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# Basicranial evidence suggests picrodontid mammals are not stem primates

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The Picrodontidae from the middle Palaeocene of North America are enigmatic placental mammals that were allied with various mammalian groups but are generally now considered to have close affinities to paromomyid and palaechthonid plesiadapiforms based on proposed dental synapomorphies. The picrodontid fossil record consists entirely of dental and gnathic remains except for one partial cranium of *Zanycteris paleocenus* (AMNH 17180). Here, we use µCT technology to unveil previously undocumented morphology in AMNH 17180, describe and compare the basicranial morphology of a picrodontid for the first time, and incorporate these new data into cladistic analyses. The basicranial morphology of *Z. paleocenus* is distinct from plesiadapiforms and shares similarities with the Palaeogene Apatemyidae and Nyctitheriidae. Results of cladistic analyses incorporating these novel data suggest picrodontids are not stem primates nor euarchontan mammals and that the proposed dental synapomorphies uniting picrodontids with plesiadapiforms and, by extension, primates evolved independently. Results highlight the need to scrutinize proposed synapomorphies of highly autapomorphic taxa with limited fossil records.

## 1. Background

Plesiadapiforms are a likely non-monophyletic group of placental mammals known from the Palaeocene and Eocene of North America, Europe, and Asia that have been regarded as close fossil relatives of crown clade primates based mostly on aspects of dental morphology [1–5]. Results of recent phylogenetic analyses support plesiadapiforms as euarchontan mammals and either support members of this group as stem primates [6–10], stem colugos or stem primatomorphans (Primates + Dermoptera) [11,12].

The Picrodontidae consists of three genera (*Picrodus*, *Zanycteris*, and *Draconodus*) known from the Torrejonian and Tiffanian North American Land Mammal Ages (NALMA) of western North America [13–15]. Due to the autapomorphic dental morphology of picrodontids and the lack of an obvious sister group, researchers have allied picrodontids with caenolestid marsupials [16], chiropterans [17], insectivorans [18], and most recently primates (*sensu lato*) [13]. Over the past half-century, picrodontids have often been viewed as plesiadapiforms and more recently belonging to the superfamily Paromomyoidea (Paromomyidae + Palaechthonidae + Picrodontidae) based on the shared presence of dental features such as a strong postprotocingulum and expanded distolingual basin of the upper molars (figure 1*a*) [5,15,19]. However, picrodontid dental morphology differs significantly from plesiadapiforms (e.g. greatly enlarged M1/m1 with a decrease in molar area to M3/m3, absence of m3 hypoconulid) [13,15]. Because the picrodontid fossil record consists only of autapomorphic dentitions, except for one partial cranium, they are usually excluded from cladistic analyses aimed at assessing primate supraordinal relationships and/or interrelationships among plesiadapiforms. Here, we use µCT scanning technology to describe

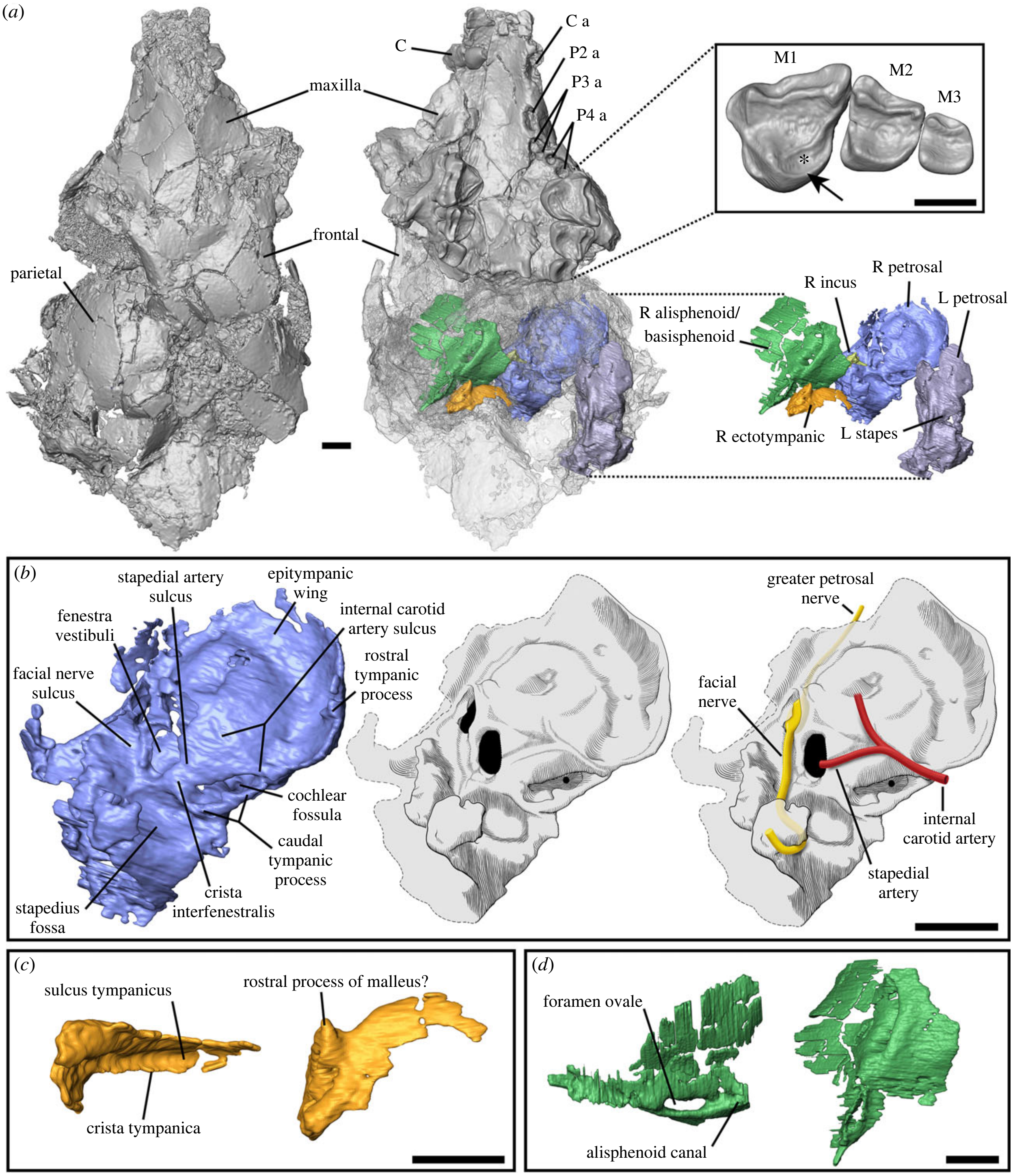


**Figure 1.** Three-dimensional models derived from µCT scan data of *Zanycteris paleocenus* (AMNH 17180) with descriptions and orientations of skeletal elements organized from left to right. (*a*) Cranium in dorsal and ventral views with basicranial region transparent showing original position of digitally extracted bones. Box illustrates left upper molars rotated into occlusal view with distolingual basin (asterisk) and postprotocingulum (arrow). (*b*) Three-dimensional model of right petrosal in ventral view, composite line drawing incorporating preserved morphology from right and left petrosal, and composite line drawing with major neurovascular structures; (*c*) R partial ectotympanic in oblique posterior and ventral view; (*d*) R partial alisphenoid/basisphenoid in lateral and ventral view. Scale bars, 1 mm. Abbreviations: C = upper canine; C a = upper canine alveolus; M = upper molar; P a = upper premolar alveolus.

and compare previously undocumented morphology from the only known partial cranium of a picrodontid and include these novel data in cladistic analyses to assess the phylogenetic affinities of the Picrodontidae.

## 2. Material and methods

The partial cranium of *Z. paleocenus* (AMNH 17180), from the late Tiffanian (Ti-4) Mason Pocket locality in the San Juan Basin of Colorado, includes two separate cranial portions that were submerged in plaster: a rostral portion including the palate and right C, M1–3 and left M1–3 and a caudal portion that includes several partial basicranial elements, including left and right petrosals, right ectotympanic, right incus, left stapes, and part of the right sphenoid complex (figure 1*a*). Both portions were µCT scanned at the Microscopy and Imaging Facility of the American Museum of Natural History (AMNH), and µCT scan data were manually segmented using the segmentation tool in Avizo 9.0.1. Comparisons were made to plesiadapiforms, other

Palaeogene mammals, extant euarchontans, and other placental mammals (electronic supplementary material, SI1).

Maximum parsimony analyses were performed in TNT (v. 1.5) [20] using a character–taxon matrix (electronic supplementary material, SI3) that was modified from previously published versions [8,21,22] to include three picrodontids, one palaechthonid, one microsyopid, and one apatemyid (electronic supplementary material, SI2). Unconstrained and constrained analyses were performed generally following previous methods [22] and well-supported supraordinal groups in molecular-based phylogenetic analyses were constrained (Afrotheria, Xenarthra, Laurasiatheria, Euarchontoglires) [23–26].

## 3. Basicranial descriptions and comparative morphology

### (a) Petrosal

The petrosals of *Z. paleocenus* possess a ventrally projecting rostral tympanic process arising from the medial aspect of the rounded promontorium that is confluent with an anteriorly projecting epitympanic wing (figure 1*b*). The caudal tympanic process is posterior to and roughly level in its ventral extent to the aperture of the cochlear fossula and meets the crista interfenestralis via a curved ridge. Two subequal sulci on the surface of the promontorium correspond to the stapedial and promontory branches of the internal carotid artery, which enters the middle ear in a posteromedial position. There is an open sulcus for the facial nerve, which exits the middle ear space via the stylomastoid notch.

Unlike *Z. paleocenus*, all non-microsyopid plesiadapiforms possess a posterior septum that shields the aperture of the cochlear fossula in ventral view with additional septa originating from the promontorium (figure 2, electronic supplementary material, figure SI4) [9,27–30]. *Zanycteris paleocenus* is like the carpolestid *Carpolestes simpsoni* in having an unreduced internal carotid artery with a posteromedial entrance into the middle ear [29], but differs from other non-microsyopid plesiadapiforms, which have a reduced internal carotid artery that enters the middle ear in a more posterolateral position [9,27,28,30]. *Zanycteris paleocenus* is like micromomyid plesiadapiforms in exhibiting an open sulcus for the facial nerve [9], but differs from other non-microsyopid plesiadapiforms, which enclose the facial nerve within a bony canal [27,28,30,31].

Microsyopids have long been considered distinct from non-microsyopid plesiadapiforms in their petrosal morphology [32–34]. Overall, microsyopids are like *Z. paleocenus* in exhibiting a posteromedial position for the internal carotid artery in which both the stapedial and promontorial branches are preserved, an open sulcus for the facial nerve, and the absence of an auditory bulla derived from the petrosal [7]. However, microsyopids differ from *Z. paleocenus* in lacking a well-developed, ventrally projecting rostral tympanic process that is confluent with an epitympanic wing and a well-developed caudal tympanic process that forms a complete rim around the aperture of the cochlear fossula (figure 2).

Outside Euarchonta, *Z. paleocenus* shares basicranial similarities with *Labidolemur kayi*, an apatemyid known from the late Palaeocene of North America that has been interpreted as a basal member of Euarchontoglires based on cladistic results [7]. Like *Z. paleocenus*, *L. kayi* exhibits an open sulcus for the internal carotid artery that enters the middle ear in a posteromedial position, an open sulcus for the facial nerve, and a caudal tympanic process that forms a rim around the aperture of the cochlear fossula (figure 2). However, the rostral tympanic process and epitympanic wing of *L. kayi* are much less developed than that of *Z. paleocenus*.

*Zanycteris paleocenus* also shares basicranial similarities with the Nyctitheriidae, a family of small-bodied insectivorous mammals known from the Palaeogene of North America, Europe, and Asia that has been supported as a member of Euarchonta [35] or Lipotyphla [22]. Like *Z. paleocenus*, nyctitheriids have an open sulcus for an unreduced internal carotid artery that enters the middle ear in a posteromedial position, an open sulcus for the facial nerve, and a prominent caudal tympanic process that forms a rim around the aperture of the cochlear fossula and meets the crista interfenestralis via a curved ridge (figure 2) [22]. However, the rostral tympanic process and epitympanic wing of nyctitheriids are not as prominent as those of *Z. paleocenus*.

### (b) Ectotympanic

The partial right ectotympanic of *Z. paleocenus*, which preserves the anterior crus, has the shape of a ring with some lateral expansion (figure 1*c*), like that of several groups including nyctitheriids [22], apatemyids [7], and extant lipotyphlans [36,37]. Unlike that of euarchontans, *Z. paleocenus* does not exhibit a simple ring-like element (i.e. no lateral expansion) such as that in lemuriform primates [36], treeshrews [38], micromomyids [9], and paromomyids [28] (but see [27]), it lacks bony struts on the ventral surface to fuse to the lateral bullar wall as in plesiadapids [30], and it is not greatly expanded to form a significant component of the auditory bulla as in colugos [39,40].

### (c) Auditory bulla composition

Current evidence suggests a limited contribution of the petrosal, either from the rostral or caudal tympanic processes in the tympanic floor of *Z. paleocenus*. Therefore, *Z. paleocenus* is distinct from that of crown primates and that which has been inferred for micromomyid, carpolestid, and plesiadapid plesiadapiforms [9,29,30] in lacking a complete bulla derived from the petrosal. The absence of a large entotympanic element and associated articular surfaces on the petrosal makes *Z. paleocenus* distinct from that of treeshrews [38] and paromomyid plesiadapiforms [27,28], which possess an entotympanic bulla. The ectotympanic does not expand medial to the crista tympanica, suggesting that the ectotympanic did not entirely floor the middle ear space like the condition found in lipotyphlans [36,37], apatemyids [7], and nyctitheriids [22]. Given the lack of evidence for other bullar elements, the ectotympanic of *Z. paleocenus* appears to retain the reconstructed primitive condition for Eutheria of not being covered by an auditory bulla [41,42]. See the electronic supplementary material for more details of the basicranium.

## 4. Phylogenetic results

Phylogenetic results do not support Picrodontidae within Euarchonta and instead support Picrodontidae as the sister taxon to the apatemyid *L. kayi* (figure 2). The strict consensus of the unconstrained cladistic analysis recovers a monophyletic Euarchonta that is sister to a broad clade containing lipotyphlans, afrosoricids, nyctitheriids, and picrodontids as

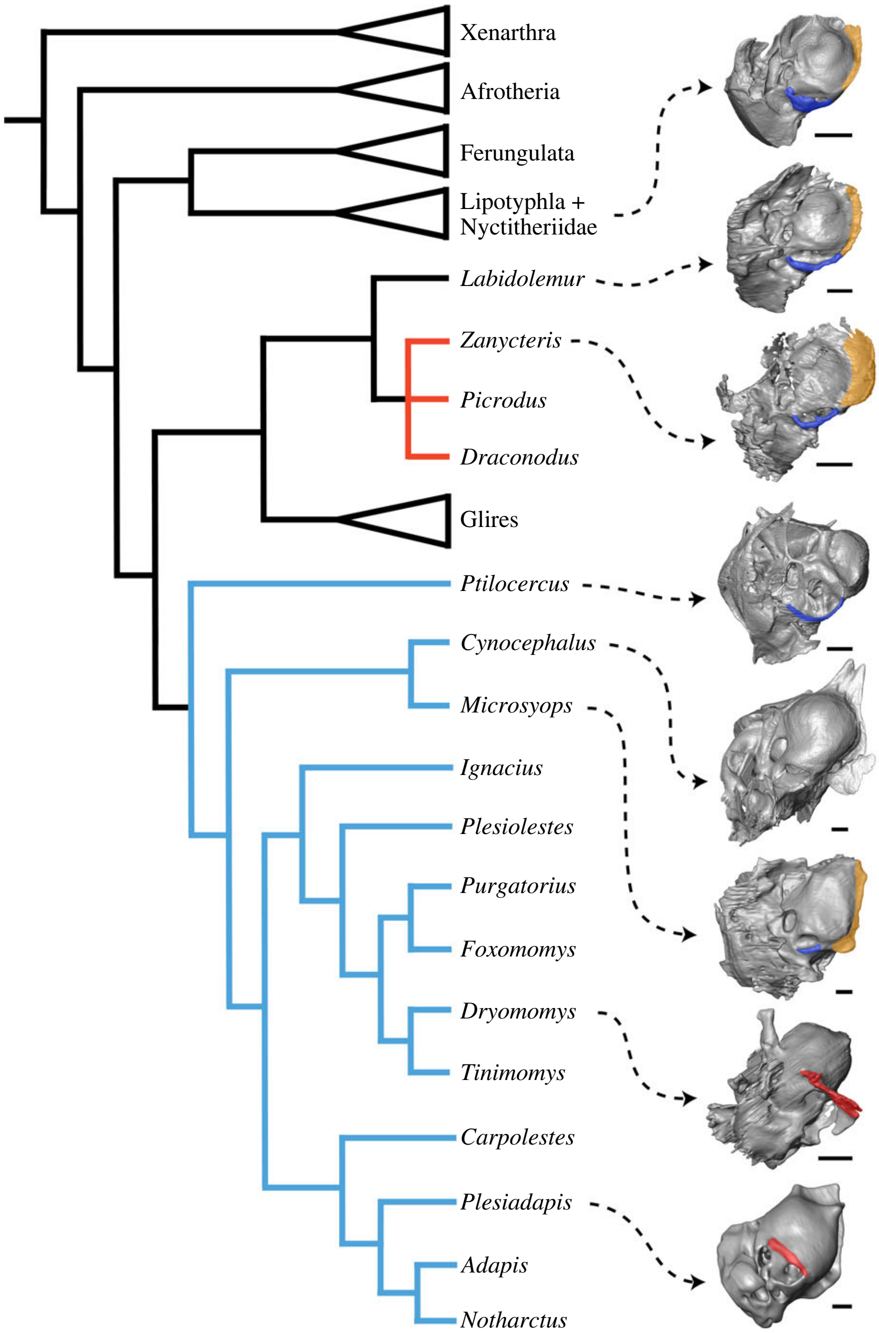


**Figure 2.** Hypothesis of evolutionary relationships of *Zanycteris paleocenus* and other picrodontids among eutherian mammals. Simplified strict consensus resulting from cladistic analysis forcing the monophyly of Afrotheria, Xenarthra, Laurasiatheria, and Euarchontoglires. See electronic supplementary material for full strict consensus tree. Three-dimensional models of petrosals illustrated to the right are, from top to bottom, Nyctitheriidae sp. (UM 85176), *Labidolemur kayi* (USNM 530208), *Zanycteris paleocenus* (AMNH 17180), *Ptilocercus lowii* (USNM 481107), *Cynocephalus volans* (FMNH 56521), *Microsyops annectens* (UW 12362), *Dryomomys szalayi* (UM 41870), *Plesiadapis tricuspidens* (MNRH BR 17418). *Zanycteris paleocenus* and other picrodontids (red) are not recovered within a monophyletic Euarchonta (blue) which includes all plesiadapiforms. Highlighted features of petrosals illustrate comparisons among taxa including a caudal tympanic process (blue), rostral tympanic process (orange), and posterior septum (red). Note that the plesiadapiforms *Dryomomys* and *Plesiadapis* have posterior septa which are absent in *Z. paleocenus*. Scale bars, 1 mm.

sister to *L. kayi* (electronic supplementary material, figure SI1). In contrast, the strict consensus of the constrained cladistic analysis forcing Afrotheria, Xenarthra, Laurasiatheria, and Euarchontoglires supports a monophyletic Euarchonta that is sister to a clade comprised of Glires and picrodontids as sister to *L. kayi* (figure 2). Nyctitheriids and extant lipotyphlans are recovered in a clade within Laurasiatheria.

## 5. Discussion

Over the past half a century, picrodontids have been hypothesized to be early primates [13] and supported as stem primates based on results of phylogenetic analyses [19]. These views have been mostly due to picrodontids exhibiting several dental features that are like those of plesiadapiforms, but their uniquely derived dentitions lack common features found in all plesiadapiform families [5,13,15]. Our observations of the basicranial morphology of *Z. paleocenus* indicate that it is distinct from that of all plesiadapiforms and is more like that of nyctitheriids and apatemyids, which likely retain the primitive condition of Placentalia [41].

Given our results that *Z. paleocenus* is not a stem primate, proposed dental similarities between picrodontids and primates (*sensu lato*) are most likely independently evolved. This conclusion might not be that surprising given the numerous dental and basicranial differences between *Z. paleocenus* and that of plesiadapiforms. In each basicranial bone examined, *Z. paleocenus* lacks any clear synapomorphies linking it with plesiadapiforms and instead resembles nyctitheriids, some extant lipotyphlans, and apatemyids. While many of these similarities among these taxa are likely symplesiomorphies for placental mammals, it might be worth further investigating our recovered dental synapomorphies uniting picrodontids and apatemyids (e.g. a parastylar lobe anterior to the paracone on M1). Also, *Z. paleocenus* exhibits a caudal tympanic process that meets the crista interfenestralis via a curved ridge, which was recovered as a lipotyphlan synapomorphy in previous cladistic results and is found in nyctitheriids [21,22]. This character is recovered as a synapomorphy of the broader clade including extant lipotyphlans, nyctitheriids, and picrodontids in our unconstrained analysis (electronic supplementary material, SI1) and of the clade including lipotyphlans and nyctitheriids in our constrained analysis (figure 2; electronic supplementary material, SI2).

Although unlikely, if *Z. paleocenus* is a stem primate as previously proposed [13,19], the primitive primate (*sensu lato*) and, by extension, primatomorphan and euarchontan basicranial morphology would likely be indistinguishable from that of a primitive placental mammal. A similar conclusion was reached regarding microsyopids [34], which retain basicranial morphology like that which has been reconstructed for the ancestral placental [41]. Unfortunately, the ancestral primate morphotype is difficult to reconstruct in part because cranial remains of Palaeocene representatives of non-plesiadapiform euarchontans and of *Purgatorius*, the oldest and likely most basal plesiadapiform [43], are not yet known.

The results of our phylogenetic analyses generally support our morphology-based interpretations that *Z. paleocenus* and other picrodontids are not stem primates, primatomorphans, or even euarchontan mammals. Our chosen character–taxon matrix provides a robust test of the evolutionary relationships of picrodontids among eutherian mammals given the elements preserved in AMNH 17180, the character sampling of the cranial partition, and the taxon sampling of eutherian mammals. This character–taxon matrix was not designed specifically to elucidate plesiadapiform interrelationships, which likely led to some differences in the resulting topologies for plesiadapiforms compared to those that are generally recovered [7,8,9]. However, *Z. paleocenus* was never recovered as a stem primate or euarchontan in any of our results. Provided the likely independent evolution of plesiadapiform and/or primate-like dental features in picrodontids, our results indicate a need to better scrutinize proposed synapomorphies, especially when evaluating poorly known, uniquely derived fossil taxa.

Ethics. This work did not require ethical approval from a human subject or animal welfare committee.

Data accessibility. Associated data are available in the electronic supplementary material. µCT tiff stacks are available via Morphosource (www.morphosource.org) [44]. The character–taxon matrix is available via https://morphobank.org/ [45].

The data are provided in the electronic supplementary material [46].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. J.W.C.: conceptualization, data curation, formal analysis, investigation, methodology, writing—original draft, writing—review and editing; J.R.W.: formal analysis, investigation, writing—review and editing; S.G.B.C.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, supervision, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare no competing interests.

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