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New Jurassic Mammals from Patagonia, Argentina: A Reappraisal of Australosphenidan Morphology and Interrelationships

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ABSTRACT

A new mammal, *Henosferus molus*, n.gen. and n.sp., from the Callovian–Oxfordian (latest Middle to earliest Late Jurassic) Cañadón Asfalto Formation from Chubut Province (Argentina) is described. This taxon corresponds to a new species clearly different from *Asfaltomylos patagonicus* from the same locality and stratigraphic level. This new species is based on three lower jaws with relatively well-preserved dentition. The lower jaw shows a primitive morphology having a Meckelian groove, a prominent medial flange associated with a lateral ridge of the dentary, and a deep dentary trough, which possibly indicates the presence, even though reduced, of postdentary bones still attached to the dentary. The lower dental formula is i4, c1, p5, m3. The premolars are simple, bearing a main cusp, while the molars appear to be tribosphenic, with an obtuse to right-angled trigonid and a basined talonid with three cusps. This association of plesiomorphic features in the jaw and derived features in the molars is documented in several taxa of the recently proposed Australosphenida. A phylogenetic analysis of mammaliaforms nests the new species with *Asfaltomylos* from the same locality and stratigraphic level; Henosferidae, new family, is recognized for *Asfaltomylos* and *Henosferus*, representing the basal radiation of Australosphenida. Henosferidae is the sister group to *Ambondro* from the Middle Jurassic of Madagascar, which, in agreement with previous phylogenies, is the sister taxon to the remaining australosphenidans. Additionally, our phylogenetic analysis does not support

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the inclusion of australosphenidans within eutherians. Henosferids likely retained some connection of the postdentary elements with the dentary; therefore, if the inclusion of Monotremata within Australosphenida is confirmed, final freeing of the postdentary elements and development of a triossicular middle ear would be convergent events in Monotremata and Theria. Finally, the distinctiveness of the yet sparse South American record of Jurassic mammals when compared with the slightly better documented Cretaceous data is emphasized. The clear faunistic break between the Middle Jurassic and Early/Late Cretaceous underlies our rudimentary understanding of the evolution of Mesozoic mammals in Gondwana.

INTRODUCTION

The record of Jurassic mammaliaforms from Gondwana is restricted to a few localities from Africa, Madagascar, and South America, where their known diversity and abundance are, as yet, much lower than those of boreal landmasses (Bonaparte, 1986a, 1990, 1995; Bonaparte and Kielan-Jaworowska, 1987; Luo et al., 2002; Kielan-Jaworowska et al., 2004). *Megazostrodon rudnerae* and *Erythrotherium parringtoni* (Crompton and Jenkins, 1968, 1979; Crompton, 1974; Jenkins and Parrington, 1976; Gow, 1986) are the only relatively complete Gondwanan mammaliaforms from the Early Jurassic (Stormberg Group of Lesotho and South Africa). Isolated teeth from the likely Early Jurassic of India are suggestive of a large diversity of "triconodontid" and "symmetrodont" animals, but their incomplete nature makes them difficult to integrate into more general interpretations of the early diversification of the mammalian lineage (Datta et al., 1978; Datta, 1981; Yadagiri, 1984, 1985; Datta and Das, 1996; Prasad and Manhas, 1997, 2002).

On the other hand, the Gondwanan latest Middle through Late Jurassic shows a relatively greater diversity of mammaliaforms, including the archaic "triconodont" *Tendagurodon janenschi* (Heinrich, 1998), the first occurrence of cladotherians *Brancatherulum tendagurense* and *Tendagurutherium dietrichi* (Branca, 1916; Dietrich, 1927; Simpson, 1928a; Prothero, 1981; Heinrich, 1998), and the probable haramiyid *Staffia aenigmatica* (Heinrich, 1999, 2001) from the Late Jurassic Tendaguru beds (Tanzania). Tribosphenic-like forms are represented by the Middle Jurassic *Ambondro mahabo* (Flynn et al., 1999) from the Isalo III levels of Mahajanga Basin, Madagascar, and *Asfaltomylos patagonicus* from the latest Middle to earliest Late Jurassic Cañadón Asfalto Formation, Chubut Province, Argentina (Rauhut et al., 2002; Martin and Rauhut, 2005).

Asfaltomylos patagonicus represents the only *bona fide* mammaliaform hitherto known from the South American Jurassic (Rauhut et al., 2002; Martin and Rauhut, 2005). The ichnospecies *Ameghinichnus pataganicus* from the Middle Jurassic La Matilde Formation (Chubut, Argentina) has traditionally (Casamiquela, 1961, 1964; Bonaparte, 1978; Kielan-Jaworowska and Gambaryan, 1994) been interpreted as representing a mammal (or mammaliaform). In addition, *Brasilichnium elusivum* and an unnamed ichotaxon from the lower Jurassic Botucatu Formation (São Paulo, Brazil; Leonardi, 1994; Rainforth and Lockley, 1996) have also been regarded as mammals, but the systematic status of these species is uncentain.

The Cretaceous record of mammaliaforms in Gondwana is incomplete, but relatively more diverse and abundant than that from older rocks. Mammals or close relatives have been described from the Early Cretaceous of Australia (Archer et al., 1985; Flannery et al., 1995; Rich et al., 1997, 1999a, 2001a,b, 2002; Rich and Vickers-Rich, 2004), Morocco (Sigogneau-Russell, 1991a,b, 1995, 2003; Sigogneau-Russell and Ensom, 1998), Cameroon (Brunet et al., 1988, 1990; Jacobs et al., 1988), and probably Tanzania (Krause et al., 2003), and from the Late Cretaceous of Madagascar (Krause et al., 1994; Krause and Grine, 1996; Krause, 2001) and India (Prasad and Sahni, 1988; Prasad et al., 1994; Prasad and Godinot, 1994; Anantharaman and Das Sarma, 1997; Krause et al., 1997). In South America, the diversity of mammaliaforms is relatively better known than in the rest of Gondwana; they have been discovered in the Early and Late Cretaceous of Argentina (Bonaparte, 1986a, 1990, 1994, 1995, 2002; Bonaparte and Rougier, 1987; Pascual et al., 2000) and in the Late Cretaceous of Brazil

(Bertini et al., 1993) and Bolivia (Gayet et al., 2001). Among these finds, several taxa are based on fragmentary and isolated elements that result in a uncertain taxonomic position for many of them. Moreover, some of these remains show a peculiar combination of characters that has opened new questions about the evolutionary history of mammalian features. A wealth of new materials has recently been reported on briefly from a variety of Cretaceous formations from Patagonia, Argentina (e.g., Rougier et al., 2003a) that span a wide geographical, temporal, and systematic range. These new specimens will enrich the material basis for discussion of the faunal changes in the late Mesozoic of South America and of Gondwana in general.

The discovery of taxa interpreted as having a tribosphenic molar pattern, in some cases associated with primitive mandibular features in the Middle Jurassic of Madagascar (Flynn et al., 1999) and Argentina (Rauhut et al., 2002; Martin and Rauhut, 2005) and the Early Cretaceous of Australia (Archer et al., 1985; Rich et al., 1997, 1999a, 2001a, b), has led to the postulation of a diphyletic acquisition of the tribosphenic molar pattern (Luo et al., 2001a, 2002). The core of this new interpretation is that the tribosphenic molar pattern evolved in two distinctive lineages, named Australosphenida and Boreosphenida by Luo et al. (2001a, 2002); this view has been supported by new findings (Rauhut et al., 2002; Martin and Rauhut, 2005). The gondwanan clade Australosphenida would have acquired a molar pattern functionally equivalent to the tribosphenic molar as defined by Simpson (1936) independently from the Laurasian clade Boreosphenida, defined by *sensu stricto* tribosphenic dentitions. McKenna (1975) defined the formal name Tribosphenida to "reflect the view that their [i.e., eutherians and marsupials] acquisition of a protocone is synapomorphous and is meant to be the cladistic taxonomic equivalent of Simpson's (1936: 8) descriptive term tribosphenic" (McKenna, 1975: 27). Under the new interpretation of the "dual origin of tribosphenic mammals", Boreosphenida and Tribosphenida are equivalents (Kielan-Jaworowska et al., 2004). Australosphenida not only includes *Asfaltamylos*, *Ambondro*, *Ausktribosphenos*, and *Bishops* but also Monotremata as well (Luo et al., 2001a, 2002; Rauhut et al., 2002; Martin and Rauhut, 2005). This hypothesis of inclusion of monotremes within Australosphenida was critized by some (e.g., Rich et al., 2002; Woodburne, 2003; Woodburne et al., 2003) who alternatively suggested that australosphenidans (excluding Monotremata) are a monophyletic group, although these authors placed it close to, or inside, Placentalia. Under this hypothesis of a restricted, mostly Mesozoic Australosphenida (i.e., excluding Monotremata), monotremes would be basal to Multituberculata plus Zatheria (Woodburne et al., 2003). In short, under both competing hypotheses there is a clade of Mesozoic gondwanan mammals that can be dubbed Australosphenida; its various phylogenetic positions (nested inside Eutheria, forming a monophyletic group together with Monotremata, or anywhere in between) are still controversial.

In this contribution, we report new Jurassic mammalian specimens from South America discovered during several field seasons carried out jointly by staff of the University of Louisville, American Museum of Natural History, and Museo Paleontológico "Egidio Feruglio" during 2002–2004 at the Queso Rallado locality (fig. 1), Cañadón Asfalto Formation (Callovian-Oxfordian; Tasch and Volkheimer, 1970), Chubut Province, Argentina. The new mammalian taxon is based on three isolated lower dentaries with much of the dentition, which provide new information about the complex interplay between jaw and molar morphology occurring during the Jurassic in western Gondwana (Forasiepi et al., 2004a,b).

INSTITUTIONAL ABBREVIATIONS: **AMNH**: American Museum of Natural History, New York, USA; **MPEF**: Museo Paleontológico Egidio Feruglio, Trelew, Argentina.

GEOLOGICAL SETTING

The Cañadón Asfalto Formation (Stipanicic et al., 1968) combines a series of calcareous, silicoclastic, and volcanic deposits developed during the rifting of the Golfo San Jorge Basin, as a consequence of the opening of the South Atlantic Ocean (Figari and

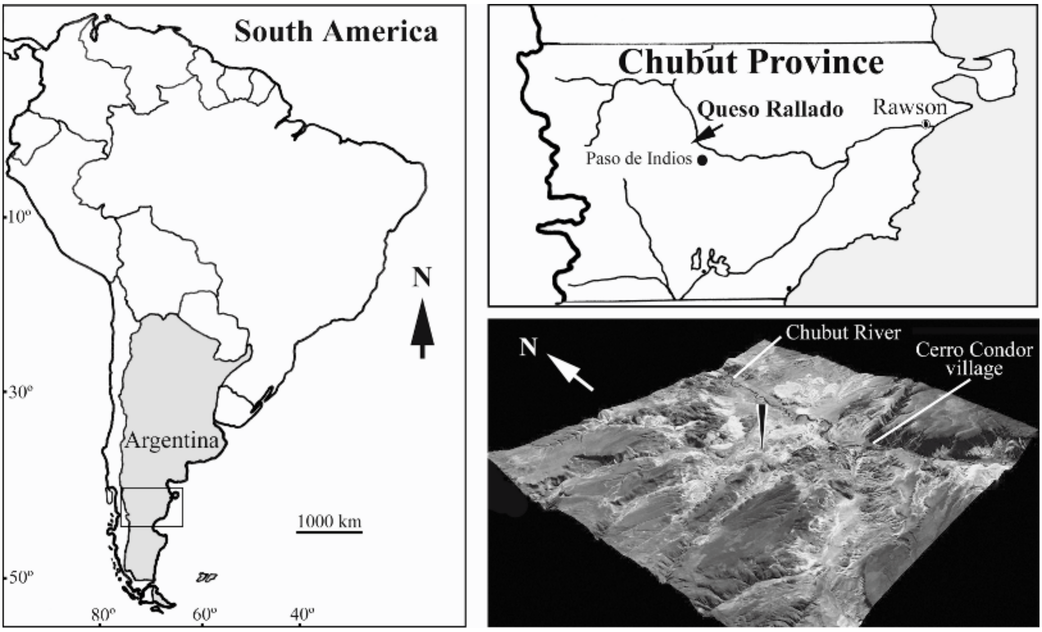

Fig. 1. Location map of Queso Rallado Locality where the specimens of *Henosferus molus* were found, Chubut Province, Argentina. The black and white arrow indicates the locality of Queso Rallado in the topographic map.

Courtade, 1993). The holotype section of the formation is located on the west-southwestern slope of the Chubut River, between the Cañadón Asfalto and the Estancia Berwyn localities (Stipanicic et al., 1968). In the vicinity of Cerro Cóndor, the Cañadón Asfalto Formation is widely exposed, with a maximum thickness of approximately 450 m. The lithological variation exhibited in the area of study allowed recognition of a lower and an upper section.

The lower section of the Cañadón Asfalto Formation is approximately 180 m thick, corresponding to the Las Chacritas Member of Silva Nieto et al. (2003). These levels are composed of carbonatic deposits and biohermal bodies developed over lacustrine basins. The sporadic intercalation of basaltic flows, pyroclastic sediments, and mudflows indicate the presence of a contemporaneous but intermittent vulcanism (A.C. Garrido, personal communication). The upper section of the sequence is approximately 270 m thick, corresponding to the Puesto Almada Member (Silva Nieto et al., 2003). It is characterized by the association of sandstones, calcareous limestones, and a small conglomeratic lens, intercalated by thin layers of tuff, tuffites, limestones, and evaporitic rocks. This sedimentary sequence suggests the presence of an ephemeral meandering fluvial system developed over an alluvial floodplain associated with small, shallow, and transient lacustrine bodies; sporadic ash rains would provide the pyroclastic material. The passage from the lower to the upper member of the Cañadón Asfalto Formation is transitional, with a conspicuous transgression from the fluvial system in the northwest of the basin to the lacustrine system in the area of Cerro Cóndor (A.C. Garrido, personal communication).

The three specimens of the new mammal species studied here were collected at the locality of Queso Rallado (fig. 1), in the uppermost part of the section exposed in the area of Cerro Cóndor, at levels corresponding to the upper part of the Puesto Almada Member (*sensu* A.C. Garrido, personal communication, *contra* Martin and Rauhut, 2005). The fossiliferous level is 0.80 m thick, principally formed by thin, laminated carbonatic deposits, intercalated by tuffs and opals. These deposits would have originated in a small, shallow, and ephemeral lacustrine body located between the coastal sector of the lacustrine basin and the alluvial floodplain of the fluvial system (A.C. Garrido, personal communication).

The Cañadón Asfalto Formation has yielded a large variety of vertebrates. Among them, and besides the already mentioned *Asfaltamylos patagonicus*, are the sauropods *Patagosaurus fariasi* Bonaparte 1979, *Volkheimaria chubutensis* Bonaparte 1979, and *Tehuelchesaurus benitezii* Rich et al. 1999b, and the theropods *Piatnitzkysaurus floresi* Bonaparte 1979 and *Condorraptor currumili* Rauhut, 2005 (Bonaparte, 1979, 1986b; Rich et al. 1999b; Rauhut et al., 2002; Rauhut, 2003, 2005). Additionally, recent fieldwork in the area has also provided fishes, anurans, turtles, lepidosaurs, crocodyliforms, pterosaurs, and new dinosaur remains (see also Rauhut and Puerta, 2001; Rauhut et al., 2001; Martin and Rauhut, 2005).

SYSTEMATIC PALEONTOLOGY

MAMMALIA LINNAEUS, 1758

AUSTRALOSPHENIDA LUO, CIFELLI AND KIELAN-JAWOROWSKA, 2001a

FAMILY HENOSFERIDAE, NEW FAMILY

FAMILIAR DEFINITION: Henosferidae is the clade including the most recent common ancestor of *Henosferus* and *Asfaltomylos* and all its descendants.

Henosferus, new genus

ETYMOLOGY: From the Greek *henos* (old) and from the Latin *ferus* (animal).

HOLOTYPE AND ONLY KNOWN SPECIES: *Henosferus molus*.

DIAGNOSIS: This new taxon is diagnosed by the combination of the following characters (autapomorphic traits are indicated with an asterisk): lower dental formula consisting of i4, c1, p5, m3; variously developed diastemata between most premolars; molars with an obtuse to right-angled trigonid and a basined talonid with two well-developed cusps and a ridgelike structure in the position of entoconid/entocristid; procumbent paraconid in a more labial position than the metaconid; talonid slightly wider and much lower than trigonid; talonid wider than long; blunt prominent hypoconid cusp not fully differentiated from broad, bulbous hypoconulid connected by a broad, low crest (hypocristid); talonid lingually closed by a strong rounded entocristid, well-developed lingually*; lack of talonid wear; slender lower jaw having a Meckelian groove, a prominent medial flange associated with a lateral ridge of the dentary, and a deep dentary trough (possibly indicating presence, even though reduced, of postdentary bones still attached to dentary); and prominent, transversely wide, spoonlike angular process with a medial crest occupying a position homologous to pterygoid crest of other mammals*.

Henosferus molus, new species

ETYMOLOGY: From the Latin *mola*, meaning millstone in reference to the well-developed talonid of the lower molars.

DIAGNOSIS: As for the genus, for monotypic attribution.

HOLOTYPE: MPEF 2353: Right lower jaw with the dentary well preserved, bearing the distal half of p1 and p2, and almost complete m1 (fig. 2). The posterior portion of the dentary shows a deep trough and a medial flange; it also bears a deep and small coronoid facet, a remarkable Meckelian groove, and a transversely wide angular process. This specimen is chosen as the holotype because it preserves an almost complete molar that bears numerous diagnostic features, making it possible to compare with most other Mesozoic mammals.

HYPODIGM: MPEF 2354: Left lower jaw bearing the roots of the first and second incisors, the broken crown of the third and fourth incisors, a complete canine, five premolars, and three damaged molars (fig. 3). Behind the level of the coronoid process, the dentary is partially broken and preserved mostly as a natural cast of the medial aspect. MPEF 2357: Left lower jaw exposed in labial view preserving the canine, four premolars, and a molar with the trigonid mostly damaged (fig. 4). Floating in the matrix near the jaw are two teeth here identified as p1 and m2 (not shown in figures). The p1 is complete but the m2 is missing the protoconid and a small

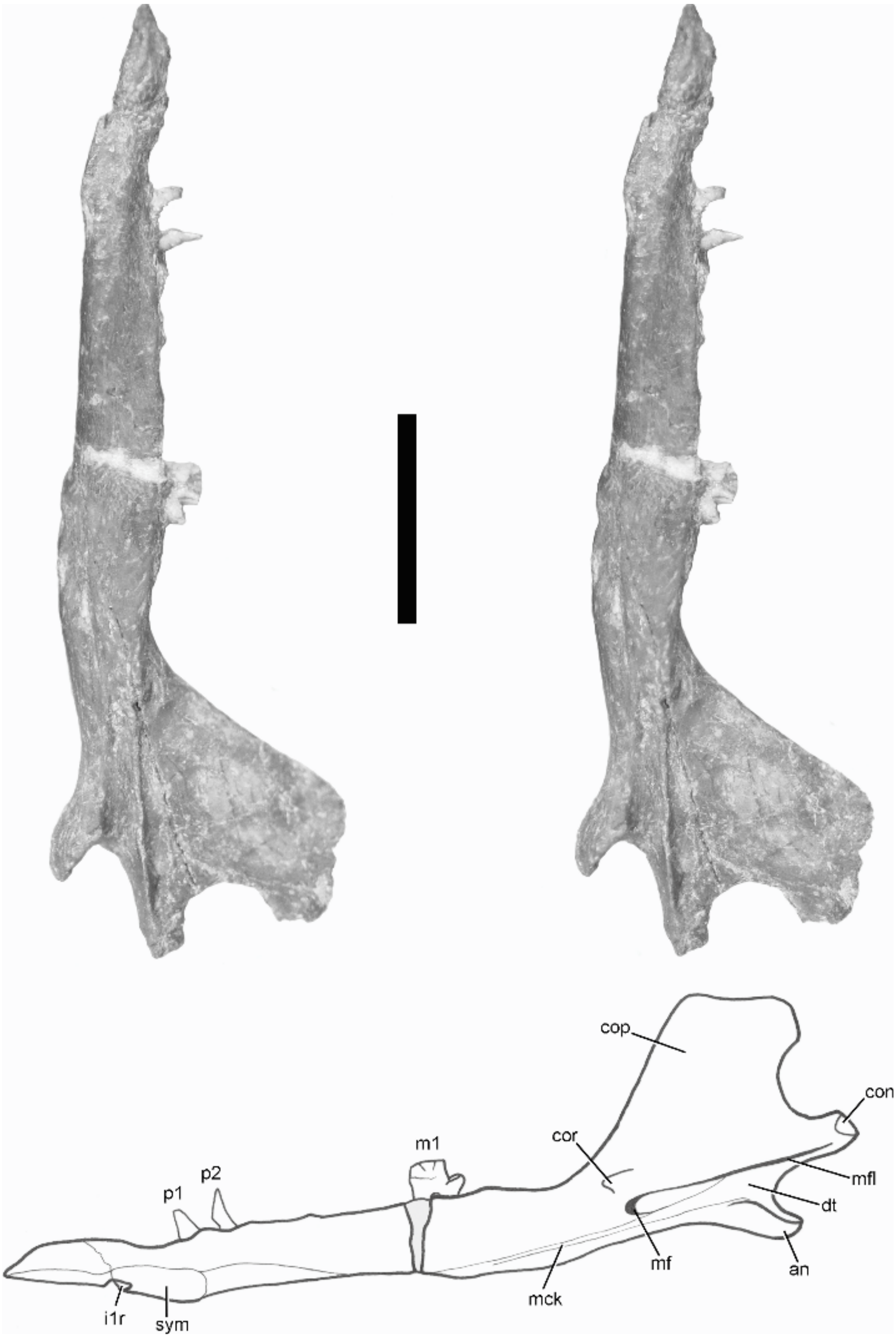

Fig. 2. *Henosferus molus* holotype MEFP 2353. Stereophotograph of the right lower jaw in lingual view and accompanying line drawing. Gray pattern indicates broken bone and matrix. Scale bar is 5 mm. Abbreviations: an = angular process; con = condyle; cop = coronoid process; cor = scar for the paradentary coronoid bone; dt = dentary trough; i1r = root of the lower first incisor; m1 = lower first molar; mck = Meckelian groove; mf = mandibular foramen; mfl = medial flange; p1 = lower first premolar; p2 = lower second premolar; sym = mandibular symphysis. The p1 and p2 are broken, preserving only the distal halves of their crowns; the premolars appear thus to be like single-rooted but they are in fact double-rooted.

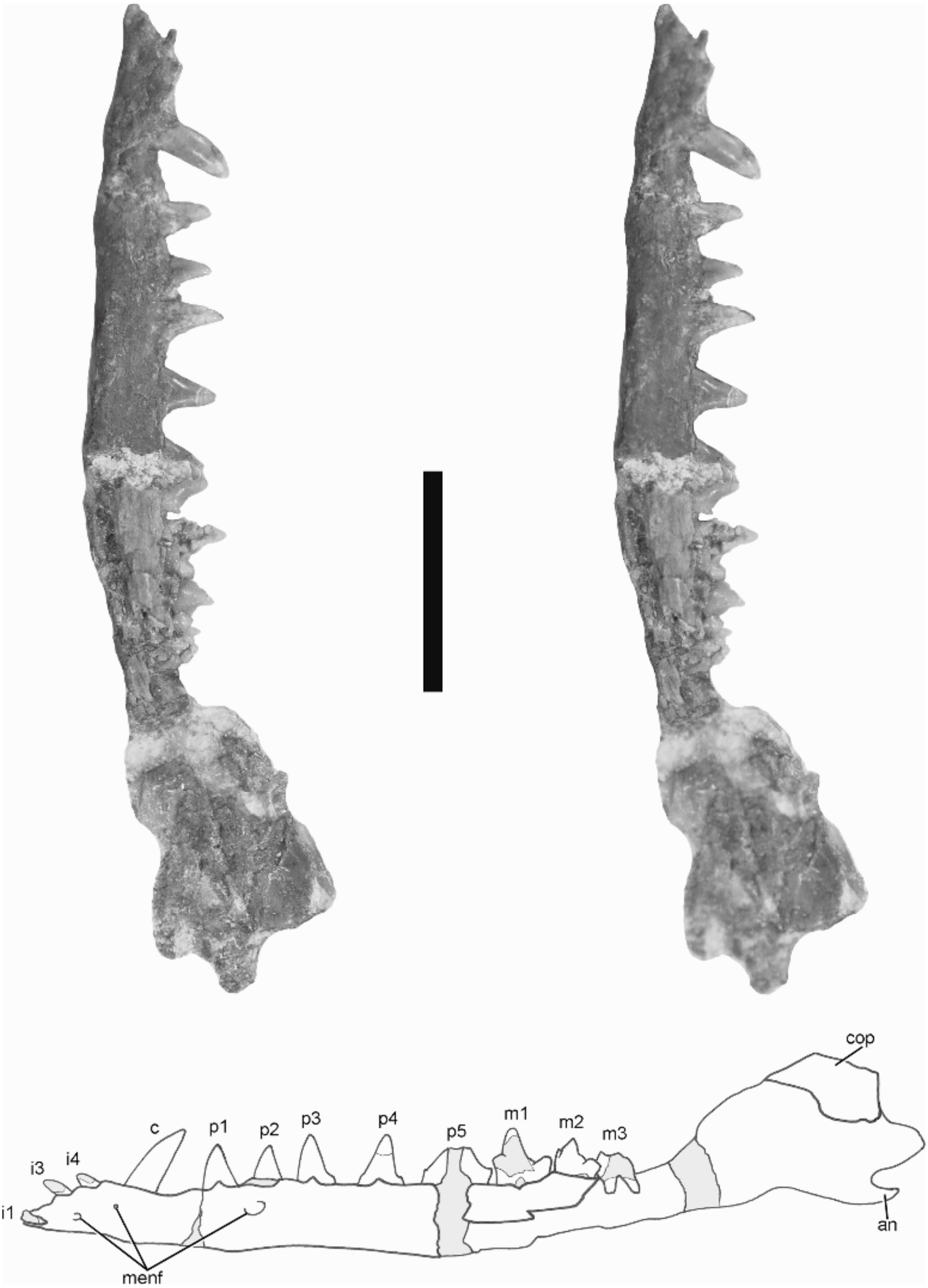

Fig. 3. *Henosferus molus* referred specimen MEFP 2354. Stereophotograph of the left lower jaw in labial view and accompanying line drawing. Gray pattern indicates broken bone and matrix. Scale bar is 5 mm. Abbreviations: an = angular process; c = lower canine; cop = coronoid process; menf = mental foramina; i1= lower first incisor; i3 = lower third incisor; i4 = lower fourth incisor; p1 = lower first premolar; p2 = lower second premolar; p3 = lower third premolar; p4 = lower fourth premolar; p5 = lower fifth premolar; m1 = lower first molar; m2 = lower second molar; m3 = lower third molar.

portion of the talonid. The posterior part of the dentary is complete, adding information on the lateral view of the jaw not accessible in the other specimens.

Tentatively Referred Specimen: MPEF 2355: isolated upper premolar enclosed in a small block, which also includes indeterminate fragments of bone (not figured).

Locality and Horizon: All specimens come from the Queso Rallado locality (43°24′33.55″S/69°13′50.1″W), about 3 mi west-northwest of the village of Cerro Condor, Chubut Province, Argentina (fig. 1); Puesto Almada Member (Silva Nieto et al., 2003), Cañadón Asfalto Formation, Callovian-Oxfordian (Stipanicic et al., 1968; Tasch and Volkheimer, 1970).

DESCRIPTION

This contribution is based on three mandibular specimens and a possible upper premolariform. The holotype MPEF 2353 (fig. 2) consists of a right lower jaw with the dentary exceptionally well preserved but fractured at the level of the symphysis and the m1, where it slightly bends ventrally. The jaw also bears the distal halves of the crowns of p1 and p2 and a fairly complete m1. The lateral surface of this specimen, with the exception of m1, is still embedded in the limestone matrix. The specimen MPEF 2354 (fig. 3) consists of a left lower jaw with the horizontal ramus of the dentary well preserved, but the posterior portion of the dentary heavily damaged. Most dental elements are represented, but all of the molars have sustained extensive damage, thereby hampering their interpretation. The lingual side of the dentary and the teeth, excepting p5 and the molars, are still embedded in the matrix. The specimen MPEF 2357 (fig. 4) is a left lower jaw preserving the canine, four premolars, and a molar. In the same fragment of rock, an isolated premolar is preserved (fig. 4) approximately 5 mm from the dentary; this tooth would correspond to the p1, because it is the only premolar missing on the jaw and agrees with the morphology of the specimen MPEF 2354. The m2 is preserved on a separate little block, but is damaged, adding little to the known morphology of the molars. The dentary is well preserved, in particular the angular region, adding information on the labial view of the coronoid process and masseteric fossa that is missing, or not accessible, on the other specimens.

The specimen MPEF 2354 is slightly larger, with longer diastemata, than the holotype and MPEF 2357, both of which are subequal in length and tooth spacing. These differences are unlikely to be caused by age difference because the holotype shows the m1 more worn than in MPEF 2354 and 2357, suggesting a relatively older individual age; small discrepancies in tooth size, robustness, etc. are interpreted here as within the normal range of intraspecific variation, which likely accounts for the differences. The size of *Henosfenus* is relatively large by Mesozoic standards, about twice as large as *Asfaltomylos* (Rauhut et al., 2002; Martin and Rauhut, 2005) from the same locality and stratigraphic level. Measurements of the specimens are listed in appendix 1.

Lower Jaw: The holotype and the referred specimens have a well-preserved dentary morphology, providing several features relating to an understanding of the evolution of the mammalian middle ear (see Discussion). The default specimen used to describe the jaw is the holotype (figs. 2, 5); discordant or accessory information provided by the hypodigm is noted.

The horizontal ramus of the dentary is low and elongated with the alveolar and ventral edges almost parallel. In cross section, the labial surface of the dentary is convex while the lingual is almost flat (in specimen MPEF 2357, the labial surface is somewhat concave, especially below the molar area, but this feature appears to be related to deformation). The minimum depth of the lower jaw is located at the level of the posterior diastema of the canine, clearly shown in MPEF 2354. The incisor alveolar border is facing anterodorsally, intersecting obliquely the ventral edge in the most anterior point of the dentary.

In labial view of MPEF 2354, the wall of the i1 alveolus is partially broken, exposing the root of this incisor. An interdental process between the incisors is clearly observable. Both the holotype and MPEF 2357 show four somewhat damaged incisor alveoli. The alveolar borders of the cheek teeth of the holotype

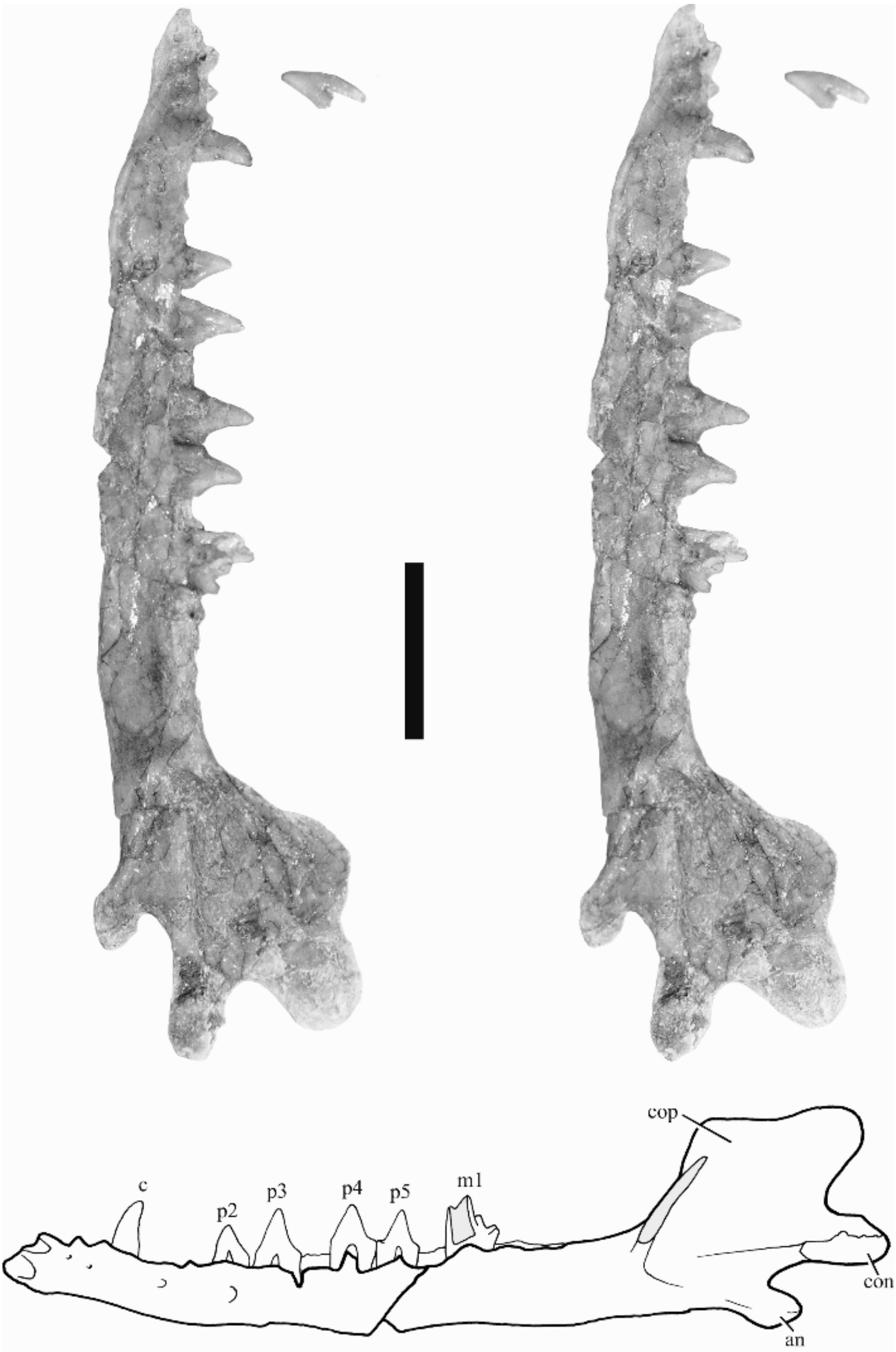

Fig. 4. *Henosferus molus* referred specimen MEFP 2357. Stereophotograph of the left lower jaw in labial view and accompanying line drawing. The isolated premolar in the stereophotograph corresponds to p1 of the same specimen. Gray pattern indicates broken bone and matrix. Scale bar is 5 mm. Abbreviations: an = angular process; c = lower canine; con = condyle; cop = coronoid process; p2 = lower second premolar; p3 = lower third premolar; p4 = lower fourth premolar; p5 = lower fifth premolar; m1 = lower first molar.

and MPEF 2354 are well preserved. The p1, p3, and p4 have sharp interadicular processes (still covered by rock in the p2) that are taller than the interdental processes. In all of the specimens of *Henosferus*, the labial alveolar edge is set below the level of the lingual alveolar edge. There are four mental foramina in MPEF 2354 and 2357, with little variation in their positions (figs. 3, 4). The anteriormost foramen is located below the i3–i4 diastema, near the ventral edge; the second one is located below the mesial border of the canine or slightly in front of it; the third one is found under the diastema between the canine and the p1. All three foramina are small, with some variation in their relative sizes. The fourth, located below the anterior root of the p2, is the largest. All of the anterior mental foramina face anteriorly, but the fourth foramen seems to face laterodorsally; we believe its ventral edge, which is formed by a thick ventral rim, to be natural, but it could also be caused by postmortem deformation. The labial view of the posterior portion of the jaw is available only in MPEF 2357. The coronoid process is well developed, twice as high as the horizontal ramus. The anterior border is straight, with a thick coronoid crest. The coronoid process, as determined by its anterior edge, is inclined posteriorly 115° with respect to a horizontal alveolar edge. The dorsal border was probably straight (as suggested by the medial view in the holotype), although slight damage in MPEF 2357 gives it the appearance of being dorsally concave. The posterior border of the coronoid process parallels the anterior border to the level of the pedicle of the condyle. The most conspicuous feature in labial view is the development of the lateral ridge of the dentary (fig. 4); this ridge extends horizontally from the level of the condyle to the anterior base of the coronoid process, forming the ventral edge of a distinct masseteric fossa (although the masseter muscle probably extended beyond this crest into the flatter area ventral to the ridge). The lateral ridge is a blunt and relatively robust crest, equally developed along the entire preserved portion. A small section of the crest is missing immediately in front of the condyle; however, we believe it is clear that the lateral ridge was confluent with the pedicle of the condyle, as seen, for example, in *Morganucodon* (Kermack et al., 1973), and the lack of connection is artificial. The anterior extension of the ridge is distorted by a low, round depression, probably an artifact. The crest seems to become weaker anteriorly and probably reached the anterior margin of the masseteric fossa, showing once more a condition not dissimilar to that of *Morganucodon* (Kermack et al., 1973, 1981; Crompton and Luo, 1993) and other basal mammaliaforms (Crompton, 1974; Jenkins et al., 1983; Gow, 1986; Lillegraven and Krusat, 1991). The bulk of the masseteric fossa is dorsal to the lateral ridge (i.e., it is restricted to the dorsal area of the coronoid process, about the level of the alveolar margin) and could correspond with the attachment of the portion of the masseter mucle identified by Turnbull (1970) as M. zigomaticomandibularis. The dorsal portion of the masseteric fossa is relatively deep, roughly rectangular in shape, with shallow horizontal scars for muscular attachment. This fossa, probably associated with portions of the temporalis muscle group (Turnbull, 1970), is deeper in the area immediately in contact with the lateral ridge and does not extend ventrally to it. The surface below the lateral ridge, ventrally bordered by the massseteric crest (see below), which becomes more distinct posteroventrally, probably served for the attachment of a small portion of the masseter muscle. No masseteric foramen is recognized in *Henosferus*.

The general features of the angular process are described in detail under the medial view (figs. 2, 5); particular features of the labial aspect include the masseteric crest and the concave surface between the angular process and the bottom of the condylar pedicle. The masseteric crest is developed on the ventral border of the angular process; it is blunt but becomes more distinct posteriorly and protrudes laterally more pronouncedly. Coupled with the larger development of the masseteric crest is the deepening of the portion of the dentary immediately below the lateral ridge; these combined factors result in a progressively more concave surface for the dentary in the vicinity of the angular notch. The development of a concave surface between the angular process and the lateral ridge is also found

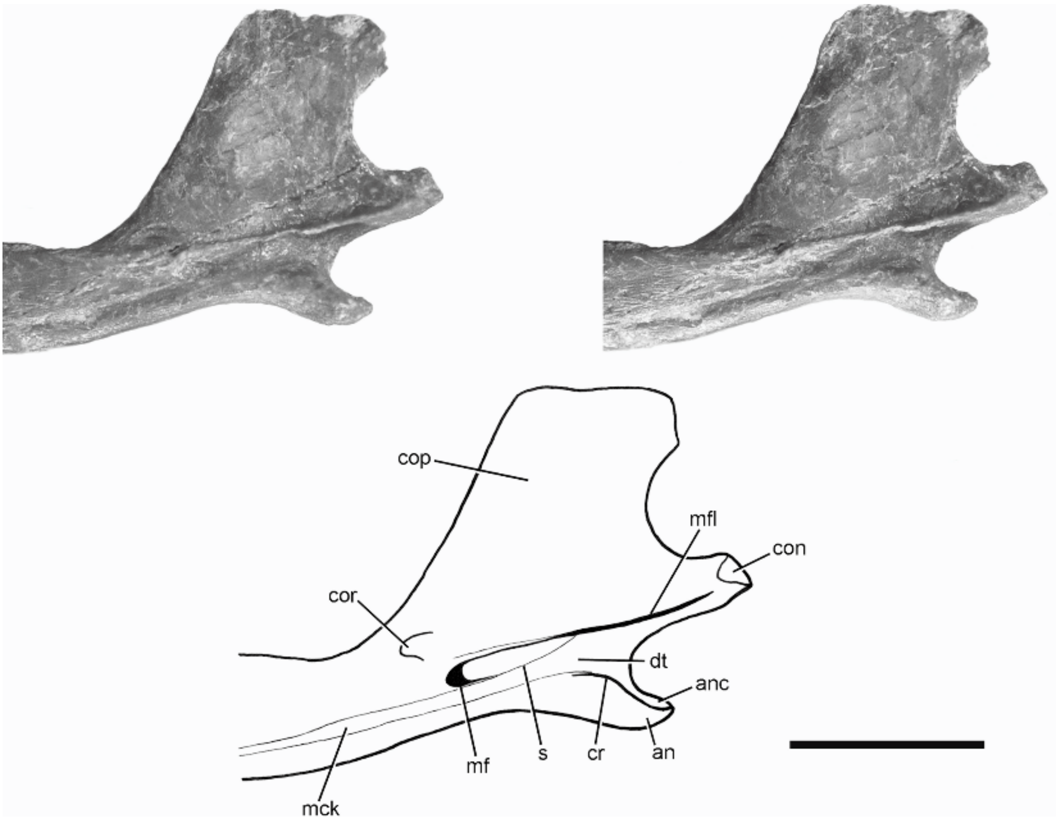

Fig. 5. *Henosferus molus* holotype MEFP 2353. Stereophotograph of the posterior portion of the right lower jaw in lingual view and accompanying line drawing. Scale bar represents 5 mm. Abbreviations: an = angular process; anc = concave surface of the angular process; con = condyle; cop = coronoid process; cor = scar for the paradentary coronoid bone; cr = medial crest of the angular process; dt = dentary trough; mck = Meckelian groove; mf = mandibular foramen; mfl = medial flange; s = step may be homologous to the "diagonal ridge" of *Morganucodon* (Kermack et al., 1973).

in *Morganucodon* (Kermack et al., 1973), *Megazostrodon* (Gow, 1986), *Haldanodon* (Krusat, 1980; Lillegraven and Krusat, 1991), *Castorocauda* (Ji et al., 2006), and most other mammaliaforms with a pronounced angular notch and lateral ridge (Allin, 1975; Clack and Allin, 2004).

The medial view of the dentary is well preserved in the holotype (figs. 2, 5). The mandibular symphysis is unfused, smooth, and roughly oval, anteroposteriorly elongated and extending posteriorly to the level of p1. Posterior to the symphysis, the ventral edge of the dentary is fairly straight back to the level of m2, where it curves dorsally, resulting in a concave outline that extends to the angular process.

Subtle scars near the dorsal border of the extensive coronoid process indicate the attachment area of deep temporal muscle fibers. The condyle is eroded in the holotype and the shape is not clearly defined, but specimen MPEF 2357 suggests that the condyle is mostly spherical. The articular surface of the condyle is incompletely preserved and faces posterodorsally, lacking a well-defined constriction (neck) at the base of the condyle. The main axis of the condylar process in the holotype forms an angle of approximately 160° with the alveolar edge and results in a condyle located above the level of the tooth row. The holotype has suffered a fracture that artificially masks this feature.

The angular process is prominent, protrudes posteroventrally, and it is located below the level of the tooth row. The holotype has sustained a sharp break just in front of the anterior root of the m1, resulting in a lower and forward position for the anterior end of the jaw and thus giving the exaggerated impression that the angle is far below the tooth row. The angular process is located posteriorly, relatively close to the condyle (fig. 5), and therefore the angular notch is proportionately narrow and small compared to *Morganucodon*. The anteriormost extent of the notch is at the level of the posterior border of the coronoid process. The angular process is transversely wide, more expanded lingually than labially; its medial border is determined by a round crest that decreases in size anteriorly. This crest, medial to the angular process, runs along the ventromedial edge of the dentary and occupies a position homologous to the pterygoid crest of other mammals. This crest, however, is well developed only in the vicinity of the angular notch, helping to delimit the ventral edge of the dentary trough, and does not continue anteriorly much further. The posterodorsal surface of the angular process is concave, almost spoonlike, and with a rounded posterior edge. A similar morphology was found in basal mammaliaforms for accommodating the reflected lamina of the angular (ectotympanic) (Crompton and Luo, 1993). The posterior orientation of the concavity of *Henosferus* resembles more that of docodontans (Lillegraven and Krusat, 1991; Ji et al., 2006) than that of *Morganucodon* and *Sinoconodon*, which is medially exposed (Kermack et al., 1973; Crompton and Luo, 1993). Both the medial crest of the angular process and the medial flange of the dentary project lingually to the same degree.

There is a relatively small, concave surface for the coronoid bone (not preserved), located at the level of the alveolar edge, above the mandibular foramen (fig. 5). The anterior and dorsal edges of this facet are round and clearly defined, while the posterior and posteroventral borders are not clearly delineated. The coronoid facet faces posteromedially, having its deepest point adjacent to the anterodorsal border.

The mandibular foramen is relatively distinct and located posteroventral to the coronoid facet (figs. 2, 5). This elliptical foramen faces posteriorly and is continuous with the dentary trough. A sharp crest forms the dorsal edge of the foramen and decreases in size posteriorly before becoming continuous with the protruding medial flange. The dorsal rim of the mandibular foramen is very close to the medial flange of the dentary in *Henosferus* (fig. 5). In contrast, in other basal mammaliaformes such as *Morganucodon*, these two structures seem to be separated by a wider gap (Kermack et al., 1973; Crompton and Luo, 1993). The gap between the dorsal rim of the mandibular foramen and the medial flange would permit the passage of the inferior alveolar nerve and artery from the infratemporal fossa into the dentary.

The medial flange, medial trough, and Meckelian groove are the most remarkable features in the medial view of the lower jaw of *Henosferus* (fig. 5). The medial flange is sharp and prominent, forming a protruding shelf extending posteriorly from the mandibular foramen and continuing to the ventral surface of the condyle. The flange forms an angle of approximately 170° with the alveolar border. The medial-most projection of the medial flange occurs at the level of the angular process, and as mentioned above, has an extension similar to that of the medial crest of the angular process. There is limited evidence of articulation of the medial flange with other elements, as most of its surface shows parallel lineation of the periosteum similar to that in other portions of the dentary, but along its mid-length there is a smooth, elongated surface that could be interpreted as a facet, probably indicating the presence of postdentary bones (see Discussion).

The dentary trough is deep and develops below the medial flange and posterior to the mandibular foramen (fig. 5). In the dentary trough, two different surfaces can be observed separated by a blunt and not very distinct ridge of bone likely homologous to the diagonal ridge of *Morganucodon* (Kermack et al., 1973). Accepting the homology of this feature between *Morganucodon* and *Henosferus*, we use the same terminology, although the morphology is somewhat different. The surface dorsal to the diagonal ridge is placed immediately posterior to the mandibular foramen and below the notch of the

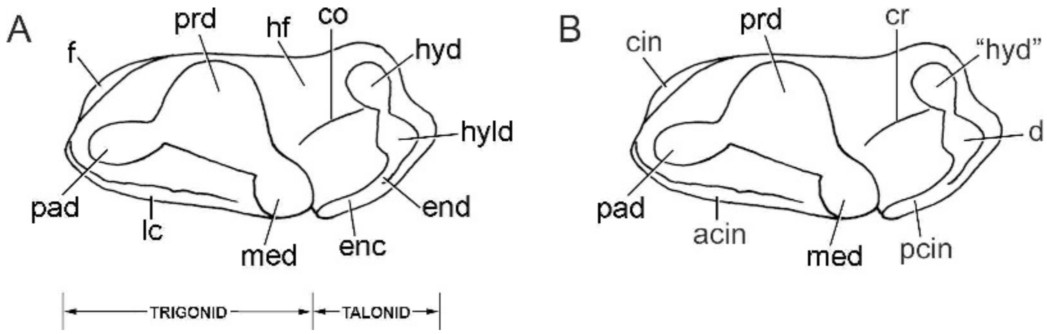

Fig. 6. Schematic drawing of the m1 of *Henosferus molus* (MEFP 2353) in occlusal view depicting the tribosphenic nomenclature (**A**) and an alternative interpretation of the australophenidan molar homologies (**B**). Abbreviations: acin = anterior cingulid; cin = cingulid; co = cristid obliqua; cr = crest; d = cusp d; enc = entocristid; end = entoconid; f = cingular cuspule f; hf = hypoflexid; hyd = hypoconid; hyld = hypoconulid; lc = lingual cingulid; med = metaconid; pad = paraconid; pcin = posterior cingulid; prd = protoconid.

medial flange, interpreted here as allowing transmission of the inferior alveolar nerve and accompanying vessels. We, therefore, believe that this surface dorsal to the diagonal ridge is occupied mostly by the vascular and nervous structures just mentioned. The second surface, below the diagonal ridge, is mainly related to the Meckelian groove and passes below the mandibular foramen to the posterior portion of the horizontal ramus of the dentary. The Meckelian groove is broader and deeper porteriorly between the medial flange and the angular process.

Behind the mandibular foramen, the dentary trough connects the Meckelian groove with the concave posterodorsal surface of the angular process (fig. 5). The trough becomes wider posteriorly, its direction suggested by a different bony texture indicating that the groove is directed dorsally toward the ventral surface of the medial flange. The dentary trough is delimited ventrally by the forward continuation of the pterygoid crest. In the area of the angular notch, the dentary is mediolaterally expanded, forming a sharply concave surface. This surface is wider along the dorsal edge of the angular process, resulting in a well-delimited space between the angular process, the edge of the angular notch, and the ventral surface of the medial crest, including its continuation as the condylar process.

The surface ventral to the diagonal ridge narrows strongly in front of the mandibular foramen and continues anteriorly as a continuous Meckelian sulcus, which reaches the posterodorsal surface of the symphysis without losing much width along the way, although it becomes progressively shallower (figs. 2, 5). The Meckelian sulcus curves ventrally from the area around the mandibular foramen to reach the ventral margin of the jaw, at the level of the posterior premolars, and then curves upward to reach the symphysis.

DENTITION: For descriptive purposes, we followed the dental nomenclature of Crompton (1971), Crompton and Kielan-Jaworowska (1978), and Bown and Kraus (1979) (fig. 6A); however, an alternative nomenclatural hypothesis is also suggested (fig. 6B; see further explanation in the Discussion).

With the exception of the m1 (fig. 7), the description of the dentition is based on the referred specimen (MPEF 2354; fig. 3). The lower dental formula of *Henosferus* is interpreted as i4, c1, p5, m3; tooth morphology has been the sole deciding criterion for distinguishing premolars from molars, because tooth replacement evidence is lacking. The incisors are placed close to one another and are separated by small diastemata that increase slightly in size among the posterior elements. The i1 and i2 are only represented by their roots; these teeth are circular in cross section and strongly procumbent. More posterior incisors are less procumbent, with a mesiodorsal orientation of the crowns. The alveolus of i1 is parallel to the ventral edge of

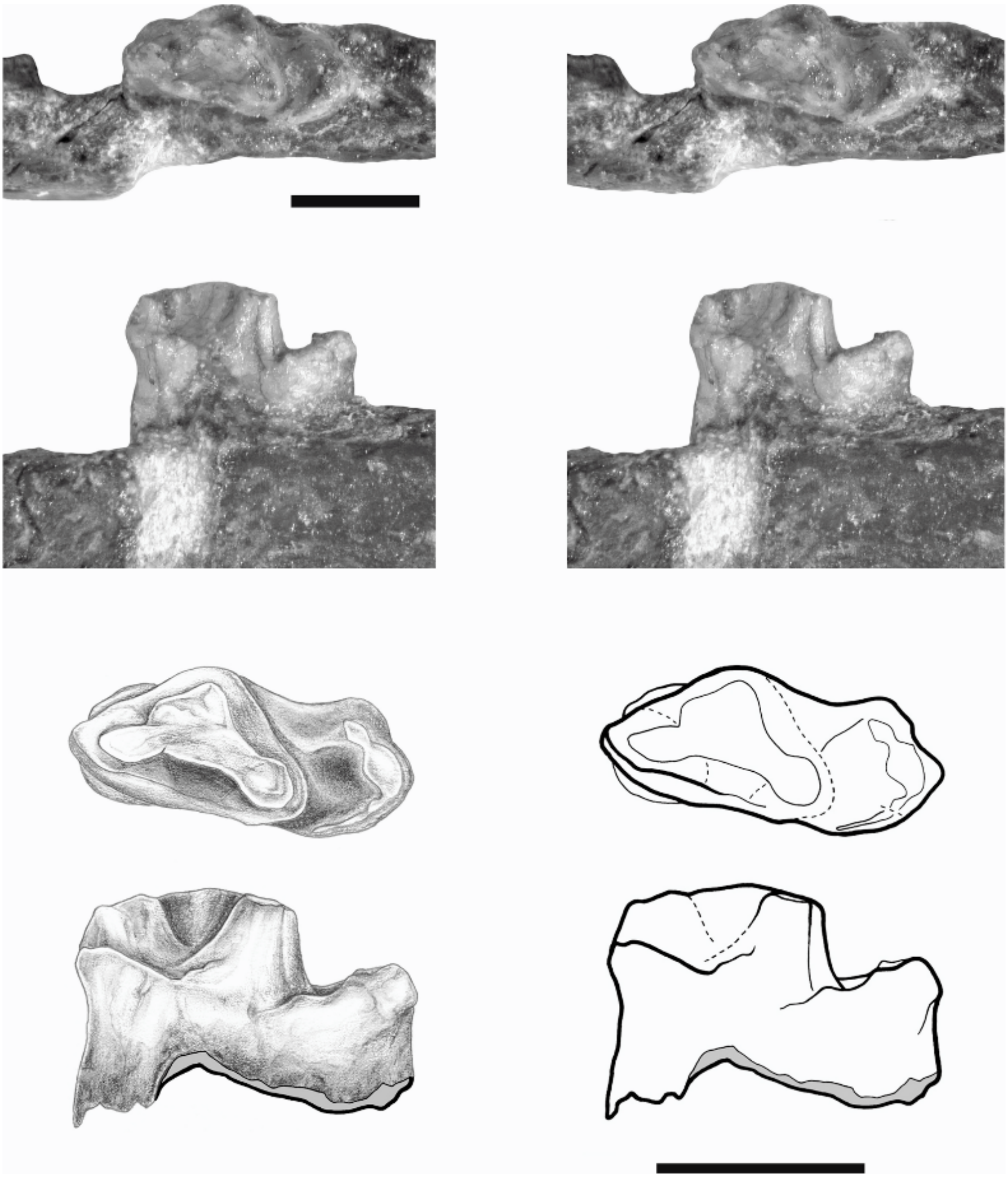

Fig. 7. *Henosferus molus* holotype MEFP 2353. Stereophotograph of the m1 in lingual and occlusal views, with accompanying drawings. Scale bar represents 1 mm.

the dentary, as clearly shown by the exposed root of i1 in the holotype, reaching back at least to the middle of the symphysis, but likely extending back to the level of the canine. According to the size of the alveoli and the cross section of the teeth, all incisors seem to have been of similar size, although the i1 could be slightly larger. In the holotype, all incisors are broken off (fig. 2), but some of the alveoli are clearly visible and agree with the morphology of MPEF 2354. The tip of the crowns of the i3 and i4 of MPEF 2354 are damaged, preserving only their subcircular bases, where no individual cusps can be identified.

The canine is complete in MPEF 2354 and MPEF 2357 and represented only by the alveolus in the holotype. It is the tallest tooth of the entire dentition, single rooted, and approximately cylindrical with a blunt apex that develops abruptly. The canine is posterodorsally projected in both specimens preserving it, although its inclination is more pronounced in MPEF 2354 than in MPEF 2357. We believe the canine of MPEF 2357 approaches the normal condition (fig. 4), while that in MPEF 2354 is a preservational artifact. The mesial edge is rounded and convex near the tip of the crown, while the distal edge is straight and slightly sharper than the mesial one. The canine is supported by a robust single root that makes a shallow bulge on the labial surface of the dentary. The canine is separated from the incisors by a smaller diastema than that separating the canine from the premolars (but see below). The canine is absent in the holotype, and although they are difficult to identify, it seems that the alveolus and diastemata are smaller than in MPEF 2354.

We interpret that *Henosferus* has five premolars (fig. 3); however, in the holotype, in addition to the five premolars, there are unambiguous indications of an extra alveolus partially plugged by bone between the canine and the alveolus of the mesial root of p1. Reabsorption of alveoli occurs widely among Mesozoic mammals, when a tooth is shed and not replaced or when the replacement tooth erupts behind the tooth being replaced (Luckett, 1993), so that both generations of a single tooth family are present at the same time in an individual. We believe this alveolus represents a somewhat more persistent deciduous p1, which was shed and replaced by a p1 occupying a more distal position in the jaw; plugging of alveoli is common among basal mammaliaforms (Crompton and Luo, 1993; Rougier et al., 2001). The dentaries MPEF 2354 and MPEF 2357 do not show unambiguous evidence of alveoli in the corresponding portion of the lower jaw. The premolars occupy about 45% of the total length of the horizontal ramus of the dentary. The premolars are separated from each other by proportionately large and subequal diastemata, resulting in a very open premolar series with teeth positioned at regular intervals (figs. 3, 4). The premolars are transversely narrow, almost four times longer than wide. All premolars have two cylindrical roots subequal in size. The main cusp is centrally located in the crown with the roots supporting the anterior and posterior halves of the teeth respectively in the p4–p5. In the anterior premolars (p1–p3), the main cusp is located mesially (i.e., over the anterior root) or close to the midline. The roots diverge slightly ventrally and are continuous with the crown, without a distinct neck. The limit between the roots and crown is determined by the presence of a distinct enamel–dentine juncture.

The crowns of the p1 and p2 are very similar; both teeth are dominated by a prominent main cusp (protoconid) that determines a trenchant, triangular outline for the teeth. The p1 and p2 lack accessory cusps and cingula, at least on their labial surface (fig. 3). The tip is acute, located slightly mesially on the crown, resulting in a nearly symmetrical tooth, with the mesial edge slightly convex and the distal edge slightly concave. The p1 seems to be slightly more robust than the p2.

The p3 is taller than the preceding premolars and slightly shorter than the p4. The apex of the main cusp is mesially displaced; the anterior edge is fairly straight and the distal one is slightly concave, resulting in a more asymmetrical tooth than the preceding premolars. This feature is accentuated by the presence of a small posterior accessory (cingular) cuspule at the base of the crown (fig. 3).

The p4 is slightly taller than the p3 and almost symmetrical in lateral view. The tip of p4 is acute, centrally placed in the crown, and both mesial and distal edges are fairly straight (fig. 3). There is a distinct posterior accessory cuspule that has its tip truncated by wear. The posterior accessory cuspule of the p4 is more prominent, closer to the alveolar margin, and more lingually located than that of the p3. The p4 has an incipient mesiolingual cingulid at the base of the crown, which is higher than the posterior accessory cusp, although this condition might be exaggerated by the distal inclination of the tooth.

The p5 seems to be subequal in height (once the missing tip is considered) but longer than the p4 (fig. 3). The jaw MPEF 2354, however, is fractured through the p5, the main cusp being almost bisected by this crack, which is slightly open, increasing the distance between the two fragments of p5 and giving the impression that the tooth is much longer than it actually is. This tooth is better preserved on the MPEF 2357 (fig. 4). On the lateral aspect, the crown is almost symmetrical, bearing anterior and posterior cuspules located at the same level near the base of the crown. The mesial border of the protoconid is straighter than the distal border, which is slightly concave. The lateral surface of the protoconid is slightly convex, while the medial surface is flat. The anterior accessory cusp is tiny, placed slightly lingually at the base of the crown and separated from the main cusp by a transverse groove. The posterior accessory cusp is located at the distolingual corner of the main cusp, and a small flake of enamel has been displaced anteriorly. The posterior half of the tooth is broader buccolingually than the anterior half, especially in the immediate vicinity of the posterior accessory cusp, where in specimen MPEF 2357 there is abundant wear. No basined talonid is present on this premolar.

In the holotype, the alveoli for p3–p5 are discernible; these alveoli differ from MPEF 2354 in the size and number of the diastemata. Instead of the regular, subequal diastemata of the referred specimen, the holotype lacks diastemata between the p1–p2 and p4–p5; furthermore, only very small diastemata are present between p2–p3 and p3–p4. This difference in diastema size cannot be explained as an age difference between the two specimens, because we would expect to have larger diastemata in older individuals. However, based on relative wear of the molars, the holotype is older than MPEF 2354. The specimen MPEF 2357 agrees more closely with MPEF 2354 than with the holotype, although there is a wide diastema between p3 and p4. We interpret these differences as reflecting individual variations and preservational differences.

There are three double-rooted molars implanted close to one another (i.e., there are no intermolar diastemata) in *Henosferus*. The molars decrease in size posteriorly, the last one being considerably smaller than the others. The last molar is located at the base of the anterior edge of the coronoid process, without leaving any substantial space between the tooth and the coronoid process.

The holotype preserves a fairly complete m1, providing good information on talonid morphology (fig. 7). The molars of MPEF 2354 and MPEF 2357 are damaged, making their interpretation challenging. The m1of the holotype shows a pattern with a trigonid and a fully basined talonid to which tribosphenic terminology can be readily applied. The trigonid is open with an angle of approximately 110° (fig. 7). The talonid is slightly wider and much lower than the trigonid. The labial surface of the trigonid is somewhat worn, even though a small cuspule (f) is present on the mesiolabial edge at the base of the trigonid. This cuspule seems to be a mesial elaboration of an anterior cingulid and, at least as preserved, lacks a conspicuous apex. The cingulid is also poorly individualized, and it is mostly expressed as a thickening of the crown base immediately above the root.

In the holotype, the tips of the three main cusps of the trigonid are truncated by wear, resulting in a single amalgamated wear surface that is horizontally oriented; in addition, the metaconid is also worn on its disto-labial surface (fig. 7). The protoconid is the most prominent cusp, followed by the paraconid and then by a small metaconid. On the mesiolingual and lingual base of the trigonid, there is a slightly crenulated cingulid that ends just anterior to the mesial edge of the metaconid. There is some damage on the mesial surface of the paraconid, which partially obscures the area, but enough is preserved to show that the lingual cingulid extends mesially to form part of the interlocking system between the p5 and m1. As preserved, the m1 of the holotype does not show a distinct cusp e. The mesiolingual corner of the trigonid, formed by the sharp base of the paraconid and the mesial extension of the cingulid, extends further mesially than the small cusp f; therefore, the interlock between p5 and m1 was oblique, with a greater lingual than buccal overlap. The trigonid is broad but not basined (fig. 7); most of it is occupied by the prominent base of the protoconid and only a small surface is present between the slopes of the three main cusps and the lingual cingulid that marks the medial edge of the trigonid. The paraconid is slightly procumbent and certainly occupies a more labial position than the metaconid, which constitutes the most lingual feature on the molar.

A heavily worn distal metacristid occurs in the holotype; the relevant area of the tooth on MPEF 2354 is truncated by a broad wear facet. The m1 of MPEF 2357, however, has a well-preserved talonid and distal face of the metaconid showing unequivocal evidence of a distal metacristid. The crest is broad and descends from the metaconid apex distolabially toward the weak cristid obliqua and prominent hypoconid.

The talonid is fully basined, rectangular in shape, and wider than long (fig. 7). The hypoconid is located on the distolabial corner of the talonid. Much of the hypoconid has been worn off in the holotype, but in MPEF 2354 and MPEF 2357, it is a blunt prominent cusp that is not fully differentiated from the hypoconulid; both cusps are connected by a broad, low hypocristid (Martin and Rauhut, 2005) crest. The labial face of the hypoconid bulges strongly labially beyond the base of the supporting root. From the mesiolingual face of the hypoconid arises the cristid obliqua, which determines the labial border of the basin of the talonid; this crest meets the trigonid slightly labial to the base of the metaconid. A wide hypoflexid is defined between the labial edge of the cristid obliqua and the hypoconid. The deep hypoflexid narrows the talonid basin to only two-thirds of the total width of the talonid. As in other Mesozoic mammals, the area of the hypoflexid is oblique and not fully vertical as seen in many later therians; therefore, there is not a great difference in height between the basin of the talonid and the portions of the talonid immediately labial to the cristid obliqua.

In the holotype, the hypoconulid is broad and bulbous and is the most prominent cusp of the talonid. In posterior view, the hypoconulid is partially obscured by some remnant sediment, but in the rear slope of the talonid a distinct vertical grove separates the hypoconid and hypoconulid. The hypoconulid would project posteriorly to participate in the interlocking mechanism as a broad crest descending posteriorly from the apex of the cusp and anchoring the posterior portion of the tooth between cusp f and the mesial extension of the paraconid on the succeeding tooth. The entoconid is hard to recognize due to wear; however, the talonid is lingually closed by a strong rounded entocristid. This crest is well developed lingually. The entoconid would be very close to the hypoconulid; therefore, the postcristid would also be very short. The best evidence for the position of the entoconid is produced on the lingual surface and expressed as a rounded eminence thought to represent the base of the entoconid (fig. 7). The entocristid is separated from the metaconid by a small but deep entoflexid (talonid notch); the entocristid is not directed mesially toward the base of the metaconid, but instead extends lingually, forming the posterior edge of the talonid notch.

In the referred specimen MPEF 2354, the trigonid and talonid of the m1 are crushed, and the paraconid, the labial basal part of the protoconid, the distal face of the metaconid, and the distolingual border of the talonid are missing. Despite breakage, the height of the protoconid is probably complete, showing remnants of a mesiobuccal wear facet on its tip. In posterior view, the hypoconid and the hypoconulid are not separated by a vertical groove, as happens in the holotype. MPEF 2357 adds further variability to the hypoconid–hypoconulid relationship and size. The talonid of this latter specimen seems to be complete and well preserved; while the hypoconid is of identical position and relative size as the holotype and MPEF 2354, the hypoconulid is very small and apparently closely apressed against the entoconid, which is quite distinct. MPEF 2357 resembles *Ausktribosphenos* and *Bishops* in these features (Rich et al., 1999a, 2001a). We are unsure about the meaning of the differences in the observed variability of the talonid cusps and relationships.

The remaining molars (m2–m3) are preserved in the referred specimen MEPF 2354 (fig. 3), but not in the holotype, and are the sole elements on which this description is based; the m2 of MPEF 2357 awaits preparation. The m2 is the best preserved molar of MPEF 2354. Missing or broken are the mesiolingual border of the base of the paraconid, the tip of the protoconid, most of the metaconid, and the lingual rim of the talonid. The main cusps of the trigonid form an angle of 85°. This angle is approximately 25° more acute than that in the m1 of the holotype (the m1 is too damaged in MPEF 2354 to estimate an angle). The protoconid is the tallest preserved cusp and likely the tallest in the crown. The protoconid has a bulbous base and a somewhat flattened mesial face. The lingual slope is flat, almost vertical, and occupies most of the surface of the trigonid; this feature, added to the separation between the bases of the paraconid and metaconid and the proximity of the lingual cingulid, results in the almost complete absence of a trigonid basin.

The relative heights of the paraconid and metaconid are impossible to estimate because the metaconid is broken at its base. The paraconid seems to be a fairly conical cusp truncated by an oblique wear facet on the labial aspect. Although a fair amount of wear is present, there is no well-developed metacristid; that is, the crest is not a vertical structure aligned with the posterior base of the trigonid. The condition in *Henosferus* resembles that of more generalized forms in which wear removes a substantial amount of material from the facet of the cusp bases to elaborate continuous wear facets; nevertheless, the condition here does not seem to be as primitive as that seen among Zhangheotheriidae (Rougier et al., 2003b; Tsubamoto et al., 2004). The protocristid also seems to be produced by a mixture of innate morphology and wear. A thin lingual cingulid can be distinguished from the base of the paraconid, extending lingually to the base of the metaconid. The cuspule f of the m2 is not as individualized as that of the m1 of the holotype and extends posteroventrally to the level of the base of the protoconid. The cuspule f delimits labially a notch for the interlocking with the hypoconulid, which strongly projects posteriorly in the m1 preserved only in the holotype. Some damage to the mesial portion of the crown of the m2 of MPEF 2354 may exacerbate the depth of the notch for interlocking. The notch is completed lingually by the procumbent paraconid, which, as in the m1 of the holotype, projects mesially beyond the position of cusp f. The talonid is mesiodistally shorter and probably subequal to or wider than the trigonid. The hypoconid is unworn, but a thin flake of its posterior face has been broken off. The cristid obliqua is low and reaches the base of the metaconid just lingual to the metacristid notch. The hypoconulid is rounded, bulbous, and massive, missing most of the labial surface and separated from the hypoconid by a shallow groove. The entoconid and entocristid are missing in this tooth, resulting in a molar basin that is artificially open lingually.

The last molar only preserves part of the trigonid and a small piece of tooth placed posterior to the metaconid. The labial portions of the trigonid (protoconid) are missing. As in m2, the paraconid bears a wear facet on the labial face of the tip. The lingual cingulid along the margin of the trigonid is more pronounced than in m2 and m1 and extends only between the bases of the paraconid and metaconid without reaching the mesial surface of the paraconid. The cingulid bears two small, blunt cuspules interrupted by a groove, located at the level of the protoconid. These grooves that delimit the small cingular cusps are the lingual continuation of the groove that demarcates the bases of the three main cusps (protoconid, paraconid, and metaconid), converging on the surface of the trigonid basin. Grooves such as these are commonly seen in forms with broad, open molariforms, such as amphilestids and "symmetrodonts" (Kielan-Jaworowska and Dashzeveg, 1998; Cifelli and Gordon, 1999; Cifelli and Madsen, 1999; Kielan-Jaworowska et al., 2004).

All of the molars have two vertically implanted cylindrical or slightly oval roots. The anterior one supports the trigonid and the posterior one the talonid. The posterior roots may be somewhat more compressed buccolingually than the anterior and seem to be longer mesiodistally.

WEAR FACETS: For nomenclature of the wear facets of lower molars, we follow Crompton (1971) and later amendments by Crompton and Kielan-Jaworowska (1978). In the holotype specimen, the only molar preserved (m1) has the trigonid and talonid strongly worn (attrition and apical wear), making recognition of the wear facets difficult.

The lower molars of *Henosferus* seem to have all major cusps present in tribosphenic mammals; however, the occlusal features do not appear to conform to that expected among members of Tribosphenida.

Facet 1, covering the metacristid and the posterior slope of the trigonid and extending into the hypoflexid, is completely preserved on the m2 of the referred specimen (MPEF 2354) and partialy on the m1 in the same specimen. Facet 1 is the most prominent of all the facets of *Henosferus* and results from the wear produced by a presumably robust paracone and preparacrista of the upper molar. Facet 2 extends from the protoconid to the paraconid along the paracristid on the anterior surface of the trigonid, and can be best observed on the mesiolabial face of the m2 of the referred specimen hypodigm and is complemented with partial views of the same from the m1 and m3 of the same specimen. This facet determines a relatively deep gully stretching from the labial surface of the paraconid and extending down to the anterior basal cingulid; along the anterior surface of the trigonid, facet 2 is flat and ornamented with striae directed inferiorly and labially. Facet 3 is developed on the mesiolabial face of the hypoconid and extends labially to merge with facet 1 at the deepest point of the hypoflexid. A deep trough is determined jointly by facets 1 and 3. Facet 3 is clearly seen on the m2 of the referred specimen and partially on the m1 of the same specimen and in the holotype. The holotype shows that facet 3 covers the mesial slope of the hypoconid and obliquely truncates the apex of this cusp when wear progresses. Facet 4 would be present on the distolabial face of the hypoconulid, but it cannot be clearly recognized in the holotype of *Henosferus*; the only possibility for the presence of this facet is on the m2 of MPEF 2354, in which the appropriate area displays a roughened surface that could either be a chipped piece of enamel or the facet. Based on the texture of other, unambiguously identified, facets, we lean toward the first of the two alternatives. Among tribosphenic mammals facet 5 develops on the distal face of the metaconid and extends down into the mesiolingual portion of the talonid, resulting from the likely shearing action of the mesial surface of the protocone along the preprotocrista. As interpreted here, facet 5 is likely not present in *Henosferus*. In the m2 of MPEF 2354, there could be a very small and limited area of wear on the base of the metaconid, lingual to the distal metacristid; this possible wear may only represent an artificial change in texture produced by the preparation of the specimen. Despite adequate preservation, neither the holotype nor the referred specimen MPEF 2357 show any evidence of a putative facet 5 in the relevant areas of the talonid. Facet 6, developed in mesiolabial surface of the entoconid in tribosphenic mammals (Crompton, 1971), is absent in *Henosferus*; evidence in favor of the absence of wear in this area of the talonid is furnished more definitively by MPEF 2357, where, despite extensive wear of the metaconid and distal metacristid, the mesial surface of the talonid cusps still preserve rounded bases and no wear.

A reconstruction of the jaw in *Henosferus* (fig. 8) is presented as a way to summarize the morphology in this early australosphenidan and to facilitate comparisons with other taxa.

PHYLOGENETIC ANALYSIS

In this study we have used as primary reference the data matrix of Luo et al. (2002) and subsequent modification by Woodburne (2003), Woodburne et al. (2003), and Martin and Rauhut (2005). Modifications to character wording and the actual scoring of taxa were made; some characters were deleted (see details in appendix 2) either because they were considered redundant with regard to other characters already included in the analysis or because we failed to see the proposed morphological variation. A few extra characters were added (characters 276 to 278), and, for one character (118), enamel microstructure was split into five individual states following Wood and Rougier (2005). Characters deleted from the analysis were, however, retained in the data matrix so as to preserve the original numeration of Luo et al. (2002) for ease of comparison of results and scoring between previous studies and ours. In the data matrix, the deleted character-states in *Henosferus* are indicated as "?". The primary results discussed here resulted from unweighted analysis of multistate characters. Subsequent runs explored the effects of ordering a subset of characters that included characters 5, 25, 34, 42, 45, 52, 56, 61, 63, 64, 74, 75, 79, 80, 93, 95, 97, 98, 108, 110, 111, 141, 147, 149, 150, 164, 170, 172, 191, 193, 194, 202, 204, 206, 237, 240, 241, 252, 254, 256, 259, 264, 278, 279, and 282. The results of the ordered runs preserve the basic tree topology of the unordered analysis.

The resulting data matrix of 271 characters and 48 taxa (appendix 3) was analyzed by using the programs NONA version 2.0 (Goloboff, 1993) and TNT (Goloboff et al., 2003) using heuristic search with 1000 replications and multiple tree bisection-reconnection (TBR) algorithms and other search strategies afforded by TNT (Ratchet, etc.), and edited using Winclada (Nixon, 1999).

The ordered analysis resulted in a strict consensus of three trees (fig. 9) of 903 steps with a consistency index of 0.43 and a retention index of 0.74 that collapse the eutherians into an unresolved tetrachotomy and also collapse *Kielantherium* and *Aegialodon* in a position basal to Theria. The unordered analysis resulted in a single most parsimonious tree of 872 steps, a consistency index of 0.45 and a retention index of 0.74 that resolved the eutherian clade, the relationships of *Kielantherium* and *Aegialodon* (grouping them in a monophyletic sister-group to therians), and, most surprisingly, moved *Haramiyavia* from a sister-group relationship to tritylodontids (fig. 9; a position somewhat similar to that defended by Jenkins et al., 1997) to a position basal to Multituberculata, a result along the lines of the review by Butler (2000), following earlier proposals by Hahn et al. (1989).

DISCUSSION

In light of the phylogenetic position of *Henosferus* and its geographic and geologic precedence, the most obvious comparison for *Henosferus molus* is *Asfaltomylos patagonicus* Rauhut et al. 2002 from the same locality and age. *Henosferus* is about twice the size of *Asfaltomylos*, with large diastemata between premolars, a proportionately low horizontal ramus of the dentary, a well-defined medial ridge on the dentary, a low coronoid process with the anterior edge less vertical, lower condyle, shorter retromolar space, distal metacristid on m1–m2 very weak in *Henosferus* and probably better developed in *Asfaltomylos*, and stronger lingual cingulid in the latter that extends from the paraconid to the metaconid on the molars. Despite these differences, there is a very close morphological resemblance between the two forms and they certainly belong to the same group of mammals. Great difference in size is known to occur in some Mesozoic mammals for which a relatively large sample is known and sexual dimorphism can be postulated (Rougier, 1993). In *Vincelestes neuquenianus*, known by 11 specimens found in association, absolute cranial size, sagittal crest, lambdoidal crests, and canine size seem to reflect sexual dimorphism. Based on skull length and mandibular length, the size difference proposed as an expression of sexual dimorphism in *Vincelestes* is roughly 25% and 20%, respectively. We have no other model against which to evaluate potential size disparities due to dimorphism among Mesozoic mammals; a size range such as that in *Asfaltomylos* and *Henosferus* is too great to result from variation within a single species. We are, therefore, quite confident that *Asfaltomylos* and *Henosferus* are distinct taxa. The qualitative characters enumerated above further reinforce the distinctiveness of these closely related taxa.

DENTAL FEATURES

TOOTH FORMULA: The lower dental count of *Henosferus molus* is i4, c1, p5, m3; this interpretation agrees with the reformulation of dental homologies proposed for *Asfaltomylos* by Martin and Rauhut (2005; *contra* Rauhut et al., 2002). The presence of four lower incisors and five lower premolars is a trait commonly found in the earliest eutherians, such as *Eomaia*, *Prokennalestes*, and zhelestids (Kielan-Jaworowska, 1975; Kielan-Jaworowska and Dashzeveg, 1989; Nessov et al., 1998; Ji et al., 2002). Among nontribosphenic mammals, a high number of premolars (five or more) is known in *Amphitherium* (Simpson, 1928b) and *Peramus* (McKenna, 1975; Butler and Clemens, 2001; but see Clemens and Mills for a different interpretation). As far as the

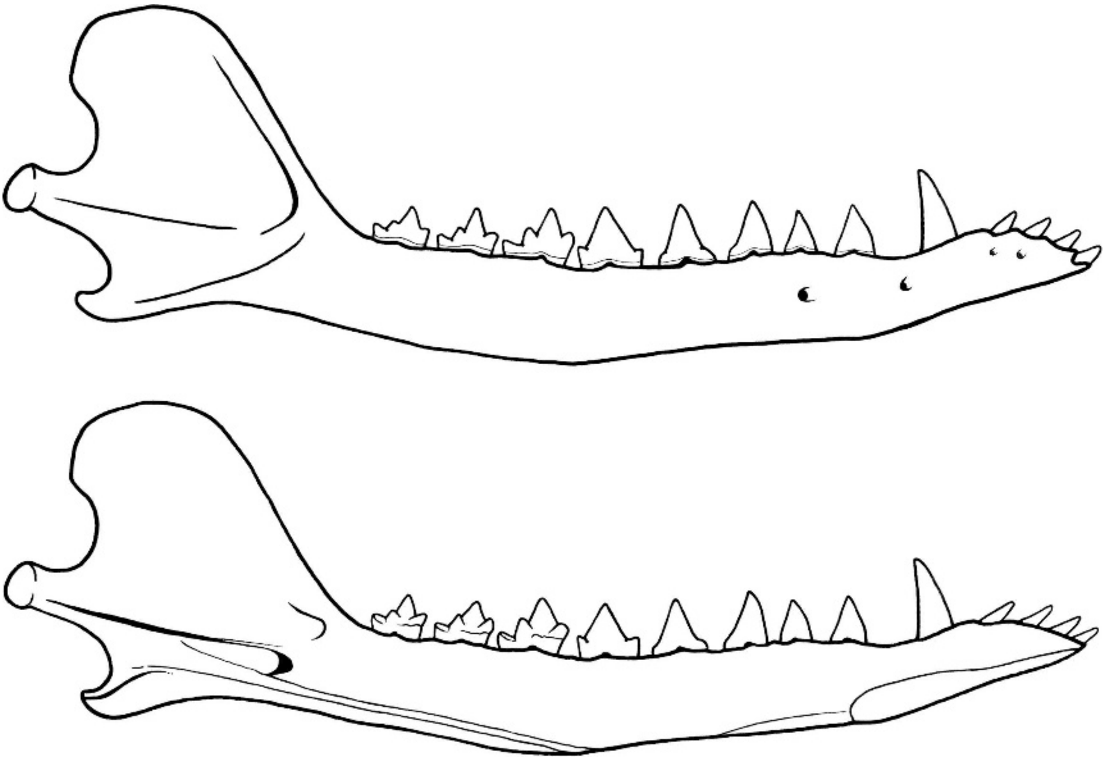

Fig. 8. Reconstruction of the right lower jaw of *Henosferus molus* in labial and lingual views.

interpretation permits, the number of premolars in the Early Cretaceous genera of Australia is six in *Bishops* (Rich et al., 2001a) and five in *Ausktribosphenos* (Rich et al., 1997, 1999a). In these taxa, the transition between premolars and molars is gradual and, together with the lack of replacement evidence, complicates the interpretation of the count of the postcanine teeth. There is a clear morphological break between the premolar and molar series in *Henosferus*; this is a purely morphological (and somewhat arbitrary) determination, because we do not have any evidence bearing on tooth replacement. Among early eutherians, the break between permanent premolars and molars is not as evident as that observed in metatherians (Clemens and Lillegraven, 1986; Rougier et al., 1998). The likely reduced, and derived, number of three molars is also present in *Ausktribosphenos*, *Bishops*, and derived monotremes (*Teinolophos* has four or more molars; Rich et al., 2005) (Archer et al., 1985, 1992, 1993; Rich et al., 1997, 1999a, 2001a) and in the nontribosphenic cladotheres *Peramus* (McKenna, 1975; Butler and Clemens, 2001; Kielan-Jaworowska et al., 2004) and *Vincelestes* (Bonaparte, 1986a), and it is traditionally recognized as synapomorphic at the base of Eutheria. Three molars is one of the most clear plesiomorphic traits for many extant placentals (e.g., Rougier et al., 1998). Plotting tooth count in the cladogram results in the recognition of multiple events of molariform/premolariform gains and losses, suggesting also a probable plastic boundary between premolar and molars (i.e., a premolar position becomes a molar or vice versa). Most notable are the extremes, such as six premolars in *Kuehneotherium* and *Bishops* and up to nine molariforms occuring among some dryolestoids (*Amblotherium*, not included in the analysis but implied by the position of reference taxa). Tooth count is, therefore, a problematic character for phylogenetic reconstruction. The risk of nonhomologous

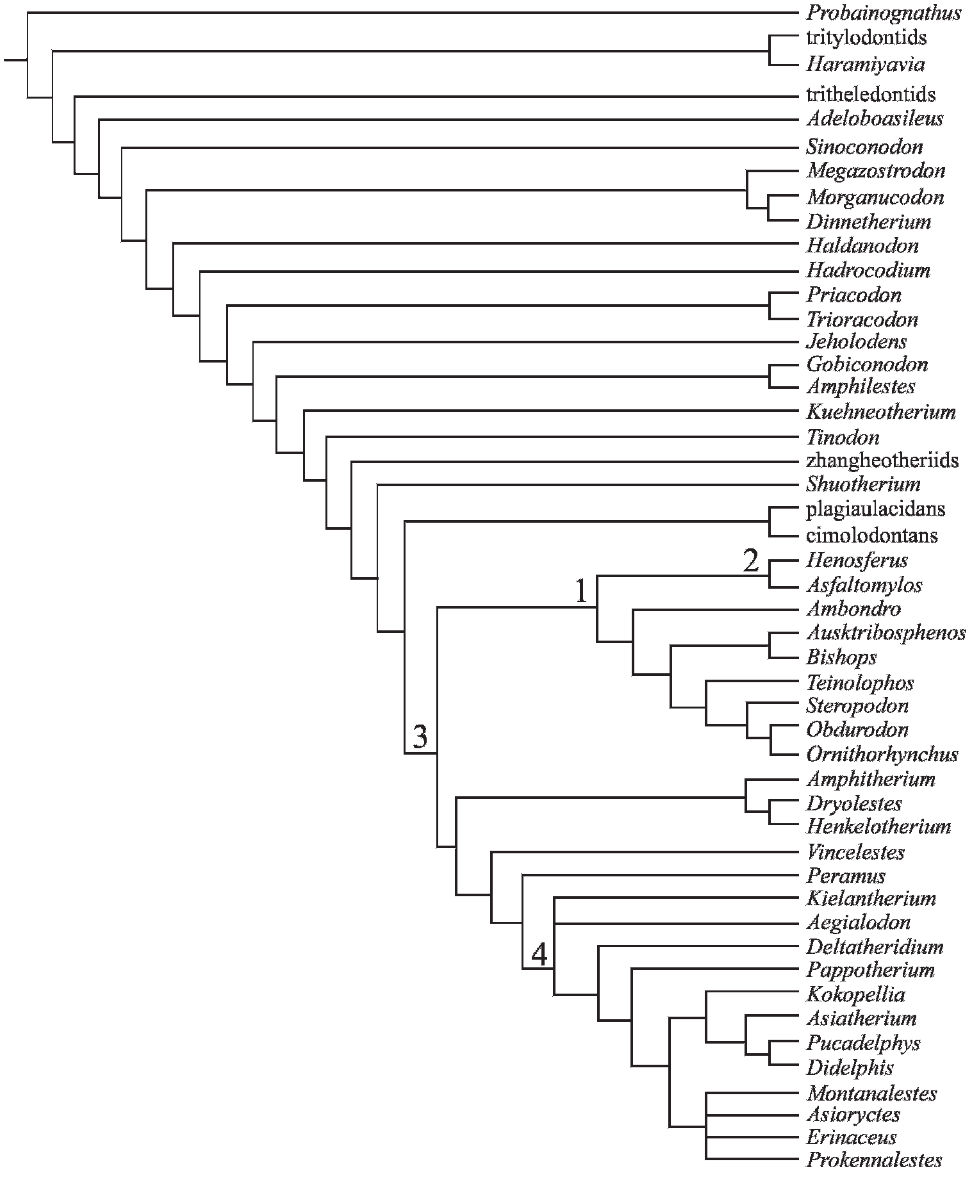

Fig. 9. Strict consensus tree of three trees obtained by the analysis of the data matrix containing 45 ordered characters. Individual MPT values: length: 903 steps; CI: 0.43; and RI: 0.74. Clade names: 1 = Australosphenida, 2 = Henosferidae, 3 = Mammalia, 4 = Tribosphenida.

comparison entailed by the pure count of teeth grouped by morphological discontinuities is enormous. Within a limited phylogenetic framework, a minimum of homology can be secured (e.g., among therians) and characters such as these are helpful. However, when comparing the m1 of a triconodont, multituberculate, monotreme, and placental, it is unclear to us that we are actually comparing homologous structures. Wide ranging statements of homology that can bridge widely disparate groups are tempting and help tidy up distinct portions of a cladogram defined by characters with highly localized distributions. Dental count is one such character, but until a better understanding of tooth formula evolution is reached, topologies based on, or supported by, tooth count should be regarded as provisional.

Tribosphenic Molars: The term tribosphenic was first used by Simpson (1936) to indicate the mortar and pestle opposing action of protocone and talonid and a wedgelike, alternating and shearing action of trigon and trigonid. The tribosphenic lower molar consists of an anterior triangle of cusps (the trigonid) and a posterior basin (the talonid) flanked by two or three cusps. The cusps of the trigonid are the labial protoconid, mesiolingual paraconid, and distolingual metaconid. The cusps of the talonid are the lingual entoconid, labial hypoconid, and distomedial hypoconulid (Osborn, 1907; Patterson, 1956; Bown and Kraus, 1979).

The traditional view of molar evolution of tribosphenic mammals (Crompton, 1971; Crompton and Kielan-Jaworowska, 1978) can be summarized as follows: *Kuehneotherium* and other basal mammaliaforms from the Late Triassic and Jurassic have the three main cusps of the trigonid of later therians forming an obtuse angle with a heel formed by the cusp d (the hypoconulid; Crompton and Jenkins, 1968; Kermack et al., 1968) and without a basin. In later forms of cladotherians from the Early Cretaceous, including *Amphitherium*, *Arguimus*, *Palaeoxonodon*, *Arguitherium*, and *Vincelestes*, the talonid heel becomes wider and larger than in basal "symmetrodonts" but a basined talonid and a hypoconid cusp are still absent (e.g., Dashzeveg, 1979, 1994; Freeman, 1976; Rougier, 1993). The talonid becomes larger in *Peramus* and *Kielantherium* from the Early Cretaceous; in those taxa a hypoconid and an incipient basin are present (Clemens and Mills, 1971; Dashzeveg, 1975; Butler and Clemens, 2001). Finally and completing the basic talonid morphology, an entoconid cusp is developed in *Aegialodon* (Kermack et al., 1965; Crompton, 1971), *Tribactonodon* (Sigogneau-Russell et al., 2001), *Pappotherium* (Butler, 1978), and therians (e.g., Cifelli, 1999; Kielan-Jaworowska et al., 2004).

The assumption of a double origin of the tribosphenic molar (Luo et al., 2001a, 2002; Sigogneau-Russell et al., 2001; Rauhut et al., 2002; Kielan-Jaworowska et al., 2004; Martin and Rauhut, 2005) accepts this series of homologous transformations (or most of them; see discussion of *Kuehneotherium* in Rougier et al., 1996a and Godefroit and Sigogneau-Russell, 1999), but argues that an independent tribosphenic molar was achieved among australosphenidans.

Simpson's (1936: 797) definition of the tribosphenic molar ("suggestive of the mortar and pestle, opposing action of protocone and talonid and the wedge-like, alternating and shearing action of trigon and trigonid") implies that the components involved in the formation of the tribosphenic molar (protocone, entoconid, hypoconid, etc.) must be homologous, preserving a specific and particular hypothesis of homology. Not just any cusp occluding on a basin will make a tooth tribosphenic. The definition of tribosphenic employed by Luo et al. (2001a) is based only on general functional terms ("The tribosphenic lower molar is defined by a basin-like heel (talonid), which grinds (*tribein*) with the large inner cusp (protocone) on the upper molar–functionally analogous to mortar-to-pestle grinding. This is in addition to a wedge-like trigon (*sphen*) to shear with the crests of the corresponding upper tooth." Luo et al., 2001a: 55). Defining a group or structure on a functional basis is a nonhierarchical procedure per se, which obviates ancestor–descendant relationships and phylogenetic internesting of characters. Despite similarity of function, there is no reason to, a priori, give the same name to two structures believed to have different phylogenetic origins; that is to say if the "tribosphenic" molar of asutralosphenidans and that of therians is not homologous, there is no compelling argument to apply to them the same term and, in particular, to be surprised by the independent acquisition of nonhomologous but morphologically indistinguishable functional complexes (Luo et al., 2001a, 2002; Kielan-Jaworowska et al., 2004). The independent acquisition is a corollary of the nonhomology, or lack of phylogenetic continuity, between these character complexes. Chow and Rich (1982) and Wang et al. (1998), when faced with a similar problem of a functional equivalent of the therian tribosphenic molar, opted to called the molar "pseudotribosphenic" and the protocone "pseudoprotocone", a solution we believe to be a sensible one. In fact, a similar nomenclatorial approach has been followed by Martin and Rauhut (2005) for the australosphenidan *Asfaltomylos*. The relatively well-established term such as Tribosphenida (McKenna, 1975), referring to a character-defined taxon (i.e., a group of mammals diagnosed by having a protocone, occluding on the talonid) was changed to Boreosphenida, based on the fact that a nonhomologous, similar functional complex was present in the unrelated australosphenidans (Luo et al., 2001a, 2002, 2003; Kielan-Jaworowska et al., 2004). The naturalness of Tribosphenida, supported among other features by the synapomorphic acquisition of a prominent protocone and basined talonid, is not questioned by Luo and coauthors or by any recent study (e.g., Woodburne et al., 2003; Martin and Rauhut, 2005). Only tribosphenic mammals (i.e., members of Tribosphenida) have a protocone and a basined talonid that is homologous among members of the group. Tribosphenida is an unambiguous term that refers to a clearly monophyletic group. Australosphenidans do not have a tribosphenic molar, although they may possibly have a functional equivalent of it, a question explored below.

The functional equivalence of the austalosphenidan molar and the tribosphenic molar seems to be at present tenuously supported. The basal members of the australosphenidan radiation are known only by mandibular elements and lower dentitions; therefore, the presence of an upper protocone or functionally equivalent cusp must be deduced from the lower tooth morphology and wear facets. Martin and Rauhut (2005: 422) wrote: "The talonid wear pattern of *Asfaltomylos* differs fundamentally from that of Laurasian tribosphenic boreosphenidans, because it shows no wear within the talonid basin itself"; the same applies to *Henosferus* and Ausktribosphenidae (Hunter, 2004; G.W.R., personal observation, 2004). No wear facets are distinguishable in the talonid of the Australian australosphenids. In the Middle Jurassic (*Ambondro*) facets 5 and 6 have been identified (Flynn et al., 1999), but Martin and Rauhut (2005) have subsequently challenged this interpretation. We are uncertain about this feature in *Ambondro*; whatever the case, most of the wear is nonetheless labial to the cristid obliqua in *Ambondro*.

The information summarized above calls into question the presence of a single major cusp occluding in the basin, a *sine qua non* trait of tribosphenic molars. Furthermore, the only putative (see Woodburne, 2003 and Woodburne et al., 2003) australosphenidan group known by upper teeth, Monotremata, is almost universally interpreted as missing a protocone cusp, either truly homologous or functionally analogous (Greene, 1936; Luckett and Zeller, 1989; Pascual et al., 1992a,b, 2002; Woodburne, 2003), with teeth functioning in a very different way from those of tribosphenic mammals (Kielan-Jaworowska et al., 1987; Archer et al., 1992; Pascual et al., 1992a,b, 2002). Luo et al. (2002: 26) identified a small cuspule in *Monotrematum* as the sole remnant of a functional protocone that later would be lost in more derived members of Monotremata. Pascual et al. (2002) argued against such identification. We concur with Pascual et al. (2002) in considering such homology unlikely. There is, then, no direct homology between therian dentitions and the arguably modified monotreme "tribosphenia" (Luo et al., 2001a, 2002, 2003; Kielan-Jaworowska et al., 2004), because of the radical lack of protocone in monotremes and a very lax if at all present functional correspondence in the molars. To the extent of the known materials, the same arguments can be extended to most of the remaining australosphenidans. Therefore, the presence of a true protocone or a functional analog is yet to be documented, and overall occlusion as evidenced by wear facets does not seem to agree closely with those of tribosphenic mammals. The presence of a small protoconal cusp in *Vincelestes* (Bonaparte and Rougier, 1987) that determines no evident wear on the talonid serves also as a cautionary note against deducing upper molar morphology based on lowers and vice versa. An even more dramatic example is provided by the large "protocone" of *Shuotherium* (Wang et al., 1988) that determines no wear on the talonid (Chow and Rich, 1982). We believe the presence of a "protocone" cusp (but with limited or no occlusal function in the talonid [Martin and

Rauhut, 2005]) in the upper molars of australosphenids is probable.

AN ALTERNATIVE VIEW OF AUSTRALOPHENIDAN MOLARS: Based on the homologies accepted here and on the resulting cladogram, Australosphenida and Tribosphenida share the major trigonid cusps and the primitive posterior talonid cusp, traditionally viewed as the hypoconulid (Kermack, 1968; Crompton, 1971). The hypoconid and the entoconid would be independently acquired in the austrilosphenid and tribosphenid clades.

Following this interpretation, an alternative view of the austalosphenidan talonid cusps can be offered (fig. 6B). Australosphenidans are bracketed between "symmetrodonts" (*Tinodon*, *Zhangheotherium*) and basal cladotheres (*Amphitherium*, dryolestoids); therefore, it is appropriate to keep in mind symmetrodonts and dryolestoids when evaluating australosphenidans and attempting to understand their morphology. The lingual view of the molars of *Ausktribosphenos*, *Bishops*, *Ambondro*, and to a lesser degree *Asfaltomylos* and *Henosferus*, resembles closely a basal "symmetrodont" like *Zhangheotherim* or *Maotherium* (Hu et al., 1997; Rougier et al., 2003b), in particular the last premolar of the Ausktribosphenidae. As suggested by serial homology (Van Valen, 1994), the posterior cingular cusp of the last premolar must be the homolog of the large posterolingual cusp of the talonid (see Rich et al., 1999a, 2001a), which in turn is cusp d of therians and other mammals. We view as compelling the close morphological correspondence between the anterior cingular cusp, anterior portion of the lingual cingulid, position of the metaconid, posterior portion of the lingual cingulid, and posterior cingular cusp of the last premolar of ausktribosphenids and *Ambondro* on one hand and the "wrapping cingulid", lingual metaconid, and "preentocristid offset and past the base of metaconid" of the molars in the remaning australosphenidans on the other. Under this view, the anterior cingular features used by Luo et al. (2001a, 2002) to diagnose australosphenidans become simply the retention of the anterior half of the lingual cingulid of basal trechnotheres, which, as in those basal forms, extends to the front of the tooth to reach an anterior cingular cusp. The primitive lingual cingulid becomes partially interrupted by the lingual position of the metaconid, and the distal portion of the cingulid is enlarged, reaching a relatively large posterior cingular cusp (cusp d or hypoconulid). This large cusp is the core of the australosphenidan talonid, and, therefore, the basin of the talonid would be formed by a buccal expansion. The "hypoconid" would be a neomorphic or enlarged cingular cusp (Hunter, 2004). The cristid obliqua can be directed to the hypoconulid (Hunter, 2004) or possibly more labially, contacting the lingual slopes of the "hypoconid" as in *Henosferus*. The nonhomology of the hypoconid is dictated by the phylogenetic position of the australosphenidans and is, in turn, reinforced under the interpretation suggested above. The elongated and crestlike entoconid of australosphenidans would be simply small cuspules of the posterior portion of the lingual cingulid. These cuspules vary in development and position in *Ausktribosphenos* and *Henosferus*, suggesting a cusp under no occlusal control. For a summary of homologies see figure 6B. Toothed monotremes would have greatly modified dentitions, with a complete anterior cingulid and anterior cingular cusp, a hypoconulid enormously developed, and a large "hypoconid".

Following the logical implications of this alternative interpretation affects the scoring of characters 47, 48, 55, 56, 63–65, 67, 70–74, and 99. The searches with these changes, using the same set of ordered characters as in previous runs, result in two trees of 903 steps that agree closely with the one illustrated here in figure 9. The only substantive difference is the inclusion of multituberculates inside Australosphenida as the sister group of Monotremata, a result also obtained during the standard runs under certain conditions. *Zhangheotherium* and *Tinodon* are moved basal to dryolestoids. When the matrix was run unordered, 33 MPT trees of 857 steps were obtained. The consensus was poorly resolved and the 50% majority rule identified many poorly supported nodes. The branches in the vicinity of, and inside, Australosphenida either failed to form monophyletic clusters or had very low support. Not even the node *Asfaltomylos*/*Henosferus* was recovered in all the trees.

This area of the tree is obviously very labile and susceptible to drastic topological collapses, probably due to the lack of cranial, postcranial, and upper dental information for most of the australosphenidans.

Regardless of which of the two main hypotheses of cusp homology are followed, ausktribosphenids are not clustered within eutheria. Addmittedly, our sample of crown-group Theria is poor to the extreme but several alternatives of character weighting, additivity, and reinterpretation have repeatedly failed to dislodge ausktribosphenids from a basal position in Mammalia. A southern (Gondwanan) origin for Eutheria based on australosphenidan taxa is at present unparsimonious.

Postdentary Bones

The origin of the typical mammalian middle ear is well documented by the fossil record and embryological data (e.g., Reichert, 1837; Gaupp, 1913; Hopson, 1966; Allin, 1975, 1986; Maier, 1990; Allin and Hopson, 1992; Clack and Allin, 2004). All the elements of the mammalian middle ear with the exception of the stapes can be homologous to either endochondral or dermal bones that in basal tetrapods are mechanical constituents of the jaw. The dentary is the dominant mandibular element, bears teeth, and occupies a mesial position in the jaw. Two sets of elements can be recognized in the jaw with respect to their relations to the dentary: paradentary and postdentary bones. Paradentary elements are of dermal origin, closely apressed to the medial (lingual) surface of the dentary, and in mammalian forerunners serve to close structurally the medial gap in the dentary caused by a large mandibular canal and a prominent Meckel's cartilage. The postdentary elements occupy a posterior (distal) position with regard to the dentary and serve for the attachment of masticatory musculature, in addition to forming part of the suspensorium.

The two paradental elements, coronoid and splenial, are absent in the crown-group Mammalia, although reduced coronoids and even splenials have been postulated for some stem therians (Krebs, 1971; Martin, 1999). It is possible that a vestigial coronoid survives in basal eutherians (Kielan-Jaworowska and Trofimov, 1981; Kielan-Jaworowska and Dashzeveg, 1989; Nessov et al., 1994). There is a degree of uncertainty about the persistence of the coronoid in later mammals because in basal forms such as *Vincelestes* (Rougier, 1993) and *Henosferus* (fig. 5), the position is marked by a clear rugose depression, but in eutherians it is usually identified as a raised area (Wible et al., 2004). Unambiguous evidence of a splenial is not known in members of Theria, either living or fossil. Neither one of these elements raises any serious problems of homology beyond their identification as such based on scars or facets.

The postdentary elements are the angular (ectotympanic), prearticular (goniale), articular (malleus), and surangular. With the exception of the articular (that is an endochondral assification of the posterior part of the Meckel's cartilage) the remaining elements are dermal in origin and partially surround Meckel's cartilage or form the medial boundary of the cartilage (De Beer, 1937).

Transformation from mechanically robust elements with an unequivocal suspensorial function as seen in nonmammalian therapsids into the minute, solely auditory elements of the crown group Mammalia was gradual (Allin, 1975; Crompton and Hylander, 1986; Clack and Allin, 2004; Vater et al., 2004). The enlargement of the dentary as the only bone of the lower jaw that articulates directly with the squamosal is arguably a driving force that, in turn, affects the reduction and detachment of the articular and angular elements (including the tympanum-bearing reflected lamina) from the dentary. Concomitant modification affects the cranial elements, in particular the quadrate, quadratojugal (which seems to disappear without mammalian homolog), and the basicranial region (e.g., Allin, 1975; Rougier et al., 1996b; Rowe, 1996; Vater et al., 2004). The reduction and transition of the postdentary elements from the jaw into the middle ear is relatively well documented (Allin, 1975, 1986; Maier, 1990; Allin and Hopson, 1992; Clack and Allin, 2004) and this documentation is one of the great achievements of comparative anatomy (Reichert, 1837; Gaupp, 1913). The fossil support for this transformation is less substantive, in particular, among basal mammaliaforms where the elements involved are already of small size and loosely attached to the dentary. Except for a few exceptions, most Mesozoic mammal jaws are preserved as an isolated dentary, and the postdentary elements, if ever present, have been lost. Using nonmammalian cynodonts and basal mammaliaforms in which the dentary, paradental, and postdentary elements are known as a model, a great deal of morphology can be extracted from the dentary as a predictor of the size and relationships of postdentary bones and Meckel's cartilage, in particular, when prominent ridges and facets are present.

Henosferus shows a peculiar set of ridges and grooves on the posteromedial aspect of the dentary resembling the morphology of the Late Triassic and Liassic mammaliaform *Morganucodon* (Kermack et al., 1973) and the Jurassic docodonts *Haldanodon* (Lillegraven and Krusat, 1991) and *Castorocauda* (Ji et al., 2006); based on comparison with those taxa, we believe that *Henosferus* also retained a basal mandibular arrangement with relatively well-developed postdentary elements and possibly a robust and persistent Meckel's cartilage.

MECKELIAN GROOVE AND CARTILAGE: In medial view, the dentary of *Henosferus* has a sigmoid groove near the ventral border of the horizontal ramus that, from the level of the symphysis, extends backward to the area of the mandibular foramen (figs. 2, 5). The small groove descends toward the ventral border of the jaw and at the level of the m1 disappears; posteriorly it rises again and finally becomes confluent with the medial trough.

A thin medial groove, supposed for the Meckel's cartilage, has been widely reported for a variety of Mesozoic mammaliaform lineages (De Blainville, 1838; Owen, 1871; Osborn, 1888; Simpson, 1928b,c, 1929; later contributions are summarized in Kielan-Jaworowska et al., 2004). The groove was variously interpreted as an osteological correlate of the presence of a Meckel's cartilage (e.g., Flower, 1883; Bensley, 1902) or as a scar of a nerve or artery related to the mylohyoid groove of some current mammals (e.g., Owen, 1838; Simpson, 1928c). Usually, this groove extends from the symphysis back to the level of the mandibular foramen. The arrangement in the dentary is variable in each group; even specimens of same species show differences in the location and depth of the dentary medial groove.

Repenomamus robustus from the Early Cretaceous of Liaoning (China) and *Gobiconodon zofiae* (Li et al., 2003) have preserved an ossified Meckel's cartilage in its natural position, providing clear data for understanding the significance of the so-called Meckelian groove in Mesozoic mammals. As was noted by Meng et al. (2003), the split of the groove in the anterior and mid-portion of the dentary represents a trace left when the dentary wraps over the cartilage during ontogeny. Only the most posterior portion of the groove was occupied by the ossified cartilage in *Repenomamus* (Meng et al., 2003). However, the presence of the Meckelian groove does not directly imply the persistence of the Meckelian cartilage in the adult; the Meckel's cartilage could occupy the groove only during early ontogenetic stages and later disappear, as is the case among perinatal didelphids (Maier, 1993; Meng et al., 2003). The Meckelian groove in *Henosferus* passes ventral to the mandibular foramen (figs. 2, 5), as in many Mesozoic mammaliaforms (e.g., *Morganucodon* and *Repenomamus*). This ventral location of the groove in relation to the mandibular foramen is also evident in the development of the mandibule of the extant eutherians. The embryo of *Rattus* shows the mandibular foramen appearing dorsal to the Meckel's cartilage on day 19 (Tomo et al., 1997); in *Ornithorhynchus*, histological cross sections of the lower jaw of an immature individual show that the Meckel's cartilage runs ventromedial to the mandibular nerve (Zeller, 1989). The same is observed in marsupials (Toeplitz, 1920; personal observation). Comparisons with fossil mammaliaforms possessing similar structures on the medial side of the dentary and with ontogenetic data strongly suggest that the medial groove of *Henosfenus* corresponds to a Meckelian groove, which may or may not have had a persistent cartilage in the adult form. The evidence observed in *Repenomamus* and *Gobiconodon zofiae* (Wang et al., 2001; Li et al., 2003; Meng et al., 2003) indicates that possibly the medial groove of the dentary in most Mesozoic mammals such as cladotherians does not correspond to a Meckelian groove *sensu stricto*, but instead is a trace remnant left when the dentary wraps over the cartilage during ontogeny (Meng et al., 2003). The known interactions during embryology of the dentary and Meckel's cartilage (Zeller, 1989; Starck, 1995; Tomo et al., 1997) provide additional support to a dual nature for the Meckelian groove of Mesozoic mammals, with a wide array of morphologies, from forms with a cartilage almost completely exposed through life and extending from the symphysis to the back of the jaw to other forms in which the "groove" is more properly a suture of two dentary lips. In summary, *Henosferus* has a Meckelian groove extending from the symphyseal area to the level of the coronoid process, but the presence of Meckel's cartilage in this groove in the adult form is not demonstrated but could potentially remain lodged in the posterior portion of the trough, perhaps continuous with the malleus.

DENTARY TROUGH AND CONTENTS: The dentary trough, or medial trough, of *Henosfenos* is clearly defined, limited dorsally by the medial flange and ventrally by the medial crest of the angular process (fig. 5). The medial trough of *Henosferus* is considerably shorter anteroposteriorly than in *Morganucodon* (Kermack et al., 1981) and docodonts (Krusat, 1980; Lillegraven and Krusat, 1991). Additionally, in *Henosferus* the condylar and angular processes are proportionately close to each other, restricting the anteroposterior extension of the groove. In contrast, *Morganucodon* has a condylar process lying well back from the level of the angular process, resulting in a broad dentary trough. *Haldanodon* (Lillegraven and Krusat, 1991), *Castorocauda* (Ji et al., 2006), and *Docodon* show an intermediate position of these processes with regards to *Morganucodon* and *Henosferus*. The dentary trough of *Henosferus* is clearly divided into two surfaces: one posterior to the mandibular foramen and leading into it, the other ventrally located to the surface mentioned above, connecting anteriorly with the Meckelian groove (fig. 5). There is a low, blunt ridge that separates these surfaces. Basal mammaliaforms such as *Morganucodon*, *Haldanodon*, and *Castorocauda* are known to have postdentary bones attached to the lower jaw and clear surfaces for their attachment (Kermack et al., 1973, 1981; Allin, 1975, 1986; Jenkins et al., 1983; Lillegraven and Krusat, 1991; Allin and Hopson, 1992; Clack and Allin, 2004; Ji et al., 2006). *Morganucodon* has a diagonal ridge running from the anterior end of the medial flange to the lower edge of the mandibular foramen, separating the prominent dentary trough from the posterior wall of the mandibular foramen (Kermack et al., 1973). A clear diagonal ridge is absent is *Henosferus*, but the blunt ridge between the two surfaces of the lateral trough seems to be homologous with the diagonal ridge of *Morganucodon*, so that a less complete subdivision into two surfaces is present in *Henosferus*. The area posterior to the mandibular foramen is interpreted here as being for the passage of the inferior alveolar nerve and artery that supply the body of the mandible and teeth and continue anteriorly as cutaneous branches to exit the dentary as a series of mental nerves through the mental foramina. If living mammals serve as analogs, these soft structures would reach the mandibular foramen from the posterodorsally located infratemporal fossa of the skull (see Zeller, 1989, for monotremes, and Spatz, 1964, for eutherians). The medial flange is slightly notched, or less developed, immediately distal to the mandibular foramen, a trait also present in *Morganucodon*, which suggests the path of a neurovascular bundle extending toward the mandibular foramen. The ventral facet, continuous with the Meckelian groove, requires further explanation. This facet widens posteriorly and, at the level of the angular process, is bordered ventrally by a distinct crest. In this region, the medial flange extends inward to approximately the same degree as the medial crest of the angular process, thus defining the dorsal border of the facet. The angular process is conspicuously wide transversely and concave posteriorly; the peculiar morphology of the process results in the formation of a restricted post-mandibular area, which, when considered in unison with the likely position of the angular (tympanic), hints to the presence of a middle ear diverticulum in connection with the postdentary tympanum, similar in position to that suggested for basal mammaliamorphs (Allin, 1986; Allin and Hopson, 1992; Luo et al., 2001b). *Morganucodon* (Kermack, 1973) bears a clear facet bordered dorsally by the medial flange and ventrally by a low crest, which supports the articular–prearticular and angular–surangular complex. Even though proportions and degree of crest development differ between *Henosferus* and *Morganucodon*, these taxa share a common morphology, absent in more derived mammaliaforms, that strongly supports the idea of the presence of postdentary bones in the specimen from Cerro Cóndor. It is probable that the postdentary complex was enclosed between the medial flange and the medial crest of the angular process and that the concave angular process was likely closely associated with the reflected lamina of the angular process where the tympanic membrane was attached. The relatively anteroposteriorly shorter medial trough suggests the presence of relatively smaller postdentary bones in comparison with *Morganucodon*, but we believe the close morphological similarities warrant the assumption that all major postdentary and paradentary elements were still present and substantially anchored to the dentary. The paradentary elements, coronoid and splenial, were not particularly large; the scar for the coronoid is distinct but occupies a small area at the base of the coronoid process (fig. 5), while the evidence for the splenial is less distinct. The splenial would be expected to cover medially the distal portions of the Meckelian groove (and cartilage if present) and extend posteriorly below the proximal portions of the dentary trough, but the ridges and rugosities in these areas are not particularly distinct, and, therefore, although we are convinced about the presence of the splenial, we are not certain about its extent. The postdentary elements would be proportionately smaller than in *Morganucodon*, *Haldanodon*, and *Castorocauda* and more loosely attached to the dentary, because distinct facets are not present in *Henosferus*. We believe this to be a natural feature because of the exquisite preservation of the *Henosferus* jaw MPEF 2353 (figs. 2, 5). Size and attachment of the postdentary complex has direct implication on the predicted dual cranio-mandibular joint. In *Henosferus* the dentary condyle is distinct, robust, and certainly the major structural link between skull and jaw; the predicted mandibular location for the tympanum in *Henosferus* has as a corollary the involvement of prearticullar (goniale), articular (malleus), and quadrate (incus) in a dual auditory and suspensory function. The degree of participation of the archaic mandibular articulation on the distribution of masticatory forces would depend on the strength of their attachments to the dentary (see below).

Unlike *Morganucodon*, but similar to *Haldanodon* (Lillegraven and Krusat, 1991) and *Docodon* (Simpson, 1929), the medial flange of *Henosferus* lies at the blevel of the inferior edge of the condylar process. If present, the postdentary bones would be supported dorsally by the medial ridge, and therefore the quadrate (incus)/articular (malleus) articulation would occur substantially below the major axis of the dentary condyle. The presence of two articulations that are not coaxial poses a biomechanical challenge whose details we are unsure how to resolve at present. Obvious models for a dual mandibular articular system are offered by embryos and perinatal mammals, in which the middle part of Meckel's cartilage and the first arch derivatives (such as the articular/malleus) are reduced or resorbed late in ontogeny (e.g., Maier, 1987, 1990, 1993; Zeller, 1989; Rowe, 1996; Meng et al., 2003), and by exceptional fossils (Wang et al., 2001; Meng et al., 2003). Coaxial dual articulations are mechanically simple and have been present in the temporomandibular joint (TMJ) in most of the basal mammaliaforms (Allin, 1975, 1986; Crompton and Hylander, 1986; Allin and Hopson, 1992; Rosowski, 1992). However, alternative noncoaxial contacts between the postdentary elements and/or Meckel's cartilage are likely to have occurred in fossils (Meng et al., 2003; Ji et al., 2006) and are present at least during some stages of development of recent mammals, thus offering a possible model for fossils like *Henosferus*. The tree topology obtained in this study includes *Henosferus* as a basal australosphenidan; monotremes appear to be a terminal group of this clade and would constitute the closest models for *Henosferus*. In fact, Rich et al. (2005a,b) have recently postulated the retention of postdentary elements in Mesozoic toothed monotremes, which makes consideration of monotreme anatomy even more relevant for the understanding of australosphenidan morphology.

Rich et al. (2005a) proposed an independent origin of the middle ear bones in monotremes and therians based on their interpretation that a basal toothed monotreme (i.e., *Teinolophos trusleri*) possessed middle ear bones still attached to the dentary. Rich et al. (1999a, 2002), however, do not accept links between australosphenidans and monotremes, but consider australosphenidans as members of basal Eutheria (Woodburne, 2003; Woodburne et al., 2003).

The presence of postdentary elements in *Teinolophos* (and by extension, ancestrally in monotremes) was challenged (Bever et al., 2005; Rougier et al., 2005) and reasserted by the original authors (Rich et al., 2005b). All of the known specimens of *Teinolophos* are fragmentary and represented only by dentaries; therefore, the actual morphology of any putative postdentary element is not known, but deduced from the morphology of the dentary. There is no objection against this practice (we ourselves have done so to understand the morphology in *Henosferus*), but the quality of preservation of the dentary is crucial for extrapolating the anatomy of the postdentary elements. In our view (Rougier et al., 2005), the specimen assigned to *Teinolophos* lacks unambiguous facets indicating the presence, or location, of any of the middle ear bones (articular, goniale, and incus), and even if the argument is relaxed to include the angular/tympanic (not a middle ear ossicle), we see no compelling evidence of a facet for the prearticular–articular complex. The presence of a "facet" for the angular/ectotympanic is ambiguous at best; based on all of the specimens, we are confident that the surface identified as a "facet" for the angular, in fact, extends inside the mandibular canal, a trait not seen in other nonmammaliaform cynodonts and mammaliaforms. The arrangment proposed by Rich et al. (2005a,b) is not supported by any model either living or fossil and can be more plausibly understood as the bottom of the enlarged mandibular foramen of monotremes that transmits a hypetrophied trigeminal system (Griffiths, 1978; Kuhn and Zeller, 1987; Zeller, 1989). *Teinolophos* has the distinct medial process that overhangs the mandibular foramen and determines an inordinately large mandibular foramen. A very large mandibular foramen is a rare condition in mammals but present in living and fossil monotremes (Musser, 2003), indicating the presence of a hyperdeveloped trigeminal system in the Cretaceous monotremes. This morphology lends support to our (Rougier et al., 2005) interpretation of the "facet" and flattened area of Rich et al. (2005a) as preservation artifact and floor of the mandibular canal, respectively. Despite troublesome preservation, we accept that ridges may be present in the back of the *Teinolophos* jaw. However, it does not show a suitable morphology to provide attachment of a sizable postdentary complex, no real medial flange is present (*contra* Rich et al., 2005a,b), and the weak ridge runs directly into the mandibular foramen, a fact more easily explained in connection to soft structures than postdentary elements.

In addition, Bever et al. (2005) remarked on the ambiguity of assigning the new specimens of *Teinolophos* to this species and argued for separated treatments of the specimens as different terminal taxa. We have argued (Rougier et al., 2005) that, even accepting the assumptions of the original authors (Rich et al., 2005a), the optimization is equivocal; under one of the two possible optimizations of the cladogram originally presented, independent origin of the middle ear in monotremes and therians is not supported. Therefore, the same cladogram also supported a single origin for the postdentary elements. In cases with ambiguous support, as here, it is a safe systematic practice not to regard only one optimization as supporting a given character transformation. The results of the optimization of this feature in the cladogram presented originally by Rich et al. (2005a) becomes a moot point when a larger set of relevant taxa, as we do here, is studied. If indeed *Henosferus* and monotremes are both members of Astralosphenida, the conclusion that the freeing of the middle ear elements in monotremes and therians is independent seems unavoidable. Rougier et al. (2005) recognized "other Mesozoic forms may question the monophyletic origin of the mammalian middle ear"; our more extensive study of *Henosferus* here further substantiates this challenge. According to our view, as deduced from the cladogram, the henosferids would retain a generalized mammaliaform arrangement of postdentary elements, reduced from the condition in *Morganucodon* and allies but still essentially mandibular in nature. Later australosphenids including ausktribosphenids and monotremes would have already achieved free, or mostly free, ear ossicles.

To sum up, *Henosferus* and the australosphenidans are interpreted as one of the basal branches of Mammlia and potentially forming part of the stem lineage leading to monotremes. Eutherian affinities for Australosphenida as a whole or for any of its members are here not supported and therefore a Southern continet origin for placentals is considered unlikely. The medial trough of *Henosferus* and its associated structures suggest the presence of postdentary bones at least partially attached to the dentary. These elements would be reduced in comparison with those of *Morganucodon* (Kermack et al., 1981). *Henosferus* presents the strongest evidence of postdentary elements for any australosphenidan, and, under the present cladogram, implies independent detachment of the angular and articular bones from the dentary of basal australosphenidans and therians. Obviously, the inclusion of Monotremata among australosphenidans is crucial for the postulation of independent liberation of postdentary elements among members of the crown group Mammalia. The inclusion of Monotremata in Australosphenida is a controversial topic (Luo et al., 2001a, 2002; Rich et al., 2002; Woodburne, 2003; Woodburne et al., 2003; Martin and Rauhut, 2005); our cladogram supports this membership (although the support of this branch is low; Bremer suport: 2), but we do not regard this study as a thorough exploration of this problem. Several preservational issues, such as the lack of upper dentitions, cranial, or postcranial material for any australosphenidans, make our results tentative. Better specimens of australosphenidans have the potential to drastically change the topology of the tree and the conclusions that can be drawn from it.

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APPENDIX 1

TABLES OF MEASUREMENTS OF *HENOSFERUS MOLUS* AND RECONSTRUCTION OF M1 INDICATING MEASUREMENTS OF THE MOLAR

All measurements are given in millimeters. Asterisks (*) indicate estimated measurements.

DENTARY

	MPEF 2353	MPEF 2354
Length of dentary	22.24	22.48*
Depth of dentary below posterior root of p1	1.67 (lingual)	1.73 (labial)
Depth of dentary below anterior root of m1	2.14 (lingual)	—
Length of symphysis	5.75	—
Length of incisor row	2.77*	2.83
Length between c and m3	11.02*	12.69*
Length between p1and m3	10.06*	11.02*
Length between m1 and m3	3.50*	3.49*

LOWER DENTITION

The measurements of premolars were taken from MPEF 2354. The molar measurements are shown in figure 10.

	p1	p2	p3	p4	p5
Length	0.68	0.72	0.95	1.13	1.20*
Height	1.09	1.17	1.32	1.35	1.40*

	MPEF 2353 m1	MPEF 2354 m1	MPEF 2354 m2	MPEF 2354 m3
1	1.70	1.69*	1.56	—
2	0.74	0.75	—	—
3	0.74	—	0.75	—
4	0.99	—	0.95	—
5	1.14	—	1.03	0.95
6	0.83	—	0.83	—
7	—	1.45	—	—
8	0.55	0.96	—	—
9	110°*	—	85°*	95°*

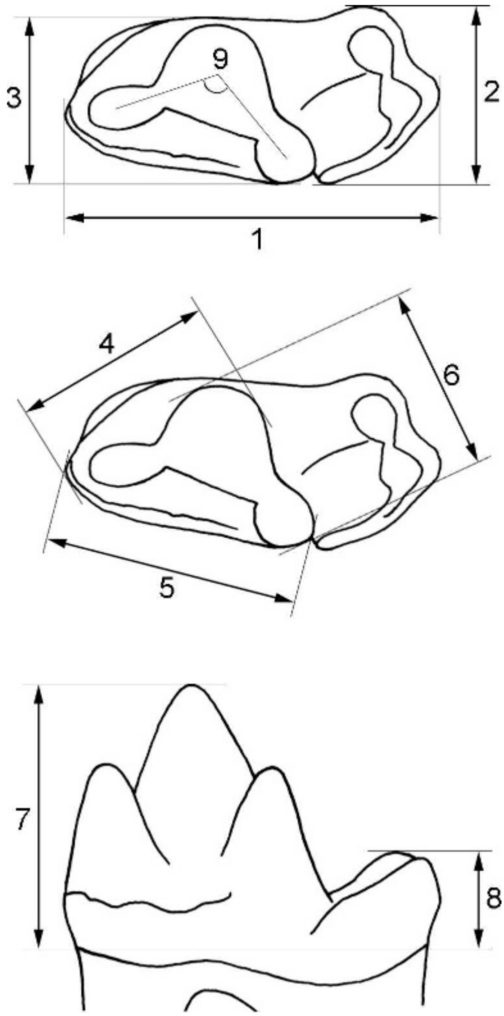

Fig. 10. Measurements of the lower molar.

APPENDIX 2

CHARACTER LIST

INGROUP TAXA: In this study we have incorporated *Asfaltomylos patagonicus* (Rauhut et al., 2002; Martin and Rauhut, 2005) and *Henosferus molus*, the new taxon described here, to the data matrix of Luo et al. (2002). The codification for *Asfaltomylos patagonicus* follows Martin and Rauhut (2005); otherwise we comment on our changes below. We consider zhangeotheriids as represented by *Zhangeotherium quinquecuspidens* (Hu et al., 1997) and *Maotherium sinensis* (Rougier et al., 2003b). Most of the scorings of each taxon were based on personal observation of the specimens and also from published sources.

CHARACTER LIST MODIFICATIONS: Recently, Woodburne et al. (2003) published a revision of the data matrix of Luo et al. (2001a) in order to review the hypothesis of the dual origin of the tribosphenic molar pattern. They introduced several modifications to characters 1–55 enunciated in the first matrix (of 125 characters) of Luo et al. (2001a), and the character states for each taxa were review and in many cases recoded. Unfortunately, the extensive work of Woodburne et al. (2003) was based on the first data matrix (Luo et al., 2001a) and not on the subsequent contribution in which 150 more characters were added (Luo et al., 2002).

Some modifications proposed in definition of the character or in the codification of states for taxa by Woodburne et al. (2003) had been included and/or modified (and amplified) in Luo et al. (2002); these characters are 5, 22, 32, 36, 37, 44, 47, and 54. Characters 6, 11, 21, and 44 were also amplified in Luo et al. (2002). For our purposes, we used the data matrix of Luo et al. (2002), and additionally we evaluated the modification suggested by Woodburne et al. (2003).

MODIFICATIONS TO THE DATA MATRIX OF LUO ET AL. (2002)

Character 1. Changed the character state in *Steropodon* from 0 to ?. Woodburne et al. (2003) suggested scoring *Steropodon* as 1, but this is not followed here. *Ausktribosphenos* and *Bishops* change from 0 to 1. The postdentary trough in both *Ausktribosphenos* and *Bishops* does not qualify as a groove; it is extremely shallow and with essentially no extension behind the mandibular foramen.

Character 2. Deleted because a separated scar for the surangular and prearticular is not evident in most specimens still having a dentary trough and the interpretation of this feature is ambiguous.

Character 3. This feature is deleted because we considered it redundant with character 1. A medial ridge is present in all taxa in which a medial trough is known.

Character 4. *Teinolophos* and *Bishops* change from ? to 1; *Gobiconodon* from 0 to 1; *Jeholodens* from 0 to ?. We keep the presence of a Meckel's groove in *Steropodon*; it is very faint and runs subparallel to the jaw. *Obdurodon* changes from ? to 0. In *Obdurodon* a crease indicates the position of Meckel's groove; it is small and very faint, but better seen in the anterior half.

Character 5. *Steropodon* changes from 0 to 1; *Teinolophos* from 2 to 1, based on a new dentary (Rich et al., 2005). *Jeholodens* changes from 1 to 1 + 2.

Character 6. Changed the character state in tritylodontids (e.g. *Kayentatherium wellesi*; Sues, 1986) from 0 to 1. *Ausktribosphenos* and *Bishops* change from ? to 1. *Hadrocodium* and zhangeotheriids changes from 2 to 1. *Obdurodon* change from 2 to ? because the front of the jaw is unknown.

Character 8. Character wording and states changed. We merge conditions 1, 5, and partially condition 0 of Luo et al. (2002) into our condition 0. As stated here, condition 0 reflects the absence of a distinctive angular process (or poor development) among basal members of the mammalian lineage. The character state modification results in the following transformations: In addition to the original taxa the condition 0 is now present in *Megazostrodon*, *Dinnetherium*, *Khueneotherium*, *Shuotherium*, *Ornithorhynchus*, *Gobiconodon*, *Amphilestes*, *Jeholodens*, *Priacodon*, *Trioracodon*, *Haramiyavia*, plagiaulacidans, cimolodontans, *Tinodon*, and *Zhangheotherium*. The following taxa were originally coded as 0, but are here included in condition 1 (straight, posteriorly directed process): *Peramus*, *Amphitherium*, *Dryolestes*, *Henkelotherium*, *Vincelestes*, *Kielantherium*, *Prokennalestes*, and *Erinaceus*. *Obdurodon* is coded as 3 to account for the medially inflected, well-developed angle, which is, however, not continued as a shelf (metatherian condition).

Character 9. Slight changes to the character states; we suppress additional information in the character states because the reference changes and makes the scoring confusing. Position of angular process (antero-posterior position relative to the dentary condyle): anterior position (the angular process is below the main body of the coronoid process) (0); posterior position (the angular process is placed at the same level as the posterior end of the coronoid process) (1). *Ausktribosphenos*, *Bishops*, *Teinolophos*, and *Obdurodon* change from 0 to 1. *Ornithorhynchus* changes from ? to 1 based on specimens with a small angular process. It is difficult to know where it would be with regard to the posterior edge of the coronoid process, but, comparing with *Obdurodon*, it seems to be in the same relative position.

Character 10. Slight change in wording of condition 1; we suppress additional information without changing the original meaning of the enunciate. Position of angular process (vertical position): low, at or near the level of the ventral border of the mandibular horizontal ramus (0); high, at or near the level of the molar alveolar line (1). *Obdurodon* and *Teinolophos* change from 1 to 0. *Ausktribosphenos* changes from 1 to 0 + 1 because the two known specimens show different conditions: the type has the angular process at the level of the alveolar margin and a referred specimen has it clearly at the level of the bottom of the mandibule. *Ornithorhynchus* changes from ? to 1 based on specimens with preserved remnants of the angular process.

Character 11. *Bishops* changes from ? to 0; the sutures are not clear at all, but there is a change in texture in all three specimens preserving the pertinent area. *Obdurodon* changes from 1 to 0 because it seems to have a change in texture in the area. *Asioryctes* changes from 1 to 0 to be consistent when scoring similar depressions in *Montanalestes* and *Prokennalestes* as representing the coronoid either fused or a facet for it.

Character 12. Deleted because this character depends on the presence of dentary trough (Ch. 1) and has the same distribution of character states as character 1.

Character 13. Wording of the character and character states changed to: medial concavity (fossa) on the dentary angular process: present (0) or absent (1), because references to support to the reflected lamina are difficult to determine even in well-preserved specimens. *Shuotherium*, *Gobiconodon*, *Amphilestes*, *Jeholodens*, *Priacodon*, *Trioracodon*, multituberculates, *Tinodon*, and zhangheotheriids change from 1 to ? because an angular process is absent in all these forms (Ch. 8), and therefore the character is not comparable. *Kielantherium* changes from 1 to ?.

Character 14. Deleted because it is almost impossible to distinguish a separate scar for the splenial in most taxa.

Character 15. Deleted because in most taxa an individual surangular bone is not known and determination of the presence/absence of this trait based solely on dentary morphology is unwarranted and equivocal. The surangular has been positively identified only in *Morganucodon* (Kermack et al., 1973: plate 4) and *Megazostrodon* (Gow, 1986: fig. 6) among basal mammaliaforms.

Character 16. We consider a pterygoid fossa a continuous depression interpreted for the pterygoid musculature (both the superficial and deep pterygoids) that approaches the ventral edge of the jaw. *Haldanodon* changes from 1 to 0 following our interpretation (Luo et al. also recognized that the pterygoid fossa of *Haldanodon* was unlike that of therians and basal member of that lineage).

Character 17. The character state (0) was deleted. All taxa originally scored as lacking the pterygoid fossa (condition 0) in Luo et al. (2002) are now score as (?) with the exception of multituberculates, which have condition 1.

Character 18. There are differences with regard to the way in which the border is marked; in some taxa the crest is better developed anteriorly and in others posteriorly. However, we consider them all to be expressions of the same feature. *Ausktribosphenos* and *Bishops* change from 2 to 1.

Character 19. Conditions 1 (crest along the anterior border of masseteric fossa present) and 2 (present and laterally flaring) were merged as a single state indicating the presence of a conspicuous crest along the anterior edge of the masseteric process. We found it difficult and ambiguous to determine between conditions 1 and 2 in Luo et al. (2002). The wording of the amended character and character states is: crest of the masseteric fossa along the anterior border of the coronoid process: absent or weakly developed (0); forming a distinct anterior border (1). Because of the change, all the taxa codified as 2 in Luo et al. (2002) are now changed to 1, with the exception of *Ornithorhynchus*, which is changed to ?, because it does not have a developed coronoid process, and therefore an anterior margin cannot be determined.

Character 21. We changed the wording of the character states to reflect the similar morphology found in taxa like the Australian forms and dryolestoids, *Vincelestes* and therians; scoring was modified according to the new character states. Orientation of the dentary peduncle and condyle: (0) dentary peduncle is posteriorly directed (forms an angle of 35° or less to the alveolar margin); (1) dentary condyle is continuous with the semicircular posterior margin of the dentary; (2) dentary articulation extends vertically for the entire depth of the horizontal ramus of mandible; it is confluent with the horizontal ramus and lacks a peduncle; (3) vertically directed dentary peduncle (above 35°). *Peramus* changes from 1 to 0; *Tinodon*, *Pucadelphys*, *Didelphis* from 0 to 1; *Deltatheridium*, *Asiatherium*, *Erinaceous*, *Asioryctes*, and *Montanalestes* from 0 to 3; *Amphitherium*, *Dryolestes*, *Henkelotherium*, and *Vincelestes* from 1 to 3; *Shuotherium* from ? to 0 + 3. *Obdurodon* changes from 3 to 0; one of the main differences of the preserved portions of the dentary is the angle of the peduncle, which in *Obdurodon* is very low. Other scorings follow Luo et al. (2002).

Character 22. Changed the character state in *Kuehnotherium* from 0 to ?, because among published sources there is no complete condyle for *Kuehnotherium*, and the authors are unaware of specimens preserving this area. *Asiatherium* changes from ? to 1. *Obdurodon* changes from 1 to ?, because it is unknown. The condyle in both zhangheotheriids considered here does not conform too closely to any of the states employed here; nevertheless and with some trepidation we retain zhangheotheriids as condition 1.

Character 23. Character wording changed to: ventral inferior border of the dentary peduncle: posteriorly tapering without a condyle (0); robust process, columnar or ridgelike (1); ventrally flaring (probably correlated to the presence of a pseudangular process) (2); or robust and short (3). *Peramus*, *Dryolestes*, *Henkelotherium*, *Amphitherium*, and *Vincelestes* change from 3 to 1. Taxa scored as (4) in Luo et al. (2002) are now coded as (1).

Character 24. *Shuotherium* changes from ? to 1. Cimolodontans change from 0 + 1 to 0, because condition 0 can be optimized as plesiomorphic for the group as a whole under the tree topologies recovered by most recent phylogenetic studies (Kielan-Jaworowska and Hurum, 1997; Rougier et al., 1997).

Character 25. *Ornithorhynchus* actually lacks the coronoid process; it changes from 2 to ?.

Character 26. Wording of the character and states changed in order to avoid reference to the time of eruption; the meaning of the character is the same as in Luo et al. (2002). Alignment of ultimate molar to the anterior margin of the dentary coronoid process: ultimate functional molar is medial to the coronoid process (0); or ultimate functional molar is in alignment with the anterior margin of coronoid process (1). *Jeholodens* changes from 0 to ?, because it is based on a juvenile specimen.

Character 27. *Vincelestes* and *Erinaceous* change from 1 to 0; *Ambondro* from 1 to 0; *Jeholodens* from 0 to 1. Woodburne et al. (2003) added character state 2 (Ch. 15) for *Obdurodon*: asymmetric, with the posterior edge of the cusp a longer and more convex in outline than the anterior edge. The introduction of this character as a sole autapomorphy of *Obdurodon* has no bearing on the resolution of the affinities of monotremes. Although we recognize that the tooth in question is slightly asymmetrical, we believe this is mostly due to the lingual development of a small basin; the cusp preserves a fairly symmetrical outline in labial view and is with some hesitation scored as such in this study.

Character 28. We changed the wording of the character states to deal with the cingular nature of cusp b in some taxa, the absence of a cusp c in some others, and refer the comparisons to cingular cusps when the main cusps are not available. Ultimate lower premolar–anterior cusp b (paraconid): (0) present (at least subequal to cusp c, or posterior cingular cusp of the same tooth); or (1) small (much smaller than cusp c or posterior cingular cusp of the same tooth) or absent. *Gobiconodon* changes from 1 to ?, because the last premolar is reduced and not well known. *Prokennalestes* changes from 1 to 0. *Obdurodon* changes from 0 to 1 based on Archer et al. (1992, 1993), Woodburne (2003), and Woodburne et al. (2003).

Character 29. Changed the character state in *Obdurodon* from 1 to 0. *Peramus* changes from 0 to 1. *Ambondro* changes from 1 to 0 following Woodburne et al. (2003).

Character 30. *Dryolestes*, *Henkelotherium*, and *Amphitherium* change from 0 to 1; *Vincelestes* from 0 to 1; and *Jeholodens* from 1 to 0.

Character 31. We changed wording of character states to: (0) laterally compressed, outline of the crown longer than wide; (1) bladelike, close to twice as long as wide; (2) or transversely wide, crown outline subequal or wider than long. *Ambondro* and *Erinaceus* change from 2 to 0.

Character 32. Changed the character state in *Bishop* from ? to 0, and in *Ambondro* and *Ausktribosphenos* change from 1 to 0. The illustration of the cingulum in *Ausktribosphenos* in Rich et al. (1999a) is exaggerated based on observation of the specimens. *Gobiconodon* changes from 1 to 0. Zhangeotheriids change from 0 to 1. Most of these changes agree with Woodburne et al. (2003).

Character 33. *Henkelotherium* and *Vincelestes* change from 0 to 1.

Character 34. *Megazostrodon*, *Dinnetherium*, *Morganucodon*, *Kuehneotherium*, *Shuotherium*, *Tinodon*, zhangeotheriids, and *Vincelestes* change from 0 to 1. *Obdurodon* changes from ? to 0.

Character 35. *Jeholodens* changes from ? to 0.

Character 36. *Jeholodens* changes from 0 to ?; zhangeotheriids from 0 to 1. Tritylodontids, *Haramiyavia*, plagiaulacidans, and cimolodontans are changed from 2 to ?, because condition 2 is redundant with conditions 2 and 3 of character 29. Therefore, condition 2 is deleted here.

Character 37. This character is deleted because condition 2 is redundant on character 36 (2) and therefore coded as ? here to avoid redundant information. The cusps do not seem to be triangular either in *Ausktribosphenos* or in *Bishops*.

Character 39. We changed character state 2. The original condition 2 (Luo et al., 2002) was deleted because it is logically dependent on the same character state as 38 (3), cusps in line, and therefore tritylodontids, *Haramiyavia*, plagiaulacidans, and cimolodontans were scored as ?. In addition, we added character state: (2) obtuse angle; because of the presence of this condition in *Henosferus*. *Kuehneotherium* and *Tinodon* change from 0 to 2 and zhangheotheriids and *Vincelestes* from 1 to 2.

Character 40. Deleted because it is exactly the same as character 95, and logically the same as 38.

Character 41. *Shuotherium* changes from 0 to 1 following Wang et al. (1998).

Character 43. *Jeholodens* changes from 1 to 2 based on personal observations, and *Kokopellia* changes from 0 to 1 based on specimens.

Character 44. Change in wording of condition 1 of Luo et al. (2002) in order to clearly make the character state contrary to condition 0. Relative height of the primary cusp a (protoconid) to cusp c (metaconid) of the anterior lower molars (measured as the height ratio of a and c from the bottom of the valley between the two adjacent cusp, on m1): (0) posterior cusp c is less than 40% of the primary cusp a; or (1) posterior cusp c is more than 40% of cusp a (1). *Amphitherium* and *Peramus* change from 0 to 1. *Asiatherium* changes from 1 to 0. *Didelphis* changes from 2 to 0 based on specimens

Character 45. We changed the character order as Woodburne et al. (2003). We are following traditional understanding of docodont cusps and in the previous character, therefore, *Haldanodon* is not comparable (?). The relative size of the paraconid and metaconid in *Henosferus* is difficult to establish without caveats, but both the type and MPEF 2357 suggest that the bases of the paraconid are higher and more robust than that of the metaconid; therefore, we score *Henosferus* as 2.

Character 46. Modified based on personal communication from Z.-X. Luo A.C. Garrido, personal communication; this character refers in fact to the relative position of the cusp base and not to the cingulid: Relative elevation of the bases of the paraconid (cusp b) and metaconid (cusp c): (0) at the same level; (1) base of paraconid higher than base of metaconid; or (2) base of metaconid higher than base of the paraconid. Changed the character state from 1 to 2 in *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, and *Obdurodon*. *Ornithorhynchus* changes from 1 to ?.

Character 47. *Ambondro* changes from 3 to 1, *Vincelestes* from 0 to 1.

Character 48. We changed the character wording considering only the condition of the "pre-entocristid" (presence of "pre-hypoconulid crest" is considered in a new character below). Change in wording of condition 3 in order to include the new taxon. We deleted character states (2); therefore, taxa scored as 2 in Luo et al. (2002) are now ?. In *Henosferus* the "pre-entocristid" crest does not pass the base of the metaconid and, therefore, the wording of the new character state 2 is: "pre-entocristid" crest is offset from the metaconid (and postmetacristid if present) and the "pre-entocristid" is lingual to the base of the metaconid. Taxa scored originally as 3 in Luo et al. (2002) are now scored (2). *Amphilestes* changes from ? to 0.

Character 51. *Kuehneotherium* changes from 0 to 1.

Character 52. *Jeholodens* changes from 0 to 1.

Character 53. Changed the character state in *Steropodon* and *Obdurodon* from 0 to 1, in part following Woodburne et al. (2003). The presence of a cingulum has not been equated to the presence of a cusp. In *Deltatheridium* the m1 has a very small bulge in the position of cusp e we interpret as homologous with that of more posterior positions; this taxon is therefore changed from 0 + 1 to 1. *Jeholodens* changes from 1 to 0.

Character 54. We are not considering cingula. We change *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, and *Erinaceus* from 1 to 0 following, in part, Woodburne et al. (2003). *Jeholodens* changes from 0 to ?.

Character 55. Condition 1 (discontinuous cingulum present as cusp e, f, or both, but not connected) is merged with condition 0 (absence) and the consideration is of the derived complete mesial cingulum. All taxa originally scored as 3 are now 2. All taxa originally scored as 2 are now 1. All taxa scored as 1 are now 0. *Morganucodon*, *Dinnetherium*, *Kuehneotherium*, *Tinodon*, and zhangheotheriids change from 0 to 1.

Character 56. This character has been modified from Luo et al. (2002); character state 3 was deleted. The amended character and character states are: cingulid shelf wrapping around the anterior-internal corner of the molar to extend to the lingual side of the trigonid below the paraconid: (0) absent; (1) present, weakly developed, restricted to the mesial aspect of the paracone base; or (2) present, strongly developed, running along most of the lingual base of the paraconid. *Obdurodon* changes from 1 to 0 + 1 because of the incertitude about its morphology. Taxa with lingual cingulid were considered and the character states were changed from 0 to 2 for *Morganucodon*, *Dinnetherium*, *Kuehneotherium*, *Tinodon*, and zhangheotheriids. *Megazostrodon* changes from 0 to 1; *Haldanodon* from 3 to 0; *Shuotherium* from 3 to 2.

Character 57. *Shuotherium* changes from 2 to 0, based on study of s cast and figures.

Character 58. Condition 1 changed to reflect criticism of the character by Woodburne et al. (2003). Character states (1) is: interlocking present, posterior cuspule d (or the base of the hypoconulid) of the preceding molar fits in between cingular cuspules e and f of the succeeding molar or teeth meet flat surfaces of the mesiolabial cingulum. Changed the character state in zhangeotheriids from 0 to 1. *Jeholodens* changes from 3 to 1. *Asfaltomylos is* scored as 1 instead of 0 contra Martin and Rauhut (2005).

Character 59. It is likely that *Asfaltomylos* should be coded as 0 for this character, based on the broken base of the root in the type; however, as it is equivocal at present we follow the original scoring by Rauhut et al. (2002) and Martin and Rauhut (2005). *Jeholodens* changes from 1 to ?, because m4 is erupting and there is likely another molar to emerge (m5). *Teinolophos* changes from ? to 1 based on the fact that the type preserves the last molar and that NMV 575 preserves the penultimate and two other more mesial molars. *Ornithorhynchus* changes from ? to 0 based on juvenile dentition.

Character 60. Deleted because partially overlaps with character 61 and covers only part of the variability of character 61 (only taxa with trigonid). Character states (0) and (1) of character 60 are grouped together in character 61 (1).

Character 61. *Bishops* changes from 2 to 1.

Character 62. *Jeholodens* changes from ? to 0.

Character 64. *Peramus* and *Amphitherium* change from 0 to 1; *Henkelotherium* from ? to 0. *Ambondro* changes from 2 to 1 following Woodburne et al. (2003).

Character 65. Slight changes in the wording of character states 0–4. Morphology of the talonid: (0) absent or present as a cingulid or cingular cusp d; (1) present as an incipient heel, that is, a small horizontal surface; (2) present as a heel (with at least one functional cusp); (3) present as a transverse V-shaped basin, two major cusps; or (4) present as a functional basin, rimmed with 3 major cusps. *Probainognathus* and tritheledontids change from ? to 0; *Kuehneotherium* and zhangeotheriids from 1 to 0; *Ornithorhynchus* from 3 to ?.

Character 66. Slight changes in the wording of character states 0 and 1 and deletion of character state 2, because this condition is different from that evaluated in conditions 0 and 1. Hypoconulid (= cusp d): (0) hypoconulid at the cingulid level; or (1) hypoconulid elevated above the cingulid level. *Dryolestes* and *Henkelotheriun* coded as 2 in Luo et al. (2002) were changed to the new condition 1.

Character 67. Redefined as suggested by Luo (personal communication, 2004). The character wording was considered a mistake. New definition: hypoconid as part of a talonid: (0) absent, or (1) present. *Vincelestes* changes from 1 to 0; *Gobiconodon*, *Amphilestes*, *Priacodon*, *Trioracodon*, *Jeholoden* from ? to 0.

Character 68. Character changed from Luo et al. (2002). The characters states and the character definition consider different features not mutually excluding (i.e., character definition refers solely to the hypoconulid, but the character states consider in addition aspects of the posterior wall of the trigonid and the slant of the area). Our states consider solely the inclination of the cusp. Hypoconulid anteroposterior orientation: (0) erect or procumbent; or (1) recumbent (reclined). Taxa scored as (2) in Luo et al. (2002) are now scored as (0). Taxa scored as (1) in Luo et al. (2002) are now scored as (0). Taxa scored originally as (0) in Luo et al. (2002), excepting *Kielantherium*, are now scored as 1. *Kuehnotherium*, *Jeholodens*, *Tinodon*, zhangeotheriids, and *Vincelestes* change from ? to 0; *Amphitherium* from ? to 1.

Character 69. *Jeholodens*, zhangeotheriids, and *Vincelestes* change from ? to 0, and *Didelphis* changes from 1 to 0.

Character 70. Small wording changes in definition of character state (1): present but far from hypoconulid (at least equal to one cusp size). *Ornithorhynchus* changes from ? to 0. *Deltatheridium* changes from 0 + 1 to 1: the m4 is the only molar lacking the entoconid; it is small in the m3 but well developed in the m1–2. We believe this variation is probably related to the reduction of the posterior molariforms in *Deltatheridium*. *Aegialodon* changes from 1 to 0. *Kielantherium* changes from 0 + 1 to 0, based on original description (Dashzeveg and Kielan-Jaworowska, 1984).

Character 71. State 0 deleted because it is redundant with condition 0 of character 70. Entoconid: (0) lower than the hypoconulid; or (1) subequal in height as the hypoconulid. Taxa scored originally as 0 in Luo et al. (2002) are now scored as ?. We score *Asfaltomylos* as 0 based on study of a cast.

Character 72. *Ambondro* changes from 1 to 0 based on personal observation. *Kielantherium* and *Aegialodon* changes from 0 to ?, because of the lack of the entoconid. *Erinaceus* and *Deltatheridium* change from 0 to 1 based on specimens.

Character 73. *Tinodon*, zhangheotheriids, *Amphitherium*, *Dryolestes*, and *Henkelotherium* change from ? to 0. The sole cusp on the back of the tooth is considered homologous to a talonid. *Ambondro* changes from 1 to 1 + 2, because the m1 and m2 show different conditions.

Character 74. We change the word hypoconid for hypoconulid as was written in the original character of Luo et al. (2002); however, this mistake was fixed in Luo et al. (2003). Character states (3) and (4) are merged; the difference of 10% is seen among different elements in the same tooth row and within the margin of error produced by wear and deformation. Condition 3 is reworded as ratio 50% or higher. *Ambondro* changes from 3 to 1, based on estimated height of the protoconid when complete. *Dryolestes* and *Henkelotherium* change from 1 to 0 based on specimens. All taxa scored originally as (4) in Luo et al. (2002) are now score as (3). *Aegialodon* changes from 2 to 1, based on the extensive wear of the protocone, which we believe changes the proportion of the cusps.

Character 75. Character states 2 and 3 are merged as (2): stylar shelf present and broad (we are not here considering the presence of ectoflexus; this feature is considered in the new character 285). All taxa originally scored as (3) in Luo et al. (2002) are now scored as (2).

Character 76. Zhangeotheriids change from 1 to 2. *Haramiyavia*, plagiaulacidans, and cimolodontans change from 0 to ?, because under most hypotheses concerning the origin of multituberculate upper molars, both the labial and lingual cingulum are involved in the formation of cusps rows. We prefer to score these groups as ?, because we are uncertain about the details of the contributions of the cingula.

Character 77. Character wording was changed in order to reflect homology of the protocone (pseudoprotocone is not considered in the amended character). *Haldanodon* and *Shuotherium* change from 1 to 0. *Haramiyavia*, plagiaulacidans, and cimolodontans change from 0 to ?, because we are uncertain about the homologies of multituberculate cusps with those of tribosphenic molars.

Character 78. *Vincelestes* and *Peramus* change from ? to 0.

Character 79. *Deltatheridium* changes from 0 to 0 + 1 based on specimens (variation along the tooth row).

Character 81. *Asiatherium* changes from 1 to 0 based on Szalay and Trofimov (1996).

Character 82. *Asiatherium* changes from 1 to 0 based on Szalay and Trofimov (1996) and personal observation of the specimen.

Character 83. *Haramiyavia*, plagiaulacidans, and cimolodontans change from 1 to ?, because the homologies between multituberculate and tribosphenic dentitions are uncertain.

Character 86. Deleted, because it repeats information in character 85. Serial homology explains similar morphology of M1/m1 (Van Valen, 1994).

Character 93. *Haramiyavia* and zhangheotheriids change from 2 to 1, because the cusps are bulbous upon eruption and the flat wear facets are developed by substantial removal of the cusp slopes.

Character 94. Condition 0 is redundant on condition 0 of character 93; this state is therefore here removed and taxa with condition (0) are now scored as (?) so as not to be redundant. *Jeholodens* changes from 2 to 1.

Character 95. Zhangheotheriids change from 2 to 1 based on specimens.

Character 97. *Vincelestes* changes from 0 to 1 based on specimens.

Character 98. *Ausktribosphenos* and *Bishops* change from 1 to ?, because the facets are not evident based on Rich et al. (2001a) and personal observations. *Ornithorhynchus* changes from 2 to ?; no wear facets can be recognized on the juvenile teeth. We keep state 2 for *Steropodon*; nevertheless, there is not a clear indication of facet 4. *Vincelestes* has clearly developed facet 3, but 4 is not easily recognized; if at all present it would be small, distal to the hypoconulid; the character is nevertheless changed from 0 to 1 in this taxon.

Character 99. *Vincelestes* changes from ? to 0. *Ausktribosphenos* and *Bishops* change from 1 to ? following with character 98.

Character 100. This character is deleted, because it is correlated and redundant with character 99 (when the facet is transverse the posterior face is angular).

Character 101. *Ausktribosphenos* and *Bishops* are changed from 1 to 0 based on personal observation and in agreement with Martin and Rauhut (2005). *Ambondro* is scored as ?, because the presence of wear facts in the talonid is controversial (see Martin and Rauhut, 2005).

Character 102. *Teinolophos* changes from 1 to 0; there is a crest that goes down from the tip of the metaconid into the talonid, which is ambiguously aligned with the crista obliqua or the lingual edge of the molar in the direction of the hypoconid. *Steropodon* has the same prominent crest, but this time unambiguously aligned with the crest from the hypoconid; therefore, *Steropodon* changes from 1 to 0. *Ornithorhynchus* changes from 1 to ?.

Character 103. This character is deleted, because it is very similar to character 101; the only difference in the scoring was in *Aegialodon*, *Kielantherium*, and *Deltatheridium*. All these taxa have small talonids and, with the exception of *Deltatheridium*, are known by a single specimen. Determination of the presence or absence of facet 6 is equivocal; however, the talonid has an occlusal function. A facet 5 is certainly present in all three. Therefore, the only potential difference between this character and 101 rests on the equivocal absence of a facet 6 in the taxa mentioned above. Until a better determination of the wear in the talonid is possible, we prefer to treat characters 101 and 103 as redundant.

Character 105. *Tinodon* changes from ? to 0 based on Simpson (1925, 1928b). *Kuehneotherium* changes from ? to 0 based on Gill (1974).

Character 106. Deleted because we consider it causally correlated to character 107.

Character 107. Wording changed from "lower canine" to "canine"; following the new wording, plagiaulacidans change from 2 to 1.

Character 108. *Ausktribosphenos* changes from ? to 0 following Rich et al. (1997).

Character 109. Character wording changed. A diastema is considered present when the length is equal or larger than half the length of the P1. *Haramiyavia*, plagiaulacidans, *Amphilestes*, *Tinodon*, *Amphitherium*, *Kielantherium*, *Montanalestes*, and *Prokennalestes* change from ? to 0 based on specimens. *Henkelotherium* (Krebs, 1991: 43), *Deltatheridium*, *Pucadelphys*, and *Asiatherium* change from 1 to 0. Zhangeotheriids change from ? to 1.

Character 110. Wording in character state 2 is restricted to 3 molar/molariforms. *Teniolophos* changes from ? to 1 based on Rich et al. (2005).

Character 112. Zhangeotheriids change from 1 to ?.

Character 113. *Deltatheridium* changes from ? to 1 based on available specimens.

Character 114. *Amphilestes* changes from 1 to ?, because of the lack of material showing dental replacement evidence. *Jeholodens* changes from 1 to ?.

Character 115. Tritheledontids, *Vincelestes*, and *Erinaceus* change from 0 to 1 based on original observation.

Character 117. The character and character states were modified: enlarged diastema in the lower incisor premolar region (rodentiform): (0) absent; or (1) present. All the taxa originally scored as (0) and (1) in Luo et al. (2002) are now score as (0).

Character 118. This character is deleted because we added five new characters (279 to 283; taken from Wood and Rougier, 2005) with regard to this feature.

Character 119. *Vincelestes* changes from 1 to ?.

Character 120. Cimolodontans and *Vincelestes* change from ? to 0, based on specimens.

Character 121. *Jeholodens* changes from 0 to ?. Cimolodontans change from 0 to 1 based on PSS-MAE 101. The absence of a transverse foramen was interpreted as an expression of an unfused atlas rib; this is a likely possibility, but we prefer to score this condition based on well-preserved specimens such as PSS-MAE 101.

Character 124. *Jeholodens* changes from 0 to ?.

Character 125. *Jeholodens* changes from 0 to ?.

Character 126. *Vincelestes* changes from 0 to ?.

Character 128. *Jeholodens* changes from 0 to ?.

Character 129. *Jeholodens* changes from 1 to ?.

Character 130. *Jeholodens* changes from 1 to ?.

Character 131. *Jeholodens* changes from 1 to ?.

Character 133. *Vincelestes* changes from ? to 1.

Character 136. We change the character wording to: scapula with a distinct fossa or process for the *Teres Major* muscle on the lateral aspect of the scapular plate. *Vincelestes* changes from 0 to 1.

Character 137. We change character state (0): present as a free element.

Character 139. *Jeholodens* changes from 1 to ?.

Character 140. We do not consider the adult condition as in the original character wording in order to score *Jeholodens*.

Character 143. Character state (0) is changed to concave instead of convex.

Character 145. *Zhangheotherium* and *Henkelotherium* change from 1 to 0, because they show a morphology closer to *Vincelestes* and other basal mammaliaforms than to therians.

Character 147. *Henkelotherium* changes from 1 to 0. Zhangheotheriids change from 1 to 0 + 1 based on the humerus of *Maotherium*.

Character 151. Cimolodontans change from 0 + 1 to 1 based on character optimization within cimolodontans. *Lambdopsalis* (condition 0) is a highly derived terminal taeniolabidoid (Simmons, 1987; Miao, 1988).

Character 152. *Vincelestes* changes from 0 to 1.

Character 153. *Henkelotherium* changes from 1 to 0 based on original description (Krebs, 1991).

Character 155. *Vincelestes* changes from ? to 0.

Character 156. Zhangeotheriids change from 1 to 0.

Character 157. *Jeholodens* changes from 0 to ?.

Character 158. Character wording change and character states 0 and 2 were merged; therefore, character is: ischiatic tuberosity: (0) dorsal margin with a small or absent ischiatic tuberosity; (1) or dorsal margin concave and ischiatic tuberosity hypertrophied. Taxa scored as 2 in Luo et al. (2002) change to 0.

Character 160. Zhangheotheriids change from ? to 1.

Character 164. *Vincelestes*, *Henkelotherium*, and zhangheotheriids change from 2 to 1.

Character 167. *Jeholodens* and zhangheotheriids change from 1 to 0.

Character 170. *Vincelestes* changes from 2 to 1. *Jeholodens* changes from 0 to 1.

Character 171. *Jeholodens* changes from 0 to ?, because the orientation of the sustentacular facet is somewhat horizontal; however, it is not clear in the specimen if it is smaller than 70°.

Character 173. *Vincelestes* changes from 1 to 0.

Character 175. Zhangheotheriids, *Vincelestes*, *Pucadelphys*, and *Didelphis* change from 1 to 2. *Deltatheridium* changed from ? to 2 based on Horovitz (2000) and specimens.

Character 176. *Vincelestes* and zhangheotheriids change from 0 to 1.

Character 177. This character is deleted because it is redundant with character 171.

Character 178. *Vincelestes* changes from 2 to ?; zhangheotheriids from ? to 1.

Character 179. *Vincelestes* changes from 0 to ?.

Character 180. *Vincelestes* changes from ? to 0.

Character 181. *Vincelestes* changes from 0 to ?.

Character 182. Zhangheotheriids and plagiaulacidans change from ? to 0.

Character 183. *Vincelestes* changes from 1 to 0; zhangheotheriids from ? to 0.

Character 184. *Deltatheridium* changes from 1 to ?; *Asiatherium*, *Pucadelphys*, *Didelphis*, *Erinaceus*, and *Asioryctes* change from 1 to 0.

Character 186. *Jeholodens* changes from 0 to ?.

Character 193. *Jeholodens* changes from 1 to 0 + 1. The petrosal in both *Ornithorhynchus* and *Obdurodon* is rounded and somewhat bulbous, certainly far more similar to the condition in *Vincelestes* than those of triconodontids and others. *Ornithorhynchus* and *Obdurodon* change from 1 to 2 based on specimens.

Character 194. *Jeholodens* and zhangeotheriids change from 0 to ?.

Character 195. *Deltatheridium* changes from ? to 3 based on specimens.

Character 201. *Jeholodens* changes from 1 to ?.

Character 204. Character states 1 and 2 are merged. The new conditions are: (0) ventrally open; (1) partially enclosed by petrosal or lateral flange; (2) enclosed by both the alisphenoid and the petrosal. Taxa scored originally as (2) in Luo et al. (2002) are now scored as (1). Taxa scored originally as (3) are now scored as (2). Zhangeotheriids change from ? to 1.

Character 205. Zhangeotheriids change from ? to 1. *Deltaheridium* changes from ? to 3 because the lack of anterior lamina eliminates states 0–2. Cimolodontans change from 2 + 3 to 2 based on optimization of the characters states (*Lambdopsalis*: condition 3, is a very derived teaniolabidoid and the presence of an ascending process of the alisphenoid is suspect).

Character 206. The character states are reworded: (0) "quadrate ramus" of the alisphenoid forming a rod overlapping with the anterior part of the lateral flange; (1) present but not extending back too far, mostly a laminar process in the vicinity of the oval foramen; or (2) absent. *Trioracodon* changes from 1 to ?. The quadrate remus in monotremes is very small if there is one and borders ventrally the foramen ovale. Two juveniles specimens of *Ornithorhynchus* from the Museum of Victoria (25093 and c5569) have very clear sutures around the ossified ala temporalis.

Character 207. Zhangheotheriids change from ? to 1.

Character 208. This character is deleted because the lateral flange is considered to be the thickened ventral edge of the anterior lamina and therefore the "vertical component of the lateral flange" is seen here as part of the characters dealing with the anterior lamina and structures bounding the cavum epiptericum.

Character 209. *Vincelestes* changes from 1 to 0.

Character 216. Cimolodontans change from 0 + 1 to 1.

Character 218. *Didelphis* changes from ? to 0. *Jeholodens* changes from 0 to ?.

Character 221. This character is deleted and replaced by new character 284 (taken from Rougier et al., 1996).

Character 222. *Deltaheridium* changes from 1 to ? based on specimens.

Character 227. Zhangheotheriids change from ? to 1.

Character 229. Deleted. The "center of mass" alignment is difficult to evaluate in most Mesozoic mammals and seems to be dependent of the geometry of the articulation between the middle ear elements (Character 228).

Character 233. *Ornithorhynchus* changes from 1 to ? because the crus longus is not distinct based on specimens.

Character 235. Zhangheotheriids and *Vincelestes* change from ? to 1.

Character 236. Cimolodontans change from 1 to 2 based on *Kryptobaatar* and other djadochtatherians (Rougier et al., 1996); the columeliform stapes of *Lambdopsalis* is not considered here based on phylogenetic position.

Character 239. *Vincelestes* changes from 1 to 0.

Character 240. *Vincelestes* changes from 1 to ?.

Character 243. Zhangheotheriids change from ? to 1.

Character 244. Cimolodontans change from 0 + 1 to 1, based on the condition of djadochatatherians.

Character 246. Zhangheotheriids change from ? to 0.

Character 247. *Vincelestes* changes from 1 to 0. *Obdurodon* changes from ? to 1 based on specimen.

Character 249. Zhangheotheriids change from ? to 0.

Character 250. *Vincelestes* has a ratio around 8% and therefore falls in between the ranges established for the character. We scored *Vincelestes* as 0 + 1.

Character 252. *Obdurodon* changes from ? to 0. *Deltatheridium* changes from ? to 2 based on the lack of grooves for the arterial system on petrosals.

Character 253. *Jeholodens* changes from 0 to ?.

Character 254. Zhangheotheriids change from ? to 1. *Deltatheridium* changes from ? to 1 based on undescribed specimens.

Character 256. *Vincelestes* changes from 1 to 2 based on specimens.

Character 257. *Vincelestes* changes from 0 to 1.

Character 258. Both *Obdurodon* and *Ornithorhynchus* change from 0 to 1 because of the presence of a large epiphanial foramen interpreted as a branch of the CN V1. Zhangheotheriids change from ? to 0. Plagiaulacidans change from ? to 1, based on paulchofatiid specimens.

Character 259. Zhangheotheriids change from ? to 1. Plagiaulacidans change from ? to 2 based on paulchofatiid specimens (*contra* Hahn and Hahn, 1994).

Character 260. Zhangheotheriids change from ? to 1.

Character 261. Zhangheotheriids change from ? to 1. *Deltatheridium* changes from ? to 1 based on Rougier et al. (1998).

Character 262. In the skull of *Obdurodon*, there are numerous fragments of bone across the area of the ethmoidal plate (cribriform), and a normal plate seems to have been present; therefore, *Obdurodon* changes from ? to 1.

Character 265. *Pucadelphys* and *Didelphis* change from 1 to 0. *Jeholodens* and *Deltatheridium* change from 1 to ?.

Character 266. *Obdurodon* changes from ? to 1. *Jeholodens* changes from 1 to ?.

Character 274. *Shuotherium*, *Ambondro*, *Ausktribosphenos*, and *Bishops* change from 0 to 1 based on tooth form and orientation of wear facets. *Obdurodon* changes from 0 to 0 + 2, following Woodburne's (2003) assessment of an increased palinal component in the mastication of the Tertiary monotremes. *Aegialodon* and *Pappotherium* change from ? to 1.

Character 275. This character is deleted because it is congruent with the conditions of unfused/fused symphysis considered in character 6.

NEW CHARACTERS:

Character 276. Masseteric foramen (labial mandibular foramen inside the masseteric fossa): (0) absent; or (1) present (modified from Rougier et al., 1998; Martin and Rauhut, 2005: Ch. 24X).

Character 277. Position of the mandibular foramen: (0) below or near to the base of the anterior border of the coronoid process; or (1) posterior to the base of the anterior edge of the coronoid process (modified from Rougier et al., 1998).

Character 278. Position of the posteriormost mental foramen: (0) below the canine and anterior premolariform region; (1) below the penultimate premolar; (2) below the ultimate premolar; or (3) between the ultimate premolar and the first molar junction (Martin and Rauhut, 2005: Ch. 23X).

Character 279. Enamel prism shape: (0) absent; (1) arc; or (2) enclosed.

Character 280. Enamel prism seams: (0) present; or (1) absent.

Character 281. Enamel prism packing: (0) hexagonal; (1) erratic; or (2) in rows.

Character 282. Interprismatic matrix: (0) on all sides, widely separated prisms; (1) distinct interrow sheets; or (2) prisms "shoulder to shoulder", little IPM.

Character 283. Outer aprismatic zone: (0) present; or (1) absent.

Character 284. Tensor tympani fossa: (0) indistinct; (1) deep recess on lateral trough anterior to hiatus Fallopii; (2) deep recess on lateral trough posterior to secondary facial foramen (modified from Rougier et al., 1996). This character replaces deleted character 221 of Luo et al. (2002).

Character 285. Staggered incisor: (0) absent, or (1) pressent (Hershkovitz, 1982; Rougier et al., 1998).

Character 286. Deep ectoflexus: (0) present only on penultimate molar; (1) on penultimate and preceding molar; or (2) strongly reduced or absent (Rougier et al., 1998). We added this character because we do not use the features of the ectoflexus in character 75 of Luo et al. (2002).

Character 287. "Pre-hypoconulid" crest (a crest connecting the metaconid with the hypoconulid along the lingual edge of the tooth): (0) absent; or (1) present.

Character 288. "Mylohyoid process" at the level of the anterior basal edge of the coronoid process: (0) absent; or (1) present.

Deleted Characters from the Data Matrix of Luo et al. (2002): 2, 3, 12, 14, 15, 37, 40, 60, 69, 86, 100, 103, 106, 118, 177, 208, 221, 229, 275.

New Characters: 13 (from 276 to 288).

Additive Characters: 5, 25, 34, 42, 45, 52, 56, 61, 63, 64, 74, 75, 79, 80, 93, 95, 97, 98, 108, 110, 111, 141, 147, 149, 150, 164, 170, 172, 191, 193, 194, 202, 204, 206, 237, 240, 241, 252, 254, 256, 259, 264, 278, 279, 282.

APPENDIX 3

Data Matrix

Distribution of character states for 288 characters among 47 ingroup terminal taxa and 1 outgroup taxon considered in the analysis. 0 to 5 = character states, ? = missing or inapplicable information. Polymorphic scorings are: a = 0–1, b = 0–2, c = 0–3, d = 1–2, e = 0–1–2, f = 1–2–3.

Probainognathus

```
0000000000 000000?000 0?0?00???? ???????00?
?00??????? 00??0?00?? ????0????? ????000???
??00??01?? ??0??????? ????000?0? 00000000?0
0??00?0??? ?0?000000? 0000000000 0000?0??00
0000?00000 ???00????0 ?00000??00 0??0000000
1000001110 10000?000? 000?000000 0000000000
0000000000 0000000000 000000??00 0000100f00
??000??0
```

Tritylodontids

```
0000011000 000000?000 0?0?30??2? ??0????3??
?24??????? 00??0?00?? ?????????? ?????00???
??10aa54a0 0022?????? ????122??a d?11101000
00000?0000 0000000000 0000000a00 0000?00000
0000000000 0000000??0 000000??00 0??0100000
0000100000 00101?100? 0000010000 100000000a
0010100000 0000000000 a010100?00 0002000f00
??000??0
```

Ttritheledontids

```
0000010000 000000?000 001?20???? ??0????00?
?00??????? 00??0?00?? 0???0????? ????040???
??000001?? ??0??????? ????000?0? 00001a02??
0???0?00?1 101000000? 0000000000 0000?0??0?
000???0??? ?????????? ?000100?00 0??0?00000
0000000110 00000?000? 0000000001 00?1101000
0000100000 0000010?00 1?001????? ???0000?10
00100??0
```

Adelobasileus

```
?????????? ?????????? ?????????? ????????0?
????????0? 00???????? ?????????? ??????????
??????00?? ?????????? ?????????? ??????????
?????????? ?????????? ?????????? ??????????
?????????? ?????????? ?10??????0 1?0????000
1100201101 10000?0000 0000001??? ??0?????0?
```

Adelobasileus (continued)

```
1110??00?? 1101120??? ???01????? ??????????
???0????
```

Sinoconodon

```
0000010000 000000?000 0110001000 0000?0000?
?00000??00 10a000001? 0???00???0 ????000???
??000010?? ??0?00?0?? 0?0?000311 a0100001?0
0???0??000 0000000000 0000000000 0000????00
0000??0??? ?????????? ?000100001 1000100000
1111200000 00101?0000 0001011100 0001101101
1010100001 1000000000 0010100000 0000000?10
10000?00
```

Morganucodon

```
0001010000 000000?000 0a10000000 0001?10000
?11000??00 120012020? 0???00???0 ????040???
??000010?? ??1000?0?? 0?0?000001 11110001?0
01000?10?1 ?0010?000? 0000000000 0000?00001
00010?0?00 0000000??? ?00110aa01 2110200000
1111201101 0011201000 1001011001 10?2101101
1010100001 1001110110 0010100000 0000100010
10010?00
```

Megazostrodon

```
0001010000 000000?000 0020100100 0001?10000
?12000??00 120001020? 0???00???0 ????040???
??000010?? ??1000?0?? 0?0?000001 1??00002??
01000?1??? ?0?100000? 0000000000 00?0000001
000?000000 00000?0000 00?110??01 201020?000
1111011?1 0011201000 ?001011001 ?0?21?11?1
1?101??001 ?001?10??? ????1????? ???0100010
00110?00
```

Dinnetherium

```
0001011000 0000?0?000 0220100000 0001?10000
?11020??00 120112010? 0???00???0 ????040???
```

Dinnetherium (continued)

```
??000010??  ??1000?0??  0?0?000001  1??10001??
??????????  ??????????  ??????????  ??????????
??????????  ??????????  ?????????1  2110???000
11111?11?1  0011201000  10010110??  10?21??1??
1?????????  ??????????  ????1?????  ???0100010
10010?00
```

Haldanodon

```
0000011000  000000?000  0110100000  0010?10000
?11??0??00  120021000?  0???00???0  ????010???
??000053??  ??1000?0??  0?0?000201  11?10000??
??????????  ???100????  00?00?0100  000?????0?
000?0?????  ??????????  ?001201101  2000200000
1111001???  ?010201000  200111100?  ???2?02112
2110100000  ?101111110  000000????  10?0100000
??000??0
```

Hadrocodium

```
11??11?300  ?11??0?000  00102?1100  00?0???000
?12000??00  1?0000000?  0???00???0  ????000???
??000010??  ??1000?0??  0?0?0003?2  1???000???
??????????  ??????????  ??????????  ??????????
??????????  ??????????  ?100210101  212????000
1111?11102  1000211000  1001011???  ???2??2112
2110101001  111212101?  00?21???11  111010????
????0?00
```

Kuehneotherium

```
0001011000  0000?0?000  0?10000100  00010??121
0120200011  1101120100  10000000?0  ???0110??0
0?00??21??  ??111100??  00000??0?0  a?11???0??
??????????  ??????????  ??????????  ??????????
??????????  ??????????  ??????????  ??????????
??????????  ??????????  ??????????  ??????????
??????????  ??????????  ??????????  ???0100000
????0?00
```

Shuotherium

```
00010?10??  00?1?0?0?0  c??1011001  0111?00211
11?0100011  0101220001  1000110??0  ???0220??0
0000??32??  ??211100??  0100?????1  1?????????
??????????  ??????????  ??????????  ??????????
??????????  ??????????  ??????????  ??????????
??????????  ??????????  ??????????  ??????????
??????????  ??????????  ??????????  ???11?0???
??????00
```

Ambondro

```
??????1???  ???1??????  ??????0?02  0011???212
?131?1121?  00011200?1  1021411001  00d1??????
??????3???  ??2111?110  ?010??????  1?????????
??????????  ??????????  ??????????  ??????????
??????????  ??????????  ??????????  ??????????
```

Ambondro (continued)

```
??????????  ??????????  ??????????  ??????????
??????????  ??????????  ??????????  ???11?????
??????0?
```

Ausktribosphenos

```
101101121a  0011?0?110  ??11211012  2011?10212
?13102321?  0000120002  2021411002  1123??????
??????5???  ??2121???1  0111???0?2  1?????????
??????????  ??????????  ??????????  ??????????
??????????  ??????????  ??????????  ??????????
??????????  ??????????  ??????????  ??????????
??????????  ??????????  ??????????  ???11000??
??????00
```

Henosferus

```
0?0101121a  000??0?210  0011211001  00?0?00221
?13121121?  0011000101  102141100d  a021??????
??????3???  ??2111?100  00000?10?2  1???000???
??????????  ??????????  ??????????  ??????????
??????????  ??????????  ??????????  ??????????
??????????  ??????????  ??????????  ??????????
??????????  ??????????  ??????????  ???11000??
????0?00
```

Asfaltomylos

```
0?1???1210  ?0???0?210  3a1121??01  0011???212
?13??13?1?  0011000111  102141100d  0021??????
??????????  ??2111??00  0100?????2  1?????????
??????????  ??????????  ??????????  ??????????
??????????  ??????????  ??????????  ??????????
??????????  ??????????  ??????????  ??????????
??????????  ??????????  ??????????  ???1?000??
??????00
```

Bishops

```
1?11111211  0011?0?110  3111211012  2011?10212
?13102321?  0000120012  1021411002  1123??????
??????5???  ??2121???1  0111???0?2  1?????????
??????????  ??????????  ??????????  ??????????
??????????  ??????????  ??????????  ??????????
??????????  ??????????  ??????????  ??????????
??????????  ??????????  ??????????  ???11000??
????0?00
```

Steropodon

```
???01?1???  ?0?1??????  ?????1????  ???????212
?131122?1?  0010112002  2022311000  ??23??????
??????5???  ??2121?211  0000?????2  1?????????
??????????  ??????????  ??????????  ??????????
??????????  ??????????  ??????????  ??????????
??????????  ??????????  ??????????  ??????????
??????????  ??????????  ??????????  ???0???e??
??????1?
```

Teinolophos

```
11111?1210  0111?0?210  311121????  ???????212
?131122?1?  0000112012  2022311000  ??23??????
??????5???  ??2121?211  0000?????1  1?????????
??????????  ??????????  ??????????  ??????????
??????????  ??????????  ??????????  ??????????
??????????  ??????????  ??????????  ??????????
??????????  ??????????  ??????????  ???0100???
??????11
```

Obdurodon

```
11?02?1310  0111110210  0?11211102  0110?00212
?131122?1?  00101a2002  2022311000  ??2321????
???0??54??  ??2121?211  01001223?2  2??????2?1
??????????  ??????????  ??????????  ??????????
??????????  ??????????  ?000111001  212????000
2111111112  1001201000  1000000???  ???2??2112
2111121?11  1012121111  01?211????  ???b110?21
21?0??11
```

Ornithorhynchus

```
11??221011  11111102?0  3111?1????  ??????????
?1????????  0???1?2002  2022?11000  ??2321????
???0??54??  ??????????  ????1223?2  2??1???31?
1110111000  0000010100  0000000100  0000?11100
0002010000  0000210111  1000101001  2121300000
2111111112  1001201000  1000000220  12?2112112
2111121?11  1012121111  0002110110  111b110001
???0???1
```

Gobiconodon

```
11?11110??  01?1?11210  1110101?01  0001?00000
?12010??01  110100010?  0???000??0  ????010???
??000010??  ??1101?0??  0?0?111101  1?101002??
?????00???  ?1?21?1?1?  1110000110  000??00000
000100100?  ??????????  1001201101  2?10?0?000
?1?1?111??  ?????0?0??  200???????  ??????21??
????10??10  12001?0?1?  0??01?????  ???0110310
100?0?00
```

Amphilestes

```
11?11110??  11?1?112??  1110201101  0001?00000
?12010?00?  110100010?  0???000??0  ????0?????
????0010??  ??1101?0??  0?0?0?0101  1?1???0??0
??????????  ??????????  ??????????  ??????????
??????????  ??????????  ??????????  ??????????
??????????  ??????????  ??????????  ??????????
????????1?  ??????????  ??????????  ???01003??
????0?00
```

Jeholodens

```
11??d110??  ?1?1?11?10  12101?1000  00010?0000
?12010??00  110?0001??  00??000000  ????0a0???
??000010??  ??1100?0??  0?0?011311  1???100???
```

Jeholodens (continued)

```
?10??10???  ?112111??0  1110??0110  100000?000
0001000001  ?000010010  00012?110?  ??a?2?????
??????????  ??????????  ??????????  122????1??
????10??11  ???11??01?  0??1??????  ???01?0???
????0?00
```

Priacodon

```
11?01110??  11?1?11210  1210100101  0002?00000
?11110??00  111000031?  0???000??0  ????010???
??110010??  ??1000?0??  0?0?000201  1??10001??
??????????  ??????????  ???????110  100???????
??????????  ??????????  ??????????  21102??000
11111?1111  00??20??00  2??1021???  ???2??21??
??????????  11???2????  ??????????  ???0110110
10010?00
```

Trioracodon

```
11?01110??  11?1?11210  1210100101  0002?00000
?11110??00  11a000031?  0???000??0  ????010???
??110010??  ??1000?0??  0?0??00102  11110?0???
??????????  ??????????  ??????????  ??????????
??????????  ????0?????  ?????????1  21102??000
11111?1111  0011201?00  2??102????  ???2???1??
??????????  11????????  ???1?11101  11001101??
???10?00
```

Haramiyavia

```
0?000?1000  ?0?????000  0?1110??2?  000????3??
?24???????  00??0?000?  ??????????  ??????????
???0115411  0112??????  ????011102  1???1100??
??????????  ??????????  ????????00  ??????????
??????????  ??????????  ??????????  ??????????
??????????  ??????????  ??????????  ??????????
??????????  ??????????  ??????????  ???20?0000
????0??0
```

Plagiaulacidans

```
11??2110??  a1?1110211  221010??3?  100????3??
?24???????  00??0?000?  ??????????  ??????????
???0115411  1122??????  ????1d1d03  11111110?0
??????????  ??????????  ??????????  ??????????
??????????  ??????????  ?001111001  21102??000
111122211?  ??012110?0  3001021???  ???2??0102
21??21??11  12??12012?  ??2?1?????  ???2000000
???20??0
```

Cimolodontans

```
11??2110??  11?1110211  2210d0??3?  100????3??
?24???????  00??0?000?  ??????????  ??????????
???0115400  1022??????  ????1223?3  11111a1210
1110001000  1111101110  110100d000  1010001111
1102010001  0001211112  10011a1001  2110d0010a
d111222112  1a012110a0  3001a2122?  122212010d
```

Cimolodontans (continued)

```
2111200?11  12ad1d0121  102d111101  1102000011
00?20??0
```

Tinodon

```
11?11?10??  01???111?0  1111311001  0001?00121
?120100011  0101120101  10001000?0  ??00110??0
0?00??21??  ??1111?0??  00000?1201  1?????????
??????????  ??????????  ??????????  ??????????
??????????  ??????????  ??????????  ??????????
??????????  ??????????  ??????????  ??????????
??????????  ??????????  ??????????  ???01?00??
????0?00
```

Zhangheotheriids

```
11?01110??  01?0111210  1111011001  0101010222
0120100011  0100120101  1000000000  ??00220??0
0?00??42??  ??111100??  0000011210  1?1110021?
1110001010  1112111110  111101a111  1000000011
1101100001  100121d1?2  1001211101  211????111
11?11?1?12  1001212000  ?001?21???  ???21??1??
??1??0??01  ???1???011  1?????????  ???11002??
???10?00
```

Peramus

```
11?1111110  0111?10210  0111210111  0001000212
0131201011  0001000100  1a01211100  ??01210000
0000??31??  ??21111100  00000?0002  1?????0???
??????????  ??????????  ??????????  ??????????
??????????  ??????????  ??????????  ??????????
??????????  ??????????  ??????????  ??????????
??????????  ??????????  ??????????  ???1101d??
????0100
```

Amphitherium

```
11?1111110  0111?10210  3111210101  0010?00211
0131001011  0011000100  10012111?0  ??01110??0
0?00??41??  ??21111100  00000?0000  1?????0???
??????????  ??????????  ??????????  ??????????
??????????  ??????????  ??????????  ??????????
??????????  ??????????  ??????????  ??????????
??????????  ??????????  ??????????  ???11000??
????0?00
```

Dryolestes

```
11?0111110  0111?10210  3111210001  0010000211
0131000011  0010000001  1000211??0  ??00100??0
0?00??42??  ??211100?0  0100000100  11110?02??
??????????  ??????????  ???????111  100???????
??????????  ??????????  ??????????  ??????????
??????????  ??????????  ??????????  ??????????
```

Dryolestes (continued)

```
??????????  ??????????  ??????????  ???1100010
000?0200
```

Henkelotherium

```
11?0111110  0111?10210  3111210001  0?10000211
0131000011  001?000001  1000211??0  ??00100??0
0?00??42??  ??211100?0  0100?00100  1?????0??0
??????1???  ?112111?1?  11110?0011  1000??0011
110111010?  ???1??????  11?12?110?  ?1????????
??????????  ???????0??  ??????????  ???????1??
?????1??01  ??????????  ??????????  ???11?0010
00?0020?
```

Vincelestes

```
11??211110  0111?10110  3111210101  0011000221
0130101011  0010000000  1000210000  ??01210000
0?00??31??  ??21111100  0000100302  1???1102?0
11111?1121  1112111110  1111010011  1100001011
1001110101  1001211??0  ?100211101  21211?1111
1111111102  1101212011  2001121???  ???21?110?
111011000a  1200121111  0??11?????  ???1101210
00000200
```

Kielantherium

```
11?0111110  01?1?10110  ???1310100  0000?00211
0130201111  00a1000101  1001411000  0?01??????
??????3???  ??2121?100  1000??0101  1?????0???
??????????  ??????????  ??????????  ??????????
??????????  ??????????  ??????????  ??????????
??????????  ??????????  ??????????  ??????????
??????????  ??????????  ??????????  ???1111d??
??????00
```

Aegialodon

```
??????????  ??????????  ??????????  ???????211
?13??0111?  00010001?1  1001411100  0?01??????
??????3???  ??2121?100  1000??????  ??????????
??????????  ??????????  ??????????  ??????????
??????????  ??????????  ??????????  ??????????
??????????  ??????????  ??????????  ??????????
??????????  ??????????  ??????????  ???1??????
??????0?
```

Deltatheridium

```
11??211410  1111?10110  3131310101  0001000212
0131201111  0011000111  1011411101  01012210a1
0000??32??  ??21212100  1000000201  1?110?02??
??????????  ??????????  ??????????  ??????????
????????12  1??12?1???  ?11?2111?1  21223??111
1212323?1?  ??00212?00  3??1121???  ???2??2111
101?11??01  12?1???02?  1?????????  ???1101310
00001100
```

Asiatherium

```
11??1?1410  1111110110  31?1310101  0001000212
1131003111  0011001111  1121411111  1113211022
0000??32??  ??21212100  1110?0?201  1?????????
????101???  ?11210111?  2111112022  1111?0101?
111111101?  ?????????2  0110211111  2122???111
?2?2323???  ??00?121??  ?1111?1???  ???21?2111
10101???01  ???11200??  ???21?????  ???11013??
????1000
```

Kokopellia

```
?1??1114??  1??1?1?110  ????310101  0001?00212
1131103111  0011001110  1121411111  1103221012
0000??32??  ??21212100  1110000 2?1  1??10?02??
??????????  ??????????  ??????????  ??????????
??????????  ??????????  ??????????  ??????????
??????????  ??????????  ??????????  ??????????
??????????  ??????????  ??????????  ???11113??
????0a0?
```

Pucadelphys

```
11??111410  1111110110  1131310101  0001000212
1131003111  0011001110  1121411112  1113231022
1100??32??  ??21212100  1110000201  1?11000211
1111101121  1112101111  2111112022  1111?11011
1111111012  111120120?  0110211111  21223??111
1212323?1?  ??00212100  3011121???  ???21?2111
1010111101  1201120021  1?210?????  ???11013??
???01000
```

Didelphis

```
11??211410  1111110110  1131310101  0001000212
1131003111  0011001111  1121411102  1113231020
1100??32??  ??21212100  1110000211  1111000211
1111101121  1112101111  2111112022  1111111011
1111111012  1111201202  0110211111  2122311111
1212323?1?  ??00212000  3111121111  1112122111
1010111101  1200120021  1121000110  1111101211
22101000
```

Pappotherium

```
??????1???  ??????????  ??????0100  0000???212
0131001111  00110001?0  1011411101  1002231001
0000??32??  ??21212100  1110??????  1?????????
```

Pappotherium (continued)

```
??????????  ??????????  ??????????  ??????????
??????????  ??????????  ??????????  ??????????
??????????  ??????????  ??????????  ??????????
????????????????????  ??????????  ???1??????
?????00?
```

Erinaceus

```
11??211110  1111110110  3131310011  0000100212
1130003111  0010000101  1021411001  1113211122
0000??52??  ??21212111  1110111302  1111100211
1111101121  1112101111  2111112022  1010111011
1112110122  1211102202  0110211111  2122311112
0212323?1?  1100212011  3001121111  1112122111
1010111101  1201121021  1122100110  1111101111
22100200
```

Asioryctes

```
11??211310  0111110110  3131311101  0000100212
1130001111  0011000120  1011411101  1003221112
0000??32??  ??21212100  1110000102  1?11000?10
11111?????  ??????????  ??????????  ?0101?????
?????10122  ?21110220?  0110211111  2122???112
0212323?1?  1100212010  3001121???  ???21?2111
1010111101  1201121021  1??1100110  1111101d??
???00000
```

Prokennalestes

```
11?0111110  0111?10110  0131211001  0000100212
1130001111  0011000120  1011411101  1003231111
0000??32??  ??21212100  1110010002  1??1??02??
??????????  ??????????  ??????????  ??????????
??????????  ??????????  ?????????1  2122311112
2212??3?1?  110021??11  3??1121???  ???2??????
??????1???  ??????????  ??????????  ???1111d10
00000000
```

Montanalestes

```
11??2?1310  0111?10110  3131311101  0010?00212
?130101111  0011100120  1011411101  1003??????
??????3???  ??2121?100  1110???002  1?????????
??????????  ??????????  ??????????  ??????????
??????????  ??????????  ??????????  ??????????
??????????  ??????????  ??????????  ??????????
??????????  ??????????  ??????????  ???11013??
????0?00
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