

THE EARLIEST TERTIARY THERIAN MAMMAL FROM SOUTH AMERICA

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We describe the oldest South American Tertiary therian mammal from Danian-equivalent strata of northwestern Chubut province, Argentina (Fig. 1). The specimen is an isolated lower molar most likely pertaining to a polydolopimorphian marsupial, a group known from the Late Cretaceous of North America as well as later Paleocene and Eocene deposits in South America. The derived nature of this bunodont marsupial provides evidence for an evolutionary radiation of marsupials in the earliest Paleocene or Late Cretaceous of the Americas. Whereas the presence of this radiation had been suspected previously, the Lefipán specimen (Fig. 2) narrows the interval within which that radiation may have occurred.

Up to now, the earliest glimpse of the diversity of therian mammals of South America has been gained from the Tiupampa local fauna of Bolivia and tentatively correlated to late Paleocene sites in Argentina (Selandian; 58.7–61.7 Ma) (Somoza et al., 1995; Marshall et al., 1997; radioisotopic ages after Luterbacher et al., 2004). In addition to relict gondwanan monotremes and sudamericids, taxa from these sites reflect a growing diversity of marsupial and placental immigrants from North America. For marsupials, these include a few derived members of the basal peradectian radicle (e.g., *Roberthoffstetteria*), along with ameridelphians represented by early didelphoids, with some (*Didelphopsis*, *Eobrasilia*, *Gaylordia*) showing probable affinities with North American forms (Case et al., 2005). In addition, a relatively broad array of ameridelphian taxa is allocated to groups currently endemic to South America as far as their origin is concerned: derorhynchid didelphids (*Derorhynchus*, *Gaylordia*, *Miniscalodelphys*), protodidelphids (*Bobbschaefferia*, *Guggenheimia*, *Procaroloameghinia*, *Protodidelphis*, *Robertbutleria*), sternbergiids (*Itaboraidelphys*), ?sparassodontan carnivores (*Maylestes*, *Allqokirus*, ?*Nemolestes*), and a variety of polydolopimorphians, including epidolopine bonapartheriids (*Epidolops*). A third group consists of endemic microbiotheriid australidelphians (*Khasia*, *Mirandatherium*), with potential significance for dispersal to, and radiation within, Australia. Most of these taxa imply that an extensive evolutionary radiation took place in South America prior to the medial Paleocene, and this usually is taken as evidence in favor of a Late Cretaceous entry of the necessary ancestral stocks (Muizon and Brito, 1993), for which there is evidence of Late Cretaceous polydolopimorphians having originated in North America (Case et al., 2005). The placental mammals are comprised mostly of condylarths and condy-

larth-like taxa considered to have had a likely early Paleocene source in North America, with the possible exception of the Pantodontia.

Of the immigrant groups, the presence in Danian-equivalent deposits of a marsupial (with a possible age range of 61.7–65.5 Ma) was expected, but the derived nature of this taxon, if its proposed polydolopimorphian affinity is borne out by further material, further strengthens the implications in favor of a Late Cretaceous entry of marsupials to South America. The presence of polydolopimorphian taxa in Judithian as well as Lancian (Maastrichtian) deposits in North America (Case et al., 2005) indicates that the evolution of this group was underway by about 75 Ma, so that a member of this relatively derived marsupial group in Danian-equivalent deposits of South America is compatible with the North American data.

SYSTEMATIC PALEONTOLOGY

MAMMALIA Linnaeus, 1758
Supercohort MARSUPIALIA Illiger, 1811
Cohort AMERIDELPHIA Szalay, 1982
Order ?POLYDOLOPIMORPHIA Ameghino 1897
COCATHERIUM LEFIPANUM, gen. et. sp. nov.
(Fig. 3)

Etymology—For “Coca” San Martín, of the Estancia San Ramón, whose invaluable assistance to scientists of the Museo de La Plata and particularly to us for many years, made our work in the western Chubut River region possible (Fig. 1). *Lefipanum* from Lefipán, name of one of the most prominent native (mapuche) inhabitants of the region.

Holotype—LIEB-PV 1001, an isolated right lower molar.

Locality, Horizon, and Age—The Grenier section (Fig. 2) of the Lefipán Formation is located at grid coordinates 42° 46' S and 69° 51' W, on Grenier Farm, about 20 km west of the town of Paso del Sapo (Fig. 1), in the middle Chubut region, Chubut Province, Argentina. The regional geology (Spalletti, 1996) shows that the Lefipán Formation (and underlying Paso del Sapo Formation) unconformably overlies older Cretaceous strata referable to the Chubut Group. In turn, the Lefipán Formation is unconformably overlain by lower Tertiary (Eocene) strata of the Laguna del Hunco Series (Wilf et al., 2003 and references therein). The Lefipán Formation is a 200-m thick, marine silici-

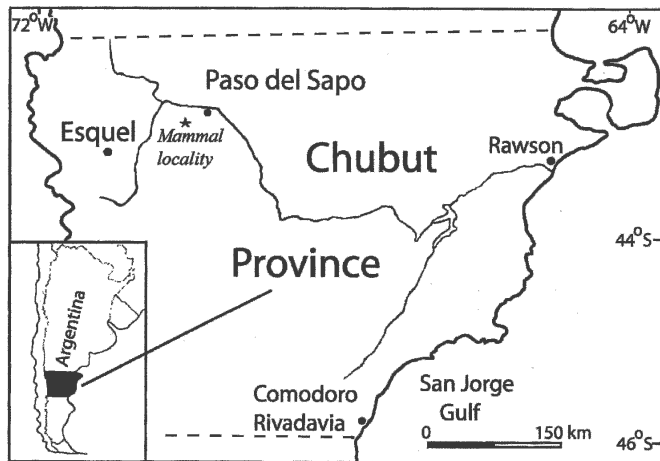


FIGURE 1. Map of Chubut Province, Argentina and *Mammal Locality* yielding *Cocatherium*. Chubut Province is black area in index map of Argentina.

clastic unit, mainly composed of massive and heterolithic mudstones with several intercalations of sandstone packets and coquina beds that have a well preserved molluscan fauna of Maastrichtian-Paleocene age (Spalletti, 1996). Sandstone beds are massive, or display parallel or cross-bedding. Sometimes they show well preserved bioturbation of the *Skolithos-Cruziana* like ichnofacies and contain phosphatic concretions. The whole unit was deposited in a shallow epeiric sea, in which the sandstones were interpreted as bars and shoals that accumulated in a shoreface environment. The lower part of the Lefipán Formation (Spalletti, 1996) corresponds to strata assigned to Asociación I (Medina et al., 1990) of Late Maastrichtian age. The upper part of the Lefipán Formation begins with a maximum flooding surface considered to mark the beginning of the Paleocene (Spalletti, 1996), and is equivalent to Asociación II in Medina et al. (1990) paleontologically determined to be of Danian-equivalent age. Although the part of the Lefipán Formation that yielded *Cocatherium* is not discussed in either Spalletti (1996) or Medina et al. (1990) paleontologically determined to be of Danian-equivalent age. Although the part of the Lefipán Formation that yielded *Cocatherium* is not discussed in either Spalletti (1996) or Medina et al. (1990) paleontologically determined to be of Danian-equivalent age. Although the part of the Lefipán Formation that yielded *Cocatherium* is not discussed in either Spalletti (1996) or Medina et al. (1990) paleontologically determined to be of Danian-equivalent age. Although the part of the Lefipán Formation that yielded *Cocatherium* is not discussed in either Spalletti (1996) or Medina et al. (1990) paleontologically determined to be of Danian-equivalent age.

A stratigraphic section 65m thick (Fig. 2) has been developed in the upper part of the Lefipán Formation at the Grenier Farm site. The lower 12 m of the section are characterized by brown mudstone with calcareous concretions and rare heterolithic bedding, and rusty-brown massive sandstone beds. The mudstone beds contain remains of *Pterotrionia windhausenii* (Wilckens), indicative of a Maastrichtian age. The brown mudstones are overlain by about 5 m of massive sandstone that contains the bivalves *Meretrix chalconica* and *Venericardia*, gastropods, shark and ray teeth and claws of callianassid crabs.

The holotype specimen (LIEB-PV 1001) was found at the *Meretrix-Venericardia* level, about 15 m stratigraphically above the base of the measured section displayed in Figure 2. The lower and middle stakes shown in Figure 2 denote the interval within which the K-T boundary is considered to occur based on the fossils recovered by one of us (MCU). The *Meretrix* level occurs about 5 m stratigraphically above the K-T interval in the upper member of the Lefipán Formation (Spalletti, 1996), who considered the entire upper member of the Lefipán Formation to represent the earliest Paleocene Series. Medina et al., (1990) assign the relevant strata to Asociación II, with fossils of Danian-equivalent age. The stratigraphic section in Figure 2 was prepared by some of us (MCU, RAS, FAM) and colleagues as a refinement of the previous work. Although the new investigation

Profile of Lefipán Formation at Grenier Farm

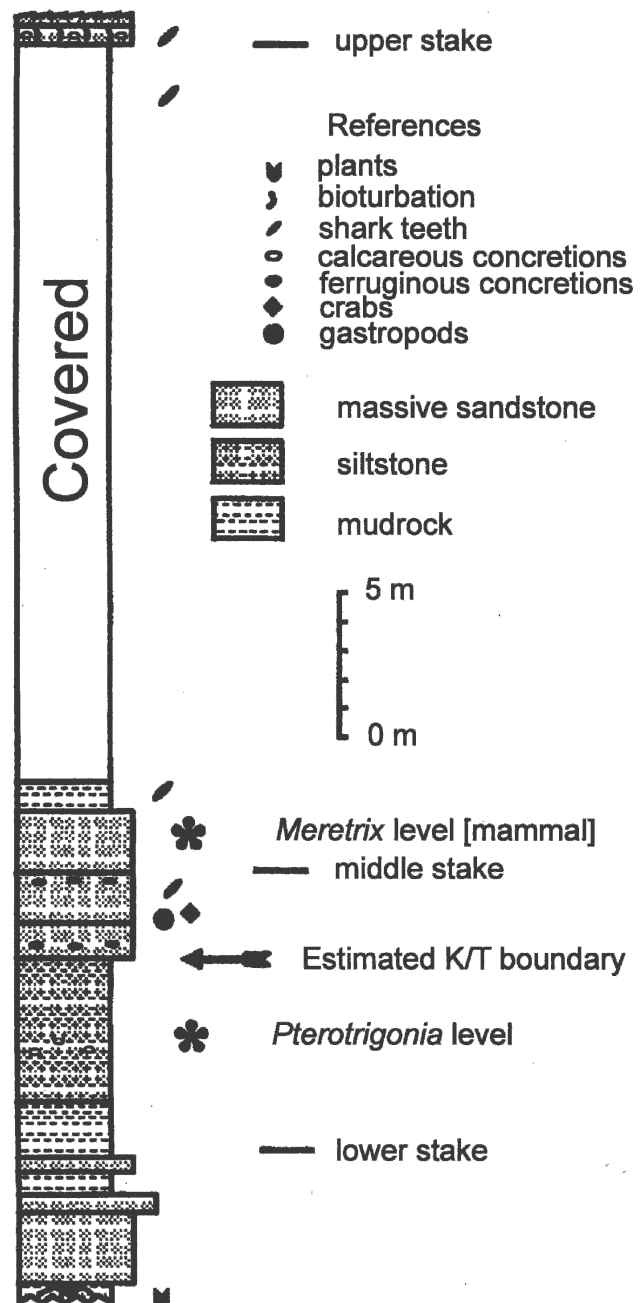


FIGURE 2. Stratigraphic section at Grenier Farm locality showing position of *Cocatherium* level with respect to temporal indicators discussed in the text.

cannot yet precisely identify the stratigraphic location of the K-T boundary in Figure 2, it is clear that *Cocatherium* and its associated invertebrate fossils occur stratigraphically above this interval, and are of Danian-equivalent age. In addition, *Meretrix chalconica* is restricted to Asociación II, the oldest of the two Paleocene biostratigraphic assemblages recognized in the Lefipán Formation by Medina et al. (1990). Actinopterian fish and neoselachians found stratigraphically 2–3 m above and below the *Meretrix* horizon are consistent with a Danian-equivalent age for the deposit. Neoselachian teeth are comprised mostly of

Carcharias, not known prior to the Paleocene, and remains of *Hypolophodon*, a taxon previously known only from Eocene deposits (Kemp et al., 1990). The presence of this genus in this part of the Lefipán Formation apparently represents a downward range extension. It also is notable that neoselachian groups otherwise typical of Cretaceous strata are absent in this part of the Lefipán Formation (Hybodontidae, Acrodontidae, Anacoracidae, Polyacrodontidae, Sclerorhynchidae, Ptychodontidae, Rhombodontidae, *Scapanorhynchus*, *Igdabatis*), consistent with its correlation to the Danian.

Diagnosis—Bunodont marsupial of relatively large size; trigonid with distinct paraconid; protoconid and metaconid transversely opposite each other; cristid obliqua attaches to trigonid posterior to protoconid and well labial to protocristid notch; hypoconulid distinct, terminal, and closely appressed with, but distinctly separate from, much taller entoconid; entoconid with distinctly curved preentocristid that meets the postmetacristid to block the talonid basin; talonid shorter than trigonid, with shallow talonid basin; lingual surface of hypoconid flat to labially slightly concave, rather than basally rounded. Labial surface of the tooth slopes basally and is deeper than the nearly vertical lingual surface. This diagnosis is provisional pending discovery of additional materials of this or other South American Paleocene polydolopimorphian marsupials.

Measurements—Total length, 2.90 mm; trigonid width, 2.20 mm; talonid width, 2.27 mm.

Description—LIEB-PV 1001 is a fully tribosphenic bunodont well-worn right lower molar. Although somewhat shortened due to the angulate paracristid, the trigonid is distinctly longer than the talonid. The talonid is slightly wider than the trigonid. The anterior and posterior roots are anteroposteriorly compressed. A narrow anterior cingulum is present at the anterior base of the tooth, and apparently was somewhat wider at the anterolabial surface of the protoconid than at the anterior base of the parconid. No other cingula are present.

The paraconid is set somewhat labially relative to the metaconid but, judging from the well-developed wear pattern, still was a distinct cuspid. The paraconid portion of the paracristid extended directly transversely to meet the anterolingually oriented protocristid portion at a distinct, although oblique, angle, at the anterior midpoint of the tooth. The paraconid is set closely adjacent to the anterolinguale base of the metaconid, with the two cusps being separated by a distinct, narrow, crevice. Thus the trigonid basin likely was very narrow.

The protoconid and metaconid are set transversely opposite to each other, and are about equally large. The labial surface of the protoconid slopes strongly toward the base of the tooth, whereas the lingual border of the metaconid is more nearly vertical. It is likely that the protoconid and metaconid were connected by a transverse protocristid. The enamel surface preserves a weak, short, postmetacristid. Based on the current wear pattern, it appears that the metaconid and protoconid were the tallest cusps of the tooth, with the hypoconid, entoconid, paraconid and hypoconulid being progressively lower.

The talonid is shorter than typical of the plesiomorphic therian condition. The hypoconid is about as strongly worn as the trigonid cusps. As for the protoconid, the labial surface of the hypoconid slopes basally, in contrast to the more nearly vertical lingual surface of the entoconid. The cristid obliqua apparently was anterolingually oriented. It now reaches the rear of the trigonid at the posterior side of the protoconid; at this stage of wear, it is continuously connected to the worn trigonid surface. Previous to this stage of wear it is likely that the cristid obliqua abutted the rear of the trigonid below the occlusal edge of the trigonid wall. The short posthypocristid extends posterolingually to the hypoconulid, which apparently also was oriented obliquely. A remnant of a valley that separates the posterior surface of the hypoconid from that of the hypoconulid suggests that the

posthypocristid sloped basally toward a comparably sloping pre-hypoconulid cristid. The entoconid still preserves much of its original structure, and is a relatively tall cuspid that is laterally compressed. It also is inclined labially and slightly anteriorly. In contrast to the other cusps which have nearly flat occlusal wear surfaces, that of the entoconid clearly slants labially. The entoconid is separated from the adjacent base of the hypoconulid by a sharp, distinct, crevice, which broadens slightly anteriorly to separate the entoconid from the lingual slope of the hypoconid. The talonid basin thus is shaped as an asymmetrical valley, with a steeper lingual than labial surface, rather than as a basin. The lingual surface of the hypoconid is not expanded and does not occlude the talonid basin. A distinct preentocristid extends anteriorly from the entoconid and weakly meets the opposing postmetacristid so that the talonid basin is closed lingually. The hypoconulid is very close to the entoconid, although distinctly separated from it.

An interdental wear facet is present on both the anterior and posterior surfaces of the tooth so that it is most likely an intermediate molar, neither the first nor the last. In anterior and posterior views (Fig. 3d, e), the asymmetrical slope of the tooth is apparent with much more sloping, and taller, labial rather than lingual surfaces.

Discussion

Based on its Danian-equivalent age, *Cocatherium* is the oldest Paleocene record of a marsupial or any therian mammal in the Southern Hemisphere. As preserved, its morphology and worn occlusal surfaces show that *Cocatherium* had a full complement of therian cusps and cusps, including a protocone in the upper dentition.

LIEB-PV 1001 contains all the features characteristic of a therian mammal, including the requisite cusps, their appropriate locations in the trigonid and talonid, and pertinent wear facets. A numbered series of surfaces has been documented (Crompton, 1971) for shearing occlusion between the upper and lower molars which define the tribosphenic molar morphology of therian mammals. Even though LIEB-PV 1001 is very worn, it still retains evidence of three distinct shearing surfaces. A large occlusal wear facet is present on the anterolabial surface of the protoconid along the paracristid prior to its lingual bend, which

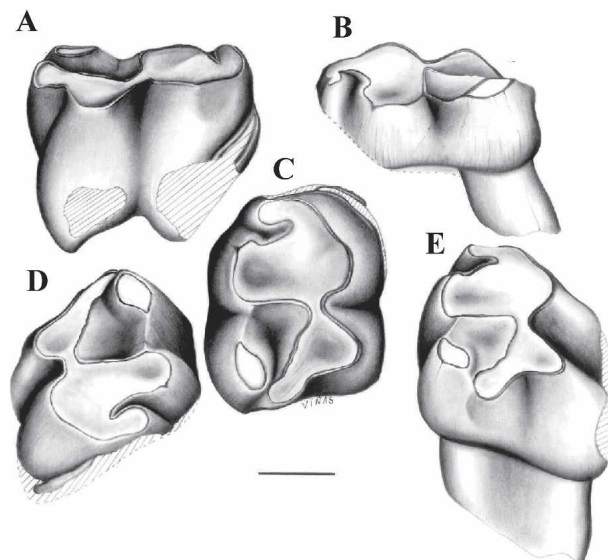


FIGURE 3. Drawings of the lower molar LIEB-PV 1001, *Cocatherium lefipanum*. Labial (a), lingual (b), occlusal (c), anterior-occlusal (d), and posterior-occlusal (e) views. Scale: 1 mm.

corresponds to shearing surface N° 2 (Crompton, 1971; and all subsequent numbered surfaces), that occludes with the post-metacrista on the upper molar. A second, but smaller, occlusal facet on the anterolabial surface of the hypoconid is referred to shearing surface N° 3, which would occlude with the upper molar's postparacrista. The posterolabial surface of the hypoconid also possesses a wear facet; it corresponds to shear facet N° 4, and occludes with the premetacrista of the upper molar. In short,

the cusps and observable shearing surfaces correspond with those of a therian mammal. We interpret that the peculiar, extended, and almost continuous wear facets of the masticatory surface resulted from the prolonged medial movement of the lower jaw that followed its upward movement during occlusion. The almost continuous surface that extended throughout the trigonid—to connect the paracristid and the metacristid—appears to have been produced by the joint action of the post-metacrista

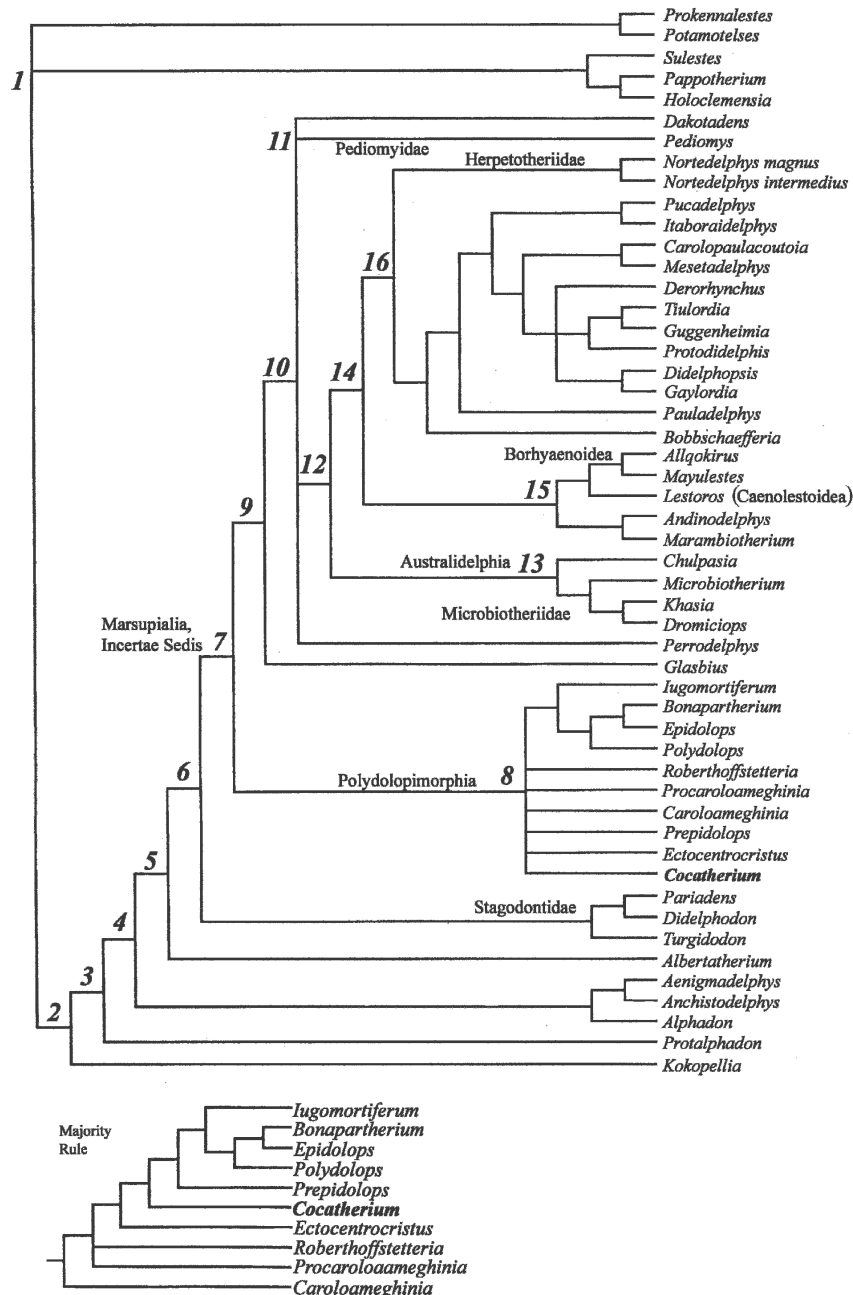


FIGURE 4. Cladogram of selected marsupial and other therian taxa. Strict Consensus of 25 equally parsimonious trees. TL = 1175; CI = 0.402; RI = 0.829; HI = 0.598. *Cocatherium* is shown within polydolopimorphians. **Boldface numbers** refer to nodes. Unless otherwise indicated, the classification follows Case et al. (2005, hereafter C'05, which includes Marshall et al., 1990). Node 1 comprises the outgroup. Node 2 includes Metatheria (*Kokopellia*; Cifelli, 1993). Nodes 3-5 comprise Peradectia. Node 6 is after C'05, plus *Turgidodon*. Nodes 7, 8, and 9 comprise Marsupialia, *Incertae Sedis*, after C'05, with *Caroloameghiniidae* (minus *Glasbuis*) grouped with *Polydolopimorphia*. Node 10 is Alphadelphia; with *Perrodelyphs* homoplasiously added. Node 11 is an unnamed plesion including *Pediomyidae* and *Dakotadens*. Node 12 is an unnamed plesion containing Ameridelphia and Australidelphia. Node 13 is Australidelphia (C'05) plus *Chulpasia*, likely a homoplasy. Nodes 14 and 15 are Ameridelphia (C'05) plus *Caenolestoidea* and *Borhyaenoidea*. Node 16 is *Didelphimorphia* (C'05), with *Herpetotheriidae* indicated. The other taxa (*Pucadelphys* – *Bobbschaefferia*) are variously allocated in C'05 to *Pucadelphidae*, “*Didelphidae*,” *Eobrasiliinae*, *Derorhynchidae*, and *Protodidelphidae*. The Majority Rule insert (below) shows *Cocatherium* nested within *Polydolopimorphia*.

crista and the post-metacrista. The wear surface that joins the hypoconid and hypoconulid must have been produced by the joint action of the post-paracrista and the pre-metacrista of the upper molars. In turn, the wear surface affecting the entoconid must have been produced by the action of the protocone.

As a therian, *Cocatherium* also may be considered as a member of the Boreosphenida (Luo et al., 2001), and even though therian-like australosphenidans are known in late Jurassic strata of Chubut Province, South America (Rauhut et al., 2002), there is no evidence that this group persisted into the Cenozoic of that continent. In addition to its own apomorphic bunodonty in this context, *Cocatherium* lacks any australosphenidan apomorphies, such as a 'wrapping mesial cingulid.' Although the specimen is well worn, enough can be seen of its morphology to suggest polydolopimorphian affinities for *Cocatherium*. Chief among these features is the strong association of hypoconulid and entoconid in conjunction with the large size and elevation of the entoconid, which typically is a marsupial characteristic (Cifelli and Muizon, 1997). Among South American marsupials, only the polydolopimorphians also are as bunodont and relatively as large as shown in Figure 3 (Goin and Candela, 2004). The relative development of the other cuspids, and the longer (and sloping) labial versus the shorter (and more nearly vertical) lingual surface of the tooth combine to suggest a polydolopimorphian affinity. In *Epidolops* and polydolopines, in particular, there is a tendency to reduce the hypoconulid and increase the size of the entoconid (Goin and Candela, 2004). In the Prepidolopidae and Bonapartheriidae the entoconid is large and strongly developed, but doesn't show the anterior and posterior crests of *Cocatherium*. In contrast to some polydolopimorphians (e.g., Bonapartheriids), the paraconid still is relatively strong, and still lingual of the midline of the tooth. A phylogenetic analysis of therian molar characters (Fig. 4) based on PAUP 4.0b (Swofford, 2001), using a combination of ordered, unordered, and unique character trees (Appendixes I, II, Supplementary Data; www.vertpaleo-org/jvp/JVPcontents.html). Whereas aspects of the cladogram reflect the homoplasious nature of molar characters, *Cocatherium* clearly is contained within polydolopimorphian marsupials at Node 8 (also Majority Rule insert, Fig. 4), and separated from Alphadelphia and Ameridelphia at Node 12. Other examples of homoplasia include the diversity of associations among Didelphimorphia at Node 16, and within the Polydolopimorphia in Node 8, but the overall affinities of *Cocatherium* are consistent with its limited known morphology. With respect to therians, Fig. 5 is a phylogenetic analysis of South American condylarth and 'ungulate' taxa based on the character states refined in Gelfo (2004) and shown in Appendix III (Supplementary Data, www.vertpaleo-org/jvp/JVPcontents.html). In this analysis, *Cocatherium* shows virtually plesiomorphic states comparable to the hypothetical ancestor out-group and exhibits no compelling affinity with any American condylarth or 'ungulate.'

Although a few of the more plesiomorphic 'ungulates,' condylarths and condylarth-like taxa reviewed in Cifelli and Muizon (1997) reveal individual and selected similarities to *Cocatherium*, the trigonid of *Cocatherium* is derived in the appressed paraconid and metaconid, the trigonid being virtually closed lingually, and the protoconid and metaconid lie opposite each other transversely. *Cocatherium* probably had a planar posterior surface of the trigonid, a plesiomorphic character, and a weak precingulid also is plesiomorphic. An affinity of *Cocatherium* with condylarths and other South American ungulates is virtually ruled out by the paracristid in *Molinodus* and other South American condylarths (and didolodontids and primitive litopterns) having a distinctively arcuate pattern where it actually extends anteriorly from the protoconid before curving lingually (and almost recurving) to reach the paraconid. It is one of the strongest synapomorphies to unite Kollpaniinae + Didolodontidae + litopterns

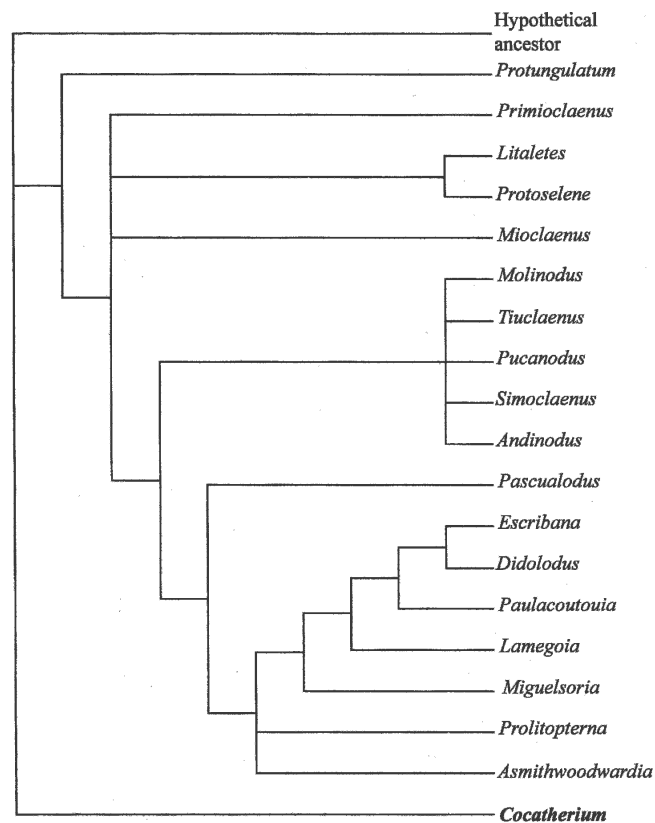


FIGURE 5. Cladogram of selected condylarth and condylarth-like taxa. Consensus of 30 equally parsimonious trees, 1000 random input orders. TL = 59; CI = 0.644, RI = 0.817; HI = 0.356. *Cocatherium* is shown outside of all condylarth taxa.

(Muizon and Cifelli, 2000), and its absence in *Cocatherium* virtually excludes this genus from an 'ungulate' association.

Polydolopimorphians have been recently reported (Case et al., 2005) from the Late Cretaceous of North America, suggesting that the evolution of this otherwise South American group was already underway. In this context it is not surprising to find a relatively derived member of that group in Danian-equivalent deposits of South America. The North American presence of polydolopimorphians also raises questions about the timing, as well as place of evolution, of other nominally South American groups with potential links to North American clades. The new polydolopimorphian reported upon here not only narrows the focus on the timing of the implied evolutionary diversification of the group to the Late Cretaceous (as opposed to early Paleocene), but also implies that a significant record of this radiation is to be expected in South America, hopefully to stimulate further search for its expected manifestation.

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