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A new didolodontid mammal from the late Paleocene–earliest Eocene of Laguna Umayo, Peru

JAVIER N. GELFO and BERNARD SIGÉ



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A previously undescribed tooth from the Muñani Formation at the Laguna Umayo locality, Peru, represents the new didolodontid *Umayodus raimondi* gen. et sp. nov., here diagnosed by the presence of a well developed metastylid and ectostylid, and a twinned hypoconulid. This taxon is closely related to the middle Paleocene genera *Escribania* and *Raulvaccia* from the locality of Punta Peligro in Patagonia, Argentina. Phylogenetic analysis here performed indicates that they constitute a monophyletic group within Didolodontidae, supported by five derived characters: the hypocone well developed and close to the protocone; the strongly concave precingulum; the contact between the postcristid and the entoconid; the contact of the crista pre-paraconular, precingulum and parastyle; and the mesiodistal enlargement of the m3 talonid. Their paleogeographic distribution fit with those of the actual Andean Region of the Austral Kingdom. The previously assumed Thanetian–Ypresian age assignment for the Laguna Umayo LU3 fauna is here reinforced by faunistic comparisons with the earliest Eocene Murgon fauna, in Australia, and the Itaboraian South American Land Mammal Age, represented from faunas of Patagonia, Argentina and São José de Itaboraí, Brazil.

Key words: Mammalia, Didolodontidae, Condylarthra, Paleocene, Eocene, Austral Kingdom, South America, Peru.

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Introduction

Since first reported after the Maurice Mattauer fossil discovery (Grambast et al. 1967), the brownish red strata that crop out on the northwestern shore of Laguna Umayo, southeastern Peru, have been of great paleontological interest. Their fossil contents include the Laguna Umayo local fauna LU-3 and the later discovered Chulpas level, located ca. 140 m stratigraphically higher than the former. These widely diverse assemblages, comprising charophytes, several osteichthyan orders and representatives of Anura, Chelonia, Squamata, Crocodylia, and Mammalia (updated list in Sigé et al. 2004) pertain to the lower Muñani Formation of the Puno Group (Sempere et al. 2000; Sigé et al. 2004). This red mudstone sequence belongs to a long reversed polarity zone which allows three alternative age inferences: a Late Cretaceous–early Paleocene one related to Chron 29r (Maastrichtian–Danian); a middle Paleocene one matching with Chron 26r (Selandian); and the one supported by evidence provided by the LU-3 and Chulpas faunas, a late Paleocene–early Eocene age, in coincidence with Chron 24r (Thanetian–Ypresian) (Sigé et al. 2004).

Even though several mammals have been reported from

Laguna Umayo local faunas, only some of them have been fully described up to now. They include several metatherians belonging to indeterminate Didelphimorphia and Peradectia, and *Peradectes austrinum* (Sigé 1971, 1972; Crochet 1980; Sigé et al. 2004); placentals, assigned to the endemic ?notoungulate *Perutherium altiplanense* (Grambast et al. 1967; Marshall et al. 1983) and, a condylarthran ?Didolodontidae (Kerourio and Sigé 1984; Sigé et al. 2004; Gelfo and Sigé 2008). Indeterminate placentals reported as Proteutheria and Notoungulata, together with two polydolopimorphians, *Chulpasia mattaueri* (Crochet and Sigé 1993) and *Sillustania quechuense* (Crochet and Sigé 1996), have been described from the overlying Chulpas level (Crochet and Sigé 1993).

In this contribution, we confirm the presence of a didolodontid in the LU-3 level, in association with charophyte algae and various vertebrate fossils including mammals, among them peradectid and didelphimorph marsupials, and the ?notoungulate *Perutherium altiplanense*. We describe this didolodontid as a new taxon and analyze its phylogenetic relationships, the biochronologic and paleobiogeographic importance of this record, and the possible relationships of Laguna Umayo with other Gondwanan Paleogene faunas.

Institutional abbreviations.—AMNH, American Museum of Natural History, New York, USA; LIEB-PV, Laboratorio de Investigaciones en Evolución y Biodiversidad, Universidad Nacional Patagónica San Juan Bosco, Esquel, Argentina; CPSGM-MA1, Collections Paléontologiques du Service Géologique du Maroc, Ministère de l’Energie et des Mines, Rabat, Morocco; LU, Laguna Umayo, Service des Collections, Laboratoire de Paléontologie, Université Montpellier-2, France; MACN-CA, Museo Argentino de Ciencias Naturales Bernardino Rivadavia-Colección Ameghino, Buenos Aires, Argentina; MCT, Museu de Ciências da Terra, Rio de Janeiro, Brazil; MHNC, Museo de Historia Natural de Cochabamba, Bolivia; MN, Museu Nacional, Rio de Janeiro, Rio de Janeiro, Brazil; MLP, Museo de La Plata, La Plata, Buenos Aires, Argentina; MPEF-PV, Museo Paleontológico Egidio Feruglio, Trelew, Argentina; PVL, División Paleontología de Vertebrados, Fundación Miguel Lillo, Tucumán, Argentina; UNPSJB-PV, Universidad Nacional Patagónica San Juan Bosco, Comodoro Rivadavia, Argentina; YPFB Pal, Yacimientos Petrolíferos Fiscales Bolivianos, Colección Paleontología, Santa Cruz, Bolivia.

Other abbreviations.—SALMA, South American Land Mammal Age. Uppercase letter indicates a tooth in the maxillary series, and a lowercase letter a tooth in the dentary series. “P” and “p” were used for premolars, and “M” and “m” for molars. The number following the tooth abbreviation indicates locus position (e.g., M1 is a first upper molar, p2 a second lower premolar). Accessory cusps were referred as “ac” plus a number.

Material and methods

Cusp and crest homologies.—Several comments are necessary regarding the dental nomenclature of the material here described. There are several bulges of the enamel or protuberances, which may be isolated or joining the principal cusps through low and rounded ridges, most of them probably subject to individual variation and without systematic value. In contrast, there are several supplementary cusps, usually not present among bunodont South American endemic ungulates. When it was possible, we relate them to cusps previously defined in the dental nomenclature, while others will be mentioned just as accessory cusps.

The cusp located on the distolingual wall of the trigonid or postvallid sensu Van Valen (1966), which is closely appressed to the metaconid, was termed metastylid (Osborn 1907). However, the metastylid is not formed by a cingulid, as the suffix-stylid would suggest (Stirton 1941; Evander 2004). In contrast, this cusp seems to originate from the division of the metaconid, as could be inferred via the study of the enamel dental junction. The latter is responsible for the degree of expression of dental traits in the outer enamel surface. In the case of the metastylid, the enamel dental junction appears as a protuberance at the end of a shoulder on the dis-

tal ridge of the metaconid dentine (see cusp 7 grade 1A in Skinner et al. 2008). Other synonyms of metastylid found in the literature are “postmetastylid” (e.g., Marshall et al. 1983) and, particularly in anthropology, “metaconulid”, “cusp 7” or “tuberculum intermedium” (Turner et al. 1991). Even though no consensus have been reached about this, probably postmetaconulid (Hershkovitz 1971) should be preferred if the origin of this cusp is considered. In the following description, we still use metastylid, since it has been broadly used for ungulate molars.

We use the term cristid obliqua in the sense of Szalay (1969). Postmetacristid indicates here the cristid that projects distolingually from the metaconid, which could be in contact with the metastylid. Hershkovitz (1971), in contrast, used postmetacristid as the cristid that joins the hypoconid and the hypoconulid. A small cusp distolabial to the protoconid, related to the labial cingulid, is here mentioned as ectostylid, without distinction between the several cusps described as ectostylid j, k, l, or m according to their position (Hershkovitz 1971). Another name that could be found for this cusp is styloconid, but this one seems to be no more than a synonym of ectostylid (Hershkovitz 1971). The cusps related to the entoconid are here named: postentoconulid (Hershkovitz 1971) for the cusp distal to the former; and entoconulid, for the cusp located mesial to it and related with the entocristid (Van Valen 1966). Centroconid is here used for the cusp present on the cristid obliqua, in contrast to mesoconid (Van Valen 1966), which was also used as a synonym of the hypoconulid (see comments in Hershkovitz 1971).

Phylogenetic analysis.—Phylogenetic analysis was performed using TNT 1.1 software (Goloboff et al. 2003) with the implicit enumeration option. The data matrix has 41 dental characters partially modified from previous analyses (Muizon and Cifelli 2000; Gelfo 2004, 2007a, 2010) plus new characters (see Appendix 1), and 20 taxa (*Protungulatum donnae*, *Phenacodus primaevus*, 5 Kollpaniinae, 12 Didolodontidae, and LU3-801). The systematic arrangement follows Muizon and Cifelli (2000) and Gelfo (2006, 2010); but see Williamson and Carr (2007) for an alternative interpretation of the Kollpaniinae.

Systematic paleontology

Class Mammalia Linnaeus, 1758

Infraclass Placentalia Owen, 1837

Order Panameriungulata Muizon and Cifelli, 2000

Family Didolodontidae Scott, 1913

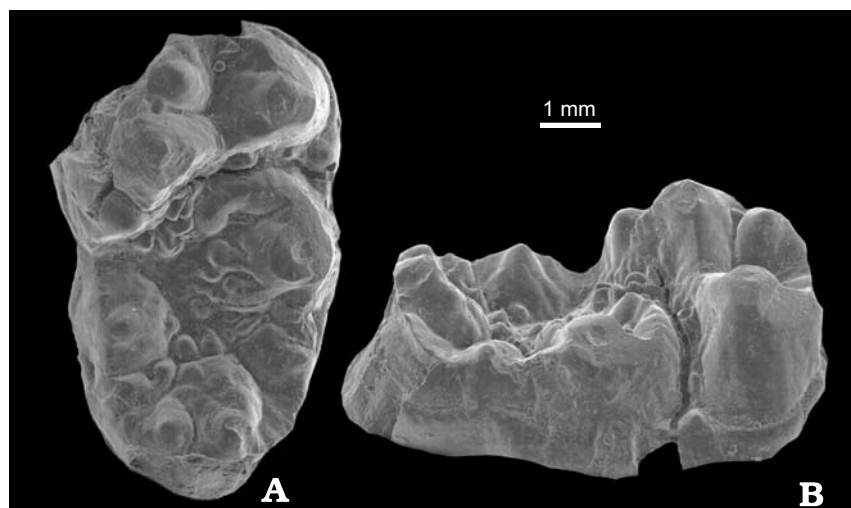
Genus *Umayodus* nov.

Type and included species: *Umayodus raimondi* sp. nov.; by monotypy, see below.

Etymology: From Umayo, for the Laguna Umayo locality; and the Greek *odous*, tooth; commonly used for Didolodontidae names.

Diagnosis.—In contrast to the rest of didolodontids, well de-

Fig. 1. Didolodontid mammal *Umayodus raimondi* gen. et sp. nov. from the Muñani Formation (late Paleocene–earliest Eocene) of Laguna Umayo, Peru; LU3-801 (holotype), in occlusal (A) and labial (B) views.



veloped metastylid, ectostylid, and twinned hypoconulid. Medium sized didolodontid, larger than *Raulvaccia peligrensensis* and smaller than *Lamegoia conodonta*. Trigonid higher and wider than the talonid. The m3 with small but well-developed paraconid placed mesiolabially with respect to the metaconid. Metastylid and ectostylid present. Entoconid subequal in size to hypoconulid, cristid obliqua curved and not contacting the distal wall of trigonid.

Umayodus raimondi sp. nov.

Figs. 1, 2.

Etymology: In honor of the Italian geographer and scientist, Antonio Raimondi (1824–1890) who dedicated most of his life to study of Peruvian nature.

Holotype: LU3-801 isolated right m3 (Figs. 1, 2).

Type locality: Laguna Umayo, Puno department, southern Peru.

Type horizon: Lower Muñani Formation (Puno Group).

Material.—Only the type.

Diagnosis.—The same as the genus, by monotypy.

Description.—The only known specimen of the hypodigm is a right m3 (LU3-801), partially broken in the lingual and mesial side of the trigonid and with the distal portion of hypoconulid enamel missing. Its minimum size is 5.4 mm labiolingually (width) and 8.95 mm mesiodistally (length), so it is larger than any Kollpaniinae and is comparable in size to the lesser didolodontids (Fig. 3). The crown is low and bunodont, and the talonid bears numerous small cuspules. The trigonid is higher and mesiodistally shorter than the talonid. Between the trigonid and the talonid, there is a narrow labiolingual fracture, which ends distal to the ectostylid and does not affect the morphological interpretation (Figs. 1, 2). Even though it is partially broken, the presence of a continuous cingulid surrounding the base of the trigonid may be inferred from the remnant of cingulid, mesial to the protoconid and lingual to the metaconid. The cingulid projects from the low ectostylid on the distolabial base of the protoconid, up to the distolingual side of the metaconid. The cingulid is absent labial to the hypoconid, but, distal to it, a weak labial rim runs over the preserved portion of the talonid.

The metaconid is the highest cusp, followed by the lower and rounded protoconid. The paraconid is small, placed mesiolabial to the metaconid. In the trigonid, wear only appears at the top of the metaconid and protoconid, where the dentine is exposed. The paracristid is only partially preserved, labially at its contact with the protoconid basis, and lingually near the paraconid. A short and low metacristid runs mesiolabially from the metaconid to the paraconid. The oblique distal wall of the trigonid (or postvallid) is vertical, particularly distal to the metaconid, which does not invade the talonid basin as in Kollpaniinae or in *Escribania chubutensis*. The metastylid is strong and located distolingual to the metaconid. A short and smooth crest descends from the apex of the metaconid, up to the transverse furrow that separates it from the metastylid.

The talonid is almost twice the mesiodistal length of the trigonid but somewhat narrower. The bases of the talonid cusps are not in contact, so the talonid basin is relatively wide and lingually open. The walls of the cusps delimit a sloped talonid basin, with its deeper portion located mesial to the entoconid. The hypoconid, the only talonid cusp with significant evidence of wear, is the largest talonid cusp, followed in size by the hypoconulid and the entoconid. The base of the hypoconid is connected by projections of its base to several small protuberances, placed in the central part of the talonid basin (Figs. 1, 2).

The cristid obliqua is strongly arcuate, extending a short distance mesially from the hypoconid before curving lingually about 90° and pointing distolingually at its ending. The base of the cristid obliqua is bulky and the surface of the cristid very irregular. No evident centroconid is present, but a small cusp is located at the end of the cristid (Figs. 1, 2). The trajectory of the cristid obliqua does not contact either the protoconid or the metaconid distal walls, but surrounds the base of the postvallid, distal to the above cited fracture between trigonid and talonid. Several bulges lie distal to the postvallid and on its lingual base. Most of them are placed distal to the metastylid and metaconid, and lingual to the

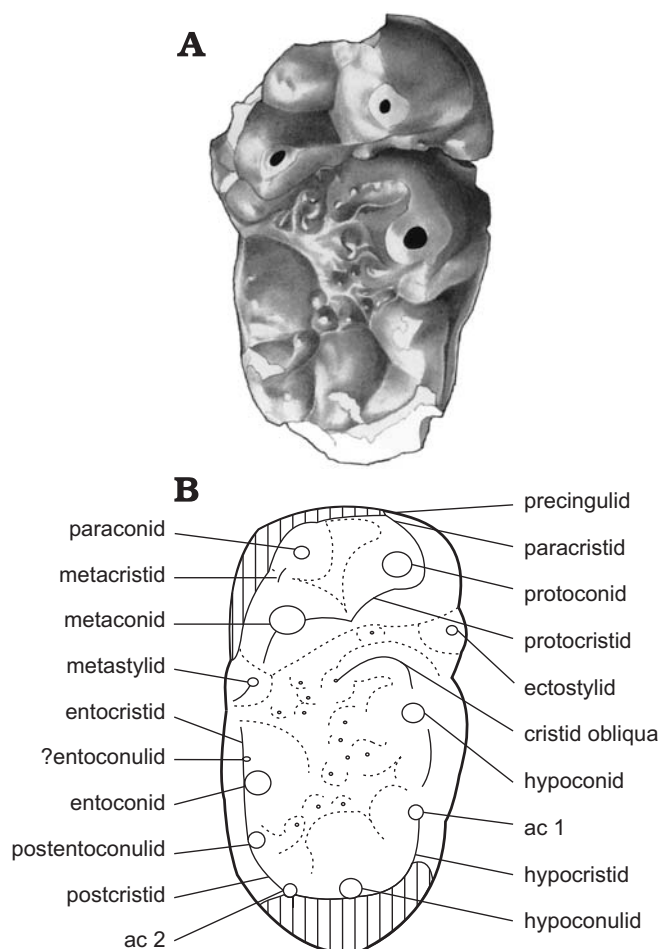


Fig. 2. Didolodontid mammal *Umayodus raimondi* gen. et sp. nov. from the Muñani Formation (late Paleocene–earliest Eocene) of Laguna Umayo, Peru; LU3-801 (holotype) in occlusal view. A. Jean R. Remy's artistic drawing. B. Diagram of LU3-801 specimen showing the nomenclature of cusp mentioned in the text. Abbreviation: ac 1, accessory cusp 1; ac 2, accessory cusp 2.

cristid obliqua, except for one located over the postvallid, distal to the protocristid and mesial to the cristid obliqua.

The mesial base of the hypoconulid bears two small protuberances. Labially, the hypoconulid looks taller than the hypoconid, partly due to the wear encompassed (Fig. 1). The hypocristid descends from the hypoconulid, delimiting the labial side of the talonid up to the contact with the hypoconid. A massive accessory cusp (ac 1) lies over the mesial side of the hypocristid, close to the hypoconulid base but separated from it by a conspicuous furrow. The postcristid gradually descends from the hypoconulid, first lingually and then turning mesially up to the entoconid. A second accessory cusp of the talonid (ac 2) is associated with the postcristid and is twinned to the lingual side of the hypoconulid. The postcristid is interrupted by a postentoconulid, which has a low and rounded projection through the talonid basin. This projection separates the distolabial base of the entoconid from the mesiolingual side of the hypoconulid, ending in a small and rounded protuberance. The entoconid is a large cusp

though smaller than the hypoconid. It occupies almost all of the lingual side of the talonid. The lingual flank of the entoconid forms a vertical plane. The labial side is bulbous and its base expands within the talonid basin. The mesial portion of the entoconid could be interpreted as having a smooth entocristid, which descends to the distal wall of the trigonid without contacting it, thus leaving the talonid basin open lingually. A small ?entoconulid lies mesial to the entoconid as a protuberance of the entocristid.

Discussion

Character comparisons.—Particularly among bunodont dentitions, the differences between m1–2 and m3 could be significant. Among South American “condylarths” the m3 not only has a different outline compared with m1–2, but may also show slight differences in the relationships between cusps and their relative positions (e.g., hypoconulid position). This of course constrains the interpretation of the affinities of *Umayodus raimondi* mostly to comparison with the last lower molar of other taxa. *Umayodus* shows some peculiarities compared to other bunodont South American ungulates: the presence of an ectostylid and a metastylid is unique within Paleogene bunodont ones (i.e., didolodontids, protolipternids and kollpaniines). Nevertheless, the appearance of several supernumerary cusps in several Didolodontidae lineages (e.g., *Raulvaccia peligrensis*, *Escribania talonicuspis*, *Didolodus multicuspis*) makes their presence in *Umayodus* not completely unparalleled. An ectostylid is variably present particularly in different lineages of bunodont condylarths as also in non South American ungulates (e.g., *Mioclaenus turgidus* AMNH 3135) but in contrast, in these taxa the distal side of the metaconid is not related to a metastylid as in *Umayodus*. In fact, the metaconid may be expanded distally through the talonid basin as in kollpaniinaes, or may be almost vertical, as in most didolodontids (with the exception of *Escribania chubutensis*) and protolipternids. The metastylid of *Umayodus* is more comparable to the condition present in North American Phenacodonta (Thewissen 1990), in which it is a conspicuous cusp of the m1–3 and sometimes is present on p4. Considering this serial homology in phenacodontids, the presence of a metastylid could be inferred, at least for the m1–2 of *Umayodus*. In *Tetraclaenodon puercensis* (AMNH 3866) the m1–3 develop a faint metastylid, proportionally much smaller than the one in *Umayodus*. However, in the p4–m3 of *Ectocion osbornianus* (AMNH 3866) and *Phenacodus primaevus* (AMNH 15777), the metastylid is larger and placed very close to the metaconid, separated from it by a well-marked furrow.

The metastylid was considered as one of the synapomorphies supporting the monophyly of Phenacodonta (Thewissen and Domning 1992), and as a derived feature to tentatively link problematic taxa with the former (Gheerbrant et al. 2001). Thus, one hypothesis to be discussed is whether *Umayodus* could be linked with Phenacodonta due to the

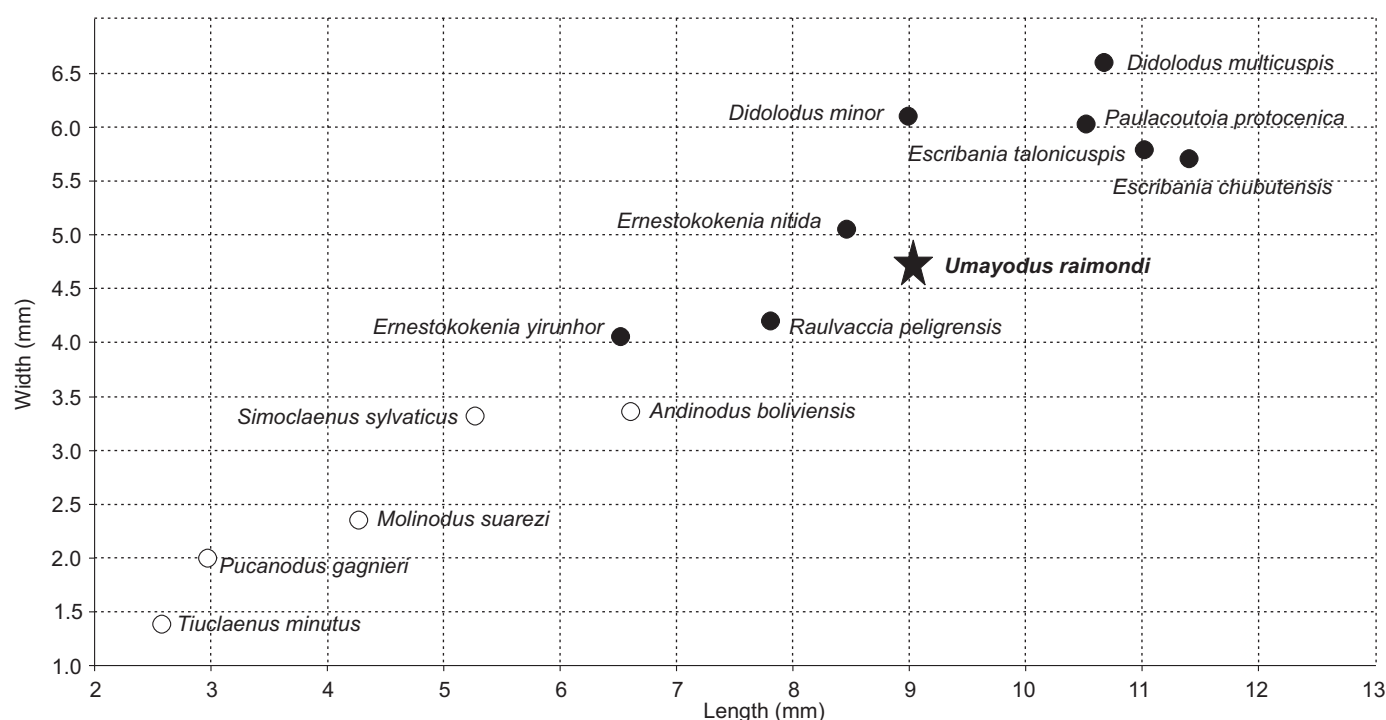


Fig. 3. Plot of the maximum length and width relationship of the last lower molars in Kollpaniinae (white circles) and Didolodontidae (black circles). *Umayodus raimondi* gen. et sp. nov. (star). Measurements of Kollpaniinae and Didolodontidae represent an average of several specimens and were taken from the literature (Muizon and Cifelli 2000; Gelfo 2006, 2007a).

presence of the metastylid. The data matrix of 52 characters and 13 taxa of Thewissen and Domning (1992) was reanalyzed including *Umayodus*. Most of its characters were coded as missing data, except for the presence of metastylids (character 9 state 1) and hypolophid (character 10 state 1). In the original analysis, the branch-and-bound option of PAUP (version 3.0) was used to obtain two most parsimonious trees of 117 steps (Thewissen and Domning 1992). In contrast, we applied the implicit enumeration option of TNT (version 1.1; Goloboff et al. 2003), considering the characters as unordered and equally weighted. We found four most parsimonious trees of 115 steps, two steps shorter than the trees found in the original analysis. The relationships in the new 116-step consensus tree are as follows: (Outgroup ((*Arctocyon*, *Diacodexis*) (*Hyopsodus* (*Pleuraspidotherium* (*Meniscotherium*, *Hyracotherium*, *Umayodus* (*Phenacodus*, *Ectocion*) (*Hyracoidea* (*Moeritherium*, *Sirenia*, *Desmostylia*)))))). This tree strongly supports one of the proposals of Thewissen and Domning (1992), namely that *Phenacodus* and *Ectocion* are sister groups. Other statements, such as the close link suggested between Hyracoidea and Tethytherians, with Perissodactyla, have already been rejected by more recent molecular and morphological analyses (e.g., Wible et al. 2007) and will not be discussed here. Particularly Phenacodonta as considered by Thewissen and Domning (1992) are in the present analysis paraphyletic. The metastylid is a shared character within phenacodontids, but this character does not support a monophyletic group including *Umayodus* and Phenacodonta. Indeed, *Umayodus* shows several differences with re-

spect to the phenacodontids, for example the distal side of the metaconid has a smooth crest, which descends from its apex, reaching the transverse furrow mesial to the metastylid. This structure could represent an incipient postmetacristid, which is not present in *Tetraclaenodon puericensis*, *Ectocion osbornianus*, or *Phenacodus primaevus*. In contrast, a stronger postmetacristid is present in *Ocepeia daouiensis* (CPSGM-MA1 and MNHN PM20) a basal ungulate from the ?Eocene of Morocco, Africa, which was first referred as cf. Phenacodonta by Gheerbrant et al (2001) and later as family incertae sedis within ?Paenungulata (Gheerbrant 2010). The postmetacristid of *Ocepeia* ends in an inflated metastylid, but proportionally much smaller and different than the one present in *Umayodus*.

To sum up, the metastylid of *Umayodus* was probably acquired independently from that of phenacodontids and it only represents a parallelism, as suggested by the strong differences among them. In contrast to phenacodontids, *Umayodus* has a proportionally higher trigonid, strong development of the talonid in m3, the position of the hypoconulid distant from the hypoconid and not forming a third lobe as in phenacodontids (Thewissen 1990), and the development of hypocristid and postcristid, associated with additional cusps. In order to assess the possible homoplastic nature of metastylid, this character was tested by incorporating it to the main cladistic analysis of South American taxa, and adding *Phenacodus primaevus* (see below).

Another peculiar character of *Umayodus raimondi* is the unusual cristid obliqua. It presents a trajectory comparable to

that of the kollpaniine *Simoclaenus sylvaticus* (MHNC 8332). On the m1–2 of *SSimoclaenus sylvaticus* the cristid obliqua meets the trigonid on the lingual edge of the protoconid (Muizon and Cifelli 2000), but on the m3 the cristid obliqua is projected lingually, pointing to the distolingual side of the metaconid, and without contact with the trigonid. However, in *Umayodus* the robust cristid obliqua is strongly arcuate from the hypoconid, whereas in *S. sylvaticus* it is almost straight and faint. In other Kollpaniinae the development of the cristid obliqua in the m3 is variable. For example, this structure is absent in some specimens of *Tiucloaenus minutus* (MHNC 8335) or if present, it is usually short, low and rounded, contacting the distolabial side of the metaconid. The cristid obliqua in most didolodontids follows the same trajectory, from the hypoconid up to the labial side of the metaconid, and it may be related with a strong centroconid (e.g., *Didolodus*) or not (e.g., *Ernestokokenia*). *Lamegoia conodonta* is the only didolodontid with a straight cristid obliqua, projected from the hypoconid up to the protoconid. The Protolipternidae show a low and rounded cristid obliqua, as in didolodontids, but never with centroconid.

Associated with the entoconid, *Umayodus* shows a smooth entocristid with a very small protuberance, here considered, with doubts, as a small entoconulid. In fact, an entoconulid has never been reported as such for kollpaniinae, didolodontids or protolipternids. However, in several specimens referred to these taxa, some cusps are in fact present in association with the entocristid and the entoconid. At least one m2 of *Lamegoia conodonta* (MN1463-V) shows a duplicated entoconid. This is not a constant character, since no accessory cusp or duplication of the entoconid is present in other specimens of *L. conodonta* (e.g., m2 of MCT 1487). In the m3 of some Mioclaenidae, several minor cusps are present over the entocristid, which may extend up to the distal wall of the metaconid, and so closing the talonid basin as in the type of *Mioclaenus turgidus* (AMNH 3135) or, as in some specimens of *Molinodus suarezi* (MHNC 1247), not closing this basin. Within didolodontids, the entocristid is very strong and bears a small cusp on the m3 of *Raulvaccia* (MLP 90-II-12-69) but is not present on the m2. An isolated cusp not related with an entocristid is present mesial to the entoconid, and obliterating the talonid basin, in the m2 of *Escribania chubutensis* (type material UNPSJB-PV 916) but is absent in the m3 of the same specimen, as well as in several second lower molars referred to this taxon (i.e., MPEF-PV 1860, MLP 93-XII-10-2). There is also some variation in the presence of an ?entoconulid in the ?protolipternid *Asmithwoodwardia*. In some remains corresponding to the m1–2 of *A. subtrigona* (syntype MACN-CA10723 and LIEB-PV 1623), a small cusp is present on the mesial face of the entoconid. No cusp is present in the m3 but the entocristid is well developed. In contrast, neither ?entoconulid nor entocristid occurs in specimens referred to *A. scotti*. In summary, the presence of a cusp mesial to the entoconid, related or not to the entocristid, is highly variable within these forms. Cusps related with the entocristid possibly appeared several

times during the evolution of these lineages, in contrast to the metastylid in Phenacodonta.

A peculiar accessory cusp (ac 1) is present in *Umayodus* over the hypocristid, and distal to the hypoconid. Such structures are absent in Kollpaniinae and Protolipternidae, and are not very common among didolodontids. For example, in the m3 of *Escribania chubutensis* (UNPSJB PV 916), the hypocristid is present, and projects from the labial surface of the hypoconulid to the mesiolabial side of the talonid (Bonaparte et al. 1993), but in contrast to *Umayodus*, without contacting the hypoconid and without accessory cusp. In the m3 of *Escribania talonicuspis* (MPEF-PV 1861), the strong and low hypocristid extends from the hypoconulid labial face to the hypoconid distal and basal side (Gelfo et al. 2007). However, m3 of *Umayodus* more closely resembles that of *Raulvaccia peligrensis* in which a rounded and low cusp interrupts the continuity of a strong hypocristid, which connects the hypoconulid to the hypoconid (Gelfo 2007a).

The presence of a duplicated hypoconulid (ac 2) in *Umayodus* (Fig. 2) is a peculiar character among South American ungulates. In the didolodontid *Raulvaccia peligrensis*, the hypoconulid is associated with a very smooth and cuspidate posteristid, but there is not a well-defined cusp comparable to the ac 2 here described. The hypocristid of *Raulvaccia* is stronger and more bulbous than the posteristid, but because of its wear-obscured condition, it is not possible to check for the presence of any cusp (Gelfo 2007a). In *Escribania talonicuspis* there is a similar accessory cusp labial to the hypoconulid, as a swelling in the posteristid (Gelfo et al. 2007). In contrast with *Umayodus*, this accessory cusp is not separated by a deep furrow.

Outside the Paleogene South American endemic ungulates, the duplicated or twinned hypoconulid of *Umayodus* is comparable to that of some primates, in which an enlarged hypoconulid is usually present in the m3. This could form an undivided hypoconulid lobe or heel, or be more squared, with distal and mesial fissures dividing the heel (Gingerich 1976). In particular, some Paromomyidae from the Eocene of North America have two distinct but very close cusps, the hypoconulid and a smaller one located mesiolabially in relation to the hypocristid, which runs through the hypoconid (Silcox et al. 2008). However, ac 2 in *Umayodus* is lingual to the hypoconulid, and it seems to be larger and more separated from the hypoconulid.

The presences of additional cuspules or enamel protuberances in the talonid of *Umayodus raimondi* were not included as characters in our phylogenetic analysis since they probably represent a variable trait among this species. Notwithstanding, it is interesting to mention that comparable structures are variably present in some other didolodontids. They are present in the bottom of the postvallid and in the talonid of some specimens of *Lamegoia conodonta* (MCT 1487 and MN 1463-V). In *Escribania talonicuspis* (MPEF-PV 1861) no minor cuspules are present but, in contrast, there is a large accessory cusp obliterating the talonid basin

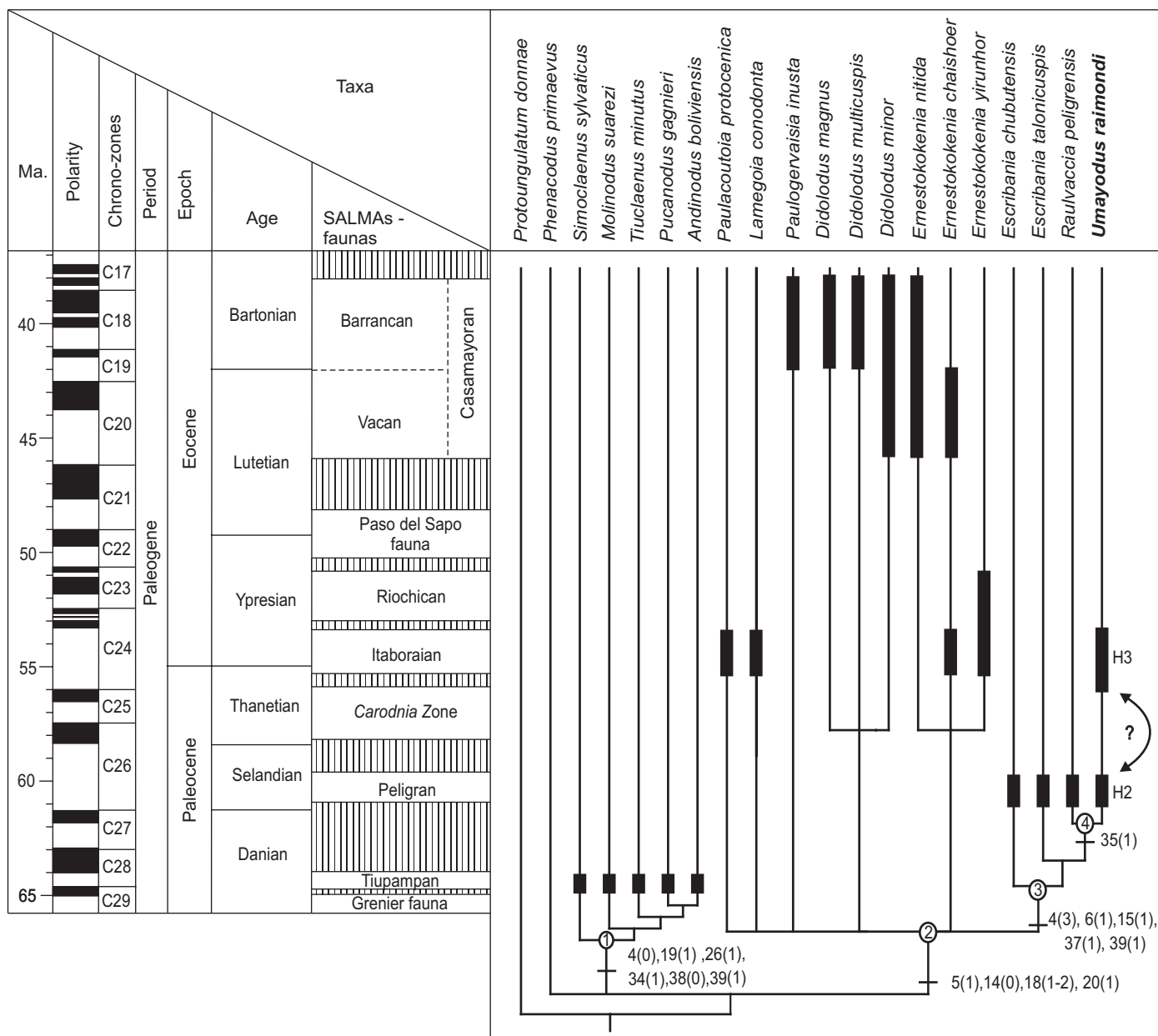


Fig. 4. Phylogenetic relationships of *Umayodus raimondi* gen. et sp. nov. Strict consensus (115 steps) from two most parsimonious trees of 110 steps, indicating the common synapomorphies of the most important nodes and the biochron of the taxa included. Geochronology and magnetostratigraphy follow Luterbacher et al. (2004). Biochronological units follow Gelfo et al (2009) for SALMAs and faunas.

and contacting the hypoconid labially and the entoconid linguallly (Gelfo et al. 2007).

Phylogenetic analysis.—In order to test the relationships of *Umayodus* within the South American Paleogene ungulates, a data matrix was built using 41 characters and involving 20 taxa. Some of the characters (Appendices 1 and 2) were taken and modified from previous analyses (Muizon and Cifelli 2000; Gelfo 2004, 2007a, 2010). Characters 0 to 21 correspond to the upper teeth and characters 22 to 40 to the lower dentition. Some taxa are considered as polymorphic for characters 7, 8, 13, 14, and 26. The taxa included along with *Umayodus raimondi* are *Protungulatum donnae* as an out-

group, *Phenacodus primaevus*, five Kollpaniinae (*Molinodus suarezi*, *Pucanodus gagnieri*, *Simoclaenus sylvaticus*, *Tiucloaenus minutus*, and *Andinodus boliviensis*) and 12 valid Didolodontidae sensu Gelfo (2006, 2010) (*Raulvaccia peligrans*, *Escribania chubutensis*, *Escribania talonicusps*, *Paulacoutoia protocenica*, *Lamegoia conodonta*, *Didolodus multicusps*, *Didolodus minor*, *Didolodus magnus*, *Paulogervaisia inusta*, *Ernestokokenia nitida*, *Ernestokokenia chaisioer*, and *Ernestokokenia yirunhor*). A constraint for monophyly was enforced for South American taxa, except for *Umayodus raimondi*, which was considered as floating, in order to evaluate its possible relationship with *Phenacodus primaevus*.

The Protolipternidae *Protolipterna ellipsodontoides* and *Miguelsoria parayirunhor*, which retain a didolodontid-like dentition, were not included in the present phylogenetic analysis. They were considered as litopterns, due to the association hypotheses of postcranial elements to dental remains (Cifelli 1983a; Bergqvist 1996). Since there is no unambiguous dental character that separates protolipternids from didolodontid, and, no unquestioned didolodontid postcranial remain that could be used as characters (Gelfo 2006) we set them aside from the present analysis.

The analysis of the data matrix under the implicit enumeration option of TNT (version 1.1; Goloboff et al. 2003) resulted in two most parsimonious trees of 110 steps. The analysis supports the inclusion of *Umayodus raimondi* within Didolodontidae. Kollpaniinae and Didolodontidae are both monophyletic groups, but it should be emphasized that their monophyly needs to be tested in a wider context, including several litopterns and notoungulates families. The strict consensus of 115 steps (Fig. 4) shows a basal polytomy that separates *Phenacodus primaevus*, Kollpaniinae, and Didolodontidae. Kollpaniinae are fully resolved (Fig. 4: node 1) and comparison of most parsimonious trees indicates six common synapomorphies. They correspond to the absence of hypocone in M1–2 (character 4 state 0); protocone mesiodistally expanded (character 19 state 1); the posterior slope of the metaconid invading the talonid basin (character 26 state 1); the hypoconid of m3 large and extending in the lingual half of the talonid (character 34 state 1); m3 postentoconulid absent (character 38 state 0) and, m3 talonid length not expanded mesiodistally (character 39 state 1). The projection to the talonid of the posterior slope of the metaconid is also present in *Escribania chubutensis* (Bonaparte et al. 1993; Muizon and Cifelli 2000), but not in *E. talonicuspis* or *Raulvaccia peligrensis*. *Umayodus raimondi* shows a molar morphology more derived than that of kollpaniines from the early Paleocene (Tiupampan SALMA) of Tiupampa, Bolivia (Muizon and Cifelli 2000; Gelfo et al. 2009). The main distinguishing characteristics of *Umayodus* are: larger size; mesiodistally expanded talonid with well defined and wide basin; distal wall of the metaconid not inflated nor projected through the talonid; presence of new structures as metastylid, ectostylid, hypocristid and postcristid. All these morphological features clearly set *Umayodus* apart from the primitive Kollpaniinae.

Didolodontidae share four synapomorphies: hypocone on M3 (character 5 state 1); crista postmetaconular in contact with the postcingulum distally (character 14 state 0); the development of protostyle (character 18 state 1–2) and, subequal size of the para- and metacone in M1–2 (character 20 state 1). In the strict consensus tree, the didolodontids comprise a polytomy (Fig. 4: node 2) formed by three groups plus three isolated terminal taxa *Paulacoutoia protocenica*, *Lamegoia conodonta*, and *Paulogervaisia inusta*. The first of these groups is formed by the *Didolodus* species. The relationships among the *Ernestokokenia* clade, the second group, are not resolved. It should be mentioned that *Ernestokokenia*

patagonica was excluded from the present analysis because only two upper molars are known for this taxon (MACN-CA 10687 and 10688). The last clade is formed by all the taxa from the middle Paleocene (Peligran SALMA) from Punta Peligro in Patagonia, Argentina (Gelfo et al. 2009), plus the new taxon here described. Within this clade, *Umayodus raimondi* appears as the sister taxon of *Raulvaccia peligrensis*, and the two species of *Escribania*, here recovered as paraphyletic, as their sister group. This node (Fig. 4: node 3) is supported by five common synapomorphies: M2 with well developed hypocone appressed to the protocone (character 4 state 3); precingulum of M2 strongly concave (character 6 state 1); crista preparaconular in contact with the precingulum at the parastyle (character 15 state 1); the postcristid of m3 contacting the entoconid (character 37 state 1) and, the mesiodistal enlargement of the m3 talonid (character 39 state 1). At node 4 (Fig. 4) *Umayodus* shares the hypocristid of m3 (character 35 state 1) as a derived character with *Raulvaccia*. Additionally, they also share several characters, such as mesiolabial position of the paraconid in respect to the metaconid; labial cingulid at the base of the protoconid; talonid expanded mesiodistally; development of postcristid; and entocristid developed with an ?entoconulid (much smaller in *Umayodus*). In contrast, *Umayodus raimondi* differs from *Raulvaccia peligrensis* by several exclusive characters, as its wider talonid, the direction of the cristid obliqua, and the duplicated hypoconulid or ac 2. It also differs from the Eocene (Casamayoran SALMA) didolodontids *Didolodus* and *Ernestokokenia*, particularly as regards the size and position of the paraconid, which usually is lacking in geologically younger taxa, and the location of the main talonid cusps.

Even though they were not included in this analysis (see above), *Umayodus* is also distinct from the bunodont and low-crowned protolipternid litopterns (Cifelli 1983b). It differs from the better known of them *Protolipterna ellipsodontoides* (e.g., DNPM LE 444A–E) for the following characters: the paraconid presence; the distal talonid outline not V-shaped as in *P. ellipsodontoides*, but U-shaped; the entoconid separation from the hypoconulid, and the cristid obliqua bending lingually without contacting the protocristid.

Systematic position of *Umayodus*.—The complex morphology of the *Umayodus* molar highlights the importance of establishing a common dental nomenclature, based on homologies, for the different orders of endemic South American ungulates (Gelfo 2007b). Several cusps of *Umayodus* (e.g., metastylid, twinned hypoconulid, or ac 2) are comparable to non-South American mammals, for example phenacodontid “condylarths” and plesiadapiform primates. These molar novelties seem to have evolved independently and convergently in different lineages of bunodont mammals, probably in relation to similar selective pressures as shared adaptive advantage. Specimen LU3-801 was originally mentioned as a doubtful didolodontid condylarth (Kerourio and Sigé 1984), and its attribution later improved as “Didolodontid indet.” (Sigé et al. 2004: 784). The present phylogenetic

analysis confirms its inclusion within the Didolodontidae. *Umayodus* shares more characters with them than with any other bunodont South American group, such as the Kollpaniinae (early Paleocene), the litopterns Protolipternidae (late Paleocene–early Eocene), or even the more derived protheriids Megadolodinae (late Miocene). The phylogenetic analysis shows *Umayodus* nested in a monophyletic clade with all the Peligran taxa (Fig. 4: node 3), and within the latter, more closely related to *Raulvaccia peligrensis* than to the *Escribania* species.

The biochron of Didolodontidae shows a wide temporal distribution, from the middle Paleocene up to the late Eocene (Gelfo et al. 2009). Only an isolated species, *Salladolodus deuterotheroides*, has been recorded from the late Oligocene of Bolivia, but its placement within the didolodontids has been questioned due to the temporal gap and probable affinities with litopterns (see comments in Gelfo 2006). The temporal distribution of the taxa included in the present phylogenetic analysis is in most cases restricted to a particular SALMA. The exceptions are *Ernestokokenia yirunhor* recorded for the Itaboraian and Riochican; and *Ernestokokenia chaishoer* present in the Itaboraian and Vacan subage of the Casamayoran SALMA, but not in the Riochican and Paso del Sapo faunas (Fig. 4). The absence of these species from the Riochican SALMA is very probably due to sample bias, since very few didolodontid species have been recorded for this span, in contrast to previous and succeeding SALMAs (Gelfo 2006). Even so, the absence of *E. chaishoer* from the Paso del Sapo fauna, in which only small bunodont ungulates have been recorded, could be of paleogeographic nature, since this is the only locality in central-western Patagonia (Tejedor et al. 2009; Gelfo and Tejedor 2007). In this context, *Umayodus* represents the westernmost and northernmost record for the Didolodontidae. Its phylogenetic relationships with more southerly forms, such as *Raulvaccia peligrensis* from the middle Paleocene of Punta Peligro (Gelfo 2007a), suggests a wide geographical distribution during the Paleocene, in contrast to other groups like Notoungulata, which were first recorded in lower latitudes from South America, like Tiupampa in Bolivia for the early Paleocene and seems to be first recorded in Patagonia for the late Paleocene–early Eocene (Itaboraian SALMA) in Las Flores Formation (Bond et al. 1995; Gelfo et al. 2009).

Temporal and paleobiogeographic relationships of Laguna Umayo.

The age assignment of LU-3, alternatively regarded as Late Cretaceous or early Tertiary, has been discussed previously (e.g., Grambast et al. 1967; Kielan-Jaworowska et al. 1979). The most recent stratigraphic, paleomagnetic and faunistic revision favors a Paleogene age for this fauna, considering the single and long reverse polarity zone including LU-3 level, to be preferably correlated to Chron 24r (Thanetian–Ypresian) or, as another but less reliable alternative, to Chron 26r (Selandian) (see hypotheses two and three of Sigé et al. 2004). Even though a close phylogenetic relation between *Umayodus raimondi* and the middle Paleocene didolodontids, from the Peligran SALMA (Gelfo et al. 2009), have been pro-

posed here, it should be noted that these relationships do not contradict nor reinforce any of the previous hypotheses concerning the Paleogene age assignment of LU-3 level (Fig. 4: H2, H3). Excepting didolodontids, the Punta Peligro faunistic assemblage (Bonaparte et al. 1993) is very different from that of LU-3 one in its taxonomic content. The Peligran SALMA could be characterized by the following facts: (a) the presence of relictual Mesozoic non-therian mammals such as Gondwanatheria (Pascual et al. 1999) and Dryolestoidea (Gelfo and Pascual 2001); (b) exclusive Gondwanan lineages such as monotremes (Pascual et al. 1992); (c) the presence of derived native ungulates such as the notonychopid litopterns (Bonaparte and Morales 1997); and (d) the striking absence of Notoungulata. Since no new biostratigraphic constraint arises from the phylogenetic relationships of *Umayodus raimondi*, we follow the Thanetian–Ypresian age assignment for LU-3 fauna as the more probable inference (Sigé et al. 2004).

The Paleocene–Eocene age inferred as most probable for LU-3 (Sigé et al. 2004) agrees with the most recent age assignment for the Itaboraian SALMA (Gelfo et al. 2009), which had previously been considered as late Paleocene (e.g., Marshall 1985; Bonaparte et al. 1993). It is important to record that the stratigraphic levels bearing Itaboraian fauna, Las Flores (Patagonia, Argentina) and Itaboraí (Brazil) formations, have never been dated by isotopic or magnetostratigraphic methods. Thus, the age of the Itaboraian SALMA was inferred from the stratigraphic position of Las Flores Formation (Bellosi and Madden 2005) and the evolutionary grade of the mammals (Gelfo et al. 2009).

LU-3 (represented in Peru) and the Itaboraian SALMA (Patagonia, Argentina and Brazil) could be referred to a similar age with independence of their faunistic composition. LU-3 is characterized by the presence of the ?notoungulate *Perutherium altiplanense* and several marsupials, some of them indeterminate (i.e., ?Pediomyidae or ?Microbiotheriidae and Didelphimorphia) and *Peradectes austrinum* (Sigé et al. 2004). Some new peradectids have also been recorded from the Las Flores (Goin et al. 1997) and Itaboraí formations, and at least those from Brazil seem to be more related with the forms from LU-3 than with North American and European species of *Peradectes* (Oliveira 1998). Another similarity between the LU-3 and Itaboraian faunas is the common presence of didolodontids. *Umayodus raimondi* retains a well-developed paraconid, as do *Paulacoutoia protocenica* and *Lamegoia conodonta* from Itaboraí, Brazil. However, the presence of a paraconid only represents the retention of a primitive character, not a derived feature that could relate these taxa to each other. In fact, *Umayodus* is similar to and phylogenetically more related to the older Peligran didolodontids, as suggested in the present analysis and previously (Sigé et al. 2004; Gelfo and Sigé 2008), due to several common characters, such as the talonid expansion, hypocristid, development of accessory cusps, postcrisid, and entocristid development.

The Itaboraian SALMA is also characterized by a wide diversity of mammals, none of which have been recorded in LU-3. These groups are represented by several marsupial lin-

eages (i.e., Borhyaenidae, Caroloameghiniidae, Derorhynchidae, Didelphidae, Microbiotheriidae, Bonapartheriidae, and Protodidelphidae); and Xenarthra (Dasypodidae), Xenungulata (Carodniidae), Astrapotheria (Trigonostylopidae), Notoungulata (Henricosborniidae, Oldfieldthomasiidae), Litopterna (Protolipternidae), and Sparnotheriodontidae, which were considered both as Litopterna (e.g., Bond et al. 2006) or “Condylarthra” (Cifelli 1983a, b).

Despite the differences with LU-3, the Itaboraian fauna could also be compared to the Chulpas local fauna at Peru, discovered southward along the exposed Laguna Umayo profile, and stratigraphically ca. 140 m above the LU-3 level (Crochet and Sigé 1993; Sigé et al. 2004: fig. 7). In addition to several indeterminate therians, two marsupials have been described for this level. The first, *Sillustania quechuense* (Crochet and Sigé 1996) shares derived characters with *Epidolops ameghinoi* from Itaboraí and *Epidolops* sp. from Patagonia (Sigé et al. 2004). Among these similitudes are the earliest occurrence of a large “metaconular hypocone”, which could be suggestive of a similar time span for the Chulpas and Itaboraian levels.

The other Chulpas marsupial described is the polydolopimorphian *Chulpasia matteni*. It shares primitive features with *Glasbius* from the Late Cretaceous of North America (Crochet and Sigé 1993), but it is particularly close related to *Chulpasia jimthorselli* from the earliest Eocene Murgon local fauna of southeastern Queensland, Australia (Sigé et al. 2004, 2009). Both *Chulpasia* species, plus another Murgon marsupial, *Thylacotinga bartholomaii*, were regarded as part of a transantarctic therian land mammal group, the Chulpasiinae.

Two alternative hypotheses about the evolution of polydolopimorphians were postulated: They were already present in the Late Cretaceous of North America, and then dispersed to South America (Case et al. 2005); or they have a completely Gondwanan history (Beck et al. 2008). Even though a complete analysis of these statements or of the biogeographic history of polydolopimorphian are out of the scope of the present work, the Peruvian Chulpas and Australian Murgon record suggest a close link between these faunas (Sigé et al. 2004, 2009).

The widespread polydolopimorphian assemblage was considered as indicative of a short time span, between the stratigraphic occurrences of Peruvian Chulpas and Australian Murgon faunas (Sigé et al. 2004, 2009). Considering that, the mammal bearing horizon in Murgon was dated by K^{40} -Ar 40 at 54.6 ± 0.05 Ma. (Godthelp et al. 1992), so an early Eocene age is possible for the Chulpas fauna. Disregarding the real amount of time involved between LU3 and Chulpas faunas, which depends on the sedimentary rates within the red-beds of the Muñani Formation, the stratigraphic span between them (ca. 140 m) indicates a necessarily different and somewhat older age for the LU3 faunistic assemblage, which reinforces the Thanetian–Ypresian age assignment (Sigé et al. 2004).

Up to now, no relationship was suggested between these Peruvian and Australian faunas and the Itaboraí SALMA, the latter of which is considered as probably late Paleocene–early

Eocene (Gelfo et al. 2009). Even considering the time involved between LU3 and Chulpas faunas (Peru), they could be assigned to a similar wide time span (i.e., late Paleocene–early Eocene) together with Murgon (Australia), Las Flores (Patagonia, Argentina) and Itaboraí (Brazil). If this temporal assignment could be established by independent evidence, the variation in taxonomic composition among these faunas could be explained by paleobiogeographic differences.

South America has usually been considered as part of the Neotropical Region together with Central and different parts of southern North America. This was criticized, since the development of panbiogeography and cladistic biogeography challenged the traditional phytogeographical and zoogeographical systems, emphasizing that some of the units recognized in them, do not represent natural units (Cox 2001; Morrone 2002). The southern temperate areas in South America, South Africa, Australasia, and Antarctica, were considered as part of the Austral Kingdom (Morrone 2002 and literature therein). In contrast, the biota of the northern and central South America was considered as part of the Neotropical region of the Holotropical Kingdom, which incorporates the tropical areas of the world, between 30° south and 30° north latitudes (Morrone 2002, 2006). The Austral kingdom seems to match with the western portion of Gondwana (Crisci et al. 1993) and with the known Late Cretaceous to early Paleogene biotic distribution (e.g., Woodburne and Case 1996; Pascual 1996, 2006; Ortiz Jaureguizar and Cladera 2006; Pascual and Ortiz Jaureguizar 2007).

Considering their geographic locations, Murgon, Chulpas and Las Flores faunas could be related with the Austral Kingdom, whereas the Itaboraí fauna, from the Rio de Janeiro State in Brazil, is with the Holotropical Kingdom (Morrone 2002). A significant difference among these faunas could be the presence of the Polydolopinae in Las Flores and their absence from Itaboraí locality (Chornogubsky 2008). Polydolopines have been recorded in the Paleogene of southern South America and West Antarctica, and have been postulated as a marsupial radiation that was restricted to the Austral Kingdom (Chornogubsky et al. 2009). The origin of microbiotherians marsupials and, probably, of other lineages of the Australidelphian radiation, was suggested to be restricted to this biogeographic region (Goin et al. 2007). The Austral Kingdom could also be related with the distribution of the Chulpasiinae (Sigé et al. 2009), and the Ornithorhynchidae, represented by *Monotrematum sudamericanum* from the middle Paleocene of Punta Peligro and *Obdurodon* from the Oligo-Miocene of Australia (Pascual et al. 1992). These groups have been suggested as relicts, vicariant members of groups that spanned large parts of the Austral Kingdom during the Paleogene (Sigé et al. 2009). Eutherian mammals in contrast had a more restricted distribution. With the exception of *Tingamarra porteri*, described as a possible condylarth from Australia (Godthelp et al. 1992) and the record of an archaeonycterid bat (Hand et al. 1994) they were only recorded in South America and Antarctica and, particularly didelodontid fossil record, are by now restricted to the first landmass.

The present phylogenetic analysis suggests that *Umayodus*, *Escribania*, and *Raulvaccia* were part of a monophyletic group (Fig. 4: node 3), supported here by five synapomorphies: the well developed hypocone appressed to the protocone in M2; the concave precingulum of M2; the crista preparaconular in contact with the precingulum at the parastyle; the posteristid of m3 contacting the entoconid; and, the mesiodistal enlargement of the m3 talonid. They could be also characterized by the enlargement and multiplication of cusps in the m3 talonid, in contrast to the mesiodistally short and simple talonids of kollpaniinaes. The creation of a subfamily for this group seems to be premature since the relationships among the rest of didolodontids is not fully resolved (Fig. 4). Nonetheless, it is interesting to note that their distribution fit well with the proposed Andean Region of the Austral Kingdom, which includes southern South America below 30° south latitude, extending through the Andean highlands north of this latitude, to the Puna and North Andean Paramo (Morrone 2002).

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Appendix 1

Character list used for the phylogenetic analysis from 0 to 40.

0. Postprotocrista of P3: (0) P3 with incipient or small protocone and non-expanded distal border, (1) small to medium sized protocone present and postprotocrista expanded distally.
1. Metacone of P4: (0) absent, (1) small projection of the postparacrista, (2) well developed.
2. Outline of P4: (0) triangular, (1) quadrangular.
3. P2–3 metacone: (0) absent, (1) smaller than paracone, (2) subequal to the paracone.
4. Hypocone on M2: (0) absent, (1) small lingual cusp in the postcingulum, (2) large cusp distal or distolingual to the protocone (3) large cusp appressed to the protocone.
5. Hypocone in M3: (0) absent, (1) present.
6. M2 precingulum: (0) more or less straight (1) strongly distally concave.
7. Labial cingulum M1–2: (0) reduced to a labial rim with no separation of the bases of paracone and metacone, (1) interrupted labially to the paracone, (2) interrupted labially to the mesostyle, (3) well developed mesio-distally.
8. Labial cingulum M3: (0) absent, (1) reduced to a labial rim with no separation of the bases of paracone and metacone, (2) interrupted labially to the paracone, (3) interrupted labially to the mesostyle, (4) well developed mesio-distally, (5) interrupted labial to the metacone.
9. Mesostyle: (0) absent, (1) small, (2) large.
10. Parastyle-stylocone relationship: (0) separated, (1) fused and small, (2) fused and large structure.
11. Size of the conules: (0) small to medium, (1) large.
12. Position of the conules: (0) closer to the labial side of the protocone, (1) in a middle position.
13. Preparacrista: (0) bent labially, (1) projected mesially, (2) bent lingually, (3) reduced or absent.
14. Crista postmetaconular: (0) in contact with the postcingulum distally, (1) in contact with the postcingulum at the metastyle, (2) reduced or absent.
15. Crista preparaconular: (0) not related with the precingulum, (1) in contact with the precingulum at the parastyle, (2) projected between the parastyle and paracone, (3) reduced or absent.
16. Crista premetaconular: (0) present, (1) absent.
17. Crista postparaconular: (0) present, (1) absent.
18. Protostyle: (0) absent, (1) small, (2) large.
19. Protocone: (0) not mesio-distally expanded, (1) mesio-distally expanded, (2) not expanded but with a wide base.
20. Paracone and metacone: (0) paracone larger and higher than the metacone, (1) both cusps subequal.
21. Centrocrista: (0) labially projected, (1) mesio-distally straight, (2) bent labially.
22. Mandibular symphysis: (0) not fused, (1) ankylosed.
23. p4 metaconid: (0) small and appressed to the protoconid; (1) enlarged and separated from the protoconid.
24. p4 talonid: (0) formed by a simple cusp, (1) presence of hypoconulid in labial position and incipient talonid.
25. Paracristid: (0) not distally arched (1) distally arched.
26. Posterior slope of the metaconid: (0) not inflated or invading the talonid, (1) strongly inflated, invading the talonid basin.
27. m1–2 entoconid and hypoconulid relation: (0) distantly separated, (1) almost fused, (2) near but not fused.
28. m1–2 hypoconid: (0) comprises the labial half or less of the talonid, (1) large extending also in the lingual half of the talonid.
29. m1–2 entoconid size: (0) smaller than the hypoconulid, (1) subequal, (2) larger than the hypoconulid.
30. m3 entoconid: (0) smaller than the hypoconulid, (1) subequal.
31. m1–2 cristid obliqua: (0) strong, (1) with centroconid, (2) reduced or almost absent.
32. m3 cristid obliqua: (0) strong, (1) with centroconid or cusps associated, (2) reduced or almost absent.
33. m3 entoconid and hypoconulid relation: (0) distantly separated, (1) almost fused.
34. m3 hypoconid: (0) comprises the labial half or less of the talonid, (1) large extending also in the lingual half of the talonid.
35. m3 hipocristid: (0) absent, (1) present.
36. m3 postentoconulid: (0) absent, (1) present.
37. m3 postcristid: (0) absent, (1) present and contacting the entoconid (2) without contacting the entoconid.
38. m1–2 talonid width: (0) narrower or subequal to the trigonid, (1) wider than the trigonid.
39. m3 talonid length: (0) short or subequal to trigonid length, (1) longer than the trigonid, (2) two times or more the trigonid length.
40. m3 metastylid: (0) absent, (1) small, (2) large and in contact to the metaconid through a crest or postmetacristid.

Appendix 2

Data matrix.

Characters	0–19	20–40
<i>Protungulatum donnae</i>	0000100340000011??00	0100000202?000?????00
<i>Molinodus suarezi</i>	000?0003101001131101	010101111000011100010
<i>Tiuclaenus minutus</i>	00000000101001031001	110001111002211000010
<i>Pucanodus gagnieri</i>	00000000101001031001	010001[01]11112211000010
<i>Simoclaenus sylvaticus</i>	???0003401001111001	010101101210011100010
<i>Andinodus boliviensis</i>	???????????????????	?????111102211000010
<i>Escribania chubutensis</i>	???2311350111011112	11???1100100021001120
<i>Escribania talonicuspis</i>	???????????????????	?????1???????01011?20
<i>Lamegoia conodonta</i>	1110210010111031122	11?1110001?0?????0?0
<i>Paulacoutoia protocenica</i>	11102101001111031112	110111001200020000100
<i>Didolodus multicuspis</i>	11112102321111[02]00122	101111000101120100100
<i>Didolodus minor</i>	11122?02321111[02]00122	?0?1110001?11?????1?0
<i>Didolodus magnus</i>	???2102?21112000122	10???10001???????1?0
<i>Paulogervaisia inusta</i>	???210??11012001122	12?1110???100?????100
<i>Ernestokokenia nitida</i>	???210120101[12]221122	11???1021200020102100
<i>Ernestokokenia chaishoer</i>	???2?01?01011201122	?1???10201000?????1?0
<i>Ernestokokenia yirunhor</i>	?????10?201011201102	?1???10201?0?2000?100
<i>Raulvaccia peligrensis</i>	???23?11?01112010112	?1???100010?000111120
<i>Umayodus raimondi</i>	???????????????????	?????1???????00111?22
<i>Phenacodus primaevus</i>	1211200[01][12]11213231102	000112000210000000101