

The “condylarths” (archaic Ungulata, Mammalia) from the early Palaeocene of Tiupampa (Bolivia): implications on the origin of the South American ungulates

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ABSTRACT

The oldest known “condylarth” fauna of the Tertiary of South America comes from basal Palaeocene strata of the Santa Lucía Formation at Tiupampa (Bolivia). It includes five genera and seven species: *Molinodus suarezi*, *Tiuclaenus minutus*, *T. cotasi* n. sp., *T. robustus* n. sp., *Pucanodus gagnieri*, *Andinodus boliviensis*, and *Simoclaenus sylvaticus*, n. gen., n. sp. This work presents a thorough revision of all the fossils previously described, which are interpreted in the light of recently discovered specimens including materials belonging to three new taxa. The sample contains 33 jaws and 43 isolated teeth. The Tiupampa “condylarths” are included in the Kollpaniinae Marshall, Case & Woodburne, 1990 (= Molinodinae Bonaparte, Van Valen & Kramartz, 1993), a subfamily of the Mioclaenidae (*Kollpania tiupampina* Marshall & Muizon, 1988, the type species of the type genus of the Kollpaniidae Marshall, Case & Woodburne, 1990 is regarded as a junior synonym of *Tiuclaenus minutus* Muizon & Marshall, 1987). Some of the taxa (e.g., *Molinodus suarezi*, *Tiuclaenus cotasi*) are well represented and the cheek dentition of the former is almost completely known. However, other genera such as *Andinodus* and *Simoclaenus* are still poorly known (a few lower teeth only in the case of *Andinodus*). Because of their scant representation, their position within the Kollpaniinae still has to be confirmed by the discovery of new specimens, especially upper molars of *Andinodus*. The Tiupampa “condylarths” are clearly related to the North American Mioclaenidae, although it is not possible to securely relate them to a specific genus. They share with the North American taxa the following derived characters when compared to *Protungulatum*: bulbous cusps, the apices of which are approximated in occlusal view; protocone enlarged; styler shelf greatly reduced or

lost; styles reduced and tending to be aligned with para- and metaconidae; paraconid appressed against metaconid; entoconid and hypoconulid connate to fused, and forming an obliquely oriented posterolingual crest. The major characteristics of the Kollpaniinae are: metaconid well posterior to protoconid, strongly inflated, and invading the talonid basin posteriorly; loss of the entocristid; hypoconid extremely inflated, occupying at least the medial half of the talonid (generally more); talonid basin reduced to an obliquely oriented groove that is widely opened lingually; posterior slope of the hypoconulid of m3 less convex than in the other mioclaenids. The Kollpaniinae (Tiupampa “condylarths” and *Escribania*) are also regarded as closely related to the Didolodontidae and Litopterna (especially the Protolipternidae). The key synapomorphy of the three groups is the morphology and development of the paracristid, which is narrower than half the width of the trigonid, deeply arched posteriorly, projected anteriorly, and attaching on the anterior to anterolingual side of the proto- and paraconids. Study of the Tiupampa “condylarths” confirms that the South American Didolodontidae and Litopterna have their origins in North American Mioclaenidae. A parsimony analysis establishes the monophyly of the clade including the North American Mioclaenidae, the Kollpaniinae (South American Mioclaenidae), the Didolodontidae, and the Litopterna. This clade is formally designated as a new order of mammals, the Panameriungulata. Because no close relationships based on dental characters were found with the other groups of South American ungulates (or so-called ungulates) — Astrapotheria, Pyrotheria, Xenungulata, Notoungulata —, it reinforces the unlikelihood of a single origin of the South American ungulates and therefore brings into question the monophyly of the Meridiungulata.

KEY WORDS

“Condylarths”,
Didolodontidae,
Litopterna,
Panameriungulata,
early Palaeocene,
Bolivia,
taxonomy,
phylogeny.

RÉSUMÉ

Les « condylarthres » (ongulés archaïques, Mammalia) du Paléocène inférieur de Tiupampa (Bolivie) : implications sur l'origine des ongulés sud-américains.

La plus ancienne faune de « condylarthres » du Tertiaire sud-américain provient du Paléocène basal de la Formation Santa Lucía à Tiupampa (Bolivie). Elle comprend cinq genres et sept espèces : *Molinodus suarezi*, *Tiuclaenus* (*T. minutus*, *T. cotasi* n. sp., *T. robustus* n. sp.), *Pucanodus gagnieri*, *Andinodus boliviensis* et *Simoclaenus sylvaticus*, n. gen., n. sp. Ce travail présente une revue de tous les fossiles précédemment décrits, lesquels sont interprétés à la lumière de nombreux spécimens récemment découverts, incluant trois nouveaux taxons. L'échantillon contient 33 mâchoires et 43 dents isolées. Les « condylarthres » de Tiupampa sont inclus dans les Kollpaniinae Marshall Case & Woodburne, 1990 (= Molinodinae Bonaparte, Van Valen & Kramartz, 1993), une sous-famille des Mioclaenidae (*Kollpania tiupampina* Marshall & Muizon, 1988, l'espèce-type de la famille des Kollpaniidae Marshall, Case & Woodburne, 1990, est considérée comme un synonyme plus récent de *Tiuclaenus minutus* Muizon & Marshall, 1987). Certain des taxons (*Molinodus suarezi*, *Tiuclaenus cotasi*) sont bien représentés et les dents jugales de ces derniers sont presque toutes connues. Cependant, certains genres comme *Andinodus* et *Simoclaenus*, sont encore mal connus (par quelques dents inférieures seulement pour *Andinodus*) et, en raison de la pauvreté de cet échantillon, leur position au sein des Kollpaniinae devra être confirmée par la découverte de nouveaux spécimens, en particulier de dents supérieures d'*Andinodus*. Les « condylarthres » de Tiupampa sont, de toute

évidence, apparentés aux Mioclaenidae nord-américains, bien qu’il ne soit pas possible de les relier avec certitude à un genre précis. Ils partagent avec les formes nord-américaines les caractères dérivés suivants, par comparaison avec *Protungulatum* : cuspides bulbeuses dont les apex sont rapprochés en vue occlusale ; grand protocone ; plate-forme styloïde très réduite ou perdue ; styles réduits et tendant à s’aligner avec les para- et metacristas ; paraconide plaqué contre le métaconide ; entoconide et hypoconulide accolés, voire fusionnés, et formant une crête postéro-linguale oblique. Les principales caractéristiques des Kollpaniinae sont : très gros métaconide renflé, très postérieur au protoconide et envahissant partiellement le bassin du talonide postérieurement ; perte de l’entocristide ; hypoconide extrêmement gonflé occupant au moins la moitié labiale du bassin du talonide ; bassin du talonide réduit à un sillon oblique largement ouvert lingualement ; flanc postérieur de l’hypoconulide de $m3$ moins gonflé et moins convexe que chez les autres Mioclaenidae. Les Kollpaniinae (« condylarthes » de Tiupampa et *Escribania*) sont également considérés comme ayant des relations étroites avec les Didolodontidae et les Litopterna (particulièrement les Protolipternidae). La synapomorphie majeure qui réunit les trois groupes réside dans la morphologie et le développement de la paracristide. Celle-ci est plus étroite que la moitié de la largeur du trigonide, profondément arquée postérieurement, fortement saillante antérieurement et prend attache sur les bords antérieurs à antéro-internes des para- et protoconides. L’étude des « condylarthes » de Tiupampa confirme donc l’origine septentrionale, au sein des Mioclaenidae, des Didolodontidae et des Litopterna d’Amérique du Sud. Une analyse de parcimonie conduit à la monophylie probable du clade incluant les Mioclaenidae d’Amérique du Nord, les Kollpaniinae (Mioclaenidae d’Amérique du Sud), les Didolodontidae et les Litopterna. Le clade est formellement désigné comme un nouvel ordre de mammifères, les Panameriungulata. Étant donné qu’aucune relation étroite fondée sur des caractères dentaires n’a pu être mise en évidence avec les autres groupes d’ongulés (ou considérés comme tels) sud-américains, — Astrapotheria, Pyrotheria, Xenungulata, Notoungulata —, cette étude donne du poids à l’in vraisemblance d’une origine unique des ongulés sud-américains et met en question la monophylie des Meridiungulata.

MOTS CLÉS

« Condylarthes »,
Didolodontidae,
Litopterna,
Panameriungulata,
Paléocène inférieur,
Bolivie,
taxonomie,
phylogénie.

INTRODUCTION

The origin of the unique Tertiary ungulate fauna of South America has long captivated the attention of palaeontologists and evolutionary biologists (e.g., Patterson & Pascual 1972; Simpson 1980). Such groups as notoungulates, pyrotheres, astrapotheres, trigonostylopoids, litopterns, and xenungulates are unknown on other continents and the problem of their origin remains unresolved (McKenna 1981; Cifelli 1983a; 1985; Bergqvist 1996). It is generally believed that some or all of these groups evolved

in situ, having their ancestry among North American “condylarths” that migrated to South America sometime in the Late Cretaceous or early Tertiary (Simpson 1978). Hence, the less derived of the South American ungulates, which are included among the “condylarths” (see p. 68 for understanding of the term *Condylarthra* vs “*Condylarthra*” or “condylarths”), are pivotal to understanding the origin of a substantial part of South America’s endemic mammalian fauna (Simpson 1948). South American “condylarths” were first recorded from what would later become known as the

Casamayoran land-mammal age, presumed to be early Eocene in age (Marshall *et al.* 1983), in some of the initial descriptions of the fauna (e.g., Ameghino 1897, 1901, 1902, 1904). In his great summary treatise of 1906, Ameghino referred then known taxa to various Holarctic families (see reviews by Simpson 1948; Cifelli 1983a). Later workers (e.g., Scott 1913) referred South America's Eocene "condylarths" to the endemic family Didolodontidae. It has long been recognized that these taxa are rather similar to certain North American forms, particularly among the somewhat specialized family Phenacodontidae. However, at the same time it is clear that Casamayoran and later didolodonts are too late in time to present much in the way of direct, compelling evidence that would speak to their ancestry among North American "Condylarthra" (Simpson 1948).

An important new venue on the problem appeared in the 1950s, with the recovery of a vastly better represented "condylarth" fauna from fissure fill deposits at the Itaboraí locality in Brazil, which is presumed to be late Palaeocene in age and therefore older than the Casamayoran (e.g., Bonaparte *et al.* 1993; Muizon & Brito 1993). Paula Couto (1952) initially referred the "condylarths" of Itaboraí to the Didolodontidae (*Ernestokokenia protocenica* Paula Couto, 1952; *E. parayirunhor* Paula Couto, 1952; *Lamegoia conodonta* Paula Couto, 1952) and Hyopsodontidae (*Asmithwoodwardia scotti* Paula Couto, 1952). This latter referral is particularly significant in that it represents the first formal recognition by a modern worker of a close tie between a South American "condylarth" and an otherwise Holarctic family. However, Paula Couto later (1978) recanted his view, opting for the more conservative placement of *Asmithwoodwardia* Paula Couto, 1952 in the Didolodontidae. More recent revision of the Itaboraí fauna (Cifelli 1983a) upheld the distinctiveness of South America's native "condylarth" family. Most taxa were referred to the Didolodontidae, although *Miguelsoria parayirunhor* (= *Ernestokokenia parayirunhor*) and, tentatively, *A. scotti* were transferred to the Litopterna. This view reflects the long-standing belief in a relationship between the two: "The Litopterna are, in effect,

no more than advanced 'condylarths' surviving in South America long after this general structural grade had been replaced elsewhere..." (Simpson 1948: 97.) Hence, although Itaboraí's "condylarths" possess a rather generalized dentition (as do those of the Casamayoran), they appear to have been already specialized along lines seen in members of later South American faunas. Cifelli (1983a: 38) suggested that Mioclaeninae were best suited among North American "Condylarthra" as structural antecedents for the South American Didolodontidae, using arguments based on morphotype reconstruction and the development of a hypothesized ancestral morphology for South American taxa. Evidently, Itaboraí's "condylarths" — important though they are — significantly postdate faunal exchange between the two American subcontinents.

A few years later, the discovery of substantially older South American "condylarths", in the early Palaeocene of Tiupampa (Bolivia), offered some support for Cifelli's assumption. *Molinodus suarezi* and *Tiucloaenus minutus* (see Muizon & Marshall 1987 a, b; Marshall & Muizon 1988) were referred to the mioclaenine Hyopsodontidae. *Andinodus boliviensis*, the third "condylarth" of the fauna, was referred to the didolodontids or phenacodontids (Muizon & Marshall 1987b). Another condylarth, *Pucanodus gagnieri*, was described by Muizon & Marshall (1991) and was also referred to the Mioclaeninae. Van Valen (1988) and Bonaparte *et al.* (1993) followed this interpretation and accepted the mioclaenine affinities of *Molinodus*, *Tiucloaenus*, and *Pucanodus*, although they gave the subfamily a family rank (an arrangement which we follow for reasons given below), therefore assigning the three taxa to the Mioclaenidae. They were followed in this respect by Muizon (1998: 24).

Since their first description, the "condylarths" of Tiupampa have been discussed several times, based on material originally described (Marshall & Muizon 1988; Van Valen 1988; Muizon & Marshall 1991; Muizon 1992; Muizon & Brito 1993; Bonaparte *et al.* 1993). Numerous new specimens are now available, considerably augmenting knowledge of described species, as well as providing the basis for recognition of several

additional new taxa, including two new species of *Tiuclaenus* and one new genus of Mioclaenidae (Muizon 1998: 24). This new material also provides more substantial basis for the attribution of some of the previously described specimens and a clearer understanding of the relationships of the Tiupampa “condylarths” to the North and South American taxa. The new fossils, therefore, shed light on the phylogenetic origin of the South American “condylarths”.

Our present intents are to provide a general study of Tiupampa’s “condylarths”, including a more detailed description of the previously described taxa on the basis of both published and new material, and to describe the new taxa mentioned above. We shall also present a character analysis and a discussion including most of better known South American taxa and the relevant North American genera.

The age of the Tiupampa beds has been extensively discussed in the recent literature (Muizon *et al.* 1984; Van Valen 1988; Ortiz Jaureguizar & Pascual 1989; Marshall 1989; Gayet *et al.* 1992; Muizon & Brito 1993; Bonaparte *et al.* 1993; Marshall *et al.* 1995; Bonaparte & Morales 1997; Marshall *et al.* 1997; Muizon 1998), and needs no further consideration here. In agreement with Muizon & Brito (1993), Bonaparte *et al.* (1993), Bonaparte & Morales (1997), and Muizon (1998) we regard the fossiliferous horizon at Tiupampa (Santa Lucía Formation) to be of earliest Palaeocene age, and older than the mammalian fauna of Punta Peligro (Bonaparte *et al.*, 1993) from Patagonia. The Tiupampa “condylarths” are, therefore, the oldest known on the South American continent.

MATERIALS AND METHODS

BASIS FOR TAXONOMIC COMPARISONS

We studied available fossils and casts of numerous specimens, as well as published descriptions and illustrations. Because systematic and material bases for “condylarth” comparisons are often unclear, we list below the taxonomic concept and principal specimens (and their origin) that are most central to this study.

1. “Zhelestidae” (Archibald 1998; Nessov *et al.* 1998)

The “Zhelestidae” are the most primitive known Ungulatomorpha and represent a useful basis for evaluating the polarity of character states. They are essentially from central Asia (but also present in North America and western Europe) and were recently revised by Nessov *et al.* (1998).

Aspanlestes aptap Nessov, 1985: CCMGE 6/12176, 1/12455 (Bissetky Formation, Uzbekistan; Turonian-Coniacian).

Parazhelestes minor Nessov *et al.*, 1998, *P. robustus* Nessov, 1993: CCMGE 11/12353, 11/12953 (holotype of *P. minor*), 70/12455 (holotype of *P. robustus*), 20/12953 (Bissetky Formation, Uzbekistan; Turonian-Coniacian).

Eoungulatum kudukensis Nessov *et al.*, 1998, *E. cf. kudukensis*: CCMGE 2/12455 (holotype), 35/12176, 16/12953, 17/12953 (Bissetky Formation, Uzbekistan; Turonian-Coniacian).

2. Arctocyoniidae (Van Valen 1978; Cifelli 1983a)

Protungulatum donnae Sloan & Van Valen, 1965: SPSM 62-2028 (holotype), UCMP 100824, 112110; UMVP 1563, 1567; UM 5206 (also figures in Kielan-Jaworowska *et al.* 1979) (Bug Creek Anthills, Montana; earliest Palaeocene). *Protungulatum* is a primitive taxon from the early Palaeocene of North America (see Archibald & Lofgren 1990, Eberle & Lillegraven 1998). It was classified within the arctocyonids by Van Valen (1978) but Prothero *et al.* (1988) excluded it from this family and regarded this genus as part of a trichotomy with peryptichiids and hyopsodontids. For Archibald (1998), *Protungulatum* is part of a trichotomy with the arctocyonids on the one hand and all the other “condylarths” (including cetaceans and paenungulates, on the other. Prothero *et al.* (1988), McKenna & Bell (1997), and Archibald (1998) regard *Protungulatum* as an *incertae sedis* ungulate although Eberle & Lillegraven (1998) included it in the oxyclaenines arctocyonids. Regardless of its higher taxonomic placement, because of its age and its primitive morphology, this genus is regarded as important in

the analysis of the relationships of the Kollpaniinae (see below for definition).

Oxyprimus galadriellae Van Valen, 1978: YPM(PU) 16217, 16703, 16712, 16863, 16866 (holotype), 17297, 21109, 21122. The position of the taxon has not reached a consensus. Van Valen (1978) included it in the oxyclaenine Arctocyonidae, McKenna & Bell (1997) in the separate family Oxyclaenidae, and Archibald (1998) in the Hyopsodontidae. However, because the genus *Oxyprimus* has been regarded by Luo (1991) as possessing more primitive character states than *Protungulatum* and *Mimatuta*, we regard this taxon as a useful comparative element for basal “condylarths”.

Baiococonodon (= *Ragnarok*) *nordicum* (Van Valen, 1978): YPM(PU) 14473, 14475, 16694, 16720, 16854, 21081, 21123 (Mantua lentil, Wyoming; earliest Palaeocene). We follow Van Valen (1988) and McKenna & Bell (1997), who regard *Ragnarok* Van Valen, 1978 as a junior synonym of *Baiococonodon* Gazin, 1941. *Ragnarok* and *Baiococonodon* are regarded as distinct genera by Archibald (1998) and are both included in the Cetungulata.

3. Mioclaenidae (Osborn & Earle, 1895; see Van Valen 1978; Van Valen 1988; Johnston & Fox 1984)

A new generic name is proposed for *Promioclænus wilsoni* Van Valen 1978: KU 9446 (holotype) (San Juan Basin, New Mexico; Puercan). “*Promioclænus*” *wilsoni* has been regarded by Van Valen as the most primitive species of *Promioclænus* and the only one known in the Puercan. Other specimens referred to this species have been recently described from the Western Hanna Basin, Wyoming (Eberle & Lillegraven 1998) from the Pu2 and Pu3 zones of the Puercan.

We regard the differences between “*Promioclænus*” *wilsoni* and the other species of *Promioclænus* as of generic rather than specific level. Following we propose a diagnosis of the new genus and provide comments and discussion.

Valenia n. gen.

Type species: “*Promioclænus*” *wilsoni* Van Valen, 1978 by original designation.

Included species: the type species only.

Distribution: Puercan (early Palaeocene), New Mexico and Wyoming.

Etymology: for Leigh Van Valen, in recognition of his substantial contributions to knowledge of early ungulates, particularly those of the North and South American Palaeocene.

Diagnosis: small mioclaenid differing from the otherwise similar *Promioclænus* in having the following primitive characters: p4 less inflated; P3-4 with smaller, anteroposteriorly shorter protocone; P4 with less distinct pre- and postcingula; upper molars with broader labial cingulum (remnant of stelar shelf); pre- and postcingulum smaller, postcingulum not attaching as high on the protocone and not extending labially to the styles; prepraconular and postmetaconular cristae complete, extending labially to styles, not captured by the cingula; M3 unreduced.

Comments and discussion: *Promioclænus* was established by Trouessart (1904) to include the Torrejonian species *P. acolytus* and *P. lemuroides*, the former earlier referred to *Hyopsodus* (e.g., Cope 1882; Matthew 1897) or *Mioclaenus* (e.g., Osborn 1902), and the latter to *Mioclaenus* (see Matthew 1897). A type species was not specified, although *P. acolytus* was listed first and has been regarded as the type (Gazin 1956). Later workers generally ignored the generic name, placing these species in *Ellipsodon*, until *Promioclænus* was resurrected in the 1950s (Gazin 1956; Wilson 1956). Van Valen (1978) expanded the concept of *Promioclænus*, including the aforementioned Torrejonian species, plus Tiffanian *P. pipiringosi* and two Puercan species, *P. vanderhoofi* and *P. wilsoni*. The former was described by Simpson (1936) under the genus *Tiznatzinia*; its synonymy with *Promioclænus* has been debated without apparent consensus (e.g., Cifelli 1983a; Archibald 1998; McKenna & Bell 1997; Van Valen 1988).

Van Valen (1978; 1988) considered *Promioclænus* to be the most primitive mioclaenid and regarded “*P.*” *wilsoni* as a suitable morphological and temporal ancestor for Torrejonian and later species of *Promioclænus*, and perhaps for other Mioclaenidae as well. We concur. However, as noted in the character analysis and comparisons below, we believe “*P.*” *wilsoni* to be sufficiently distinct to warrant placement in its own genus,

Valenia – thereby permitting later species of *Promioclænus* to be recognized as a unit on the basis of shared, derived characters, while at the same time allowing *V. wilsoni* to be recognized (or not) as their ancestor (indeed, clarifying its ancestral status, if *V. wilsoni* is ancestral to other mio-claenids as Van Valen suggests).

The foregoing diagnosis is based on the type of *V. wilsoni*, KU 9446, which preserves the lower dentition in poor condition, hence we were unable to give consideration to the lower molars (Van Valen 1988 figured additional specimens of the species, we do not have casts of these available). Of the taxa with which *V. wilsoni* is most meaningfully compared, we considered only the holotype of *Tiznatzinia vanderhoofi*, a partial lower dentition (Simpson 1936); similarly, *P. pipiringosi* is confidently known only from parts of the lower dentition (Gazin 1956). The originally referred (Torrejonian) species, *P. acolytus* and *P. lemuroides*, are both well-known (e.g., Matthew 1937; Simpson 1937).

Promioclænus acolytus (Cope, 1882) (see Van Valen 1978): AMNH 15949, BUNM 77-183, USNM 15294 (San Juan Basin, New Mexico; Torrejonian), AMNH 35728, 35778, USNM 9575 (Gidley Quarry, Montana; Torrejonian). *Promioclænus* is a primitive mioclaenid known during most of the Palaeocene of North America. It is very similar in size and morphology to *Molinodus*.

Litaletes disjunctus (Simpson, 1935) (see Simpson 1937): USNM 9338, AMNH 35871, 35874, 35883, 35885, 35889, 35890, 35933 (Gidley Quarry, Montana; Torrejonian). *Litaletes* is a primitive mioclaenid from the Torrejonian of North America and was regarded by Cifelli (1983a) as a possible ancestor for the didolodontids and litopterns.

Choeroclaenus turgidunculus (Cope, 1888): AMNH 3291 (holotype), 16402, 16404, 16489, USNM 15465 (San Juan Basin, New Mexico; Puercan).

Bubogonia saskia Johnston & Fox, 1984, *B. bombadili*: (Van Valen 1978) UALVP 15105 (holotype of *B. saskia*; Ravenscrag W-1, Saskatchewan;

earliest Palaeocene), USNM 23285 (holotype of *B. bombadili*; San Juan Basin, New Mexico; Puercan). *Bubogonia* is a primitive mioclaenid from the middle Puercan of North America and regarded by Van Valen (1988) as belonging to the same clade as *Molinodus*.

Escribania chubutensis Bonaparte *et al.*, 1993: UNPSJB PV 916 (Punta Peligro, Argentina; early Palaeocene). *Escribania* has been referred to the Mioclaenidae by Bonaparte *et al.* (1993) and is from the early Palaeocene of Punta Peligro (Argentina). It is slightly younger than *Molinodus* and probably has an age close to the North American Tiffanian. *Raulvaccia* from the same locality is known by a single badly broken lower m1 (not an m2), which is likely to belong to the same genus as the holotype and single specimen of *Escribania chubutensis* (see below).

4. Hyopsodontidae (see Van Valen 1978; Archibald 1998).

Litomylus dissentaneus Simpson, 1935 (see Simpson 1937): USNM 9425 (holotype), AMNH 35920, 35922, 35924, 35927, 35932, 35933 (Gidley Quarry, Montana; Torrejonian).

Haplaletes disceptatrix Simpson, 1935 (see Simpson 1937): USNM 9500 (holotype), 9555, AMNH 35894, 35897, 35898, 35901, 35902 (Gidley Quarry, Montana; Torrejonian).

5. Periprychidae (see Archibald *et al.* 1983a, b; Archibald 1996; Archibald 1998)

Maiorana noctiluca Van Valen, 1978 (see also Cifelli 1983a): YPM (PU) 14171, 16667 (holotype), 16715, 21124 (Mantua lentil, Wyoming; earliest Palaeocene).

Mimatuta minuial: Van Valen, 1978 YPM (PU) 14172, 14211 (holotype), 21012, 21018 (Mantua lentil, Wyoming; earliest Palaeocene).

6. Didolodontidae

Paulacoutoia protocenica (Paula Couto, 1952) (see also Cifelli 1983a): MNRJ 1431V, 1432V, 1433V, 1434V, 1438V, 1439V, 1441V, 1444V, 1448V, 1449V, 1450V, 1454V, 1460V, 1461V, DNPM 908M (Itaboraí, Brazil; Itaboraian).

Lamegoia conodonta Paula Couto, 1952 (see also Cifelli, 1983a): MNRJ 1463V (holotype), 1464V, 1465V, 1841V, 1842V, AMNH 109552 (Itaboraí, Brazil; Itaboraian).

Didolodus multicuspis Ameghino, 1897 (see Simpson 1948): MACN A-10690 (holotype), MACN A-10725, 10730, MLP 59.11.28.14 (Argentina; Casamayoran).

Ernestokokenia nitida Ameghino, 1901 (see Simpson 1948): MACN A-10735 (holotype), MACN A-10722, AMNH 28447. MNHN CAS 683 [a relatively unworn upper molar (M2?) described by Simpson (1964: 11), one of the two upper molars of “No. 6”] and MNHN CAS 681, a mandible fragment with M1-3 (not seen by Simpson). The two latter specimens are referred to *E. cf. nitida* (Argentina, Casamayoran).

Ernestokokenia has been regarded as a junior synonym of *Asmithwoodwardia* by McKenna & Bell (1997). The great similarity between the two genera had been mentioned twice by Simpson in his 1948 monograph. Nevertheless, mainly because of the great size difference between the type species of the genera, he retained Ameghino’s generic assignation. Because the analysis of this synonymy stands outside the scope of the present work, we follow Simpson’s interpretation, although we admit that McKenna & Bell may have been correct. In the following comparisons and discussions reference to *Ernestokokenia* will concern *E. nitida* and more specifically MNHN CAS 681 and 683.

7. Protolipternidae

Asmithwoodwardia scotti Paula Couto, 1952 (see also Paula Couto 1978; Cifelli 1983a): DGM 358M (holotype), 410M, MCT 2313M (Itaboraí, Brazil; Itaboraian). *Asmithwoodwardia* is a small dentally primitive ungulate from the late Palaeocene of Brazil and Patagonia. *A. scotti* was initially referred by its author (Paula Couto 1952) to the hyopsodontine hyopsodontids. Later, Paula Couto (1978) referred this genus to the didolodontids, and Cifelli (1983a, 1993a) regards *Asmithwoodwardia* as a primitive litoptern. *Miguelsoria parayirunhor* (Paula Couto, 1952) (see also Cifelli 1983a): MNRJ 1460V, 1468V

(holotype), 4094V, DGM 249M, 296M, 330M, AMNH 109556 (Itaboraí, Brazil; Itaboraian).

Protolipterna ellipsodontoides Cifelli, 1983a: DNPM LE 444A (holotype) through 444 I, DGM 1308M, 1392D (Itaboraí, Brazil; Itaboraian)

In the following description and discussion the lower teeth will be represented by lower case letters and the upper teeth by capital letters. All measurements are in millimetres and were taken with a Wild MMS 235 digital length-measuring system mounted on a stereo microscope. The back background of the photographs has been cropped using Adobe Photoshop 4.0

Dental nomenclature is given in Figure 1. However, a short comment must be made about the use of the terms pre- and postprotocrista, preparaconular and postmetaconular cristae, and para- and metacingulum. The preparaconular and postmetaconular cristae are the parts of the pre- and postprotocrista labial to the para- and metaconules respectively. The paracingulum corresponds to the labial part of the preparaconular crista and the groove posterior to it, which borders the paracone anteriorly. The same definition is adaptable to the metacingulum (Van Valen 1966; Szalay 1969; Gheerbrant 1992; Nessov *et al.* 1998). Therefore para- and metacingulum are “geographically” related to the para- and metacone and correspond to a functional structure of the preparaconular and postmetaconular cristae. The pre- and postprotocrista will be regarded as the crests connecting the apex of the protocone to the conules (Nessov. *et al.* 1998).

In Figure 1 the taxon on which the nomenclature is based is *Molinodus suarezi*. The upper molars of this species have a conspicuous labial cingulum, i.e. a crest separated from the para- and metacones by a valley. In other taxa (e.g., *Pucanodus*) there is no true cingulum. The bases of the para- and metacones are swollen but there is no crest and valley as are observed in *Molinodus*. In this case the structure observed will be termed “labial rim” in order to better describe the actual morphology of this part of the tooth.

On the upper premolars, the crista joining the paracone to the metastyle has been termed

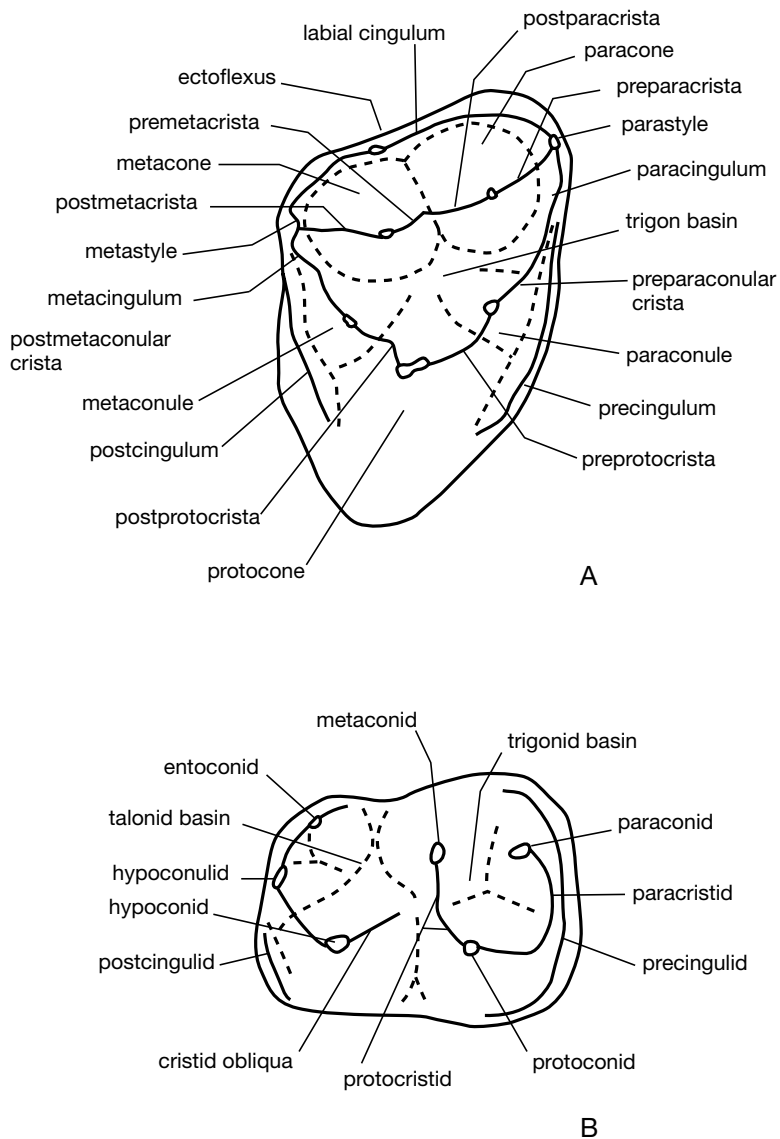


FIG. 1. — Terminology used for molar morphology; **A**, right upper molar; **B**, right lower molar; both in occlusal view.

paracrista rather than metacrista (as in Nessov *et al.* 1998) mainly because none of the known upper premolars of Kollpaniinae bears a metacone even incipient.

In the discussion, the term “primitive”, when applied to taxa, is regarded as a synonym of “archaic” or “generalized” according to recommendations of Prothero *et al.* (1988), i.e. a taxa which retains many plesiomorphic character states.

ABBREVIATIONS FOR INSTITUTIONS CITED IN THE TEXT

AMNH	American Museum of Natural History, New York, USA;
BUNM	Bureau of Land Management Collection, University of New Mexico, Albuquerque, New Mexico, USA;
CCMGE	Chernyshev’s Central Museum of Geological Exploration of Saint Petersburg, Russia;
DGM	Divisão Nacional de Produção Mineral, Rio de Janeiro, Brazil; and DNP
DMNH	Denver Museum of Natural History, Denver, Colorado, USA;
KU	Museum of Natural History, University of Kansas, Lawrence, Kansas, USA;
MACN	Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina;
MCT	Museu de Ciencia da Terra, Rio de Janeiro, Brazil;
MHNC	Museo de Historia Natural de Cochabamba, Bolivia;
MLP	Museo de La Plata, Division de Paleontología de Vertebrados, La Plata, Argentina;
MNHN	Muséum national d’Histoire naturelle, Paris, France;
MNRJ	Departamento de Geología e Mineralogía, Museu Nacional de Rio de Janeiro, Brazil;
SPSM	Saint Paul Science Museum, Saint Paul, Minnesota, USA;
UALVP	Laboratory for Vertebrate Palaeontology, University of Alberta, Edmonton, Canada;

UCMP	University of California, Museum of Paleontology, Berkeley, California, USA;
UM	Museum of Paleontology, University of Michigan, Ann Arbor, Michigan, USA;
UMVP	University of Minnesota, Vertebrate Paleontology Collection, Minneapolis, Minnesota, USA;
UNPSJB PV	Palaeontology collections of the Universidad Nacional de la Patagonia, Comodoro Rivadavia, Argentina;
USNM	United States National Museum of Natural History, Washington, DC, USA;
YPFB Pal	Yacimientos Petrolíferos Fiscales Bolivianos, Colección de Paleontología, Santa Cruz, Bolivia;
YPM (PU)	Princeton Collection, Yale Peabody Museum, New Haven, USA.

SYSTEMATIC PALAEONTOLOGY

Supergrandorder UNGULATOMORPHA
Archibald, 1996

Order PANAMERIUNGULATA nov.

Family MIOCLAENIDAE Osborn & Earle, 1895

INCLUDED GENERA. — *Andinodus*, *Bubogonia*, *Choeroclaenus*, *Ellipsodon*, *Escribania*, *Litaletes*, *Mioclaenus*, *Molinodus*, *Orthaspidothierium*, *Pleuraspidotherium*, *Promioclaenus*, *Protoselene*, *Pucanodus*, *Simoclaenus*, *Tiucloaenus*, *Tiznatzinia*, *Valenia*.

DIAGNOSIS. — Bulbous cusps, the apices of which are approximated in occlusal view; protocone enlarged; styler shelf reduced to a labial cingulum or lost; styles of M1-2 reduced and tending to be aligned with para- and metacristae; paraconid reduced, tends to merge with the metaconid; entoconid and hypoconulid connate to fused, forming an obliquely oriented posterolingual crest; entoconid compressed transversely on P4 parastyle reduced and postparacrista straight, not curved labially.

The character states presented in this diagnosis are derived when compared to *Protungulatum*, *Oxyprimus* and “zehlestids”. However, it is noteworthy that most of these characters are highly homoplastic and are observed in several other groups of “condylarths”.

Subfamily KOLLPANIINAE Marshall,
Case & Woodburne, 1990

As documented below (in the *Tiuclaenus minutus* section), the genus *Kollpania* Marshall & Muizon, 1988 is regarded as a junior synonym of *Tiuclaenus*. Therefore and unfortunately, the family name Kollpaniidae Marshall, Case & Woodburne, 1990 must be retained as a subfamily and has priority over Molinodinae Bonaparte, Van Valen & Kramartz, 1993. See p. 144.

INCLUDED GENERA. — *Andinodus*, *Escribania*, *Molinodus*, *Pucanodus*, *Simoclaenus*, *Tiuclaenus*.

DIAGNOSIS. — Metaconid well posterior to protoconid, strongly inflated, and invading the talonid basin posteriorly; paracristid short transversely and strongly arcuate posteriorly; loss of the entocristid; hypoconid extremely inflated and occupying the medial half of the talonid (at least); talonid basin reduced to an obliquely oriented groove widely opened lingually; posterior slope of the hypoconulid of m3 less convex than in the other mioclaenids.

Genus *Molinodus* Muizon & Marshall, 1987

TYPE SPECIES. — *Molinodus suarezi* Muizon & Marshall, 1987

DIAGNOSIS. — Same as for the species.

Molinodus suarezi Muizon & Marshall, 1987

HOLOTYPE. — A partial left dentary with m1-3 (YPFB Pal 6112).

HYPODGM. — The holotype and the following specimens: YPFB Pal 6113, partial right dentary with m1-2 and m3 erupting; YPFB Pal 6114, partial right dentary with m2-3; YPFB Pal 6117, left M1, YPFB Pal 6118, right M2 with apices of proto-, para-, and metacone broken; MHNC 1238, right m1; MHNC 1243, partial right dentary with root of c, alveolus of p1, and p2; MHNC 1244, left p4; MHNC 1245 right p4; MHNC 1247, partial right maxilla with P3-M2; MHNC 1248, left M3; MHNC 1261, broken right m1; MNHNC 8269, partial left dentary with m1-3; MHNC 8274, right mandible fragment with dp4, m1; MHNC 8280, a partial maxilla with dp4, M1-2; MHNC 8329, worn right M1; MHNC 8330, left M1 with broken protocone; and MHNC 8344, partial right dentary with m1-2.

TYPE LOCALITY. — The holotype and MHNC 8344 were discovered at site 2 of the locality of Tiupampa as defined by Muizon & Marshall 1992. The other specimens come from site 1, the "quarry".

HORIZON AND AGE. — Santa Lucía Formation; Tiupampian (early Palaeocene), approximately equivalent to the Puercan of North America (Muizon & Brito 1993; Bonaparte *et al.* 1993; Muizon 1998; see Archibald *et al.* 1987 and Eberle & Lillegraven 1998 for definition, age, and subdivision of the Puercan land-mammal age).

DIAGNOSIS. — Size similar to that of *Promioclaenus*; dental formula I?/?; C?/1, P?/4, M3/3; P3 triangular, with a strong parastyle anterior to paracone; pre- and postparacristae well-developed; protocone slender with slight pre- and postcingula; P4 more massive, shorter, and wider than P3, with small conules; well-marked pre- and postcingula, and strong labial cingulum; M1 triangular and almost symmetrical in relation to its transverse axis; metacone only slightly lingual to the paracone; well-developed cingula (pre-, post- and labial); styles slightly to not projected labially; no hypocone; M2 subquadrangular and strongly asymmetrical, with oblique labial edge; well-developed pre- and postcingula, not reaching the para- and metastyles (but close to them); labial cingulum very strong; protocone large, bulbous, and anteroposteriorly elongated with a tendency to duplication; conules large; well-developed para- and metacingula reaching para- and metastyles; paracone higher and more voluminous than metacone; metacone much more lingual than paracone; centrocrista straight; para- and metastyles almost aligned with para- and metacones but parastyle still slightly shifted labially; no hypocone; M3 much wider than long; strongly bent posteriorly; labial edge strongly oblique; not reduced (i.e., nearly as long as M2); metacone and metaconule reduced; p2 triangular in lateral view; transversely flattened; small posterior cusp; p4, much larger; variable in shape from triangular to quadrate, with a large metaconid appressed against protoconid; anterior crest of protoconid possessing a tiny paraconid; large talonid cusp; lower molars with bulbous cusps; trigonid and talonid basin reduced; strong pre- and small postcingulids (on m1 and m3 only); paraconid clearly smaller than and appressed against metaconid; paracristid transverse and arched posteriorly; metaconid posterolingual to and slightly smaller than protoconid; cristid obliqua variable in size and reaching labial edge of metaconid; talonid basin small and open lingually (more an oblique groove than a basin); hypoconid large, inflated, circular, and only slightly smaller than protoconid; entoconid and hypoconulid almost completely fused forming a posterolingual oblique crest; talonid of m3 larger than on m1-2 with hypoconulid as large as hypoconid. Among Tiupampa "condylarths", *Molinodus* more resembles *Simoclaenus* than the other taxa. However, *Molinodus* differs from *Simoclaenus* in its smaller size, its jugal teeth more elongated anteroposteriorly, its upper molar less transverse and its M2 more asymmetrical with an anterolabially projected parastyle. *Molinodus* differs from *Promioclaenus* in its

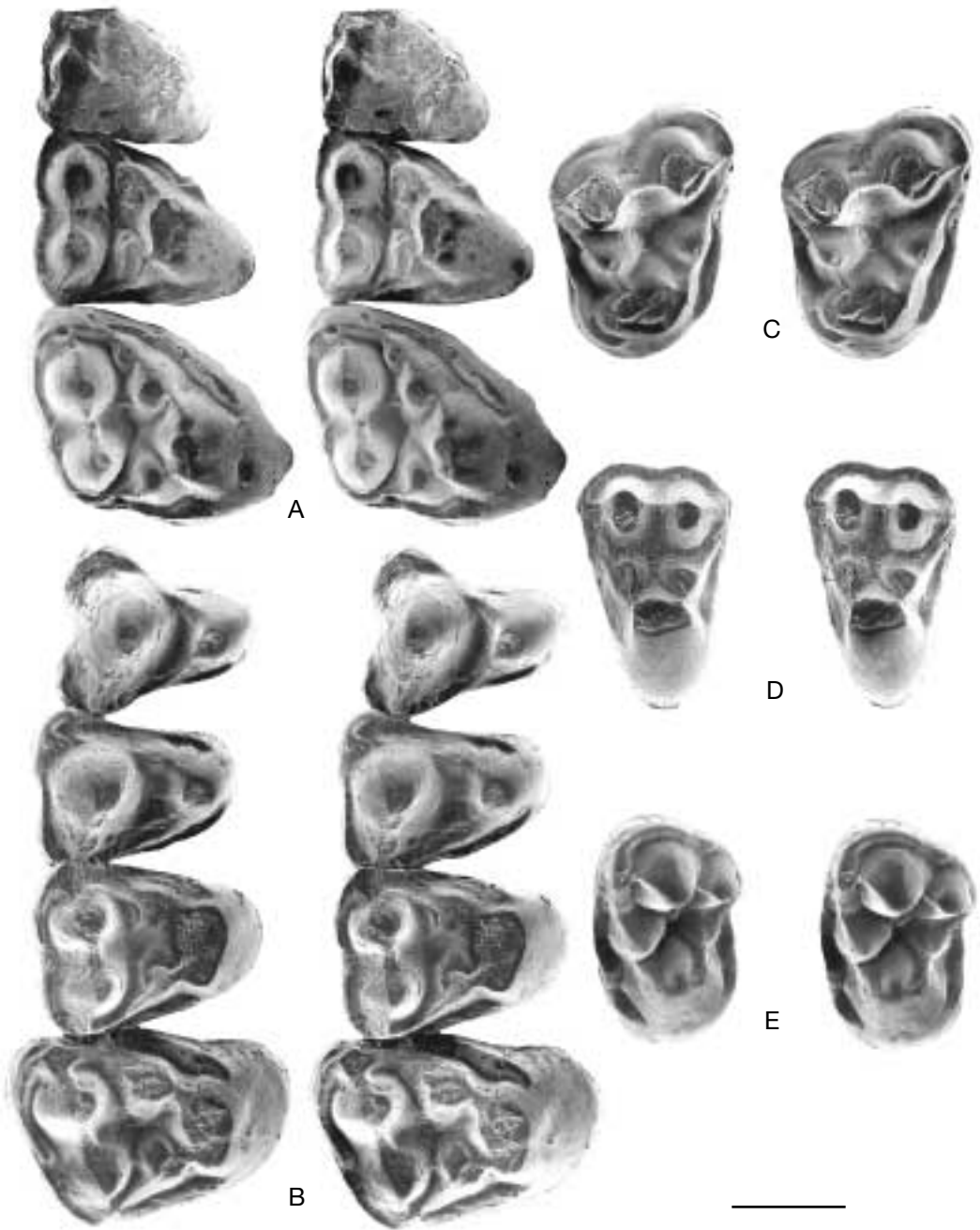


FIG. 2. — *Molinodus suarezi*, stereopairs of upper dentition: **A**, partial right maxilla with DP4-M2 (cast of MHNC 8280); **B**, partial right maxilla with P3-M2 (cast of MHNC 1247); **C**, isolated right M2 (cast of YPFB Pal 6118); **D**, isolated left M1 (cast of YPFB Pal 6117); **E**, isolated left M3 (cast of MHNC 1248). Scale bar: 2 mm.

TABLE 1. — Measurements (mm) and descriptive statistics of the upper dentition of *Molinodus suarezi*.

Measurement	N	Min	Max	Mean	CV
P3 L	1	3.02	3.02	3.02	1.000
P3 W	1	3.46	3.46	3.46	1.000
P4 L	1	2.74	2.74	2.74	1.000
P4 W	1	3.82	3.82	3.82	1.000
M1 L	5	2.78	3.07	2.95	0.036
M1 W	4	3.90	4.20	4.03	0.037
M2 L	3	3.31	3.41	3.37	0.015
M2 W	3	4.51	5.05	4.72	0.062
M3 L	1	2.62	2.62	2.62	1.000
M3 W	1	3.96	3.96	3.96	1.000

molars, which are more bulbous with apices of the cusps more approximated, in the longer trigonid of the lower molars with a paraconid less appressed against the metaconid, in the presence of a generally distinct labial cingulum, in the non-reduced m3, in the more transverse and less bulbous upper molars, in the thinner postcingulum, in the strong asymmetry of the M2 with an anterolabially projecting parastyle, and in the unreduced M3.

DESCRIPTION

Upper dentition (Fig. 2; Table 1)

Upper premolars. P3 (Fig. 2B) is triangular in occlusal view, with clearly concave anterior and posterior edges, though a distinct “waist” between the protocone and paracone is not present. The labial side bears a slight ectoflexus. The main cusp is the paracone, which is at least twice as voluminous and elevated as the protocone. Its anterior edge is rounded and does not bear a preparacrista, but a large parastyle is present at its base. The posterior edge of the paracone presents a fairly well-developed postparacrista, terminating at a weak metastyle that extends anterolabially a short distance as a labial cingulum, disappearing above the posterior root of the tooth. On the labial edge of the tooth are two small, conspicuous cingula at the antero- and posterolabial angles of the paracone. The protocone is a small and inflated cusp, slightly recurved labially (in anterior view). A short preprotocrista, unworn on the single specimen available (MHNC 1247), links the apex of the protocone to the anterolabial base of the paracone. The postprotocrista is

lower but longer than the preprotocrista and unites the apex of the protocone to the metastylar region; it bears a prominent wear facet that appears to reflect shear that took place *en échelon* (see Kay & Hiiemäe 1974) with the postparacrista, which bears a similar wear facet. A faint cingulum is present at the anterolabial angle of the protocone, while a thicker and longer cingulum is observed on its posterior flank. There is no true trigon basin but a saddle-shaped vallum separates paracone and protocone.

P4 (Fig. 2B) is also triangular in occlusal outline but is more molariform in appearance. Its labial edge is shorter and straighter (an ectoflexus is lacking) than on P3 and its lingual border is anteroposteriorly thicker and more rounded. Contrary to the condition observed on P3, the anterior border of the tooth is hardly concave (almost straight) and the posterior border is slightly convex. The paracone is about 30% lower than on P3 (when the teeth are viewed labially) and slightly less voluminous. The preparacrista, if present (the tooth is slightly worn), was faint, and there is a large parastyle at the anterolabial base of the paracone. The postparacrista is more pronounced than on P3 and links the apex of the paracone to a small metastyle located exactly posterior to the cusp. The styles are connected by a labial cingulum that is almost continuous, being interrupted only briefly, just at the anterolabial base of the paracone. The protocone is slightly larger than on P3 and more inflated. It bears pre- and postcingula that are thicker than on P3. In spite of the slight wear of the tooth, it is possible

to observe very faint conular swellings on the pre- and postprotocristae, respectively. A small trigon basin is observed because of the presence of the conules.

Upper molars. M1 (Fig. 2A, B, D) is subtriangular in occlusal view; the anterior border is approximately as long as the posterior border but slightly more convex. The labial edge of the tooth is parallel to the axis of the tooth row and bears a thick labial cingulum that is continuous from the parastyle to the metastyle. A shallow ectoflexus is present. The pre- and postcingula are thick, salient, and subequal in development. They extend labially up to the bases of the paracone and metacone, respectively, but do not reach the parastyle and metastyle on unworn specimens (e.g., MHNC 8330); the precingulum more closely approximates the parastyle than the postcingulum does the metastyle. In lingual view, the lingual extremities of the cingula are at the same level on the base of the protocone. The lingual slope of the protocone is smooth and does not bear a cingulum. The protocone is large, swollen, and anteroposteriorly elongated, with a flattened lingual side. This elongation is due to an inflation of the posterior edge of the protocone, which is responsible for the development of a small, triangular fossula limited by the metaconule anterolabially, the posterior bulge of the protocone anterolingually, and the postcingulum posteriorly (Fig. 2A-C). The protocone is flanked by large para- and metaconules which are closer to it than to the para- and metacone, respectively. They are connected to the protocone by small pre- and postprotocristae, respectively. The preparaconular and postmetaconular cristae extend labially to the parastyle and metastyle, respectively, and form strong para- and metacacula in their labial portions (Van Valen 1966). There are no postparaconular and premetaconular cristae except on MHNC 8330, on which a small postparaconular crista is present. This feature, therefore, shows some individual variation. The edges of the conules overhanging the trigon basin are rounded and inflated. Para- and metastyles are very small and almost of the same size (the parastyle is slightly larger than the metastyle). They are connected to the para- and metacones by prepara- and postmetacristae

respectively. The paracone is slightly higher and more voluminous than the metacone. They are widely separated from each other, as well as from the conules. The metacone is slightly more lingual than the paracone. The centrocrista is straight. In occlusal view, parastyle, preparamacrista, paracone, postparamacrista, premetacrista, metacone, postmetacrista, and metastyle are not perfectly aligned anteroposteriorly as stated by Bonaparte *et al.* (1993). On two of the three M1 and on the three M2s the para- and metastyle are slightly shifted labially. On one M1 only (YPFB Pal 6117), the para- and metastyle are anterior and posterior to the para- and metacone respectively. This condition of YPFB Pal 6117 is regarded here as the result of some individual variation of this character in *Molinodus suarezi*. The trigon basin is fairly large and has a cross-shaped morphology due to the inflation of the internal edges of the conules.

Muizon & Marshall (1987a) referred to *M. suarezi* an M1 (YPFB Pal 6117) which closely resembles the M2 that they referred to the same taxon (YPFB Pal 6118). The only differences existing between the two specimens are the slightly smaller size of 6117, and its more symmetrical morphology in relation to a transverse axis. These differences were regarded as owing to different positions on the maxilla. Van Valen (1988) referred YPFB Pal 6117 to cf. *Mimatuta* on the basis of the great lingual slope of the protocone of the tooth, which is reminiscent of the condition observed in the Peripitychidae. However, Van Valen, who subsequently studied the specimen, retrieved it from the genus *Mimatuta* and considered it to represent a new species of *Molinodus* (pers. comm. of Van Valen to C. de Muizon, September 1991, Chicago). Materials now available, which include five specimens of M1 belonging to *M. suarezi* (two of which are directly associated in maxillary fragments with M2), uphold the original interpretation of Muizon & Marshall (1987a). The size of YPFB Pal 6117 falls perfectly into the range of variation seen in the available sample of *Molinodus suarezi* (Table 1).

The three known specimens of M2 (Fig. 2A-C) are much larger than the M1 in width and length (Table 1). However, in contrast to what is observed on M1, the M2s are asymmetrical in

relation to a transverse axis. The anterior border of the tooth is convex anteriorly and much longer than the posterior one. Furthermore, the labial border is clearly oblique in relation to the axis of the tooth row. The tooth has a subquadrangular outline, its anterior and labial borders being respectively longer than its posterior and lingual ones. As a consequence, the medial half of the tooth seems to have been shifted posteriorly, a feature absent on M1 but strongly accentuated on M3. The labial cingulum is thick and continuous from para- to metastyles. There is a faint cuspule on the labial cingulum at the level of the ectoflexus on two of the three specimen (MHNC 1247 and 8280). This cuspule could represent the incipient development of a mesostyle, which is absent as such in *Molinodus*. The ectoflexus is shallow but distinct. The pre- and postcingula are thicker and transversely longer than on M1. They do not reach the styles labially and do not contact the preparaconular and postmetaconular cristae, although they approximate these crests closely. Lingually, the pre- and postcingula do not contact on the lingual edge of the protocone, although a small cingular cusp is present on MHNC 8280. The protocone is the largest cusp of the tooth. It is elongated anteroposteriorly and, on MHNC 8280 (the only specimen where the apex is well preserved), it clearly shows an incipient duplication process. The labial edge of the protocone is swollen. The pre- and postprotocristae are short but sharp and connect the apex of the protocone to the large conules, which are only slightly smaller than the para- and metacones. The preparaconular and postmetaconular cristae reach the para- and metastyles, respectively. Because of the asymmetry of the tooth, the preparaconular crista is much longer than the postmetaconular crista. On MHNC 8280 a small cuspule is present at the labial base of the paraconule, on the preparaconular crista. The conules are separated from the para- and metacones by a deep valium. The para- and metacones are separated by a straight centrocrista and the former is clearly more voluminous and higher than the latter. The metacone is strongly lingual to the paracone, a position which is responsible for the oblique orientation of the labial edge of the tooth.

The parastyle and preparamacrista are better developed than the metastyle and postmetacrista, respectively; the parastyle is slightly shifted labially, while the metastyle is directly posterior to the metacone. The parastyle is small as generally observed in mioclaenids, but it is relatively large for a member of this family. It is larger on MHNC 8280 than on the two other specimens. On MHNC 8280, posterolabial to the parastyle, at its junction with the labial cingulum, is a small cuspule (in fact it is more a swelling of the posterolabial crest of the parastyle than a cusp). A similar structure is present on the lingual crest, which connects the apex of the parastyle to the accessory cuspule of the preparaconular crista mentioned above (see discussion for possible homologies of these cusp and cuspules). The trigon basin is deep and well enclosed by the five bulbous cusps of the tooth. The tooth, as on M1, lacks a hypocone.

M3 (Fig. 2E) is smaller than M2. It is only slightly narrower transversely, but its labial edge is clearly shorter anteroposteriorly. It shows a characteristic posterior curvature. As is observed on M2, but to a greater extent, the labial edge is strongly oblique in relation to the tooth row. The protocone is only slightly smaller than on M2 and has the same morphology. The major difference with M2 is the great reduction of the metacone and metaconule, which are approximately half the size of the paracone and paraconule. As on M2, the cingulum is incomplete lingually, but the lingual face of the protocone bears faint swellings at the level of the pre- and postcingula.

Lower teeth (Fig. 3; Table 2)

Lower premolars. The p1 of *Molinodus suarezi* is only known by its alveolus on MNHN 1243, which indicates a single rooted tooth. The distance from this alveolus to the posterior margin of the canine alveolus is greater than to p2, suggesting the possibility of a small diastema between p1 and c.

The p2 (Fig. 3O, P) is known by one specimen (MHNC 1243). It is double-rooted, and the crown has two cusps: a large protoconid, triangular in lateral view with a spatulate apex, and a small posterior cusp (the talonid) at the posterior base of the protoconid. Faint keels descend the

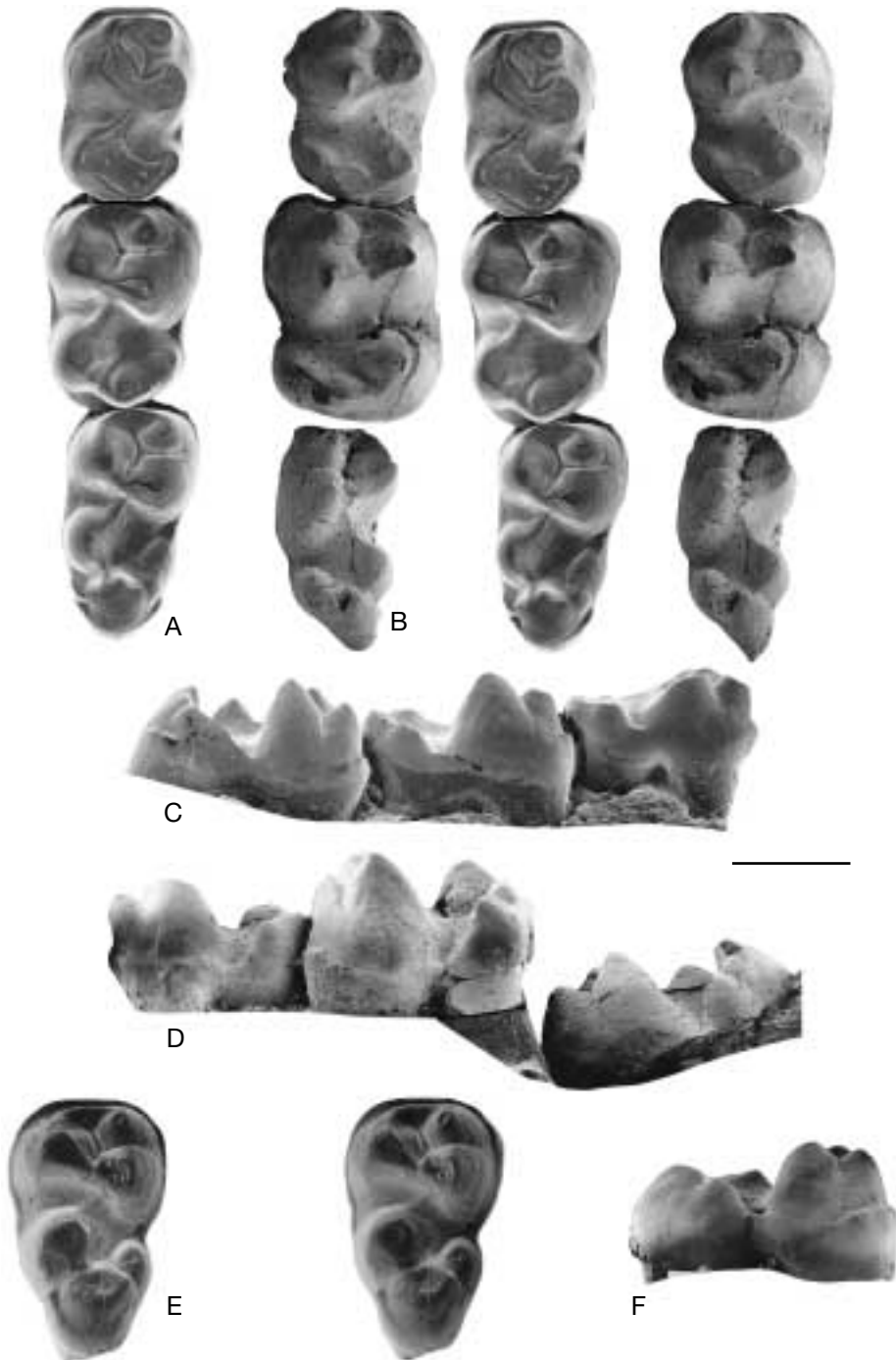


FIG. 3. — *Molinodus suarezi*, lower dentition; **A**, stereopair of partial left dentary with m1-m3 (cast of YPFB Pal 6112, holotype) in occlusal view; **B**, the same in lingual view; **C**, stereopair of partial right dentary with m1-m3 (m3 erupting) (cast of YPFB Pal 6113) in occlusal view; **D**, the same in lingual view; **E**, left m3 (cast of MHNC 1238) in occlusal view; **F**, the same in lingual view.

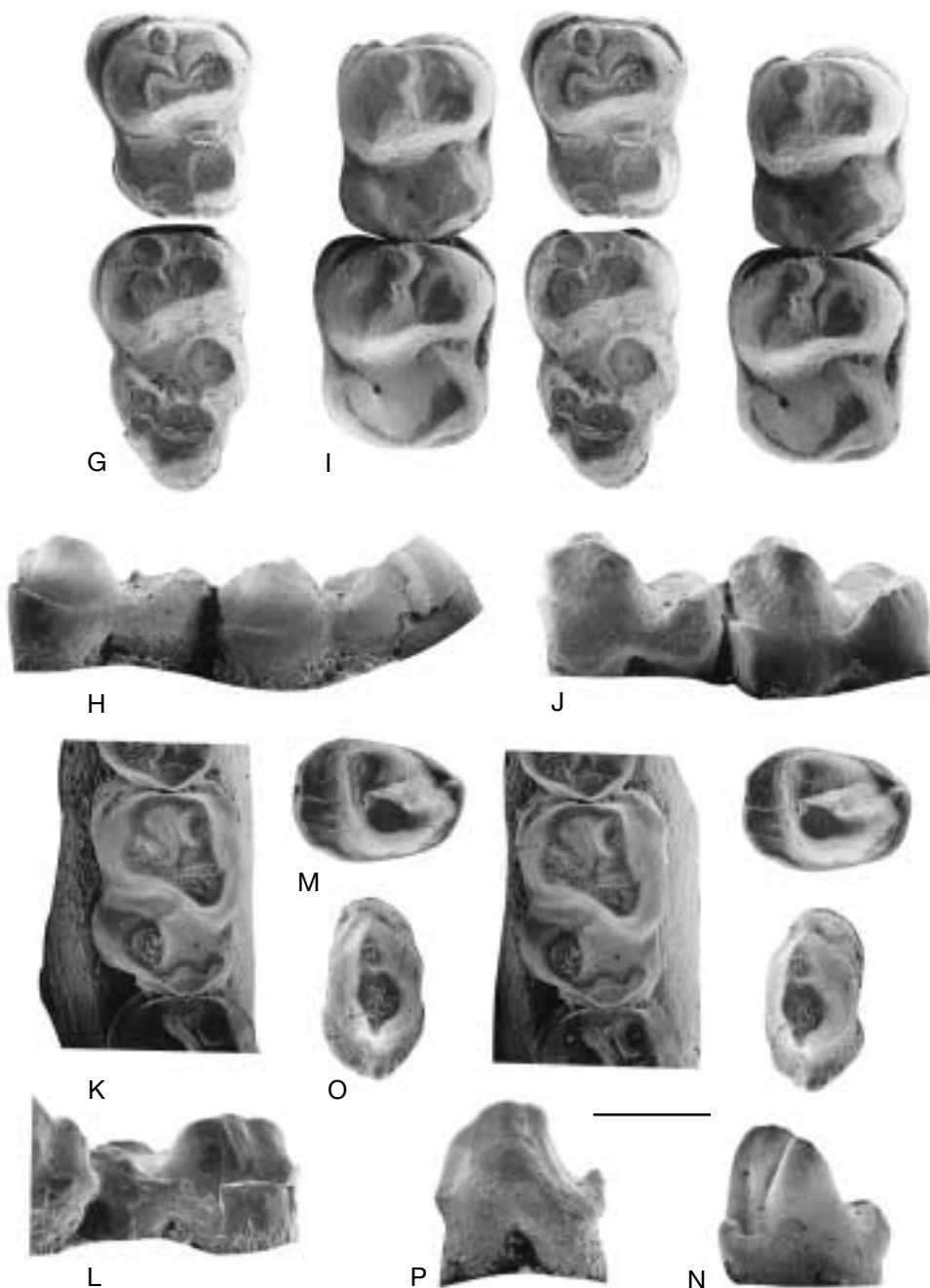


FIG. 3. — **G**, partial right mandible with m2-m3 (cast of YPFB Pal 6114) in occlusal view; **H**, the same in lingual view; **I**, partial right mandible with m1-m2 (cast of MHNC 8344) in occlusal view; **J**, the same in lingual view; **K**, left m2 (cast of MHNC 8269) in occlusal view; **L**, the same in lingual view; **M**, right p4 (cast of MHNC 1244) in occlusal view; **N**, the same in lingual view; **O**, right p2 (cast of MHNC 1243) in occlusal view; **P**, the same in lingual view. A, C, E, G, I, K, M, O, stereopairs. Scale bars: 2 mm.

TABLE 2. — Measurements (mm) and descriptive statistics of the lower dentition of *Molinodus suarezi*.

Measurement	N	Min	Max	Mean	CV
p2 L	1	2.89	2.89	2.89	1.000
p2 tri W	1	1.71	1.71	1.71	1.000
p4 L	2	2.82	2.92	2.87	0.025
p4 tri W	2	2.01	2.19	2.10	0.061
dp4 L	1	3.13	3.13	3.13	1.000
dp4 tri W	1	1.67	1.67	1.67	1.000
dp4 tal W	1	1.78	1.78	1.78	1.000
m1 L	6	2.88	3.28	3.15	0.045
m1 tri W	5	2.27	2.89	2.47	0.106
m1 tal W	6	1.98	2.54	2.24	0.097
m2 L	5	3.36	3.69	3.58	0.037
m2 tri W	5	2.80	3.26	2.96	0.066
m2 tal W	5	2.42	3.07	2.66	0.095
m3 L	5	3.88	4.69	4.28	0.075
m3 tri W	5	2.14	3.09	2.65	0.140
m3 tal W	5	1.80	2.50	2.24	0.138

anterior and posterior faces of the protoconid. Cingula apparently are lacking, although there is a slight swelling just labial to the base of the anterior keel.

Three p4s (MHNC 1244, 1245, and 8274) are referred to *Molinodus suarezi*. The p4 MHNC 8274 was extracted from a jaw fragment with dp4 and m1 and, in spite of some crushing, it is clear that it is extremely similar to MHNC 1245. MHNC 1244 (Fig. 3M, N) is fairly different from the two other teeth and, if it is actually referable to *Molinodus suarezi*, the p4 of this species denotes some variation in shape and position of the metaconid. MHNC 1245 and 8274 are larger and grossly triangular with the trigonid narrower than the talonid. The metaconid is well-developed but much smaller than the protoconid in height and volume, and is located posterolingual to it. At the anterolingual base of the protoconid is a small paraconid connected to the apex of the cusp by a sharp and almost straight paracristid (which is in fact the preprotocristid). The talonid is a thick, transverse crest that bears a labial main cusp connected to the posterolingual base of the protoconid by a small cristid obliqua. On MHNC 8274, lingual to the main cusp (hypoconid), are three cusps, subequal in size and aligned transversely. The talonid is separated from the trigonid by a transverse vallum which is closed by the hypoconid labially on MHNC

8274, thus recalling the talonid basin of the molars. In MHNC 1245 the transverse vallum is open both lingually and labially. A well-developed precingulid is present at the anterolabial base of the trigonid but it is weak on MHNC 1245.

MHNC 1244 is so different that we describe it separately. It is more massive than the other two p4s but its major characteristic is its semimolariform aspect. The tooth is more rectangular, and has a trigonid wider than the talonid. The trigonid approaches the condition of the molars, and the metaconid is only slightly smaller than the protoconid; both cusps are taller than on the molars, and the trigonid basin is well-formed. The metaconid is almost lingual to the protoconid. The paraconid is appressed against the anterolabial base of the metaconid. The paracristid is longer and much more recurved posteriorly than on the two other p4s and runs posterolabially from the paraconid, ascending vertically the anterior face of the protoconid. It resembles the condition observed on the molars (i.e. it forms a rounded right angle, see below). A strong precingulid is present at the base of the trigonid below the paracristid and extends further on the anterolabial angle of the protoconid than on MHNC 1245. The talonid is a thick, transverse crest that appears to be weakly cuspidate. The cristid obliqua is faint and the talonid crest is

separated from the trigonid by a transverse valium opened labially and lingually. There is no talonid basin.

The differences existing between the three p4s described above could be explained by the referral of MHNC 1245 to a p3. However, this interpretation is rejected here for the following reasons: 1) MHNC 1245 closely resembles MHNC 8274, which is an undoubted p4 (extracted below the dp4) and 2) with the exception of some very derived taxa (*Didolodus*, *Phenacodus*), "condylarths" generally do not present a well-developed metaconid on p3. Then, the strong differences that exist between MHNC 1244 (especially on the trigonid) and the two other p4s could warrant referral to a different taxon. However, it is noteworthy that, on MHNC 1244, the trigonid is morphologically very close to that of the molar, while, on MHNC 8274 (which is an unquestionable p4 of *Molinodus suarezi*), it is the talonid which strongly approaches the molar condition. In other respects, on MHNC 1245, neither the trigonid nor the talonid resemble that of the molars. Therefore, it is likely that the p4 of *Molinodus* is extremely variable in structure and cusp organization, but clearly denotes a tendency towards molarization.

Lower molars. The lower molars of *Molinodus* increase in length from m1 to m3 and, as with the upper molar series, m1 is considerably smaller than m2 (Table 2). The trigonid of m1 is always narrower than on m2. The trigonids of m2 and m3 are rather variable in absolute and relative width, with comparatively high coefficients of variation recorded for the sample (Table 2). Most of this variation is accounted by a single specimen, YPFB Pal 6113, in which the trigonids of m1-2 are quite broad but the m3 is somewhat smaller than the remaining teeth.

On m1 and m2 (Fig. 3A-D, G-L), the trigonid is consistently higher and wider than the talonid, although the difference on some specimens (e.g., m1 of MHNC 8344) is slight. The labial and lingual sides of the trigonid are sloping and the lingual edge of the trigonid is not subvertical as is observed in many primitive North American taxa (e.g., *Protungulatum*, *Oxyprimus*, *Mimatuta*). Therefore, in anterior view, the trigonid of the m2 of *Molinodus* is symmetrical in relation to the mid-

line of the tooth. The trigonid cusps are bulbous, and their apices are approximated in occlusal view. As a consequence, the trigonid basin is small, shallow and triangular. In the unworn condition, the classical trihedron of the primitive pattern is clearly observable (e.g., YPFB Pal 6112). The valley between the paraconid and protoconid is well-developed, and the two cusps are still well-individualized. The anterior edge of the trigonid bears a robust precingulid, which extends slightly on the lingual and labial edges of the tooth. The paraconid is either directly anterior to the metaconid or slightly more labially situated; it is approximately half the size of that cusp. The paraconid and metaconid are fused at their bases but on unworn teeth their apices are well-separated. The apex of the paraconid is oriented anteriorly because the cusp itself is anteriorly recumbent (this feature is especially clear on the m1 of YPFB Pal 6113). The paracristid is complete and strongly recurved, extending anteriorly from the protoconid before curving lingually and then posterodorsally to reach the apex of the paraconid. The transverse length of the paracristid is approximately half the width of the trigonid. On most of the specimens, the preprotocristid is oriented anteroposteriorly and the preparacristid transversely. Both cristids form a rounded angle of approximately 90° at the anterior base of the protoconid. The preparacristid is strongly concave posteriorly and originates on the anterior border of the paraconid. The protocristid is slightly V-shaped in occlusal view, with the apex of the V pointed posteriorly. The protoconid is massive and inflated anteriorly. It is subequal in volume and height to the metaconid. The latter is posterior to the protoconid in such a way that the posterior side of the trigonid has an anterolabial-posterolingual orientation. The talonid is slightly shorter than the trigonid and bears a shallow basin that is open lingually. The hypoconid is the largest cusp of the talonid and is only slightly smaller than the protoconid. The cristid obliqua runs from its apex toward the notch in the protocristid between protoconid and metaconid. The hypoconulid is higher than the entoconid and slightly larger. Both cusps are compressed anterolabial-posterolingually (sometimes almost anteroposteriorly, as in YPFB Pal 6113 and MHNC 8269) and always merge to

form a thick, oblique crest that is sometimes smooth, sometimes mamillated, and that occupies the posterolingual angle of the talonid. As a consequence of this crest and of the inflation of the hypoconid, the talonid basin is reduced to a kind of oblique groove opening lingually just behind the metaconid. *Contra* Van Valen (1988), there is no entocristid except on the m3 of YPFB Pal 6114, in which a faint cuspule anterior to the entoconid could represent a possible relict of such a structure.

The m2 is identical to m1 except its size is approximately 25% larger. Furthermore, the five specimens of m2 known so far show some differences that we interpret as individual rather than specific variation. The trigonid is almost as wide as the talonid in YPFB Pal 6113, it is slightly wider in YPFB Pal 6112, MHNC 8269 and 8244, and it is much wider in YPFB Pal 6114. This latter specimen is much wider than the other four. Among other features we interpret as variable within the species, the cristid obliqua is well-developed in YPFB Pal 6112 and MHNC 8344, it is small but present in YPFB Pal 6113 and MHNC 8269, and is absent in YPFB Pal 6114; the trigonids of YPFB Pal 6112, 6114, MHNC 8269, and 8344 are clearly more elevated than the talonid, while this difference is weaker on YPFB Pal 6113.

On the m3 (Fig. 3A-G, H), the trigonid is essentially identical to those of m1 and m2 (except, variably, for being more anteroposteriorly elongate; e.g., YPFB Pal 6113) and the major difference of this tooth is in its much longer talonid. This morphology is mainly due to the size of the hypoconulid, which is subequal in size to the hypoconid. The posterior edge of the hypoconulid is not inflated and is only weakly convex. On YPFB Pal 6112 and 6114, the entoconid as such is very small or lacking, being developed as a crest that runs from the labial border of the hypoconulid toward the base of the metaconid. As a consequence, the talonid basin is widely open lingually. On the labial edge of the hypoconulid, a small crest connects the apex of the cusp to the posterolabial base of the hypoconid. On YPFB Pal 6113 and MHNC 1238, the entoconid is not so crest-like, and the labial crest of the hypoconulid is smoother

(almost absent on YPFB Pal 6113). The hypoconulid of MHNC 8269 is damaged.

Deciduous dentition

The ultimate upper and lower deciduous premolars can be unambiguously assigned to *Molinodus suarezi* because they are known from jaw fragments that also include parts of the adult molar series (MHNC 8280, dp4, M1-2; MHNC 8274, dp4, p4-m1). Furthermore, one isolated unworn dp4 is referred to *Molinodus suarezi* because it compares favourably to dp4 of MHNC 8274. dp4 is, unfortunately, very heavily worn and reveals little details as to coronal morphology. In occlusal outline, it is similar to but smaller than M1, differing in being lower crowned, with thinner enamel and a weaker precingulum. The dp4 is approximately the same length as m1 but is much narrower, and in this and other respects it differs from the adult teeth in ways that have been reported for other "condylarths" (e.g., West 1971). The paraconid is rather low compared to the condition on m1-3. It is more distinctly separated from the metaconid than on the molars, and is much more anteriorly placed, so that the angle formed between paraconid, protoconid, and metaconid is greater and the trigonid more open lingually than on succeeding teeth. As a consequence, the paracristid is more open and does not form a rounded right but obtuse angle. The posterior face of the trigonid is less vertical than on the molars, sloping more gently in a posterior direction. The hypoconid is the largest of the talonid cusps (as with the molars) but is rapidly diminished in height by apical wear. As with the molars, the hypoconulid and entoconid are joined by a crest, and the talonid basin is open lingually.

Dentary (Fig. 4)

The posterior part of the dentary is preserved in MHNC 8269 and some other parts of this element are represented by several specimens, including MHNC 1243, which preserves p2 in place. The symphysis apparently was unfused, but is broadly developed as a rugose surface extending posteroventrally from just below the alveolar border adjacent to the canine, terminating adjacent to the posterior margin of p2. No specimen preserves the canine, but evidently it



FIG. 4. — *Molinodus suarezi*, partial left dentary with m1-m3 (MHNC 8269); **A**, lateral view; **B**, medial view. Scale bar: 5 mm.

was a large tooth, judging by its preserved base and by the fact that the labial surface of the dentary bulges adjacent to the presumed position of the root. MHNC 1243 does not preserve the incisor region, but it must have been small (with incisors correspondingly small, tightly packed, and bearing short roots) as judged by the close approximation of the lingual face of the canine to the symphysis. A well-marked mental foramen is present on the labial face of the dentary, adjacent to the bony septum separating the anterior alveolus of p2 from the single alveolus of p1.

The angular process is complete on MHNC 8269, but the condyle and the coronoid process are lacking. The most notable feature of the dentary is the large, posteriorly projecting angular process. It bears a sharp lingual ridge, which we interpret as being for the insertion of the *M. pterygoideus medialis*. This ridge is concave dorsally and continues posteriad to the apex of the angular process. The mandibular foramen, located approximately at the alveolar level of the horizontal ramus and adjacent to the anterior margin of the angular process, is well-developed, faces posteriorly, and bears sharp dorsal and ventral rims. The ventral

border of the dentary at the base of the angular process is slightly concave. On the lateral border of the bone, the masseteric fossa is deep and limited anteriorly by an elevated crest which forms an angle of about 50° with the tooth row. The ventral margin of the masseteric fossa is poorly defined.

COMPARISONS

In this section, we compare the dental and mandibular morphology of *Molinodus suarezi* with that of other primitive ungulates, from both North and South America. *Molinodus* warrants special consideration in this regard, as previous studies have identified it as the most primitive of South America's native ungulates. Therefore, in many ways, *Molinodus* is most comparable to North American “condylarths” (Van Valen 1988; Bonaparte *et al.* 1993). Further reasons for focusing attention on *Molinodus suarezi* are that, it is the best known of Tiupampa's “condylarths”; and that, because of its size, specimens cannot be confused with those belonging to any other taxon from Tiupampa. In later sections, we will compare the remaining “condylarths” of Tiupampa to *M. suarezi* and to other South and North

American taxa, focusing mainly on the features in which they differ from *Molinosus*. In order to provide a framework for assessment of character polarity, we first discuss the concept and contents of “Condylarthra” (with some comments on the use of this term), and our reasons for including certain taxa in the comparisons, while ignoring others. This clarification is necessary because the concepts and morphology of some taxa, most especially at the genus and family level, are heterogeneous, and it is not possible to provide character states for these without making implicit assumptions. The main taxa and specimens we consulted are listed above.

Basis for comparisons

Ungulatomorpha. Archibald (1996) and Nesson *et al.* (1998) have recently provided comprehensive studies of primitive ungulates or ungulate-like mammals (depending on definition) from the Late Cretaceous, including the “zhelestids” of Uzbekistan and apparently affiliated taxa from the Campanian and Maastrichtian of North America and Europe. This work provides welcome new data on the phylogeny of ungulates, in the form of outgroup taxa that are critical to evaluating character polarity among “condylarths”. For this reason, we included “zhelestids” in our comparisons, focusing on the best represented taxa, *Aspanlestes*, *Parazhelestes* (two species), and *Eoungulatum* (one species). Nesson *et al.* (1998) treated early Palaeocene North American *Protungulatum donnae* as representing an ungulate morphotype, as have virtually all other workers. We follow that course here and include *Protungulatum* in our comparisons, although, as noted below, we tentatively identify several features of the dentition in which we suspect *P. donnae* may be derived with respect to a common ancestor of remaining ungulates. This interpretation is not contradicted by Luo (1991) who observe more plesiomorphic character states in *Oxyprimus ericksoni* than in *P. donnae*. Consequently, *Oxyprimus* will also be regarded as a referral for definition of character polarity.

“**Condylarthra**”. Grouping of archaic mammals generally recognized as archaic ungulates into a formal taxonomic unit has long been recognized

as unsatisfactory because shared similarities are, in most instances, plesiomorphies (see discussion in Prothero *et al.* 1988 and Archibald 1998). In some instances, such as with the Mesonychidae, long placed in the Condylarthra (Simpson 1945), detailed study has resulted in the establishment of reasonably well-corroborated hypotheses of relationships to more derived groups (in this case Cetacea), with consequent taxonomic revisions (see review of literature in O’Leary & Rose 1995). Unfortunately, the relationships of most remaining “condylarths” are far more uncertain. Some authors have advocated abandonment of the concept of Condylarthra altogether, arguing that its retention has deleterious consequences for public and professional communities alike (Prothero *et al.* 1988; Archibald 1998). Yet one alternative, distributing “condylarth” taxa among more derived groups based on the perceived significance of a very few, subtle nuances in morphology, is likely to be unstable and arguable at best. Another, considering all taxa as *incertae sedis* results in a non-classification leaves one with no syntactical tool as a basis for communication. For these reasons, we retain a traditional concept of the Condylarthra, essentially that of Simpson (1945), as revised by Van Valen (1978) (see also Cifelli 1983a; Van Valen 1988). Our concept of Condylarthra is equivalent to that of Archibald (1998) although this author does not use the same term. It is also similar to the arrangement given by McKenna & Bell (1997), except that we find it useful to include Arctocyonidae, as more traditionally conceived. However, we are conscious that our understanding of Condylarthra probably represents a paraphyletic taxon as expressed by Prothero *et al.* (1988) and Archibald (1998). We, therefore, follow recommendations of the latter in adding quotation marks to the term “condylarth” in order to emphasize its probable paraphyly. As a matter of fact, Archibald (1998) in his review of the North American “condylarths” also needs found for a syntactical tool since this author uses the term “archaic ungulates”, which, according to him is equivalent of “condylarths” (*sensu* Simpson, 1945). Furthermore, Salles (1996), in a study of early ungulates phylogeny, agrees with Prothero *et al.* (1988) and Archibald (1998) — this reference is

cited (1994, in press) in the references section of Salles (1996) and corresponds to a preprint of Archibald (1998) — on the fact that the Condylarthra represent a “waste basket” but still retains the term “condylarths”, probably because he finds it useful. Therefore, whatever the term is used for, there is a clear syntactical need to refer to an entity including the taxa that Simpson (1945) placed in his Condylarthra and which are unanimously regarded as primitive (or archaic) ungulates. *Contra* Prothero *et al.* (1988) and Archibald (1998), we think that the term “condylarths” (Simpson, 1945) is not misleading. As properly stated by Archibald (1998), this name is familiar to non-specialist readers and we now all know that it very probably represents a non-monophyletic group, as “archaic ungulates”, “primitive ungulates” or “generalized ungulates” do. If its context is clarified, the use of any denomination is a minor matter of semantics, not of science.

In addition to *Protungulatum* and *Oxyprimus*, we included in our comparisons the arctocyonid *Baioconodon* (= *Ragnarok*) *nordicum*, which is well known and which appears to represent a basal loxolophine (see Van Valen 1978; Johnston & Fox 1984). Our comparisons also included, for similar reasons, *Maiorana noctiluca*, which may either be an extremely primitive periptychid or an arctocyonid (see Van Valen 1978; Cifelli 1983a). Although there remain some controversies regarding relationships within the Periptychidae (e.g., Cifelli *et al.* 1995), the group is rather well understood (in the context of “Condylarthra”) and its monophyly has been universally upheld. Despite the suggestion of possible periptychid affinities for poorly known *Perutherium* (Van Valen 1978), it is clear that the typical, specialized members of the family are irrelevant to the origin of South America’s native ungulates — whether or not periptychids are ultimately related to mioclaenids (see below), as has been suggested (Prothero *et al.* 1988; Archibald 1998). Accordingly, we restricted extensive comparisons to well-known basal taxa: *Maiorana noctiluca* (mentioned above) and *Mimatuta minuial*.

Students have long found South America’s Eocene didolodontids to be similar to North American Phenacodontidae, a well-defined, well-known

monophyletic group (Thewissen 1990). Ameghino (1904) and Gaudry (1904), for example, referred Casamayoran *Ernestokokenia patagonica* to the Puercan phenacodontid *Tetraclaenodon* (then commonly known by the names *Protogonia* and *Euprotogonia*). Similarly, the Casamayoran macrauchenioid *Proectocion* was described by Ameghino (1904) in allusion to the Palaeocene and Eocene *Ectocion* of North American faunas. Simpson (Simpson 1948: 97-98) noted that, were *Didolodus* (the best known didolodontid) “found in North America it would probably be referred to the Phenacodontidae without question,” but astutely added that, “the family (i.e. Didolodontidae) considered as a whole is an assemblage too advanced to be compared with Palaeocene Holarctic condylarths”. Later study upholds this view: basic phenacodontid specializations are lacking from *Didolodus* itself, and a morphotype for didolodontids (and other South American “condylarths”), based on study of Palaeocene and Eocene taxa, suggests origin from a considerably more primitive “condylarth” (Cifelli 1983a; see also Van Valen 1988). We therefore considered Phenacodontidae only peripherally in the course of this study.

The most problematic and, for present purposes, relevant assemblage of “condylarths” is the hyopsodonts which, prior to recognition of Arctocyonidae as basal ungulates in the mid-1960s, served as the taxonomic “wastebasket” for generally small, primitive ungulates (Cifelli 1983a). The now-traditional concept of Hyopsodontidae stems largely from the work of Matthew (1937) and Simpson (1937); most important in the present context is the union of Hyopsodontidae (previously considered as insectivores or primates) and Mioclaenidae. Van Valen (1978) separated the two into distinct families, later explaining that this is because they have separate origins among Arctocyonidae (Van Valen 1988). Later workers generally have adopted the distinction between Mioclaenidae and Hyopsodontidae (e.g., Johnston & Fox 1988; McKenna & Bell 1997), although a clear basis for this remains somewhat elusive (see excellent discussion in Archibald 1998). We do not attempt to solve this problem — which in fact lies outside the scope of the present undertaking — although we make a

few comments on the basis of our comparisons. In view of the close resemblance of Tiupampa's "condylarths" to North American Mioclaenidae, we have included as many of the well-known taxa as possible in our comparisons: *Promioclænus acolytus*, *Valenia wilsoni*, *Litaletes disjunctus*, *Bubogonia* spp., *Choeroclaenus turgidunculus*, and *Mioclænus turgidus*. Among hyopsodontids, we focused on the earlier, more primitive taxa: *Litomylus dissentaneus* and *Haplaletes disceptatrix*. Remaining taxa generally or occasionally included in Hyopsodontidae, including Louisiinae and Apheliscinae, have never been suggested in connection with South American ungulates and are ignored for present purposes.

South American ungulates. We include detailed comparisons with the better represented members of South America's native "condylarth" family, Didolodontidae (*Didolodus multicuspis*, *Ernestokokenia nitida*, *Paulacoutoia protocenica*, and *Lamegoia conodonta*). *Paulogervaisia* is so inadequately known that it can be considered only in passing. Some members of Litopterna are equally primitive, or even more so, in terms of the dentition. Their recognition as litopterns is based on postcranial criteria, which cannot be applied to many of the Early Tertiary taxa (Cifelli 1983a; Cifelli 1983b; Bergqvist 1996; Muizon *et al.* 1998). We have included in our comparisons only the basal taxa *Miguelsoria parayirunhor*, *Protolipterna ellipsodontoides*, and *Asmithwoodwardia scotti*. The latter, traditionally regarded as a didolodontid, has been tentatively referred to the litopterns by Cifelli (1983). This interpretation is followed by McKenna & Bell (1997).

The origin of remaining South American ungulate groups – Notoungulata, Astrapotheria, Pyrotheria, and Xenungulata – is of great interest. Dentitions of even the earliest members of these groups are, however, already highly specialized. When comparison is made to the Tiupampa "condylarths", only vague resemblances or differences (of uncertain significance) can be noted, resulting in evidence that is permissive but not strongly suggestive (see, e.g., Cifelli 1993). Accordingly, we treat remaining South American ungulate groups only briefly.

Comparison of dentition of Molinodus

Upper dentition. Upper premolars: the P3-4 of *Molinodus* are more derived than those of *Protungulatum*, *Promioclænus* and *Litaletes* in the greater development of their protocone and in their greater transverse width (especially on P3). The relatively large protocone of the P3 of *Protungulatum* and *Molinodus* is more derived than the condition observed in *Promioclænus* and *Litaletes* (which have a very small protocone on P3). The fact that an incipient swelling only of the posterolingual margin of the paracone is observed on the penultimate premolar of *Zhelestes* and *Parazhelestes* would confirm the plesiomorphy of the mioclaenid condition when compared to *Molinodus* (but see below).

The P4 of *Molinodus* presents incipiently developed conules. A small paraconule is present in several "zhelestids" (*Aspanlestes*, *Parazhelestes*) and para- and metaconules are present in *Prokennalestes*, which would support the plesiomorphy of the feature. However, there are no conules on the P4 of the oldest and most primitive known "condylarths" (*Protungulatum*, *Oxyprimus*, *Mimatuta*, *Valenia wilsoni*).

Upper molars: the molars of *Molinodus* retain some plesiomorphic features that are present in *Protungulatum* but absent in the other genera.

The paracone of M1-2 is higher and larger than the metacone (difference is weak on M1), as in "zhelestids" while in certain other mioclaenids (*Bubogonia*, *Protoselene*, *Litaletes*), the paracone and metacone are subequal in height and volume. The condition of *Molinodus* resembles that observed in most didolodontids and primitive litopterns (*Paulacoutoia*, *Didolodus*, *Lamegoia*, *Miguelsoria*, *Asmithwoodwardia*), in which the paracone is slightly larger in height and volume than the metacone.

The pre- and postcingula of M1-2 do not reach the styles labially (although they are very close to it) (Fig. 5). Their labial extremities are more labial than in *Protungulatum*. They are dorsal to the para- and metacingula respectively (i.e. not contacting them), but less dorsal than in *Protungulatum*. In several other mioclaenids (but see character analysis section below), the pre- and postcingula are connected to the styles labially, and the preparaconular and postmetaconular

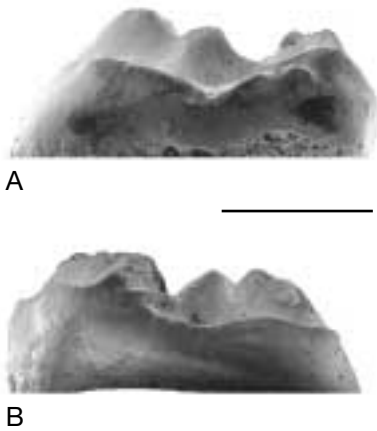


FIG. 5. — Anterior and posterior views of the M2 in *Molinodus* (cast of YFPB Pal 6118) to show the relationships between the pre- and postcingula and the preparaconular and postmetaconular cristae; **A**, anterior view; **B**, posterior view. Scale bar: 2 mm.

cristae are either reduced or their labial extremities connect the pre- and postcingula before they reach the styles. In other words, the condition of *Molinodus* is clearly intermediate between that of a *Protungulatum* primitive morphotype and a North American mioclaenid morphotype (a condition similar to that of *Molinodus* is also found in *Valenia*, *Protoselene*, and *Choeroclaenus*). A condition even more plesiomorphic than that of *Protungulatum* is observed in *Parazhelestes*, in which the pre- and postcingula do not extend labially further than the level of the conules and in which the preparaconular and postmetaconular cristae do not reach the styles labially (Nessov *et al.* 1998).

As is generally observed in *Protungulatum*, most didolodontids, and primitive litopterns, *Molinodus* lacks postparaconular and premetaconular cristae (although a faint postparaconule crista is still observable on the M2 of MHNC 8280). This is a derived condition when compared to what is observed in the “zhelestids”, in which the conules bear both pre- and postcristae. Such cristae are also present in North American mioclaenids as well as in the primitive periprychid *Mimatuta*. Although absent on most specimens of *Protungulatum* observed during this study, these cristae can be present in this genus as an individual variation but, if so, they are very weak.

Postparaconular and premetaconular cristae are variably present in some didolodontids and early litopterns, sometimes as an individual variation (see below in the character analysis section).

The labial cingulum of *Protungulatum* and *Molinodus* is well-developed and continuous from para- to metastyles. This plesiomorphic condition is found in most other primitive mioclaenids.

The ectoflexus of *Molinodus* is shallower than in *Protungulatum* and much shallower than in “zhelestids”. Other mioclaenids do not have an ectoflexus except *Litaletes*, in which it is a little more pronounced than in *Molinodus*.

The postcingulum of *Molinodus* is less derived than that of *Protungulatum*, *Mimatuta*, North American mioclaenids, hypsodontids, didolodontids, and litopterns, because it does not present a lingual cusp (or is not thickened lingually) and does not present any kind of hypocone, even incipiently developed. In this respects the condition of *Molinodus* is similar to that of “zhelestids”. It is more primitive than the North American mioclaenids, which have a clearly thickened lingual extremity although they do not develop a true hypocone even in the most advanced genera. The pre- and postcingula reach the anterior and posterior edges of the protocone at its base and their extremities are at the same level in lingual view. This condition is observed in the “zhelestids”, *Protungulatum*, and *Oxyprimus*. In the North American mioclaenids, the postcingulum is generally higher on the protocone than the precingulum, which represents a derived condition.

The parastyle of *Molinodus* is much smaller than that of *Protungulatum*, *Mimatuta*, and “zhelestids”. The prominent anterior projection of the parastyle and its conspicuous labial shifting (regarded here as plesiomorphic) which is observed in those taxa, are lacking in *Molinodus*. Among mioclaenids, the parastyle and preparacrista are slightly shifted labially in *Bubogonia*, *Valenia*, *Litaletes*, *Protoselene*, and *Choeroclaenus* (it is variable in the last genus). The condition in these taxa is intermediate between those observed in *Protungulatum* and *Molinodus*. In *Promioclaenus* and *Mioclaenus* the preparacrista and parastyle are aligned with the labial edge of the

tooth. In *Molinodus* the anterolabial angle of the upper molars — i.e. the parastyle — is rounded and not salient as in the plesiomorphic condition. The condition of *Molinodus* is closer to those of *Promioclænus* and *Mioclænus* than to those of the other mioclænids, although the parastyle of *Molinodus* is slightly larger and has a more labial position. The evolutionary sequence from the plesiomorphic to the apomorphic state is: “zhelestids”, *Protungulatum*, *Litaletes*, *Molinodus*, *Promioclænus*.

The structure of the parastyle of MHNC 8280 is noteworthy in the presence of posterolabial and lingual accessory cusps. In a basal eutherian such as *Prokennalestes* (Kielan-Jaworowska & Dashzeveg 1989) as well as in “zhelestids” (Nessov *et al.* 1998), the parastylar lobe is composed of three cusps: 1) the stylocone, which is labial to anterolabial to the paracone and connected to it by the preparacrista; 2) the parastyle, which is just anterior to the paracone; and 3) the preparastyle, which is lingual to the parastyle. The stylocone on the one hand and the parastyle + preparastyle on the other are separated by the parastylar groove (Crompton & Kielan-Jaworowska 1978; Nessov *et al.* 1998), where the shearing action of the protoconid produces an important transverse wear facet. In primitive “condylarths” (e.g., *Protungulatum*, *Oxyprimus*, *Mimatuta*), the stylocone is smaller and closer to the parastyle than in *Prokennalestes*, but a small parastylar groove is clearly present. In fact in those genera, the stylocone is reduced to a simple elevation of the junction between the preparacrista and the labial cingulum. In *Baioconodon*, the stylocone is connate to the parastyle (almost fused to it), but is still connected to the paracone by the preparacrista; the parastylar groove has disappeared and the wear facet affects the whole lobe, is relatively flat, and is subhorizontal or anteriorly sloping. Therefore, the trend toward the “condylarth” pattern of the parastylar lobe seems to be a fusion of the stylocone and the parastyle. In “condylarths” that are more derived, in this respect, than *Protungulatum* (for example) the parastyle seems to “capture” the preparacrista which therefore links the paracone to the parastyle. The morphology of the parastylar region of *Molinodus* (as

observed on MHNC 8280) thus is reminiscent of the plesiomorphic condition, and the posterolabial and lingual cusps mentioned in the description could represent relicts of the stylocone and preparastyle, respectively. The condition of MHNC 8280 has not been observed during this study in other mioclænids and, is intermediate between those of *Protungulatum* and the other mioclænids.

The conules of *Molinodus* are larger than in *Protungulatum*, and the trigon basin is deep and wide. As is observed in *Protungulatum*, the conules are located closer to the protocone (relative to paracone and metacone) *vs* midposition. This condition is also present in the other mioclænids, but absent in the “zhelestids”, in which the conules are closer to midposition of the tooth than to the protocone. The “zhelestid” condition is regarded by Nessov *et al.* (1998) as plesiomorphic, whereas the morphology of *Protungulatum* and *Molinodus* are apomorphic. Following Nessov *et al.* (1998), we give preference to this definition of the position of the conules *vs* that given by Bonaparte *et al.* (1993), who consider the shape of the polygon formed by conules and para- and metacone. This polygon is longer than wide (i.e. derived for Bonaparte *et al.* 1993) in mioclænids, didolodontids, and “zhelestids”, wider than long (i.e. primitive for Bonaparte *et al.* 1993) in *Protungulatum*, and as long as wide in *Oxyprimus*. In the case of *Molinodus*, the state of the character varies according to its definition: in spite of the lingual position (derived for Nessov *et al.* 1998) of the conules, the polygon is clearly longer than wide (i.e. primitive for Bonaparte *et al.* 1993).

Molinodus resembles *Protungulatum*, *Valenia* and *Litaletes* in the absence of reduction of M3, and differs from *Promioclænus* and *Mioclænus*, which have a reduced M3. This feature, however, is difficult to evaluate because *Parazhelestes robustus* has a small M3 (probably autapomorphic for the genus, Archibald, pers. comm.), but *Zhelestes temirkazyk* has an unreduced M3 (Nessov *et al.* 1998). Furthermore, a large M3 is present in most didolodontids and litopterns, which could indicate a tendency to increase the size of this molar. However, *Molinodus* shows some obviously derived features. *Molinodus* is derived in the



FIG. 6. — *Lamegoia conodonta* from the late Palaeocene of Itaboraí (Brazil); **A**, right M2 (cast of MNRJ 1465-V, referred specimen) in occlusal view; **B**, left m2 (cast of MNRJ 1463-V, holotype) in occlusal view. Stereopairs. Scale bar: 1 cm.

incipient duplication of its protocone, which confers it an anteroposteriorly elongated morphology with an expanded posterior edge. This condition is absent in *Protungulatum*, peripitychids, the other mioclaenids, litopterns, and most didolodontids. A similar condition is present in one upper molar (MNRJ 1463-V) referred to *Lamegoia* by Paula Couto (1952) (Fig. 6). However, it is not clear whether this cusp observed on this specimen represents a duplication of the protocone or a hypocone closely appressed against the protocone. Other specimens referable to *Lamegoia* are needed to clarify this point.

Another derived feature of *Molinodus* is the asymmetrical outline of the M2 (while the M1 is approximately symmetrical in relation to a transverse axis), with an anterolabial expansion of its anterolabial angle and a metacone in a more lingual position than the paracone. As noted by Bonaparte *et al.* (1993), the lingual position of the metacone is also observed on the M1, although in the three available specimens this condition is very weakly developed. The position of the metacone observed on M2 is absent to this extent in *Protungulatum*, "zhelestids", most other mioclaenids, and most didolodontids, but it is present in *Mioclaenus*, *Ellipsodon*, and an M2 (MNRJ 1463-V) referred to *Lamegoia* (Paula Couto 1952).

Furthermore, contrary to the statement by Bonaparte *et al.* (1993), the protocone of *Molinodus* does not bear a less inclined lingual slope than in *Protungulatum*. This character shows some variation in *Protungulatum* and in *Molinodus* (three specimens), and in some cases

we have observed in *Molinodus* a lingual slope more pronounced than in *Protungulatum*. Furthermore, as is clearly observed on the three specimens, the protocristae do not form an obtuse (Bonaparte *et al.* 1993) but rather an acute angle as in *Protungulatum* and most plesiomorphic taxa. The pre- and postcingula of *Molinodus* are not almost continuous on the lingual side of the protocone as claimed by Bonaparte *et al.* (1993), but are clearly separated. In this respect, the condition of *Molinodus* is not different from that of *Protungulatum*, other mioclaenids, and didolodontids.

Lower dentition. Lower premolars: the p4 of *Molinodus* has a well-developed metaconid, smaller in volume and height than the protoconid and located posterior to it. However, as mentioned above, this tooth probably shows some variation in the size of the metaconid, which can be almost as voluminous as the protoconid (as in MHNC 1244). A well-developed metaconid (but clearly smaller than and posteromedial to the protoconid) is present on the p5 (= ultimate premolar) of the "zhelestid" *Aspanlestes* and the penultimate premolar has a swollen lingual edge. A small metaconid on p4 (smaller than and posteromedial to the protoconid) is also present in *Protungulatum*, *Oxyprimus*, and *Mimatuta* (it is smaller in *Protungulatum* than in the first two genera). Therefore, the presence of a metaconid on p4 is likely to represent a plesiomorphic character state for ungulatomorphs. In North American mioclaenids the metaconid of p4 is generally absent (it probably disappears because of the apomorphic inflation of the p4) except in *Litaletes* where the p4 is distinctly semi-

molarized. The condition of *Litaletes* (AMNH 35890) is very similar to that observed on MHNC 8274. The only differences are that, in *Molinodus*, the metaconid is slightly smaller and the paraconid distinctly smaller. We regard both genera as having a premolariform p4. The presence of a small metaconid on p3 of *Litaletes* is a clear indication of the tendency to molarization of the premolars. This tooth is unknown in *Molinodus*. Among didolodontids and primitive liopterns, the p4 is semi-molarized (i.e. the metaconid is almost lingual and subequal to or only slightly smaller in volume and height than the protocone, the talonid bears a small and shallow basin) in *Paulacoutoia*, *Didolodus*, *Lamegoia*, *Paulogervaisia*, *Miguelsoria*, and *Asmithwoodwardia*. The p4 of *Ernestokokenia* (the p4 referred to this genus by Simpson 1964 probably belongs to *Didolodus*) is unknown, and *Protolipterna* resembles the North American mioclaenids (except *Litaletes*) in having an inflated p4, in which the metaconid is merged with the protoconid. The fact that p3 also has a small metaconid in *Litaletes*, *Didolodus*, and *Lamegoia* is another indication of their tendency to semi-molarization of the premolars. Therefore, the lower premolars of *Molinodus* present a slightly less pronounced molarization than in *Litaletes*, didolodontids, and primitive liopterns (excluding *Protolipterna*) and are therefore slightly less derived than the premolars of these taxa. Comparisons of *Molinodus* with the North American mioclaenids (except *Litaletes*) in terms of degree of specialization is difficult because they are specialized in two different ways. In the North American mioclaenids (except *Litaletes*) and *Protolipterna*, the increase of abrading surface of the premolars is achieved by inflation of the teeth, in which the cusps tend to merge. In *Molinodus*, *Litaletes*, didolodontids and liopterns (except *Protolipterna*), the premolars tend to multiply their cusps by molarization.

Lower molars: the lower molars of *Molinodus* retain some primitive features found in *Protungulatum* and *Bubogonia saskia* but absent in the other mioclaenids and in didolodontids. The presence of a well-individualized and relatively large (for a mioclaenid) paraconid is attested by the presence of a conspicuous valley that

separates para- and metaconid and that gives the trigonid basin its classical trihedron shape, characteristic of the plesiomorphic pattern where the three valleys are subequal in length. This condition is also found in *Mimatuta* and in *Sorlestes* and *Eoungulatum* (in those “zhelestids” the para-metaconid valley is generally slightly longer than in the others). In more derived forms, like other mioclaenids and didolodontids, the para-metaconid and para-protoconid valleys disappear or are reduced; the main valley of the trigonid is that which separates the proto- and metaconid and has an almost anteroposterior orientation. The condition of *Escribania* is apparently similar to that of *Molinodus*, but the only specimen known is relatively worn and this feature is not clearly observable.

In *Molinodus*, the trigonid of m2 is always clearly wider than the talonid. This condition is generally (but not always) present in *Protungulatum* and *Escribania*. In *Oxyprimus galadriela*, the trigonid is as wide as the talonid. In the North American mioclaenids, the trigonid is generally slightly wider than the talonid. In the didolodontids, the trigonid is either as wide as or narrower than the talonid. A trigonid wider than the talonid is generally regarded as a plesiomorphic condition for eutherians. However, the fact the trigonid of *Eoungulatum*, *Aspanlestes*, and *Sorlestes* is narrower than the talonid would indicate the contrary for Ungulatomorpha, although these genera could very well be derived for this feature.

Contrary to the condition of some other mioclaenid, the m3 of *Molinodus* is not reduced but resembles that of *Protungulatum*, *Mimatuta* and the didolodontids. Apparently, the reduction of m3 is a derived character state present in some “condylarths” (some mioclaenids, hypsodontids, arctocyonids, and phenacodontids). However, the distribution of this feature is variable according to genus.

Molinodus differs from *Protungulatum* in its more bulbous cusps of the trigonid of lower molars, with apices in a more internal position. This is a major feature of Mioclaenidae, which was formulated by Bonaparte *et al.* (1993: 27): “cusps of the trigonid closer to median line of the tooth; edges of the trigonid more inclined towards the centre of the tooth”. It is noteworthy, however, that the

condition of this character in *Molinodus* is even more derived than in primitive mioclaenids such as *Promioclænus* and *Litaletes*.

Another important difference of *Molinodus* with respect to *Protungulatum* is the inclination of the labial and lingual sides of the trigonid of m2, a feature probably related to the position of the apices of the trigonid cusps. In *Protungulatum*, the lingual edge of the trigonid is subvertical and the labial side is sloping. Therefore, in anterior view, the trigonid has an asymmetrical aspect. In *Molinodus*, both sides of the trigonid are sloping and the anterior view is symmetrical in relation to the median axis. The *Protungulatum* pattern is found in *Oxyprimus*, primitive mioclaenids (*Bubogonia*, *Promioclænus*, *Litaletes*, *Choeroclaenus*) and represents the plesiomorphic character state. The derived condition of *Molinodus* is found in some mioclaenids (*Mioclaenus*, *Protoselene*, *Escribania*), didolodontids (*Paulacoutoia*, *Ernestokokenia*, *Lamegoia*, *Didolodus*) and primitive litopterns (*Asmithwoodwardia*, *Miguelsoria*, *Protolipterna*). It is noteworthy that the *Molinodus* (derived) pattern is also present in *Mimatuta*, a primitive periptychid, and *Baiocodon*, a primitive arctocyonid, and which would indicate that this character state evolved several times independently in the "Condylartha".

The trigonid of *Molinodus* is longer anteroposteriorly than in *Protungulatum* and in North American mioclaenids. One of the major characteristics of the trigonid of *Molinodus* is the posterior extension of the metaconid, which is located in a posterior position in relation to the protoconid. This condition gives to the protocristid a strongly oblique orientation, and the posterior slope of the trigonid is slightly concave posteriorly. This feature is not nearly so well-developed in *Protungulatum* and in most North American mioclaenids. However, an approaching condition is observed in *Protoselene* (although in this genus the metaconid is not so posterior) and *Bubogonia*. In other South American "condylarths" (*Didolodus*, *Paulacoutoia*, *Ernestokokenia*, *Lamegoia*, *Escribania*), and primitive litopterns (*Miguelsoria*, *Asmithwoodwardia*, *Protolipterna*) the metaconid is also well posterior to the protoconid. The condition in *Protolipterna* and *Miguelsoria*, because of some individual variation, is more subtle

although we regard it as more similar to that observed in South American ungulates than in North American mioclaenids. As a matter of fact, in the oldest known litoptern, *Requisia vidmari* from the early Palaeocene of the "Banco Negro Inferior" (Bonaparte & Morales 1997), the metaconid clearly is well posterior to the protoconid and partially invades the talonid basin posteriorly. The same condition is observed in the m3 referred by Simpson (1948) to *Wainka tshotshe* from the late Palaeocene of the Río Chico Formation (Argentina). However, the most striking similarity is observed in MNRJ 1463-V, the holotype of *Lamegoia conodonta* (Fig. 6). On this specimen (an m2), the paraconid is almost the size of the metaconid (i.e. larger than in *Molinodus*), merged to it at its base and located almost lingual to the protoconid. The metaconid has a strong posterior position and is located lingually at the level of the ectoflexid labially. Although clearly much more derived, this specimen bears the same lower molar pattern as in *Molinodus*. In *Paulacoutoia* and *Miguelsoria*, the paraconid is similar in size to that of *Molinodus*. In *Didolodus*, the paraconid, although sometimes more appressed against the metaconid, has a morphology and a position that remains in the range of variation observed in *Molinodus*. Therefore, considering that *Molinodus* commonly has a paraconid larger than in *Protungulatum*, it is possible that some early didolodontids as well as *Molinodus* encompassed an apomorphic development of the paraconid and metaconid followed by a reduction in some lineages. For instance, *Asmithwoodwardia* clearly possess the apomorphic condition of the metaconid but has no (or a very reduced) paraconid. Furthermore, in litopterns, which are commonly accepted as the sister-group of didolodontids (Cifelli 1983a; 1993 and see below), the primitive forms (*Miguelsoria*, *Protolipterna*) have a *Molinodus*-like pattern of the trigonid while the paraconid is lost in some more derived genera (*Proectocion*, *Polymorphis*, *Cramauchenia*, *Proadiantus*). Therefore, it is possible that from a relatively large (in relation to *Protungulatum*) paraconid (*Molinodus* pattern), the cusp tends to reduce and disappear in some litopterns, and elsewhere tends to increase in size, as is observed in *Lamegoia*.

The condition of the paracristid of *Molinodus* is also relatively specialized when compared to that of *Protungulatum*. As mentioned in the description, the preprotocristid and the labial part of the preparacristid form a rounded angle of 90°, and the extremities of the paracristid attach on the anterior side of the cusps. In *Protungulatum*, *Oxyprimus* (Bonaparte *et al.* 1993), “zhelestids” (Nessov *et al.* 1998), and North American mioclaenids, the attachments of the paracristid are more on the anterolabial and anterolingual edges of the paracone and protocone, respectively. The *Molinodus* pattern is present in *Escribania* and is emphasized in most didolodontids (*Didolodus*, *Paulacoutoia*, *Ernestokokenia*, *Lamegoia*) and early litopterns (*Asmithwoodwardia*, *Protolipterna* and *Miguelsoria*), in which the paracristid has a relatively symmetrical, anteriorly protruding, and bowed to “quadrate-bowed” morphology.

The hypoconid of *Molinodus* is as voluminous as the protoconid. It is strongly inflated, enlarged, and occupies the whole labial half of the talonid on m1-2. As a consequence, the talonid basin is small, shallow, and reduced to a sort of transverse groove that is open lingually. In *Protungulatum* and “zhelestids”, the hypoconid is smaller and less inflated than in *Molinodus*. In the North American mioclaenids, the hypoconid is larger than in *Protungulatum* but does not reach the size observed in *Molinodus* (although it sometimes approaches the size of the protocone) and the talonid basin is slightly larger. The condition of *Escribania* is extremely similar to that of *Molinodus*. In didolodontids (*Lamegoia*, *Paulacoutoia*, *Ernestokokenia*, and in some specimens of *Didolodus*) and primitive litopterns (*Asmithwoodwardia*, *Miguelsoria*, *Protolipterna*), the hypoconid is more voluminous than the protocone but the talonid basin is larger than in *Molinodus* and *Escribania*.

The cristid obliqua of *Molinodus* connects the trigonid at the posterolabial base of the metaconid or at the centre of the protocristid. In *Protungulatum* and in the North American mioclaenids, the cristid obliqua generally reaches the posterolingual base of the protoconid or the centre of the protocristid. The condition of *Molinodus* also is generally present in didolodontids and primitive litopterns.

The hypoconulid and entoconid of *Molinodus* are compressed and merged. They form an anterolinguo-posterolabially (sometimes almost transversely) oriented crest, which borders the talonid basin posterolingually. In *Protungulatum*, the cusps are not (or very little) flattened and are approximated but not connate; in North American mioclaenids, the cusps are generally flattened, connate but not merged (except in some species of *Ellipsodon*). In didolodontids, the cusps are conical and well-individualized. In fact, the condition of *Molinodus* seems to be the result of further development of the condition of the North American mioclaenids and could be an autapomorphy of the genus. The condition of *Escribania* is intermediate between that of *Molinodus* and didolodontids; it is fairly similar to that of North American mioclaenids.

As noted by Bonaparte *et al.* (1993), the hypoconulid of *Molinodus* is larger than the entoconid on m1-2. The plesiomorphic condition is observed in “zhelestids”, in which they are grossly subequal in height and volume. In *Protungulatum* and *Oxyprimus*, the hypoconulid is smaller than the entoconid. In North American mioclaenids and primitive litopterns, the hypoconulid is generally smaller than the entoconid. In didolodontids, the entoconid is a large, conical cusp, larger than the hypoconulid. It is generally smaller in *Ernestokokenia*, *Asmithwoodwardia*, *Miguelsoria*, and *Escribania*; it is either smaller or subequal to it in *Protolipterna*, *Paulacoutoia* and *Didolodus*. On the holotype of *Lamegoia*, the entoconid is slightly lower than the hypoconulid but more voluminous. The condition of *Molinodus* appears to be derived.

Bonaparte *et al.* (1993) noted that the posterior edge of the hypoconulid of *Molinodus* is not bulbous, differing in this respect from the condition observed in *Protungulatum* and *Oxyprimus*. The “zhelestid” *Eoungulatum kudukensis* has a posterior edge of the hypoconulid that is more concave than that of *Molinodus* but approaches the condition of *Protungulatum*. The profile of the hypoconulid of the m3 of *Molinodus* also differs from that of the other mioclaenids, primitive peripitychids (e.g., *Mimatuta*, *Maiorana*), and *Baiococonodon*. We therefore assume that the condition of *Molinodus* represents a derived character

state. The posterior slope of the hypoconulid is relatively inflated and convex in lateral view in didolodontids and primitive litopterns, except in some specimens of *Protolipterna* (DNPM LE 444B and E) and *Miguelsoria* (MNRJ 1468V).

An entocristid is absent in most specimens of *Molinodus*. A well-developed entocristid is present in "zhelestids". *Protungulatum*, *Oxyprimus*, and North American mioclaenids have a small but clear entocristid. There is no entocristid in *Escribania*; however, as noted by Bonaparte *et al.* (1993), there is a small cuspule between the entoconid and the metaconid. Among didolodontids and primitive litopterns the condition varies. A small entocristid is clearly present in *Ernestokenia nitida*, but it is absent in *Didolodus*, *Paulacoutoia*, *Miguelsoria*, and *Asmithwoodwardia*. *Molinodus* and most other primitive South American ungulates therefore appear to be characterized by an apomorphic reduction of the entocristid.

Genus *Tiuclaenus* Muizon & Marshall, 1987

Kollpania Marshall & Muizon, 1988: 39. – Marshall, Case & Woodburne 1990: 486. – Muizon 1992: 614. – Bonaparte, Van Valen & Kramartz 1993: 32. – Muizon & Brito 1993: 257. – Muizon 1998: 24.

TYPE SPECIES. — *Tiuclaenus minutus* Muizon & Marshall, 1987

SPECIES INCLUDED IN THE GENUS. — *T. minutus*, *T. cotasi* n. sp., and *T. robustus* n. sp.

DIAGNOSIS. — Small-sized mioclaenids approximately 15 to 30% smaller than *Molinodus*; tooth cusps bulbous but more gracile than those of *Molinodus*. Dental formula I $\frac{2}{3}$, P $\frac{2}{4}$, M $\frac{3}{3}$; M1-2 subquadrangular with large conical conules clearly separated from the para-, meta- and protocone; paracone larger and in a more labial position than metacone on M2; trigon basin small, cross-like, or star-like on M2 because of swelling of the cusps; premetaconular and postmetaconular cristae absent (or present as a faint, rounded elevation) on M1-2 but strong pre- and postcingula joining the base of protocone to para- and metastyle, respectively; no labial cingulum; no hypocone; M1 and M2 more transverse than in *Molinodus*; M3 small, oval-shaped, with strong reduction of metacone and metaconule; lower canine small, as high as the premolars; lower premolars with large central cusp, minute anterior cusp and talonid cusp increasing in size from p2 to p4; p4 with small metaconid on posterolabial side of protoconid; lower molars with well-developed paraconid

fused at base to metaconid; paraconid more closely appressed against metaconid than in *Molinodus* and, as a consequence, trigonid basin often almost reduced to an anteroposterior sulcus; talonid with a large hypoconid; hypoconulid and entoconid generally connate and forming an oblique posterolingual crest; talonid basin reduced to an oblique groove opened lingually; talonid of m3 generally small and narrow.

Tiuclaenus minutus Muizon & Marshall, 1987

HOLOTYPE. — YPFB Pal 6115, a left dentary with alveoli of i1 and i3, i2, c, alveolus of p1 and p2-m3.

HYPODIGM. — The holotype; YPFB Pal 6119, maxilla fragment with M3; MHNC 1240, right maxilla fragment with M1-3 [referred by Muizon & Marshall (1991) to *Pucanodus gagnieri*]; MHNC 1253, dentary fragment with p3-p4, MHNC 1250 a left m2; MHNC 1252, left m3; MHNC 1258, right M1; MHNC 8334, left m2 lacking anterior part of para- and protoconids; MHNC 8335, left m3, MHNC 8346, left M1 lacking the enamel of para- and metacones.

HORIZON AND AGE. — Santa Lucía Formation; Tiupampian (early Palaeocene), approximately equivalent to the Puercan of North America (Muizon & Brito 1993; Bonaparte *et al.* 1993; Muizon 1998; see Archibald *et al.* 1987 and Eberle & Lillegraven 1998 for definition, age, and subdivision of the Puercan land-mammal age).

TYPE LOCALITY. — Site 1 ("the quarry") at Tiupampa, Cochabamba Department, Bolivia.

DIAGNOSIS. — Size clearly smaller than the two other species of the genus; upper molars less transverse than in *T. cotasi* and *T. robustus*; p4 slightly more gracile with a metaconid larger than in *T. cotasi*; m3 relatively short.

SPECIAL COMMENTS ON THE GENUS *KOLLPANIA* Marshall & Muizon, 1988. — *Kollpania tiupampina* was established on a single, molariform upper tooth, thought to belong to a caroloameghiniid marsupial (Marshall & Muizon 1988). The specimen (YPFB Pal 6135), however, is so atypical for a marsupial that Marshall *et al.* (1990) established the family Kollpaniidae (within the Caenolestoidea) to contain it. They also referred to the Kollpaniidae *Zeusdelphys*, a genus generally placed in the Protodidelphidae (e.g., McKenna & Bell 1997), from Itaboraí, Brazil (Marshall 1987). Based on comparisons with ontogenetic series of the mioclaenid *Promioclænus*, Muizon subsequently (1992) pointed out that YPFB Pal 6135 is a deciduous tooth (dP4) of a condylarth, a conclusion supported by Bonaparte *et al.* (1993) and Marshall *et al.* (1995, 1997). These papers were evidently not seen by McKenna and Bell (1997), who continued to recognize *Kollpania* as a distinct genus of marsupials, representing its own family.

TABLE 3. — Width relationship of dP4 to M1 in “Condylarthra”. Data on *Hyopsodus* “*markmani*” (used of quotes denotes uncertain status of species) measured from Gazin (1968: plate 9, fig. 13); data for Phenacodontidae measured from West (1971: figs 3C, 4A, 5A, 9A, 10A, 11A, 13A, B, 18C). Taxonomy for Phenacodontidae follows Thewissen (1990).

Taxon	Specimen	W dP4/W M1
Mioclaenidae		
<i>Molinodus suarezi</i>	MNHC 8280	0.752
Phenacodontidae		
<i>Tetraclaenodon puercensis</i>	AMNH 3841	0.773
<i>Tetraclaenodon puercensis</i>	AMNH 16648	0.789
<i>Tetraclaenodon puercensis</i>	PU 17498	0.778
<i>Phenacodus primaevus</i>	PU 13048	0.783
<i>Phenacodus primaevus</i>	USNM 20070	0.868
<i>Phenacodus vortmani</i>	AMNH 15763	0.815
<i>Phenacodus grangeri</i>	PU 19561	0.864
<i>Copecion brachypternus</i>	PU 13115	0.824
<i>Ectocion osbornianus</i>	PU 13325	0.912
Hyopsodontidae		
<i>Hyopsodus</i> “ <i>markmani</i> ”	DMNH 486	0.814
		min. 0.752
		max. 0.912
		mean 0.816

Unfortunately, deciduous teeth of “condylarths” have neither been widely studied nor illustrated, a notable exception being the work of West (1971) on Phenacodontidae. The only “condylarth” from Tiupampa known by specimens preserving parts of the deciduous and adult dentitions together is *Molinodus suarezi*, for which both dp4 and dP4 are known. In order to assess the identity of YPFB Pal 6135, we compared it with dP4 of *Molinodus* (which is not well preserved) and available illustrations of “condylarth” specimens preserving dP4 and M1 (Gazin 1968; West 1971). Given the measurements of YPFB Pal 6135 (L = 2.6; W = 2.4) and the proportional relationships of dP4 to M1 in this sample of Mioclaenidae, Hyopsodontidae, and Phenacodontidae (Table 3), the width of M1 in the species represented by YPFB Pal 6135 can be estimated as being between 2.63 and 3.19 mm (95% confidence interval). The sample (N = 11) mean, 2.94 mm, is almost exactly the width of the two measurable M1s known for *Tiuclaenus minutus* (MHNC 1240, W = 3.09; MHNC 1258, W = 2.99), and even the maximum estimated value falls far outside the ranges of variation for the next largest species of “condylarth” from Tiupampa, *Tiuclaenus cotasi* n. sp. and *Pucanodus gagnieri* Muizon & Marshall, 1991 (see below).

YPFB Pal 6135 can, therefore, be referred reasonably to *Tiuclaenus minutus* and we place *Kollpania tiupampina* Marshall & Muizon, 1988 in synonymy with *T. minutus* Muizon & Marshall, 1987. Ironically, however, Kollpaniidae Marshall *et al.* 1990 – a taxon created to contain what was considered to be an aberrant marsupial represented by a species known by a single, non-

diagnostic tooth now found to belong to a previously described species – represents the first suprageneric taxon containing South America’s endemic Mioclaenidae. Therefore, Kollpaniinae Marshall, *et al.*, 1990 is the senior synonym of Molinodinae Bonaparte *et al.*, 1993. This example illustrates the hazards of basing higher taxa on poorly known species.

DESCRIPTION

In the following sections, the three species of *Tiuclaenus* will be described first. Although the discussion will concern the three taxa together, it will in fact refer mainly to qualities of the genus *Tiuclaenus* in general.

Upper dentition (Fig. 7C-E; Table 4)

Upper molars. The maxilla with M1-3 (MHNC 1240) referred by Muizon & Marshall (1991) to *Pucanodus* is regarded here as belonging to *Tiuclaenus minutus* [following Muizon & Brito (1993) and Bonaparte *et al.* (1993)]. This interpretation was made possible by the discovery of a new maxilla with M1-3, which more likely represents *Pucanodus* because of its size, close occlusal relationship to the lower molar dentition, and morphological appropriateness. M2 of MHNC 1240 is nearly identical to the M2 (YPFB Pal 6119) initially referred to *T. minutus*, also favouring the current arrangement.

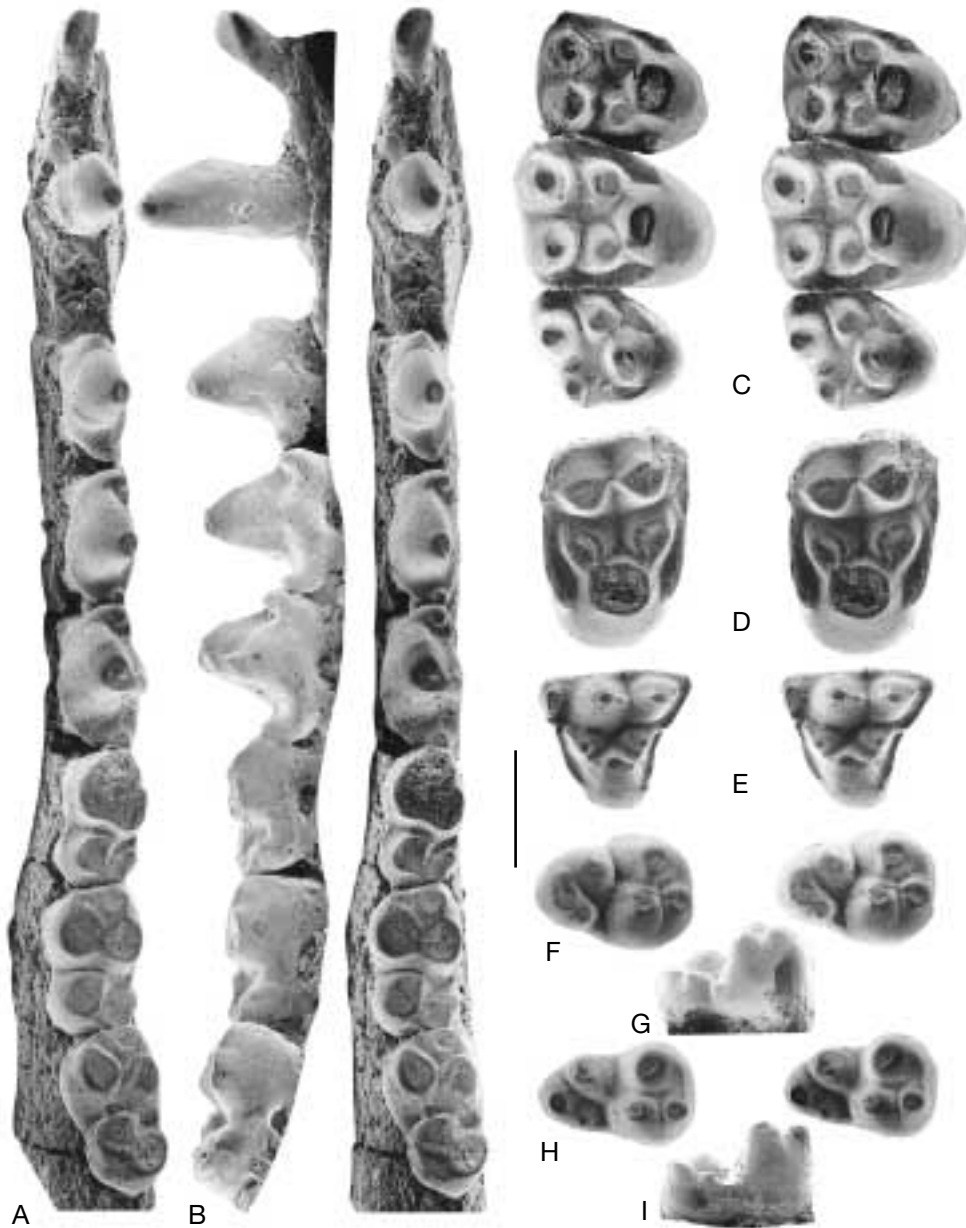


FIG. 7. — *Tiuclaenus minutus*, upper and lower dentition; **A**, left mandible with i2, c, p2-m3 (cast of YPFB Pal 6115, holotype) in occlusal view; **B**, the same in medial view; **C**, partial right maxilla with M1-M3 (cast of MHNC 1240) in occlusal view; **D**, right M2 (cast of YPFB Pal 6119) in occlusal view; **E**, left dP4 (holotype of *Kollpania tiupampina* cast of YPFB Pal 6135) in occlusal view; **F**, left m3 (cast of MHNC 8335) in occlusal view; **G**, the same in medial view; **H**, left m3 (cast of MHNC 1252) in occlusal view; **I**, the same in medial view. A, C-F, H, stereopairs. Scale bar: 2 mm.

TABLE 4. — Measurements (mm) and descriptive statistics of the upper dentition of *Tiuclaenus minutus*.

Measurement	N	Min	Max	Mean	CV
M1 L	3	2.23	2.41	2.31	0.040
M1 W	3	2.99	3.09	3.04	0.023
M2 L	2	2.45	2.48	2.47	0.009
M2 W	2	3.52	3.58	3.55	0.012
M3 L	2	1.90	2.06	1.98	0.057
M3 W	1	2.83	2.83	2.83	1.000

M1 and M2 each (Fig. 7C, D) bear five well-defined cusps that are clearly separated from one another. The protocone is the largest and is almost twice as large as the paracone. It forms alone the lingual third of the crown. Its lingual edge slopes gently (rather than subvertically) toward the maxilla, so that its apex occupies a relatively labial position. The cusp is linked to the conules by short and low pre- and postprotocrista. The paraconule is slightly larger than the metaconule. The conules are not connected to the styles by conular cristae, and therefore are totally separated from the para- and metacones by a conspicuous anteroposterior valley. On YPFB Pal 6119, however, a small inflation of the antero- and posterolabial edges of the para- and metaconules respectively, represent slight remnants of the preparaconular and postmetaconular cristae. The paracone is slightly larger in height and volume than the metacone on M2, but the two cusps are subequal on M1. The metacone is slightly lingual to the paracone on M2 but not on M1. The centrocrista is very low and rounded. Weak preparaconular and postmetacristae connect the apices of the para- and metacone to the para- and metastyles, respectively. The latter are small and perfectly aligned with para- and metacone; that is, they are anteroposteriorly aligned. They are connected to the protocone by strong pre- and postcingula, which are thickened in their lingual portion dorsal to the pre- and postprotocrista. They do not contact on the lingual side of the protocone, and the postcingulum does not develop any kind of swelling that might be interpreted as an incipient hypocone. The quadrangular morphology of the M1-2 is essentially the result of the large size of the conules and protocone.

There is neither labial cingulum nor labial rim. The trigon basin is small and mostly filled by the inflated postero- and anterolabial angles of the para- and metaconules, respectively; however, internal conular crests (premetaconular and postparaconular cristae) are lacking. The infilling of the trigon basin and distribution of cusps produces a characteristic, cross-like pattern on M2. This condition is not so conspicuous on M1 because of the smaller size of the conules and the consequently larger trigon basin.

M2 also differs from M1 in its larger size and in being slightly asymmetrical. This character is faint on YPFB Pal 6119, which is probably an individual variation.

M3 (Fig. 7C) is much smaller than M1 and M2. It is strongly asymmetrical, a morphology that results from reduction of the metacone and metaconule. In fact, the latter is totally fused to the postcingulum. The paracone of M3 is almost as strong as that of M2, but its metacone is smaller than the metaconule of M1. On M3, the para- and metacones are not linked by a centrocrista. The protocone is still the largest cusp of the tooth, but it is slightly smaller than that of M1. Its lingual side slopes lingually and its apex is in a relatively labial position. A strong precingulum is present and joins the anterior base of the protocone to the small parastyle. The latter is aligned with para- and metacone and the minute metastyle. The paraconule is large and bears a small but clear preparaconular crista, which connects to the precingulum at the level of the anterolingual angle of the paracone. The trigon basin is relatively wide compared to that of M2 because of reduction of the metaconule.

TABLE 5. — Measurements (mm) and descriptive statistics of the lower dentition of *Tiulaenus minutus*.

Measurement	N	Min	Max	Mean	CV
p2 L	1	2.11	2.11	2.11	1.000
p2 W	1	1.18	1.18	1.18	1.000
p3 L	2	2.31	2.35	2.33	0.012
p3 W	2	1.29	1.33	1.31	0.022
p4 L	2	2.48	2.64	2.56	0.044
p4 W	2	1.46	1.56	1.51	0.047
m1 L	1	2.37	2.37	2.37	1.000
m1 tri W	1	1.43	1.43	1.43	1.000
m1 tal W	1	1.41	1.41	1.41	1.000
m2 L	2	2.53	2.53	2.53	0.000
m2 tri W	2	1.75	1.80	1.78	0.020
m2 tal W	2	1.52	1.64	1.59	0.040
m3 L	3	2.61	2.83	2.70	0.043
m3 tri W	3	1.67	1.93	1.79	0.074
m3 tal W	3	1.29	1.44	1.36	0.055

Lower dentition (Fig. 7A, B, F-I; Table 5)

Lower incisor and canine. Only one lower incisor (Fig. 7A, B) is known, on the holotype. The i2 is a small, spatulate, and procumbent tooth. It is anteroposteriorly compressed and its crown is higher than wide. Its anterior face is strongly convex while its posterior face is more or less flat. In occlusal view, its apex is slightly arcuate posteriorly. There is no diastema, either between the incisors or between i3 and the canine.

The canine (Fig. 7A, B) is small and has a low crown that is approximately as high as the p2. It possesses a rounded apex. In lateral view, the anterior face of the tooth is convex and the posterior face is almost rectilinear in continuation to the portion of the root external to the dentary. In anterior view, the canine is slightly recurved lingually.

Lower premolars. The premolars are relatively low. The p1 is known only by its single alveolus, which has a subcircular outline and is clearly smaller than that of the canine. On the three premolars known (p2, p3, p4), the crown is longer than high (Fig. 7A, B). The p2 has a simple main cusp (protoconid) that is slightly recurved lingually. Its anterior base bears a very slight bulge and its posterior base has a minute talonid cusp. The p3 is longer and higher than p2. Its main cusp is more recurved lingually, and its lingual side is more concave than on p2. The p3 bears a clear anterolingual cusp (paraconid) and a small posterolingual talonid cusp. The p4 is more mas-

sive, longer, wider, and slightly higher than the two other premolars. It differs from p3 mainly in the presence of a small but high metaconid fused to the posterolingual angle of the protoconid. The metaconid is distinguishable only as a slight swelling on the lingual side of the protoconid, and a corresponding anterior sulcus. The anterior (paraconid) and posterior (talonid) cusps are well-developed and larger than on p3. The talonid is represented by a single cusp as on p3.

Lower molars. The molars (Fig. 7A, B, F-I) are relatively gracile for a mioclaenid. The m1 is approximately 7% shorter but nearly 20% narrower than the m2 and differs from the latter in having a trigonid that is narrower than the talonid. The trigonid is wider than the talonid on m2-3. The three molars have a trigonid that is higher and, for m1-2 only, longer than the talonid. On m3, talonid and trigonid have approximately the same length. The lower molars have a very weak precingulid but no postcingulid. The m1 of the holotype is the only one known for *T. minutus*. It is too worn to be informative as regards the cusp morphology and organization. However, the m2 is in better condition and its structure appears to be similar to that of m1. The trigonid possesses a large protoconid that forms the labial half of the trigonid. Lingually the metaconid is almost as large as the protoconid and is located slightly posterior to it. The paraconid is located anterolabial to the metaconid and merged

to it at its base. It is large for a mioclaenid paraconid but is considerably smaller than the protoconid. The paracristid is relatively worn on the m2 of the holotype, but it can be observed on the m3 (MHNC 8335). It is rather short; its transverse length comprises only about half of the width of the trigonid. The paracristid is deeply arched posteriorly and has the same configuration as observed in *Molinodus*: the preprotocristid is directed anteriorly and forms a rounded right angle at the anterolabial corner of the tooth, where it turns lingually before ascending posteriorly up the face of the paraconid. The trigonid basin is difficult to observe on the m2 of the holotype because of wear. This basin is small on the three m3s known. It has a trihedron shape, but the angle between the proto-paraconid and proto-metaconid valleys is larger than the two others and the angle between the proto-metaconid and para-metaconid valleys is almost 90°. Furthermore, the proto-paraconid valley is much longer than the two others. The protocristid is short and deeply notched in posterior view. The talonid has a very large hypoconid that is only slightly smaller than the protoconid. The cristid obliqua is low and rounded. It connects the anterolingual edge of the hypoconid to the posterolabial edge of the metaconid. The presence of a cristid obliqua on m3 is variable since it is absent on MHNC 8335. The hypoconulid and entoconid are smaller than the hypoconid but the hypoconulid is clearly larger than the entoconid on m1-2. The entoconid is not observable on the m3 of the holotype because of wear of the tooth. The hypoconulid has a subcircular cross-section and the entoconid is only slightly compressed in an anterolabial-posterolingual direction. Both cusps are fused at their bases. The talonid basin is partially filled by the swollen hypoconid labially and is reduced to an oblique groove that is open lingually, with a posterolabial-anterolingual orientation. On m3 the talonid is narrower, and the hypoconulid is larger than on m1-2. There is no entocristid.

Deciduous dentition (Fig. 7E)

One upper deciduous premolar, the holotype of *Kollpania tiupampina* (YPFB Pal 6135), is referred to *T. minutus* (see above). The tooth is

very low-cusped and almost forms an equilateral triangle in occlusal outline. The labial edge is subrectilinear, the anterior is slightly convex, and the posterior slightly concave. The protocone is large but gracile and in posterior view is recurved labially. The pre- and postprotocristae are short and link its apex to the relatively large conules. The latter are subconical and the paraconule is slightly larger in height and volume than the metaconule. The para- and metaconules are in an anterior position with respect to the para- and metacones. This position is a characteristic of deciduous teeth; for example it is present on the dP4 of *Promioclaenus acolytus* and the dP4 of the Tiupampian pantodont, *Alcidedorbignya inopinata*. As is observed on the molars, the conules do not have postparaconular and premetaconular cristae. The postmetaconular crista is sigmoid and joins the metastyle labially. Contrary to the condition observed on the molars, the postcingulum does not contact the postmetaconular crista, although it is very close to it, posterior to the posterolabial angle of the metaconule. The postcingulum is relatively thick. It almost reaches the posterolingual angle of the protocone lingually but remains at the base of the cusp. The preparaconular crista is weaker than the postmetaconular crista. It does not contact the precingulum, which is continuous from the anterior base of the protocone to the parastyle. In fact, as explained below, the precingulum “captures” the paracingular portion of the preparaconular crista and, in the case of YPFB Pal 6135, separates the two portions. The parastyle is very large and contrasts with the condition observed on the molars. However, this is not surprising because, as mentioned by West (1971), the styles of dP4s are generally more developed than on the molars. As is observed on the molars, the paracone is higher and more voluminous than the metacone. On the labial edge of the tooth there is no labial cingulum, but a tiny cuspule is present between the para- and metacones.

Dentary

The dentary (holotype) is gracile and its horizontal ramus is low. Its depth increases regularly from the anterior region to the level of m1 where it reaches its maximum elevation (4.4 mm). It

decreases slightly below m3. The ventral border of the horizontal ramus is regularly convex while the alveolar border is almost straight. Beneath the ascending ramus, adjacent to the anteroventral corner of the masseteric fossa, the ventral border ascends as it extends posteriorly, unlike the condition in *Molinodus*, where it is relatively straight. There are four small mental foramina, each one placed below the root of p1, the anterior root of p2, posterior root of p3, and anterior root of p4. On the medial face of the bone, the symphysis is an elongated surface slightly widened below the root of p1. Its posterior extremity is below the posterior root of p2. The symphysis is considerably less massive than in *Molinodus*, particularly posteriorly, where it tapers out more gradually. The vertical ramus is only partially preserved and shows the anterior region of the coronoid process and masseteric fossa. The latter is well-excavated, and its anterior border is a subvertical pillar with a triangular cross-section. The anterior border of the coronoid process, forms an angle of approximately 100° with the alveolar border. The anterior extremity of the coronoid process begins about a half a molar's length posterior to the talonid of m3.

Tiuclaenus cotasi n. sp.

HOLOTYPE. — MHNC 1231, a left mandible fragment with p3-m3.

HYPODIGM. — The holotype, MHNC 1232, left dentary fragment with m3; MHNC 1235, partial right dentary with p4-m1; MHNC 1236, left dentary fragment with m2-3; MHNC 1251, right m3; MHNC 1253, right dentary fragment with p3-4; MHNC 1254, right dentary fragment with m3; MHNC 1255, right m1; MHNC 1256, left m2; MHNC 1257, right M3; MHNC 1259, right m1; MHNC 1262, left m3; MHNC 1263, left m1; MHNC 1267, right M1, incomplete; MNHC, 1270, right M2 lacking the protocone; MHNC 1271, right M3; MHNC 1272, right M3; MHNC 8272, mandible fragment with m2; MHNC 8273, left dentary with p4-m3; MHNC 8336, left m1; MHNC 8341, right maxilla with P2-M2; MHNC 8342, left M2; MHNC 8347, left P4.

TYPE LOCALITY. — All specimens except MHNC 1236 are from site 1, the "quarry" at Tiupampa as defined by Muizon & Marshall 1992. MHNC 1236 is from site 5 at Tiupampa.

HORIZON AND AGE. — Santa Lucía Formation; Tiupampian (early Palaeocene), approximately equivalent

to the Puercan of North America (Muizon & Brito 1993; Bonaparte *et al.* 1993; Muizon 1998; see Archibald *et al.* 1987 and Eberle & Lillegraven 1998 for definition, age, and subdivision of the Puercan land-mammal age).

ETYMOLOGY. — For the Cotas, indigenous people of the region prior to arrival of the Incas.

DIAGNOSIS. — *Tiuclaenus cotasi* differs from *T. minutus* in the following features: larger size; upper molars more transverse, with a labial rim and protocone placed more posteriorly; lower premolars slightly more robust with a smaller metaconid on p4; m1-2 hypoconulid more anteroposteriorly compressed and subequal to or only slightly larger than entoconid; m3 proportionately longer. *T. cotasi* differs from *T. robustus* in its smaller size, more transverse M2, and narrower lower molars.

DESCRIPTION

Upper dentition (Fig. 8; Table 6)

Upper premolars. The P2 (Fig. 8A) is relatively short anteroposteriorly and bears a single cusp (paracone). The anterior edge of the paracone is steep and does not bear any basal cusps. The posterior edge of the paracone is more inclined and probably (the only P2 known is worn) has a small cusp at its base.

The P3 (Fig. 8A) has an outline that almost forms an equilateral triangle because of the presence of a small protocone. The paracone is relatively massive and is flanked anteriorly and posteriorly with small para- and metastyles, respectively. The styles are slightly labial to the paracone, and the anterior and posterior angles of the tooth are swollen labially. The anterior border of the tooth is weakly concave but the posterior is straight.

The P4 (Fig. 8A, B) is much more transverse mainly because of the large size of the protocone. As on P3 the anterior border is concave and the posterior is straight. The metastyle is slightly more labial than the parastyle. The paracone is approximately the same size as that of P3. The P4 of MHNC 8341 is very worn but MHNC 8347 is a fresh P4. The anterior border of the paracone is rounded and does not bear any crista, whereas a sharp postparacrista connects its apex to the metastyle. The protocone is clearly recurved labially (in anterior view). There are no conules even incipiently

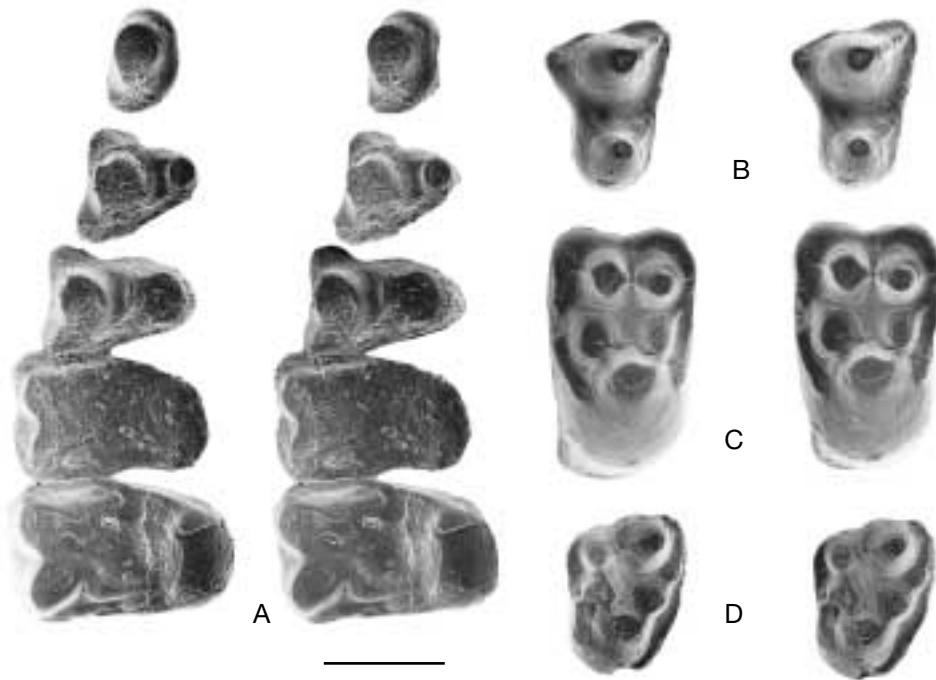


FIG. 8. — *Tiucloaenus cotasi*, upper dentition; **A**, partial right maxilla with P2-M2 (cast of MHNC 8341), in occlusal view; **B**, left P4 (cast of MHNC 8347) in occlusal view; **C**, left M2 (MHNC 8342) in occlusal view; **D**, right M3 (cast of MHNC 1271) in occlusal view. Stereopairs. Scale bar: 2 mm.

developed. No precingulum is observed, but the posterior base of the protocone bears a weak rim that connects the labial extremity of the postprotocrista to the posterolingual base of the protocone.

Upper molars. The M1 (Fig. 8A) of MHNC 8341 is the only one known and its coronal features have been almost completely obliterated by wear. However, it is possible to note that this tooth was very transverse and that the protocone was slightly deflected posteriorly. Furthermore, the labial edge of the tooth bears a thick labial rim, which is a small cingulum labial to the metacone.

The M2 (Fig. 8A, C) is badly worn on MHNC 8341, but MHNC 8342 is well-preserved. The tooth is much more transverse than the M2 of *T. minutus*, essentially because of the lingual projection of the lingual side of the protocone. The cusp is very inflated and forms more than the lingual third of the tooth. In anterior view, the protocone is asymmetrical; its lingual side is much

steeper than the labial face, and its apex has a very labial position. The pre- and postprotocristae are small and low and the conules are large, although slightly smaller than in *T. minutus*. As a consequence of this condition, the trigon basin is slightly more open than in *T. minutus*, and is star-shaped rather than cross-shaped. There is no prepraconular crista, and a weak, short, and low postmetaconular crista links (albeit barely) the posterolabial angle of the metaconule to the labial third of the postcingulum. Pre- and postcingula are strong and connect the anterior and posterior bases of the protocone to the para- and meta-styles, respectively. Because of the posterior shifting of the protocone, the lingual extremity of the postcingulum is slightly more labial than that of the precingulum. The lingual extremities of the pre- and postcingula are slightly but equally thickened, and there is no hypocone, even incipiently developed. The styles are relatively thick when compared to those of *T. minutus* and are located slightly lingual to the para- and meta-

TABLE 6. — Measurements (mm) and descriptive statistics of the upper dentition of *Tiuclaenus cotasi*, n. sp.

Measurement	N	Min	Max	Mean	CV
P2 L	1	1.81	1.81	1.81	1.000
P2 W	1	1.34	1.34	1.34	1.000
P3 L	1	2.07	2.07	2.07	1.000
P3 W	1	2.01	2.01	2.01	1.000
P4 L	1	1.93	1.93	1.93	1.000
M1 L	3	2.28	2.58	2.41	0.063
M1 W	2	3.51	3.74	3.63	0.045
M2 L	3	2.45	2.58	2.52	0.026
M2 W	3	3.75	4.02	3.85	0.039
M3 L	2	2.02	2.15	2.09	0.044
M3 W	1	2.77	2.77	2.77	1.000

cones, respectively. From each style descends a thick rim that borders the antero- and postero-labial edges of the para- and metacones. The metacone rim is thicker than the paracone rim. On MHNC 1270 (an M2 lacking the lingual side of the protocone), the metastylar rim is extremely salient labially and develops a small labial cusp. Because those rims do not meet in the middle of the labial edge of the tooth there is a small ectoflexus. Rims and ectoflexus are absent in *T. minutus*. The paracone is slightly higher and more voluminous than the metacone but this difference in size is much less conspicuous than in *T. minutus*. A well-marked valley separates the conules from the para- and metacones. The latter are connected by a weak centrocrista, straight in occusal view and V-shaped in labial view. The point of contact of the cusps on the centrocrista is located more dorsally than in *T. minutus*, which means that the para- and metacones are more closely appressed than in the smaller species.

The M3 (Fig. 8D) of *Tiuclaenus cotasi* shows the characteristic reduction of the metacone and metaconule. As generally observed on the M3 of the "condylarths" from Tiupampa, the paraconule and, occasionally, the metaconule have a well-developed preparaconular (or postmetaconular) crista joining the precingulum (or postcingulum). The labial edge of the tooth is damaged on the three known specimens; however, it is possible to observe that the anterolabial side of the paracone was swollen as is observed on M2.

Lower dentition (Fig. 9, Table 7)

The lower teeth are known from p3 to m3.

Lower premolars. The general pattern of the premolars is similar to that of *T. minutus*. However, the p3 of *T. cotasi* differs from that of *T. minutus* in having a higher and shorter protoconid (Fig. 9A, B).

The p4 (Fig. 9A, B) is taller and shorter than that of *T. minutus*. It is more robust and the metaconid is smaller, perhaps partially obliterated by the inflation of the tooth. The most striking difference between the two species is the size disparity between p4 and m1 when compared to *T. minutus*. The m1 of *T. cotasi* is proportionately much larger, especially in width, when compared to p4 than in *T. minutus*. In other words, the p4s of the two species are approximately the same size but the m1 of *T. cotasi* is about 25% wider than that of *T. minutus*.

Lower molars. The m1 (Fig. 9A-F) of *T. cotasi* has a basic pattern very similar to that of *T. minutus* although it is proportionately wider. Morphologically, the m1 of *T. cotasi* is rather similar to m2 of *T. minutus*. The trigonid is generally slightly narrower than the talonid on most specimens or subequal in width (on m2 the trigonid is always wider than the talonid). The major morphological difference between the two species is the compression and slightly smaller size of the hypoconulid of *T. cotasi*. In that species, the hypoconulid is generally subequal to the entonconid, while it is larger and relatively more conical in *T. minutus*.

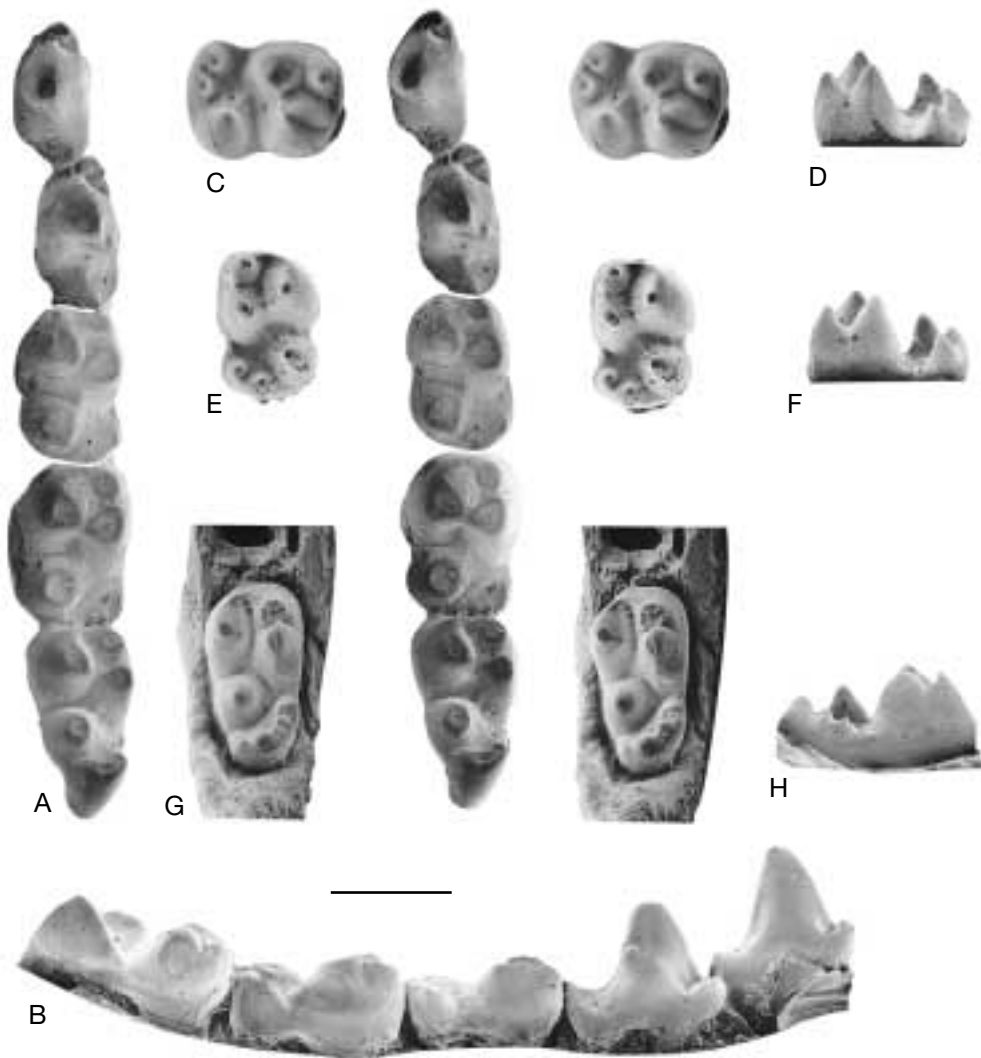


FIG. 9. — *Tiulaenus cotasi*, lower dentition; **A**, partial left dentary with p3-m3 in occlusal view (cast of MHNC 1231, holotype); **B**, the same in medial view; **C**, right m1 or m2 (cast of MHNC 1255) in occlusal view; **D**, the same in medial view; **E**, right m1 in occlusal view (cast of MHNC 1259); **F**, the same in medial view; **G**, left m3 in occlusal view (cast of MHNC 1232); **H**, the same in medial view. A, C, E, G, stereopairs. Scale bar: 2 mm.

The m2 (Fig. 9A-D) differs from m1 in its larger size and in the fact that its trigonid is clearly wider than the talonid. The protoconid, the largest cusp of the tooth, is slightly larger than the metaconid. The trigonid basin is essentially reduced to an anteroposterior groove formed by long proto-paraconid and small proto-metaconid grooves. The metaconid is slightly posterior to

the protoconid and its posterior face is projected posteriorly. It partially fills the talonid basin that is, in fact, reduced to an oblique groove open lingually.

The m3 (Fig. 9A, B, G, H) has a smaller trigonid than m2 as well as a narrow talonid that is elongated because of the increase in size (especially anteroposteriorly) of the hypoconulid. The ento-

TABLE 7. — Measurements (mm) and descriptive statistics of the lower dentition of *Tiuclaenus cotasi*, n. sp.

Measurement	N	Min	Max	Mean	CV
p3 L	1	2.42	2.42	2.42	1.000
p3 W	1	1.26	1.26	1.26	1.000
p4 L	3	2.18	2.51	2.29	0.082
p4 W	3	1.56	1.63	1.59	0.022
m1 L	7	2.33	2.64	2.47	0.042
m1 tri W	7	1.70	2.01	1.82	0.057
m1 tal W	6	1.79	1.92	1.85	0.030
m2 L	5	2.71	2.80	2.76	0.015
m2 tri W	5	1.99	2.19	2.12	0.048
m2 tal W	5	1.73	2.07	1.92	0.071
m3 L	7	2.86	3.21	3.00	0.050
m3 tri W	6	1.67	2.11	1.85	0.080
m3 tal W	7	1.31	1.56	1.46	0.065

conid often bears a slight entocristid on its anterior face, but the talonid basin is never closed. The third lower molar of *T. cotasi* has a small precingulid but no postcingulid.

Dentary

The dentary is stouter than in *T. minutus* but not significantly larger; as with *T. minutus*, it differs from the dentary of *Molinodus* in having a posteroventral border that is noticeably concave in lateral view. The height of the horizontal ramus is similar in the two species; maximum height of the horizontal ramus is 4.91 mm on MHNC 8273 and 4.74 mm on MHNC 1232, and is located below the trigonid of m2. On MHNC 8273, there is a well-marked mylohyoid groove below m1-3 but this structure is much weaker on the holotype. This weaker nature is certainly because MHNC 8273 represents a younger individual, as indicated by the significantly lesser degree of molar wear. The condyloid process is located well above the occlusal plane, and in this respect departs from a morphotype for Ungulatomorpha (see Nessov *et al.* 1998). The condyloid process is small and placed medial to the ascending ramus. Its articular facet faces posterolingually, is approximately as wide as long, and is broadly convex, with a tighter curvature laterally than medially. The masseteric fossa is deep but does not extend as far ventrally on the horizontal ramus as it does in *T. minutus*. The tip of the coronoid process is broken, but it is possi-

ble to note that it was fairly elevated and recurved posteriorly. Its anterior edge is abrupt and forms an angle of approximately 100° from the alveolar plane of the cheek teeth. The angular process is broken adjacent to the incurved posterior margin of the jaw, ventral to the condyle. However, it is probable that it was much longer than high, as is observed in *Molinodus*, but contrary to the condition in primitive litopterns (e.g., *Miguelsoria*) in which it is large and wide. On the lingual side of the angular process (as preserved) there is no dorsally recurved ridge for attachment of the *pterygoideus medialis* muscle as in *Molinodus* and *Simoclaenus*. The notch between the condyle and the angular process is well-marked and deeper than in *Miguelsoria*.

Tiuclaenus robustus n. sp.

HOLOTYPE. — MHNC 1233, left dentary fragment with m2-3.

HYPODIGM. — The holotype; MHNC 1234, right dentary fragment with m1-2; MHNC 1246, right lower p3; MHNC 1264, right M2; MHNC 1266, right maxilla fragment with P3-4; MHNC 8331, left M3 (lacking the labial edge of the para- and metacones).

TYPE LOCALITY. — Site 1 ("the quarry") at Tiupampa, Cochabamba Department, Bolivia.

HORIZON AND AGE. — Santa Lucía Formation; Tiupampian (early Palaeocene), approximately equivalent to the Puercan of North America (Muizon &

Brito 1993; Bonaparte *et al.* 1993; Muizon 1998; see Archibald *et al.* 1987 and Eberle & Lillegraven 1998 for definition, age, and subdivision of the Puercan land-mammal age).

ETYMOLOGY. — *Robustus* (Latin), in allusion to the larger, more robust cheek teeth in comparison to other described species of the genus.

DIAGNOSIS. — Larger and more massive than the two other species of *Tiucloenus*; width differential between talonid and trigonid on m1-2 much greater than in *T. minutus* and *T. cotasi*. Upper molars larger and, especially, proportionally longer than in the two other species; also differs from them in the presence of a strong labial rim on M2.

DESCRIPTION

This species of *Tiucloenus* has large and robust molars, a feature especially obvious on M2 and m2.

Upper dentition (Fig. 10F, J; Table 8)

Upper premolars. The upper premolars are known by worn P3 and P4 only (Fig. 10G). The teeth have a morphological pattern apparently similar to that of *T. cotasi*, but they are slightly larger, anteroposteriorly longer, and stouter. The anteroposterior constriction separating the protocone from the paracone is less developed and the posterior edge of P4 is straight, whereas it is slightly concave in *T. cotasi*. The parastyle is more strongly developed and is slightly shifted labially. The metastyle is small, but its labial rim is well-developed. The protocone of P4 is large and bears a small paraconule on its anterolabial edge. No metacone is developed, even incipiently.

Upper molars. The only M2 (Fig. 10H-J) known is about 10% longer than its homologue in *T. cotasi* and 15% than in *T. minutus*; it is significantly less transverse than that of *T. cotasi*, being of similar width. The protocone is large and anteroposteriorly extended. As is observed in *T. cotasi*, the protocone is shifted posteriorly and the anterior edge of the tooth is convex whereas the posterior edge is straight. The pre- and postcingula are continuous from the anterior and posterior faces of the protocone to the para- and metastyles respectively. The paraconule is not connected to the precingulum by a preparaconular crista. The metaconule is too worn to allow this observation. The paracone is slightly higher

and more voluminous than the metacone. The styles are slightly labial to their respective cones. Para- and metacones bear, on their labial side an antero- and posterolabial rim and the posterior rim is thicker than the anterior. Therefore, the basic morphological pattern of the M2 of *T. robustus* is similar to that of the other species of *Tiucloenus*.

One incomplete M3 is known (Fig. 10J). It is slightly more transverse than the M3 of *T. cotasi*. With exception of this characteristic, the teeth of the two species are highly similar.

Lower dentition (Fig. 10A-E; Table 8)

The lower teeth are known by one p3 and the three molars.

Lower premolars. The p3 (Fig. 10E, F) is much larger than in *T. cotasi*. Its protoconid is lower and longer and is slightly recurved lingually. A very small paraconid cusp is observable at the base of the protoconid, and a single talonid cusp is present posteriorly. The tooth is transversely narrow.

Lower molars. The m1 (Fig. 10C, D) is significantly smaller than m2 (Fig. 10A-D). The size difference between the teeth is greater than in *T. minutus* and *T. cotasi*, more resembling what is observed in *Molinodus suarezi*. The m1 has a trigonid that is slightly narrower than the talonid. The contrary is true on the m2, with the trigonid being much wider on the holotype. On this specimen, the width difference between trigonid and talonid is closer to what is observed in *Molinodus*. Except for this feature and its larger size, the m2 of *T. robustus* is very similar to that of *T. cotasi*. The trigonid has a well-individualized protoconid but the main valley of the trigon basin is the para-protoconid valley. This condition indicates that (as is observed in *T. minutus* and *T. cotasi*) the paraconid is more appressed against the metaconid than in *Molinodus*. The paraacristid is strongly concave posteriorly. The metaconid is well-expanded posteriorly and its apex is slightly posterior to that of the protoconid. The large hypoconid is connected to the posterolabial edge of the metaconid by a weak cristid obliqua, which is almost absent on the holotype. The talonid is open lingually but, contrary to what is observed in *T. cotasi* and *T. minutus*, it is more transverse

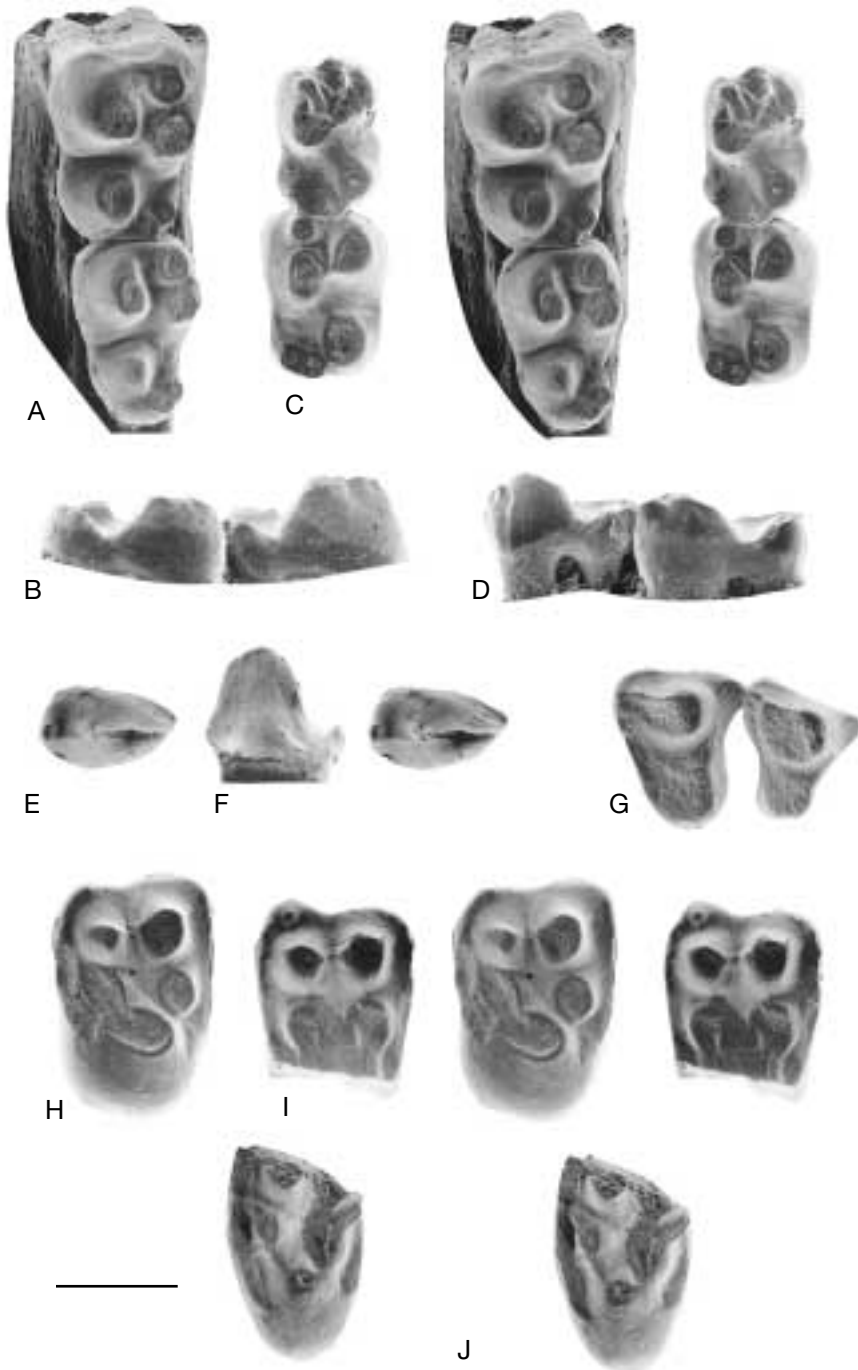


FIG. 10. — *Tiulaenus robustus*, upper and lower dentitions; **A**, partial left dentary with m2-3 in occlusal view (cast of MHNC 1233, holotype); **B**, the same in medial view; **C**, partial right dentary with m1-2 in occlusal view (cast of MHNC 1234); **D**, the same in medial view; **E**, right p2 in occlusal view (cast of MHNC 1246); **F**, the same in labial view; **G**, partial right maxilla with P3-4 in occlusal view (cast of MHNC 1266); **H**, right M2 in occlusal view (MHNC 1264); **I**, right M1 lacking the lingual portion of the protocone (cast of MHNC 1267); **J**, left M3 in occlusal view (cast of MHNC 831). A, C, E, F-I, stereopairs. Scale bar: 2 mm.

TABLE 8. — Measurements (mm) and descriptive statistics of the upper and lower dentitions of *Tiucloenus robustus*, n. sp.

Measurement	N	Min	Max	Mean	CV
p2 L	1	2.44	2.44	2.44	1.000
p2 W	1	1.57	1.57	1.57	1.000
m1 L	2	2.66	2.68	2.67	0.005
m1 tri W	2	1.86	1.93	1.90	0.026
m1 tal W	2	2.00	2.13	2.07	0.045
m2 L	2	2.94	3.16	3.05	0.051
m2 tri W	2	2.33	2.60	2.47	0.077
m2 tal W	2	2.06	2.13	2.10	0.024
m3 L	1	3.06	3.06	3.06	1.000
m3 tri W	1	2.03	2.03	2.03	1.000
m3 tal W	1	1.42	1.42	1.42	1.000
P3 L	1	2.19	2.19	2.19	1.000
P3 W	1	2.26	2.26	2.26	1.000
P4 L	1	2.15	2.15	2.15	1.000
P4 W	1	2.68	2.68	2.68	1.000
M1 L	2	2.62	2.88	2.75	0.067
M2 L	1	2.73	2.73	2.73	1.000
M2 W	1	3.85	3.85	3.85	1.000
M3 L	1	2.42	2.42	2.42	1.000

than oblique. This condition apparently is the result of the greater proximity of the hypoconulid and the entoconid, which are more closely appressed to one another. As in *T. cotasi*, the entoconid and the hypoconulid are subequal in size and connate. Neither precingulid nor postcingulid is present.

The m3 (Fig. 10A, B) is relatively small, as in the other species of *Tiucloenus* (it is relatively smaller than in *T. cotasi*), differing in this respect from *Molinodus*. Although the m2 is much larger than that of *T. cotasi*, the m3s of the two species are close in size. The m3 of *T. robustus* is approximately as long as the m2, whereas it is longer in *T. cotasi* and its trigonid is clearly narrower.

COMPARISONS OF *TIUCLAENUS*

Upper dentition

In the following section, the dental morphology of the three species of *Tiucloenus* will be compared to the same genera as those to which *Molinodus* was compared and with *Molinodus* itself. In fact, *Molinodus*, the “condylarth” genus of the Tiupampa fauna which retains the greatest number of plesiomorphic characters, is, in many respects, intermediate between some primitive North American “condylarths” (*Protungulatum*, *Mimatuta*) and *Tiucloenus*. Furthermore, because

Molinodus is a primitive mioclaenid, it will be regarded as a basic taxon for comparison with the more derived *Tiucloenus*.

Upper premolars. The P3-4 of *Tiucloenus* resemble those of *Molinodus* in having a greater protocone on P3 than in the North American mioclaenids, some didolodontids (*Paulacoutoia*, *Didolodus*) and primitive litopterns (*Asmithwoodwardia*). However, as in *Molinodus*, the protocone of P4 is shorter anteroposteriorly, smaller when compared to the paracone, and more gracile. Also, the P4 is more triangular than in the didolodontids in which the protocone is subequal in height and volume to the paracone and in which the P4 is more quadrangular. *Tiucloenus* is clearly more primitive than the didolodontids in the general morphology of the P4.

Upper molars. The cusps of the molars of *Tiucloenus* are extremely bulbous, a condition slightly more pronounced than in *Molinodus* and the North American mioclaenids. The premolars of *Tiucloenus*, however, are not as inflated as in this group of mioclaenids and the didolodontids. In this respect, *Tiucloenus* resembles *Molinodus*; the two genera, therefore, retain a plesiomorphic condition.

The cingular pattern of *Tiucloenus*, in which the pre- and postcingula are continuous from the

protocone to the styles (Fig. 5), is similar to that observed in most mioclaenids (*Promioclænus*, *Litaletes*, *Mioclænus*). Exceptions include *Choeroclænus* and *Protoselene*, both of which have a cingular pattern close to that observed in *Molinodus*. In *Protoselene* and *Molinodus*, the pre- and postcingula do not reach the styles labially and are not connected to the preparaconular and postmetaconular cristae (they are very close to the styles in *Molinodus*). The condition of *Tiucclaenus* is therefore more derived than that of *Molinodus* and resembles that observed in South American “condylarths” or primitive litopterns (*Paulacoutoia*, *Asmithwoodwardia*, *Lamegoia*, *Didolodus*, *Miguelsoria*, *Protolipterna*).

Tiucclaenus resembles *Molinodus*, the other South American “condylarths”, and primitive litopterns in lacking postparaconular and premetaconular cristae, which indicates a derived condition. *Tiucclaenus*, however, as in *Molinodus*, differs from the condition of North American mioclaenids, which clearly have small postparaconular and premetaconular cristae. This condition of the Tiupampa taxa is more derived and could represent a synapomorphy shared by South American “condylarths” and litopterns.

Tiucclaenus differs from *Molinodus* and the North American mioclaenids in lacking a continuous labial cingulum. This is a derived condition (see above), which apparently is absent in the other South American “condylarths” and early litopterns. The condition of *Tiucclaenus minutus* is especially characteristic because this species does not even bear antero- and posterolabial swellings found, with variable development, in *T. cotasi* and *T. robustus*.

The postcingulum of *Tiucclaenus* resembles the primitive condition of *Molinodus* in lacking hypocone. As in *Molinodus*, and contrary to the condition in North American mioclaenids, the lingual extremity of the postcingulum of *Tiucclaenus* is not thicker than that of the precingulum. The condition of the North American mioclaenids is regarded here as more derived than that of *Tiucclaenus*.

The pre- and postcingula of *Tiucclaenus* reach the anterior and posterior faces of the protocone at its base, and their extremities are at the same level in lingual view. This plesiomorphic (see above) con-

dition is similar to that observed in *Molinodus* and, in this respect, the North American mioclaenids are more derived than *Tiucclaenus*.

The small para- and metastyles of *Tiucclaenus*, almost aligned with the para- and metacone, resemble those of *Molinodus*, other South American “condylarths”, and primitive litopterns. This condition is derived when compared to that of *Protungulatum* and some North American mioclaenids (*Litaletes*, *Choeroclenus*, *Valenia*). Other North American mioclaenids resemble *Tiucclaenus* in having almost aligned styles (*Promioclænus*, *Mioclænus*). As mentioned above, it is noteworthy that in *Tiucclaenus* and *Molinodus* the styles are slightly shifted labially in a few specimens (more constantly, however, in the latter than in the former).

The M3 of *Tiucclaenus* is slightly reduced, i.e. it is narrower transversely than the M2. This represents a derived feature also present in *Promioclænus*, *Mioclænus*, *Ellipsodon*, and *Choeroclænus* (less so in this genus). This feature is absent (or not clearly present) from the other North American mioclaenids (*Litaletes*, *Protoselene*, *Valenia*). The condition of *Tiucclaenus* differs from that of *Molinodus*, in which the M3 is unreduced and apparently retains the plesiomorphic condition. In the other South American “condylarths” and primitive litopterns, the M3 is either unreduced (*Asmithwoodwardia*) or even enlarged (*Paulacoutoia*, *Didolodus*, *Protolipterna*, *Miguelsoria*). *Tiucclaenus* is probably more derived in this respect than *Asmithwoodwardia* but the condition of the other four South American “condylarths” and primitive litopterns is probably derived. Whether it represents a reversal from a *Tiucclaenus* pattern or derived character state from a *Molinodus* plesiomorphic condition is difficult to evaluate.

The conules of *Tiucclaenus* are more inflated than in *Molinodus* and the trigon basin is reduced and has a distinct cross-shaped morphology (best developed in *T. minutus*). The conules are located closer to the protocone than to the para- and metacones, which represent a derived condition also found in *Protungulatum* (see above). The derived condition is also present, although less pronounced, in the North American mioclaenids. The condition in the other South American

“condylarths”, and primitive litopterns, which approaches the plesiomorphic character state is probably a reversal due to the inflation of the conules. It is noteworthy, however, that in spite of the position of the conules (closer to the protocone), the polygon formed by the para- and metacones and the conules is longer than wide (not wider than long as in *Protungulatum*). The same condition is observed in *Molinodus*, in which, however, the conules are located slightly closer to the midline of the tooth than in *Tiucloaenus*.

Lower dentition

Lower premolars. A small metaconid is observed on the posterolingual side of the protoconid of the p4 of *Tiucloaenus* but not on p3. In this respect, *Tiucloaenus* resembles *Molinodus* and *Litaletes*. In the other North American mioclaenids, the inflation of p4 reduces the size of the metaconid, which is barely present. Younger South American “condylarths” and primitive litopterns have a clearly semi-molarized p4 with a metaconid as large as the protoconid and often totally lingual to it.

Lower molars. The trigonid of m2 of *Tiucloaenus* differs from that of *Molinodus* in having a paraconid more appressed against the metaconid. This condition results in a different morphology of the trigonid basin, which has a reduced parametaconid valley and an enlarged para-protoconid valley. In this respect, *Tiucloaenus* resembles the condition of North American mioclaenids. It is more derived than *Molinodus* (and apparently *Escribania*), which has the plesiomorphic trihedron shape present in *Protungulatum*, *Mimatuta*, and “zhelestids”. It is more primitive than didolodontids, where the trigonid basin is reduced to an approximately anteroposterior or slightly oblique median valley (*Paulacoutoia*, *Ernestokokenia*, *Didolodus*) or to a simple pit (*Asmithwoodwardia*).

The trigonid of m2 of *Tiucloaenus* is generally slightly wider than (but can be as wide as) the talonid. Therefore, the condition of *Tiucloaenus* would be more derived than that of *Molinodus* and *Escribania* (which have a trigonid wider than the talonid), but resembles the North American mioclaenids. It is apparently more primitive in

this respect than the didolodontids and primitive litopterns, where the trigonid is generally narrower than (sometimes as wide as) the talonid. However, as mentioned above, this feature is fairly variable and its polarity is not securely established.

The m3 of *Tiucloaenus* is slightly reduced and in this respect approaches the condition observed in some North American mioclaenids (*Promioclauenus*, *Mioclauenus*, *Choeroclauenus*). *Molinodus*, didolodontids and primitive litopterns generally do not have a reduced m3 and, in this respect, would be more primitive than *Tiucloaenus*. However, as noted for the M3, it is probable that the m3 of several South American ungulates is enlarged (*Escribania*, *Paulacoutoia*, *Lamegoia*, *Didolodus*, *Ernestokokenia*, *Miguelsoria*, *Protolipterna*).

As in *Molinodus*, the lower molars of *Tiucloaenus* have a metaconid which is posterior to the protoconid and expanded posteriorly. This feature is not observed to such an extent in most North American mioclaenids but it is well-developed in the other South American “condylarths” and in primitive litopterns. As a consequence, the protocrista is clearly oblique, sometimes concave posteriorly (*Tiucloaenus*, *Andinodus*, most specimens of *Molinodus*, *Simoclaenus*, *Escribania*). Among North American mioclaenids, *Bubogonia* (*B. saskia*) has a metaconid clearly posterior to the protoconid, but in this genus the protocristid is straight.

Genus *Pucanodus* Muizon & Marshall, 1991

TYPE SPECIES. — *Pucanodus gagnieri* Muizon & Marshall, 1991.

DIAGNOSIS. — Same as for the species.

Pucanodus gagnieri Muizon & Marshall, 1991

HOLOTYPE. — MHNC 1239, a right dentary with p3-m3.

HYPODIGM. — The holotype; MHNC 1230, fragment of right dentary with c, p2-m1; MHNC 1235, fragment of right dentary with p4-m1; MHNC 1242, fragment of left maxilla with P3-4 (referred to cf. *Mimatuta* by Muizon & Marshall 1991); MHNC

1265, left M2; MHNC 1267, right M2; MHNC 1268, right M1; MHNC 1269, left M2; MHNC 1271, right M3; MHNC 1272, right M3; MHNC 8271, fragment of maxilla with M1-2; MHNC 8338, left P3; MHNC 8340, right M1; MHNC 8343, fragment of right maxilla with M1-3.

TYPE LOCALITY. — The holotype and MHNC 8344 were discovered at site 2 of the locality of Tiupampa as defined by Muizon & Marshall (1992). The other specimens come from the site 1, the "quarry".

HORIZON AND AGE. — Santa Lucía Formation; Tiupampian (early Palaeocene), approximately equivalent to the Puercan of North America (Muizon & Brito 1993; Bonaparte *et al.* 1993; Muizon 1998); see Archibald *et al.* (1987) and Eberle & Lillegraven (1998) for definition, age, and subdivision of the Puercan land-mammal age.

DIAGNOSIS. — Small-sized mioclaenid differing from *Tiuclaenus* in the proportion of its lower molars and premolars, which are shorter and wider; in particular the m3 presents a shorter talonid than in any other Tiupampa "condylarths". The p4 bears a small metaconid on the lingual side of the protoconid. The lower molars have a well-developed paraconid, and the entoconid is fused to hypoconulid to form a posterolingual crest. Upper molars are devoid of hypocone and bear a clear labial rim (but no true cingulum), thickened labial to the para- and metastyles. As in *Tiuclaenus*, but contrary to what is observed in *Molinodus*, the pre- and postcingula reach the styles labially. *Pucanodus* differs from *Molinodus* and *Tiuclaenus* in having a straight labial edge of M1-2 and salient styles, which give a quadrate morphology to the labial side of the upper molars. The preparacunar and postmetaconular cristae connect the pre- and postcingula at the level of the valley separating the para- and metacone. M3 is not reduced and is as wide as M1.

DESCRIPTION

Upper dentition (Fig. 11; Table 9)

One maxilla fragment with M1-3 (MHNC 8343) has been referred to *Pucanodus* because it fits in size more closely with the holotypic mandible. Because the specimens are contralateral jaws it was not possible to observe their occlusion directly. Therefore, we have compared the length of apex of protocones of M1-M3 to length of bottom of talonid of m1-3, which appeared to be identical. Furthermore, the molars of MHNC 8343 are slightly larger than the M1-2 referred to *T. cotasi*, clearly larger than the maxilla referred to *T. minutus* and much smaller than the M2 referred to *T. robustus*. Finally, the M1-2 are less

transverse than in *T. cotasi* and *T. robustus*. The maxilla fragment referred to cf. *Mimatuta* by Muizon & Marshall (1991) is here referred to *Pucanodus* mostly because the premolars are slightly larger than those observed on the maxilla referred to *T. cotasi* (see above) and slightly smaller than those referred to *T. robustus*. However, it is noteworthy that some variation has been observed in the tooth morphology and size of *Molinodus* and *Tiuclaenus*, and referral of these specimens has to be confirmed by discovery of associated dentitions.

Upper premolars. The P3 (Fig. 11B) has a large paracone, three times longer and twice as tall as the small protocone. The anterior edge of the paracone is rounded. Its posterior edge is a sharp crest, which connects the apex to the metastyle. The protocone is very short anteroposteriorly and its apex is recurved labially. A weak preprotocrista connects the anterolabial angle of the protocone to the anterior base of the paracone or to the parastyle. The posterior edge of the paracone does not present a metacone even incipiently developed. The styles are well-developed. The parastyle is a well-individualized small cusp anterior to the paracone, and the metastyle is shifted labially. Both the anterior and posterior edges of the tooth are concave. There are no cingula.

The P4 (Fig. 11B) is a triangular tooth that is slightly shorter than P3 but more transverse. It has a paracone subequal in size to that of P3 but the protocone is much more expanded lingually and anteroposteriorly. The apex of the protocone is recurved lingually. The protocone is linked to the styles by thin pre- and postprotocristae, and the preprotocrista is more developed than the postprotocrista. A hint of postcingulum is present at posterior base of the protocone. The lingual face of the paracone is less vertical than in P3, and therefore its apex is shifted lingually. Anteriorly, a sharp and well-individualized parastyle is present, but there is no preparacrista. The metastyle is large and massive. It is connected to the apex of the paracone by a strong postparacrista, very concave labially. The metastyle is clearly shifted labially.

Upper molars. On the unworn specimens of molars (MHNC 1268 and 8340, M2s) (Fig. 11D, E), the cusps are fairly sharp and appear to be less inflated in general than in

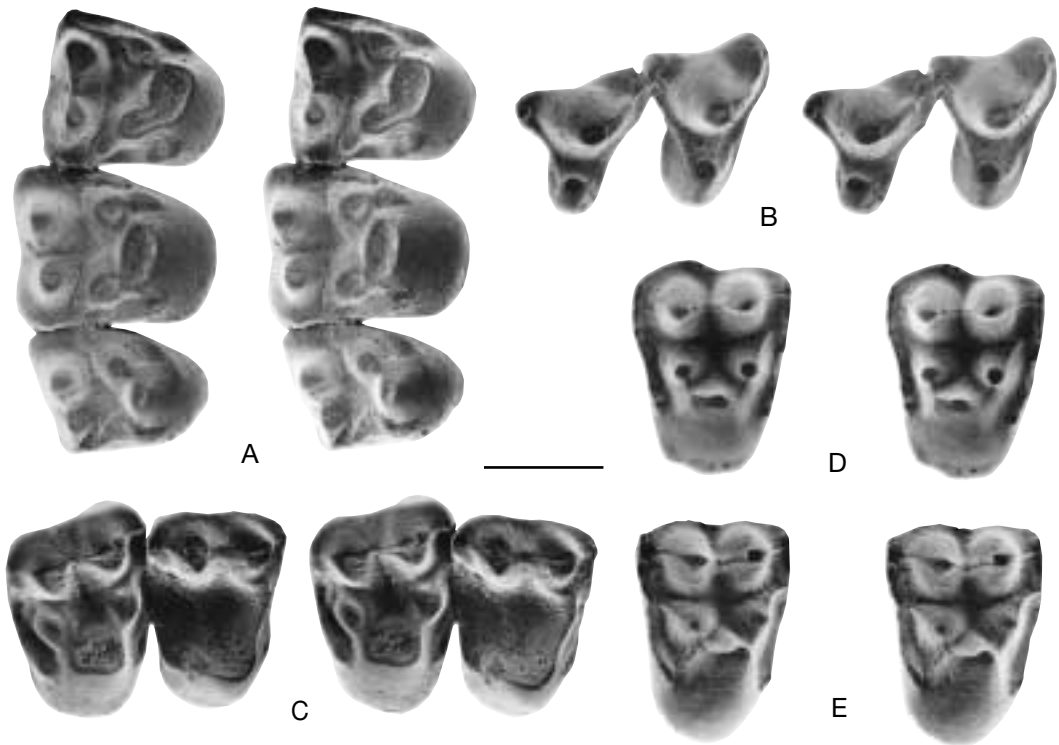


FIG. 11. — *Pucanodus gagnieri*, upper dentition; **A**, partial right maxilla with M1-M3 (cast of MHNC 8343) in occlusal view; **B**, partial left maxilla with P3-P4 (cast of MHNC 1242) in occlusal view; **C**, partial right maxilla with M1-M2 (cast of MHNC 8271) in occlusal view; **D**, isolated right M2 (cast of MHNC 8340) in occlusal view; **E**, isolated right M2 (cast of MHNC 1268) in occlusal view. Stereopairs. Scale bar: 2 mm.

Tiuclaenus. On MHNC 8343 (Fig. 11A), the anterior edge of M1-2 is convex and the posterior is concave. Although this feature is less pronounced than in *T. robustus*, a slight but distinct shifting of the protocone is observed in this specimen, but is hardly discernible on MHNC 8271 (Fig. 11C). In their basic morphological pattern, the upper molars of *Pucanodus gagnieri* are very similar to those of *Tiuclaenus*. An important similarity between the two genera is the morphology of the pre- and postcingula, which connect the anterior and posterior bases of the protocone to the styles. The preparaconular and postmetaconular cristae do not direct toward the styles, as in the plesiomorphic condition observed in *Protungulatum*, but are connected to the pre- and postcingula respectively at the level of the valley between the para- and metacones and conules. In fact, in the case of *Pucanodus*, again, the pre- and postcingula seem to “capture” the para- and

metacingular portions of the preparaconular and postmetaconular cristae. There is no true labial cingulum as in *Molinodus*, but a weak labial rim is present. On MHNC 8340 (Fig. 11D), a small cusplule is present on the labial rim at the level of the anterolabial edge of the metacone. This cusplule is variably present in *Pucanodus* and could represent the incipient development of a mesostyle. The lingual extremity of the postcingulum is not thickened and there is no hypocone. In lingual view, the lingual extremities of the cingula are both located at the base of the protocone. The protocone is large and somewhat elongated anteroposteriorly on M2 of MHNC 8343. The paracone is slightly larger in height and volume than the metacone on M2. This feature is generally hardly discernible on M1. The styles are grossly aligned with the para- and metacones, although in some specimens they are slightly labial to the cusps. The conules are large. Because

TABLE 9. — Measurements (mm) and descriptive statistics of the upper dentition of *Pucanodus gagnieri*.

Measurement	N	Min	Max	Mean	CV
P3 L	2	2.19	2.30	2.25	0.035
P3 W	2	2.19	2.25	2.22	0.019
P4 L	1	2.27	2.27	2.27	1.000
P4 W	1	2.94	2.94	2.94	1.000
M1 L	4	2.25	2.70	2.51	0.075
M1 W	3	3.36	3.47	3.40	0.019
M2 L	2	2.60	2.81	2.71	0.055
M2 W	1	3.91	3.91	3.91	1.000
M3 L	1	2.21	2.21	2.21	1.000
M3 W	1	3.30	3.30	3.30	1.000

they are less inflated than in *Tiuclaenus*, the trigon basin is relatively wider than in this genus. The conules do not have postparaconular and premetaconular cristae. The M3 is almost as wide as M2 and only slightly shorter. Its metacone and metaconule are reduced, as in all M3s.

Lower dentition (Fig. 12; Table 10)

Lower incisors and canine. The lower incisors are unknown but their alveoli are preserved on MHNC 1230 (Fig. 12C, D). The largest alveolus is that of i2 and the smallest, that of i1. The lower canine is a small tooth but it is slightly higher than in *Tiuclaenus*. The canine is also higher than the p2. It is slightly recurved posteriorly. In anterior view, its labial flank is subvertical whereas its lingual flank is oblique.

Lower premolars. The lower premolars of *Pucanodus* are proportionally shorter anteroposteriorly, higher, and wider than those of *Tiuclaenus cotasi* and *T. minutus*. The p1 is unknown but its single root remains in the alveolus on MHNC 1230. The p2 (Fig. 12C, D) is clearly shorter than p3; its protoconid is elevated and has subvertical flanks. A minute cusp is observed at the anterolingual base of the protoconid, and a small and low talonid cusp is present at its posterolingual base. The p3 (Fig. 12A-D) is longer and wider than the p2 but approximately of the same height. Its protoconid is slightly less voluminous, but the anterior and talonid cusps are more developed. On p4 (Fig. 12A-F), these cusps are still larger, especially the talonid cusp, which is central and tends to become duplicated lingually. The protoconid bears a small metaconid appressed

against its posterolingual angle, the apex of which is much lower. On the holotype, no metaconid is observed probably because it was obliterated by the wear of the tooth. On MHNC 1235, a clear metaconid is present.

Lower molars. The m1 (Fig. 12A-F) is badly worn on the holotype but it is well-preserved on MHNC 1230. Its trigonid is higher and narrower than the talonid. The protoconid is thick and inflated, the paraconid is small but well-developed compared to the condition of *Tiuclaenus*, and the metaconid is intermediate in volume between the paraconid and the protoconid. Paraconid and metaconid are approximately the same height, but both are much lower than the protoconid. The metaconid is clearly posterior to the protoconid, as is observed in the other "condylarths" from Tiupampa. On MHNC 1230, the posterior flank of the metaconid is not inflated as in *Tiuclaenus*. This condition, however, not observable on the holotype because of the wear of the specimen, is present on MHNC 1235. The trigonid basin is triangular and has a trihedron shape, although the paraconid-metaconid valley is shorter than the two others. This morphology is always more pronounced on m1 than on m2 (Fig. 12A, B, G, H). The trigonid basin overhangs the talonid basin. The talonid is short and bears a large hypoconid that is almost as voluminous as the protoconid. The cristid obliqua is small and low but clearly present. It contacts the trigonid at the posterolabial angle of the metaconid. The hypoconulid and the entoconid are flattened in a vertical plane and partly fuse to form an oblique posterolingual crest

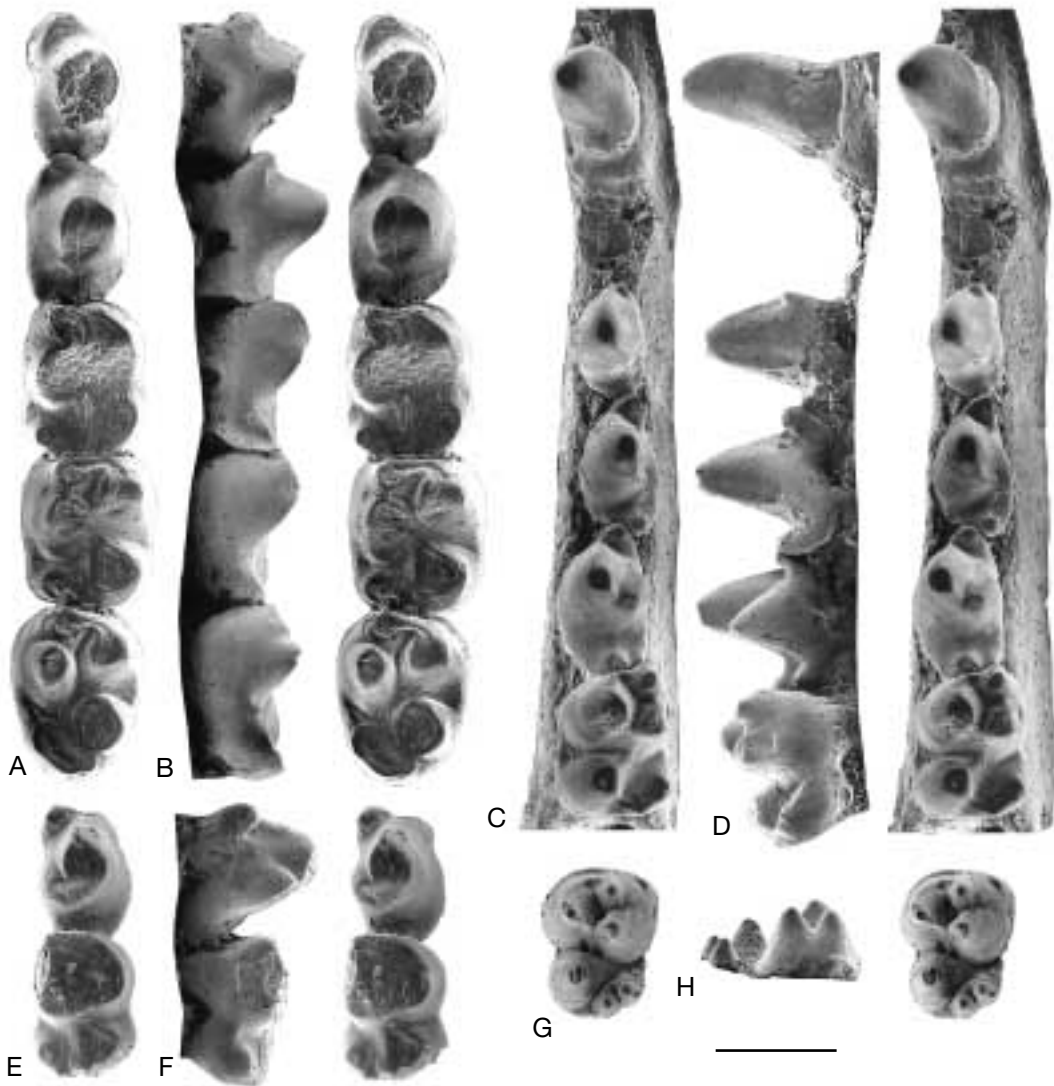


FIG. 12. — *Pucanodus gagnieri*, lower dentition; **A**, partial right dentary with p3-m3 (cast of MHNC 1239, holotype) in occlusal view; **B**, the same in medial view; **C**, partial left dentary with c, p2-m1 (cast of MHNC 1230) in occlusal view; **D**, the same in medial view; **E**, partial right dentary with p4-m1 (cast of MHNC 1235) in occlusal view; **F**, the same in medial view; **G**, isolated left m2 (cast of MHNC 1265) in occlusal view; **H**, the same in medial view. A, C, E, G, stereopairs. Scale bar: 2 mm.

as in all the other Tiupampa “condylarths”. The entoconid does not contact the posterolingual edge of the metaconid and, therefore, the talonid is open lingually. In fact, as in *Molinodus* and *Tiuclaenus*, the talonid basin is reduced to an oblique groove opened lingually. A weak precingulum is observed on the m1 of the holotype. The m2 of the type specimen (Fig. 12A, B) is relatively worn. Its basic

pattern is similar to that of the m1, from which it differs in that its trigonid is slightly wider than the talonid. An unworn m2 (MHNC 1265) has been referred to *P. gagnieri*. This tooth differs from that of the holotype in its cristid obliqua that is almost absent; however it is well known that this structure shows a significant individual variation. The two known m2s present a small precingulum.

TABLE 10. — Measurements (mm) and descriptive statistics of the lower dentition of *Pucanodus gagnieri*.

Measurement	N	Min	Max	Mean	CV
p2 L	1	1.86	1.86	1.86	1.000
P2 W	1	1.29	1.29	1.29	1.000
p3 L	2	2.23	2.42	2.36	0.058
p3 W	2	1.44	1.65	1.55	0.096
p4 L	2	2.47	2.49	2.48	0.006
m1 L	2	2.51	2.51	2.51	0.000
m1 tri W	2	2.00	2.15	2.05	0.034
m1 tal W	2	2.04	2.15	2.10	0.037
m2 L	1	2.64	2.64	2.64	1.000
m2 tri W	2	2.10	2.30	2.20	0.064
m2 tal W	1	2.20	2.20	2.20	1.000
m3 L	1	2.97	2.97	2.97	1.000
m3 tri W	1	2.30	2.30	2.30	1.000
m3 tal W	1	2.00	2.00	2.00	1.000

The only m3 known is that of the holotype (Fig. 12A, B). It is characteristic in its oval-shaped outline and in its shortness, although the trigonid is not narrower than that of m2. The morphology of the trigonid is almost identical to that of m2. The paraconid is slightly lower than the metaconid; the trigonid basin is small and almost reduced to an anteroposterior groove. It is widely open posteriorly on the talonid basin. The posterior border of the metaconid is inflated and partially fills the anterior region of the talonid basin. On m3, the talonid basin is smaller than on m2. The cristid obliqua is rounded and low. It connects the anterolingual angle of the hypoconid to the posterolingual edge of the protoconid, a condition that allows opening of the trigonid basin into the talonid basin. The oval morphology of the tooth is caused by the great reduction of the hypoconulid, which is not strongly developed as in *Molinodus* and *Tiuclaenus*. The talonid is hardly longer than on m2, clearly narrower, and its posterior border is rounded. The hypoconid is slightly less voluminous than on m2. The posterolingual crest formed by the fusion of the entoconid and hypoconulid is more developed than on m2 and extends anteriorly in a small entocristid, which closes the basin lingually.

Dentary

The dentary of *Pucanodus* is slightly more robust below m2 than those of *Tiuclaenus*. Its height is

4.7 mm and its width 3 mm; a small mental foramen is present on the lateral face below the anterior root of p4. The ventral border of the bone is slightly convex below the tooth row and concave below the anterior extremity of the masseteric fossa. On the medial face of the dentary the mylohyoid groove is deep and extends posteriorly below the m3. The symphysis was clearly articulated and its posterior extremity is below the anterior root of p2.

COMPARISONS

Pucanodus gagnieri is a species that appears to be closer in some derived features to *Tiuclaenus* than to *Molinodus*. However, the three genera share certain specializations and differ from the North American mioclaenids.

Upper dentition

Upper premolars. The P3 has a relatively larger protocone than in the North American mioclaenids, some didolodontids (*Paulacoutoia*) and primitive litopterns (*Asmithwoodwardia*). In *Didolodus*, the protocone of P3 is large and subequal in size to that of P4. As mentioned in the section dealing with *Molinodus*, the great size of the protocone of P3 is a derived character state. Among North American "condylarths", a relatively large protocone of P3 is also found in *Oxyprimus*, *Maiorana* and *Mimatuta*. In those

genera, however, the protocone of P3 is not as high as in *Pucanodus* and the anterior and posterior edges of the tooth are not as concave.

The P4 of *Pucanodus* resembles that of *Tiuclaenus* and *Molinodus* in being triangular in occlusal outline (i.e. anterior and posterior border are not parallel). It is more quadrate (i.e. the anterior and posterior borders of the tooth are almost parallel) in didolodontids and primitive liopterns (*Paulacoutoia*, *Didolodus*, *Asmithwoodwardia*, *Protolipterna*). In North American mioclaenids, the P4 is clearly triangular as it is in many primitive taxa (*Protungulatum*, *Oxyprimus*, *Mimatuta*, *Maiorana*, *Baiiconodon*, *Loxolophus*, *Tetraclaenodon*). Some North American “condylarths”, however, also have a subquadrate P4 (e.g., *Mioclaenus*, *Phenacodus*).

Upper molars. The pre- and postcingula of the upper molars are continuous from the anterior and posterior faces of the protocone to the para- and metastyle; the preparaconular and postmetaconular cristae connect to cingula at the level of the valley separating the labial cones and the conules. As mentioned above in the *Molinodus* section, the conule cristae reach the styles labially whereas the pre- and postcingula do not. The conditions of *Pucanodus* and *Tiuclaenus* are similar to those of most North American mioclaenids (except *Choeroclaenus*). They resemble the condition of didolodontids and primitive liopterns, in which the pre- and postcingula connect the para- and metacingular portions of the preparaconular and postmetaconular cristae.

Pucanodus and *Tiuclaenus* have lost the strong labial cingulum observed in such plesiomorphic taxa as *Protungulatum* and *Mimatuta* and only show a variably developed rim generally more emphasized in the styler regions. In this respect, they are more derived than *Molinodus* and the North American mioclaenids. A labial cingulum is generally present in most didolodontids and primitive liopterns. Therefore, *Tiuclaenus* would be more derived than these ungulates in this respect.

Pucanodus, *Tiuclaenus*, and *Molinodus* share the lack of postparaconular and premetaconular cristae, a derived condition absent in North American mioclaenids and *Protungulatum* but found in the didolodontids and primitive liopterns.

The three genera also share the position of the styles, which are almost aligned with the para- and metacone (or only slightly shifted labially). This condition differs from the plesiomorphic condition observed in *Protungulatum* and *Mimatuta*, in which the styles are clearly labial to the para- and metacones. The condition of North American mioclaenids is variable as the styles are slightly but clearly labial in *Bubogonia*, *Litaletes*, *Choeroclaenus*, and *Valenia*, whereas they are aligned in *Promioclaenus* and *Mioclaenus*. The styles are aligned in didolodontids and primitive liopterns, which represents a derived condition.

The conules of *Pucanodus* are less inflated than in *Tiuclaenus* and the trigon basin is larger. As in *Molinodus* and *Tiuclaenus*, the conules are closer to the protocone than to midline position of the tooth. This is a derived condition which is found in *Molinodus* and *Tiuclaenus*, and *Protungulatum*. It is generally absent in didolodontids and the primitive lioptern, in which the conules are closer to midline position. It probably represents a derived condition (reversal) related to the acquisition of massive molar cusps (see below).

Furthermore, the M2 of *Pucanodus* is more quadrate and more symmetrical in relation to a transverse axis than in *Molinodus*. It clearly resembles the condition in *Tiuclaenus* in this respect. The condition of *Tiuclaenus* and *Pucanodus* represents a plesiomorphic character state.

Lower dentition

Lower premolars. A small metaconid is observed on the posterolingual angle of the protoconid of p4. This condition, regarded here as primitive, is similar to that observed in *Tiuclaenus*, *Molinodus*, *Protungulatum*, *Oxyprimus*, *Mimatuta* and some North American mioclaenids (*Litaletes*). It is lost in certain North American mioclaenids (*Promioclaenus*, *Choeroclaenus*, *Mioclaenus*, *Protoselene*), which represents a derived condition. Another derived condition is observed in didolodontids and primitive liopterns, in which the metaconid of p4 is greatly enlarged and generally the same size as the protoconid and sometimes located directly medial to it.

Lower molars. As in *Tiuclaenus*, the trigonid of *Pucanodus* differs from that of *Molinodus* in having a paraconid more appressed against the meta-

conid. Therefore, the trigonid basin tends to reduce the paraconid-metaconid valley and give an oblique orientation to the paraconid-protoconid and metaconid-protoconid valleys. In other words, these two valleys show a tendency to be anteroposterior as is observed in didolodontids and primitive litopterns. This condition is generally better observed on m2 than on m1 or m3.

The trigonid of the m2 of *Pucanodus*, which is slightly wider than the talonid (as in *Molinodus* and *Tiuclaenus*) is more primitive than the condition observed in didolodontids and primitive litopterns, in which the trigonid is generally narrower than (although it is sometimes as wide as) the talonid. *Escribania* resembles *Pucanodus* in having a trigonid clearly wider than the talonid. The m3 of *Pucanodus* is reduced in length (but not in its trigonid width), which represents a derived condition. In this respect, *Pucanodus* resembles *Tiuclaenus minutus* (although the m3 of this species is not so reduced as in *Pucanodus*) but differs from *Molinodus*, *Escribania*, didolodontids, and primitive litopterns. The m3 also is reduced in some North American mioclaenids (*Promioclænus*, *Mioclænus*, *Choeroclænus*) but not in *Litaletes*. Therefore *Pucanodus* is more derived in this respect than the other South American mioclaenids, didolodontids and primitive litopterns.

On the m2 of *Pucanodus*, the metaconid is similar to that of *Molinodus* and *Tiuclaenus* in its posterior position and inflation of its posterior wall. This condition gives the posterior side of the trigonid a strongly oblique orientation. Although protoconid and metaconid are worn on the holotype, it is clear that this condition was present. Associated to the posterior position of the metaconid is the concavity of the posterior wall of the trigonid, which is also present in the other "condylarths" from Tiupampa. Similarly, in *Escribania*, didolodontids, and primitive litopterns, the metaconid is strongly posterior to the protoconid. This condition is much more pronounced than in "zhelestids" and *Protungulatum*, which are likely to bear the plesiomorphic condition (i.e. metaconid very slightly posterior to the protoconid). Among North American mioclaenids, a metaconid significantly posterior to protoconid is present in *Bubogonia*

and *Protoselene* (see Bonaparte *et al.* 1993). This means that the metaconid of these genera is more posterior to the protoconid than in other mioclaenids (*Promioclænus*, *Mioclænus*, *Choeroclænus*) or *Protungulatum*, but see discussion below.

On m1-2 of *Pucanodus*, the entoconid is subequal in size to the hypoconulid. In this respect, *Pucanodus* resembles *Tiuclaenus* but differs from *Molinodus*, in which the entoconid is clearly smaller than the hypoconulid. In North American mioclaenids, *Protungulatum*, and *Oxyprimus*, the hypoconulid is smaller (to slightly smaller) than the entoconid. In didolodontids and primitive litopterns, the same condition is observed, although in some specimens of *Protolipterna* the difference in size is sometimes very subtle. The condition of *Pucanodus* is similar to that observed generally in North American mioclaenids and probably represents derived character state.

Furthermore, in *Pucanodus* and *Tiuclaenus* the two cusps are connate (but the hypoconulid retains a median position) whereas they are fused in *Molinodus*. The condition of *Tiuclaenus* and *Pucanodus* is similar to that of primitive North American mioclaenids (e.g., *Promioclænus*, *Litaletes*, *Choeroclænus*, *Bubogonia*), although in these genera, the hypoconulid generally is smaller than the entoconid. In *Protungulatum* and *Oxyprimus*, the cusps are also connate but their condition is less conspicuous in *Mimatuta* and *Maiorana*. In didolodontids and primitive litopterns, the entoconid and hypoconulid generally are not as connate as in *Tiuclaenus* and *Pucanodus* although the distribution of this character shows some variation. In *Protolipterna*, the condition of the entoconid and hypoconulid is close to that of *Tiuclaenus* and *Pucanodus*. In didolodontids and other primitive litopterns, the cusps should not be regarded as connate, but they are approximated. In *Asmithwoodwardia*, they are almost totally separated.

Genus *Andinodus* Muizon & Marshall, 1987

TYPE SPECIES. — *Andinodus boliviensis* Muizon & Marshall, 1987.

DIAGNOSIS. — Same as for the species.

TABLE 11. — Measurements (mm) and descriptive statistics of the lower dentition of *Andinodus boliviensis*.

Measurement	N	Min	Max	Mean
m2 L	2	4.79	5.09	4.94
m2 tri W	2	4.09	4.16	4.13
m2 tal W	2	3.61	3.87	3.74
m3 L	1	6.76	6.76	6.76
m3 tri W	1	3.89	3.89	3.89
m3 tal W	1	3.36	3.36	3.36

Andinodus boliviensis Muizon & Marshall, 1987

HOLOTYPE. — YPFB Pal 6120, a fragment of right dentary with m2.

HYPODYGM. — The holotype; MHNC 1241, a fragment of right dentary with talonid of m1 and m2-3.

TYPE LOCALITY. — The holotype and MHNC 1241 were discovered at site 2 of the locality of Tiupampa as defined by Muizon & Marshall, 1992.

HORIZON AND AGE. — Santa Lucía Formation; Tiupampian (early Palaeocene), approximately equivalent to the Puercan of North America (Muizon & Brito 1993; Bonaparte *et al.* 1993; Muizon 1998; see Archibald *et al.* 1987 and Eberle & Lillegraven 1998 for definition, age, and subdivision of the Puercan land-mammal age).

DIAGNOSIS. — Medium to large-sized mioclaenid; much larger than the other taxa from Tiupampa; approximately 40% larger than *Molinodus*; lower molars with relatively low cusps and with posterior side of the trigonid sloping more gently than in *Molinodus*; trigonid of m2 and m3 higher and wider than talonid; paraconid well-developed and metaconid only slightly smaller than protoconid; metaconid strongly posterior to protoconid and with a swollen posterior edge partially filling the talonid basin (this feature is more pronounced in *Andinodus* than in any other known members of the Kollpaniinae), and giving to the posterior wall of the trigonid a distinct sigmoid morphology; very large hypoconid (almost as large as the protoconid), which forms the labial half of the talonid; entoconid and hypoconulid of m2 not as connate as in the other Kollpaniinae, but forming a transverse to oblique posterolingual barrier of the talonid basin; m3 long and unreduced, and presenting a tendency to increase the length of the talonid. *Andinodus* differs from *Molinodus* in its: much larger size; more sigmoid posterior side of the trigonid (it is only slightly concave in *Molinodus*); larger entoconid which is not fused to the hypoconulid but relatively well separated from the latter; much deeper masseteric fossa.

Furthermore, *Escribania chubutensis* differs from *A. boliviensis* in the following characters: approximately 50% larger; presence of a labial cingulid on the talonid; paraconid slightly more labial; smaller size of the protoconid; development of accessory cuspules between the metaconid and the entoconid lingually and on the paracristid (on the anterior edge of the protoconid); anterolingual expansion of the trigonid of m2 (although this feature could well represent individual variation when compared to that observed in *Molinodus*); and in the greater length of the talonid of m3 (see below for discussion).

DESCRIPTION (Fig. 13; Table 11)

Andinodus boliviensis is the largest “condylarth” found at Tiupampa. It is approximately 40% larger than *Molinodus*. The m2 and m3 present a trigonid that is higher and wider than the talonid. The protoconid is a large, bulbous cusp that is only slightly more voluminous than the metaconid. On MHNC 1241 the protoconid is only slightly smaller than the combined metaconid and paraconid. The metaconid is located well posterior to the protoconid when compared to the condition of the North American mioclaenids. The major characteristic of *Andinodus boliviensis* is the presence of a well-developed swelling of the posterior side of the metaconid. This condition is found in *Escribania* and in the other kollpaniines. Although this condition is relatively pronounced in one specimen of *Molinodus* (MHNC 8269), probably as an individual variation, it is generally more developed in *Andinodus* than in the other kollpaniines from Tiupampa. On the anterior side of the metaconid is a relatively large paraconid that is approximately 50% less voluminous than the metaconid. It is connected to the anterior side of the protoconid by a strongly arcuate and transverse paracristid, which is shorter than half the trigonid width. Because the paraconid is closely appressed against the metaconid, the paraconid-metaconid sulcus is located more dorsally than the protoconid-paraconid sulcus; the trigonid basin is reduced almost to an anteroposterior sulcus. The protocristid is reasonably observable on the holotype only. It closes the trigonid basin posteriorly and is not V-shaped in posterior view. The posterior slope of the trigonid is deeply concave and has a conspicuous sigmoid morphology in occlusal view. It is

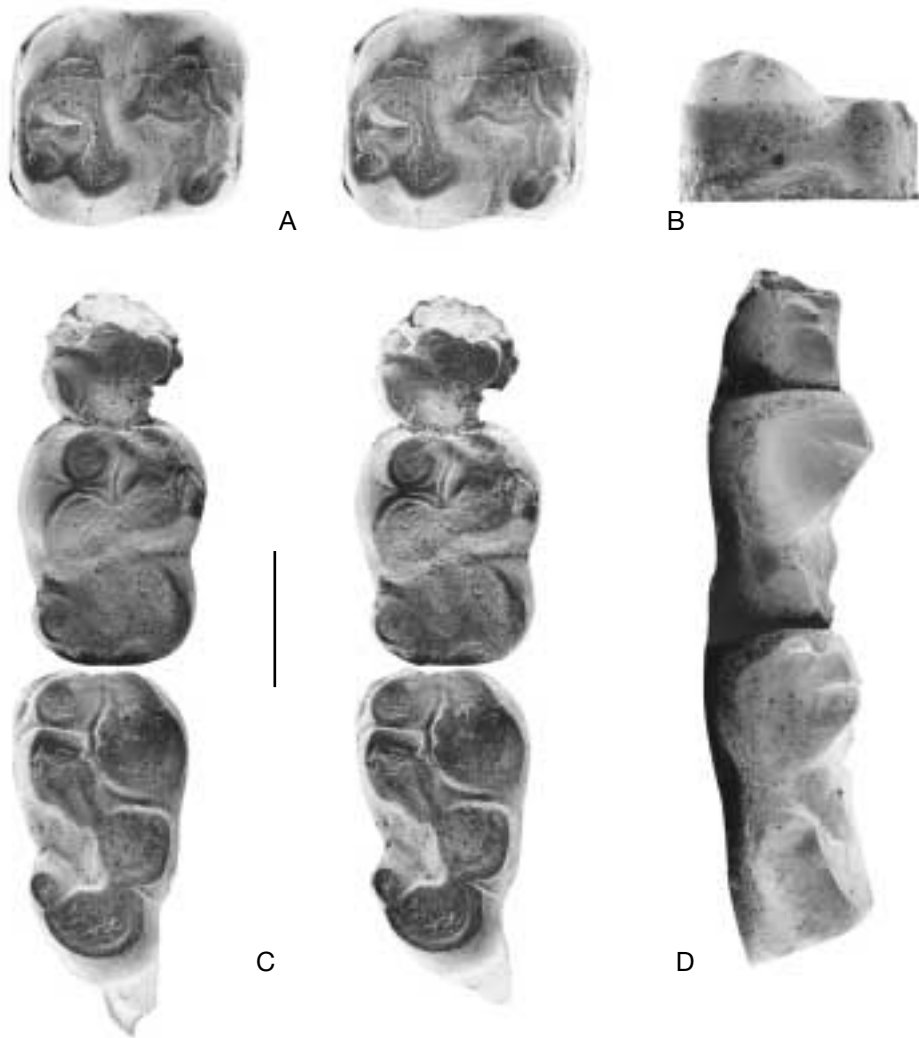


FIG. 13. — *Andinodus boliviensis*, lower dentition; **A**, right m2 (cast of YPFB Pal 6120, holotype) in occlusal view; **B**, the same in lateral view; **C**, partial right dentary with talonid of m1-m3 (cast of MHNC 1241) in occlusal view; **D**, the same in medial view. A, C, stereopairs. Scale bar: 3 mm.

gently sloping towards the talonid basin, which indicates that the lower-molars of *Andinodus* probably were lower-cusped than those of *Molinodus*. The talonid is small and bears an enormous hypoconid which is as large as the metaconid. The hypoconid forms more than two thirds of the talonid. The talonid basin is very small and clearly reduced because of the posterior projection of the posterior wall of the metaconid. It is open lingually and limited posteriorly by a

barrier formed by the hypoconulid and entoconid, two cusps which are fused at their bases but not as connate or fused as in the other kollpaniines. There is no entocristid. On m2 the hypoconulid is slightly larger than the entoconid. A short and low cristid obliqua connects the anterolingual angle of the hypoconid to the centre of the protocristid in YPFB Pal 6120 and to the labial angle of the metaconid in MHNC 1241. The talonid of m3 is very long

and narrow and its hypoconulid is slightly larger than the hypoconid.

The dentary is very robust and has a high (10 mm) and thick (6.6 mm) horizontal ramus below the middle of m2. The anterior border of the vertical ramus is lateral to the protoconid of m3 contrary to the condition observed in the other Kollpaniinae. The anteriormost region of the masseteric fossa only is preserved on MHNC 1241. Apparently it was relatively shallow and differs in this respect from the conditions of *Molinodus* and *Simoclaenus*.

COMPARISONS

Andinodus boliviensis is a large, poorly known (two specimens only) taxon of the “condylarth” fauna from Tiupampa. It clearly differs from *Molinodus*, *Tiucloaenus* and *Pucanodus* in its much larger size. It is only slightly larger than *Simoclaenus* n. gen., and comparison with this genus will be given in the section describing it. *Andinodus* also differs from *Molinodus* in the lower crowns of its lower molars, a feature materialized in the more gentle sloping of the posterior side of the trigonid. *Andinodus boliviensis* also differs from *Molinodus* in the stronger posterior projection of the metaconid. As a consequence, the posterior face of the protocristid is more conspicuously concave (in occlusal view) and is sigmoid-shaped as is observed in *Escribania*. The talonid of *Andinodus* is more specialized than that of *Molinodus* in its larger hypoconid, which forms more than two thirds of the talonid. Specializations also exist in its entoconid and hypoconulid, which are fused only at their bases rather than totally fused as in *Molinodus*. On the dentary, the anterior root of the coronoid process is more anterior and the masseteric fossa is shallower than in *Molinodus*.

It has been suggested to one of us (pers. comm. of K. Rose to C. de Muizon) that *Andinodus* could represent a junior synonym of *Molinodus*. It is true that *Andinodus boliviensis* and *Molinodus suarezi* have a very similar basic pattern in the morphology and arrangement of the cusps of the lower molars. However, this pattern is the plesiomorphic mioclaenid condition. Furthermore, *Andinodus* is more specialized than *Molinodus* in the stronger posterior projection of the meta-

conid and in the larger hypoconid. Finally, *Molinodus* is apomorphic in the fusion of the entoconid and hypoconulid. We consider that these features, along with the greater robustness and the lower crowns of the lower molars, are probably indicative of generic level. Nevertheless, we do not discard the possibility that the two species may ultimately prove to be congeneric. In other respects, it is noteworthy that only m2 and m3 of *Andinodus* are known (whereas all the molars and most of the premolars of *Molinodus* have been discovered). Thus we defend here the hypotheses of Muizon & Marshall (1987b; 1991) and Muizon (1992) that refer the two species to different genera. More complete representation of *A. boliviensis* is required however, especially upper molars.

Escribania chubutensis was described by Bonaparte *et al.* (1993) on the basis of a single specimen (a mandible fragment with m2 and m3 lacking most of the metaconid and part of the paraconid) from beds of early Palaeocene age from Punta Peligro (Argentina). The strata of Punta Peligro are younger than those of Tiupampa. *Raulvaccia peligrensis* comes from the same locality, and its holotype and only known specimen is a poorly preserved tooth identified by its authors (Bonaparte *et al.* 1993) as m2. The type specimen of *Raulvaccia peligrensis* has a trigonid slightly narrower than the talonid. Therefore, if the molar preserved is an m2, the root alveolus observed on the specimen anterior to the tooth is too narrow to be the posterior root of an m1 (it is approximately 25 to 30% narrower than the anterior root of the tooth preserved on the specimen). The tooth better corresponds to the size of a p4 (when compared to what is observed in *Paulacoutoia* and *Simoclaenus* n. gen.). Furthermore, the size difference between the holotype of *Raulvaccia* and the m2 of *Escribania* is similar to that observed between m1 and m2 in *Paulacoutoia* or *Molinodus*. For these reasons, and because Bonaparte *et al.* (1993) did not give argument to defend their position, we regard the holotype of *Raulvaccia peligrensis* as an m1. Some characters of the m2 of *Escribania chubutensis* are also observable on the holotype of *R. peligrensis*. As in the former, the metaconid of *Raulvaccia* is very large and expanded posteriorly in the talonid basin. Consequently, the posterior

edge of the trigonid is strongly oblique and probably had a sigmoid morphology. The paraconid of *Raulvaccia* is large as in *Escribania* and, because the trigonid of these genera is larger than in any other “condylarths”, we regard this feature as derived. Therefore, for the reasons given above, we believe that the holotype of *Raulvaccia peligrensis* is an m1 of *Escribania chubutensis* and consider the two species as synonyms. The difference observed in the cristid obliqua of the two m2s is minor and agrees perfectly with the variation observed in other “condylarths” (*Molinodus*, *Paulacoutoia*) or primitive litopterns (*Miguelsoria*). We formally propose to retain the name *Escribania chubutensis* rather than *Raulvaccia peligrensis* because of the better quality of its type specimen [although *Raulvaccia peligrensis* appears in a page (Bonaparte *et al.* 1993: 22) anterior to that of *Escribania chubutensis* (Bonaparte *et al.* 1993: 24)]. In fact, the page position in such a case is not considered by the International Code of Zoological Nomenclature.

Escribania and *Andinodus* present some derived character states that apparently are not found in other kollpaniine “condylarths”. The two genera have an enlarged metaconid that strongly projects posteriorly and partially invades the talonid basin (to a stronger extent than in the other Kollpaniinae). As a consequence, the lingual side of the trigonid is much longer than that of the talonid and the limit between the two parts of the tooth is clearly sigmoid whereas it is only oblique in the other kollpaniines and in didolodontids. Furthermore, the tendency to increase the lingual length of the trigonid is reinforced by the large size of the paraconid which probably must be regarded as a derived feature. Such a large paraconid is not observed in any of the North or South American “condylarths” (even in primitive forms such as *Protungulatum* or *Mimatuta*) except *Lamegoia*. *Molinodus* approaches the condition of *Andinodus* and *Escribania*, although its lower molars generally have a smaller paraconid than those of the latter. Another similarity between *Escribania* and *Andinodus* is the tendency in the two genera to increase the length of the m3. The m2/m3 ratio is 0.694 in *Escribania*, 0.723 in *Andinodus*, 0.83 in *Molinodus* (mean of four specimens), 0.845 in *Protungulatum* (mean of two specimens), and

0.863 in *Mimatuta* (mean of two specimens). Among the didolodontids, *Ernestokokenia* (MNHN CAS 681) has a ratio of 0.798, *Paulacoutoia* 0.813, and the litoptern *Miguelsoria* 0.872 (mean of three specimens) (Table 12). If the condition of *Protungulatum* and *Mimatuta* can be regarded as primitive, then it is probable that *Andinodus* and *Escribania* shared the same apomorphic tendency to increase the length of m3, contrary to what is generally observed in the other mioclaenids.

Nevertheless, the two genera differ in some features. For example, *Escribania* is approximately 50% larger than *Andinodus*. The protoconid of *Escribania* is relatively smaller and its hypocoenid is smaller than the entoconid whereas it is larger in *Andinodus*. The labial cingulid in *Escribania* is more developed, it presents small cuspsules between the metaconid and the entoconid of m2 and on the paracristid anterior to the protoconid, and its dentary is relatively much larger than in *Andinodus*. Furthermore, *Escribania* presents a characteristic anterolingual expansion of the m2 that gives an oblique orientation of the anterior edge of the tooth, a feature which is also present but less pronounced on m3. It has not been observed during this study in any other mioclaenid except in *Mioclaenus*, the m2 of which is amazingly similar to that of *Escribania*. In fact, if found isolated in North America, the m2 of *Escribania* probably would be referred to a new species of *Mioclaenus*, and certainly to the same clade. *Escribania* differs from *Mioclaenus* in the size of its m2 (approximately 30% larger), in its proportionally longer m2 and m3 (especially in its m3 which is 30% longer than the m2), whereas it is reduced in *Mioclaenus* (approximately 20% shorter than the m2).

The great resemblance and the derived features shared by *Escribania* and *Andinodus* (especially the enlarged m3) indicate a close relationship in the same clade. It is also possible that the two species are congeneric and that both should be placed in the genus *Andinodus*. However, the poor knowledge of both species (m2-3 only, upper molars unknown), does not allow a secure comparison and they will be retained here, conservatively, as distinct genera.

TABLE 12. — Relative lengths of m2 and m3 in various “condylarths”. (Values for *Promioclænus* are an average of 30 specimens; see Table 17 in Appendix 1.)

Taxon	L m2	Lm3	Lm2/Lm3	Mean
<i>Protungulatum donnae</i> SPSM 62-2028	4.25	4.95	0.858	0.866
<i>Protungulatum donnae</i> UC 100894				
	3.84	4.39	0.874	
<i>Mimatuta minuial</i> PU 14172	4.15	4.77	0.870	0.891
<i>Mimatuta minuial</i> PU 14453				
	4.58	5.02	0.912	
<i>Promioclænus aquilonius</i>				
	3.6	3.67	0.98	0.98
<i>Bubogonia saskia</i> UA 15105				
	6.4	6.35	1.007	
<i>Choeroclaenus turgidunculus</i> USNM 15465	4.21	4.22	0.997	0.997
<i>Choeroclaenus turgidunculus</i> AMNH 16404				
	4.28	4.29	0.997	
<i>Protoselene opisthacus</i> KU 7852	5.61	6.23	0.9	
<i>Protoselene opisthacus</i> AMNH 16614	5.36	6.13	0.874	0.879
<i>Protoselene opisthacus</i> MNHN AN				
	5.13	5.94	0.863	
<i>Molinodus suarezi</i> YPFB Pal 6113	3.69	4.33	0.852	
<i>Molinodus suarezi</i> YPFB Pal 6114	3.62	4.31	0.853	0.823
<i>Molinodus suarezi</i> MHNC 8269				
	3.59	4.69	0.765	
<i>Tiuclaenus minutus</i> YPFB Pal 6115				
	2.53	2.83	0.893	0.893
<i>Tiuclaenus cotasi</i> MHNC 8273	2.73	2.87	0.951	
<i>Tiuclaenus cotsis</i> MHNC 8349	3	3.1	0.967	0.934
<i>Tiuclaenus cotasi</i> MHNC 1231				
	2.8	3.16	0.886	
<i>Tiuclaenus robustus</i> MHNC 1233				
	3.16	3.1	1.02	1.02
<i>Pucanodus gagnieri</i> MHNC 1239				
	2.64	2.97	0.888	0.888
<i>Andinodus boliviensis</i> MHNC 1241				
	5.09	7.04	0.723	0.723
<i>Simoclaenus sylvaticus</i> MHNC 8332				
	4.35	5.27	0.825	0.825
<i>Escrivanja chubutensis</i> UNPSJB PV 916				
	9.04	12.6	0.717	0.717
<i>Ernestokokenia yirunhor</i> AMNH 28539	5.89	6.81	0.865	0.831
<i>Ernestokokenia cf. nitida</i> MNHN Cas 681				
	6.8	9.1	0.747	
<i>Paulacoutoia protocenica</i> MNRJ 1431-V				
	8.25	10.3	0.801	0.801
<i>Didolodus multicuspis</i> MACN A 10689	9.1	11.7	0.777	0.781
<i>Didolodus multicuspis</i> MLP 59.11.28.14				
	9.2	11.7	0.786	
<i>Miguelsoria parayirunhor</i> MNRJ 1468-V	5.52	6.83	0.808	
<i>Miguelsoria parayirunhor</i> DGM 296-M	5.64	7.07	0.797	0.798
<i>Miguelsoria parayirunhor</i> DGM 249-M				
	5.12	6.38	0.802	
<i>Protolipterna ellipsodontoides</i> DNPM LE444A	4.36	5.35	0.814	
<i>Protolipterna ellipsodontoides</i> DNPM LE 444C	4.05	4.98	0.813	0.808
<i>Protolipterna ellipsodontoides</i> DGM 1308 M				
	4.35	5.44	0.799	
<i>Asmithwoodwardia scotti</i> DGM 410M	3.84	4.25	0.903	
<i>Asmithwoodwardia scotti</i> DGM 1358 M	3.9	4.37	0.892	0.880
<i>Asmithwoodwardia scotti</i> MCT 2312 M	3.78	4.47	0.845	

McKenna & Bell (1997) have authoritatively included *Andinodus* within the Meridiungulata as an *incertae sedis* taxon, therefore excluding the genus from the Mioclaenidae. We do not follow this hypothesis because the two poorly preserved specimens of *Andinodus* do not present (certainly no more than *Molinodus*) derived features that could relate them, even tenuously, to any of the orders included by these authors in the Meridiungulata. The only meridiungulate group to which *Andinodus* could eventually be referred is the Litopterna. However, *Miguelsoria parayirunhor* and *Asmithwoodwardia scotti* from Itaboraí, initially referred to the Didolodontidae (Paula Couto 1978), were referred by Cifelli (1983a) to the litopterns on the basis of their tarsal bones. The same is true for *Protolipterna* which, in the absence of probable correlation to tarsal bones, would probably be referred to the Didolodontidae (see Cifelli 1983a). It is noteworthy that none of the "condylarth" tarsal bones from Tiupampa have been referred to litopterns (Muizon *et al.* 1998). As mentioned below, the three Itaboraí genera also share with the other Litopterna the derived fusion of the mandibular symphysis; however, this feature cannot be used in the case of *Andinodus* because this region is not preserved on the available specimens.

Genus *Simoclaenus* n. gen.

TYPE SPECIES. — *Simoclaenus sylvaticus* n. gen., n. sp.

ETYMOLOGY. — From *simo* (Greek), short-snouted, in relation to the anteroposterior compression of the lower molars and premolars which indicates a relatively short snout; and *claus* (Greek), closed, a suffix commonly used for genera of "condylarths".

DIAGNOSIS. — Same as for the species.

Simoclaenus sylvaticus n. gen., n. sp.

TYPE SPECIMEN. — MHNC 8332, a fairly complete right dentary with the alveoli of c, p1, the roots of p2, the alveolus of p3, and p4-m3. The dentary is lacking the anterior region with the incisor alveoli and most of the coronoid process.

HYPODIGM. — The type specimen and MHNC 8348, a right maxilla with M1 lacking the parastylar region and part of the paracone and M2-3 complete.

TYPE LOCALITY. — The holotype was discovered at site 2 and MHNC 8348 at site 1 (the quarry) of the locality of Tiupampa as defined by Muizon & Marshall 1992.

HORIZON AND AGE. — Santa Lucía Formation; Tiupampian (early Palaeocene), approximately equivalent to the Puercan of North America (Muizon & Brito 1993; Bonaparte *et al.* 1993; Muizon 1998; see Archibald *et al.* 1987 and Eberle & Lillegraven 1998 for definition, age, and subdivision of the Puercan land-mammal age).

ETYMOLOGY. — *Sylvaticus* from the Greek *sylva*, forest, referring to the inferred tropical forest environment of Tiupampa during the early Palaeocene.

DIAGNOSIS. — Dental formula: I ?/?, C ?/1, P ?/4, M 3/3; relatively large kollpaniine mioclaenid characterized by the strong anterior compression of its lower molars and premolars, which is correlatively observed on the M2; low crown of molars; m2 almost square in occlusal outline but asymmetrical with oblique anterior and posterior edges; p4 with a well-developed metaconid medial to protoconid; molars with a large metaconid, posterior to the protoconid and with a posterior projection that partially fills the talonid basin; protoconid distinctly smaller than in *Andinodus*; posterior wall of trigonid sigmoid in occlusal view; paraconid and paracristid smaller than in *Andinodus*; large hypoconid with a labial slope less vertical than in *Andinodus*; cristid obliqua meets trigonid on lingual edge of protoconid.

DESCRIPTION (Fig. 14; Table 13)

Lower premolars

The main characteristic of the lower teeth of *Simoclaenus* is their anteroposterior compression. Table 14 give the ratio of the average width of m2 (width trigonid + width talonid/2) on the length of the tooth in several kollpaniine and in the primitive litoptern *Miguelsoria*). *Simoclaenus*, with a ratio of 0.951, has an m2 which is almost quadrate and is distinctly separated from the other taxa considered in Table 14.

The teeth anterior to p4 are lacking on the only known lower jaw of *Simoclaenus sylvaticus*, but the roots of p2 and the alveoli of the canine, p1, and p3 are preserved. The alveolus of the canine indicates a small tooth whose root had a triangular section. The canine is separated from the p1 by a short diastema. The p1 is small, single-rooted, and its root has a circular section. It is as wide as the anterior root of p2. The p2 is two-rooted and the posterior root is slightly wider than the anterior. The alveoli of p3 indicate a tooth that was wider (especially the posterior root) but not longer. The p4 is well-preserved and little worn. The tooth is massive, strongly bulbous, and has a higher crown than the molars. It is very short

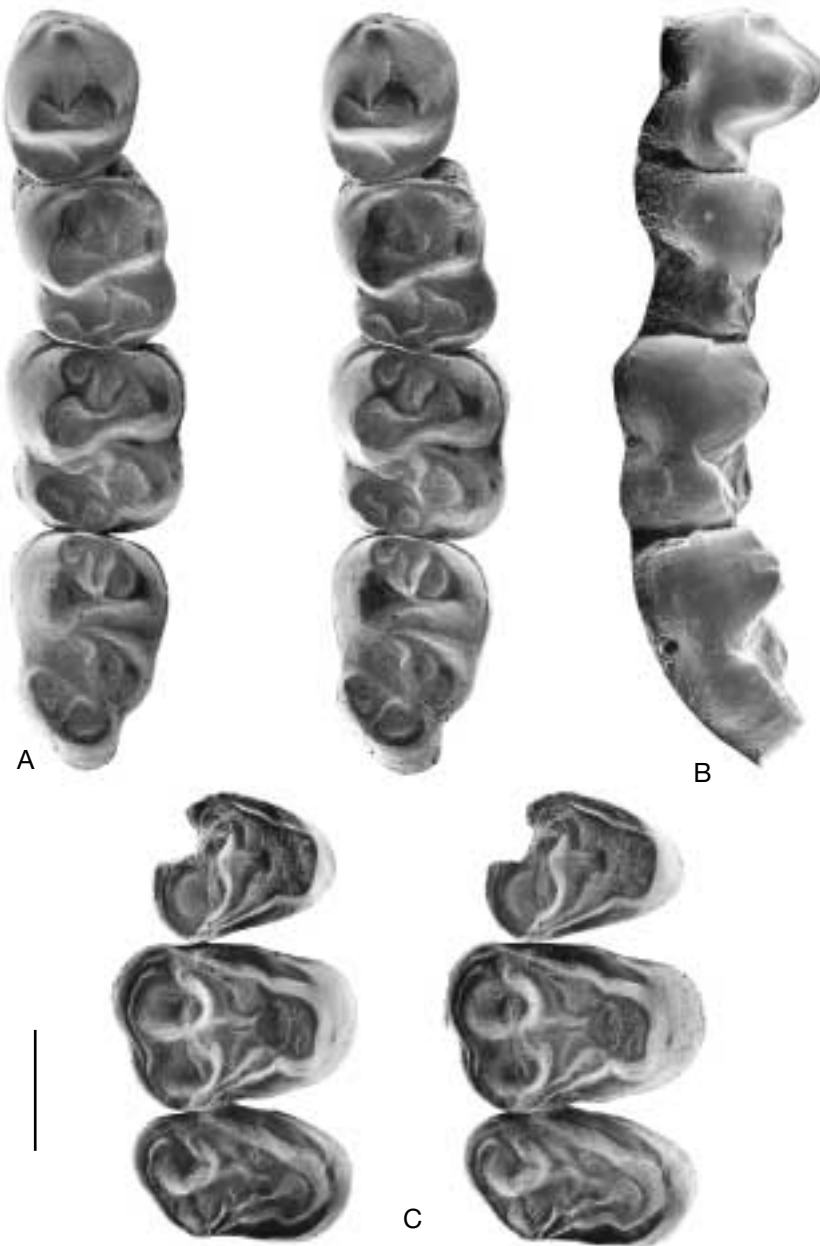


FIG. 14. — *Simoclaenus sylvaticus* n. gen., n. sp., upper and lower dentitions; **A**, partial right dentary with p4-m3 (cast of MHNC 8332, holotype) in occlusal view; **B**, the same in medial view; **C**, partial right maxilla with M1-M3 (cast of MHNC 8348) in occlusal view. A, C stereopairs. Scale bar: 3 mm.

TABLE 13. — Measurements (mm) of the lower (MHNC 8332, holotype) and upper (MHNC 8348) dentition of *Simoclaenus sylvaticus*, n. gen., n. sp.

Measurement	L	W trig or max W	W tal
p4	3.46	3.20	—
m1	3.71	3.48	3.30
m2	4.45	4.11	3.90
m3	5.27	3.78	3.31
M2	3.8	6.2	—
M3	3.14	5.6	—

anteroposteriorly and almost circular in occlusal view (L = 3.46; W = 3.2). The protoconid is large and inflated, and the metaconid is relatively larger than in the other kollpaniines (except one p4 from Tiupampa referred to *Molinodus suarezi*; MHNC 1244). The volume of the metaconid is approximately two thirds that of the protoconid and, although the apices of the cusps are slightly worn, it is possible to note that the height of the metaconid was approaching that of the protoconid. The metaconid is strictly lingual to the protoconid and the posterior wall of the trigonid is transverse, very steep, and flat. At the anterolingual base of the protoconid is a small paraconid cuspule that is linked to the apex of the protoconid by an anteroposteriorly directed, small paracristid. On the anterolabial side of the protoconid is a faint precingulid; a similar, but more developed, structure is observed on the anterolingual angle of the metaconid. The talonid is a strong posterolingual crest, obliquely oriented and located posterior to the metaconid. Labially, the crest is strongly recurved (cristid obliqua) anterolingually and ascends the base of the posterolabial angle of the metaconid. The labial side of the talonid has no large cusp (such as the hypoconid of the molars) but rather exhibits a gentle slope that has a weak angulation with the posterior side of the protoconid.

Lower molars

The m1 is relatively worn and the trigonid structure is not as clearly observable as on the m2. The m1 is much smaller than m2. As is observed in Table 14, it is relatively smaller than in any other "condylarth" from Tiupampa. Among the other mioclaenids, didolodontids, and primitive

litopterns, only *Paulacoutoia* has an m1 slightly smaller (relative to m2) than in *Simoclaenus*. No complete m1 of *Andinodus* is known. However, the talonid (badly worn) and the anterior alveolus of m1 are partially preserved on MHNC 1241; it is probable that this tooth was larger when compared to m2 than in *Simoclaenus*. Because of the wear of the m1 of the holotype of *Simoclaenus*, the following description will refer to the m2. This tooth is very compressed anteroposteriorly and is asymmetrical. As shown in Table 15, the m2 of *Simoclaenus* is more compressed anteroposteriorly than other known kollpaniines, didolodontids, primitive litopterns, and most North American taxa. Its anterior edge is oblique in relation to the axis of the tooth row, and the anterolingual angle of the tooth is acute; its anterolabial angle is obtuse. The metaconid is the largest cusp of the trigonid. As in the other Kollpaniinae, it is expanded posteriorly and partially fills the talonid basin. In the anterolingual angle of the trigonid is a small paraconid that is strongly appressed against the metaconid. The trigonid basin is small and forms an anteroposterior valley. The metaconid-paraconid sulcus is reduced and clearly overhangs the metaconid-protoconid and metaconid-paraconid sulci, both of which have an almost anteroposterior orientation. A short paracristid links the paraconid to the anterior side of the protoconid and closes the trigonid basin anteriorly. It is strongly arcuate posteriorly and resembles the condition observed in the other "condylarths" from Tiupampa. The protoconid is bulbous and, although the tooth is worn, it is possible to note that the distance between its apex and that of the metaconid was less than half the trigonid width. At the anterior edge of the trigonid is a well-developed precingulid that extends labially to the ectoflexid; it does not extend further than the anterolingual angle of the tooth. The posterior side of the trigonid is strongly oblique and concave posteriorly. It slopes gently, which indicates a low-crowned tooth. The talonid is short anteroposteriorly and its basin is very reduced (because of the posterior expansion of the metaconid) and is open lingually. The hypoconid is very bulbous and is slightly larger than the protoconid. It is connected to the posterolabial angle of the metaconid by a conspicuous and relatively sharp cristid obliqua.

TABLE 14. — Comparison of the surface of m1 and m2 in various “condylarths”. (Value for *Promioclaenus* is an average of 30 specimens; see Table 17.)

Taxon	Lm1	WTr m1	Wta m1	Wtr+ Wta/2	Sm1	Lm2	Wtr m2	Wta m2	Wtr+ Wta/2	Sm2	Sm1/ Sm2
<i>Protungulatum donnae</i> SPSM 62-2028	3.84	2.67	2.81	2.74	10.52	4.25	3.35	3.08	3.16	13.43	0.783
<i>Baiococonodon nordicum</i> PU 16720	5.26	3.63	4.02	3.82	20.1	5.83	4.86	4.92	4.89	28.5	0.705
<i>Baiococonodon nordicum</i> PU 14475	5.18	3.84	3.68	3.76	19.49	5.9	4.74	4.58	4.66	27.49	0.7.08
<i>Oxyprimus galadriellae</i> PU 16863	3.32	2.28	2.45	2.36	7.83	3.82	2.9	2.79	2.84	10.84	0.722
<i>Oxyprimus galadriellae</i> PU 16712	3.25	2.12	2.41	2.26	7.34	3.47	2.71	2.69	2.7	9.37	0.783
<i>Mimatuta minuial</i> PU 14453	3.86	2.75	2.76	2.75	10.61	4.58	3.22	3.27	3.24	12.84	0.826
<i>Mimatuta minuial</i> PU 14172	3.87	2.62	2.68	2.65	10.25	4.05	3.16	2.87	3.01	12.19	0.84
<i>Maiorana noctiluca</i> PU 16715	3.01	2.35	2.37	2.36	7.1	3.42	2.83	2.87	2.85	9.74	0.728
<i>Tetraclaenodon puercensis</i> AMNH 3866	7.84	7.04	6.88	6.96	54.56	8.58	7.51	7.37	7.44	63.83	0.854
<i>Tetraclaenodon puercensis</i> AMNH 3832	8.17	6.42	6.47	6.44	52.61	8.6	7.35	7	7.17	61.66	0.853
<i>Promioclaenus acolytus</i> (Mean, see Table 16)	3.4	2.77	2.91	2.84	9.65	3.6	3.24	3.1	3.17	11.41	0.845
<i>Protoselene opisthacus</i> KU 7852	5.8	4.38	4.41	4.39	25.62	5.69	4.89	4.65	4.77	27.14	0.944
<i>Protoselene opisthacus</i> AMNH 16614	5.35	3.92	3.9	3.91	20.91	5.31	4.17	4.22	4.19	22.24	0.94
<i>Choeroclaenus turgidunculus</i> USNM 15465	4.19	2.89	3.02	2.95	12.36	4.41	3.65	3.51	3.58	15.78	0.783
<i>Choeroclaenus turgidunculus</i> AMNH 16402	3.87	2.78	2.8	2.79	10.8	4.2	3.71	3.3	3.5	14.7	0.734
<i>Litaletes disjunctus</i> AMNH 35874	4.17	2.87	3.06	2.96	12.34	4.17	3.61	3.54	3.57	14.88	0.829
<i>Haplaletes disceptatrix</i> USNM 9500	2.46	2.05	2.1	2.05	5.04	2.79	2.47	2.42	2.44	6.8	0.741
<i>Haplaletes disceptatrix</i> USNM 21008	3.1	2.17	2.28	2.22	6.88	3.32	2.61	2.58	2.59	8.59	0.8
<i>Molinodus suarezi</i> YPFB Pal 6112	3.15	2.35	2.19	2.27	7.15	3.68	2.82	2.42	2.62	9.64	0.741
<i>Molinodus suarezi</i> YPFB Pal 6113	3.28	2.89	2.54	2.71	8.88	3.69	3.26	3.07	3.16	11.67	0.761
<i>Molinodus suarezi</i> MHNC 8269	3.16	2.28	2.05	2.16	6.82	3.59	2.8	2.59	2.69	9.67	0.716
<i>Molinodus suarezi</i> MHNC 8344	3.14	2.56	2.44	2.5	7.85	3.56	2.96	2.69	2.82	10.04	0.785
<i>Tiuclaenus minutus</i> YPFB Pal 6115	2.37	1.43	1.41	1.42	3.36	2.53	1.75	1.52	1.63	4.12	0.815
<i>Tiuclaenus cotasi</i> MHNC 1231	2.64	1.85	1.83	1.84	4.85	2.8	2.15	1.98	2.06	5.77	0.84
<i>Tiuclaenus cotasi</i> MHNC 8273	2.33	1.96	2.03	1.99	4.63	2.73	2.19	2.03	2.11	5.76	0.803
<i>Tiuclaenus robustus</i> MHNC 1234	2.68	1.93	2	1.96	5.25	2.94	2.33	2.13	2.23	6.55	0.801
<i>Simoclaenus sylvaticus</i> MHNC 8332	3.71	3.48	3.3	3.39	12.57	4.35	4.26	4.02	4.14	18	0.698
<i>Didolodus multicuspis</i> MACN-A 10689	9.42	7.14	8.27	7.7	72.53	10.17	7.84	8.68	8.26	84.25	0.86
<i>Paulacoutoia protocenica</i> MNRJ 1431-V	6.95	5.26	5.45	5.35	37.18	8.35	6.8	6.94	6.87	57.36	0.648
<i>Ernestokokenia cf. nitida</i> MNHN CAS 681	6.2	4.8	5.34	5.07	31.43	7.07	5.68	6.06	5.87	41.5	0.757
<i>Asmithwoodwardia scotti</i> MCT 2312 M	3.54	2.43	2.65	2.54	9	3.67	2.84	2.84	2.84	10.42	0.86
<i>Asmithwoodwardia scotti</i> DGM 358-M	3.76	2.73	2.87	2.8	10.52	3.71	3	3	3	11.13	0.945
<i>Asmithwoodwardia scotti</i> DGM 410-M	3.66	2.85	2.77	2.81	10.24	3.79	3.13	3	3.06	11.59	0.88
<i>Miguelsoria parayirunhor</i> MNRJ 1468-V	5.23	3.79	3.88	3.83	20.03	5.52	4.59	4.35	4.47	24.67	0.81
<i>Miguelsoria parayirunhor</i> DGM 249 M	4.86	3.82	3.8	3.81	18.51	5.24	4.52	4.19	4.35	22.79	0.812
<i>Miguelsoria parayirunhor</i> DGM 330-M	5.2	3.68	3.95	3.83	19.8	5.6	4.75	4.68	4.71	26.37	0.75
<i>Protolipterna ellipsodontoides</i> DNPML LE 444 A	4.06	3.1	3.15	3.12	12.66	4.33	3.6	3.57	3.58	15.5	0.81
<i>Protolipterna ellipsodontoides</i> DNPML LE 444 B	3.83	2.88e	3.07e	2.97	11.37	4.3	3.54	3.33	3.43	14.75	0.77
<i>Protolipterna ellipsodontoides</i> DNPML LE 444 C	3.94	2.9	3	2.95	11.62	4.13	3.38	3.44	3.41	14.08	0.82
<i>Protolipterna ellipsodontoides</i> DNPML LE 444 E	3.85	2.87	3.05	2.96	11.39	3.98	3.5	3.52	3.51	13.96	0.81

The entoconid is more voluminous than the hypoconulid but the two cusps probably were subequal in height. They are connate but not fused as observed in *Molinodus*. The postcingulid is weak and restricted to the base of the hypoconulid. As for the m2, the m3 is short when compared to other mioclaenids, didolodontids, and early litopterns (Table 15). This condition reflects the general anteroposterior shortening of the tooth row also observed on m2, m1, p4, and M2. However, the m3 of *Simoclaenus* (relative to m2) is proportionally longer than in most of the taxa considered in Table 15 (except *Andinodus*, *Paulacoutoia* and *Escribania*). Therefore, if the m3 of *Simoclaenus* is short in absolute value, it is relatively long when compared to the m2. The trigonid is similar to that of m2. The talonid is larger than on m2 and the talonid basin is broader. The hypoconid is slightly smaller than on m2 and the hypoconulid is much larger. It is subequal in volume to the entoconid and is connate (not fused) to it. The molars of *Simoclaenus* have no entocristid.

Upper molars

A right maxilla (MHNC 8348) with M1-M3 has been referred to the holotype of *Simoclaenus sylvaticus* because it matches the size of the lower teeth and perfectly occludes with them. Furthermore, it presents the same anteroposterior compression observed in the lower molars. The comparison of the W/L ratio of the upper and lower M2s of *Molinodus* and *Simoclaenus* is highly relevant. In *Molinodus*, in which the molars are much less compressed anteroposteriorly than in *Simoclaenus* the W/L and ratios of the m2 and M2 (Table 1) are 0.71 and 1.21 respectively. Values for the ratio in *Simoclaenus* are 0.61 and 10.8. Therefore, because the differences between the ratio for the M2s (0.1) and for the m2 (0.13) are almost identical, the anteroposterior compression of the M2 of *Simoclaenus* (when compared to that of *Molinodus*) is similar to that observed on m2. Furthermore, *Simoclaenus* is, so far as known, the only large “condylarth” in the fauna from Tiupampa that bears major anteroposterior compression of the cheek teeth.

M1 is poorly preserved; it lacks the parastyle, most of the paracone, and is relatively worn. The major morphology and relationships of the cusps

and crests will be described in the M2 section. As observed on lower teeth, M1 is much smaller than M2. However, because the tooth is incomplete, the relative proportions of M1 and M2 of *Simoclaenus* cannot be compared to the other “condylarths” of Tiupampa. The occlusal outline of the tooth seems to have been triangular. The labial side of the relatively large protocone is slightly flattened, and its posterior side is expanded. As a consequence, a small triangular fossa is present on the posterolabial edge of the cusp. It is limited posteriorly by the postcingulum, anterolabially by the metaconule, and anterolingually by the protocone. The conules are large and, although very worn, it is clear that the paraconule was larger than the metaconule. The postmetaconular crista is pronounced, low, and rounded, but its relationships with the metastyle are not observable due to wear. There is no premetaconular crista but a faint postparaconular rim is present. The metacone is bordered by a strong labial cingulum, which bears a small cusplule in median position. The metastyle is small and located posterior to the metacone (i.e. the postmetacrista and metastyle are not deflected labially). A thick precingulum is present.

The M2 is complete and moderately worn. It is very transverse and forms an elongated triangle. The protocone is large and has a flattened lingual side. It is expanded posteriorly and forms, with the metaconule and the postcingulum, a small triangular fossa as is observed on M1. The conules are large and the paraconule is larger than the metaconule. The preparaconular crista is well-developed and sharp. It is oblique (in relation to the transverse axis of the tooth) and meets the parastyle labially. A distinct postparaconular crista is present. It is low and rounded, but better pronounced than on M1. It is grossly parallel to the transverse axis of the tooth and connects the posterolabial edge of the paraconule to the posterolingual edge of the paracone. There is no premetaconular crista, but a thick obliquely oriented postmetaconular crista connects the posterolabial edge of the metaconule to the metastyle. The para- and metacones are regularly conical in occlusal view and the former is more voluminous and higher than the latter. The parastyle is relatively well-developed and appar-

TABLE 15. — Proportions (W/L) of the m2 and m3 in various “condylarths”. (Value for *Promioclaenus* is an average of 30 specimens; see Table 17 in Appendix 1.) Abbreviations: L, length; Wta, width of talonid; Wtr, width of trigonid.

Taxon	Lm2	Wtrm2	Wtam2	Wavm2	Wavm2 /Lm2	Wtrm2 /Lm2	Lm3	Wtrm3	Wtrm3 /Lm3
<i>Protungulatum donnae</i> SPSM 62-2028	4.25	3.35	3.08	3.21	0.755	0.793	4.95	3.08	0.622
<i>Protungulatum donnae</i> UC 100894	3.84	2.99	2.71	2.85	0.742	0.799	4.39	2.66	0.606
<i>Mimatuta minuial</i> PU 14172	4.15	3.16	2.87	3.01	0.725	0.761	4.77	2.77	0.58
<i>Mimatuta minuial</i> PU 14453	4.58	3.22	3.27	3.24	0.707	0.703	5.02	2.93	0.583
<i>Molinodus suarezi</i> YPFB Pal 6112	3.68	2.82	2.42	2.62	0.711	0.766	4.09	2.42	0.59
<i>Molinodus suarezi</i> YPFB Pal 6113	3.69	3.26	3.07	3.16	0.856	0.883	4.33	2.14	0.494
<i>Molinodus suarezi</i> YPFB Pal 6114	3.62	3.04	2.51	2.77	0.824	0.863	4.31	2.79	0.64
<i>Molinodus suarezi</i> MHNC 8269	3.59	2.8	2.59	2.69	0.749	0.78	4.69	2.78	0.592
<i>Molinodus suarezi</i> MHNC 8344	3.56	2.86	2.69	2.77	0.778	0.803	*	*	*
<i>Andinodus boliviensis</i> YPFB Pal 6120	4.79	4.16	3.87	4.01	0.837	0.868	*	*	*
<i>Andinodus boliviensis</i> MHNC 1241	5.09	4.09	3.61	3.85	0.756	0.803	7.04	3.89	0.552
<i>Simoclaenus sylvaticus</i> MHNC 8332	4.35	4.26	4.02	4.14	0.951	0.98	5.27	3.78	0.707
<i>Escribania chubutensis</i> UNPSJB.PV 916	9.04	7.19	6.56	6.87	0.759	0.795	12.4	*	*
<i>Paulacoutoia protocenica</i> MNRJ 1434 V	*	*	*	*	*	*	10.28	6.4	0.623
<i>Paulacoutoia protocenica</i> MNRJ 1432 V	*	*	*	*	*	*	10.58	6.75	0.638
<i>Paulacoutoia protocenica</i> MNRJ 1433 V	*	*	*	*	*	*	9.42	6.17	0.655
<i>Paulacoutoia protocenica</i> MNRJ 1431 V	8.25	6.6	6.88	6.74	0.816	0.8	10.33	6.88	0.666
<i>Miguelsoria parayirunhor</i> DGM 249 M	5.12	4.5	4.1	4.3	0.839	0.878	6.38	4.22	0.661
<i>Miguelsoria parayirunhor</i> DGM 296 M	5.64	4.9	4.8	4.85	0.859	0.868	7.07	4.68	0.661
<i>Miguelsoria parayirunhor</i> DGM 330 M	5.6	4.75	4.96	4.85	0.866	0.848	*	*	*
<i>Miguelsoria parayirunhor</i> MNRJ 1468 V	5.52	4.59	4.35	4.47	0.809	0.831	6.83	4.48	0.656

ently (it is slightly worn) located anterior to the paracone. The metastyle is small and posterior to the metacone. In other words, the styles are not deflected labially (or tenuously for the parastyle), and the components of the labial wall of the tooth (parastyle, preparacrista, paracone, postparacrista, premetacrista, metacone, postmetacrista, and metastyle) are aligned. The three cingula (anterior, posterior, and labial) are thick, sharp, and well-marked. The labial extremity of the precingulum does not contact the labial extremity of the preparaconular crista and the parastyle, but ends very close to them. The lingual extremities of the pre- and postcingula reach the anterolingual and posterior edge of the protocone, respectively. Both cingula contact the protocone at its base. The labial cingulum is continuous from the parastyle to the metastyle and bears a small cuspule just posterior to the shallow ectoflexus, at the level of the anterolabial edge of the metacone. This cuspule is in the same position as the mesostyle observed in *Didolodus* and could represent the incipient development of this cusp in *Simoclaenus*. There is no hypocone. The M3 differs from M2 in the much smaller size of the metacone and metaconule. However, the tooth is not reduced and is almost as wide as M2. The protocone is slightly smaller than on M2 and the antero- and posterocingula are almost in contact lingually.

Dentary (Fig. 15)

The dentary of *Simoclaenus* is robust and stout. Anteriorly on the lingual side is a well-defined symphysis. Although it clearly was not fused, its robust indentations indicates a solid articulation. The posterior extremity of the symphysis is at the level of the posterior root of p2. There are two mandibular foramina. The more anterior is the largest and is located below the anterior root of p2. The more posterior foramen is at the same height on the dentary but is positioned below the posterior root of p3. The ventral edge of the dentary is gently convex below the tooth row and becomes slightly concave below the vertical ramus. The concavo-convex morphology of the ventral side of the dentary is less pronounced than in *Tiucloaenus*, *Protungulatum* and *Mimatuta*, but resembles the condition of *Pucanodus*

The ascending ramus is large and long, which denotes large insertion for the masseter muscle and therefore a powerful masticatory musculature. It differs from the condition of *Protungulatum* and *Protolipterna*, in which the ascending ramus of the dentary is relatively gracile. The ascending ramus does, however, reach the size observed in *Miguelsoria* (DGM 249M). The masseteric fossa is extremely deep and limited anterolabially by an elevated and sharp crest. The angular process is well-developed and robust but, although its apex has been slightly abraded, it is probable that it was relatively shorter than in *Molinodus*. It is also relatively shorter than in *Protungulatum* but wider and more robust. On the lingual face of the angular process are two small crests, concave dorsally, for insertion of the *pterygoideus medialis*. The ventral crest is much more pronounced than the dorsal and both crests join at their posterior extremity, at the apex of the angular process. The posterior border of the ascending ramus, between the angular and condyloid processes, is less concave than in *Tiucloaenus* (the only other "condylarth" from Tiupampa in which this region is preserved). The depth of concavity is especially less than in *Protungulatum*. It resembles the condition of *Miguelsoria* and *Protolipterna* (although more concave than in either of these genera). This condition is due to the important elevation of the condyloid process which, as in *Tiucloaenus*, is higher than in *Protungulatum* but resembles the condition in *Mimatuta*. In lateral view, the condyle of *Simoclaenus* is dorsal to the base of the angular process as in *Protungulatum*. In *Tiucloaenus* the condyle is slightly posterior whereas in *Mimatuta* the condyle is displaced anteriorly. The condyle of *Simoclaenus* is slightly more developed medially than labially but is not clearly shifted lingually as in *Tiucloaenus*. On the labial side of the base of the condyloid process is a sharp crest that enters the masseteric fossa and received part of the origin of the masseter. The articular facet of the condyle has two elements. One part is oriented almost dorsally, is oval-shaped, and transverse; the other part is smaller, relatively rounded, located on the posterolingual side of the condyle, and faces posteriorly. This condition has not been observed in *Tiucloaenus* or *Protungu-*

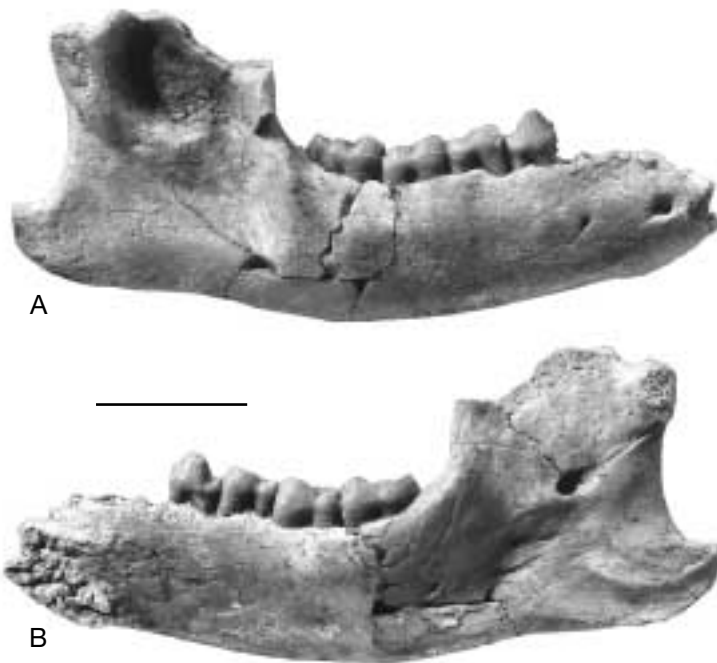


FIG. 15. — *Simoclaenus sylvaticus* n. gen., n. sp., partial right dentary with p4-m3 (MHNC 8332, holotype); **A**, lateral view; **B**, medial view. Scale bar: 1 cm.

latum. As a whole, the dentary of *Simoclaenus* denotes a more powerful masticatory musculature than in *Tiucloaenus* and *Protungulatum*.

COMPARISONS

Lower dentition

Simoclaenus is the second largest “condylarth” of Tiupampa. As indicated by its generic name, its main characteristic is the anteroposterior compression of the upper and lower tooth rows, which is likely to have been reflected on the global morphology of the head. Among the other kollpaniines, *Pucanodus* also presents anteroposteriorly compressed cheek teeth but conditions in that genus do not reach the extremes observed in *Simoclaenus*. *Andinodus* is slightly larger than *Simoclaenus*, but its lower cheek teeth are more elongated anteroposteriorly, as shown in Table 11. The proportions of the two m2s known of *Andinodus* show some variation (see Table 11), as the W/L ratio is 0.837 on the holotype (YPFB Pal 6120) and 0.756 on

MHNC 1241. However, the difference in ratios between *Simoclaenus* (0.98) and the holotype of *Andinodus* is almost 50% greater than that existing between the two specimens of *Andinodus*. Furthermore, the proportions and relative length of m3 differ considerably in the two genera. The m3 of *Andinodus* is not only proportionally much longer than that of *Simoclaenus* but it is also much longer in relation to the m2 (see Tables 13 and 14).

Morphologically, *Simoclaenus* also differs from *Andinodus* in its shorter trigonid, smaller paracoid and paracristid, and more gracile dentary, with a deeper masseteric fossa.

However, *Simoclaenus* greatly resembles *Andinodus* and *Escribania* in the important posterior expansion of the metaconid, which partially fills the talonid basin, and the very oblique and concave posterior slope of the trigonid. This feature is not so pronounced in any other kollpaniine. In the size of its m1, which is small relative to m2, *Simoclaenus* more resembles

Paulacoutoia than any other known “condylarth” or early litoptern.

Upper molars

The upper molars of *Simoclaenus* are extremely similar to those of *Molinodus*. It is worthy to recall, however, that the upper molars of *Andinodus* are unknown. They differ from *Molinodus* only in their larger size, and in the anteroposterior compression of the M2. Furthermore, the upper molar of *Simoclaenus* present two features that are variably present in *Molinodus*: the presence of a small cusplule on the labial cingulum and a low postparaconular crista.

CHARACTER ANALYSIS OF THE KOLLPANIINAE

In the following section we present and discuss the major dental characters that are commonly referred to in studies of “condylarths” and/or that we believe important in understanding evolution of the group. Reference is made to the taxa listed in the “Material and methods” section and comparisons are focused on relationships between “condylarths” from Tiupampa and North American mioclaenids and South American mioclaenids, didolodontids, and litopterns.

UPPER DENTITION

Posterior upper premolars (P3-4).

Comparison of premolars beyond “Condylarthra” (and its presumed descendants) is complicated by the fact that some fossils of archaic eutherians preserve five premolariform teeth, or at least evidence for five teeth, between the canine and first molariform tooth (e.g., Lillegraven 1969; Kielan-Jaworowska 1981; Kielan-Jaworowska & Dashzeveg 1989). This has suggested either that five premolars were originally present in Eutheria (McKenna 1975; Novacek 1986; Archibald & Averianov 1997) or, alternatively, that one of the teeth represents a retained deciduous tooth rather than a separate tooth locus (Luckett 1993). The tooth in question lies at the third position distal to the canine. Five premolars, or alveoli representing five premolars, are present in the “zhelestids” *Zhelestes*, *Sorlestes*, and

an unidentified genus (Nessov *et al.* 1998). Whatever the significance and identity of the third tooth in the premolar series of these and other early eutherians, positional and morphological evidence favours homology of the succeeding two premolars with the posteriormost two premolars of “condylarths” and remaining ungulates. For convenience, then, we ignore the anterior premolars (except P1, p1, mentioned briefly above), and simply refer to the last two premolars as penultimate and ultimate premolar for “zhelestids” and P3-4, p3-4 for “condylarths”.

Penultimate premolar. Judged from various “zhelestids”, the penultimate premolar was primitively simple in ungulatomorphs. In *Zhelestes temirkazyk*, the tooth (P4) consists almost entirely of a paracone without supporting crests other than the postparacrista, or cusps other than a faint protocone. In *Parazhelestes robustus*, the penultimate premolar is wholly premolariform, lacking a postparacrista and protocone (see Nessov *et al.* 1998: figs 9, 11). In basal “condylarths” (e.g., *Baioconodon*), the protocone of P3 (penultimate premolar) is consistently present. It is relatively larger than in the penultimate premolar of “zhelestids”, and generally bears faint pre- and postprotocristae that attach to weak parastyle and metastyle at the anterolabial and posterolabial corners of the tooth, respectively. We believe this to approximate the primitive condition for “condylarths”. We have no available specimens preserving P3 in *Protungulatum donnae*. Judged from Kielan-Jaworowska *et al.* (1979: fig. 12-9), the pre- and postprotocristae appear to have been lacking in this species. The paracone of P3 may be anteroposteriorly expanded in some Mioclaenidae (e.g., *Promioclaenus acolytus*), but here the general inflation of the premolars makes interpretation problematic. In *Litaletes*, at least, the P3 appears to be somewhat more advanced. The protocone is larger, with better developed protocristae, parastyle, and metastyle. A faint “metacone” (seen as an irregularity in the postparacrista) is present. Of early hyopsodontids, only *Haplaletes* was available to us for comparison. Here a metacone is lacking, and the protocone is somewhat larger than in Mioclaenidae. P3 of *Molinodus* is rather close to the hypothetical primitive pattern, being similar to that of

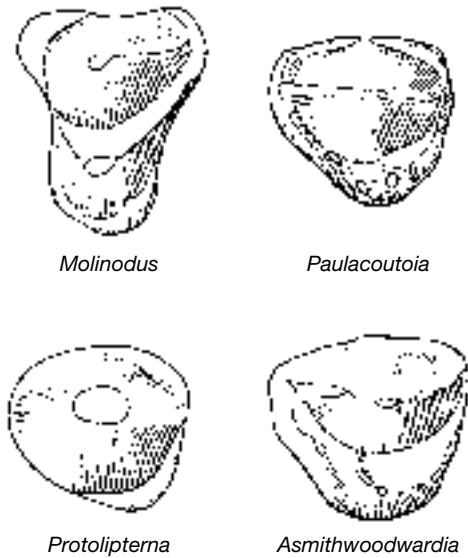


FIG. 16. — Occlusal view of the left P3 of some South American ungulates; *Molinodus suarezi* (MHNC 1247, reversed); *Paulacoutoia protocenica* (MNRJ 1461-V); *Protolipterna ellipsoidontoides* (MCT 1626-M); *Asmithwoodwardia scotti* (DGM 358-M). Not to scale.

Baiococonodon except for having a somewhat taller protocone. We find no evidence suggestive of relationships based on this tooth.

Didolodontids and primitive litopterns, on the other hand, have a somewhat more modified P3. In *Paulacoutoia*, a distinct preparacrista is present, as it is in some mioclaenids (but not *Molinodus*). The protocone is small but bears protocristae (faint or lacking in *Molinodus*) and is posteriorly placed. The P3 of *Protolipterna* (Fig. 16) is inflated; the protocone is small but, significantly, also has a peculiar posterior position, as in *Paulacoutoia*. The same is true of the P3 protocone in *Asmithwoodwardia*. Here, the paracone is antero-posteriorly elongate and bears a preparacrista, as in some mioclaenids (but not *Molinodus*). A small metacone, as in that of *Litaletes*, also is present. A preprotocrista is lacking, but the postprotocrista (and/or the postcingulum) defines a moderately large platform as it sweeps posterolabially from the protocone. This platform has been observed in *Paulacoutoia*, *Didolodus*, *Asmithwoodwardia*, and *Protolipterna*. The P3 of *Miguelsoria* is unknown, but P2 presents a condition similar to

that of P3 in these four genera of South American ungulates. It is therefore probable that the P3 of *Miguelsoria* also had an expanded posterior border.

Ultimate premolar. The ultimate premolar of known “zhelestids” (P5) and early “condylarths” (P4) is somewhat variable. The protocone in “zhelestids” is generally small (somewhat larger in *Eoungulatum*) and retains a distinct “waist” formed by an anterior concavity between protocone and paracone when the tooth is seen in occlusal view. This “waist” seems to be lost in “condylarths”, in which the protocone is better developed and the occlusal outline of the tooth more nearly triangular. A preparacrista is lacking in “condylarths”, but the postparacrista generally forms a trenchant cutting surface that terminates at the metastyle. The parastyle is generally strong, and the presence of a nearly complete labial cingulum is widely distributed and also probably primitive for ungulates. The ultimate premolar of *Aspanlestes*, *Zhelestes* and *Parazhelestes* bears a small but distinct metacone and a faint paracone. Because these features are lacking in early “condylarths” (e.g., *Protungulatum*, *Oxyprimus*, *Baiococonodon*) we believe that “zhelestids” may be precociously specialized in this respect. The absence of these cusps probably should be considered primitive for “Condylarthra”.

At least a small postcingulum is also probably primitive for ungulates. The presence of a precingulum is variable (it is present, for example, in *Mimatuta*, but lacking in *Baiococonodon*). If present primitively, it probably was weak. Similarly, the protocristae are generally weak and probably did not reach the respective styles.

In Mioclaenidae, the postparacrista tends to be straight, not curving labially, a condition that we interpret to be derived. Additionally, the parastyle is reduced relative to the condition seen, for example, in *Protungulatum*. Mioclaenids are also characterized by a moderate (e.g., *Valenia*, *Litaletes*, *Promioclaenus*, *Protoselene*) to strong (e.g., *Choeroclaenus*, *Mioclaenus*) degree of inflation of P4. Faint conules are present in some taxa (a metaconule is variably present in *P. acolytus*; both metaconule and paraconule are present in *Litaletes*). A metacone is also variable in presence. The significance of this is hard to judge because

of the confounding factor of tooth inflation. The metacone is present in two of the species with the least inflated P4, *Litaletes disjunctus* and *Valenia wilsoni*. As stated above for the metaconid, the condition of *Choeroclaenus* and *Mioclaenus* (lack of incipiently developed conules and metacone) may be a reversal due to the inflation of the P4.

P4 of the hyposodontids compared is rather different. That of *Litomylus* is extremely transverse, with a large anterior concavity. A large parastyle is retained in this taxon and *Haplaletes*, and there are neither metacone nor conules.

A metacone is lacking from P4 of *Molinodus*, but incipiently developed conules are present (see description above). The P4 of *Molinodus* resembles that tooth in North American mioclaenids, particularly in reduction of the parastyle and the straight postparacrista. In both didolodontids (e.g., *Paulacoutoia*, *Lamegoia*, *Didolodus*) and primitive litopterns (*Miguelsoria*, *Asmithwoodwardia*, *Protolipterna*), P4 is somewhat more advanced: in all, pre- and postcingula extend labially to the parastyle and metastyle, respectively, which are both reduced; a metacone is developed in a characteristic position, close to the apex of the paracone and “twinned” with that cusp. Furthermore, the protocone of P4 in didolodontids and early litopterns is enlarged, which gives the tooth a quadrangular outline. This morphology is regarded as derived when compared to the triangular morphology present in most mioclaenids and primitive North American “condylarths” (e.g., *Protungulatum*, *Oxyprimus*, *Mimatuta*, and *Baiococonodon*). It is noteworthy, however, that a condition similar to that in didolodontids and litopterns is present in *Mioclaenus* and *Protoselene*.

Inflation of premolars. Premolars of “zhelestids” are gracile and slender. They are regarded as not inflated and represent a plesiomorphic character state. All mioclaenids have inflated premolars (uppers and lowers), although the degree of inflation varies. P3s and P4s are only slightly inflated in *Valenia* and *Litaletes*. They are moderately inflated in *Promioclaenus*, *Ellipsodon*, *Protoselene*. They are strongly swollen in *Mioclaenus* and *Choeroclaenus*. The premolars of kollpaniines are slightly inflated (*Tiucloaenus*, *Pucanodus*) to moderately inflated (*Molinodus* and *Simoclaenus*).

Premolars are also moderately to strongly inflated in didolodontids and early litopterns.

Archibald (1998) has created the taxon Bulbulodentata to include the Periptychidae and the Mioclaenidae on the single basis of the swollen aspect of their premolars. Although this possible synapomorphy of the Bulbulodentata represent a relatively weak support, which can certainly be homoplastic, a review of this character in most “condylarths” taxa seems to favour his interpretation. Swollen p3-4 are also present in the didolodontids and early litopterns such as protolipternids. Because these groups probably originated among North American mioclaenids, they should be included in the Bulbulodentata. However, it is noteworthy that the p3-4 of *Tiucloaenus minutus* and *Asmithwoodwardia scotti* are only moderately swollen. This raises the problem of subjectivity of appreciation when diagnosing taxa with qualitative character states (i.e. very often when dealing with teeth). Where is the limit between a swollen and a not swollen premolar? In spite of this restriction, which was clearly pointed out by Archibald (1998: 309), we accept, as a working hypothesis, the taxon Bulbulodentata, which we regard as also including the Didolodontidae and litopterns.

Upper molars

As suggested by their hypothesized position as basal ungulatmorphs (see Nessov *et al.* 1998), “zhelestids” have upper molars that are, in many respects, morphologically intermediate between those of primitive eutherians such as *Prokennalestes* (Kielan-Jaworowska & Dashzeveg 1989), and early “condylarths”. In *Aspanlestes*, for example, a moderate-sized stylar shelf is retained, together with a small stylocone; the postmetacrista and preparacrista are labially directed and retain important shearing function (see Crompton 1971); paracone and metacone are tall and sharp, with the paracone noticeably taller than the metacone; conules have salient “wings” (conular cristae, particularly postparaconular crista and premetaconular crista) and are placed close to the bases of paracone and metacone; the preparaconular and postmetaconular cristae terminate labially adjacent to the base of the paracone and metacone respectively (i.e. they do not

reach the parastyle and metastyle lingually; i.e. there are no para- and metacingula; parastylar and metastylar projections are prominent.

Comparison of the various taxa included in this study suggests that the following features of the upper molars probably are derived for “condylarths”, with respect to “zhelestids”: cusps lower, more rounded; stylar shelf greatly reduced, stylocone fused to parastyle (sometimes not completely in primitive forms such as *Protungulatum*, *Oxyprimus*, and *Mimatuta*); protocone antero-posteriorly broader, with better developed pre- and postcingulum; postmetaconular crista extends labially to metastyle (appearance of a metacingulum). *Protungulatum*, otherwise suitable as an ancestor for all ungulates (see Sloan & Van Valen 1965; Van Valen 1978; Van Valen 1988), appears to diverge from this morphotype in two important ways: a small hypocone is present, and the conules are more lingually placed. The same is true concerning *Oxyprimus* although this genus has been regarded by Luo (1991: 454) as more primitive in some character states than *Protungulatum*.

Stylar shelf and labial cingulum. It is notable that primitive periprychids (e.g., *Maiorana*, *Mimatuta*) and various basal arctocyonids (e.g., *Baioconodon*, *Protungulatum*, *Oxyprimus*) retain (when compared to “zhelestids”) a narrow stylar shelf. In contrast, it is reduced to a strong labial cingulum in most “condylarth” groups, including both Mioclaenidae and Hyopsodontidae. There is some suggestion that the reduction of the stylar shelf occurred independently, as the condition in *Valenia wilsoni* appears to be intermediate between what is observed in *Protungulatum* and *Promioclænus acolytus* (in which the shelf is reduced to a strong labial cingulum). The labial cingulum of *Molinodus* resembles that of primitive mioclaenids or hyopsodontids. *Tiucloenus* and *Pucanodus* are more derived than *Molinodus* as their labial cingulum is either reduced (to a labial rim) or, lost. Because of the presence of this synapomorphy in the two kollpaniine genera, they probably belong to the same clade. An interesting characteristic exists in some specimens of *Pucanodus* and *Tiucloenus* on the one hand and some didolodontids and early litopterns on the other. In MHNC 8342 (*Tiucloenus cotasi*),

MHNC 8340, 1268 (*Pucanodus gagnieri*), a weak cingulum (rim) is present on the labial edge of the metacone only. This cingulum is not present in all specimens and is variably developed. A relatively well-developed metacone labial cingulum (more developed than in *Tiucloenus* and *Pucanodus*) is variably observed in some didolodontids (*Paulacoutoia*, *Lamegoia*, *Ernestokokenia*) and in early litopterns (*Miguelsoria*). However, the cingulum is continuous in some specimens referred to these taxa. In other taxa (*Didolodus*, *Protolipterna*, *Asmithwoodwardia*), a continuous cingulum is generally present. In these genera, although more continuous from parastyle to metastyle, the labial cingulum is often interrupted labial to the paracone. Therefore, the plesiomorphic continuous cingulum observed in most North American mioclaenids (e.g., *Litaletes*, *Choerocloenus*, *Protoselene*, and *Promioclænus*) and some South American taxa (e.g., *Molinodus*, *Simocloenus*) is probably not homologous to the labial cingulum observed in several didolodontids and early litopterns. The South American ungulates seem to be characterized by a tendency to lose the labial cingulum in a first stage (*Tiucloenus* and *Pucanodus*) followed by a reversal trend to increase the cingulum, essentially labial to the metacone.

Parastyle. As mentioned in the section comparing *Molinodus*, the parastylar lobe of early eutherians (e.g., *Prokennalestes*, “zhelestids”) is made of the stylocone (labial to anterolabial to the paracone), the parastyle (anterior to the paracone) and the preparastyle (lingual to the parastyle). In early “condylarths”, the preparastyle is generally not clearly present (it possibly disappears or merges with the parastyle), and the parastyle and stylocone are closely approximated (*Protungulatum*) or sometimes connate (*Oxyprimus*, *Mimatuta*, *Maiorana*). In more derived “condylarths”, there is only one cusp at the anterolabial angle of the molars. The morphology observed on the specimen of *Molinodus* MHNC 8280 (in which possible relicts of the stylocone and preparastyle are present) favours the hypothesis that what is called the parastyle in the great majority of “condylarths” is, in fact, the result of the fusion of the three cusps of the parastyle *s.s.*, the stylocone and the preparastyle. Note, however,

that the parastyle is clearly larger than the two other cusps. In fact, as mentioned above, the stylocone, when distinct in "condylarths" is often reduced to a small elevation at the junction of the preparacrista and the labial cingulum. The fusion of the stylocone to the parastyle seems to be, in fact, a simple capture of the preparacrista (and therefore the stylocone) by the parastyle. Therefore, the parastyle of most "condylarths" is probably not homologous to the parastyle *s.s.* observed in *Prokennalestes*, "zhelestids", or *Protungulatum*, but would be homologous to the parastylar lobe. The parastyle on M1-2 of *Protungulatum*, as in that of "zhelestids", is rather large, and this is also the case in *Baioconodon* and primitive peripitychids (*Mimatuta*, *Maiorana*). As mentioned above, in these genera, the parastyle *s.s.* is separated from the stylocone. Like the styler shelf, the parastylar lobe of M1-2 tends toward reduction early in various lineages, perhaps independently. The parastylar lobe of M1-2 (commonly called parastyle) of primitive hyposodontids is reduced (*Haplaletes*) or absent (*Litomylus*). Among mioclaenids, *Valenia wilsoni* retains a medium-sized parastyle of M1-2, whereas it is extremely reduced or lost in its presumed descendant (see Van Valen 1978), *Promioclænus acolytus*. In other North American mioclaenids, the parastylar lobe of M1-2 is either medium-sized (*Litaletes*, *Bubogonia*) or small (*Choeroclaenus*). The parastylar lobe on M1-2 of *Molinodus* is small to medium-sized and relatively large for a mioclaenid in MHNC 8280. It is extremely reduced or lacking in didolodontids and early litopterns. In some respect, M3 often appears to "lag behind" the preceding molars in terms of acquisition of derived character states, and this seems to be the case for the parastylar lobe, which we address separately for this tooth locus. All arctocyonids, peripitychids, and hyposodontids that we studied retained a relatively larger and more salient parastylar lobe on M3 than on M2. Among Mioclaenidae, this feature was present in *Litaletes* and *Valenia*. In *Choeroclaenus* and *Protoselene*, the parastylar lobe of M3 is similar in size to that of M2 but M3 is slightly smaller than in *Litaletes* and *Valenia*. *Promioclænus acolytus* and *Mioclænus* have a parastylar lobe clearly smaller on M3 than on M2. Notably, in *Molinodus* the parastylar

lobe of M3 is smaller than on M2. The parastyle of Didolodontidae and primitive Litopterna is so reduced (when present) that there is hardly a size difference between the parastyle of M2 and M3 (*Paulacoutoia*, *Didolodus*, *Asmithwoodwardia*). However, in *Protolipterna* and *Miguelsoria*, a small parastyle is still present and is smaller on M3 than on M2.

Mesostyle. A mesostyle is absent in primitive taxa (e.g., "zhelestids", *Protungulatum*, *Mimatuta*, *Maiorana*, *Baioconodon*), which represents a plesiomorphic state. This structure is also absent in most mioclaenids, with the exception of *Protoselene*, *Mioclænus*, *Pleuraspidotherium*, and *Orthaspidotherium*. A well-developed mesostyle also is present in *Didolodus* [*Enneoconus* and *Paulogervaisia*, which also bear a mesostyle, are regarded by McKenna & Bell (1997) as junior synonyms of *Didolodus*], and all derived litopterns (Lopholipterna of Cifelli 1983a). The Protolipternidae (*Protolipterna*, *Asmithwoodwardia*, and *Miguelsoria*) lack a mesostyle. Cifelli (1983a) regarded the morphology of *Didolodus* and Lopholipterna as a convergence. The same is probably true for the mesostyle of the Pleuraspidotheriinae. The Kollpaniinae have no mesostyle, but the M2 of *Molinodus* and *Simoclaenus* present a small inflation or cuspule, respectively, on the labial cingulum in a mesostyle position. This inflation or cuspule could represent an incipient development of a mesostyle.

Para- and metacristae. Primitively, the preparacrista and postmetacrista bear some of the most important shearing surfaces of tribosphenic upper molars (see Crompton 1971). The crests extend more or less labially from paracone to stylocone and from metacone to metastyle, respectively. In the trend toward bunodonty which characterizes early ungulates, these crests are reduced, although retained in basal members of most groups. The crests are directed more or less labially in basal arctocyonids (e.g., *Protungulatum*, *Baioconodon*) and peripitychids (e.g., *Maiorana*, *Mimatuta*). In primitive hyposodonts, both crests are oriented more or less anteroposteriorly in *Haplaletes*; in *Litomylus*, the preparacrista is absent, but the postmetacrista retains the primitive (labial) orientation. Among Mioclaenidae, the primitive (somewhat labially directed, at least) condition is retained in the basal

genera *Bubogonia* and *Valenia* for both crests. The preparacrista of *Litaletes*, *Choeroclaenus*, and *Protoselene* is also labially directed. In remaining North American mioclaenids, both crests have an approximately anteroposterior orientation (i.e. they are aligned with the paracone and metacone). *Molinodus* has a postmetacrista that is posteriorly directed, but the anterior extremity of the preparacrista (at the junction with the parastyle) extends somewhat anterolabially from the paracone (this feature is present in MHNC 1247 and 8082; it is absent in YPFB Pal 6118). We interpret the condition of *Molinodus* to be a retention of a primitive feature (the condition in *Molinodus* and *Protoselene* shows some individual variation). In *Promioclauenus acolytus*, *Mioclauenus*, *Tiucloaenus*, *Pucanodus*, primitive litopterns, and didolodontids, both crests are more or less anteroposteriorly oriented. *Paulacoutoia* is unusual and probably derived, in that the preparacrista extends anterolingually from the paracone. A condition approaching that of *Paulacoutoia* is also found in *Ernestokokenia*.

Paracone and metacone. In “zhelestids”, *Protungulatum*, *Oxyprimus*, *Mimatuta*, *Baiococodon*, and North American mioclaenids (except *Mioclauenus*), the metacone of M2 is posterior to slightly lingual to the paracone. This condition is not observed on M1. Therefore, a posterior to slightly lingual position of the metacone in regard to the paracone on M2 probably represents a plesiomorphic character state. This state is retained in *Pucanodus*, most didolodontids, and primitive litopterns. A derived condition is found in *Molinodus*, *Simoclaenus*, and *Tiucloaenus*, in which the metacone of M2 is strongly lingual to the paracone. The lingual displacement of the metacone is also observable on M1, although to a lesser extent than on M2. The condition of *Molinodus* and *Simoclaenus* is clearly more pronounced than on *Tiucloaenus*. This derived character state is present on the M2 and M1 of *Mioclauenus*, *Ellipsodon*, and on the M2 (MNRJ 1465 V) referred to *Lamegoia* by Paula Couto (1952). However, it is noteworthy that the metacone is not conspicuously lingual to the paracone on the M1 (MNRJ 1464 V) referred to *Lamegoia* by Cifelli (1983a) and that no M1 is associated with the M2 mentioned above. The lingual displace-

ment of the metacone could represent a synapomorphy of *Molinodus*, *Simoclaenus*, and *Tiucloaenus*. Whether or not *Lamegoia* could be associated to these two genera is pending upon the discovery of more complete upper dentition of this genus (e.g., with associated M1 and M2). The condition of *Mioclauenus* and *Ellipsodon* is probably the result of homoplastic evolution.

As mentioned by Nesson *et al.* (1998), the paracone of M2 in “zhelestids” is higher and more voluminous than the metacone, which represents the plesiomorphic condition. It is also present in *Protungulatum*, *Oxyprimus*, and *Baiococodon*. The two cusps are subequal in size in *Mimatuta* and *Maiorana*. In North American mioclaenids, the size difference is extremely subtle and variable within the same taxon. The paracone is generally slightly larger than the metacone in *Valenia*, *Promioclauenus*, *Mioclauenus*, and *Choeroclaenus*. The paracone and metacone are generally subequal in volume and height in *Bubogonia*, *Protoselene* and *Litaletes*. The paracone is always higher and almost always more voluminous than the metacone in kollpaniines, didolodontids and primitive litopterns. Therefore, the Tiupampa “condylarths”, the didolodontids, and the primitive litopterns retain the plesiomorphic condition and are more primitive than the North American mioclaenids.

Precingulum, postcingulum, preparaconular and postmetaconular cristae (Figs 17, 18). The nature, extent, and attachments of anterior and posterior crests also vary significantly among upper molars of ungulates and ungulate-like mammals (Van Valen 1988; Nesson *et al.* 1998). Primitively, among tribosphenic mammals, the preparaconular and postmetaconular cristae probably terminated near the lingual bases of paracone and metacone in line with the apices of the para- and metacones, respectively. The cristae did not extend into the interstitial regions of the tooth (Fox 1975; Cifelli 1993b; Nesson *et al.* 1998). In “zhelestids”, this primitive pattern for the postmetaconular crista is retained. The primitive pattern for the preparaconular crista is retained only in *Aspanlestes*, while in *Parazhelestes* and *Eoungulatum* the preparaconular crista extends labially to attach to the stylocone (Nesson *et al.* 1998: 52, 57, 59) but the postmetaconular

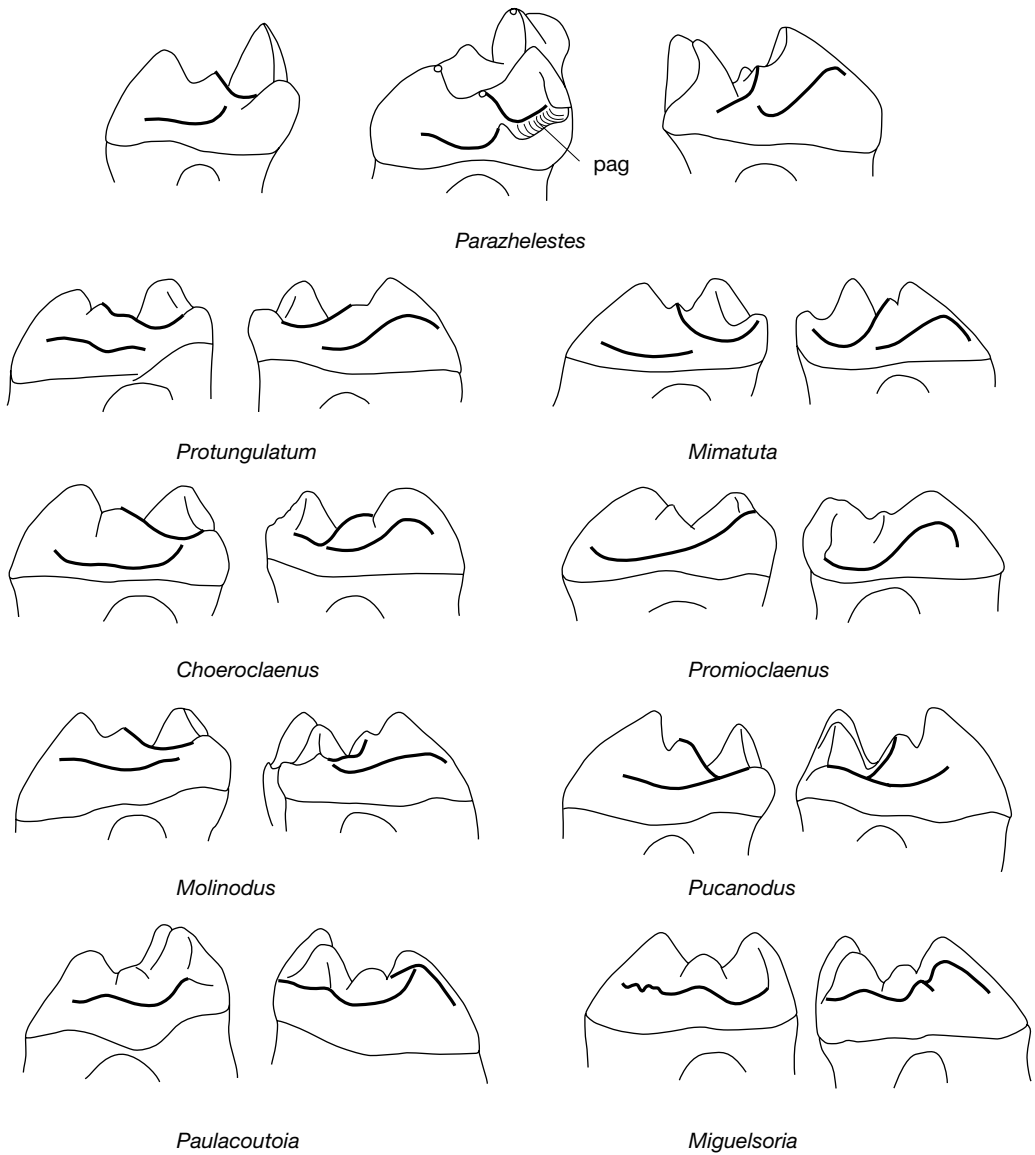


FIG. 17. — Anterior (left) and posterior (right) views of the left M2 of some ungulatormorphs to show the relationships of the labial extremities of the pre- and postcingula to the premetaconular and postmetaconular cristae. The middle view of *Parazhelestes* is anteroventral and shows the parastylar groove (**pag**). *Parazhelestes minor* (CCMGE 11/12953); *Protungulatum donnae* (UM 5206); *Mimatuta minual* (PU 14211, reversed); *Choeroclaenus turgidunculus* (reconstructed from AMNH 3291 and 16499); *Promioclaenus acolytus* (AMNH 35778); *Molinodus suarezi* (MHNC 8280); *Pucanodus gagnieri* (MHNC 1268); *Paulacoutoia protocenica* (MNRJ 1458-V, reversed); *Miguelsoria paryirunhor* (DGM uncatalogued). Not to scale.

crista does not reach the metastyle. In basal “condylarths” (as in *Alostera*; see Nesson *et al.* 1998: 66), the postmetaconular crista is complete and extends to the metastyle or to the metastylar region of the tooth. This labial extension of the preparaconular and postmetaconular cristae are called para- and metacingula by Van Valen 1966. The acquisition of connection of preparaconular and postmetaconular cristae to the styles, which we believe to be primitive for “Condylarthra”, takes place with the development of pre- and postcingula, and their “capturing” of the para- and metacingular crests (i.e. the labial portions of the preparaconular and postmetaconular cristae) (Figs 17, 18). As a consequence of this “capture” of the para- and metacingula by the pre- and postcingula, linguolabial continuity of the conule cristae is disrupted. However, it is noteworthy that there are few individual instances in which both cristae and cingula independently attach to a style without capture of the conular cristae by the cingula (Fig. 18). As with so many other changes in the molars, this character apparently changed states independently a number of times in “Condylarthra”, and, in most cases, appears to have done so during the early Palaeocene.

In basal arctocyonids (*Protungulatum*, *Oxyprimus*, *Baiococonodon*) and early peripitychids (*Maiorana* and *Mimatuta*), both preparaconular and postmetaconular cristae are attached to parastyle and metastyle and pre- and postcingula do not reach the styles remaining independent from the conular cristae. This condition is regarded here as plesiomorphic for “condylarths”. It is noteworthy that in *Baiococonodon* the precingulum almost contacts the preparaconular crista midway between the paraconule and the parastyle. In the earliest phenacodontid (*Tetraclaenodon*), by contrast to the condition of early arctocyonids and peripitychids, the pre- and postcingulum attach to the styles and no crest connects the conules to the cingula. This condition is regarded here as derived. Among hyopsodontids, *Litomylus* retains the primitive condition both anteriorly and posteriorly on its M1-2. *Haplaletes*, on the other hand, presents the derived condition and has a derived cingular attachment to the parastyle and metastyle. A similar condition is found in *Haplomyilus* and *Hyopsodus*.

Assuming monophyly of the group as conventionally defined (e.g., Archibald 1998), changes in crest-style attachments also occur within Mioclaenidae. *Valenia wilsoni* and *Choeroclaenus turgidunculus* retain attachment of preparaconular and postmetaconular cristae to parastyle and metastyle, respectively, but the labial extremities of the pre- and postcingula are above (and very close to) the labial edge of the conules or the lingual edge of the para- and metacone, respectively. In *Bubogonia* and *Protoselene*, the preparaconular crista-parastyle attachment is retained, but both postcingulum and post-metaconular crista attach to the metastyle. In remaining North American taxa studied (*Promioclænus*, *Litaletes*, *Mioclænus*), the cingula have completely “captured” style attachments. In these genera, the conular part of the conular cristae is reduced. *Molinodus suarezi* is of considerable interest in this regard, because it appears to be one of a few “intermediate” taxa known. The preparaconular and postmetaconular cristae of *M. suarezi* are complete, extending labially to their respective styles, but the cingula approximate the styles closely or join with the conular cristae in meeting them. In *Tiuclaenus*, *Pucanodus*, didolodontids, and primitive litopterns, the stylar connections (= para- and metacingular crests) have been “captured” by the pre- and postcingula.

Figure 18 presents a summary of the various morphotypes that we observed in the evolution of the relationships of the postmetaconular crista and meta- and postcingula and as expressed in the parsimony analysis below. Type 1 is present in “zhelestids”; type 2 is present in *Protungulatum*, *Oxyprimus*, and *Mimatuta*; type 3 is present in *Bubogonia*, *Protoselene*, *Molinodus*, and *Simoclaenus*; type 4 is present in *Choeroclaenus*, *Valenia*; type 5 is present in *Pucanodus*; type 6 is present in *Promioclænus*, *Litaletes*, *Mioclænus*, *Ellipsodon*, *Tiuclaenus*, and primitively in didolodontids and litopterns. Type 4 and 5 are regarded as the same character state since the “capture” of the metacingulum is incipiently present in type 4.

Conules and internal conular cristae. As noted above, the primitive condition for the conules (paraconule, metaconule) probably involved their placement near the bases of paracone and metacone, respectively, and the presence of well-marked “wings” (internal conular cristae; see

above). This condition is present in “zhelestids” (Nessov *et al.* 1998: 75-76). Conules placed near the bases of protocone and weak (when compared to “zhelestids”) internal conular cristae are present, with minor variations, throughout basal members of all condylarthran families. *Molinodus* represents an unusual departure in that the internal conular cristae (postparaconular crista, premetaconular crista) are lacking. This same condition is seen in some Didolodontidae (*Paulacoutoia*, *Didolodus*, *Lamegoia*) and primitive Litopterna (e.g., *Asmithwoodwardia scotti*, *Miguelsoria*, *Protolipterna*). It is noteworthy that these cristae are occasionally present in *Paulacoutoia*, *Miguelsoria*, and *Protolipterna*, but always very faint. The loss of postparaconular and premetaconular cristae could represent a synapomorphy of the Kollpaniinae, Didolodontidae, and Litopterna. However, postparaconular and premetaconular cristae are present in molars observed during this study and referable to *Ernestokokenia cf. nitida* (MLP 59. II. 24-11 and 541; MNHN CAS 683), on the holotype of *Asmithwoodwardia subtrigona* (MACN 10723), and on one M3 referable to *Proectocion argentinus* (MACN 10673). Therefore, this feature is not constant and may not represent a synapomorphy of the three groups. Furthermore, postparaconular and premetaconular cristae are variably present in basal arctocyonids, and North American mioclaenids. Luo (1991) stated that those crests were present in *Oxyprimus* and absent in *Protungulatum*. However, we have observed specimens of *Oxyprimus* lacking them and individuals of *Protungulatum*, in which they were present. Among the “condylarths” taxa that we have observed, this character appears to show great individual and interspecific variations. The only statement that we can confidently make on the development of postparaconular and premetaconular cristae is that they are well-developed and sharp in “zhelestids” and tend to get reduced or disappear in “condylarths” and litopterns. This condition could be related to the increase in the size of the conules observed in didolodontids. However, it is noteworthy that the conules of *Protolipterna* and *Asmithwoodwardia* are not strongly enlarged and do not present conspicuous conular crests.

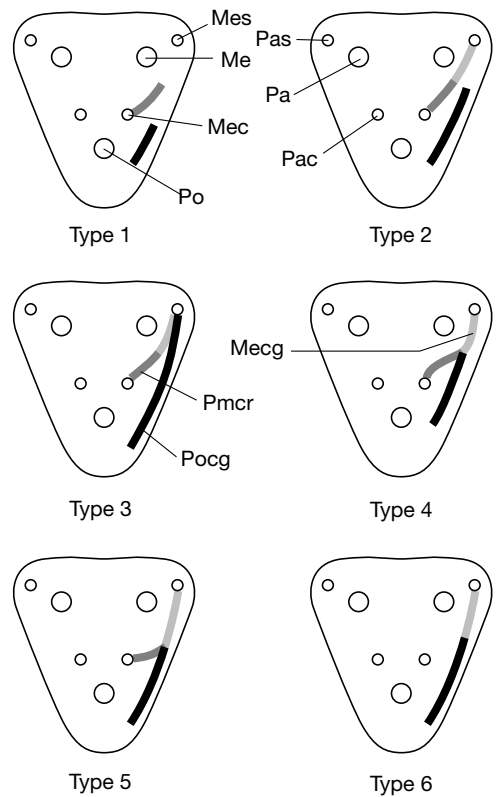


FIG. 18. — Schematic representation of the various conditions of the relationships between the postcingulum, the postmetaconular crista and the metacingulum as observed during this study and discussed in text. Type 1 is present in “zhelestids”; type 2 is present in *Protungulatum*, *Oxyprimus*, and *Mimatuta*; type 3 is present in *Bubogonia*, *Protoselene*, *Molinodus*, and *Simoclaenus*; type 4 is present in *Choeroclaenus*, *Valenia*; type 5 is present in *Pucanodus*; type 6 is present in *Promioclaenus Litaletes*, *Ellipsodon*, *Tiucclaenus*, and primitively in didolodontids and litopterns. Abbreviations: **Me**, metacone; **Mec**, metaconule; **Mes**, mesostyle; **Mecg**, metacingulum; **Pa**, paracone; **Pac**, paraconule; **Pas**, parastyle; **Pmcr**, premetaconular crista; **Po**, protocone; **Pocg**, postmetaconular crista.

Hypocone. As noted, we suggest the lack of hypocone on M1-2 to be a plesiomorphy for “condylarths”. This cusp is lacking in “zhelestids”, but obtains a wide distribution in “condylarths” (Fig. 19). A small hypocone (sometimes suggested by little more than a faint swelling of the postcingulum) is present on M1-2 of *Protungulatum*, *Baiococonodon*, and early Periptychidae such as *Maiorana* and *Mimatuta*, whereas this cusp is large and well-established in early Phenacodontidae (*Tetraclaenodon*) and Hyposodontidae (*Litomylus*,

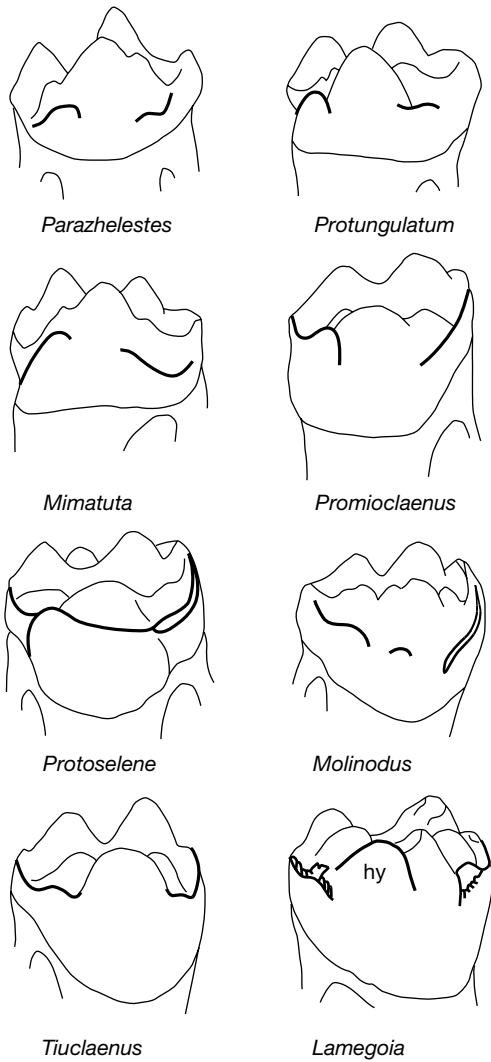


FIG. 19. — Lingual views of the left M2 of some ungulatiforms to show the lingual extremities of the pre- and postcingula and the development of a hypocone; *Parazhelestes minor* (CGME 11/12953, reversed); *Protungulatum donnae* (UM 5206); *Mimatuta minual* (PU 14211, reversed); *Promioclænus acolytus* (AMNH 35778); *Protoselene opisthacus* (KU 13997, reversed); *Molinodus suarezi* (MHNC 8280); *Tiuclaenus minutus* (MHNC 1240); *Lamegoia conodonta* (MNRJ 1465-V). Not to scale. Abbreviation: **hy**, hypocone.

Haplaletes). Mioclaenidae are distinctive in primitively lacking a hypocone on M1-2, as noted in the diagnosis of the family by Simpson (1937). The cusp is lacking in *Bubogonia*, *Valenia wilsoni*, and

Promioclænus acolytus, but in these genera, the lingual extremity of the postcingulum is clearly swollen and thicker than that of the precingulum. This is regarded here as an initial step in the development of a cusp and, therefore, we consider that a hypocone is incipiently developed in these genera. Depending on definition, a hypocone may be present in *Litaletes* (in which it would be defined by an abrupt, lingual, cusped termination of the postcingulum) and in *Choeroclænus*, in which the condition observed in *Litaletes* is slightly more emphasized. This cusp is completely lacking from M1-2 of *Molinodus*, *Tiuclaenus*, and *Pucanodus*, in which the lingual extremities of the pre- and postcingulum are subequal in thickness. All Didolodontidae and Litopterna have a strongly developed hypocone (Cifelli 1983a). Therefore, the Tiupampa “condylarths” mentioned above are more primitive for this character state than all North American “condylarths” (apparently), didolodontids and litopterns.

Contacts of the pre- and postcingula to the protocone. Lingually, the pre- and postcingula both contact the protocone at the base of its anterior and posterior slopes in “zhelestids”, basal arctocyonids (*Protungulatum*, *Oxyprimus*, *Baioconodon*) and early peripitychids (*Mimatuta*, *Maiorana*). This condition is regarded here as primitive for ungulates. In mioclaenids the condition varies. The plesiomorphic state is present in *Valenia*, *Bubogonia*, *Protoselene*, and *Ellipsodon*. In *Promioclænus*, *Litaletes*, *Mioclaenus*, and *Choeroclænus*, the lingual extremity of the postcingulum is more elevated on the posterior flank of the protocone than that of the precingulum on the anterior flank. This condition is derived. The plesiomorphic character state is present in the kollpaniines. The derived condition is present in primitive litopterns (*Miguelsoria*, *Asmithwoodwardia*, *Protolipterna*). It is absent in some didolodontids (*Didolodus*, *Ernestokokenia*, *Lamegoia*) but present in *Paulacoutoia*.

Precingular cusp. A distinct cusp is present on the precingulum anterior to the paraconule in all didolodontids and early litoptern considered in this study except *Asmithwoodwardia*. This condition is absent in “zhelestids”, *Protungulatum*, *Oxyprimus*, *Mimatuta*, and all mioclaenids except *Mioclaenus*. The presence of this cusp is regarded

as a derived character state convergently developed in *Mioclaenus*.

DENTARY AND LOWER DENTITION

The dentary and anterior dentition are so poorly represented for the "condylarths" of Tiupampa, as well as for primitive ungulates in general, that they are not yet useful for interpreting relationships. Nonetheless, they are worth passing mention because there appears to be some variation that, when better understood, may be of systematic relevance.

Mandibular symphysis

The symphysis was primitively unfused in mammals (Crompton & Hylander 1986), and this condition appears to be general to primitive members, at least, of the "Condylarthra" (e.g., *Protungulatum* and *Mimatuta*). What we interpret to be the plesiomorphic condition is retained in *Molinodus*, *Tiucloaenus*, and *Simocloaenus*, in which the symphysis is unfused (condition in *Pucanodus* and *Andinodus* is unknown). An unfused symphysis also exists in *Paulacoutoia*, the only didolodontid available to us in which the condition can be observed. However, the dentally similar taxa, *Asmithwoodwardia*, *Protolipterna*, and *Miguelsoria* (from Itaboraí, Brazil) have a fused symphysis. The last two genera were included in the Lipterna based on postcranial criteria; *Asmithwoodwardia* was also tentatively included in that order, but with little supporting evidence (Cifelli 1983a, b). As judged from figures and descriptions, the symphysis is fused in all advanced families of lipterns – Macraucheniiidae, Proterotheriidae, and Adianthidae (see Scott 1910; Cifelli 1993a, b, c). The condition in *Asmithwoodwardia*, *Protolipterna*, and *Miguelsoria* thus supports their referral to this order, and suggests that fusion of the symphysis occurred early in the differentiation of the group. Among other groups of South American ungulates, it would appear that the symphysis is fused in primitive notoungulates, such as the henricosborniid *Simpsonotus* (see Pascual *et al.* 1978) as well as the notostyloid *Notostylops* (see Simpson 1948). This also appears to be true of primitive astrapotheres such as *Tetragonostylops* but not, apparently, in xenungulates,

as represented by *Carodnia* (see Paula Couto 1952).

Lower canine

Bonaparte *et al.* (1993) noted that the lower canine of "Molidodinae" (= Kollpaniinae) (presumably reference is to *Tiucloaenus minutus*, the only kollpaniine species known by the lower canine in place) is reduced with respect to the condition seen in *Protungulatum* and *Oxyprimus*. A relatively large canine seems to be widespread among primitive "condylarths", judged from the comparisons we have made. A large canine is also present in *Baioconodon* and *Maiorana* (Van Valen 1978). The lower canine tends to be reduced in several mioclaenids (*Promioclaenus*, *Litaletes*, *Protoselele*, *Ellipsodon*, and *Miocloaenus*; see Simpson 1937), although it is apparently less reduced in those genera than in *Tiucloaenus*. The other kollpaniine in which the canine is known is *Pucanodus*. In this taxon, the canine is reduced although to a lesser extent than in *Tiucloaenus*. It is noteworthy, however, that the anterior cheek teeth of *Pucanodus* are taller than those of *Tiucloaenus* (Figs 7B, 12D). Unfortunately, the canine region is not known for many of South America's early ungulates. The canines are not known for Didolodontidae. Among early lipterns, the canine is quite small in *Miguelsoria* (in which it strongly resembles that of *Tiucloaenus*), moderately large in *Asmithwoodwardia* (see Paula Couto 1952), and hypertrophied in *Protolipterna* (see Cifelli 1983a). The canine is reduced in primitive notoungulates (see Simpson 1948; Pascual *et al.* 1978). In astrapotheres, on the other hand, they are developed into large tusks (Simpson 1967), and the canine of the xenungulate *Carodnia* is also a rather large, robust tooth. We tentatively regard the small canine of *Tiucloaenus* and *Pucanodus* as a derived character state. The very large canine of *Protolipterna* is probably an autapomorphy of this genus. However, given the small amount of taxa known by their canines, we are conscious that the significance of this character is difficult to establish.

Lower premolars

First premolar. At least the lower (and presumably also the upper) first premolar (or retained

dp1, see Luckett 1993) is two-rooted in primitive marsupials (Cifelli 1993c; Cifelli & Muizon 1997; Muizon 1998) and primitive eutherians such as *Prokennalestes* (see Kielan-Jaworowska & Dashzeveg 1989). The condition in “zhelestids” is known from a left partial dentary referred to *Sorlestes budan*, and a large, unnamed taxon, which have a two-rooted p1 (Nessov *et al.* 1998). It is noteworthy, however, that the type and only known specimen of *Zhelestes temirkazyk* (a left maxilla) has a single-rooted P1. In all “condylarths” we examined, as well as primitive members of Litopterna, Notoungulata, and Astrapotheria, both p1 and P1 (where present) are single-rooted. This suggests that reduction or fusion in the roots of p1 and P1 took place early in the history of Ungulatomorpha, and that the character may eventually prove useful for diagnosing some taxon within the group.

Penultimate premolar. To judge from *Aspanlestes*, the penultimate premolar (p4 of “zhelestids” and p3 of “condylarths”) was primitively a simple, premolariform tooth with a lanceolate protoconid and a small anteroposteriorly elongate, blade-like talonid. However, although there is no metaconid on the p4 of *Aspanlestes aptap* (Nessov *et al.* 1998: 52), it is noteworthy that a metaconid swelling is present (Archibald, pers. comm.). The condition in basal arctocyonids such as *Protungulatum* and *Baioconodon* is not much different, save for the presence of a small, antero-basal cuspule, presumably the paraconid. Interpreting premolar morphology in certain taxa, including some peripitychids, mioclaenids, and primitive litopterns is problematic. For example, it cannot be determined if their simple morphology is really primitive, or if accessory cusps have undergone secondary reduction as a result of the inflation of the teeth in general. With this caveat in mind, p3 of mioclaenids is generally simple; a paraconid may be absent or developed as a small crest (e.g., *Promioclauenus acolytus*), or basal cuspule (e.g., *Litaletes disjunctus*). The protoconid of p3-4 is quite inflated in *Choeroclaenus*, *Mioclauenus*, and to a lesser extent in some species of *Promioclauenus* (e.g., *P. lemuroides*). It is also quite inflated in some didolodontids (*Lamegoia*, *Didolodus*) and litopterns (*Protolipterna*).

Trigonid of p3-4. There are certain resemblances among the p3-4 of some hyopsodontids and some mioclaenids, but we have not been able to interpret an intelligible pattern to these similarities. For example, the posterior face of the trigonid on p3-4 (unless the latter tooth is strongly molarized) in *Litomylus*, *Litaletes*, and *Promioclauenus acolytus* has a characteristic flat or slightly fluted appearance, because of its sharply defined lingual and lateral edges. A similar condition is found on the p4 of *Protungulatum*, although less pronounced and without the sharp lateral edges. This feature is observable, but weak, on the p4 of *Haplaletes* (another of the hyopsodontids included in the comparisons) but it is not clear whether or not it is present on the p3. This condition is attenuated or disappears in other mioclaenids, such as *Protoselene*, *Choeroclaenus*, and *Mioclauenus* because of the strong inflation of the last two premolars. In *Tioclauenus* and *Pucanodus*, the posterior face of the trigonid of the p3 is not flattened and the condition of the p4 resembles that of *Protungulatum*. In *Simoclaenus* and *Molinodus*, the posterior wall of the p4 is distinctly flattened but the tooth does not bear any lateral crests as observed in *Promioclauenus* (the p3 of *Molinodus* and *Simoclaenus* is unknown). In fact, the widening and flattening of the posterior wall of the trigonid of p3-4 corresponds to a tendency to molarization of the premolars and, in this respect, *Promioclauenus* and *Litaletes* are more specialized than *Protungulatum*, *Tioclauenus* and *Pucanodus*. Another similarity between the premolars of mioclaenids and hyopsodontids, is the anteroposterior elongation of the trigonid of p3-4 in some taxa of the two families (e.g., *Promioclauenus acolytus*, *Litaletes*, *Litomylus*) but not others (*Choeroclaenus*, *Haplaletes*).

In mioclaenids such as *Promioclauenus*, *Mioclauenus*, *Choeroclaenus*, and *Protoselene*, it seems clear that it is the strong inflation of p4 that hides the posterior flattening of the trigonid and that incorporates the metaconid with the protoconid. These mioclaenids have increased the crushing surface of their premolars by inflating them whereas other “condylarths” have performed it by a tendency to molarize their last premolars (*Litaletes*, *Haplaletes*, *Molinodus*, and *Simoclaenus*). However, it is noteworthy that *Litaletes*,

Molinodus and *Simoclaenus* have a more inflated p4 than *Hapalestes*. *Tiucloaenus* and *Pucanodus*, in which the p4 is only slightly more inflated than in *Protungulatum*, are more plesiomorphic than the North American mioclaenids in this respect.

Paraconid of ultimate premolar. Of "zhelestids" included in our comparisons, the ultimate lower premolar is known for *Aspanlestes* and *Sorlestes*. In these genera, there is no paraconid, the metaconid is small, the posterior wall of the trigonid is not flattened. A low, somewhat lingually placed paraconid is present in *Protungulatum* and certain other archaic ungulates, in which the cusp is slightly more strongly developed (e.g., *Baioconodon*, *Mimatuta*). The condition in *Valenia wilsoni* appears to approximate most closely the primitive condition for "Condylartha": the paraconid is a tiny cusp shifted only slightly lingually and the metaconid is a small cusp that is much more reduced in height and volume than the protoconid, placed posterolingual to the protoconid and connate with it. Under this interpretation, *Molinodus*, with its small, centrally-placed paraconid, does not depart significantly from the ungulate morphotype.

Metaconid of ultimate premolar. A metaconid is absent on the ultimate lower premolar of *Prokennalestes* (Kielan-Jaworowska & Dashzeveg 1989; Sigogneau-Russell *et al.* 1992). The step (extremely faint indeed) noted by Sigogneau-Russell *et al.* (1993: 206) on the posterior crest of p5 of *Prokennalestes trofimovi* (PSS 10-41) is not regarded as an incipient metaconid, *contra* the authors, because it is not located on the lingual side of the protoconid. A small metaconid is present in "zhelestids" (*Aspanlestes* and *Sorlestes*), in which it is small but distinct. It is placed high on the lingual side of the protoconid but is poorly differentiated from that cusp. A similar condition is found on the p4 of primitive ungulates, such as *Protungulatum*, *Oxyprimus*, *Baioconodon*, *Valenia*, and *Maiorana*. Contrary to statement by Luo (1991), we have not observed a significant size difference between the metaconids of *Protungulatum* and *Oxyprimus*. This condition is probably the plesiomorphic character state for Ungulatomorpha (Archibald pers. comm.). This is also generally the condition in hyopsodontids. In some North American mioclaenids (e.g.,

Choeroclaenus, *Protoselene*, and *Mioclaenus*), the metaconid is generally obliterated by the inflation of the p4. This derived condition is less pronounced in *Promioclaenus*, where a small metaconid is still observable in spite of the inflation of the p4. In *Litaletes*, although the p4 is swollen, the metaconid is rather tall and almost transversely aligned with the protoconid, which we regard as an autapomorphy of the genus. The condition of *Litaletes* is similar to what is seen in *Molinodus* (on MHNC 1244) and *Simoclaenus*. In the other Tiupampa "condylarths" (*Tiucloaenus*, *Pucanodus*), the condition of the metaconid approaches the plesiomorphic (or suggested as such) condition of *Protungulatum*. The condition is variable in other primitive ungulates of South America. The metaconid is transverse with respect to the protoconid in the didolodontid *Paulacoutoia* but more posteriorly placed in *Lamegoia*, and tends to be transversely placed in primitive litopterns (e.g., *Asmithwoodwardia*, *Miguelsoria*). In *Protolipterna*, the metaconid is generally lacking or small. However, in DGM 1392 D-M (a partial dentary with unworn p4-m1), the metaconid of p4 is clearly large and is medial to the protoconid, although appressed against it. In this genus the metaconid probably merges secondarily with the protoconid as a consequence of inflation of p4 (as in *Choeroclaenus*). Therefore, the pattern of distribution of this character is probably highly homoplastic but denotes a clear tendency of "condylarths" to increase the size of the metaconid and to place it in a more transverse position relative to the protoconid, which we regard as a tendency to molarization of the p4.

Talonid of ultimate premolar. The talonid of p4 probably consisted primitively of a single, blade-like cusp (Luo 1991). This condition is general to the plesiomorphic arctocyonids such as *Protungulatum*, *Oxyprimus*, and *Baioconodon*. In the "zhelestids" *Aspanlestes* and *Sorlestes*, the talonid of the ultimate premolar also bears an incipient basin lingually. We regard this condition as derived when compared to that of the arctocyonids mentioned above. As with so many other features of the dentition, elaboration of the talonid almost surely occurred numerous times in various lineages. A basined talonid, usually with at least two cusps, occurs in primitive peripity-

chids (*Mimatuta*, *Maiorana*, though separate cusps are lacking in the latter), mioclaenids (*Promioclænus*, *Litaletes*, *Ellipsodon*, *Choeroclaenus*; two to three cusps in the latter), hypsodontids (*Haplaletes*, *Litomyllus*; the basin is large in the latter but separate cusps cannot be distinguished) and other taxa, such as the basal phenacodontid *Tetraclaenodon*, in which a large talonid basin, rimmed by (variably) three cusps is present. That molarization of the talonid of the p4 occurred independently is suggested by the fact that, in the Puercan mioclaenid *Valenia wilsoni*, which otherwise is strikingly plesiomorphic, the talonid of p4 resembles that of *Protungulatum* in being unicuspid and unbasined. In *Mioclaenus*, the talonid is also unicuspid and unbasined; however, the extreme inflation of the premolars observed in this genus is probably responsible for their secondary simplification. The talonid of the p4 in *Molinodus* and *Simoclaenus* differs from the presumed primitive condition in having a transversely expanded, posterior swelling. They are sometimes multicuspid in *Molinodus*; they are connected to the trigonid by an anteroposteriorly aligned crest (cristid obliqua), and they present sometimes a small basin (in *Molinodus*). The talonid of the p4 of *Tiucloenus* and *Pucanodus* is extremely similar to those of *Protungulatum* and *Oxyprimus* in having a single cuspid and unbasined talonid of the p4. On this basis, we interpret the talonid of the p4 in *Tiucloenus* and *Pucanodus* to approximate the primitive ungulate condition whereas those of *Molinodus* and *Simoclaenus* are more specialized and intermediate between the plesiomorphic condition and the very derived one observed in didolodontids and early litopterns.

Lower molars

Primitive condition of the trigonid. Based on “zhelestids” and basal arctocyonids (e.g., *Protungulatum*, *Baiocoenodon*), we interpret the primitive conditions for ungulatomorph lower molar trigonids to include cusps that are sharply conical and well-separated. They have good separation of paraconid and metaconid (only slightly appressed), with trigonid open lingually, and the valleys between major cusps (protoconid-paraconid, protoconid-metaconid, paraconid-meta-

conid) form a trihedron with approximately equal arms. The paraconid is lower than other cusps and placed near the lingual margin of the tooth. The paraconid has lingual and labial slopes vertical, or nearly so. The metaconid is distinctly lower than protoconid and placed only slightly posterior to that cusp, with a protocristid that is relatively transverse and posterior wall of trigonid forming a nearly planar surface. The paracristid is obliquely oriented and broadly arcuate. A weak precingulid is present.

Relative height of the trigonid. Assuming correct placement of taxa and monophyly of their respective groups (see caveats above and below), the trigonid/talonid height differential became reduced in various condylarthran lineages: it remains relatively great in primitive peripitychids such as *Mimatuta*, for example, and becomes reduced in later taxa such as *Anisonchus*. The situation is similar among Mioclaenidae: *Bubogonia saskia* for example retains a rather tall trigonid, particularly on m2, whereas the trigonid is only slightly taller than the talonid in later species of *Promioclænus* (e.g., *P. acolytus*). The trigonid is only moderately taller than the talonid on lower molars of *Molinodus*. In early litopterns (e.g., *Protolipterna*, *Miguelsoria*) and, especially, didolodontids (e.g., *Paulacoutoia*, *Ernestokokenia*), the differential is further reduced. The differential in trigonid to talonid height is moderate on the hypsodontids included in our comparisons.

Precingulid. A weak precingulid is present in “zhelestids”, which we regard as the plesiomorphic character state for Ungulatomorpha. A precingulid stronger than in “zhelestids” is present in early arctocyonids *Protungulatum*, *Oxyprimus*, and *Baiocoenodon* and probably represents the plesiomorphic condition for “Condylarthra”. While a well-developed precingulid is retained in most peripitychids, this structure can be variably lost elsewhere. Among the hypsodontids, it is present in *Haplaletes* and, variably, *Litomyllus*. It is weak in the basal mioclaenids (*Bubogonia* and *Valenia*, apparently), moderately developed in *P. acolytus*, and somewhat stronger in *Litaletes*. A strong precingulid is present in *Molinodus*, *Simoclaenus* and *Andinodus* (probably the plesiomorphic condition), but the precingulid is very weak (when present) in

Tiuclaenus and *Pucanodus*. A strong precingulid is also found in basal litopterns (e.g., *Miguelsoria*, *Asmithwoodwardia*, *Protolipterna*) and didolodontids (e.g., *Paulacoutoia*, *Ernestokokenia*). In early litopterns and didolodontids, it is difficult to determine whether the relatively strong precingulid represents a plesiomorphic condition or a secondary specialization related to a tendency to increase the crushing morphology of the dentition.

Slopes of the flanks of the molar trigonid. Van Valen (1988) indicated that “condylarths”, specifically mioclaenids, vary in the degree to which the lateral walls of the lower molars are vertical. By our interpretation, this refers to the fact that, in certain taxa, the labial (protoconid) and lingual (paraconid, metaconid) trigonid cusps appear to be more closely approximated relative to the width of the tooth. This is because the lingual wall of the tooth forms a more inclined, convex surface, a characteristic that gives the cusps an inflated appearance. The trigonid thus appears more symmetrical when viewed anteriorly. This feature is even more subject to alternative interpretation than most other continuously varying molar characters of primitive ungulates, and is difficult to determine on worn teeth. We define the primitive (“vertical”) condition for “condylarths” as asymmetrical, because the lingual face of the trigonid is more vertical than the labial face. The derived condition we consider symmetrical, because the inclination of the lingual surface matches, more or less, that of the labial surface. An asymmetrical trigonid is clearly present in *Protungulatum*. In “zhelestids” and *Oxyprimus*, the asymmetrical condition is not always as distinct as in *Protungulatum*. Because the trigonid of “zhelestids” and *Oxyprimus* is higher, its flanks are sometimes subvertical and roughly parallel. Nevertheless, we have observed that, when not subparallel, the labial slope was generally slightly more inclined than the lingual one. Therefore, we consider that the *Protungulatum* condition is incipiently present in the “zhelestids” and *Oxyprimus*, which are regarded as plesiomorphic for this character. Again, assuming monophyly of “condylarth” groups as conventionally defined (but see below), it would appear that the symmetrical condition, which we associ-

ate with increased molar bunodonty, arose multiple times within “Condylarthra”. The “pinched” appearance of trigonid cusps in Periptychidae (Cifelli 1983a) is an expression of this character. Symmetry of trigonid walls also characterizes certain Mioclaenidae, although we interpret the distribution somewhat differently than did Van Valen (1988); see also Bonaparte *et al.* (1993: 27, character 2). Most taxa (e.g., *Bubogonia*, *Litaletes*, *Promioclænus*, *Choeroclænus*) are characterized by primitive, asymmetrical trigonids, whereas the symmetrical condition is seen in *Mioclaenus*, *Protoselene*, and *Molinodus* – which, according to Van Valen (1978; 1988) represent at least two separate lineages within the family (see also discussions in Johnston & Fox 1984; Bonaparte *et al.* 1993). The advanced condition is also seen in remaining “condylarths” from Tiupampa [e.g., *Tiuclaenus*, *Pucanodus* (in these genera it is less pronounced than in *Molinodus*), *Simoclaenus*, *Andinodus*]. It is also present in *Escribania*, didolodontids (*Paulacoutoia*, *Ernestokokenia*, *Didolodus*, *Lamegoia*), and some early litopterns (e.g., *Miguelsoria*, *Protolipterna*, *Asmithwoodwardia*).

Paraconid. The lower molar paraconid undergoes various changes in size and position in “condylarths” (Fig. 20). In “zhelestids” and early arctocyonids (*Protungulatum*, *Oxyprimus*, *Baiococonodon*), the paraconid is large and well separated from the metaconid, and closer to a lingual than a median position. This morphology probably represents the plesiomorphic condition for ungulatomorphs. In the hyopsodontids studied (*Litomylus*, *Haplaletes*), the trigonid remains rather open lingually and the paraconid does not become appressed to the metaconid (as is observed in advanced Hyopsodontidae such as *Haplomyilus* and *Hyopsodus*), but becomes reduced in height and occupies a more median position. This condition also occurs within the advanced Periptychidae (e.g., *Anisonchus*, *Hemithlaeus*). More primitive members of the family, such as *Mimatuta*, however, retain a paraconid, essentially as in *Protungulatum*, i.e. large, well separated from the metaconid and lingually placed. Mioclaenids are distinctive among “condylarths” in retaining a more primitive lingual position of the metaconid, as Simpson (1937) noted in his

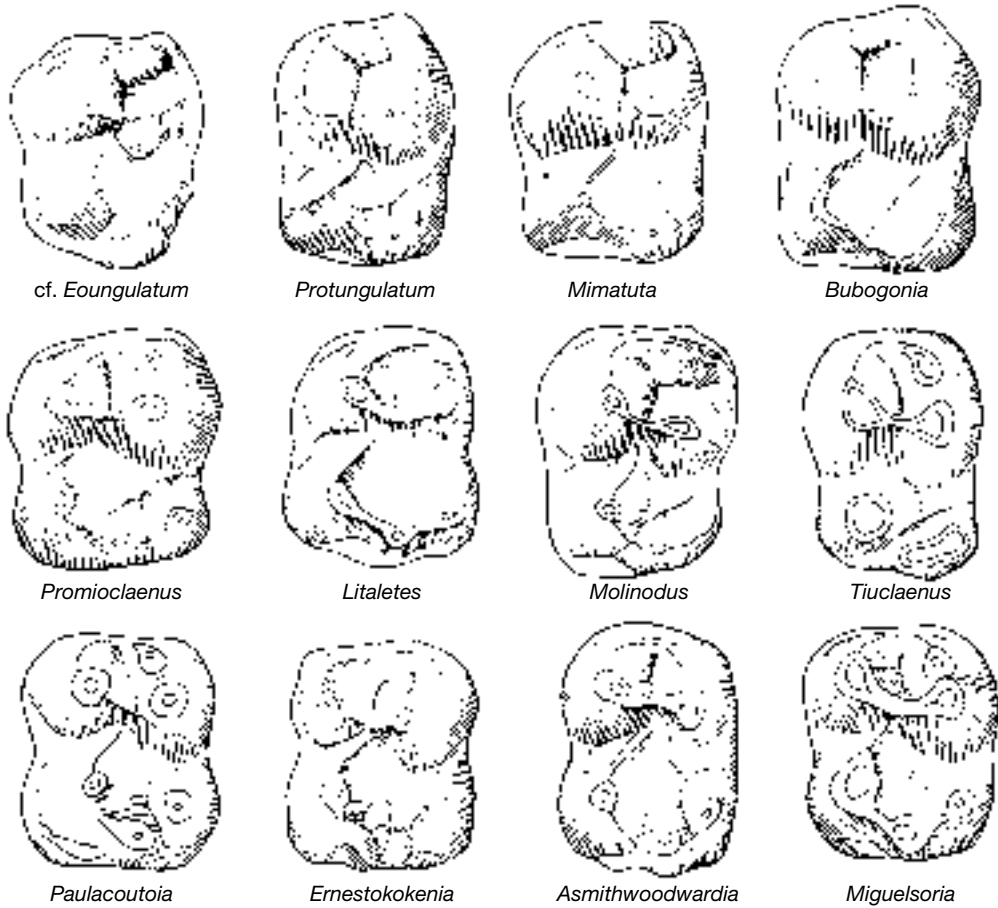


FIG. 20. — Occlusal views of left m2 in some unguatormorphs to show the morphology of the paracristid (cf. *Eoungulatum* and *Litaletes* are represented by m3 and m1 respectively because well-preserved m2s were not available during this study). cf. *Eoungulatum kudukensis* (E. CCGME 16/12953); *Protungulatum donnae* (SPSM 62-2028); *Mimatuta minual* (PU 14172); *Bubogonia saskia* (UA 15105, reversed); *Promioclænus acolytus* (AMNH 35778, reversed); *Litaletes disjunctatus* (AMNH 35889, reversed); *Molinodus suarezi* (MHNC 8344, reversed); *Tiulaenus cotasi* (MHNC 1231); *Paulacoutoia protocenica* (MNRJ 1431-V); *Ernestokokenia cf. nitida* (MNHN CAS 681, reversed); *Asmithwoodwardia scotti* (DGM 358-M); *Miguelsoria parayirunhor* (MNRJ 1468-V, reversed). Not to scale.

diagnosis of the group. In *Bubogonia*, the paraconid is positioned essentially as in *Protungulatum*. Nevertheless, the paraconid is taller in this and other mioclaenids, perhaps a derived feature of the group. In remaining mioclaenids (e.g., *Promioclænus*, *Litaletes*, *Choeroclænus*, *Mioclaenus*), the paraconid is more posteriorly placed, being close to and connate with (but not fused to) the metaconid. In these genera of North American mioclaenids, the paraconid-metaconid valley almost disappears; the protoconid-meta-

conid valley is anteroposteriorly oriented and divides the trigonid into a labial protoconid and a lingual para-metaconid. *Molinodus* resembles mioclaenids (except *Bubogonia*) in this respect. The condition of *Protoselele* is relatively atypical because the paraconid is shifted labially, is almost equidistant from the labial and lingual edges of the trigonid, and is located at the anterior edge of the trigonid between the proto- and metaconids (probably a derived condition). In primitive didolodontids, the paraconid variably remains

distinct (e.g., *Paulacoutoia*, *Lamegoia*). However, there is a tendency toward merging of this cusp with the metaconid, as in *Didolodus*, in which the paraconid is hardly observable, and *Ernestokenia* in which it is no longer distinct (Fig. 21). The same occurs, apparently independently, in Litopterna. The paraconid in *Miguelsoria* remains distinct (though less so than in *Molinodus*), whereas it is almost or completely merged with the metaconid in other early, primitive taxa (*Asmithwoodwardia*, *Protolipterna*). The paraconid of didolodontids and early litopterns are always in a position that is more lingual than labial.

The variation of the condition of the paraconid in ungulatomorphs is a continuum from a plesiomorphic well-individualized cusp to its total loss through fusion to the metaconid. This evolution occurs in all major groups of "condylarths" (mioclaenids, arctocyonids, hypsodontids, phenacodontids, and didolodontids) with the apparent exception of the Periptychidae. Although the polarity of this highly homoplastic character is clear, its use in phylogenetic reconstruction is problematic because of its high degree of homoplasy. Furthermore, as we have observed several times in this study, a major difficulty is, once again, to determine the limit between a well-individualized paraconid and a closely appressed paraconid in the case of a continuous morphological series.

Paracristid. As noted by Bonaparte *et al.* (1993), the paracristid of *Molinodus* is atypical among the "Condylarthra". It is more strongly arcuate, extending anteriorly from the protoconid before curving lingually and, later, posteriorly to reach the paraconid. This unusual condition is not met, to our knowledge, in North American taxa, but it appears to be true of remaining South American "condylarths" and primitive litopterns.

Metaconid. The size and position of the metaconid on molars also varies among condylarthrans. Johnston & Fox (1984) referred *Bubogonia* to the Mioclaenidae, in part on the large size of the metaconid relative to the condition in primitive oxyclaenines. We are unable to confirm the presence of an enlarged metaconid in all taxa referred to the family. However, it is clearly so for *Protoselene* (grouped with *Pleura-*

spidotherium by Van Valen 1978), as Johnston & Fox (1984) recognized, suggesting divergence of this clade of mioclaenids within early Palaeocene time (see Van Valen 1988). *Molinodus* and the other kollpaniines are distinctive in having a rather posteriorly placed metaconid. As Van Valen (1988) noted, this is a similarity to *Bubogonia* and *Protoselene* among North American taxa. Because of the posterior position of the metaconid, the posterior face of the trigonid, primitively (as in *Protungulatum*) almost transverse, is markedly oblique with respect to the axis of the dentary. It is noteworthy, however, that the posterior position of the metaconid noted by Van Valen in *Bubogonia* and *Protoselene* is sometimes only slightly more pronounced than in *Protungulatum*. A markedly posteriorly placed metaconid is also present in all didolodontids and early litopterns observed during this study.

The condition of kollpaniines, however, differs from that observed in *Bubogonia* and *Protoselene* in the posterior inflation and projection of the posterior wall of the metaconid, which partially fills the talonid basin. This unusual condition of the metaconid is conspicuous but moderately developed in *Molinodus*, *Tiuclaenus*, and *Pucanodus*. It is strongly emphasized in *Simoclaenus*, *Andinodus*, and *Escribania*. No posterior projection of the metaconid exists in the didolodontids and early litopterns.

Primitive condition of talonid cusps and crests. Comparison of "zhelestids" with primitive arctocyonids such as *Protungulatum* suggests that the following features are primitive for the talonids of "condylarth" lower molars: major cusps (hypoconid, hypoconulid, entoconid) well-defined and well-separated; hypoconid most voluminous cusp, but subequal to others in height and with a concave lingual face, not dominating talonid or filling talonid basin; entoconid and hypoconulid subequal (hypoconulid is slightly smaller in early "condylarths"), hypoconulid slightly closer to entoconid than hypoconid and connected to the former by a low cristid but not connate; and entocristid extending anteriorly from entoconid on the base of the posterior face of metaconid and enclosing talonid basin linguallly. Some "zhelestids" (*Aspanlestes* and *Sorlestes*)

have a weak labial postcingulid; when present in cf. *Eoungulatum*, it is extremely faint (Nessov *et al.* 1998). A well-developed postcingulid is observed in *Avitotherium* (see Cifelli 1990) and primitive “condylarths” (*Protungulatum*, *Maiorana*, *Mimatuta*, *Baiococonodon*) have a strong labial postcingulid. We tentatively regard the presence of a faint postcingulid as primitive for Ungulatomorpha and the presence of a strong postcingulid as primitive for the “Condylarthra”. The morphological difference between the weak labial postcingulid of “zhelestids” and the strong one of the early “condylarths” is clear so far. However, we are conscious that the discovery of ungulatomorphs bearing a labial postcingulid morphologically intermediate between the two states mentioned above may make difficult the use of this character.

Cristid obliqua. The condition for the anterior attachment of the cristid obliqua is unclear and appears to be rather variable. In “zhelestids” (cf. *Eoungulatum* and *Sorlestes*, for example), the attachment is on the posterolingual side of the protoconid. In *Protungulatum*, the cristid obliqua generally attaches below the notch in the protocristid (as it does in *Mimatuta* and *Maiorana*), or below the posterolabial edge of the metaconid. In *Baiococonodon*, it attaches to the posterolabial side of the metaconid. Among North American mioclaenids, the condition varies. In *Litaletes*, *Choeroclaenus* and *Protoselene*, the cristid obliqua generally connects the trigonid below the protocristid notch. The condition of *Protoselene*, however, is more variable than in the two other genera and the cristid obliqua frequently connects the trigonid at the posterolabial edge of the metaconid. In *Promioclænus* and *Mioclænus*, the connection is at the posterolingual base of the protoconid and, in *Bubogonia*, at the posterolabial base of the metaconid. In the Kollpaniinae, the connection is generally at the posterolabial base of the metaconid. It is more variable in *Molinodus* than in the other genera and frequently contacts the trigonid below the protocristid notch. In didolodontids, the contact is below the protocristid notch in *Paulacoutoia* and *Ernestokenia*, at the posterolabial base of the metaconid in *Didolodus* and at the posterolingual base of protoconid in *Lamegoia*. In early litopterns, the

contact is generally below the protocristid notch in *Asmithwoodwardia*, at the posterolabial base of the metaconid in *Miguelsoria* and at the posterolabial base of the metaconid or below the protocristid notch in *Protolipterna*. Therefore, the condition in South American mioclaenids, didolodontids and early litopterns is far from being homogeneous, although the position “at posterolabial base of metaconid” appears to be more frequent than in North American taxa. This condition is probably derived for “condylarths”, but the strong inter- and intraspecific variation of the position of the anterior end of the cristid obliqua, is indicative of a high degree of homoplasy. This variability and homoplasy hampers interpretation of character transformation, and makes the character of questionable utility on phylogenetic reconstruction.

Entoconid and hypoconulid of m1-2. Of the talonid cusps, the entoconid is perhaps most often cited for variability of systematic relevance; the primitive pattern described above is subject to a number of variations in “Condylarthra”. The relative size and position of the hypoconulid and entoconid is of interest in the case of the relationships between the North and South American mioclaenids. In “zhelestids”, the entoconid and hypoconulid are similar in size (volume and height) and the hypoconulid is salient posteriorly; they are approximated but not connate. In early “condylarths” (e.g., *Protungulatum*, *Oxyprimus*, *Baiococonodon*, *Mimatuta*, *Promioclænus*), the hypoconulid is smaller than the entoconid and is not salient posteriorly (i.e. the flexids which separate it from the entoconid and hypoconid are reduced), which we regard as the primitive condition for ungulates. This condition is probably derived when compared to that of the “zhelestids”. In other words, a reduced hypoconulid of m1-2 is regarded as a derived condition of the early “condylarths” when compared to the “zhelestids”. In all mioclaenid taxa we studied, the entoconid tends to be posteriorly placed and partly joined, at least at the base (sometimes fused) to the hypoconulid. *Prima facie*, this characteristic would appear to be identical with a feature (hypoconid more anterior than entoconid) cited by Van Valen (1988) as seen in *Bubogonia*, *Protoselene*, and *Molinodus*. We have also

observed that the entoconid of North and South American mioclaenids tends to be transversely compressed, a relatively constant derived character state of the North American mioclaenids. The reduction of the entoconid noted by Simpson in his 1937's definition of the Mioclaenidae is not constant. In some cases, it was not observed or very weak (*Bubogonia*, *Promioclaenus*, *Choeroclaenus*, *Litaletes*). It is conspicuous, however, in derived taxa (*Mioclaenus*, *Ellipsodon*). Furthermore, the talonid basin in most mioclaenid taxa (*Bubogonia*, *Promioclaenus*, *Litaletes*, *Choeroclaenus*, *Ellipsodon*) is more open lingually than in *Protungulatum* or *Oxyprimus* because of the tendency to reduce the entocristid and entoconid (see below). This condition develops a wide lingual notch between the trigonid and talonid lingually. In *Protoselene*, the talonid basin is relatively more widely open than in several other North American mioclaenids. The presence of a relatively wide lingual notch is probably a derived character state of the Mioclaenidae. However, the talonid basin is secondarily closed in *Mioclaenus* by the multiplication of accessory cusps anterior to the entocristid and in *Ellipsodon*, in which a continuous crest unites the hypoconulid to the posterior edge of the metaconid.

Van Valen (1978: fig. 5) recognized a number of lineages within Mioclaenidae. He assumed a major clade being constituted by *Protoselene* and other taxa, including highly derived *Pleuraspidotherium* and *Orthaspidotherium*. This view has attained general acceptance (McKenna & Bell 1997). Johnston & Fox (1984) followed Van Valen's (1978) arrangement, but noted that, in Pleuraspidotheriinae, the entoconid tends to become enlarged, whereas the cusp remains small or become reduced in Mioclaeninae. Hypsodontidae have a large entoconid, especially in *Litomylus*, in which it is always much larger than the hypoconulid. In hypsodontids, the hypoconid is also generally well-developed.

Molinodus and the remaining kollpaniines from Tiupampa are similar to North American Mioclaenidae in the close appression of the entoconid to the hypoconulid and the transverse compression of the entoconid. Indeed, the two cusps are hardly distinct in *Molinodus*. Because entoconid and hypoconulid of *Molinodus* are

almost completely fused, the condition of this genus seems to be more specialized than most of the North American mioclaenids. Furthermore, because of the loss of the entocristid (see below), the talonid basin is more open lingually than in the North American mioclaenids.

The condition of *Protolipterna*, an early litoptern, is similar to that of North American mioclaenids. The entoconid is posteriorly placed, connate with hypoconulid, compressed transversely, and slightly larger than hypoconulid. A well-marked talonid notch is present.

In the Didolodontidae and other early litopterns (*Asmithwoodwardia* and *Miguelsoria*) included in our comparisons, the talonid basin is widely open lingually but the entoconid and hypoconulid are more separated and are never partially or totally fused as is observed in mioclaenids. Furthermore, whereas in the "condylarths" from Tiupampa the entoconid and the hypoconulid of m1-2 are generally subequal in height and volume (sometimes the entoconid is smaller than the hypoconulid as in *Molinodus*), didolodontids and *Escrivanbia* have an entoconid larger than the hypoconulid as is observed in several North American mioclaenids. In several taxa, the entoconid is much larger (*Paulacoutoia*, *Ernestokokenia*, *Didolodus*, *Miguelsoria*). Therefore, if the didolodontids and litopterns have their origin in a kollpaniine (or in a more generalized mioclaenid) stock, they seem to be characterized by tendencies to increase the size of the entoconid, reduce the hypoconulid, and separate the two cusps. However, because many North American "condylarths" also present this feature, it is probable that it represents a very homoplastic character state of problematic use in phylogenetic reconstruction.

Entocristid. An entocristid is present in "zhelestids" (*Sorlestes*, *Aspanlestes*, *Eoungulatum*), early arctocyonids (e.g., *Protungulatum*, *Oxyprimus*, *Baiocodon*) and early peripitychids (*Mimatuta*). However, "zhelestids" differ from early "condylarths" in the fact that their entocristid extends anteriorly and dorsally on the base of the posterior face of the metaconid. In basal arctocyonids and peripitychids, it remains at the base of the metaconid and extends on the posterolingual face of the cusp. As a consequence, the talonid of "zhelestids" is closed lingually and only partially

closed in early “condylarths”. All North American mioclaenids have a more or less distinct entocristid. In most members of this family, however, it tends to reduce and does not contact the posterior edge of the metaconid. Therefore, the talonid of mioclaenids tends to be more open lingually than in basal “condylarths” (e.g., *Protungulatum*, *Oxyprimus*). Nevertheless, as mentioned above, in some mioclaenids the talonid basin is secondarily closed by the development of a continuous neomorphic crest (smooth in *Ellipsodon* and cusped in *Mioclaenus*) that connects the hypoconulid to the posterior slope of the metaconid. In peripitychids, the entocristid is enhanced, even in primitive taxa (e.g., *Mimatuta*, *Maiorana*), and in more advanced taxa (e.g., *Anisochnus*, *Haploconus*) extends as a sharp crest to the metaconid, forming a distinctive lingual wall to the talonid basin. In primitive phenacodontids (e.g., *Tetraclaenodon*), the entoconid is generally doubled, with an entocristid present anterior to the entoconid itself. Because an entocristid seems to be widely distributed among early “condylarths” and in “zhelestids”, we regard its presence as a plesiomorphic character state within Ungulatomorpha. Van Valen (1988) cited the presence of an incipient entocristid as a derived character shared by *Molinodus* and certain North American mioclaenids (*Bubogonia*, *Protoselene*). However, if an entocristid is obviously present in *Bubogonia* and *Protoselene* (as in all North American mioclaenids) it is absent in *Molinodus* (we have observed it on the m3 of one specimen only, in which it is very small). Furthermore, an entocristid is clearly absent from all the other “condylarths” from Tiupampa and *Escribania*, in which the talonid basin is widely open lingually. Therefore, the reduction of the entocristid in most North American mioclaenids would be derived within the Ungulatomorpha and the lack of entocristid in the kollpaniines would be derived within the mioclaenids. In didolodontids and primitive litopterns included in our comparisons, the entocristid is always absent (except in *Ernestokokenia nitida*) and the talonid basin is broadly opened lingually (Fig. 21).

Hypoconid. In the Tribosphenida, the hypoconid is the largest cusp of the talonid. This condition

is observed in “zhelestids”, in which the hypoconid forms approximately the labial half of the talonid and has a concave lingual flank. A similar condition is found in early arctocyonids (*Protungulatum*, *Oxyprimus*, *Baiococonodon*), in peripitychids (*Mimatuta*), and North American mioclaenids. The hypoconid of the kollpaniines is enlarged and its lingual flank is either flat or convex. It extends lingually and partially invades the talonid basin anterior to the hypoconulid. A similar condition is present in didolodontids, but is apparently absent in the early litopterns.

Hypoconulid of m3. In “zhelestids” (*Aspanlestes*, cf. *Eoungulatum*, and *Sorlestes*), the hypoconulid of m3 is only slightly more voluminous than that of m2. In early “condylarths” (e.g., *Protungulatum*, *Oxyprimus*, *Baiococonodon*, *Mimatuta*, *Promioclaenus*), the hypoconulid of m3 is clearly larger than that of m2 and strongly protruding posteriorly. We regard the condition observed in early “condylarths” as plesiomorphic within the Ungulata but apomorphic within the Ungulatomorpha.

Lower m2 trigonid-talonid proportions. The trigonid of m2 is wider than the talonid primitively in tribosphenic mammals (Clemens & Lillegraven 1986) and in most early eutherians, such as *Prokennalestes* (see, e.g., Kielan-Jaworowska & Dashzeveg 1989: fig. 27). In “zhelestids”, according to measurements by Nessov *et al.* (1998), the trigonid of m2 is as wide as the talonid. As indicated in Table 14, in most basal “condylarths” that we have examined, the trigonid is wider than the talonid. It is noteworthy, however, that the difference is weak in some specimens, probably more reflecting individual variation than true taxonomic significance. Considering the plesiomorphic condition for tribosphenic mammals, a trigonid of m2 slightly wider than the talonid is probably the plesiomorphic condition for Ungulatomorpha, the condition of “zhelestids” being interpreted as an autapomorphy.

As in many other dental features discussed herein, changes in width proportions of trigonid to talonid seem to occur independently among most condylarthran groups. In primitive Phenacodontidae (e.g., *Tetraclaenodon*), the m2 talonid is as wide or wider than the trigonid. The m2

talonid becomes broadened in various Arctocyoniidae (e.g., *Loxolophus*, *Thryptacodon*, *Claenodon*); however, most periptychids (with the variable exception of *Conacodon*) do not greatly widen the talonid. In North American mioclaenids, the trigonid is slightly larger than the talonid in several taxa such as *Valenia wilsoni* (assuming referral of AMNH 59788 to the species is correct: see Van Valen, 1988: fig. 5), *Promioclænus*, and *Mioclænus*. *Choeroclaenus* and *Protoselele opisthacus* show variation of the trigonid width from slightly wider than the talonid to subequal or slightly narrower. Curiously, the type specimen of *Bubogonia saskia*, which is probably one of the most plesiomorphic of known mioclaenids, is derived in having a talonid slightly wider than the trigonid [we ignore the condition of this character on the two other m2s referred to this taxon by Johnston & Fox (1984)]. Among South American taxa, *Molinodus*, *Tiuclaenus*, *Pucanodus*, *Andinodus*, *Simoclaenus* and *Escribania* retain the primitive condition of a narrow talonid, whereas the talonid of m2 is broadened in didolodontids and litopterns. Clearly, the evolutionary trend in all groups of “condylarths” is to reduce the width of the trigonid and to widen the talonid, a process that occurred independently in the various lineages.

Relative size of the lower molars. The relative size of sequential molars also varies considerably in “Condylarthra”. For example, m3 of *Protoselele opisthacus* is noticeably longer than m2, whereas the reverse is true for a number of other mioclaenids (Cifelli 1983a; Archibald 1998). On some specimens of *Molinodus suarezi* and especially on the holotype of *Simoclaenus sylvaticus*, m1 is considerably smaller than m2, even given the predictable differences according to locus (Table 12). The same is true of the didolodontid *Paulacoutoia protocenica* [see Cifelli (1983a: fig. 2F); Table 12]. We examined these variations quantitatively, including molar series of Arctocyoniidae, Periptychidae, Hyopsodontidae, Mioclaenidae, Phenacodontidae, Didolodontidae, and primitive Litopterna. Comparisons of length, width, and calculated measurements (e.g., molar area) failed to show any consistent or meaningful patterns among these variations. Indeed, we were impressed by the considerable

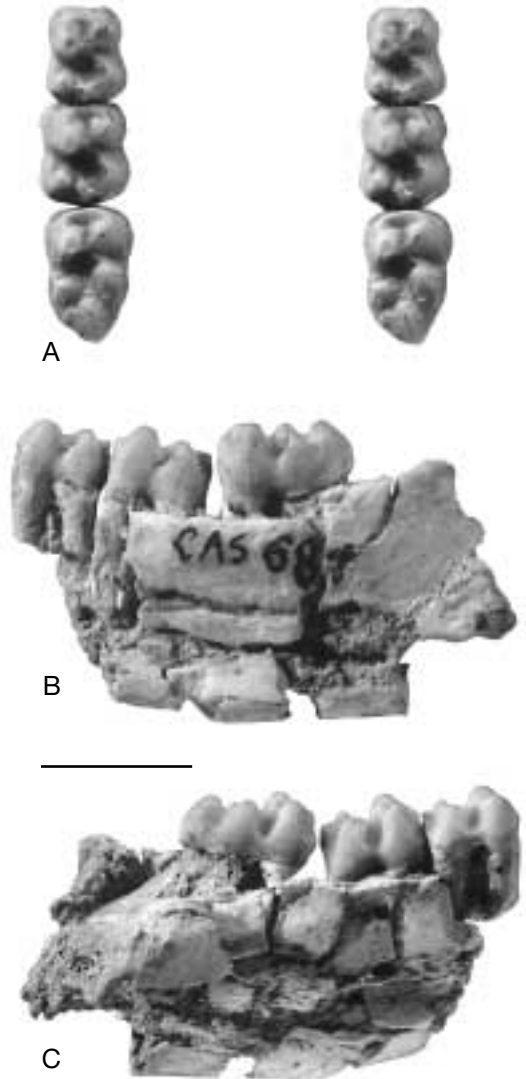


FIG 21. — *Ernestokokenia* cf. *nitida*, partial right dentary (MNHN CAS 681) with m1-3 from Cerro Negro (Chubut, Argentina), Casamayorian; **A**, occlusal view; **B**, lingual view; **C**, labial view. Scale bar: 1 cm.

within-species variations, such as the relative size of m1 in *Molinodus suarezi* (Table 12). However, *Simoclaenus* and *Paulacoutoia* are the genera that show the greatest difference in surface area between m1 and m2.

DISCUSSION

TIUPAMPA'S "CONDYLARThS" AND NORTH AMERICAN MIOCLAENIDAE

As should be clear from the foregoing (and as any student of the subject will readily attest), the assessment of relationships among "condylarths" is fraught with numerous difficulties. Most importantly these include general primitiveness of included taxa, the apparent acquisition of numerous apomorphies independently in various lineages, reversals, problematic definition of subtle, continuously varying morphological features, and considerable within-species variation. Indeed, it is no coincidence that students have long relied on temporal and geographic data, as well as the negative evidence presented by plesiomorphy (see below), given the ambiguities of a strictly morphology-based approach. Although we do not adopt the methodology advocated by Van Valen (1988; see also Gingerich 1976), we can appreciate the rationale behind it. In spite of the difficulties evoked above, we insist in presenting a parsimony-based, computer-assisted phylogenetic analysis. Nevertheless, we are conscious of the weakness of this approach in the case of the early ungulates considered in the present study because it is based almost exclusively on dental characters (37 out of 38). It is clear that the discovery of reasonable cranial remains of every taxon will considerably modify (or clarify) the relationships presented in Figure 22.

Below, we discuss the identification of primitive and derived features among the "condylarths" from Tiupampa and their possible relatives, based on the comparisons just given, and on the possible significance of these character distributions.

As we have noted above, students in the past have compared the most primitive of South America's native ungulates, the didolodontids, with various North American "condylarths", notably Phenacodontidae and Periptychidae. With the discovery of pre-Casamayoran didolodonts (e.g., Paula Couto 1952) and more primitive taxa, such as the "condylarths" from Tiupampa, it is now clear that such similarities as exist with these groups are largely convergent, as Simpson (1948) implicitly recognized. This emphasizes the fact that through the Early Tertiary, numerous specializa-

tions were acquired independently and, apparently, almost synchronously, in a stepwise fashion by various separate lineages. In this context, the primitive features of *Molinodus* and other taxa from Tiupampa are of considerable interest: they help to date divergence from potential North American relatives (Van Valen 1988; Williamson 1996), and, though they do not help to securely identify the relatives, they do help to eliminate certain (more derived) groups as potential close allies.

Our comparisons failed to produce tangible evidence for close relationship between the Tiupampa "condylarths" and Arctocyonidae or Hyopsodontidae. The most compelling resemblances are with taxa generally referred to the Mioclaenidae, as has been previously suggested by various studies, either based on taxa from Tiupampa (Muizon & Marshall 1987 a, b; Marshall & Muizon 1988; Muizon & Marshall 1991; Muizon 1992; Van Valen 1988; Bonaparte *et al.* 1993) or on the younger Didolodontidae and Litopterna of Itaboraí, Brazil (Cifelli 1983a). Mioclaenidae are diagnosed on the basis of a combination of primitive and advanced features (see discussions in Simpson 1937; Cifelli 1983a; Johnston & Fox 1984; Archibald 1998; and below). Within the family, Van Valen (1978, 1988) identified *Bubogonia* and *Promioclænus* as the most primitive genera. Whether or not the species included by Van Valen in *Promioclænus* form an ancestor-descendant sequence, Puercan *Valenia wilsoni* (= *Promioclænus wilsoni*) is morphologically distinctive and retains more primitive characters than the various species of *Promioclænus*. Therefore, *Promioclænus* is not necessarily the most primitive representative of the group (see also Johnston & Fox 1984). By the same token, inclusion of *Bubogonia* (which in many respects appears to differ only subtly from *Protungulatum*) and *Valenia* makes characterization of the Mioclaenidae more difficult simply because these genera retain so many primitive characters. Van Valen (1978: fig. 5) also produced a provisional phylogeny of Mioclaenidae, including a number of lineages within Mioclaeninae, and a major clade (Pleuraspidotheriinae) to hold *Pleuraspidotherium* and suspected allies. Johnston & Fox (1984) allied their then new

species, *Bubogonia saskia*, with the Mioclaeninae, viewing it as a suitable structural antecedent for a *Choeroclaenus-Mioclaenus* lineage. They also noted, however, that *B. saskia* could be close, structurally, to the ancestry of Pleuraspi dotheiriinae. Van Valen (1988) subsequently considered *Bubogonia* to be a member of the clade including *Protoselene* (Pleuraspidotheriinae, as conceived by Van Valen 1978), to which he also referred *Molinodus*, citing a number of derived character states shared in common. We have no quarrel with the specifics of these proposed relationships. However, in view of the many primitive retentions of some of the taxa involved (illustrated by the partly conflicting results of the latter two studies), we prefer to avoid formal recognition of these clades. Below, we discuss characters cited by Van Valen (1988) and those included in our comparisons in evaluating relationships of *Molinodus*.

When considered independently from the other South American ungulates, we find some support for a monophyletic Mioclaenidae (but see below, the results of the parsimony analysis), and placement of *Molinodus* in the group, through the structure of the lower molars. The paraconid is appressed to the metaconid but still distinct and remaining in a lingual position. Somewhat less equivocal, the talonid bears a distinct lingual notch, and the entoconid is posteriorly placed, transversely compressed, and connate or fused with the hypoconulid. On the upper molars, the styler shelf is reduced, and the parastyle is reduced on M1-2. Other derived similarities that are possible synapomorphies for Mioclaenidae (including *Molinodus*) are on P4: the parastyle is reduced and the postparacrista is straight, not curved labially.

As noted, *Molinodus* is remarkably primitive in certain respects. Most notable is the complete lack of a hypocone, which is already present in most "condylarth" groups, except Mioclaenidae (although incipiently present in all North American taxa), at first appearance. The lack of a hypocone in *Molinodus* and other "condylarths" from Tiupampa argues against reference to Hyopsodontidae, Periptychidae, Phenacodontidae, and most clades of Arctocyonidae (as conceived by Van Valen 1978; Cifelli 1983a), in

which it is already developed. Within Mioclaenidae, a small hypocone is arguably present in some Torrejonian taxa (such as *Choeroclaenus* and *Litaletes*), suggesting that the ancestor of Kollpaniinae was more primitive than these forms. *Molinodus* is also primitive in the extent and relationships of upper molar pre- and postcingula with respect to preparaconular and postmetaconular cristae. Within Mioclaenidae, our survey revealed the primitive pattern in *Bubogonia* (*B. bombadili*), on the postcingulum only, and *Protoselene*. In the remaining taxa (*Valenia*, *Choeroclaenus*, *Promioclaenus*, *Mioclaenus*, *Ellipsodon*, *Tiucclaenus*, and *Pucanodus*), the cingula have fully "captured" attachment to the styles (incipiently in *Valenia* and *Choeroclaenus*, see Fig. 18). Similarly, *Molinodus* retains a somewhat labially oriented preparacrista on M1-2, reminiscent of the condition seen in early Arctocyonidae and Periptychidae. Within Mioclaenidae, the preparacrista is slightly labially oriented in *Bubogonia* (*B. bombadili*), *Valenia*, *Litaletes*, *Protoselene*, and *Choeroclaenus* (although variable in the last two genera). In *Promioclaenus*, *Mioclaenus*, *Tiucclaenus* and *Pucanodus*, the preparacrista is anteriorly directed.

What of characters that appear to be derived within Mioclaenidae? As noted by Van Valen (1988), the lower molar metaconid of *Molinodus* is more posteriorly located than it is, for example, in *Protungulatum*. *Molinodus* and other "condylarths" from Tiupampa are rather extreme in this respect (see below), but the condition appears to be present, in incipient form at least, in *Protoselene* and *Bubogonia*. The latter was deemed an ancestor of Pleuraspidotheriinae by Van Valen (1988) but considered a basal mioclaenine by Johnston & Fox (1984). Another feature worthy of note in this connection is the symmetry of labial and lingual trigonid walls, owing to "pinching" of the trigonid. As noted above, this characterizes *Molinodus* and certain North American Mioclaenidae. It seems to be present in *Protoselene* and *Mioclaenus*, placed in different subfamilies, but not their suggested antecedents (see Van Valen 1988). Hence the significance of this character is unclear.

Summing up, present evidence favours origin of the Tiupampa "condylarths" from within the

North American Mioclaenidae as that family is currently conceived. The limited and somewhat equivocal data are insufficient, in our view, to identify with some level of security a specific ancestor of, or sister-taxon to, Tiupampa “condylarths” among the North American radiation.

However, given the progressive changes that occurred within Mioclaenidae (and adumbrated in other “condylarth” groups) through the course of the North American Palaeocene, the repeated plesiomorphic similarities of *Molinodus* to primitive, Puercan taxa (e.g., *Valenia*, *Bubogonia*) are strongly suggestive of a Puercan (at least) divergence of the South American lineage, as suggested by Van Valen (1988) and Williamson (1996).

TIUPAMPA’S “CONDYLARTHS”, DIDOLODONTIDAE, AND LITOPTERNA

Didolodontids and primitive litopterns appear to share all of the derived similarities seen in *Molinodus* and some or all North American Mioclaenidae. Notable among these are: 1) the symmetrical walls of the lower molars (seen in certain members of Mioclaeninae and Pleuraspidotheriinae); 2) the posterior position of the metaconid (also present in *Bubogonia* and *Protoselene*); 3) the posterior placement of the entoconid, which is connate with the hypoconulid (this feature is not present in didolodontids); 4) the development of a lingual talonid notch (all Mioclaenidae); and 5) the reduction or loss of the postparaconular and premetaconular cristae (this feature, however, is not clearly present in *Ernestokokenia nitida*, *Asmithwoodwardia subtrigona*, and *Proectocion argentinus*).

Given the generally primitive nature of *Molinodus* and other “condylarths” from Tiupampa, and the fact that previous workers have found considerable difficulty in framing dentally-based diagnoses that would distinguish didolodontids either from litopterns or from North American “Condylarthra” (Simpson 1948; Cifelli 1983a), one of the most surprising results of this study was the identification of several possible synapomorphies uniting the South American taxa (i.e. kollpaniines, didolodontids and litopterns).

The first of these involves a more extreme condition of the posterior placement of the metaconid. In *Molinodus*, the metaconid is in a more posteri-

or position (in relation to the protoconid) than in most of the North American “condylarths” and projects posteriorly into the talonid basin. Among other kollpaniines this condition is greatly emphasized in *Andinodus*, *Simoclaenus*, and *Escribania* but is nevertheless also present in *Tiuclaenus* and *Pucanodus*. The posterior position of the metaconid observed in *Molinodus* is found in didolodontids and early litopterns. However, it is noteworthy that in these groups the posterior projection of the metaconid into the talonid basin is never as clearly observed as it is in the Kollpaniinae.

The paracristid of “condylarths” from Tiupampa (see Bonaparte *et al.* 1993), didolodontids, and primitive litopterns is distinctive in being strongly arcuate and extending anteriorly from the protoconid before turning lingually and, finally, posteriorly to reach the anterior side of the paraconid. This condition is present in most didolodontids and primitive litopterns but disappears in derived taxa because of reduction of the paraconid and paracristid. It is absent in North American taxa and probably represents one of the strongest synapomorphies of the Kollpaniinae + Didolodontidae + Litopterna.

A final, more equivocal resemblance between *Molinodus* (MHNC 1244) and *Simoclaenus* on the one hand and didolodontids and early litopterns on the other is the fact that the p4 metaconid is transversely aligned with the protoconid and almost the same size. However, it is noteworthy that this morphology of p4 is absent in *Tiuclaenus* and *Pucanodus*, whereas it is present in *Mimatuta* and *Litaletes*.

DIDOLODONTIDAE AND LITOPTERNA

We also tentatively identify some dental synapomorphies shared by Didolodontidae and Litopterna to the exclusion of Tiupampa’s “condylarths”. Didolodontids (*Paulacoutoia*, *Didolodus*) and early litopterns (*Asmithwoodwardia*, *Protolipterna*, and probably *Miguelsoria*) have a broadly sweeping postprotocrista on P3 that forms a distinctive posterior platform on this tooth. Both in didolodontids and primitive litopterns, the P4 has reduced styles, strong pre- and postcingula, and presence of a metacone. A metacone apparently developed independently on P4 in many

different eutherian lineages, as posterior premolars became molarized. However, in didolodontids and litopterns, the metacone does not appear in a distal position on the postparacrista, as it commonly does elsewhere among Eutheria. To the contrary, it is closely appressed to, and connate with, the paracone itself, an unusual condition among mammal. Because such an atypical metacone is present on P4 of all Itaboraian and later didolodonts and primitive litopterns, it was earlier assumed that this cusp may have characterized the morphotypic South American ungulates (Cifelli 1983a). Discovery of *Molinodus* and similarly primitive taxa from Tiupampa, however, shows this is not the case. The P4 metacone, with its unusual placement, can accordingly be regarded as a didolodontid-litoptern synapomorphy.

The P4 of didolodontids and litopterns has a relatively enlarged protocone with thick lingual extremities of the pre- and postcingula. This condition gives the P4 a quadrangular morphology (i.e. with subparallel anterior and posterior edges). In the other "condylarths", the P4 is triangular. However, a condition approaching (but different from) that of didolodontids and Litopterns is found in *Mioclaenus* (because of the strong inflation of the tooth) and *Protoselene*. Nevertheless, in these genera, the P4 still retains a roughly triangular outline.

Two somewhat more equivocal characters may also be cited as potential synapomorphies of these groups: 1) the labial cingulum of upper molars (remnant of the styler shelf), well-developed in *Molinodus* as in most other archaic ungulates, is incomplete in didolodontids and litopterns; 2) on lower molars of these groups, the paraconid and metaconid are more closely appressed.

Distinction of Didolodontidae from Litopterna, a problem that, excepting postcranial criteria (Cifelli 1983b), has survived repeated attempts to defeat it (Simpson 1948; Cifelli 1983a), was not of primary concern to us. Nonetheless, we identified one feature that, when better known, may prove to be useful in this regard. Didolodontids for which the jaw is known retain an unfused mandibular symphysis, whereas the symphysis was fused even in small, dentally primitive litopterns such as *Miguelsoria*, *Protolipterna*, and *Asmithwoodwardia*.

PHYLOGENETIC ANALYSIS

The characters used in this study are almost exclusively dental characters and we are aware of the high degree of homoplasy of these data. However, in spite of this restriction, we present the results of a parsimony analysis of the phylogenetic relationships between 24 taxa. The outgroup includes three taxa: "zhelestids", *Oxyprimus*, and *Protungulatum*. The ingroup includes one peripitychid (*Mimatuta*), seven North American mioclaenids (*Protoselene*, *Bubogonia*, *Promioclaenus*, *Litaletes*, *Choeroclaenus*, *Ellipsodon*, and *Mioclaenus*), six kollpaniine mioclaenids (*Molinodus*, *Simoclaenus*, *Tiuclaenus*, *Pucanodus*, *Andinodus*, and *Escribaniania*), four didolodontids, (*Lamegoia*, *Paulacoutoia*, *Didolodus*, and *Ernestokokenia*), and three litopterns (*Miguelsoria*, *Protolipterna*, and *Asmithwoodwardia*). Thirty-eight characters were selected among the 24 taxa of ungulatomorphs (Table 16) and were analysed using heuristic algorithm (general) of Paup 3.1.1. The character list is organized as follows: 1-21, upper dentition; 22, dentary; 23-37, lower dentition; 38, postcranial skeleton. Characters 2, 4, 7, 8, 21, 23, 24, 27, 29, 31, 32, 36, 38 were regarded as ordered; the others were regarded as unordered.

Character and character states of 24 taxa of ungulatomorphs as listed in Table 16 and Figure 22. See text for character analysis.

1. Premolars number:

0 - five.

1 - four.

2. Inflation of premolars:

0 - not inflated.

1 - slightly inflated.

2 - strongly inflated.

3. Postprotocrista of P3:

0 - P3 with an incipient or small protocone and a posterior edge not expanded posteriorly.

1 - small or medium-sized protocone present and postprotocrista expanded posteriorly.

4. Metacone of P4:

0 - absent.

1 - present as a small swelling of the post-paracrista.

2 - well-developed cusp, almost as high as the paracone and connate to it.

5. Outline of P4:

0 - triangular.

1 - quadrangular.

6. Size of the conules:

0 - small to medium-sized.

1 - enlarged and swollen.

7. Position of conules of M1-2 (see Nesson *et al.* 1998: 75) relative to paracone and metacone *vs* protocone:

0 - conules closer to midposition.

1 - conules closer to protocone than to midposition.

2 - conules on labial flank of protocone but approximately equidistant from the labial and lingual edges of the tooth.

8. Styler shelf:

0 - present but narrow.

1 - reduced to a labial cingulum.

2 - loss of a true labial cingulum and presence of a faint to small labial rim (i.e. not separated from the labial face of the para- and metacones by a sulcus).

3 - increase of the size of the labial rim, labial to metacone; it is generally interrupted labial to paracone and when present weak. The rim labial to metacone is sometimes a true cingulum. State 3 is regarded as a derived condition non-homologous to state 1 because: 1) the rim or cingulum is clearly asymmetrical and not continuous along the labial edge of the tooth and 2) it is weaker on basal taxa and more developed in younger taxa.

9. Mesostyle:

0 - absent.

1 - present.

10. Stylocone and parastyle:

0 - separated (i.e. parastylar groove present).

1 - fused (i.e. parastylar groove absent).

11. Orientation of the preparacrista (i.e. position of the parastyle):

0 - conspicuously oriented laterally.

1 - oriented approximately in line with the paracones.

12. Relative size of paracone and metacone:

0 - paracone larger and taller than metacone.

1 - both cusps subequal in height and volume.

13. Relative position of paracone and metacone of M2:

0 - metacone posterior to paracone.

1 - metacone posterolingual to paracone.

14. Relation of paracone and metacone at base:

0 - paracone and metacone in contact at base, V-shaped or narrow U-shaped centrocrista (i.e. trigon basin small).

1 - paracone and metacone not in contact at base with a wide U-shaped centrocrista (i.e. trigon basin expanded).

15. Pre- and postcingula:

0 - do not extend further labially than the conules or, at least, the lingual edge of the para- and metacones.

1 - reach (or almost reach) the para- and metastyles.

16. Relations of postmetaconular crista and postcingulum:

0 - independent from the postcingulum.

1 - connects to the postcingulum at the metastyle.

2 - meets the postcingulum below the metacone (i.e. the postcingulum has "captured" the metaconular portion of the postmetaconular crista).

17. Extension of the postmetaconular crista:

0 - ends below the metacone labially.

1 - reaches the metastyle labially.

18. Preparaconular and postmetaconular cristae:

0 - well-marked.

1 - strong reduction or loss of the conular portion.

19. Postparaconular and premetaconular cristae:

0 - present and well-marked.

1 - reduced or absent (important individual variation).

20. Lingual extremity of the postcingulum:

0 - at the same level as precingulum on protocone slopes.

1 - located much higher on protocone than precingulum.

21. Hypocone:

0 - absent.

1 - present as a thickening of the lingual extremity of the postcingulum, and much lower than the protocone.

2 - large cusp almost as high as the protocone.

22. Cusp on precingulum anterior to paraconule:

0 - absent.

1 - present.

23. Mandibular symphysis:

0 - unfused.

1 - ankylosed.

24. Size of lower canine:

0 - unreduced.

1 - reduced.

2 - enlarged.

25. Metaconid of p4:

0 - small to medium-sized and appressed against protoconid.

1 - enlarged and distinctly separated from the protoconid.

26. Talonid of p4:

0 - formed of one single cusp in a median position on the talonid).

1 - presence of a labially positioned hypoconid with an incipient talonid basin.

27. Slopes of flanks of the trigonid:

0 - labial slope slightly to strongly oblique and lingual slope subvertical.

1 - both slopes oblique.

28. Paracristid:

0 - asymmetrical in relation to the anteroposterior axis of the tooth, paraconid portion straight and forms an obtuse angle with the protoconid portion.

1 - deeply arched posteriorly and approximately symmetrical in relation to the anteroposterior axis of the tooth, paraconid portion makes an

angle of approximately 90° with the protoconid portion.

29. Metaconid:

0 - lingual to protoconid.

1 - slightly posterior to protoconid.

2 - strongly posterior to protoconid.

30. Posterior slope of metaconid:

0 - not inflated with straight protocristid.

1 - strongly inflated, invading the talonid basin with concave protocristid.

31. Entocristid:

0 - present and extends anterodorsally on the base of the posterior wall of the metaconid (talonid basin closed lingually).

1 - present and extends anteroventrolingually on posterolingual base of metaconid.

2 - present but anterior extremity remains at lingual base of metaconid.

3 - absent or extremely faint.

4 - talonid basin secondarily closed by development of a continuous neomorphic crest (smooth or cusped) that connects hypoconulid to posterior slope of metaconid.

32. Entoconid and hypoconulid of m1-2:

0 - entoconid subequal in size to hypoconulid and hypoconulid salient posteriorly.

1 - hypoconid smaller than entoconid and not salient posteriorly (i.e. reduction of the flexids separating the hypoconulid from the entoconid and hypoconid).

2 - entoconid reduced, subequal to or smaller than hypoconulid.

3 - entoconid tends to increase in size.

33. Hypoconulid and entoconid:

0 - approximated but well-individualized.

1 - connate or fused.

2 - well-separated.

34. Hypoconid:

0 - forms labial half of talonid or less, does not invade talonid basin anterior to the hypoconulid.

1 - large, conical; extends on lingual half of talonid and invades talonid basin anterior to hypoconulid.

35. Hypoconulid of m3:

- 0 - only slightly larger than hypoconulid of m1-2.
- 1 - proportionally much larger than hypoconulid of m1-2 (strongly enlarged when compared to condition in 0).

36. Postcingulid:

- 0 - weak with talonid cusp not inflated.
- 1 - medium-sized to strong.
- 2 - weak with strongly inflated talonid cusps.

37. M3s:

- 0 - unreduced.
- 1 - moderately to greatly reduced.
- 2 - enlarged.

38. Tarsus:

- 0 - portion of the calcaneum distal to ectal facet and neck of astragalus not expanded.
- 1 - expanded.

The result of the analysis produced 2280 shortest trees (length: 100; CI: 0.550; HI: 0.440; RI: 0.793; RC: 0.436). Figure 22 presents the strict consensus (A), the 50% majority rule consensus trees (B), and two of the 2280 trees obtained (C, D). The analysis resulted in the paraphyly of the Mioclaenidae as traditionally conceived. In the strict consensus tree, the South American taxa are included in a single monophyletic group (Kollpaniinae + Didolodontidae + Litopterna). However, the relationships of this group with the North American genera *Mioclaenus* and *Ellipsodon* are unresolved. The relationships of the six Kollpaniinae are unresolved. These genera are part of a polytomy which also includes a monophyletic group made of the Didolodontidae (paraphyletic) and the Litopterna (monophyletic). In the 50% majority rule the Kollpaniinae are monophyletic. Within the Kollpaniinae, *Molinodus* + *Simoclaenus* are sister-taxa and form an unresolved polytomy with the four other taxa (*Tiuclaenus*, *Pucanodus*, *Andinodus*, and *Escribania*).

The two major aspects of the parsimony analysis undertaken in this work are the relatively good support of nodes 44, 39, and 38 in tree of Figure 22C (Kollpaniinae monophyletic). Node 44 is supported by seven synapomorphies (char. 4: 0 → 1;

8: 0 → 1; 10: 0 → 1; 15: 0 → 1; 24: 0 → 1; 31: 1 → 2; 33: 0 → 1). This node substantiate the close affinities of the South American ungulates to the North American mioclaenids. Node 39 substantiate the monophyly of the Kollpaniinae + Didolodontidae + Litopterna, which confirms the close links existing between the Kollpaniinae and some other South American ungulates. It is supported by six synapomorphies (char. 25: 0 → 1; 28: 0 → 1; 29: 1 → 2; 34: 0 → 1; 35: 2 → 1; 37: 1 → 2). Node 38 is supported by eight synapomorphies (char 3: 0 → 1; 4: 0 → 2; 6: 0 → 1; 7: 1 → 2; 8: 2 → 3; 21: 1 → 2; 22: 0 → 1; 32: 2 → 3). This node is supportive of the monophyly of the didolodontid + litoptern group. Therefore, the present analysis confirms the close relationships of the “condylarths” from Tiupampa to the North American mioclaenids and to the other South American ungulates. It diverges from the statement by Williamson (1996: 70) who sees no strong evidence of special relationships of *Molinodus* and *Tiuclaenus* with North American mioclaenids. However, contradictorily, this author also states that *Molinodus* and *Tiuclaenus* “are perhaps derived from a primitive mioclaenid similar to *Tiznatzinia*”.

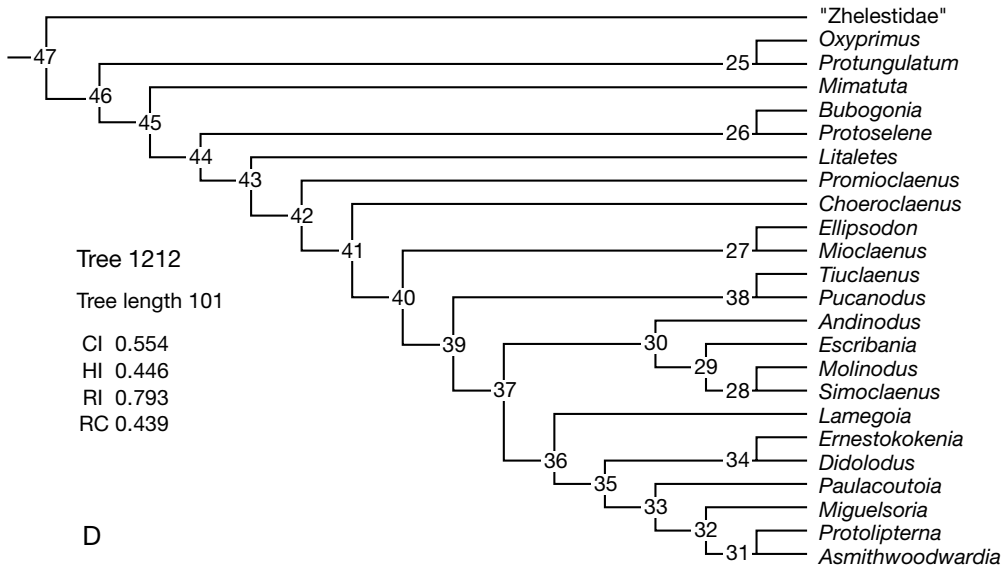
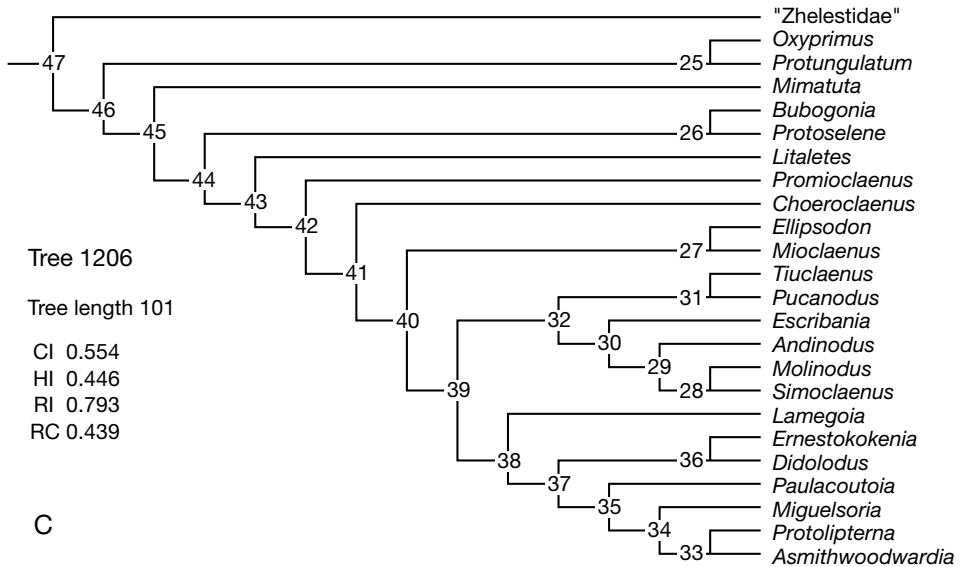
Node 32 supports the monophyly of the Kollpaniinae. However, this node is based on four synapomorphies, three of which are reversals (char. 5: 1 → 0; 19: 1 → 0; 22: 1 → 0; 31: 0 → 1). Therefore, this node is not very strong and the kollpaniines could very well be paraphyletic as shown on the tree of Figure 22D.

We are conscious that introduction of other North American “condylarths” taxa in the matrix could modify the result of the analysis, for instance, the Mioclaenidae could result in a monophyletic group. Furthermore, in spite of the relationships resulting of the present analysis, whether the Mioclaenidae are actually monophyletic or paraphyletic and whether they should include the Kollpaniinae or not is still doubtful given the relatively high homoplasy index of the trees (HI = 0.446) and the weakness of the monophyly of the Kollpaniinae. For that reason, we regard as legitimate the use of the classification term Mioclaenidae (including Kollpaniinae), at least as a working hypothesis, although it may not represent a monophyletic taxon. The “condy-

TABLE 16. — Data matrix for the distribution of the 38 characters listed above among the 24 taxa considered.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
1 "zhelestids"	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2 <i>Oxyprimus</i>	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1
3 <i>Protungulatum</i>	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1
4 <i>Mimatuta</i>	1	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	1	0	1
5 <i>Bubogonia</i>	?	?	?	?	?	0	1	1	0	1	0	1	0	0	1	0	1	0	1
6 <i>Promioclaenus</i>	1	1	0	1	0	0	1	1	0	1	1	0	0	0	1	2	1	1	1
7 <i>Litaletes</i>	1	1	0	1	0	0	1	1	0	1	0	1	0	0	1	2	1	1	1
8 <i>Choeroclaenus</i>	?	2	?	0	0	0	1	1	0	1	0	0	0	0	1	2	1	0	1
9 <i>Protoselene</i>	1	1	0	2	0	0	1	1	1	1	0	1	0	0	1	1	1	0	1
10 <i>Ellipsodon</i>	?	1	?	?	?	0	1	2	0	1	1	0	1	0	1	2	1	1	1
11 <i>Mioclaenus</i>	1	2	0	0	1	0	1	1	1	1	1	0	1	0	1	2	1	1	1
12 <i>Molinodus</i>	1	1	0	0	0	0	1	1	0	1	1	0	1	0	1	1	1	0	1
13 <i>Tiuclaenus</i>	1	1	0	0	0	0	1	2	0	1	1	0	1	0	1	2	1	1	1
14 <i>Pucanodus</i>	1	1	0	0	0	0	1	2	0	1	1	0	0	0	1	2	1	0	1
15 <i>Simoclaenus</i>	?	1	?	?	?	0	1	1	0	1	1	0	1	0	1	1	1	0	1
16 <i>Andinodus</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
17 <i>Escribania</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
18 <i>Lamegoia</i>	?	1	?	2	1	1	2	3	0	1	1	0	1	0	1	2	1	1	1
19 <i>Paulacoutoia</i>	?	1	1	2	1	1	2	3	0	1	1	0	0	0	1	2	1	1	1
20 <i>Ernestokokenia</i>	?	1	?	?	?	1	2	3	0	1	1	0	0	0	1	2	1	1	1
21 <i>Didolodus</i>	1	1	1	2	1	1	2	3	1	1	1	0	0	0	1	2	1	1	1
22 <i>Miguelsoria</i>	1	1	?	?	1	1	2	3	0	1	1	0	0	0	1	2	1	1	1
23 <i>Protolipterna</i>	1	1	1	2	1	0	1	3	0	1	1	0	0	1	1	2	1	1	1
24 <i>Asmithwoodwardia</i>	1	1	1	2	1	0	1	3	0	1	1	0	0	1	1	2	1	1	1

	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38
1 "zhelestids"	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	?
2 <i>Oxyprimus</i>	0	1	0	0	0	0	0	0	0	1	0	1	1	0	0	1	1	0	?
3 <i>Protungulatum</i>	0	1	0	0	0	0	0	0	0	1	0	1	1	0	0	1	1	0	0
4 <i>Mimatuta</i>	0	1	0	0	0	1	1	1	0	1	0	1	1	0	0	1	1	0	?
5 <i>Bubogonia</i>	0	1	0	?	?	?	?	0	0	2	0	2	1	1	0	1	1	1	?
6 <i>Promioclaenus</i>	1	1	0	0	1	0	1	0	0	1	0	2	1	1	0	1	1	1	0
7 <i>Litaletes</i>	1	1	1	0	1	1	1	0	0	1	0	2	1	1	0	1	1	0	?
8 <i>Choeroclaenus</i>	1	1	0	0	?	0	1	0	0	1	0	2	1	1	0	1	1	1	0
9 <i>Protoselene</i>	0	1	0	0	1	0	1	1	0	2	0	2	1	1	0	1	1	0	?
10 <i>Ellipsodon</i>	0	1	0	?	1	0	1	1	0	1	0	4	2	1	0	1	2	1	?
11 <i>Mioclaenus</i>	1	1	0	0	1	0	0	1	0	1	0	4	2	1	0	1	2	1	?
12 <i>Molinodus</i>	0	0	0	0	?	1	1	1	1	2	1	3	2	1	1	1	1	2	0
13 <i>Tiuclaenus</i>	0	0	0	0	1	0	0	1	1	2	1	3	2	1	1	1	1	1	0
14 <i>Pucanodus</i>	0	0	0	0	1	0	0	1	1	2	1	3	2	1	1	1	1	0	0
15 <i>Simoclaenus</i>	0	0	0	0	?	1	1	1	1	2	1	3	2	1	1	1	1	2	0
16 <i>Andinodus</i>	?	?	?	?	?	?	?	1	1	2	1	3	2	1	1	1	1	2	?
17 <i>Escribania</i>	?	?	?	?	?	?	?	1	1	2	1	3	1	1	1	1	1	2	?
18 <i>Lamegoia</i>	0	2	1	?	?	1	1	1	1	2	0	3	3	1	1	1	1	2	0
19 <i>Paulacoutoia</i>	1	2	1	0	?	1	1	1	1	2	0	3	3	2	1	1	1	2	0
20 <i>Ernestokokenia</i>	0	2	1	?	?	1	?	1	1	2	0	2	3	2	1	1	1	2	?
21 <i>Didolodus</i>	0	2	1	?	?	1	1	1	1	2	0	3	3	2	1	1	1	2	?
22 <i>Miguelsoria</i>	1	2	1	1	1	1	1	1	1	2	0	3	3	1	0	1	1	2	1
23 <i>Protolipterna</i>	1	2	1	1	2	1	1	1	1	2	0	3	1	1	0	1	1	2	1
24 <i>Asmithwoodwardia</i>	1	2	0	1	0	1	1	1	1	2	0	3	3	1	0	1	1	0	1



larths" from Tiupampa and *Escribania* are therefore included here in the Mioclaenidae. The major result of this study is the discovery of close phylogenetic relationships of the Kollpaniinae with both the North American Mioclaenidae and the South American ungulate groups

Didolodontidae and Litopterna. The monophyly of the group Mioclaenidae + Didolodontidae + Litopterna is confirmed by the parsimony analysis. Although the relationships within this group are still partially unclear and in order to emphasize these panamerican relationships, we formally

propose a new suprageneric taxon to include the North American Mioclaenidae, the Kollpaniinae, the Didolodontidae, and the Litopterna: the order Panameriungulata. This new ungulate order includes the following suprageneric taxa:

- Mioclaenidae
 - Mioclaeninae
 - Pleuraspidotheriinae
 - Kollpaniinae
- Didolodontidae
- Litopterna (suborder)
 - Protolipternidae
 - Macrauchenidae
 - Adianthidae
 - Protheroheriidae
 - Notonychopidae

CONCLUSIONS: TAXONOMY, PHYLOGENY, AND BIOGEOGRAPHY

A close phylogenetic link of Tiupampa's "condylarths" to similar taxa from the North American Palaeocene has been recognized since their initial discovery (e.g., Muizon & Marshall 1987a, b; 1991; Marshall & Muizon 1988; Van Valen 1988; Bonaparte *et al.* 1993). Additional materials (including those belonging to new taxa), coupled with the comparisons cited above, also suggest an equally important phylogenetic tie with southern groups. The Tiupampa taxa appear to be ultimately related to at least two endemic groups of ungulates that characterized land-mammal faunas later in the Tertiary of South America: the Litopterna and Didolodontidae. These comparisons further suggest that the latter two groups can be recognized as a monophyletic unit with respect to the Kollpaniinae (Tiupampa's "condylarths" + *Escribania*) and, more distally, with respect to North American Mioclaenidae (Panameriungulata). Assuming that North American mioclaenids represent a monophyletic entity (although it is probably not the case), a tempting basis for discussion and further research would be to regard the Didolodontidae and the Litopterna as sister-groups, both in turn being the sister-group of the Kollpaniinae and the three groups of South American ungulates representing the sister-group

of the North American Mioclaenidae (an interpretation approaching the results of the parsimony analysis presented above). Of course, this hypothesis is not fully satisfactory. First, either the Kollpaniinae should therefore be excluded from the Mioclaenidae and erected to a family rank or the Didolodontidae and the Litopterna should be included in the Mioclaenidae. Second, the Kollpaniinae (except *Molinodus*) are still poorly known and the upper teeth of certain taxa (*Andinodus*, *Escribania*) are unknown; because of this the monophyly of the subfamily is far from being securely established. The same is to be said for some didolodontid genera (*Lamegoia*, *Ernestokokenia*) that are still very poorly represented in the fossil record. Third, the parsimony analysis has not considered all the taxa of each group, which obviously biased the results presented in Figure 22. Furthermore, as evidenced in Figure 22, the Mioclaenidae probably do not represent a monophyletic taxon. In fact, it seems that, given the available data (almost exclusively teeth and jaws), the difficulty raised by the definition of characters and their variation (of any kind), their homoplasy, and the unavoidable subjectivity in the appreciation of qualitative characters (most of them in this case), hypotheses on the phylogenetic relationships of these groups of ungulates remains highly conjectural. Even if the "condylarth" fauna of Tiupampa represents a substantial increase in the knowledge and understanding of the evolution of the early South American ungulates, as it stands, the available material in South as well as in North America does not allow the establishment of more precise relationships, whatever method is used. As noted above, the major result of this study is the evidence for close phylogenetic relationships of the Kollpaniinae with both the North American Mioclaenidae and the South American ungulates Didolodontidae and Litopterna, the four groups being included in the new ordinal taxon Panameriungulata.

These results have implications for higher level classification of South American ungulates. At the most inclusive level (Kollpaniinae + Didolodontidae + Litopterna), consideration must first be given to remaining groups of native South American ungulates, specifically, the Astra-

pothoria, Xenungulata, Pyrotheria, and Notoungulata. Can one, some, or all of these justifiably be united into a larger group, e.g., the Meridiungulata of McKenna (1975; see also McKenna 1981; McKenna & Bell 1997)? Earlier comparisons, based on Itaboraian and later ungulates (Cifelli 1983a) suggested that dental evidence was permissive, but not suggestive, of such a grouping, except for Astrapotheria, which contain forms decidedly more primitive than a suitable hypothetical ancestor for then known didolodontids and litopterns. With the discovery of "condylarths" at Tiupampa, which are even more primitive than the proposed morphotype of the South American ungulates, morphological contradictions to common ancestry with Astrapotheria were removed (Cifelli 1993a).

Dental evidence from the "condylarths" of Tiupampa, based on all known material and on the comparisons presented above, provides no additional insight into the monophyly of the Meridiungulata. There is no clear, or even suggestive, data to support a relationship, based on shared derived characters, with Astrapotheria, Pyrotheria, or Xenungulata. However, tarsals assigned to *Tiuclaenus* suggest some notoungulate-like features (Muizon *et al.* 1998). Nevertheless, Notoungulata had already diverged from a shared common ancestor (proximally or distally), since they were clearly present in the Tiupampa fauna, although they remain known by a single, incomplete upper molar (Muizon *et al.* 1984; Muizon 1992). In other respects, it is noteworthy that referral of "condylarth" tarsal bones to dental "condylarth" specimens from Tiupampa will remain hypothetical until articulated skeletons are discovered. Our summary judgement regarding a comprehensive grouping to include South American ungulates (Meridiungulata) is that existing data does not corroborate such a monophyletic taxon. Furthermore, the close relationships evidenced here between Kollpaniinae, Didolodontidae and Litopterna, as well as the lack of dental characters susceptible to link them to other South American ungulates (or so-called ungulates, see Lucas 1993) is suggestive of a separate origin and would support the paraphyly or polyphyly of the Meridiungulata (*sensu* McKenna 1975), as suggested by Soria (1988).

Given the lack of applicable morphological evidence, we are reluctant to accept this higher taxon based strictly on geographic criteria. Caution on this point is especially appropriate because of: 1) the divergent nature of the groups in question, 2) the possibility of independent North American affinities for some (Lucas 1993), and 3) the presence at Tiupampa (the South America's oldest ungulate fauna) of Pantodonta, a group that has clear holarctic ties, but is unrelated to other South American eutherians (Muizon & Marshall 1992; Muizon 1992). Therefore, the interpretation of the affinities of the eutherian fauna of Tiupampa apparently favours multiple eutherian dispersal events from North America to South America.

Based on phylogenetic relationships, three dispersal events, at least, could be hypothesized. The probable monophyly of the kollpaniine-didolodont-litoptern group could favour a mioclaenid (or panameriungulate) dispersal event. This event could possibly have given rise to the notoungulate radiation. Dinoceratan affinities of the xenungulates and/or pyrotheres (Uintatheriamorpha = Dinocerata + Xenungulata + Pyrotheria) have been proposed by Schoch & Lucas (1985), Gingerich (1985), Lucas (1986, 1993), and Prothero *et al.* (1988). Bergqvist (1996) regarded astrapotheres, pyrotheres and xenungulates as belonging to the same monophyletic group and Cifelli (1993a) found possible relationships between pyrotheres and notoungulates (see also Patterson 1977) on the one hand and xenungulates and astrapotheres on the other. Therefore, if Lucas (1993) and others (see above) are correct in assuming dinocerate affinities for some of the South American ungulate groups, a uintatheriamorph second dispersal event is to be considered. A third event could involve pantodonts, which is irrelevant in the case of the Meridiungulata.

Although we have identified some dental synapomorphies linking Tiupampa "condylarths" with Didolodontidae and Litopterna, we are reluctant to propose a higher taxon to include them. Our conservatism reflects current lack of diagnosing features that would exclude the various other groups of South American ungulates. For instance, as noted by Cifelli (1993a), the notoun-

gulates could readily have derived from a *Tiuclaenus*-like ancestor. This statement is reinforced by the similarities between the tarsus referred to *Tiuclaenus* and primitive notoungulates which could represent evidence for a kollpaniine origin of the Notoungulata (Muizon *et al.* 1998). However, if the hypothesis of Cifelli (1993a) is confirmed by the discovery of new evidences, then the Notoungulata should also be included in the Panameriungulata.

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APPENDIX 1

TABLE 17. — Measurements and descriptive statistics for lower molars of *Promioclaenus acolytus*. **L**, mesiodistal length; **Wtri**, labiolingual width of trigonid; **Wtal**, labiolingual width of talonid. Sample includes the following AMNH specimens, all from Gidley Quarry (Torrejonian, Montana; see Simpson 1937): 35729, 35736, 35738, 35742, 35748, 35749, 35752, 35758, 35761, 35767, 35769, 35771, 35779, 35782, 35786, 35787, 35791, 35792, 35793, 35794, 35799, 35800, 35801, 35802, 35804, 35807, 35808, 35809, 35811, 35816.

Measurement	N	Min	Max	Mean	CV
m1 L	29	3.22	3.64	3.40	0.032
m1 Wtri	27	2.54	3.18	2.77	0.057
m1 Wtal	29	2.57	3.43	2.91	0.056
m2 L	33	3.33	3.99	3.60	0.042
m2 Wtri	33	2.94	3.53	3.24	0.049
m2 Wtal	31	2.87	3.43	3.10	0.044
m3 L	30	3.34	3.99	3.67	0.037
m3 Wtri	30	2.45	2.98	2.67	0.048
m3 Wtal	28	2.02	2.43	2.20	0.042