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RE-DESCRIPTION OF THE AUDITORY REGION OF THE PUTATIVE BASAL ASTRAPOTHERE (MAMMALIA) *EOASTRAPOSTYLOPS RIOLORENSE* SORIA AND POWELL, 1981. SYSTEMATIC AND PHYLOGENETIC CONSIDERATIONS

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ABSTRACT

Eoastrapostylops riolorense Soria and Powell, 1981, is a primitive meridiungulate mammal known by two specimens from the early Paleogene Río Loro Formation, in NW Argentina. The holotype and most complete specimen is an almost complete skull, mandible, and a few associated postcranial elements. *Eoastrapostylops* is one of the oldest South American ungulates with a well-preserved skull; although its original description included some cranial characters, its attribution to the endemic South American Order Astrapotheria and the concomitant phylogenetic consequences were based on dental features. New preparation and examination of the holotype (PVL 4216) revealed features not mentioned and/or incorrectly interpreted in previous studies; particularly important are those of the auditory region. The cranial anatomy is here re-described and compared with that of *Astrapotherium* Burmeister, 1879, providing the first detailed description of a basal meridiungulate auditory region. The general structure of the preserved elements of *E. riolorense* resembles more closely that of archaic "ungulates" (i.e., condylarths) and litopterns than that of *Astrapotherium* or other astrapotheres with known skulls (e.g., *Trigonostylops* Ameghino, 1897, *Astraponotus* Ameghino, 1901); the more remarkable differences are: presence of distinct apertures (foramen ovale) for passage of the mandibular ramus of the trigeminal nerve, surfaces on the alisphenoid and squamosal for attachment of the ectotympanic bone, low and crest-like postglenoid process, postglenoid foramen medial to the postglenoid process and not piercing its base, almond-shaped promontorium with a strong caudal tympanic process almost obliterating the post-promontorial tympanic sinus, and the mastoid process exposed laterally and posteriorly. We performed three sets of cladistic analyses based on previously published matrices, including dental, cranial, and postcranial features scored in a wide sample of South American ungulates and "archaic" ungulates. The results suggest that *Eoastrapostylops* represents a basal meridiungulate lineage that diverged before the differentiation among astrapotheres, pyrotheres, and notoungulates, and thus it can be classified neither within Astrapotheria nor another clade of ordinal rank. Other groups of still uncertain status (e.g., Notopterna, Indalecidae) also would represent independent basal radiations, which would have characterized the early meridiungulate evolution, although this topic needs a more exhaustive exploration.

KEY WORDS: early Paleogene, Meridiungulata, South America, Systematics

INTRODUCTION

The Cenozoic South American record documents a remarkable diversification of endemic ungulate-like placental mammals. These mammals, traditionally grouped in at least six orders (Condylarthra, Notoungulata, Litopterna, Astrapotheria, Xenungulata, and Pyrotheria), evolved in geographic isolation during most of the Paleogene; the last survivors became extinct in the late Quaternary (see Bond 1999 and references therein). These groups are usually classified together in a separate placental superorder, the Meridiungulata (McKenna 1975), although its validity is still under debate (Muizon and Cifelli 2000; O'Leary et al. 2013, etc.). Many hypotheses of relationships of these groups to one another and to the main placental clades have been proposed since the end of XIX century (e.g., Ameghino 1906; Gregory 1910), and especially during the last decades (e.g., McKenna 1975; Billet 2010; Agnolin and Chimento 2011; O'Leary et al. 2013; Welker et al. 2015; Billet et al. 2015). However, despite a much refined phylogenetic framework and far more comprehensive data matrices, the relationships of the native South American ungulates are still unclear, mainly because even the earliest and more generalized representatives of each one of the traditional six orders are already distinct and show very specialized features with respect to the putative common ancestor of all these lineages (Cifelli 1993).

Eoastrapostylops riolorense Soria and Powell, 1981, is known through an almost complete skull and mandible and a few associated postcranial bones of a sub-adult individual, and an additional, less complete skull and mandible, recovered from early Paleogene deposits in northwestern Argentina. Thus, it is one of the oldest South American ungulates for which cranial anatomy is well documented. Soria (1987) provided an extensive description of the dentition and of the preserved parts of the skull. However, he

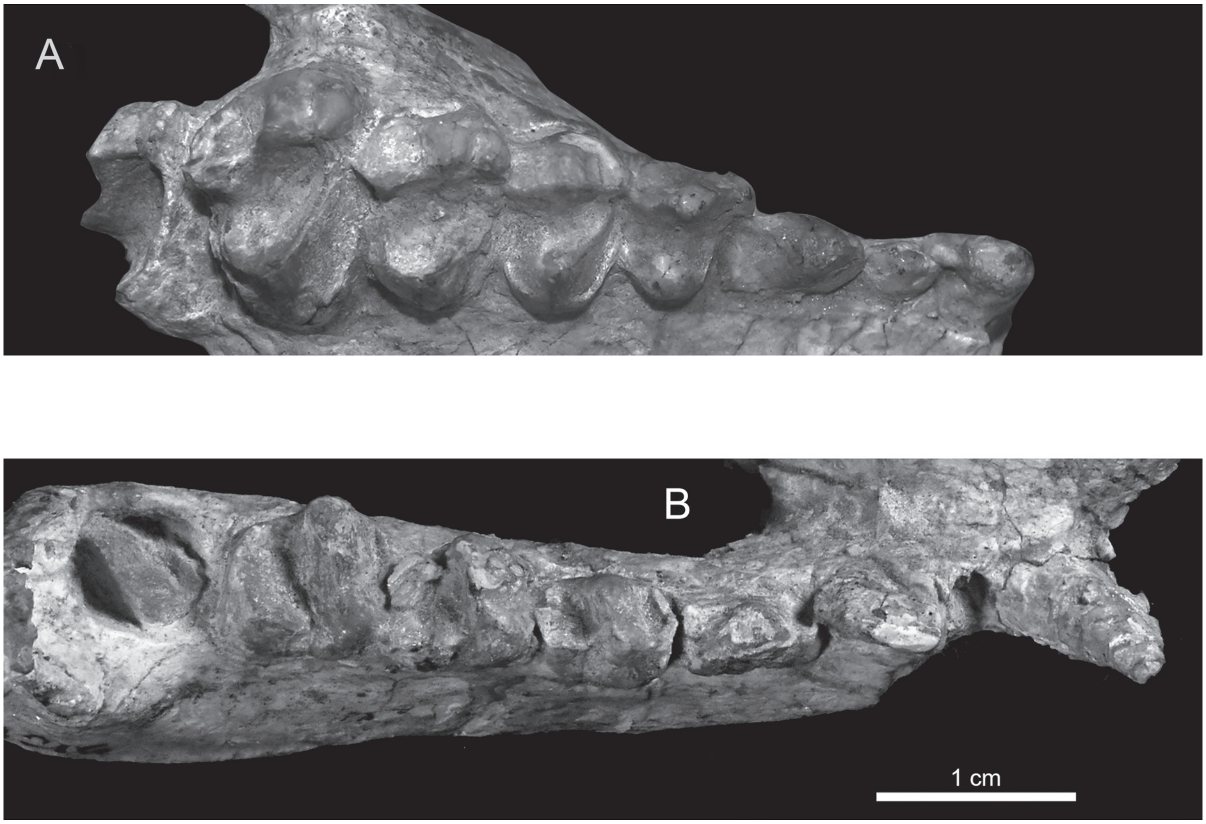

Fig. 1.—Holotype of *Eoastrapostylops riolorense* Soria and Powell, 1981 (PVL 4216). **A,** right C1-M2 and erupting M3, in occlusal view; **B,** right c1, alveolous for p1, p2-m2, and encrypted m3, in occlusal view.

stated that the auditory region was difficult to interpret due to its deficient preservation, and described this region superficially. Later, Soria (1988) concluded that *E. riolorense* would correspond to the basal astrapothere stock from which the later astrapotheres (i.e., trigonostylopids and astrapotheriids) would have diverged. Soria (1987) identified some dental features shared by *Eoastrapostylops* and some basal astrapotheres (i.e., *Trigonostylops* Ameghino, 1897, *Tetragonostylops* Paulo Couto, 1963), although he did not compare these characters with other South American ungulates. However, the only feature that he remarked as shared with the Astrapotheria in general is the possession of enlarged canines, which seems to be essentially the only support for his phylogenetic proposal.

The recent re-preparation of the type specimen of *E. riolorense* (PVL 4216) revealed that many relevant cranial structures were still embedded in the matrix when Soria described it, and thus these structures were incorrectly interpreted or simply were not mentioned in the description. The aim of this contribution is the re-description of the auditory region of *E. riolorense* and the re-interpretation of some related structures, which after re-preparation furnished the bulk of novel information on *Eoastrapostylops*. Additionally, we herein provide comparisons with the typical astrapothere *Astrapotherium* Burmeister, 1879, and with other astrapotheres for which the auditory anatomy is known: *Trigonostylops apthomasi* (Price and Paulo Couto, 1950), as described by Simpson (1933) and Billet (2010), and *Astraponotus* Ameghino, 1901 (Kramarz et al. 2010). Based on these observations, we test the proposed astrapothere affinities of *E. riolorense* within a cladistic framework including a wide taxonomic sample of SA ungulates. Finally, we present a preliminary discussion of the main evolutionary history of *E. riolorense*, astrapotheres, and other clades of SA ungulates.

MATERIALS AND METHODS

The type specimen of *E. riolorense* (PVL 4216) is an almost complete skull with associated mandible and some incomplete postcranial elements. It comes from the lower section of the Río Loro Formation, a continental unit exposed at Sierra de Medina (Tucumán Province, NW Argentina, Soria and Powell 1981). These deposits have been assigned to the Paleocene (Soria and Powell 1981; Woodburne et al. 2014) or to the early Eocene (Woodburne et al. 2014 and references therein).

The specimen is a juvenile with all the teeth in adult

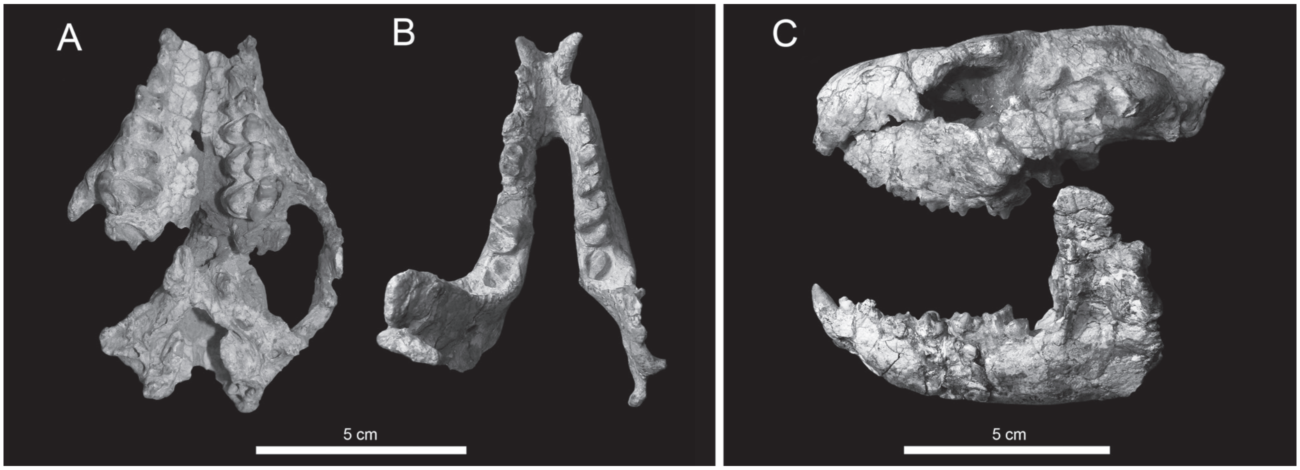

Fig. 2.—Holotype of *Eoastrapostylops riolorense* Soria and Powell, 1981 (PVL 4216). **A,** ventral view of the skull; **B,** occlusal view of the mandible; **C,** lateral aspect of the skull and jaws.

position, except for the still-erupting M3/m3 (see Fig. 1). The re-preparation revealed a large breakage on the right maxillary, exposing the roots of the premolars. There is no trace of replacement teeth within the maxillary, indicating that the premolars are the permanent ones, and thus this is a near-adult specimen. Other features of the dentition exposed during the re-preparation of the holotype and of the paratype are described in Appendix 1. The skull lacks the premaxillae, the ectotympanics, and the occipital bones (except for a minute portion of the right exoccipital) (see Fig. 2). The mesocranium and the intraorbital region are poorly preserved; except for the alisphenoid, all the bones of this area are incomplete and the sutures and the foramina are not discernible or are equivocal.

The re-preparation of the studied specimen involved the removal of a thin layer of sandy pelitic matrix, which was still covering some portions of the skull (especially the basicranium and the rostrum) when Soria and Powell (1981) and Soria (1987) described the specimen. The removal of the matrix was performed manually with steel needles.

For comparisons, we used two skulls of *Astrapotherium* preserving most parts of the basicranium, MACN A 8580 (a sub-adult specimen with erupting M3) and MACN A 3208 (an adult specimen with fully erupted M3), and supplementary observations on the skulls AMNH 8278, FMNH 13170, and YPM PU 15332.

Anatomical terminology for the skull essentially follows works by Wible and coauthors (Wible 2008, 2011; Wible and Spaulding 2013) and other works that follow the same anatomical school such as Billet et al. (2015) and Muizon et al. (2015).

The parsimony analysis was conducted with the TNT program (Goloboff et al. 2008) by a traditional search with 1000 replications using the tree bisection reconnection algorithm (TBR) option. The Bremer support values were also calculated with the TNT program. The cladograms were edited using the Winclada interface (WinClada, vers. 1.00.08, Nixon 2002).

Institutional Abbreviations

AMNH, American Museum of Natural History, New York, USA; **FMNH,** Field Museum of Natural History, Chicago, USA; **MACN A,** Colección Nacional Ameghino, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia,” Buenos Aires, Argentina; **MNHN,** Muséum National d’Histoire Naturelle, Paris, France; **PVL,** Colección de Paleontología de Vertebrados Lillo, Facultad de Ciencias Naturales e Instituto Miguel Lillo, Universidad Nacional de Tucumán, San Miguel de Tucumán, Argentina; **YPM PU,** Princeton University collection housed in the Yale Peabody Museum, Yale University, New Haven, USA.

SYSTEMATIC PALEONTOLOGY

Class Mammalia Linnaeus, 1758
Infraclass Eutheria Gill, 1872
Superorder Meridiungulata McKenna, 1975

Eoastrapostylops riolorense Soria and Powell, 1981
(Figs. 1–6)

Description of the basicranium of *Eoastrapostylops riolorense*.—Only a short portion of the anterior part of the basisphenoid is preserved (Fig. 3); the hypophysial fossa and neighboring structures are missing. The preserved part of the basisphenoid is moderately narrow, convex ventrally, and forms almost the entire roof of the basipharyngeal canal.

Pterygoids preserved only their posteriormost portions, just flanking the basisphenoid and delimiting the posteriormost limit of the choanal passage. The pterygoids do

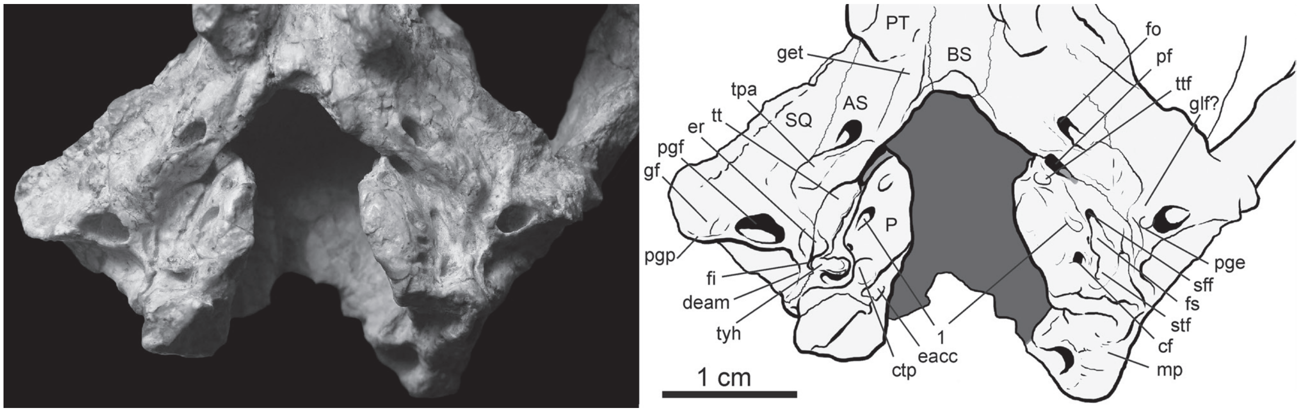

Fig. 3.—Holotype of *Eoastrapostylops riolorense* Soria and Powell, 1981 (PVL 4216), photo and line drawing of basicranium in ventral view. Abbreviations: **1,** eroded promontorium showing cochlear endocast; **AS,** alisphenoid; **BS,** basisphenoid; **cf,** cochlear fossula; **ctp,** caudal tympanic process of petrosal; **deam,** dorsal edge of external acoustic meatus; **eacc,** external aperture of the cochlear canaliculus; **er,** epitympanic recess; **fi,** fossa incudis; **fo,** foramen ovale; **fs,** facial sulcus; **get,** groove for the Eustachian (auditory) tube; **gf,** glenoid fossa; **glf?,** Glaserian fissure?; **mp,** mastoid process of petrosal; **P,** petrosal; **pf,** piriform fenestra; **pge,** postglenoid eminence; **pgf,** postglenoid foramen; **pgp,** postglenoid process; **PT,** pterygoid; **sff,** secondary facial foramen; **SQ,** squamosal; **stf,** stapedius fossa; **tyh,** tympanohyal; **tpa,** tympanic process of alisphenoid; **tt,** tegmen tympani; **ttf,** tensor tympani fossa.

not meet in the midline; their ventral margins are missing, thus, the presence of a hamular process is unknown. The entopterygoid processes originate from the base of the pterygoid flanges; they are moderately high and ventrolaterally directed. In this portion, the basipharyngeal canal is at least as high as wide. Posterior to the pterygoids, the preserved skull base is essentially a large V-shaped structure, with the arms diverging from the basisphenoid and extending posterolaterally up to the postglenoid processes. Because the squamosal-alisphenoid suture is less oblique than the main axis of the arms, the alisphenoid composition of each arm narrows towards the back, whereas the squamosal narrows to the front (Fig. 3). The alisphenoid forms the bulk of the ventral aspect of the skull between the pterygoids and the postglenoid process; however, the extension of the alisphenoid into the orbitotemporal region cannot be determined. On the ventral aspect, a deep groove for the Eustachian tube runs from the posteromedial base of the entopterygoid process to the posteromedial margin of the alisphenoid; this groove narrows anteriorly and becomes shallower at the base of the pterygoids where they merge into the rear of the choana. Soria (1987) interpreted *Eoastrapostylops* as lacking foramina ovale. The re-preparation of the holotype revealed the presence of well-defined bilateral foramina; these foramina are near the ventral edge of the alisphenoid, oval in shape, relatively large, and anterolaterally directed (Fig. 3). The position and relationships of these foramina are consistent with the foramen ovale of other mammals, for the exit of the mandibular branch of the trigeminal nerve (V_3). As is often the case in generalized therians and most SA ungulates, the foramen ovale is located near the middle of the anteroposterior length of the alisphenoid and forward from the anterior edge of the glenoid fossa. The foramina are single, with the main axis oblique (anteromedial – posterolateral), and entirely within the alisphenoids. The medial and lateral margins of the oval foramen are raised and converge posterolaterally, forming a prominent, oblique ridge directed to, but not reaching, the postglenoid foramen. The ridge is herein interpreted as a tympanic process of the alisphenoid. In this region, the exact course of the squamosal – alisphenoid suture is uncertain, but the squamosal surely contributes to the posterior or to the posterolateral portion of this elevated ridge, which would form an entoglenoid process of the squamosal. The combined tympanic process of the alisphenoid and entoglenoid process of the squamosal form the preotic crest (sensu McDowell 1958; Novacek 1986), whose rough ventral surface would have provided attachment to a now missing ectotympanic. A deep notch separates the preotic crest from the postglenoid foramen (Figs. 3–4); in other SA ungulates this feature has been interpreted as for the passage of the chorda tympani from the tympanic cavity into the temporal fossa (see Billet et al. 2015; Muizon et al. 2015, etc.). Thus, the notch represents the roof of the Glaserian fissure (or petrotympanic fissure), which was likely made into a foramen by the ectotympanic. No distinct structure for the passage of the ramus inferior of the stapedial artery could be identified; thus, this notch also could have transmitted the ramus inferior or tributaries as in other mammals (Novacek 1986; Wible 2008); a vascular occupant for the groove and notch is inviting given the large size of the structure, which is in sharp contrast with the minute size of the chorda tympani in other mammals. Posterior to the oval foramen and posteromedial to the preotic crest, the alisphenoid turns up almost vertically, deep into the tympanic cavity. There, the alisphenoid forms almost the entire anterolateral wall of the cavity (see Figs. 3–4), abutting directly with the petrosal and the tegmen tympani.

The squamosal contribution to the skull base is slightly concave anteroposteriorly and almost featureless. The glenoid fossa is barely insinuated by the concavity in front of the postglenoid process and the raised anterior margin of the postglenoid foramen (Fig. 3). The glenoid fossa is a single concavity restricted to the posterior root of the zygoma, merging into the braincase medially. There is no distinct neck and the articular surface is somewhat inclined anteroventrally with its main axis oblique. The postglenoid process is not rounded and anteroposteriorly broad, as described by Soria (1987), but a low, thin, and oblique ridge (Figs. 3, 5), very different from *Astrapotherium* and *Trigonostylops*. The postglenoid foramen is very large (as in *Astrapotherium* and *Trigonostylops*), oval (wider than longer), located entirely within the squamosal, immediately medial to the postglenoid process and well exposed in ventral view (Figs. 3–4). The margins of the foramen form a thin lip that projects ventrally, especially on the medial and posterior sides. On the left side, the elevated medial margin of the foramen bears a small tubercle (Figs. 3–4), similar to the postglenoid eminence described for *Alcidedorbignya* Muizon and Marshall, 1992, and *Pantolambda* Cope, 1882 (Muizon et al. 2015); on the right side, the tubercle is much smaller, so probably some part was lost during the preparation. The postglenoid foramen leads to a cavity within the substance of the squamosal situated medial to the postglenoid process, and thus it does not pierce the base of the process. This intra-squamosal space is part of the venous sinuses that surround the ear region in a variety of placental mammals including some native SA ungulates (Martinez et al. 2016). The posttympanic process of the squamosal is markedly more medial than the postglenoid process; it is very low, plate-like, and abuts the mastoid process of the petrosal (Figs. 4–6). A short but prominent ridge of the squamosal connects obliquely the raised posterior margin of the postglenoid foramen with the posttympanic process, and forms the dorsal edge of the external acoustic meatus; thus, the external acoustic meatus opens posterolaterally instead of the more common lateral orientation (Figs. 3–4). Because the postglenoid and the posttympanic processes are vertically short and the dorsal edge of the external acoustic meatus is prominent, the notch for the meatus is very shallow (Fig. 5) compared with that of other astrapotheres. Lateral and dorsal to the dorsal edge of the external acoustic meatus, the squamosal forms a conspicuous suprameatal fossa immediately dorsal to the external acoustic meatus, ventral to the temporal line (Fig. 5). Medial to the dorsal edge of the external acoustic meatus, the squamosal is recessed and forms part of the lateral wall of the epitympanic recess (Figs. 3–4). There is no preserved evidence of accessory sinuses of the squamosal in the auditory region (e.g., epitympanic sinus).

The petrosal is sutured to the squamosal and to the posterior portion of the alisphenoid (Figs. 3–4). Although the basisphenoid and the basioccipital are not preserved, the space surrounding the petrosal appears to be natural and very likely had no (or very little) contact with these bones, as in *Astrapotherium*. The promontorium is amygdaloid (almond-shaped), longer than wide, with its main mesiodistal axis oblique and its dorsoventral axis sloping from lateroventral to dorsomedial (Figs. 3–4). The external surface of both promontoria is partially eroded or even broken, and thus parts of the cochlear endocasts are exposed (Figs. 3, 6). At least in those parts where the external surface is preserved, there is no trace of transpromontorial sulci and we interpret this as the natural condition. There is a round depression on the rostrolateral aspect of the promontorium, posterior to the minute epitympanic wing (Figs. 3–4, 6); this fossa could be for the attachment of the tensor tympani muscle, and it is located very anterior to the fenestra vestibuli, much more than in litopterns, notoungulates, and euungulates (see O'Leary 2010; Billet et al. 2015). The fenestra vestibuli is low and long [stapedial ratio (Segall 1970) is greater than 3]; it opens laterally, at the same level as the posterior edge of the postglenoid foramen (Fig. 6). The fenestra cochleae sits in a shallow depression, the cochlear fossula, which is similar in size but more rounded, more ventral, and faces posterolaterally (Figs. 3–4, 6). The crista interfenestralis is narrow, almost horizontal, and bears no posterolateral process. The crista extends posteriorly, reaching the lateral continuation of the paroccipital process into the caudal tympanic process.

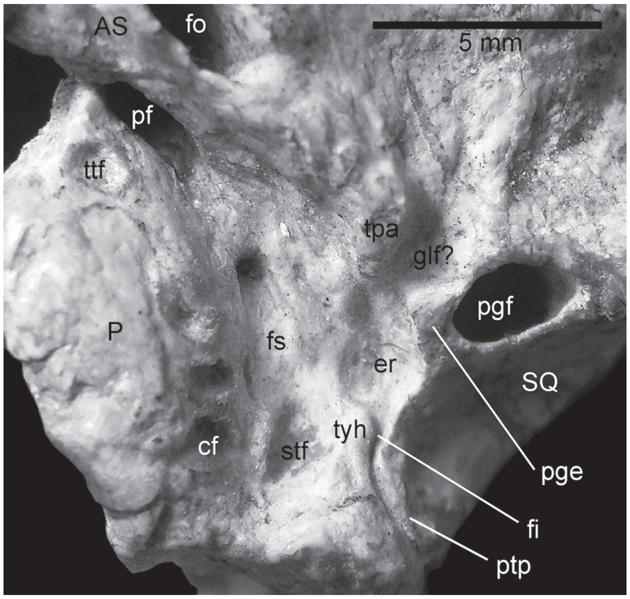

Fig. 4.—Holotype of *Eoastrapostylops riolorense* Soria and Powell, 1981 (PVL 4216), detail of left the auditory region, in ventral view. Anterior to the top. Abbreviations: **AS,** alisphenoid; **cf,** cochlear fossula; **er,** epitympanic recess; **fi,** fossa incudis; **fo,** foramen ovale; **fs,** facial sulcus; **glf?,** Glaserian fissure?; **P,** petrosal; **pf,** piriform fenestra; **pge,** postglenoid eminence; **pgf,** postglenoid foramen; **ptp,** posttympanic process of squamosal; **SQ,** squamosal; **stf,** stapedius fossa; **tyh**, base of tympanohyal; **tpa,** tympanic process of alisphenoid; **ttf,** tensor tympani fossa.

There is no evidence of an opening for the perilymphatic duct, and thus the duct almost surely runs through an enclosed canal (cochlear canaliculus). The pars cochlearis

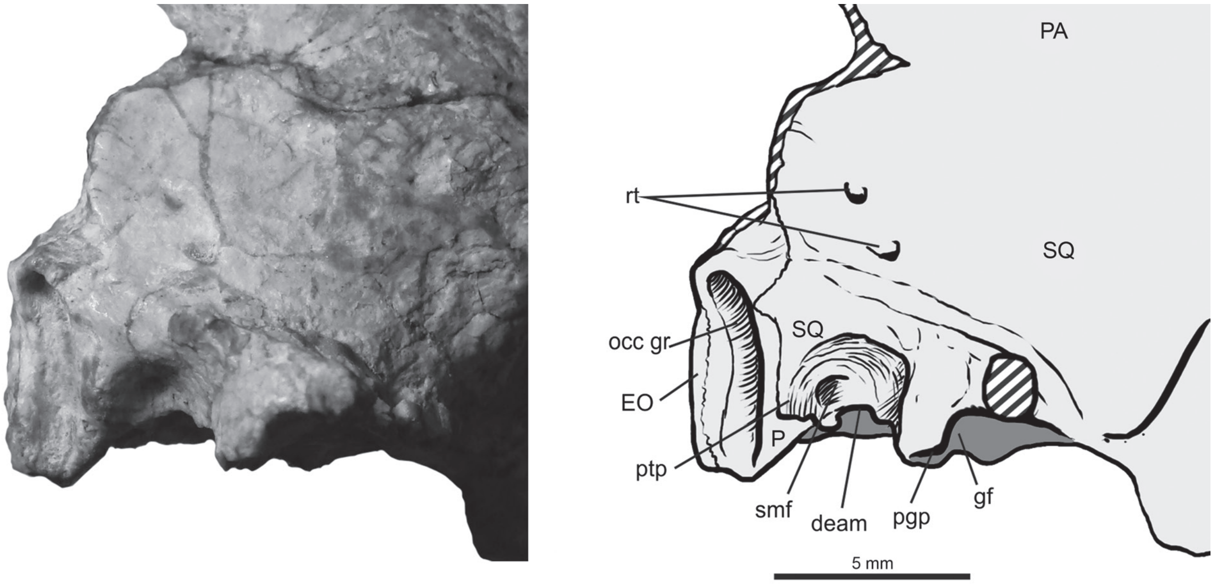

Fig. 5.—Holotype of *Eoastrapostylops riolorense* Soria and Powell, 1981 (PVL 4216), photograph and line drawing of the right braincase in lateral view. Abbreviations: **deam,** dorsal edge of the external acoustic meatus; **EO,** exoccipital; **gf,** glenoid fossa; **occ. gr.,** occipital groove; **P,** petrosal; **PA,** parietal; **pgp,** postglenoid process; **ptp,** posttympanic process of squamosal; **rt,** foramina for temporal rami; **smf,** suprameatal fossa; **SQ,** squamosal. Hatched areas indicate damaged or incomplete.

shows no trace of anterior or medial outgrowths except a small, spine-like anterior projection of the promontorium, likely representing a small, or reduced, epitympanic wing, which reaches the alisphenoid (Figs. 4, 6). Lateral to this spine, there is a narrow, long, mostly oblique gap between the posteromedial margin of the alisphenoid and the anterolateral border of the promontorium (Figs. 3–4, 6), corresponding to the piriform fenestra (McDowell 1958; MacPhee 1981). Medial to the anterior spine, the promontorium also seems to have been isolated from the alisphenoid (and probably also from the basisphenoid) by a small gap, where the medium lacerate foramen would be located. The wide and laminar tegmen tympani stretches anterolaterally from the promontorium, impinging in the lumen of the piriform fenestra, is somewhat concave, and confined to the anterolateral roof of the tympanic cavity between the alisphenoid and the promontorium (Figs. 3, 6). The tegmen tympani's anterior end is horizontal, and there are no preserved traces of ventrolateral tuberosity or epitympanic crest. The hiatus Fallopii was not identified, but the canal for the greater petrosal nerve, exposed on the right petrosal, runs anteriorly and surely opens at the anterior edge of the tegmen tympani (Fig. 3). A distinct foramen for the superior ramus of the stapedial artery appears to be absent. The crista parotica is a long, oblique (anteromedial-posterolateral) ridge, separating clearly the facial sulcus (medially) from the epitympanic recess (laterally). The epitympanic recess is a rounded, distinct depression posteromedial to, and converging with, the notch interpreted as for the passage of the chorda tympani (Figs. 3–4, 6). The medial portion of the depression is formed by the petrosal. Posteriorly, the epitympanic recess merges with a smaller, much narrower cavity, tightly appressed between the dorsal edge of the external acoustic meatus and the base of the tympanohyal (Figs. 3–4), likely to receive the crus breve of the incus, indicating this would be the fossa incudis.

The tympanohyal is attached to the posteriormost part of the crista parotica, posterior to the fenestra vestibuli; it is strongly incurved medially and its distal end contacts the caudal tympanic process of the petrosal, just posterior to the cochlear fossula (Fig. 3), although such curvature could be accentuated by post mortem deformation. The stylomastoid notch is wide, posterior to the tympanohyal and anterior to the paraoccipital process of the petrosal. The facial sulcus (MacPhee 1981) is long and open along its entire length (i.e., not a canal). The secondary facial foramen is located anterior to the fenestra vestibuli. The primary facial foramen (partially visible on the right side, where the floor of the cavum supracochleare is not preserved) is larger than the fenestra vestibuli and occupies almost the entire medial wall of the cavity for the geniculate ganglion. The stapedius fossa is deep, sub-circular, and placed posterolateral to the crista interfenestralis (Figs. 3–4, 6).

The caudal tympanic process forms a high and broad posterolateral projection of the promontorium, immediately medial to the cochlear fossula, and forms the posterior wall of the post-promontorial tympanic sinus (which is almost obliterated) and the petrosal contribution of the jugular foramen (Figs. 3, 6). The proximal portion of the caudal tympanic process bears a very superficial

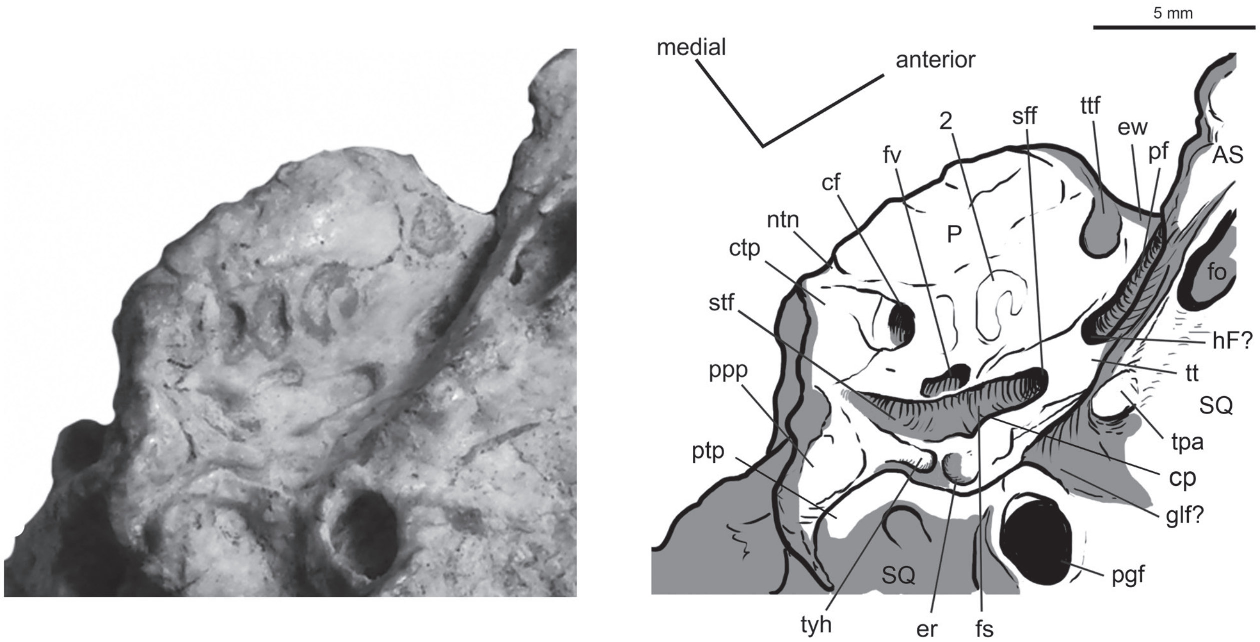

Fig. 6.—Holotype of *Eoastrapostylops riolorense* Soria and Powell, 1981 (PVL 4216), photograph and line drawing of the left ear region in ventrolateral view. Abbreviations: **2,** cochlear endocast exposure; **AS,** alisphenoid; **cf,** cochlear fossula; **cp,** crista parotica; **ctp,** caudal tympanic process of petrosal; **ew,** epitympanic wing; **fo,** foramen ovale; **fs,** facial sulcus; **fv,** fenestra vestibuli; **glf?,** Glaserian fissure?; **hF,** hiatus Fallopii; **ntn,** notch for the tympanic nerve; **P,** petrosal; **pf,** piriform fenestra; **pgf,** postglenoid foramen; **ppp,** paraoccipital process of petrosal; **ptp,** posttympanic process of squamosal; **sff,** secondary facial foramen; **SQ,** squamosal; **stf,** stapedius fossa; **thy,** base of tympanohyal; **tpa,** tympanic process of alisphenoid; **tt,** tegmen tympani; **ttf,** tensor tympani fossa.

notch close to the cochlear fossula (Fig. 6), likely for the tympanic nerve, which exits the skull at the jugular foramen (MacPhee 1981; Wible 2008, 2010). The posterior section of the caudal tympanic process joins the anterior aspect of the paraoccipital process of the petrosal, completing the posteromedial wall of the stapedius fossa. The mastoid process is a large wedge between the posttympanic process of the squamosal and the exoccipital (Fig. 3). A robust ventral expansion of the mastoid process (paraoccipital process of the petrosal) forms the posterior portion of the posttympanic process, and it extends ventrally to the squamosal contribution of the process (Fig. 6). In lateral view (Fig. 5), the mastoid exposure extends dorsally on the skull wall at least up to the level of the dorsal margin of the zygomatic arch. In the dorsalmost portion of the lateral exposure of the mastoid, a large foramen opens into a deep vertical groove, which extends ventrally almost the entire height of the mastoid, almost reaching the ventral tip of the paraoccipital process (Fig. 5). Because of its position, size, and relationships, this foramen is herein interpreted as more likely the posterior opening of the posttemporal canal (for transmission of arteria and vena diploëtica magna), instead of a mastoid foramen, and the associated groove as the occipital artery groove, a pattern similar to that predicted as primitive for eutherians (Wible 1987; Rougier et al. 1992). A very small portion of the exoccipital and its suture with the mastoid process of the petrosal is preserved on the right side of the skull (Fig. 5), probably representing the base of the paracondylar process. The external surface of this piece of bone faces posteriorly and very probably corresponds to the occipital plane. If so, at least a part of the mastoid portion of the petrosal forms a lateral part of the occipital plane and is exposed in occipital view.

The only structures discernible in endocranial view is the notch housing the external aperture of the cochlear canaliculus. It is a deep depression at the posteroventral corner of the cerebellar aspect, anterior to the proximal section of the caudal tympanic process, and thus partially visible in ventral view (Fig. 3).

In lateral view, the squamosal bears at least two conspicuous foramina for passage of the temporal rami (Fig. 5). On the left side of the skull, the anteriormost foramen is above the exit for the external acoustic meatus, dorsal to the suprameatal crest (inferior temporal line); the posterior foramen is near the contact with the lateral exposure of the mastoid process, which probably contributes to the posterior margin of the foramen. On the right side (Fig. 5), the posterior foramen is placed somewhat more anterior than on the left side, entirely within the squamosal.

Comparisons with *Astrapotherium magnum and other astrapotheres*.—In *A. magnum*, the entopterygoid processes are comparatively lower than in *E. riolorense* and the pterygoid crests extend backwards along the alisphe-

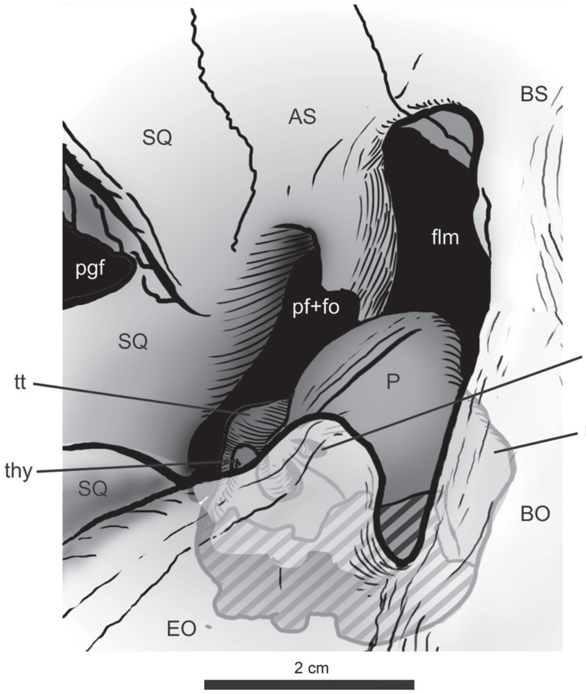

Fig. 7.—Reconstruction of the right auditory region of *Astrapotherium magnum* in ventral view, based on MACN A 3208 and 8580. Shaded areas of the petrosal represent the portions concealed by basi- and exoccipital bones. Hatched areas indicate damaged or incomplete. Abbreviations: **AS,** alisphenoid; **BO,** basioccipital, **BS,** basisphenoid; **cf,** cochlear fossula; **EO,** exoccipital; **flm,** foramen lacerum medium; **fo,** foramen ovale; **mf,** medial flange of petrosal; **P,** petrosal; **pf,** piriform fenestra; **pgf,** postglenoid foramen; **SQ,** squamosal; **thy,** tympanohyal; **tt,** tegmen tympani.

noids up to the anterior border of the tympanic cavity (as in *Trigonostylops* and *Astraponotus*). In front of the auditory cavity, the braincase base is narrow and mostly formed by the basisphenoid and alisphenoids. The basisphenoid, as well as the basipharyngeal canal, is proportionally wider than in *E. riolorense*. The grooves for the Eustachian tube run in the juncture of the basisphenoid and the pterygoid crest of the alisphenoids (i.e., not entirely within the alisphenoid). Lateral to the pterygoid crest, the alisphenoids are strongly convex anteroposteriorly and slightly concave transversally. The suture with the squamosal is oriented longitudinally, as in *Trigonostylops* and *Astraponotus* (oblique in *Eoastrapostylops*). Caudally, the alisphenoid rises very deep within the tympanic cavity forming most of its anterior wall (Fig. 7). The posterior margin does not contact the petrosal, except through a slender, somewhat triangular posterior process that forms part of the roof of the tympanic cavity. This structure is not equivalent to the tympanic process of the alisphenoid observed in *Eoastrapostylops*, which contributes to the anterior wall of the cavity. There is a large fissure between the posterior process of the alisphenoid, basisphenoid, basioccipital, and petrosal (Fig. 7). The anteromedial margin of the fissure bears a shallow notch for the Eustachian tube, flanked by the basisphenoid and the posteriormost expression of the pterygoid crest. A second fissure, more lateral and smaller, partially incising the alisphenoid, lies between the posterior process of the alisphenoid, the squamosal, and the petrosal (Fig. 7). A separate aperture for the mandibular branch of the trigeminal nerve could not be identified, neither for the carotid foramen nor the aperture of the vidian foramen. Therefore, we interpret that the largest medial fissure housed the passage for the internal carotid artery, if present, and the nerves of the pterygoid canal. The smaller, more lateral fissure would correspond in part to the piriform fenestra and would have also housed the passage of the mandibular branch of the trigeminal nerve (piriform fenestra + oval incisure).

In *Astrapotherium*, the squamosals are almost completely restricted to the base of the zygomas (as in *Astraponotus*), which are very enlarged, both laterally and anteroposteriorly. The glenoid fossa is a slight, almost transverse concavity occupying nearly the entire width of the ventral face of the zygoma. A faint ridge arises from the anterolateral base of the postglenoid process and runs obliquely up to the lateral rear of the ventral surface of the zygoma, forming the posterior limit of the glenoid cavity. The postglenoid process is very massive, somewhat wider than longer, higher on the lateral than on the medial face, and located posteromedial to the glenoid cavity, as in *Trigonostylops* and *Astraponotus*. The postglenoid foramen is very large, irregular, and located entirely within the squamosal, on the posterior (or posteromedial) base of the postglenoid process, as in *Trigonostylops* (*Astraponotus* lacks a postglenoid foramen). As noted by Billet (2010), in *Astrapotherium* (as in *Trigonostylops*), the postglenoid foramen pierces the base of the postglenoid process defining a large sinus within it. The posttympanic process of the squamosal is roughly in line (cranio-caudally) with the postglenoid process; consequently, the external acoustic meatus opens laterally, as in *Astraponotus*. The posttympanic process is plate-like, almost as high as the postglenoid process, and entirely attached to the anterior aspect of the paracondylar process of the exoccipital. Because both processes are vertically long and there is no distinct ridge connecting the processes, the notch for the external acoustic meatus in *Astrapotherium* (and in *Astraponotus*) is much deeper than in *E. riolorense*. In *Trigonostylops*, the posttympanic process is much reduced, similar to *Eoastrapostylops*, and does not connect to the paracondylar process of the exoccipital. In *Astrapotherium*, the roof of the external meatus is long (mediolaterally), featureless, with no signs of a suprameatal fossa. In all examined skulls, there is no preserved medial extension of the squamosal within the tympanic cavity; thus, its contribution to the fossa incudis is unknown. No area for attachment of the ectotympanic could be identified (nor in *Astraponotus*).

In *Astrapotherium*, the petrosal is set very deep within the auditory cavity, dorsal to, and partially hidden by the basioccipital (Fig. 7). Thus, only the ventrolateral portion of the promontorium is exposed in ventral view. The

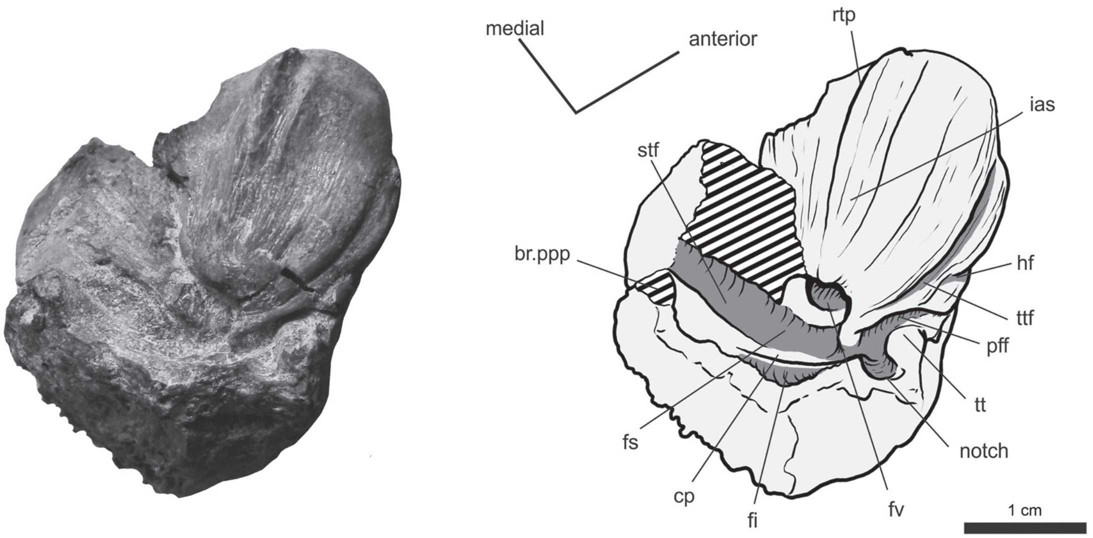

Fig. 8.—*Astrapotherium magnum*, MACN A 8580, photograph and line drawing of the left petrosal in lateroventral view. Abbreviations: **br.ppp,** broken paraoccipital process of petrosal; **cp,** crista parotica; **fi,** fossa incudis; **fs,** facial sulcus; **fv,** fenestra vestibuli; **hF,** hiatus Fallopii; **ias,** possible sulcus for the internal carotid artery; **pff,** primary facial foramen; **rtp,** rostral tympanic process; **stf,** stapedius fossa; **tt,** tegmen tympani; **ttf,** tensor tympani fossa. Hatched areas indicate damaged or incomplete

basioccipital and part of the exoccipitals and squamosals were removed from the sub-adult MACN A 8580 in order to get a better exposure of the petrosal. In ventral view, the petrosal is roughly triangular, narrower but hemispherical anteroventrally, and wider and flat posterodorsally (Fig. 7). Unlike in *E. riolorense*, there is a moderate crest-like medial outgrowth running along the posterior half of the pars cochlearis, although it has no contact with the basioccipital bone. Anteriorly, there is no preserved trace of the epitympanic wing, and the only contact with the alisphenoid is through the slender posterior process of the latter described above. Laterally, it would have a feeble, likely un-sutured contact with the squamosal. The promontorium in *Astrapotherium* is globular (Figs. 7–8), as in *Astraponotus*, proportionally much higher and shorter than in *Eoastrapostylops*. A crest-like rostral tympanic process crosses obliquely the ventrolateral aspect of the promontorium, from its ventral apex to the crista interfenestralis. The tympanic surface of the promontorium is sculptured by a set of crests and grooves slightly diverging from a point near the fenestra vestibuli, roughly parallel to the rostral tympanic process (Fig. 8). Among these grooves, the deeper one is set on the anterolateral face of the promontorium, and probably accommodated the tensor tympani muscle. Another conspicuous groove, possibly for the internal carotid artery, is defined between the rostral process and an anterior accessory crest. The hiatus Fallopii is represented by a constricted orifice on the anterior base of the promontorium (Fig. 8). The fenestra vestibuli and cochlear fossula are minute apertures on the base of the promontorium. The former faces laterally; the latter faces posteriorly. The crista interfenestralis is broad and almost vertical. The anterior portion of the pars canalicularis is represented by a narrow platform between the promontorium and the squamosal, which sinks anteriorly very deep into the auditory cavity (inclined posteroventrally–anterodorsally) (Fig. 7). The only structures distinguishable on this platform are an extremely faint crista parotica running from the base of the tympanohyal, and the very shallow facial sulcus medial to the crista (Fig. 8). A narrow depression lateral to the crista parotica likely represents the fossa for the crus breve of the incus, with no distinct depression for the epitympanic recess. The tegmen tympani is a massive and short knob at the anterolateral corner of the petrosal. It is separated from the crista parotica by a semicircular notch that leads to the canal for the greater petrosal nerve (Fig. 8). This notch could be for the passage of the ramus superior of the stapedial artery, although the passage could be anterior to the tegmen tympani (following the pattern suggested by Billet and Muizon 2013: fig. 8), where the tegmen is likely damaged. The stapedius fossa is very deep and continuous with the facial sulcus. The post-promontorial tympanic sinus is ample and shallow, separated from the stapedius fossa by a distinct crest derived from the lateral margin of the cochlear fossula. The caudal tympanic process is low and does not isolate the post-promontorial tympanic sinus from the very developed jugular notch. The mastoid process is not completely preserved in the dissected specimen MACN A 8580 of *Astrapotherium*; the proximal portion is robust and somewhat irregular. As noted by Simpson (1933), there is no exposure of the mastoid process due to the strong extroversion of the exoccipital on the occipital plane, and thus the exposed portion of the posttemporal canal is formed exclusively by the squamosal and the exoccipital. A similar structure is observed in *Astraponotus*, whereas in *Trigonostylops* there is not extroversion of

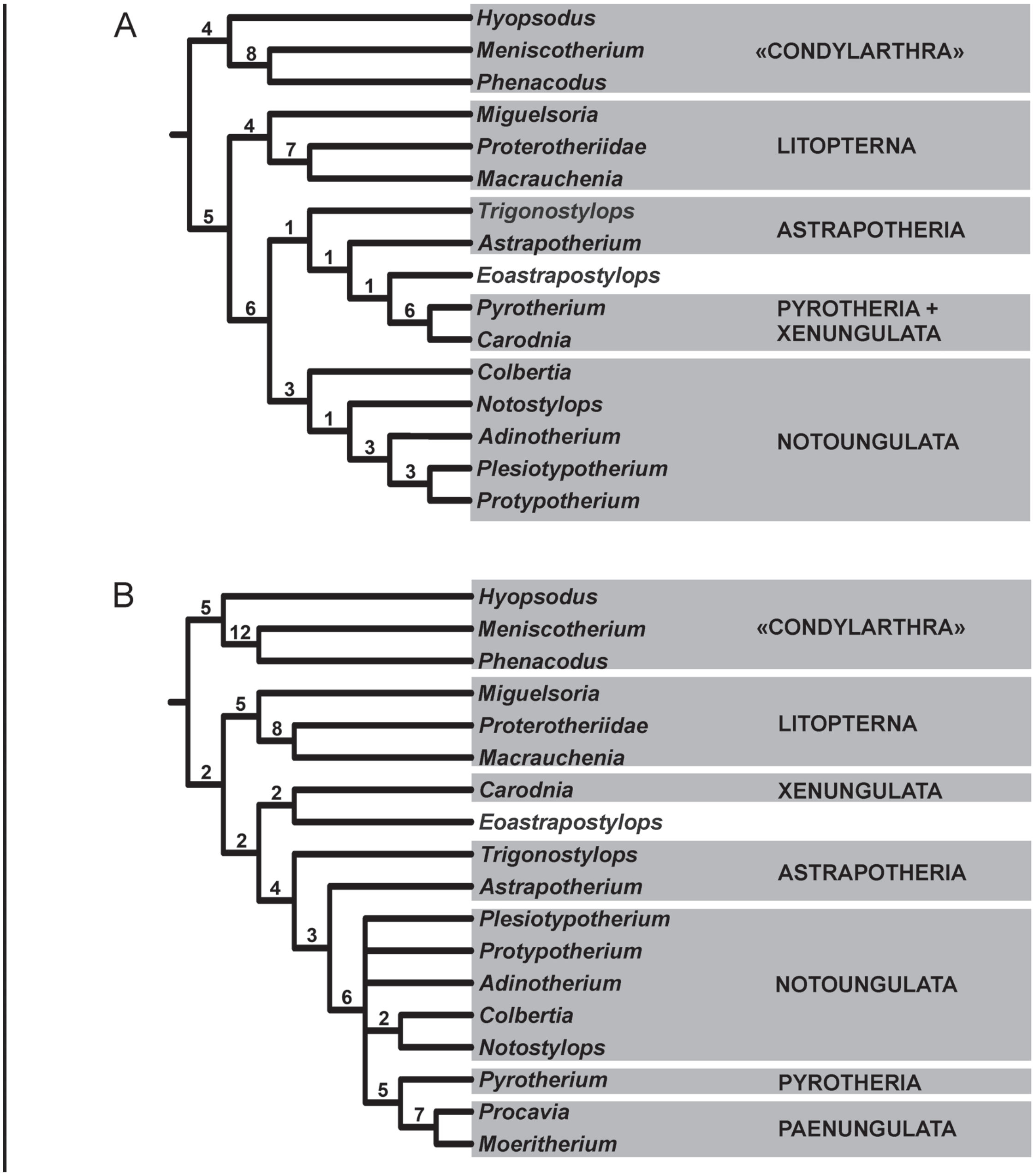

Fig. 9.—Results of the cladistics analyses based on the revised version of the data matrix of Muizon et al. (2015) and enlarged with the inclusion of *Eoastrapostylops*. **A**, detail of the strict consensus tree (3494 steps) of the three most parsimonious trees (3476 steps, ci = 0.176, ri = 0.493) obtained with the backbone constraint as defined by Muizon et al. (2015: figs. 121–122); **B**, detail of the strict consensus tree of the six most parsimonious trees (3423 steps, ci = 0.178, ri = 0.502) obtained from the unconstrained analysis. Numbers above the nodes are Bremer support values. The complete data matrix is shown in Appendix 4.

the exoccipital and thus the mastoid is well exposed.

In lateral view, the squamosal of *Astrapotherium* bears a variable number of foramina for passage of the temporal rami. In *Eoastrapostylops*, additional foramina are set within the parietals and near the suture with the squamosal, as in *Astraponotus* and *Trigonostylops*.

PHYLOGENETIC AFFINITIES

Soria and Powell (1981) and Soria (1987) interpreted that *Eoastrapostylops* is morphologically closer to *Astrapo-*

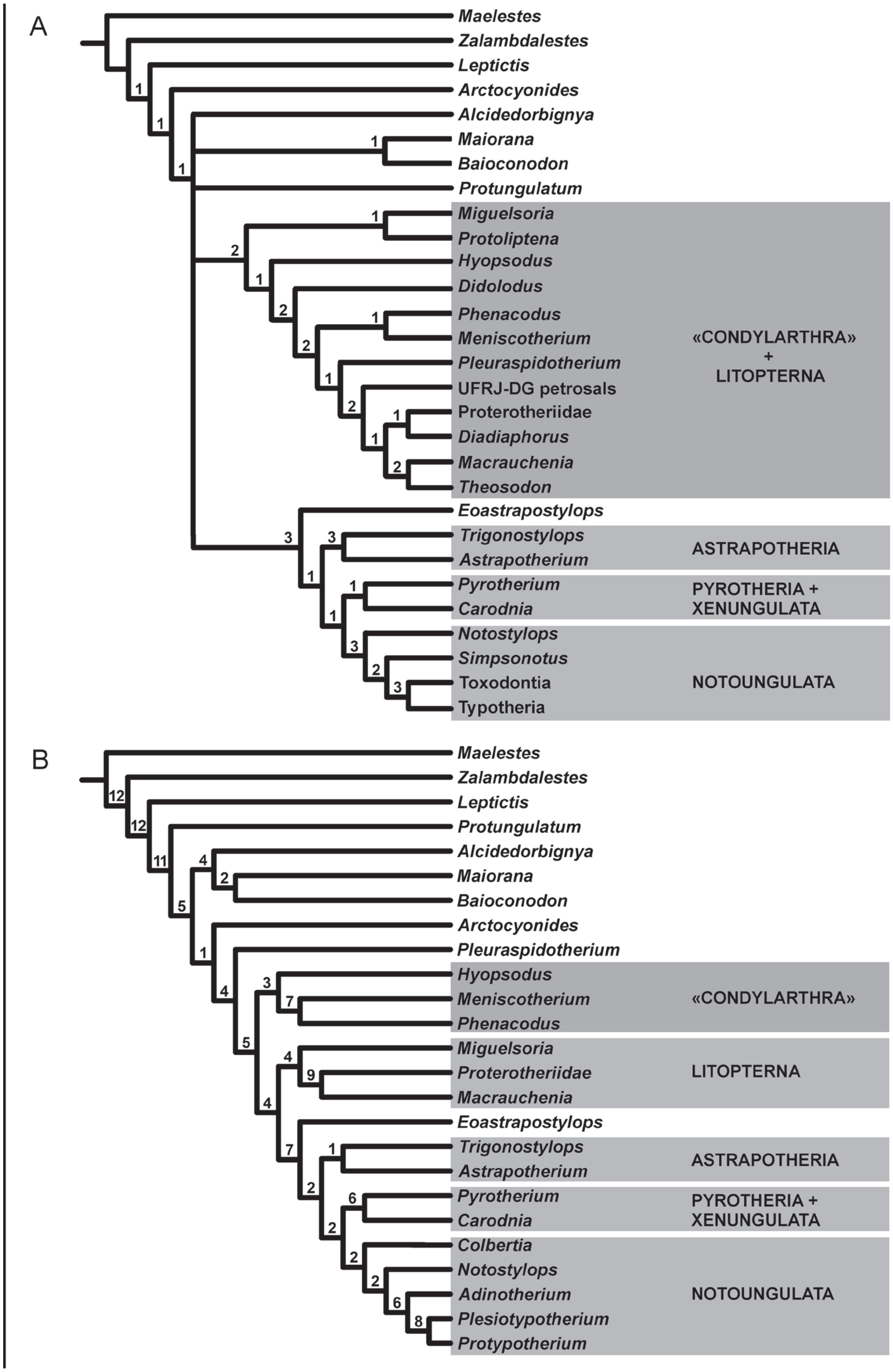

Fig. 10.—Results of the cladistics analyses based on the revised version of the data matrix of Billet et al. (2015) and enlarged with the inclusion of *Eoastrapostylops*. **A**, strict consensus tree of the 12 most parsimonious trees (482 steps, ci = 0.37, ri = 0.71) obtained from the parsimonious analysis based on the data matrix of Billet et al. (2015). Except *Notostylops* and *Simpsonotus*, the notoungulate taxa are depicted grouped by subordinal rank for graphical purpose. The complete data matrix is shown in Appendix 7; **B**, single most parsimonious trees (1275 steps, ci = 0.41, ri = 0.47) resulted from the parsimony analysis of the combined matrices of Muizon et al. (2015) and Billet et al. (2015), with the exclusion of the xenarthran taxa. Numbers above the nodes are Bremer support values. The complete data matrix is shown in Appendix 9.

theria and Trigonostylopoidea than to any other group of South American ungulates, and concluded that *Eoastrapostylops* is the most primitive astrapothere known so far. Certainly, the dentition of *Eoastrapostylops* resembles in many aspects that of the early diverging astrapothere *Trigonostylops* (see Soria 1987, 1988), but it strongly differs from that of *Astrapotherium* and other advanced astrapotheres, except by the presence of enlarged canines. Concerning the cranial morphology, Soria (1987) found very few simliarities with the compared astrapotheres, and also remarked on some superficial resemblances with some pantodonts. Our comparisons between the auditory region of *Eoastrapostylops* and *Astrapotherium* also revealed significant differences in the shape and relationships of the preserved structures. On the other hand, *Eoastrapostylops* exhibits many features that more closely resemble those known in condylarths and litopterns: foramen ovale distinct from piriform fenestra, petrosal with flat promontorium, with no trace of medial flange, large stapedial ratio, epitympanic recess distinct from fossa incudis, etc., although some of these features very likely are plesiomorphies. Additionally, other features are shared with the pantodont *Alcidedorbignya*, such as the presence of a strong preotic crest and the very unusual presence of a postglenoid eminence of the squamosal. It is thus clear that different sets of characters bear slightly different, and partially conflicting, phylogenetic information, suggesting a broader approach is desirable.

In order to test the putative astrapothere affinities of *Eoastrapostylops* integrating dental and basicranial features, we conducted a set of cladistics analyses based on modified versions of previously published data matrices. For these analyses, we used both the holotype of *E. riolorense* and the paratype (PVL 4217, a partial anterior portion of skull and mandible with fully erupted m3).

The first analysis is based on the data matrix recently published by Muizon et al. (2015), which is modified from that of Wible et al. (2009). This data matrix (72 taxa x 426 characters) was essentially conceived in order to test the relationships of *Alcidedorbignya* and Pantodonta within placentals; it encompasses a large sample of fossil and extant mammals corresponding to the main placental clades (Afrotheria, Xenarthra, Euarchontaglires, and Laurasitheria), as well as many non-placental mammals as outgroups. It also includes representatives of the main groups of native South American “ungulates” (three Litopterna, two Astrapotheria, one Pyrotheria, one Xenungulata, and five Notoungulata); thus, it is also suitable for evaluation of the relationships of the endemic South American groups in a large systematic scale, but not for a detailed discussion of the relationships among these groups. The complete list of characters, as defined by Muizon et al. (2015), is provided in Appendix 2. In addition to *Eoastrapostylops*, we incorporated some modifications to the scoring of the two astrapothere taxa originally included in this data matrix, *Astrapotherium* and *Trigonostylops*; some of these changes are based on the above description of the ear anatomy of *Astrapotherium*. The re-scoring of these characters in the astrapothere taxa are discussed in the Appendix 3. The terminal taxa “*Proterotherium*” included in the original matrix by Muizon et al. (2015) is herein re-named as Proterotheriidae, as the specimens used for scoring (Muizon et al. 2015: appendix 2), all from the early Miocene Santacrucian Age, are not congeneric with the genotype species *Proterotherium cervioides* Ameghino, 1883 (late Miocene), but they belong to different species of *Tetramerorhinus* Ameghino, 1894, and *Anisolophus* Burmeister, 1885 (see Soria 2001). The complete new data matrix, with the scoring of the 426 characters defined by Muizon et al. (2015) in *Eoastrapostylops* and the corrected scorings in *Trigonostylops* and *Astrapotherium*, is shown in Appendix 4. The parsimony analysis was conducted with the TNT program (Goloboff et al. 2008) by a traditional search with 1000 replications using the TBR algorithm option. The analysis was performed using the backbone constraint defined by Muizon et al. (2015) forcing the monophyly of the four major extant placental clades (Xenarthra, Afrotheria, Euarchontoglires, Laurasiatheria) based on molecular phylogenies (e.g., Stanhope et al. 1998; Waddell et al. 1999; Madsen et al. 2001; Murphy et al. 2001; Springer et al. 2007; O’Leary et al. 2013), but with *Macrauchenia* Owen, 1838, as the only South American ungulate included in the molecular scaffold, following Welker et al. (2015).

The constrained analysis resulted in three most parsimonious trees (3476 steps, consistency index = 0.176, retention index = 0.493). The strict consensus (3494 steps) is shown in Figure 9A. In all the MPTs, *Eoastrapostylops* is nested within the clade including all the analyzed astrapotheres, notoungulates, pyrotheres, and xenungulates (the Meridiungulata clade), but more closely related to the clade formed by *Pyrotherium* Ameghino, 1888, and *Carodnia* Simpson, 1935, than to the astrapotheres. This affiliation is supported by dental and mandibular features [(characters 63(0), 140(0), 142(0), 146(1), and 159(2)]. Moreover, Astrapotheria is not recovered as monophyletic, and *Pyrotherium* is recovered closer to astrapotheres than to notoungulates. The same results are obtained when the constrained analysis is performed with the same molecular scaffold as in Muizon et al. (2015) (i.e., all the notoungulates, litopterns, and *Pyrotherium* included within Laurasitheria). These results contrast with those of Muizon et al. (2015) and to other previous phylogenetic proposals focused on phylogeny of the South American ungulates (Billet 2010; Billet and Muizon 2013; Billet et al. 2015), in which *Pyrotherium* is closer to (or even nested within) Notoungulata, and Astrapotheria (i.e., *Trigonostylops* and *Astrapotherium*) is recovered as monophyletic. Additionally, we performed a further parsimony analysis without backbone constraints. The unconstrained analysis resulted in six MPTs (3423 steps, see Fig. 9B), in which *Eoastrapostylops* clusters with *Carodnia* in a clade separate from that encompassing the astrapotheres, notoungulates, and *Pyrotherium.* Nevertheless, these results reveal a high level of homoplasy in the dataset, and therefore the resulting trees are very unstable as minor modifications of taxa or characters may alter significantly their topology.

A second parsimony analysis was conducted with the data matrix of Billet et al. (2015; 48 ingroup taxa x 156 morphological characters). As remarked by Billet et al. (2015), this matrix was not conceived primarily for the discussion of the relationships of the extinct South American ungulates with the main placental clades, but rather to test the affinities of an individual South American taxon identified by a particular set of characters (mostly dental and petrosal). This latter data matrix provides the most exhaustive covering of South American endemic placentals and other extinct "ungulates" to date (mostly notoungulates), and focuses on dental and petrosal characters, most of which are well documented in *Eoastrapostylops*. Assuming the meridiungulate affinities of *Eoastrapostylops* inferred in the previous analysis, this matrix is suitable for the discussion of its relationships with the astrapotheres and other South American ungulates at a lower systematic scale. The complete list of characters and character states, as defined by Billet et al. (2015), is provided in Appendix 5.

In addition to *Eoastrapostylops*, we included in the analysis the xenungulate *Carodnia* (not considered by Billet et al. 2015) and we excluded the xenarthran taxa because the assessment of the affinities of *Eoastrapostylops* within Meridiungulata does not require comparisons with xenarthrans. Moreover, we incorporated some changes to the scoring of *Astrapotherium* and *Trigonostylops*. The re-scoring of these characters in the astrapothere taxa are discussed in the Appendix 6. The terminal taxa "*Proterotherium*" in the original matrix by Billet et al. (2015) is herein re-named as Proterotheriidae, as discussed above. The complete data matrix includes the 156 characters defined by Billet et al. (2015) scored in 47 ingroup taxa (*Maelestes* Wible et al., 2007, as the outgroup), shown in Appendix 7.

The analysis resulted in 12 most parsimonious trees of 482 steps, with a comparatively lower degree of homoplasy (retention index = 0.71). The strict consensus tree is shown in Figure 10A. *Eoastrapostylops* clusters with none of the astrapothere taxa sampled in this analysis (*Astrapotherium* and *Trigonostylops*), but it is recovered as the sister group of the clade containing the astrapotheres, pyrotheres, xenungulates, and notoungulates analyzed here. *Eoastrapostylops* is excluded from this latter clade by lacking the following synapomorphies: metaloph in upper molars (character 25), foramen ovale merged with piriform fenestra (character 110), promontorium globose (character 128), expanded medial flange of petrosal (character 129), and low stapedial ratio (character 136). *Astrapotherium* and *Trigonostylops* share three synapomorphies: choanae posterior to last molar (character 81), postglenoid foramen piercing deeply postglenoid process (character 108), and hypoglossal and jugular foramina in a common depression (character 113); the first two characters are absent in *Eoastrapostylops* and the last is unknown. Additionally, *Eoastrapostylops* shares a single apomorphy with *Trigonostylops* (metacone distinct from paracone on posterior premolars, character 41), and shares no apomorphy with *Astrapotherium*. The possession of enlarged canines (character 18), implicitly interpreted by Soria (1987, 1988) as linking *Eoastrapostylops* with the astrapotheres, is rendered a plesiomorphy by the tree topology.

A third parsimony analysis was conducted with a new data matrix built by combination of the matrices of Muizon et al. (2015) and Billet et al. (2015). The new matrix includes those taxa shared by both matrices, with the addition of *Eoastrapostylops* and the xenungulate *Carodnia* (not included by Billet et al. 2015), and the exclusion of the xenarthran taxa, as discussed above. The character sampling includes the 426 characters of the matrix by Muizon et al. (2015) (although many characters become non-informative with this new taxon sampling), and 87 characters selected from Billet et al. (2015) (the remaining characters are totally or partially redundant). All the characters and characters states taken from Muizon et al. (2015: characters 1 to 426) are treated as in the Appendix 2, except the character 271 (absence/presence of postglenoid process), to which a third state was added in order to capture the condition in *Eoastrapostylops* and in astrapotheres (i.e., very large postglenoid foramen). The character states are redefined as follows: Postglenoid foramen: (0) absent; (1) present, small, width less than one third the width of the postglenoid process; (2) present, large, width more than one third the width of the postglenoid. The remaining characters were scored as in the original matrices of Muizon et al. (2015) and Billet et al. (2015), except the same modifications to the scoring of the two astrapothere taxa *Astrapotherium* and *Trigonostylops* discussed in the Appendices 3 and 6. The complete new data matrix includes 513 characters scored in 24 ingroup taxa (*Maelestes* as the outgroup), as shown in the Appendix 9.

The analysis resulted in a single most parsimonious tree (Fig. 10B) of 1275 steps, also with a high degree of homoplasy (retention index = 0.47). As in the preceding analyses, *Eoastrapostylops* clusters with none of the astrapothere taxa sampled in this analysis (*Astrapotherium* and *Trigonostylops*), but it is recovered as the sister group of the clade containing the astrapotheres, pyrotheres, xenungulates, and notoungulates analyzed here. *Eoastrapostylops* is excluded from this latter clade by lacking the following synapomorphies: enlarged upper diastema (character 4(2)), procumbent anteriormost lower incisor (20(1)), metaconid and paraconid distinctly separated on p3 (58(2)), large lower molars entoconid (130(2)), exit of V_3 between petrosal and alisphenoid (259(1)), foramen ovale on ventral surface of the skull facing ventrally (260(1)), entoglenoid process of the squamosal absent (276(0)), globose promontorium (293(1)), and presence of upper molars metaloph (437(1)). *Astrapotherium* and *Trigonostylops* share three synapomorphies: enlarged lower diastema (5(1)), postglenoid foramen piercing deeply the postglenoid process (487(1)), and hypoglossal and jugular foramina in a common depression (490(1));

the first two are absent in *Eoastrapostylops* and the last is unknown. Additionally, *Eoastrapostylops* does shares apomorphies with *Astrapotherium* or with *Trigonostylops*. The possession of enlarged canines (character 433), interpreted by Soria (1987, 1988) as linking *Eoastrapostylops* with the astrapotheres, is rendered a plesiomorphy by the tree topology

Although weakly conclusive due to high homoplasy, our results have interesting implications for the relationships of other meridiungulate taxa that can be compared with those of previous analyses. Billet (2010, 2011) concluded that *Pyrotherium* is closely related to *Notostylops* Ameghino, 1897, both nested within Notoungulata; the same result was obtained by Billet et al. (2015), although these analyses did not include *Carodnia* or other xenungulate taxa. The unconstrained analysis of Muizon et al. (2015: fig. 120), as well our unconstrained analysis (Fig. 9B), also supports the inclusion of *Pyrotherium* and Notoungulata in a clade that also encompasses the paenungulates, and separated from *Carodnia*. On the contrary, when the analysis is constrained to the evolutionary scenario defined by molecular phylogenies, the results of Muizon et al. (2015: figs. 121–122) and our results (Fig. 9A) do not support the inclusion of *Pyrotherium* within Notoungulata, but *Pyrotherium* clusters with *Carodnia* as sister group of Notoungulata. The results of the unconstrained analysis of Muizon et al. (2015: fig. 120) support the inclusion of the xenungulate *Carodnia* within Pantodonta (see Muizon et al. 2015 for discussion). Our results of the same analysis, modified essentially by the simple addition of *Eoastrapostylops*, do not support the affinity of *Carodnia* with Pantodonta, but with the meridiungulates, closely related to *Eoastrapostylops* (Fig. 9B).

CONCLUSIONS

Eoastrapostylops was originally interpreted as a basal astrapothere by Soria (1987, 1988), essentially by having enlarged canines, as in all later astrapotheres. The re-preparation of the basicranum of *E. riolorensis* generated novel anatomical information and the recognition of a relatively generalized ear region. The new data led us to reassess the affinities of *E. riolorensis* within a broad cladistics framework combining dental, cranial, and mandibular characters.

The results of the cladistics analyses presented here are derived from modifications of the matrices of Muizon et al. (2015) and Billet et al. (2015). The first one was conceived for the evaluation of the relationships of *Alcidedorbignya* with the main placental clades and with the SA ungulates, whereas the latter was intended for exploring the contribution of new petrosal data to the reconstruction of the relationships among the SA ungulates (Billet et al. 2015: 958). A third analysis was conducted combining both matrices. Although we find no conflict with the combination of these large datasets that were previously aimed at different taxonomic scopes, further analyses could eventually reveal that some characters require a redefinition to apply to a larger taxonomic scale.

As identified in previous analyses of deep nodes of placental mammals phylogeny (e.g., Muizon et al. 2015 and references therein), the results of the analyses performed herein detected a high level of homoplasy in the dataset. Consequently, the results are labile and not fully conclusive, but they bring motivating implications on the relationships of *Eoastrapostylops* with other SA ungulates.

Our results of the cladistic analyses based on the matrix of Muizon et al. (2015) suggest that *Eoastrapostylops* is part of the meridiungulate radiation that gave origin to astrapotheres, pyrotheres, and notoungulates. The results of the analyses based on the data matrix of Billet et al. (2015) and on that built assembling the latter with the matrix of Muizon et al. (2015) give rise to a consistent scenery for SA ungulate systematics, especially when xenarthrans are removed from the analysis. Opposed to Soria`s (1987) opinion, *Eoastrapostylops* would have diverged before the differentiation of astrapotheres, pyrotheres, and notoungulates. Therefore, *Eoastrapostylops* can be included neither within Astrapotheria nor within another clade of ordinal rank. Based on these results, and accepting the early Eocene age of the Itaboraian fauna (Woodburne et al. 2014), there is no Paleocene record for Astrapotheria yet. *Tetragonostylops apthomasi* (Itaboraian) and the putative astrapothere *Shecenia ctineru* Simpson, 1935 (Cañadon Hondo fauna, Itaboraian?) represent the oldest record of the order. The occurrence of a possible notoungulate in the Tiupampa fauna (early Paleocene of Perú, Muizon 1992) suggests that the absence of astrapotheres in the pre-Itaboraian record is due to a sampling bias.

Additionally, our results highlight the absence of a clear phylogenetic signal concerning pyrotheres and xenungulates. The inclusion of *Pyrotherium* within Notoungulata, as proposed by Billet (2010, 2011) is not supported in our analyses, but its position as the sister group of Notoungulata is weakly supported. The inclusion of *Pyrotherium* and *Carodnia* within Notoungulata (as sister groups of *Notostylops*) requires only two additional steps. We prefer to keep Pyrotheria as a separate group; the recognition of it as an order or not is semantic, but for the sake of stability it should be kept until more information becomes available, especially regarding basal pyrotheres.

Eoastrapostylops and other Early Paleogene meridiungulates still have unclear ordinal position. This is particularly the case of the Notopterna, considered by Soria (1989) as a separate, short-lived lineage that diverged from the common ancestor of Astrapotheria, Pyrotheria, and Notoungulata, but later considered as a subclade of Litopterna (Bonaparte and Morales 1997). More recently, García López and Babot (2014) presented a preliminary result of a cladistics analysis in which the notoptern *Indalecia grandensis* Bond and Vucetich, 1983, resulted as the sister-taxon of astrapotheres and notoungulates, which is essentially the same position we recover in our analyses for *Eoastrapostylops* (Fig. 10). The mounting evidence suggests that these SA ungulates represent independent basal radiations of the early evolution of the meridiungulates before the differentiation of most of the main clades (i.e., Astrapotheria, Pyrotheria, and Notoungulata). If the tree topology presented here is corroborated by further studies and new materials, the evolution of the native SA ungulates involved a more diverse and time-layered process than previously recognized. Much is yet to be discovered, both by study of the detailed anatomy of the known specimens and by the recovery of new forms in the field. SA ungulate studies have focused on dental morphology out of necessity and by tradition; the incorporation of the complex and rich data afforded by craniomandibular anatomy, postcranial morphology, and to some extent molecular research are harbingers of great promise.

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We dedicate this contribution to the memory of our friend and colleague, the late geologist and paleontologist Jaime Eduardo Powell (Jimmy) from Facultad de Ciencias Naturales e Instituto Miguel Lillo, Universidad Nacional de Tucumán. He was well known for his pioneering contributions to the geology and paleontology of northwestern Argentina. Jaime was the finder of the specimens of *Eoastrapostylops riolorense* studied here from the locality of Río Loro, and he loaned to one of us (MB) the materials for the re-study presented herein. His unexpected and premature death in February 2016 was a great loss to all of us. We are especially indebted to Guillaume Billet (MNHN, Paris) and an anonymous reviewer for their very useful and constructive suggestions that greatly improved a previous version of the manuscript. Our thanks also to Maximiliano Iberlucea for the skillful mechanical preparation of the studied specimens, to the artist Jorge Gonzalez for his help with the making of the schematic drawings, to Dr. Cynthia Corbitt for language and editing help, and to M. Ezcurra (MACN) for his help with the phylogenetic analysis. This project was partially supported by the Consejo Nacional de Investigaciones Científicas y Técnicas de Argentina (CONICET) and the Department of Anatomical Sciences and Neurobiology, University of Louisville, USA.

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APPENDIX 1

Additional comments on the skull of *Eoastrapostylops riolorense*

The description made by Soria and Powell (1981) of the holotype PVL 4216 and paratype PVL 4217, with the supplementary descriptions and comments made by Soria (1984, 1987, 1988) described fairly well all the principal features observed in the skull and teeth as they were originally prepared. Subsequent to this, additional preparation of the known specimens (excepting MACN 19040, which to the present could not be located again) was made, allowing us to observe new aspects and features of the skull, especially of the basicranial region, which is the main object of this work. The cleaning of the skulls also uncovered some other aspects that deserve comments.

As stated by Soria and Powell (1981) and Soria (1988), the absence of the P1 in PVL 4217 and its presence in PVL 4216 could be interpreted as a case of sexual dimorphism. Cleaning of the area around the C1 in PVL 4127 shows the presence on both sides of the root of the P1. Therefore, this tooth is present in both specimens, PVL 4216 and 4217, and there is no argument to presume a sexual difference between them.

Also, the removal of the matrix on the top of the skull of PVL 4216 shows that part of the dorsal surface of the rostrum was lost, and there are two cavities on each side of the cranium, lateral to the remaining parts of the long nasals. These cavities, instead of being some kind of sinus area, are interpreted as the open, wide base of the C1, which are very profoundly implanted in the cranium and extend almost to the anterior limit of the orbits.

APPENDIX 2

(continued on next page)

List of characters and character states used for the phylogenetic analysis based on the data matrix of Muizon et al. (2015) presented in Figures 9A–B.

Dentition general

1. Teeth: (0) present; (1) absent (Wible et al. 2009: ch. 1).
2. Teeth: (0) differentiated into morphological type (incisors, canines, premolars, molars) with enamel; (1) homodont and peg-like without enamel (Wible et al. 2009: ch. 2).
3. Number of postcanine tooth loci: (0) eight or more; (1) seven; (2) six; (3) or five or less (Rougier et al. 1998: ch. 7); ORDERED.
4. Upper diastema: (0) small, between incisors and canine; (1) small, between canine and premolars; (2) enlarged; (3) absent (Wible et al. 2009: ch. 4).
5. Lower diastema behind incisors: (0) absent or small; (1) enlarged (Wible et al. 2009: ch. 5).
6. Dental eruption timing vs cranial growth: (0) early; (1) late (adult size reached prior to complete eruption of permanent cheek teeth; specimens with 95% median adult jaw length and less than 60% of their permanent, occluding premolars and molars erupted (Asher and Lehmann 2008).

Incisors

7. Incisor shape: (0) root and crown are straight and continuous in length; (1) form a continuous curve (Asher et al. 2005: ch. 3).
8. Number of upper incisors: (0) five; (1) four; (2) three; (3) two; (4) one; (5) none (Wible et al. 2009: ch. 7); ORDERED.
9. Number of lower incisors: (0) four; (1) three; (2) two; (3) one; (4) none (Wible et al. 2009: ch. 8); ORDERED.
10. Position of anteriormost upper incisors (or alveoli): (0) contacting medially or closely approximated; (1) widely separated (Wible et al. 2009: ch. 9).
11. Upper incisors relative size: (0) subequal; (1) anteriormost is the largest (close to twice the size of following incisors); (2) second anteriormost is the largest (close to twice the size adjacent incisors); (3) third anteriormost is the largest (close to twice the size adjacent incisors) (Muizon et al. 2015: ch. 11).
12. Anteriormost upper incisor shape: (0) conical; (1) mediolaterally compressed; (2) anteroposteriorly compressed; (3) cuspate (one major and one minor); (4) spatulate (Wible et al. 2009: ch. 11).
13. Anteriormost lower incisor shape: (0) conical; (1) mediolaterally compressed; (2) anteroposteriorly compressed; (3) cuspate (one major and one minor); (4) spatulate (Wible et al. 2009: ch. 16).
14. Anteriormost upper incisor procumbent: (0) absent; (1) present (Muizon et al. 2015: ch. 14).
15. Second anteriormost upper incisor projecting anteriorly: (0) absent; (1) present (Billet 2010: ch. 9, modified).
16. Anteriormost upper incisor root: (0) closed; (1) open extending in premaxilla only; (2) open extending in maxilla (Asher et al. 2005: ch. 52; Wible et al. 2009: ch. 12).
17. Anteriormost incisor enamel: (0) surround tooth; (1) discontinuous posteriorly (Asher et al. 2005: ch. 49; Wible et al. 2009: ch. 13).
18. Ultimate upper incisor: (0) in premaxilla; (1) between maxilla and premaxilla; (2) or in maxilla (Wible et al. 2009: ch. 14).
19. Anteriormost lower incisor size: (0) small and subequal to subsequent incisors; (1) greatly enlarged; (2) greatly reduced (Archibald et al. 2001: ch. 28; Wible et al. 2009: ch. 15).
20. Procumbent anteriormost lower incisor: (0) absent; (1) present (Archibald et al. 2001: ch. 29; Wible et al. 2009: ch. 17).
21. Anteriormost lower incisor root: (0) closed; (1) open (Archibald et al. 2001: ch. 32; Wible et al. 2009: ch. 18).
22. Anteriormost lower incisor root length: (0) not extended posteriorly below p1; (1) extending posteriorly below p1; (2) extending posteriorly below penultimate or ultimate premolar; (3) extending posteriorly below molars (Archibald et al. 2001: ch. 32); ORDERED.
23. Anteriormost lower incisor enamel: (0) covers the whole incisor or (1) discontinous posteriorly (Archibald et al. 2001: ch. 30).
24. Procumbent posterior lower incisors: (0) absent; (1) present (Wible et al. 2009: ch. 21).
25. Staggered lower i3: (0) absent; (1) present (Hershkovitz 1982).
26. Shape of incisor arcade: (0) transverse; (1) U-shaped; (2) sharply angled at I1s (V-shaped) or parallel-sided (Muizon et al. 2015; modified from Springer et al. 1997: ch. 25; Horovitz and Sánchez-Villagra 2003: ch. 161; Ladevèze and Muizon 2007: ch. 8).

Canines

27. Upper canine: (0) large; (1) reduced; (2) absent (Meng et al. 2003: ch. 23); ORDERED.
28. Roots of upper canines: (0) two roots; (1) one root (Rougier et al. 1998: ch. 10; Wible et al. 2009: ch. 24).
29. Lower canine: (0) large; (1) reduced; (2) absent (Meng et al. 2003: ch. 25); ORDERED.
30. Roots of lower canines: (0) two roots; (1) one root (Rougier et al. 1998: ch. 44; Wible et al. 2009: ch. 26).
31. Procumbent lower canine: (0) absent; (1) present (Wible et al. 2009: ch. 27).
32. Canines diverging externally, uppers and/or lowers: (0) absent; (1) present (Muizon et al. 2015).

APPENDIX 2
(continued from previous page)

Premolars

33. Number of premolars: (0) five; (1) four; (2) three; (3) less than three (Rougier et al. 1998: ch. 1); ORDERED.
34. Tall, trenchant premolar: (0) ultimate premolar; (1) penultimate premolar; (2) absent (Rougier et al. 1998: ch. 3).
35. Procumbent first upper premolar: (0) absent; (1) present (Luo and Wible 2005: ch. 151, modified).
36. First upper premolar (P1 in placentals, cf. Wible et al. 2009 matrix) roots: (0) one; (1) two; (2) three: eutherians with lost P1 are coded non-applicable (Muizon et al. 2015); ORDERED.
37. Diastema posterior to first upper premolar: (0) absent; (1) present (Luo and Wible 2005: ch. 43; Wible et al. 2009: ch. 34).
38. Shape of the premolar cusps: (0) sharp and uninflated; (1) inflated with apical wear strongly developed (Cifelli 1993; Rougier et al. 1998: ch. 2; Wible et al. 2001: ch. 2).
39. Protocone of the penultimate premolar: (0) absent; (1) lingual bulge; (2) basined (Rougier et al. 1998: ch. 12).
40. Metacone of penultimate upper premolar: (0) absent; (1) swelling; (2) large (Wible et al. 2009: ch. 37).
41. Penultimate upper premolar parastylar lobe: (0) absent or small; (1) well developed (Wible et al. 2009: ch. 38).
42. Vertically developed cylindrical parastyle separated from paracone by a deep vertical sulcus on labial edge of upper cheek teeth (at least PM): (0) absent; (1) present (Muizon et al. 2015: ch. 42).
43. Penultimate upper premolars roots: (0) one; (1) two; (2) three; (3) four (Wible et al. 2009: ch. 39); ORDERED.
44. Ultimate upper premolar protocone: (0) absent or narrow cingulum; (1) present but distinctly smaller than paracone; (2) similar in thickness and height to paracone (Rougier et al. 1998; Wible et al. 2009: ch. 40); ORDERED.
45. Last upper premolar metacone: (0) absent; (1) swelling (metacone connate to paracone); (2) large (metacone and paracone distinctly separated) (Luo and Wible 2005: ch. 39).
46. Last upper premolar para- and metastylar lobes: (0) absent or insignificant; (1) present and subequal; (2) parastylar lobe larger; (3) metastylar lobe larger (Wible et al. 2009: ch. 42).
47. Ultimate premolar precingulum: (0) absent; (1) present (Wible et al. 2009: ch. 43).
48. Ultimate premolar postcingulum: (0) absent; (1) present (Muizon et al. 2015; Wible et al. 2009: ch. 44, modified).
49. Ultimate premolar conules: (0) absent or very weak; (1) present as a distinct cusp (prominent) (Wible et al. 2009: ch. 45).
50. Ultimate upper premolar size (occlusal surface, L x W) relative to first upper molar: (0) smaller or subequal; (1) larger (Meng et al. 2003: ch. 41).
51. Double V-shaped penultimate and ultimate upper premolars (paracone and protocone V-shaped): (0) absent; (1) present (Muizon et al. 2015).
52. First lower premolar orientation: (0) in line with the jaw axis; (1) oblique (Rougier et al. 1998: ch. 45; Wible et al. 2009: ch. 47).
53. First lower premolar roots: (0) two; (1) one (Wible et al. 2009: ch. 48).
54. Diastema separating first and second lower premolars: (0) absent (gap less than one tooth root diameter); (1) present (subequal to or larger than one tooth root diameter) (Luo and Wible 2005: ch. 152, modified; Wible et al. 2009: ch. 49).
55. Third lower premolar size compared to second (only scored for taxa with five lower premolars): (0) longer or (1) shorter (Wible et al. 2009: ch. 50).
56. Third lower premolar roots (only scored for taxa with five lower premolars): (0) two or (1) one (Wible et al. 2009: ch. 51).
57. Penultimate lower premolar paraconid: (0) vestigial or absent; (1) distinctive (Luo and Wible 2005: ch. 52, modified; Wible et al. 2009: ch. 52).
58. Penultimate lower premolar metaconid: (0) absent; (1) swelling or metaconid connate to paraconid; (2) metaconid and paraconid distinctly separated (Wible et al. 2009: ch. 53).
59. Penultimate lower premolar talonid cusps: (0) one; (1) two; (2) three (Wible et al. 2009: ch. 54); ORDERED.
60. Ultimate lower premolar paraconid: (0) absent (there may be a small swelling at the anterior base of the protoconid but a well-defined cusp is not present); (1) present but low: less than half the height of protoconid (the paraconid is generally a small cusp at the anterior base of the protoconid); (2) present and high, half the height of protoconid or more (Muizon et al. 2015; Wible et al. 2009: ch. 55, modified); ORDERED.
61. Ultimate lower premolar metaconid: (0) absent; (1) metaconid present as a small bulge on posteromedial side of protoconid (swelling); (2) metaconid distinctly individualized (separate, large) (Wible et al. 2009: ch. 56).
62. Ultimate lower premolar talonid: (0) narrower than anterior portion of the crown; (1) as wide as anterior portion of the crown; (2) absent (Archibald and Averianov 2006: ch. 25).
63. Ultimate lower premolar talonid cusps: (0) one; (1) two; (2) three (Wible et al. 2009: ch. 58); ORDERED.
64. Length of ultimate lower premolar relative to penultimate premolar: (0) longer; (1) equal or shorter (Archibald and Averianov 2006: ch. 24).
65. Ultimate lower premolar anterolingual cingulid: (0) absent or (1) present (Wible et al. 2009: ch. 60).

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Upper molars

66. Number of molars: (0) four or more; (1) three; (2) two (Wible et al. 2009: ch. 61); ORDERED.
67. Size (area) of M1 vs M2: (0) M1 much larger (>120%); (1) subequal (80%<>120%); (2) M1 much smaller (80%<) (Muizon et al. 2015); ORDERED.
68. Size (area) of M1 vs M3: (0) M1 much larger (>120%); (1) subequal (80%<>120%); (2) M1 much smaller (80%<) (Muizon et al. 2015); ORDERED.
69. Size (area) of m1 vs m2: (0) m1 much larger (>120%); (1) subequal (80%<>120%); (2) m1 much smaller (80%<) (Muizon et al. 2015); ORDERED.
70. Size (area) of m1 vs m3: (0) m1 much larger (>120%); (1) subequal (80%<>120%); (2) m1 much smaller (80%<) (Muizon et al. 2015); ORDERED.
71. Molar cusps form: (0) sharp and gracile; (1) inflated and robust; (2) crest-like (Wible et al. 2009: ch. 63).
72. Upper molar shape: (0) as long as wide or longer; (1) wider than long (length more than 75% but less than 99%of the width); (2) much wider than long (length less than 75% of the width) (Wible et al. 2009: ch. 64); ORDERED.
73. Upper molar stylar shelf maximum width: (0) 50% or more of total width; (1) between 50% and 25% of width; (2) less than 25%; (3) absent (Wible et al. 2009: ch. 65); ORDERED.
74. Labial extent of parastylar and metastylar lobes: (0) parastylar lobe more labial; (1) lobes subequal; (2) metastylar lobe more labial; (3) lobes absent (Wible et al. 2009: ch. 66).
75. M1 parastylar lobe relative to paracone: (0) anterolabial to paracone; (1) anterior to paracone (Archibald and Averianov 2006: ch. 7; Wible et al. 2009: ch. 67) (if parastylar lobe is absent, scored as non-applicable).
76. Length of the parastylar lobe (measured to stylocone or stylocone position) relative to total length on penultimate molar: (0) more than 30% of the tooth length; (1) between 30% and 20%; (2) 20% or less. (Wible et al. 2009: ch. 68); ORDERED.
77. Preparastyle: (0) absent; (1) present (Rougier et al. 1998: ch. 21).
78. Stylar cusp A: (0) subequal to or larger than stylar cusp B; (1) distinct but smaller than B; (2) very small to indistinct (Muizon et al. 2015; Wible et al. 2009: ch. 70). Taxa in which both stylar cusps A and B are not identifiable are scored non-applicable.
79. Size of stylar cusp B relatively to paracone: (0) vestigial to absent; (1) smaller but distinct; (2) subequal (Rougier et al. 1998: ch. 22) Taxa scored non-applicable for character 78 are also coded non-applicable for this character; ORDERED.
80. Stylar cusp C, mesostyle: (0) absent; (1) present (Rougier et al. 1998: ch. 23).
81. Stylar cusp D: (0) absent; (1) smaller or subequal to B (Rougier et al. 1998: ch. 24).
82. Stylar cusp E: (0) lingual to D or to D position; (1) distal to D; (2) small to indistinct (Rougier et al. 1998: ch. 25).
83. Paracingulum (= preparacingulum of Wible et al. 2009): (0) absent; (1) interrupted between stylar margin and paraconule; (2) continuous between stylar margin and paraconule (taxa with a protoloph with indistinct paraconule are coded 2 as the labial portion of the protoloph is hypothesized as corresponding to the paracingulum) (Wible et al. 2009: ch. 75).
84. Deep ectoflexus: (0) present on penultimate molar; (1) present on penultimate and preceding molars; (2) very small or absent (Wible et al. 2009: ch. 76).
85. Relative size of the paracone and metacone on penultimate molar: (0) metacone smaller than paracone; (1) cusps subequal; (2) paracone smaller than metacone (Wible et al. 2009: ch. 77, modified); ORDERED.
86. Metacone position relative to paracone: (0) labial; (1) approximately at the same level; (2) lingual (Rougier et al. 1998: ch. 28); ORDERED.
87. Paracone and metacone at base: (0) fused at base; (1) distinctly separated; (Muizon and Marshall 1992: ch. 13).
88. Preparacrista: (0) strong, from labial edge of paracone to stylocone; (1) weak (from base of paracone) or absent (Wible et al. 2009: ch. 80).
89. Orientation of the preparacrista on penultimate and ante-penultimate molars and premolars (in the case of molariform premolars): (0) deflected labially and tend to be aligned with or sub parallel to paracone-protocone axis; (1) shifted anteriorly, forming a distinct angle with paracone-protocone axis. Taxa without a distinct preparacrista are scored non-applicable (Muizon et al. 2015).
90. Cuspate preparacrista: (0) present; (1) absent (Wible et al. 2009: ch. 81).
91. Centrocrista: (0) straight; (1) V-shaped (2) absent (Wible et al. 2009: ch. 82).
92. Postmetacrista: (0) prominent from side of metacone to metastyle; (1) salient (expanded posterolabially); (2) absent or weak (Wible et al. 2009: ch. 83).
93. Cuspate postmetacrista: (0) present; (1) absent (Wible et al. 2009: ch. 84).
94. Preprotocrista: (0) does not extend labially below the paracone; (1) extends labially below the paracone (double rank prevallum/postvallid shearing); (2) absent (Wible et al. 2009: ch. 85). Taxa with a protoloph are coded (1).
95. Postprotocrista: (0) extends to mid-lingual surface of metacone; (1) extends distal to metacone; (2) absent (Wible et al. 2009: ch. 86). Taxa with a metaloph are coded (1).

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96. Development of postvallum shear: (0) present, but only by the first rank: postmetacrista; (1) present, with the addition of a second rank (postprotocrista below postmetacrista) but the second rank does not reach labially below the base of the metacone; (2) present, with second rank extending to metastylar lobe: metacingulum; (3) absent (Luo and Wible 2005: ch. 57). All taxa with a hypocone subequal to protocone are scored as non-applicable.
97. Labial edges of paracone and metacone: (0) distinctly swollen; (1) slightly convex; (2) flat to concave (Muizon et al. 2015); ORDERED.
98. Paraconule: (0) weak or absent; (1) prominent, closer to protocone; (2) or prominent, mid-way or closer to paracone (Wible et al. 2009: ch. 88).
99. Metaconule: (0) weak or absent; (1) prominent, closer to protocone; (2) or prominent, mid-way or closer to metacone (Wible et al. 2009: ch. 89).
100. Internal conular cristae: (0) indistinct; (1) distinctive and wing-like (Luo and Wible 2005: ch. 107). Taxa without prominent conules are scored as non-applicable.
101. Protocone: (0) lacking; (1) small; without trigon basin; (2) or with distinct trigon basin (Rougier et al. 1998: ch. 36).
102. Protocone anteroposterior expansion: (0) absent and protocone subequal to paracone; (1) present and protocone larger than paracone (Wible et al. 2009: ch. 93).
103. Protocone procumbency: (0) absent; (1) present (Rougier et al. 1998: ch. 37).
104. Protocone labial shift: (0) no shift (10-20%); (1) moderate shift (21-30%); (2) substantial labial shift (more than 31%) (Luo and Wible 2005: ch. 97, modified); ORDERED.
105. Height of the protocone: (0) low, clearly lower than paracone and/or metacone; (1) approaching, equal or higher than paracone and/or metacone (Wible et al. 2009: ch. 96, modified).
106. Precingulum: (0) absent or weak; (1) labial edge of the precingulum, lingual to paraconule; (2) labial edge of the precingulum labial to paraconule (= reaching labially past the paraconule or paraconule position) (Wible et al. 2009: ch. 97)
107. Postcingulum: (0) absent or weak; (1) labial edge of the postcingulum lingual to metaconule; (2) labial edge of the postcingulum labial to metaconule; (3) postcingulum extending to labial margin (Wible et al. 2009: ch. 98).
108. Hypocone on postcingulum: (0) absent; (1) present lower than protocone; (2) present subequal to protocone (Wible et al. 2009: ch. 99); ORDERED.
109. Pre- and postcingulum: (0) separated lingually; (1) continuous lingually. If cingula absent coded as non-applicable (Wible et al. 2009: ch. 100).
110. Number of roots of upper molars except ultimate molar: (0) three; (1) four; (2) more than four (Wible et al. 2009: ch. 101); ORDERED.
111. Ultimate upper molar number of roots: (0) one; (1) two; (2) three; (3) four or more (Wible et al. 2009: ch. 102); ORDERED.
112. Metastylar lobe on ultimate molar: (0) absent; (1) present (Wible et al. 2009: ch. 105).
113. M1–M2 metaconular hypocone: (0) absent; (1) present (Williamson and Carr 2007: ch. 22, modified).
114. Presence of a crochet (oblique loph joining the ectoloph (or centrocrista?) to the metaloph (or posterior edge of molar between metacone and protocone): (0) absent; (1) present (Cifelli 1993; Billet 2010: ch. 27, modified).

Lower molars

115. Paraconid: (0) present (distinctive); (1) absent (or vestigial) (Wible et al. 2009: ch. 106).
116. Paraconid height relatively to metaconid: (0) lower; (1) subequal; (2) taller (Wible et al. 2009: ch. 107); ORDERED.
117. Paraconid on lingual margin: (0) absent; (1) present (Wible et al. 2009: ch. 108).
118. Mesiolingual edge of paraconid: (0) rounded; (1) keeled (Wible et al. 2009: ch. 109).
119. Paracristid: (0) notched; (1) continuously curved without notch (Wible et al. 2009: ch. 110).
120. Trigonid configuration: (0) open with the paraconid in anteromedial position, paracristid-protocristid angle more than 50°; (1) acute with paraconid more posteriorly placed, paracristid-protocristid angle between 36° and 49°; (2) anteroposteriorly compressed, paracristid-protocristid angle 35° or less (Wible et al. 2009: ch. 111, modified); ORDERED.
121. Protoconid height: (0) tallest of trigonid; (1) subequal to lower than other cusps (Wible et al. 2009: ch. 112, modified).
122. Protocristid orientation: (0) oblique (1) transverse (Wible et al. 2009: ch. 113).
123. Talonid: (0) small heel; (1) multicusped basin (Rougier et al. 1998: ch. 49).
124. Cristid obliqua: (0) incomplete; (1) complete attaching lingual to notch in protocristid; (2) complete attaching at or labial to notch in protocristid; (3) complete attaching below middle posterior face of protoconid; (4) complete, labially placed (Wible et al. 2009: ch. 116, modified).
125. Trigonid height relative to talonid: (0) twice or more; (1) less than twice; (2) subequal (Wible et al. 2009: ch. 117); ORDERED.
126. Anteroposterior shortening of trigonid (at base) relative to talonid: (0) long > 75% tooth length; (1) moderately long < 75% and > 50% tooth length; (2) short < 50% tooth length (Luo and Wible 2005: ch. 78); ORDERED.

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127. Talonid width: (0) talonid very narrow, subequal to base of metaconid, (1) talonid narrower than trigonid, (2) subequal or wider than trigonid (Rougier et al. 1998: ch. 50); ORDERED.
128. Hypoconulid: (0) absent; (1) in median position on posterior edge of talonid; (2) lingually placed with slight approximation of entoconid; (3) connate to entoconid (Wible et al. 2009: ch. 120).
129. Hypoconulid of last lower molar: (0) short and erect; (1) tall and sharply recurved; (2) posteriorly procumbent; (3) absent. (Wible et al. 2009: ch. 121).
130. Entoconid: (0) absent; (1) smaller than hypoconid and/or hypoconulid; (2) subequal to larger than hypoconid and/or hypoconulid (Wible et al. 2009: ch. 122); ORDERED.
131. Postcristid (between entoconid and hypoconulid) taller than hypoconulid and nearly transverse: (0) absent; (1) present (Wible et al. 2009: ch. 123).
132. Mesoconid: (0) absent or (1) present. (Meng et al. 2003: ch. 79).
133. Hypolophid (loph joining hypoconid to hypoconulid): (0) absent; (1) present (Meng et al. 2003: ch. 82).
134. Labial postcingulid: (0) absent; (1) present (Rougier et al. 1998: ch. 55).
135. Entoconid transversely expanded into entolophid and not connected to hypoconulid: (0) absent; (1) present (Cifelli 1993; Billet 2010: ch. 55, modified; Muizon et al. 2015).

Dentary

136. Number of mental foramina: (0) two or more; (1) one (Meng et al. 2003: ch. 87).
137. Anteriormost mental foramen: (0) below incisors; (1) below p1; (2) below p2; (3) more posterior (Wible et al. 2009: ch. 129). Taxa with only one mental foramen are scored here. ORDERED.
138. Posteriormost mental foramen: (0) in canine and anterior premolar region; (1) below penultimate premolar; (2) below ultimate premolar; (3) posterior to ultimate premolar (Wible et al. 2009: ch. 130); ORDERED.
139. Depth of dentary body: (0) slender and long; (1) deep and short (Meng et al. 2003: ch. 86).
140. Retromolar space in adults (i.e. in which ultimate molar exhibits wear process): (0) absent; (1) present (Wible et al. 2009: ch. 132). Comment: we scored this character for *Eoastrapostylops riolorense* based on the paratype (PVL 4217, a partial anterior portion of skull and mandible with fully erupted m3) because in the holotype the m3 is still unerupted.
141. Coronoid process height: (0) higher than condyle; (1) even with condyle (Wible et al. 2009: ch. 133).
142. Coronoid process width: (0) broad, roughly two molar lengths; (1) narrow, one molar length or less (Wible et al. 2009: ch. 134).
143. Angle between anterior border of coronoid process and horizontal alveolar border of cheek teeth: (0) distinctly obtuse (anterior border of coronoid process strongly oblique posteriorly); (1) slightly obtuse or more or less right angle (anterior border of coronoid process slightly oblique posteriorly or sub-vertical; (2) acute angle (anterior border of coronoid process shifted anteriorly) (Wible et al. 2009: ch. 135, modified); ORDERED.
144. Coronoid crest (crest of the masseteric fossa along the anterior border of the coronoid process): (0) absent or weakly developed; (1) present and transversely thick; (2) hypertrophied and laterally flaring with a very deep masseteric fossa posterior to it (Luo and Wible 2005: ch. 21, modified); ORDERED.
145. Portion of the mandibular ramus ventral to the masseteric fossa: (0) dorsoventrally narrow crest or ridge with a dorsoventral height less than half that of the mandibular body; (1) dorsoventrally broad ridge (or elevated area) with a dorsoventral height more than half that of the mandibular body. Taxa in which the ventral limit of the masseteric fossa is indistinct are scored as non-applicable (Luo and Wible 2005: ch. 20, modified).
146. Anterior extension of masseteric fossa on the body of the dentary, below the last molars: (0) absent; (1) present (Luo and Wible 2005: ch. 22). Comment: as for character 140, we scored this character for *Eoastrapostylops riolorense* based on the paratype.
147. Labial mandibular foramen: (0) absent; (1) present (Rougier et al. 1998: ch. 70).
148. Condyloid crest: (0) absent; (1) present (Wible et al. 2009: ch. 140).
149. Posteroventral shelf of the masseteric fossa: (0) absent; (1) present (Rougier et al. 1998: ch. 68).
150. Angular process: (0) process on posterior aspect of dentary ramus; (1) shelf along ventral border of dentary ramus (Wible et al. 2009: ch. 142).
151. Angular process length: (0) less than dentary ramus length; (1) equal or greater than dentary ramus length (Wible et al. 2009: ch. 144).
152. Angular process shape: (0) hook-like with width (in lateral view) of base lesser than length; (1) hook-like with width of base subequal to (or wider than) length; (2) plate-like (no hook distinct), more or less rounded or sub rectangular; (3) triangular (Wible et al. 2009: ch. 145, modified).
153. Angular process apex vertical position: (0) low: below the level of the alveolar border; (1) elevated: at the level of or above the alveolar border (Luo and Wible 2005: ch. 9, modified).
154. Anteroposterior position of the dorsal root of the angular process: (0) level with or posterior to the level of the condyloid process;

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(1) anterior to it (Wible et al. 2009: ch. 147, modified).
155. Condylar process: (0) with posteriorly directed peduncle (1) or not (Wible et al. 2009).
156. Condyle shape: (0) wider than long ovoid; (1) wider than long cylindrical; 2) as long as wide or longer, anteroposteriorly elongate (Rougier et al. 1998: ch. 71, modified; Wible et al. 2009: ch. 149).
157. Condyle position relative to the tooth row: (0) approximately at the same level or slightly above; (1) above by approximately one molar length; (2) above by two molars length or more (Wible et al. 2009: ch. 150, modified); ORDERED.
158. Symphysis shape: (0) tapered; (1) deep (Meng et al. 2003: ch. 86).
159. Symphysis posterior extent: (0) p1 or more anterior; (1) p2; (2) p3 or more posterior (Wible et al. 2009: ch. 152) ORDERED.
160. Mandibular symphysis: (0) unfused; (1) fused (Luo and Wible 2005: ch. 36).
161. Meckelian groove: (0) present; (1) absent (Rougier et al. 1998: ch. 75).
162. "Coronoid facet": (0) present; (1) absent (Rougier et al. 1998: ch. 76; Wible et al. 2009: ch. 156).
163. Mandibular foramen vertical position: (0) near ventral margin of dentary; (1) recessed dorsally from ventral margin; (2) at the level of alveolar plane; (3) above alveolar plane (Wible et al. 2009: ch. 157, modified); ORDERED.
164. Mandibular foramen dorsal to prominent longitudinal ridge: (0) present; (1) absent (Wible et al. 2009: ch. 158).

Skull: rostrum
165. Facial process of the premaxilla: (0) does not reach the nasal posterodorsally; (1) reaches the nasal (Rougier et al. 1998: ch. 80).
166. Posterior extent of the facial process of the premaxilla: (0) up to the canine (not beyond); (1) between the canine and the frontal (=beyond canine); (2) up to the frontal (Luo and Wible 2005: ch. 406; Wible et al. 2009: ch. 161, modified); ORDERED.
167. Facial process of the premaxilla: (0) finger-like process wedged between the maxilla and the nasal posterodorsally; (1) not wedged (no finger-like process) (Wible et al. 2009: ch. 162).
168. Paracanine fossa between posterior incisor and upper canine: (0) absent; (1) distinctly excavated in the tooth row with a crest-like lateral margin; (2) opened laterally but remaining on the tooth row; (3) opened laterally and dorsally expanded on the lateral edge of the rostrum (Muizon et al. 2015: ch. 168).
169. Paracanine fossa: (0) excavated in maxilla; (1) excavated in maxilla and premaxilla; (2) excavated in premaxilla (Rougier et al. 1998: ch. 81, modified; Wible et al. 2009: ch. 163, modified). All taxa coded (0) for character 168 are coded as non-applicable.
170. Exit(s) of infraorbital canal: (0) multiple; (1) single; (2) absent. (Rougier et al. 1998: ch. 82, modified).
171. Infraorbital foramen position: (0) dorsal to penultimate premolar or more anterior; (1) dorsal to ultimate premolar; (2) dorsal to first molar or more posterior (Geisler 2001: ch. 65, modified, Wible et al. 2009: ch. 165, modified); ORDERED.
172. Infraorbital canal length: (0) long (longer than greater diameter of the anterior opening); (1) short (shorter than or roughly equal to greater diameter of the anterior opening). In the case of multiple openings the diameter is that of the circle with a surface corresponding to the sum of the surfaces of all foramina (Wible et al. 2009: ch. 166, modified).
173. Width of the nasals: (0) much wider posteriorly than anteriorly; (1) sides subparallel; (2) widest anteriorly (Asher et al. 2005: ch. 110, modified; Wible et al. 2009: ch. 168); ORDERED.
174. Shape ratio of the nasals (length/mean width): (0) nasals length less than (or equal to) five times their mean width; (1) nasals length more than five times their mean width (Muizon et al. 2015: ch. 174).
175. Nasals overhang external nasal aperture: (0) present; (1) absent (Wible et al. 2009: ch. 169).
176. Nasal of adults fused together but not to surrounding bones: (0) absent; (1) present (Muizon et al. 2015: ch. 176).
177. Anterior processes of the frontals wedged between the nasals: (0) present; (1) absent. (Rougier et al. 1998; Wible et al. 2009).
178. Nasofrontal suture: 0) suture level with or posterior to the anterior edge of the orbit; 1) all points of the suture well anterior to anterior edge of the orbit: (Wible et al. 2009: ch. 171, modified).
179. Nasal foramina: (0) present; (1) absent (Rougier et al. 1998: ch. 84).
180. Frontal-maxillary contact on rostrum: (0) absent; (1) present (Rougier et al. 1998: ch. 86).
181. Anterior (maxillary) process of the frontal wedged between the nasal and the maxilla: (0) absent or weak; (1) present, elongated and thin (Asher et al. 2005: ch. 109).
182. Preorbital length (measured from the anterior edge of the orbit to anterior end of the skull): (0) less than one-third total length; (1) more than one-third (Rougier et al. 1998: ch. 90, modified).
183. Lacrimal: (0) present; (1) absent (Asher et al. 2005: ch. 103).
184. Facial process of the lacrimal: (0) large external wing on the rostrum at the anterior edge of the orbit; (1) no wing: either the external part of the lacrimal is totally absent or it is reduced to a narrow crescentic rim on the anterior edge of the orbit (Asher et al. 2005: ch. 105, modified; Wible et al. 2009: ch. 177, modified).
185. Lacrimal tubercle: (0) present; (1) absent. Taxa without lacrimal are scored non-applicable (Rougier et al. 1998: ch. 87).
186. Lacrimal foramen "on face" (because lateral edge of the foramen is reduced or missing): (0) present; (1) absent (Rougier et al. 1998: ch. 88).

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187. Lacrimal foramen (0) double; (1) simple (Rougier et al. 1998 : ch. 89).
188. Lacrimal foramen composition: (0) enclosed within lacrimal; (1) with maxillary contribution; (2) with jugal contribution (Asher et al. 2003: ch. 100; Wible et al. 2009: ch. 181).
189. Translacrimal canal (see Wible et al. 2004): absent (0) or present (1) (Wible et al. 2009). Taxa without lacrimal are scored non-applicable.
190. Narial processes of the premaxillae (tuberosity at the anterior apices of the premaxillae, on the anterior floor of the narial opening): (0) absent; (1) present (Billet 2010: ch. 77).

Skull: palate

191. Palatal process of the premaxilla: (0) does not reach the alveolus; (1) does reach or nearly reach the canine alveolus (Rougier et al. 1998: ch. 79).
192. Incisive foramina length: (0) short, half or less than half the maximal palatal length of the premaxilla along the sagittal plane; (1) long, more than half the length of the premaxilla (Luo and Wible 2005: ch. 409, modified).
193. Incisive foramina composition: (0) between premaxilla and maxilla; (1) within premaxilla (Wible et al. 2009, ch. 186).
194. Palatal vacuities: (0) absent; (1) present (Rougier et al. 1998 : ch. 93).
195. Major palatine foramina: (0) well-individualized, within maxilla and/or palatine; (1) multiple small foramina in palatine and/or maxilla (Wible et al. 2009: ch. 188, modified). Taxa without major palatine foramina are scored as non-applicable.
196. Anterior extent of palatine: (0) posterior to M1; (1) level with M1; (2) more anterior (Wible et al. 2009: ch. 189, modified); ORDERED.
197. Palatal expansion with regard to ultimate molar: (0) posterior; (1) even with; (2) anterior (Wible et al. 2009: ch. 190); ORDERED.
198. Postpalatine torus: (0) absent; (1) present (Rougier et al. 1998: ch. 95).
199. Posterior palatine spine: (0) weak or absent; (1) prominent (Wible et al. 2009: ch. 192).
200. Passageway of the minor palatine artery (minor palatine foramen or groove): (0) totally enclosed in the minor palatine foramen; (1) in a groove on the posteromedial edge of the palate as a result of the posterior opening of the minor palatine foramen (no posterior bony bridge); (2) absent (no groove nor foramen) (Wible et al. 2009: ch. 193, modified; Muizon et al. 2015).
201. Minor palatine foramen composition: (0) palatine or maxilla-palatine or (1) palatine-pterygoid. (Wible et al. 2009: ch. 194).
202. Maxilla with shelf-like expansion posterior to ultimate molar with a length at least equal to half a tooth and lateral to minor palatine notch or foramen: (0) absent; (1) present (Wible et al. 2009: ch. 195, modified).

Skull: zygoma

203. Posterior edge of the anterior zygomatic root aligned: (0) with last molar or more posterior; (1) with more anterior molars; (2) with premolars (Meng et al. 2003: ch. 123; Wible et al. 2009: ch. 196, modified); ORDERED.
204. Zygomatic process of the maxilla: (0) present; (1) vestigial; (Wible et al. 2009: ch. 197).
205. Jugal: (0) present; (1) absent (Wible et al. 2009: ch. 198).
206. Jugal contribution to anteroventral edge of the orbit: (0) present; (1) absent (Wible et al. 2009: ch. 199, modified).
207. Maxilla-jugal suture bifurcated: (0) absent; (1) present (Rougier et al. 1998: ch. 91).
208. Jugal-lacrimal contact: (0) present; (1) absent (Meng et al. 2003: ch. 137).
209. Zygomatic arch: (0) stout; (1) delicate; (2) incomplete (Wible et al. 2009: ch. 199); ORDERED.
210. Orientation of the anterior root of zygoma in anterior view: (0) oblique, extends dorsally; (1) transverse, roughly horizontal; (2) extends ventrally (Muizon et al. 2015); ORDERED.
211. Vertical position of posterior root of zygoma relative to foramen magnum: (0) even; (1) clearly higher (Muizon et al. 2015).
212. Shape of zygomatic arches in dorsal view: (0) not protruding much laterally, smoothly curved or parallel to sagittal plane; (1) protruding laterally (largely exceeding other parts of skull laterally), with a large posterior elbow (Muizon et al. 2015).

Skull: orbit

213. Roots of molars exposed in orbit floor: (0) absent; (1) present (Asher et al. 2005: ch. 126.
214. Palatine enters the posterior opening of the infraorbital canal (maxillary foramen): (0) present; (1) absent (Rougier et al. 1998: ch. 98).
215. Lacrimal contributes to maxillary foramen: (0) present; (1) absent (Luo and Wible 2005: ch. 376, modified).
216. Groove connects maxillary to sphenopalatine foramina: (0) absent; (1) present (Asher et al. 2005: ch. 97).
217. Sphenopalatine foramen: (0) within palatine; (1) between palatine and maxilla; (2) between palatine, maxilla and frontal (Asher et al. 2005: ch. 133, modified).
218. Sphenopalatine foramen: proximal (= approximated) to maxillary foramen: (0) absent; (1) present (Wible et al. 2009: ch. 208).
219. Maxilla in the orbit: (0) no participation in orbital wall; (1) large dorsal process participating in medial orbital wall (Wible et al.

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2009: ch. 209, modified).

220. Frontal and maxilla contact in medial orbital wall: (0) absent; (1) present (Geisler 2001: ch. 52).
221. Orbital process of the palatine: (0) present; (1) absent (Asher et al. 2005: ch. 127, modified).
222. Ethmoid exposure in medial orbital wall: (0) absent; (1) present (Wible et al. 2009: ch. 212).
223. Ethmoidal foramen: (0) between frontal and orbitosphenoid; (1) within frontal (Wible et al. 2009: ch. 213).
224. Foramina for the frontal diploic vein: (0) absent; (1) present (Wible et al. 2009: ch. 214).
225. Position of frontal diploic foramina vs postorbital process or tuberosity: (0) posterior; (1) anterior or even (Muizon et al. 2015). Taxa lacking a postorbital process or tuberosity and/or frontal diploic foramina are coded non-applicable.
226. Supraorbital foramina: (0) absent; (1) present on the skull roof, often extending anteriorly as a groove on the maxilla and/or nasal; (2) present more laterally on the dorsal orbital edge and/or postorbital process, groove variably present (Thewissen et al. 2001: ch. 41, modified).
227. Postorbital process of the frontal: (0) present and prominent; (1) present weak (tuberosity); (2) absent (Wible et al. 2009: ch. 216); ORDERED.
228. Postorbital process (main) composition: (0) frontal; (1) parietal (Wible et al. 2005: ch. 67, modified).
229. Postorbital bar: (0) absent; (1) present (Meng et al. 2003: ch. 145).
230. Dorsal process of the jugal: (0) absent or weak (hump); (1) strong (Meng et al. 2003: ch. 142).
231. Optic foramen: (0) confluent with sphenorbital fissure; (1) well separated from sphenorbital fissure (Rougier et al. 1998: ch. 102).
232. Optic foramen position: (0) narrowly separated from sphenorbital fissure; (1) broadly separated from sphenorbital fissure (Wible et al. 2009: ch. 221, modified).
233. Orbitosphenoid: (0) expanded anteriorly from optic foramen (or with anterior process for forms without optic foramen); (1) expanded dorsally from optic foramen (or with dorsal process for forms without optic foramen); (2) not expanded anteriorly or dorsally (Wible et al. 2009: ch. 222).
234. Suboptic foramen: (0) absent; (1) present (Wible et al. 2009: ch. 223).
235. Orbitotemporal canal: (0) present; (1) absent (Rougier et al. 1998: ch. 103).
236. Frontal-alisphenoid contact: (0) present: small contact at the anterodorsal corner of the alisphenoid; (1) present: more extensive contact on approximately 50% of the dorsal margin of the alisphenoid; (2) absent (Luo and Wible 2005: ch. 382, modified).
237. Sphenorbital fissure confluent with foramen rotundum (i.e., there is no foramen rotundum per se and V_2 exits with V_1 through the sphenorbital fissure): (0) absent; (1) present (Muizon et al. 2015).

Skull: braincase

238. Frontal length on midline: (0) less than half that of the parietal; (1) subequal to slightly smaller than parietal; (2) more than 50% longer than parietal (Wible et al. 2009: ch. 226); ORDERED.
239. Frontoparietal suture: (0) transverse; (1) with anterior process of the parietal off the midline; (2) with anterior process of the parietal on the midline (Wible et al. 2009: ch. 227).
240. Temporal lines meet on midline to form a sagittal crest: (0) present; (1) absent (Geisler 2001: ch. 33, modified).
241. Nuchal crest: (0) level with or anterior to foramen magnum; (1) posterior to foramen magnum (Wible et al. 2009: ch. 230).
242. Nuchal crest in dorsal view: (0) deeply notched on medial line: bilobate morphology and V-shaped opening posteriorly; (1) transverse: roughly straight; (2) median point posterior to lateral parts of the crest: V-shaped morphology opening anteriorly (Muizon et al. 2015); ORDERED.
243. Anterior lamina of the petrosal: (0) present and exposed on lateral braincase wall; (1) internal to braincase and small to vestigial; (2) absent (Wible et al. 2009: ch. 231, modified).
244. Squama of the squamosal: (0) absent; (1) present (Rougier et al. 1998: ch. 113).
245. Foramina for temporal rami (including suprameatal foramen when present) of the stapedial artery: (0) in the petrosal; (1) in parietal and/or squama of the squamosal; (2) absent (Rougier et al. 1998: ch. 143).

Skull: mesocranium

246. Choanae: (0) almost as wide as posterior palate; (1) distinctly narrower (Wible et al. 2009: ch. 234).
247. Vomer contacts pterygoids: (0) present; (1) absent (Wible et al. 2009: ch. 235).
248. Pterygoids contact in midline: (0) present; (1) absent (Rougier et al. 1998: ch. 99).
249. Pterygopalatine crests: (0) present; (1) absent (Rougier et al. 1998: ch. 100).
250. Midline crest in basipharyngeal canal: (0) absent; (1) present (Wible et al. 2009: ch. 238).
251. Entopterygoid process (posterior extension): (0) absent; (1) ends at anterior basisphenoid; (2) approaches ear region (Wible et al. 2009: ch. 239).
252. Midline rod-shaped eminence on basisphenoid: (0) absent; (1) present (Wible et al. 2009: ch. 240).
253. Ectopterygoid process of the alisphenoid: (0) absent (or fused with entopterygoid crest); (1) present: ends at anterior basisphenoid;

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(2) present: approaches ear region (Rougier et al. 1998: ch. 101, modified).

254. Ectopterygoid process shape: (0) long crest or triangular blade; (1) narrow process, spine or tubercle (Wible et al. 2009: ch. 242).
255. Ectopterygoid crests (blades) or tubercles orientation: (0) sub-parallel and facing ventromedially; (1) diverging and facing mostly posteriorly (Billet 2010: ch. 74, modified; Muizon et al. 2015).
256. Transverse canal: (0) absent; (1) present (Rougier et al. 1998: ch. 104).
257. Exit for maxillary nerve (V_2) (foramen rotundum) relative to alisphenoid: (0) between the posterior edge of the alisphenoid anteriorly and the anterior lamina of the petrosal posteriorly; (1) within the alisphenoid; (2) at the anterior edge of the alisphenoid (Rougier et al. 1998: ch. 110, modified); ORDERED.
258. Number of exits for the mandibular branch of the trigeminal nerve (V_3): (0) two or more; (1) one (Luo and Wible 2005: ch. 317).
259. Foramen ovale composition: (0) in anterior lamina of the petrosal; (1) between petrosal and alisphenoid; (2) in alisphenoid; (3) between alisphenoid and squamosal (Rougier et al. 1998: ch. 111, modified).
260. Foramen ovale position: (0) on lateral wall of the braincase; (1) on ventral surface of the skull facing ventrally; (2) on the ventral side of the skull, facing anteroventrally (Rougier et al. 1998: ch. 112, modified).
261. Alisphenoid canal: (0) absent; (1) present (Rougier et al. 1998: ch. 107).
262. Posterior opening of alisphenoid canal: (0) separated from foramen ovale; (1) in common depression with foramen ovale (Wible et al. 2009: ch. 249). Taxa without alisphenoid canal are scored non-applicable.
263. Posterior border of hypophyseal fossa (located just anterior to basisphenoid-basioccipital suture) position relative to posterior edge of foramen ovale: (0) anterior to or roughly even with; (1) well posterior to (Muizon et al. 2015).

Skull: basicranium

264. Position of the dentary articulation relative to fenestra vestibuli: (0) at the same level; (1) anterior (Rougier et al. 1998: ch. 114).
265. Glenoid fossa position: (0) on zygoma; (1) partly below braincase (Wible et al. 2009: ch. 251).
266. Glenoid fossa shape: (0) concave (or concave posteriorly and flat anteriorly), open anteriorly; (1) trough-like; (2) anteroposteriorly elongate, with the major axis of fossa directed anteroposteriorly; (3) anteroposteriorly short, with the major axis of fossa directed anteroposteriorly or flat; (4) concavo-convex (Rougier et al. 1998: ch. 115; Archibald et al. 2001: ch. 137; Wible et al. 2009: ch. 252, modified)
267. Glenoid fossa dorsoventral position relative to roof of basipharyngeal canal: (0) approximately level with; (1) dorsal to it (Wible et al. 2009: ch. 253).
268. Glenoid process of the jugal: (0) present with articular facet; (1) present without facet; (2) absent (Wible et al. 2009: ch. 254).
269. Glenoid process of the alisphenoid: (0) absent; (1) present (Rougier et al. 1998: ch. 117).
270. Postglenoid process: (0) absent or very small; (1) present: subequal in width to (or slightly narrower than) glenoid cavity; (2) present: approximately half the width of the glenoid cavity. (Rougier et al. 1998: ch. 118, modified).
271. Postglenoid foramen: (0) absent; (1) present (Wible et al. 2009: ch. 257).
272. Postglenoid foramen position: (0) posterior to postglenoid process (or glenoid fossa if postglenoid process is absent); (1) medial or anteromedial to the postglenoid process (within glenoid fossa); (2) on lateral aspect of braincase (Rougier et al. 1998: ch. 120, modified).
273. Postglenoid eminence of the squamosal: (0) absent; (1) present (Muizon et al. 2015)
274. Postglenoid foramen composition: (0) within squamosal or (1) on posterior edge of squamosal. Taxa without postglenoid foramen are scored non-applicable (Wible et al. 2009: ch. 259, modified).
275. Suprameatal foramen: (0) absent; (1) present (Wible et al. 2009: ch. 260).
276. Entoglenoid process of the squamosal: (0) absent; (1) present, separated from the postglenoid process; (2) present, continuous with the postglenoid process (Luo and Wible 2005: ch. 284).
277. Posttympanic crest of the squamosal: (0) absent; (1) present (Wible et al. 2009: ch. 262).
278. Carotid foramen: (0) within basisphenoid; (1) between petrosal and basisphenoid; (2) absent (Rougier et al. 1998: ch. 105, modified).
279. Floor of cavum epiptericum composition: (0) petrosal; (1) petrosal and/or alisphenoid; (2) primarily or exclusively squamosal; (3) primarily open as piriform fenestra (Rougier et al. 1998: ch. 109, modified).
280. Posterodorsal extension of the tympanic process of the alisphenoid, which forms the roof of the anterior region of the tympanic cavity: (0) absent; (1) present (Rougier et al. 1998: ch. 121, modified).
281. Basisphenoid tympanic process: (0) absent; (1) present (Wible et al. 2009: ch. 266).
282. Basicochlear fissure: (0) closed; (1) patent (Thewissen et al. 2001: ch. 59, modified)
283. Medial flange of petrosal: (0) absent; (1) present; (Rougier et al. 1998: ch. 122, modified).
284. Rostral tympanic process of petrosal: (0) absent or low ridge; (1) moderate ridge contributing to posterodorsomedial bulla; (2) tall ridge contributing to ventral bulla (Rougier et al. 1998: ch. 130, modified).

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285. Course of the internal carotid artery: (0) lateral (transpromontorial); (1) medial (perbullar or extrabullar) (Wible et al. 2009: ch. 270, modified).
286. Bony canals for intratympanic carotid system (transpromontorial internal carotid and +/- stapedial artery): (0) absent; (1) present (Wible et al. 2009: ch. 271 and 288, modified). Taxa lacking a transpromontorial internal carotid artery are scored non-applicable.
287. Deep groove for the internal carotid artery excavated in the apex of the promontorium: (0) absent; (1) present (Rougier et al. 1998: ch. 148).
288. Perbular carotid canal (for medial internal carotid): (0) absent; (1) present (Wible et al. 2009: ch. 273). Taxa with transpromotorial course are scored non-applicable.
289. Sulcus or canal for stapedial artery on promontorium: (0) present; (1) absent (Asher et al. 2005: ch. 161, modified).
290. Stapedial ratio (length/width fenestra vestibuli): (0) rounded less than 1.8; (1) elliptical more than 1.8 (Rougier et al. 1998: ch. 127).
291. Coiling of the cochlea: (0) less than 360°; (1) more than 360° (Rougier et al. 1998: ch. 129).
292. Pars cochlearis length: (0) more than 13% of skull length; (1) less than 10% of skull length (Wible et al. 2009: ch. 277).
293. Promontorium shape: (0) flat; (1) globose (Wible et al. 2009: ch. 278).
294. Kidney (or bean-) -shaped promontorium: (0) absent; (1) present (Billet 2010: ch. 127, modified; Muizon et al. 2015).
295. Promontorium depth (most ventral point) relative to basioccipital: (0) level or ventral; (1) dorsal (Wible et al. 2009: ch. 279).
296. Intratympanic course of facial nerve: (0) open in sulcus; (1) open anteriorly, canal posteriorly; (2) in canal (Meng et al. 2003: ch. 169, modified).
297. Aperture of hiatus Fallopii: (0) on cerebral face of petrosal; (1) at anterior edge of petrosal; (2) on tympanic face of petrosal; (3) via fenestra semilunaris: (Rougier et al. 1998: ch. 123, modified; Sánchez-Villagra and Wible 2002: ch. 12, modified).
298. Prootic canal: (0) present; (1) absent (Rougier et al. 1998: ch. 124, modified).
299. Prootic canal length and orientation: (0) long and vertical; (1) short and vertical; (2) short and horizontal. (Rougier et al. 1998: ch. 124, modified).
300. Lateral flange: (0) parallels length of the promontorium, (1) greatly reduced or absent (Rougier et al. 1998: ch. 126, modified).
301. Anterior extension of bony shelf lateral to promontorium (lateral trough or tegmen tympani): (0) does not reach the apex of the promontorium anteriorly and confined posterolaterally; (1) extends as far anteriorly as the apex of the promontorium; (2) extends further anteriorly than the apex of the promontorium (Wible et al. 2009: ch. 285, modified); ORDERED.
302. Width of bony shelf lateral to promontorium (lateral trough or tegmen tympani): (0) uniform; (1) expanded anteriorly (Wible et al. 2009: ch. 286).
303. Inflation of bony shelf lateral to promontorium (lateral trough or tegmen tympani): (0) absent; (1) present (Cifelli 1982; Geisler and Luo 1998; Thewissen et al. 2001: ch. 52).
304. Tensor tympani fossa on petrosal: (0) shallow; (1) deep circular fossa (Wible et al. 2009: ch. 289, modified).
305. Area occupied by tensor tympani fossa: (0), small and/or poorly excavated; (1) large (Muizon et al. 2015).
306. Location of tensor tympani fossa: (0) mostly medial (or ventromedial) to the cavum supracochleare; (1) strictly ventral or lateral to it, not medial (Billet and Muizon 2013: ch. 138; Muizon et al. 2015).
307. Medial process of squamosal in tympanic cavity: (0) absent; (1) present (Muizon 1994).
308. Hypotympanic sinus: (0) absent; (1) formed by squamosal, petrosal and alisphenoid; (2) formed by alisphenoid and petrosal; (3) formed by petrosal (Muizon 1994, modified).
309. Epitympanic recess vs fossa incudis: (0) subequal; (1) epitympanic recess larger; (2) no visible depression for epitympanic recess (Wible et al. 2009: ch. 292).
310. Epitympanic recess lateral wall: (0) with small contribution of squamosal to posterolateral wall; (1) with extensive contribution of squamosal; (2) with no squamosal contribution (Rougier et al. 1998: ch. 138, modified).
311. Fossa incudis relationship with epitympanic recess: (0) continuous with; (1) separated from (Rougier et al. 1998: ch. 137).
312. Squamosal epitympanic sinus: (0) absent; (1) present (Billet 2010: ch. 124; Muizon et al. 2015).
313. Floor ventral to fossa incudis: (0) absent (the fossa is open ventrally); (1) formed by squamosal; (2) formed by ectotympanic; (3) formed by the petrosal (Wible et al. 2009: ch. 295, modified).
314. Fossa incudis position relative to fenestra vestibuli: (0) lateral; (1) anterolateral (Wible et al. 2009: ch. 296).
315. Foramen for superior ramus of the stapedial artery: (0) in petrosal; (1) in petrosal-squamosal suture; (2) absent (Rougier et al. 1998: ch. 145).
316. Position of the ramus superior foramen relative to fenestra vestibuli: (0) posterior or lateral; (1) anterior (Luo and Wible 2005: ch. 326).
317. Ascending canal (passage for the ramus superior of the stapedial artery): (0) intramural in the petrosal, (1) intracranial, or (2) absent. (Rougier et al. 1998: ch. 152).
318. Diameter of the stapedius fossa: (0) approximately twice the size of that of the fenestra vestibuli; (1) distinctly less than twice the

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size of the diameter of the fenestra vestibuli (= small and shallow) (Rougier et al. 1998: ch. 139, modified).
319. Cochlear canaliculus visible in middle ear space: (0) absent; (1) present (Wible et al. 2009: ch. 301).
320. Stapedial fossa and postpromontorial tympanic sinus: (0) distinct, separated by a break in slope or a crest; (1) merged, almost indistinct (Billet and Muizon 2013: ch. 139; Muizon et al. 2015).
321. External aperture of cochlear fossula (fenestra cochleae in Wible et al. 2009: ch. 303) position relative to fenestra vestibuli: (0) posteromedial, (1) posterior (Wible et al. 2009: ch. 303).
322. Posterior septum shields fenestra cochleae: (0) absent; (1) present (Wible et al. 2009: ch. 304).
323. Mastoid process (= paroccipital process of Wible et al. 2009): (0) distinctly present and vertical; (1) slanted, projecting anteroventrally; (2) indistinct to absent (Wible et al. 2009: ch. 305).
324. Posterior border of the middle ear cavity medial to the stylomastoid notch and lateral to the lateral edge of the jugular foramen: (0) straight or convex anteriorly; (1) concave or deeply notched (Wible et al. 2009: ch. 306 and 310, modified).
325. Crista interfenestralis and lateral caudal tympanic process of petrosal (= caudal tympanic process of Wible et al. 2009: ch. 307) connected by curved ridge: (0) absent; (1) present (Rougier et al. 1998: ch. 133, modified).
326. Medial caudal tympanic process (sensu MacPhee, 1981) of the petrosal (= “tympanic process” of Wible et al. 2009: ch. 308): (0) absent; (1) present (low); (2) present (high) (e.g., inflated into bullar wall) (Rougier et al. 1998: ch. 134, modified); ORDERED.
327. Medial caudal tympanic process (sensu MacPhee 1981) of the petrosal (= “tympanic process” of Wible et al. 2009: ch. 309) composition: (0) petrosal; (1) petrosal and exoccipital (Wible et al. 2009: ch. 309).
328. Inferior petrosal sinus: (0) intrapetrosal; (1) horizontal between petrosal and basioccipital; (2) intracranial: entering cranial cavity on anterior edge of the jugular foramen; (3) intracranial: entering cranial cavity via a foramen at mid-length of the medial border of the promontorium (Rougier et al. 1998: ch. 151, modified).
329. Size of the jugular foramen: (0) smaller or subequal to external aperture of cochlear fossula; (1) larger (Rougier et al. 1998: ch. 149).
330. Jugular foramen and inferior petrosal sinus: (0) confluent; (1) separated (Rougier et al. 1998: ch. 150).
331. Hypoglossal foramen: (0) two or more; (1) one; (2) absent (Luo and Wible 2005: ch. 349).
332. Hypoglossal foramen housed in opening larger than jugular foramen (0) absent; (1) present (Wible et al. 2009: ch. 315).
333. Hypoglossal foramen ventral opening on exoccipitals: (0) in a fossa; (1) on a flat to convex bony surface (Muizon et al. 2015).
334. Paroccipital (paracondylar of Wible et al. 2009) process of the exoccipital: (0) weak or absent; (1) prominent vertical; (2) prominent posteriorly directed (Rougier et al. 1998: ch. 135, modified).
335. Ectotympanic: (0) phaneric or visible in ventral view; (1) aphaneric, hidden by auditory bulla (Wible et al. 2009: ch. 317).
336. Ectotympanic: (0) ringlike; (1) fusiform; (2) transversely expanded (Rougier et al. 1998: ch. 142).
337. Anterior crus of ectotympanic broad articulation with squamosal: (0) absent; (1) present (Wible et al. 2009: ch. 319).
338. Anterior crus of ectotympanic articulation with petrosal: (0) absent; (1) present (Muizon et al. 2015).
339. Elongate ossified external acoustic canal: (0) absent; (1) present (Wible et al. 2009: ch. 320).
340. Roof of external acoustic meatus: (0) petrosal; (1) squamosal (Wible et al. 2009: ch. 321).
341. Entotympanic distinct in adults: (0) absent; (1) present (Luo and Wible 2005: ch. 363).
342. Pit for hyoid on ectotympanic (or between ectotympanic and exoccipital): (0) absent; (1) present (Wible et al. 2009: ch. 323, modified).
343. Hyoid arch contributes to bullar floor: (0) absent; (1) present (Wible et al. 2009: ch. 324).
344. Dorsum sellae: (0) tall; (1) low (Rougier et al. 1998: ch. 106).
345. Posterior clinoid process contacts apex of the promontorium: (0) absent; (1) present (Wible et al. 2004).
346. Position of sulcus for anterior distributary of transverse sinus relative to fossa subarcuata: (0) anterolateral; (1) posterolateral; (2) absent (Rougier et al. 1998: ch. 125).
347. Wall separating the cavum supracochleare from the cavum epiptericum: (0) absent; (1) incomplete with fenestra semilunaris; (2) complete (Rougier et al. 1998: ch. 128, modified).
348. Crista petrosa: (0) vestigial or absent; (1) tall and thin crest (Wible et al. 2009: ch. 329).
349. Subarcuate fossa morphology: (0) subspherical with constricted aperture: diameter of aperture is smaller than maximum diameter of the fossa; (1) cylindrical, diameter more or less constant; (2) conical or shallow depression: aperture is the widest diameter (Wible et al. 2009: ch. 330, modified) ORDERED.
350. Internal acoustic meatus: (0) deep with thick prefacial commissure; (1) shallow with thin prefacial commissure (Wible et al. 2009: ch. 332).

Skull occiput
351. Posttemporal canal: (0) present; (1) absent (Wible et al. 2009: ch. 333, modified).
352. Posttemporal canal composition (posterior opening): (0) between petrosal and squamosal; (1) within petrosal (Wible et al. 2009: ch. 334).

Appendix 2
(continued from previous page)

353. Mastoid foramen l: (0) absent; (1) present (one or more) (Meng et al. 2003: ch. 114, modified).
354. Amastoidy or lack of occipital exposure of the mastoid: (0) absent; (1) present (Geisler 2001: ch. 38).
355. Dorsal margin of the foramen magnum: (0) formed by the exoccipitals; (1) formed by the exoccipitals and the supraoccipital (Rougier et al., 1998, ch. 156).
356. Dorsal relief of lambdoid crest continuous with dorsal margin of zygomatic arch: (0) absent; (1) present (Billet, 2010, ch. 95; Muizon et al., 2015).

Postcranial characters
357. Atlantal foramen: (0) present; (1) absent (Horovitz and Sánchez-Villagra 2003: ch.1, modified).
358. Atlas neural hemiarches fused: (0) absent; (1) present (Luo and Wible 2005: ch. 169, modified).
359. Atlas neural arch and intercentrum fused: (0) absent; (1) present (Luo and Wible 2005: ch. 167).
360. Suture between atlantal and axial parts of the axis: (0) present; (1) absent (Luo and Wible 2005: ch. 169, modified).
361. Axis with extra pair of transverse processes on ventral surface of body: (0) present; (1) absent (Horovitz and Sánchez-Villagra 2003: ch. 11, modified).
262. Axis anterior facets (prezygapophyses) and dens connection: (0) not linked; (1) linked; facets extend ventral to dens (Horovitz and Sánchez-Villagra 2003: ch. 12, modified).
363. Inferior lamellae on posterior cervical vertebrae (essentially on C6 and occasionally on C5): (0) present; (1) absent (Wible et al. 2009: ch. 345).
364. C7 transverse foramen: (0) present; (1) absent (Horovitz and Sánchez-Villagra 2003: ch. 231, modified).
365. Number of thoracic vertebrae: (0) 13 or fewer; (1) 15 or more (Luo and Wible 2005: ch. 172).
366. Number of lumbar vertebrae: (0) 6 or more; (1) 5 or fewer Wible et al. 2009: ch. 348).
367. Xenarthrous articulations on lumbar vertebrae: (0) absent; (1) present (Luo and Wible 2005: ch. 176).
368. Number of sacral vertebrae: (0) 2; (1) 3; (2) 4 or more (Geisler 2001: ch. 131, modified); ORDERED.
369. Sacral vertebrae fused to pelvis: (0) absent; (1) present (Wible et al. 2009: ch. 351).
370. Infraspinous fossa position to supraspinous fossa: (0) different planes (in part medial to); (1) coplanar (Rougier 1993: ch. 13, modified).
371. Suprascapular incisure: (0) absent; (1) present (Luo and Wible 2005: ch. 196).
372. Apex of acromion: (0) distal to glenoid articulation; (1) proximal; (2) absent (Asher et al. 2005: ch. 174, modified).
373. Metacromion: (0) weak or absent; (1) well-developed process (Wible et al. 2009).
374. Elevation of the greater tubercle of the humerus relatively to the humeral head: (0) ventral (distal); (1) even or dorsal (proximal) (Asher et al. 2005: ch. 175).
375. Extension of deltopectoral crest: (0) limited to proximal half of the humerus; (1) reaches distal half (Horovitz and Sánchez-Villagra 2003: ch. 50).
376. Epicondylar crest (= sigmoidal shelf for supinator ridge extending proximally from ectepicondyle: (0) weak or absent; (1) present and patent (Luo and Wible 2005: ch. 206).
377. Entepicondyle: (0) Robust and projecting medially; (1) weak or absent (Geisler 2001: ch. 134).
378. Entepicondylar foramen: (0) present; (1) absent (Geisler 2001: ch. 135).
379. Supratrochlear foramen: (0) absent; (1) present (Asher et al. 2005: ch. 178).
380. Ulnar articulation of the humerus: (0) cylindrical trochlea in posterior view with a vestigial ulnar condyle in anterior view; (1) cylindrical trochlea without an ulnar condyle (cylindrical trochlea extending to the anterior/ventral side) (Luo and Wible 2005: ch. 203, modified).
381. Radial articulation: (0) rounded radial condyle (= capitulum) anteriorly but cylindrical posteriorly; (1) capitulum forming a continuous synovial surface with the ulnar trochlea (cylindrical in both anterior and posterior views) (Luo and Wible 2005: ch. 204, modified).
382. Humeral articulation on radius: (0) single fossa; (1) two fossae (Geisler 2001: ch. 141, modified).
383. Central process of radial head: (0) small or absent; (1) present (Asher et al. 2005: ch. 181).
384. Radius and ulna distal fusion: (0) absent; (1) present (Thewissen et al. 2001: ch. 81).
385. Radial articulation with carpals: (0) single fossa; (1) two fossae (Thewissen et al. 2001: ch. 80).
386. Scaphoid and lunate: (0) separate; (1) fused (Asher et al. 2005: ch. 183).
387. Os centrale: (0) present; (1) absent (Asher et al. 2005: ch. 184).
388. Pubic symphysis: (0) extensive; (1) narrow (Meng et al. 2003: ch. 22).
389. Epipubic bone: (0) present; (1) absent (Luo and Wible 2005: ch. 218).
390. Articular surface of femoral head: (0) extended posterolaterally; (1) limited to the sphere of the head (Asher et al. 2005: ch. 186).
391. Fovea for ligamentum teres on femoral head: (0) surrounded by articular surface; (1) interrupt margin of articular surface; (2)

APPENDIX 2
(continued from previous page)

absent (MacPhee 1994: ch. 27).

392. Greater trochanter relative to femoral head: (0) lower; (1) even; (2) higher (Horovitz and Sánchez-Villagra 2003: ch. 79); ORDERED.
393. Size of lesser trochanter of femur: (0) large, surpassing half of the medial extension of the femoral head; (1) small (Luo and Wible 2005: ch. 228; Flores 2009: ch. 93).
394. Third trochanter of femur: (0) absent; (1) present (Asher et al. 2005: ch.188).
395. Pectineal tubercle: (0) absent or vestigial; (1) distinct (Wible et al. 2009: ch. 377).
396. Proportions of the distal extremity of the femur: (0) as long as wide; (1) longer than wide (Asher et al. 2005: ch. 189).
397. Patellar facet of the femur: (0) weakly developed; (1) broad and shallow; (2) narrow and elevated (deep) (Luo and Wible 2005: ch. 230, modified).
398. Ossified patella: (0) absent; (1) present (Luo and Wible 2005: ch. 273).
399. Articulation between femur and fibula: (0) absent; (1) present (Horovitz and Sánchez-Villagra 2003: ch. 84).
400. Tibia and fibula proximal fusion: (0) absent; (1) present (Asher et al. 2005: ch. 190).
401. Tibia and fibula distal fusion: (0) absent; (1) present (Horovitz and Sánchez-Villagra 2003: ch. 87).
402. Depth of trochlear groove of the astragalus: (0) shallow (slightly concave articular surface); (1) moderately deep (section of the groove U-shaped); (2) deep (V-shaped) (Zack et al. 2005: ch. 40, modified); ORDERED.
403. Angle between medial and lateral facet for the tibia on the astragalar body: (0) 180°; (1) intermediate; (2) 90° (Horovitz and Sánchez-Villagra 2003: ch. 94, modified); ORDERED.
404. Angle between facet for the fibula and the lateral facet for the tibia: (0) 180°; (1) intermediate; (2) 90° (Horovitz and Sánchez-Villagra 2003: ch. 99); ORDERED.
405. Radius of curvature of the lateral trochlear ridge of the astragalus relatively to the medial trochlear ridge: (0) greater; (1) subequal (Zack et al. 2005: ch. 41).
406. Cotylar fossa on the medial edge of the astragalus trochlea: (0) absent; (1) present (Zack et al. 2005: ch. 44, modified).
407. Contact between sustentacular and navicular facets of the astragalus: (0) absent; (1) present (Asher et al. 2005: ch. 204).
408. Medial extension of the astragalar sustentacular facet: (0) reaches the medial edge of the neck; (1) does not reach the medial edge (Horovitz and Sánchez-Villagra 2003: ch. 102).
409. Astragalar medial plantar tuberosity: (0) weak or absent; (1) protruding (Horovitz and Sánchez-Villagra 2003: ch. 98, modified).
410. Astragalar neck: (0) absent; (1) present shorter than body width; (2) present and similar in length to body width (Horovitz and Sánchez-Villagra 2003: ch. 100).
411. Convex astragalar head: (0) absent; (1) present (Thewissen et al. 2001: ch. 92, modified).
412. Facet on astragalus for cuboid: (0) absent; (1) present (Asher et al. 2005: ch. 208).
413. Astragalar canal: (0) present; (1) dorsal foramen only; (2) absent (Horovitz and Sánchez-Villagra 2003: ch. 104, modified).
414. Posterior trochlear shelf of the astragalus: (0) weak or absent; (1) strong (Asher et al. 2005: ch. 198).
415. Calcaneal width: (0) broad with sustentacular and ectal facet extending from body; (1) narrow with sustentacular and ectal facets in line with long axis (Asher et al. 2005: ch. 210).
416. Ectal (or posterior calcaneoastragalar) facet orientation of longest axis: (0) anteromedial to posterolateral, (1) anteroposterior (proximodistal), (2) posteromedial to anterolateral (Horovitz and Sánchez-Villagra 2003: ch. 113, modified); ORDERED.
417. Anteroposterior overlap between calcaneal ectal and sustentacular facets: (0) no overlap; (1) partial overlap; (2) nearly complete overlap (Zack et al. 2005: ch. 32, modified); ORDERED.
418. Calcaneal sustentacular facet orientation: (0) medial; (1) dorsal (Horovitz and Sánchez-Villagra 2003: ch. 118).
419. Calcaneal sustentacular facet expanded onto body: (0) absent; (1) present (Wible et al. 2009: ch. 401).
420. Calcaneal peroneal process: (0) Protruding distally beyond calcaneo-cuboid facet; (1) distal but non-protruding; (2) at a distance from distal end of calcaneum; (3) absent (Horovitz and Sánchez-Villagra 2003: ch. 117).
421. Calcaneal plantar tubercle: (0) absent; (1) present at distal margin; (2) present more proximal than distal margin (Horovitz and Sánchez-Villagra 2003: ch. 122, modified).
422. Tuber calcis ventral curvature: (0) present; (1) absent (Horovitz and Sánchez-Villagra 2003; ch. 125, modified).
423. Calcaneal facet for the fibula: (0) present; (1) absent (Horovitz and Sánchez-Villagra 2003: ch. 125, modified).
424. Orientation of mediolateral axis of the cuboid facet relative to the long axis of the calcaneum: (0) less than 70°; (1) c. 70°-80°; (2) c. 90° (Zack et al. 2005: ch. 37); ORDERED.
425. Proportions of the cuboid facet on the calcaneum: (0) facet much deeper (dorsoplantar) than wide (mediolateral); (1) facet depth and width subequal; (2) facet much wider (mediolateral) than deep (dorsoplantar) (Zack et al. 2005: ch. 38); ORDERED.
426. Deep groove for the tendon of the flexor hallucis longus (= flexor fibularis) on the posterior edge of the sustentaculum calcaneum: (0) absent; (1) present (Wible et al. 2009: ch. 408).

APPENDIX 3

Re-scoring of the characters from the data matrix by Muizon et al. (2015) in *Trigonostylops* and *Astrapotherium*

Character 9. All available specimens of *Trigonostylops* have three lower incisors (state 1). (see Soria and Bond 1984).

Character 78. *Trigonostylops* has no stylar cusp B, re-scored as non-applicable.

Character 91. *Trigonostylops* has straight centrocrista (state 0).

Character 108. The nature of the hypocone in molars of *Astrapotherium* is uncertain. It is re-scored as non-applicable.

Characters 110 and 111. All upper molars of *Astrapotherium* have undoubtedly three roots (state 0).

Character 128. The presence of hypoconulid in lower molars of *Astrapotherium* is uncertain.

Character 170. All specimens of *Astrapotherium* examined by us have a single exit of the infraorbital canal (state 1).

Character 243. The anterior lamina of petrosal is absent in *Astrapotherium* (state 2) and unknown in *Trigonostylops*.

Character 271. *Astrapotherium* and *Trigonostylops* are re-scored as having postglenoid foramen (state 1), following Billet (2010) and Billet et al. (2015).

Character 285. *Astrapotherium* has conspicuous sulcus indicating a transpromontorial course of the internal carotid artery (state 0).

Character 287. Groove for the internal carotid artery is present in *Astrapotherium* (state 1).

Character 293. *Astrapotherium* has globose promontorium (state 1).

Character 301. *Astrapotherium* has a short tegmen tympani (state 0).

Character 306. In *Astrapotherium*, the depression interpreted herein as the fossa for the tensor tympani is ventromedial to the cavum supracochleare (state 0).

Character 309. *Astrapotherium* has no distinct depression for epitympanic recess (state 2).

Character 314. In *Astrapotherium*, the fossa incudis is lateral to fenestra vestibuli (state 0).

Character 323. *Trigonostylops* has a distinctly present and vertical mastoid process (state 0).

APPENDIX 4

(continued on next page)

Data matrix (modified from Muizon et al. 2015) used for the first set of phylogenetic analyses (Figs. 9A–B). All taxa are scored as in Muizon et al. (2015), except *Astrapotherium* and *Trigonostylops* (see Appendix 3).

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APPENDIX 4

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APPENDIX 4

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Azygonyx

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11001001100002121001111002000001002101202110210000000210000200000?2?11?201111?????0?100??
00?0???00100000????00?11?10?0000?001010?1?????????102???11????001010?111??1110100?2122100
110020210100101300?00?00?01?100002??121000000011000011?00000010101??1?00???11??????????00
?0?0??????????????????????????????0???????????????????????????????????????

Trogosus

000200?13211210011011121102111100{23}200012000221100000010??120220?00122?20120010??002021
00001001100000?21001011?020000110011011121201100000231?0?1200010002011010211131110{03}?10
0000010110101001000110000110100010010010101002000000{01}1010?010?0?1100012?111??1?1?10002
12210010012020?0?0101?00?0??0?????????????????????00??????????????1??????2??1????1???????
????????10011???????0??110011100011010100??11101??110000121?00?11101021102???00

Protungulatum

0001???0???????????00?000??01010?12???1101022{01}111000010??10011000112122022102000002221
2110102111201102102122000200000{01}00110111{12}1312000100{12}{12}010001000100010010201011
11??{12}???
??????????????????????????????????00000?011?10?021?11??000??211??0{12}?{12}00000210101???
????????1?00??020011??0???022100?011100022101
110120

Vulpavus

000{12}00?0210000000000000000{01}010100{12}010100000212300000011??00000000?10000022002020
00222111111021111000?2101111{01}10200000110021011122131000000{12}{12}0?0001000?000001111??
011??1{01}03{12}110{12}0001011000111100010?00{12}???1?01?0010{01}001?0??????????0000110?
01??11011?11??110?0????21221111010?011000?011300000000?0?110010?1?120010002{01}1{01}00010
{01}000000100?{12}101002???01?00??????????0?0??????????00??1?001??000110000{01}???1021100
1???00220001021010021102011100

Appendix 4

(continued from previous page)

Miacis
```
000100?021000000000000000?1010100101010000011230001001???00010000010000002200?020002220011
01021111000?21001{02}{01}0102000011001001111023100000{01}?1010001?000?0?0?1110???11{012}1
???3211020?010?100011110001000020011?0110010?00?100100000001100000?10?010011011?1111?10101
10?21{23}21111010?0110000111{13}00000000?01110010?1?120011011110000???0000001010{12}10000
2????01?00??????????0?0??????????0010????10?000????0?00??????1?????000????????1?1?0???????
1???
```
Cynodictis
```
00023???2?03??000?0???????001???010000000100112310000??0??01001?00020?0?022002021002221211
010011111000210011101 02?00011001001201123100000 0{12}{01}0100010001000101110?101111103211
020001011100111100010000200110010001010011101000000000?0000110001?01?010?11100101011002122
111101020110000011{13}10000000?11?10010?1?110011002110000???00000010101101002????01?00000
??001?10?0???????????????????????????????????????????????????????????????????????
```
Diacodexis
```
000100?021?0040000?0000000101110?1201112000220011000011??0002010011{12}1{12}2112002020002
2211111102111102212102123000200000 0?0210112222120001002{12}0100010000000200102010????1100
?1000???0011010101 1000??????0101?00000000200??0020010011110000100000?10010?111??1?1010002
1210?11000101 1000???130000000 0??11?01??1???0?110??????????????0?02?????11{01}0?102??01000
????1011?10?????????1???010????10011??11?010101??211?121000122100102012011 1101210110
```
Dichobune
```
0001?0???1?????????01000101?111101?0001210022101100001 0??0001111101111111130020??002221111
11021111012020021221002000101012111222210200010011010101000000002001020101121???0?1001??01
1110?0001000????001{12}11100000000?20?10100100101111000?100?0?110001?110??11?0???02121??0
1000?0110000101110000000????11000???11011100210000001?00000010103111101???011??????210?00
10?????????????????????????????????????????????????????????????????????????
```
Acotherulum
```
0001?0??????????????100?101?11110{12}200012100221011000010??10001101011111113002 0?1002221
1111102111?01002002113200200010101211112221020001001{12}010?010000000200102010112 1111??10
00??01001??0001000???00{12}21?1?0100010?20?110000000001111000?101000110001?110001??0??02
121??01000?0110000101300000000????100001??100?00000???100011?0?0001?103111101021?11?1????
20211?10?1???????????????????????????????????????????????????????????????????????
```
Hyopsodus
```
000130?02101000000000000011111001210011000220011000010??0{01}1121100121{12}{12}11200200?
0022211111102112?{01}220210112{23}2002000{01}010021011222221000100{012}2010101?0000002001
110{01}011111100?100000010110001011000110001110 1?00000000100001000 1000?1?02??01101?110101
{01}2110111010100021221?0100020110000101100100000?0111000011?1101110000{01}00002??0000001
010{12}1011010????1?00?0020{12}10000?0??111?0?1?02001011100011111010101100?10021000012100
1021120021101110100
```
Meniscotherium
```
000110?0210044000000000001111100120111200022201110001 1??0002211001{12}1112120020??102221
1111112122?020121011232102000000000110112220 31?0??0002110111?00000020010102111211100?1{01}
00000{01}011010001100011100120010000000001000110001000111000?01100?200001{01}211011101010
00{12}1221101001202100001013001 00000?0111001011?1101000001100002??0000001010{12}001101???
1?1?00?0???2?0000?00111101110020111110010111110101011121100210000120000021000021101111120
```
Phenacodus
```
000100?0211044000000000000101{01}1011200012100222011100011??0{012}0221{12}001101111200?0?
?102221211111 2122?022021021232102000001002101122221100010002 0100{01}1?00?0002001110101121
1100?1{01}00000?01101010110001100021101?00000{01}0010000100000001 0?110?011010210?011?110?
???10100?2122110100020210000101300100000?1111001011?110100000?1?0?02??{01}00000100?2100{0
1}010????1?00?0?????0000?001111???10020111?1001011111010101012110121000022?001021?0002110
1?112?0
```
Pleuraspidotherium
```
000220?02101?000000?0000002110100{12}2001122102222111000 11??001{12}21100111111030020??102
```

APPENDIX 4

(continued from previous page)

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2211111?10111?01112002121011211000001010122220321000001311001000000001200102020111111101110
0000010???10??1???01100011??1000000000100010100000000???010?010??00101000211100111010002122
1011000102101011011100000000?011110?021?120111000110000001?00000010101001100???001?0010020{
12}1??10?0011110????0?011??0100101111000???0010100110000121001111000020101100121
```

Maiorana

```
0001???????????????????????111???012000110102102010000???????11100012112012102001002221110
11001112011121021221002000000001101201210110000???11??1??00??????????????1?111100?10011001
0?1?101111000???0??11?0000000??11001?11000000?0?110?011000?001011?111??1010100?2122101100
010210001101300100?00?00?100?0???110?00000110000???000000010101101000???01?00?0????????0?
0??????????????????????????????????????????????012100??11100????????????
```

Baioconodon

```
0001????????????????????????01???01200011000210201000010??10022100012022122102001011221110
110011120111210212210020000000002101201210110010?1110001100000000200101010112111???1000?000
0????0?11100????0??11?100100010?0001??0?00?00???110??11?????0?011?111??1?10?????120111100
0?0210001201300100000?011100?0???110?00000???00001?0000001010110{01}000???01?00?0???1???
10?0???????????????????????????????????????????????????????????????????????
```

Arctocyonides

```
0001{01}0??2?00??000?0?????1?1010100120011100021021000000?0??00011100112121103{13}120??002
1211111?021000011021021221002000100001111312210100010021100001000100000111001011211103110
0000000110100111000010001210100100010010110100000000010?010?0110?00001012?11100101010002122
110101020110000101110000000?011100?01??110?0000011000001?00000010103111112???001?00?0?2??
?011010???????????????????????????????????????????????????????????????????????
```

Arctocyon

```
000100?0210311000000100010101011012000110002102100000???000101000110211033120??002121111
1?02100002202102122100020001?????111322210100010?01100011000100000111002011111103110000?00
0?1010001100000000111010{01}100010010111100000000?0?010?010??00001012?1110010101000212?110
101020110000101110000?00?01?110?0???110?00000110000???0000000101010?1112???001?00?0?????01
1??00111100???0?011001110001101000???000010011000012100{01}111100021102100011
```

Ptilocercus

```
00200?03110010000021000102101100200100100021020100?????000221001110100122020??0022122110
1001101200?211112201020000001011013122312000100310100{01}0000000000010101011211200?11{01}
2000001110011010001000011110001000111100111100100011?00011101002111101211011101010?021201
00100000210001101100000010?0111100211?121001002111100{01}11100002000?20110001010011001002
1011?101001111?11{01}101011110010001100000011100010011000022101102102001112111100
```

Plesiadapis

```
000{23}{01}1?031013000000011020?0?{12}12?00{23}20{01}012{01}0022{12}011{01}00????0000{01}
1{12}0012222122{01}020??{01}02221{12}111102110?022021021232002000010002101312210200010032
10001100000000011011101121120??1202?001011010010100000000011111001000000010101000011001??02
??010?11?{01}020012111?1112?201011200?0110020210000101100012000?1111100011?1210010031??1{
02}02?21101120020{12}111000110?11000?????0?1?10?1111???1??00101???000000110000???110{012}
01?01???00220011011001021112111101
```

Northarctus

```
000100?0320044000000000000000010101120011200012{12}011000010??0{01}02211001101111221020??002
2211111102110?0221210112320020001?????1012222202000100121{01}0011?0000000001021{12}111211
100?1101010101100011011001?00011011?0000001010101?000??0????0001110?0?{01}002001?110?1111
02000?1200??1100?0110?00001100012010?0111100211?12100??031111?0{01}11?1?1120020{12}1110?0
100?11000?????0?1?10?111111???00010??0?00100011000010?10?001002100002210100210?1111112211
221
```

Adapis

```
000130?03200440000000000000001{01}11100120001{12}000122011000010??00022110011112122{01}020??
002221{12}111102110?0200210112320020001?????1012222002?0010012100012?0000000101021{12}111
211100?{01}{01}02?10101100011011001100001111000000{01}0010101100011011??0001110?010002002
2110?110102000112?0?0110010210000001100012010?0111100211?12100100311?1?0{01}11?1?1120020{
12}111000100?1100010??0??1?10?1????????????????????0???10?00???1????????2????0221010021011
```

APPENDIX 4

(continued from previous page)

111112211121
Tribosphenomys
000321?14301220021?11131?0?2?2???32???100000???????0????????0210?0110111220020??002221211
0122?101222021021031?021001?????1113122102010001?2100?100100?0??0???102011211????101?????
??????????????????????????10???????1???
???
??0002210010110200211011111?0
Paramys
000321?14301220021?11131?0?2?2???{23}2???10000022011100????????0211?0111221{01}33?????1??
22{01}2111?22?22?1220210212320021001?????111322210101000{01}32100110010000??0102202011211
20??1012?0000110001111100?000012112?0200000010001???011001??02??0101000?11001?11011102020
?02020110102120012?00001300010000?0111100001?111000000120?0001110?002100?11110120?0?01000
?0?????1??0?0011110??00010??0?0000{01}011?10?00?11221100210000220001011020021101111210
Rhombomylus
00032101430122002 1?11131?0?2?2???32???12{01}00?2{01}101000?????01122020011{12}221233?????
0??0202011?22?20?100?21021032?1?1001?????11131211120000003{12}100011010000100000202011111
20??101200000110001111100?000012002?010000102001110101100 10?00001101012102001?11111112020
002120{01}0010212001 1?00002{13}00010????1111110{12}11?1210110031200202?2?0?002000?210{01}
002021?110000000 20011?1010???1??1??0?1?1?0110000111010???11021101210000221001011020022101
110120
Gomphos
000{23}21?1320122001101113110?2?2???{23}2???12100?21000000?????02202120011?121233?????1??
020211??22?20?102021021032?0?1001?????11131221020100003210001101000010010020201111120??10
11000001?01??111100?100?1200100100001010011?010??00???02??01??0??11??01?111?11010100??120
1?1103110012?0000210?000???????1????????????????????????????????????1??0??021?01000??????
???10?0?111??????000110?001?011????????10?211?1?10000220001021020112101111100
Mimotona
000{23}21?1320122001101113110?2?2???{23}2???12000120000000?????000021000110121233?????{01
}??020211??22?20?100?21021032?0?1001?????11131221020000003?1??????10??????????02?????1{12
}0??101???????1??01?1????????????????000000????1???
???
???
Blarina
000{23}30?02{23}11210001{01}1103100211{12}?10{23}0???01000012001010????000222?001{01}000
0110020001020222110110100?200?21101022?110000011011113112332000001?3010010000000001111102
011211100?120101{01}1111101101?00?0?001010000011???2?0?1?00?1?????1?02???1??00?100001211
1111010101021{23}10?11100??20????111300001000?0111100031?12000100011001000100000 21?202101
01001000100100?10011?00??01111001{01}00001001100000110000011100201001100102200011210000 21
1011101?1
Erinaceus
000{23}00002211000000{01}11000102101110{23}0???1{01}000{12}10001000????000220000100{01}0
0120020??0002212111?02100?000?201012320110000010021113122032?0010{01}3{23}0101{12}1?00000
001110202011311200?11011101011110?0{01}110010010101100010010111 0011?1101110{01}1002??0100
1001120012111111010100021210?1104020211 0?110111100100 0?0111100021?11100100210000001100000
0101021010020100 0{01}000100200101101001111101100101101100110110000111102011001100102210 11
011120121101010110
Solenodon
000230?021013000001200000 0?10110021010010002102010 00????0002200001101{12}02000201101221?
??101201111?00?20100011?020000000002010100020 0?00000{12}30100111000000210101 02011{23}11100
?1{12}1111010111101111000100001011000001???210?111010111001002???1000001100{01}{01}?11101
10100??021211111100?02100?120130000{01}000?01111000{012}02100000000110000111000000 21020210
000001110100110???0?1?101?011101011102011010100001101010011002010011000002210010211?002110
1010211

APPENDIX 4

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Eoryctes
```
0002?0?0?{23}????????????0??????01??21???010002122000 10?????0001000?0111??0220020100022{0
1}010111021120100?20?0100??0?000000?0200110203?2000000{23}2???????????????????020????????
?110???0?0?10?01?110?????0?2210000?0????2???????????00?0???2???10?00?110?01?111?11??0?????2
1211111100?0?100?1{12}0111101?010?0?11100???12100?002110100{01}11000000101 0?1000??01??01
?????????????0??????????????????????????????????????????????????????????????????????????
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Potamogale
```
0002301021012300000200001021011002201002000222100000????1102200111112202110201211221{01}
0010100111200?2000100??020000000021111020202?000000301001000000000001100010112111 00?12111
111011111??111?010001200000000 1???200?10?001000010?02???10011010100011110010100??02122111
1100?02100?021121110100 0?0111000011?1000000111100101110000000102021010100110010011002 00100
001?011111011100010101101101100000111100 10?02100101200?11110201??1?00102?0
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Tenrec
```
00022010311022100000100010{12}01010022011{01}0100220111000001??01012101?111120202?201?012
22???101201??0?00?2?10?111001?0000100201 0?012200?000002301001000000000111121020112111 01212
111011011110 0{01}0100010001{12}011000101???210?111000110010?02???1020001100{01}2111100101
10??021221011100?00100?020111?100000?01?1000011?10100{01}?0211001011100000 21020{13}101002
0110010011002101 1?10??011111011102011011110001100000111100110011000022001111112002110110 1
221
```
Orycteropus
```
001{23}??0?54??????????????????2?2???{23}2???1????1??????0??????????????0?110{12}0?0???????
?????????????????????????????????????????????????????00{123}010110?1000001101220001131
101??{01}200010111101001 01200?000?101000100000012000000001000000111000010100011 0001?1100110
100??021220?010412010???0201100000000?0111001011?11000000011110011010000210 0?111100001100
10001022021 1?1011?11110??00020110111100111000101010121110 2?1101220101111 00002?101?112??
```
Rhynchocyon
```
0002101051???3????10100010?0010001201101200212201010001??11{01}02120020?0?2033?????001020
2111?02?101000?2101100??0??0000001110122220?2?00000120111 00?0000001101020001121100 0?11011
0011110100111000100002001 1?10000101200000000100000110010010111012000 1?121011010110021220?0
104020010?101011110?1010?01110?0031?11100??0112012?011?0???1??20{12}?1000001 1?11101100210
11?00110111110100010111111010111000101010021101211111122110112112012010101020 1
```
Procavia
```
0001211{01}4201230021?0100010?2?2??01202012200322011000000??1212211001{12}1112033?????101
0212111?12?12?200?2101123202310000001011111220 32?0100001111120?1000002101020{012}1111111
1??100000010110001011000?00001{01}{01}1{12}01{01}000000110011110110 00{01}?001011010120 10
00121211110101110212110010410020???0101100110 1?0011111100 11?1100101001201002?2101002?00?2
101001021011110102102 11?011101111001100201120100111111001010101211{01}121011022011111 0120
120103010220
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Moeritherium
```
000211?{01}2202020000101000102112??022???1220022201100 0?????12122111012222 1033?????002021
2111?02?02?000?2101123210 21?01?????111422210200100 1?1101111?10100020010201111??1100?1001?
0?0011001??????00?000{01}010?00200101010 0?1?1?0011010?02??010?010010101?11001101000?011?1
10010400000???0001?00?????????1?0?1????????????????????????0??02?????102??0????01?0???0?12
0???1?10111100?1102011201101101 1????????0021000 1?????????????????????????????
```
Chaetophractus
```
001130?054?????????0?????????1111????????1??????????????????????????????????????????????????
?????????????????????????????????????????????????0000001101001000210012 0?01121101??1?010000
101010000100010101?000????00000002000110100110110010?01020011201012111111 0200??121210?1103
120211011201100010 1?0111111001 21?100000001221000 2?2001002000?1011100021?1110010020 2101001
00111101111121110010100011000101110120100210110220000011020021101110010
```
Dasypus
```
001??01?54?????????????????????????????1????????????????????????????????????????????????????
?????????????????????????????????????????????????00301010010010001110220?011211?1??1?110000
1110100101000?0101?000????00000002000010110 0{01}111?02??0102000120101211111 10200??121210?1
```

APPENDIX 4

(continued from previous page)

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1021202100011013001001?0?1111100021?1200001001110002?2000002000?1101100001101100100202101
001001111010011211100101000110000011111201002101101200000110200211011 10110
```

Bradypus

```
00133???54?????????????????112????????1??????????????????????????????????????????????????
???????????????????????????????????????????????0031001 10?1010000001211?11121001??2??1010{
01}0110001101000 0?00{01}?100????000002200011000110011?02??0102010010101?1201110200??021{2
3}10?111202000???00011000001?0110111000?1?1000000111211002?2000002000?200{01}000021?01110
1001021000010011110101112110100000101100000111120100021000032000101002011010100 1000
```

Tamandua

```
01???????????????????????????????????????????????????????????????????????????????????????
???????????????????????????????????????????????1?00?0?00??0100020112?0?011111?1??1?010001
111010110{01}000?1001?000???00100220??000000000001102??0102010020101?120?111200??021210?1
11202000???0101100000000?1111100021?1?000???????0??2?2?00002000?2101100021?011001002001{0
1}000??01111001111211000001000110001011110010002100002200110100200201010 11000
```

Colbertia

```
000130?02100000000001000001111110120001201122011100001 0??0200211011{12}122212012000001221
2111?00112?000?2002122000 21?11???0?1012222102001010?311??11000?000210102 1111?111110?10000
00101??0???????00000{12}000100{01}000?001100??????????????1?00???????0?001?111??10?0111??
1110?01041?0210?????{12}?0001??00?????1100???????????????1??????????????????1?0?02??11???
?????{12}??????1???????????????????1001100????????02110??????0220101111000?1101?10101
```

Plesiotypotherium

```
000321?{01}420?220?11?111?0???2?2???32?????011??0????00????????021???1????20??????????22?
????????1??{12}??????????????1?????????11222?????????0{12}3110010000000002101020211111111?
?12110000011010001{01}001?110000000100000000210?111100110111100001111{01}01111001211111101
0111021110?0104110211?001?{12}?0001??00???1111?????????????0???1?????????0??0??21?{01}?01
02??11?101???02?0000?{01}111?????????????1110011100000???00111?01??0002201111111100011101
210110
```

Protypotherium

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Adinotherium

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Notostylops

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Pyrotherium

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APPENDIX 4
(continued from previous page)

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end;
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ctype ord: 4 9 10 23 28 30 34 37 44 45 60 61 64 67 68 69 70 71 73 74 77 80 86 87 98 105 109 111 112 117 121 126 127 128 131 138 139 144 145 158 160 164 167 172 174 197 198 204 210 211 228 239 243 258 302 327 350 369 393 403 404 405 417 418 425 426 ;

begin trees ;
tree tnt_1 = [&U]
(1,((24,25,26,27,28,29,47,48,49,61,62,63,64,65,66,67,68,69),(38,39,40,41,42,43,44,45,46)),(51,52,53,54,55,56),(57,58,59,60));

end ;

APPENDIX 5

(continued on next page)

List of characters and character states used for the phylogenetic analysis based on the data matrix of Billet et al. (2015) presented in Figure 10A.

Teeth

1. Presence of variable upper and lower precanine diastemae (= elongation of the premaxillary relative to teeth size): (0) absent; (1) present.
2. Presence of variable upper postcanine diastemae (= elongation of the anterior maxillary part relative to teeth size): (0) absent; (1) present.
3. I1: (0) absent; (1) present.
4. I2: (0) absent; (1) present.
5. I2-C labio-lingually compressed: (0) absent; (1) present.
6. I1 relative size vs. other incisors: (0) smaller or subequal to other incisors; (1) enlarged relatively to other incisors.
7. I1 crown highly curved: (0) absent; (1) present.
8. I1 comma-shaped in section: (0) absent; (1) present.
9. I1 obliquely implanted, meeting at tips: (0) absent; (1) present.
10. Procumbent I1-2, occluding in an angle of 90° (or less) with procumbent i1-2? (wear forms a bevel on upper incisors): (0) absent; (1) present.
11. I1 crown height and robustness: (0) brachydont or slightly hypsodont, not tusk-like; (1) hypsodont and/or tusk-like; (2) hypselodont and tusk-like. Hypsodonty corresponds here to enamel-band or dentine hypsodonty sensu Koenigswald 2011. ORDERED.
12. (I1-)I2 caniniform, circular in cross-section: (0) absent; (1) present.
13. I2 trihedral tusk and diverging: (0) absent; (1) present.
14. I2 position relatively to I1: (0) I2 lateral to I1; (1) posterolateral to I1; (2) I2 immediately posterior to I1 (I1 and I2 brought into line anteroposteriorly). ORDERED.
15. I3 (+-i3): (0) present; (1) absent.
16. Lingual cingulum on upper incisors forms a fossa: (0) absent; (1) present.
17. Canine (upper and +- lower): (0) present; (1) vestigial, often absent; (2) always absent. ORDERED.
18. Tusk-like upper and lower canines: (0) absent; (1) present.
19. Canine (upper and lower): (0) massive and caniniform; (1) incisiform and subequal to other incisors.
20. P1: (0) absent; (1) present.
21. Cheek teeth: (0) brachyodont; (1) hypsodont (sidewall hypsodonty sensu Koenigswald 2011); (2) hypselodont. ORDERED.
22. Distal cingulum isolating a deep fossette (postcingulum fossette) on upper cheek teeth: (0) absent; (1) present.
23. Protoloph (high crest (loph) joining paracone-parastyle and protocone, in paracingulum position) on upper molars (and premolars): (0) absent; (1) present; (2) paracingulum high but not connecting to parastyle-paracone.
24. Ectoloph (high crest joining paracone and metacone) on upper molars (and premolars): (0) absent; (1) present.
25. Metaloph (high crest joining metacone and hypocone) on M1-2 (and premolars): (0) absent; (1) present.
26. Long crochet on upper cheek teeth connected to the ectoloph, thus isolating a posterolabial fossette: (0) absent; (1) present.
27. Anterolabial fossette on upper cheek teeth: (0) absent; (1) present.
28. B29- Central fossette on upper cheek teeth: (0) absent; (1) present.
29. Deep labial extension of central fossette between the protoloph (-crista 1) and the crochet (-crista 2) on upper molars: (0) absent; (1) present.
30. Multiple cristae individualized mesially to the crochet on upper cheek teeth: (0) absent; (1) present.
31. Crista intermedia running lingually from the ectoloph between the protoloph and the crochet on upper cheek teeth: (0) absent; (1) present.
32. Crista intermedia: (0) not-well individualized but suggested by a bulge; (1) completely individualized .
33. Posterolabial fossette on upper molars: (0) co-occurs with the central fossette; (1) disappears before the closure of the central fossette.
34. Crochet originating lingually at mesial edge of hypocone: (0) absent; (1) present.
35. Para- and metaconule: (0) absent or indistinct; (1) present.
36. Upper cheek teeth parastyle: (0) absent or indistinct; (1) present.
37. Upper cheek teeth parastyle (at least on molars): (0) not projected labially (not more labial than paracone); (1) projected labially relative to metacone.
38. Subvertical parastyle-paracone sulcus on upper cheek teeth (at least premolars): (0) absent; (1) present.
39. Subvertical parastyle-paracone sulcus on upper premolars: (0) shallow; (1) deep.
40. Prominent mesostyle (stylar cusp C) (at least on M): (0) absent; (1) present.

APPENDIX 5

(continued from previous page)

41. Metacone (fold or cusp) on (P3-)P4: (0) absent, connate with paracone or not visible; (1) present-distinctly individualized from paracone.
42. Deep mesial valley on P2-3 (-4) due to incomplete development of protoloph: (0) absent; (1) present.
43. Persistent lingual sulcus after the isolation of the central fossette on upper molars: (0) absent; (1) present.
44. Persistent lingual sulcus (enamel infolding; tooth not trilobed) between protoloph and metaloph on upper molars: (0) absent; (1) present.
45. Upper molars trilobed when little worn, with large and rounded median lobe: (0) absent; (1) present but disappears with wear; (2) trilobation persists throughout all wear stages. ORDERED.
46. Prominent hypocone on upper molars (M1-2 +-M3): 0. absent; (1) formed by bulge of posterocingulum; (2) formed by displaced and expanded metaconule; (3) formed by an additional cusp, possibly from split of protocone.
47. Size (area) of M1 vs. M2: (0) M1 much larger (>120%); (1) subequal (80%<>120%); (2) M1 much smaller (80%<).
48. Size (area) of M1 vs. M3: (0) M1 much larger (>120%); (1) subequal (80%<>120%); (2) M1 much smaller (80%<).
49. Size (area) of m1 vs. m2: (0) m1 much larger (>120%); (1) subequal (80%<>120%); (2) m1 much smaller (80%<).
50. Size (area) of m1 vs. m3: (0) m1 much larger (>120%); (1) subequal (80%<>120%); (2) m1 much smaller (80%<).
51. MC22- Cusp on precingulum anterolingual to paraconule: (0) absent; (1) present. Non-applicable for hypsodont and hypselodont taxa.
52. Separation between paracone and metacone on upper molars (at tip and base): (0) small to moderate, (1) large.
53. First lower incisor: (0) well developed; (1) reduced relative to other incisors.
54. Lingual vertical ridge on lower incisors and canine: (0) absent; (1) present.
55. Lingual face of i1-2 (only i2 when i1 is absent; and vice-versa): (0) without vertical sulcus; (1) with a shallow vertical sulcus; (2) with a deep vertical sulcus (bifid incisors). ORDERED.
56. Lower incisors: (0) implanted subvertically; (1) highly procumbent.
57. Third lower incisor large (larger than canine) and canine-like (pointed): (0) absent; (1) present.
58. Tusk-like third lower incisor: (0) absent; (1) present.
59. Leaf shaped lower incisors: (0) absent; (1) present.
60. Metaconid of p4 (or ultimate premolar): (0) small to medium-sized and appressed against protoconid; (1) enlarged and distinctly separated from the protoconid.
61. Mesial lophid (paralophid?) in a paraconid position on lower cheek teeth: (0) absent (or just a faint cristid); (1) present.
62. Lower cheek teeth with short mesiodistal protolophid, transverse metalophid and mesiodistal hypolophid slightly convex labially (double crescent): (0) absent; (1) present.
63. Lower cheek teeth with entoconid transversely expanded into entolophid: (0) absent; (1) transversely expanded; (2) less transverse and attached to the trigonid.
64. Isolated cuspid in front of the metalophid-metaconid on lower cheek teeth: (0) absent; (1) small mesiodistal crest running mesially from the distolingual extremity of the metalophid-metaconid; (2) completely isolated cusp.
65. Lingual connection of lophids of the trigonid and talonid (entolophid connects to metalophid with wear) on lower cheek teeth: (0) absent; (1) isolating a trigonid-talonid fossettid in conjunction with the preceding more labial connection of hypolophid with trigonid; (2) lingual connection trigonid-talonid precedes the labial connection and isolation of fossettid; (3) single lingual connection, producing a deep labial sulcus between trigonid and talonid.
66. Hypoconid: (0) forms labial half of talonid or less, does not invade talonid basin anterior to the hypoconulid. (1) large, conical; extends on lingual half of talonid and invades talonid basin anterior to hypoconulid.
67. Fossettid of entolophid: (0) absent; (1) present.
68. Trigonid of lower molars with a tiny trigonid fossettid partially or entirely isolated lingually by a crest (premetacristid) running mesially from metalophid: (0) absent; (1) present.
69. Transversely elongated fossettid isolated between entolophid (mesially) and hypolophid (labially and distally) with advanced wear: (0) absent; (1) present.
70. Distolabial crest on trigonid of lower premolars made by a distolabial extension of protolophid: (0) absent; (1) present.
71. Talonid extending well distal to entolophid on lower molars: (0) absent; (1) present.
72. Deep labial and lingual sulci dividing trigonids and talonids on lower cheek teeth at all wear stages (all along the crown): (0) absent; (1) present.
73. Flat and straight lingual face on lower molars at all wear stages (on all the crown height): (0) absent; (1) present.
74. Teeth: (0) differentiated into morphological types (incisors, canines, premolars, and molars) with enamel or, (1) simple peglike teeth without enamel (or very thin layer in unworn teeth).

APPENDIX 5
(continued from previous page)

Skull

75. Rostrum length/braincase length<0.5 (braincase more than twice larger than rostrum): (0) absent; (1) present.
76. Premaxillaries defining a strong and long ridge connecting the narial processes to the anterior alveolar border (the nares open much higher than the alveolar border): (0) absent; (1) present.
77. Development of incisive foramina: (0) small; (1) large (=anteroposteriorly elongated).
78. Triangular incisive foramina (distal extremities converging): (0) absent; (1) present.
79. Medial platform of palatines expanding palate posteriorly and fully continuous with it: (0) absent; (1) present.
80. Orientation of the blades of the ectopterygoid crests: (0) sub-parallel and facing ventromedially; (1) diverging and facing mostly posteriorly.
81. Position of choanae: (0) mostly anterior to last molar; (1) even with last molar; (2) mostly posterior to last molar. ORDERED.
82. Choanae divided by a vomerian/palatine process: (0) absent; (1) present.
83. Premaxillary-maxillary suture course on palate: (0) medially: directed anteriorly; (1) medially: grossly transverse; (2) medially: directed posteriorly; (3) directed posteriorly in its entire course. ORDERED.
84. Narial processes of the premaxillaries: (0) absent; (1) present.
85. Posterodorsal extremity of maxillary contacting nasal: (0) does not reach posterior extremity of nasals; (1) does approximately reach posterior extremity of nasals; (2) reaches much further than posterior extremity of nasals. ORDERED.
86. Infraorbital foramen in adult: (0) above premolars; (1) above molars.
87. Strong vertical descending process (masseteric spine) of maxillary: (0) absent; (1) present.
88. Anterior tips of nasals: (0) extends anterior to ascending process of premaxillary; (1) does not extend anterior to ascending process of premaxillary.
89. Anterior edge of ascending process of premaxillary shifted posteriorly: (0) absent; (1) present.
90. Length of nasals reduced relative to width: (0) absent; (1) present.
91. Large facial extent of lacrimal toward nasal bone: (0) absent; (1) present.
92. Post-orbital constriction: (0) strong; (1) weak.
93. Jugal excluded from anterior orbital border: (0) absent; (1) present.
94. Squamosal contacts with frontal at level of postorbital apophysis: (0) absent; (1) present.
95. Zygomatic arches in dorsal view: (0) parallel to anteroposterior axis; (1) semi-circular and well-expanded laterally.
96. Zygomatic plate below and in front of orbit: (0) absent; (1) present.
97. Anterior root of zygomatic arch grossly situated at level of M1 anteriorly (or more anterior) and removed from M3 posteriorly: (0) absent; (1) present.
98. Orbit shape: (0) round; (1) oval (higher than long, dorsal edge of zygomatic arch excavated below orbit).
99. Jugal-squamosal suture strongly curved anteriorly (large part directed dorsally): (0) absent; (1) present.
100. Sphenopalatine foramen: (0) well individualized at limit between medial orbital wall and orbital floor; (1) poorly individualized, within a groove at limit between medial orbital wall and orbital floor.
101. Position of sphenopalatine foramen: (0) in posterior part of orbit floor; (1) at level of middle of orbit floor antero-posterior length.
102. Very large orbit (the orbit occupies almost all the orbitotemporal fossa): (0) absent; (1) present.
103. Temporal lines (forming sagittal crest): (0) fused temporal lines, sagittal crest well-developed; (1) fusion of temporal lines only in most posterior part; (2) no fusion between temporal lines. ORDERED.
104. Auditory region (basicranium) large and short (= auditory region much wider than longer, from level of anterior edge of squamosal root of zygomatic process to posterior border of paroccipital processes): (0) absent; (1) present.
105. Glenoid fossa shape: (0) concave (or concave posteriorly and flat anteriorly), open anteriorly; (1) mostly flat anteroposteriorly; (2) concavo-convex (deep and narrow fossa posteriorly).
106. Extent of glenoid surface: (0) elongate transversally; (1) reduced transversally, almost as large anteroposteriorly; (2) elongate anteroposteriorly. ORDERED.
107. Postglenoid foramen: (0) posterior or posteromedial to the postglenoid process; (1) anterior to the postglenoid process.
108. Postglenoid foramen piercing deeply postglenoid process postero-dorsally and defining a large sinus within its base: (0) absent; (1) present.
109. Alisphenoid canal: (0) absent; (1) present.
110. Foramen ovale: (0) within alisphenoid and separated from piriform fenestra; (1) mandibular branch of trigeminal passes through sphenotympanic fissure and/or piriform fenestra.
111. Long and large groove on the lateral face of ecto-(ento-)pterygoid process immediately in front of the foramen ovale/sphenotympanic fissure: (0) absent; (1) present.
112. Inflated ossified auditory bulla well (tightly) attached to basicranium: (0) absent; (1) present.
113. Position of hypoglossal foramen relative to posterior lacerate (jugular) foramen: (0) well separated from it; (1) in a common

APPENDIX 5

(continued from previous page)

depression.

114. Basicochlear fissure: (0) closed; (1) patent.
115. Large foramen medial to promontorium midlength and/or auditory bulla and lateral to basioccipital: (0) absent; (1) present.
116. Large quadrangular auditory bulla with an anterior border grossly transverse and a medial border defining a long straight line: (0) absent; (1) present.
117. Posterior bulla laps up onto paraoccipital process: (0) absent; (1) present.
118. Crista meatus: (0) absent; (1) present.
119. Crista meatus: (0) small; (1) well developed.
120. Ossified tubular external auditory meatus strongly attached to the basicranium: (0) absent; (1) present.
121. Ossified tubular external auditory meatus: (0) short, does not reach lateral edge of skull (especially lateral edge of postglenoid process); (1) long, reaches lateral edge of skull.
122. Postglenoid process appressed or almost fused on all its length to crista meatus and/or to external auditory meatus and defining a channel for postglenoid foramen: (0) absent; (1) present.
123. Crista meatus and post-tympanic process of squamosal: (0) widely separated; (1) very close to or appressed against each other.
124. Posterior border of tympanohyal recess: (0) formed by paroccipital process; (1) formed by a tympanic extension and/or post-tympanic process.
125. Very small tympanohyal recess located on posterolateral slope of bulla: (0) absent; (1) present.
126. Epitympanic sinus in posterodorsal part of squamosal: (0) absent; (1) present.
127. Epitympanic sinus in a large swollen triangular area delimited by a medial crest continuous with posterior root of zygomatic arch and with lambdoid crest: (0) absent; (1) present.
128. Promontorium shape: (0) flat; (1) globose.
129. Expanded and fanlike medial flange of tympanic face of petrosal, well demarcated from the bean-shaped promontory: (0) absent; (1) present.
130. Location of tensor tympani fossa: (0) largely (ventro-)medial to the cavum supracochleare; (1) strictly ventral or lateral to it, not medial.
131. Facial sulcus (here the distance from fenestra vestibuli to crista parotica): (0) wide; (1) moderate; (2) narrow. ORDERED.
132. Subquadrangular outline of tensor tympani fossa outline on the promontorium, elongated anteroposteriorly: (0) absent; (1) present.
133. Vascular (internal carotid and stapedial) sulci on promontorium: (0) absent; (1) present.
134. Epitympanic recess vs. fossa incudis: (0) subequal; (1) epitympanic recess larger; (2) reduced or no visible depression for epitympanic recess.
135. Posttemporal canal (or groove) and foramen: (0) absent; (1) present.
136. Stapedial ratio: (0) less than 1.8; (1) more than 1.8.
137. Stapedial fossa and postpromontorial tympanic sinus: (0) distinct, separated by a break slope; (1) merged, almost indistinct.
138. Hiatus Fallopii location: (0) opening at anterior edge of petrosal; (1) opening on the tympanic surface of petrosal.
139. Strongly curved promontorium of petrosal (excavated by a deep notch just anterior to the fenestra vestibuli): (0) absent; (1) present.
140. Tegmen tympani: (0) inflated ventrolaterally; (1) thin, not inflated ventrolaterally.
141. Pierced tegmen tympani: (0) absent; (1) present.
142. Location of crest separating foramen acusticus superius and foramen acusticus inferius in internal auditory meatus (IAM): (0) shallow in IAM; (1) deep in IAM.
143. Subarcuate fossa morphology: (0) deep, diameter of aperture is smaller than maximum diameter of the fossa; (1) deep, cylindrical or slightly conical, with diameter more or less constant; (2) conical or shallow depression: aperture is the widest diameter. ORDERED.
144. Cochlear canaliculus within a large notch at posteromedial edge of promontorium (=lateral wall of cochear canaliculus notched in a (large) right angle): (0) absent; (1) present.
145. Number of cochlear turns: (0) less than 2 (or 2); (1) more than 2.
146. Relative sizes of SCs (from inner perimeter and/or R): (0) ASC clearly the largest (>1.10 from the others); (1) subequal (at least ASC and PSC); (2) PSC the largest (>1.10 from the others).
147. Secondary common crus: (0) present; (1) just a contact; (2) absent.
148. Anterior (and posterior) ampullae dorsoventral girth relative to semicircular canal cross-sectional diameter: (0) ampullae girth in the dorsoventral direction extend well beyond the SSC boundaries; (1) ampullae are not noticeably expanded anterodorsally beyond the plane of the SSC.
149. Dorsal extent of ASC and PSC above the crus commune: (0) only the ASC extends well dorsal to the crus; (1) ASC and PSC both

APPENDIX 5
(continued from previous page)

extend well dorsal to the crus commune; (2) neither canal extends well dorsal to the crus.
150. Pars mastoidea of petrosal: (0) well extended; (1) absent or reduced to a thin strip of bone appearing between squamosal and exoccipital, disrupted in surface from non-mastoid portion of petrosal.
151. Very high sagittal and lambdoid crests, this latter crest being inclined backward: (0) absent; (1) present.
152. Coronoid process of dentary: (0) rectilinear; (1) bent medially.
153. Mandibular foramen: (0) below alveolar border; (1) at level of alveolar border.
154. Shape of dentary body: (0) deep, robust; (1) slender.
155. Neck and head of astragalus: (0) not expanded and axis oblique relative to tibial trochlea; (1) expanded and axis subaparallel to tibial trochlea.
156. Cotylar fossa on the astragalus: (0) absent; (1) present.

APPENDIX 6

Re-scoring of the characters from the data matrix by Billet et al. (2015) in *Trigonostylops* and *Astrapotherium*

Character 15: the presence of I3 in *Trigonostylops* should be scored as unknown.
Character 20: The P1 is present in *Trigonostylops* (see Soria and Bond 1984) (state 1).
Characters 88 and 89: *Astrapotherium* has no ascending process of the premaxillary. These characters should be scored as non-applicable.
Character 90. *Trigonostylops* has no reduced nasals (see Soria and Bond 1984, Ameghiniana 21: 43-51) (state 0)
Character 128: *Astrapotherium* is re-scored as having globose promontorium (state 1)
Character 129: *Astrapotherium* is re-scored as having a well demarcated medial flange of the petrosal (state 1)
Character 130: *Astrapotherium* is re-scored as having tensor tympani fossa (ventro)medial to the cavum supracochleare (state 0).
Character 133: *Astrapotherium* is re-scored as having vascular sulci on promontorium (state 1).
Character 134: *Astrapotherium* is re-scored as lacking distinct depression for epitympanic recess (state 2).
Character 151: Billet et al. (2015) scored *Trigonostylops* and *Astrapotherium* with state 3, but only two states were defined for this character. We herein re-scored both taxa with state 1.

APPENDIX 7

(continued on next page)

Data matrix (modified from Billet et al., 2015) used for the second phylogenetic analyses (Fig. 10A). All taxa are scored as in Billet et al. (2015), except *Astrapotherium* and *Trigonostylops* (see Appendix 6).

```
#NEXUS
begin data;
dimensions ntax=48 nchar=156;
format missing=? symbols=»0~3»;
matrix
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??00??000?10000?00000000101001????0?0?????0???????????????????????01011??
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Periphragnis
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Puelia
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APPENDIX 7
(continued from previous page)

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Leontinia
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00100010001000100020000101000110?11??111111 1100??1111???20?????1100000
Cochilius
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0001000100??00020???1?10?011??1?1?0?11????????????????????02210100 00??
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Mesotherium
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01000000001000020 00?1?10?100111110 1010??????????????????????????11000??
Hegetotherium
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APPENDIX 7

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Carodnia
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;
end;
ctype ord: 11 14 17 21 45 55 81 83 85 103 106 131 143 ;
end ;
```

APPENDIX 8

(continuedon next page)

List of characters and character states used for the phylogenetic analysis based on the COMBINED matrices of Muizon et al. (2015) (characters 1-426) and Billet et al. (2015) (characters 427-513) presented in Figure 10B.

Dentition general

1. Teeth: (0) present; (1) absent (Wible et al. 2009: ch. 1).
2. Teeth: (0) differentiated into morphological type (incisors, canines, premolars, molars) with enamel; (1) homodont and peg-like without enamel (Wible et al. 2009: ch. 2).
3. Number of postcanine tooth loci: (0) eight or more; (1) seven; (2) six; (3) or five or less (Rougier et al. 1998: ch. 7); ORDERED.
4. Upper diastema: (0) small, between incisors and canine; (1) small, between canine and premolars; (2) enlarged; (3) absent (Wible et al. 2009: ch. 4).
5. Lower diastema behind incisors: (0) absent or small; (1) enlarged (Wible et al. 2009: ch. 5).
6. Dental eruption timing vs cranial growth: (0) early; (1) late (adult size reached prior to complete eruption of permanent cheek teeth; specimens with 95% median adult jaw length and less than 60% of their permanent, occluding premolars and molars erupted (Asher and Lehmann 2008).

Incisors

7. Incisor shape: (0) root and crown are straight and continuous in length; (1) form a continuous curve (Asher et al. 2005: ch. 3).
8. Number of upper incisors: (0) five; (1) four; (2) three; (3) two; (4) one; (5) none (Wible et al. 2009: ch. 7); ORDERED.
9. Number of lower incisors: (0) four; (1) three; (2) two; (3) one; (4) none (Wible et al. 2009: ch. 8); ORDERED.
10. Position of anteriormost upper incisors (or alveoli): (0) contacting medially or closely approximated; (1) widely separated (Wible et al. 2009: ch. 9).
11. Upper incisors relative size: (0) subequal; (1) anteriormost is the largest (close to twice the size of following incisors); (2) second anteriormost is the largest (close to twice the size adjacent incisors); (3) third anteriormost is the largest (close to twice the size adjacent incisors) (Muizon et al. 2015: ch. 11).
12. Anteriormost upper incisor shape: (0) conical; (1) mediolaterally compressed; (2) anteroposteriorly compressed; (3) cuspate (one major and one minor); (4) spatulate (Wible et al. 2009: ch. 11).
13. Anteriormost lower incisor shape: (0) conical; (1) mediolaterally compressed; (2) anteroposteriorly compressed; (3) cuspate (one major and one minor); (4) spatulate (Wible et al. 2009: ch. 16).
14. Anteriormost upper incisor procumbent: (0) absent; (1) present (Muizon et al. 2015: ch. 14).
15. Second anteriormost upper incisor projecting anteriorly: (0) absent; (1) present (Billet 2010: ch. 9, modified).
16. Anteriormost upper incisor root: (0) closed; (1) open extending in premaxilla only; (2) open extending in maxilla (Asher et al. 2005: ch. 52; Wible et al. 2009: ch. 12).
17. Anteriormost incisor enamel: (0) surround tooth; (1) discontinuous posteriorly (Asher et al. 2005: ch. 49; Wible et al. 2009: ch. 13).
18. Ultimate upper incisor: (0) in premaxilla; (1) between maxilla and premaxilla; (2) or in maxilla (Wible et al. 2009: ch. 14).
19. Anteriormost lower incisor size: (0) small and subequal to subsequent incisors; (1) greatly enlarged; (2) greatly reduced (Archibald et al. 2001: ch. 28; Wible et al. 2009: ch. 15).
20. Procumbent anteriormost lower incisor: (0) absent; (1) present (Archibald et al. 2001: ch. 29; Wible et al. 2009: ch. 17).
21. Anteriormost lower incisor root: (0) closed; (1) open (Archibald et al. 2001: ch. 32; Wible et al. 2009: ch. 18).
22. Anteriormost lower incisor root length: (0) not extended posteriorly below p1; (1) extending posteriorly below p1; (2) extending posteriorly below penultimate or ultimate premolar; (3) extending posteriorly below molars (Archibald et al. 2001: ch. 32); ORDERED.
23. Anteriormost lower incisor enamel: (0) covers the whole incisor or (1) discontinous posteriorly (Archibald et al. 2001: ch. 30).
24. Procumbent posterior lower incisors: (0) absent; (1) present (Wible et al. 2009: ch. 21).
25. Staggered lower i3: (0) absent; (1) present (Hershkovitz 1982).
26. Shape of incisor arcade: (0) transverse; (1) U-shaped; (2) sharply angled at I1s (V-shaped) or parallel-sided (Muizon et al. 2015; modified from Springer et al. 1997: ch. 25; Horovitz and Sánchez-Villagra 2003: ch. 161; Ladevèze and Muizon 2007: ch. 8).

Canines

27. Upper canine: (0) large; (1) reduced; (2) absent (Meng et al. 2003: ch. 23); ORDERED.
28. Roots of upper canines: (0) two roots; (1) one root (Rougier et al. 1998: ch. 10; Wible et al. 2009: ch. 24).
29. Lower canine: (0) large; (1) reduced; (2) absent (Meng et al. 2003: ch. 25); ORDERED.
30. Roots of lower canines: (0) two roots; (1) one root (Rougier et al. 1998: ch. 44; Wible et al. 2009: ch. 26).
31. Procumbent lower canine: (0) absent; (1) present (Wible et al. 2009: ch. 27).
32. Canines diverging externally, uppers and/or lowers: (0) absent; (1) present (Muizon et al. 2015).

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(continued from previous page)

Premolars

33. Number of premolars: (0) five; (1) four; (2) three; (3) less than three (Rougier et al. 1998: ch. 1); ORDERED.
34. Tall, trenchant premolar: (0) ultimate premolar; (1) penultimate premolar; (2) absent (Rougier et al. 1998: ch. 3).
35. Procumbent first upper premolar: (0) absent; (1) present (Luo and Wible 2005: ch. 151, modified).
36. First upper premolar (P1 in placentals, cf. Wible et al. 2009 matrix) roots: (0) one; (1) two; (2) three: eutherians with lost P1 are coded non-applicable (Muizon et al. 2015); ORDERED.
37. Diastema posterior to first upper premolar: (0) absent; (1) present (Luo and Wible 2005: ch. 43; Wible et al. 2009: ch. 34).
38. Shape of the premolar cusps: (0) sharp and uninflated; (1) inflated with apical wear strongly developed (Cifelli 1993; Rougier et al. 1998: ch. 2; Wible et al. 2001: ch. 2).
39. Protocone of the penultimate premolar: (0) absent; (1) lingual bulge; (2) basined (Rougier et al. 1998: ch. 12).
40. Metacone of penultimate upper premolar: (0) absent; (1) swelling; (2) large (Wible et al. 2009: ch. 37).
41. Penultimate upper premolar parastylar lobe: (0) absent or small; (1) well developed (Wible et al. 2009: ch. 38).
42. Vertically developed cylindrical parastyle separated from paracone by a deep vertical sulcus on labial edge of upper cheek teeth (at least PM): (0) absent; (1) present (Muizon et al. 2015: ch. 42).
43. Penultimate upper premolars roots: (0) one; (1) two; (2) three; (3) four (Wible et al. 2009: ch. 39); ORDERED.
44. Ultimate upper premolar protocone: (0) absent or narrow cingulum; (1) present but distinctly smaller than paracone; (2) similar in thickness and height to paracone (Rougier et al. 1998; Wible et al. 2009: ch. 40); ORDERED.
45. Last upper premolar metacone: (0) absent; (1) swelling (metacone connate to paracone); (2) large (metacone and paracone distinctly separated) (Luo and Wible 2005: ch. 39).
46. Last upper premolar para- and metastylar lobes: (0) absent or insignificant; (1) present and subequal; (2) parastylar lobe larger; (3) metastylar lobe larger (Wible et al. 2009: ch. 42).
47. Ultimate premolar precingulum: (0) absent; (1) present (Wible et al. 2009: ch. 43).
48. Ultimate premolar postcingulum: (0) absent; (1) present (Muizon et al. 2015; Wible et al. 2009: ch. 44, modified).
49. Ultimate premolar conules: (0) absent or very weak; (1) present as a distinct cusp (prominent) (Wible et al. 2009: ch. 45).
50. Ultimate upper premolar size (occlusal surface, L x W) relative to first upper molar: (0) smaller or subequal; (1) larger (Meng et al. 2003: ch. 41).
51. Double V-shaped penultimate and ultimate upper premolars (paracone and protocone V-shaped): (0) absent; (1) present (Muizon et al. 2015).
52. First lower premolar orientation: (0) in line with the jaw axis; (1) oblique (Rougier et al. 1998: ch. 45; Wible et al. 2009: ch. 47).
53. First lower premolar roots: (0) two; (1) one (Wible et al. 2009: ch. 48).
54. Diastema separating first and second lower premolars: (0) absent (gap less than one tooth root diameter); (1) present (subequal to or larger than one tooth root diameter) (Luo and Wible 2005: ch. 152, modified; Wible et al. 2009: ch. 49).
55. Third lower premolar size compared to second (only scored for taxa with five lower premolars): (0) longer or (1) shorter (Wible et al. 2009: ch. 50).
56. Third lower premolar roots (only scored for taxa with five lower premolars): (0) two or (1) one (Wible et al. 2009: ch. 51).
57. Penultimate lower premolar paraconid: (0) vestigial or absent; (1) distinctive (Luo and Wible 2005, ch. 52 modified; Wible et al. 2009: ch. 52).
58. Penultimate lower premolar metaconid: (0) absent; (1) swelling or metaconid connate to paraconid; (2) metaconid and paraconid distinctly separated (Wible et al. 2009: ch. 53).
59. Penultimate lower premolar talonid cusps: (0) one; (1) two; (2) three (Wible et al. 2009: ch. 54); ORDERED.
60. Ultimate lower premolar paraconid: (0) absent (there may be a small swelling at the anterior base of the protoconid but a well-defined cusp is not present); (1) present but low: less than half the height of protoconid (the paraconid is generally a small cusp at the anterior base of the protoconid); (2) present and high, half the height of protoconid or more (Muizon et al. 2015; Wible et al. 2009: ch. 55, modified); ORDERED.
61. Ultimate lower premolar metaconid: (0) absent; (1) metaconid present as a small bulge on posteromedial side of protoconid (swelling); (2) metaconid distinctly individualized (separate, large) (Wible et al. 2009: ch. 56).
62. Ultimate lower premolar talonid: (0) narrower than anterior portion of the crown; (1) as wide as anterior portion of the crown; (2) absent (Archibald and Averianov 2006: ch. 25).
63. Ultimate lower premolar talonid cusps: (0) one; (1) two; (2) three (Wible et al. 2009: ch. 58); ORDERED.
64. Length of ultimate lower premolar relative to penultimate premolar: (0) longer; (1) equal or shorter (Archibald and Averianov 2006: ch. 24).
65. Ultimate lower premolar anterolingual cingulid: (0) absent or (1) present (Wible et al. 2009: ch. 60).

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(continued from previous page)

Upper molars

66. Number of molars: (0) four or more; (1) three; (2) two (Wible et al. 2009: ch. 61); ORDERED.
67. Size (area) of M1 vs M2: (0) M1 much larger (>120%); (1) subequal (80%<>120%); (2) M1 much smaller (80%<) (Muizon et al. 2015); ORDERED.
68. Size (area) of M1 vs M3: (0) M1 much larger (>120%); (1) subequal (80%<>120%); (2) M1 much smaller (80%<) (Muizon et al. 2015); ORDERED.
69. Size (area) of m1 vs m2: (0) m1 much larger (>120%); (1) subequal (80%<>120%); (2) m1 much smaller (80%<) (Muizon et al. 2015); ORDERED.
70. Size (area) of m1 vs m3: (0) m1 much larger (>120%); (1) subequal (80%<>120%); (2) m1 much smaller (80%<) (Muizon et al. 2015); ORDERED.
71. Molar cusps form: (0) sharp and gracile; (1) inflated and robust; (2) crest-like (Wible et al. 2009: ch. 63).
72. Upper molar shape: (0) as long as wide or longer; (1) wider than long (length more than 75% but less than 99%of the width); (2) much wider than long (length less than 75% of the width) (Wible et al. 2009: ch. 64); ORDERED.
73. Upper molar stylar shelf maximum width: (0) 50% or more of total width; (1) between 50% and 25% of width; (2) less than 25%; (3) absent (Wible et al. 2009: ch. 65); ORDERED.
74. Labial extent of parastylar and metastylar lobes: (0) parastylar lobe more labial; (1) lobes subequal; (2) metastylar lobe more labial; (3) lobes absent (Wible et al. 2009: ch. 66).
75. M1 parastylar lobe relative to paracone: (0) anterolabial to paracone; (1) anterior to paracone (Archibald and Averianov 2006: ch. 7; Wible et al. 2009: ch. 67). If parastylar lobe is absent, scored as non-applicable.
76. Length of the parastylar lobe (measured to stylocone or stylocone position) relative to total length on penultimate molar: (0) more than 30% of the tooth length; (1) between 30% and 20%; (2) 20% or less. (Wible et al. 2009: ch. 68); ORDERED.
77. Preparastyle: (0) absent; (1) present (Rougier et al. 1998: ch. 21).
78. Stylar cusp A: (0) subequal to or larger than stylar cusp B; (1) distinct but smaller than B; (2) very small to indistinct (Muizon et al. 2015; Wible et al. 2009: ch. 70). Taxa in which both stylar cusps A and B are not identifiable are scored non-applicable.
79. Size of stylar cusp B relatively to paracone: (0) vestigial to absent; (1) smaller but distinct; (2) subequal (Rougier et al. 1998: ch. 22) Taxa scored non-applicable for character 78 are also coded non-applicable for this character; ORDERED.
80. Stylar cusp C, mesostyle: (0) absent; (1) present (Rougier et al. 1998: ch. 23).
81. Stylar cusp D: (0) absent; (1) smaller or subequal to B (Rougier et al. 1998: ch. 24).
82. Stylar cusp E: (0) lingual to D or to D position; (1) distal to D; (2) small to indistinct (Rougier et al. 1998: ch. 25).
83. Paracingulum (= preparacingulum of Wible et al. 2009): (0) absent; (1) interrupted between stylar margin and paraconule; (2) continuous between stylar margin and paraconule (taxa with a protoloph with indistinct paraconule are coded 2 as the labial portion of the protoloph is hypothesized as corresponding to the paracingulum) (Wible et al. 2009: ch. 75).
84. Deep ectoflexus: (0) present on penultimate molar; (1) present on penultimate and preceding molars; (2) very small or absent (Wible et al. 2009: ch. 76).
85. Relative size of the paracone and metacone on penultimate molar: (0) metacone smaller than paracone; (1) cusps subequal; (2) paracone smaller than metacone (Wible et al. 2009: ch. 77, modified); ORDERED.
86. Metacone position relative to paracone: (0) labial; (1) approximately at the same level; (2) lingual (Rougier et al. 1998: ch. 28); ORDERED.
87. Paracone and metacone at base: (0) fused at base; (1) distinctly separated; (Muizon and Marshall 1992: ch. 13).
88. Preparacrista: (0) strong, from labial edge of paracone to stylocone; (1) weak (from base of paracone) or absent (Wible et al. 2009: ch. 80).
89. Orientation of the preparacrista on penultimate and ante-penultimate molars and premolars (in the case of molariform premolars): (0) deflected labially and tend to be aligned with or sub parallel to paracone-protocone axis; (1) shifted anteriorly, forming a distinct angle with paracone-protocone axis. Taxa without a distinct preparacrista are scored non-applicable (Muizon et al. 2015).
90. Cuspate preparacrista: (0) present; (1) absent (Wible et al. 2009: ch. 81).
91. Centrocrista: (0) straight; (1) V-shaped (2) absent (Wible et al. 2009: ch. 82).
92. Postmetacrista: (0) prominent from side of metacone to metastyle; (1) salient (expanded posterolabially); (2) absent or weak (Wible et al. 2009: ch. 83).
93. Cuspate postmetacrista: (0) present; (1) absent (Wible et al. 2009: ch. 84).
94. Preprotocrista: (0) does not extend labially below the paracone; (1) extends labially below the paracone (double rank prevallum/postvallid shearing); (2) absent (Wible et al. 2009: ch. 85) (taxa with a protoloph are coded (1)).
95. Postprotocrista: (0) extends to mid-lingual surface of metacone; (1) extends distal to metacone; (2) absent (Wible et al. 2009: ch. 86). Taxa with a metaloph are coded (1).

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96. Development of postvallum shear: (0) present, but only by the first rank: postmetacrista; (1) present, with the addition of a second rank (postprotocrista below postmetacrista) but the second rank does not reach labially below the base of the metacone; (2) present, with second rank extending to metastylar lobe: metacingulum; (3) absent (Luo and Wible 2005: ch. 57). All taxa with a hypocone subequal to protocone are scored as non-applicable.
97. Labial edges of paracone and metacone: (0) distinctly swollen; (1) slightly convex; (2) flat to concave (Muizon et al. 2015); ORDERED.
98. Paraconule: (0) weak or absent; (1) prominent, closer to protocone; (2) or prominent, mid-way or closer to paracone (Wible et al. 2009: ch. 88).
99. Metaconule: (0) weak or absent; (1) prominent, closer to protocone; (2) or prominent, mid-way or closer to metacone (Wible et al. 2009: ch. 89).
100. Internal conular cristae: (0) indistinct; (1) distinctive and wing-like (Luo and Wible 2005: ch. 107). Taxa without prominent conules are scored as non-applicable.
101. Protocone: (0) lacking; (1) small; without trigon basin; (2) or with distinct trigon basin (Rougier et al. 1998: ch. 36).
102. Protocone anteroposterior expansion: (0) absent and protocone subequal to paracone; (1) present and protocone larger than paracone (Wible et al. 2009: ch. 93).
103. Protocone procumbency: (0) absent; (1) present (Rougier et al. 1998: ch. 37).
104. Protocone labial shift: (0) no shift (10-20%); (1) moderate shift (21-30%); (2) substantial labial shift (more than 31%) (Luo and Wible 2005: ch. 97, modified); ORDERED.
105. Height of the protocone: (0) low, clearly lower than paracone and/or metacone; (1) approaching, equal or higher than paracone and/or metacone (Wible et al. 2009: ch. 96, modified).
106. Precingulum: (0) absent or weak; (1) labial edge of the precingulum, lingual to paraconule; (2) labial edge of the precingulum labial to paraconule (= reaching labially past the paraconule or paraconule position) (Wible et al. 2009: ch. 97)
107. Postcingulum: (0) absent or weak; (1) labial edge of the postcingulum lingual to metaconule; (2) labial edge of the postcingulum labial to metaconule; (3) postcingulum extending to labial margin (Wible et al. 2009: ch. 98).
108. Hypocone on postcingulum: (0) absent; (1) present lower than protocone; (2) present subequal to protocone (Wible et al. 2009: ch. 99); ORDERED.
109. Pre- and postcingulum: (0) separated lingually; (1) continuous lingually. If cingula absent coded as non-applicable (Wible et al. 2009: ch. 100).
110. Number of roots of upper molars except ultimate molar: (0) three; (1) four; (2) more than four (Wible et al. 2009: ch. 101); ORDERED.
111. Ultimate upper molar number of roots: (0) one; (1) two; (2) three; (3) four or more (Wible et al. 2009: ch. 102); ORDERED.
112. Metastylar lobe on ultimate molar: (0) absent; (1) present (Wible et al. 2009: ch. 105).
113. M1-M2 metaconular hypocone: (0) absent; (1) present (Williamson and Carr 2007: ch. 22, modified).
114. Presence of a crochet (oblique loph joining the ectoloph (or centrocrista?) to the metaloph (or posterior edge of molar between metacone and protocone): (0) absent; (1) present (Cifelli 1993; Billet 2010: ch. 27, modified).

Lower molars

115. Paraconid: (0) present (distinctive); (1) absent (or vestigial) (Wible et al. 2009: ch. 106).
116. Paraconid height relatively to metaconid: (0) lower; (1) subequal; (2) taller (Wible et al. 2009: ch. 107); ORDERED.
117. Paraconid on lingual margin: (0) absent; (1) present (Wible et al. 2009: ch. 108).
118. Mesiolingual edge of paraconid: (0) rounded; (1) keeled (Wible et al. 2009: ch. 109).
119. Paracristid: (0) notched; (1) continuously curved without notch (Wible et al. 2009: ch. 110).
120. Trigonid configuration: (0) open with the paraconid in anteromedial position, paracristid-protocristid angle more than 50°; (1) acute with paraconid more posteriorly placed, paracristid-protocristid angle between 36° and 49°; (2) anteroposteriorly compressed, paracristid-protocristid angle 35° or less (Wible et al. 2009: ch. 111, modified); ORDERED.
121. Protoconid height: (0) tallest of trigonid; (1) subequal to lower than other cusps (Wible et al. 2009: ch. 112, modified).
122. Protocristid orientation: (0) oblique (1) transverse (Wible et al. 2009 : ch. 113).
123. Talonid: (0) small heel; (1) multicusped basin (Rougier et al. 1998: ch. 49).
124. Cristid obliqua: (0) incomplete; (1) complete attaching lingual to notch in protocristid; (2) complete attaching at or labial to notch in protocristid; (3) complete attaching below middle posterior face of protoconid; (4) complete, labially placed (Wible et al. 2009: ch. 116, modified).
125. Trigonid height relative to talonid: (0) twice or more; (1) less than twice; (2) subequal (Wible et al. 2009: ch. 117); ORDERED.
126. Anteroposterior shortening of trigonid (at base) relative to talonid: (0) long > 75% tooth length; (1) moderately long < 75% and > 50% tooth length; (2) short < 50% tooth length (Luo and Wible 2005: ch. 78); ORDERED.

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127. Talonid width: (0) talonid very narrow, subequal to base of metaconid, (1) talonid narrower than trigonid, (2) subequal or wider than trigonid (Rougier et al. 1998: ch. 50); ORDERED.
128. Hypoconulid: (0) absent; (1) in median position on posterior edge of talonid; (2) lingually placed with slight approximation of entoconid; (3) connate to entoconid (Wible et al. 2009: ch. 120).
129. Hypoconulid of last lower molar: (0) short and erect; (1) tall and sharply recurved; (2) posteriorly procumbent; (3) absent. (Wible et al. 2009: ch. 121).
130. Entoconid: (0) absent; (1) smaller than hypoconid and/or hypoconulid; (2) subequal to larger than hypoconid and/or hypoconulid (Wible et al. 2009: ch. 122); ORDERED.
131. Postcristid (between entoconid and hypoconulid) taller than hypoconulid and nearly transverse: (0) absent; (1) present (Wible et al. 2009: ch. 123).
132. Mesoconid: (0) absent or (1) present. (Meng et al. 2003: ch. 79).
133. Hypolophid (loph joining hypoconid to hypoconulid): (0) absent; (1) present (Meng et al. 2003: ch. 82).
134. Labial postcingulid: (0) absent; (1) present (Rougier et al. 1998: ch. 55).
135. Entoconid transversely expanded into entolophid and not connected to hypoconulid: (0) absent; (1) present (Cifelli 1993; Billet 2010: ch. 55, modified; Muizon et al. 2015).

Dentary

136. Number of mental foramina: (0) two or more; (1) one (Meng et al. 2003: ch. 87).
137. Anteriormost mental foramen: (0) below incisors; (1) below p1; (2) below p2; (3) more posterior (Wible et al. 2009: ch. 129). Taxa with only one mental foramen are scored here. ORDERED.
138. Posteriormost mental foramen: (0) in canine and anterior premolar region; (1) below penultimate premolar; (2) below ultimate premolar; (3) posterior to ultimate premolar (Wible et al. 2009: ch. 130); ORDERED.
139. Depth of dentary body: (0) slender and long; (1) deep and short (Meng et al. 2003: ch. 86).
140. Retromolar space in adults (i.e. in which ultimate molar exhibits wear process): (0) absent; (1) present (Wible et al. 2009: ch. 132). Comment: we scored this character for *Eoastrapostylops riolorense* based on the paratype (PVL 4217, a partial anterior portion of skull and mandible with fully erupted m3) because in the holotype the m3 is still unerupted.
141. Coronoid process height: (0) higher than condyle; (1) even with condyle (Wible et al. 2009: ch. 133).
142. Coronoid process width: (0) broad, roughly two molar lengths; (1) narrow, one molar length or less (Wible et al. 2009: ch. 134).
143. Angle between anterior border of coronoid process and horizontal alveolar border of cheek teeth: (0) distinctly obtuse (anterior border of coronoid process strongly oblique posteriorly); (1) slightly obtuse or more or less right angle (anterior border of coronoid process slightly oblique posteriorly or sub-vertical; (2) acute angle (anterior border of coronoid process shifted anteriorly) (Wible et al. 2009: ch. 135, modified); ORDERED.
144. Coronoid crest (crest of the masseteric fossa along the anterior border of the coronoid process): (0) absent or weakly developed; (1) present and transversely thick; (2) hypertrophied and laterally flaring with a very deep masseteric fossa posterior to it (Luo and Wible 2005: ch. 21 modified); ORDERED.
145. Portion of the mandibular ramus ventral to the masseteric fossa: (0) dorsoventrally narrow crest or ridge with a dorsoventral height less than half that of the mandibular body; (1) dorsoventrally broad ridge (or elevated area) with a dorsoventral height more than half that of the mandibular body. Taxa in which the ventral limit of the masseteric fossa is indistinct are scored as non-applicable (Luo and Wible 2005: ch. 20, modified).
146. Anterior extension of masseteric fossa on the body of the dentary, below the last molars: (0) absent; (1) present (Luo and Wible 2005: ch. 22). Comment: as for character 140, we scored this character for *Eoastrapostylops riolorense* based on the paratype.
147. Labial mandibular foramen: (0) absent; (1) present (Rougier et al. 1998: ch. 70).
148. Condyloid crest: (0) absent; (1) present (Wible et al. 2009: ch. 140).
149. Posteroventral shelf of the masseteric fossa: (0) absent; (1) present (Rougier et al. 1998: ch. 68).
150. Angular process: (0) process on posterior aspect of dentary ramus; (1) shelf along ventral border of dentary ramus (Wible et al. 2009: ch. 142).
151. Angular process length: (0) less than dentary ramus length; (1) equal or greater than dentary ramus length (Wible et al. 2009: ch. 144).
152. Angular process shape: (0) hook-like with width (in lateral view) of base lesser than length; (1) hook-like with width of base subequal to (or wider than) length; (2) plate-like (no hook distinct), more or less rounded or sub rectangular; (3) triangular (Wible et al. 2009: ch. 145, modified).
153. Angular process apex vertical position: (0) low: below the level of the alveolar border; (1) elevated: at the level of or above the alveolar border (Luo and Wible 2005: ch. 9, modified).
154. Anteroposterior position of the dorsal root of the angular process: (0) level with or posterior to the level of the condyloid process;

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(1) anterior to it (Wible et al. 2009: ch. 147, modified).

155. Condylar process: (0) with posteriorly directed peduncle (1) or not (Wible et al. 2009).
156. Condyle shape: (0) wider than long ovoid; (1) wider than long cylindrical; 2) as long as wide or longer, anteroposteriorly elongate (Rougier et al. 1998: ch. 71, modified; Wible et al. 2009: ch. 149).
157. Condyle position relative to the tooth row: (0) approximately at the same level or slightly above; (1) above by approximately one molar length; (2) above by two molars length or more (Wible et al. 2009: ch. 150, modified); ORDERED.
158. Symphysis shape: (0) tapered; (1) deep (Meng et al. 2003: ch. 86).
159. Symphysis posterior extent: (0) p1 or more anterior; (1) p2; (2) p3 or more posterior (Wible et al. 2009: ch. 152); ORDERED.
160. Mandibular symphysis: (0) unfused; (1) fused (Luo and Wible 2005: ch. 36).
161. Meckelian groove: (0) present; (1) absent (Rougier et al. 1998: ch. 75).
162. "Coronoid facet": (0) present; (1) absent (Rougier et al. 1998, ch. 76; Wible et al. 2009: ch. 156).
163. Mandibular foramen vertical position: (0) near ventral margin of dentary; (1) recessed dorsally from ventral margin; (2) at the level of alveolar plane; (3) above alveolar plane (Wible et al. 2009: ch. 157, modified); ORDERED.
164. Mandibular foramen dorsal to prominent longitudinal ridge: (0) present; (1) absent (Wible et al. 2009: ch. 158).

Skull: rostrum

165. Facial process of the premaxilla: (0) does not reach the nasal posterodorsally; (1) reaches the nasal (Rougier et al. 1998: ch. 80).
166. Posterior extent of the facial process of the premaxilla: (0) up to the canine (not beyond); (1) between the canine and the frontal (=beyond canine); (2) up to the frontal (Luo and Wible 2005: ch. 406; Wible et al. 2009: ch. 161, modified); ORDERED.
167. Facial process of the premaxilla: (0) finger-like process wedged between the maxilla and the nasal posterodorsally; (1) not wedged (no finger-like process) (Wible et al. 2009: ch. 162).
168. Paracanine fossa between posterior incisor and upper canine: (0) absent; (1) distinctly excavated in the tooth row with a crest-like lateral margin; (2) opened laterally but remaining on the tooth row; (3) opened laterally and dorsally expanded on the lateral edge of the rostrum (Muizon et al. 2015: ch. 168).
169. Paracanine fossa: (0) excavated in maxilla; (1) excavated in maxilla and premaxilla; (2) excavated in premaxilla (Rougier et al. 1998: ch. 81, modified; Wible et al. 2009: ch. 163, modified). All taxa coded (0) for character 168 are coded as non-applicable.
170. Exit(s) of infraorbital canal: (0) multiple; (1) single; (2) absent. (Rougier et al. 1998: ch. 82, modified).
171. Infraorbital foramen position: (0) dorsal to penultimate premolar or more anterior; (1) dorsal to ultimate premolar; (2) dorsal to first molar or more posterior (Geisler 2001: ch. 65, modified, Wible et al. 2009: ch. 165, modified); ORDERED.
172. Infraorbital canal length: (0) long (longer than greater diameter of the anterior opening); (1) short (shorter than or roughly equal to greater diameter of the anterior opening). In the case of multiple openings the diameter is that of the circle with a surface corresponding to the sum of the surfaces of all foramina (Wible et al. 2009: ch. 166, modified).
173. Width of the nasals: (0) much wider posteriorly than anteriorly; (1) sides subparallel; (2) widest anteriorly (Asher et al. 2005: ch. 110, modified; Wible et al. 2009: ch. 168); ORDERED.
174. Shape ratio of the nasals (length/mean width): (0) nasals length less than (or equal to) five times their mean width; (1) nasals length more than five times their mean width (Muizon et al. 2015: ch. 174).
175. Nasals overhang external nasal aperture: (0) present; (1) absent (Wible et al. 2009: ch. 169).
176. Nasal of adults fused together but not to surrounding bones: (0) absent; (1) present (Muizon et al. 2015: ch. 176).
177. Anterior processes of the frontals wedged between the nasals: (0) present; (1) absent. (Rougier et al. 1998; Wible et al. 2009).
178. Nasofrontal suture: 0) suture level with or posterior to the anterior edge of the orbit; 1) all points of the suture well anterior to anterior edge of the orbit: (Wible et al. 2009: ch. 171, modified).
179. Nasal foramina: (0) present; (1) absent (Rougier et al. 1998 : ch. 84).
180. Frontal-maxillary contact on rostrum: (0) absent; (1) present (Rougier et al. 1998: ch. 86).
181. Anterior (maxillary) process of the frontal wedged between the nasal and the maxilla: (0) absent or weak; (1) present, elongated and thin; (Asher et al. 2005: ch. 109).
182. Preorbital length (measured from the anterior edge of the orbit to anterior end of the skull): (0) less than one-third total length; (1) more than one-third (Rougier et al. 1998: ch. 90, modified).
183. Lacrimal: (0) present; (1) absent (Asher et al. 2005: ch. 103).
184. Facial process of the lacrimal: (0) large external wing on the rostrum at the anterior edge of the orbit; (1) no wing: either the external part of the lacrimal is totally absent or it is reduced to a narrow crescentic rim on the anterior edge of the orbit (Asher et al. 2005: ch. 105, modified; Wible et al. 2009: ch. 177, modified).
185. Lacrimal tubercle: (0) present; (1) absent. Taxa without lacrimal are scored non-applicable (Rougier et al. 1998: ch. 87).
186. Lacrimal foramen "on face" (because lateral edge of the foramen is reduced or missing): (0) present; (1) absent (Rougier et al. 1998: ch. 88).

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187. Lacrimal foramen (0) double; (1) simple (Rougier et al. 1998: ch. 89).
188. Lacrimal foramen composition: (0) enclosed within lacrimal; (1) with maxillary contribution; (2) with jugal contribution (Asher et al. 2003: ch. 100; Wible et al. 2009: ch. 181).
189. Translacrimal canal (see Wible et al. 2004): absent (0) or present (1) (Wible et al. 2009). Taxa without lacrimal are scored non-applicable.
190. Narial processes of the premaxillae (tuberosity at the anterior apices of the premaxillae, on the anterior floor of the narial opening): (0) absent; (1) present (Billet 2010: ch. 77).

Skull: palate

191. Palatal process of the premaxilla: (0) does not reach the alveolus; (1) does reach or nearly reach the canine alveolus (Rougier et al. 1998: ch. 79).
192. Incisive foramina length: (0) short, half or less than half the maximal palatal length of the premaxilla along the sagittal plane; (1) long, more than half the length of the premaxilla (Luo and Wible 2005: ch. 409, modified).
193. Incisive foramina composition: (0) between premaxilla and maxilla; (1) within premaxilla (Wible et al. 2009: ch. 186).
194. Palatal vacuities: (0) absent; (1) present (Rougier et al. 1998: ch. 93).
195. Major palatine foramina: (0) well-individualized, within maxilla and/or palatine; (1) multiple small foramina in palatine and/or maxilla (Wible et al. 2009: ch. 188, modified). Taxa without major palatine foramina are scored as non-applicable.
196. Anterior extent of palatine: (0) posterior to M1; (1) level with M1; (2) more anterior (Wible et al. 2009: ch. 189, modified); ORDERED.
197. Palatal expansion with regard to ultimate molar: (0) posterior; (1) even with; (2) anterior (Wible et al. 2009: ch. 190); ORDERED.
198. Postpalatine torus: (0) absent; (1) present (Rougier et al. 1998 : ch. 95).
199. Posterior palatine spine: (0) weak or absent; (1) prominent (Wible et al. 2009: ch. 192).
200. Passageway of the minor palatine artery (minor palatine foramen or groove): (0) totally enclosed in the minor palatine foramen; (1) in a groove on the posteromedial edge of the palate as a result of the posterior opening of the minor palatine foramen (no posterior bony bridge); (2) absent (no groove nor foramen) (Wible et al. 2009: ch. 193, modified; Muizon et al. 2015).
201. Minor palatine foramen composition: (0) palatine or maxilla-palatine or (1) palatine-pterygoid. (Wible et al. 2009: ch. 194).
202. Maxilla with shelf-like expansion posterior to ultimate molar with a length at least equal to half a tooth and lateral to minor palatine notch or foramen: (0) absent; (1) present (Wible et al. 2009: ch. 195, modified).

Skull: zygoma

203. Posterior edge of the anterior zygomatic root aligned: (0) with last molar or more posterior; (1) with more anterior molars; (2) with premolars (Meng et al. 2003: ch. 123; Wible et al. 2009: ch. 196, modified); ORDERED.
204. Zygomatic process of the maxilla: (0) present; (1) vestigial; (Wible et al. 2009: ch. 197).
205. Jugal: (0) present; (1) absent; (Wible et al. 2009: ch. 198).
206. Jugal contribution to anteroventral edge of the orbit: (0) present; (1) absent (Wible et al. 2009: ch. 199, modified).
207. Mx-Ju suture bifurcated: (0) absent; (1) present (Rougier et al. 1998: ch. 91).
208. Jugal-lacrimal contact: (0) present; (1) absent (Meng et al. 2003: ch. 137).
209. Zygomatic arch: (0) stout; (1) delicate; (2) incomplete (Wible et al, 2009: ch. 199); ORDERED.
210. Orientation of the anterior root of zygoma in anterior view: (0) oblique, extends dorsally; (1) transverse, roughly horizontal; (2) extends ventrally (Muizon et al. 2015); ORDERED.
211. Vertical position of posterior root of zygoma relative to foramen magnum: (0) even; (1) clearly higher (Muizon et al. 2015).
212. Shape of zygomatic arches in dorsal view: (0) not protruding much laterally, smoothly curved or parallel to sagittal plane; (1) protruding laterally (largely exceeding other parts of skull laterally), with a large posterior elbow (Muizon et al. 2015).

Skull: orbit

213. Roots of molars exposed in orbit floor: (0) absent; (1) present (Asher et al. 2005: ch. 126.
214. Palatine enters the posterior opening of the infraorbital canal (maxillary foramen): (0) present; (1) absent (Rougier et al. 1998: ch. 98).
215. Lacrimal contributes to maxillary foramen: (0) present; (1) absent (Luo and Wible 2005: ch. 376, modified).
216. Groove connects maxillary to sphenopalatine foramina: (0) absent; (1) present (Asher et al. 2005: ch. 97).
217. Sphenopalatine foramen: (0) within palatine; (1) between palatine and maxilla; (2) between palatine, maxilla and frontal (Asher et al. 2005: ch. 133, modified).
218. Sphenopalatine foramen: proximal (= approximated) to maxillary foramen: (0) absent; (1) present (Wible et al. 2009: ch. 208).
219. Maxilla in the orbit: (0) no participation in orbital wall; (1) large dorsal process participating in medial orbital wall (Wible et al.

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2009: ch. 209, modified).
220. Frontal and maxilla contact in medial orbital wall: (0) absent; (1) present (Geisler 2001: ch. 52).
221. Orbital process of the palatine: (0) present; (1) absent (Asher et al. 2005: ch. 127: modified).
222. Ethmoid exposure in medial orbital wall: (0) absent; (1) present (Wible et al. 2009: ch. 212).
223. Ethmoidal foramen: (0) between frontal and orbitosphenoid; (1) within frontal (Wible et al. 2009: ch. 213).
224. Foramina for the frontal diploic vein: (0) absent; (1) present (Wible et al. 2009: ch. 214).
225. Position of frontal diploic foramina vs postorbital process or tuberosity: (0) posterior; (1) anterior or even (Muizon et al. 2015). Taxa lacking a postorbital process or tuberosity and/or frontal diploic foramina are coded non-applicable.
226. Supraorbital foramina: (0) absent; (1) present on the skull roof, often extending anteriorly as a groove on the maxilla and/or nasal; (2) present more laterally on the dorsal orbital edge and/or postorbital process, groove variably present (Thewissen et al. 2001: ch. 41, modified).
227. Postorbital process of the frontal: (0) present and prominent; (1) present weak (tuberosity); (2) absent (Wible et al. 2009: ch. 216); ORDERED.
228. Postorbital process (main) composition: (0) frontal; (1) parietal (Wible et al. 2005: ch. 67, modified).
229. Postorbital bar: (0) absent; (1) present (Meng et al. 2003: ch. 145).
230. Dorsal process of the jugal: (0) absent or weak (hump); (1) strong (Meng et al. 2003: ch. 142).
231. Optic foramen: (0) confluent with sphenorbital fissure; (1) well separated from sphenorbital fissure (Rougier et al. 1998: ch. 102).
232. Optic foramen position: (0) narrowly separated from sphenorbital fissure; (1) broadly separated from sphenorbital fissure (Wible et al. 2009: ch. 221, modified).
233. Orbitosphenoid: (0) expanded anteriorly from optic foramen (or with anterior process for forms without optic foramen); (1) expanded dorsally from optic foramen (or with dorsal process for forms without optic foramen); (2) not expanded anteriorly or dorsally (Wible et al. 2009: ch. 222).
234. Suboptic foramen: (0) absent; (1) present (Wible et al. 2009: ch. 223).
235. Orbitotemporal canal: (0) present; (1) absent (Rougier et al. 1998: ch. 103).
236. Frontal-alisphenoid contact: (0) present: small contact at the anterodorsal corner of the alisphenoid; (1) present: more extensive contact on approximately 50% of the dorsal margin of the alisphenoid; (2) absent (Luo and Wible 2005: ch. 382, modified).
237. Sphenorbital fissure confluent with foramen rotundum (i.e. there is no foramen rotundum per se and the V_2 exits with the V_1 through the sphenorbital fissure): (0) absent; (1) present (Muizon et al. 2015).

Skull: braincase
238. Frontal length on midline: (0) less than half that of the parietal; (1) subequal to slightly smaller than parietal; (2) more than 50% longer than parietal (Wible et al. 2009: ch. 226); ORDERED.
239. Frontoparietal suture: (0) transverse; (1) with anterior process of the parietal off the midline; (2) with anterior process of the parietal on the midline (Wible et al. 2009: ch. 227).
240. Temporal lines meet on midline to form a sagittal crest: (0) present; (1) absent (Geisler 2001: ch. 33, modified).
241. Nuchal crest: (0) level with or anterior to foramen magnum; (1) posterior to foramen magnum (Wible et al. 2009: ch. 230).
242. Nuchal crest in dorsal view: (0) deeply notched on medial line: bilobate morphology and V-shaped opening posteriorly; (1) transverse: roughly straight; (2) median point posterior to lateral parts of the crest: V-shaped morphology opening anteriorly (Muizon et al. 2015); ORDERED.
243. Anterior lamina of the petrosal: (0) present and exposed on lateral braincase wall; (1) internal to braincase and small to vestigial; (2) absent (Wible et al. 2009: ch. 231, modified).
244. Squama of the squamosal: (0) absent; (1) present (Rougier et al. 1998: ch. 113).
245. Foramina for temporal rami (including suprameatal foramen when present) of the stapedial artery: (0) in the petrosal; (1) in parietal and/or squama of the squamosal; (2) absent (Rougier et al. 1998: ch. 143).

Skull: mesocranium
246. Choanae: (0) almost as wide as posterior palate; (1) distinctly narrower (Wible et al. 2009: ch. 234).
247. Vomer contacts pterygoids: (0) present; (1) absent (Wible et al. 2009: ch. 235).
248. Pterygoids contact in midline: (0) present; (1) absent (Rougier et al. 1998: ch. 99).
249. Pterygopalatine crests: (0) present; (1) absent (Rougier et al. 1998: ch. 100).
250. Midline crest in basipharyngeal canal: (0) absent; (1) present (Wible et al. 2009: ch. 238.
251. Entopterygoid process (posterior extension): (0) absent; (1) ends at anterior basisphenoid; (2) approaches ear region (Wible et al. 2009: ch. 239).
252. Midline rod-shaped eminence on basisphenoid: (0) absent; (1) present (Wible et al. 2009: ch. 240).

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253. Ectopterygoid process of the alisphenoid: (0) absent (or fused with entopterygoid crest); (1) present: ends at anterior basisphenoid; (2) present: approaches ear region (Rougier et al. 1998: ch. 101, modified).
254. Ectopterygoid process shape: (0) long crest or triangular blade; (1) narrow process, spine or tubercle (Wible et al. 2009: ch. 242).
255. Ectopterygoid crests (blades) or tubercles orientation: (0) sub-parallel and facing ventromedially; (1) diverging and facing mostly posteriorly (Billet 2010: ch. 74, modified; Muizon et al. 2015).
256. Transverse canal: (0) absent; (1) present (Rougier et al. 1998 : ch. 104).
257. Exit for maxillary nerve (V_2) (foramen rotundum) relative to alisphenoid: (0) between the posterior edge of the alisphenoid anteriorly and the anterior lamina of the petrosal posteriorly; (1) within the alisphenoid; (2) at the anterior edge of the alisphenoid (Rougier et al. 1998: ch. 110, modified); ORDERED.
258. Number of exits for the mandibular branch of the trigeminal nerve (V_3): (0) two or more; (1) one (Luo and Wible 2005: ch. 317).
259. Foramen ovale composition: (0) in anterior lamina of the petrosal; (1) between petrosal and alisphenoid; (2) in alisphenoid; (3) between alisphenoid and squamosal (Rougier et al. 1998: ch. 111, modified).
260. Foramen ovale position: (0) on lateral wall of the braincase; (1) on ventral surface of the skull facing ventrally; (2) on the ventral side of the skull, facing anteroventrally (Rougier et al. 1998: ch. 112, modified).
261. Alisphenoid canal: (0) absent; (1) present (Rougier et al. 1998: ch. 107).
262. Posterior opening of alisphenoid canal: (0) separated from foramen ovale; (1) in common depression with foramen ovale (Wible et al. 2009: ch. 249). Taxa without alisphenoid canal are scored non-applicable.
263. Posterior border of hypophyseal fossa (located just anterior to basisphenoid-basioccipital suture) position relative to posterior edge of foramen ovale: (0) anterior to or roughly even with; (1) well posterior to (Muizon et al. 2015).

Skull: basicranium

264. Position of the dentary articulation relative to fenestra vestibuli: (0) at the same level; (1) anterior (Rougier et al. 1998: ch. 114).
265. Glenoid fossa position: (0) on zygoma; (1) partly below braincase (Wible et al. 2009: ch. 251).
266. Glenoid fossa shape: (0) concave (or concave posteriorly and flat anteriorly), open anteriorly; (1) trough-like; (2) anteroposteriorly elongate, with the major axis of fossa directed anteroposteriorly; (3) anteroposteriorly short, with the major axis of fossa directed anteroposteriorly or flat; (4) concavo-convex (Rougier et al. 1998: ch. 115; Archibald et al. 2001: ch. 137; Wible et al. 2009: ch. 252, modified)
267. Glenoid fossa dorsoventral position relative to roof of basipharyngeal canal: (0) approximately level with; (1) dorsal to it (Wible et al. 2009: ch. 253).
268. Glenoid process of the jugal: (0) present with articular facet; (1) present without facet; (2) absent (Wible et al. 2009: ch. 254).
269. Glenoid process of the alisphenoid: (0) absent; (1) present (Rougier et al. 1998: ch. 117).
270. Postglenoid process: (0) absent or very small; (1) present: subequal in width to (or slightly narrower than) glenoid cavity; (2) present: approximately half the width of the glenoid cavity. (Rougier et al. 1998: ch. 118, modified).
271. Postglenoid foramen: (0) absent; (1) present, small, width less than one third the width of the postglenoid process; (2) present, large, width more than one third the width of the postglenoid (Wible et al. 2009: ch. 257, modified).
272. Postglenoid foramen position: (0) posterior to postglenoid process (or glenoid fossa if postglenoid process is absent); (1) medial or anteromedial to the postglenoid process (within glenoid fossa); (2) on lateral aspect of braincase (Rougier et al. 1998: ch. 120, modified).
273. Postglenoid eminence of the squamosal: (0) absent; (1) present (Muizon et al. 2015)
274. Postglenoid foramen composition: (0) within squamosal or (1) on posterior edge of squamosal. Taxa without postglenoid foramen are scored non-applicable (Wible et al. 2009: ch. 259, modified).
275. Suprameatal foramen: (0) absent; (1) present (Wible et al. 2009: ch. 260).
276. Entoglenoid process of the squamosal: (0) absent; (1) present, separated from the postglenoid process; (2) present, continuous with the postglenoid process (Luo and Wible 2005: ch. 284).
277. Posttympanic crest of the squamosal: (0) absent; (1) present (Wible et al. 2009: ch. 262).
278. Carotid foramen: (0) within basisphenoid; (1) between petrosal and basisphenoid; (2) absent (Rougier et al. 1998: ch. 105, modified).
279. Floor of cavum epiptericum composition: (0) petrosal; (1) petrosal and/or alisphenoid; (2) primarily or exclusively squamosal; (3) primarily open as pyriform fenestra (Rougier et al. 1998: ch. 109, modified).
280. Posterodorsal extension of the tympanic process of the alisphenoid, which forms the roof of the anterior region of the tympanic cavity: (0) absent; (1) present (Rougier et al. 1998: ch. 121, modified).
281. Basisphenoid tympanic process: (0) absent; (1) present (Wible et al. 2009: ch. 266).
282. Basicochlear fissure: (0) closed; (1) patent (Thewissen et al. 2001: ch. 59, modified)
283. Medial flange of petrosal: (0) absent; (1) present; (Rougier et al. 1998: ch. 122, modified).

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284. Rostral tympanic process of petrosal: (0) absent or low ridge; (1) moderate ridge contributing to posterodorsomedial bulla; (2) tall ridge contributing to ventral bulla (Rougier et al. 1998: ch. 130, modified).
285. Course of the internal carotid artery: (0) lateral (transpromontorial); (1) medial (perbullar or extrabullar) (Wible et al. 2009: ch. 270, modified).
286. Bony canals for intratympanic carotid system (transpromontorial internal carotid and +/- stapedial artery): (0) absent; (1) present (Wible et al. 2009: ch. 271 and 288, modified). Taxa lacking a transpromontorial internal carotid artery are scored non-applicable.
287. Deep groove for the internal carotid artery excavated in the apex of the promontorium: (0) absent; (1) present (Rougier et al. 1998: ch. 148).
288. Perbular carotid canal (for medial internal carotid): (0) absent; (1) present (Wible et al. 2009: ch. 273). Taxa with transpromotorial course are scored non-applicable.
289. Sulcus or canal for stapedial artery on promontorium: (0) present; (1) absent (Asher et al. 2005: ch. 161, modified).
290. Stapedial ratio (length/width fenestra vestibuli): (0) rounded less than 1.8; (1) elliptical more than 1.8 (Rougier et al. 1998: ch. 127).
291. Coiling of the cochlea: (0) less than 360°; (1) more than 360° (Rougier et al. 1998: ch. 129).
292. Pars cochlearis length: (0) more than 13% of skull length; (1) less than 10% of skull length (Wible et al. 2009: ch. 277).
293. Promontorium shape: (0) flat; (1) globose (Wible et al. 2009: ch. 278).
294. Kidney (or bean-) -shaped promontorium: (0) absent; (1) present (Billet 2010: ch. 127, modified; (Muizon et al. 2015).
295. Promontorium depth (most ventral point) relative to basioccipital: (0) level or ventral; (1) dorsal (Wible et al. 2009: ch. 279).
296. Intratympanic course of facial nerve: (0) open in sulcus; (1) open anteriorly, canal posteriorly; (2) in canal (Meng et al. 2003: ch. 169, modified).
297. Aperture of hiatus Fallopii: (0) on cerebral face of petrosal; (1) at anterior edge of petrosal; (2) on tympanic face of petrosal; (3) via fenestra semilunaris: (Rougier et al. 1998: ch. 123, modified; Sánchez-Villagra and Wible 2002: ch. 12, modified).
298. Prootic canal: (0) present; (1) absent (Rougier et al. 1998: ch. 124, modified).
299. Prootic canal length and orientation: (0) long and vertical; (1) short and vertical; (2) short and horizontal. (Rougier et al. 1998: ch. 124, modified).
300. Lateral flange: (0) parallels length of the promontorium, (1) greatly reduced or absent (Rougier et al. 1998: ch. 126, modified).
301. Anterior extension of bony shelf lateral to promontorium (lateral trough or tegmen tympani): (0) does not reach the apex of the promontorium anteriorly and confined posterolaterally; (1) extends as far anteriorly as the apex of the promontorium; (2) extends further anteriorly than the apex of the promontorium (Wible et al. 2009: ch. 285, modified); ORDERED.
302. Width of bony shelf lateral to promontorium (lateral trough or tegmen tympani): (0) uniform; (1) expanded anteriorly (Wible et al. 2009: ch. 286).
303. Inflation of bony shelf lateral to promontorium (lateral trough or tegmen tympani): (0) absent; (1) present (Cifelli 1982; Geisler and Luo 1998; Thewissen et al. 2001: ch. 52).
304. Tensor tympani fossa on petrosal: (0) shallow; (1) deep circular fossa (Wible et al. 2009: ch. 289, modified).
305. Area occupied by tensor tympani fossa: (0), small and/or poorly excavated; (1) large (Muizon et al. 2015).
306. Location of tensor tympani fossa: (0) mostly medial (or ventromedial) to the cavum supracochleare; (1) strictly ventral or lateral to it, not medial (Billet and Muizon 2013: ch. 138; Muizon et al. 2015).
307. Medial process of squamosal in tympanic cavity: (0) absent; (1) present (Muizon 1994).
308. Hypotympanic sinus: (0) absent; (1) formed by squamosal, petrosal and alisphenoid; (2) formed by alisphenoid and petrosal; (3) formed by petrosal (Muizon 1994, modified).
309. Epitympanic recess vs fossa incudis: (0) subequal; (1) epitympanic recess larger; (2) no visible depression for epitympanic recess (Wible et al. 2009: ch. 292).
310. Epitympanic recess lateral wall: (0) with small contribution of squamosal to posterolateral wall; (1) with extensive contribution of squamosal; (2) with no squamosal contribution (Rougier et al. 1998: ch. 138 modified).
311. Fossa incudis relationship with epitympanic recess: (0) continuous with; (1) separated from (Rougier et al. 1998: ch. 137).
312. Squamosal epitympanic sinus: (0) absent; (1) present (Billet 2010: ch. 124; Muizon et al. 2015).
313. Floor ventral to fossa incudis: (0) absent (the fossa is open ventrally); (1) formed by squamosal; (2) formed by ectotympanic; (3) formed by the petrosal (Wible et al. 2009: ch. 295, modified).
314. Fossa incudis position relative to fenestra vestibuli: (0) lateral; (1) anterolateral (Wible et al. 2009: ch. 296).
315. Foramen for superior ramus of the stapedial artery: (0) in petrosal; (1) in petrosal-squamosal suture; (2) absent (Rougier et al. 1998: ch. 145).
316. Position of the ramus superior foramen relative to fenestra vestibuli: (0) posterior or lateral; (1) anterior (Luo and Wible 2005: ch. 326).

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317. Ascending canal (passage for the ramus superior of the stapedial artery): (0) intramural in the petrosal, (1) intracranial, or (2) absent. (Rougier et al. 1998: ch. 152).
318. Diameter of the stapedius fossa: (0) approximately twice the size of that of the fenestra vestibuli; (1) distinctly less than twice the size of the diameter of the fenestra vestibuli (= small and shallow) (Rougier et al. 1998: ch. 139, modified).
319. Cochlear canaliculus visible in middle ear space: (0) absent; (1) present (Wible et al. 2009: ch. 301).
320. Stapedial fossa and postpromontorial tympanic sinus: (0) distinct, separated by a break in slope or a crest; (1) merged, almost indistinct (Billet and Muizon 2013: ch. 139; Muizon et al. 2015).
321. External aperture of cochlear fossula (fenestra cochleae in Wible et al. 2009: ch. 303) position relative to fenestra vestibuli: (0) posteromedial, (1) posterior (Wible et al. 2009: ch. 303).
322. Posterior septum shields fenestra cochleae: (0) absent; (1) present (Wible et al. 2009: ch. 304).
323. Mastoid process (= paroccipital process of Wible et al. 2009): (0) distinctly present and vertical; (1) slanted, projecting anteroventrally; (2) indistinct to absent (Wible et al. 2009: ch. 305).
324. Posterior border of the middle ear cavity medial to the stylomastoid notch and lateral to the lateral edge of the jugular foramen: (0) straight or convex anteriorly; (1) concave or deeply notched (Wible et al. 2009: ch. 306 and 310, modified).
325. Crista interfenestralis and lateral caudal tympanic process of petrosal (= caudal tympanic process of Wible et al., 2009, ch. 307) connected by curved ridge: (0) absent; (1) present (Rougier et al. 1998: ch. 133, modified).
326. Medial caudal tympanic process (sensu MacPhee 1981) of the petrosal (= “tympanic process” of Wible et al. 2009: ch. 308): (0) absent; (1) present (low); (2) present (high) (e.g., inflated into bullar wall) (Rougier et al. 1998: ch. 134, modified); ORDERED.
327. Medial caudal tympanic process (sensu MacPhee 1981) of the petrosal (= “tympanic process” of Wible et al. 2009: ch. 309) composition: (0) petrosal; (1) petrosal and exoccipital (Wible et al. 2009: ch. 309).
328. Inferior petrosal sinus: (0) intrapetrosal; (1) horizontal between petrosal and basioccipital; (2) intracranial: entering cranial cavity on anterior edge of the jugular foramen; (3) intracranial: entering cranial cavity via a foramen at mid-length of the medial border of the promontorium (Rougier et al. 1998: ch. 151, modified).
329. Size of the jugular foramen: (0) smaller or subequal to external aperture of cochlear fossula; (1) larger (Rougier et al. 1998: ch. 149).
330. Jugular foramen and inferior petrosal sinus: (0) confluent; (1) separated (Rougier et al. 1998: ch. 150).
331. Hypoglossal foramen: (0) two or more; (1) one; (2) absent (Luo and Wible 2005: ch. 349).
332. Hypoglossal foramen housed in opening larger than jugular foramen (0) absent; (1) present (Wible et al. 2009: ch. 315).
333. Hypoglossal foramen ventral opening on exoccipitals: (0) in a fossa; (1) on a flat to convex bony surface (Muizon et al. 2015).
334. Paroccipital (paracondylar of Wible et al. 2009) process of the exoccipital: (0) weak or absent; (1) prominent vertical; (2) prominent posteriorly directed (Rougier et al. 1998: ch. 135, modified).
335. Ectotympanic: (0) phaneric or visible in ventral view; (1) aphaneric, hidden by auditory bulla (Wible et al. 2009: ch. 317).
336. Ectotympanic: (0) ringlike; (1) fusiform; (2) transversely expanded (Rougier et al. 1998: ch. 142).
337. Anterior crus of ectotympanic broad articulation with squamosal: (0) absent; (1) present (Wible et al. 2009: ch. 319).
338. Anterior crus of ectotympanic articulation with petrosal: (0) absent; (1) present (Muizon et al. 2015).
339. Elongate ossified external acoustic canal: (0) absent; (1) present (Wible et al. 2009: ch. 320).
340. Roof of external acoustic meatus: (0) petrosal; (1) squamosal (Wible et al. 2009: ch. 321).
341. Entotympanic distinct in adults: (0) absent; (1) present (Luo and Wible 2005: ch. 363).
342. Pit for hyoid on ectotympanic (or between ectotympanic and exoccipital): (0) absent; (1) present (Wible et al. 2009: ch. 323, modified).
343. Hyoid arch contributes to bullar floor: (0) absent; (1) present (Wible et al. 2009: ch. 324).
344. Dorsum sellae: (0) tall; (1) low (Rougier et al. 1998: ch. 106).
345. Posterior clinoid process contacts apex of the promontorium: (0) absent; (1) present (Wible et al. 2004).
346. Position of sulcus for anterior distributary of transverse sinus relative to fossa subarcuata: (0) anterolateral; (1) posterolateral; (2) absent (Rougier et al. 1998: ch. 125).
347. Wall separating the cavum supracochleare from the cavum epiptericum: (0) absent; (1) incomplete with fenestra semilunaris; (2) complete (Rougier et al. 1998: ch. 128, modified).
348. Crista petrosa: (0) vestigial or absent; (1) tall and thin crest (Wible et al. 2009: ch. 329).
349. Subarcuate fossa morphology: (0) subspherical with constricted aperture: diameter of aperture is smaller than maximum diameter of the fossa; (1) cylindrical, diameter more or less constant; (2) conical or shallow depression: aperture is the widest diameter (Wible et al. 2009: ch. 330, modified); ORDERED.
350. Internal acoustic meatus: (0) deep with thick prefacial commissure; (1) shallow with thin prefacial commissure (Wible et al. 2009: ch. 332).

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Skull occiput

351. Posttemporal canal: (0) present; (1) absent (Wible et al. 2009: ch. 333, modified).
352. Posttemporal canal composition (posterior opening): (0) between petrosal and squamosal; (1) within petrosal (Wible et al. 2009: ch. 334).
353. Mastoid foramen l: (0) absent; (1) present (one or more) (Meng et al. 2003: ch. 114, modified).
354. Amastoidy or lack of occipital exposure of the mastoid: (0) absent; (1) present (Geisler 2001: ch. 38).
355. Dorsal margin of the foramen magnum: (0) formed by the exoccipitals; (1) formed by the exoccipitals and the supraoccipital (Rougier et al. 1998: ch. 156).
356. Dorsal relief of lambdoid crest continuous with dorsal margin of zygomatic arch: (0) absent; (1) present (Billet 2010: ch. 95; Muizon et al. 2015).

Postcranial characters

357. Atlantal foramen: (0) present; (1) absent (Horovitz and Sánchez-Villagra 2003: ch.1, modified).
358. Atlas neural hemiarches fused: (0) absent; (1) present (Luo and Wible 2005: ch. 169, modified).
359. Atlas neural arch and intercentrum fused: (0) absent; (1) present (Luo and Wible 2005: ch. 167).
360. Suture between atlantal and axial parts of the axis: (0) present; (1) absent (Luo and Wible 2005: ch. 169, modified).
361. Axis with extra pair of transverse processes on ventral surface of body: (0) present; (1) absent (Horovitz and Sánchez-Villagra 2003: ch. 11, modified).
262. Axis anterior facets (prezygapophyses) and dens connection: (0) not linked; (1) linked; facets extend ventral to dens (Horovitz and Sánchez-Villagra 2003: ch. 12, modified).
363. Inferior lamellae on posterior cervical vertebrae (essentially on C6 and occasionally on C5): (0) present; (1) absent (Wible et al. 2009: ch. 345).
364. C7 transverse foramen: (0) present; (1) absent (Horovitz and Sánchez-Villagra 2003: ch. 231, modified).
365. Number of thoracic vertebrae: (0) 13 or fewer; (1) 15 or more (Luo and Wible 2005: ch. 172).
366. Number of lumbar vertebrae: (0) 6 or more; (1) 5 or fewer Wible et al. 2009: ch. 348).
367. Xenarthrous articulations on lumbar vertebrae: (0) absent; (1) present (Luo and Wible 2005: ch. 176).
368. Number of sacral vertebrae: (0) 2; (1) 3; (2) 4 or more (Geisler 2001: ch. 131, modified); ORDERED.
369. Sacral vertebrae fused to pelvis: (0) absent; (1) present (Wible et al. 2009: ch. 351).
370. Infraspinous fossa position to supraspinous fossa: (0) different planes (in part medial to); (1) coplanar (Rougier 1993: ch. 13, modified).
371. Suprascapular incisure: (0) absent; (1) present (Luo and Wible 2005: ch. 196).
372. Apex of acromion: (0) distal to glenoid articulation; (1) proximal; (2) absent (Asher et al. 2005: ch. 174, modified).
373. Metacromion: (0) weak or absent; (1) well-developed process (Wible et al. 2009).
374. Elevation of the greater tubercle of the humerus relatively to the humeral head: (0) ventral (distal); (1) even or dorsal (proximal) (Asher et al. 2005: ch. 175).
375. Extension of deltopectoral crest: (0) limited to proximal half of the humerus; (1) reaches distal half (Horovitz and Sánchez-Villagra 2003: ch. 50).
376. Epicondylar crest (= sigmoidal shelf for supinator ridge extending proximally from ectepicondyle: (0) weak or absent; (1) present and patent (Luo and Wible 2005: ch. 206).
377. Entepicondyle: (0) Robust and projecting medially; (1) weak or absent (Geisler 2001: ch. 134).
378. Entepicondylar foramen: (0) present; (1) absent (Geisler 2001: ch. 135).
379. Supratrochlear foramen: (0) absent; (1) present (Asher et al. 2005: ch. 178).
380. Ulnar articulation of the humerus: (0) cylindrical trochlea in posterior view with a vestigial ulnar condyle in anterior view; (1) cylindrical trochlea without an ulnar condyle (cylindrical trochlea extending to the anterior/ventral side) (Luo and Wible 2005: ch. 203, modified).
381. Radial articulation: (0) rounded radial condyle (= capitulum) anteriorly but cylindrical posteriorly; (1) capitulum forming a continuous synovial surface with the ulnar trochlea (cylindrical in both anterior and posterior views) (Luo and Wible 2005: ch. 204, modified).
382. Humeral articulation on radius: (0) single fossa; (1) two fossae (Geisler 2001: ch. 141, modified).
383. Central process of radial head: (0) small or absent; (1) present (Asher et al. 2005: ch. 181).
384. Radius and ulna distal fusion: (0) absent; (1) present (Thewissen et al. 2001: ch. 81).
385. Radial articulation with carpals: (0) single fossa; (1) two fossae (Thewissen et al. 2001: ch. 80).
386. Scaphoid and lunate: (0) separate; (1) fused (Asher et al. 2005: ch. 183).
387. Os centrale: (0) present; (1) absent (Asher et al. 2005: ch. 184).

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388. Pubic symphysis: (0) extensive; (1) narrow (Meng et al. 2003: ch. 22).
389. Epipubic bone: (0) present; (1) absent (Luo and Wible 2005: ch. 218).
390. Articular surface of femoral head: (0) extended posterolaterally; (1) limited to the sphere of the head (Asher et al. 2005: ch. 186).
391. Fovea for ligamentum teres on femoral head: (0) surrounded by articular surface; (1) interrupt margin of articular surface; (2) absent (MacPhee 1994: ch. 27).
392. Greater trochanter relative to femoral head: (0) lower; (1) even; (2) higher (Horovitz and Sánchez-Villagra 2003: ch. 79); ORDERED.
393. Size of lesser trochanter of femur: (0) large, surpassing half of the medial extension of the femoral head; (1) small (Luo and Wible 2005: ch. 228; Flores 2009: ch. 93).
394. Third trochanter of femur: (0) absent; (1) present (Asher et al. 2005: ch.188).
395. Pectineal tubercle: (0) absent or vestigial; (1) distinct (Wible et al. 2009: ch. 377).
396. Proportions of the distal extremity of the femur: (0) as long as wide; (1) longer than wide (Asher et al. 2005: ch. 189).
397. Patellar facet of the femur: (0) weakly developed; (1) broad and shallow; (2) narrow and elevated (deep) (Luo and Wible 2005: ch. 230, modified).
398. Ossified patella: (0) absent; (1) present (Luo and Wible 2005: ch. 273).
399. Articulation between femur and fibula: (0) absent; (1) present (Horovitz and Sánchez-Villagra 2003: ch. 84).
400. Tibia and fibula proximal fusion: (0) absent; (1) present (Asher et al. 2005: ch. 190).
401. Tibia and fibula distal fusion: (0) absent; (1) present (Horovitz and Sánchez-Villagra 2003: ch. 87).
402. Depth of trochlear groove of the astragalus: (0) shallow (slightly concave articular surface); (1) moderately deep (section of the groove U-shaped); (2) deep (V-shaped) (Zack et al. 2005: ch. 40, modified); ORDERED.
403. Angle between medial and lateral facet for the tibia on the astragalar body: (0) 180°; (1) intermediate; (2) 90° (Horovitz and Sánchez-Villagra 2003: ch. 94, modified); ORDERED.
404. Angle between facet for the fibula and the lateral facet for the tibia: (0) 180°; (1) intermediate; (2) 90° (Horovitz and Sánchez-Villagra 2003: ch. 99); ORDERED.
405. Radius of curvature of the lateral trochlear ridge of the astragalus relatively to the medial trochlear ridge: (0) greater; (1) subequal (Zack et al. 2005: ch. 41).
406. Cotylar fossa on the medial edge of the astragalus trochlea: (0) absent; (1) present (Zack et al. 2005: ch. 44, modified).
407. Contact between sustentacular and navicular facets of the astragalus: (0) absent; (1) present (Asher et al. 2005: ch. 204).
408. Medial extension of the astragalar sustentacular facet: (0) reaches the medial edge of the neck; (1) does not reach the medial edge (Horovitz and Sánchez-Villagra 2003: ch. 102).
409. Astragalar medial plantar tuberosity: (0) weak or absent; (1) protruding (Horovitz and Sánchez-Villagra 2003: ch. 98, modified).
410. Astragalar neck: (0) absent; (1) present shorter than body width; (2) present and similar in length to body width (Horovitz and Sánchez-Villagra 2003: ch. 100).
411. Convex astragalar head: (0) absent; (1) present (Thewissen et al. 2001: ch. 92, modified).
412. Facet on astragalus for cuboid: (0) absent; (1) present (Asher et al. 2005: ch. 208).
413. Astragalar canal: (0) present; (1) dorsal foramen only; (2) absent (Horovitz and Sánchez-Villagra 2003: ch. 104, modified).
414. Posterior trochlear shelf of the astragalus: (0) weak or absent; (1) strong (Asher et al. 2005: ch. 198).
415. Calcaneal width: (0) broad with sustentacular and ectal facet extending from body; (1) narrow with sustentacular and ectal facets in line with long axis (Asher et al. 2005: ch. 210).
416. Ectal (or posterior calcaneoastragalar) facet orientation of longest axis: (0) anteromedial to posterolateral, (1) anteroposterior (proximodistal), (2) posteromedial to anterolateral (Horovitz and Sánchez-Villagra 2003: ch. 113, modified); ORDERED.
417. Anteroposterior overlap between calcaneal ectal and sustentacular facets: (0) no overlap; (1) partial overlap; (2) nearly complete overlap (Zack et al. 2005: ch. 32, modified); ORDERED.
418. Calcaneal sustentacular facet orientation: (0) medial; (1) dorsal (Horovitz and Sánchez-Villagra 2003: ch. 118).
419. Calcaneal sustentacular facet expanded onto body: (0) absent; (1) present (Wible et al. 2009: ch. 401).
420. Calcaneal peroneal process: (0) Protruding distally beyond calcaneo-cuboid facet; (1) distal but non-protruding; (2) at a distance from distal end of calcaneum; (3) absent (Horovitz and Sánchez-Villagra 2003: ch. 117).
421. Calcaneal plantar tubercle: (0) absent; (1) present at distal margin; (2) present more proximal than distal margin (Horovitz and Sánchez-Villagra 2003: ch. 122, modified).
422. Tuber calcis ventral curvature: (0) present; (1) absent (Horovitz and Sánchez-Villagra 2003: ch. 125, modified).
423. Calcaneal facet for the fibula: (0) present; (1) absent (Horovitz and Sánchez-Villagra 2003: ch. 125, modified).
424. Orientation of mediolateral axis of the cuboid facet relative to the long axis of the calcaneum: (0) less than 70°; (1) c. 70°-80°; (2) c. 90° (Zack et al. 2005: ch. 37); ORDERED.

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425. Proportions of the cuboid facet on the calcaneum: (0) facet much deeper (dorsoplantar) than wide (mediolateral); (1) facet depth and width subequal; (2) facet much wider (mediolateral) than deep (dorsoplantar) (Zack et al. 2005: ch. 38); ORDERED.
426. Deep groove for the tendon of the flexor hallucis longus (= flexor fibularis) on the posterior edge of the sustentaculum calcaneum: (0) absent; (1) present (Wible et al. 2009: ch. 408).

Characters derived primarily from Billet et al. (2015)

427. I1 comma-shaped in section: (0) absent; (1) present (Billet et al. 2015: ch. 8; Billet 2010: ch. 5).
428. I1 obliquely implanted, meeting at tips: (0) absent; (1) present (Billet et al. 2015: ch. 9; Billet 2010: ch. 7).
429. I1 crown height and robustness: (0) brachydont or slightly hypsodont, not tusk-like; (1) hypsodont and/or tusk-like; (2) hypselodont and tusk-like (Billet et al. 2015: ch. 11; Billet 2010: ch. 6 and 9, modified); ORDERED
430. (I1-)I2 caniniform, circular in cross-section: (0) absent; (1) present (Billet et al. 2015: ch. 12; Billet 2010: ch. 10).
431. I2 trihedral tusk and diverging: (0) absent; (1) present (Billet et al. 2015: ch. 13; Billet 2010: ch. 11).
432. Lingual cingulum on upper incisors forms a fossa: (0) absent; (1) present (Billet et al. 2015: ch. 16; Billet 2010: ch. 15).
433. Tusk-like upper and lower canines: (0) absent; (1) present (Billet et al. 2015: ch. 18; Billet 2010: ch. 18).
434. Canine (upper and lower): (0) massive and caniniform; (1) incisiform and subequal to other incisors (Billet et al. 2015: ch. 19; Billet 2010: ch. 19).
435. Cheek teeth: (0) brachyodont; (1) hypsodont (sidewall hypsodonty sensu Koenigswald, 2011); (2) hypselodont (Billet et al. 2015: ch. 21; Billet 2010: ch. 20); ORDERED.
436. Distal cingulum isolating a deep fossette (postcingulum fossette) on upper cheek teeth: (0) absent; (1) present (Billet et al. 2015: ch. 22; Billet 2010: ch. 21).
437. Metaloph (high crest joining metacone and hypocone) on M1-2 (and premolars): (0) absent; (1) present (Billet et al. 2015: ch. 25; Billet 2010: ch. 26).
438. Anterolabial fossette on upper cheek teeth: (0) absent; (1) present (Billet et al. 2015: ch. 27; Billet 2010: ch. 28).
439. Central fossette on upper cheek teeth: (0) absent; (1) present (Billet et al. 2015: ch. 28; Billet 2010: ch. 29).
440. Deep labial extension of central fossette between the protoloph (-crista 1) and the crochet (-crista 2) on upper molars: (0) absent; (1) present (Billet et al. 2015: ch. 29; Billet 2010: ch. 30).
441. Multiple cristae individualized mesially to the crochet on upper cheek teeth: (0) absent; (1) present (Billet et al. 2015: ch. 30; Billet 2010: ch. 31).
442. Crista intermedia running lingually from the ectoloph between the protoloph and the crochet on upper cheek teeth: (0) absent; (1) present (Billet et al. 2015: ch. 31; Billet 2010: ch. 32).
443. Crista intermedia: (0) not-well individualized but suggested by a bulge; (1) completely individualized (Billet et al. 2015: ch. 32; Billet 2010: ch. 33, modified).
444. Posterolabial fossette on upper molars: (0) co-occurs with the central fossette; (1) disappears before the closure of the central fossette (Billet et al. 2015: ch. 33; Billet 2010: ch. 34).
445. Crochet originating lingually at mesial edge of hypocone: (0) absent; (1) present (Billet et al. 2015: ch. 34; Billet 2010: ch. 35).
446. Subvertical parastyle-paracone sulcus on upper premolars: (0) shallow; (1) deep (Billet et al. 2015: ch. 39; Billet 2010: ch. 38).
447. Prominent mesostyle (stylar cusp C) (at least on M): (0) absent; (1) present (Billet et al. 2015: ch. 40; Cifelli 1993: ch. 13).
448. Deep mesial valley on P2-3 (-4) due to incomplete development of protoloph: (0) absent; (1) present (Billet et al. 2015: ch. 42; Billet 2010: ch. 40).
449. Persistent lingual sulcus after the isolation of the central fossette on upper molars: (0) absent; (1) present (Billet et al. 2015: ch. 43; Billet 2010: ch. 44).
450. Persistent lingual sulcus (enamel infolding; tooth not trilobed) between protoloph and metaloph on upper molars: (0) absent; (1) present (Billet et al. 2015: ch. 44; Billet 2010: ch. 45).
451. Upper molars trilobed when little worn, with large and rounded median lobe: (0) absent; (1) present but disappears with wear; (2) trilobation persists throughout all wear stages; (Billet et al. 2015: ch. 45; Billet 2010: ch. 46); ORDERED.
452. Cusp on precingulum anterolingual to paraconule: (0) absent; (1) present (Billet et al. 2015: ch. 51; Muizon and Cifelli 2000: ch. 22). Non-applicable for hypsodont and hypselodont taxa.
453. Lingual vertical ridge on lower incisors and canine: (0) absent; (1) present (Billet et al. 2015: ch. 54; Billet 2010: ch. 47).
454. Lingual face of i1-2 (only i2 when i1 is absent; and vice-versa): (0) without vertical sulcus; (1) with a shallow vertical sulcus; (2) with a deep vertical sulcus (bifid incisors) (Billet et al. 2015: ch. 55; Billet 2010: ch. 48); ORDERED.
455. Third lower incisor large (larger than canine) and canine-like (pointed): (0) absent; (1) present (Billet et al. 2015: ch. 57; Billet 2010: ch. 51).
456. Tusk-like third lower incisor: (0) absent; (1) present (Billet et al. 2015: ch. 58; Billet 2010: ch. 52).
457. Leaf shaped lower incisors: (0) absent; (1) present (Billet et al. 2015: ch. 59).

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458. Mesial lophid (paralophid?) in a paraconid position on lower cheek teeth: (0) absent (or just a faint cristid); (1) present (Billet et al. 2015: ch. 61; Billet 2010: ch. 53).
459. Lower cheek teeth with short mesiodistal protolophid, transverse metalophid and mesiodistal hypolophid slightly convex labially (double crescent): (0) absent; (1) present (Billet et al. 2015: ch. 62; Billet 2010: ch. 54).
460. Lingual connection of lophids of the trigonid and talonid (entolophid connects to metalophid with wear) on lower cheek teeth: (0) absent; (1) isolating a trigonid-talonid fossettid in conjunction with the preceding more labial connection of hypolophid with trigonid; (2) lingual connection trigonid-talonid precedes the labial connection and isolation of fossettid; (3) single lingual connection, producing a deep labial sulcus between trigonid and talonid (Billet et al. 2015: ch. 65; Billet 2010: ch. 57).
461. Hypoconid: (0) forms labial half of talonid or less, does not invade talonid basin anterior to the hypoconulid. 1, large, conical; extends on lingual half of talonid and invades talonid basin anterior to hypoconulid (Billet et al. 2015: ch. 66; Muizon and Cifelli 2000: ch. 34).
462. Fossettid of entolophid: (0) absent; (1) present (Billet et al. 2015: ch. 67; Billet 2010: ch. 58).
463. Trigonid of lower molars with a tiny trigonid fossettid partially or entirely isolated lingually by a crest (premetacristid) running mesially from metalophid: (0) absent; (1) present (Billet et al. 2015: ch. 6; Billet 2010: ch. 59).
464. Transversely elongated fossettid isolated between entolophid (mesially) and hypolophid (labially and distally) with advanced wear: (0) absent; (1) present (Billet et al. 2015: ch. 69; Billet 2010: ch. 60).
465. Distolabial crest on trigonid of lower premolars made by a distolabial extension of protolophid: (0) absent; (1) present (Billet et al. 2015: ch. 70; Billet 2010: ch. 61).
466. Talonid extending well distal to entolophid on lower molars: (0) absent; (1) present (Billet et al. 2015: ch. 71; Billet 2010: ch. 62).
467. Deep labial and lingual sulci dividing trigonids and talonids on lower cheek teeth at all wear stages (all along the crown): (0) absent; (1) present (Billet et al. 2015: ch. 72; Billet 2010: ch. 63).
468. Flat and straight lingual face on lower molars at all wear stages (on all the crown height): (0) absent; (1) present (Billet et al. 2015: ch. 73; Billet 2010: ch. 64).
469. Premaxillaries defining a strong and long ridge connecting the narial processes to the anterior alveolar border (the nares open much higher than the alveolar border): (0) absent; (1) present (Billet et al. 2015: ch. 76; Billet 2010: ch. 69).
470. Triangular incisive foramina (distal extremities converging): (0) absent; (1) present. (Billet et al. 2015: ch. 78; Billet 2010: ch. 72).
471. Medial platform of palatines expanding palate posteriorly and fully continuous with it: (0) absent; (1) present (Billet et al. 2015: ch. 79; Billet 2010: ch. 73).
472. Choanae divided by a vomerian/palatine process: (0) absent; (1) present (Billet et al. 2015: ch. 82; Billet 2010: ch. 75).
473. Premaxillary-maxillary suture course on palate: (0) medially: directed anteriorly; (1) medially: grossly transverse; (2) medially: directed posteriorly; (3) directed posteriorly in its entire course (Billet et al. 2015: ch. 83; Billet 2010: ch. 76); ORDERED.
474. Posterodorsal extremity of maxillary contacting nasal: (0) does not reach posterior extremity of nasals; (1) does approximately reach posterior extremity of nasals; (2) reaches much further than posterior extremity of nasals (Billet et al. 2015: ch. 85; Billet 2010: ch. 78); ORDERED.
475. Strong vertical descending process (masseteric spine) of maxillary: (0) absent; (1) present (Billet et al. 2015: ch. 87; Billet 2010: ch. 80).
476. Anterior tips of nasals: (0) extends anterior to ascending process of premaxillary; (1) does not extend anterior to ascending process of premaxillary (Billet et al. 2015: ch. 88; Billet 2010: ch. 83).
477. Anterior edge of ascending process of premaxillary shifted posteriorly: (0) absent; (1) present (Billet et al. 2015: ch. 89; Billet 2010: ch. 84).
478. Post-orbital constriction: (0) strong; (1) weak (Billet et al. 2015: ch. 92; Billet 2010: ch. 87).
479. Squamosal contacts with frontal at level of postorbital apophysis: (0) absent; (1) present (Billet et al. 2015: ch. 94; Billet 2010: ch. 89).
480. Zygomatic plate below and in front of orbit: (0) absent; (1) present (Billet et al. 2015: ch. 96; Billet 2010: ch. 91).
481. Orbit shape: (0) round; (1) oval (higher than long, dorsal edge of zygomatic arch excavated below orbit) (Billet et al. 2015: ch. 98; Billet 2010: ch. 93).
482. Jugal-squamosal suture strongly curved anteriorly (large part directed dorsally): (0) absent; (1) present (Billet et al. 2015: ch. 99; Billet 2010: ch. 94).
483. Sphenopalatine foramen: (0) well individualized at limit between medial orbital wall and orbital floor; (1) poorly individualized, within a groove at limit between medial orbital wall and orbital floor (Billet et al. 2015: ch. 100; Billet 2010: ch. 96).
484. Position of sphenopalatine foramen: (0) in posterior part of orbit floor; (1) at level of middle of orbit floor antero-posterior length (Billet et al. 2015: ch. 101; Billet 2010: ch. 97).
485. Very large orbit (the orbit occupies almost all the orbitotemporal fossa): (0) absent; (1) present (Billet et al. 2015: ch. 102; Billet 2010: ch. 98).

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486. Auditory region (basicranium) large and short (= auditory region much wider than longer, from level of anterior edge of squamosal root of zygomatic process to posterior border of paroccipital processes): (0) absent; (1) present (Billet et al. 2015: ch. 104; Billet 2010: ch. 100).
487. Postglenoid foramen piercing deeply postglenoid process postero-dorsally and defining a large sinus within its base: (0) absent; (1) present (Billet et al. 2015: ch. 108; Billet 2010: ch. 105).
488. Long and large groove on the lateral face of ecto-(ento-)pterygoid process immediately in front of the foramen ovale/sphenotympanic fissure: (0) absent; (1) present (Billet et al. 2015: ch. 111).
489. Inflated ossified auditory bulla well (tightly) attached to basicranium: (0) absent; (1) present (Billet et al. 2015: ch. 112; Billet 2010: ch. 107).
490. Position of hypoglossal foramen relative to posterior lacerate (jugular) foramen: (0) well separated from it; (1) in a common depression (Billet et al. 2015: ch. 113; Billet 2010: ch. 108).
491. Large foramen medial to promontorium midlength and/or auditory bulla and lateral to basioccipital: (0) absent; (1) present (Billet et al. 2015: ch. 115; Billet 2010: ch. 112, modified).
492. Large quadrangular auditory bulla with an anterior border grossly transverse and a medial border defining a long straight line: (0) absent; (1) present (Billet et al. 2015: ch. 11; Billet 2010: ch. 113).
493. Posterior bulla laps up onto paraoccipital process: (0) absent; (1) present (Billet et al. 2015: ch. 117; Billet 2010: ch. 114).
494. Crista meatus: (0) absent; (1) present (Billet et al. 2015: ch. 118; Billet 2010: ch. 115).
495. Crista meatus: (0) small; (1) well developed (Billet et al. 2015: ch. 119; Billet 2010: ch. 116).
496. Ossified tubular external auditory meatus: (0) short, does not reach lateral edge of skull (especially lateral edge of postglenoid process); (1) long, reaches lateral edge of skull (Billet et al. 2015: ch. 121; Billet 2010: ch. 118).
497. Postglenoid process appressed or almost fused on all its length to crista meatus and/or to external auditory meatus and defining a channel for postglenoid foramen: (0) absent; (1) present (Billet et al. 2015: ch. 122; Billet 2010: ch. 119).
498. Crista meatus and post-tympanic process of squamosal: (0) widely separated; (1) very close to or appressed against each other (Billet et al. 2015: ch. 123; Billet 2010: ch. 120).
499. Posterior border of tympanohyal recess: (0) formed by paroccipital process; (1) formed by a tympanic extension and/or post-tympanic process (Billet et al. 2015: ch. 124; Billet 2010: ch. 122).
500. Very small tympanohyal recess located on posterolateral slope of bulla: (0) absent; (1) present (Billet et al. 2015: ch. 125; Billet 2010: ch. 123).
501. Epitympanic sinus in a large swollen triangular area delimited by a medial crest continuous with posterior root of zygomatic arch and with lambdoid crest: (0) absent; (1) present (Billet et al. 2015: ch. 127; Billet 2010: ch. 126).
502. Facial sulcus (here the distance from fenestra vestibuli to crista parotica): (0) wide; (1) moderate; (2) narrow (Billet et al. 2015: ch. 131); ORDERED.
503. Subquadrangular outline of tensor tympani fossa outline on the promontorium, elongated anteroposteriorly: (0) absent; (1) present (Billet et al. 2015: ch. 132).
504. Strongly curved promontorium of petrosal (excavated by a deep notch just anterior to the fenestra vestibuli): (0) absent; (1) present. (Billet et al. 2015: ch. 139; Billet and Muizon 2013: ch. 141).
505. Cochlear canaliculus within a large notch at posteromedial edge of promontorium (=lateral wall of cochear canaliculus notched in a (large) right angle): (0) absent; (1) present (Billet et al. 2015: ch. 144).
506. Number of cochlear turns: (0) less than 2 (or 2); (1) more than 2 (Billet et al. 2015: ch. 154).
507. Relative sizes of SCs (from inner perimeter and/or R): (0) ASC clearly the largest (>1.10 from the others); (1) subequal (at least ASC and PSC); (2) PSC the largest (>1.10 from the others) (Billet et al. 2015: ch. 146).
508. Secondary common crus: (0) present; (1) just a contact; (2) absent (Billet et al. 2015: ch. 147; Macrini et al. 2013: ch 21 and 22, modified).
509. Anterior (and posterior) ampullae dorsoventral girth relative to semicircular canal cross-sectional diameter: (0) ampullae girth in the dorsoventral direction extend well beyond the SSC boundaries; (1) ampullae are not noticeably expanded anterodorsally beyond the plane of the SSC (Billet et al. 2015: ch. 148; Macrini et al. 2013: ch. 8).
510. Dorsal extent of ASC and PSC above the crus commune: (0) only the ASC extends well dorsal to the crus; (1) ASC and PSC both extend well dorsal to the crus commune; (2) neither canal extends well dorsal to the crus (Billet et al. 2015: ch. 149; Macrini et al. 2013: ch. 14).
511. Very high sagittal and lambdoid crests, this latter crest being inclined backward: (0) absent; (1) present (Billet et al. 2015: ch. 151; Billet 2010: ch. 134).
512. Coronoid process of dentary: (0) rectilinear; (1) bent medially (Billet et al. 2015: ch. 152; Billet 2010: ch. 135).
513. Neck and head of astragalus: (0) not expanded and axis oblique relative to tibial trochlea; (1) expanded and axis subaparallel to tibial trochlea (Billet et al. 2015: ch. 155; Cifelli 1993: ch. 5, modified).

Supplemental Appendix 9

(continued on next page)

Data matrix (modified from Muizon et al. 2015 with the addition of 87 characters selected from Billet et al. 2015) used for the second set of phylogenetic analyses (Fig. 10B). All taxa are scored as in Muizon et al. (2015) and Billet et al. (2015), except *Astrapotherium* and *Trigonostylops* (see Supplemental Appendices 3 and 6).

In character 271, a third state was added in order to capture the condition in *Eoastrapostylops* and in astrapotheres (i.e., very large postglenoid foramen). The character states are redefined as follow: Postglenoid foramen: (0) absent; (1) present, small, width less than one third the width of the postglenoid process; (2) present, large, width more than one third the width of the postglenoid process (modified from Wible et al. 2009: ch. 257; Muizon et al. 2015: ch. 271). *Maiorana*, *Baioconodon*, and *Arctocyonides* were scored as missing data because the size of the postglenoid foramen could not be compared based on the available literature.

```
#NEXUS
begin data;
dimensions ntax=25 nchar=513;
format missing=? symbols=”0~5”;
matrix

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???0?0???10??1000????101210010010000100111011000000 1??{01}000????0??01???111?01121200???
{23}????1100?0120001010300010000?01111000?021000000000010001{12}?{12}0000001111{12}00{01}1
000?0??00??100210101?010100010???????000?1000011100??????????????????????????????????????
?????????????000?????????0????00000000?0?????00??00?00??1?00?00000?000??0???????0?0??????
?0?
‘Zalambdalestes’
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02000002120111110210110 00?2001100??0200000100211131223121000001101010100{01}1000001102010
11111000?10000000110?1000100100000011{01}00101000001101110120011010?0000010100101 1{01}01?
111001111200011 3{02}0?11000{12}0111001210300010 1?00011110001 1?1100000000100111 1{01}000002
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?0???????000?0000010?
‘Leptictis’
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1021111122120111120002000000000211131221120000001201010100010000001120?011111000?121110011
1101010110001000021110000000010110001100000000011 02??0110101010100{12}11111102010012120101 1
10020210001101110000000000111100021?110011001?100001?100000210 0?111100000100110010021011??
010?111????00020111100000111 0?000101002110 02?00102200010210200211011 11210???00000000?????
????0????00000000?0?????00?000100001000001000000 0??0???????100010001100
‘Alcidedorbignya’
00130002110440000000000000010101011200012010220101001010??1202201011212221200201100221011 00
1111112120021011220002000001002101111110110010001100022010000010010112111211001110000000 0
0101000100001000011101 00{01}0001011011110000000011112??01010000010101111011010100021221001
00020210100101300100000?011100002 1?1000010001100000110000000101011010100011010001002121001
01001111001000201100101000110100000110201001100001210010111000011011001000000000 10000?????
????0????00000000?0?????00??0000000100000100000 0???0???????01000000{01}000
‘Protungulatum’
001???0???????????00?000??01010?12???1101022{01}111000010??1001100011212202210200000 22212
110102111201102102122000200000{01}00110111{12}1312000100{12}{12}0100010001000100102010111
1?????????????????????????????????????????????????????????????????????????????????{12}???
??????????????????????????????????00000?011?10?021?11??000??211??0{12}?{12}00000210101??
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01110120????????000?????????0????0?????00?0??????00????????????????????????????????0000??
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SUPPLEMENTAL APPENDIX 9

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‘Hyopsodus’

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00130?0210100000000000000011111001210011000220011000010??0{01}1121100121{12}{12}11200200?0
0222111111102112?{01}220210112{23}2002000{01}010021011222221000100{012}2010101?00000020011
10{01}011111100?1000000101100010110001100011101?0000000001000010001000?1?02??01101?110101{
01}2110111010100021221?0100020120000101100100000?0111000011?1101110000{01}00002??00000010
10{12}1011010????1?00?0020{12}10000?0??111?0?1?02001011100011111010101100?100210000121001
021120021101110100000000001000?????????0????{01}0?00100?0?????00?00?0?0001?000??000?00???0
???????0100?????0?0
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‘Meniscotherium’

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00110?02100440000000000000111110012011120002220111000011??0002211001{12}1112120020??1022211
111112122?0201210112321020000000011011222031?0??0002110111?00000020010102111211100?1{01}0
0000{01}011010001100011100120010000000001000110001000111000?01100?200001{01}2110111010100
0{12}122110100120220000101300100000?0111001011?1101000001100002??0000001010{12}001101???1
?1?00?0???2?0000?001111011100201111100101111101010111211002100001200000210000211011111200
0000001000?????????1????10000001?0?0???00?000200000000000000000???0???????0100?????100
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‘Phenacodus’

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00100?0211044000000000000101{01}1011200012100222011100011??0{012}0221{12}001101111200?0??
10222121111112122?0220210212321020000010021011222211000100020100{01}1?00?00020011101011211
100?1{01}00000?01101010110001100021101?00000{01}001000010000000010?110?011010210?011?110??
??10100?2122110100020210000101300100000?1111001011?110100000?1?0?02??{01}00000100?2100{01
}010????1?00?0?????0000?001111???10020111?1001011111010101012110121000022?001021?00021101
?112?0000000000000?????????1????00000?00?0??????00?000210010000000000?00???0???????0000????
?10?
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‘Pleuraspidotherium’

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00220?02101?000000?0000002110100{12}200112210222211100011??001{12}2110011111030020??1022
211111?10111?01112002121011211000001010122220321000001311001000000001200102020111111011100
000010???10??1???01100011??1000000000100010100000???010?010??001010002111001110100021221
011000102201011011100000000?011110?021?12011100011000001?0000001010100110???001?0010020{1
2}1??10?0011110????0?011??0100101111000???0010100110000121001111000020101100121???1000100
0?????????1????0???001?0?0?0?00?000?00?00000000000?000??0???????000000001000
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‘Maiorana’

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001???????????????????????111???012000110102102010000???????111000121120121020010022211101
10011120111210212210020000000001101201210110000???11??1??00??????????????1?111100?100110010
?1?101111000???0??11?0000000??11001?11000000?0?110?011000?001011?111??1010100?21221011000
102?0001101300100?00?00?100?0???110?00000110000???000000101011010000???01?00?0?????????0?0
?????????????????????????????????????????012100??11100??????????????????????000????????
?0????0????????????????????0??00??100000000000???0???????0?0?????????
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‘Baioconodon’

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001????????????????????????01???01200011000210201000010??100221000120221221020010112211101
10011120111210212210020000000002101201210110010?111000110000000200101010112111???1000?0000
????0?11100????0??11?100100010?0001??0?00?00???110??11?????0?011?111??1?10?????1201111000
?02?0001201300100000?011100?0???110?00000???00001?0000001010110{01}000???01?00?0???1???1
0?0????????????????????????????????????????????????????????????????????????????1?000?????
????0????????????00?0??????00??0????0??0?00?0000?000???0?????????0000000???
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‘Arctocyonides’

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001{01}0???2?00??000?0?????1?101010012001110002102100000?0??00011100112121103{13}120??0021
211111?0210000110210212210020001000011113122101000100211000010001000001110010112111031100
0000001101001110000100012101001000100101101000000010?010?0110?00001012?111001010100021221
101010201?00001011100000000?011100?01??110?0000011000001?00000010103111112???001?00?0?2????
011010???????????????????????????????????????????????????????????????????????0???000??
???????0????0??????00?0??????00?000000001?000000000001??0???????01010000000??
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‘Colbertia’

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00130?02100000000000100000111111012000120112201110000010??0200211011{12}1222120120000012212
111?00112?000?200212200021?11???0?1012222102001010?311??11000?0002101021111?111110?100000
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SUPPLEMENTAL APPENDIX 9

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0101??0????????00000{12}000100{01}000?001100?????????????1?00???????0?001?111??10?0111??1
110?01041?0220?????{12}?0001??00?????1100????????????????1??????????????????1?0?02??11????
????{12}??????1???????????????????1001100???????02110??????0220101111000?1101?101010000
000100111010?{01}00001000000000010000000000010??0000?000??000?10010??0????0?????????100
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'Plesiotypotherium'

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00321?{01}420?220?11?111?0???2?2???32?????011??0????00????????021???1????20????????????22??
???????1??{12}??????????????1??????????11222?????????0{12}31100100000000210102021111111??
12110000011010001{01}001?11000000100000000210?11110011011110000111{01}01111001211111010
11102111?0104110211?001?{12}?0001??00????1111??????????????0???1??????????0??0??21?{01}?010
2??11?101???02?0000?{01}111????????????????1110011100000???00111?01??00022011111100011012
1011001 2?????2?1?0???????00??02?01??0??3?0???000011010000000100100000100011111100?0???????
110
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'Protypotherium'

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0013010210122000100100010111111012000?2011??0????00010????2?{12}20?0?1????20????????????22?2
1??????1??2????????????????1??1???1?1011222?????1??00311??10000000021010201111111110?1{12}1
1000101101010 1{01}{01}0101000100 01?11001010210?000{12}10000???10000101??0111001{12}111111
010111?21110?0104110210?000?{12}?00010?00?11?111002??11??101?0???1?????10100??0??2101?010
2??11?10????121000 1?1111110??????01?1110000{01}11000???0?00211002??01122100{01}1110200111
01210101000000012?1?0???????100?10?02000110?0???010001012001000000010000100110?1??1111010??
???100
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'Adinotherium'

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001{01}00{01}2102220001001000001 11{12}10012000?2011??0????00011??121{12}2110?1????20?????
??????22?21??????1??1???2?0???200??1?10?1010101{12}222??????1?100311011000010002101020211 12
11110?120100000110101111??10010000102?000000001 10?010{12}000001??10000102001111001211111 1
010111021110?0104120210?1{01}0?{12}?00110?00?1??111102??1111???01??1?????10100??0??{12}1
?????02??11?10????02000?0?10111100?110001?{12}11111111000???0100111001??10022011101 1?200
1{12}10?2101?100001?0?11101001101000000?00010111?10111000000300000?01100010010?0011111000
0000?????100
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'Notostylops'

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00{12}2000{23}{12}1110110102100{01}??2{12}1{12}100{12}20001201122031100001 0??02102110
011112212012000001221{12}111?0010{02}?100?21021{12}200021?11???0?101222102001010{01}
{23}1101110100000200102 0{12}{01}11211100?1100000001100011 11001?0?001111100100000011 00?10{
12}01??????01?0010????1020012111??10101100?1{12}10?0104120210?1?0?{12}?00010?00?10111110?
??1????????0???1???????0?00??????20?1?0102??11?10????121000 0?1???????????????????????????????
??????????????????????????????????????????0010000?00101000?00000100000000010000000000000100
0000000000000100001100 1000?00?1111110?
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'Pyrotherium'

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00221?03300101111??1111??22?2????{23}2???????00{23}22011?00?????02?021?10122222 1????????002?
2???????2???????????????????{12}30{01}130?01?????111?222???????1???3101?120100000 2?0102021 1?21??
???01{01}??????????0???11??1?0?0000001001?????01000??0?111?????????0010??0?1???????1?1??1010
?11??1110???001??21{01}????0?{12}?00????????????????????????????????1????????????????????1?0?0
2??11??????????????????0111111??????11??0110101110 01????010100011?0001110110001201121 13210?
?0002000??00100??0????00?00000??0?0?????????00000??0????00???00001??0011????????????????????00
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'Miguelsoria'

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00????????????????????????????110012???1???0?2011100001 0??001120100121{12}2112012000011202
111?00101002202001122100200000000111011122102000100?301????000?00020????0111?21????????????
???????????????????????11?1000000???1??1??0?0?????????????????????????2??????????????????????
?????????????????????01000?001?00?011?1000000??2?1?00011000000100?1?????????????????????12100?
0?????????????????????????????????????????????????2221011021010021 10??101?1?????????000?????
????0????1?????00?0?????00???????????????????????????????????010{01}1000{01}??1
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'Proterotheriidae'

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00120?022??120?1102100010?2?11001201012210222111100010??021{12}2111111{01}1{12}1120020001
01121{12}11??101020222020011221013000000011101122220100110002010110000000002?0102011111110
1??{01}{01}00000?0010100011000?10002?10{12}000?0000010010?0000000???{12}001110??0??110112
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SUPPLEMENTAL APPENDIX 9

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110??10100??0?1220?1100020210000101?00101000?0011001011?10000000021100001??00000100?11011
01????01??0????12100?0?0??????????0??11?110011111000??????0211?11??001221011021?2002{12}1
0?210200???01???001?????????1????0000101100?0?0?00?0000000000000??000100???0???????010111
201101
'Macrauchenia'
00130?12100220000?0000000111110012010??010222111100000??011{12}211101???20?10??0?1?112?1
1???1010??2?????????2?0??0?001101110112222010011002301010000000002100221011111???0??20?01
0?0???10??????0?1000?1?01010000001100???????????11{12}0?11?????????10121?0??111?0????1220
?11001?021000?1?{12}?00100?00??01100101??1100000??1?1000???000000100?{12}101101????01????
????2000?0??????????????011?1100110110011011101111011??111221000011?1002110221021{01}0000
0001111?????????1?????1000111???0?0?00?001?001?0?00???000100???0???????01011{12}201101
'Trigonostylops'
00121?0?1?????????0100?10?01010112?0112211222111000011??0211212001{12}2222120120?00012212
111?001100000?210112200021001???0?101222220200100000?0101110000000??01020{01}11121?????000
???????1??0110100????0011111001??????100?111100110????100?1001?11?1011?111??10100??021110
?01000?022???00?{12}?00??????????????????????????????0??????????0???????100102??01?00????
??????0?0????????????????????????????????????????????????????????????????????????????1000
{01}00??0???000???0000000100?0?0?000?01??0??0100?00001001???0???????????????10?
'Astrapotherium'
003210051???4?????0100010?01010132????2011?20111?00????????{12}20??11????20???????0012212
11??0011??1???2?0??{12}2?0001?1??????101{23}222???0?100???01011000000002101020?111210?10?
0{12}01010?0?1?101????000100?100??010000?01{01}0???0?????????{12}1?00??????11?0112111??1
0100??0?1110?010002022???000{12}?00100001?1011101011?1000000?02??0?0???10000??0??{12}1?10
01????01??0????1200001?001?11101??02?1?001101101100000?0??00?0??11000022011?1110???1110??
112????????1011100?00???000?00?010001100?0?0?00?0002?0??1?0001?001001???0???????000?01201
100
'Eoastrapostylops'
00130??????????????0?0?0??01010112000121112221111000010??1001210{01}1122{12}22220120?00012
212111?001100000?2101122000?1001???0?101{02}12210{01}00110??1000021?100000??01020211121??
???10?11?????1?????????????0?1??????1?00??01010?????????????1000?????????0??211???1?10???
0?1220??1001?022110010??0??00?????1??00?011?100000000110000???100000?010?????????1?01????
??????01?0?0???????????????????????????0???????????????0????????????????????????????????1
000000??0???00????00?0??0000?0?0?00??0???0??0?00???0000????????????000????????0?
'Carodnia'
00110?0?1???4???0?0100010?0101011200012000220111000010??0100200111222221???????002?2?????
?2??????????????{12}3?00??01??????111?121002???10???100022010000021010212{01}1121????????
?????????????????????0????????1??????1???????????????????????????????????1???????????????
????????2????????????????????????????????????????????????????????????1?1?????????????????
??????0111100???0??1???11101011110001??10??1?001?0002100111010200221 0?200120?????01000100
???????00?00001000000??0?0?00?????????????????????0?????????????????????00
;
end;

ctype ord: 3 8 9 22 27 29 33 36 43 44 59 60 63 66 67 68 69 70 72 73 76 79 85 86 97 104 108 110 111 116 120 125 126 127 130 137
138 143 144 157 159 163 166 171 173 196 197 203 209 210 227 238 242 257 271 301 326 349 368 392 402 403 404 416 417 424 425
429 435 451 454 473 474 503 ;

begin trees ;
tree tnt_1 = [&U]
(1,(2,(3,(5,((4,(10,11)),(12,(9,((6,(7,8)),((24,(((13,(17,(16,(14,15)))),(18,25)),(22,23))),(19,(20,21)))))))))));

end ;
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