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A subantarctic reigitheriid and the evolution of crushing teeth in these enigmatic Mesozoic mammals

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Mesozoic mammals from Gondwana remain poorly understood, with most species known only from isolated teeth. Nevertheless, these tantalizing fossils point to a diversity of families that were distinct from Laurasian forms. Among these, the enigmatic South American family Reigitheriidae was proposed based on the unique crushing teeth of its sole representative, *Reigitherium*, from Northern Patagonia. Here, we report a new mammal, *Yeutherium pressor* gen. et sp. nov., which is only the second known taxon of Reigitheriidae. This is based on a partial maxilla bearing an upper molar from the Late Cretaceous Dorotea Formation in the Río de Las Chinas valley, Sub-Antarctic Chile. Parsimony and Bayesian phylogenetic analyses indicate a close relationship between *Reigitherium* and *Yeutherium*. Shared features between both taxa—such as expanded preparacristae and postparacristae, a lingual cingulum at the paracone base, interradicular crests and enamel crenulations—help define Reigitheriidae. Cingula development and molar morphology of *Yeutherium* differ from that of the related Mesungulatidae, suggesting independent evolution of the crushing adaptations in Reigitheriidae. Additionally, we suggest a reinterpretation of the dental formula of Reigitheriidae. The discovery of *Yeutherium* highlights the specialized dentition of Reigitheriidae as a significant functional innovation in a radiation of Gondwanan mammals that is starting to be understood.

1. Introduction

Current understanding of mammalian evolution during the dusk of the dinosaur age is heavily biased towards fossils of northern continents. Comparatively, very little data are available about mammal evolution on the southern continents [1]. One intriguing group of Gondwanan mammals, the meridiolestidans, first appeared in the Late Cretaceous [2,3]. They underwent significant morphological and ecological diversification with various diets (i.e. insectivory, omnivory and herbivory) and body sizes [3–6] and survived the end-Cretaceous extinction, persisting into the Miocene [7]. These morphologically unique mammals fall in a phylogenetic position outside of crown Theria [4,6–13], but little is understood about their origins, affinities and evolution. Among the meridiolestidans, the enigmatic family Reigitheriidae was proposed based on a sole representative, the shrew-sized taxon *Reigitherium* from Northern Patagonia [5,8,14,15] because of the unique adaptations for herbivory in its bunodont teeth (teeth designed for crushing and grinding). Most phylogenetic studies have placed *Reigitherium* as the sister taxon of the family Mesungulatidae, together forming the clade Mesungulatoidea [4,6,7,9–13]. Mesungulatids have a crushing, bunodont dentition and a great range of sizes, including the wolf-sized early Palaeocene *Peligrotherium tropicalis* [4,6]. According to some studies, *Peligrotherium* could be a sister taxon of *Reigitherium* based on similarities in their teeth and mandibles [5,8,9], despite the differences in body size and their difference in geological ages.

Here, we describe the second-ever encountered species of Reigitheriidae, *Yeutherium pressor* gen. et sp. nov., based on a fragmentary maxilla recovered from the Upper Cretaceous Dorotea Formation in Chilean Patagonia (figure 1), at the fossil site of Río de Las Chinas valley, more than 600 km south of the Argentinian sites that yielded previous reigitheriid fossils. We present new phylogenetic analyses using a modified version of previous matrices [6,8] that support a close affinity between *Reigitherium* and *Yeutherium*, making *Yeutherium* the second and southernmost known reigitheriid. *Yeutherium* provides new information on the evolutionary trajectory of bunodonty in the upper molars of reigitheriids, and the diagnostic features that set them apart from mesungulatids.

2. Material and methods

(a) Fossil specimen

The holotype of *Y. pressor* gen. et sp. nov. is housed at the Museo Nacional de Historia Natural, Santiago, Chile, under the acronym SGO.PV 12964. SGO.PV 12964 was collected by picking at the 'Black Bone' locality, 200 metres north of the Mammal Quarry. More information about the geologic context and radiometric age from the locality is in the electronic supplementary material, S1. Comparisons with other mammals were made through direct observation of specimens housed at MACN-Pv (Colección Nacional Paleovertebrados, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Buenos Aires, Argentina) and MPEF-PV (Vertebrate Paleontology, Museo Paleontológico Egidio Feruglio, Chubut, Argentina), as well as through reference to the bibliographic sources cited throughout the text.

(b) Micro-CT scanning and processing

The specimen SGO.PV 12964 was scanned in SkyScan1272 scanner at the Laboratorio de Microscopía, Departamento de Ingeniería Química y Bioprocesos, Pontificia Universidad Católica de Chile, Santiago, Chile, using a source voltage of 80 kV, a current of 125 μA and a voxel size of 10 μm, generating TIFF files. The scans were segmented with the software 3D Slicer and 3D models were generated and used in some of the figures of this article. The 3D models are available as STL files in MorphoSource (morphosource.org) under the project ID 000748825 (https://www.morphosource.org/projects/000748825/temporary_link/GEp7kjeT4JKjzjRMUtGPJG4M?locale=en). In addition, we added two CT movies as electronic supplementary material, S2 and S3.

(c) Phylogenetic analyses

We modified the matrix of Rougier *et al.* [8] and scored *Y. pressor* and *Orretherium tzen*. The modifications involved separating characters that mixed neomorphic (presence/absence of a structure) with transformational (variation of a structure) characters following recommended practices [16,17], removing some redundancies, modifying some character scores and adding two characters. A detailed list of changes is present in the electronic supplementary material, S1.

A recent development in TNT v.1.6 [18] permits taking into consideration different types of dependencies between characters by using step–matrix costs, including inapplicability owing to contingent coding, which theoretically finds ancestral reconstructions that maximize homology [19,20]. Therefore, we ran the matrix in TNT twice, in one analysis applying this method in cases of inapplicable characters owing to the absence of a structure, and in the other, using the same parameters but without using this method in order to compare the effect in the topology of the tree/s recovered with both methods.

Undated and tip-dated Bayesian analyses were performed in MrBayes v.3.2.7a [21]. In both analyses, a single partition was used for the morphological data, applying the Mkv model of morphological evolution, assuming that only variable characters were scored. To model rate heterogeneity across characters, we used a lognormal distribution with eight rate categories. For the tip-dated analysis, a truncated normal prior was used for calibrating the root of the tree, with a minimum age of 242 million years ago (Mya), a standard deviation of 1 Mya and a mean age of 242.1 Mya, and we accounted for stratigraphic uncertainty by incorporating the temporal interval between the first appearance datum (FAD) and last appearance datum (LAD) known for each taxon. The prior distribution of the clock rate parameters was a lognormal-distributed clock rate prior with a mean of −4.354890166 and a standard deviation of 0.482226338. Branch rate variation was modelled using the Independent Gamma Rate relaxed clock model with an exponential distribution of rate 10. We used the fossilized birth–death model [22] as a prior on divergence times, incorporating an exponential net diversification prior (rate = 1), a beta turnover prior ($\alpha = 1$, $\beta = 1$), a beta fossil sampling proportion prior ($\alpha = 1$, $\beta = 1$) and allowing fossil taxa to be sampled as ancestors. The extant sampling proportion for the analysis was set to 0.00045. The undated and tip-dated analyses ran for 10 and 40 million Markov chain Monte Carlo generations, respectively, with two independent runs of four chains, discarding the first 25% as burn-in. Upon completion, the effective sample size for parameters exceeded 200 and the split frequency deviation was below 0.01 in both

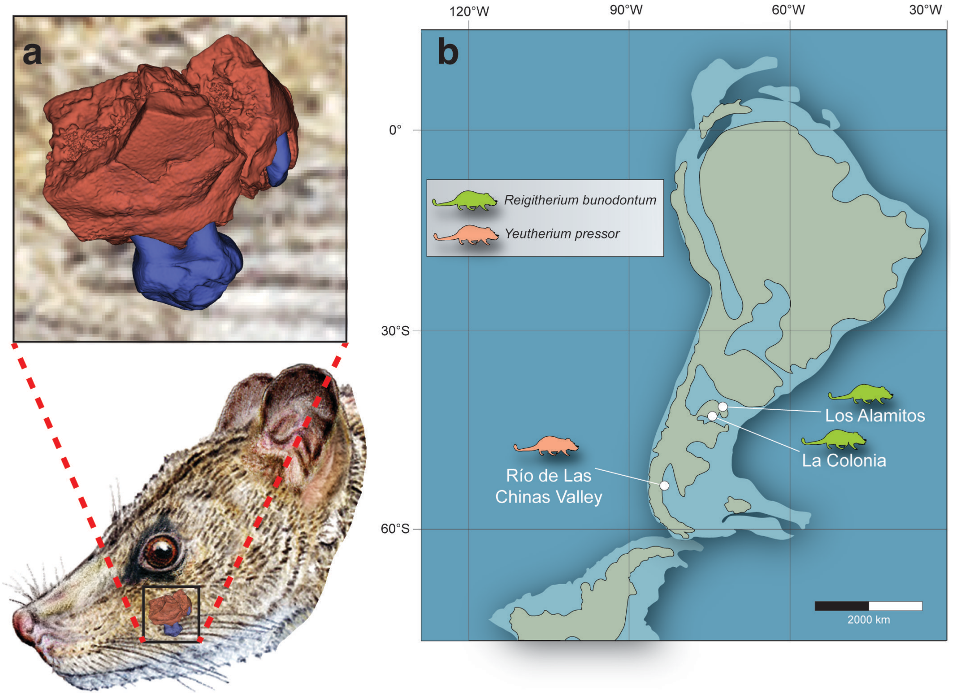

Figure 1. (a) Artistic reconstruction of the head of *Yeutherium pressor* highlighting the left maxilla fragment and M1 preserved in SGO.PV 12964. (b) Late Cretaceous localities with records of reigitheriids plotted in a palaeomap of South America (74 Ma) and the locality where *Y. pressor* was found. Artistic reconstruction by Mauricio Álvarez.

analyses. Convergence and stationarity were confirmed using Tracer v.1.7.1 [23]. See electronic supplementary material, S1 for an extended phylogenetic protocol.

3. Results and discussion

(a) Systematic palaeontology

Mammalia Linnaeus 1758
Meridiolestida Rougier, Apesteguía, and Gaetano 2011
Mesungulatoidea Rougier, Apesteguía, and Gaetano 2011
Reigitheriidae Bonaparte 1990

Diagnosis: Small-sized mesungulatoids with seven upper/lower postcanine teeth, instead of six as in mesungulatids. The cingulids in the lower molars are tall and hypertrophied (based on *Reigitherium*) and the cingula in the upper molars is generally mesially and distally reduced because of expanded preparacristae and postparacristae, presenting a lingual cingulum at the paracone base, unlike mesungulatids that show strongly developed mesial cingula and distal cingula , but lack a lingual cingulum. Unlike mesungulatids, reigitheriids present interradicular crests linking the roots of the upper molars, a distal accessory root and an ectostyle in the last premolar and first upper molar. Reigitheriids have a variably developed median ridge connecting the paracone and the stylocone, and mesially and distally from it, marked enamel crenulations.

(i) *Yeutherium*, gen. nov.

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Figures 2–3 and electronic supplementary material, figure S2

Type species: Yeutherium pressor

Diagnosis: Small-sized reigitheriid meridiolestidan, being somewhat smaller (approx. 1/3) than *Reigitherium bunodontum*. *Yeutherium* differs from *Reigitherium* in exhibiting the M1 with a shorter median ridge, a subrectangular outline instead of a rhomboid one, a shorter preparacrista ending in a mesiobuccally concave area, a mesial cingulum with a developed lingual component having a small mesiolingual cusp separated from a small buccal component by a mesially expanded preparacrista, a continuous lingual cingulum embracing base of the paracone with a tiny lingual cusp, large enamel crenulations or crests between the stylocone and the paracone, small metastyle and a small ectostyle appressed to the base of the stylocone.

Age and distribution: Late Campanian to early Maastrichtian, Dorotea Formation, Río de Las Chinas valley, Última Esperanza Province, Magallanes and Chilean Antarctic Region, Chile. See geologic context and radiometric age in electronic supplementary material, S1.

Etymology: From the combination of the words 'yeut' ('hill' in Aonikenk language) and 'therium' ('beast' in Greek). The name makes reference to the finding of this mammalian specimen on the slope of a hill in the 'Black Bone' locality.

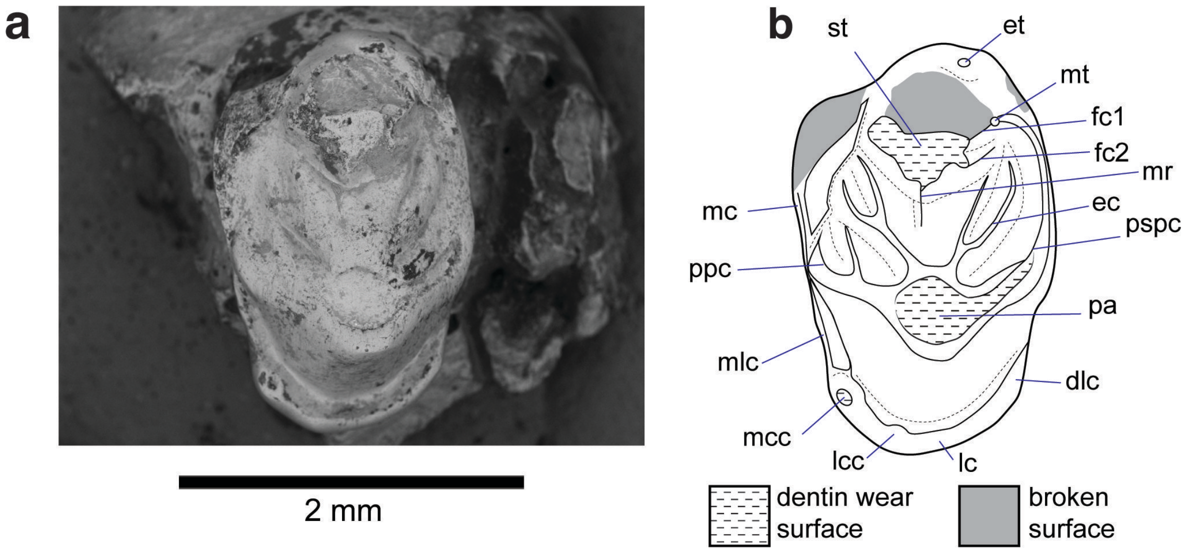

Figure 2. *Yeutherium pressor* gen. et sp. nov. (SGO.PV 12964, holotype) (a) SEM image of the left M1 in occlusal view. (b) Illustration of the left M1. Abbreviations: dlc, distolingual cingulum; ec, enamel crenulation; et, ectostyle; fc, frenular crest; lc, lingual cingulum; lcc, lingual cingulum cuspule; mc, mesial cingulum; mcc, mesial cingulum cusp; mlc, mesiolingual cingulum; mr, median ridge; mt, metastyle; pa, paracone; ppc, preparacrista; pspc, postparacrista; st, stylocone.

(ii) *Yeutherium pressor*, sp. nov.

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Holotype: The specimen SGO.PV 12964 corresponds to a left maxilla fragment with M1, roots of M2 and mesial roots of M3.

Etymology: From the word ‘pressor’, ‘one that presses or squeezes’ in Latin. The name refers to the shape and presence of crests and crenulations of the M1 of this species, which reminds of an orange or a lemon squeezer.

Horizon and locality: From the ‘Black Bone’ locality (50° 42′ S /72° 32′ W), an outcrop of the Dorotea Formation in the Río de Las Chinas valley located 200 m north of the Mammal Quarry (figure 1 and electronic supplementary material, S1).

Age and distribution: As for the genus.

Diagnosis: As for the genus.

(b) Description

Only the crown of M1 of SGO.PV 12964 is preserved (figures 2 and 3) and it has a length of 1.49 mm and a width of 2.37 mm (electronic supplementary material, S1, tables S1 and S2). There are two main cups in M1: the stylocone, located close to the buccal margin, and the paracone, positioned close to the lingual margin. Both cusps are considerably worn, and the buccal half of the stylocone is missing. The paracone and the stylocone are aligned at the same mesiodistal level in M1, very similar to the cusp arrangement exhibited in *Reigitherium*’s M1, and unlike P4 [5,8]. The stylocone presents three crests preserved: two distal frenular crests, one of which is connected to the metastyle, and also a short lingually directed median ridge [8,24,25]. The median ridge ends at the base of the paracone and is notched half-way along in a basin between the stylocone and the paracone, being considerably shorter than that of *Reigitherium* [8]. In the same basin, mesial and distal to the median ridge, there are two somewhat worn crests that run obliquely from the paracone and quickly bifurcate into two smaller crests that we interpret as expanded enamel crenulations (definition in electronic supplementary material, S1). *Reigitherium* also presents crenulations, but these are finer and presenting small rugosities and pits that are absent in *Yeutherium*.

The paracone presents strong and worn crests running from its worn apex: the preparacrista, with a mesiobuccal orientation, and the postparacrista, with a distobuccal orientation. Starting from the paracone, the postparacrista continues towards the distal margin of M1 and then is directed buccally, connecting to the metastyle. In contrast, the preparacrista progressively becomes thinner and ends abruptly in a mesiobuccally extended concave and somewhat worn area. Mesial to the preparacrista, there is an almost continuous mesial cingulum extended from the lingual to the buccal margin of M1, presenting a small interruption at the level of the maximum mesial bulge of the preparacrista (figure 3b,e). The lingual component of the mesial cingulum of *Yeutherium*’s M1 is more developed than its distolingual counterpart and presents a small cusp that exhibits some apical wear, and distal from it, a tiny incipient cusp (figure 3h). Lingually, there is a somewhat expanded lingual cingulum that is continuous with the lingual component of the mesial cingulum and the distolingual cingulum, which together embrace the paracone. In the buccal margin of M1, there are two stylar cusps: a metastyle, close to the distal margin of the molar, and mesial to it, an ectostyle, which is slightly distal to the mesiodistal midpoint of M1. The parastyle is not preserved owing to breakage of the crown in that area. The degree of the development of the cingula and stylar cups in the M1 of *Yeutherium* differs notably from *Reigitherium*, the latter presenting a thin and lingually restricted cingulum and hypertrophied stylar cusps (e.g. MPEF 2394 [8]).

M1 presents three main roots, two buccal and one lingual, and also a distal accessory root (figure 3f–i). The buccal roots are mesiodistally compressed and mostly straight, whereas the lingual root has a subcircular contour and its apex is mesiobuccaly

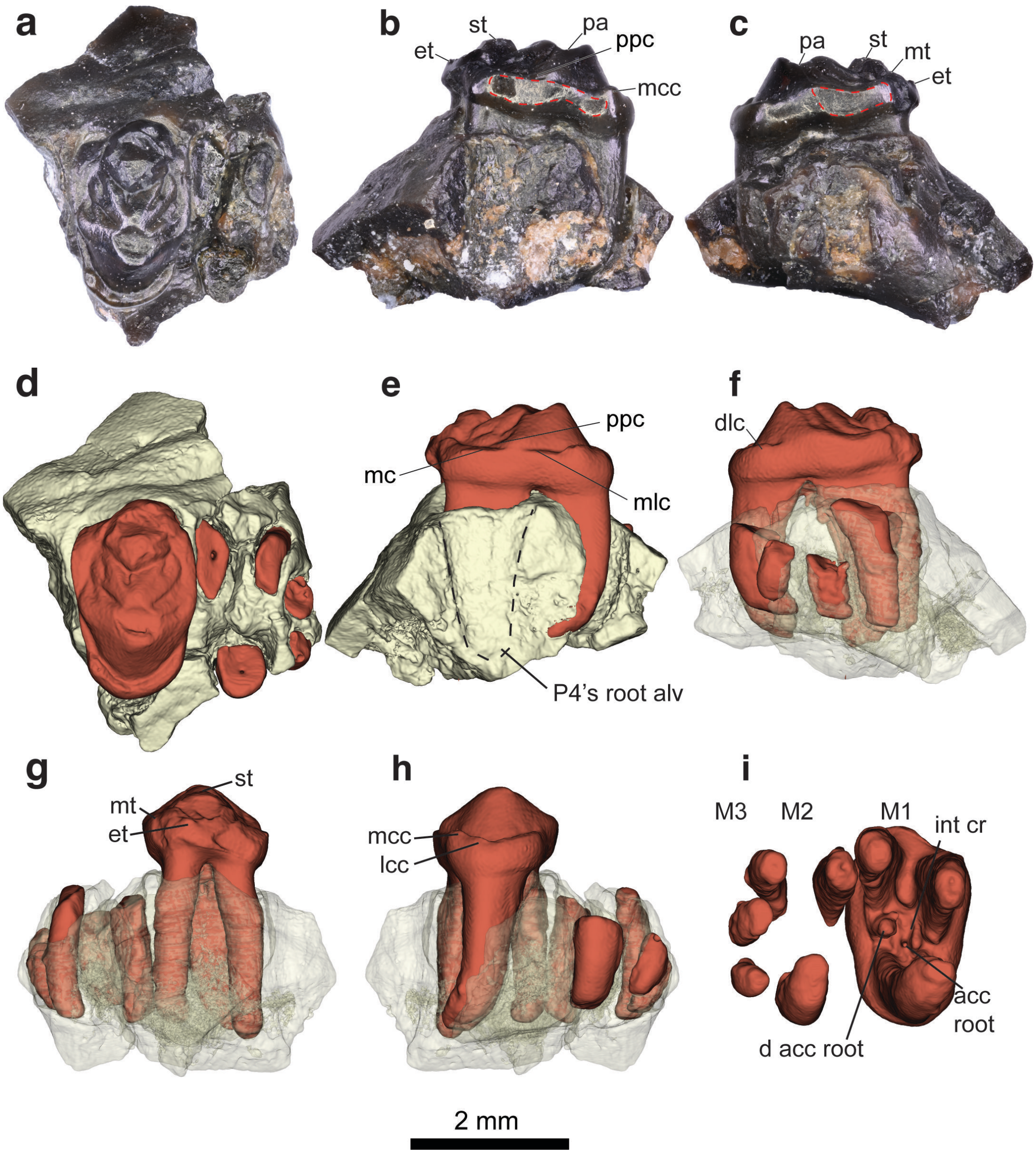

Figure 3. *Yeutherium pressor* gen. et sp. nov. (SGO.PV 12964, holotype) left maxilla fragment with M1, roots of M2 and mesial roots of M3 (a–c) photos in (a) occlusal, (b) mesial and (c) distal views. (d–i) 3D renderings in (d) occlusal, (e) mesial, (f) distal, (g) buccal, (h) lingual and (i) dorsal (radicular) views. The white dashed lines in (b–c) represent the extension of the interdental wear facets in M1. In (f–g) the maxilla is transparent to show the molars' roots. In (i), the maxilla was removed to uncover the molars' roots. Abbreviations: acc root, accessory root; alv, alveolus; d acc root, distal accessory root; dlc, distolingual cingulum; et, ectostyle; int cr, interradicular crests; lcc, lingual cingulum cuspule; mc, mesial cingulum; mcc, mesial cingulum cusp; mlc, mesiolingual cingulum; mt, metastyle; pa, paracone; ppc, preparacrista; st, stylocone.

oriented. Among the buccal roots, the distal one is more buccally located than the mesial one. The distal accessory root is small and straight, being located between the distal buccal root and the lingual root. The four roots are connected by interradicular crests that appear to be cross-shaped, with an interradicular crest connecting the distal buccal root and the lingual root, and another interradicular crest crossing the former and connecting the mesial buccal root and the distal accessory root. Buccal and close to the lingual root, there is a tiny protuberance that seems to be another accessory root, although this is much smaller than the previous one. The radicular structure of the M1 *Yeutherium* is very similar to the radicular structure of the same molar in *Reigitherium* (MPEF 2394) sharing: (i) a distal buccal root that is more buccally placed than the mesial buccal root, (ii) the presence of a distal accessory root in a similar position and (iii) a similar pattern of interradicular crests.

SGO.PV 12964 also preserves the three roots of M2 and two roots of M3. Overall, the roots of M2 are similar to those of M1. The main difference with the roots of M1 is that in M2 the distal root is in the same buccolingual plane as the mesial root, instead of having a more buccally projected distal root (i.e. as in M1). This probably indicates that M2 is a more symmetrical molar than M1, similar to the condition present in the same molar in *Reigitherium* (MPEF 2394 [8]). M3 has a buccal root and a lingual root of similar size, which are aligned in the same mesiodistal plane. M3 was probably half the size of the two former molars. Directly anterior from the mesial buccal root of M1, almost half of the alveolus for the distal buccal root of P4 is preserved, being wider than the former (figure 4d). Therefore, the distal buccal root of P4 was larger than the roots of M1 and M2, which suggests that P4 was larger than any of the molars of *Yeutherium*. Additional features of *Yeutherium* are described in the electronic supplementary material, S1.

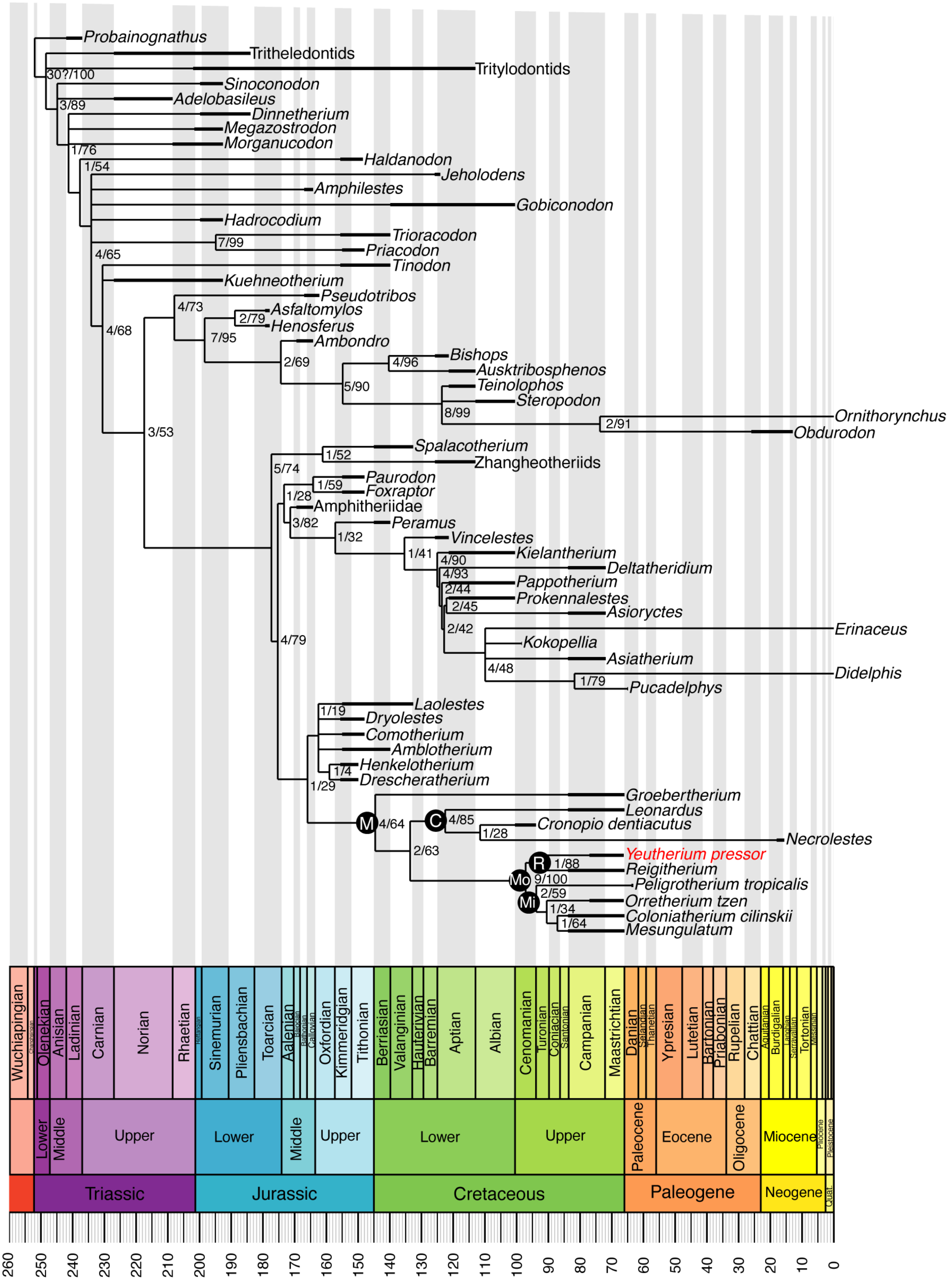

Figure 4. Strict consensus from trees of the maximum parsimony analysis considering dependency (i.e. inapplicability) between characters represented on a timescale. For more details on the approach, see electronic supplementary material, S1. The numbers next to each node indicate the absolute Bremer support on the left and the Jackknife resampling support on the right. The nodes do not represent divergence-time estimates; for that, see the Tip-Dated Bayesian results in the electronic supplementary material, S1. *Yeutherium pressor* is indicated in red. Abbreviations: C, Cronopioidea; M, Meridiolestida; Mo, Mesungulatoidea; Mi, Mesungulatidae; R, Reigitheriidae.

(c) The family Reigitheriidae: a specialized radiation among South American mammals

When Bonaparte [14] created the family Reigitheriidae, he included only one taxon, *R. bunodontum*, which was justified considering the great morphological distance between this taxon and other known mesungulatids such as *Mesungulatum*. Later Pascual *et al.* [26] interpreted *Reigitherium* as a derived docodont, based on the crenulation of the molar crown similar to that of *Docodon* [27]. Although this systematic designation is not followed by more recent studies [4–13,28], it nonetheless highlights the complex and highly distinctive molar morphology of *Reigitherium*.

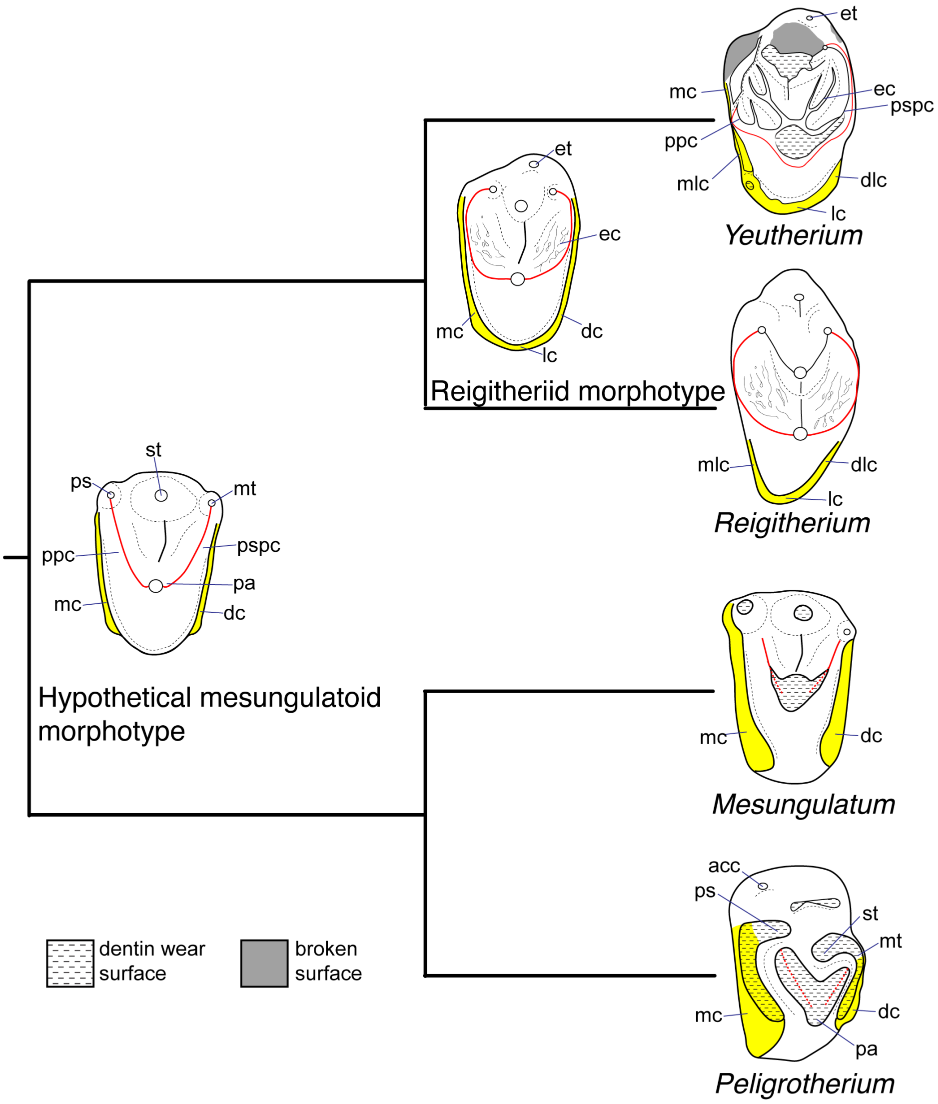

Figure 5. Cingula development in the upper molars of mesungulatoids based on the left M1 mapped into the phylogeny of figure 4. The diagram represents the hypothesis that from a putative archaic mesungulatoid with narrow buccolingually extended mesial and distal cingula, two lineages emerge: reigitheriids and mesungulatids. In reigitheriids, a lingual cingulum develops and the pseudotrigon is expanded with the preparacrista and postparacrista expanding towards the mesial and distal cingulum, respectively. In *Reigitherium*, this expansion is complete and the buccal component of the mesial and distal cingulum is completely lost, whereas in *Yeutherium*, a small remnant of the buccal component of the mesial cingulum still persists. In mesungulatids such as *Mesungulatum*, the mesial and distal cingula are expanded. In *Peligrotherium*, the mesial and distal cingula are even more expanded and elevated. The mesial, lingual and distal cingula are highlighted in yellow and the preparacrista and postparacrista are highlighted in red. The M1 drawings were based on the following specimens: *Yeutherium* (SGO.PV 12964), *Reigitherium* (MPEF 2394; mirrored) and *Peligrotherium* (MPEF 2351). Abbreviations: acc, accessory cusp; dc, distal cingulum; dlc, distolingual cingulum; ec, enamel crenulation; et, ectostyle; lc, lingual cingulum; mc, mesial cingulum; mlc, mesiolingual cingulum; mt, metastyle; pa, paracone; ps, parastyle; ppc, preparacrista; pspc, postparacrista; st, stylocone.8

The discovery and description of *Y. pressor* from the Dorotea Formation in the Río de Las Chinas valley, at the ancient gateway between Antarctica and South America [29], expands the geographic distribution and diversity of this poorly known radiation of meridiolestidans (including reigitheriids) [6]. Although *Yeutherium* is distinct from *Reigitherium* from Northern Patagonia, they share several derived characters of the upper molars: (i) a continuous lingual cingulum at the paracone base, (ii) the mesial cingulum and the distal cingulum are reduced because of the expansion of the preparacristae and postparacristae, (iii) interradicular crests linking the roots, (iv) large stylar cusps with an ectostyle in M1 (and P4 in *Reigitherium*; contra Rougier *et al.* [8]) and (v) marked enamel crenulations between the paracone and the stylocone. These derived features shared by *Yeutherium* and *Reigitherium* are absent in otherwise closely related mesungulatids and also absent in other meridiolestidans. Some of these features were recovered as unambiguous synapomorphies by parsimony analyses (see electronic supplementary material, S1). More importantly, in all the phylogenetic analyses conducted here, *Reigitherium* and *Yeutherium* were consistently recovered forming a monophyletic group (Reigitheriidae) with strong support (figure 4 and electronic supplementary material, S1, figures S3 and S4). These results allow us to forward a new definition of the family Reigitheriidae as the clade composed of the reigitheriid *Reigitherium bunodontum* Bonaparte, 1990 and all taxa more related to it than *Mesungulatum houssayi* Bonaparte and Soria, 1985, *Peligrotherium tropicalis* Bonaparte, Van Valen & Kramarz, 1993 and *Cronopio dentiacutus* Rougier *et al.* 2011. Notice that this definition stands regardless of the position of *Peligrotherium*.

Although among the meridiolestidans interradicular crests have been only described in reigitheriids and *Peligrotherium* [8,30], these connecting ridges are also developed in some dryolestoideans, such as *Dryolestes leiriensis*, *Henkelotherium*

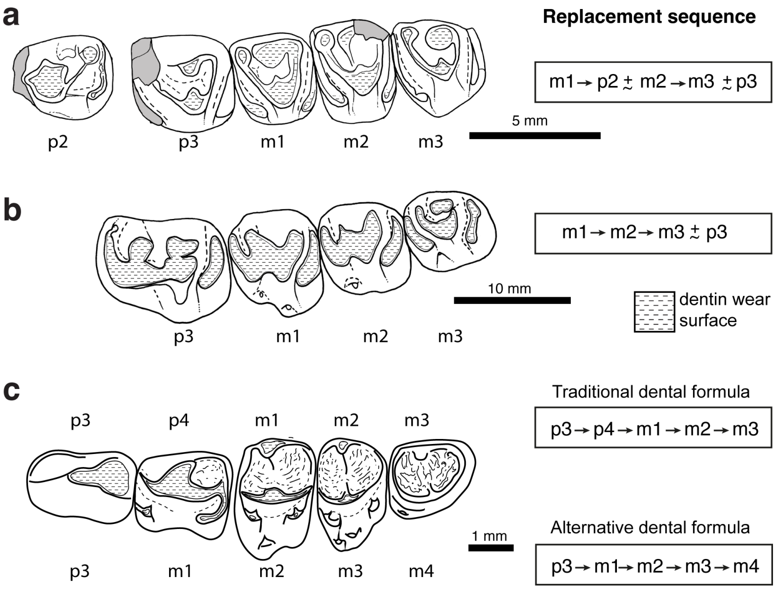

Figure 6. Dental replacement sequence of the lower dentition and inferred dental formula of mesungulatoid meridiolestidans. (a) *Orretherium tzen* (CPAP—5007), (b) *Peligrotherium tropicalis* (MPEF-PV 2351), and (c) *Reigitherium bunodontum* (based on MPEF-PV 606 [lp3–m1], MPEF-PV 2338 [rp3–m1], MPEF-PV 2393 [rm1–m2], MPEF-PV 2390 [rm3] and MPEF-PV 2391 [rm3]). In (c) two dental formula hypotheses are given for *Reigitherium*: the traditional hypothesis defended by Rougier *et al.* [8] and the alternative hypothesis here suggested based on the dental wear and inferred dental replacement.

guimarotae and *Hercynodon germanicus* (Luo & Martin [31]: Y-shaped dentine ridges, figs 4 and 5). These connecting ridges also have been observed in some members of other mammalian lineages such as eulipotyphlans (erinaceids [32] and soricomorphs [33]), allotherians (multituberculates [34] and gondwanatherians [35]), the eutherian *Azilestes* [36], mixodectids, lepticids, plesiadapiforms and primates (omomyids [37]). Interradicular crests originated independently in most of the above-mentioned lineages, and their distribution and potential function in mammals are mostly unknown. Apart from reigitheriids, enamel crenulations have been observed in *Docodon victor*, *Agilodocodon scansorius* and *Simpsonodon oxfordensis* [27,38] but are otherwise absent or poorly developed in other docodonts [39,40]. The enamel crenulations present in some docodonts, such as *Simpsonodon*, seem finer and deeper than the crenulations of reigitheriids. The systematic pattern of enamel crenulations among docodonts and meridiolestidans strongly suggests these two lineages acquired this fine structure independently, as implied by our present phylogenetic analyses and also elsewhere [40]. Enamel crenulations have arisen independently in different mammalian lineages (e.g. periptychids, dermopterans, primates, rodents) [41] and have been considered to increase tooth volume, prolonging functional life against abrasive wear [42], in an adaptation that facilitated feeding on hard dietary items [43–45] and/or to increased the ability to fracture fibrous seeds [46].

(d) The position of Reigitheriidae among meridiolestidans and other mesungulatoids and the origin of bunodonty in mesungulatoids

A relevant aspect of *Y. pressor* is that it narrows the morphological gap between *Reigitherium* and mesungulatids. In particular, the mesial cingulum of *Yeutherium* gives clues about how the condition displayed by *Reigitherium*, of lingually restricted mesial and distal cingula, can evolve from a more generalized mesungulatoid, with mesial and distal cingula that extended from the lingual to the buccal margin, as in mesungulatids (figure 5). In *Yeutherium*, the mesial cingulum extends from the lingual to the buccal margin (as in mesungulatids), although it is interrupted by an inflated preparacrista at its midsection (unlike mesungulatids). The distal cingulum of *Yeutherium* is lingually restricted as in *Reigitherium*, and there is a distally inflated postparacrista. We think that at some point in the evolution of Reigitheriidae, the preparacrista and postparacrista got mesially and distally expanded, inflating the pseudotrigon, which increased the crushing and grinding area; coupled with the enamel crenulations, these were probably adaptations to a harder herbivorous diet. In this scenario, the buccal component of the mesial cingulum and distal cingulum got fused with the expanded preparacrista and postparacrista, respectively, a process that was partially completed in *Yeutherium* and fully completed in *Reigitherium*.

Our upper molar evolution interpretation also has implications regarding the affinities between reigitheriids and the mesungulatid *Peligrotherium*. A close relationship between *Reigitherium* and *Peligrotherium* has been defended in some studies based on similarities such as high occlusally functional cingulids, the presence of labial accessory cusps/cuspulids, inflated and intermittent condition of the primary trigon/trigonid crests, the position of the posterior-most mental foramen and the position of maximal convexity of the dentary [5,8,47]. Although some phylogenetic analyses have supported this sister relationship between *Reigitherium* and *Peligrotherium* [5,8,9], most phylogenetic studies have recovered *Reigitherium* in a basal position among mesungulatoids [4,6,7,9–13], a result firmly supported by differences in crown configuration [6]. Our phylogenetic analyses displayed ambiguous results. Although Reigitheriidae was recovered consistently across the phylogenetic analyses, its position among meridiolestidans differed between the parsimony and Bayesian analyses, being in the former at the stem of mesungulatids (figure 4 and electronic supplementary material, S1, figure S3) and in the latter in a nested position among mesungulatoids and as the sister taxon with *Peligrotherium* (electronic supplementary material, S1, figure S4a–b).

Although the position of *Peligrotherium* as a sister of Reigitheriidae remains possible, we suggest that the anatomical features of *Peligrotherium* are more consistent with those of a mesungulatid. From a hypothetic archaic mesungulatoid, in mesungulatids such as *Mesungulatum* there is an expansion of the mesial and distal cingula, probably connected to an increase in the consumption and processing of vegetable matter (figure 5). *Peligrotherium*, with an extremely expanded mesial and distal cingula and relatively high molar crowns, may have continued the same evolutionary trajectory set by Late Cretaceous mesungulatids, increasing the specialization towards an herbivorous diet. As Martinelli *et al.* [6] previously argued, some of the dental similarities between *Reigitherium* and *Peligrotherium* might be related to their well-developed bunodonty specialized for herbivory, potentially influenced more by a convergent dietary ecology than by a close phylogenetic ancestry. Accordingly, the upper molars of reigitheriids are characterized by reduced cingula that do not have an important role in occlusion, which is opposite to the wider cingula for occlusal contact that are seen in mesungulatids such as *Peligrotherium*. It is important to mention that although a sister relationship between Reigitheriidae and *Peligrotherium* is unlikely, in our review of current evidence, the only way to solve this debate is with more fossils that could help to determine the dental identity of postcanine teeth in reigitheriids and also by gaining more corroboration from non-dental characteristics, across more mesungulatoid taxa.

(e) Current uncertainties in the dental formula of Reigitheriidae

Our interpretation of the teeth loci for *Yeutherium* was based on the similarities with *Reigitherium* and its inferred dental formula of I?/i?, C1/c1, P4/p4, M3/m3 from previous work [5,8]. Although we agree with most of the cusp interpretations (see discrepancies concerning the presence of an ectostyle in P4 in electronic supplementary material, S1) and the presence of seven postcanine teeth in the upper and lower dentition from these works [5,8], we think that the identity of premolars and molars for *Reigitherium* is still poorly understood. The identity of the last premolar (P4/p4) in *Reigitherium* was justified in these works mostly by putative similarities of this tooth with the same position in *Cronoprio* and *Peligrotherium*, which present three molars and a robust last premolar that is generally molarized and one of the largest teeth. In these taxa, the last premolar was less worn in comparison with the first molar (M1/m1), which strongly suggests that the last premolar erupted later than the first molar and it was a replacement tooth [5,8,30,47]. A similar replacement pattern has been inferred recently for *Orretherium* [6]. However, close observation of several specimens of *Reigitherium* showed that this taxon does not have this replacement pattern, and this wear contrast between a more worn M1 and considerably less worn P4 does not exist; instead, the opposite is observed. For instance, in MPEF 2394, P4 exhibits more wear than M1 and M2, being in the order of (more to less wear) P4, M1 and then M2. The lower molars show the same pattern as the upper being in the order of (more to less wear) p3, p4, m1 and then m2 (figure 6). This would suggest a different replacement pattern sequence from the common pattern of other meridiolestidans (i.e. *Cronoprio*, *Peligrotherium* and *Orretherium*). This raises questions about the exact boundary between molars and premolars of the seven postcanine teeth present in *Reigitherium*. The molars are traditionally defined as any tooth posterior to the last postcanine showing evidence of replacement [48]. By the current interpretation of the dental formula for *Reigitherium* [5,8], the last premolar would appear to be more worn than the first molar (M1/m1; Figure 6). But it is the opposite for most mammals, in which the permanent tooth of the ultimate premolar locus erupts after the first molar, and as such the ultimate permanent premolar should be less worn than M1/m1 (e.g. figure 6a, *Orretherium*). If *Reigitherium* has turned out to have four molars, its premolar and molar wearing pattern would be consistent with other meridiolestidans (figure 6).

4. Conclusions

The discovery and description of *Y. pressor* from the Dorotea Formation in the Río de Las Chinas valley allow us to formally recognize the family Reigitheriidae as a distinct diversification within Mesungulatoidea and also to bridge the anatomy of the automorphic *Reigitherium* with that of mesungulatids. *Yeutherium* is also key to separating the distinct evolutionary trajectory of the upper molars of reigitheriids from that of mesungulatids, the former with small mesial and distal cingula and expanded pseudotrigon and the latter with large mesial and distal cingula that participate in occlusion. Thus, the previously described dental similarities between *Reigitherium* and *Peligrotherium* [5,8,47] are probably more related to a convergent tendency of increased crushing and grinding capacities for herbivory in both lineages instead of being directly inherited from their last common ancestor. Our phylogenetic analyses partly support this conclusion and also placed *Yeutherium* and *Reigitherium* in a strongly supported monophyletic group, the Reigitheridae. This family is characterized by upper molars with expanded preparacristae and postparacristae, a lingual cingulum at the paracone base, interradicular crests, enamel crenulations and an ectostyle (only in M1). At ~55° S of paleolatitude and with a set of distinctive dental features, *Yeutherium* represents the southernmost record of this family and expands the taxonomic and ecological richness of meridiolestidans from the Dorotea Formation.

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

Data accessibility. All the data generated in this study are accessible. The matrix and two CT movies of SGO.PV 12964 segmented are available within the published article and its electronic supplementary material in Proceedings of the Royal Society B online. These files, alongside the code used in the phylogenetic analyses, can also be found in the Dryad repository [49]. Additionally, the matrix can be accessed on MorphoBank (morphobank.org) under project number 5011 (http://morphobank.org/permalink/?P5011) and the 3D models generated from the segmentation of SGO.PV 12964 are available as STL files in MorphoSource (morphosource.org) under the project ID 000748825 (https://www.morphosource.org/projects/000748825).

Supplementary material is available online [50].

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

Authors' contributions. H.P.P.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, resources, software, validation, visualization, writing—original draft, writing—review and editing; A.G.M.: conceptualization, validation, visualization, writing—review and editing; S.S.-A.: conceptualization, funding acquisition, validation, visualization, writing—review and editing; H.O.: writing—review and editing; M.L.: writing—review and editing; A.O.V.: conceptualization, funding acquisition, project administration, 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 we have no competing interests.

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