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A new South American mioclaenid (Mammalia: Ungulatomorpha) from the Tertiary of Patagonia, Argentina

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Resumen. UN NUEVO MIOCLAENIDO SUDAMERICANO (MAMMALIA: UNGULATOMORPHA) DEL TERCIARIO DE PATAGONIA, ARGENTINA. Se describe un nuevo "condilartro" Mioclaenidae, proveniente de la Edad Mamífero Casamayorense, Subedad Barranquense, de Paso de Indios, Provincia del Chubut. El nuevo taxón *Pascualodus patagoniensis* gen. et sp. nov., representado por un molar superior izquierdo, es comparado con otros Mioclaenidae, con los Didolodontidae y los más primitivos Litopterna. Una hipótesis filogenética provisoria es expresada a través de un cladograma de consenso estricto y uno de compromiso de mayoría. Si bien el análisis confirma la agrupación de los taxa sudamericanos en un grupo monofilético, existen numerosos puntos sin resolver. *Pascualodus patagoniensis* se ubica como un taxón terminal, en una politomía que reúne por un lado a los Mioclaenidae sudamericanos y por el otro, a los Didolodontidae y Litopterna. Por otra parte la consideración de caracteres dentales superiores de *Escribania chubutensis*, previamente el único Mioclaenidae patagónico conocido, modifica sus relaciones filogenéticas vinculándolo al Didolodontidae *Didolodus* sp. La asignación de *Pascualodus patagoniensis* a los Mioclaenidae constituye el registro más moderno y el más austral de la familia.

Abstract. A new Mioclaenidae "condylarth" of the Casamayoran Land Mammal Age, Barrancan subage, from Paso de Indios, Chubut Province is described. The new taxon *Pascualodus patagoniensis* gen. *et* sp. nov., represented by a left upper first molar, is compared with other Mioclaenidae; the Didolodontidae and some primitive litopterns. A provisory phylogenetic hypothesis is represented by a strict consensus tree and a 50 percent majority rule consensus tree. Although the analysis confirms the inclusion of the South American taxa in a single monophyletic group, some relationships remain unresolved. *Pascualodus patagoniensis* is a terminal taxon in an unresolved politomy which also includes the South American Mioclaenidae and a clade comprising the Didolodontidae + Litopterna. The addition of upper dental characters of *Escribania chubutensis*, previously the only known Patagonian Mioclaenidae, clearly changes its relationships and allies it with the Didolodontidae *Didolodus*. The assignation of *Pascualodus patagoniensis* to the Mioclaenidae represents the geologically youngest and southernmost record for this family.

Key words. Eocene. Casamayoran. Mammalia. "Condylarthra". Mioclaenidae. Patagonia. Argentina.

Palabras clave. Eoceno. Casamayorense. Mammalia. "Condylarthra". Mioclaenidae. Patagonia. Argentina.

Introduction

The Mioclaenidae were first recognized as a family by Osborn and Earle (1895). Many subsequent workers (e.g. Matthew, 1937; Simpson, 1937; Muizon and Marshall, 1987a,b) have included them as a subfamily within the Hyopsodontidae. More recently they have been recognized as a family on the basis of the probable monophyly of most of the comprised genera (Van Valen, 1978; McKenna and Bell, 1997; Archibald, 1998; Muizon and Cifelli, 2000).

The Mioclaenidae have been recorded for the Paleocene in various localities of Puercan, Torrejonian and Tiffanian ages in North America; Cernaysian in Europe; and Tiupampan in South America. Additionally Gheerbrant *et al.* (2001) have described a posible Eocene? Mioclaenidae for the north of Africa based on a single left mandibular fragment with p3-m2. In South America, the Mioclaenidae are represented by the "Kollpaniinae", which include the Tiupampan forms *Andinodus boliviensis*, *Molinodus suarezi*, *Pucanodus gagnieri*, *Simoclaenus sylvaticus*, *Tiuclaenus cotasi*, *T. minor* and *T. robustus* from Bolivia; but not *Escribania chubutensis* from the Paleocene of Punta Peligro (Gelfo, 1999).

The purpose of this work is to present a description of a new "condylarth", from the Casamayoran of Paso de Indios, (43°52'S, 69°02'O) Chubut Province, which represents the southernmost record for the Mioclaenidae. The material is deposited in the collection of Departamento de Paleontología de Vertebrados of Museo de La Plata and according to its collection data it was collected by members of the mu-

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seum staff on 13 February 1959, in an outcrop located between La Escondida and El Batistín "aguadas" (*watering places*).

Materials and methods

In the following description and discussion the lower teeth will be represented by lower case letters and the upper teeth by capital letters. Al measurements are in millimeters and were taken with calipers. Dental nomenclature is given in figure 1.B. The phylogenetic analysis was performed using the genera as terminal taxa. The program NONA 2.0 (Goloboff, 1993) was used to obtain the most parsimonious trees. For the comparisons and the elaboration of the list of characters used in the phylogenetic analysis, original materials and casts were studied, as well as descriptions and illustrations from diverse published works. In the text the Kollpaniinae is named between brackets because the monophyly of this group is questioned (see below). The abbreviations for the institutions mentioned in the text correspond to AMNH (American Museum of Natural History, New York, USA); MACN (Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina.); MCT (Museu de Ciências da Terra, Rio de Janeiro, Brazil); MNHN: (Muséum national d´Histoire Naturelle, París France); MNRJ (Museu Nacional de Rio de Janeiro, Rio de Janeiro, Brazil); MPEF-PV (Museo Paleontológico Egidio Feruglio, Trelew, Argentina); UNPSJB-PV (Universidad Nacional Patagónica San Juan Bosco, Comodoro Rivadavia, Argentina); and YPFB Pal (Yacimientos Petrolíferos Fiscales Bolivianos, Colección de Paleontología, Santa Cruz Bolivia)

Systematic Paleontology

Class MAMMALIA Linnaeus, 1758
Order PANAMERIUNGULATA Muizon and Cifelli, 2000
Family MIOCLAENIDAE Osborn and Earle, 1895

Pascualodus gen. nov.

Type species. *Pascualodus patagoniensis* sp. nov.
Etymology. "*Pascual*" after Dr. Rosendo Pascual + "*odus*" from the Greek name (οδουσ) meaning "*tooth*"; a suffix generally used for condylarth genera.

Diagnosis. Larger than the rest of the "Kollpaniinae" (not considering *Escribania chubutensis* as a member of this family); approximately 50% larger than *Molinodus suarezi*. M1 with sub-quadrangular outline, three-rooted, nearly symmetrical with respect to its transverse axis; labial cingulum cuspate and interrupted at the paracone; anterior and posterior cinguli well developed, broader lingually than labially; no mesostyle; very reduced premetaconular crista; paracone barely larger and somewhat more labial in position with respect to the metacone; protocone not elongated anteroposteriorly; trigon basin wide; hypocone absent. *Pascualodus* differs from others "Kollpaniinae" for the distinct cusp present on the precingulum anterior to the preprotocrista, and for the labial cingulum interrupted labially to the paracone. In contrast to *Simoclaenus* and *Molinodus*, the postmetaconular crista is unit to the postcingulum and not reaching the metastyle, and the preparaconular crista and the anterior cingulum reaching the parastyle without contacting each other.
Type locality, horizon and age. Pink tuff and bentonites from Paso de Indios, Chubut Province, Argentina. Casamayoran Age, Barrancan subage.

Pascualodus patagoniensis sp. nov.

Holotype. MLP 59-II-24-39 left first upper molar.
Hypodigm. The holotype.
Etymology. "*patagoniensis* " Patagonia (by contrast with the "Kollpaniinae" found in Tiupampa, Bolivia) + *ensis*: latin suffix meaning "from" or "belonging to".
Diagnosis. Same as for the genus.
Description. (figure 1.A-B) This species is represented by a left M1 (length: 6.15 mm and wide: 7.85 mm) in good condition, with the whole protocone root and two labial roots that are broken close to the tooth neck. The tooth is brachydont, with bunoid cusps more slender than in other "Kollpaniinae". The anterior and posterior margins are not markedly convergent towards the lingual sector as in other Mioclaenidae but somewhat more parallel. The labial cingulum is narrow, cuspate and interrupted at the paracone. It extends from the parastyle to the anterolabial sector of the paracone, bearing two small cuspules, and from a very slightly insinuated ectoflexus to the area where the absent mesostyle would be. The cingulum is cuspate around the metacone. There are three small cusps posterolabial to the metacone, three on its labial side and one more anterior, in the position usually occupied by the mesostyle in other taxa. Similar characteristics on the labial margin may be observed in MNHN CAS 681, a right M2? from the Tournouër collection assigned by Gaudry (1904) to *Protogonia* (*Euprotogonia*) *patagonica*, and described as *Ernestokokenia* sp. (Simpson, 1964). This molar has a basal cuspule between the paracone and the metacone on the labial side, followed by a series of denticles along the base of the metacone. There is a slight basal thickening along the buccal side of the paracone that doesn't form a real cingulum. The presence of these "denticles" or conules on the cingulum at the level of the metacone, and the interruption of the cin-

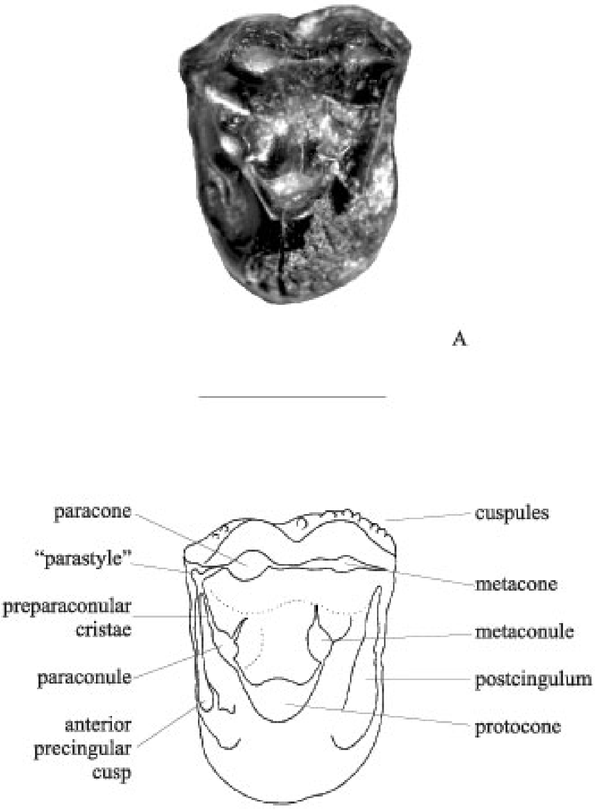

Figure 1. A, Oclusal view of *Pascualodus patagoniensis* (MLP 59-II-24-39). **B,** Diagram of the same tooth with the principal characters. Scale 5 mm. / ***A,*** *Vista oclusal de* Pascualodus patagoniensis. ***B,*** *Diagrama del mismo diente con los principales caracteres. Escala 5 mm.*

gulum labially to the paracone, are also observed in other specimens referred to *Ernestokokenia* sp. (MLP 59-II-24-11 and MLP 61-VIII-3-105).

The anterior and posterior cinguli are practically parallel and thinner labially than lingually. The anterior cingulum extends from the parastyle to the anterior edge of the protocone. The cingulum has a small precingular cusp between the paraconule and the protocone. The posterior cingulum extends from the labial area to the posterior margin of the protocone. Although a localized hypoplasy is observed in the posterolingual sector of the tooth, affecting the lingual sector of the posterior cingulum, there is no hypocone, nor a well developed cusp closer to the protocone neither a small lingual cusp on the postcingulum, as is the case in the Didolodontidae. Both the anterior and the posterior cingula broaden lingually. In lingual view, the precingulum and postcingulum are located at the same height on the base of the protocone. The lingual margin of the protocone does not bear any cingulum. The protocone is not elongated anteroposteriorly as in *Molinodus suarezi*; it is rather a bulbous but more slender cusp with a more important transverse component. The conules are considerably smaller than in the other "Kollpaniinae", and in contrast with these latter, not so bulbous, so that they leave a wide trigon basin. The conules are placed close to the labial sector of the protocone. Their apices are not buccolingually aligned with the paracone and metacone but are somewhat anteriorly shifted. This condition is more evident in the paraconule, situated in an anterolingual rather than lingual position with respect to the paracone. The paraconule is somewhat larger than the metaconule and has a rounded posterior margin. The conules are connected to the protocone by means of a pre- and a postprotocrista. The preprotocrista projects towards the paraconule in the same direction as that of the preparaconular crista towards the parastyle. The preparaconular crista and the anterior cingulum reach the parastyle independently. The postparaconular crista is absent, but there is a small remnant of the premetaconular crista, which extends towards the anterolingual margin of the metacone. The postmetaconular crista projects towards the metastyle but doesn't contact the latter or the posterior cingulum. The paracone is slightly larger than the metacone and somewhat more labial in position. These cusps are well separated and united by means of a straight centrocrista. The parastyle and metastyle are not labially shifted with respect to the paracone and metacone, but rather aligned anteroposteriorly with respect to those cusps. The location of the conules, especially the paraconule, and the slenderness of the protocone contribute to the delimitation of a wide trigon basin.

Comments. During the study of the tooth described in the present paper, and aiming at the correct interpretation of its place in the dental series, three mutually exclusive hypotheses were considered: that the specimen could correspond to a permanent premolar, a deciduous P4 or a molar. The material had been originally entered in the collection as an upper premolar referred to *Ernestokokenia* sp. The distribution of the cusps, and especially the strong development of a metacone subequal to the paracone, as well as the defined separation of these cusps, indicate that, if the material were a premolar, it would correspond to a highly molarized P4. Of all the materials ever referred to species of *Ernestokokenia*, the only known upper premolars belong to *Paulacoutoia protocenica* (= *E. protocenica*). In this Didolodontidae the P4 is a tooth almost as large as the M1, with the protocone and paracone forming subequal bulbous cusps. There is no paraconule or metaconule; the metacone is appressed to the posterior side of the paracone as a small prominence and never forms an independent cusp. The metastyle, as well as the slightly smaller parastyle, correspond to small cusps in the cingulum. The latter is well developed and is only interrupted at the lingual margin of the protocone.

Following the observations of Simpson (1948), McKenna and Bell (1997) consider *Ernestokokenia* as a junior synonym of the primitive Litopterna *Asmithwoodwardia*. The premolars of *Asmithwoodwardia*, as well as those of *Protolipterna*¸ always show a relatively simple structure, and never a well-defined trigon comparable to the condition in *Pascualodus*. In fact, the P4 of *Asmithwoodwardia scotti* has a large paracone that constitutes the main cusp of the tooth and makes the labial length greater than the lingual length. The labial side is virtually flat, with a weak cingulum at its base. The protocone is a smaller, more bulbous cusp, with a convex lingual margin. The metacone is a small cusp appressed to the posterior side of the paracone, never attaining important development or good individualization. The metastyle is somewhat larger than the parastyle. The anterior cingulum extends lingually less than the posterior cingulum. The paraconule is a large, clearly defined cusp, without associated cristas, united to the protocone by means of a weak preprotocrista. The metaconule is absent.

In *Protolipterna* the protocone and paracone are bulbous, large, subequal and facing each other on the same transverse axis. The metacone , when present, is small, appressed to and weakly differentiated from the paracone apex in specimens where the wear is not marked. The parastyle and metastyle are small cusps. The cingulum is thicker at its anterior and posterior ends, labially reduced and absent lingually to the protocone. No paraconule or metaconule were seen in the study cast, but, in most specimens a not very much developed paraconule is present (Bergqvist *com. pers.*). Cifelli (1983a) mentions a protostylar cusp of variable occurrence associated with the anterior cingulum, in anterolingual position with respect to the protoconule. However, in the materials available for the present study which have preserved the P4, a small cusp posterolabial with respect to the protocone was observed only in a cast of MCT 1392i-M. Neither in the latter nor in MCT 1392f-m it was possible to distinguish the paraconule or any cusp associated with the anterior cingulum.

Among the Didolodontidae, *Didolodus* and *Lamegoia* have a transversely elongated P4 which in the latter, is also larger than the M1. The paracone and protocone are subequal and are the most developed cusps; the first is generally somewhat larger than the second. In contrast with *Lamegoia*, where the paracone and protocone are somewhat separated, in *Didolodus* the bases of both cusps contact each other, obliterating the central area of the premolar. As in *Pascualodus*, the labial side of the paracone has a convex base, in contrast with the condition observed in *Asmithwoodwardia* and *Proectocion* where the labial development of this sector is clearly flat. However, in *Didolodus* and *Lamegoia* the labial portion of the tooth is formed by a robust paracone, while in *Pascualodus* it comprises the subequal paracone and metacone. *Didolodus* has a well-defined paraconule that contacts the bases of the paracone and protocone. The metaconule cannot be observed in the holotype of *Didolodus multicuspis*; in fact, it is extremely small and early removed by wear in case of its occurrence (Simpson, 1948). In *Lamegoia* the paraconule is a well developed cusp, closer to the base of the protocone than to the base of the paracone, and projecting anterolabially a low short preparaconular crista. The possible presence of a metaconule on the P4 of *Didolodus* (Cifelli, 1983a) would not be an exclusive feature, since is also present and even better defined in at least one specimen of *Lamegoia* (MNRJ 1842 V). In the latter specimen, the metaconule is somewhat smaller than the paraconule, more lingual, and has a short postmetaconular crista that does not project labially as much as the preparaconular crista. Both *Didolodus* and *Lamegoia* have well developed anterior, labial and posterior cingulum, interrupted lingually to the protocone.

The main difference between all P4s referred to Didolodontidae and the single specimen of *Pascualodus* is the great development of the metacone and its clear separation from the paracone (in *Pascualodus*), which clearly defines a trigon area comparable to the condition observed in the molars but not in the premolars of diverse condylarths.

Apart from that, *Oxybunotherium praecursor* from the Casamayoran fauna of Paso de Indios was described by Pascual (1965) as a doubtful Didolodontidae on the basis of a right mandibular fragment with part of the m2 and a complete m3. Cifelli (1985) mentions a mandibular fragment with m2-3 (AMNH-28769) from the Casamayoran of Colhue Huapi as indistinguishable from *Oxybunotherium* and, based on the fitting size of the molars, their morphology, geographical and possibly temporal distribution, refers all these lower molars to the upper molars of *Proectocion*, conditioning such assignation to the synonymy of *Proectocion precisus* (a fragment of right maxilla with P4-M3) and *Proectocion argentinus* (based on a right M3). The P4 of the adiathid Litopterna *Proectocion* is highly molarized and to a certain extent comparable to the material studied here. Both *Pascualodus* and *Proectocion* have symmetrical teeth, with similar size, well separated paracone and metacone; development of a robust preparaconular crista that contacts the weak parastyle, and absence of mesostyle and hypocone. However, the P4 of Proectocion is clearly different due to its smaller size, slight transverse development, straight and flat structure of the labial sides of the paracone and metacone (particularly at their bases), the presence of mesostyle, absence of a labial cingulum, and position of the paraconule and metaconule, which are nearer to the paracone and metacone respectively than to the protocone.

Among the Northern Hemisphere condylarths, molarization of the P4 by development of bulbous cusps is seen among the Phenacodontidae. *Ectocion osbornianum*, for instance, the base of the paracone are closely associated with a well developed metacone, and a strong parastyle. The labial edge of the tooth corresponds to its greater axis, in contrast with the condition observed in the molars or in *Pascualodus*. Apart from that, the molars of *Ectocion* differ from the P4 by the clear separation of the labial cusps, smaller parastyle, well-developed mesostyle, conspicuous conules, especially the metaconule, which are not appressed against the base of the protocone, and strong development of the hypocone.

The morphology of *Pascualodus* does not correspond to any premolar known for the Didolodontidae, nor to the most primitive Litopterna.

The second hypothesis to consider is that, due to the degree of molarization, it could be a dP4. Study of the deciduous dentition in condylarths reveals that the dP4 shows a distorted morphology similar to that of the molars. Muizon and Cifelli (2000) described the deciduous dentition of some "Kollpaniinae". The dP4 of *Tiuclaenus minutus* (YPFB Pal 6135) is very low cusped and almost form an equilateral triangle in occlusal outline. As in *Promioclaenus acolytus*, the paraconule and the metaconule are in an anterior position with respect to the paracone and metacone respectively. Contrary to the condition observed in the molars, dP4 have a large parastyle, a weak precingulum and a thin postcingulum which does not contact the postmetaconular crista. The dP4 of *Molinodus suarezi* (MNHC 8280) is very heavily worn to make a full comparison with the M1. In occlusal outline it is similar to but smaller than M1, differing in being lower crowned, with thinner enamel and a weaker precingulum.

Among other condylarths for which the deciduous dentition is well known, such as *Phenacodus primaveus*, *Tetraclaenodon puercensis* and *Ectocion osbornianum*, the dP4 does not predict the structure of the permanent P4 but rather the general appearance of the molars (West, 1971). When we consider that one of the most remarkable characters of *Pascualodus* is the absence of hypocone, it is clear that this doesn't resemble the morphology of the molariforms of any known Didolodontidae or Litopterna. *Pascualodus* does not resemble any of the named dP4 and in contrast, deciduous teeth are characterized by the presence of thin enamel, a slight constriction at the tooth neck, roots, when present, are generally divergent and the styles are generally more developed than on molars.

On the basis of the available information and especially on the similarity to the molars of the "Kollpaniinae", it may be claimed that the material assigned to *Pascualodus* corresponds to a molar, and in high probability to a M1, due to the slight lingual orientation of the metacone.

Discussion

1. Considerations about the age of Pascualodus

Pascual (1965) recognizes two faunal assemblages assignable to the Casamayoran for the area of Paso de Indios, and on this basis he suggested splitting this age into two smaller subunits. One of these assemblages, from the pink tuffs and bentonites, comprises Polydolopidae, Didolodontidae, and Notoungulata Oldfieldthomasiidae and Isotemnidae. However, some noteworthy particularities are the occurrence of *Proectocion* (=*Oxybunotherium*), Notoungulata Isotemnidae assignable to *Thomashuxleya* or *Periphragnis* (Bond *com. pers.*), and the remarkable absence of *Notostylops*; that would make this assemblage closer to the more modern Mustersan.

The other assemblage, for which no faunal list is mentioned, comes from sediments formed exclusively by very light-colored tuff, containing the most typical assemblage of Casamayoran genera and species, different from the previous one. This unit underlies the first one, and is separated by an erosive discordance, in the outcropping sediments at Cerro Guacho. Additionally, a paleosol with scarabeid nests over the erosive plane is widespread in the area and marks the boundary between these two lithostratigraphic entities (Pascual, 1965).

Cifelli (1985) correlates the fauna from the pink tuffs and bentonites from Paso de Indios, as well as the fauna from Valle Hermoso, with the lower portion of the Gran Barranca member of the southern area of Colhue Huapi Lake. This comprises the fauna on which the Barrancan subage, the younger of the Casamayoran subages (Vacan and Barrancan), was based. At the same time, this author recognizes informally an early Barrancan, characterized by *Notopithecus adapinus*, *Oldfieldthomasia debilata*, *Pleurostylodon modicus*, *Notostylops murinus*, and a late Barrancan with *Homalostylops parvus*, *Ultrapithecus rutilans*, *Anthepithecus brachystephanus*. It is probable that, if the pink tuff and bentonites do indeed correspond to the early Barrancan, the underlying light-colored tuff stratum is assignable to the Vacan subage.

The Casamayoran has been traditionally assigned to the early Eocene (Flynn and Swisher, 1995; Flynn and Wyss, 1998), but Kay *et. al.*, (1999) by means of the determination of isotopes (Ar^{40}/Ar^{39}) and associated magnetic polarity obtained a considerably younger age (Late Eocene), for the area of Gran Barranca. Taking these data into account, and providing that the correlation between the strata bearing the Paso de Indios and Gran Barranca faunas is correct, the presence of *Pascualodus* would represent the most recent and southernmost record for a Mioclaenidae (Gelfo, 2002). In fact, with the exclusion of *Apheliscus* from the Clarkforkian (Early Eocene), of the Northern Hemisphere, doubtfully assigned to the Mioclaenidae (Archibald, 1988), the presence of *Pascualodus* would extend the family biocron in approximately 21 MY, from the last records of *Promioclaenus*, *Protoselene* and, with doubts, *Litaletes*? from the Tiffanian (Late Paleocene) of the Northern Hemisphere, to the Casamayoran (late Eocene) of Patagonia.

2. Phylogenetic Analysis

Despite the constraints imposed by the use of exclusively dental characters, a phylogenetic analysis including 19 taxa was performed. The outgroup comprises an hypothetical ancestor and *Protoungulatum*. The ingroup includes diverse Mioclenidae: Mioclaeninae and the "Kollpaniinae", the Didolodontidae and some primitive Litopterna. The 27 dental characters used were selected based on previous works (Cifelli, 1983a; Luo, 1991; Cifelli, 1993; Salles, 1996), especially Muizon and Cifelli, (2000), and personal observations. The data matrix (table 1) includes characters 1 to 17 correspond to the upper dentition and 18 to 27 to the lower one, listed in the Appendix. Within the text characters are denoted by their corresponding number from the Appendix Characters were considered equally weighted and multistate characters were coded as unordered.

Some considerations are due with respect to the characters and their codification. No mesostyle (character 7) is present in the "Kollpaniinae", as well as in primitive ungulates such as *Protoungulatum*. However, *Molinodus* and *Simoclaenus* have a labial cusp or protuberance in the M2 that has been interpreted as an initial state in the appearance of mesostyle (Muizon and Cifelli, 2000). Among the Mioclaeninae, this cusp is observed, for instance, in *Protoselene* and *Mioclaenus*. In *Pascualodus*, *Asmithwoowardia subtrigonia*, and those specimens originally referred to *Ernestokokenia*, the anteriormost cusp of the labial cingulum that encircles the metacone also occupies the topographic position of the mesostyle. However, it is noteworthy that there never exists a labial projection of the postparacrista and the premetacrista toward this cusp. This condition is observed in those forms with well developed mesostyle. In *Didolodus* the mesostyle corresponds to a large cusp that interrupts the continuity of the labial cingulum. The postparacrista and the premetacrista are thus posterolabially and anterolabially projected, respectively, towards the mesostyle. This is also observed in *Protoselene opisthacus*, where the postparacrista and the premetacrista form a "v"-shaped structure with its apex directed towards the mesostyle, and in *Mioclaenus turgidus* where the cristae also project toward the mesostyle, but forming a "u"-shape.

If the cingular cusp that is present in certain Mioclaenidae represents an incipient state in the formation of mesostyle (Muizon and Cifelli, 2000), it is to be expected that in some instance it would be accompanied by labial projections of the postparacrista and premetacrista toward the aforesaid cusp. However, the cingular cups could be non-homologous to the mesostyle, and an alternative scenario could be the development of the mesostyle independently from the cusp on the labial cingulum. The mesostyle could develop as a cusp independent from the labial cingulum, directly onto the centrocrista, acquiring variable development and shifting more or less in labial direction.

Protoselene (cast belonging to *P. opisthacus* AMNH 101654) has a stylar shelf (character 6) reduced to a continuous labial cingulum; this is the case on M2 and M3, but the cingulum is virtually interrupted in labial position with respect to the paracone in M1.

Some of the characters taken from Muizon and Cifelli (2000) were modified on the basis of study of various materials. In *Didolodus*, the presence of an external cingulum interrupted labial to the paracone was considered (Muizon and Cifelli, 2000). However, in the holotype of *Didolodus multicuspis* (MACN 10690) as well as in other studied materials (such as MLP 61-VIII-3-208) the cingulum is only interrupted labial to the strong mesostyle, but is well developed labial to the paracone. Muzion and Cifelli (2000) suggest the possibilities of discriminating the Didolodontidae and primitive Litopterna on the basis of the presence of non-fused versus ankylosed symphysis (character 18), respectively. But the state for the mandibular symphysis of *Didolodus* was assessed in this paper as ankylosed on account of the consideration of specimen MACN 10689 corresponding to a right mandibular fragment with p3-m3, fused to a small anterior portion of the left side. This most certainly suggests the possibility that the state may be a synapomorphy with Litopterna. However, the situation is not quite simple, because the dentaries are unfused in *Paulocoutoia*. So, it could be that *Didolodus* is simply convergent to Litopterna or that a fused manibular symphisis may be common to both Litopterna and Didolodontidae (except *Paulocoutoia*).

In the present work, a cingulum interrupted labially respect to the paracone was considered like the character state for stylar shelf (character 6) in *Asmith-*

Table 1. Data matrix for the distribution of the 27 characters listed above among the 19 taxa considered / *Matriz de datos para la distribución de 27 caracteres para los 19 taxa considerados.*

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
Hypothetical ancestor	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Protungulatum	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1	1
Promioclaenus	1	1	0	0	0	1	0	1	0	1	1	2	2	1	0	0	0	0	0	1	0	1	0	1	0	1	1
Litaletes	0	1	0	1	0	1	0	1	0	1	0	2	2	1	1	0	1	0	1	1	0	1	0	1	0	1	1
Protoselene	0	2	0	1	0	1	1	1	0	1	0	1	1	1	0	0	1	0	0	1	0	2	0	1	0	1	1
Mioclaenus	0	0	1	1	?	1	1	1	0	1	1	2	2	1	0	0	0	0	0	0	0	1	0	1	0	1	2
Molinodus	0	0	0	0	0	1	0	1	0	1	1	1	1	1	0	1	0	0	1	1	1	2	1	1	1	1	1
Tiuclaenus	0	0	0	0	0	2	0	1	0	1	1	2	2	1	0	1	0	0	0	0	1	2	1	1	1	1	1
Pucanodus	0	0	0	0	0	2	0	1	0	1	1	2	2	1	0	1	0	0	0	0	1	2	1	1	1	1	1
Simoclaenus	?	?	?	0	0	1	0	1	0	1	1	1	1	1	0	1	0	0	1	1	1	2	1	1	1	1	1
Andinodus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	2	1	1	1	1	1
Pascualodus	?	?	?	0	?	3	0	1	0	1	1	2	1	1	1	0	0	?	?	?	?	?	?	?	?	?	?
Escribania	?	?	?	2	1	1	0	1	1	2	1	2	2	1	1	2	0	?	?	?	1	2	1	2	1	1	1
Lamegoia	1	2	1	2	1	3	0	1	1	2	1	2	2	1	1	2	0	?	1	1	1	2	0	1	1	1	1
Paulacoutoia	1	2	1	2	1	3	0	1	1	2	1	2	2	1	1	2	0	0	1	1	1	2	0	2	1	1	1
Didolodus	1	2	1	2	1	1	1	1	1	2	1	2	2	1	1	2	0	1	1	1	1	2	0	2	1	1	1
Miguelsoria	?	?	1	2	0	3	0	1	1	2	1	2	2	1	1	2	0	1	1	1	1	2	0	1	0	1	1
Protolipterna	1	2	1	2	0	3	0	1	0	1	1	2	2	1	1	2	0	1	1	1	1	2	0	1	0	1	1
Asmithwoodwardia	1	2	1	2	0	3	0	1	0	1	1	2	2	1	0	2	0	1	1	1	1	2	0	1	0	1	1

woodwardia. However, it is important to point out that this state is found in *Asmithwoodwardia subtrigonia* (MACN 10723), as it was described by various authors (Simpson, 1948; Paula Couto, 1978); but not in *A. scotti* (MACN 18888) in whose molars the cingulum, albeit weak, is complete labially with respect to the paracone.

In the case of *Escribania chubutensis*, characters pertaining to the upper molars were included (Gelfo, 1999). In addition, the entoconid and hypoconulid (character 24), previously considered as fused, are indeed well individualized, as can be observed in the holotype (UNPSJB PV 916) as well as various studied materials (MPEF- PV 1860 and MLP 93-XII-10-2).

In the phylogenetic analysis performed by Muizon and Cifelli, (2000), the South American taxa are part of a single monophyletic group which was not named and included the Kollpaniinae (sic.) -South American Mioclaenidae-, the Didolodontidae and the Litopterna. Only in the 50 percent majority rule, the "Kollpaniinae" were considered as monophyletic, but because this was supported by four sinapomorphies, three of which are reversals, the node is not very strong and the authors agree that the "Kollpaniinae" could very well be paraphyletic. In this paper, the "Kollpaniinae" are not monophyletic, nor in the strict consensus tree neither in the majority rule tree. The relationships between the genera traditionally included in this subfamily are part of a politomy.

The outcome of the analysis consisted of 41 equally parsimonious trees (length: 65; CI: 58; RI: 79). Figure 2 shows one strict-consensus tree and one majority rule consensus tree. Both show a grouping of the South American taxa in a monophyletic group that includes the "Kollpaniinae", Litopterna and Didolodontidae, as has been traditionally proposed. Although the strict-consensus tree shows the separation of the South and North American Mioclaenidae, the relationships within the two groups are unresolved. In the 50% majority rule consensus cladogram, this group is represented by the polytomy comprising *Pascualodus*, all the Tiupampan Mioclaenidae and lastly a monophyletic group formed by the Didolodontidae and the Litopterna. Probably due to the large number of non-comparable characters of *Andinodus* and *Pascualodus*, the status of the "Kollpaniinae" is not supported by the phylogenetic analysis. The relationships between the Southamerican Mioclaenidae are unresolved. These genera are part of a polytomy that includes *Pascualodus* and *Andinodus*, and two clades that share an anteroposteriorly expanded protocone (character 16: 1). The first clade is formed by *Tiuclaenus* and *Pucanodus* sharing a labial rim with no separation of the bases of paracone and metacone by a sulcus (character 6: 2). The second clade including *Molinodus* and *Simoclaenus*, is supported by the union of the postmetaconular crista with the postcingulum at the metastyle (character 12: 1; shared with *Protoselene*); and the union of the

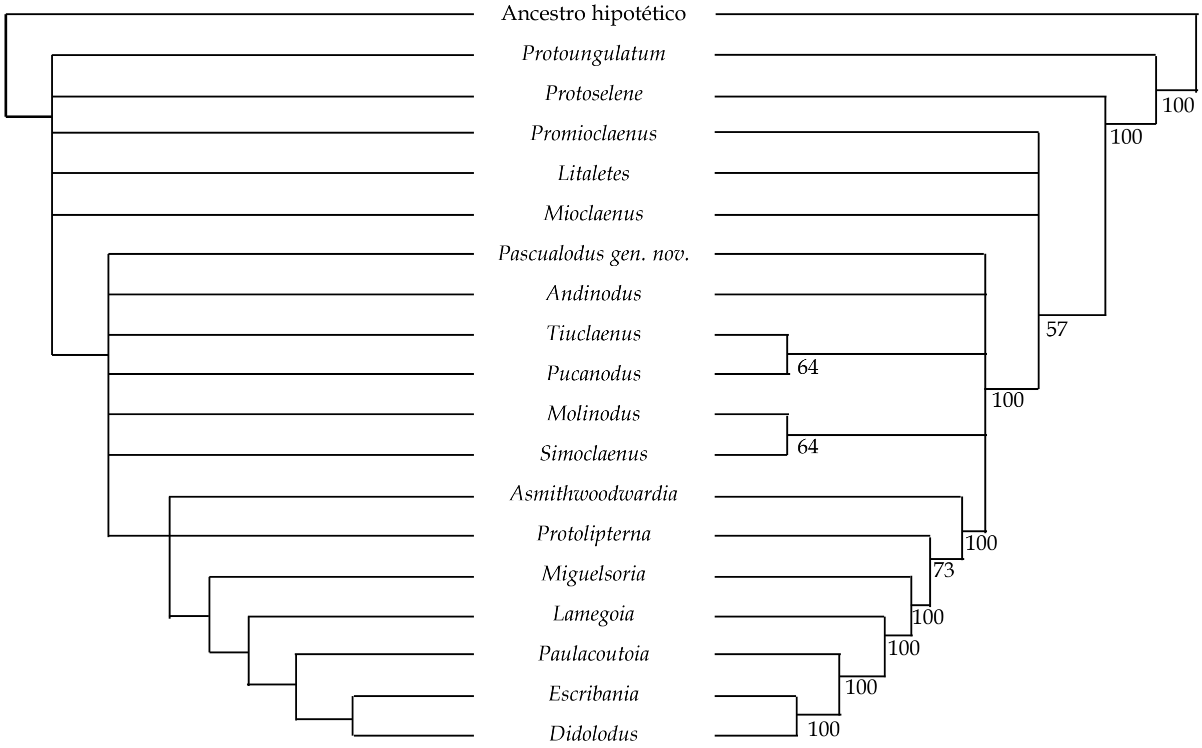

Figure 2. A strict-consensus tree and a majority rule consensus tree of the 19 taxa included on the phylogenetic analysis / *Árbol de consenso estricto y consenso de mayoría de los 19 taxa incluidos en el análisis filogenético.*

preparaconular crista with the anterior cingulum at its distal tip, (character 13: 1; sheared also with *Protoselene* and *Pascualodus*).

The only character that *Escribania chubutensis* shares with "Kollpaniinae" (within which it was previously grouped), is the strongly inflated metaconid of the lower molars, which invades the talonid basin (character 23:1). The inclusion of upper molar characters in the analysis (Gelfo, 1999) drastically changes their phylogenetic relationships. In fact, *Escribania* is set apart from the "Kollpaniinae" and clearly appears as sister group of *Didolodus*. The Didolodontidae and Litopterna form a monophyletic group supported by 2 synapomorphies: a large hypocone on M1-2 (character 4: 2) and unexpanded protocone (character 16: 2). However, in contrast with the conclusions of other phylogenetic analyses (Muizon and Cifelli, 2000), the small group of Litopterna here considered is paraphyletic and the Didolodontidae are monophyletic. In fact, *Asmithwoodwardia*, *Protolipterna* and *Miguelsoria*, were considered to be primitive Litopterna because of the absence of hypocone in the M3, and on the basis of the reassociation of postcranial elements, particularly tarsals, to dental elements (Cifelli 1983a-b; 1993, Bergqvist, 1996). But here they are placed in a very basal position within the clade. This appears to be more consequential with the considerations of Soria (2001) who recognized those genera as Didolodontidae. Nevertheless, due to the high degree of homoplasy that may be found in dental characters such as those used in the present analysis, it is not possible to draw strong conclusions with respect to these statements.

Conclusions

To date, *Pascualodus patagoniensis* is the most recent and the southernmost record for the Mioclaenidae. The occurrence of this taxon, whose dental characters are more primitive than those found in contemporaneous ungulates of Casamayoran age, and even than those referred to the oldest Riochican age, raises a series of questions. Thus, if the preceding analysis is correct, there are at least two hypotheses to be contrasted in the near future, on the basis of new studies. The first is the consideration that *Pascualodus* might correspond to an "anachronistic" form in whose lineage the selective pressures have been different than for other ungulate groups, where the trend towards hypsodonty and especially selenodonty are more accentuated by this time. Secondly, *Pascualodus* might represent, as *Megadolodus* for the middle Miocene of Colombia (Cifelli and Villarroel, 1997), a form with primitive and conservative dental characters, but whose postcranial elements are more specialized and derived than that of a "condylarth".

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Bibliography

Archibald, J.D. 1998. Archaic ungulates ("Condylarthra"). In: C.M. Janis, K.M. Scott and L.L. Jacobs (eds.), *Evolutionary of Tertiary Mammals of North America*. Cambridge University Press, pp. 292-331.

Bergqvist, L.P. 1996. [*Reassociação do pós-cranio as espécies de ungulados da bacia de S.J. de Itaboraí (Paleoceno), estado do Rio de Janeiro, e filogenia dos "Condylarthra" e ungulados sul-americanos com base no pós-cranio.*] Porto Alegre, Universidade Federal do Rio Grande do Sul. Doctoral thesis: 1-407.

Cifelli, R.L. 1983a. The origin and affinities of the South American Condylarthra and Early Tertiary Litopterna (Mammalia). *American Museum Novitates* 2772: 1-49.

Cifelli, R.L. 1983b. Eutherian tarsals from the late Paleocene of Brazil. *American Museum Novitates* 2761: 1-31.

Cifelli, R.L. 1985. Biostratigraphy of the Casamayoran, early Eocene of Patagonia. *American Museum Novitates* 2820: 1-26.

Cifelli, R.L. 1993. The phylogeny of the Native South American Ungulates. In: F.S. Szalay, M.J. Novaceck and M.C. McKenna, (eds.), *Mammal Phylogeny, Placentals*. Springer-Verlag, pp. 195-216.

Cifelli, R.L. y Villarroel C. 1997. Paleobiology and affinities of *Megadolodus*. In: R. F. Kay, R.H. Madden, R.L. Cifelli, and J. J. Flynn, (eds.), *Vertebrate Paleontology in the Neotropics: The Miocene fauna of La Venta, Colombia*. Smithsonian Institution Press, Washington DC. pp. 265-288.

Flynn, J.J. and Swisher, C.C. 1995. Cenozoic South American land mammal ages: correlation to global geochronologies. In: W.A. Berggren, D.V. Kent, M.P. Aubry and J. Hardenbol (eds.), *Geochronology, Times Scales, and Global Stratigraphic Correlation*. Society for Sedimentary Geology, Tulsa, OK, Special Publication, 54 pp. 317-333.

Flynn, J.J. and Wyss, A.R. 1998. Recent advances in South American mammalian paleontology. *TREE*. 13: 449-454.

Gaudry, A. 1904. Fossiles de Patagonie. Dentition de quelques mammiferes. *Mémoires de la Société Géologique de France* 12: 1-27.

Gelfo, J.N. 1999. New aspects of the paleocene genus *Escribania* (Mammalia: Condylarthra) *Ameghiniana* 36, *Suplemento*: 12R.

Gelfo, J.N. 2002. Análisis preliminar de un nuevo Mioclaenidae sudamericano (Mammalia Ungulatomorpha), del Paleoceno de Patagonia, Argentina. *Ameghiniana* 39, *Suplemento*: 11-12R.

Gheerbrant, E., Sudre, J., Iarochene M. y Mounmi, A. 2001. First ascertained African "Condylarthra" mammals (primitive ungulates: cf. Bulbulodentata and cf. Phenacodonta) from the earliest Ypresian of the Ouled Abdoun Basin, Morocco. *Journal of Vertebrate Paleontology*, 21: 107-118.

Goloboff, P.A. 1993. NONA 2.0 MS-DOS tree-searching program and documentation.

Kay, R.F., Madden, R.H., Vucetich, M.G., Carlini, A.A., Mazzoni, M.M., Re G.H., Heizler, M. y Sandeman H. 1999. Revised geochronology of the Casamayoran South American land mammal age: climatic and biotic implications. *PNAS* 96, 23:13235-13240.

Luo, Z. 1991. Variability of dental morphology and the relationships of the earliest arctocyonid species. *Journal of Vertebrate Paleontology*, 11,4: 452-471.

McKenna M.C. and Bell, S.K. 1997. *Classification of Mammals, Above the Species Level*. Columbia University Press, 631 pp.

Matthew, W.D. 1937. Paleocene faunas of the San Juan Basin, New Mexico. *Transactions of the American Philosophical Society*, n.s., 30, 1-510.

Muizon, C. de And Marshall, L.G. 1987a. Le plus ancien condylarthre (Mammalia) sud-américan (Crétacé supérieur, Bolivie). *Comptes Rendus de l´Académie des Sciences*, Série II, 304: 771-774.

Muizon, C. de and Marshall, L.G.1987b. Deux nouveaux condylarthres (Mammalia) du Maastrichtien de Tiupampa (Bolivie). *Comptes Rendus de l´Académie des Sciences*, Série II, 304, 947-950.

Muizon, C. de and Cifelli, R. L. 2000. The "condylarths" (archaic Ungulata, Mammalia) from the early Paleocene of Tiupampa (Bolivia): implications on the origin of the South American ungulates. *Geodiversitas* 22, 1: 47-150

Pascual, R. 1965. Un nuevo Condylarthra (Mammalia) de Edad Casamayorense de Paso de los Indios (Chubut, Argentina). Breves consideraciones sobre la Edad Casamayorense. *Ameghiniana* 4, 2: 57-65.

Paula Couto, C. De. 1978. Ungulados fósseis do Riochiquense de Itaboraí, RJ, Brazil. II-Condylarthra e Litopterna. *Anales de la Academia Brasileira de Ciencias* 50: 209-218.

Osborn, H.F. and Earle, C. 1895. Fossil mammals of the Puerco beds. Collection of 1892. *Bulletin of the American Museum of Natural History* 4, 6-147.

Salles, L.O. 1996. Roting ungulates within placental mammals: Late Cretaceous/Paleocene fossil record and upper molar morphological trends. B*ulletin du Muséum National d´Histoire Naturelle* 18: 417-450.

Simpson, G.G. 1937. The Fort Union of the Crazy Mountain Field, Montana and its mammalian faunas. *United States National Museum Bulletin* 169, 1-287.

Simpson, G.G. 1948. The begining of the age of mammals in South America. Part 1. Introduction. Systematics: Marsupialia, Edentata, Condylarthra, Litopterna, Notioprogonia. *Bulletin of the American Museum of Natural History* 91: 1-232.

Simpson, G.G. 1964. Los mamíferos Casamayorenses de la colección Tournouer. *Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia"* 1: 1-21.

Soria, M.F. 2001. Los Proterotheriidae (Litopterna, Mammalia), sistemática, origen y filogenia. *Monografías del Museo Argentino de Ciencias Naturales* 1: 1-167.

Van Valen, L. 1978. The beginning of the age of mammals. *Evolutionary Theory* 4: 45-80.

West, R.W. 1971. Deciduous dentition of the early Tertiary Phenacodontidae (Condylarthra, Mammalia). *American Museum Novitates* 2461: 1-37.

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Appendix

The description and coding for the characters used is the following : **1** postprotocrista of P3, (0) P3 with incipient or small protocone and non-expanded posterior border, (1) small- to medium-sized protocone present and postprotocrista expanded posteriorly; **2** metacone of P4 (0) absent, (1) small projection of the post-paracrista, (2) well developed cusp appressed to the paracone; **3** outline of P4, (0) triangular, (1) quadrangular; **4** hypocone on M1-2 (0) absent, (1) small lingual cusp in the postcingulum, (2) large cusp appressed to the protocone; **5** hypocone in M3 (0) absent, (1) present; **6** stylar shelf (0) narrow, (1) reduced to a continuous labial cingulum, (2) reduced to a labial rim with no separation of the bases of paracone and metacone by a sulcus; (3) cingulum interrupted labially to the paracone; **7** mesostyle (0) absent, (1) present; **8** parastyle-stylocone relationship (0) separated, (1) fused; **9** size of the conules (0) small to medium, (1) large; **10** position of the conules with respect to the paracone and metacone (0) approx middle position, (1) closer to the protocone than to a middle position, (2) conules on the labial edge of the protocone but in a relatively middle position; **11** orientation of the preparacrista (0) labially projected, (1) in line with the paracone and metacone; **12** relation of the postmetaconular crista with the postcingulum (0) independent structures, (1) crista united to the postcingulum at the metastyle, (2) crista united to the postcingulum anteriorly to the metastyle -development of the metacingulum portion-; **13** development of the preparaconular crista with the anterior cingulum (0) independent structures, (1) crista united to the precingulum at its distal tip, (2) crista united to the precingulum but not to its distal tip -development of the paracingulum portion-; **14** postparaconular and premetaconular cristae (0) present and well defined, (1) strongly reduced or absent; **15** cusp on the precingulum approximately anterior to the paracone (0) absent, (1) present; **16** development of the protocone (0) without anteroposterior expansion, (1) anteroposteriorly expanded or with a trend towards duplication, (2) not expanded in occlusal view but with a wide base; **17** relative size of the paracone and metacone (0) paracone larger and higher than the metacone, (1) both cusps have subequal size and height; **18** mandibular symphysis (0) not fused, (1) ankylosed; **19** metaconid of p4 (0) small to medium size and appressed to the protoconid; (1) enlarged and separated from the protoconid; **20** talonid of p4 (0) formed by a simple cusp in middle position, (1) presence of hypoconulid in labial position and incipient talonid; **21** paracristid (0) asymmetric with respect to the anteroposterior axis of the tooth, the paraconid portion is straight and forming an obtuse angle with the protoconid portion, (1) deeply arched posteriorly and approximately symmetric with respect to the antero-posterior axis of the tooth, the paraconid portion forming a 90º angle with the protoconid portion; **22** metaconid (0) lingual to the protoconid, (1) slightly posterior to the protoconid, (2) markedly posterior to the protoconid; **23** Posterior slope of the metaconid (0) not inflated, with straight protocristid, (1) strongly inflated, invading the talonid basin, with concave protocristid; **24** hypoconulid and entoconid, (0) close to each other but well individualized, (1) connate or fused, (2) well separated; **25** hypoconid (0) comprises the labial half or less of the talonid but does not invade the talonid basin anteriorly to the hypoconulid, (1) large and conical, extending in the lingual half of the talonid and invading its basin anteriorly to the hypoconulid; **26** hypoconulid of m3 (0) slightly larger than that of m1-2, (1) markedly larger; **27** postcingulid, (0) weak, with non-inflated talonid cusp, (1) moderate to large size, (2) weak but strongly inflated talonid cusps.