Historical Biology

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Submission ID	246728970
Article Type	Research Article
Keywords	Argyrolagidae, Middle Miocene, Palaeothentoidea,, Patagonia, Paucituberculata, Polydolopimorphia
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Title page:

New metatherians from Collon Cura Formation at Cerro Zeballos (Middle Miocene), Chubut province, Argentina

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ABSTRACT

High latitude metatherians from the Middle Miocene of Patagonia (Argentina and Chile) are only known from medium-sized Sparassodonta, and undescribed taxa collected in several fossil localities of Collon Cura (Argentina) and Río Frías (Chile) Formations, although the latter has several species reported and mostly recognized for the slightly older Santa Cruz Formation. In this contribution we describe five new genera and six new species of metatherians from Collon Cura Formation at Cerro Zeballos, Chubut province (Argentina), based on 11 specimens that notably increased the diversity of Collon Cura Formation. The specimens were assigned to the orders Paucituberculata (Palaeothentoidea), Sparassodonta (Hathliacynidae), and Polydolopimorphia (Argyrolagidae), and are taxa of small size, including the smallest palaeothentoids known to date. Also, the Palaeothentoidea of Cerro Zeballos are amongst the youngest of the superfamily in Patagonia. The new specimens described herein show morphological differences with other metatherian associations already known, probably related to adaptive changes coincident with the Middle Miocene Climatic Transition and the beginning of a faunal turnover, including a time range that is virtually unknown for the Patagonian Miocene.

Keywords: Argyrolagidae, Middle Miocene, Palaeothentoidea, Patagonia, Paucituberculata, Polydolopimorphia.

Funding details.

Nothing to declare.

Disclosure statement.

No potential conflict of interest was reported by the authors.

Introduction

Metatherians from the Middle Miocene of South America are better known from lower and middle latitude localities in Bolivia, Perú, and Colombia, more abundant and diverse than in the southernmost regions of the continent perhaps due to more intense work there. In Bolivia, the records include Palaeothentidae (*Acdestis maddeni*, *Palaeothentes serratus*, *Palaeothentes relictus*, *Chimeralestes ambiguus,* Palaeothentidae indet.), Thylacosmilidae (*Patagosmilus goini*), Hathliacynidae (*Acyon myctoderos*), Hathliacynidae (*Australogale leptognathus*), Sparassodonta gen. et sp. indet., and Argyrolagidae (*Hondalagus altiplanensis*) (Sanchez Villagra et al. 2000; Forasiepi et al. 2006, Engelman and Croft 2014; Engelman et al. 2016; Suárez-Gómez 2018; Echarri et al. 2021). The Peruvian records include descriptions of ?Sparassodonta gen et sp. indet., Hathliacynidae (*Sipalocyon* sp.), Didelphidae (*Marmosa* cf. *laventica*, cf. *'Thylamys.' colombianus*), Palaeothentidae (*Palaeothentes* sp.), Abderitidae (*Pitheculites ipururensis*) (Antoine et al. 2013 Tejada-Lara et al. 2015; Stutz et al. 2022), and mentions of Sparassodonta, Argyrolagidae, Didelphimorphia, and ?Caenolestidae (Antoine et al. 2016; Stutz et al. 2022). In Colombia, the records are attributed to Microbiotheriidae (*Pachybiotherium minor*, ?*Pachybiotherium*), Didelphidae ("*Thylamys" minutus*, "*T". colombianus* – see Stutz et al. (2022) for comments on the identity of *Thylamys* from La Venta –, *Marmosa* (*Micoureus*) *laventica*, Marmosini cf. *Tlacuatzin*, Marmosini gen. et sp. indet., Didelphinae gen. et sp. indet.), Hondadelphidae (*Hondadelphis fieldsi*, ?*Hondadelphis*, *Hondadelphys* sp. indet), Thylacosmilidae (*Anachlysictis gracilis*), Borhyaenoidea fam. et. gen. indet., Sparassodonta fam. et. gen. indet., Palaeothentidae (*Hondathentes cazador*), Abderitidae (*Pitheculites chenche*), Borhyaenidae (*Lycopsis longirostrus*, cf. *Lycopsis*, *Dukecynus magnus*), Boryaenoidea (*Lycopsis padillai*) (Marshall 1976, 1977; Dumont and Bown 1997; Goin 1997; Forasiepi et al. 2004; Engelman et al. 2016; Suárez-Gómez 2018).

In contrast, high latitude metatherians from the Middle Miocene of Patagonia (Argentina and Chile) comprise a particular array of taxa collected mainly in several fossil localities of Collon Cura

(Argentina) and Río Frías (Chile) Formations. There are mentions of metatherians from Collon Cura Formation that include Borhyaenidae (cf. *Arctodictis* sp., Borhyaenidae indet.), Caenolestidae (*Stilotherium* cf. *dissimile*, Caenolestidae indet.), Palaeothentidae (*Acdestis owenii*), Abderitidae (*Abderites meridionalis*, *Pitheculites* sp.) from Neuquén province (Abello 2007; Kramarz et al. 2011); Borhyaenidae (*Prothylacynus* sp.), Palaeothentidae (*Palaeothentes* sp.), Abderitidae (*Abderites* sp.) from Río Negro province (Pascual et al. 1984); Hatlyacynidae, Palaeothentidae, Argyrolagidae (Villafañe et al. 2008), and Caenolestidae (Caenolestidae gen. et sp. indet), Palaeothentidae (*Palaeothentes* cf. *serratus*), and Argyrolagidae (cf. *Hondalagus* sp.) from Chubut province (Bucher et al. 2021). However, none of them have been formally described or accompanied by collection numbers (with the exception of cf. *Hondalagus* sp.; Bucher et al. 2021).

There are three formally described species from Collon Cura Formation, two Hathliacynidae (*Pseudonotictis chubutensis* and *Cladosictis patagonica*), one from Cerro Zeballos in Chubut Province (Martin and Tejedor 2007) and another from Estancia La Alemana in Río Negro Province (Echarri et al. 2021), respectively, as well as one Thylacosmilidae (*Patagosmilus goini*) from Río Chico in Río Negro province (Forasiepi and Carlini 2012). For Río Frías Formation at Alto Río Cisnes, Chile, the record includes 11 described species of the families Microbiotheriidae (*Microbiotherium tehuelchum*), Hathliacynidae (*Sipalocyon gracilis*, *Cladosictis patagonica*), Borhyaenidae (*Borhyaena tuberata*, *Prothylacynus patagonicus*), Caenolestidae (*Phichipilus? halleuxi*), Palaeothentidae (*Palaeothentes minutus*, *Palaeothentes intermedius*, *Palaeothentes lemoinei*), and Abderitidae (*Abderites meridionalis*, *Pitheculites rothi*) (Marshall, 1990), as well as mentions of Abteritidae (*Abderites*) (Bostelmann et al. 2012).

In this context, and although there are several specimens of metatherians mentioned for the Collon Cura Formation, the previously described species are only three from different fossil localities, making the known diversity of each locality lower compared to other localities from the Middle Miocene of South America (e.g., Alto Río Cisnes in Chile, Quebrada Honda in Bolivia, La Venta in Colombia; Marshall 1990; Croft 2016).

In this contribution we describe five new genera and six new metatherian species from Collon Cura Formation at Cerro Zeballos, Chubut province, Argentina, expanding the knowledge of their diversity during the Middle Miocene in Patagonia.

Materials and methods

The specimens described in this work (see below) were collected throughout different field trips from 2010 to 2022, and are housed at the Laboratorio de Investigaciones en Evolución y Biodiversidad (LIEB), Esquel, Chubut province, Argentina.

The taxonomy of Paucituberculata and Argyrolagidae follows Abello et al. (2021) and Goin et al. (2016), respectively (but see Eldridge et al. 2019 for a discussion of argyrolagoid phylogenetic relationships). Dental nomenclature and homologies follows Abello (2013) for Paucituberculata, and Babot and García-López (2015) for Argyrolagidae. Incisors, canines, premolars, and molars are abbreviated as i, c, p and m, respectively, all for the lower dentition. Photographs were taken with a Zess Stemi DV4 and Zeiss Sigma 300 VP: D Scanning Electron Microscope (SEM) (see Supplemental online material Figure 1). Measurements were taken using a stereoscopic microscope (Zess Stemi DV4) equipped with an ocular micrometer, or using a digital caliper taken to the nearest 0.01 mm. Dental measurements include premolar maximum length and width, and molar maximum length (L) and width (W). Length and width were defined as the greatest anteroposterior distance and labio-lingual width, respectively. Body mass was estimated using the formula of Dumont et al. (2000): body mass = e ^ $(2.419 + (1.727 \times \ln \text{m2 area}))$.

Geological setting

The Collón Curá Formation was deposited in the extra-Andean Patagonian region of Neuquén, Río Negro and Chubut provinces, and is represented mainly by volcaniclastic limestones and sandstones accumulated in continental environments, ranging from alluvial to lacustrine depositional systems (Yrigoyen, 1969; Rabassa, 1978; Ramos et al. 2011; Bilmes et al. 2014;

Bucher et al. 2018). Several published U-Pb and Ar-Ar absolute ages of the Collon Cura Formation indicate that the formation spans at least from *ca.* 16 Ma to *ca*. 11 Ma (Burdigalian-Tortonian) (Brandoni et al. 2019; Bucher et al 2021; Bilmes et al., 2022).

The specimens described in this contribution were collected from Cerro Zeballos (42° 34' 46.5"S, 70° 19' 55"W), located 22 Km east of the town of Gualjaina, northwestern Chubut Province, Argentina (see Fig. 1 in Brandoni et al. 2019). The fossils were recovered from a volcaniclastic section dominated by tuffs, chonites and subordinate epiclastic sediments, which corresponds to the Collon Cura Formation (Lage 1982; Lizuain et al. 1995; Martin and Tejedor, 2007; Brandoni et al. 2019). The stratigraphic correlation of the section of Collon Cura Formation at Cerro Zeballos in relation with other sections described (Vucetich et al. 1993; Bucher et al 2021) is still unknown.

Institutional abbreviations

FCNyM, Facultad de Ciencias Naturales y Museo, Buenos Aires, Argentina; LIEB-PV, Laboratorio de Investigaciones en Evolución y Biodiversidad, Esquel, Argentina; MACN, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Buenos Aires, Argentina; MACN-PV, Colección Nacional de Paleovertebrados of the MACN; MPEF-PV, Museo Paleontológico 'Egidio Feruglio,' paleovertebrate collection, Trelew, Argentina.

Systematic Palaeontology

Infraclass Metatheria Huxley, 1880

Superorder Marsupialia Illiger, 1811

Order Paucituberculata Ameghino, 1894

Superfamily Palaeothentoidea (Sinclair, 1906)

Panchothentes gen. nov. Figure 1

Type species: *Panchothentes goini* sp. nov.

Included species: The type species only.

Diagnosis

Palaeothentoid marsupial with a transversally wide p3, m1 with a large trigonid and a shorter talonid; m2-m3 talonids clearly longer than trigonids, with a labially displaced hypoconid and longer cristid obliqua reaching the protocristid in m1, shorter and oriented distally to the protoconid in m2; a strait and crest-like entoconid (instead of being lingually concave) with the postentocristid directed posteriorly and not inflected towards the talonid basin or joined with the postcristid, except in m4; presence of a paraconid in m2.

Etymology

The genus name *Panchothentes* is in honor of the Argentine paleontologist Francisco "Pancho" Goin, for his contributions to our understanding of metatherian and marsupial evolution. The ending *thentes* is commonly used for palaeothentoid marsupials, associated with an (erroneous) interpretation of the word *thereutes*, meaning hunter, derived from a *nomen nudum* according to Marshall (1980, p. 54).

Comparisons

Panchothentes differs from other genera within Palaeothentoidea by an m1 with a long trigonid and shorter talonid. The genus differs from any abderitine by the lack of a plagialaucoid m1; from palaeothentids by the presence of a clear paraconid in m2 (Supplemental online material Figure 2); from acdestines by the large size of its p3, and non-reduced m3; and from palaeothentines by a well-developed paraconid in m1, and the metaconid not posteriorly displaced with respect to the protoconid in m2-m3. The genus differs from *Palaeothentes* by a shallow and rather vertical basin between paraconid and metaconid in m1, lack of accesory cusps in the entocristid. The genus differs from *Antawallathentes* by the lack of a mesolabial cinguid in m1, a V-shaped gap between metaconid and entocristid in m1, and more obliquely oriented cristid obliqua in m2.

Panchothentes goini gen. et sp. nov.

Holotype

LIEB-PV 7594, a left mandible with p3-m4.

Diagnosis

As for the genus

Etymology

The species epithet is the surname of Francisco “Pancho” Goin.

Referred material

The type specimen (LIEB-PV 7594), an isolated left m1 (LIEB-PV 7596), and an isolated right m2 (LIEB-PV 7597) (Supplemental online material Figure 1).

Zoobank registration

Will be generated upon manuscript acceptance

Measurements

See Table 1.

Description and comparisons

The specimen is a left mandible with the basal portion of the ascending ramus, almost complete, partially worn p3-m4, and four alveoli for four unicuspid teeth, and a broken procumbent incisor. In occlusal view, the tooth row is partially curved lingually, with alveoli for what appears to be four single rooted teeth between p3 and the procumbent incisor, with a vertical orientation in the first, and more procumbent in the anterior alveoli. The p3 is a large tooth (length = 2.85 mm; width = 1.53 mm) as in most palaeothentids, almost equal in length to m3, has a central robust cusp with a larger anterior cristid, and with a cutting edge that reaches the posterior portion of the tooth; it has no accessory cusps, exhibiting a triangular shape in occlusal view, with a broad posterior area.

Comparisons in molar size shows a very large m1, and the posterior teeth decreasing in size to approximately two thirds of the previous tooth, the talonid being longer than the trigonid in m2-m4 (Table 1). The cristida obliqua is consistently less oblique from m3 to m4, where the labial margin of the tooth is straight. In labial view, the tooth row is curved with its shortest distance to the mandibular base between m2-3.

The mandible has two foramina on the labial side, an anterior deep one below the fourth alveolus, and a second foramen located below the anteriormost portion of m1's anterior root; both opening to the side. In lingual view, the symphysis reaches a point below the anterior root of p3.

The first molar is broken on its labial side, but still preserves the paraconid, metaconid and entoconid. The most notable feature of m1 is its very large trigonid and a short talonid, a unique feature within Palaeothentoidea. The tallest cusp appears to be the paraconid, followed by a large metaconid worn at the tip, and the entoconid. The paraconid is anterolingually placed, and although broken on its labial side, seems to have a long mostly vertical anterior cristid that reaches p3. The area between paraconid and metaconid in m1 is relatively narrow and shallow, forming a basin like in most *Palaeothentes* spp. probably due to the lingual displacement of the paraconid, and possibly related to a lingual displacement of the protoconid (implying also short paracristid and postprotcristid). The metaconid is a large and blunt cusp rounded at its posterior base, and separated from the tall entoconid by a well-marked med-entocristid gap. Although broken in its labial side, m1 has a well-developed shelf-like hypoconulid.

The m2 is about 2/3 the size of m1, has a longer talonid than trigonid, the former is slightly narrower, and the trigonid is slightly higher than the talonid. The labial side of this tooth is highly worn, but the lingual cusps are present showing a taller metaconid but a larger (in area) crest-like entoconid. The lingually open trigonid has a small, labially-displaced paraconid, with an oblique postparacristid, what appears to have been a large protoconid and a short oblique protocristid that joins a transversal postmetacristid. The metaconid is bucolingually compressed, longitudinally oriented, but without a posterior crest (mdpc *sensu* Abello 2013). The metaconid transversally aligned with the somewhat larger protoconid. The talonid has a well-developed, crest-like entoconid (laterally compressed), which is longer than the metaconid. The hypoconulid is a small shelf-like structure below the crest formed by the junction of the postentocristid and the posthypoconid crest.

The following molars (m3 and m4) decrease in size, being m4 almost one half the size of m3, but are similar to m2 in general structure, with a shorter trigonid than talonid, and large metaconid and entoconid, with the former being smaller. The cristid obliqua is slightly concave labially in m3, but reaches the trigonid wall distal to the protoconid. The metaconid is anteriorly displaced in m3 with respect to the protoconid giving an oblique orientation to the distal trigonid wall. This tooth has a small hypoconulid, located closer to the entoconid and not in the midline of the tooth. The fourth molar is small, with a well-developed metaconid, entoconid and hypoconid, the latter two cusps bulbous and close each other separated by a small medial notch.

Panchothentes goini is similar in size and estimated mass to *Acdestis maddeni* and *Acdestoides praecursor* (Tables 1 and 2). The new species differs from *A. maddeni* and other Acdestidae in the presence of a large p3 which is not overlain by the m1 trigonid, a characteristic of Acdestidae. *Panchothentes* has small trigonids in m2-m3 in which the metaconid is large, the trigonid basin is shorter than wide, and has a more triangular shape than the more rounded one in *A. maddeni*; this is due to the long paracristid in *P. goini*, reduced towards the metaconid. Also, *P. goini* has a larger and pointed paraconid in m2, a very large and crest-like entoconid, with a posteriorly oriented postentocristid (this crest is L-shaped in *A. maddeni* closing the posterolingual border of the tooth).

Talonids in m2-m4 are clearly longer than trigonids in *P. goini*, while in *A. maddeni* the trigonid is longer in m2 and subequal in m3. Although clearly different in size, *P. goini* also differs from *Palaeothentes serratus* by its wider and not laterally compressed p3, m1 trigonid longer than its talonid, less labially displaced hypoconid with a more strait cristida obliqua, oriented towards the protoconid instead of a medial area of the protocristid, and a strait and crest-like entoconid. Although apparently similar in size to *P. lemoinei*, *P. goini* differs by its longer p3 which lacks an anterior cusp, longer m1 trigonid, anteriorly displaced hypoconid in m1 (the hypoconid position is transverse or posterior to the entoconid in *P. lemoinei*), less angular cristid obliqua, more robust entoconids and well-developed hypoconulids in m2-m3.

Lemmythentes gen. nov. Figure 2

Type species: *Lemmythentes kilmisteri* sp. nov.

Included species: The type species only.

Diagnosis

Palaeothentoid marsupial with a very long anterior mandibular region, with a distance between the procumbent incisor alveolus and the anteriormost alveolus of m1 equal (or longer) to the molar toothrow; large and deep anterior mental foramen located labially below the alveolus of the third unicuspid tooth that opens anteriorly, m1 is slightly longer than m2, the trigonid and talonid of m1-m3 are subequal, and with a larger trigonid in m4. The talonid is distally open where the postentocristid and posthypocristid are not joined, leaving a small notch between them.

Etymology

The genus name *Lemmythentes* is in honor to Ian "Lemmy" Kilmister, for his outstanding achievements in the history and development of Rock and Roll with the band Motörhead. See above for the meaning of *thentes* and its usage.

Comparisons

Lemmythentes differs from other genera within Palaeothentoidea (except *P. lemoinei*) by its long antemolar region (length from anterior most (broken) point of the mandible to the anterior most point of m1 = 10.58 mm; molar tooth row length = 10.78 mm), and very reduced postmetacristid and postprotocristid in m2. The genus differs from any abderitids by the lack of a plagialaucoid m1; from palaeothentids by a triangular trigonid and deep labial and lingual inflections separating trigonid from talonid in m2-m3; from acdestines by the large size of its (inferred) p3, and non-reduced m3; and from palaeothentines by a metaconid not posteriorly displaced with respect to the protoconid in m2-m3, and C-shaped entoconid. *Lemmythentes* differs from *Palaeothentes* by the lack of posteriorly directed metaconid crests in m2 and m4 (the portion of the m3 is broken), and lack of accessory cusps in the entocristid. *Lemmythentes* differs from *Antawallathentes* by the lack of a mesolabial cingulid in m1, a V-shaped gap between metaconid and entocristid in m1, and more obliquely oriented cristid obliqua in m2-m3.

Lemmythentes kilmisteri sp. nov.

Holotype

LIEB-PV 7591, a right mandible with partial m1 and complete m2-m4 (Figure 2)

Referred material

The holotype only (Supplemental online material Figure 1)**.**

Etymology

The species epithet is the surname of Ian “Lemmy” Kilmister, founder, bassist and singer of the band Motörhead.

Zoobank registration

Will be generated upon manuscript acceptance

Measurements

See Table 1.

Description and comparisons

The specimen is a right mandible with the basal portion of the ascending ramus, almost complete m1-4, and alveoli for six antemolar teeth including the procumbent incisor, a double rooted p3, and four single rooted teeth (the incisor-like teeth of Martin 2013, Abello et al. 2020). In occlusal view, the tooth row is partially curved lingually, with alveoli of what appears to be a double rooted p3, and four teeth between p3 and the procument incisor, which changes in orientation from posterior to anterior, from almost vertical to clearly procumbent. The trigonid is apparently subequal to the talonid in m1 (the anterior portion is broken although the root is observed), slightly larger trigonid in m2, and the trigonid is increasingly larger in m3-4. A well-developed (complete only in m2) entocristid is obliquely oriented joining the postmetacristid forming an inflection towards the middle of the tooth, deeper in m2-m3, becoming closer to the cristid obliqua in m1, or the crest formed by the junction of the postprotocristid, and the cristid obliqua in m2-3. In labial view, the tooth row is highly curved with its shortest distance to the mandibular base between m2-3. The mandible has two foramina on the labial side, an anterior deep one that opens anteriorly and is enclosed by the bone on the labial side, below the third alveolus, and a second foramen that opens more dorsally and is located below the posterior root of p3, which also has a very small accessory foramen anterior to it. In lingual view, the mandibular symphysis reaches a point between the posterior root of dp2 and the anterior root of p3.

The m1 is mesially broken, preserving only the posterolabial portion of the trigonid and almost complete talonid (the lingual side is also broken); although broken, the inferred size of the trigonid seems subequal to the talonid. The protoconid is medially displaced, and has a short protocristid, oblique to the antero-posterior tooth axis. The metaconid was probably a large cusp, and although the lingual side of the tooth is missing, it shows a small posterior crest that joins the entocristid. The entoconid, although broken, has C-shaped entocristid, with the cusp at the most distal edge. The anterior portion forms a deep notch that joins with a posterior transversal crest that originates in the metaconid. Although broken in its lingual side, a deep notch separates the metaconid from the entocristid-entoconid. The hypoconid is a relatively robust cusp, slightly displaced anteriorly from the entoconid, and shows a well-marked, posterior wear area, implying the presence of a very large metacone in the upper molars. The posthypocristid does not contact the postentocristid, the posterior edge of the talonid is open through a narrow shelf.

The m2 shows the talonid of slightly larger area than the trigonid. The separation between trigonid and talonid is well-marked by labial and lingual inflections, the apex of the labial inflexion is anterior to that of the lingual side, with crests formed by the postprotocristid-cristid obliqua, and postmetacristid-preentocristid, respectively. The highest cusp in the m2 is a robust (albeit broken) metaconid, which also has a small anterior cuspule on the metacristid. A very large, C-shaped entoconid follows in height, which has a robust entocristid, longer than that of m1. This entocristid appears to have an anterior cuspule, which is also present in m1, albeit smaller sized. The trigonid is slightly taller than the talonid, but both areas appear connected due to wear. The posterior edge of the talonid shows the same open pattern described in m1, i.e., the posthypocristid does not join the postentocristid. As in m1, the hypoconulid is not well-developed. The cristid obliqua becomes progressively less oblique and shorter from m1 to m4, forming a narrow and not very deep hypoflexid (this same wear can be seen in m2 and m3).

The m3 is worn, and its lingual side is broken. Despite this, some features are clearly observable in this tooth. The trigonid is clearly larger in total occlusal surface than the talonid. Although highly worn, the tooth shows traces of the entoconid and its anterior portion, showing the same C-shape described above, with a very narrow and posteriorly curved med-entocristid gap.

The m4 shows the same pattern described for m3, in which the trigonid is clearly larger than the talonid. It has a large metaconid and, comparatively, a large, partially broken entoconid. Despite its worn surface, the cristid obliqua still shows an oblique trajectory, forming a small and narrow but clearly visible hypoflexid.

Similar in size to *P. lemoinei*, *L. kilmisteri* differs by its smaller m1, the similar length of trigonid and talonid in m2 (in *P. lemoinei* the trigonid is clearly shorter than the talonid), and a very large entoconid in m2. The new species differs from *Antawallathentes quimsacruza* and *Antawallathentes illimani* by a shorter and broader talonid in m1, a short and slightly curved cristid obliqua oriented towards the protoconid (oblique to the dental axis in *A. quimsacruza* and *A. illimani*), slightly larger trigonids of m2–m3 (trigonid is clearly shorter than talonid in *A. quimsacruza*), the metaconid position is transversal to the protoconid in m2 (it is anterolingual to the protoconid in *A. quimsacruza*), and lacks a posteriorly oriented crest that is present in *Antawallathentes*. The new species is similar in body mass to *Pilchenia lucina*, but differs in having a shorter m1, larger trigonids in m2–m3, and for lacking a projecting, shelf-like hypoconulid, which is well developed in m1-3 of *P. lucina*. Also, *L. kilmisteri* has a larger entoconid in m1 and with a curved entocristid (the entoconid is robust in *P. lucina* but the entocristid is not labially curved), a very large and C-shaped entoconid in m2 (*P. lucina* has a robust but not C-shaped entoconid). Although similar in m2 area and mass to *Abderites meridionalis* and in size to *Acdestis spegazzini* and *Trelewthentes rothi*, *L. kilmisteri* is not an acdestine or an abderitine marsupial, based on the size of the roots of p3, which suggest a rather large tooth.

Minusculothentes gen. nov. Figure 3

Type species: *Minusculothentes zeballoensis* sp. nov.

Included species: The type species only.

Diagnosis

This is the smallest known palaeothentoid, smaller than all living Caenolestidae and slightly larger than *Phonocdromus gracilis*. Other than its small size, the most remarkable characteristic is the lack of an anterior crest (the preparacristid) of m1 trigonid, a medium-sized and narrow p3 which lacks an anterior cusp, a conical entoconid without an entocristid, and a very small hypoconulid.

Etymology

Minusculothentes is for minusculus, small. See above for the meaning of *thentes* and its usage.

Comparisons

The specimen is the smallest known palaeothentoid marsupials, almost ⅓ smaller than *Palaeothentes minutus* (MACN-PV 15). *Minusculothentes* differs from other palaeothentoids by a well-developed paraconid, that can be distinguished in the paracristid, but the anterior crest is not developed (a typical feature of palaeothentoids). It differs from other non-palaeothentid marsupials by the larger size of its p3, from *Palaeothentes* by the lack of an anterior crest in m1 trigonid, poorly developed hypoconulids in all molars, triangular trigonid in m2-3, with a larger trigonid than talonid in m3, mostly conical metaconid and entoconid in m2-3. *Minusculothentes* can be distinguished from decastines (Decastinae) and abderitids (Abderitidae) by its larger p3.

Minusculothentes zeballoensis gen. et sp. nov.

Holotype

LIEB-PV 10004, a right mandible with complete p3-m3.

Referred specimens

The holotype only (Supplemental online material Figure 1).

Zoobank registration

Will be generated upon manuscript acceptance

Measurements

See Tables 1 and 2.

Diagnosis

As for the genus.

Etymology

The species epithet is for the type locality Cerro Zeballos.

Description and comparisons

The specimen is a right mandible with complete p3-m3, a broken procumbent incisor, four alveoli for a double-rooted p2, two unicuspid teeth or four single-rooted teeth, the root of m4, and part of the ascending ramus. The mandible is ventrally straight, but the posterior portion is dorsally curved, with an oblique and robust coronoid crest, what appears to be a relatively deep masseteric fossa, and dorsally curved toothrow. The mandible also has a very deep and large, oval-shaped anterior mental foramen, extending from the middle of the root of p3 to the bone separating the two alveoli of the p3. A second mental foramen is located at the level of the posterior root of m1.

The p3 is large, triangular in lateral shape with its main cusp at the middle of the tooth's length; it is similar in length to the trigonid of m1, and its posterior portion is slightly under the trigonid of m1; the talon is not developed.

The m1 is slightly longer than m2, and both are clearly longer than m3. The trigonid of m1 is shorter and taller than the talonid, similar-sized in m2, and larger (both longer and wider) in m3. The tall protoconid occupies most of the trigonid with the preprotocristid elevated and oriented anteriorly. The trigonid basin is shallow and reduced, open lingually and totally separated from the talonid by the contact between the postprotocristid, and the poorly developed metaconid. The protoconid is positioned rather anterolingual to the metaconid. In m1, the paraconid appears to be well-developed, and can be distinguished in the paracristid, but the anterior crest is not developed (a typical feature of palaeothentoids). There is no trace of a well-formed anterior cingulum. The protocristid has a well-marked notch that continues to the metaconid. The cristid obliqua is long and joins the metaconid, which has no posterior crest. The entoconid is a large, conical cusp with no entocristid; the hypoconid is well-developed and positioned slightly anterolabial to the entoconid forming an oblique postentocristid+postcristid, with a very small hypoconulid.

The m2 differs from m1 by the larger trigonid and talonid basins, especially that of the trigonid due to the labially displaced, transversally oriented protoconid. The paraconid is present in m2, has a well-developed postparacristid and joins the protoconid by an oblique preprotocristid, which although broken, has the same orientation as the cristid obliqua of m1. The conical metaconid is better developed than in m1, and is the largest cusp in m2, followed by an also conical and large entoconid. The protoconid is larger than the hypoconid, and both cusps are labially projected in a similar way. The cristid obliqua is not attached to the metaconid as in m1, but is attached to a point between the protocristid notch (which is not highly visible) and the protoconid. The posterior edge of the tooth shows a low shelf-like hypoconulid, and the postentocristid+postcristid is not as oblique and strait as in m1, with a slight medial inflection.

The trigonid of m3 is slightly larger (longer and wider) than the talonid, and with a relatively well-developed paraconid. Metaconid and entoconid are the largest cusps, similar in size and mostly conical (i.e., with no anterior nor posterior crests). As in m2, the lingual side is worn, but the hypoconid appears larger than the protoconid, being the hypoconid not as lingually projecting as in m2. The cristid obliqua is almost strait and directed towards the protoconid. The postpostcristid is rounded, and joins the postentocristid by a notch closer to the entonconid. The tooth has a poorly developed but clearly visible hypoconulid, which is located at the middle of the tooth.

The root of a single-rooted m4 is present but broken at the level of the alveolus.

Minusculothentes zeballoensis differs from *P. minutus*, *P. pascualii* and other small palaeothentids by the lack of an anterior crest in m1 trigonid, and poorly developed hypoconulids in all molars. It differs from *P. minutus* by the smaller trigonid in m1, less medially inflected centrocrista in m2-3 (in the m2 of *P. minutus* the centrocrista is oriented towards the midline of the protocristid), and the lack of an anterior cusp in the entocristid of all mollars (clearly visible in *P. minutus*, even in m4), a character also commonly occurring in *P. pascuali* (MACN PvSC1293) and *P. migueli* (MACN Pv CH1338; see also Bown and Fleagle, 1993). *Minusculothentes zeballoensis* also differs from *P. migueli* in features of its trigonid (i.e., lack of anterior crest of m1, long paracristid with distant paraconid and protoconid, longer trigonid in m2 with a narrower and pointed paraconid), comparatively narrower p3, and non-crestiform entocristid.

Zeballothentes gen. nov. Figure 4.

Type species: *Zeballothentes incertus* sp. nov.

Included species: Type species only.

Diagnosis

Small palaeothentoid with m2 in which the paraconid area is almost equally distant from the metaconid and protoconid; postmetacristid and entocristid almost joined at their base (slightly separated by a notch); hypoconulid not developed in m2.

Etymology

The genus name *Zeballothentes* is from the locality Cerro Zeballos. See above for the meaning of *thentes* and its usage.

Comparisons

Even when this specimen is worn, it is clearly different from *Palaeothentes* by its triangular m2 trigonid, continuous crest formed by the postmetacristid and entocristid (there is usually a notch between these crests in the genus *Palaeothentes*), and the lack of a hypoconulid in m2 (m3 is distally broken). Although similar in size to *Palaeothentes minutus* (MACN-PV-SC 9599), this specimen can be easily differentiated by its narrower talonid in m1, which has a broader hypoconid in contact with the anterior portion of the m2 trigonid, an absent postmetacristid in m2, a pointed entoconid different from the robust and crestlike entoconid in MACN-PV-SC 9599, a cristid obliqua that is not as medially inflected as in MACN-PV-SC-15, a postcristid that does not enclose the talonid but is directed towards the paraconid in m3, and is separated from the entonconid by a notch, an apparently poorly developed hypoconulid in m2, m3 with a larger trigonid basin, and less developed entoconid. The specimen can be differentiated from *Minusculothentes* by its larger size, and an m2 with laterally aligned protoconid and metaconid, and hypoconid and entoconid (the protoconid and hypoconid are anteriorly displaced in *Minusculothentes*) (Supplemental online material Figure 1).

Zeballothentes incertus gen. et sp. nov.

Holotype

LIEB-PV-10003, a left mandible with talonid of m1, complete m2-m3, and alveolus for the second root of m4.

Referred material

The holotype only (Supplemental online material Figure 1).

Zoobank registration

Will be generated upon manuscript acceptance

Measurements

See Tables 1 and 2.

Diagnosis

As for the genus.

Etymology

The species epithet is because of its uncertain relationships within Palaeothentoidea.

Description

The talonid of m1, although broken, appears to have a well-developed hypoconid and entoconid. The trigonid of m2 is shorter than the talonid, with well-developed protoconid and metaconid, and a poorly developed paraconid, located at the most anteromedial position of the trigonid, equidistant to the protoconid and the metaconid, giving the trigonid a triangular shape. The trigonid is closed in all lower molars, with laterally aligned protoconid and metaconid. The hypoconid and entoconid are also well developed, having a long cristid obliqua running from the hypoconid to the middle of the distal trigonid wall; the hypoconid is slightly posterolingual to the entoconid, and the latter has a small, worn cuspule on the postentocristid. The hypoconulid is worn and appears to have been poorly developed, but there is a notch separating the postcristid. The hypoflexid is relatively deep, with a weak lingual cingulum.

The m3 is broken distally in the talonid, and appears slightly smaller than m2. Although the occlusal surface is heavily worn, and the lingual portion of the trigonid is broken, m3 has a small but evident paraconid. The hypoflexid is not as deep as in m2. The hypoconid is more labially projected than the protoconid, which appears to have been smaller than the metaconid.

Order Polydolopimorphia Archer (1984)

Suborder Bonapartheriiformes Pascual (1980)

Superfamily Argyrolagoidea Ameghino (1904)

Family Argyrolagidae Ameghino (1904)

Zeballolagus gen. nov. Figure 5.

cf. *Hondalagus* sp. Bucher et al. 2021. Table 1 and Figure 6.

Type species: *Zeballolagus ronniejamesdioi* sp. nov.

Included species: The type species and *Z. separatus*.

Diagnosis

The new genus is characterized by a narrow trigonid in m1, with a poorly developed groove between protoconid and ectostylid, large and rounded trigonids in m2-4 with shorter and narrower talonids (the hypoconid not extending labially to the level of the ectostylid), broad contact between the talonid of the preceding tooth and the trigonid of the following tooth, less developed entoflexids but more developed ectoflexids.

Etymology

The genus name *Zeballolagus* is for the locality Cerro Zeballos; *lagus* is from the greek λαγός (lagós), meaning hare, rabbit, a common usage for argyrolagid metatherians.

Comparisons

The new genus is similar in size to *Microtragulus* (Simpson 1970 a and b; Goin and Abello 2013; Babot and García-López 2015; García-López and Babot 2015) from which it differs in having a larger trigonid than talonid, clearly separated ecto and entoflexids (the labial border of

Microtragulus lacks a well developed entoflexid), more rounded trigonid than in *Microtragulus*, rounded entocristid closing the entoflexid and clearly separating the lingual portion of the talonid (the entocristid is strait or mostly strait in *Microtragulus*), larger and more robust hypoconid in m1, but not as labially salient and anteroposteriorly compressed as in *Microtragulus*, and m2 is the largest tooth in the toothrow (m2-3 are subequal in *Microtragulus*).

The new genus differs from *Anargyrolagus* (Carlini et al. 2007; Goin and Abello 2013) by a narrower and longer m1, narrower and longer trigonid in m1 with a less labially salient talonid, less developed entoflexid in m1 (it is well-marked in *Anargyrolagus*, which also has a clearly longer talonid), more anteriorly compressed hypoconid, shorter and narrower talonid in m2, more angular ectostylid but not as labially developed as in *Anargyrolagus*, longer trigonid in m3-4 with a shorter and narrower talonid (narrower in m4), and a poorly developed hypoconid in m4.

The new genus differs from *Argyrolagus* (Simpson 1970 a and b; Goin and Abello 2013) by its less angular teeth (more rounded ectostylid, metaconid, entostylid, giving the trigonids of m2-4 a circular shape) that in *Argyrolagus* clearly separate the trigonid from the talonid by a very narrow area, longer trigonid in m1 than in *Argyrolagus* but without the groove at the anterior portion of the ectostylid, smaller talonids in m2-4, circular trigonids which differ from the more triangular trigonids in *Argyrolagus*.

The new genus differs from *Proargyrolagus* (Wolff 1984) in the overall shape of all molars, larger trigonids than talonids (in *Proargyrolagus* trigonid and talonid are subequal, or with a longer talonid -see Goin and Abello, 2013; Fig. 4 for *P. bolivianus*), more developed ectoflexid than in *Proargyrolagus* but with more rounded crests.

The new genus differs from *Hondalagus* (Sanchez Villagra et al. 2000) by its shorter talonids, m1 with a groove between protoconid and ectostylid, less developed entoflexid and more developed ectoflexid in m1, clearly separating trigonid from talonid (the ectoflexid is less developed in *Hondalagus*' m1), circular trigonids of m2-4 (triangular in *Hondalagus*), larger metaconid in m2-4 which is closer to the hypoconid of the previous tooth, talonid of m3 narrower than its trigonid, the hypoconid in *Hondalagus* anteriorly displaced, with the an oblique posterior edge of the talonid (it is somewhat strait in *Zeballolagus*), broader m4 talonid in *Hondalagus*, with a larger and posteriorly salient hypoconulid which is not posteriorly developed in *Zeballolagus.*

Bucher et al. (2021: Fig 6) mentioned and figured an argyrolagid (MPEF-PV 11465) for Collon Cura Formation in Chubut province, and provisionally assigned it to cf. *Hondalagus*. Although we did not have direct access to that specimen, its dental morphology (i.e., circular trigonids of m2-m4, shorter talonids, m1 with a groove between protoconid and ectostylid, less developed entoflexid and more developed ectoflexid in m1) allows us to assign this specimen to *Zeballolagus* sp.

Zeballolagus ronniejamesdioi gen. et sp. nov.

Holotype

LIEB-PV-10002 (Supplemental online material Figure 1)**.**

Referred material

The holotype and LIEB-PV 3071, LIEB-PV 7598, and LIEB-PV 7600

Zoobank registration

Will be generated upon manuscript acceptance.

Measurements

See Table 3.

Diagnosis

An argyrolagid metatherian with well-developed protoconids in m1-4, broad and long talonids and deep entoflexids in m2-3, and long m4 with a narrow talonid.

Etymology

The species name *ronniejamesdioi* is in honor of Ronnie James Dio, for his outstanding contributions to hard rock and heavy metal music with the bands Rainbow, Black Sabbath, and Dio.

Description and comparisons

The type specimen is a left mandible with a broken root of the procumbent incisor, root for a p3, complete although worn m1-4, and part of the coronoid crest. The referred specimens are a right mandible with complete m1-2 and the broken root of the procumbent incisor (LIEB-PV 3071), and a right mandible with alveoli for at least three antemolar teeth and complete m1-3 (LIEB-PV 7598). The mandible of the holotype is ventrally curved, probably tallest below m3, and has two mental foramina, the first is rounded and small, and is located below the alveolus of p3, the second one is large and oval-shaped and located below m1, posteroventrally from the first alveolus. LIEB-PV 3071 has two mental foramina, one is large and oval located below a portion of the mandible that is broken (probably containing the alveolus of p3) extending posteriorly to a point below the ectoflexid of m1; and a second foramina below the talonid of m1, posteroventral to the anterior mental foramen. The molars are all euhypsodont, subequal in length, with m1 smaller than m2-3 (which are subequal, but m3 is the longest tooth) and a slightly smaller m4. The enamel is mostly continuous throughout the edges of each molar, with the exception of the labial edge of the protoconid of m1, thicker in the ectostylid of all molars as well as in the hypoconid.

The first molar has a trigonid narrower than the talonid, deep ectoflexid separating the trigonid from the talonid, but a poorly developed entoflexid (slightly deeper than in LIEB-PV 7600). The paraconid is absent, and the crestiform metaconid is the largest cusp, obliquely oriented, which has a slight anterolingual flexion towards the protoconid, especially in m2. The metaconid is broken in LIEB-PV 3071, but the anterolingual flexion and clearly distinct protoconid can be easily distinguished. The ectostylid of the holotype is lower than the metaconid, and joins the protoconid in a strait line (without a groove), similar to LIEB-PV 7600. The m1 talonid is wider than the trigonid, and approximately ⅓ to ¼ in length, with its main axis transversal to the toothrow, and it is longer (anteroposteriorly) in the lingual side than in the labial side, with a well-developed and round entoconid, and a narrow, labially projecting hypoconid (narrower than in LIEB-PV 7600). The hypoconulid is absent.

The m2 is the widest of the series, has a large and almost circular trigonid, a short and narrow talonid (albeit proportionally wider than all other molars), separated clearly from the trigonid by a deep ectoflexid and entoflexid. The protoconid is well-developed and labially displaced, with a clear inflection of the ectostylid, similar to the pattern observed in m2 of both *Proargyrolagus bolivianus* and *Anargyrolagus primus* (Fig. 1 in Goin and Abello 2003). The metaconid is well-developed, its main cusp almost at the anterolingual edge of the tooth, and the premetacristid bordering half of the posterior edge of m1 towards its labial side (in LIEB-PV 7600 the length of the anterior portion of m2 extends from the postentocristid to the begining of hypoconid's posterior end). The postmetacristid is mostly rounded, not extending lingually past the level of the entoconid, posteriorly curved to form an entoflexid, which is more open compared to LIEB-PV 7600. The entoconid is larger than in LIEB-PV 7600, and is partially broken in its posterior edge. The posterior cristid of the talonid is curved towards the hypoconid, and the enamel in this portion is thin. The hypoconid is well-developed, and extends labially almost to the level of a robust ectostylid. The labial border of the ectostylid between the main cusp and the displaced protoconid, is almost strait, expanding labially in the protoconid.

The m3 is the longest in the series, similar in outline to m2, albeit slightly narrower in both trigonid and talonid, being the talonid narrower. The metaconid is well-developed and is the largest cusp, with its anterior crest transversal to the toothrow, and in contact with m2 in the portion where the enamel is thin (see above). The posterior portion of the metaconid is almost strait, which curves to form a slightly shallower entoflexid compared to m2, mainly due to a less developed entoconid. The posterior cristid of the talonid is strait, and the enamel is thin, as in m2, notoriously expanding towards the hypoconid labially from a point where the protoconid of m4 is located. The hypoconid is robust, slightly larger than that of m2, with its anterior crest forming an oblique angle towards the posterior portion of the ectostylid, forming a shallower ectoflexid when compared to that of m2. The ectostylid is labially more projecting than in m2, clearly open V-shaped, and with its anterior portion (towards the protoconid) lingually oblique. The protoconid is developed but oriented anteriorly, extending past the premetacristid, and more V-shaped than in m2.

The m4 is different in shape from m2-3, being narrower with a very narrow talonid separated from the trigonid by poorly developed ecto and entoflexids. It has a pointy metaconid with a well-developed postmetacristid, an almost crest-like entoconid, a poorly developed hypoconid that forms a very shallow ectoflexid, and an open V-shaped ectostylid.

The new species differs from *Z. separatus* (see below) by the more procumbent orientation of its first lower incisor, what appears to be a longer antemolar area, m1 with more developed protoconid and longer entoconid, m2 with well-developed, labially salient protoconid with longer and wider talonids in m2-3, and smaller m3 (this tooth appears to be the longest in *Z. separatus*, while it is similar in size to m2 in *Z. ronniejamesdioi*). These size differences are beyond what can be considered part of the species variability.

Zeballolagus separatus sp. nov. Figure 6.

Holotype

LIEB-PV 7600 (Supplemental online material Figure 1).

Referred material

The holotype only.

Zoobank registration

Will be generated upon manuscript acceptance

Measurements

See Table 3.

Diagnosis

An argyrolagid with poorly developed protoconids in m1-2, deep entoflexids in m2-3, m3 longer than m1-2 and possibly the longest tooth in the toothrow.

Etymology

The species name *separatus* is for its distinct morphology separating it from its co-generic species *Z. ronniejamesdioi.* See above for the meaning of *lagus* and its usage.

Description and comparisons

The specimen is a left mandible with a broken root of the procumbent incisor, the alveolus for what appears to be a p3; complete and worn m1-3, with open roots for m3. The mandible is ventrally curved, appears to have been tallest below m2, and has two foramina (the first is oval-shaped and is located below the alveolus of p3, the second one is round and located below m1, posteroventrally from the first alveolus). The molars are all euhypsodont, subequal in length, with a slightly smaller m1. The enamel is mostly continuous throughout the edges of each molar, with the exception of the labial edge of the protoconid of m1, thicker in the ectostylid of all molars, the hypoconid (especially of m1 and m2), the metaconid and entoconid.

The m1 has a well-marked ectoflexid separating the trigonid from the talonid, but a poorly developed entoflexid. The paraconid is absent, and the crestiform metaconid is the largest cusp, obliquely oriented from the mandible. The ectostylid is lower than the metaconid, and joins the protoconid in a strait line (without a groove). The talonid is wider than the trigonid and approximately ⅓ to ¼ in length, with its main axis transversal to the toothrow. It has a well-developed, open U-shaped hypoconid, a well-developed entoconid, and the hypoconulid is absent.

The m2 is the largest of the series, has a large and almost circular trigonid, an a short and narrow talonid. Unlike m1, the talonid is narrower than the trigonid. The metaconid is well-developed, its main cusp almost at the anterolingual edge of the tooth, its anterior crest bordering the posterior edge of m1, extending lingually and curving to form a narrow entoflexid, joined posteriorly by the entocristid and a rounded entoconid. It has a well-developed, robust and rounded ectostylid, more labially developed than the hypoconid, and with its main cusp anteriorly displaced.

The third molar is similar in outline to m2, albeit slightly narrower in both trigonid and talonid. The metaconid is well-developed being the largest cusp, more anteriorly directed than in m2, with its anterior crest transversal to the toothrow, and an almost strait posterior crest that curves to form an entoflexid shallower than in m2. The entoconid is slightly V-shaped, open and with a mostly strait entocristid (not rounded as in m2). The ectoflexid is deep and well-developed, more rounded and not extending labially as much as in m2. The hypoconulid is pointed and narrower (i.e., anteroposteriorly less developed) than in m2.

See comparisons above for differences between this species and *Zeballolagus ronniejamesdioi*.

Order Sparassodonta Ameghino, 1894

Family Hathliacynidae Ameghino, 1894

Genus *Pseudonotictis* Marshall, 1981

Type species

Pseudonotictis pusillus (Ameghino, 1891)

Included species

The type species and *P. chubutensis* Martin and Tejedor, 2007

Pseudonotictis chubutensis Martin and Tejedor, 2007

Referred material

The type specimen, and LIEB-PV-7601.

Emended diagnosis

Pseudonotictis chubutensis is a small-sized sparassodont with a deep trigon basin, large difference between paracone and metacone height, labiolingually flat metacone; slightly developed preparacrista that does not extend toward the labial cingulum; metacrista lower than the protocone; p2 with anteriorly displaced main cusp, homogenous in width; m1 with a vertically oriented, anteriorly displaced main cusp, and a broad talonid.

Description and comparisons

The new specimen is a broken left mandible with complete p1 and p3, alveolus of the procumbent anterior central incisor, two roots of p2 and two roots of m1. The specimen was assigned to *P. chubutensis* due to its size, which appears to be complementary in size to the upper dentition, and only known specimen. The mandible has three foramina, an anterior one located below the posterior root of p1 and the anterior root of p2, a middle one located below the central portion of p3, and a posterior one located below the posterior root of m1. The unicuspid p1 has a triangular shape in lateral view, with the cusp anteriorly displaced, and a longer talon, and is homogenous in width throughout. The p3 is robust, its main cusp and anterior portion partially broken, the main cusp is vertically oriented, has a talon with a central and well-developed cusp. Although p2 is not present, it appears to have been longer than p3. All premolars and m1 have two roots each.

Pseudonotictis chubutensis differs from *P. pusillus* by its smaller size and less developed stylar shelf; relatively smaller trigon in M2 with deeper trigon basin; bigger difference in height between paracone and metacone, being the metacone labiolingually flatter; preparacrista slightly developed and not extending towards the labial cingulum; metacrista proportionally higher than the protocone. About the lower dentition, p1 has a longer talon than *P. pusillus* and appears to be shorter in comparison to p3; the p3 has a broader talon, the main cusp more centrally oriented and robust, and a mesially less expanded trigonid.

Discussion

This work represents a comprehensive study of the fossil metatherians from the locality Cerro Zeballos, adding six new species of the orders Paucituberculata (*Panchothentes goini, Lemmythentes kilmisteri, Minusculothentes zeballoensis, Zeballothentes incertus*) and Polydolopimorphia (*Zeballolagus ronniejamesdioi,* Z. *separatus*) to this metatherian association, for which the only taxon previously reported was the hathliacynid sparassodont *Pseudonotictis chubutensis* described by Martin and Tejedor (2007). These findings increase the metatherian richness of the Collon Cura Formation in Chubut province, along with preliminary reports of Hathliacynidae, Palaeothentidae, and Argyrolagidae at El Petiso (Villafañe et al. 2008), and Caenolestidae (Caenolestidae gen. et sp. indet), Palaeothentidae (*Palaeothentes* cf. *serratus*), and Argyrolagidae (cf. *Hondalagus* sp.= *Zeballolagus*, this paper) at Cruces Infinitos and Los Yeguarizos (Bucher et al. 2021).

Preliminary reports from Collon Cura Formation of the neighboring Río Negro and Neuquén Provinces included Borhyaenidae (*Prothylacynus* sp.) at Pilcaniyeu Viejo, Palaeothentidae (*Palaeothentes* sp.) at Puesto Marileo, Abderitidae (*Abderites* sp.) at Valle Huahuel Nieyu, Cantera

Lif Mahuida and Pilcaniyeu Viejo, Borhyaenidae (cf. *Arctodictis* sp.), Caenolestidae (*Stilotherium* cf. *dissimile*, Caenolestidae indet.), Palaeothentidae (*Acdestis owenii*), Abderitidae (*Abderites meridionalis*, *Pitheculites* sp.) from Cañadón del Tordillo, and Borhyaenidae (Brorhyaenidae indet.) at Quebrada Azul (Cerro Las Huitreras) (Pascual et al., 1984; Abello 2007; Kramarz et al. 2011).

The palaeothentoids of Collon Cura Formation (Middle Miocene) at Cerro Zeballos are amongst the youngest described for the superfamily in Patagonia, together with *Pitheculites chenche*, *Acdestis maddeni*, *Palaeothentes serratus* and *P. relictus* (Abello et al. 2020). Our work adds not only to the knowledge of the metatherian association from Collon Cura Formation, but also represent the youngest well-documented high-latitude palaeothentoids. As noted by Engelman et al (2017), the Middle Miocene palaeothentoids developed an extensive radiation with several species distributed in geographically distant regions. Apparently, some biotic or climatic-environmental episode occurred and determined their synchronous extinction by the late Middle Miocene or early Late Miocene. The new taxa described herein could represent a moment of changes in the palaeothentoid assemblage of this period, and their eventual disappearance.

The metatherian taxa at Cerro Zeballos suggest a guild of mostly animalivorous and omnivorous species represented by four different paucituberculatans and a sparassodont, and two granivorous species (which might include twigs and plant shoots in their diet) represented by argyrolagids. It is interesting to mention that, despite many years of fieldwork in Collon Cura Formation at Cerro Zeballos, we did not recover any Abderitidae nor Microbiotheriidae marsupials which are present at slightly more northern outcrops of Collon Cura Formation (i.e., Neuquén province; Abello 2007, Kramarz et al. 2011). These taxa are usually suggested to be more frugivorous or frugivorous-animalivorous species associated with well forested environments (Abello et al. 2012, 2020; Zimicz 2012), and their absence might indicate more open environments for Collon Cura Formation at Cerro Zeballos. Also, the occurrence of two species of Argyrolagidae can be associated with subhumid to semiarid environments as proposed by Abello and Candela (2019), who suggested their presence in habitats with heterogeneous vegetation cover. In sum, all these taxa occurred before the Late Miocene cooling (sensu Goin and Martin 2022), or coincident with the Middle Miocene Climatic Transition (Flower and Kennett 1994), and could represent a drier environmental period consistent with more open environments than those characterizing the more northern outcrops of Collón Curá Formation.

The estimated mass of the Palaeothentoidea and Argyrolagidae metatherians from Cerro Zeballos ranges from 400 g to 5 g, including the smallest palaeothentoids known up to date (Tables 1), even smaller than the mass calculated for caenolestoids (Abello et al. 2020). The two largest species from Cerro Zeballos (*P. goini,* the largest of the Paucituberculata from Cerro Zeballos, and *L. kilmisteri*) fall within the range of species from Quebrada Honda (Bolivia), *A. maddeni* (554 g) and *P. serratus* (100 g), showing that mass remained within medium to low body sizes throughout the Middle Miocene for some species at different latitudes. However, we found a marked decrease in overall mass for the clade, as calculated for our two smaller species (*Z. incertus* and *M. zeballoensis*) (Tables 1 and 2). The presence of these species might indicate that mouse-sized niches in South American ecosystems prior to the Great American Biological Interchange were occupied by small metatherians, absent from previous studies probably due to sampling methods. The incorporation of screen-washing techniques could aid in the collection of these overlooked taxa.

Both argyrolagid species from Cerro Zeballos fall within the median mass values for the family Argyrolagidae, closer to the estimated masses of *Argyrolagus palmeri*, and some *Microtragulus* species (e.g., *M. bolivianus* or *M. reigi*) (Table 3). Despite their similar estimated masses, the two species of *Zeballolagus* can be clearly differentiated by their mandibular and teeth morphologies (see description above, and Figs. 5, 6 and Supplemental online material Figure 1).

Further studies might increase the metatherian association of Collon Cura Formation at Cerro Zeballos, providing a better idea of their diversity during the Middle Miocene, and their relation to the decline of metatherian diversity, which occurred most probably during the Middle Miocene

Climatic Transition (Frigola et al. 2018; Methner et al. 2020), leading to new environmental conditions and faunal associations in Patagonia.

Acknowledgments

We thank John Fleagle for his donation of several hundreds of marsupial casts, which were invaluable during comparisons for this work. We thank Oscar Martínez, Agustina Reato, Victoria Martin Cid, Germán Alday, Sergio Vincon, and Ariel Humai for their help during the fieldwork. GMM thanks Eugene Watkins and Michael Simeon for financial support. We thank Russell Engelman and an anonymous reviewer for their constructive comments, that improved our original manuscript.

Disclosure statement

No potential conflict of interest was reported by the authors.

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Supplementary online material Figure 1

SEM occlusal views of all the metatherian species described in this work. A: *Panchothentes goini*, A1 left m1, A2 right m2; B: *Lemmythentes kilmisteri*; C: *Minusculothentes zeballoensis*; D: *Zeballothentes incertus*; E: *Zeballolagus ronniejamesdioi*; F: *Zeballolagus separatus*; and G: *Pseudonotictis chubutensis*. The scale bars represent 5 mm.

References

Abello MA. 2007. Sistemática y bioestratigrafía de los Paucituberculata (Mammalia, Marsupialia) del Cenozoico de América del Sur. Unpublished doctoral thesis, Universidad Nacional de La Plata. Available at: http://naturalis.fcnym.unlp.edu.ar/repositorio/_documentos/tesis/tesis_0942.pdf.

Abello MA. 2013. Analysis of dental homologies and phylogeny of Paucituberculata (Mammalia: marsupialia). Biol J Linn Soc. 109:441–465.

Abello MA, Candela AM. 2019. Paleobiology of Argyrolagus (Marsupialia, Argyrolagidae): an astonishing case of bipedalism among South American mammals. J Mamm Evol https://doi.org/10.1007/s10914-019-09470-z

Abello MA, Ortiz-Jaureguizar E, Candela AM. 2012. Paleoecology of the Paucituberculata and Microbiotheria (Mammalia, Marsupialia) from the late early Miocene of Patagonia. In: Vizcaíno SF, Kay RF, Bargo MS, editors. Early Miocene paleobiology in Patagonia: high-latitude paleocommunities of the Santa Cruz Formation. Cambridge: Cambridge University Press; p. 156–172.

Abello MA, Toledo N, Ortiz-Jaureguizar E. 2020. Evolution of South American Paucituberculata (Metatheria: Marsupialia): adaptive radiation and climate changes at the eocene-Oligocene boundary. Hist Biol. 32:476–493. https://doi.org/10.1080/08912963.2018.1502286.

Abello MA, Martin GM, Cardoso Y. 2021. Review of the extinct ‘shrew-opossums’ (Marsupialia: Caenolestidae), with descriptions of two new genera and three new species from the Early Miocene of southern South America. Zool J Linn Soc. 193:464–498. https://doi.org/10.1093/zoolinnean/zlaa165.

Antoine PO, Roddaz M, Brichau S, Tejada-Lara J, Salas-Gismondi R, Altamirano A, Louterbach M, Lambs L, Otto T, Brusset S. 2013. Middle Miocene Vertebrates from the Amazonian Madre de Dios Subandean Zone, Perú. J South Am Earth Sci. 42:91–102. https://doi.org/10.1016/j.jsames.2012.07.008.

Antoine PO, Abello MA, Adnet S, Altamirano Sierra AJ, Baby P, Billet G, Boivin M, Calderón Y, Candela A, Chabain J, Corfu F, Croft DA, Ganerød M, Jaramillo C, Klaus S, Marivaux L, Navarrete RE, Orliac MJ, Parra F, Pérez ME, Pujos F, Rage JC, Ravel A, Robinet C, Roddaz M, Tejada-Lara JV, Vélez-Juarbe J, Wesselingh FP, Salas-Gismondi R. 2016. A 60-million-year Cenozoic history of western Amazonian ecosystems in Contamana, eastern Peru. Gondwana Res. 31:30–59. https://doi.org/10.1016/j.gr.2015.11.001

Babot MJ, García-López DA. 2015. Redescription of the argyrolagid *Microtragulus bolivianus* (Metatheria,Polydolopimorphia, Bonapartheriiformes) based on new remains from Northwestern Argentina. Palaeontol Electron. 19.2.23A:1-23.

Bilmes A, D'Elia L, Veiga GD, Franzese JR. 2014. Relleno intermontano en el antepaís fragmentado patagónico: Evolución neógena de la cuenca de gastre. Revista de la Asociacion Geologica Argentina 71: 311-330.

Bilmes A, Cuitiño JI, D'Elia L. 2022. Los depósitos miocenos de Chubut: Análisis tectono-estratigráfico desde los Andes hasta el Océano Atlántico. In: Giacosa, R.E. (Ed.). Relatorio XXI Congreso Geológico Argentino. Puerto Madryn, 2022. 1315-1334.

Bostelmann E, Bobe R, Carrasco G, Alloway B, Santi-Malnis P, Mancuso A, Agüero B, Alemseged Z, Godoy Y, 2012. The Alto Río Cisnes Fossil Fauna (Río Frías Formation, Early Middle Miocene, Friasian SALMA): A keystone and paradigmatic vertebrate assemblage of the South American Fossil Record. III Simposio de Paleontología en Chile. Libro de Resúmenes, Punta Arenas, Chile, p. 46–49.

Bown TM, Fleagle JG. 1993. Systematics, biostratigraphy, and dental evolution of the Palaeothentidae, later Oligocene to early-middle Miocene (Deseadan-Santacrucian) caenolestoid marsupials of South America. Memoir (The Paleontological Society). 67:1–76. https://doi.org/10.1017/S0022336000062107.

Brandoni D, González Ruiz L, Reato A, Martin G. 2019. Chronological implications of the nothrotheriid '*Xyophorus'* (Mammalia, Xenarthra) from the Collón Curá Formation (Miocene of Patagonia, Argentina). Hist Biol. 31:879–887.

Bucher J, López M, García M, Bilmes A, Elia LD, Funes D. 2018. Estructura y estratigrafía de un bajo neógeno del antepaís norpatagónico: el depocentro Paso del Sapo, provincia de Chubut. Rev Asoc Geol Arg. 75:312-324.

Bucher J, Pérez ME, González Ruiz LR, D'Elía L, Bilmes A. 2021.New middle Miocene (Langhian - Serravallian) vertebrate localities in northwestern Patagonia, Argentina: A contribution to high latitude south american land mammal ages sequence. J South Am Earth Sci. 107:103024.

Carlini AA, Pascual R, Goin FJ. 2007. A new argyrolagid marsupial from the early Miocene of Patagonia. Neues Jahrb Geol Palaontol Abh. 245:323–330.

Croft DA. 2016. Horned Armadillos and Rafting Monkeys. The Fascinating Fossil Mammals of South America. Indiana University Press.

Dumont ER, Bown TM. 1997. New caenolestoid marsupials. In: Kay RF, Madden RH, Cifelli RL, Flynn JJ editors Vertebrate paleontology in the Neotropics: the Miocene fauna of La Venta, Colombia. Smithsonian Institution Press, Washington DC; p. 207–212.

Dumont ER, Strait SG, Friscia AR. 2000. Abderitid marsupials from the Miocene of Patagonia: an assessment of form, function, and evolution. J Paleont. 74:1161–1172.

Echarri S, Ulloa-Guaiquin KS, Aguirrezabala G, Forasiepi AM. 2021. *Cladosictis patagonica* (Metatheria, Sparassodonta) from the Collón Cura Formation (Middle Miocene), Río Negro, Argentina. Ameghiniana. 58:485-491.

Eldridge MDB, Beck RMD, Croft DA et al (2019) An emerging consensus in the evolution, phylogeny, and systematics of marsupials and their fossil relatives (Metatheria). J Mammal 100:802–837

Engelman RK, Croft DA. 2014. A new species of smal-bodied sparassodont (Mammalia, Metatheria) from the middle Miocene locality of Quebrada Honda, Bolivia. J Verteb Palaeontol. 34:672–688.

Engelman RK, Anaya F, Croft DA. 2016. New palaeothentid marsupials (Paucituberculata) from the middle Miocene of Quebrada Honda, Bolivia, and their implications for the palaeoecology, decline and extinction of the Palaeothentoidea, J Sys Palaeontol. DOI: 10.1080/14772019.2016.1240112.

Flower BP, Kennett JP. 1994. The middle Miocene climatic transition: East Antarctica ice sheet development, deep ocean circulation and global carbon cycling. Palaeogeogr. Palaeoclimatol. Palaeoecol. 108:537-555.

Forasiepi AM, Carlini AA. 2012. New thylacosmilid (Mammalia, Metatheria, Sparassodonta) from the Miocene of Patagonia, Argentina. Zootaxa. 2552:55–68.

Forasiepi AM, Goin FJ, Tauber AA. 2004. Las especies de *Arctodictis* Mercerat, 1891 (Metatheria, Borhyaenidae), grandes marsupiales carnívoros. Rev Esp Paleo. 19:1-22.

Forasiepi AM, Sánchez-Villagra M, Goin FJ, Takai M, Shigehara N, Kay R. 2006. A new Hathliacynidae (Metatheria, Sparassodonta) from the Middle Miocene of Quebrada Honda, Bolivia. J Verteb Paleontol. 26:670-684.

Frigola A, Prange M, Schulz M. 2018. Boundary conditions for the Middle Miocene Climate Transition (MMCT v1.0). Geoscientific Model Development. 11: 1607–1626.

García-López, DA, Babot MJ. 2015. A late Miocene Argyrolagidae (Mammalia, Metatheria, Bonapartheriiformes) from Northwestern Argentina. Ameghiniana. 52:314-323.

Goin FJ, Abello MA 2013. Los Metatheria sudamericanos de comienzos del Neógeno (Mioceno temprano, Edad–mamífero Colhuehuapense): Microbiotheria y Polydolopimorphia. Ameghiniana. 50:51–78.

Goin FJ, Woodburne MO, Zimicz AN, Martin GM, Chornogubsky L. 2016. A brief history of South American Metatherians. Evolutionary Contexts and Intercontinental Dispersals. Springer Earth System Sciences, Springer; p. 237. doi:10.1007/978-94-017-7420-8.

Goin FJ. 1997. New clues for understanding Neogene marsupial radiations. In: Kay RF, Madden RH, Cifelli RL, Flynn JJ editors Vertebrate paleontology in the Neotropics: the Miocene fauna of La Venta, Colombia. Smithsonian Institution Press, Washington DC.; p. 187–206.

Goin FJ, Martin GM. 2022. Cenozoic South American metatherians (Mammalia, Theria) as indicators of climate-environmental changes. In: Larramendy ML, Liwszyc G (eds) Non-conventional Vertebrate Species in Environmental Risk Assessment Strategies. Vol. 1: Non-conventional Mammal Species – Marsupials (Metatheria). Royal Society of Chemistry, Cambridge

Kramarz AG, Forasiepi AM, Bond M. 2011. Vertebrados Cenozoicos. XVIII Congreso Geológico Argentino. Relatorio, Neuquén, Argentina, p. 557–572.

Lage J. 1982. Descripción geológica de la hoja 43c, Gualjaina, Provincia del Chubut. Boletín del Servicio Geológico Nacional. 189:1–72.

Lizuaín A, Ragona D, Folguera A. 1995. Mapa Geológico de la Provincia de Chubut, 1:750.000. Dirección Nacional del Servicio Geológico, Secretaría de Minería, Buenos Aires.

Marshall LG. 1976. New didelphine from the la Venta fauna (Miocene) of Colombia, South America. J Paleontol. 50:402–418.

Marshall LG. 1977. A new species of *Lycopsis* (Borhyaenidae: Marsupialia) from the La Venta Fauna (Late Miocene) of Colombia, South America. J Paleontol. 51:633–642.

Marshall LG. 1980. Systematics of the South American marsupial family Caenolestidae. Fieldiana Geology, NS. 5:1–136.

Marshall LG. 1981. Review of the Hathlyacyninae, an extinct subfamily of South American “Dog-like” Marsupials. Fieldiana Geology, NS. 7:1–120.

Marshall, L. G. 1990. Fossil Marsupialia from the type Friasian Land Mammal Age (Miocene), Alto Rio Cisnes, Aisen, Chile. Rev Geol Chile. 17:19–55.

Martin GM, Tejedor MF. 2007. Nueva especie de *Pseudonotictis* Ameghino (Metatheria, Sparassodonta, Hathliacynidae) del Mioceno medio de Chubut noroccidental, Argentina. Ameghiniana. 44:747–750.

Methner K, Campani M, Fiebig J, Löffler N, Kempf O, Mulch A. 2020. Middle Miocene long-term continental temperature change in and out of pace with marine climate records. Sci Rep. 10:7989.

Pascual R, Bondesio P, Vucetich MG, Scillato-Yané GJ, Bond M, Tonni E. 1984. Vertebrados fósiles cenozoicos. IX Congreso Geológico Argentino. Bariloche, Argentina. Relatorio 2:39–561.

Rabassa J. 1978. Estratigrafía de la región de Pilcaniyeu Comallo, Provincia de Río Negro. 7º Congreso Geológico Argentino, Actas 1:731-746.

Ramos ME, Orts D, Calatayud F, Pazos PJ, Folguera A. 2011. Estructura, Estratigrafía y evolución tectónica de la cuenca de Ñirihuau en las nacientes del río Cushamen, Chubut. Revista de la Asociación Geológica Argentina 68:210–224.

Sánchez-Villagra MR, Kay RF, Anaya-Daza F. 2000. Cranial anatomy and palaeobiology of the Miocene marsupial *Hondalagus altiplanensis* and a phylogeny of argyrolagids. Palaeontol. 43:287–301.

Simpson GG. 1970a. The Argyrolagidae, extinct South American marsupials. Bull Mus Compar Zool. 139:1-86.

Simpson GG. 1970b. Additions to knowledge of the Argyrolagidae (Mammalia, Marsupialia) from the Late Cenozoic of Argentina. Breviora. 361:1-17.

Stutz NS, Abello MA, Marivaux L, Boivin M, Pujos F, Benites-Palomino AM, Salas-Gismondi R, Tejada-Lara JV, Andriolli Custódio M, Roddaz M, Ventura Santos R, Ribeiro AM, Pierre-Olivier A. 2022. Late middle Miocene Metatheria (Mammalia: Didelphimorphia and

Paucituberculata) from Juan Guerra, San Martín Department, Peruvian Amazonia. J South Am Earth Sci. 118:103902.

Suárez Gómez C. 2018. Estudios Taxonómicos y Paleobiológicos sobre los Metatheria (Mammalia) del Mioceno Medio de La Venta, Colombia. Unpublished doctoral thesis, Universidad Nacional de La Plata.

Tejada-Lara J, Salas-Gismondi R, Pujos F, Baby P, Benammi M, Brusset S, Franceschi D, Espurt N, Urbina M, Antoine PO. 2015. Life in proto-Amazonia: middle Miocene mammals from the Fitzcarrald Arch (Peruvian Amazonia). Palaeontol. 58:341–378. https://doi.org/10.1111/pala.12147.

Villafañe AL, Pérez ME, Abello MA, Bedatou E, Bond M. 2008. Nueva localidad fosilífera del Mioceno medio en el noroeste de la provincia del Chubut. III Congreso Latinoamericano de Paleontología de Vertebrados. Neuquén, Patagonia, Argentina.

Yrigoyen M. 1969. Problemas estratigráficos del Terciario de Argentina. Ameghiniana 6:349- 356.

Zimicz AN 2012. Ecomorfología de los marsupiales paleógenos de América del Sur. Unpublished doctoral thesis, Universidad Nacional de La Plata.

Figures

Figure 1. Occlusal (A), labial (B) and lingual (C) views of the mandible of *Panchothentes goini* sp. nov. The black line represents 1 cm; p3 third premolar; m1 to m4 first to fourth molars.

Figure 2. Occlusal (A), lingual (B) and labial (C) views of the mandible of *Lemmythentes kilmisteri* sp. nov. The black line represents 1 cm; m1 to m4 first to fourth molars.

Figure 3. Occlusal (A), lingual (B) and labial (C) views of the mandible of *Minusculothentes zeballoensis* sp. nov. The black line represents 0.5 cm; p3 third premolar; m1 to m3 first to third molars.

Figure 4. Occlusal (A), labial (B) and lingual (C) views of the mandible of *Zeballothentes incertus* sp. nov. The black line represents 0.5 cm; m2 and m3 second and third molars.

Figure 5. Occlusal (A), lingual (B) and labial (C) views of the mandible of *Zeballolagus ronniejamesdioi* sp. nov. The black line represents 0.5 cm; m1 to m4 first to fourth molars.

Figure 6. Occlusal (A), labial (B) and lingual (C) views of the mandible of *Zeballolagus separatus* sp. nov. The black line represents 1 cm; m1 to m3 first to third molars.

Figure 7. Occlusal (A), labial (B) and lingual (C) views of the mandible of *Pseudonotictis chubutensis* sp. nov. The black line represents 1 cm; p2 second premolar; m1 first molar.

Table 1. Comparative dental measurements of Palaeothentoidea, including the new species from Cerro Zeballos (Chubut, Argentina) described in this work (in bold) and species selected from the literature. All measurements are in mm. Length (L), width (W) and area (calculated as L × W) for each molar is presented.

Species	L m1	W m1	m1 area	L m2	W m2	m2 area	L m3	W m3	m3 area	L m4	W m4	m4 area	References
Acdestis bonapartei	4.35	2.40	10.44	2.90	2.10	6.09							Bown & Fleagle 1993
Carlothentes chubutensis	6.30	3.15	19.85	4.40	3.00	13.20							Bown & Fleagle 1993
Palaeopanorthus primus	4.00	2.30	9.20	2.60	2.00	5.20	2.05	1.50	3.07				Bown & Fleagle 1993
Palaeothentes aratae	5.53	2.84	15.69	3.98	2.84	11.31	3.03	2.23	6.76				Bown & Fleagle 1993
Palaeothentes intermedius	3.39	1.79	6.09	2.57	1.80	4.61	2.10	1.41	2.97				Bown & Fleagle 1993
Palaeothentes lemoinei	4.33	2.13	9.23	3.04	2.08	6.32	2.30	1.60	3.69				Bown & Fleagle 1993
Palaeothentes marshalli	3.78	1.85	7.00	2.42	1.74	4.21	2.05	1.53	3.14				Bown & Fleagle 1993
Palaeothentes migueli	2.50	1.31	3.27	1.89	1.33	2.50	1.54	1.05	1.62				Bown & Fleagle 1993
Palaeothentes minutus	2.63	1.42	3.73	2.10	1.45	3.04	1.77	1.20	2.12				Bown & Fleagle 1993
Palaeothentes pascuali	2.34	1.23	2.87	1.82	1.23	2.24	1.61	1.04	1.67				Bown & Fleagle 1993
Pilchenia lucina	4.30	2.10	9.03	2.90	2.10	6.09	2.45	1.90	4.66				Bown & Fleagle 1993
Anatawallathentes illimani	4.30	2.40	10.32	3.20	2.20	7.04	2.40	1.70	4.08	1.70	1.30	2.21	Rincón et al. 2015
Anatawallathentes quimsacruza	3.80	2.10	7.98	2.80	2.10	5.88	2.00	1.70	3.40	1.70	1.50	2.55	Rincón et al. 2015
Pilchenia boliviensis	5.50	3.00	16.50	4.30	3.20	13.76	3.00	2.50	7.50	2.30	1.90	4.37	Rincón et al. 2015
Palaeothentes serratus	2.58	1.55	4.00	1.53									Engelman et al. 2016
Panchothentes goini	5.20	2.40	12.48	3.60	2.20	7.92	2.40	1.90	4.56	1.80	1.20	2.16	**This work**
Lemmythentes kilmisteri	3.20	1.80	5.76	3.00	2.00	6.00	2.50	1.80	4.50	2.00	1.50	3.00	**This work**
Zeballothentes incertus			0.00	2.00	1.40	2.80	1.60	1.10	1.76				**This work**
Minusculothentes zeballoensis	2.00	1.00	2.00	1.70	1.10	1.87	1.20	0.80	0.96				**This work**

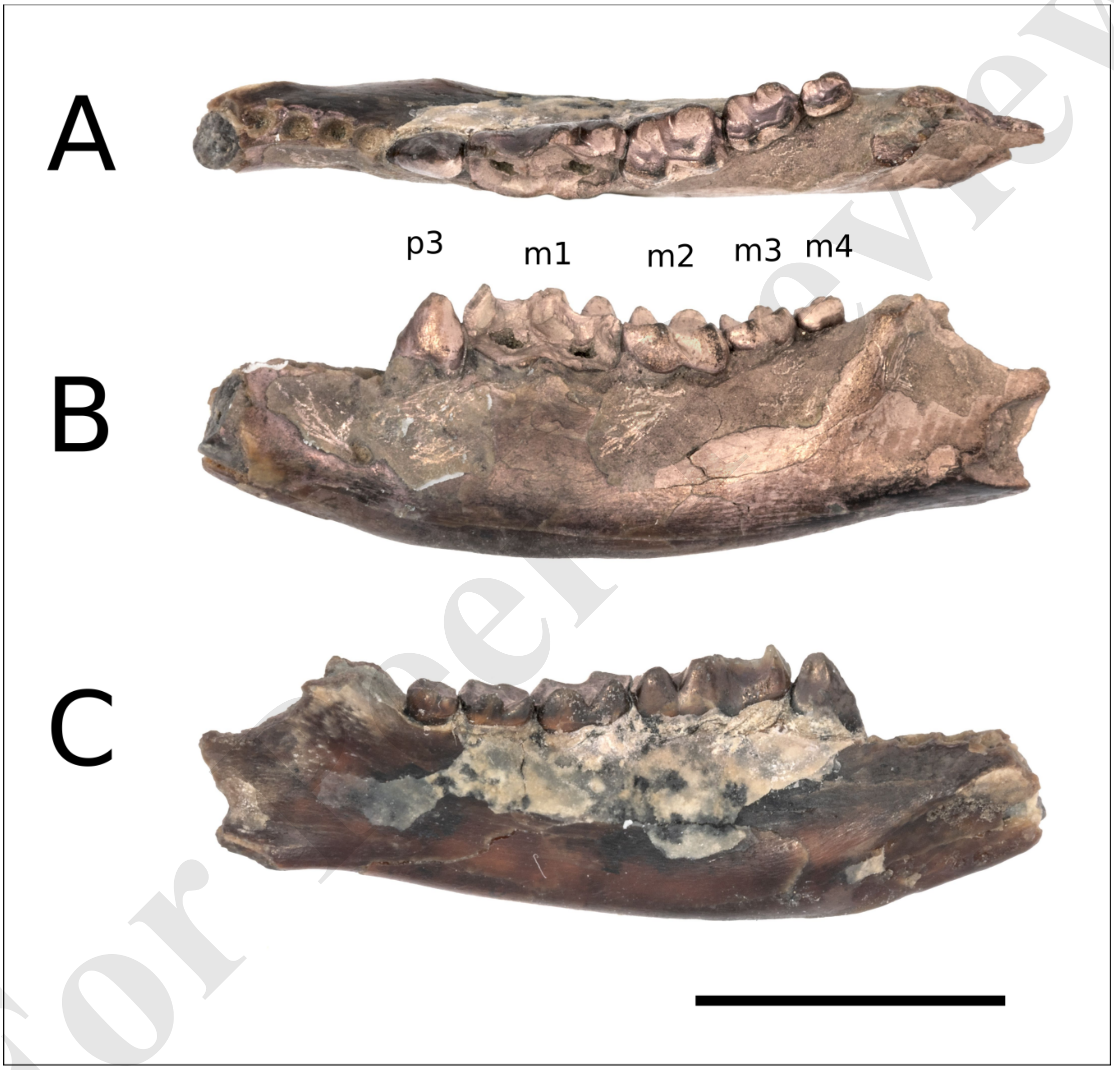
Table 2. Comparative reconstructed mass following Dumont et al. (2000) for selected species of Palaeothentoidea, with measurements taken from the literature and including the new species from Cerro Zeballos (Chubut, Argentina) described in this work (in bold).

Species	m2 área	Ln (m2 area)	Calculated Dumont index	Published mass	References
Pilchenia boliviensis	13.76	2.62177	1039.8	1040	Villaroel & Marshall 1982
Carlothentes chubutensis	13.20	2.58022	967.8	1039	Dumont et al. 2000
Palaeothentes aratae	11.30	2.42480	740.0	799	Dumont et al. 2000
Acdestis maddeni	8.62	2.15409	463.6	464	Engelman et al. 2016
Panchothentes goini	7.92	2.06939	**400.6**		**This work**
Acdestoides praecursor	7.70	2.04122	381.5	382	Marshall 1980
Antawallathentes illimani	7.04	1.95161	326.8	326	Rincón et al. 2015
Palaeothentes lemoinei	6.32	1.84423	271.5	363	Dumont et al. 2000
Acdestodon bonapartei	6.09	1.80665	254.4	273	Dumont et al. 2000
Pilchenia lucina	6.09	1.80665	254.4	273	Dumont et al. 2000
Lemmythentes kilmisteri	6.00	1.79176	**248.0**		**This work**
Antawallathentes quimsacruza	5.88	1.77156	239.5	240	Rincón et al. 2015
Palaeothentes intermedius	4.66	1.53944	160.4	173	Dumont et al. 2000
Palaeothentes relictus	4.41	1.48387	145.7	146	Engelman et al. 2016
Palaeothentes marshalli	4.21	1.43765	134.5	152	Dumont et al. 2000
Palaeothentes serratus	3.67	1.30019	106.1	106	Engelman et al. 2016
Parabderites minusculus	3.20	1.16315	83.7	84	Rincón et al. 2015
Palaeothentes migueli	2.51	0.92176	55.2	58	Dumont et al. 2000
Palaeothentes pascuali	2.24	0.80585	45.2	49	Dumont et al. 2000
Pitheculites minimus	1.54	0.43178	23.7	25	Dumont et al. 2000
Stilotherium dissimile	1.48	0.39204	22.1	24	Dumont et al. 2000

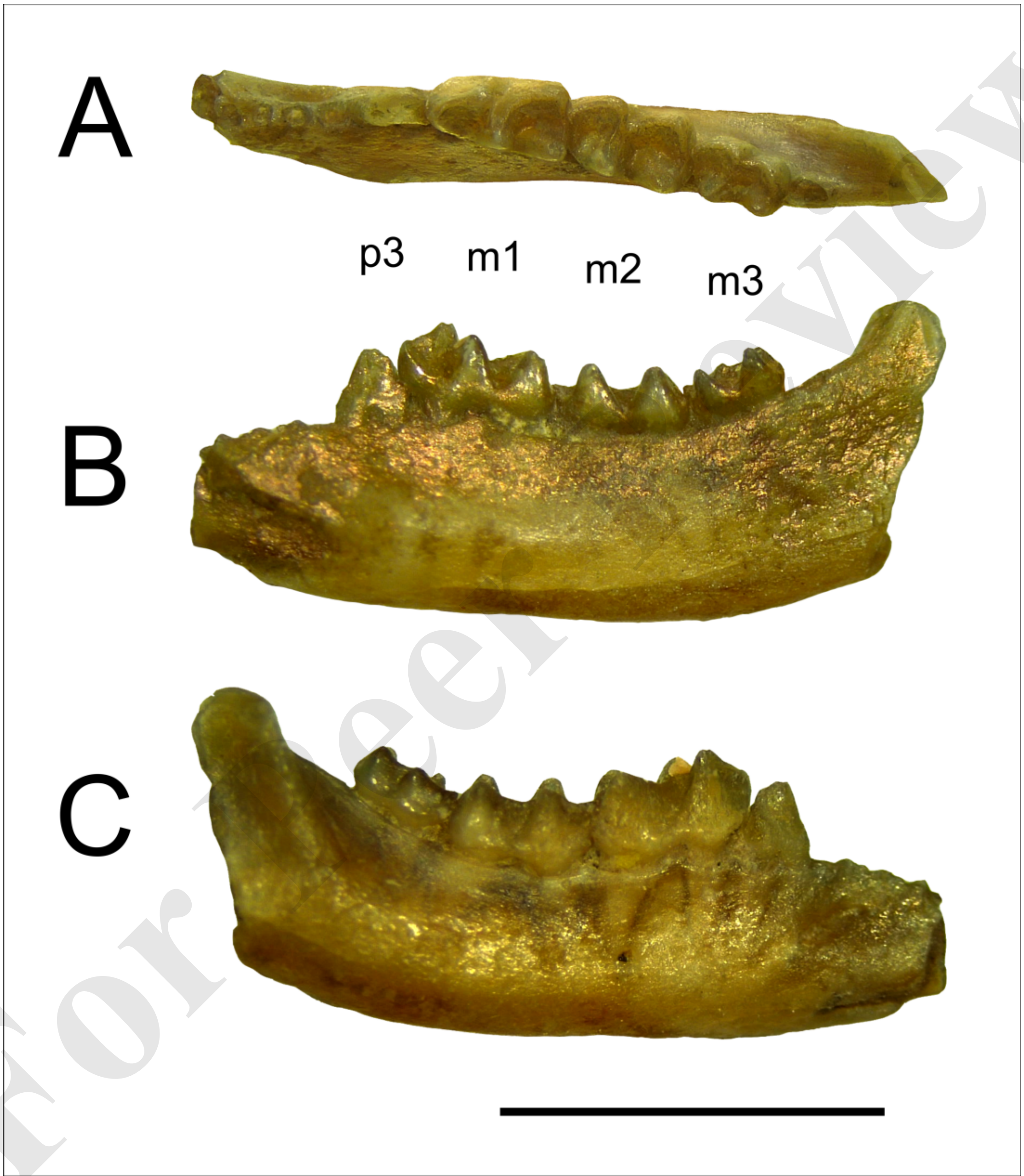
Zeballothentes incertus	1.03	0.02919	**11.8**	**This work**
Minusculothentes zeballoensis	0.63	-0.46850	**5.0**	**This work**

Table 3. Comparative dental measurements and reconstructed mass (following Dumont et al. 2000) of Argyrolagidae, including the new species from Cerro Zeballos (Chubut, Argentina) described in this work. All measurements are in mm. Length (L), width (W) and area (calculated as L × W) for each molar is presented.

Species	L m1	W m1	m1 area	L m2	W m2	m3 area	L m3	W m3	m3 area	L m4	W m4	m4 area	Ln (m² area)	Calculated Dumont index	Reference
Argyrolagus parodii	1,75	1,35	2,36	2,00	1,66	3,37	1,92	1,63	3,12	1,92	1,20	2,30	1,19	93,9	Simpson 1970, Villarroel & Marshall 1988
Argyrolagus palmeri	1,90	1,10	2,09	2,10	1,30	2,73	2,00	1,30	2,60	2,00	1,10	2,20	1,00	63,7	Simpson 1970
Anargyrolagus primus				1,43	1,18	1,69	1,35	1,17	1,58				0,52	27,7	Carlini et al. 2007
Argyrolagus scagliai	1,90	1,70	3,23	2,22	1,85	3,89	2,13	1,73	3,70	2,20	1,30	2,86	1,35	118,2	Simpson 1970
Microtragulus bolivianus	1,59	1,21	1,92	1,71	1,55	2,65	1,56	1,41	2,19	1,32	1,14	1,49	0,97	61,3	Babot & García-López 2016
Microtragulus catamarcensis	1,32	1,03	1,37	1,39	1,23	1,71	1,26	1,07	1,35	0,88	0,65	0,57	0,53	28,4	García-López & Babot 2015
Microtragulus reigi	1,60	1,50	2,40	1,50	1,50	2,25	1,70	1,60	2,72	1,50	1,10	1,65	0,81	45,6	Simpson 1970, Villarroel & Marshall 1988
Hondalagus altiplanensis	1,42	0,94	1,33	1,32	1,20	1,58	1,35	1,23	1,66	1,42	0,91	1,29	0,46	24,9	Villarroel & Marshall 1988
Zeballolagus ronniejamesdioi	1,64	0,93	1,52	1,79	1,35	2,41	1,80	1,32	2,38	1,63	1,09	1,78	0,88	**51,3**	**This work**
Zeballolagus separatus	1,55	0,91	1,42	1,73	1,30	2,24	1,60	1,30	2,07				0,81	**45,1**	**This work**


A
p3
m1
m2
m3
m4
B
C


A
m1
m2
m3
m4
B
C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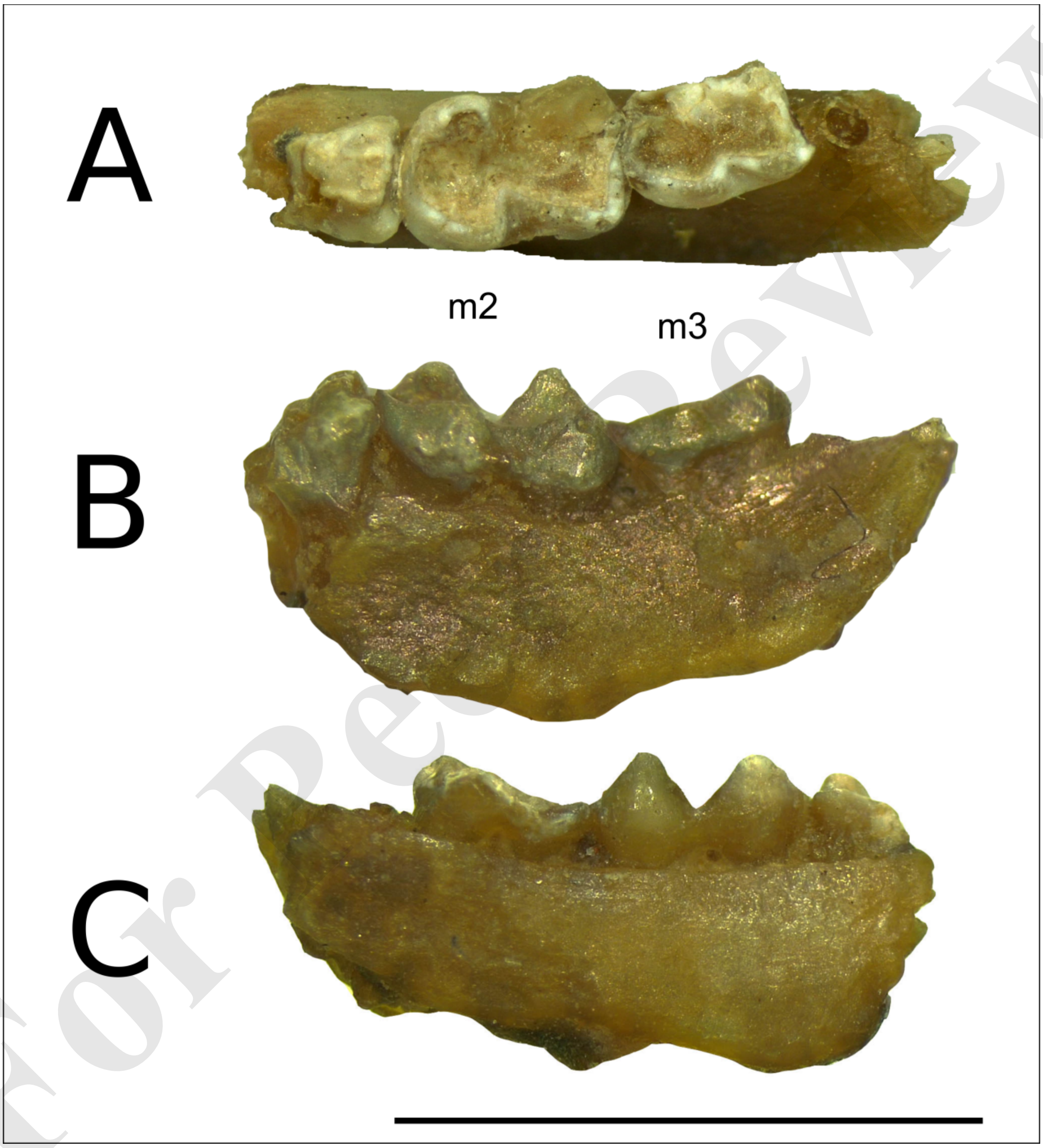
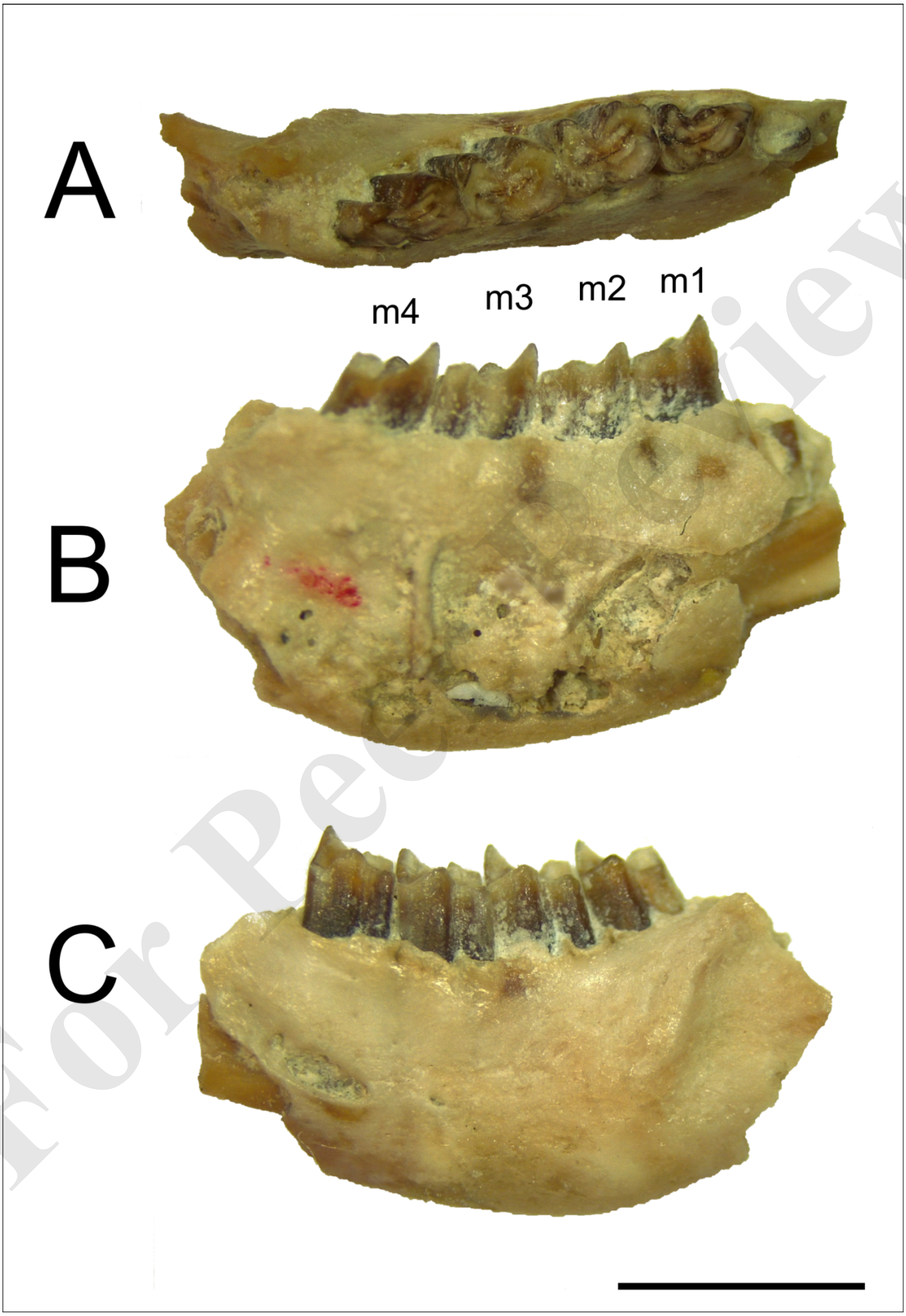
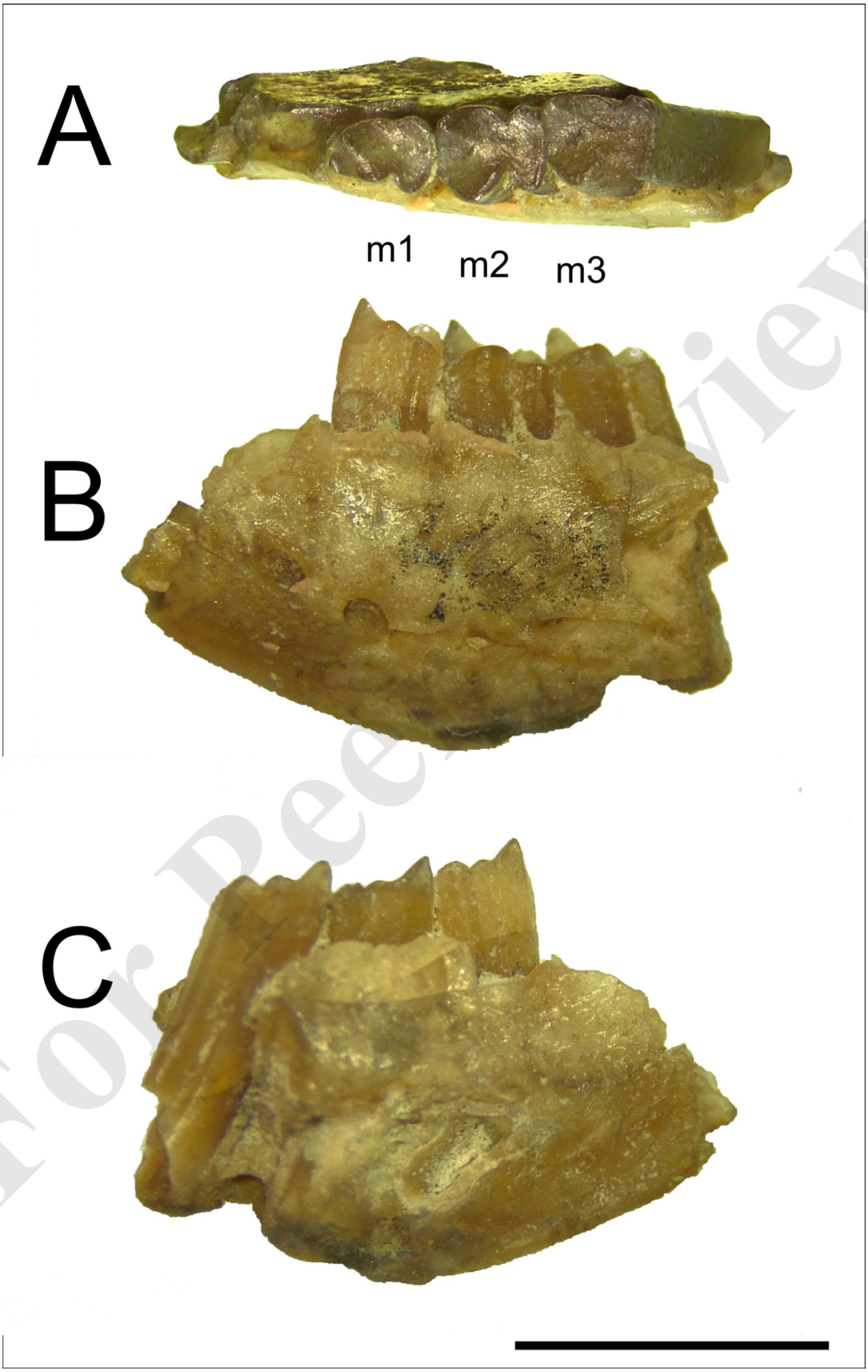
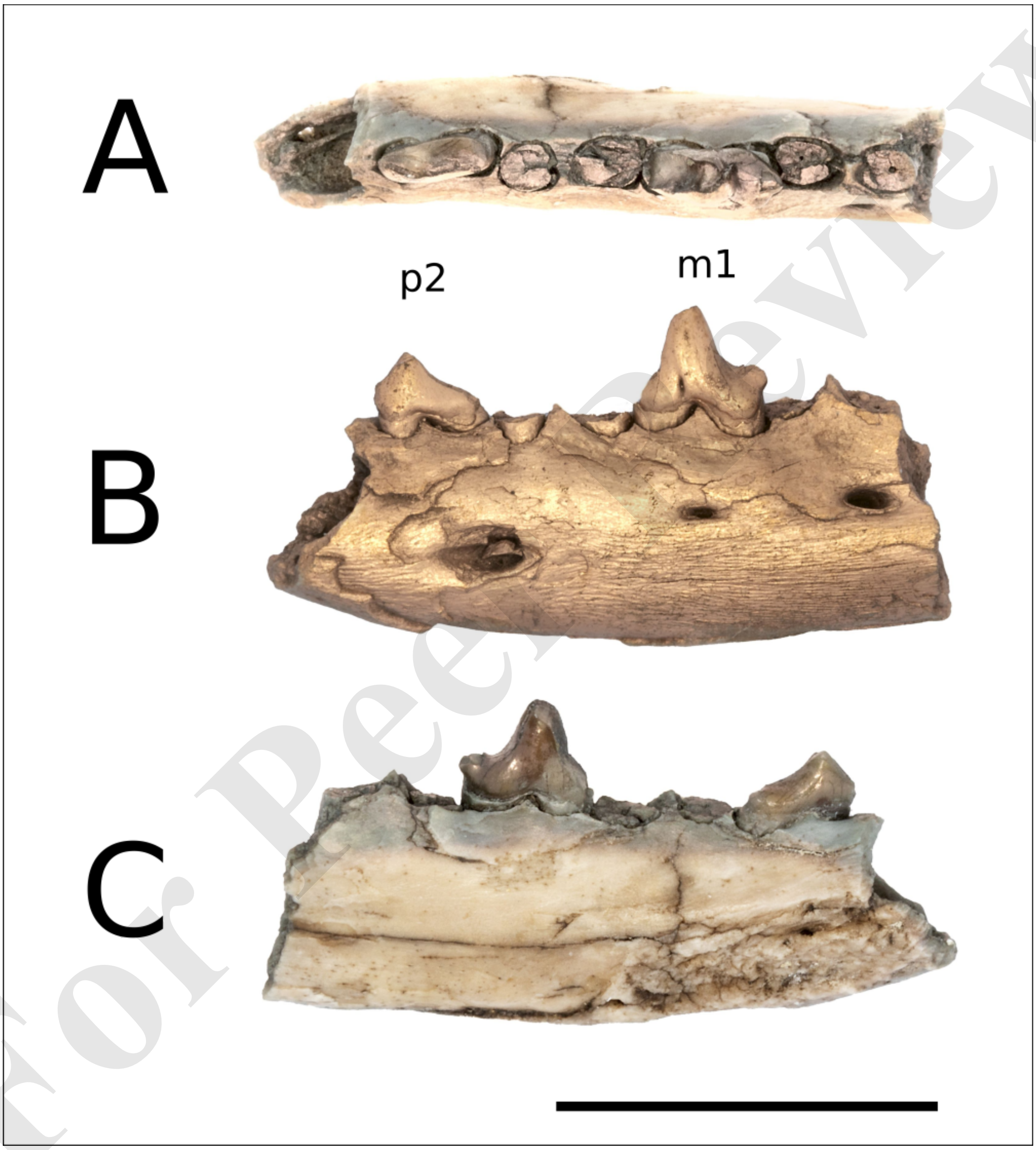
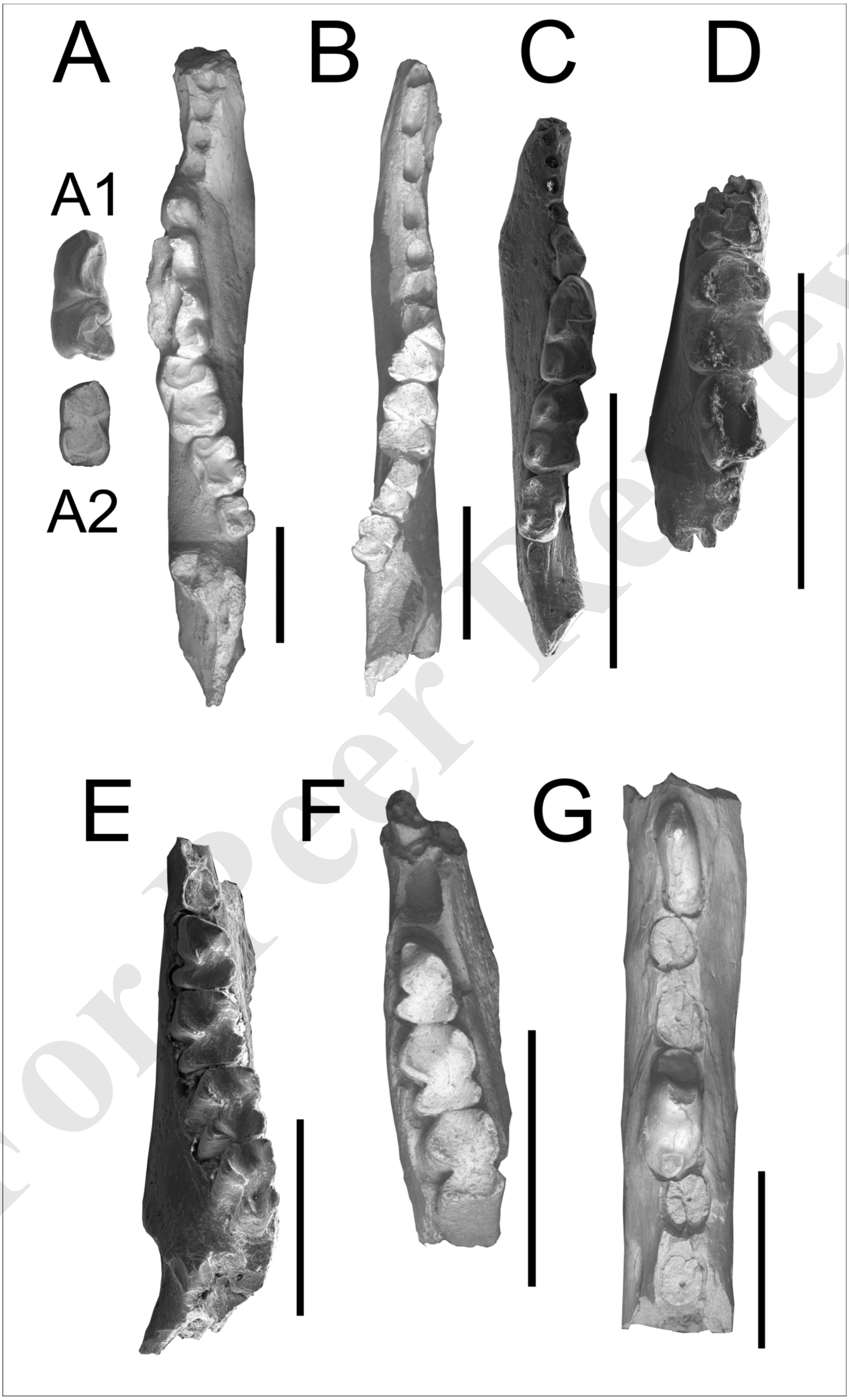
p3
m1
m2
m3
B
C

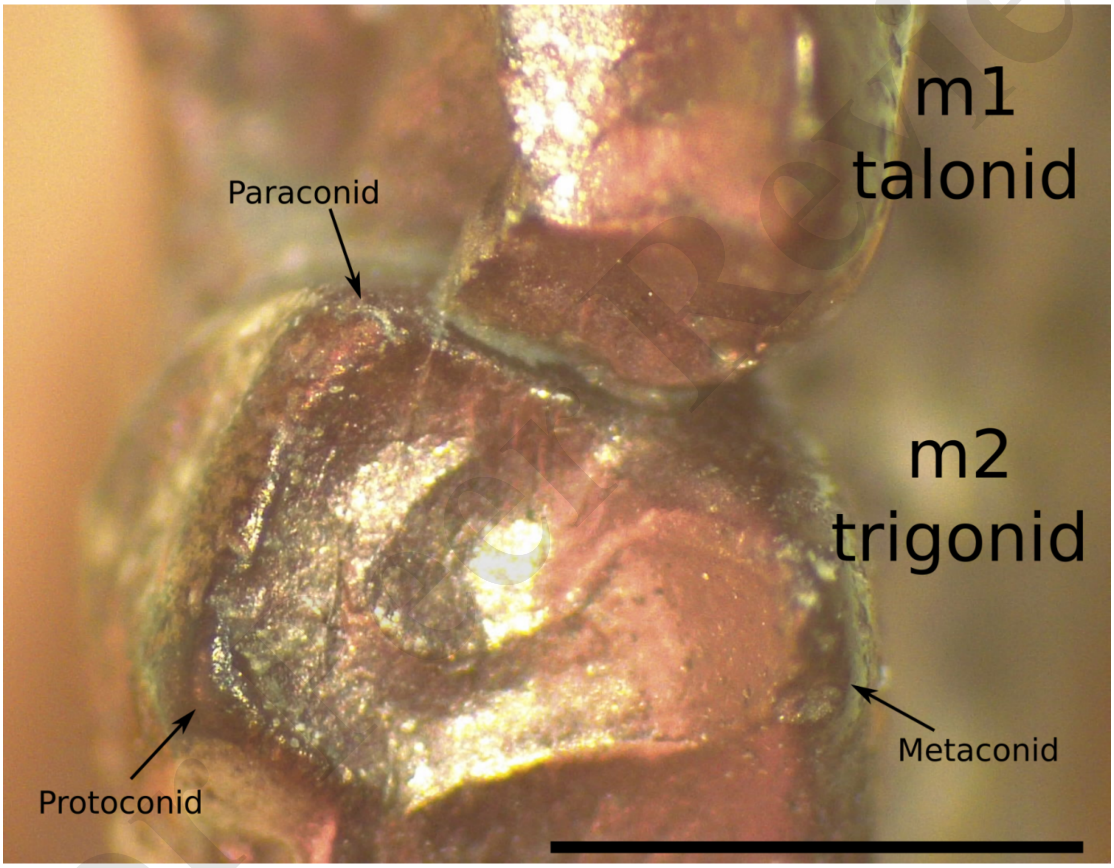

A
m2
m3
B
C


A
m4
m3
m2
m1
B
C


A
m1
m2
m3
B
C


A
p2
m1
B
C


A
B
C
D
A1
A2
E
F
G


m1
talonid
Paraconid
m2
trigonid
Metaconid
Protoconid