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'Birds' of two feathers: *Avicranium renestoi* and the paraphyly of bird-headed reptiles (Diapsida: 'Avicephala')

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ABSTRACT

The anatomy of Late Triassic drepanosauromorphs is re-examined, with a focus on the previously published surface models of the holotype of *Avicranium renestoi* from the Norian of North America. We comment on the cranial anatomy of this taxon and propose a new reconstruction of the skull and mandible. Contrary to previous interpretations, the entire rostrum and most of the palate are not preserved in this specimen. We also suggest that some proposed plesiomorphic characters may result from incomplete ossification due to immaturity. These new observations are compiled into a new morphological phylogenetic dataset designed to address the monophyly of 'Avicephala', the group comprising the Late Permian gliding reptiles Weigeltisauridae, and the Late Triassic chameleon-like Drepanosauromorpha. We recover Weigeltisauridae as stem-saurian diapsids and Drepanosauromorpha as sister-group to Trilophosauridae among archosauromorphs, thus implying the paraphyly of 'Avicephala'. Drepanosauromorphs and trilophosaurids are recovered as sister-taxa for the first time, as supported by several cranial and postcranial synapomorphies. This new phylogenetic position of Drepanosauromorpha reduces the group's ghost lineage that now does not necessarily cross the Permian–Triassic boundary. However, much remains unknown of the early history of trilophosaurids and drepanosauromorphs, and of the evolution of arboreality in Triassic archosauromorph reptiles.

Keywords: Drepanosauromorpha; Avicephala; comparative anatomy; phylogeny; Permo–Triassic

INTRODUCTION

The Late Permian Epoch witnessed the origin of both archosauromorphs and lepidosauromorphs, which together make up the clade Sauria, or crown-group reptiles (Ezcurra *et al.* 2014, Ford *et al.* 2021). These reptiles were rather modest components of terrestrial ecosystems of the Late Paleozoic, the tetrapod assemblages of which were dominated by temnospondyls and synapsids (Sahney *et al.* 2010, Sues 2019). However, during the Triassic Period, saurians, especially archosauromorphs, underwent their first major evolutionary radiation (Bernardi *et al.* 2015, Foth *et al.* 2016, 2021, Ezcurra and Butler 2018, Ezcurra *et al.* 2021). The early evolutionary history of Sauria thus straddles the Permian–Triassic Mass Extinction (PTME), the most severe ecological crisis in the history of life (e.g. Erwin 1990, Benton 2003). In this context, the study of Permian–Triassic diversity, especially that of stem-saurian diapsids—those diapsids not included in the saurian crown-group—is paramount to further our understanding of the early evolutionary history of crown-group reptiles.

Among stem-saurian diapsids, the Late Permian Weigeltisauridae, the earliest known gliding vertebrates, and the chameleon-like Drepanosauromorpha from the Late Triassic show some of the most extreme anatomical specializations for an arboreal lifestyle in tetrapods (Castiello *et al.* 2016, Pritchard *et al.* 2016, 2021, 2023, Buffa *et al.* 2021, 2022, Renesto and Saller 2023). Both taxa have been proposed to form the clade Avicephala (Merck 2003, Senter 2004, Pritchard *et al.* 2021), the earliest group of arboreal diapsids, and one of the few to survive the PTME.

However, avicephalans have a complex taxonomic history. Whereas all recent studies recover weigeltisaurids as stem-saurian diapsids (Ezcurra *et al.* 2014, Pritchard and Nesbitt 2017, Schoch and Sues 2018a, Griffiths *et al.* 2021, Pritchard *et al.* 2021, Simões *et al.* 2022), drepanosauromorphs are

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recovered either as stem-saurian diapsids (Müller 2004, Senter 2004, Pritchard *et al.* 2016, 2021, Pritchard and Nesbitt 2017) or archosauromorph saurians (Bennett 2020, Sobral *et al.* 2020, Ford *et al.* 2021, Griffiths *et al.* 2021, Martínez *et al.* 2021, Simões *et al.* 2022) in the latest phylogenetic analyses. In addition, it has been suggested that Avicephala comprises taxa that convergently evolved an arboreal lifestyle rather than actually closely related taxa (Renesto *et al.* 2010). Thus, there is no consensus regarding the monophyly of Avicephala.

Much of the uncertainty over avicephalan phylogeny arises from the highly derived morphology of drepanosauromorphs. Drepanosauromorphs are a group of small, less than 500 mm long reptiles from the Late Triassic of Laurasia that combine a bird-like head, a barrel-shaped trunk, and a laterally compressed tail. Some taxa also exhibit a hooked prehensile tail and opposable digits in the manus and pes similar to modern-day chameleons (Renesto *et al.* 2010, Castiello *et al.* 2016, Pritchard *et al.* 2016, Pritchard and Nesbitt 2017, Renesto and Saller 2023).

Our knowledge of drepanosauromorph anatomy is further hampered by the nature of preservation of most of the available specimens, comprising either fully articulated but badly crushed specimens or three-dimensional but isolated bones, with only a few incomplete specimens preserved in both articulation and three dimensions (Renesto *et al.* 2010, Pritchard *et al.* 2016). In line with this, the majority of recent phylogenetic matrices sample the European drepanosauromorphs, which are represented by specimens that were subject to postmortem compression (e.g. Bennett 2020, Sobral *et al.* 2020, Ford *et al.* 2021, Griffiths *et al.* 2021, Martínez *et al.* 2021, Simões *et al.* 2022), thus limiting our understanding of drepanosauromorph character states. Articulated material from northeastern Utah has been mentioned over the past decade (Engelmann *et al.* 2012, Chure *et al.* 2013, 2015, Britt and Chure 2016, Britt *et al.* 2019) but is yet to be formally published and described. To date, *Avicranium renestoi* Pritchard & Nesbitt, 2017 is the only published drepanosauromorph for which three-dimensional articulated cranial material is preserved. Pritchard and Nesbitt (2017) described a mosaic of highly plesiomorphic and apomorphic characters in *A. renestoi*, which formed much of their interpretation of drepanosauromorphs as stem-saurians (see also Pritchard *et al.* 2016). *Avicranium renestoi* thus provides key evidence relative to the anatomy and evolution of drepanosauromorphs and avicephalans, which prompted its re-examination in the context of recent reassessments of both weigeltisaurid (Buffa *et al.* 2021, 2022, Pritchard *et al.* 2021) and drepanosauromorph (Pritchard *et al.* 2023, Renesto and Saller 2023) anatomy.

Here, we thus provide comments on the anatomy of the Late Triassic drepanosauromorph *A. renestoi* based on the re-examination of published segmented Computed Tomography (CT) data, as well as on some more well-known drepanosauromorphs from the Late Triassic of northern Italy. We include these new data in a new morphological phylogenetic dataset designed to test the monophyly of avicephalans and to reassess the phylogenetic relationships of these reptiles, in particular drepanosauromorphs, among Permian–Triassic diapsids.

Institutional abbreviations

AMNH, American Museum of Natural History, New York, USA; CM, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, USA; MCSNB, Museo 'Caffi' di Scienze Naturali Bergamo, Bergamo, Italy; MFSN, Museo Friulano di Scienze Naturali, Udine, Italy; MNHN, Muséum national d'Histoire naturelle, Paris, France; MPUM, Museo di Paleontologia Università degli Studi di Milano, Milano, Italy; SMNK, Staatliches Museum für Naturkunde Karlsruhe, Karlsruhe, Germany; TMM, Texas Memorial Musuem, Austin, Texas, USA.

MATERIAL AND METHODS

Material examined

We studied the stereolithographic (STL) models segmented from the micro-Computed Tomography (μCT) data of the holotype and only known specimen of *Avicranium renestoi* Pritchard & Nesbitt, 2017 (AMNH FARB 30834, courtesy A. Pritchard). The μCT parameters and segmentation process are detailed in Pritchard and Nesbitt (2017). The specimen was digitally segmented by A. Pritchard, who allowed us to produce drawings (including reconstructions) rather than reproduce surface models to illustrate our comments. Based on these surface models, we produced a new reconstruction of AMNH FARB 30834 in Blender v.3.5.0.

We also conducted first-hand examinations of all specimens currently referred to *Megalancosaurus preonensis* Calzavara, Muscio & Wild, 1980 (holotype MFSN 1769a, b; MPUM 6008MPUM 8437a, b), as well as the holotype specimens of *Drepanosaurus unguicaudatus* Pinna, 1980 (MCSNB 5728) and *Vallesaurus cenensis* Renesto & Binelli, 2006 (MCSNB 4751).

All other material studied either through first-hand observations of specimens, published segmented Computed Tomography (CT) data, or photographs in order to build the phylogenetic dataset, are listed in the Supporting Information.

Phylogenetic methods

Morphological dataset

We compiled an extensive new taxon and character dataset designed to reassess the phylogenetic relationships and to test the monophyly of Avicephala, the putative clade comprising Weigeltisauridae and Drepanosauromorpha (Pritchard *et al.* 2021), and possibly the enigmatic *Longisquama insignis* (Senter, 2004). All sufficiently preserved avicephalans are included in our dataset, comprising the weigeltisaurids *Coelurosauravus elivensis*, *Rautiania* sp., and *Weigeltisaurus jaekeli*, as well as the drepanosauromorphs *Avicranium renestoi*, *Dolabrosaurus aquatilis*, *Drepanosaurus unguicaudatus*, *Hypuronector limnaios*, *Megalancosaurus preonensis*, and *Vallesaurus cenensis*. We did not include *L. insignis* in our dataset because of the very poor preservation of the available specimens.

Given the competing hypotheses regarding the systematic position of drepanosauromorphs (summarized in Renesto *et al.* 2010, Pritchard and Nesbitt 2017), our taxon sample comprises well-known representatives of non-saurian diapsids, lepidosauromorphs, and archosauromorphs, as well as relevant taxa such as the kuehneosaurid *Icarosaurus*, sister-group of drepanosauromorphs as per Müller (2004). Furthermore, given the repeated recovery of avicephalans as early diverging neodiapsids (Müller 2004, Senter 2004, Pritchard *et al.* 2016, 2021, Pritchard and Nesbitt 2017), and the possible placement

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of both varanopids and parareptiles among early diapsids as well (Laurin and Piñeiro 2017, Ford and Benson 2020, see also Simões *et al.* 2022), we increased our taxon sample stemwards to better assess character and taxon evolution at the base of the diapsid tree. We thus include two iconic anamniotic tetrapods, *Seymouria* and *Limnoscelis*, and several well-known Carboniferous, Permian, and Triassic synapsids, varanopids, parareptiles, captorhinids, and 'protorothyridids' in our dataset. Overall, the taxon sample comprises 77 operational taxonomic units (OTU, see Supporting Information for a complete taxon list).

We compiled a list of 403 morphological characters to reflect our broad taxon sample. Our character sample comprises 297 characters taken from previous phylogenetic analyses (Schoch and Sues 2018b, Ezcurra *et al.* 2020, Ford and Benson 2020, Griffiths *et al.* 2021, Pritchard *et al.* 2021, Spiekman *et al.* 2021, Simões *et al.* 2022), 91 characters compiled from these sources that were modified to fit our dataset, and 15 new characters (see Supporting Information for a complete character list). Of the total of 403 characters, 86 multistate characters represent morphological series and were considered additive, given that previous studies have shown that ordering such characters gives more reliable results, even if minor ordering errors are made (Rineau *et al.* 2015, 2018). All characters were equally weighted.

Maximum Parsimony analyses

We conducted a phylogenetic analysis under maximum parsimony in PAUP* v.4.0a (Swofford 2003). We employed a heuristic search algorithm with 1000 random additional sequence replicates and a Tree Bisection and Reconnection (TBR) branch swapping algorithm (reconnection limit = 8). Branches are collapsed if they lack transformations under all optimizations (i.e. maximum length = 0). We quantified branch support through Bremer support values and a Bootstrap resampling analysis with 1000 replicated heuristic searches, each with 50 random additional sequence replicates. Bremer support values were calculated by first incrementally increasing the number of steps retained in five successive analyses, and then by collapsing each remaining node individually using constraints when computational time became too long. *Seymouria* was designated as the outgroup.

We also computed a series of four constrained analyses (analyses C1, C2, C3, and C4) under maximum parsimony in PAUP* v.4.0a (Swofford 2003) to assess the differences in tree length, resolution, and overall topology while imposing a backbone constraint mimicking previous phylogenetic hypotheses for drepanosauromorphs. Analysis C1 constrains Drepanosauromorpha as non-saurian diapsids crownward to Araeoscelidia, which is congruent with the topologies recovered by Pritchard and Nesbitt (2017). Analysis C2 constrains the monophyly of Avicephala following the topology of Pritchard *et al.* (2021). Analysis C3 constrains Drepanosauromorpha as non-crocopodan archosauromorphs crownward to *Protorosaurus speneri*, which is congruent with those topologies that recover drepanosauromorphs within 'protorosaurs' (e.g. Dilkes 1998, Renesto *et al.* 2010). Lastly, Analysis C4 constrains the monophyly of Drepanosauromorpha and *Icarosaurus siefkeri*, which imitates the putative sister-group relationship between drepanosauromorphs and kuehneosaurids recovered by Müller (2004). See Supporting Information figures for the backbone topological constraints used and the resulting topologies.

RESULTS

Comments on the anatomy of *Avicranium renestoi*

We provide here a re-examination of the three-dimensional digital surface models of the holotype specimen of *Avicranium renestoi* AMNH FARB 30834 comprising a sub-complete skull and the first four cervical vertebrae. This specimen was initially segmented from μCT data and described by Pritchard (2015) and Pritchard and Nesbitt (2017). We refrain from providing a detailed redescription of this specimen here, but only present a statement of comparative anatomy in an effort to further our understanding of the phylogenetic position of drepanosauromorphs among Permian–Triassic diapsids. Based on our re-examination, we concur with previous identifications of the skull roof and dorsal temporal bones, which are thus not detailed here. However, we propose alternative interpretations for several structures in the cheek, palate, and braincase (Fig. 1).

Comments on maturity stage

A triangular opening can be seen between both frontals of AMNH FARB 30834, just anterior to their contact with the parietals (Fig. 1A). The location of this opening at the level of the frontoparietal contact could suggest that it is a fontanelle, that is, an opening resulting from the incomplete ossification of these bones due to immaturity. Such fontanelles are common in immature specimens of extant reptiles, although they are markedly different to that of AMNH FARB 30834 in being generally larger and separating the anterior part of the parietals as well (e.g. Rieppel 1992, Maisano 2002, Torres-Carvajal 2003, Hoffman and Rowe 2018, Pritchard *et al.* 2018, Korneisel *et al.* 2022). These openings are also found in CT-scanned fossil specimens such as the juvenile holotype of the rhynchocephalian *Colobops* (Scheyer *et al.* 2020). However, we note that some juvenile birds (but not all) do show a morphology of this opening similar to that of AMNH FARB 30834, whereby the parietals are hardly separated, if at all [e.g. *Dromaius novaehollandiae*, TMM M-6757 available on the DigiMorph repository; *Larus argentatus* (Mayr and Manegold 2021), *Pica pica* (Plateau and Foth 2021), *Struthio camelus* (Plateau *et al.* 2024)]. Given the similarity of the inflated morphology of the skull roof of AMNH FARB 30834 to that of extant birds (Fig. 2; Pritchard and Nesbitt 2017), the identification of this opening as a fontanelle cannot be excluded solely based on its relationship to the frontals and parietals. Alternatively, this opening in AMNH FARB 30834 may also be an artefact of preservation, whereby the posteromedial corner of both frontals is lost. This is plausible because these bones are exposed externally on the specimen. However, the otherwise good preservation of the left frontal and both parietals strongly suggest that the original margins of this putative fontanelle are preserved. Taking this uncertainty into account, this possible ontogenetic character is here considered equivocal but raises doubt regarding the maturity status of AMNH FARB 30834.

Beyond this putative fontanelle, it is very hard to assess the ontogenetic status of this specimen given (1) the previously noted limitations of the μCT scan data, (2) the distant phylogenetic bracket to interpret size-independent characters if

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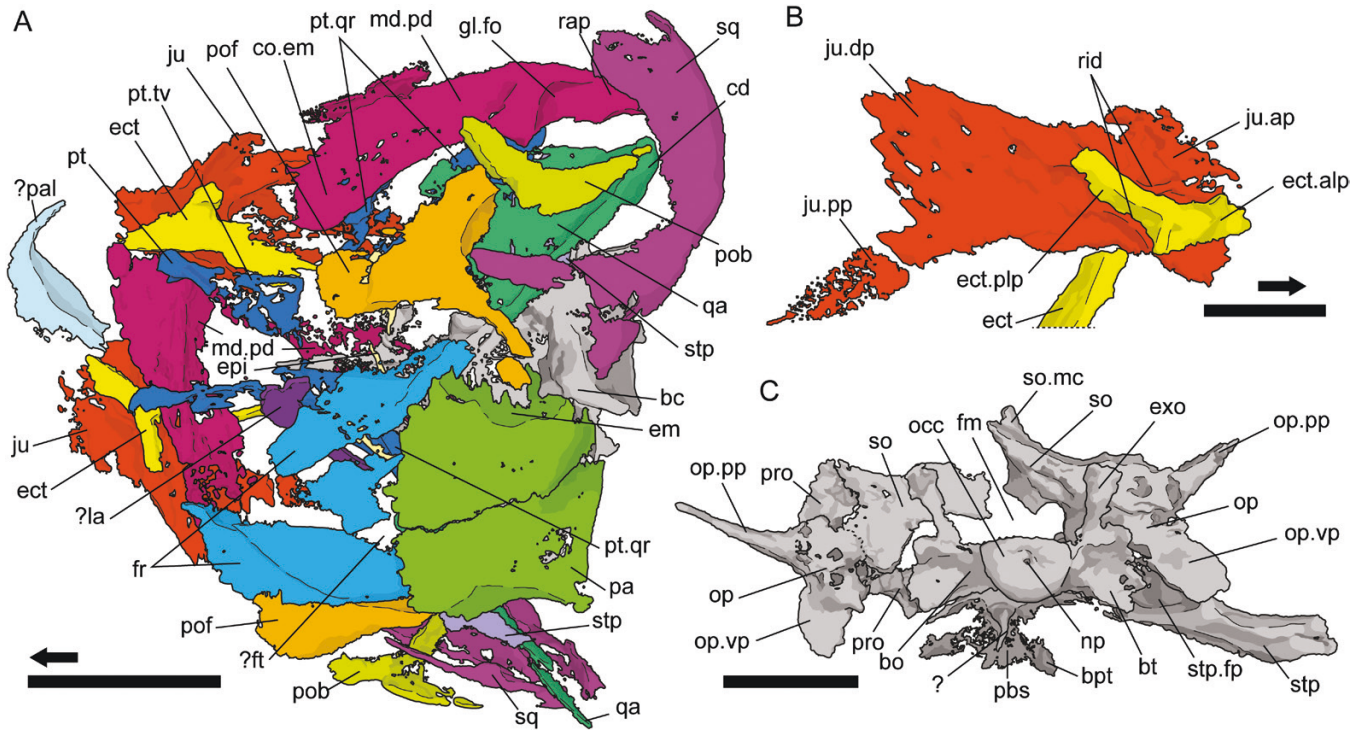

Figure 1. Cranial anatomy of the drepanosauromorph *Avicranium renestoi* Pritchard & Nesbitt, 2017 (Norian, New Mexico, USA). Interpretive drawings of surface models of holotype AMNH FARB 3083. A, sub-complete skull in dorsal view. B, left jugal in medial view. C, sub-complete braincase in posterior view. Arrows indicate anterior direction. Scale bars: 10 mm in A; 5 mm in B, C. Abbreviations: bc, braincase; bo, basioccipital; bpt, basipterygoid process; bt, basal tuberosities; cd, condyle; co.em, coronoid eminence; ect, ectopterygoid; ect.alp, anterolateral process of ectopterygoid; ect.plp, posterolateral process of ectopterygoid; em, emargination; epi, epipterygoid; exo, exoccipital; fr, frontal; ft, fontanelle; fm, foramen magnum; gl.fo, glenoid fossa; ju, jugal; ju.ap, anterior process of jugal; ju.dp, dorsal process of jugal; ju.pp, posterior process of jugal; la, lacrimal; md.pd, postdentary complex of mandible; np, notochordal pit; occ, occipital condyle; op, opisthotic; op.pp, paroccipital process of opisthotic; op.vp, ventral process of opisthotic; pa, parietal; pal, palatine; pbs, parabasisphenoid; pob, postorbital; pof, postfrontal; pro, prootic; pt, pterygoid; pt.qr, quadrate ramus of pterygoid; pt.tv, transverse flange of pterygoid; qa, quadrate; rap, retroarticular process; rid, ridge; so, supraoccipital; so.mc, medial crest of supraoccipital; sq, squamosal; stp, stapes; stp.fp, footplate of stapes.

drepanosauromorphs are non-saurian diapsids, and (3) the subjectivity in interpreting a putative immature structure as either a plesiomorphy or evidence of immaturity. Points (1) and (2) result directly from the studied material and are thus not discussed further. In contrast, point (3) is important for our understanding of *A renestoi*. Indeed, Pritchard (2015) and Pritchard and Nesbitt (2017) interpreted the short and slender paroccipital process, the large notochordal pit on the basioccipital, the poorly developed basal tuberosities, and the large oval foramen as plesiomorphies that would support an identification of drepanosauromorphs as stem-saurians. However, all of these characters have also been recognized as evidence of morphological immaturity in both extant (Rieppel 1993, Bever 2005, Bhullar 2012, Dufeau and Witmer 2015) and extinct (Scanferla and Bhullar 2014, Bullar *et al.* 2019) reptiles. Bearing this uncertainty in mind, we remain cautious with several interpretations of the cranial anatomy of AMNH FARB 30834.

Palate

The skull of AMNH FARB 30834 appears slightly dorsoventrally compressed so that the skull roof and temporal regions have been pushed to the left and slightly posteriorly, whereas the braincase and palate remain mostly in their anatomical position (Fig. 1A). Both epipterygoids remain articulated with the pterygoids, indicating that the basicranial articulation is only slightly anteromedially displaced relative to the basipterygoid processes. Anteriorly, both pterygoids are closely associated with a pair of Y-shaped bones (Fig. 1A). Given the close proximity to the quadrate ramus of the pterygoids, we suggest that these bones represent ectopterygoids, rather than palatines as previously suggested (Pritchard 2015, Pritchard and Nesbitt 2017). As such, the small portion of the pterygoid preserved anterior to the basicranial articulation likely corresponds to a part of the transverse flange rather than the palatal process. The medial part of the transverse flange and the more anterior palatal process of both pterygoids appear to be missing in AMNH FARB 30834 (Fig. 1A).

Both ectopterygoids overlap the pterygoids ventrally but their extent over the transverse flange remains unclear because the latter is incompletely preserved. Laterally, the ectopterygoids bifurcate into anterolateral and posterolateral processes which articulate with a large adjacent bone on both sides of AMNH FARB 30834 (Fig. 1A). Given the presence of a distinct articular surface on the medial surface of the left one of these bones (Fig. 1B), it is evident that it lies in its anatomical position relative to the palate but is not part of the latter. Owing to its large extension posterior to its articulation with the ectopterygoid, we identify this bone as the jugal rather than the maxilla as was previously suggested (Pritchard 2015, Pritchard and Nesbitt 2017).

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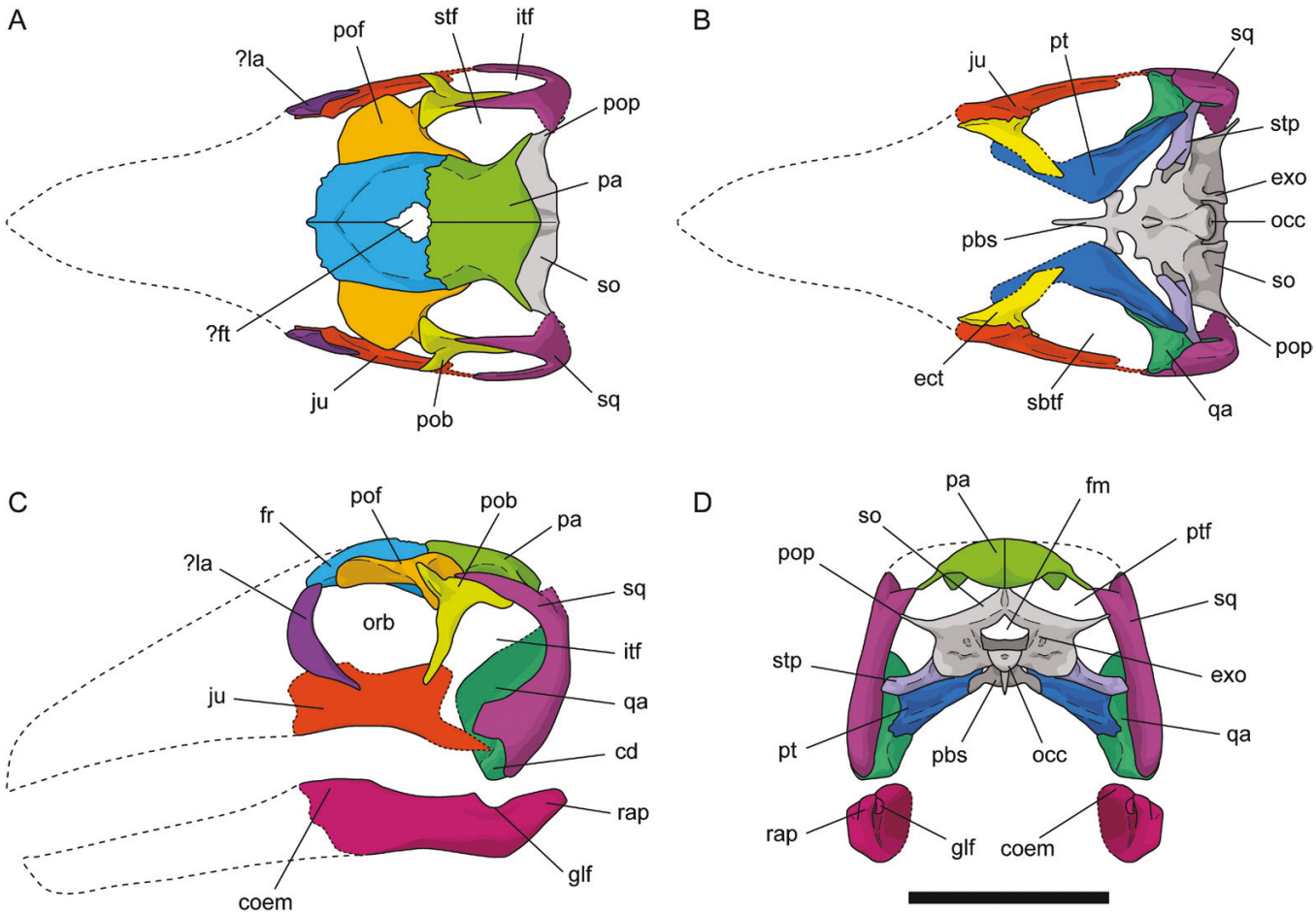

Figure 2. Cranial reconstruction of the drepanosauromorph *Avicranium renestoi* Pritchard & Nesbitt, 2017 (Norian, New Mexico, USA) based on holotype AMNH FARB 30834 in dorsal (A), ventral (B), left lateral (C), and posterior (D) views. Poorly known or unpreserved elements outlined by dashed lines, with dimensions of rostrum and anterior mandible based on reconstructions of the best-known drepanosauromorph *M. preonensis* (Renesto and Dalla Vecchia 2005). Scale bar: 20 mm. Abbreviations: cd, condyle; coem, coronoid eminence; ect, ectopterygoid; exo, exoccipital; itf, infratemporal fenestra; fr, frontal; ft, fontanelle; fm, foramen magnum; glf, glenoid fossa; ju, jugal; la, lacrimal; occ, occipital condyle; orb, orbit; pa, parietal; pbs, parabasisphenoid; pob, postorbital; pof, postfrontal; pop, paroccipital process; pt, pterygoid; ptf, posttemporal fenestra; qa, quadrate; rap, retroarticular process; so, supraoccipital; sq, squamosal; sbtf, subtemporal fenestra; stf, supratemporal fenestra; stp, stapes.

Lastly, a small bone fragment anterior to the ectopterygoid, previously identified as the premaxilla (Pritchard 2015, Pritchard and Nesbitt 2017), remains unclear. According to its position, we suggest that it might be rather a fragment of the left palatine (Fig. 1A). However, this cannot be ascertained due to its poor preservation.

Circumorbital bones

As best seen on the left side, the jugal of AMNH FARB 30834 extends beyond the anterior margin of the orbit and expands dorsoventrally anterior and posterior to its suborbital portion (Fig. 1A, B). A jugal with an anterior process extending at least to the anterior orbital margin and excluding the maxilla from the orbit is typical for archosauromorphs (Nesbitt 2011, Ezcurra 2016), but contrasts with the condition in other Permo–Triassic diapsids where this process is shorter and the maxilla contributes to the orbital margin. This is particularly true for weigeltisaurids (Bulanov and Sennikov 2015, Buffa *et al.* 2021, Pritchard *et al.* 2021), as well as rhynchocephalians (Chambi-Trowell *et al.* 2019), where the anterior process of the jugals does not reach the midpoint of the ventral orbital margin.

More posteriorly, the jugal of AMNH FARB 30834 bears a wide dorsal process for the articulation with the postorbital and a narrow and long posterior process that likely extended to the level of the squamosal, possibly even reaching the posterior margin of the skull (Fig. 1A, B). However, it remains unclear if the jugal articulated with the squamosal, thus closing the infratemporal bar, or if there was a gap between the posterior extremity of the jugal and the squamosal. This contact is similarly unclear in *M. preonensis* (MFSN 1769; Renesto and Dalla Vecchia 2005) which has a much more slender jugal, and the jugal of *V. cenensis* appears to lack a posterior process (MCSNB 4751; Renesto and Binelli 2006), which indicates an open infratemporal bar. As discussed by Buffa *et al.* (2021) for weigeltisaurids that also possess a long posterior process of the jugal, a large contribution of the posterior process of the jugal to the infratemporal bar such as that of AMNH FARB 30834 contrasts with its smaller contribution in non-saurian diapsids. Instead, it may suggest a reacquisition

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of this bar, which occurred convergently in different saurian clades, most prominently archosauriforms (Müller 2003, Abel and Werneburg 2021).

In addition, the posterior portion of the jugal of AMNH FARB 30834 is posteroventrally inclined relative to the main axis of the articular surface for the ectopterygoid. Thus, if the jugal-ectopterygoid articulation is oriented horizontally and is taken as a reference for the main axes of the palate and alveolar margin as is the case in most Triassic reptiles (e.g. Borsuk-Białynicka and Evans 2009, Evans and Borsuk-Białynicka 2009), then the jugal extends markedly posteroventral to the level of its articulation with the ectopterygoid (Fig. 1B). This would suggest that the jaw articulation laid markedly ventral to the alveolar margin of the maxilla in AMNH FARB 30834, as is only the case in other drepanosauromorphs (*M. preonensis* MFSN 1769; *V. cenensis,* MCSNB 4751; Renesto and Dalla Vecchia 2005, Renesto and Binelli 2006), weigeltisaurids (Bulanov and Sennikov 2015, Buffa *et al.* 2021), aetosaurs (Desojo *et al.* 2013), and pterosaurs (Dalla Vecchia 2013, 2014) among Permo–Triassic diapsids.

A slender and curved bone, previously identified as the jugal in AMNH FARB 30834 (Pritchard 2015, Pritchard and Nesbitt 2017) lies in a mostly dorsoventral orientation between the palate and skull roof near the expected position of the anterior orbital margin (Fig. 1A). Given the overall slenderness of this bone, as well as its location and orientation along the dorsoventral plane, we tentatively identify it as one of the circumorbital bones, likely the lacrimal, although it may alternatively correspond to the prefrontal. The interpretation of this bone as the lacrimal is supported by the morphology of the lacrimal of *Megalancosaurus preonensis* which is high and slender (MFSN 1769; Renesto and Dalla Vecchia 2005).

Pritchard and Nesbitt (2017) describe AMNH FARB 30834 with a broad squamosal extensively covering the quadrate externally through well-developed lateral and posterior laminae, a condition that is typical of early amniotes and araeoscelidians (Heaton 1979, Reisz 1981). However, this character has long been considered absent in all other diapsids where the quadrate is at least partially uncovered laterally and posteriorly (Benton 1985, Laurin 1991). As best seen on the right side, we concur with Pritchard and Nesbitt (2017) that the squamosal of this taxon bears a prominent posterior lamina (Fig. 1A). However, the lateral lamina of this bone is narrow, only forming a short anteroventral projection that likely did not cover the entire lateral surface of the quadrate (as reconstructed by Pritchard and Nesbitt 2017: fig. 3), giving the squamosal a strongly concave anterior margin (Fig. 1A). In contrast, the lateral lamina of the squamosal of other early amniotes is broad throughout its length, even if temporal fenestrae are present (e.g. *Petrolacosaurus*, Reisz 1981). However, the relatively thinner lateral lamina of AMNH FARB 30834 is very similar to that of some varanopids such as *Mesenosaurus* (Maho *et al.* 2019), and remains relatively thicker than in most neodiapdids such as *Youngina* (Gow 1975) or weigeltisaurids (Bulanov and Sennikov 2010). Conversely, neither *M. preonensis* (MFSN 1767; Renesto and Dalla Vecchia 2005) nor *Vallesaurus cenensis* (MCSNB 4751; Renesto and Binelli 2006) show a squamosal with a posterior lamina. Owing to these observations and the apical position in which Pritchard and Nesbitt (2017) recover *A. renestoi* among drepanosauromorphs, it is possible that its peculiar squamosal morphology is apomorphic.

Braincase

The braincase of AMNH FARB 30834 is nearly complete, with most portions lying in anatomical position (Fig. 1C). Pritchard (2015) and Pritchard and Nesbitt (2017) apparently used the left portion of the braincase as the main basis for their reconstruction and anatomical description. However, the right half of the braincase is much better preserved, as attested by the right stapes that lies in its anatomical position (Fig. 1C), whereas the left one is displaced. As described by Pritchard and Nesbitt (2017), the main axis of the parabasisphenoid is oriented dorsally so that the basipterygoid processes lie ventral to the basal tuberosities (Fig. 1C), a condition common in non-proterosuchid archosauriforms (Gower and Sennikov 1996, Nesbitt 2011, Ezcurra 2016) as well as in allokotosaurians and early rhynchosaurs among archosauromorphs (Flynn *et al.* 2010, Sobral and Müller 2019, Wilson *et al.* 2022). However, we concur with Pritchard and Nesbitt (2017) that there is no trace of a laterosphenoid in the surface models, the presence of which has long been considered a synapomorphy of archosauriforms (Clark *et al.* 1993, Nesbitt 2011).

Under our interpretation, the supraoccipital of AMNH FARB 30834 is dorsally convex above the foramen magnum and bears a sharp median crest (Fig. 1C), which contrasts with the dorsally concave supraoccipital reconstructed by Pritchard and Nesbitt (2017). However, our reconstruction conforms to the dorsally flat or convex supraoccipital that is typical in Permo–Triassic neodiapsids (Flynn *et al.* 2010, Gardner *et al.* 2010, Sobral *et al.* 2016a, Chambi-Trowell *et al.* 2019, Sobral and Müller 2019, Miedema *et al.* 2020, Wilson *et al.* 2022). The right opisthotic appears undistinguishably fused to the supraoccipital in the surface models of AMNH FARB 30834. Therefore, we remain cautious regarding the demarcation between the supraoccipital and left opisthotic made by previous studies (Fig. 1C). We concur with Pritchard's (2015) identification of a very slender paroccipital process in AMNH FARB 30834 (Fig. 1C). However, the latter study suggested that this process did not reach the dermal skull bones. While we concur that there is no definite distal articular surface on the paroccipital process, it may have been long enough to reach the level of the squamosal laterally (see reconstruction below). Therefore, the presence of a contact between the paroccipital process and the dermal skull is equivocal in AMNH FARB 30834. A short and slender paroccipital process that does not reach the dermal skull is uncommon among early diapsids, being present in the araeoscelidian *Petrolacosaurus* but not in *Araeoscelis* (Vaughn 1955, Reisz 1981), and in the non-saurian neodiapsids *Claudiosaurus* and *Hovasaurus* (Carroll 1981, Currie 1981) but not in *Youngina* (Gardner *et al.* 2010). In contrast, a paroccipital process that reaches the dermal skull roof laterally is prevalent throughout Permian–Triassic saurians (Laurin 1991).

While we concur with the identification of the basioccipital-exoccipital complex of previous studies, we interpret several structures of this complex differently. First, Pritchard and Nesbitt (2017) described the basioccipital of AMNH FARB 30834 as lacking well-developed basal tuberosities extending ventral to the occipital condyle. While we confirm that the basal

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tuberosities do not expand markedly ventrally, they actually extend beyond the ventral margin of the condyle for a very short distance, provided the ventral margin of the foramen magnum is oriented horizontally (Fig. 1C). In addition, they expand markedly laterally so that the bone is overall three times as wide as the occipital condyle. This differs markedly from the morphology of other taxa showing small basal tuberosities such as captorhinids or non-saurian diapsids in which the basal tuberosities are only incipient (Price 1935, Vaughn 1955). Conversely, in juvenile specimens of *Alligator mississipiensis* (e.g. TMM M-6723, available on DigiMorph repository), the basioccipital also hardly expands ventral to the occipital condyle, but is overall three time the width of the latter, whereas the bone is much taller in adult specimens (e.g. TMM M-983, available on DigiMorph repository). In fact, transversely broad but dorsoventrally short basal tuberosities seem to be indicative of an immature ontogenetic stage, as seen in juveniles of some extant (Bever 2005, Bhullar 2012, Dufeau and Witmer 2015, Palci *et al.* 2016) and extinct (Scanferla and Bhullar 2014, Bullar *et al.* 2019) reptiles in which the adults have ventrally expanded basal tuberosities. Therefore, we suggest that the dorsoventrally short basal tuberosities of AMNH FARB 30834 may reflect ontogenetic immaturity.

Second, Pritchard and Nesbitt (2017) described a large, elliptical notochordal pit on the posterior surface of the occipital condyle of AMNH FARB 30834. There is indeed a pit marking the passage of the notochord in this region (Fig. 1C). However, we argue that the notochordal pit of AMNH FARB 30834 is much smaller than that of other early amniotes such as captorhinids or non-saurian diapsids (Gardner *et al.* 2010, deBraga *et al.* 2019), or early rhynchocephalians (Evans 1980, Fraser 1982). In fact, its size resembles that of the notochordal scar of proterochampsian archosauriforms (Dilkes and Sues 2009, Trotteyn and Haro 2011), and that of the enigmatic eucrocopod *Polymorphodon* (Sues *et al.* 2020). Intra-specific variation in the size of the nothochordal pit has also been noted among Permo–Triassic archosauromorphs, where this pit can be small or absent (Wilson *et al.* 2022). Lastly, the notochordal pit closes during postnatal ontogeny in some extant taxa such as *Sphenodon* (CM 30660, available on the DigiMorph repository) or *Alligator* (Dufeau and Witmer 2015). It is therefore possible that the size of the notochordal pit of AMNH FARB 30834 is accentuated by an immature degree of ossification, although this remains tentative (see above).

Lastly, we concur with Pritchard and Nesbitt (2017) that AMNH FARB 30834 has an exceptionally robust stapes for a Triassic diapsid (Fig. 1C) that resembles that found in earlier amniotes (Price 1935, Reisz 1981). In contrast, the stapes is much more slender and rod-like in *Youngina* (Gardner *et al.* 2010) and saurians (Sobral *et al.* 2016b). However, as also noted by Pritchard and Nesbitt (2017), the stapes of AMNH FARB 30834 lacks the dorsal process typical of non-neodiapsid reptiles (Price 1935, Reisz 1981) as well as the stapedial foramen that is prevalent in the latter taxa and also present in *Youngina* (Gardner *et al.* 2010).

Mandible

Parts of both mandibular rami are preserved in AMNH FARB 30834. The right postdentary process is the best-preserved portion, showing a deep glenoid fossa and a robust and high retroarticular process (Fig. 1A), contrary to the much shorter and gracile retroarticular process of other drepanosauromorphs such as *M. preonensis* (MFSN 1769; Renesto and Dalla Vecchia 2005) and *Hypuronector limnaios* (Colbert and Olsen 2001). A large retroarticular process has long been considered a synapomorphy of saurians, contrasting with the small, spur-like retroarticular process of non-saurian neodiapsids (Laurin 1991), although some Triassic saurians also show a short and slender retroarticular process (e.g. proterochampsians; De Simão-Oliveira *et al.* 2022). What is preserved of the lateral surface of the right postdentary complex of AMNH FARB 30834 indicates that an external mandibular fenestra was absent (Fig. 1A).

More anteriorly, the dorsal margin of the right postdentary complex of AMNH FARB 30834 is markedly convex, corresponding to the posterior portion of the coronoid eminence (Fig. 1A) that is slightly shallower than that of *H. limnaios* (Colbert and Olsen 2001). Among drepanosauromorphs, both *Megalancosaurus* (MFSN 1769; Renesto and Dalla Vecchia 2005, MPUM 8437a) and *Vallesaurus* (MCSNB 4751; Renesto and Binelli 2006) lack a coronoid eminence. A marked coronoid eminence is absent in early diapsids such as araeoscelidians, *Weigeltisaurus* and *Youngina* (Gow 1975, Reisz 1981, Bulanov and Sennikov 2015) as well some archosauromorphs such as *Mesosuchus*, *Prolacerta*, *Tanystropheus*, or *Teraterpeton* (Dilkes 1998, Sues 2003, Modesto and Sues 2004, Nosotti 2007), but is present in other archosauromorphs such as *Macrocnemus*, *Trilophosaurus*, or *Pamelaria* (Sen 2003, Spielmann *et al.* 2008, Miedema *et al.* 2020) and is very common in early lepidosauromorphs (Simões *et al.* 2018, Chambi-Trowell *et al.* 2019, Ford *et al.* 2021).

Pritchard and Nesbitt (2017) identified a large structure composed of numerous bone fragments as the anterior portion of the right mandibular ramus. However, we suggest that this assemblage of fragments comprises the right jugal, which lies in articulation with the ectopterygoid, and fragments of the right mandibular ramus (Fig. 1A) that are too poorly preserved to identify. In addition, we tentatively interpret another long structure underlying the palate anteriorly, that Pritchard (2015) and Pritchard and Nesbitt (2017) considered as the left dentary, as the anterior portion of the left postdentary complex.

Comments on the skull reconstruction

The reinterpretations of some bones presented above allowed for a new reconstruction of the skull of AMNH FARB 30834 (Fig. 2), which warrant discussion in a phylogenetic context.

Firstly, *A. renestoi* has previously been reconstructed with a long, tapering, and edentulous rostrum, one of the most striking 'bird-like' characters of this taxon (Pritchard and Nesbitt 2017). However, our reinterpretation of the 'premaxilla', 'left maxilla', and 'right dentary' of previous studies (Pritchard 2015, Pritchard and Nesbitt 2017) as a possible palatine fragment and both jugals (possibly combined with non-dentigerous fragments of the mandibular rami) respectively suggests that none of the marginal tooth-bearing bones of the rostrum are preserved in this specimen (Fig. 2). Thus, owing to this interpretation nothing can be said about the rostrum morphology and marginal dentition of *A. renestoi*.

Secondly, in Pritchard and Nesbitt's (2017: fig. 7) reconstruction, the postorbital overlaps the postfrontal laterally in

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such a way that the supratemporal fossa that is present along the lateral margin of the parietal and the posterior part of the prefrontal is not continuous with the supratemporal bar formed by the postorbital and squamosal. This, combined with the newly interpreted jugal of AMNH FARB 30834, prompted a revision of the arrangement of the postorbital bones (Fig. 2). We reconstruct the postorbital as overlapping the posterior margin of the prefrontal (as is typical in diapsids, e.g. *Prolacerta*, Modesto and Sues 2004), forming a continuous supratemporal fenestra. In turn, the squamosal and quadrate are markedly inclined posterodorsally to accommodate the longer posterior extension of the postorbital compared to previous interpretations. As a result, the jaw articulation is located anterior to the occiput, and is positioned ventrally relative to the rest of the skull (Fig. 2). The resulting morphology would be similar to that of other drepanosauromorphs such as *M. preonensis* (MFSN 1769; Renesto and Dalla Vecchia 2005) and *V. cenensis* (MCSNB 4751; Renesto and Binelli 2006) that have a vaulted skull roof and a posterodorsally inclined posterior skull margin. In addition, due to the very large jugal, the orbit of AMNH FARB 30834 is much smaller than previously reconstructed.

Thirdly, our interpretation of the position of the postorbital and squamosal results in a much more transversely slender skull in the postorbital region compared to the reconstruction of Pritchard and Nesbitt (2017). In addition, our reconstruction of the braincase of AMNH FARB 30834 (principally based on the well-preserved right side), indicates that the braincase is much shorter and wider than previously thought (Fig. 2B, D). As mentioned above, the resulting reconstruction shows that the paraoccipital process reaches the level of the dermal skull bones, although it remains equivocal whether both structures were actually articulated.

Lastly, AMNH FARB 30834 was previously described with an edentulous palate (Pritchard 2015, Pritchard and Nesbitt 2017). However, our reinterpretation of the purported 'palatines' and 'anterior processes of the pterygoids' as ectopterygoids and portions of the transverse flanges of the pterygoids respectively implies that nothing of the palate anterior to the transverse flange of the pterygoid is preserved (Fig. 1A). The posterior margin of the latter is also missing on both sides. Thus, the presence or absence of teeth on this part of the pterygoid cannot be assessed. No neodiapsid shows ectopterygoid teeth, and the transverse flange of the pterygoid is edentulous in nearly all Permo–Triassic saurians, but the rest of the palate is dentigerous in most lepidosauromorphs and non-archosaurian archosauromorphs (Matsumoto and Evans 2017). Thus, given our reinterpretation of the palate of AMNH FARB 30834, the lack of dentition on its preserved portions does not imply that the palate was entirely edentulous. While some of the 'bird-like' traits of this taxon are undoubtedly present, such as a vaulted skull roof, others, such as the lack of marginal or palatal teeth cannot be assessed because the respective bones are not fully preserved or missing in the specimen.

Cervical vertebrae

AMNH FARB 30834 comprises four cervical vertebrae, whose three-dimensional preservation provides significant new information on the vertebral anatomy of drepanosauromorphs. As seen in the fourth cervical of AMNH FARB 30834, the centrum is longer than high and lacks any trace of the notochordal canal (Fig. 3). The intervertebral articulation is heterocoelous, with a saddle-shaped posterior condyle and an anterior cotyle. These features conform well with the cervical vertebrae of *M. preonensis* (MFSN 1769; MPUM 6008; MPUM 8437) and *V. cenensis* (MCSNB 4751), as well as other drepanosauromorphs known from isolated, three-dimensional material (Renesto and Fraser 2003, Dalla Vecchia and Cau 2015). Such a cervical morphology is otherwise only reported in pterosaurs among non-avian diapsids (Andres *et al.* 2010, Dalla Vecchia and Cau 2015). A marked hypapophysis expands posteroventrally from the ventral surface of the centrum in AMNH FARB 30834 and bears a marked apical transverse expansion (Fig. 3), as in other drepanosauromorphs and, to a lesser degree, in some Triassic pterosaurs (Dalla Vecchia and Cau 2015).

The neural arch is much wider than the centrum in the cervicals of AMNH FARB 30834 and is anteriorly displaced relative to it (Fig. 3). As a result, the vertebrae are T-shaped in ventral view, as is also the case in early pterosaurs and birds (Andres *et al.* 2010, Dalla Vecchia and Cau 2015). As noted by Pritchard and Sues (2019), the cervical ribs appear fused to the neural arch, as in trilophosaurid archosauromorphs. The zygapophyses of AMNH FARB 30834 are massive, with their elliptical articular facets oriented nearly vertically (Fig. 3) as in other drepanosauromorphs (*M. preonensis*; MPUM 6008; MPUM 8437; *V. cenensis*: MCSNB 4751; Renesto and Fraser 2003, Dalla Vecchia and Cau 2015), as well as in early pterosaurs (Andres *et al.* 2010, Dalla Vecchia 2014). The cervicals of AMNH FARB 30834 bear a marked postzygodiapophyseal lamina (Fig. 3A, B), which is common among archosauromorphs (Ezcurra *et al.* 2014, Ezcurra 2016). Given that only four cervicals are preserved in AMNH FARB 30834, the presence of other laminae in the presacral vertebral column remains equivocal.

The neural spines of the postaxial cervicals of AMNH FARB 30834 are triangular in lateral view and inclined anterodorsally at an angle of *c.* 25° (Fig. 3), as in most archosauromorphs (Ezcurra 2016). At least in the fourth cervical, the distal terminus of the spine is expanded transversely, resembling the expansion of the hypapophysis (Fig. 3).

Phylogenetical analyses

Main analysis

The Maximum Parsimony analysis returned 12 most parsimonious trees with a length of 2600 steps. The strict consensus (Fig. 4) has a length of 2612 steps, a consistency index (CI) of 0.2033, and a retention index (RI) of 0.6018.

Among non-diapsid taxa, our analysis recovers a monophyletic Amniota comprising the dichotomy between Synapsida and Sauropsida (Fig. 4), as recovered by most cladistic analyses [e.g. Gauthier *et al.* (1988), Laurin and Reisz (1995), deBraga and Rieppel (1997), but see Berman (2013) and Klembara *et al.* (2020) for an inclusion of diadectomorphs within Synapsida]. Among Synapsida, we recover Caseasauria as the sister-group to Eupelycosauria, the clade comprising Ophiacodontidae, Edaphosauridae, and Sphenacodontidae, which mostly coincides with previous studies (Reisz 1986, Benson 2012). Among early sauropsids, Captorhinomorpha, *Hylonomus*, and *Paleothyris* are recovered as successive sister-groups to Diapsida,

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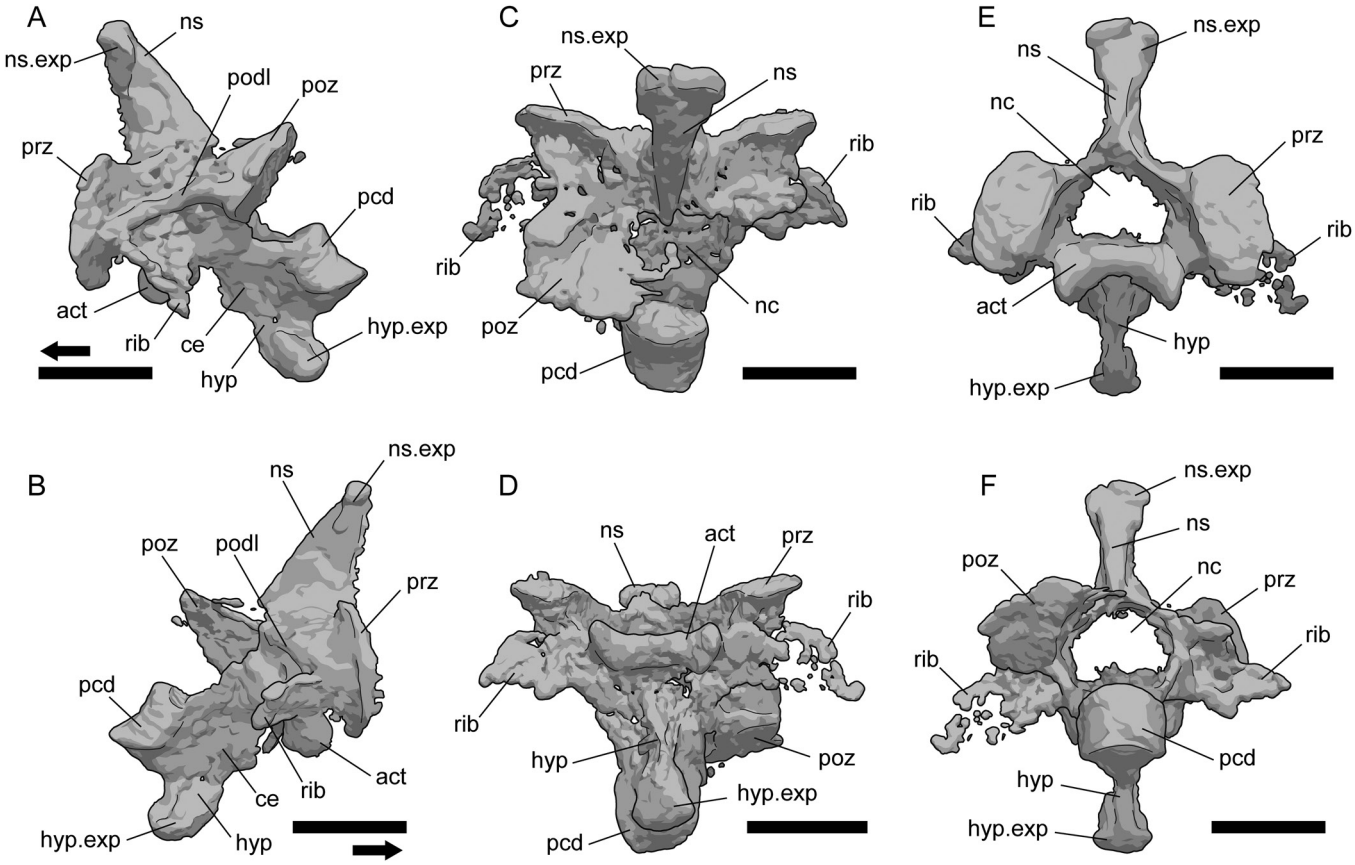

Figure 3. Fourth cervical vertebra of the drepanosauromorph *Avicranium renestoi* (Norian, New Mexico, USA). Interpretive drawings of surface model of holotype AMNH FARB 3083 in left lateral (A), right lateral (B), dorsal (C), ventral (D), anterior (E), and posterior (F) views. Arrows indicate anterior direction. Scale bars: 5 mm. Abbreviations: act, anterior cotyle; ce, centrum; hyp, hypapophysis; hyp.exp, transverse expansion of hypapophysis; nc, neural canal; ns, neural spine; ns.exp, transverse expansion of neural spine; pcd, posterior condyle; podl, postzygodiapophyseal lamina; poz, postzygapophysis; prz, prezygapophysis.

supporting the paraphyly of 'protorothyridids' as was first suggested by Müller and Reisz (2006).

Our analysis recovers an expanded concept of Diapsida, whereby Araeoscelidia and a clade comprising Varanopidae and the 'varanopid-like' diapsid *Orovenator* form successive sister-groups to Neoreptilia, the clade containing the dichotomy between Parareptilia and Neodiapsida (Fig. 4). This contrasts with the traditional view of early amniote relationships, whereby varanopids are eupelycosaurian synapsids (Romer and Price 1940, Reisz 1986, Benson 2012, Simões *et al.* 2022) and parareptiles form a dichotomy with Eureptilia at the base of Sauropsida (e.g. Gauthier *et al.* 1988, Laurin and Reisz 1995, deBraga and Rieppel 1997, Müller and Reisz 2006). However, this topology conforms to the results of several recent studies that support this expanded concept of Diapsida (Laurin and Piñeiro 2018, MacDougall *et al.* 2018, Ford and Benson 2019, 2020).

Among non-saurian diapsids, our topology differs significantly from previous studies. First, we recover a monophyletic Younginiformes at the base of Neodiapsida (Fig. 4), as in earlier studies (Currie 1982, Benton 1985, Evans 1988, Laurin 1991) but contrary to recent analyses that support the paraphyly of this clade [Bickelmann *et al.* (2009), Reisz *et al.* (2011), Hunt *et al.* (2023), but see Simões *et al.* (2022)]. This clade is supported by five unambiguous synapomorphies (listed in the Supporting Information). Given that only three taxa are included in our analysis (*Acerosodontosaurus*, *Hovasaurus*, *Youngina*), support for a monophyletic Younginiformes remains equivocal and further studies may recover this group as paraphyletic.

Second, our analysis recovers Weigeltisauridae together with the enigmatic diapsid *Claudiosaurus* in a clade forming the sister-group to Sauria, the diapsid crown-group (Fig. 4). This crownward position contrasts with most previously published analyses, which recover younginiforms crownward to weigeltisaurids and/or *Claudiosaurus* (Evans 1988, Laurin 1991, Senter 2004, Ezcurra *et al.* 2014, Pritchard *et al.* 2021, but see Müller 2004, Hunt *et al.* 2023).

Sauria, the diapsid crown-group, comprises the dichotomy between Lepidosauromorpha and Archosauromorpha (Fig. 4). The former clade comprises *Paliguana* as sister-group to Lepidosauria, which conforms to the results of Ford *et al.* (2021). Lepidosauria comprises the well-supported clades Rhyncocephalia and Squamata, and we recover *Megachirella* as a stem-squamate in agreement with Simões *et al.* (2018). The kuehneosaurid *Icarosaurus* is recovered as sister-group to Archosauromorpha (sensu Gauthier 2020), echoing previous topologies that support archosauromorph affinities for kuehneosaurids (Pritchard and Sues 2019, Simões *et al.* 2022).

The interrelationships of non-archosauriform archosauromorphs are currently unclear, notably in the position of

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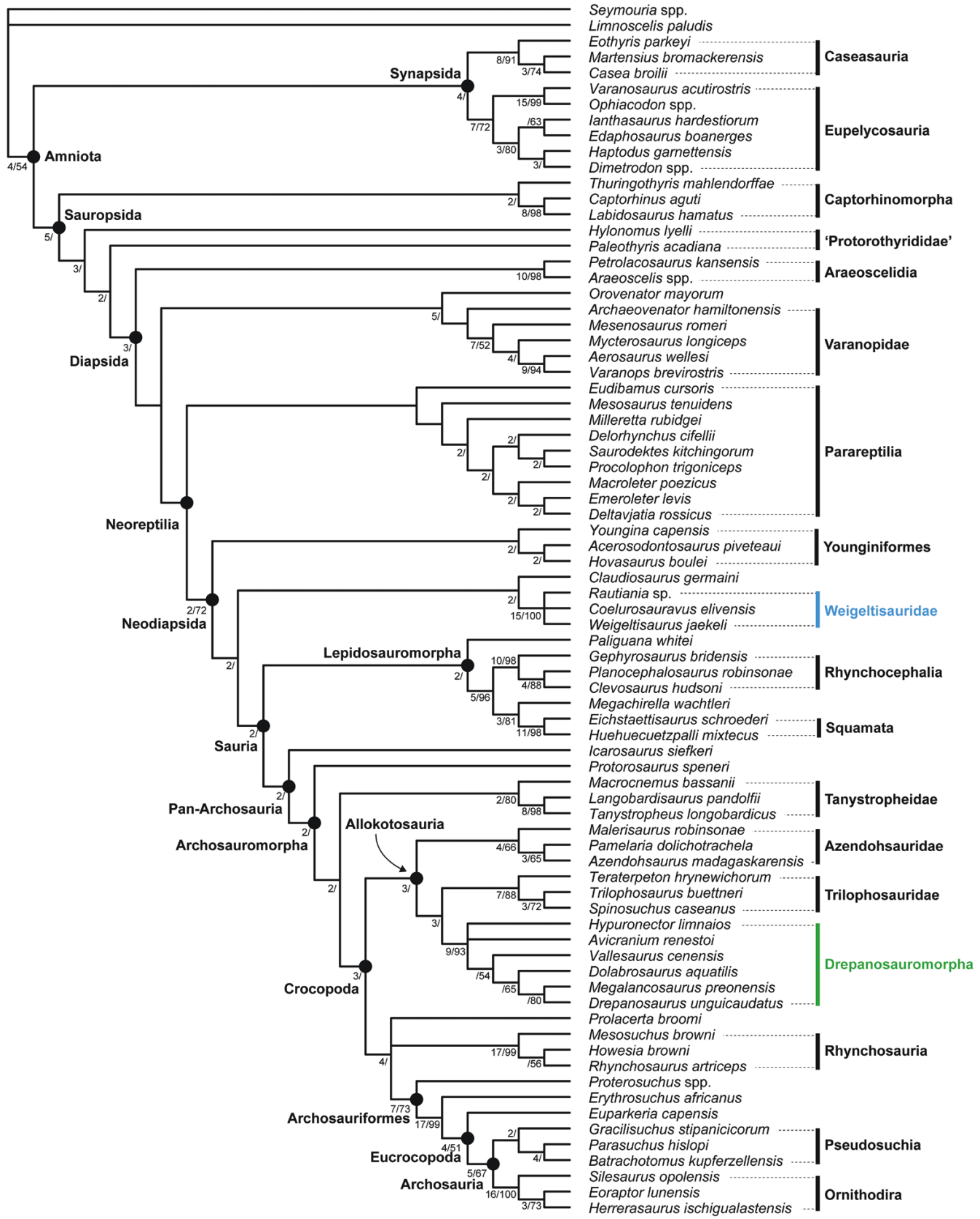

Figure 4. Strict consensus tree returned by Maximum Parsimony analysis (12 MPTs of 2600 steps; L = 2612 steps; CI = 0.2024; RI = 0.6018). Node labels: Bremer value (when > 1)/Bootstrap (when > 50%).

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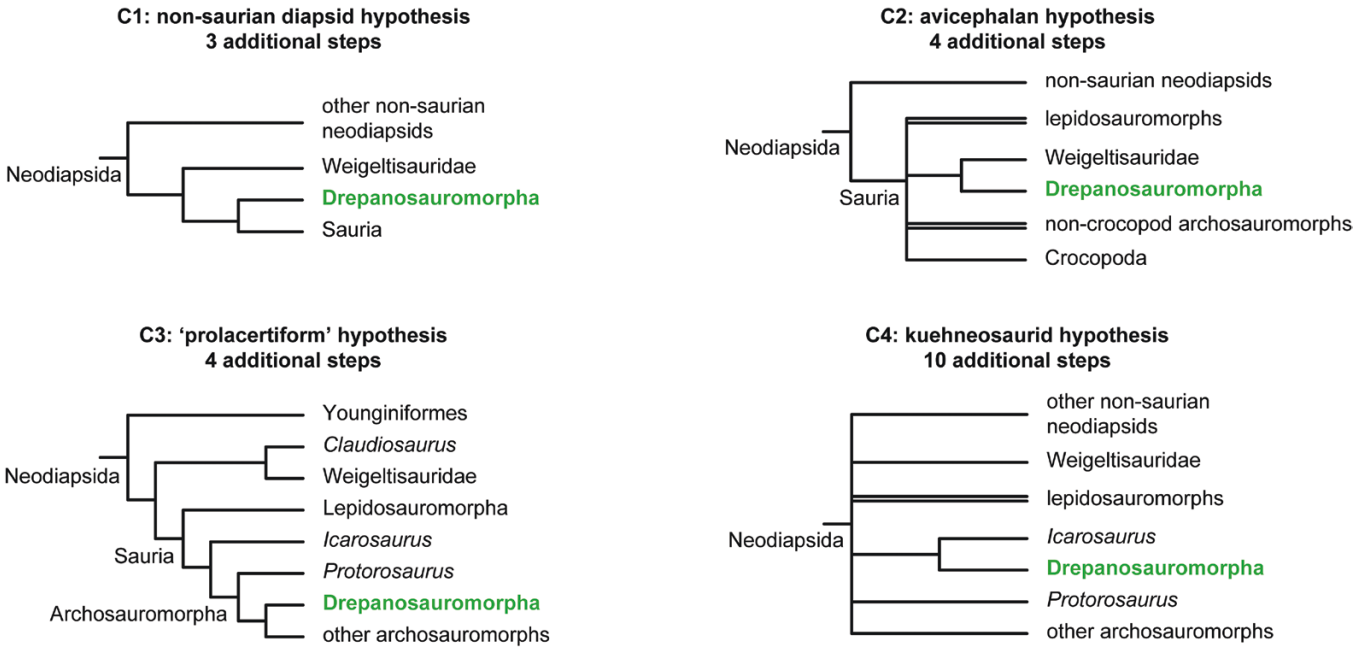

Figure 5. Simplified topologies returned by constrained Maximum Parsimony analyses C1, C2, C3, and C4. Analysis C1, 36 MPTs of 2603 steps; strict consensus: L = 2622 steps; CI = 0.2016; RI = 0.5999. Analysis C2, 639 MPTs of 2604 steps; strict consensus: L = 2754 steps; CI = 0.1919; RI = 0.5746. Analysis C3, 18 MPTs of 2604 steps; strict consensus: L = 2621 steps; CI = 0.2017; RI = 0.6001. Analysis C4, 99 MPTs of 2610 steps; strict consensus: L = 2750 steps; CI = 0.1922; RI = 0.5754. Complete topologies in the Supporting Information.

Allokotosauria as nesting stemward (Pritchard and Sues 2019, Nesbitt *et al.* 2021) or crownward (Nesbitt *et al.* 2015, Ezcurra 2016) to Tanystropheidae and/or Rhynchosauria, and in the position of *Prolacerta* (Spiekman *et al.* 2021). The topology obtained by our parsimony analysis mostly conforms to that of Ezcurra (2016) in the recovery of Tanystropheidae as sister-group to Crocopoda, the clade comprising Allokotosauria, Rhynchosauria, *Prolacerta*, and Archosauriformes (Fig. 4). However, we recover *Prolacerta* and Rhynchosauria in polytomy with archosauriforms, which further emphasizes uncertainties regarding the position of *Prolacerta* (Spiekman *et al.* 2021).

Lastly, in our analysis, drepanosauromorphs are nested within Allokotosauria as sister-group to Trilophosauridae, forming a clade supported by 10 unambiguous synapomorphies (discussed below) and strong branch support values (Fig. 4). *Avicranium* is here recovered as an early-diverging drepanosauromorph rather than a drepanosaurid drepanosauromorph as recovered by Pritchard and Nesbitt (2017). However, we suggest that drepanosauromorph interrelationships remain unclear due to the limited overlap between the preserved portions of the skeleton of various taxa (e.g. *Avicranium* and *Dolabrosaurus*).

Constrained analyses

We conducted a series of four constrained analyses (C1 to C4) to assess the differences in tree length, resolution, and overall topology when forcing the topology to be congruent with previous hypotheses of the systematic position of Drepanosauromorpha (see Material and methods). The strict consensus trees and backbone constraints for analyses C1 to C4 can be found in the Supporting Information, Figures S1 to S4.

Analysis C1, which constrains the position of Drepanosauromorpha among non-saurian diapsids, requires three additional steps compared to our main analysis and recovers Drepanosauromorpha and Weigeltisauridae as successive sister-groups of Sauria (Fig. 5). Interestingly, this analysis does not recover a monophyletic Avicephala and places Drepanosauromorphs as the immediate sister-group of Sauria in a topology that is otherwise virtually identical to our main analysis (Supporting Information, Fig. S1). This very crownward position of Drepanosauromorpha contrasts with the more basal position described by Senter (2004), Pritchard and Nesbitt (2017), and Pritchard *et al.* (2021). Müller (2004) recovered a similarly crownward position of drepanosauromorphs compared to 'younginiforms' and weigeltisaurids, but suggested drepanosauromorphs and kuehneosaurids formed a clade, which is not recovered here.

Analysis C2, which constrains the monophyly of Avicephala, requires four additional steps compared to our main analysis. Overall, the strict consensus is highly unresolved, especially regarding Sauria, which appears in a polytomy and may comprises Avicephala, non-lepidosaurian lepidosauromorphs, non-crocopodan archosauromorphs, and Crocopoda (Fig. 5; Supporting Information, Fig. S2). Despite such irresolution, our topology differs from that of Senter (2004) and Pritchard *et al.* (2021) which recover Avicephala in a more basal position among non-saurian neodiapsids. Interestingly, the unresolved strict consensus does not preclude a position of both Weigeltisauridae and Drepanosauromorpha in the saurian crown-group, which contrasts with the commonly accepted position of weigeltisaurids outside Sauria recovered by most recent studies (Ezcurra *et al.* 2014, Pritchard and Nesbitt 2017, Schoch and Sues 2018a, Griffiths *et al.* 2021, Pritchard *et al.* 2021, Simões *et al.* 2022), as well as our main analysis.

Analysis C3, which constrains the position of Drepanosauromorpha among 'prolacertiform' archosauromorphs (i.e. non-crocopodan archosauromorphs crownward to *Protorosaurus*),

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requires four additional steps compared to our main analysis. It recovers a topology that is virtually identical to our main analysis except for the position of Drepanosauromorpha as sister-group to the clade comprising Tanystropheidae and Crocopoda (Fig. 5; Supporting Information, Fig. S3). We note that this topology differs from most studies that recovered drepanosauromorphs as 'prolacertiforms', in which drepanosauromorphs generally form the sister-group to tanystropheids (Renesto *et al.* 2010, Bennett 2020, Ford *et al.* 2021) or are included in the latter group (Martínez *et al.* 2021, Simões *et al.* 2022).

Analysis C4, which constrains the monophyly of *Icarosaurus* and Drepanosauromorpha, requires 10 additional steps compared to our main analysis. Overall, the strict consensus recovers a highly unresolved Neodiapsida (Fig. 5; Supporting Information, Fig. S4), precluding reliable comparisons to Müller (2004), the only study to recover a clade comprising kuehneosaurids and drepanosauromorphs.

In light of these constrained analyses, we confirm that the topology recovered by our main analysis, whereby Drepanosauromorpha is the sister-group to Trilophosauridae, is more parsimonious than previously proposed hypotheses (Fig. 5). However, we do note that only a few steps are required to recover alternative topologies (e.g. Analyses C1 and C3), and that the topology recovered here in our main analysis is subject to some degree of lability regarding the position of Drepanosauromorpha (see Discussion below). Although we here support the sister-group relationship of drepanosauromorphs and trilophosaurids, future studies, especially of articulated drepanosauromorph specimens, may provide additional anatomical information that could support any of these hypotheses.

DISCUSSION

On the paraphyly of 'Avicephala'

Weigeltisaurids and drepanosauromorphs were first grouped into the clade Avicephala by Merck (2003) and Senter (2004), together with the enigmatic diapsid *Longisquama*. This hypothesis was subsequently criticized by Renesto and Binelli (2006) and Renesto *et al.* (2010) who recovered weigeltisaurids (represented in their analyses by *Coelurosauravus*) as stem-saurians and drepanosauromorphs as non-archosauriform archosauromorphs. More recently, Pritchard *et al.* (2021) resurrected the avicephalan hypothesis, excluding *L. insignis*, which is too poorly preserved to be considered. In this context, the recovery here of a paraphyletic 'Avicephala' warrants a discussion of the purported synapomorphies of this clade.

Senter (2004) recovered eight unambiguous synapomorphies for his Avicephala (including *L. insignis*): S1, premaxilla and dentary sharply pointed in lateral view; S2, craniomandibular joint suborbital; S3, posterior border of skull strongly inclined posterodorsally; S4, scapula elongate; S5, width of distal expansion of humerus < 1/3 humeral length; S6, length of manus ≤ humeral length; S7, metacarpal IV not longer than metacarpal III; S8, metatarsal IV not longer than metatarsal III. In contrast, Pritchard *et al.* (2021) recovered four markedly different synapomorphies for his Avicephala (excluding *L. insignis*): P1, absence of intercentra in cervical region; P2, absence of intercentra in dorsal region; P3, scapulocoracoid, ratio of anteroposterior length at base of scapular blade to dorsoventral height of scapular blade between 0.4 and 0.25; P4, outer process of fifth metatarsal absent.

A sharply pointed premaxilla is indeed present in the weigeltisaurids *Rautiania* (Bulanov and Sennikov 2010) and *Weigeltisaurus* (Fig. 6A; Bulanov and Sennikov 2015, Pritchard *et al.* 2021), and in the drepanosauromorphs *Megalancosaurus* and *Vallesaurus* (MFSN 1769; MCSNB 4751; Figs 6B, 7A, 8A), but it is also present in some tanystropheids (e.g. *Macrocnemus*; Miedema *et al.* 2020), and likely in the allokotosaur *Teraterpeton* as well, although this region is less well preserved in the latter (Sues 2003). Similarly, the craniomandibular articulation is positioned ventral to the level of the maxilla dentition in *Weigeltisaurus*, the only weigeltisaurid where this region is preserved (Fig. 6A), and in the drepanosauromorphs *Avicranium* (Figs 2, 6C) and *Megalancosaurus* (MFSN 1769; Fig. 6B). This was also likely the case in *Vallesaurus* (as reconstructed by Renesto and Binelli 2006), but the skull of this taxon is partially disarticulated, precluding a definite statement (Fig. 8A). A craniomandibular joint positioned ventral to the level of the alveolar margin of the maxilla is also present in all allokotosaurians where this region is known, namely *Azendohsaurus*, *Teraterpeton*, and *Trilophosaurus* (Fig. 6E, F; Sues 2003, Spielmann *et al.* 2008, Flynn *et al.* 2010). Lastly, we concur with Senter (2004) that all weigeltisaurids (Bulanov and Sennikov 2010, 2015, Buffa *et al.* 2021), as well as the drepanosauromorphs *Avicranium* (Fig. 2), *Megalancosaurus*, and *Vallesaurus* (MFSN 1769; MCSNB 4751) have a posterodorsally inclined posterior skull margin (Fig. 6A–C). However, in weigeltisaurids, this margin supports the parietosquamosal frill (Fig. 6A), whereas in drepanosauromorphs it is linked to the inflation of the parietal region of the skull roof, superficially resembling that of birds and pterosaurs (Figs 2, 7A). As a result, the craniomandibular articulation is located at the level of the occiput in weigeltisaurids (Buffa *et al.* 2021), whereas it is much more anterior in drepanosauromorphs (Fig. 2). Given these differences, and the topologies recovered by our main analysis, we consider the posterodorsal inclination of the posterior margin of the skull in weigeltisaurids and drepanosauromorphs as convergent.

Pritchard *et al.* (2021) considered the lack of cervical and dorsal intercentra as a synapomorphy of Avicephala. We concur that there is no trace of post-axial intercentra in the weigeltisaurids *Coelurosauravus* (MNHN.F.MAP317a, b) and *Weigeltisaurus* (SMNK-PAL 2882), nor in the drepanosauromorphs *Megalancosaurus* and *Vallesaurus* (MFSN 1769; MCSNB 4751), and probably in *Drepanosaurus* (MCNSB 5728) and *Hypuronector* (Colbert and Olsen 2001, Renesto *et al.* 2010) as well, which lack dorsal intercentra but for which the presence of cervical intercentra remains unknown due to preservation. Post-axial cervical intercentra are generally absent in non-archosauriform archosauromorphs, as is the case in *Protorosaurus* (Gottmann-Quesada and Sander 2009), most tanystropheids (Pritchard *et al.* 2015), and in the allokotosaurs *Azendohsaurus*, *Malerisaurus*, and *Teraterpeton* (Chatterjee 1980, Sues 2003, Nesbitt *et al.* 2015). However, dorsal intercentra have been reported in the allokotosaurs *Pamelaira* and *Trilophosaurus* (Sen 2003, Spielmann *et al.* 2008), and early rhynchosaurs (Dilkes 1995, 1998), while *Prolacerta* shows both cervical and dorsal intercentra (Gow 1975).

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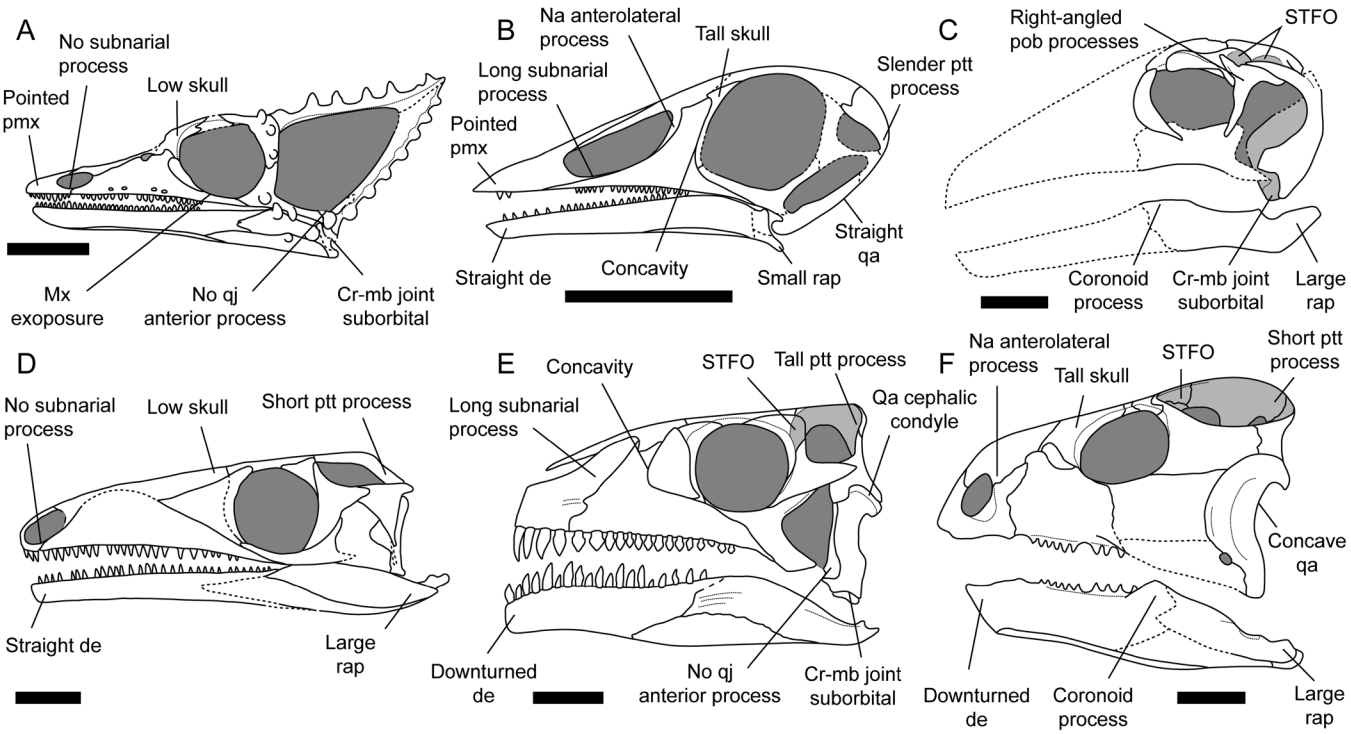

Figure 6. Skull and lower jaw reconstructions of Permo–Triassic diapsids in left lateral view. A, *Weigeltisaurus jaekeli* (modified from Bulanov and Sennikov 2015). B, *Megalancosaurus preonensis* (based on MFSN 1769a, b). C, *Avicranium renestoi* (based on surface models of AMNH FARB 30834). D, *Protorosaurus speneri* (redrawn from Gottmann-Quesada and Sander 2009). E, *Azendohsaurus madagaskarensis* (redrawn from Flynn *et al.* 2010). F, *Trilophosaurus buettneri* (redrawn from Spielmann *et al.* 2008). Scale bars: 10 mm in A–C; 20 mm in D–F. Abbreviations: Cr-mb, craniomandibular; de, dentary; Mx, maxilla; Na, nasal; pmx, premaxilla; ptt, posttemporal; qa, quadrate; qj, quadratojugal; rap, retroarticular process; STFO, supratemporal fossa.

Senter (2004) and Pritchard *et al.* (2021) both recovered a tall scapular blade as a synapomorphy of Avicephala. We concur that the scapula is extremely tall in all drepanosauromorphs where this region is preserved (Figs 7–9; Harris and Downs 2002, Renesto *et al.* 2010, Castiello *et al.* 2016). While weigeltisaurids have a markedly shorter scapular blade compared to drepanosauromorphs (Buffa *et al.* 2022), we concur that it is still tall relative to the short scapular blade of most other Permo–Triassic reptiles such as younginiforms (e.g. *Hovasaurus*; Currie 1981) and tanystropheids (e.g. *Macrocnemus*, *Tanystropheus*; Rieppel 1989, Nosotti 2007), and to other early lepidosauromorphs (e.g. *Gephyrosaurus*; Evans 1981) and archosauromorphs such as *Protorosaurus*, *Prolacerta*, azendohsaurid allokotosaurians, and rhynchosaurs, where the scapula is not as tall relative to its width (Gow 1975, Dilkes 1998, Gottmann-Quesada and Sander 2009, Nesbitt *et al.* 2015). However, scapular blades of similar dimensions to that of weigeltisaurids are also present in the trilophosaurid allokotosaurians *Trilophosaurus* and *Teraterpeton* (Sues 2003, Spielmann *et al.* 2008), as well as some eucrocopods (e.g. *Euparkeria*; Ewer 1965).

As recovered by Senter (2004), we concur that weigeltisaurids and drepanosauromorphs lack a strong expansion of the distal humerus (Fig. 7; Bulanov and Sennikov 2010, Renesto *et al.* 2010, Castiello *et al.* 2016, Buffa *et al.* 2022), although that of *Drepanosaurus* does show some degree of transverse expansion, which cannot be accurately measured due to the preservation of the material (Pritchard *et al.* 2016). All younginiforms (e.g. *Hovasaurus*, *Youngina*; Gow 1975, Currie 1981), and most Permo–Triassic lepidosauromorphs (e.g. *Clevosaurus*, *Megachirella*; O'Brien *et al.* 2018, Simões *et al.* 2018) and archosauromorphs (e.g. *Azhendohsaurus*, *Mesosuchus*, *Protorosaurus*, *Prolacerta*; Gow 1975, Dilkes 1998, Gottmann-Quesada and Sander 2009, Nesbitt *et al.* 2015) show a moderate to strong distal humeral expansion, mostly due to the expansion of the entepicondyle. However, tanystropheids lack a marked expansion of the distal humerus (e.g. *Macrocnemus*, *Tanystropheus*; Rieppel 1989, Nosotti 2007), and the humerus of '*Trilophosaurus jacobsi*' also shows little to no distal expansion (Spielmann *et al.* 2008).

We concur with Senter (2004) that 'avicephalans' have more symmetrical manus and pedes (with metapodials III and IV being subequal in length) than other Permo–Triassic reptiles. Such symmetrical metapodials are rare among non-archosauriform archosauromorphs (e.g. the manus and pes of *Tanystropheus*, the manus of *Azhendohsaurus*; Nosotti 2007, Nesbitt *et al.* 2015), but more common in later eucrocopod archosauriforms (see Nesbitt 2011). Given the topology recovered herein, we suggest these more symmetrical metapodials were acquired convergently in weigeltisaurids and drepanosauromorphs. In addition, Senter (2004) considered that 'avicephalans' shared a shorter manus than humerus. However, this character state appears to be prevalent among Permo–Triassic archosauromorphs (Ezcurra 2016). Lastly, we concur with Pritchard *et al.* (2021) on the absence of the outer process on the proximolateral corner of metatarsal V in all 'avicephalans' (e.g. *Weigeltisaurus*, SAM-PK 2882; *Drepanosaurus*, Fig. 9). This process is indeed present in

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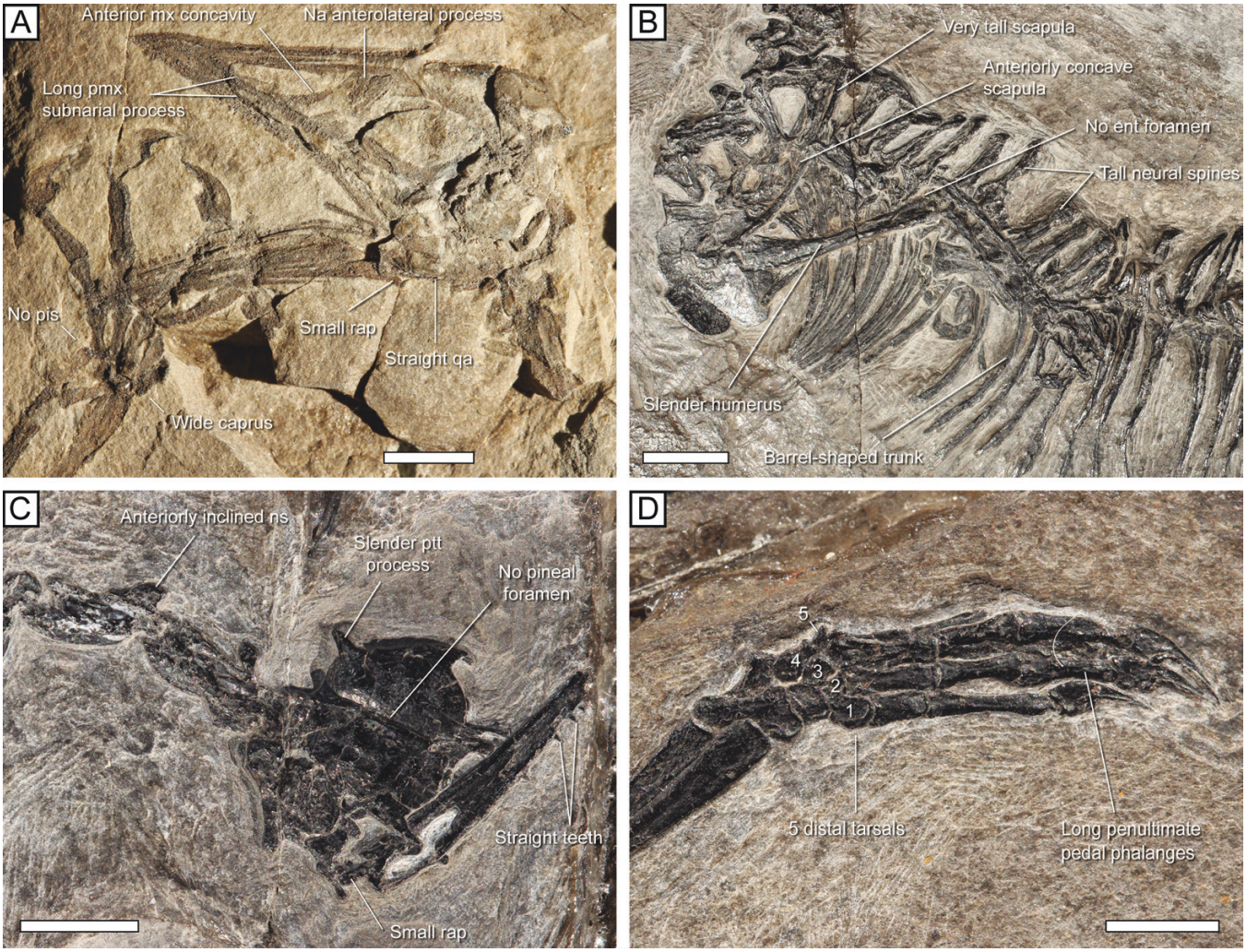

Figure 7. *Megalancosaurus preonensis* (Norian, Italy), selected anatomical regions. A, holotype MFSN 1769b, skull and left manus in left lateral view. B, MPUM 6008, anterior trunk region and left forelimb in left lateral view. C, MPUM 8437a, partial skull and mandible and articulated cervical vertebrae in mostly dorsal view. D, MPUM 8437a, right pes in dorsal view. Scale bars: 5 mm in A, C, D; 10 mm in B. Abbreviations: ent, entepicondylar; mx, maxilla; Na, nasal; ns, neural spine; pis, pisiform; pmx, premaxilla; ptt, posttemporal; qa, quadrate; rap, retroarticular process.

all younginiforms (e.g. *Hovasaurus*; Currie 1981), *Claudiosaurus* (Carroll 1981), early rhychocephalians (e.g. *Gephyrosaurus*; Evans 1981), *Protorosaurus* (Gottmann-Quesada and Sander 2009), most tanystropheids (e.g. *Macrocnemus*, *Tanystropheus*; Rieppel 1989, Nosotti 2007), *Trilophosaurus* (Spielmann *et al.* 2008), and early rhynchosaurs (Carroll 1976). Conversely, the outer process of metatarsal V is also absent in *Prolacerta* (Gow 1975) and in the allokotosaurs *Azendohsaurus*, *Pamelaria*, and *Teraterpeton* (Sen 2003, Nesbitt *et al.* 2015, Pritchard and Sues 2019).

In summary, most characters previously proposed as synapomorphies for 'Avicephala' appear very common among Permo–Triassic reptiles (characters S1, S2, S5, S6, P1, P2, P3, P4) and are coherent with many evolutionary scenarios, or are actually markedly different between weigeltisaurids and drepanosauromorphs (S3, S4). Few of these appear mostly restricted to weigeltisaurids and drepanosauromorphs (S7, S8) and are best interpreted as convergently acquired given the topology recovered herein. As suggested by Renesto *et al.* (2010), we believe that the similarities reflect convergent acquisitions of a fully arboreal lifestyle in weigeltisaurids and drepanosauromorphs. This is further supported by our constrained analysis C2 which shows that constraining the monophyly of 'Avicephala' is less parsimonious, requiring four additional steps, and results in much uncertainty about the relationships between 'avicephalans', lepidosauromorphs, and archosauromorphs.

The systematic position of weigeltisaurids

Our Maximum Parsimony analysis recovers weigeltisaurids together with the enigmatic neodiapsid *Claudiosaurus*, in a clade that constitutes the sister-group to Sauria (Fig. 4). This crownward position of both *Claudiosaurus* and weigeltisaurids contrasts with previously proposed topologies. Weigeltisaurids are indeed generally considered as stemward to younginiforms (Laurin 1991, Ezcurra *et al.* 2014, Pritchard and Nesbitt 2017, Pritchard *et al.* 2021), although some broader-scale analyses recover them more crownward than the latter (Müller 2004, Simões *et al.* 2018, 2022). There is much less consensus on

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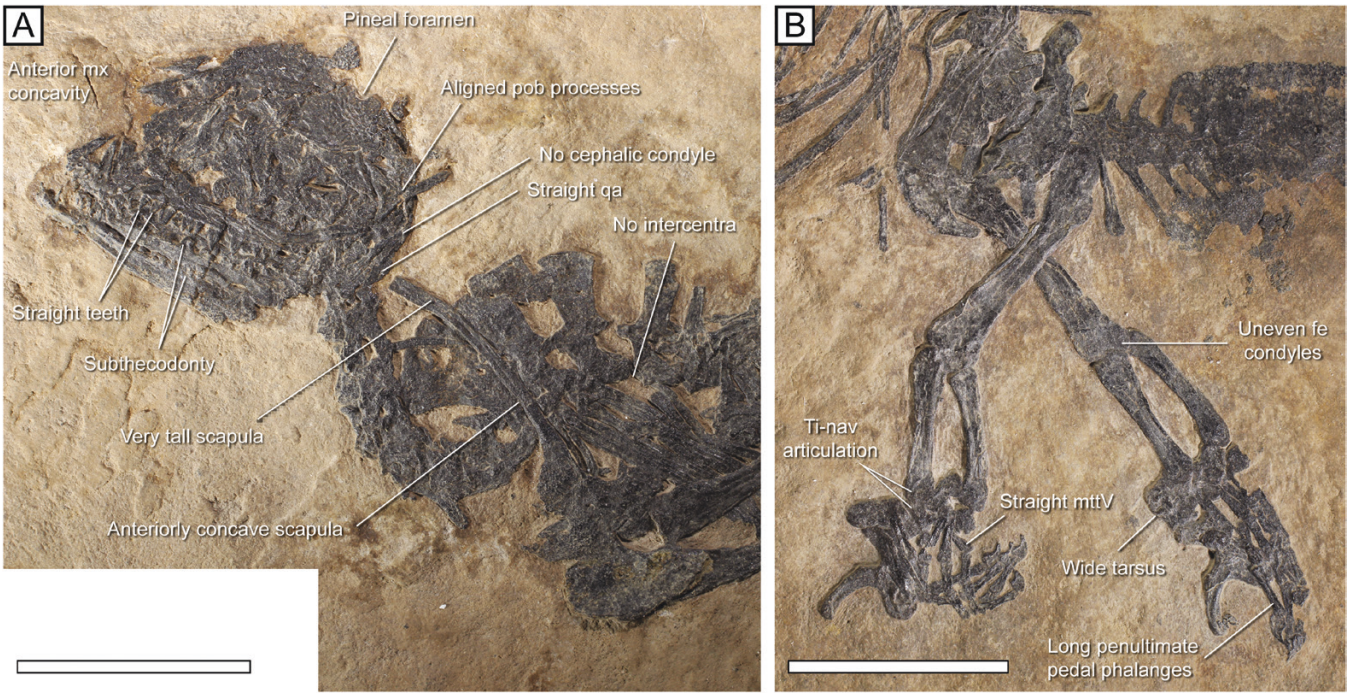

Figure 8. *Vallesaurus cenensis*, holotype MCSNB 4751 (Norian, Italy), skull, neck, and anterior trunk (A), and pelvis and legs (B) in mostly left lateral view. Scale bars: 1 cm. B. Abbreviations: fe, femur; mttV, metatarsal V; mx, maxilla; pob, postorbital; qa, quadrate; Ti-nav, tibionavicular.

Figure 9. *Drepanosaurus unguicaudatus*, holotype MCSNB 5728 (Norian, Italy). Scale bar: 5 cm. Abbreviations: fe, femur; mttV, metatarsal V.

the position of *Claudiosaurus*, which has alternatively been recovered as stemward (Pritchard and Nesbitt 2017, Ford and Benson 2020, Pritchard *et al.* 2021) or crownward (Müller 2004, Reisz *et al.* 2011, Hunt *et al.* 2023) to 'younginiforms' or even as the latter's sister-group (Simões *et al.* 2022) in recent analyses.

The crownward position of the (Weigeltisauridae + *Claudiosaurus*) clade as sister-group to Sauria is supported by eight unambiguous synapomorphies in our analysis (listed in the Supporting Information). Among these, *Claudiosaurus*, as well as all weigeltisaurids have an orbital exposure of the maxilla

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(Fig. 6A; Carroll 1981, Buffa *et al.* 2021), also seen in early lepidosauromorphs (e.g. *Paliguana*, *Clevosaurus*, *Marmoretta*; Chambi-Trowell *et al.* 2019, Ford *et al.* 2021, Griffiths *et al.* 2021). Both taxa also lack an anterior process of the quadratojugal (Fig. 6A; Carroll 1981, Bulanov and Sennikov 2010), which contrasts with the condition in *Youngina* (Gow 1975), but is common among non-archosauriform archosauromorphs (e.g. *Azendohsaurus*, *Macrocnemus*, *Mesosuchus*, *Prolacerta*; Fig. 6E; Dilkes 1998, Modesto and Sues 2004, Flynn *et al.* 2010, Miedema *et al.* 2020). Lastly, *Claudiosaurus* and *Weigeltisaurus* both have at least eight cervical vertebrae, which is recovered as an unambiguous synapomorphy of the (Weigeltisauridae + *Claudiosaurus*) clade here although *Coelurosauravus* has five (Carroll 1981, Buffa *et al.* 2022). Stem-saurian diapsids generally have a low count of around six cervicals, whereas saurians tend to have higher cervical counts (see Müller *et al.* 2010).

The (Weigeltisauridae + *Claudiosaurus*) clade recovered here is supported by six unambiguous synapomorphies (listed in the Supporting Information). However, as much of the anatomy of *Claudiosaurus* remains unclear, especially regarding the skull of this taxon (Carroll 1981), we stress that a revision of the anatomy of this taxon is warranted to confirm the putative shared synapomorphies with weigeltisaurids recovered here.

We thus provide evidence for a more crownward phylogenetic position of weigeltisaurids and *Claudiosaurus* than previously thought. However, in light of the low support values prevalent in the stem-saurian portion of our topology (Fig. 4), we stress that this interpretation remains tentative. In addition, several putative stem-saurian diapsids are poorly known and were thus provisionally excluded from our taxon sample. In particular, this includes the 'paliguanids' *Palaeagama* and *Saurosternon*, which Müller (2004) recovered as sister-group to weigeltisaurids. It is likely that these taxa, among others, could cast light on our understanding of this portion of the diapsid tree. However, a re-examination of the interrelationships of non-saurian diapsids is beyond the scope of this paper, which focuses on a re-examination of the relationship between weigeltisaurids and drepanosauromorphs.

Drepanosauromorphs as saurians

Our Maximum Parsimony analysis recovers drepanosauromorphs among saurian diapsids (Fig. 4). This contrasts with recent publications centered on drepanosauromorphs (Senter 2004, Pritchard *et al.* 2016, 2021, Pritchard and Nesbitt 2017), but conforms well with the work of Renesto *et al.* (2010), as well as several studies on saurian phylogeny (Dilkes 1998, Simões *et al.* 2018, 2022, Griffiths *et al.* 2021). Although we here support a position of drepanosauromorphs among saurians, as recovered by our main analysis (Fig. 4), we note that three additional steps are required to recover drepanosauromorphs outside the crown-group in our Analysis C1 (Fig. 5), highlighting some degree of lability regarding the position of Drepanosauromorpha.

Sauria is supported by 18 unambiguous synapomorphies in our analysis (listed in the Supporting Information). Based on these, the plesiomorphic saurian quadrate can be reconstructed as continuously concave posteriorly (character 113: state 1), bearing a lateral tympanic crest (112:1), and terminated dorsally by a cephalic condyle (116:1). This contrasts with the quadrate of stem-saurian diapsids, which lacks the cephalic condyle and tympanic crest and is posteriorly straight (e.g. *Petrolacosaurus*, *Youngina*; Gow 1975, Reisz 1981). None of these saurian character states are present in *Avicranium* (Fig. 1). The condition is harder to discern in the other drepanosauromorphs *Megalancosaurus* (MFSN 1769a, b) and *Vallesaurus* (MCSNB 4751) because they underwent severe postmortem crushing and/or remineralization, but neither has a posteriorly concave quadrate (Figs 6–8). The dorsal tip of the quadrate of *Vallesaurus* suggests that it lacks a cephalic condyle (Fig. 8). However, the quadrate of all drepanosauromorphs is very tall and inclined posterodorsally, extending ventral to the level of the maxillary tooth row, which contrasts with the shorter, more vertical quadrate of stem-saurian diapsids (e.g. *Youngina*; Gow 1975). Interestingly, the quadrate of the Italian drepanosauromorphs is very similar to that of coeval and similarly preserved pterosaurs such as *Eudimorphodon* (MCSNB 2888) or *Carniadactylus* (MPUM 6009; Dalla Vecchia 2014). While little is known at present about the evolution of the pterosaur quadrate, all known stapedes are extremely thin and cylindrical (Bennett 2001, Wang *et al.* 2023), indicating that these animals had a typical saurian tympanic ear despite apparently lacking a posterior concavity and tympanic crest on the quadrate, and in some cases, also a cephalic condyle (Prondvai and Ősi 2011). In this context, this similarity suggests that as in pterosaurs, the quadrate morphology of drepanosauromorphs may be apomorphic instead of plesiomorphic, likely linked to the similar inflation of the parietal skull roof in both taxa.

Other long-standing diagnostic characters of Sauria include the presence of a hooked metatarsal V and the absence of a distinct distal tarsal 5 in the pes (Goodrich 1916, Robinson 1975, Lee 1997; considered in characters 395 and 388 respectively here). Regardless of whether distal tarsal 5 fused to metatarsal V, making a compound element, or if distal tarsal 5 was lost independently to the hooking of metatarsal V (Joyce *et al.* 2013), no known Permo–Triassic saurian shows either a distal tarsal 5 nor a straight metatarsal V (Borsuk-Białynicka 2018). The hooked metatarsal V is commonly recovered as a synapomorphy of Sauria in phylogenetical analyses (e.g. Laurin 1991, Ezcurra *et al.* 2014), and is also recovered here (395:1). In this context, the pes of drepanosauromorphs appears problematic relative to other saurians. All known drepanosauromorph pedes have a clearly straight metatarsal V (Renesto and Paganoni 1995, Renesto *et al.* 2010, Renesto and Saller 2023), and that of *Drepanosaurus* (MCSNB 5728) and *Megalancosaurus* (MPUM 8437a) shows a distinct distal tarsal 5 (Figs 7–9). Based on our topology, drepanosauromorphs would be the only known unambiguous saurians to revert to these plesiomorphic states.

As seen in chameleons [arguably the best analogues for most drepanosauromorphs, (Steyer 2012, Castiello *et al.* 2016, Pritchard *et al.* 2023, Renesto and Saller 2023)], a fully arboreal locomotion can have an impact on mesopodial morphology. Chameleons indeed possess ossified tarsal elements that fail to ossify ancestrally in Sauria, such as distal tarsal 5, and also exhibit discrete proximal tarsals although these bones are fused ancestrally in chamaeleonids (Diaz and Trainor 2015). The peculiar tarsal morphology of chameleons has been attributed to an increased diversity of force vectors acting on the autopod aligned with the acquisition of a grasping arboreal lifestyle (Diaz and Trainor 2015). Similar changes have also been reported

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for small arboreal mammals, such as the silky anteater *Cyclopes* (Wood Jones 1953), which is often considered a good analogue for *Drepanosaurus* (Renesto *et al.* 2010, Steyer 2012, Pritchard *et al.* 2016). If drepanosauromorphs are indeed saurians, then their peculiar tarsus could be considered apomorphic rather than plesiomorphic, acquired in the context of arboreal locomotion.

Nevertheless, some drepanosauromorphs also share several characters that we recover as saurian synapomorphies, including: a small pineal foramen (95:1), present in *Vallesaurus* (Fig. 8A) but absent in *Avicranium* (Fig. 1) and *Megalancosaurus* (Fig. 7C); the absence of postparietals (97:1) in *Avicranium* (Fig. 1); a large retroarticular process (184:2) in *Avicranium* (Figs 1, 2), although much smaller in *Megalancosaurus* (Figs 6, 7) and *Hypuronector* (Colbert and Olsen 2001); a marked coronoid process (187:1), as in *Avicranium* (Figs 1, 2) and *Hypuronector* (Colbert and Olsen 2001), but much smaller in *Megalancosaurus* (MFSN 1769a, b; MPUM 8437a; Fig. 7); the absence of the pisiform in the carpus (331:1), as in *Megalancosaurus* (Fig. 7).

Drepanosauromorphs as archosauromorphs

Our main analysis recovers drepanosauromorphs as archosauromorphs (Fig. 4). Some drepanosauromorphs indeed exhibit characters recovered here as unambiguous synapomorphies of archosauromorphs (or pan-archosaurs, comprising here *Icarosaurus* and Archosauromorpha) among saurian diapsids (listed in the Supporting Information), such as: the absence of post-axial presacral intercentra (231:1, 252:1, discussed above, Fig. 8); the anterior inclination of the anterior cervical neural spines (245:1) as seen in *Avicranium* (Fig. 3) and in the Italian drepanosauromorphs (MCSNB 5728; MFSN 1769a, b; Fig. 7C); the tall dorsal neural spines (266:1) seen in all drepanosauromorphs (Figs 7–9; Berman and Reisz 1992, Colbert and Olsen 2001) except *Avicranium*, which does not preserve any dorsal vertebrae; the absence of an entepicondylar foramen (321:1), as seen in *Drepanosaurus* (MCSNB 5278), *Megalancosaurus* (MPUM 6008, 8437a; Fig. 8B), and *Vallesaurus* (MCSNB 4751).

Furthermore, we recover drepanosauromorphs crownward to the Late Permian *Protorosaurus* (Fig. 4). In our analysis, the clade comprising all archosauromorphs except *Protorosaurus* is supported by 11 unambiguous synapomorphies (listed in the Supporting Information), some of which are present in drepanosauromorphs.

These include, among others, the presence of a long subnarial process of the premaxilla (11:2), as well as a large premaxilla forming the majority of the rostrum anterior to the external naris (13:1). Such a long subnarial process of the premaxilla is currently recognized as a synapomorphy of non-*Protorosaurus* archosauromorphs (Ezcurra 2016, Spiekman *et al.* 2021), and the large relative size of the premaxilla was also proposed as a possible synapomorphy of these taxa (Ezcurra 2016). *Megalancosaurus* (MFSN 1769; Fig. 7A) and *Vallesaurus* (MCSNB 4751) show large premaxillae with subnarial processes, although that of *Vallesaurus* is shorter. Non-*Protorosaurus* archosauromorphs also show a tall dorsal process of the maxilla with a concave posterior margin (28:1), as recovered by other analyses (Spiekman *et al.* 2021). *Megalancosaurus* (MFSN 1769a, b), the only drepanosauromorph with a reasonably complete maxilla, also has a tall maxilla with a posterior concavity (Fig. 6B). All non-*Protorosaurus* archosauromorphs in our dataset share an articulation between the tibia and the navicular (383:1). This articulation is also preserved in some drepanosauromorphs, where the pes is sufficiently preserved (e.g. *Dolabrosaurus*, *Vallesaurus*; Fig. 8B; Renesto and Saller 2023), and has long been used as a character linking drepanosauromorphs with 'prolacertiform' archosauromorphs (Renesto and Binelli 2006).

Drepanosauromorphs as allokotosaurians

Our analysis recovers drepanosauromorphs inside Allokotosauria, as sister-group to Trilophosauridae (Fig. 4). This contrasts with the topologies obtained by those studies that recover drepanosauromorphs as archosauromorphs, whereby these reptiles represent early-diverging archosauromorphs, possibly related to tanystropheids (Dilkes 1998, Renesto *et al.* 2010, Simões *et al.* 2018, 2022, Griffiths *et al.* 2021). To our knowledge, a sister-group relationship between drepanosauromorphs and trilophosaurids has never been formally proposed before, which warrants a detailed discussion.

First, we recover allokotosaurians among Crocopoda, those archosauromorphs crownward to *Protorosaurus*, and tanystropheids, as in Ezcurra (2016). In our analysis, Crocopoda is supported by 14 unambiguous synapomorphies (listed in the Supporting Information), some of which are shared by drepanosauromorphs: a wide carpus relative to metacarpal IV (327:0), as seen in *Drepanosaurus*, *Megalancosaurus*, and *Vallesaurus* (Figs 7–9); the presence of a calcaneal tuber (379:1), as seen in *Drepanosaurus* (Fig. 9), *Dolabrosaurus* (Renesto and Paganoni 1995, Renesto and Saller 2023), and *Megalancosaurus* (MPUM 8437a); a metatarsal V at least half as long as metatarsal IV (393:0), as seen in all drepanosauromorphs with sufficiently preserved pedes. Some ambiguous synapomorphies recovered here for Crocopoda further support an inclusion of drepanosauromorphs, such as the presence of a subtemporal fossa extending over the postfrontal (70:1) as seen in *Avicranium* (Figs 1, 2, 6C), and the anterior concavity of the scapular blade (304:1) as seen in all drepanosauromorphs (Figs 7–9) except *Hypuronector* (Colbert and Olsen 2001). However, these synapomorphies must remain ambiguous due to the incompleteness of Triassic archosauromorph material resulting in some missing data in our scoring.

In contrast, we note some unambiguous synapomorphies of Crocopoda that are absent in drepanosauromorphs, such as: dorsoventrally tall posttemporal process of the parietal (93:1), which is low in *Avicranium* (Figs 1, 2) and *Megalancosaurus* (Fig. 7C); a thecodont tooth implantation (207:2), whereas the dentition in *Vallesaurus* is best interpreted as subthecodont (Fig. 8A) while that of *Hypuronector* (Colbert and Olsen 2001) and *Megalancosaurus* (MPUM 8437a) may either be pleurodont or subthecodont. Lastly, Crocopoda are here diagnosed by the presence of a concavoconvex articulation between the proximal tarsals, with a concavity on the astragalus (375:2). However, this character cannot be scored for any drepanosauromorph due to their state of preservation (e.g. *Drepanosaurus*, Fig. 9).

Among crocopods, Allokotosauria is supported by 11 unambiguous synapomorphies, all of which are compatible with an inclusion of drepanosauromorphs: anterodorsal margin of maxilla concave (24:1), as seen *Megalancosaurus* and *Vallesaurus* (Figs 7A, 8A); obtuse angle between posterior and ventral processes

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of postorbital (72:1), as in *Vallesaurus* (MCSNB 4751) but contrary to *Avicranium* where these processes are set at a right angle to each other (Figs 1, 2); craniomandibular joint below level of maxilla alveolar margin (110:1, discussed above); palatine teeth relatively large (126:1), which cannot be scored in any drepanosauromorph because no palatine bones are preserved; long axis of parabasisphenoid anterodorsal (161:1), as in *Avicranium* (Figs 1, 2); anterior portion of dentary turned ventrally (190:2), as in *Hypuronector* (Colbert and Olsen 2001) but contrary to *Megalancosaurus* and *Vallesaurus* (MCSNB 4751; MFSN 1769a, b) where the dentary is mostly horizontal; posterolaterally curved caudal transverse processes (279:0), as in *Hypuronector* (Colbert and Olsen 2001), but contrary to *Dolabrosaurus* (Berman and Reisz 1992), as well as *Drepanosaurus* and *Megalancosaurus*, where these processes extend laterally (MCSNB 5728; MPUM 6008, 8437b); reduced gastral basket with well separated gastralia (287:1), in line with the apparent absence of gastralia in all of the otherwise exceptionally preserved Italian drepanosauromorphs (e.g. *Drepanosaurus*, *Vallesaurus*; MCSNB 4751, 5728; Fig. 9); uneven distal femoral condyles (363:0), as in *Drepanosaurus* and *Vallesaurus* (Figs 8, 9) and as described for isolated drepanosauromorph femorae (Pritchard *et al.* 2023); wide tarsus relative to metatarsal IV (370:0), as in all drepanosauromorphs where the pes is preserved (Figs 7–9); absence of outer process on metatarsal V (394:0; discussed above).

Lastly, the sister-group relationship between trilophosaurids and drepanosauromorphs in our maximum parsimony analysis is supported by 10 unambiguous synapomorphies, discussed below.

Regarding cranial synapomorphies, all trilophosaurids have a skull that is taller than broad in the antorbital region (2:1; Sues 2003, Spielmann *et al.* 2008). Among non-archosauriform Permo–Triassic diapsids, this character is only shared with the drepanosauromorphs *Megalancosaurus* and *Vallesaurus* (Figs 6–8), the only drepanosauromorphs for a which a subcomplete rostrum is known. The skull of *Avicranium* also appears to be tall, but none of the bones of the rostrum are preserved, precluding a definite statement (Figs 1, 2). *Trilophosaurus* has a distinct anterolateral process of the nasal that separates the maxilla from the dorsal external narial margin (46:1; Spielmann *et al.* 2008), and a similar process can also be seen in *Megalancosaurus* (Figs 6, 7). As noted by Renesto and Dalla Vecchia (2005), this process superficially resembles that of early pterosaurs, the only Triassic reptiles to show this morphology of the rostrum. *Trilophosaurus buettneri* and '*Trilophosaurus jacobsi*' (scored as *Spinosuchus caseanus* in our matrix, following the synonymy suggested by Nesbitt *et al.* 2015) both lack a pineal foramen (95:1; Spielmann *et al.* 2008), as is the case in *Avicranium* (Figs 1, 2) and *Megalancosaurus* (Fig. 7C). This character state is here recovered as an unambiguous synapomorphy, with a reversal in *Vallesaurus* (Fig. 8A) which has a pineal foramen. *Trilophosaurus* and *Teraterpeton* both show slender paroccipital processes relative to the anteroposteriorly flattened ones of other crocopods (159:0; Sues 2003, Wilson *et al.* 2022), and this is also the case in *Avicranium* (Figs 1, 2). The dorsomedial processes of the exoccipital are absent or incipient in *Trilophosaurus*, in which the bone is mostly columnar (177:0; Wilson *et al.* 2022), similar to that of *Avicranium*, but contrasting with the condition in other crocopods. However, this character cannot be assessed in several crocopods where the exoccipital and opisthotic are fused (e.g. *Azhendohsaurus*; Flynn *et al.* 2010). Lastly, the teeth of *Megalancosaurus* and *Vallesaurus* (Figs 7, 8), and *Hypuronector* (Colbert and Olsen 2001) are not recurved but straight (211:0), as in all trilophosaurids (Sues 2003, Spielmann *et al.* 2008), although straight marginal teeth are also present in the allokotosaurs *Pamelaria* and *Shringasaurus* (Sen 2003, Sengupta and Bandyopadhyay 2022).

Regarding the postcranium, the cervical ribs appear fused to the vertebral costal facets in *Avicranium* (248:1; Fig. 3), as noted by Pritchard and Sues (2019) who also report this only in *Trilophosaurus* and *Teraterpeton*. All drepanosauromorphs show a strong curvature in the proximal half of the dorsal ribs, giving these reptiles a barrel-shaped trunk (272:0; Figs 7, 9; Renesto *et al.* 2010). A similar curvature of the dorsal ribs is only found in *Teraterpeton* (Sues 2003) and possibly *Trilophosaurus* (Gregory 1945) among non-archosauriform archosauromorphs. As discussed above, *Trilophosaurus* and *Teraterpeton* have tall and slender scapular blades compared to other crocopods (299:2; Sues 2003, Spielmann *et al.* 2008), and this is similar to the extremely tall and thin scapular blades of drepanosauromorphs (Figs 7–9). Lastly, the penultimate pedal phalanges are longer than the preceding ones in *Trilophosaurus* (401:1; Spielmann *et al.* 2008), the only trilophosaurid with complete pedal digits, as is only the case in the drepanosauromorphs *Drepanosaurus*, *Megalancosaurus*, and *Vallesaurus* (Figs 7–9) among non-archosauriform archosauromorphs. However, it should be noted that an increase in length of the penultimate phalanges is widespread among arboreal tetrapods, in particular in those taxa capable of claw-based clinging (Fröbisch and Reisz 2009).

In light of the numerous synapomorphies listed above, the moderate node support value recovered for the clade comprising Trilophosauridae and Drepanosauromorpha in our main analysis (Fig. 4), and the additional steps required to recover alternative hypotheses (Fig. 5), we are inclined to support a sister-group relationship between these two taxa. Nevertheless, as stressed by Renesto and Binelli (2006) and Renesto *et al.* (2010), the large amount of missing data in drepanosauromorphs resulting from their preservation still obscures the phylogenetic position of drepanosauromorphs. This is particularly striking as only few additional steps are required to recover alternative topologies (Fig. 5), highlighting some degree of lability in the phylogenetic positions of Drepanosauromorpha. The hypothesis presented herein may thus be tested by future findings of three-dimensionally preserved and articulated drepanosauromorph specimens.

In this context, the yet unpublished drepanosauromorph from the Nugget Sandstone of northeastern Utah (Engelmann *et al.* 2012, Chure *et al.* 2013, 2015, Britt and Chure 2016, Britt *et al.* 2019) may help fill this gap in our understanding of drepanosauromorph anatomy and phylogenetic relationships. In particular, the mention of 'large maxillary and dentary teeth reminiscent of *Trilophosaurus*' (Chure *et al.* 2013), if confirmed, could provide unequivocal evidence of a close relationship between trilophosaurids and drepanosauromorphs, as recovered by our analysis. The multicuspid tooth morphology of *Trilophosaurus* is indeed unique among Permo–Triassic diapsids, therefore allowing for the identification of this taxon based only on dental material (Mueller and Parker 2006,

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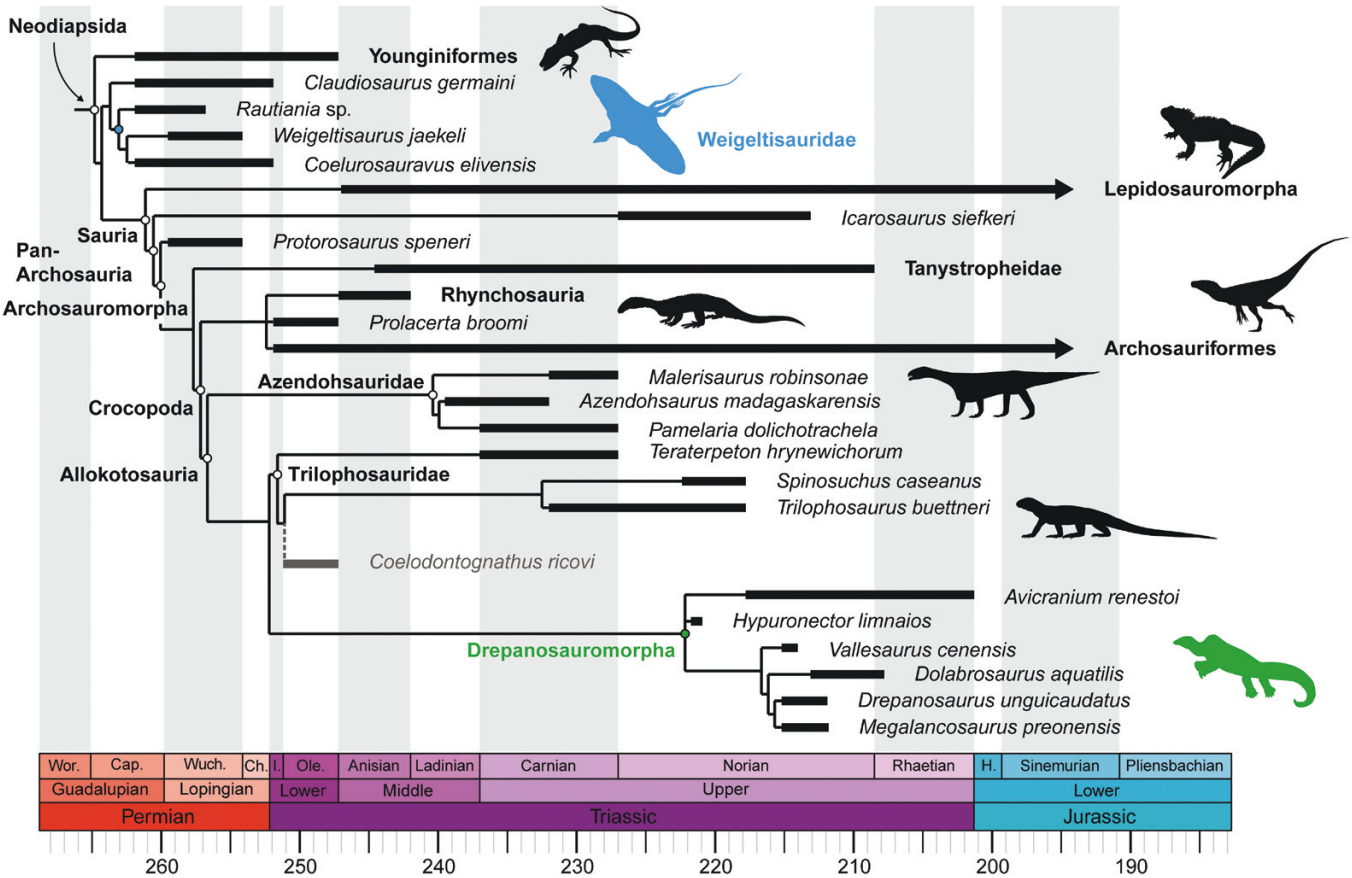

Figure 10. Time-calibrated simplified strict consensus tree of main analysis (12 MPTs of 2600 steps; L = 2612 steps; CI = 0.2024; RI = 0.6018) focused on Neodiapsida. Black bars indicate stratigraphic distribution of taxa (ages given in the Supporting Information). Dark grey dotted lines indicate the position of *Coelodontognathus ricovi*, the earliest trilophosaurid, according to Sues and Schoch (2023) as this taxon is not included in our analysis. Internal branch length minimally 500 kya for clarity. Silhouettes (top to bottom, *Youngina*, *Coelurosauravus*, *Sphenodon*, *Herrerasaurus*, *Prolacerta*, *Azendohsaurus*, *Trilophosaurus*, *Drepanosaurus*) from the PhyloPic database (public domain). Abbreviations: Cap., Capitanian; Ch., Changhsingian; H., Hettangian; I., Induan; Ole., Olenekian; Wor., Wordian; Wuch., Wuchiapingian.

Kligman *et al.* 2020, Sues *et al.* 2021). Similar teeth are found in other trilophosaurids (Chambi-Trowell *et al.* 2022, Sues and Schoch 2023), but have yet to be found in other Permo–Triassic diapsids. Although markedly different from the teeth of *Trilophosaurus*, the early-diverging trilophosaurids *Teraterpeton*, *Anisodontosaurus*, and *Variodens* also have distinctive dentitions, comprising occluding upper and lower teeth in the former taxon (Sues 2003), and heterodont dentition in the latter taxa (Chambi-Trowell *et al.* 2022, Foffa *et al.* 2022). In contrast, we note that the drepanosauromorphs *Hypuronector* (Colbert and Olsen 2001), *Megalancosaurus* (MPUM 8437a), and *Vallesaurus* (MCSNB 4751) lack *Trilophosaurus*-like multicuspid teeth, or any trace of the peculiar tooth morphologies of *Teraterpeton*, *Anisodontosaurus*, or *Variodens*, which hints at a complex dental evolutionary history of drepanosauromorphs if this is confirmed to be the case in the Nugget Sandstone drepanosauromorph.

Evolutionary implications

The topology recovered herein, whereby 'Avicephala' is paraphyletic, with weigeltisaurids as stem-saurian diapsids and drepanosauromorphs as sister-group to trilophosaurids has several evolutionary implications.

First, the paraphyly of 'Avicephala' results in one less non-saurian diapsid lineage crossing the Permo–Triassic Boundary (PTB) because weigeltisaurids are unknown beyond the Late Permian (Fig. 10). *Wapitisaurus*, a purported weigeltisaurid from the Early Triassic of British Columbia, Canada (Brinkman 1988), has recently been redescribed as a thalattosauroid marine reptile (Bastiaans *et al.* 2023), thus removing the only reported occurrence of weigeltisaurids in the Triassic. As a result, Younginiformes (here recovered as monophyletic) are the only non-saurian diapsid lineage to cross the PTB (Fig. 10; Ketchum and Barrett 2004).

Second, the recovery of drepanosauromorphs among archosauromorphs significantly reduces the ghost lineage at the base of the group. The oldest North American drepanosauromorph remains, namely *Hypuronector* from the Ewin Creek and Nursery members of the Lockatong Formation of New Jersey and isolated remains from the *Placerias* Quarry of the Bluewater Creek Formation of Arizona, place the first known drepanosauromorph occurrences in the late early Norian (late Lacian, see Supporting Information). Drepanosauromorph material from the Colorado City Formation of Texas might be slightly older (latest Carnian–earliest Norian) but their age is

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not as well constrained (Pritchard *et al.* 2023). Thus, under the 'avicephalan' hypothesis, which requires four additional steps in our analysis C2 (Fig. 5), this ghost lineage would extend at least from the Norian to the Wuchiapingian (well-dated occurrence of *Weigeltisaurus*), or possibly to the late Capitanian (conservative ages for *Coelurosauravus* and *Rautiania*; Fig. 10).

The oldest known unambiguous trilophosaurid is *Coelodontognathus ricovi* from the Olenekian of southwestern Russia (Sues and Schoch 2023). Thus, a sister-group relationship between trilophosaurids and drepanosauromorphs would imply a ghost lineage ranging at least from the Olenekian to the Norian, which reduces it by at least *c.* 8 million years compared to the 'avicephalan' hypothesis (Fig. 10). More importantly, this reduced ghost lineage does not necessarily extend across the PTB. While all major archosauromorph clades, including Allokotosauria, were already present by the end of the Permian, as implied by the presence of more crownward archosauriforms (Ezcurra *et al.* 2014), the early evolution of allokotosaurs prior to *C. ricovi* remains unknown. It is thus still unclear whether azendohsaurids, trilophosaurids, and drepanosauromorphs diversified before or after the PTB. From a palaeogeographical perspective, both trilophosaurids and drepanosauromorphs are restricted to Laurasia (Renesto *et al.* 2010, Pritchard and Nesbitt 2017, Kligman *et al.* 2020, Chambi-Trowell *et al.* 2022, Foffa *et al.* 2022, Sues and Schoch 2023), whereas azendohsaurids had a near-Pangean distribution (Nesbitt *et al.* 2021). However, given the very poor Early to Middle Triassic fossil record for trilophosaurids, with only one unambiguous taxon reported from the Early Triassic of southwestern Russia (Sues and Schoch 2023), one taxon and an isolated tooth from the Middle Triassic of North America (Sues *et al.* 2021, Foffa *et al.* 2022), and one taxon from the Middle Triassic of Germany (Sues and Schoch 2023), it remains unclear whether trilophosaurids and drepanosauromorphs originated in Western or Eastern Pangea.

Lastly, *Trilophosaurus* is generally considered as an arboreal reptile based on the morphology of its ungual phalanges (Gregory 1945, Spielmann *et al.* 2005, 2008), and the oldest and first-diverging drepanosauromorphs also show anatomical features indicative of an arboreal lifestyle (Renesto *et al.* 2010, Castiello *et al.* 2016, Pritchard and Nesbitt 2017). Facultative to obligatory climbing has been suggested for some non-archosauriform archosauromorphs based on their gracile lizard-like anatomy (e.g. *Prolacerta*; Gow 1975), including in the earliest-diverging azendohsaurid *Malerisaurus* (Chatterjee 1980), but these interpretations remain equivocal because none of these taxa exhibit evident anatomical features for climbing. Similarly, the available fossil material does not allow for an assessment of the ecology of the oldest trilophosaurids, although Sues and Schoch (2023) considered facultative climbing possible. Furthermore, the first-diverging trilophosaurid *Teraterpeton* does not show any anatomical features suggestive of an arboreal lifestyle and has been tentatively interpreted as a ground-dwelling scratch-digger, pending further study of its musculoskeletal anatomy (Pritchard and Sues 2019). Incidentally, a similar ecology has also been proposed for some stratigraphically younger drepanosauromorphs (*Ancistronynchus*, *Skybalonyx*; Jenkins *et al.* 2020). In this context, it is unclear whether the common ancestor to trilophosaurids and drepanosauromorphs could have been a facultative climber, which would not necessarily be visible in its anatomy (Sues and Schoch 2023). Thus, it remains unknown whether the clade recovered herein comprises one or two evolutionary pathways towards an arboreal lifestyle in Triassic archosauromorphs.

CONCLUSION

The re-examination of well-preserved drepanosauromorph specimens, in particular the previously published surface models of the holotype and only known specimen of *Avicranium renestoi* from the Norian of North America, results in a significant re-interpretation and reconstruction of the cranial anatomy of this taxon. We confirm that *Avicranium* has a bird-like inflated skull roof, but we demonstrate that none of the rostrum bones and very little of the palate bones are actually preserved in this specimen. It thus cannot be said that this taxon was edentulous, as was previously suggested. Furthermore, our reconstruction shows several previously unidentified similarities with other drepanosauromorphs, including a posterodorsally sloping skull with a ventrally positioned craniomandibular joint. In addition, we suggest that several of the purported plesiomophic traits of *Avicranium* such as the presence of a notochordal pit on the occipital condyle, or the lack of well-developed basal tubera, may also be interpreted as incomplete ossification due to immaturity, although this remains equivocal.

Our parsimony analysis based on an entirely new morphological phylogenetic dataset of Permo–Triassic diapsids recovers Weigeltisauridae as stem-saurian diapsids, as suggested by numerous other studies, and Drepanosauromorpha as sister-group to Trilophosauridae among allokotosaurians archosauromorphs. Thus, our analysis indicates that 'Avicephala', which was thought to be the clade that comprises weigeltisaurids and drepanosauromorphs, is paraphyletic. A close relationship between drepanosauromorphs and trilophosaurids is recovered here for the first time, as is supported by several cranial and postcranial synapomorphies. The phylogenetic position of drepanosauromorphs recovered here significantly reduces the ghost lineage at the base of drepanosauromorphs that now extends at least from the Olenekian to the Norian, and not necessarily across the Permian–Triassic boundary. However, much remains unknown regarding the early evolutionary of drepanosauromorphs, and allokotosaurs in general, as well as the evolution of arboreality in archosauromorph reptiles.

SUPPLEMENTARY DATA

Supplementary data is available at *Zoological Journal of the Linnean Society* online.

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DATA AVAILABILITY

The data underlying this article are available in the article and in its online supplementary material.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

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