

New remains and species of the ‘condylarth’ genus *Escribania* (Mammalia: Didolodontidae) from the Palaeocene of Patagonia, Argentina

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ABSTRACT: The Punta Peligro fauna includes some of the oldest Cenozoic South American mammals, and the oldest ones for Patagonia. In addition to frogs, turtles, and crocodiles, an unusual mammalian assemblage is formed by a mixture of Mesozoic lineages of Gondwanan origin and therians (eutherians and metatherians) derived from Laurasian immigrants. This paper describes new remains of the Didolodontidae ‘condylarth’ genus *Escribania* Bonaparte, Van Valen & Kramarz, 1993. The new material includes an isolated right lower third molar with talonid morphology different from the homologous structure of the type species *Escribania chubutensis* Bonaparte, Van Valen & Kramarz, 1993, justifying the recognition of a new species. The derived nature of the didolodontid ‘condylarths’ from the Banco Negro Inferior, their differences with the Mioclaenidae Kollpaniinae from the early Paleocene of Tiupampa, and the record of *bona fide* litopterns in the Banco Negro Inferior (BNI) suggest an early radiation of the panameriungulates.



KEY WORDS:

Escribania talonicuspis, Palaeogene, Peligran SALMA, South America, ungulates

The Punta Peligro locality is situated on the Argentinean Atlantic coast, 30 km north of Comodoro Rivadavia (Fig. 1). The material described here came from the ‘Banco Negro Inferior’ (BNI), which belongs to the basal section of the Hansen Member of the Danian Salamanca Formation (Andreis *et al.* 1975). The recorded fauna includes Anura, Chelonia and Crocodylia (Bonaparte *et al.* 1993), as well as a unique assemblage of mammals derived from Gondwanan and Laurasian lineages (Bonaparte *et al.* 1993; Ortiz-Jaureguizar 1996; Pascual 1996, 1998; Pascual *et al.* 1996; see Appendix). The Gondwanan lineages include the gondwanathere *Sudamerica ameghinoi* Scillato-Yané & Pascual, 1985, considered as a multituberculate (Bonaparte *et al.* 1993) or, more recently, as a Mammalia *incertae sedis* (Pascual *et al.* 1999); the dryolestoid *Peligrotherium tropicalis* Bonaparte, Van Valen & Kramarz, 1993 (Gelfo & Pascual 2001; Rougier *et al.* 2003; Rougier & Apesteguía 2004), and *Monotrematum sudamericanum* Pascual, Archer, Ortiz-Jaureguizar, Prado, Godthelp & Hand, 1992a, a monotreme related to the Australian Ornithorhynchidae taxa (Pascual *et al.* 1992a, 1992b). On the other hand, the Laurasian immigrants are represented by several metatherians (i.e., didelphimorphians, polydolopimorphians, sparassodonts; Bond *et al.* 1995; Goin *et al.* 2004) and eutherians represented by the notonychopid litoptern *Requisia vidmari* Bonaparte & Morales, 1997, and two bunodont ‘condylarths’, *Escribania chubutensis* Bonaparte, Van Valen & Kramarz, 1993, and *Raulvaccia peligrensis* Bonaparte, Van Valen & Kramarz, 1993. On the basis of this mammal assemblage, Bonaparte *et al.* (1993) recognised a new South American Land Mammal

Age (SALMA), which they named Peligran, and located chronologically between the older Tiupampan, and the younger Itaboraian SALMAs. More recently Marshall *et al.* (1997) considered the Peligran SALMA to be earlier than the Tiupampan, based on geological and palaeomagnetic data. Unfortunately, due to the lack of isotopic age data and common taxa in the Tiupampan sediments, no agreement has been reached between different authors about the relative ages of the Tiupampan and Peligran SALMAs (e.g., Bonaparte & Morales 1997; Ortiz-Jaureguizar *et al.* 1999).

Escribania chubutensis was described on the basis of a left jaw fragment with m2–3 (UNPSJB PV 916). *Raulvaccia peligrensis* is represented by only a fragment of a left jaw with a broken tooth (UNPSJB PV 915) originally considered as an m2. These two taxa were included in the South American Mioclaenidae previously known from the early Paleocene locality of Tiupampa in Bolivia (Muizon 1991), more specifically in the subfamily Kollpaniinae (=Molinodinae of Bonaparte *et al.* 1993). Muizon & Cifelli (2000) argued that *Raulvaccia* is a junior synonym of *Escribania* because the tooth in the holotype of the former is not an m2, but could correspond to the m1 of the second taxa. Finally, the latest review of the phylogenetic relationships of *Escribania* suggests that this taxon is more strongly related to the advanced Didolodontidae than to the Tiupampan Mioclaenidae (Gelfo 1999, 2004).

New specimens from the BNI are described in the present paper, including remains of *Escribania chubutensis* and a co-generic new species. Some aspects of the systematics of *Escribania* and related taxa are also discussed.

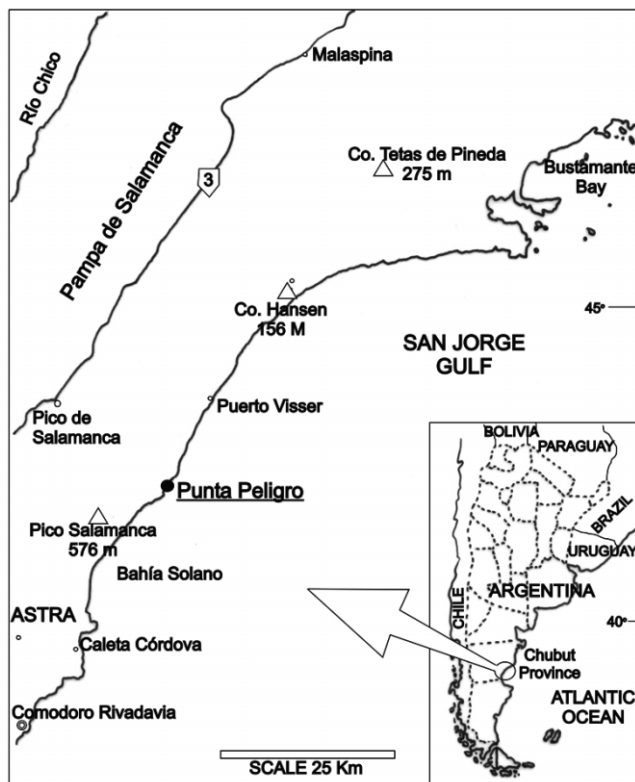


Figure 1 Map of Gulf of San Jorge Basin in the Chubut Province, Argentina.

1. Geological background

The marine Salamanca Formation (Fig. 2) (Feruglio 1949; Andreis *et al.* 1975; Lesta *et al.* 1980; Legarreta & Uliana 1994) is extensively developed within the San Jorge Gulf Basin in Chubut Province, Argentina (Fig. 1). The Salamanca Formation apparently was deposited as a result of the marine transgression ('Salamanca Sea') that ranged extensively northward and southward from the San Jorge Gulf Basin in South America during the Late Cretaceous–early Paleocene (Feruglio 1949; Andreis *et al.* 1975; Lesta *et al.* 1980; Uliana & Biddle 1988; Barcat *et al.* 1989; Legarreta *et al.* 1990).

One of the uppermost levels of the Salamanca Formation has yielded the oldest known Cenozoic mammals in Patagonia (see Bonaparte *et al.* 1993; Bond *et al.* 1995; Pascual *et al.* 1996, Ortiz-Jaureguizar 1996). This level, known by oil geologists and palaeontologists as the 'Banco Negro Inferior' (BNI), represents the retraction of the marine influence and the beginning of a sedimentary regime developed in coastal plain environments.

Exposed on the northern slopes of the San Jorge Gulf Basin, the BNI (Fig. 2) is a sequence of dark to blackish sediments varying in thickness from 1 to 8 m. From a lithostratigraphic point of view, the BNI is located within the uppermost levels (Hansen Member) of the Salamanca Formation (e.g., Simpson 1935; Andreis *et al.* 1975; Legarreta & Uliana 1992, 1994; Bonaparte *et al.* 1993; Bond *et al.* 1995; Pascual *et al.* 1996, 1999). The BNI comprised massive black clays of conchoidal fracture, and interspersed irregular conglomerates. Most of the vertebrate remains have been recovered from a level of whitish tuffaceous concretions situated at its lowest levels (Andreis *et al.* 1975).

The BNI has been considered as a lagoon deposit, formed during the withdrawal of the 'Salamanca Sea' (Andreis *et al.* 1975; Andreis 1977). During this withdrawal, the 'Salamanca Sea' left marsh areas on the continent, with freshwater and

brackish swamps. However, clays in which glauconite is an important component have been recognised in several places (e.g., Cerro Redondo, see Simpson 1935) located 10 m above the BNI. This suggests that marine conditions persisted or were re-established (but for a short lapse of time) after the BNI sedimentation (Pascual & Ortiz-Jaureguizar 1991).

Andreis *et al.* (1975) and Andreis (1977) reported the presence of nodular structures, pedotubules, and cutans inside two chloritic tuffs of the Hansen Member; the first of these layers being located in the upper part of the Salamanca Formation above the 'Banco Verde', and the second level situated amidst the BNI sediments. According to these authors, these sedimentary structures suggest the occasional establishment of a non-marine (aerial) environment. During these short aerial phases, paleosoils developed under humid climatic conditions.

2. The BNI land-mammal fauna: taxonomic richness and palaeoecology

The BNI land-mammal fauna includes a unique association of the last representatives of surviving Mesozoic mammals (including dryolestoids and monotremes), the first native 'condylarths' and marsupials. In other words, an extraordinary and surprising mixture of therians derived from Laurasian immigrants, together with a few Gondwanan relicts in southernmost latitudes (see Pascual *et al.* 1996; Ortiz-Jaureguizar 1996; Pascual 1996, 1998). Along with these mammals, fossil remains of frogs, turtles and crocodiles have been recovered in most of the localities where the Salamanca Formation is exposed. In the Punta Peligro BNI the Alligatoridae are represented by a new species of the caimanine *Eocaiman* Simpson, 1937 and the turtles by a new species of *Hydro-medusa* Wagler, 1830 (Bona 2004, see Appendix).

The taxonomic diversity of the BNI mammals is relatively low (12 species grouped in 11 genera; see Fig. 3 and Appendix). The most diverse mammals are the panameriungulates (didodontids and notonychopids), followed by didelphimorphian and polydolopimorphian marsupials. Compared to the Late Cretaceous Alamitian SALMA (see Pascual *et al.* 1996; Pascual 1998) the most outstanding differences are the extinction of most non-tribosphenic mammals (with the exception of the Gondwanatheria and the dryolestoids); the presence of a monotreme; and the appearance of marsupials and placentals (see Appendix). According to the Patagonian record, this notable compositional change occurred probably during the long hiatus between the Late Cretaceous (Campanian–earliest Maastrichtian) and the earliest Paleocene. This compositional change in the South American communities was named 'The First Great Turnover' by Pascual *et al.* (2001), as a counterpart to 'The Second Great Turnover', which involved those mammals that participated in the 'Great American Biotic Interchange' during the Late Cenozoic (see Stehli & Webb 1985).

The mammalian record from the BNI is still poor and probably biased, but based on the known fossils from this level, the land-mammal communities would have been dominated by omnivores, followed by insectivores and insectivore-frugivores (Bonaparte *et al.* 1993) (Fig. 3). According to their palaeoecological specialisation, it has been concluded that the BNI mammals were adapted to life in forested habitats, under subtropical and relatively humid climatic conditions (Pascual *et al.* 1996; Ortiz-Jaureguizar 1996; Ortiz-Jaureguizar & Cladera 2006). Despite being supported by scarce fossil remains, this inference is confirmed by other biological and geological evidences. The crocodiles and the Chelidae turtles indicate the existence of freshwater habitats (e.g., swamps,

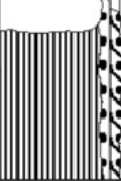
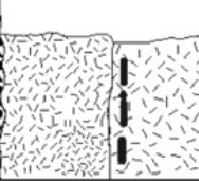
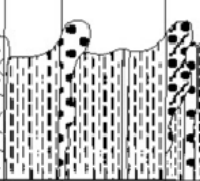

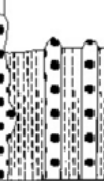
Ma	LITOSTRATIGRAPHIC UNITS	COLUMN	DEPOSITIONAL CONTEXT	CHARACTERISTIC LAND-MAMMALS	SALMAS	Ma
34	Monte León Fm.		Inner shelf to offshore. Condensed intervals littoral to inner shelf			
	San Julián Fm.		Low gradient plains covered by loess	<i>Notostylops spp.</i>	Casamayoran	
40	Casamayor Fm.		Moderate to intense edaphic processes in savanna's environments			
55	Koluel Kaike Fm.		Alluvial to ephemeral lacustrine	<i>Ernestokoenia chaishoer</i>	Riochican	40
58	Las Flores Fm.		Alluvial and minor fluvial channels. Restricted channels filled up by meandering fluvial deposits	<i>Kibenikhoria get</i>	Itaboraian	55
60	Peñas Coloradas Fm.		Fluvial of moderate to high sinuosity	<i>Carodnia feruglioi</i>	Tiupampan* or Itaboraian**	58
63	"Banco Negro Inferior" (BNI)		Lagoon, coastal marine to mangrove deposits	<i>Monotrematum sudamericanum</i>		60
	Salamanca Fm.		Inner shelf to offshore	<i>Sudamerica ameghinoi</i>	Peligran	63
71	Yacimiento Trebol Fm.		Interior basin with condensed intervals Coastal marine and beaches	<i>Peligrotherium tropicalis</i>		
			Alluvial to fluvial channels bearing high suspended load			71

Figure 2 Stratigraphical column of the Late Cretaceous–Early Miocene units recorded across the Golfo de San Jorge Basin, including the lithostratigraphic units, their depositional context and characteristic fossil mammals, and the correlated SALMAs (based on Bond *et al.* 1995). (Fm) Formation. *Tiupampan SALMA was alternatively referred as older than Peligran (Boanaparte *et al.* 1993) or younger (Marshall *et al.* 1997). **The Peñas Coloradas formation where the *Carodnia* zone was defined (Simpson 1935) could be related to the Itaboraian or even to an older SALMA.

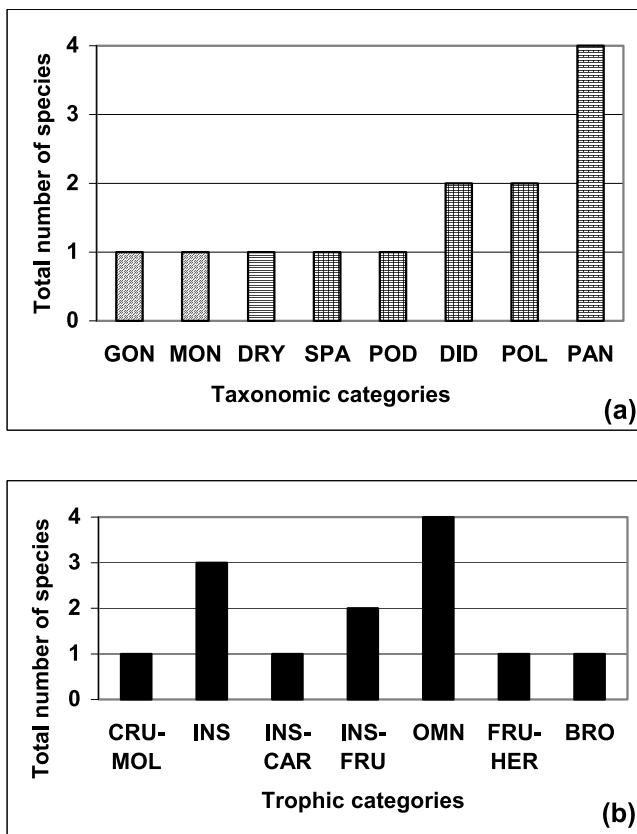


Figure 3 (a) Taxonomic richness of the BNI mammals. (diagonal lines) non-tribosphenics; (horizontal lines) pre-tribosphenics; (horizontal and vertical lines) marsupials (bricks) placentals. (GON) Gondwanatheria; (MON) Monotremata; (DRY) Dryolestida; (SPA) Sparassodonta; (POD) Peradectia or Didelphimorphia; (DID) Didelphimorphia; (POL) Polydolopimorphia; (PAN) Panameriungulata. (b) Trophic categories. (CRU-MOL) crustacean-mollusc eaters; (INS) Insectivorous; (INS-CAR) Insectivorous-carnivorous; (INS-FRU) insectivorous-frugivorous; (OMN) omnivorous; (FRU-HER) frugivorous-herbivorous; (BRO) browsers.

streams), developed under temperate-warm, humid and relatively uniform climates (Pascual & Ortiz-Jaureguizar 1991; Pascual *et al.* 1996; Ortiz-Jaureguizar 1996). Palynological evidence indicates the existence of swamp and mangrove communities near the coast, developed under humid and mainly subtropical climatic conditions (Petriella & Archangelsky 1975; Romero 1986, 1993; Troncoso & Romero 1998). Finally, sedimentological evidence suggests the presence of lagoons and swamps, and the existence of relatively humid climates (Andreis *et al.* 1975; Andreis 1977).

3. Materials and methods

In the following description and discussion the lower teeth will be represented by lower case letters, and the upper teeth by capital letters. All measurements are in millimeters (Table 1) and were taken with calipers.

3.1. Repository abbreviations

AMNH: American Museum of Natural History, New York, USA; MACN: Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia'; Ciudad Autónoma de Buenos Aires, Argentina; MLP: Depto. Científico de Paleontología de Vertebrados, Museo de La Plata, La Plata, Argentina; MHNC: Museo de Historia Natural de Cochabamba, Cochabamba, Bolivia; MN: Museu Nacional de Rio de Janeiro, Rio de Janeiro, Brazil; MPEF-PV: Museo Paleontológico

Egidio Feruglio, Paleontología de Vertebrados, Trelew, Argentina; UNPSJB-PV: Universidad Nacional Patagónica San Juan Bosco, Paleontología de Vertebrados; YPFB Pal: Yacimientos Petrolíferos Fiscales Bolivianos, Paleontología, Bolivia.

4. Systematic palaeontology

Order Panameriungulata Muizon & Cifelli, 2000

Family Didolodontidae Scott, 1913

Genus *Escribania* Bonaparte, Van Valen & Kramarz, 1993

Type Species. *Escribania chubutensis* Bonaparte, Van Valen & Kramarz, 1993.

Referred Species. *E. chubutensis* and *E. talonicuspis* nov. sp.

Escribania chubutensis Bonaparte, Van Valen & Kramarz, 1993

Holotype. UNPSJB PV 916: left jaw fragment with m2–3.

Hypodigm. The holotype; MLP 93–XII–10–2 left m2; MPEF-PV 1860 right jaw fragment with m1–2; MLP 93–XII–10–1 right jaw fragment with m3; MLP 90–II–12–67 broken left m3 with the distal root and complete talonid; MLP 90–II–12–63 right maxillary fragment with m2–3; MLP 90–II–12–68 left maxillary fragment with m2.

Horizon and age. Upper part of the Hansen Member, 'Banco Negro Inferior', Salamanca Formation, Peligran SALMA, Paleocene. Punta Peligro locality, Chubut province, Argentina.

Material referred. *MPEF-PV 1860* (Fig. 4a–b; Table 1) corresponds to a right jaw fragment, smaller than the holotype. The trigonid of the m1 is broken labially, but the m2 is well preserved. The lingual side of the jaw is broken, so that the mesial molar roots are visible. The trigonids of the m1–2 are longer lingually than labially, while the talonid is longer labially due to the distal location of the metaconid and the mesial position of the hypoconid. The trigonid of m1 preserves the lingual side of the metaconid and the paraconid, and part of the precingulid, which as preserved extends only to the more mesial and lingual side of the base of the paraconid. The hypoconid and hypoconulid have been obliterated by wear, leaving a continuous dentine surface limited by enamel distally and labially. The rounded hypoconid is the largest cusp of the talonid. The hypoconulid projects distally and is connected to the hypoconid and entoconid. The entoconid is much less worn than the other cups. The talonid basin, which cannot be defined accurately due to wear, is partially closed by the presence of a low and weak entocristid, projecting mesiolabially from the entoconid. The postcingulid, which is shorter than the precingulid, extends from the lingual side of the hypoconulid to the labial side of the entoconid. In lateral view the postcingulid of the m1 overlaps the precingulid of the m2, whose paracristid is as high as the distal border of the m1 hypoconulid.

The m2 is shorter mesiodistally than in the holotype. The trigonid cusps are very close to each other and their bulbous bases almost fill the trigonid basin, which appears in occlusal view as a groove, projecting from the distolingual side of the trigon to its mesiolabial edge. This groove bifurcates mesially, separating the distal side of the paracristid from the paraconid and protoconid; distally it divides the mesiolabial face of the metaconid from the paraconid and the protoconid. The metaconid is the highest cusp and it is placed more distally than the protoconid. The paraconid is a well-defined cusp, mesiolingual

Table 1 Measures of the lower molars described for *Escribania chubutensis* and *E. talonicuspis*

	Length in mm				Width in mm	
	Labial		Lingual		Trigonid	Talonid
	Trigonid	Talonid	Trigonid	Talonid		
MPEF-PV 1860 m1	–	3.36	4.16	2.88	–	5.92
MPEF-PV 1860 m2	3.68	4.32	5.28	2.88	6.72	6.88
MLP 93–XII-10–1 m3	4.64	6.88	5.44	5.12	6.52	5.4
MPEF-PV 1861 m3	4	6.88	5.6	5.28	5.92	5.76

to the metaconid in position, and connate to its base in lingual view. There is no metacristid in occlusal view. The paracristid runs from the mesiolabial side of the protoconid to the mesiolabial side of the paraconid. It is considerably low, arched and distally concave. Contrary to the holotype, no cuspule is present at the point where the paracristid changes its direction. The protoconid seems to be of the same size or slightly smaller than the paraconid. The protocristid is short and low.

The hypoconid is the largest cusp of the talonid. The cristid obliqua is low and rounded, and projects mesially to the labial side of the metaconid. The mesial face of the entoconid is located slightly more distally than the hypoconid. As in the m2 of the holotype (Bonaparte *et al.* 1993) and other molars assigned to this species (Gelfo 1999), no cuspule is present between the entoconid and the metaconid, so the talonid basin is lingually open. The hypoconulid is similar in size to the entoconid, and similarly to the condition of the m1, it is more distally projected than the other talonid cusp.

Each of the molars has two mesiodistally compressed roots, one located below the trigonid and the other below the talonid. In lateral view, the mesial roots of all teeth are consistently more robust and wider lingually than labially; by contrast the distal roots are wider labially. All roots are wider near the crown and narrower in the opposite direction.

MLP 93–XII-10–1 (Fig. 4c–d; Table 1) right jaw fragment with well preserved m3, and remains of the distal m2 root. Even though the trigonid is extremely worn, the general morphology of the cusps is better preserved than in the broken trigonid of the m3 of the holotype. This allows a more complete description of the cusps and their relationships. For example, the apparently greater height of the hypoconulid with respect to the other cusps in the holotype (Bonaparte *et al.* 1993) is an artifact due to the wear of the trigonid. The wear has erased the trigonid, leaving the outline of the cusp bases. The paraconid seems to have been the highest cusp, followed with a smaller metaconid and an even smaller protoconid. A short paracristid connects the mesiolabial side of the protoconid, to the mesiolabial of the paraconid; the paracristid is distally concave as in Kollpaniinae, but differs in being proportionately much shorter. Even though the paraconid is slightly more labial than the metaconid, both cusps are connate at their bases. A metacristid cannot be recognised. The metaconid is not as distal with respect to the protoconid as in the m2. The small protoconid joins to the metaconid by a bulky and short protocristid. No precingulid is observed except for a small labial rim mesial to the paracristid, which disappears in the hypoconulid notch of the m2.

As in the holotype, the talonid is much longer mesiodistally than the trigonid. The hypoconid seems to be the highest cusp, not only of the talonid but of the entire tooth. The strong cristid obliqua is distally separated from the hypoconulid by a deep valley and contacts mesially with the labial face of the metaconid. The hypoconulid practically fills the distal half of

the talonid; its distolingual side is broken, so it is not possible to confirm the presence of the cuspule located between the hypoconulid and entoconid that appears in the holotype. The entoconid is separated from the hypoconulid, and associated with a bulky and low entocristid, which does not contact the base of the trigonid. For that reason, and because the metaconid is not strongly projected distally over the talonid as in the m2, the talonid basin is open lingually. The bulbous development of the hypoconid and the entoconid fills the talonid basin, which is delimited by an oblique valley between these cusps, and opens lingually between the distal border of the metaconid and the mesial of the entocristid. No postcingulid is present.

MLP 90–II-12–67: left m3 with the talonid and almost complete distal root. It shows little wear and the same structures are observed in other m3 of this species. The hypoconulid is close to the labial edge and subequal in size to the hypoconid. A brief labial cingulum is present between the bases of these cusps. The entoconid is large, with a bulbous base, but not much differentiated from the entocristid, so that most of this cusp, which is oval in outline, runs mesio-distally. There is a smaller cusp delimited by deep enamel furrows in the lingual side between the hypoconid and the entoconid, and equidistant from both. There is an oval basin in the labial side of the distal root, located beneath the limits between the hypoconid and the hypoconulid.

MLP 90–II-12–63: right maxillary fragment with M2–3. This fragment, together with a left maxillary fragment with M2 (MLP 90–II-12–68), has been fully described and illustrated by Gelfo (2006). The M2 (Fig. 4e) is almost square in outline, but with a labio-lingual long axis. Mesial, labial and distal cingulum are well developed, but no lingual cingulum is present at the base of the protocone. The protocone is the largest cusp followed in size by the paracone and metacone, which are subequal. The paracone is somewhat more labially located than the metacone. The centrocrista is straight and no mesostyle is present. A strong parastyle, erased by wear in these remains, is present mesial to the paracone. Paraconule and metaconule are smaller than the labial cusps, and subequal in size. A strong preprotocrista links the protocone with the paraconule, whereas the preparaconular crista runs from the latter to the parastyle. The hypocone is well developed at the lingual end of the distal cingulum; it is close to the protocone but clearly separated from it by a deep lingual furrow.

The M3 shows the same characters as M2, including a well developed hypocone. The relative size of the M3 cusps differs from those of M2, as is usually observed in other 'archaic ungulates' due to their locus position.

Escribania talonicuspis nov. sp.

Diagnosis. Ungulatomorph, with m3 similar in size to *Escribania chubutensis* but with broader talonid, distally rounded and not as sharp in occlusal view. The trigonid is only

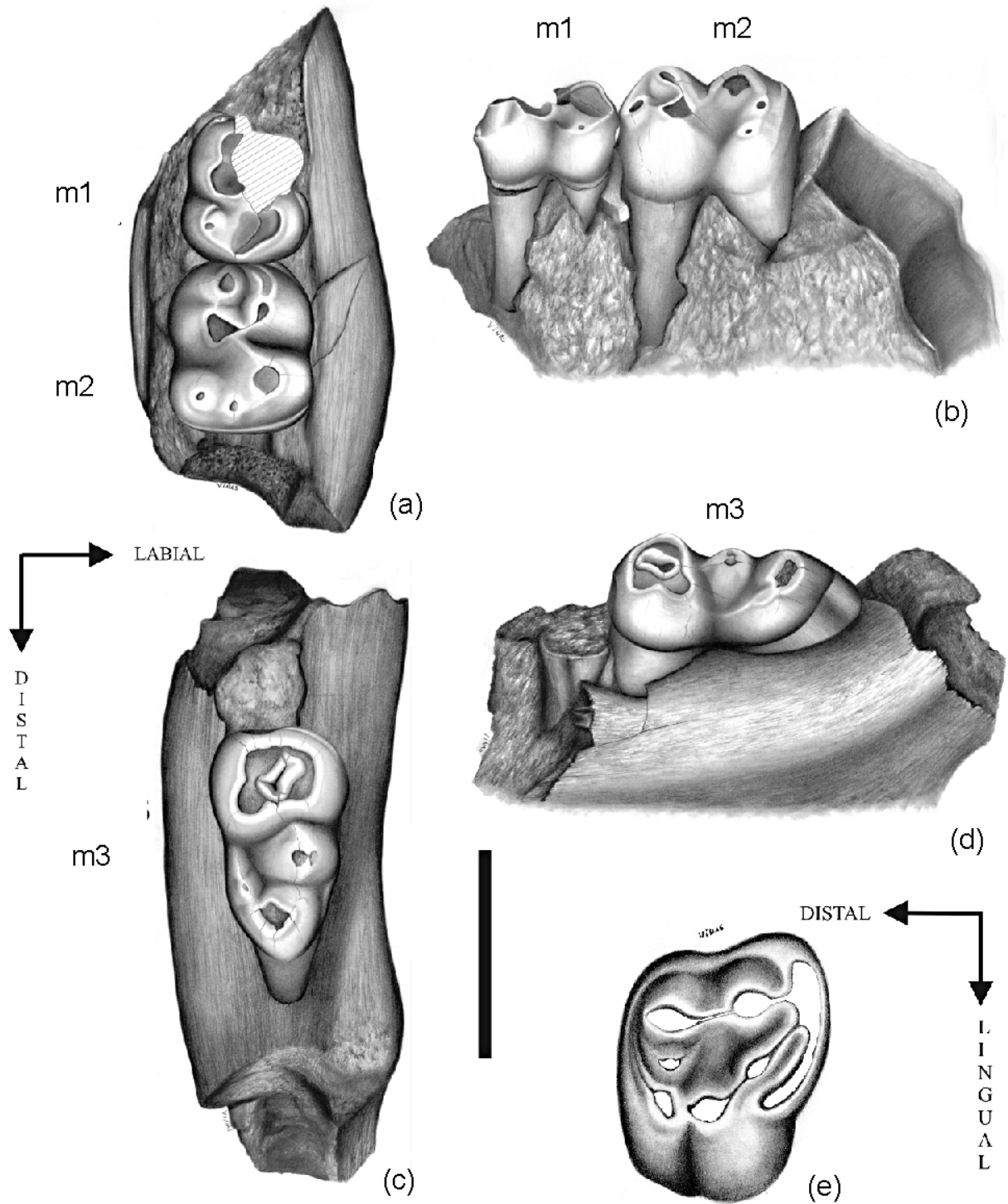


Figure 4 *Escribania chubutensis*: (a) MPEF-PV 1860 in occlusal view and (b) in lingual view. (c) MLP 93-XII-10-1 in occlusal view and (d) in lingual view. (e) right M2 from MLP 90-II-12-63 in occlusal view. Scale bar=5 mm.

slightly broader than the talonid, 2.7% vs. 13% in *E. chubutensis*. Further differs from *E. chubutensis* in: hypoconulid placed medially and far away from the hypoconid; entoconid is well defined and does not continue forward in an entocristid; talonid basin completely filled by a cusplule (accessory cusp 2 of Fig. 5) located between the hypoconid (higher and more mesial) and the entoconid (smaller and more distal); precingulid well developed from the labial side of the protoconid to the mesiolingual side of the paraconid. In contrast to *Escribania chubutensis*, in which the hypocristid joins a weak labial cingulum, in this species the strong and low hypocristid

extends from the labial face of the hypoconulid to the distal and basal side of the hypoconid.

Holotype. MPEF-PV 1861, well preserved m3 with complete roots and with well-preserved cusps.

Horizon and age. Upper part of the Hansen Member, 'Banco Negro Inferior', Salamanca Formation, Peligran SALMA, Paleocene. Punta Peligro locality, Chubut province, Argentina.

Description. MPEF-PV 1861 (Fig. 5). As in most other ungulate m3s, the talonid is longer than the trigonid. However, the tooth is shorter mesiodistally than in *Escribania chubutensis*

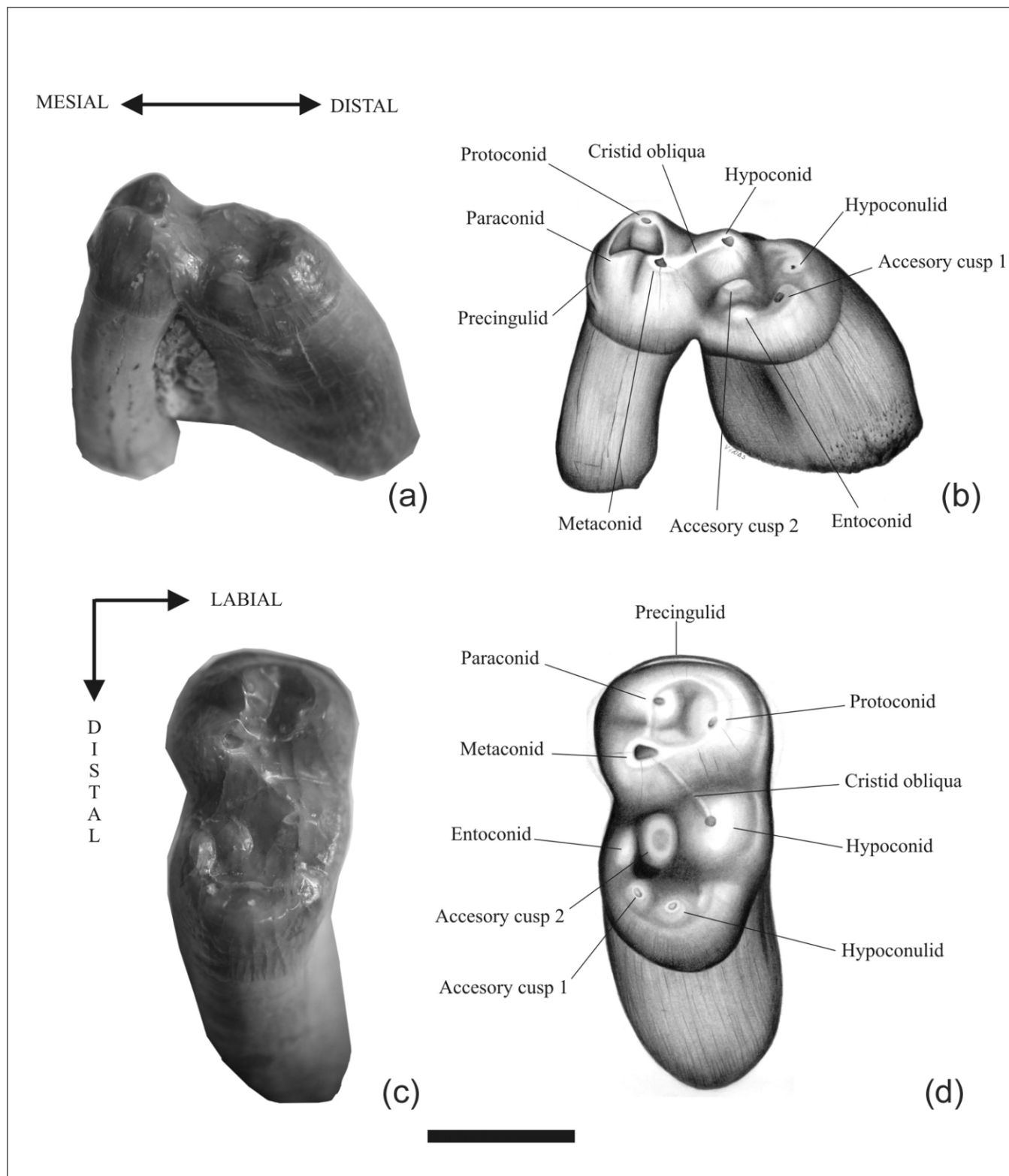


Figure 5 *Escribania talonicuspis*: MPEF-PV 1861(a) and (b) in lingual view. The same material (c) and (d) in occlusal view. Scale bar=5 mm.

and the trigonid is only slightly broader than the talonid. The position of the trigonid cusps is similar to the condition of other primitive ungulates, particularly *Escribania chubutensis*. The paraconid and the protoconid show little wear and are united by a low unworn semicircular paracristid. The proto-cristid is short but higher than the paracristid. A markedly worn metaconid is the largest and most distally located cusp of the trigonid. A well-developed precingulid runs from the labial portion of the protoconid to the mesiolingual side of the

paraconid. The contact between the m2 talonid and the m3 trigonid appears as a weak hypoconulid notch, below the paracristid and over the precingulid, but not interrupting its continuity as in the precingulid of *Escribania chubutensis* (MLP 93-XII-10-1). The major differences between the latter and *E. talonicuspis* are the number and distribution of talonid cusps. The hypoconid is the highest cusp, particularly close to the distolabial side of the metaconid and only separated from it by an abbreviated cristid obliqua that seems to be directed

lingually. The hypoconulid, the most distal cusp, is equidistant from the labial and lingual borders. The weak and low hypocristid projects from the hypoconulid labially to the apex of the hypoconid. But the degree of wear of this cristid does not mask the presence of what seems to be three low aligned cusps. There is only a relict of labial cingulid at the base of the hypoconid. Three cusps located on the lingual side of the talonid should be carefully discussed. The lesser, accessory cusp 1 (AC 1), is close to the hypoconulid and fused to its mesiolingual base. The larger cusp, accessory cusp 2 (AC 2), is distolingual to the hypoconid, and the last cusp, here interpreted as the entoconid, is located on the lingual side of the talonid, mesial to AC 1 and lingual to AC 2. Considering the variable presence of a mesial cusp mesial to the entoconid in Didolodontidae and Protolipternidae, and the reduction and adjacent location of entoconid and hypoconulid in Kollpaniinae, it is not possible to dismiss the possibility that AC1 is the correct homologue of the entoconid. The present authors reject this interpretation because of the lesser size of AC1 and because it is strongly attached to the short posteristid at the base of the hypoconulid, in the same way as three similar bulbous structures attached onto the hypocristid. Thus AC1 is interpreted as part of the cuspidate cristid related to the hypoconulid.

Although two mesial cusps, the postmetaconulid and entoconid, and one distal cusp, the postentoconulid, have been described in association with the entoconid (Hershkovitz 1971), it is very difficult to establish correct homologies for AC1 or AC2 without complete certainty about the entoconid homology.

Following this interpretation, the entoconid is better defined than in *Escribania chubutensis* and is not associated with a mesial entocristid. Even though the entoconid and the metaconid are sufficiently separated, the talonid basin does not open lingually because it is filled by the presence of AC 2, which links the mesiolabial base of the entoconid and the distolingual edge of the hypoconid. The height of AC 2 is intermediate between the entoconid and the hypoconid in lateral view. As in the holotype of *Escribania chubutensis* a small cusp (AC 1, Fig. 5) is present, lingual to the hypoconulid and separated by a faint furrow. Mesially, this cusp extends to contact the entoconid, as a high and robust posteristid in *E. chubutensis* but low and rounded in *E. talonicuspis*. The trigonid root is lightly compressed mesiodistally and concave distally. By contrast the larger distal root, beneath the talonid, is compressed labio-lingually with a straight mesial side. The apex of the angle formed by the mesial and distal roots is directed toward the distal side of the trigonid. The talonid root is strongly convex distally and, contrasting with the mesial root or the m1–2 roots of *E. chubutensis*, the greatest width is located near the middle rather than near the crown of the tooth in lateral view. Like the distal root of *E. chubutensis*, there is a small basin over the labial surface of the root, which seems to be located below the separation between hypoconulid and hypoconid.

5. Discussion

Some considerations about another taxon of the same locality and age, *Raulvaccia peligrensis*, are necessary. Bonaparte *et al.* (1993) described this species as a mioclaenid ‘condylarth’, based on a fragmentary jaw remain with a badly preserved tooth that they regarded as an m2. Muizon & Cifelli (2000) concluded that *Raulvaccia* is a junior synonym of *Escribania chubutensis* and, contrary to the original description, considered the only known tooth as an m1. Their argument is based

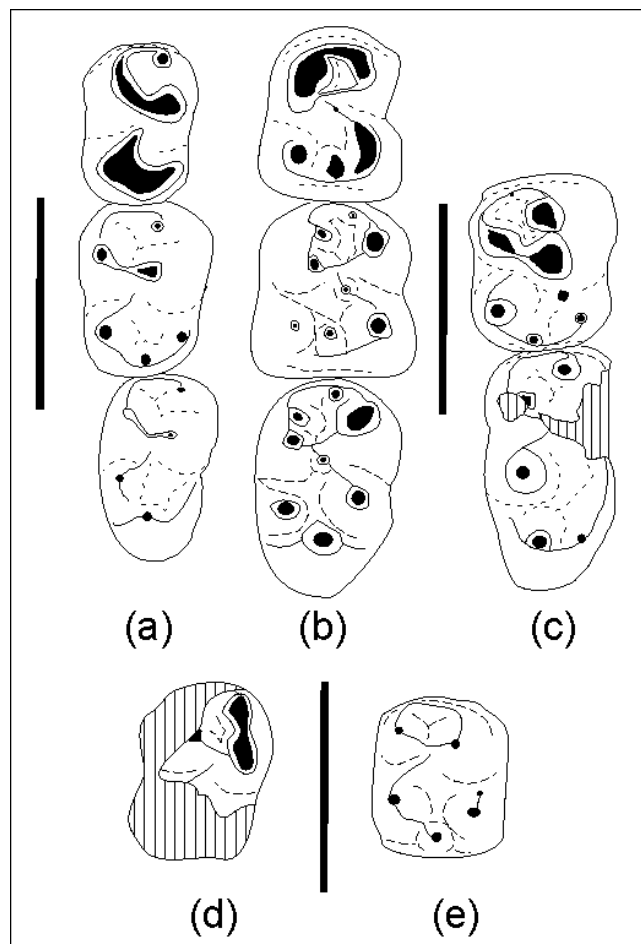


Figure 6 Occlusal sketches of (a) holotype of *Molinodus suarezi*, left m1–3 YPFB-Pal 6112, scale bar=5 mm; (b) holotype of *Didolodus crassicuspis* Ameghino, 1901 (junior synonym of *Didolodus multicuspis*), right m1–3 MACN A-10689, scale bar=10 mm; (c) holotype of *Escribania chubutensis*, left m2–3 UNPSJB PV 916, scale bar=10 mm; (d) holotype of *Raulvaccia peligrensis*, left m1? UNPSJB PV 915, scale bar=5 mm; (e) syntype of *Asmithwoodwardia subtrigona*, left m1 MACN 10723, scale bar=5 mm.

on the observation that the differences between *Raulvaccia* and *Escribania* are similar to those present between the m1 and m2 of *Paulacoutoia protocenica* (Paula Couto 1952) and *Molinodus suarezi* Muizon & Marshall, 1987 (Fig. 6a). Although the badly preserved morphology of the tooth cusps of *Raulvaccia* does not allow a precise comparison with *Escribania* (Fig. 6c, d), some details should be emphasised. The width of the alveolus of the m1, present in the holotype of *Escribania chubutensis* mesially to the m2, is greater than that observed in the *Raulvaccia* (10.95 cm and 6.95 mm, respectively). Even though the ventral portion of the dentary of *Raulvaccia* is broken, the complete size of it is more than 50% smaller than that of *Escribania*. Of all known mammalian taxa from the BNI at Punta Peligro, *Escribania chubutensis* has the most robust jaw, even larger and more heavily built than that of the dryolestoid *Peligrotherium tropicalis*. The specimen described as *Raulvaccia* seems to represent a slender and gracile taxon that, despite overall similarities with *Escribania*, can be defended as a distinct taxon.

Escribania chubutensis was described on the basis of a left jaw bearing m2–3. Some differences with *Molinodus suarezi*, were noted in the original description, including: more labial location of the paraconid, smaller trigonid basin, distally elongated m3 talonid and size three times larger. Nonetheless, this taxon was referred to the Mioclaenidae, subfamily Kollpaniinae (Bonaparte *et al.* 1993). Muizon & Cifelli (2000)

also included *E. chubutensis* with the taxa from Tiupampa, but emphasised the weakness of support for the recognition of the Kollpaniinae as a monophyletic group. Only 11 of the 38 characters included in their analysis are from the lower teeth and therefore comparable to those represented in *Escribania*. The only apomorphy shared by all the Kollpaniinae is the distal slope of the metaconid, strongly inflated, invading the talonid basin with concave protocristid, particularly evident in *Escribania* and *Andinodus boliviensis* Muizon & Marshall, 1987. However, this character is not equally conspicuous in all the Kollpaniinae, or even in all the teeth of the dental series of a single specimen. According to the degree of wear in the Kollpaniinae, the protocristid is straight in the m1–2, but concave in the m3. In *Escribania chubutensis* the metaconid and the protoconid are very close together, so that the protocristid is short and straight. Other differences with the Kollpaniinae are the smaller entoconid, and its proximity to the hypoconulid, a continuous crest usually present and linking the two cusps. In contrast, the entoconid and hypoconulid of *E. chubutensis* are well separated and never merged as in most Kollpaniinae. *E. chubutensis* seems to be similar to the Didolodontidae and primitive Litopterna in which the entoconid is similar in size, or larger than, the hypoconulid, and even if these two cusps are close together they are never fused either totally or partially. Muizon & Cifelli (2000) commented on the relationship between entoconid and hypoconulid, but in the character matrix they considered that *E. chubutensis* and the Kollpaniinae share a condition in which the hypoconulid and entoconid are connate or fused. With the exception of the m3 of *Molinodus suarezi* (YFPB Pal 6112), in which a strong and low entocristid projects mesially to the base of the metaconid, the absence of this cristid is the common condition for the Kollpaniinae, so the talonid basin is broadly open lingually. In *Escribania chubutensis* this character is variable. In the m1 there seems to be a short and low entocristid that curves labially, but is not present in the m2. Only in the m2 of the holotype is a cuspule present mesially to the entoconid and behind the metaconid, and therefore the talonid basin does not open lingually. A low entocristid that does not close the talonid basin is present in the m3 and is better defined in MLP 93–XII-10–1. On the contrary, in *Escribania talonicuspis* the entoconid does not continue in a mesial entocristid. Even though the entocristid development in the m3 of *Escribania chubutensis* is similar to that observed in the Kollpaniinae, the degree of separation between the entoconid and the hypoconulid, the absence of entocristid, and the development of an accessory cusp mesial to the entoconid are characters similar to those observed in the Didolodontidae and primitive Litopterna, and at least in one left m3 of the Kollpaniinae *Tiucloaenus cotasi* (MHNC 1232). In *Asmithwoodwardia subtrigona* Ameghino, 1901 (MACN 10723) a small cusp is present mesial to the entoconid (Fig. 6e), but none is present in *A. scotti* Paula Couto, 1952. In genus *Ernestokokenia*, which has been considered alternatively as a junior synonym of *Asmithwoodwardia* (McKenna & Bell 1997) or a valid taxon (Muizon & Cifelli 2000), the cusp mesial to the entoconid is also present in *Ernestokokenia nitida* Ameghino, 1901 (MACN 10735), but smaller than the m2 of the holotype of *E. chubutensis*. The same condition is present in some specimens of *Lamegoia conodonta* Paula Couto, 1952 (MN 1463-V). Cifelli (1983) mentioned the presence of an accessory cusp associated with the entoconid in *Didolodus*, and in the illustration of *Didolodus multicuspis* Ameghino, 1897. However, no cusp is present, mesial to the entoconid, either in the type of *Didolodus crassicuspis* Ameghino, 1901 (junior synonym of *Didolodus multicuspis*) MACN A-10689 (Fig. 6b) or in any of the studied remains; the only cusp in the area is the entoconid. It is

possible that Cifelli's cusp is present in the materials AMNH 28475 and AMNH 109618 which were, along with the holotype, the basis for his illustration. In fact, even though Simpson (1948) does not mention this cusp in his diagnosis of *Didolodus multicuspis*, he states that in closely related forms there is also a minute cuspule on the mesial slope of the entoconid, and that while it is not seen in the specimens referred to this species, it may well have been present in unworn teeth. To sum up, the cusp mesial to the entoconid present in didolodontid and protolipternid taxa could be considered variable below the species level, and probably of no systematic value.

It has been argued that the marked narrowing of the talonid width with respect to the trigonid, which occurs in the m1 of *Abdounodus hamdii* Gheerbrant *et al.*, 2001 from the early Eocene? of North Africa and in the Kollpaniinae, is peculiar and probably an apomorphic character (Gheerbrant *et al.* 2001). Notwithstanding the lack of precision of measurements of *A. hamdii*, because the lingual side of the holotype is broken, the talonid seems to be remarkably narrower than the trigonid. Given the substantial size variation of the Kollpaniinae, in which, for example, the m1s of MHNC 1234 (*Tiucloaenus robustus* Muizon & Cifelli, 2000) and MHNC 8273 (*Tiucloaenus cotasi* Muizon & Cifelli, 2000) have a talonid somewhat larger than the trigonid, the consideration of the strong shortening of talonid width as an advanced character is doubtful. A talonid narrower than the trigonid, particularly in the m2 of the Kollpaniinae, could be interpreted as plesiomorphic and different from the wider talonids present in Didolodontidae and Protolipternidae (Muizon & Cifelli 2000). The talonid of the m2 of *Escribania chubutensis* is narrower than the trigonid in UNPSJB 916 (holotype), about the same size in MLP 93–XII-10–2, and wider in MPEF-PV 1860. Although a larger sample size is necessary to draw more definitive conclusions, the talonid of *Escribania* seems to be moderately wide, more similar to the wide talonid of the Didolodontidae than to the very narrow and plesiomorphic talonids of the Tiupampan Kollpaniinae.

Several characters can be identified, such as the presence of a paraconid labial to the metaconid; the proximity of the trigonid cusps; the greater talonid expansion of the m3; a well defined entoconid not strongly associated to the hypoconulid; the variability of the talonid size in the m2; and the larger size of the teeth contrast with the condition in Kollpaniinae. The differences are emphasised by the apomorphic characters of the upper molars assigned to *Escribania chubutensis*, such as the presence of a hypocone (Gelfo 1999, 2004, 2006). In fact, the Didolodontidae are well characterised by the hypocone development in M1–3 (Cifelli 1983) in contrast to other strictly bunodont ungulates such as the Kollpaniinae, in which no trace of this cusp is present (Muizon & Cifelli 2000) or Protolipternidae such as *Miguelsoria parayirunhor* (Paula Couto 1952) or *Protolipterna ellipsodontoides* Cifelli, 1983, where the M3 hypocone is absent (Cifelli 1983). The consideration of these features of the upper and lower dentition suggests that *Escribania* is not a kollpaniinae but an advanced didolodontid, as stated in two previous cladistics analysis (Gelfo 2004, 2006).

6. Conclusions

The new remains of *Escribania chubutensis* and the new taxon *Escribania talonicuspis* here described expand the knowledge of the Peligran SALMA and represent, in the present authors' opinion, the oldest record of the South American 'condylarth' family Didolodontidae. The Didolodontidae have long been considered as the group ancestral to the Litopterna (e.g.

Simpson 1948) but another analysis considered that both didolodontids and liptoterns would have a more primitive mioclaenine-like ancestor (Cifelli 1983), which was later related to the Kollpaniinae (Cifelli 1993; Muizon & Cifelli 2000; Gelfo 2004). The species referred to *Escribania* would represent derived members of the group, distant from the hypothetical ancestral morphotype predicted for South American native ungulates; this hypothetical, generalised morphology is closer to that of the Mioclaenidae Kollpaniinae from the Tiupampán SALMA in Bolivia. Furthermore, the record of *Requisia vidmari*, a liptotern notonychopid, and also from the BNI, points to an early development of the liptoterns, which so far have not been recorded at Tiupampán. Liptoterns seems to have already been differentiated at the time when the oldest didolodontids are recorded, highlighting the pervasive presence of ghost lineages and the enduring incompleteness of the early Tertiary mammalian record.

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8. Appendix

Class Amphibia

Order Anura

Family Leptodactylidae

Gen et sp. indet. 1.

Gen et sp. indet. 2.

Family Pipidae?

Gen et sp. indet.

Class Reptilia

Order Chelonia

Family Chelidae

Hydromedusa cf. *casamayorensis* de la Fuente & Bona, 2002

Yaminuechelys maior Staesche, 1929

Order Crocodylia

Family ?Crocodylidae

Necrosuchus ionensis Simpson, 1937

Family Alligatoridae

Eocaiman nov. sp.

Class Mammalia

Order Monotremata

Family Ornithorhynchidae

Monotrematum sudamericanum Pascual, Archer, Ortiz-Jaureguizar, Prado, Godthelp & Hand, 1992a

Order Gondwanatheria

Family Sudamericidae

Sudamerica ameghinoi Scillato-Yané & Pascual, 1985

Order Dryolestida

Family Peligrotheriidae

Peligrotherium tropicalis Bonaparte, Van Valen & Kramarz, 1993

Order Peradectia or Didelphimorphia

Family, genus, and species indet.

Order Didelphimorphia

Family Derorhynchidae

Derorhynchus aff. *D. minutus* Goin, Case, Woodburne, Vizcaíno & Reguero, 1999

Family indet.

Didelphopsis nov. sp.

Order Sparassodonta

Family, genus and species indet.

Order Polydolopimorphia

Family indet.

gen. et sp. nov. Family Bonapartheriidae

gen et sp. nov.

Order Panameriungulata

Family Didolodontidae

Escribania talonicuspis nov. sp.

Escribania chubutensis Bonaparte, Van Valen & Kramarz, 1993

Raulvaccia peligrensis Bonaparte, Van Valen & Kramarz, 1993

Infraorder Liptoterna (*sensu* Muizon & Cifelli, 2000)

Family Notonychopidae*

Requisia vidmari Bonaparte & Morales, 1997

*Notonychopidae were recognised also as a distinct taxon from Liptoterna, as Order Notopterna (Soria 1988).

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