

NOTA PALEONTOLÓGICA

Femur of a monotreme (Mammalia, Monotremata)
from the Early Paleocene Salamanca Formation of
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Introduction

The Early Paleocene “Banco Negro Inferior” of the Salamanca Formation has yielded significant and diverse remains of fishes, chelid turtles, pipid and leptodactylid frogs, crocodyliforms and mammals (see Bonaparte *et al.*, 1993 and cited references).

The mammalian assemblage is represented by: 1) the gondwanatherian *Sudamerica ameghinoi*, a bizarre hypsodont toothed mammal (Bonaparte, 1990; Pascual *et al.*, 1999); 2) the dryolestoid *Peligrotherium tropicalis* (Bonaparte *et al.*, 1993; Gelfo and Pascual, 2001); 3) the condylarths *Raulvaccia peligrensis* and *Escribania chubutensis* (Bonaparte *et al.*, 1993); 4) the litoptern *Requisia vidmari* (Bonaparte and Morales, 1997); 5) the didelphimorphian, polydolopomorphian, and probably sparassodont metatherians (Goin *et al.*, 2002); and 6) the only non-Australian monotreme, *Monotrematum sudamericanum* (Pascual *et al.*, 1992a and 1992b, 2002).

A complete distal end of a left monotreme femur was discovered during the 1989-1990 field season, by staff from the Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, and the Departamento de Geología de la Universidad Nacional de la Patagonia, directed by Dr. J. F. Bonaparte. A second specimen based on a medial distal end of a right femur was recently found during the 2002 fieldwork carried out by staff of the American Museum of Natural History and of the Museo Paleontológico “Egidio Feruglio”. These femora were compared with the other mammalian taxa present at Punta Peligro and non-therian mammaliaforms. We conclude that the new materials correspond to a monotreme, tentatively referred to *Monotrematum sudamericanum*.

Abbreviations. MACN: Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires (CH: Colección Chubut; Ma: Colección

Nacional de Mastozoología; N: Colección Neuquén; Pv: Paleontología de Vertebrados); MPEF-PV: Museo Paleontológico “Egidio Feruglio”, Paleontología de Vertebrados, Trelew; MLP: Museo de La Plata, La Plata.

Material. For comparison purposes we studied specimens of *Ornithorhynchus anatinus* (MACN-Ma 26.76; MLP 1162), and *Tachyglossus aculeatus* (MACN-Ma 6.8). Other anatomical information was taken from the literature. The osteological terminology used is the same in all taxa compared regardless of the position of the femur in the living animal.

Systematic paleontology

Class MAMMALIA Linnaeus, 1758
Order MONOTREMATA Bonaparte, 1837

Monotrematum sudamericanum Pascual, Archer,
Ortiz-Jaureguizar, Prado, Godthelp and Hand,
1992b

Holotype. MLP 91-I-1-1: an upper right second molar.

Referred material. MPEF-PV 1634: an upper right second molar; MPEF-PV 1635: an incomplete upper left first molar; MACN-Pv CH 1888: a complete distal end of a left femur; and MPEF-PV 1728: a medial distal end of a right femur.

Locality, horizon and age. All specimens are from Punta Peligro, Golfo San Jorge, Chubut Province, Argentina; Hansen Member (“Banco Negro Inferior”), Salamanca Formation (Andreis *et al.*, 1975), Early Paleocene (Danian) (Andreis, 1977).

Description. The available materials consist of a complete distal end of the left femur (figure 1) and a medial distal end of a right femur. Both specimens are similar except in the slightly smaller size of the right femur. For descriptive purposes we use the left femur (MACN-Pv CH 1888) because it is better preserved.

The femoral shaft is dorsoventrally flat, being almost oval in cross section. The lateral edges of the shaft are concave; the medial one is partially broken,

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but despite of this condition it can be seen that the concavity is better pronounced and extended distally in the lateral edge than in the medial one. The epiphysis is flat and broad, with the lateral corner more prominent than the medial one.

In dorsal view (figure 1.B), the trochlea is rectangular (we define the trochlea as the anterodistal surface where the patella articulates, independent of the presence of a patellar groove); it is convex, without a patellar groove. Above the trochlea there are two supratrochlear depressions. The intercondylar notch is absent and the distal edges of both condyles are located at the same level.

In ventral view (figure 1.C), the lateral condyle is square in shape while the medial condyle is higher than wide with the main axis inclined 25° from the sagittal plane of the femur. The medial condyle is more ventrally projected than the lateral and the inner walls of the condyles define a straight angle with the intercondylar fossa. The intercondylar fossa (popliteal fossa) is deep and as wide as the lateral condyle; it has furrows and small pits. Distally, the fossa is limited by a sharp ridge, which connects both condyles.

On the lateroventral corner of the lateral condyle (figures 1.A, E) there is a process bearing the articular surface for the fibula. Furthermore, there is a

round depression for the collateral ligament on the lateral epicondyle. The medial epicondyle has a low crest reaching the femoral shaft. Ventral to this crest there is a groove probably for the origin of the *gastrocnemius* muscle (Jouffroy *et al.*, 1967)

Measurements. See table 1.

Comparisons

Monotremes. Among Monotremata the femur is known in the living *Ornithorhynchus anatinus* (Ornithorhynchidae), *Tachyglossus aculeatus*, *Zaglossus bruijni* and the fossil taxon *Z. hacketti* (Tachyglossidae) (Murray, 1978). The femora of both families show strong differences in the proximal region such as the shape and location of the trochanters, and orientation of the femoral head; however, the distal region is fairly similar (Lessertisseur and Saban, 1967; Murray, 1978) (figures 2.A, B). The distal part of the femur described herein shares with Monotremata the following derived features, which are absent in the basal mammaliaforms here considered: broad and flat distal femoral end; trochlea rectangular in shape; lack of patellar groove; and the distal edges of the lateral and medial condyles located at the same level. All these characters are typical of the Monotremata (Lessertisseur and

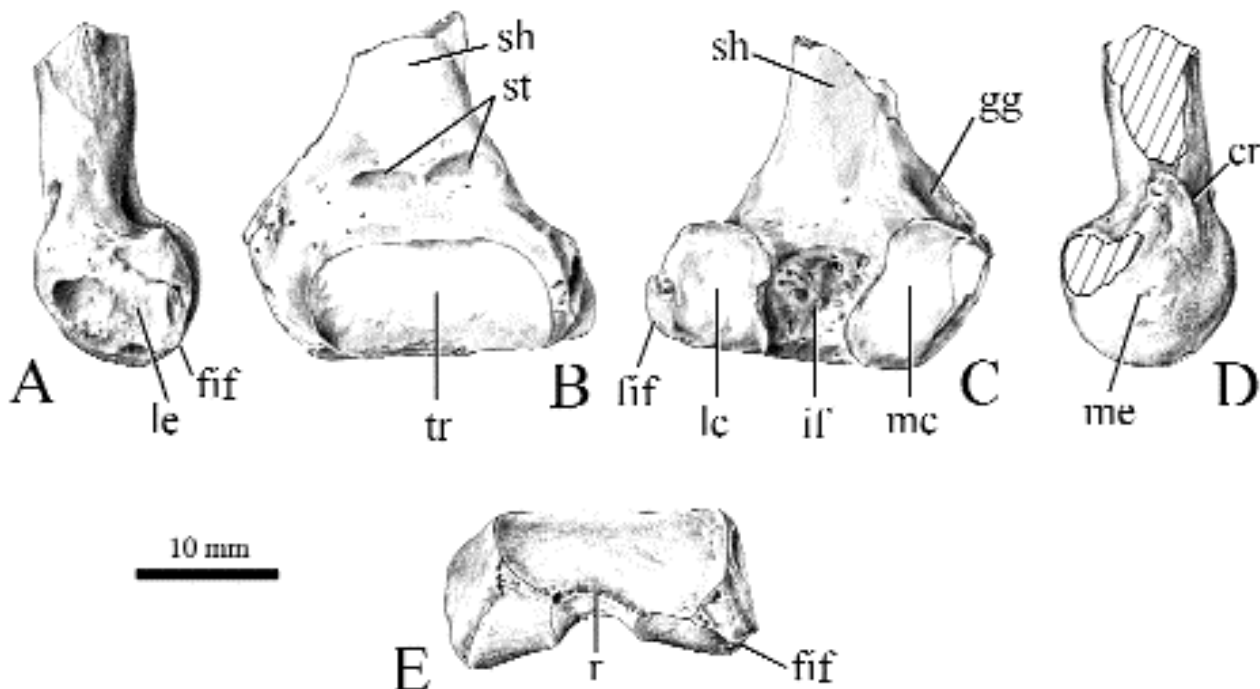


Figure 1. Distal end of the left femur of *Monotrematum sudamericanum* (MACN-Pv CH 1888) in lateral (A), dorsal (B), ventral (C), medial (D), and distal (E) views. Abbreviations: cr, crest; fif, articular facet for the fibula; gg, groove for the attach of the *gastrocnemius* muscle; if, intercondylar fossa; lc, lateral condyle; le, lateral epicondyle; mc, medial condyle; me, medial epicondyle; r, ridge; sh, distal shaft; st, supratrochlear depression; tr, trochlea. / Fragmento distal de fémur izquierdo de *Monotrematum sudamericanum* (MACN-Pv CH 1888) en vistas lateral (A), dorsal (B), ventral (C), medial (D), y distal (E). Abreviaturas: cr, cresta; fif, faceta articular fibular; gg, depresión para el músculo *gastrocnemius*; if, fosa intercondilar; lc, cóndilo lateral; le, epicóndilo lateral; mc, cóndilo medial; me, epicóndilo medial; r, borde; sh, diáfisis distal; st, depresión supratroclear; tr, tróclea.

Table 1. Measurements of the monotreme femora (figure 3). All the measurements are in mm. The measurements of *Zaglossus bruijni* were taken from Murray (1978) / *Medidas de fémures de monotremas. Todas las medidas en mm. Las medidas de Zaglossus bruijni fueron tomadas de Murray (1978)*

Fig. 3	Measurements	<i>Monotrematum sudamericanum</i> MACN-Pv CH 1888	<i>Ornithorhynchus anatinus</i> (MACN-Ma 26.76)	<i>Tachyglossus aculeatus</i> (MACN-Ma 6.8)	<i>Zaglossus bruijni</i>
A	Total length of the femur	-	31.9	57.5	75
B	Width of the proximal epiphysis	-	17.9	20.4	22
C	Width of the distal epiphysis	24.3	14	21.5	25
	Thickness of the distal shaft	7	3.9	5.7	-
D	Width of the lateral condyle	6.8	4.8	7.2	-
E	Height of the lateral condyle	11.7	5	6.6	-
F	Width of the medial condyle	9.2	4	7	-
G	Height of the medial condyle	9.4	5	6.2	-
H	Medial width of the intercondylar fossa	6.85	4	6	-
	Total body length	-	390	400	600

Saban, 1967; Murray, 1978). In particular, the general morphology of the femur from Punta Peligro resembles that of the *Ornithorhynchus* in having a considerably narrow shaft with respect to the width of the epiphysis and the main axis of the medial condyle laterally inclined. The femur of *Ornithorhynchus* differs from the femur described herein, in that the lateral epicondyle is bigger, and in the shape and size of both condyles. The femora of the echidnas differ from the femur of Punta Peligro because in echidnas the inner border of the bone is straight and flat, and both condyles are subequal in size and shape.

Morganucodontids. This group of basal mammaliaforms has a plesiomorphic femur (Jenkins and Parrington, 1976). In order to recognize the derived features of the Punta Peligro femur we used *Morganucodon*, the best known morganucodontid, for comparisons. Its femur differs from that of the Punta Peligro femur in having a shallow patellar groove, more globular condyles, inner borders of the condyles that gradually slope into the intercondylar fossa, and lateral condyle slightly lower and almost twice the size of the medial condyle (figure 2.C). Morganucodontids and the Paleocene femur share the plesiomorphic feature of having an articular facet for the fibula on the lateral epicondyle of the femur (Jenkins and Parrington, 1976) and a broad intercondylar fossa without an intercondylar notch.

Multituberculates. This group is well known in Laurasia (e.g. Clemens and Kielan-Jaworowska, 1979). In Gondwana isolated teeth and poorly preserved lower jaws of gondwanatheres were found. This group was considered Multituberculata (e.g. Bonaparte, 1990; Krause and Bonaparte, 1990) or its closest relatives (pers. com., R. Pascual and F. J.

Goin). However, the affinities of this group are a matter of discussion (e.g. Pascual *et al.*, 1999).

We compared our material with the femur of *Eucosmodon* (Granger and Simpson, 1929) since multituberculates show the same general pattern in the postcranial anatomy (Clemens and Kielan-Jaworowska, 1979). The femur of *Eucosmodon* differs from the Patagonian femur in having the following derived features: lack of contact between the femur and the fibula, a less flattened shaft, presence of a well developed patellar groove and an intercondylar notch (figure 2.D).

Dryolestoids. The presence of *Peligrotherium tropicalis* in the Salamanca Formation (Bonaparte *et al.*, 1993; Gelfo and Pascual, 2001) allows us to compare the Punta Peligro femur with that of dryolestoids. The postcranial remains of this group are poorly known, except for *Henkelotherium guimarotae* from the Upper Jurassic of Portugal (Krebs, 1991; Vázquez-Molinero *et al.*, 2001). The femoral shaft and the distal end of the femur in *Henkelotherium* are not flat and the medial condyle is clearly smaller than the lateral one as in primitive mammaliaforms. The distal epiphysis of the femur of *Henkelotherium* seems to be wide with a broad intercondylar fossa and without an intercondylar notch as in the Paleocene femur described here.

Metatherians. Understanding of the postcranium of Paleocene metatherians is based on almost complete metatherian skeletons from Tiupampa (Bolivia), including *Pucadelphys andinus* and *Mayulestes ferox* (Muizon, 1998). The presence of a probable Sparasodonta in the Salamanca Formation (Goin *et al.*, 2002) leads us to compare MACN-Pv CH 1888 with this group. The femur of sparassodonts (figure 2.E) differs from the femur described here in having a

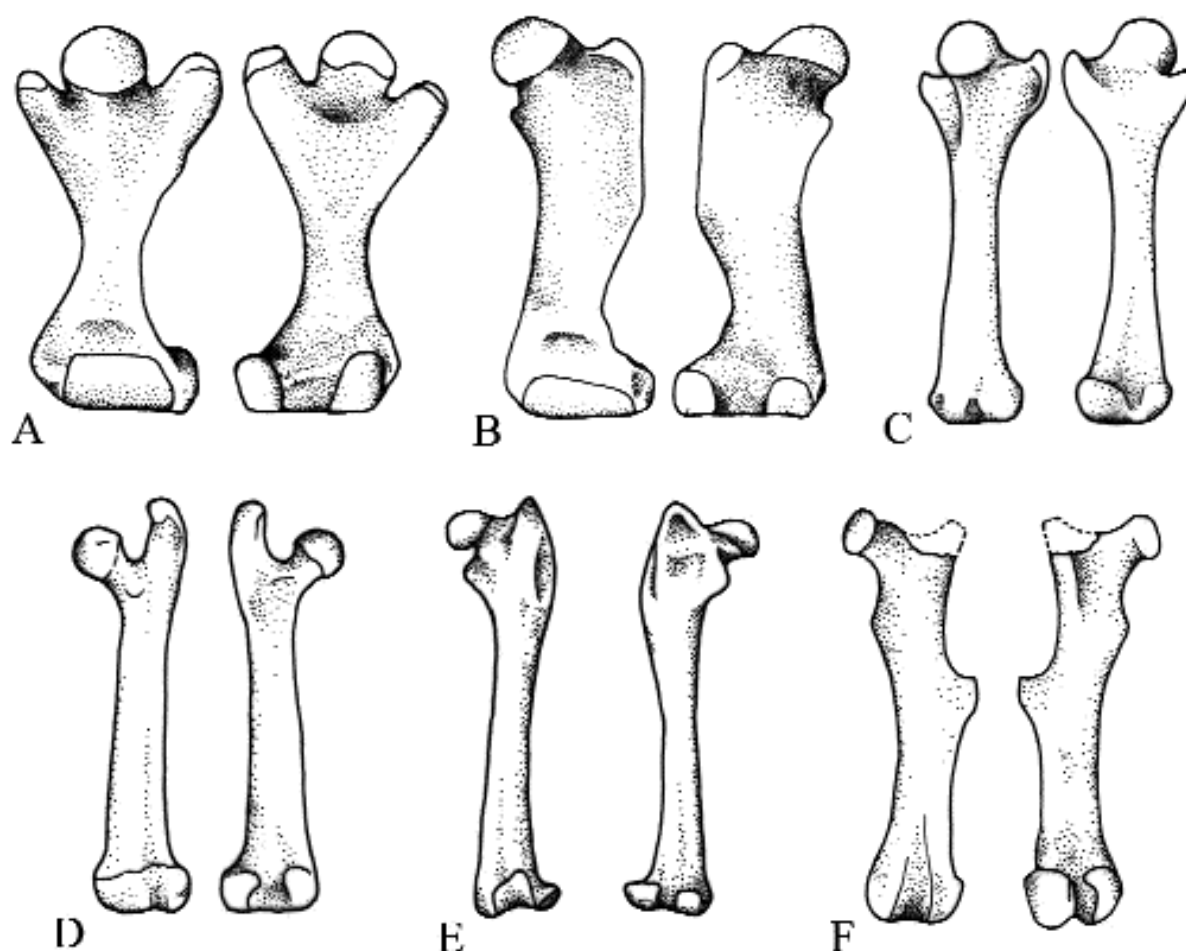


Figure 2. Comparison of the left femur among mammals in dorsal and ventral views. **A**, *Ornithorhynchus anatinus* (MACN-Ma 26.76); **B**, *Tachyglossus aculeatus* (MACN-Ma 6.8); **C**, *Morganucodon oehleri* (after Jenkins and Parrington, 1976); **D**, *Eucosmodon* sp. (after Granger and Simpson, 1929); **E**, *Mayulestes ferox* (after Muizon, 1998); and **F**, *Meniscotherium terraerubrae* (after Cope, 1884). All the figures are drawn the same size for comparison; they are not to scale. / Comparaciones del fémur izquierdo en mamíferos en vistas dorsal y ventral. **A**, *Ornithorhynchus anatinus* (MACN-Ma 26.76); **B**, *Tachyglossus aculeatus* (MACN-Ma 6.8); **C**, *Morganucodon oehleri* (según Jenkins and Parrington, 1976); **D**, *Eucosmodon* sp. (según Granger and Simpson, 1929); **E**, *Mayulestes ferox* (según Muizon, 1998); **F**, *Meniscotherium terraerubrae* (según Cope, 1884). Todas las figuras están dibujadas en un mismo tamaño a modo comparativo; no están a escala.

narrow distal epiphysis and a less flattened antero-posterior end. Sparassodonts have a large trochlea with a deep patellar groove and intercondylar notch, and a narrow intercondylar fossa. In sparassodonts the medial condyle is quadrangular and slightly lower than the lateral one. Even though the femoro-fibular articulation is unknown in *Mayulestes* this plesiomorphic condition is frequent among metatherians (Barnett and Napier, 1953a).

Eutherians. The Punta Peligro eutherian record is represented by condylarths (Mioclaenidae) and a litoptern (Notonychopidae). No postcranial elements referable to these groups have been described from Punta Peligro. Comparisons were therefore made with condylarths (*Peripitychus* and *Meniscotherium*) from the Eocene of North America (Cope, 1884). The condylarth femur (figure 2.F) differs from that of the

Punta Peligro in having a dorsoventrally thick distal end, a deep patellar groove, a medial condyle lower than the lateral one separated by an intercondylar notch, and lack of femoro-fibular articulation. In general, eutherians lost the femoro-fibular articulation, although it is present in a few basal taxa: probably in *Ukhaatherium* (Horovitz, 2000) and in some insectivores (Barnett and Napier, 1953b).

Discussion

The only South American monotreme, *Monotrematum sudamericanum*, is to date represented by isolated teeth from the “Banco Negro Inferior” (Salamanca Formation) (Pascual *et al.*, 1992 a and b; Pascual *et al.*, 2002). Recent phylogenetic studies have placed *Monotrematum* as sister taxon of *Obdurodon*,

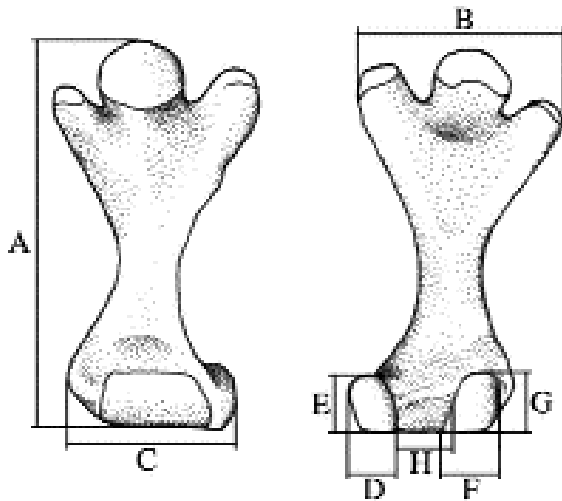


Figure 3. Left femur of *Ornithorhynchus anatinus* showing measurements taken in table 1 / Fémur izquierdo de *Ornithorhynchus anatinus* mostrando las medidas tomadas en la Tabla 1.

which and together with *Ornithorhynchus* form the Ornithorhynchidae (Musser, 1999).

The comparisons between the new femora and that of other mammalian taxa represented in the Salamanca Formation as well as with another mammaliaforms, lead us to assign these specimens to Monotremata. The presence of a femoro-fibular articulation, a broad intercondylar fossa, and the lack of an intercondylar notch in the Punta Peligro femur are plesiomorphic features also present in the remaining monotremes (i.e. *Ornithorhynchus*, *Tachyglossus*, and *Zaglossus*). The derived features shared between the new material and living monotremes are: 1) broad and flat distal femoral end; 2) rectangular trochlea; 3) lack of patellar groove, and 4) distal edges of both condyles located at the same level. As in the Ornithorhynchidae, and differing from the Tachyglossidae, the shaft is considerably narrow with respect to the distal epiphysis width; and the main axis of the medial condyle is inclined.

The measurements of the distal width of the femur, in relation to that of *Ornithorhynchus anatinus*, suggest that the total length of the specimen would have been approximately 700 mm. We also estimated the body length of *Monotrematum* by comparing its tooth length with that of a juvenile of *Ornithorhynchus anatinus* (see Simpson, 1929). This estimation also suggests that the total length of *Monotrematum sudamericanum* was approximately 700 mm. A similar measurement was estimated by Archer (1995). It is quite larger than *Obdurodon dicksoni*.

Because the estimated sizes of MACN-Pv CH 1888 and *Monotrematum sudamericanum* are quite similar, and both belong to the same stratigraphic level, we tentatively refer the femora of Punta Peligro to *Monotrematum sudamericanum*. If so, diag-

nostic features of the femur of *Monotrematum* would be the following: 1) sharp distal ridge connecting both condyles; 2) intercondylar fossa slightly narrower than in the other monotremes and 3) possibly the presence of a divided supra-trochlear depression.

In addition, *Monotrematum sudamericanum* represents the largest Ornithorhynchidae known to date (Archer, 1995; Pascual *et al.*, 2002). Moreover, the Pleistocene species *Zaglossus hacketti* (Tachyglossidae) is the largest known Monotremata (Murray, 1978).

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