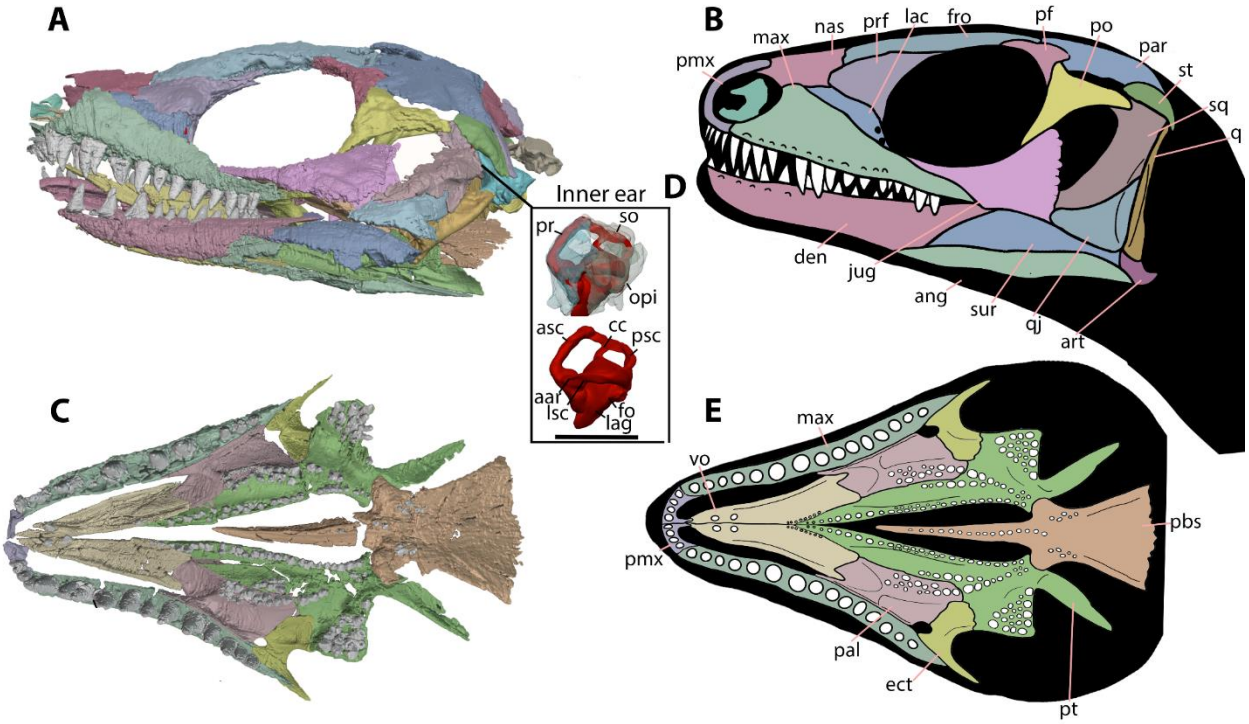

Figure 3. New information on *Milleretta* presented here. **A**, segmentation of BP/1/3822 in mirrored left lateral view and **B,** corresponding line drawing. **C**, segmentation of BP/1/3822 in palatal view; **D**, segmented endosseous labyrinth of *Milleretta* BP/1/3822 in left lateral view with bones of the otic capsules opaque and removed; and **E**, reconstruction of *Milleretta* BP/1/3822 in palatal view. Scale bar for skulls is 10 mm whereas the inner ear scale bar is 5mm. Abbreviations: aar, anterior ampullary recess; asc anterior semicircular canal; ang, angular; art, articular; cc, common crus; den, dentary; ect, ectopterygoid; fro, frontal; fo, fenestra ovalis; jug, jugal; lac, lacrimal; lag, lagena; lsc, lateral semicircular canal; max, maxilla; nas, nasal; opi, opisthotic; pal, palatine; par, parietal; pbs, parabasiphenoid; pf, postfrontal; pmx, premaxilla; po, postorbital; pr, prootic; prf, prefrontal; psc, posterior semicircular canal; pt, pterygoid; qj, quadratojugal; qu, quadrate; so, supraoccipital; st, supratemporal; sq, squamosal; sur, surangular; and vo, vomer.

Methods

Computed Tomography

BP/1/720 (*Milleropsis*), BP/1/3822 (*Milleretta*), SAM-PK-K7710 (EAZ younginiform), and other early amniote taxa (Table 1) were imaged at the ID19 beamline of the European Synchrotron Radiation Facility (Grenoble, France) using propagation phase-contrast synchrotron X-ray micro-computed tomography. The imaged specimen of BP/1/720 was of a nodule containing three skulls: individuals II, VI, and IX[8]. BP/1/4203, a fully articulated specimen of *Milleropsis*, was imaged onsite at the University of Witwatersrand. The holotypes of *Youngina capensis* (AMNH FARB 5561) and *Araeoscelis gracilis* (AMNH FARB 4686) were imaged onsite at the American Museum of Natural History. The µCT data were processed and segmented using Dragonfly2022.268(https://dragonfly.comet.tech/)[44].

Taxon	**Scanning Technique**	**Specimen Numbers**
Hylonomus lyelli	Synchrotron µCT	NHMUK R.416
Mycterosaurus sp.	Lab-based µCT	FMNH:UC:692
Heleosaurus scholtzi	Synchrotron µCT	SAM-PK-K8305
Araeoscelis casei	Lab-based µCT	AMNH FARB 4686
Saurodektes kitchingorum	Synchrotron µCT	BP/1/3189, BP/1/1395,
Sauropareion anoplus	Synchrotron µCT	SAM-PK-K11192
Procolophon trigoniceps	Lab-based µCT	BP/1/9267
Milleropsis pricei	Synchrotron µCT	BP/1/720, BP/1/4203
Milleretta rubidgei	Synchrotron µCT	BP/1/3818, BP/1/3822
Youngina capensis	Lab based and Synchrotron µCT	AMNH FARB 5561, BP/1/2871
Endothiodon Zone younginiform	Synchrotron µCT	SAM-PK-K7710
Prolacerta broomi	Synchrotron µCT	BP/1/5880

Table 1. Scan data of Paleozoic and Triassic amniotes that are accessible and under current study by one or more of the authors. Links are provided when appropriate, and scans will be released upon publication.

Phylogenetic Analysis

We evaluated the phylogenetic relationships of Paleozoic-Triassic reptiles by creating a new phylogenetic dataset using substantial new anatomical data from the scans of millerettids, neodiapsids, and other Permo-Triassic amniotes (Table 1). Our matrix (total characters = 653), includes comprehensive rescoring of skeletal anatomy informative for higher-level reptile relationships, particularly for millerettid and non-saurian neodiapsid stem reptiles (Table 1).

We expanded on previous datasets[4,24] of early amniote relationships by including 265 additional characters not used in previous analyses of early reptile phylogenetic relationships, which substantially improved representation of the early amniote neurocranium and postcranial skeleton. We attempted to incorporate all potentially relevant phylogenetic characters based on a comprehensive review of existing phylogenetic matrices that sample stem-amniote[30], parareptile[45] and saurian relationships[2,3], surveys of the descriptive literature, and observations of the early amniote neurocranium and postcranium available to the authors. These include features that were previously inaccessible in many taxa for which CT data were not available, including the detailed morphology of the orbit, tympanic recess palatoquadrate, braincase and mandible. We illustrate a fraction of this anatomical variation in these regions using *Captorhinus*, *Heleosaurus*, *Saurodektes*, *Milleropsi*s, and the EAZ younginiform as representative taxa (Figs. 4-8).

We also improved the taxonomic sampling of this matrix by adding 65 taxa typically not included in analyses of early reptile origins, including 13 recumbirostrans, 13 parareptiles, and 22 neodiapsids including saurians, bringing the total to 161 operational taxonomic units (OTUs). Notably, our dataset is the first to sample all adequately known millerettids, including: *Broomia perplexa*, *Milleropsis pricei*, *Millerosaurus nuffieldi*, and *Milleretta rubidgei* with all known early parareptile groups and the early members of Neodiapsida. The full character and taxon list (with annotations on their use in previous analyses),

optimizations, and rationale for their inclusion are provided in the SI Appendix along with the character-taxon matrix.

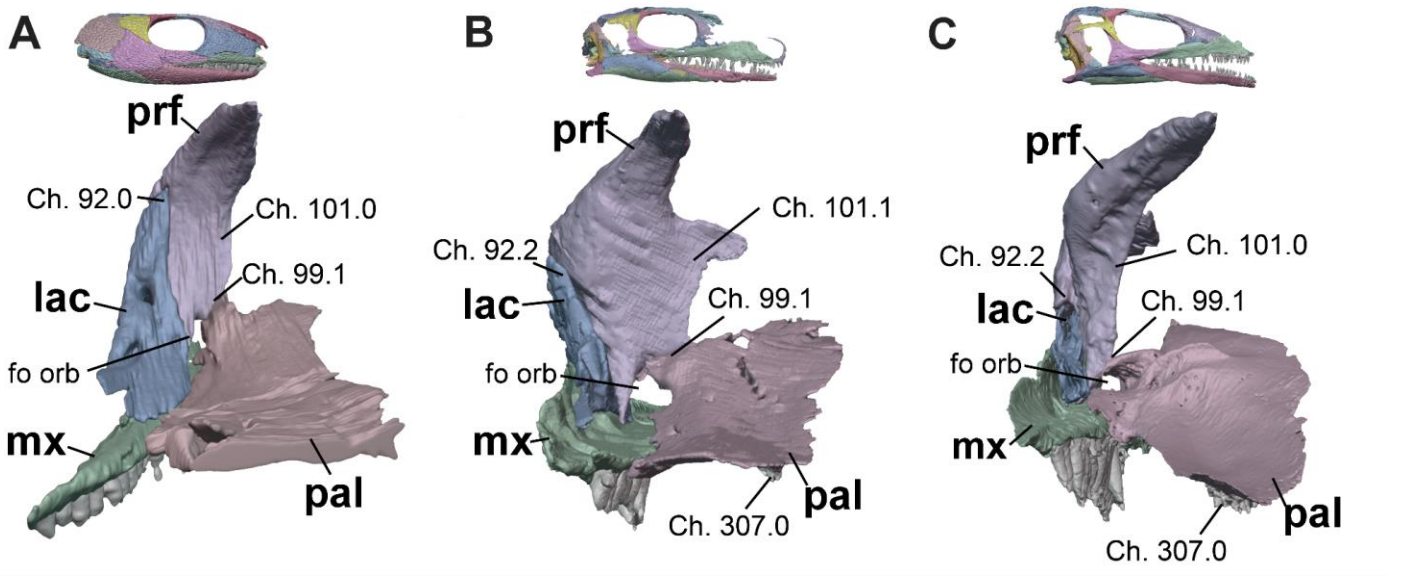

Figure 4. Anterior orbits in posterior view of **A**, *Captorhinus* (OMNH 44816)[85] , **B**, *Milleropsis* (BP/1/720), and **C**, EAZ younginform (SAM-PK-K7710) demonstrating select characters informative to early amniote evolution, including: the presence of a foramen orbitonasale*, the contribution of the lacrimal to the orbit (**Ch. 92**, mediolaterally broad in near and early amniotes), prefrontal-palatal contact* (**Ch. 99**, present in most taxa within this sampling), the width of the ventral process of the prefrontal* (**Ch. 101**, wide in edaphosaurids, procolophonians, millerettids, and rhynchosaurs), and the presence of palatine dentition (**Ch. 307**, absent in some procolophonians and archosauromorphs). * Represents former synapomorphies of Parareptilia widespread among near and crown amniotes Abbreviations: lac, lacrimal; mx, maxilla; pal, palatine; and prf, prefrontal.

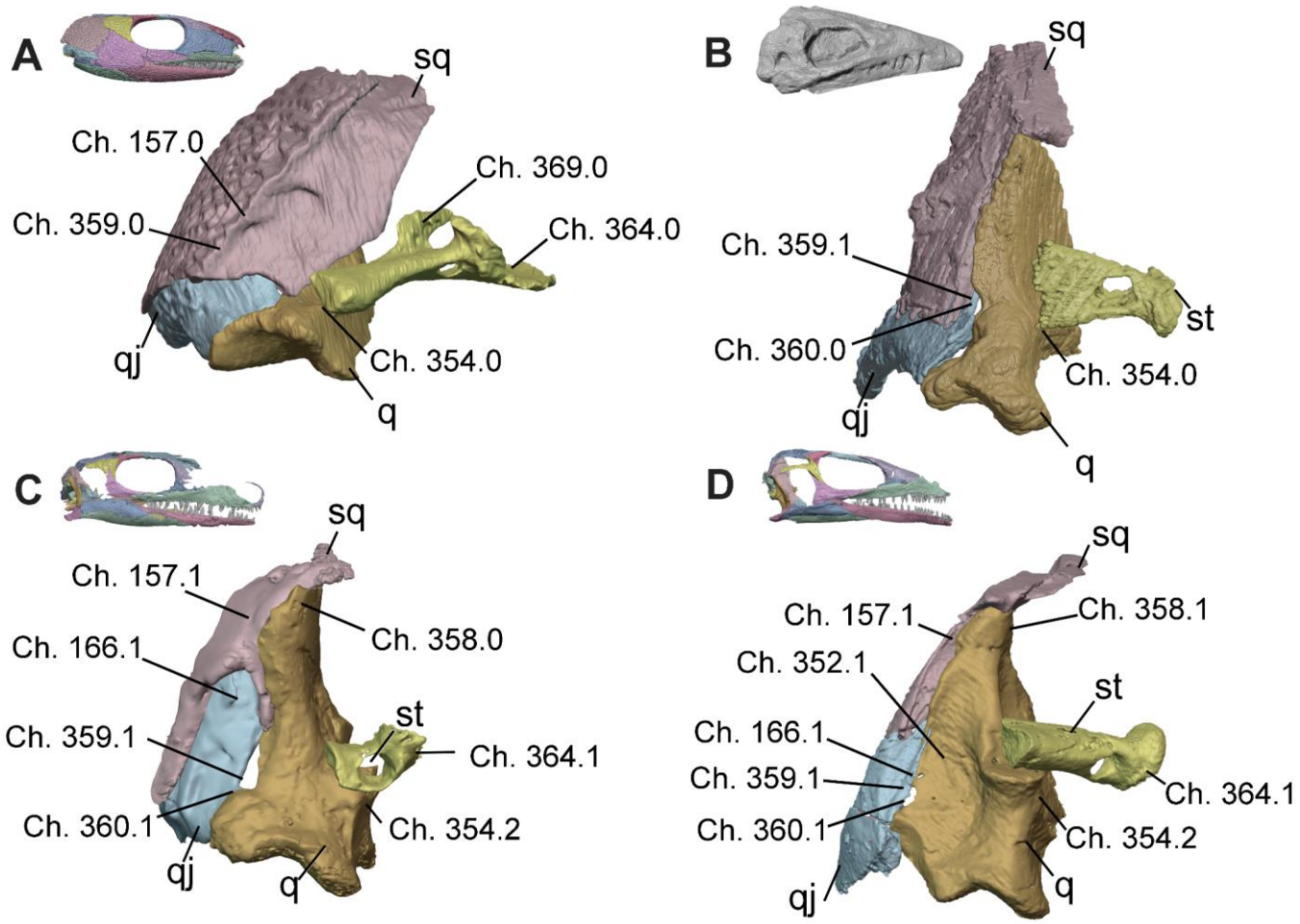

Figure 5. Tympanic and middle ear region of **A**, *Captorhinus* (OMNH 44816)[85], **B,** *Heleosaurus* (SAM-PK-K8305), **C**, *Milleropsis* (BP/1/720), and **D**, EAZ younginform (SAM-PK-K7710) in posterior views demonstrating stepwise reductions in the size and anatomy of the squamosal and stapes and the eventual appearance of a tympanic emargination. Select characters from our dataset include the occipital shelf of the squamosal (**Ch. 157**, lost in Parapleurota**)**, presence or absence of a tympanic emargination (**Ch. 166**, present in Parapleurota and convergently in Procolophonia) or quadrate (**Ch. 352**, present in Neodiapsida, although millerettids bear a small contribution here), stapedial boss of the quadrate (**Ch. 354**, present in neoreptiles), cephalic condyle of the quadrate (**Ch. 358,** present in some neodiapsids and early crown reptiles), presence (**Ch. 359**, present in all early amniotes) and location (**Ch. 360,** located between the quadratojugal and quadrate in neodiapsids) of the quadrate foramen, the presence of the dorsal process of the stapes (**Ch. 369,** lost in Parapleurota), and size of stapedial footplate (**Ch. 364**). Abbreviations:q, quadrate; qj, quadratojugal; sq, squamosal; and st, stapes.

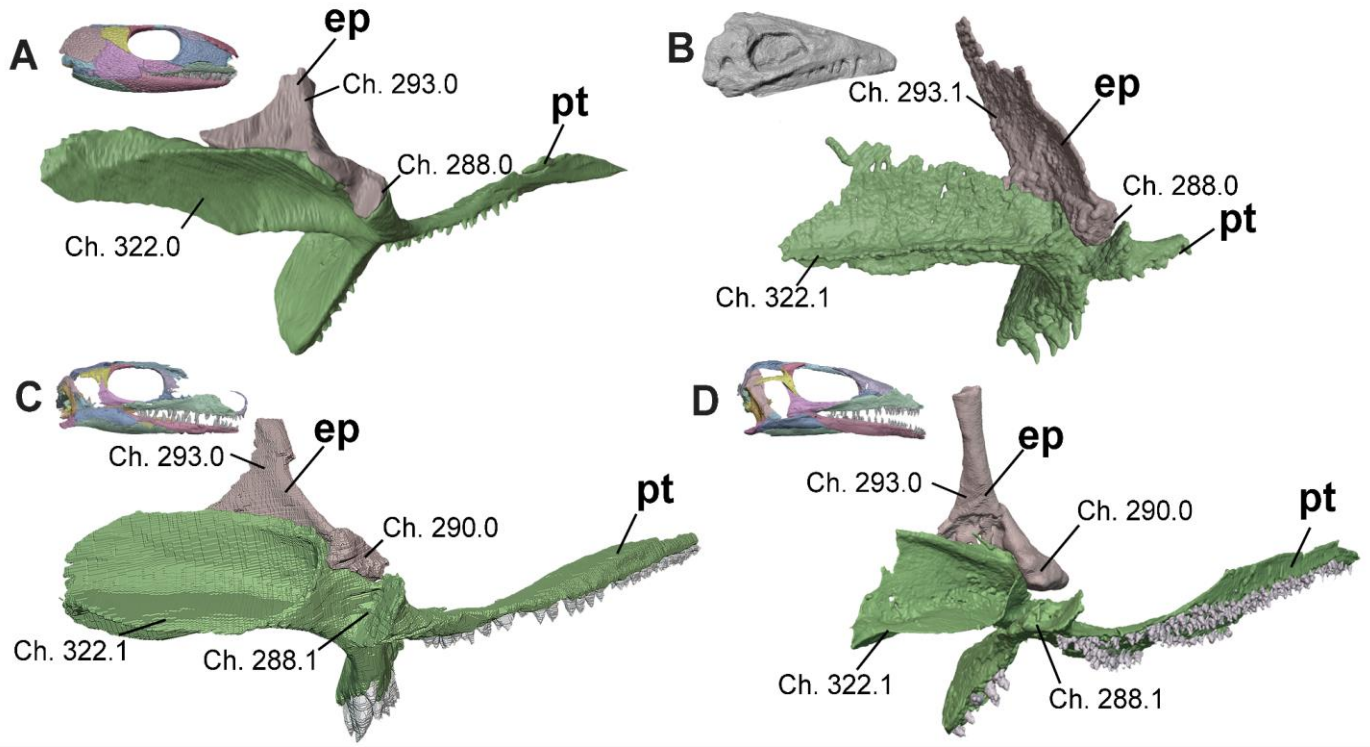

Figure 6. Basicranial region of **A**, *Captorhinus* (OMNH 44816)[85], **B,** *Heleosaurus* (SAM-PK-K8305), **C**, *Milleropsis* (BP/1/720), and **D**, EAZ younginform (SAM-PK-K7710) in oblique posterior view demonstrating the reduction and eventual absence of an the epipterygoid contributing to the basal articulation seen in Parapleurota. Select characters from our dataset include: the presence or absence of a tympanic flange of the pterygoid (**Ch. 322,** present in all early crown amniotes), contribution of the epipterygoid to the basicranial articulation (**Ch. 288**, lost in Parapleurota), the presence of a medial lip of the epipterygoid, (**Ch. 290,** lost in some lepidosauromorphs), and the morphology of the dorsal shaft of the epipterygoid (**Ch. 293,** sheetlike in synapsids including Varanopidae**)**. Abbreviations: ep, epipterygoid and pt, pterygoid

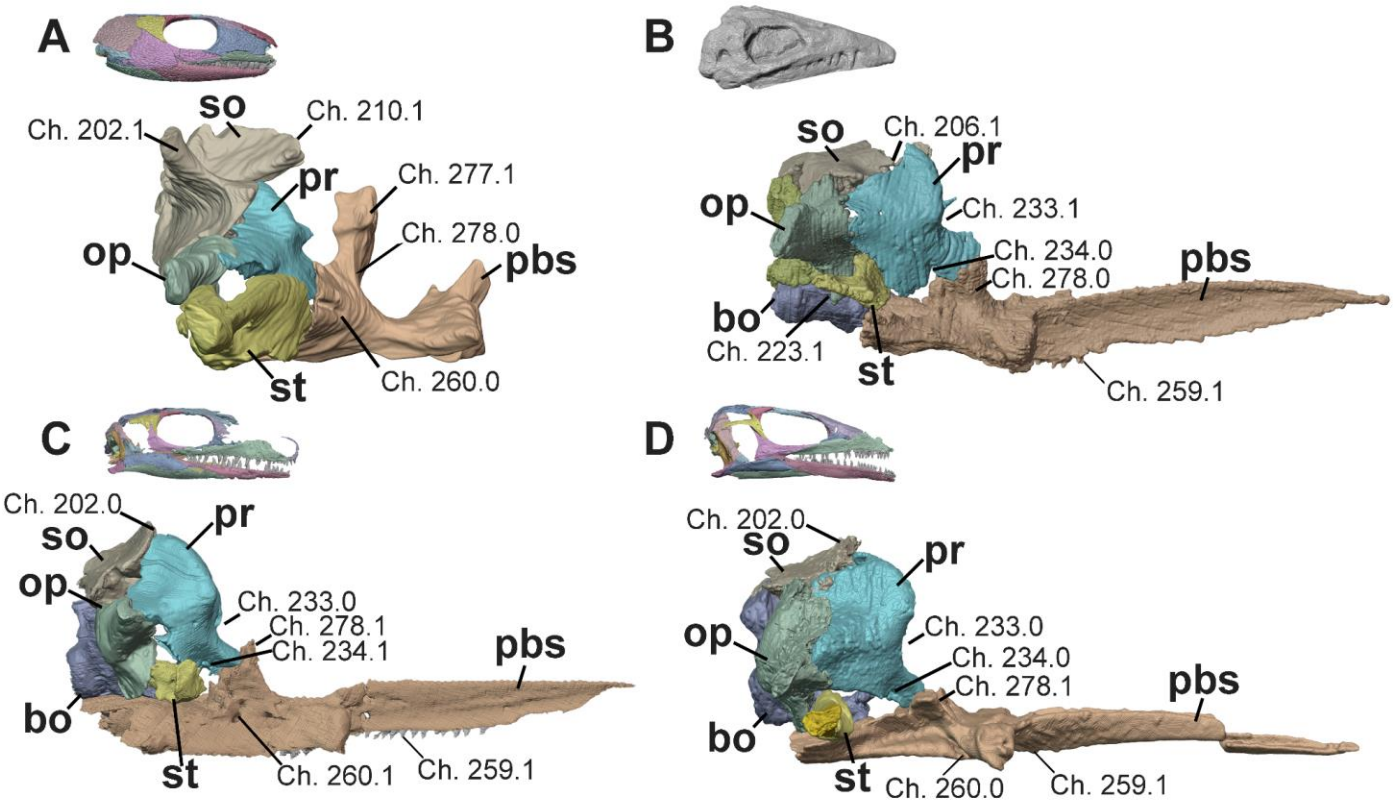

Figure 7. Braincase of **A**, *Captorhinus* (OMNH 44816)[85], **B,** *Heleosaurus* (SAM-PK-K8305), **C**, *Milleropsis* (BP/1/720), and **D**, EAZ younginform (SAM-PK-K7710) in right lateral views, focusing on the reduction of the stapes relative to the otic capsules and the pathways of the cranial nerves through the braincase. Select characters from our dataset include: the presence of lateral ascending processes of the supraoccipital (**Ch. 202**, present in captorhinids and some recumbirostrans), a supraoccipital contribution the floccular fossa (**Ch. 206**, present in synapsids including Varanopidae), the median ascending process of the supraoccipital (**Ch. 210,** present in captorhinids and some recumbirostrans), the position of the trigeminal nerve relative to the ventral process of the prootic (**Ch. 233**, located posterodorsal to to the ventral process of the prootic in synapsids including varanopids), the morphology of the facial nerve (VII; **Ch. 234**, a notch in millerettids), cultriform process dentition (**Ch. 259**, absent in most crown reptiles within this sampling), the location of the vidian canal or groove (**Ch. 260**, within the lateral wall of the braincase in procolophonians, millerettids, and some lepidosauromorphs), the height of the dorsum sellae (**Ch. 277**, tall in captorhinids and the recumbirostran *Pantylus*), and the pathway of the abducens nerve (VI) through the parabasisphenoid (**Ch. 278,** through the clinoid processes and prootic articulation in parapleurotans). Abbreviations: bo, basioccipital; op, opisthotic; pbs, parabasisphenoid, pr, prootic; so, supraoccipital; and st, stapes.

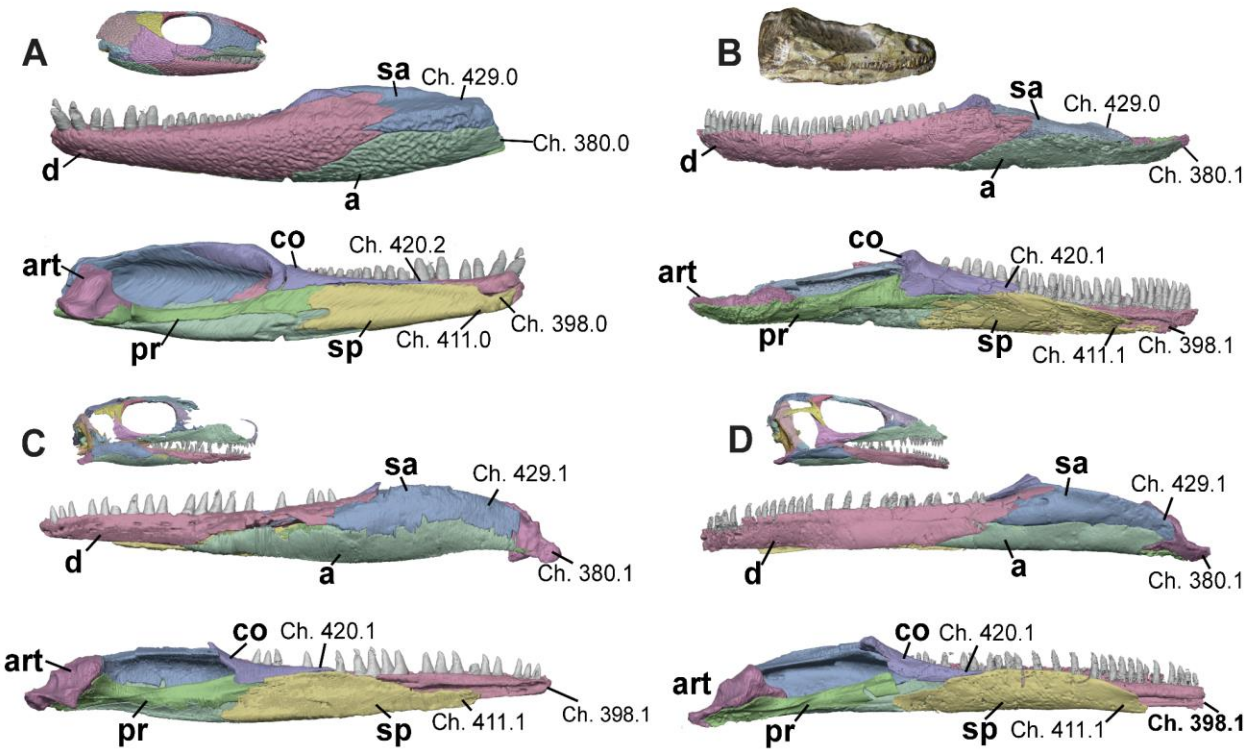

Figure 8. Left mandibles of **A**, *Captorhinus* (OMNH 44816)[85], **B,** *Saurodektes* (BP/1/1395), **C**, *Milleropsis* (BP/1/720), and **D**, EAZ younginform (SAM-PK-K7710) in lateral (upper) and medial (lower) views, emphasizing the morphology of the symphysis and articular region. Select characters include: the presence of a retroarticular process (**Ch. 380,** variably absent in this sampling), the pathway of the Meckelian canal through the anterior mandible (**Ch. 398**, piercing the dentary in total-group reptiles), the splenial contribution to the mandibular symphysis (**Ch. 411,** absent in most stem reptiles but present in other amniotes and convergently in pareiasaurs and rhynchosaurs within this sampling), the length of the coronoid (**Ch. 420**, extremely long in captorhinids), and the presence of a posterior surangular foramen (**Ch. 429**, present in many parapleurotans). Abbreviations: ang, angular; art, articular; co, coronoid; d, dentary; pr, prearticular; sa, surangular; and sp, splenial.

Parsimony Analysis

Parsimony analysis was carried out in TNT v1.6[46] using drive-search implementations of the "new technology" heuristic strategies with sectorial, drift and tree fusing algorithms following the methods of[4]. *Whatcheeria deltae* was set as the outgroup taxon. The resulting 30 MPTs of 4539 steps were then subjected to a final round of tree bisection reconnection branch swapping, with a 50% collapsing rule. Branch support was calculated using Bremer support and bootstrap resampling analyses, with 1,000 pseudoreplicates for absolute and group present/contradicted frequencies, also calculated in TNT v.1.6[46] (Fig. S2). To reconstruct the ACCTRAN/DELTRAN optimizations for each character, we conducted a heuristic search and tree bisection reconnection, with 1,000 random additional replicates in PAUP* v.4.0a[47], resulting in 30 MPTs (identical to

those found in TNT) with 4539 steps. The ACCTRAN/DELTRAN optimizations for each new character are provided in SI Appendix 8.

We ran an additional parsimony analysis following the methods above (branch length=4452, 41 MPTS) in which nine characters (118, 123, 134,135,145,146,152,153,172) regarding temporal fenestration and emargination were removed to assess the influence of patterns of temporal fenestration on amniote relationships (Fig. S2). We also computed a series of constraint analyses (analyses C1, C2, C3, and C4) under maximum parsimony in PAUP* v.4.0a[47] to assess differences in tree topology, length, and resolution when imposing backbone constraints mimicking previous phylogenetic hypotheses of early reptile evolution[2-6]. For these constrained analysis, analysis C1 constrains a monophyletic Eureptilia including *Hylonomus*, Captorhinidae, Araeoscelidia, and Neodiapsida following the hypotheses of[5-7]. Analysis C2 constrains the monophyly of Parareptilia encompassing millerettids, mesosaurids, bolosaurids, acleistorhinids, and procolophonians to the exclusion of all eureptiles[5,6,45]. Analysis C3 constrains the monophyly of Diapsida including araeoscelidians and neodiapsids following the apomorphy-based definition of this clade provided by[48]. Lastly, analysis C4 constrains Recumbirostra within the reptile total-group, congruent with recent hypotheses of a reptilian placement of this clade[25,49].

Bayesian Inference

Phylogenetic inference was carried out in MrBayes 3.2.7a using a fossilized birth–death (FBD) tree prior[50-51]. The ages of all OTUs were specified using uniform distribution spanning the minimum and maximum possible occurrence dates of each OTU. The setting for the tree age prior was set to offsetexponential (x,y), where x is the oldest fossil in the taxon list, *Whatcheeria deltae* (347.6 Ma) and y the earliest putative date of

the common tree ancestor, in this case, *Acanthostega* (365 ma). Two runs, each consisting of four chains at a temperature of .09 were performed for 100 million generations, sampling every 10,000 generations with a burn-in of 50%. We performed a second, non-time-calibrated Bayesian analysis using the Mkv model with a 'standard' datatype, coding set at 'variable' and with rates set to a gamma distribution, which allows the Mkv substitution model to allow variation in the evolutionary rates among characters. The analysis was run for 100 million generations, sampling every 10,000th generation, with a burn-in of the first 10,0000 sampled trees (50%). The effective sample size for tree length and shape of gamma distribution was greater than 3,900 and the average potential scale reduction factor was 1.01 or less on all parameters, indicating convergence. Our analytical scripts and resulting tree files are available at https://osf.io/9jac3/.

Stratigraphic Fit

To compare the stratigraphic fit of our new phylogenetic hypotheses to previous hypotheses for early reptile relationships, we performed MSM* [52], and GER*[53] stratigraphic congruence analyses. These measurements use the sum of the ghost ranges (or MIG, minimum implied gap) relative to the optimal and/or Gmin (in the case of MSM*) and/or maximally suboptimal fits to stratigraphy (GER*). These measures account for stratigraphic uncertainty by using a resampling technique over 1000 iterations that incorporate possible ranges of a given taxon using the minimum (LAD) and maximum ages (FAD)[52].

To further investigate the stratigraphic consistency of our phylogenetic hypothesis relative to more 'traditional' hypotheses of early amniote relationships, we calculated the MSM*Diff using the 30 MPTs from our parsimony analysis and 48 MPTs of a constrained version of our dataset that enforces the monophyly of Eureptilia, Parareptilia, and Diapsida. This constrained version therefore approximates the four stem-reptile

ghost lineages in prevailing phylogenetic hypotheses of early reptiles over the last three decades[5-7]. Metrics for stratigraphic fit to phylogeny are not comparable across different taxon sets, and for this reason we could not directly compare our preferred phylogenetic hypothesis to those of previous workers[50]. However, our constraint trees used here approximate the general relationship sets hypothesized in previous work. For comparative purposes, we calculated measures of stratigraphic fit (but not MSM*DIFF due to differences in taxonomic sampling in these matrices and ours) for two[20,45] recent matrices on early reptile evolution.

Ancestral State Reconstruction

Ancestral state reconstructions for the presence and morphological variation of the tympanic fossa and upper and lower temporal fenestrae were carried out in R using the phytools package[55-56] and its dependencies using the function *fitMk*, which fits a continuous-time reversible Markov model to simulate character history. We estimated the ancestral states of tympanic emarginations and temporal fenestration in four discrete analyses: testing the presence and absence of a tympanic emargination (two characters), the anatomy and location of the tympanic fossa (six characters), the presence and morphology of a lower temporal opening (four characters), and the presence or absence of an upper temporal fenestra (two characters). When the anatomy of tympanic emarginations or temporal fenestration is unknown in certain taxa (e.g., taxa in which the skull is absent or only partially preserved), the taxa were treated as uncertain following the methods of[55-56]. For each analysis, we fit two different models of evolution onto our time-calibrated FBD tree (Fig. S3): “ER”, the equal rates model and “ARD” the all-rates-different model and compare these two models using the ‘ANOVA’ function. The posterior probabilities at each ancestral node in our FBD tree were calculated and plotted for ancestral state reconstructions of tympanic emargination (Fig. 11) and temporal fenestration (Fig. 12).

Results

Phylogenetic analyses

Maximum parsimony analysis and Bayesian inference (Fig. 9, Figs. S1-3) place *Milleropsis* and other members of Millerettidae as the immediate sister group to Neodiapsida (Bremer support of 3, posterior probability=1). We propose the name Parapleurota for Millerettidae + Neodiapsida, which is supported by 18 unambiguous synapomorphies absent in traditional 'eureptiles' or 'early diapsids' including: the presence of a tympanic recess on the posterolateral surface of the skull, the loss of a lacrimal contribution to the naris, the presence of a quadrate foramen formed only by the quadrate and quadratojugal, lateral exposure of the quadrate, laterally directed caudal ribs, two lateral elements of gastralia per row or fewer, a midline gastral element, and a proximal expansion of the fifth metatarsal. The node-based phylogenetic definition of Parapleurota, as well as a redefinition of the problematic Neodiapsida, are provided in the SI Appendix.

The enigmatic 'neodiapsid' *Lanthanolania*[36] is found to be the basalmost millerettid (posterior probability =.96), supported by features including the presence of an anterior maxillary foramen (Ch. 57), an enclosed vidian canal (Ch. 260), and flat ventral plate of the parabasisphenoid which lacks the median fossa present in non-saurian neodiapsids (Ch. 265). The early amniotes *Orovenator*[35] and *Ascendonanus*[57], previously interpreted as close outgroups to Neodiapsida or Varanopidae[55], are found crownward of Ankyramorpha (posterior probability =1) as outgroups to Parapleurota (Figs. S2-3). We find *Saurosternon* as the earliest-diverging neodiapsid in our parsimony and MkV analyses (Figs. S2, S4) with 'younginiforms', tangasaurids and weigeltisaurids successively more crownward toward Sauria (Fig. 9).

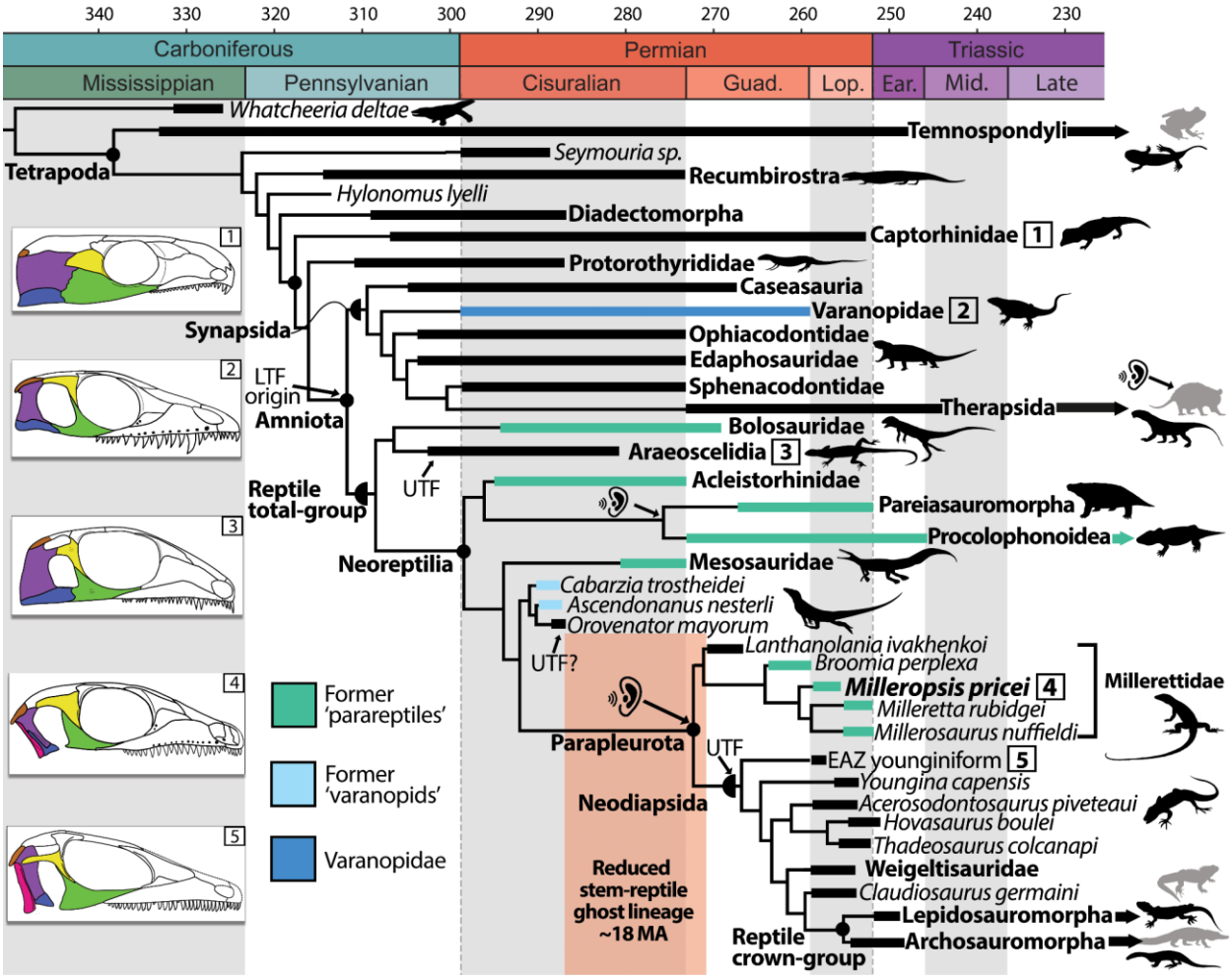

Figure 9. Simplified cladogram using parsimony and the maximum clade credibility tree recovered from Bayesian analysis using the time-calibrated FBD model on Paleozoic and Triassic tetrapods; emphasizing reptile relationships and patterns of temporal fenestration. Branch and skull coloring matches that of Fig. 1, showing the polyphyly of Varanopidae and traditional Parareptilia. The ear symbol denotes the hypothesized independent origins of tympanic hearing in Paleozoic amniotes, including a single origin ancestral to the reptile crown (see Figures 11 and 13). The amniote common ancestor is hypothesized to have possessed a lower temporal fenestra (LTF). UTF indicates the presence of an upper temporal fenestra, which may have evolved up to three times in the reptile total-group, including once in Neodiapsida (see Figure 12). Skull reconstructions: 1, *Captorhinus*; 2, *Heleosaurus*; 3, *Petrolacosaurus*; 4, *Milleropsis*; and 5, EAZ younginiform. Silhouettes are available from Phylopic (www.phylopic.org) under CC BY 3.0 licenses or within public domain.

The monophyly of the clades 'Parareptilia', 'Eureptilia', and 'Diapsida' is not supported in any of our analyses, with an additional 69 additional steps required in our parsimony analysis to force the monophyly of 'Parareptilia', 31 for 'Eureptilia' and 25 for 'Diapsida' (Fig. 10). When the monophyly of both 'Eureptilia' and 'Diapsida' were enforced in our constraint analyses, Millerettidae consistently emerges as sister to Neodiapsida, demonstrating the robust support for the novel clade Parapleurota even under alternative hypotheses of stem reptile interrelationships (Fig. 10). Our tomography data reveals the presence of classical 'parareptilian' features

in former ‘eureptiles’ including araeoscelidians, neodiapsids, and early diverging members of the reptile crown, such as prefrontal-palatal contact and a foramen orbitonasale, suggesting that these features are instead symplesiomorphies of the reptile total-group (Fig. 4). Other features previously hypothesized to support the monophyly of ‘Parareptilia’ or ‘Eureptilia’ are widespread among early amniotes (e.g., swollen dorsal vertebrae), were incorrectly optimized due to the low taxon sampling of previous studies (e.g., the presence or absence of a supraglenoid foramen), or misinterpreted for millerettids (e.g, the supposed lacrimal contribution to the naris, Figs. 2-3).

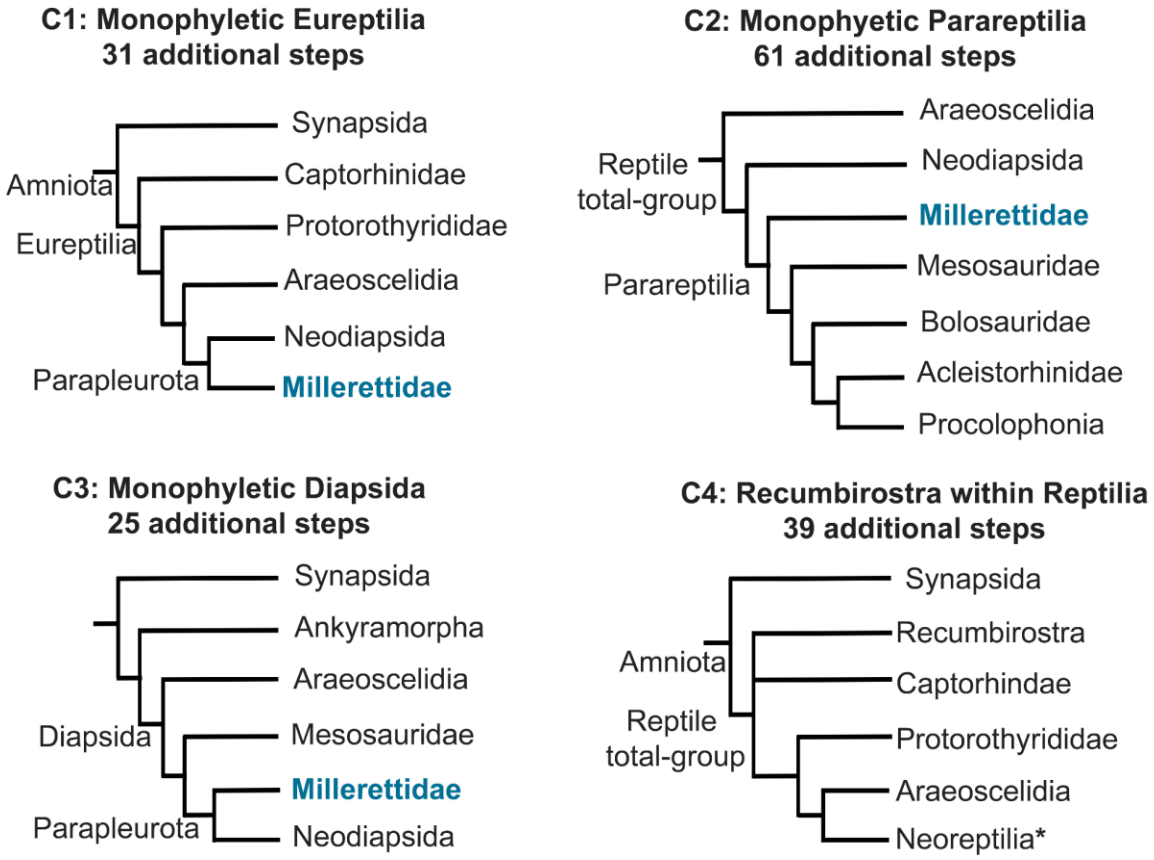

Figure 10. Simplified topologies of strict consensus trees returned by Maximum Parsimony analyses testing alternative hypotheses of early reptile evolution. Trees show cost of constraining the monophyly of Eureptilia C1 (31 additional steps); Parareptilia C2 (61 additional steps); and Diapsida C3 (25 additional steps); as well as the placement of Recumbirostra as reptiles C4 (39 additional steps). *Neoreptilia in C4 includes ankyramorph “parareptiles,” neodiapsids, and millerettids.

Araeoscelidians, conventionally interpreted as close relatives of Neodiapsida[5-6], are instead supported here as the earliest-branching group of stem-reptiles (posterior probability =.99), corroborating recent work[4,19,22]

(Fig. 9, Fig. S2-S3). Bolosaurid 'parareptiles'[10] are placed within Araeoscelidia with strong support (posterior probability =1, Bremer support = 3), although we note that this phylogenetic hypothesis merits further investigation[21]. The monophyly of Ankyramorpha[6], a group of former 'parareptiles' consisting of Acleistohinidae and Procolophonia, is strongly supported (posterior probability =1, Bremer support = 3), and ankyramorphs are placed immediately crownward of Araeoscelidia as early diverging stem reptiles (Fig. 9, Fig. S2-S3). Mesosauridae[58-59] are placed another node crownward of Ankyramorpha and Araeoscelidia, albeit with moderate support (posterior probability = .79).

Facilitated by our synchrotron tomography data of *Heleosaurus*[38], we demonstrate that Varanopidae — a contentious early amniote group that has recently been found on the reptile stem lineage,[4] but more often placed as members of the mammalian total group (Synapsida)[5,6,25] — are indeed synapsids. We find varanopids specifically as the earliest-diverging eupelycosaurs (posterior probability =0.88) supported by 15 unambiguous synapomorphies. A synapsid placement of Varanopidae is supported by synapsid-like palatal and braincase features of *Heleosaurus* revealed in our scan data that were previously never incorporated as characters in phylogenetic analyses. These features include the presence of a dorsally positioned trigeminal notch (Ch. 233, Fig. 7B), an epipterygoid contribution to the basicranial articulation (Ch. 288, Fig. 6B), a sheet-like shaft of the epipterygoid (Ch. 293, Fig. 6B) a floccular fossa that is enclosed by the supraoccipital (Fig. 7B), the pathway of the abducens nerve (CN VI) through the dorsum sellae (Ch. 279), and two coronoid ossifications (Ch. 417). Earlier hypotheses of Varanopidae relied on externally visible features such as temporal fenestration[5,6], the presence of caniniform teeth, and postcranial features such as gracile limb proportions[4] that show greater homoplasy among early amniotes, leading to some recent debates in which varanopids were proposed as possibly being stem reptiles[4].

We find evidence for the placement of early branching 'eureptiles' along the amniote stem, corroborating long standing hypotheses[8,12,60-61] of the 'Captorhinomorpha' or 'Cotylosauria' as ancestral to fenestrated amniotes[59.] Protorothyridae is found here to form the sister-group to Amniota (posterior probability =.92, Fig. S3), whereas Captorhinidae is placed rootward (posterior probability =.87, Fig. 3, Figs. S2-4), positions that remain stable even when characters relating to temporal fenestration are removed (Fig. S2B). The 'eureptile' *Hylonomus*, previously suggested to be the earliest stem reptile[27] (but see[10, 12, 60-61]), and therefore an important node age constraint in molecular phylogenetic studies of vertebrate evolution as the earliest crown amniote, is found outside of crown Amniota (posterior probability =0.89). Pre-cladistic studies similarly interpreted *Hylonomus* as far from the amniote crown either as a 'microsaur' and later as a 'cotylosaur'[61]. All features previously hypothesized to link this taxon with Reptilia[32] (e.g., presence of a transverse flange (Ch. 313) of the pterygoid, astragalus (Ch. 625), and caudal chevrons[61]) are present in early synapsids[62] and recumbirostrans[49], and are here interpreted as symplesiomorphies of Amniota. These character distributions corroborate recent studies[30,49] demonstrating the widespread presence of classical amniote or reptile features among stem and crown amniotes, including synapsids (Table S2).

Recumbirostra are found here as stem amniotes crownward of seymouriamorphs and 39 additional steps are required to place them with Reptilia (Fig. 9). Previous features suggesting a stem-reptile placement of Recumbirostra (e.g., a crista interfenestralis of the opisthotic (Ch. 224) or a single ossification of the supraoccipital (Ch. 199)) are documented in early diverging synapsids, including varanopids (Fig. 7B) and ophiacodontids[62]. The placement of Recumbirostra remains stable even when characters related to the presence of temporal fenestration are removed (Fig. S1). More detailed anatomical descriptions using 3D imaging of

fossil taxa including ‘microsaurs’, protorothyridids, *Hylonomus*, and the earliest synapsids may help resolve uncertainties in the evolutionary origin of amniotes, which merits further investigation.

Stratigraphic Fit

The results of our stratigraphic fit analyses demonstrate that our phylogenetic hypothesis of millerettids as close relatives of Neodiapsida is significantly more congruent with expectations from a stratigraphic null model than previous hypotheses of early reptile evolution by at least 28% (GER) and 29% (MSM*). Traditional phylogenetic hypotheses yielding a monophyletic Eureptilia, Parareptilia, and Diapsida are less congruent with stratigraphy (therefore implying longer ghost lineages) than hypotheses finding no support for these groups[25], including this study. The differences in MSM* values (MSM*Diff) between our phylogenetic hypothesis and our constraint analysis are summarized in Table S4. MSM*Diffs between these two topologies were positive in 100% of comparisons (Fig. S9). On average, the closure of the expansive ghost lineage for Millerettidae and three of the four major ghost lineages (‘Eureptilia’, ‘Diapsida’, and Neodiapsida ghost lineage B, Fig. 1) among the reptile stem improved stratigraphic fit by at least 29%, although a ghost lineage along the parapleurotan stem (equivalent to ‘Neodiapsid ghost lineage A’, Fig. 1) still stretches from the middle early Permian (Artinskian)[35] to the appearance of millerettids in the beginning of the middle Permian (Roadian)[36] (Fig. 9).

Ancestral State Reconstruction

Our ancestral state reconstructions mapped anatomical features related to tympanic emargination and temporal fenestration using two models of character state evolution. In each instance, the equal rates “ER”

model which assumes a single rate of evolution for all branches without our topology was best supported, outperforming the all-rates-different model “ARD” using Akaike information criterion.

Our findings suggest that the tympanic fossa of Parapleurota originated on the quadrate, squamosal, and quadratojugal and subsequently migrated to be primarily supported by the quadrate (Fig. 11B). The ancestral state estimates concerning the presence of a tympanic emargination provide robust evidence that the tympanic fossa originated twice during early reptile evolution: once within Parapleurota (including the reptile crown) and once within Procolophonia (Fig. 11A). The deep-time origins of this structure are supported by the shared presence of a tympanic fossa on the quadrate, squamosal, and quadratojugal in millerettids and early diverging neodiapsids, including SAM-PK-K7710 (Figs. 5D, 11), *Youngina* (pers. obv. BP/1/375), and *Hovasaurus* (pers. obv. MNHN.F.MAP373).

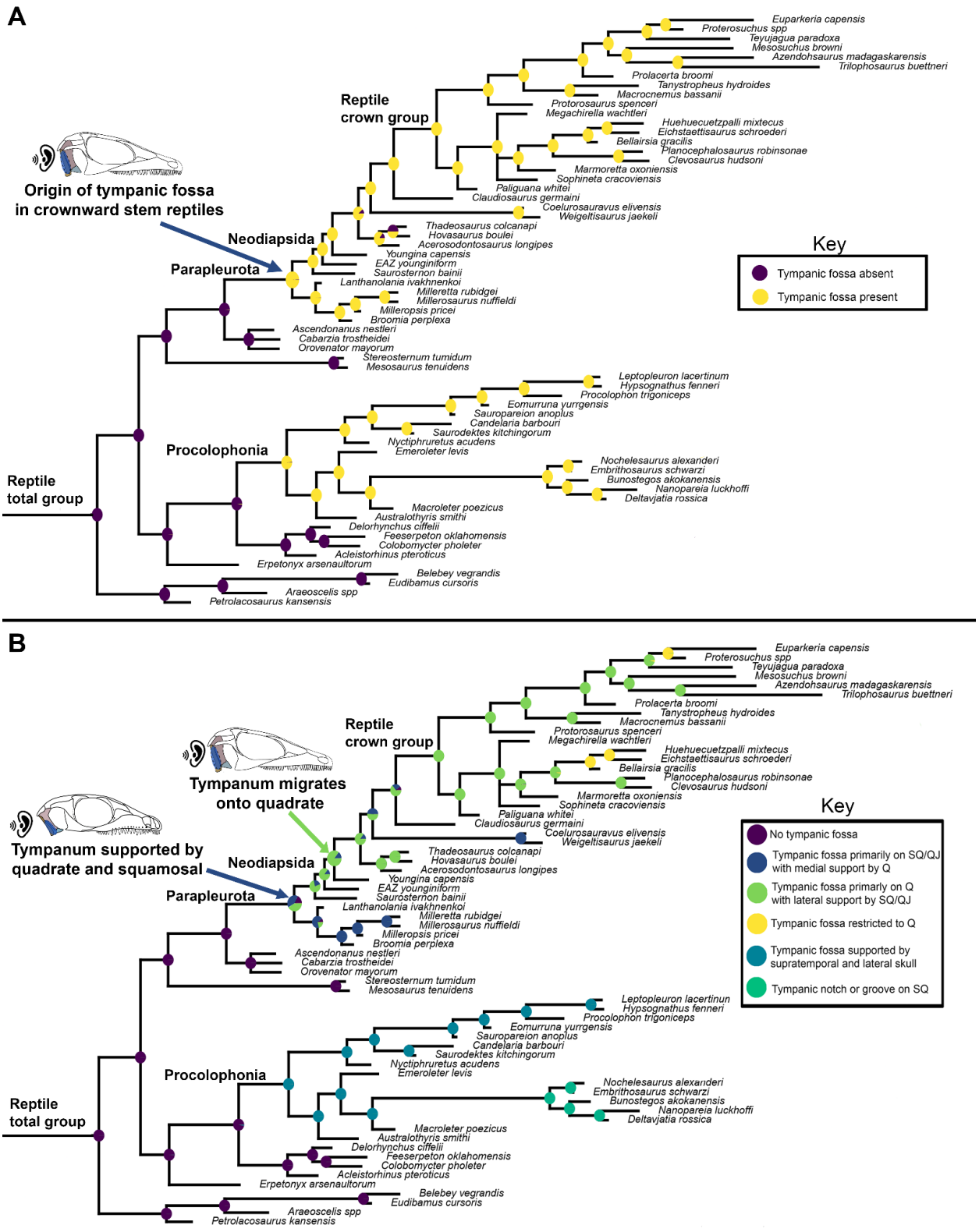

Figure 11. Ancestral state reconstruction estimates for **A**) the presence or absence of a tympanic emargination; and **B)** the anatomy of the tympanic emargination. A tympanic emargination is reconstructed as having evolved convergently in parapleurotans (supported on the quadrate/squamosal/quadratojugal) and in procolophonians (squamosal/quadratojugal/supratemporal), with a stepwise increase in the contribution of the quadrate to the tympanic emargination leading towards crown reptiles.

Our ancestral state reconstructions predict that the amniote common ancestor bore a lower temporal fenestra with subsequent closures in pareiasaurian and mesosaurid stem reptiles, and that the lower temporal bar was lost in the common ancestor of Parapleurota (Fig. 12A). These models also suggest that the lower temporal opening of procolophonoids, here termed a 'lower temporal concavity' are not homologous with the 'open' lower temporal openings of Parapleurota, although both evolved in taxa that possessed a closed lower temporal bar (Fig. 12A). The important implication of this finding is that a temporal emargination, which is also present in early neodiapsids, can no longer be interpreted as a synapomorphy of Parareptilia[6].

Our ancestral state reconstructions suggest that the upper temporal fenestra had two independent origins in reptiles, once in Late Carboniferous Araeoscelidia at the base of Reptilia and again in Neodiapsida in the late Permian, with the upper temporal fenestra being absent in nearly all other stem reptiles except possibly *Orovenator*[35](Fig. 12B). These findings corroborate interpretations from recent phylogenetic analyses which also find araeoscelidians including the famously diapsid *Petrolacosaurus* as either stem-amniotes[25-26] or the earliest-diverging group of stem reptiles[4,27].

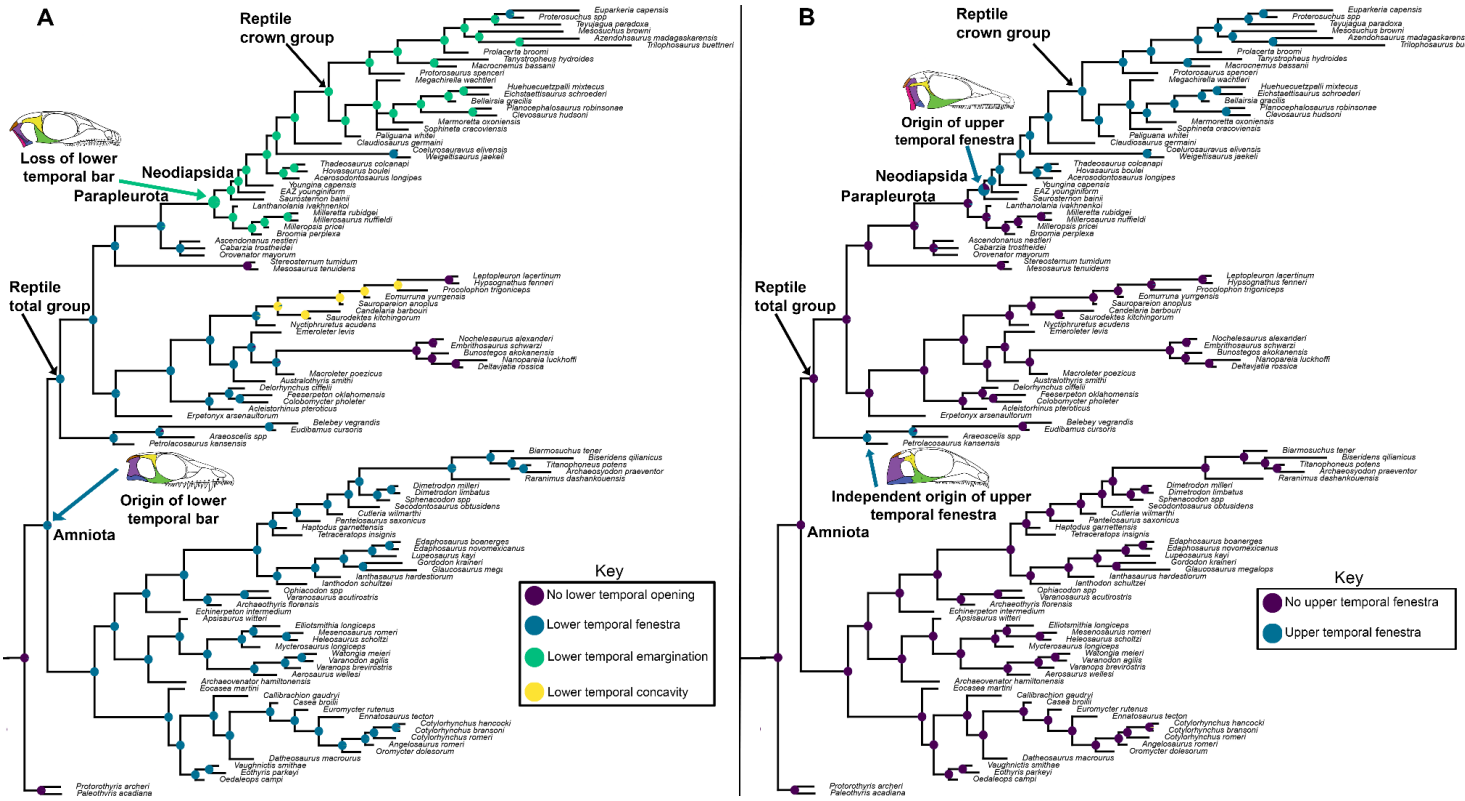

Figure 12. Ancestral state reconstruction estimates for **A**) the presence and morphology of the lower temporal fenestra/opening and **B)** the presence of the upper temporal fenestra. The amniote common ancestor is reconstructed as fenestrated, with the 'synapsid' or a single lower temporal fenestration as the plesiomorphic condition. Modifications to this lower temporal condition occur independently in araeoscelidians + bolosaurids, procolophonians, and parapleurotans. In parapleurotans the lower temporal bar is open, forming an emargination (the reconstructed ancestral condition of the reptile crown group). An upper temporal fenestra is reconstructed as having evolved independently in araeoscelidians like *Petrolacosaurus* and in neodiapsids.

Discussion

Millerettids as crownward stem-reptiles

Our phylogenetic results place various groups of middle and late Permian fossil reptiles, including millerettids, within the crownward portion of the reptile stem lineage as close outgroups of Neodiapsida (Fig. 9). The placement of Millerettidae as sister to Neodiapsida (forming Parapleurota) is robustly supported (18 unambiguous synapomorphies), even under alternative hypotheses of early reptile evolution (Fig. 10). This relationship is supported further by the relatively continuous stratigraphic record of the middle and late Permian Karoo Basin, which preserves a succession of millerettid and neodiapsid stem-reptiles[63]. Other anatomical observations are consistent with the sister-relationship of Millerettidae and Neodiapsida but are not optimized as

unambiguous synapomorphies due to the uncertain scoring of these characters in close relatives of Parapleurota (e.g., *Orovenator*), including: a quadratojugal foramen with no contribution by the squamosal (Ch. 360, Fig. 5), no contribution of the epipterygoid to the basal articulation (Ch. 288, Fig. 6), the absence of an unossified sphenethmoid (Ch. 283), the pathway of CN VI through the clinoid processes rather than the dorsum sellae (Ch. 278, Fig. 7), and a posteriorly directed ilium (Ch. 595).

Our results differ substantially from the otherwise prevailing phylogenetic paradigm in which millerettids were hypothesized to be only distant relatives of Sauria[5], specifically as parareptiles[5-7]. However, these studies were hampered by the lack of tomographic data on key taxa, which resulted in the critical undersampling of cranial characters, especially for the braincase, palatoquadrate, and palate (Figs. 4-8). Furthermore, early cladistic analyses on early reptile origins [4-6] lacked a robust sampling of non-saurian Neodiapsida (Fig. S1) and included only one representative of Millerettidae: the later-branching, youngest-occuring, and unfenestrated *Milleretta rubidgei*. Our tomography data reveal that earlier-branching representatives of Millerettidae such as *Milleropsis*[42-43] present seemingly derived features such as the lack of contact between the postorbital and supratemporal and a gastral basket consisting of a midline element and two lateral elements which are now interpreted as the plesiomorphic condition for Millerettidae (Fig. S2). Both of these features were previously interpreted as synapomorphies of Eureptilia[7] and Neodiapsida[64], respectively. Another significant factor in the sister-placement of Millerettidae and Neodiapsida are unrecognized plesiomorphies in the early neodiapsid skull revealed by our tomographic data, such as the presence of multiple rows of dentition on the transverse flange of the pterygoid and the presence of dentition on the ventral plate on the parabasiphenoid in SAM-PK-K7710. The loss of this palatal dentition was previously interpreted as a

neodiapsid synapomorphy[3], but our results instead suggest that these features are lost later in neodiapsid evolution.

Our revised Permian reptile topology reveals that successive outgroups to Sauria were taxonomically and ecologically diverse. Although reptile diversity and disparity expanded greatly among Triassic saurians[2], stem reptiles had already explored a substantial range of habitat, dietary, and locomotor spaces in the Permian: bipedal bolosaurids[65]; large-bodied herbivorous pareiasaurs[66] and their burrowing procolophonoid[67] relatives; semiaquatic mesosaurids[58-59] and tangasaurids[20]; the arboreal *Ascendonanus*[57], and gliding weigeltisaurids[21]. In this new light, Permian reptile evolution can be recognized as documenting, in greater detail, the acquisition of saurian features within an evolving lineage, akin to the established evolutionary patterns along the mammalian stem lineage[68].

Improving the stratigraphic fit of the early reptile fossil record

The placement of the middle and late Permian Millerettidae as a successive outgroup to Neodiapsida substantially improves the stratigraphic fit of the fossil record of crownward stem reptiles by 29% compared to traditional phylogenetic hypotheses of reptile relationships (Fig. S11, Table S4). This phylogenetic position for Millerettidae reduces the hypothesized ghost lineage for basal millerettids extending down to the Late Carboniferous when this clade is interpreted as branching among basal parareptiles (shortened by ~35 MA) and improves our understanding of the evolution of neodiapsid outgroups from the middle Permian (Roadian) onward (~10 MA; Neodiapsida ghost lineage B of Figure 1). Our phylogenetic hypothesis is congruent with the temporally sequential appearances of millerettid and neodiapsid stem reptiles in the well-sampled and continuous stratigraphic sections of the Karoo Basin in South Africa[69]. However, the long-recognized ghost lineage (Neodiapsida ghost lineage A) extending from *Orovenator*[35] to the earliest Parapleurotan,

Lanthanolania[36] remains an issue, as this gap aligns with known biases in the biogeography of the fossil record where early Permian rocks preserve equatorial ecosystems, and middle to late Permian rocks preferentially preserve high latitudes[70]. We suggest further fieldwork in Kungurian- to Roadian-age formations as the most likely solution.

Our phylogenetic hypothesis proposes that the groups 'Eureptilia' and 'Parareptilia'[5] , which are common textbook examples of early reptile diversification, are in fact polyphyletic assemblages of distantly related taxa. The polyphyly of this clade in our analysis falsifies the existence of the Carboniferous 'Eureptilia' ghost lineage[2] (Fig. 1). Furthermore, our placement of the 'eureptile' *Hylonomus* (~318 MA) as a stem amniote raises doubts about its suitability as a minimum-age calibration[71] for the amniote crown group and indicates a need for restudy of the anatomy of this important early taxon. Future molecular clock calibrations for the amniote crown should use more confidently assigned members such as the synapsids *Melanedaphodon*[72] (~307 MA) and *Archaeothyris*[72] (~306 MA) in the Moscovian.

The polyphyly of Parareptilia distributes various groups of former 'parareptiles' such as ankyramorphs and mesosaurids as successively crownward outgroups of Parapleurota and greatly contributes to the improvement of our hypothesis to the stratigraphic fit of the early reptile fossil record (Fig. 3). In particular, the breaking apart of Parareptilia shortens the ghost lineage for Neodiapsida by closing the 'Diapsida' ghost lineage (Fig. 1, ~15 MA) that extended from *Petrolacosaurus* in the Late Carboniferous (Ghzelian[34]) until the appearance of *Orovenator* in the early Permian (Artinskian[35]) (Fig. 3). The well-supported clade Ankyramorpha, which contains many taxa in the previous Parareptilia, bears a near-uninterrupted fossil record throughout the end-Paleozoic, in part due to their cosmopolitan distribution overcoming biases in the rock record, standing in contrast with nearly all other early reptile groups[31,73].

Tympanic hearing was initiated before the origin of Sauria

Our phylogeny and novel anatomical observations on millerettids (Fig. 2) and SAM-PK-K7710 (a non-saurian neodiapsid with a tympanic emargination on the quadrate, Fig. 3) show that tympanic hearing first evolved among early parapleurotans in the middle Permian (Fig. 13) and was later inherited by the common ancestor of crown reptiles (see also developmental work on crown homology[14]). This differs from some previous work[15] that proposed at least four separate (Triassic) origins of tympanic hearing among crown reptiles – once within Lepidosauromorpha[73], once within Testudines[74], and at least twice within Archosauromorpha, including a single shared origin for modern Archosauria[75]. Previous anatomical studies often used a narrow concept of the osteological correlates for the presence of a tympanum, restricted to the observation of an emargination on the quadrate[76]. We observe that the tympanic emargination of the quadrate of crown reptiles (Ch. 346) has antecedents on the squamosal and quadratojugal, seen in the recesses and tympanic crests in the posterior cranium of *Milleropsis* and early neodiapsids (Ch. 165, Fig. 5). Similar traits also evolved independently among procolophonians such as *Macroleter*[77] that bear a large tympanic fossa on the squamosal and quadratojugal, but which differ in their extension onto the skull roof (Ch. 185) (Fig. 13).

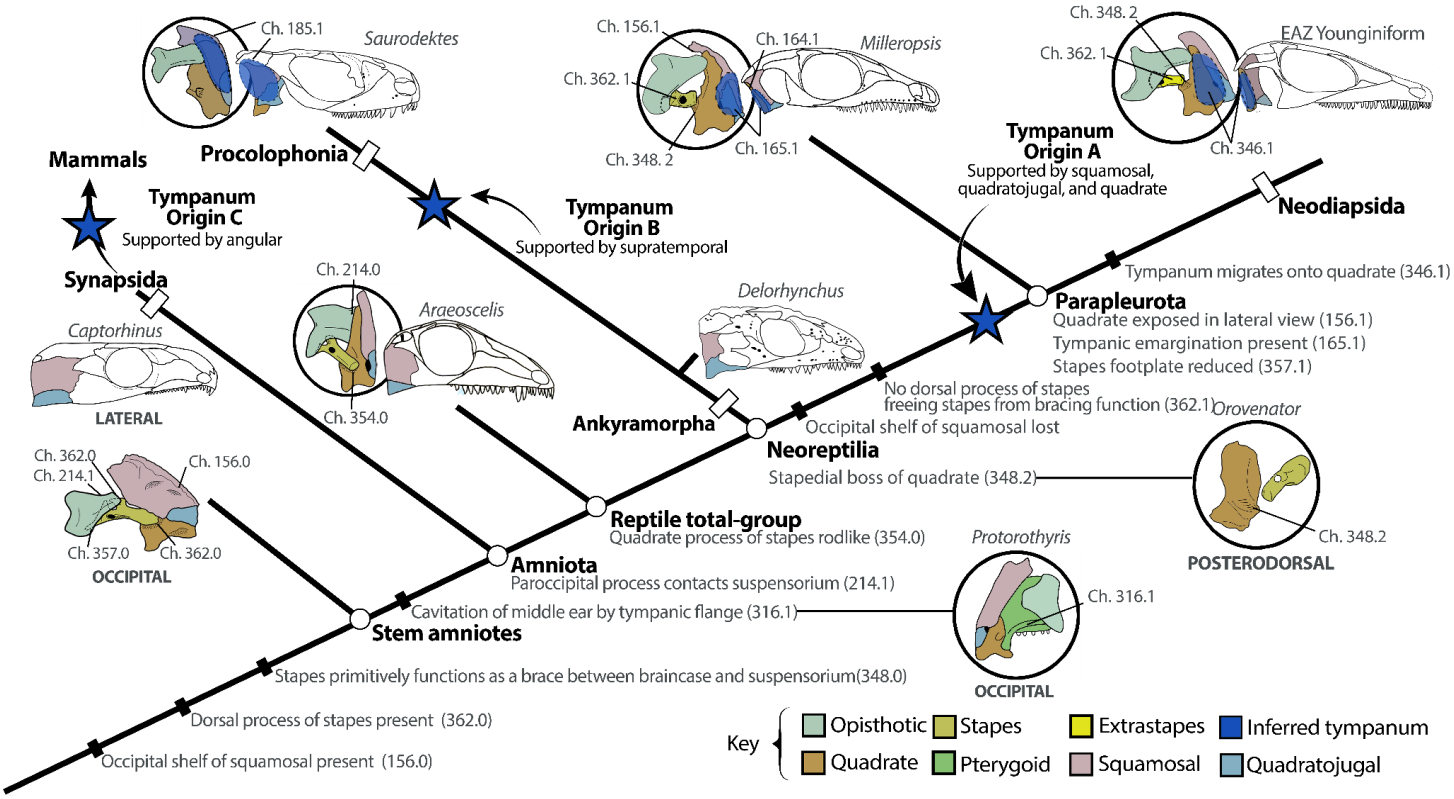

Figure 13. Evolution of amniote hearing using sensory characters of the middle ear from this study, demonstrating the stepwise reduction of the stapes, reduction in the squamosal and quadratojugal, and corresponding exposure of the quadrate in lateral view. Additionally, three independent origins of tympanic (or impedance-matching) hearing among amniotes (in Synapsida, Procolophonia, and Parapleurota) are indicated by blue stars. Skull reconstructions are from this study or modified from references: *Captorhinus*[28], Synapsida, *Araeoscelis*[92], Procolophonia (*Saurodektes*[93]), and Parapleurota (*Milleropsis* and the EAZ younginiform, this study).

Our phylogeny and ancestral state reconstruction (Fig. 11) provide evidence that a tympanum was likely already present among stem reptiles before the origin of Parapleurota, housed on the quadrate and squamosal/quadratojugal as seen in *Milleropsis* and other millerettids (Figs 2, 11A, 13). The tympanum then migrated to be primarily supported by quadrate (with a smaller contribution by the squamosal and quadratojugal) in Neodiapsida (Fig. 5D), possibly due to the evolutionary reduction of the squamosal (Ch. 156, Fig. 11B, 13), and its incorporation into the margin of the upper temporal fenestra[3]. Observations and dissections of the middle ear of both living and fossil reptiles, which unequivocally demonstrate the presence of a tympanic membrane attachment onto the squamosal and quadratojugal in lizards[77], birds[78], crocodilians[79], and turtles[80] are consistent with our proposal that the tympanic emargination of the quadrate has antecedents on other elements of the posterior skull (Figs. 9, 11).

Our observations of the stapes provide further evidence for the evolution of the reptile middle ear, which we extensively codify in our phylogenetic dataset (Fig. 5, SI Appendix). Previous studies used simplified concepts of stapedial variation, generally encoding it as a dichotomy between 'robust' and 'rod-like' morphologies[5-7]. We use a more detailed characterization of variation in stapedial morphology (SI Appendix 8, Chs. 354-364) and find evidence for an acquisition of potential auditory function of the stapes earlier in reptile evolution, by the middle Permian (Fig. 13). Stepwise reductions in the size of the stapedial footplate (Ch. 357) and columella (Ch. 355) throughout the Permian, paired with the losses of its dorsal process (Ch. 362), enlarged foramen (Ch. 360), and functional role in bracing the suspensorium (Ch. 348), suggests that the stapes of crownward stem reptiles, such as millerettids and neodiapsids, could likely transduce higher-frequency sounds than those of earlier diverging reptiles (Fig. 13). These results, corroborated by several recent developmental studies establishing the homology of the tympanic membrane[14] and extracolumella[81] in crown reptiles demonstrate that complex neurosensory innovations including enhanced auditory capabilities were present in reptiles prior to the End-Permian Mass Extinction, predating the ecomorphological diversification of Sauria in the Triassic[2].

Evolution of Temporal Fenestration in Amniota

Temporal fenestration morphologies have been pivotal in hypotheses for early amniote evolution and classification[17-18, 82-84]. These propose that distinct patterns of fenestration evolved independently on the mammal and reptile stem lineages (the 'synapsid' and 'diapsid' patterns) from a common ancestor that lacked fenestrae. Such historical schema have rarely fit neatly into phylogenetic topologies, which generally find multiple additional origins of temporal fenestration within Amniota[4-6]. We find that a lower temporal fenestra

(LTF) was present in the most recent common ancestor of the amniote crown groups, but that the subsequent evolution of temporal fenestration was remarkably homoplastic (Fig. 12). Taxa lacking temporal fenestrae, such as Protorothyrididae and Captorhinidae, which were previously posited to be early diverging crown amniotes (but see[25-26)], are here found instead as successive outgroups to crown Amniota, even when excluding characters related to temporal fenestration (Fig. S2). The amniote LTF was frequently modified in reptile evolution, including its probable closure in several groups of Paleozoic stem reptiles, including Araeoscelidia[39], Mesosauridae[56], and Pareiasauria[66] (Fig. 11). Later clades of Mesozoic reptiles continued to make substantial modifications to the ancestral LTF with closure in Pantestudines[85] and the likely opening of the ventral margin in the common ancestor of Parapleurota (Fig. 12).

Our phylogenetic topology also challenges the conventional view of homology between the doubly fenestrated 'diapsid' conditions present in the araeoscelidian *Petrolacosaurus*[34], in *Orovenator*[35], and in neodiapsids. Ancestral state estimation instead suggests that an upper temporal fenestra (UTF) evolved independently in these three groups (Fig. 12; and see[4,25]). This observation is congruent with the absence of the diapsid condition in other adequately known araeoscelidians[39], its absence in various neoreptiles, and the notably different fenestral architecture of araeoscelidians compared to both *Orovenator*[35] and neodiapsids[19].

Interestingly, millerettids such as *Milleretta rubidgei* possess a unique ventral flange of the parietal that closes an unossified gap between the parietal, postorbital, and squamosal during ontogeny, a feature that has been hypothesized to represent the secondarily closure of an upper temporal fenestra in this clade[8]. This high degree of plasticity of temporal architecture among early reptiles may result from the high functional relevance of fenestrae to jaw kinematics[83-84]. These findings necessitate future research into the homology of the upper temporal fenestra in the common ancestor of modern reptiles.

Conclusion

Our synchrotron tomography data allows new insights and interpretations into the anatomy of important stem reptile fossils, particularly for the Millerettidae. Our resulting phylogenetic hypotheses indicating the polyphyly of Eureptilia and Parareptilia and the sister relationship between Millerettidae and Neodiapsida challenge existing paradigms of early reptile evolution and allowing a reinterpretation of anatomical transformations during the evolutionary assembly of the saurian common ancestor in the middle and late Permian. This includes new hypotheses for the stepwise origins of the tympanic morphology in Parapleurota and fenestration patterns across stem reptiles. Many questions as to the origins and relationships of the earliest reptiles still remain unanswered due to the lack of anatomical data and the limited geographic distribution and temporal sampling of the earliest amniotes and their Carboniferous relatives[86], as well as the poor late Permian record for the earliest saurians, especially stem-lepidosaurs[82]. Future work reporting detailed anatomical data on these taxa will be central to our understanding of the early evolution of the reptile crown group and the rapid diversification of morphologically disparate reptile groups in the Triassic (e.g., Ichthyosauromorpha, Pantestudines, Sauropterygia, etc.).

Data availability

All computed tomography data and three-dimensional models for *Milleropsis* reported in this paper are available at MorphoSource for open download at https://www.morphosource.org/concern/media/000125334. Tomography data and links for *Heleosaurus*, *Araeoscelis*, *Milleretta*, the EAZ Younginiform, and *Youngina* are listed in SI Appendix, Table 1.

Code availability

Our phylogenetic scripts, including the matrix and full analytical settings, are available at: https://osf.io/9jac3/

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Index

Supplemental information

Document S1. Figures S4–S82 and Tables S1-S4.

Video S1. Digital rendering of *Milleropsis* BP/1/720, with the three skulls oriented horizontally.

Video S2. Digital rendering of *Milleropsis* BP/1/720, with the three skulls oriented vertically.

Video S3. Digital rendering of the articulated skeleton of *Milleropsis* BP/1/4203.