

***Peligrotherium tropicalis* (Mammalia, Dryolestida) from the early Paleocene of Patagonia, a survival from a Mesozoic Gondwanan radiation**

Javier N. GELFO

Departamento Científico de Paleontología de Vertebrados,
Museo de La Plata, Paseo del Bosque s/n (1900) la Plata, Buenos Aires (Argentina)
Comision de Investigaciones Cientificas, Provincia de Buenos Aires (Argentina)
mgelfo@intramed.net.ar

Rosendo PASCUAL

Departamento Científico de Paleontología de Vertebrados,
Museo de La Plata, Paseo del Bosque s/n (1900) la Plata, Buenos Aires (Argentina)
ropascua@museo.fcnym.unlp.edu.ar

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ABSTRACT

Peligrotherium tropicalis was originally diagnosed as a placental mammal (Peligrotheriidae, Condylarthra? Bonaparte, Van Valen & Kramartz, 1993), based on lower molariforms features and the inferred dental formula. Herein we describe the first upper cheekteeth associated with lower ones, coming from the same Patagonian locality and level (early Paleocene) as the holotype. Neither the upper cheekteeth nor the lower ones shows any tribosphenic feature. On the contrary, they show features that can be perfectly derived from a pre-tribosphenic pattern, as that characterizing the Dryolestida, and particularly from that found in the Late Cretaceous Gondwanan *Mesungulatum housayi* Bonaparte & Soria, 1984. This is not only the first Cenozoic dryolestid but also the second South American Paleocene survivor of a Mesozoic Gondwanan radiation.

KEY WORDS

Mammalia,
Dryolestida,
Peligrotherium tropicalis,
Mesungulatum housayi,
early Paleocene,
Gondwana,
Patagonia.

RÉSUMÉ

Peligrotherium tropicalis (Mammalia, Dryolestida) du Paléocène inférieur de Patagonie, un survivant de la radiation mésozoïque gondwanienne.

Peligrotherium tropicalis fut d'abord déterminé comme un mammifère placentaire (Peligrotheriidae, Condylarthra?, Bonaparte, Van Valen & Kramartz, 1993) sur la base de la formule dentaire et de caractères des molaires inférieures. Dans ce travail, les premières molaires supérieures et de nouvelles molaires inférieures d'un même individu sont décrites. Elles proviennent de la même localité et du même niveau patagonien (Paléocène inférieur) que l'holotype. Aucune molaire supérieure ou inférieure ne montre de caractères tribosphéniques. Au contraire, ces dents présentent des caractères qui peuvent être parfaitement dérivés d'un patron pré-tribosphénique, comme celui qui caractérise les Dryolestida et en particulier *Mesungulatum houisayi* Bonaparte & Soria, 1984 du Crétacé inférieur d'Argentine. *P. tropicalis* est non seulement le premier dryolestide cénozoïque connu, mais également le second représentant du Paléocène survivant d'une radiation gondwanienne mésozoïque.

MOT CLÉS

Mammalia,
Dryolestida,
Peligrotherium tropicalis,
Mesungulatum houisayi,
Paléocène inférieur,
Gondwana,
Patagonie.

INTRODUCTION

Peligrotherium tropicalis Bonaparte, Van Valen & Kramartz, 1993 was diagnosed as a placental mammal, based on the following specimens: 1) a right dentary fragment with three cheekteeth, identified as p3, p4 and m1, selected as the holotype; and 2) six fragmentary dentaries, with different degrees of preservation. These specimens come from the so-called "Banco Negro Inferior", i.e. Hansen Member of the Salamanca Formation, exposed at Punta Peligro, Chubut, Patagonia (Pascual *et al.* 1992b: fig. 1). According to Pascual & Ortiz Jaureguizar (1991), this is Tiupampan SALMA, early Paleocene, but to Bonaparte *et al.* (1993), it is younger than the Tiupampan beds and consequently recognized as Peligran SALMA. The dental formula inferred from two mandibular fragments interpreted as pertaining to the same specimen led Bonaparte *et al.* (1993) to regard this specimen as a dubious Condylarthra, assigned to the new family Peligrotheriidae. This new family was characterized by the "[...] ausencia de diastema entre canino y premolares, p3 y p4 hipertrofiados, más bien

anchos; y molares pequeños, decreciendo en tamaño hacia atrás" (Bonaparte *et al.* 1993: 21). However, six years later this taxon was referred with doubt to the Dryolestida (Pascual *et al.* 1999b); this attribution was lately confirmed by Rougier *et al.* (2000), and the genus considered as related to the family Mesungulatiidae, an endemic dryolestoid from the Patagonian Late Cretaceous. Here we report new remains of *Peligrotherium tropicalis*, coming from the same locality and level as the holotype and hypodigm. They consist of the first known maxillaries of one individual, and a fragment of a dentary, quite belonging to the same individual. The cheekteeth show unusual features, and confirm the dryolestoid attribution, thus denying its condylarth relationships.

ABBREVIATIONS

MACN-CH Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires;
MLP Museo de La Plata, Departamento Científico de Paleontología de Vertebrados, Buenos Aires;
SALMA South American Mammal-Age;
UNPSJB PV Universidad Nacional Norpatagónica "San Juan Bosco", Conodoro Rivadavia.

SYSTEMATICS

Class MAMMALIA Linnaeus, 1758

Infraclass HOLOThERIA

Wible *et al.*, 1995 *sensu* McKenna 1997

Legion CLADOTHERIA McKenna, 1975

Sublegion DRYOLESTOIDEA Butler, 1939

Order DRYOLESTIDA

Prothero, 1981 *sensu* McKenna 1993

Family PELIGROTHERIIDAE

Bonaparte, Van Valen & Kramartz, 1993

Genus *Peligrotherium* Bonaparte *et al.*, 1993

Peligrotherium tropicalis

Bonaparte, Van Valen & Kramartz, 1993

HOLOTYPE. — Right dentary with m1 and m2 (UNPSJB PV 914).

HYPODIGM. — Holotype: fragment of anterior left dentary with a not clear number of alveolus (MACN-CH 1506); fragment of right dentary with m2 and part of m3-5 (MACN-CH 1501); fragment of left dentary with m2-5 alveoli (MACN-CH 1502); left mandibular fragment with m2-5 alveoli (MACN-CH 1503); fragment of right dentary with fragmentary roots of m2 and alveoli of m3-5 (MACN-CH 1504); left dentary fragment with m3-5 alveolus (MACN-CH 1505); maxillaries fragments with right M1-M2, and left M1 fragment, M2-M4 and fragmentary alveolus of M5 (MLP 90-II-12-58); right dentary fragment with distal part of m1 alveolus, m2, and fragmentary alveolus of m3 (MLP 90-II-12-60); right isolated tooth, probably p4 (MLP 90-II-12-61).

HORIZON AND LOCALITY. — Upper levels of the Hansen Member ("Banco Negro Inferior"), Salamanca Formation (Andreis *et al.* 1975), Punta Peligro, North of the San Jorge Gulf, Chubut Province, Argentina (Pascual *et al.* 1992a, b: fig. 1), Peligran SALMA (Bonaparte *et al.* 1993; "Peligran" *sensu* Flynn & Swisher III 1995), early Paleocene.

EMENDED DIAGNOSIS. — *Peligrotherium tropicalis* is the only known species of the family; thus the following diagnosis is valid for the species, genus and family. Large specialized dryolestoid; dental formula I?/? C?/? P2?/2? M5/5; bulbous cheekteeth with the cusps low and blunt, instead of anterior and posterior cingula forming shearing crests as seen in *Mesungulatum*; M1/1 and M2/2 hypertrophied; molar size decrease from the first to the last molar (M1/1 > M2/2 > M3/3 > M4/4 > M5/5); enlarged paracone, surrounded antero-buccally and postero-buccally by figures formed by wear, slightly lower than the paracone. The antero-buccal figure became formed by union of the anterior stylar cusp with the anterior cingulum, and

the postero-buccal one by the union of the posterior cingulum, stylocone and the posterior stylar cusp, respectively seen in the Late Cretaceous *Mesungulatum*. Upper molars bearing extra-roots. Talonid anteroposteriorly compressed, low and without visible cusp; lower molars roots of m3-4 transversally wide and anteroposteriorly compressed; posterior root of m5 smaller than the anterior one.

REMARKS

In spite of the similarities with Mesungulatae, the apomorphies of *P. tropicalis* are such that they characterize a different family. Mesungulatae was diagnosed by the presence of the following characters: upper molars with well-developed anterior and posterior cingula, and lower molars with roots, mesiodistally compressed and flat (Bonaparte 1986). *Peligrotherium tropicalis* is distinguished by the elevation of the upper molars cingula which became connected with labial cusps, and for the presence of a different root pattern in the lower molars.

DESCRIPTION

Lower cheekteeth: crown morphology

The new lower cheekteeth are quite fragmentary, and few new features can be observed. For example, the right p4 (MLP 90-II-12-61) is so worn (Fig. 1B) that the entire crown features were erased. The right m2 (Fig. 1A) shows that the protoconid is somewhat lower in the holotype. The talonid, which in most dryolestid is a low shelf on the posterior side of the trigonid, triangular and with the hypoconid at the posterolabial apex (Prothero 1981), is low, with no distinguishable cusps and its labial sector is more elevated than the lingual one. The metaconid is higher than its homologue in the holotype, and extends anteriorly somewhat ahead of the protocone. The alveolar border on each side of the molars are unequal. It is markedly deeper on the labial side. This shared derived character for the dryolestids (Simpson 1929; Prothero 1981) is also recognizable in the holotype.

Upper cheekteeth: crown morphology and roots

On the upper cheekteeth, both the crown morphology and the number and arrangement of the

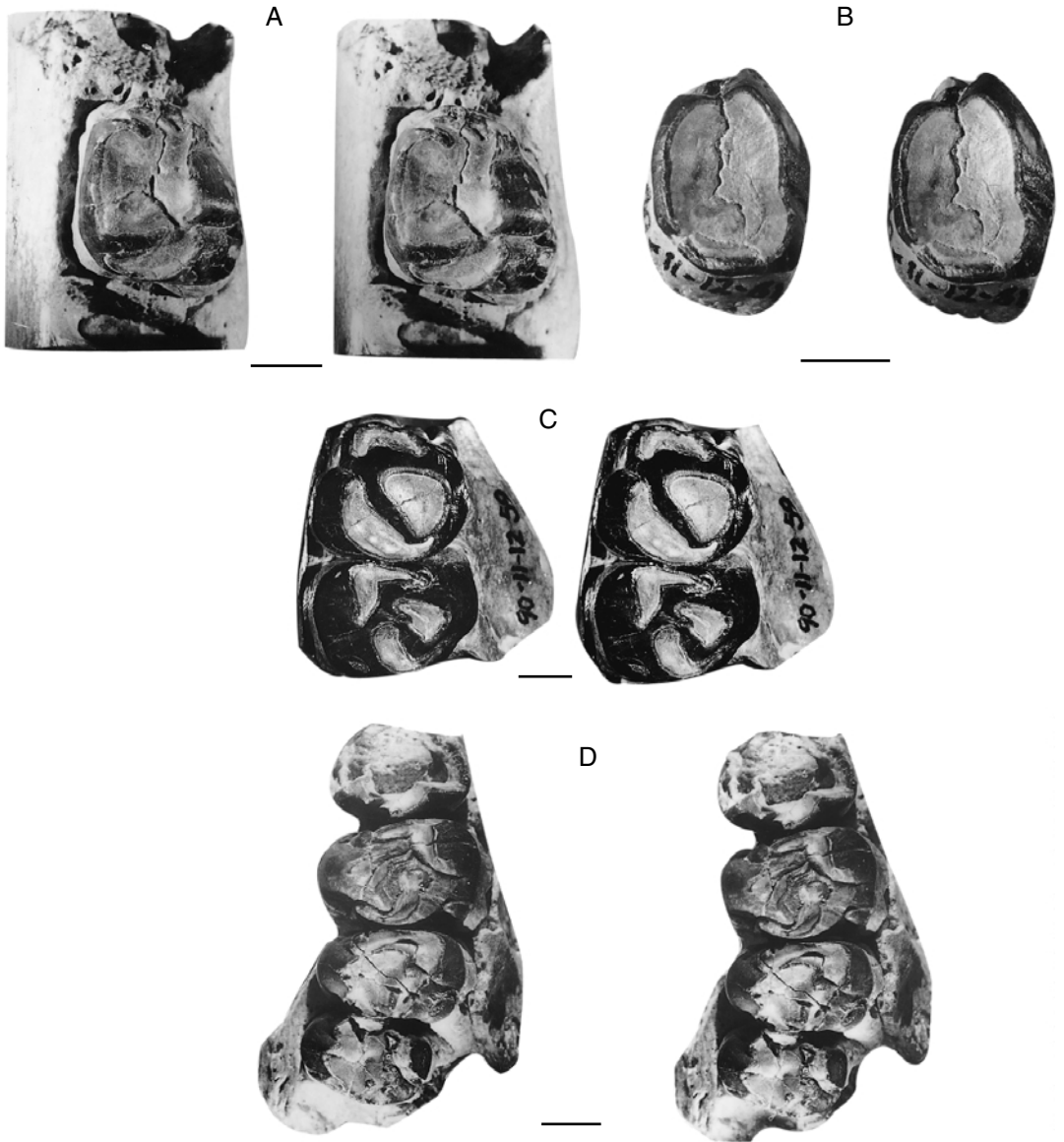


FIG. 1. — *Peligrotherium tropicalis* Bonaparte, Van Valen & Kramartz, 1993, stereopairs in occlusal view; **A**, right dentary fragment with distal part of m1 alveolus, m2, and fragmentary alveolus of m3 (MLP 90-II-12-60); **B**, right isolated tooth, probably p4 (MLP 90-II-12-61); **C**, **D**, maxillary fragment; **C**, with right M1-M2; **D**, with left M1 fragment, M2-M4 and fragmentary alveolus of M5 (MLP 90-II-12-5). Scale bars: 5 mm.

roots are quite unusual. As in the lower cheekteeth, the first and second molar are hypertrophied. The molars progressively decrease in size posteriorly, $M1 > M2 > M3 > M4 > M5$ (Figs 1C, D; 2).

The occlusal view shows that the wear has produced three figures: areas of exposed dentine surrounded by enamel. These are at the tops of vertical structures separated by relatively deep furrows. The principal and highest figure is lin-

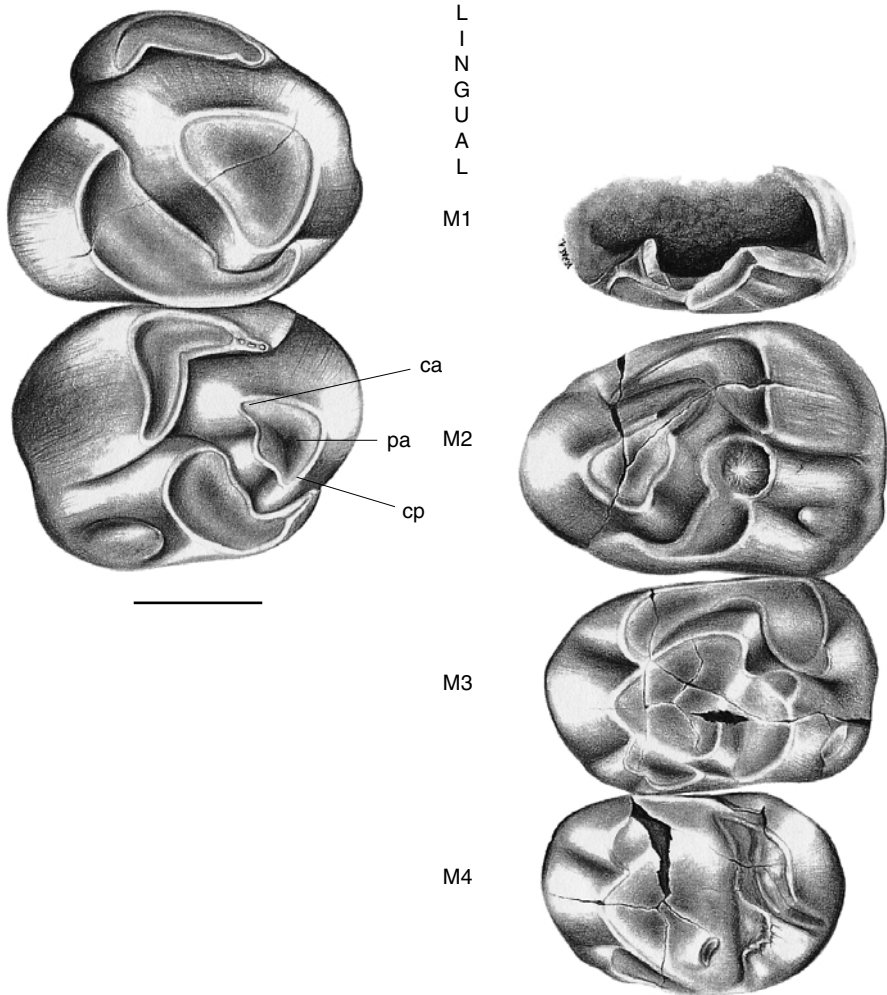


FIG. 2. — *Peligrotherium tropicalis* Bonaparte, Van Valen & Kramartz, 1993 (MLP 90-II-12-58), maxillary fragment with right M1-M2, and left M1 fragment and M2-M4, occlusal view. Abbreviations: **ca**, anterior crista; **cp**, posterior crista; **pa**, paracone. Scale bar: 5 mm.

gual, and is antero- and posterolabially surrounded by two semilunary figures, which, respectively, reach to the antero-lingual and postero-lingual portions of the principal lingual figure. In fact, these figures are compound wear facets, whose outlines and vertical extensions show that the lingual figure corresponds to the paracone, and the other two respectively correspond to an anterolabial cingulum joined to an anterior styler cusp, and to a postero-labial cingulum joined to a posterior styler cusp and to the stylocone. The cin-

gula were probably cuspidated since there persists undulations on the enamel where cusps were.

The right M1 is subquadrate. It is somewhat longer (11.65 mm) labially than lingually (9.75 mm), and a little wider posteriorly (11.80 mm) than anteriorly (10.80 mm). The lingual cusp is the main one, somewhat massive, and the outline of its wear facet is triangular, with rounded angles. Its worn surface is horizontal, although wear of the softer dentine produced a shallow basin. The anterior figure extends lingually, surpassing the middle

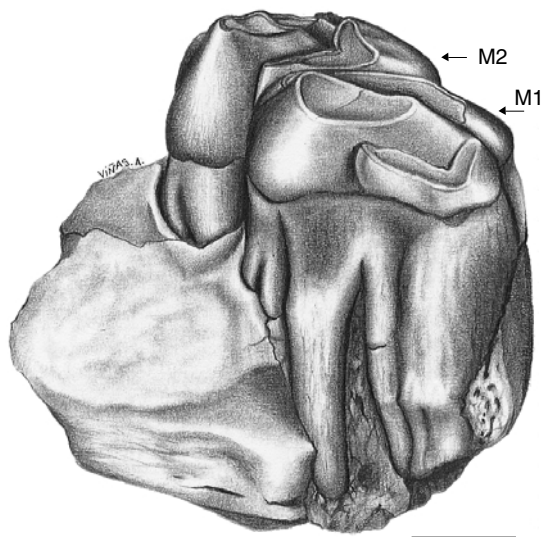


FIG. 3. — *Peligrotherium tropicalis* Bonaparte, Van Valen & Kramartz, 1993 (MLP 90-II-12-58), roots of right M1-M2, antero-internal view. Scale bar: 5 mm.

part of the anterior face (6.85 mm), and distally, forming part of the labial face (4.25 mm). Contrary to the principal figure, it is inclined anterolabially. The posterior figure is larger than the anterior one, representing most of the labial and posterior portion of the tooth. The anterolabial portion of this figure is wider, while its extension, surrounding the principal cusp posterolingually, becomes abruptly narrow. This posterior figure inclines postero-lingually. Labially it is separated from the anterior figure by a deep groove. The wear of the posterior figure is much more excavated than that of the anterior one.

The M2 is longer labially (9.85 mm on the right and 9.40 mm on the left one) than lingually (7.15 mm and 8.45 mm respectively). The features of M1 are here recognizable, although proportionally different. The principal cusp is more reduced in outline, but higher. Labial valleys of this cusp define the anterior and posterior cristae respectively (Fig. 4B). The anterior crista is slightly longer. The anterior figure is larger than the homologous in M1; it extends lingually (9.95 mm on the right and 9.40 on the left one) surrounding the anterior portion of the principal cusp. On the right M2, the lingual portion of the anterior figure

shows enamel constrictions that delimit four small in-line cuspules. On the labial face, the anterior figure extends posteriorly (5.75 mm on the right M2 and 5.25 on the left one) overlapping the most anterior portion of the posterior figure. The posterior figure is smaller than the anterior one. Its anterolabial portion (particularly on the left M2) shows a constriction in the enamel, apparently indicating that there was a cusp. Close to the posterolabial sector of this posterior figure there is a small, low and columnar cusp that has not yet been affected by wear.

M3-5 have a rectangular outline, and are smaller than the anterior molariforms. The outline of M5 is inferred by its alveolus. The labial side is anteroposteriorly larger than the lingual one (7.75 × 6.60 mm in the M3, and 7.10 × 6.20 mm in the M4); they are somewhat wider on the middle part. The cusp morphology is similar to that present on the first and second molar. The anterior figure is relatively larger than in the M1-2, more extended transversely and, apparently, bear a larger antero-labial cusp. The different degrees of wear of M2 and M3, clearly demonstrate that the posterior figure was formed by the union of the medial labial cusp, the postero-labial cusp and the posterior cingulum (see M2-3 on Fig. 2). The M4 is deeply worn, but the features that remain apparently resemble those of M2-3.

Roots

The first upper molar shows supernumerary roots. There are four principal roots, two lingual and two labial (Fig. 3). Below the principal lingual cusp there is an anterolingual root and a posterolingual one, the latter being divided by a vertical furrow, which indicates either that the root is simply bifurcated, or that it is formed by two united roots. The two labial roots are larger and bulky. The anterolabial one, situated just below the anterior figure, is also divided by a vertical furrow, which extends up to the base of the crown. The posterolabial root is massive, without a furrow and situated below the posterior figure. Apparently, there are four roots on M2, two on the labial face and two on the lingual one. The anterolabial root is the largest, and is situated

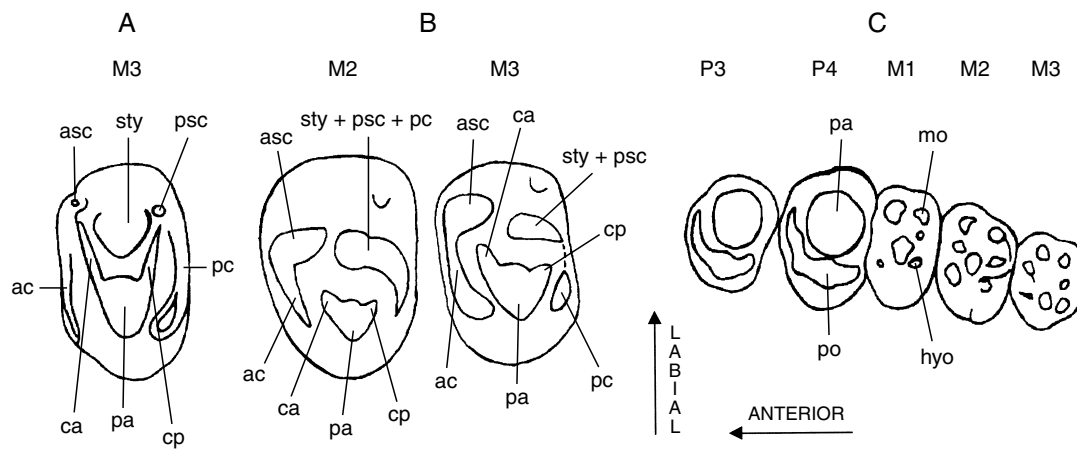


FIG. 4. — Homologies in upper molars of Mesungulatidae and Peligrotheriidae, and comparison with Periptychidae cheekteeth; **A**, left M3 of *Mesungulatum houssayi* Bonaparte & Soria, 1984; **B**, left M2-3 of *Peligrotherium tropicalis* Bonaparte, Van Halen & Kramartz, 1993; **C**, left P3-M3 of *Periptychus rhabodon* Cope, 1882. Abbreviations: **ac**, anterior cingulum; **asc**, anterior stylocone; **pc**, posterior cingulum; **psc**, posterior stylocone; **ca**, anterior crista; **cp**, posterior crista; **hyo**, hypocone; **mo**, metacone; **pa**, paracone; **po**, protocone; **sty**, stylocone. Scale bars: A, B, 5 mm; C, 10 mm.

below the anterior cingulum. The posterolabial root is situated below the posterior figure. The two lingual roots are situated just below the principal cusp. None of the roots seems to have vertical furrows or to be bifurcated.

On the contrary, M3 and M4 have only three roots, the anterolabial root, below the anterior figure, is larger than the posterolabial. There is only one lingual root, which is massive and extends along the whole antero-posterior extension of the crown.

Each lower molar of *Peligrotherium tropicalis* has an anterior and posterior root. The alveolus of m2 are almost circular in occlusal view. The roots of m3-4 are transversally wide and anteroposteriorly compressed. The posterior root of m5 is smaller than the anterior one.

DISCUSSION

Cusp homology

Based on the lower dental formula inferred by Bonaparte *et al.* (1993), *Peligrotherium tropicalis* was regarded as a placental mammal. Because of the position and size of the trigonid, and the wear of molars, it was assigned with doubt to the Condylarthra. The hypertrophy of two molariforms in *Peligrotherium tropicalis* was compared to that observed in *Periptychus* (Fig. 4B, C), but

this character appears to be convergently developed (Bonaparte *et al.* 1993). The upper molariforms of *Peligrotherium tropicalis*, herein described for the first time, add new information that requires modification of the relationships postulated by Bonaparte *et al.* (1993). They show some decisive features not compatible with condylarths, or with any other Tribosphenida (*sensu* McKenna & Bell 1997).

The principal cusp of the upper teeth of *Peligrotherium tropicalis* is lingual, and unusually large. On the contrary, the premolars of the condylarths show the labial cusp (paracone) as the most prominent, while the lingual one (protocone) is relatively reduced. If *Peligrotherium tropicalis* were a condylarth, this cusp should occlude in a proportionate large talonid. However there is no talonid basin but only a cingulum closely applied to the trigonid (Fig. 1A). None of those features that distinguish a tribosphenic pattern may be seen in the molars. On the contrary the features of the molars of *Peligrotherium tropicalis* appear to be derived from a pattern found in non-Therian mammals (*sensu* McKenna & Bell 1997) such as the Dryolestida. Among these, the molar pattern of *Mesungulatum houssayi* from the Late Cretaceous of Patagonia (Bonaparte & Soria 1985; Bonaparte 1986) shows

a primitive state of the features seen in *Peligrotherium tropicalis* and could thus be related to its ancestry. Of the five molars recognized by Bonaparte (1986) for *Mesungulatum houssayi*, only three are known, and of these, M3 shows characters that could be regarded as a stage preceding that of *Peligrotherium tropicalis* (Fig. 4A). In *Mesungulatum*, the well-developed lingual cusp, the paracone, extends antero- and posterolabially through the anterior and posterior cristae, toward the anterior styler cusp and posterior styler cusp, respectively. The cusp identifies by Bonaparte (1986) as the stylocone is the major styler cusp, while the anterior and posterior cusps are smaller. Of these, the anterior styler cusp is labially displaced with respect to the stylocone, and is lower than the latter. The anterior cingulum surrounds labially the base of the anterior styler cusp, and lingually extends up to the anterior part of the paracone, where, in some specimens, a small cusp is present. The posterior styler cusp is closer to the stylocone. The posterior cingulum extends from the posterior side of the paracone up to the base of the posterior styler cusp. Lingually, the anterior and posterior cingulum are not in contact.

If we now compare the upper molar pattern of *Peligrotherium tropicalis* with that of *Mesungulatum houssayi* (cf. compare Fig. 4A with 4B), the principal lingual cusp represent the paracone and not the condylarthran protocone. The anterior and posterior cristae became reduced, but are still evident on M2. The anterior figure of *Peligrotherium tropicalis* resulted from the fusion of the anterior styler cusp and anterior cingulum because of wear; similarly the posterior figure would result from the fusion of the stylocone, posterior styler cusp and the posterior cingulum (Fig. 4B). Those cusps and cingula of *Mesungulatum houssayi* that merged to form the peculiar anterior and posterior wearing facets shown in *Peligrotherium tropicalis* may be more clearly recognized on M2 and M3 molars than in the only known M1.

Dental formula

Peligrotherium tropicalis, as seen from the upper cheekteeth, has five molars. But neither the jaws nor the known maxillary are totally complete to

allow an unquestionable count of the premolars number. The originally inferred lower dental formula was $c1, p4, m3$ (Bonaparte *et al.* 1993). But this formula is based on a misinterpretation of the premolar-molar series. In fact the morphology of the upper cheekteeth shows that *Peligrotherium tropicalis* was a dryolestid not a condylarth, and the supposed last two premolars are molars instead. Moreover, the first lower premolar of *Peligrotherium tropicalis* was described as having one root. But the only relevant specimen for deduce this is a very badly preserved anterior jaw fragment, MACN-CH 1506, where the number of alveoli is not clear. Rougier (pers. comm.) sustains that the relative position of the symphysis and mental foramina allow the inference that the jaw alveoli were restored too forward in the reconstruction, and so two roots for the first premolar suit better than a single one. So is it possible from a new count of alveoli, that there were one less premolar.

With the actually known specimens is unlikely to infer an exact number of premolars. Although it seems that of the four premolars of dryolestids (Prothero 1981), *Peligrotherium tropicalis* reduced this number, probably to two. The tendency to decrease the number of premolars, together with the increase of molars and the reduction of the length of the talonids, were characteristic of advanced dryolestoid (Butler pers. comm. to McKenna 1975).

Occlusion

Wear on M1 and M2 erased the original cusps and cingula, connecting them to form peculiar and distinctive facets, leaving the dentine clearly exposed and shaped in shallow basins surrounded by the enamel. The relatively enormous paracone clearly forms an isolated and subhorizontal wear facet. The wear surface of the anterior figure faces somewhat mesially, and its lingual border is lower than its labial border. The wear surface of the posterior figure, particularly on M1, faces somewhat lingually and is somewhat more deeply excavated than the other surfaces. The posterior figure surface of M2 is more or less continuous with the anterior figure surface of M1. The preceding wear surfaces

are concave and were caused by mastication of food rather than by mutual teeth abrasion. On M3-4 the paracone is extremely worn apicolabially, producing a large wear basin.

Although the known lower molariform crowns are insufficiently preserved, the species holotype (UNPSJ PV 914), a right mandibular fragment with m1-3, shows that there is a transverse ridge or prominence, apparently formed by the protoconid and metaconid. From this ridge an anterior and a posterior wear facets descend, conforming V-shaped figures, as seen laterally between m1 and m2 (Fig. 5A). The direct opposition of the specimens MLP 90-II-12-58 with UNPSJ PV 914 (Fig. 5A, B) and MLP 90-II-12-60 shows that a perfect match occurred when the transversal prominence of m2 occludes on the narrow intermolar basin between M1 and M2, i.e. on the posterior figure of M1 and the anterior of M2. However, this occlusion leaves the paracones lingually displaced and out of any contact with the lower molariforms. As the paracone shows an advanced wear facet, there had to be another occlusal movement during mastication to permit its participation. Apparently *Peligrotherium tropicalis* crushed its food with a vertical jaw movement, which resulted in exposure of dentine on the tops of the cusps. Although it could also move the jaw transversely when the protoconid-metaconid ridge of the lower molars moved in the groove between two upper molars. The paracone takes some parts in this as could be deduced from its wear facet. It seems that no propalinal movement could take place between posterior molars because the anterior molars can only move transversally, owing to the groove mentioned above.

The occlusion between upper and lower molars of *Mesungulatum houssayi* shows a shearing stage of the food in which the mesial and distal cristae worked as scissors, and a crushing stage in which the lower molar cristae worked against the upper cingula (Bonaparte & Crompton 1990). The relation between upper and lower teeth in *Peligrotherium tropicalis* is essentially the same as in Dryolestidae, but in those there is shearing between vertical surfaces, whereas in *Peligrothe-*

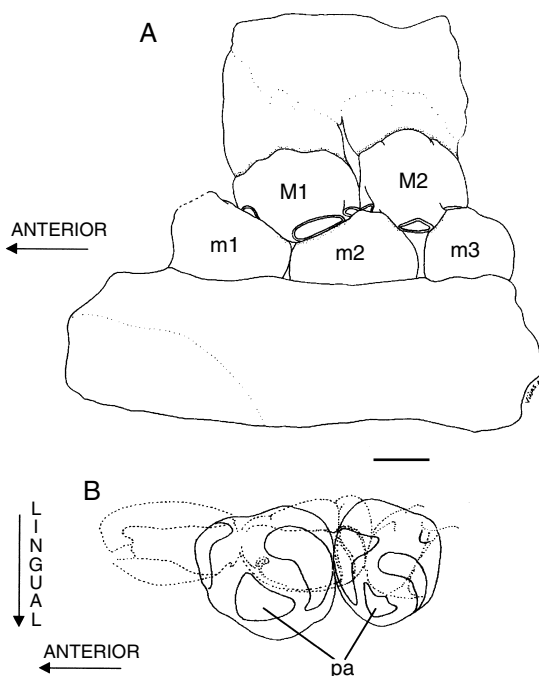


FIG. 5. — Reconstruction of the occlusion of *Peligrotherium tropicalis* Bonaparte, Van Halen & Kramartz, 1993; **A**, right M1-M2 (MLP 90-II-12-58) and right dentary with m1 and m2-3 (UNPSJB PV 914), internal view; **B**, same specimens in occlusal view. Dotted line represents the lower p4, m1-2 and continuous line upper P4-M1. Abbreviation: pa, paracone. Scale bar: 5 mm.

rium the cusps are low and blunt, and the attrition surfaces are less steeply inclined. *Peligrotherium* shows a very derived type of occlusion, which goes further than *Mesungulatum* in the crushing specialization.

Roots

The supernumerary roots of the first upper molar represent another unusual character of *Peligrotherium tropicalis*. As far as we know, the monotreme ornithorhynchids and docodonts are the only other Mammaliaformes (*sensu* Rowe 1988) that have supernumerary roots, at least on the upper postcanines. Accepting Kovacs' (1971) idea that the crown is a primary developed body and the roots a secondary developed body, we agree with him that when a significant anomaly in volume or shape occurs in the crown, it must be accompanied by a modification in the volume or shape of

the roots. At least so it was in the hypertrophied upper M1-2 of *Peligrotherium tropicalis*.

The Dryolestidae have unequal roots in the lower molars, the smaller of which is postero-internal and supports the reduced talonid (Simpson 1929; Prothero 1981). In contrast Mesungulatidae have two mesiodistally compressed and flat roots in the lower molars (Bonaparte 1986). *Peligrotherium* shared a similar root structure for m3-4 to those present on Mesungulatidae, but on the contrary, the posterior root of m5 is much smaller than the anterior one.

CONCLUSION

For a condylarth – as doubtfully regarded by Bonaparte *et al.* (1993) –, or any other Paleocene eutherian, *Peligrotherium tropicalis* has quite unusual dental features: M1/1 and M2/2 hypertrophied; M1/1 > M2/2 > M3/3 > M4/4 > M5/5; M1 with supernumerary roots; enlarged lingual cusp, and styler cusps connected by wearing to the anterior and posterior cingula. In fact, the hypertrophy of two molariforms appears as a character convergently developed with the condylarth *Periptychus* (Bonaparte *et al.* 1993), but this process affects different elements in the two forms: in the latter, these are P3/3 and P4/4. Moreover, in *Periptychus* the larger upper premolar cusp is in a labial position (Fig. 4C); and the cheekteeth show typical vertical furrows. In contrast, on the molars of *P. tropicalis*, the largest cusp is in a lingual position and vertical furrows are absent.

P. tropicalis shows dental features that do not fit the tribosphenic pattern of a condylarth. On the contrary, it shows features that can perfectly be well-derived from a pre-tribosphenic pattern, such as that found in the Late Cretaceous Gondwanan Dryolestida *Mesungulatum hussayi*. The known record of Cretaceous South American land mammals is characterized by the absence of tribosphenic taxa. It appears as the culmination of an evolutionary episode not related to the peculiar South American Cenozoic radiation which was exclusively accomplished by Tribosphenida mammals. Besides, both radiations occurred on quite

distinct geographical scenery (Pascual 1996, 1998). This culmination led to a drastic turnover in mammalian communities, including dispersal, extinction and relatively short survival of some selected groups (Pascual *et al.* 1999b). The Dryolestida *Peligrotherium tropicalis*, like the gondwanatherian *Sudamerica ameghinoi*, is an example of a South American Paleocene survivor of that Mesozoic Gondwanan history.

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