



A new thylacosmilid (Mammalia, Metatheria, Sparassodonta) from the Miocene of Patagonia, Argentina

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Abstract

A new genus and species, *Patagosmilus goini*, of the family Thylacosmilidae (Mammalia, Metatheria, Sparassodonta) is described here. The new taxon is based on a single specimen collected from the west margin of the Río Chico, in Río Negro Province, Argentina, from the middle Miocene Colloncuran SALMA. Until now, two formally recognized species were encompassed in the family Thylacosmilidae: *Thylacosmilus atrox*, from the late Miocene-late Pliocene Huayquerian to Chapadmalalan SALMA of Argentina and probably Uruguay; and *Anachlysictis gracilis*, from the middle Miocene Laventan SALMA of Colombia. Recognition of the Patagonian taxon, *Patagosmilus*, provides new anatomical data, likely to be included in future phylogenetic analyses. The overall morphology of *Patagosmilus* suggests that it has a more generalized anatomy than *Thylacosmilus*. The dental morphology suggests the new Patagonian taxon was probably closer to *Thylacosmilus* than *Anachlysictis*. Saber-tooth thylacosmilids have several autapomorphic features in the skull that differentiate them from other sparassodonts, including the delayed replacement or non-replacement of the deciduous last premolar.

Key words: saber-tooth metatherians, Cenozoic, South America

Introduction

The family Thylacosmilidae (Mammalia, Metatheria, Sparassodonta) has one of the most bizarre morphologies among the native Neogene predators of South America. The overall cranial morphology of thylacosmilids resembles that of saber-tooth felids (Eutheria, Felidae, Machairodontinae) in that both acquired large hypertrophied upper canines, a classic example of convergent evolution (e.g., Riggs 1933, 1934; Simpson 1971; Marshall 1976, 1977; Turnbull 1978; Turnbull & Segall 1984; Churcher 1985). Thylacosmilids belong to the monophyletic Sparassodonta (Marshall *et al.* 1990; Muizon 1999; Forasiepi 2009), all with carnivorous adaptive features, but different levels of specialization (e.g., Marshall 1976, 1977, 1978). Sparassodonts evolved in South America over 55 million years, from the Paleocene to the Pliocene. Thylacosmilids represent the last large-sized members of the group and the last large metatherians that inhabited South America. After their extinction, (i.e., from Chapadmalalan SALMA to present), South American metatherians are small- to medium-sized marsupials with a mostly generalized appearance, such as the living opossum, “monito de monte”, and shrew opossums (i.e., Didelphimorphia, Microbiotheria, and Paucituberculata, respectively).

The family Thylacosmilidae (Riggs 1929; see also Riggs 1933, 1934 ranked as subfamily) was originally created to accommodate a single genus: *Thylacosmilus* Riggs 1933. Several authors assigned different species to this genus (Riggs 1933, 1934; Riggs & Patterson 1939) or considered other genera closely related to it (Reig 1958; Kraglievich 1960; Ringuelet 1966; Marshall 1976). Despite these taxonomic proposals, there is at present a general consensus that all late Miocene and Pliocene remains from Argentina belong to a single species: *T. atrox* Riggs 1933 (= *Achlysictis lelongi* Ameghino 1891; see Goin & Pascual 1987 for a review of

the taxonomy; Marshall *et al.* 1990; Goin 1995, 1997; McKenna & Bell 1997; Muizon 1999; Argot 2004). *Thylacosmilus atrox* is represented by several specimens from the localities of Paraná (Entre Ríos Province, Huayquerian SALMA), Salinas Grandes de Hidalgo, and probably Quehué and El Guanaco (La Pampa Province, Huayquerian SALMA), Carhué (Buenos Aires Province, Huayquerian SALMA), Monte Hermoso (Buenos Aires Province, Montehermosan SALMA), Barranca de los Lobos and Chapadmalal (Buenos Aires Province, Chapadmalan SALMA), Valle de Nono (Córdoba Province, possible Chapadmalalan SALMA), Chiquimil (Catamarca Province, Huayquerian SALMA), and Puerta del Corral Quemado (Catamarca Province, Montehermosan SALMA) (Riggs 1933, 1934; Kraglievich 1960; Marshall 1976; Goin & Pascual 1987; Cione *et al.* 2000; Goin *et al.* 2000; Álvarez & Tauber 2004; Forasiepi *et al.* 2007). Most of these specimens are represented by fragmentary material and isolated teeth. Hitherto, the best preserved remains of *Thylacosmilus atrox* are those from Catamarca Province, originally described by Riggs (1933, 1934), that include associated crania and postcrania. Additional material of indeterminate Thylacosmilidae from the late Miocene (Huayquerian SALMA) of Uruguay (Mones & Rinderknecht 2004) was originally assigned to the family (Mones & Rinderknecht 2004); notwithstanding, it exhibits a morphology that immediately reminds to *T. atrox*.

In addition to *Thylacosmilus*, material from middle Miocene of La Venta in Colombia led to the recognition of a different thylacosmilid *Anachlysictis gracilis* Goin 1997, hitherto represented solely by its holotype (a left dentary and fragmentary associated material). *Anachlysictis* possesses a more generalized morphology than *Thylacosmilus*, but both taxa belong to the same monophyletic group (Goin 1997). *Thylacosmilus* and *Anachlysictis* share several unique derived features that characterize the family. These include: large, subvertical symphyseal flange with radially oriented, lingual bony striations; alveolar and ventral edges of the dentary subparallel and straight; low and poorly developed masseteric crest; poorly inflected angle; low condyle in relation to the alveolar plane; and bowed jugal tooth series, with its concavity lingually oriented (Goin & Pascual 1987; Goin 1997).

Finally, material tentatively assigned to the family Thylacosmilidae have been collected from La Venta (Goin 1997) and from the early Miocene (Colhuehuapian SALMA) of Patagonia (Goin *et al.* 2007). While the Laventan specimen has a more generalized morphology compared with other thylacosmilids, the symphyseal area of the dentary, the morphology of the maxilla, the shape of the upper and lower canines, and the general structure of the dentition resemble that of *Thylacosmilus* and *Anachlysictis* (Goin 1997). Despite these similarities, this form could represent a different lineage of Sparassodonta with incipient and convergent saber-tooth adaptations (Goin 1997). The Colhuehuapian specimen, in turn, is represented by an isolated upper molar. The slender aspect of the tooth, the length of the postmetacrista with a deep carnassial notch, the strong compression of the roots, and the compressed lingual portion of the protocone resemble other members of the group (Goin *et al.* 2007). If the assignation of the Patagonian specimen is correct, it is the oldest record of the family (Goin *et al.* 2007).

In summary, the family Thylacosmilidae presently encompasses two formally recognized species: *Thylacosmilus atrox* from the late Miocene to late Pliocene (Huayquerian to Chapadmalalan SALMAs) of Argentina and Uruguay, and *Anachlysictis gracilis* from the middle Miocene (Laventan SALMA) of Colombia (Riggs 1933, 1934; Marshall 1976; Goin & Pascual 1987; Goin 1997). Material tentatively assigned to this group from the early Miocene Colhuehuapian SALMA of Patagonia (Goin 1997; Goin *et al.* 2007) may extend the time span for the family from the early Miocene to the late Pliocene (Chapadmalalan SALMA).

In this contribution, we describe a new thylacosmilid, *Patagosmilus goini* gen. et sp. nov. from the west margin of the Río Chico in Río Negro Province, Argentina (Fig. 1), a fossil-bearing exposure originally described by Feruglio (1949) based on mammals collected by Carlos Ameghino. Between 1990 and 1993, the Museo de La Plata and the Duke University organized four fieldtrips in the region that resulted in new fossil finds, including the thylacosmilid specimen described here. The overall morphology of the new taxon suggests a more generalized form than *Thylacosmilus atrox*. Despite lacking homologous parts for comparison with *Anachlysictis gracilis*, observations made on the upper tooth row and upper dentition suggest that the new Patagonian taxon was probably closer to *Thylacosmilus* than *Anachlysictis*.

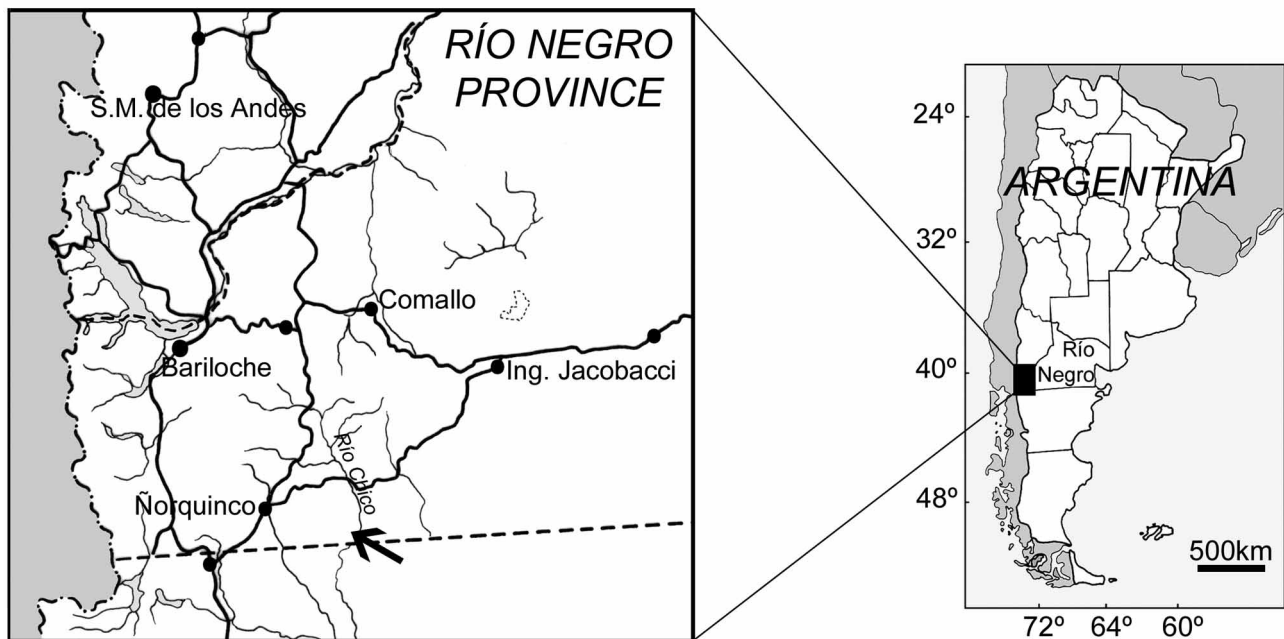


FIGURE 1. Location map of the fossil locality, at the west margin of the Río Chico (Colloncuran SALMA, middle Miocene), Río Negro Province, where the holotype of *Patagosmilus goini* (MLP 07-VII-1-1) was found.

Material and methods

For comparative purposes, the following specimens have been examined: *Thylacosmilus atrox* (FMNH P14531; FMNH P14344; MLP 35-X-41-1, ex-FMNH P14474; MLP 84-X-10-1; MMP 1443), *Borhyaena tuberata* (MACN-A 9344; MACN-A 5922; YPM PU 15701); *Prothylacynus patagonicus* (MACN-A 706-720; MACN-A 5931-5932; YPM PU 15700), *Arctodictis sinclairi* (MLP 85-VII-3-1), *Lycopsis longirostris* (UCMP38061), and *Anachlysictis gracilis* (IGM 184247). Other data were obtained from the published literature.

Capital and lower case letters, **C/c** canine, **P/p** premolar, and **M/m** molar, refer to upper and lower teeth, respectively. **D/d** refers to deciduous dentition.

Institutional abbreviation

FMNH	Field Museum of Natural History, Chicago, USA.
IGM	Instituto Nacional de Investigaciones en Geociencias, Minería y Química, Bogotá, Colombia.
MACN-A	Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Ameghino Collection, Buenos Aires, Argentina.
MLP	Museo de La Plata, La Plata, Argentina.
MMP	Museo Municipal de Ciencias Naturales de Mar del Plata “Lorenzo Scaglia”, Argentina.
MNHNA	Museo Nacional de Historia Natural y Antropología, Montevideo, Uruguay.
UCMP	University of California, Museum of Paleontology, Berkeley, USA.
YPM PU	Yale Peabody Museum, Collection of Princeton University, New Haven, USA.

Systematic Paleontology

Metatheria Huxley 1880

Sparassodonta Ameghino 1894

Thylacosmilidae (Riggs 1933)

Genus *Patagosmilus* gen. nov.

Derivation of name. *Patago*, in reference to Patagonia where the specimen was found; *smilus*, related to the carving knife appearance of the upper canine.

Type and only known species. *Patagosmilus goini*

Diagnosis. The same as for the species.

Patagosmilus goini gen. et sp. nov.

Figures 2–5

Derivation of name. *Goini*, in honor of the tireless work and patient teaching of Dr. Francisco J. Goin, Argentine paleontologist whose focus is South American metatherians.

Holotype. MLP 07-VII-1-1, most of the left side of the skull with upper dentition, right magnum, and proximal portion of ungual phalanx.

Occurrence. West margin of the Río Chico, Río Negro Province (Fig. 1), from levels of the Collón Curá Formation (Ravazzoli & Sesana 1977), Colloncuran SALMA, middle Miocene (Goin & Carlini 1993a, b).

Along the margin of the Río Chico, fossil-bearing exposures of the Collón Curá Formation (about 850 m.s.l.) overlay metamorphic basement, Tertiary basalts, and the Miocene La Pava Formation and are in turn overlaid by Pliocene deposits of the "Rionegrense" (Ravazzoli & Sesana 1977; González Díaz 1990). During fieldwork, the outcrops were subdivided into northern (Duke University/MLP Fossil Localities RCH-018 and RCH-018N) and southern exposures (RCH-018S). The specimen of *Patagosmilus* comes from the latter.

Diagnosis. *Patagosmilus goini* is smaller than *Thylacosmilus* and *Anachlysictis*. It differs from *Anachlysictis* in the following derived features: conspicuous bowed postcanine tooth row and short distance between the glenoid cavity (or condyle) and postmetacrista of M3 (or preprotocristid of m4). It differs from *Thylacosmilus* in the following plesiomorphic features: slightly longer skull, maxilla confined to the lateral side of the skull (i.e., not exposed in dorsal view), nasals widely exposed in dorsal view, presence of a subtle lacrimal process, continuous orbit and temporal fossa, lack of an anteorbital fossa and anterior notch of the orbit, longer sagittal crest, slightly shorter and straighter upper canine, P2 double rooted, molars with small protocone, M3 with narrow styler shelf and slightly shorter postmetacrista. In addition, features unique to *Patagosmilus goini* are: P2 equidistantly separated from the canine and P3, sphenopalatine foramen more anteriorly located, and anterior half of nasals extremely narrow, widening conspicuously at the level of the orbits.

Description and comparisons. Skull. The skull of the holotype of *Patagosmilus goini* is partially broken and laterally compressed (Fig. 2). The left side is better preserved, although the bone is mostly fractured. The snout is short and high with two premolars and the typical hyperdeveloped upper canine that characterizes the family. The back of the skull is also high and short, though somewhat less so than in *Thylacosmilus*. In *Patagosmilus*, the nasals are widely exposed in dorsal view; very narrow anteriorly and broad posteriorly, widening at the level of the orbit (Fig. 2). This difference in width is even more conspicuous than in other sparassodonts (Sinclair 1906; Babot *et al.* 2002; Forasiepi 2009). In *Thylacosmilus*, in contrast, the nasals are almost completely hidden in dorsal view. The nasals are apparently long, as evidenced by the section of the skull (Riggs 1934), but developed under the maxilla; the portion seen in dorsal view is triangular, narrowing posteriorly, and restricted to the anterior part of the snout (Riggs 1933, 1934). In *Patagosmilus*, the suture

between nasals and frontals defines a very open “U” outline in dorsal view, as in other sparassodonts (Sinclair 1906; Forasiepi 2009). *Thylacosmilus* is the exception: the frontal is not in contact with the nasal but with the maxilla, because of the enlargement of the latter (e.g., Riggs 1934; Marshall 1976; Goin & Pascual 1987; Muizon 1999). In *Patagosmilus*, the maxilla and the frontal are separated by the nasal and lacrimal, resembling other sparassodonts. Furthermore, the maxilla of *Patagosmilus* is anteroposteriorly short and high, and confined to the lateral aspect of the skull (Fig. 2). This condition differs from that of *Thylacosmilus*, in which the maxilla projects dorsally and posteriorly up to the level of the orbit. The root of the canine defines a prominent swelling (juga alveolaria) at the anterior border of the maxilla, which projects dorsally, following the suture with the nasal. Similar to *Thylacosmilus*, several minute vascular foramina open on this surface. The infraorbital foramen is relatively small, located dorsal to the posterior root of the last premolar (P3; see below); there is no anteorbital fossa, such as that found in *Thylacosmilus* (Riggs 1933, 1934). At the level of the postcanine teeth, the maxilla curves laterally, defining a medially concave arcade, similar to *Thylacosmilus* (Riggs 1933, 1934). In more generalized sparassodonts, in contrast, the postcanine upper tooth row is laterally straight or nearly straight (Sinclair 1906; Babot *et al.* 2002; Forasiepi 2009). There is a weakly-defined maxillary tuberosity developed above the last molars. In ventral view, the lateral border of the maxilla is nearly flat with regard to the labial border of the teeth, similar to *Thylacosmilus*. In contrast, in several more generalized sparassodonts (e.g., *Cladosictis*, *Arminiheringia*, *Callistoe*, *Borhyaena*, *Arctodictis*; Marshall 1981; Babot *et al.* 2002; Forasiepi 2009), the maxilla protrudes laterally from the labial border of the teeth, forming “cheeks”. In ventral view, the palate is mostly fractured; sutures between bones are not observable. The lateral border of the palate, which would correspond to part of the maxilla, is very high (Fig. 3B), similar to *Thylacosmilus* (Riggs 1933, 1934; Goin & Pascual 1987). There are several minute nutrient foramina on this bone surface and deep circular depressions between the molars to house the tip of the protoconid of the lower molars when the jaws are closed. The back of the palate, which would correspond to the palatine portion, is slightly thicker than the rest of the horizontal plate, forming the border of the choanae. At mid-line, the bone is broken. However, based on the fracture and the condition seen in *Thylacosmilus* and other sparassodonts, it is probable that there was a median nasal spine (Sinclair 1906; Riggs 1934; Babot *et al.* 2002; Forasiepi 2009). The posterior part of the minor palatine foramen is preserved, seen towards the lateral side of the palate and in ventral view. This foramen was apparently large and oval. As suggested by the irregular, suture-like surface of the palatine as seen in dorsal view, the minor palatine foramen was closed at the front by a now-missing portion of the maxilla, as frequently occurs among sparassodonts (Sinclair 1906; Riggs 1933, 1934; Babot *et al.* 2002; Forasiepi 2009). It is also worth mentioning that in at least one specimen of *Thylacosmilus* (MLP 35-X-41-1; Riggs 1934:figure 4), the minor palatine foramen opens entirely in the palatine bone. The palatine and maxilla are exposed in the floor of the orbit. Unfortunately, however, the bones are fractured in this area and anatomical details are not discernible. At the junction of the floor and lateral wall of the orbit, a notch in the palatine bone is observed that would represent the dorsal border of the sphenopalatine foramen (Fig. 2). This aperture is close to the anterior border of the orbit, while in other sparassodonts, including *Thylacosmilus*, this aperture is more posterior (Riggs 1934; Forasiepi 2009). In lateral view, the lacrimal is severely damaged (Fig. 2). The orbital portion of this bone is better developed than the facial part. In the rostrum, the lacrimal extends just beyond the orbit, with the height of the facial process more than half of its width. The lacrimal tubercle is relatively weak compared with that of *Thylacosmilus* (Riggs 1934). The lacrimal foramina could not be identified unequivocally on account of breakage. However, there is a shallow notch in the orbital process of the lacrimal bone that could lead to the now-missing lacrimal foramen. Among sparassodonts, a single lacrimal foramen located inside the orbit is the generalized condition (Sinclair 1906; Riggs 1934) and it seems probable that the same condition occurred in *Patagosmilus goini*.

The zygomatic arch is broken. However, the anterior base corresponding to the maxilla is deep, suggesting that the zygoma was probably robust, similar to *Thylacosmilus* (Riggs 1933, 1934). The frontal bone is partially preserved and the overall morphology resembles more generalized sparassodonts and *Anachlysictis* among thylacosmilids (Goin 1997) than *Thylacosmilus*. The postorbital process is pronounced, but does not form a postorbital bar such as in *Thylacosmilus*. It is noteworthy that the latter is the only sparassodont in which the orbit is completely separated from the temporal fossa (Riggs 1933, 1934). In

Patagosmilus, there is a small foramen below the postorbital process that opens forwards, and that would correspond to the foramen for the frontal diploic vein (*sensu* Wible 2003). The temporal lines are weak; both contact at the mid-line of the skull and broadly diverge to the lateral side. The sagittal crest, in contrast, is better defined and sharp, tall and long, resembling other sparassodonts. In *Thylacosmilus*, the temporal lines are comparatively stronger; both converge backwards in the skull, describing a sigmoid line. The sagittal crest in *Thylacosmilus* is considerably shorter and much more robust than in *Patagosmilus*.

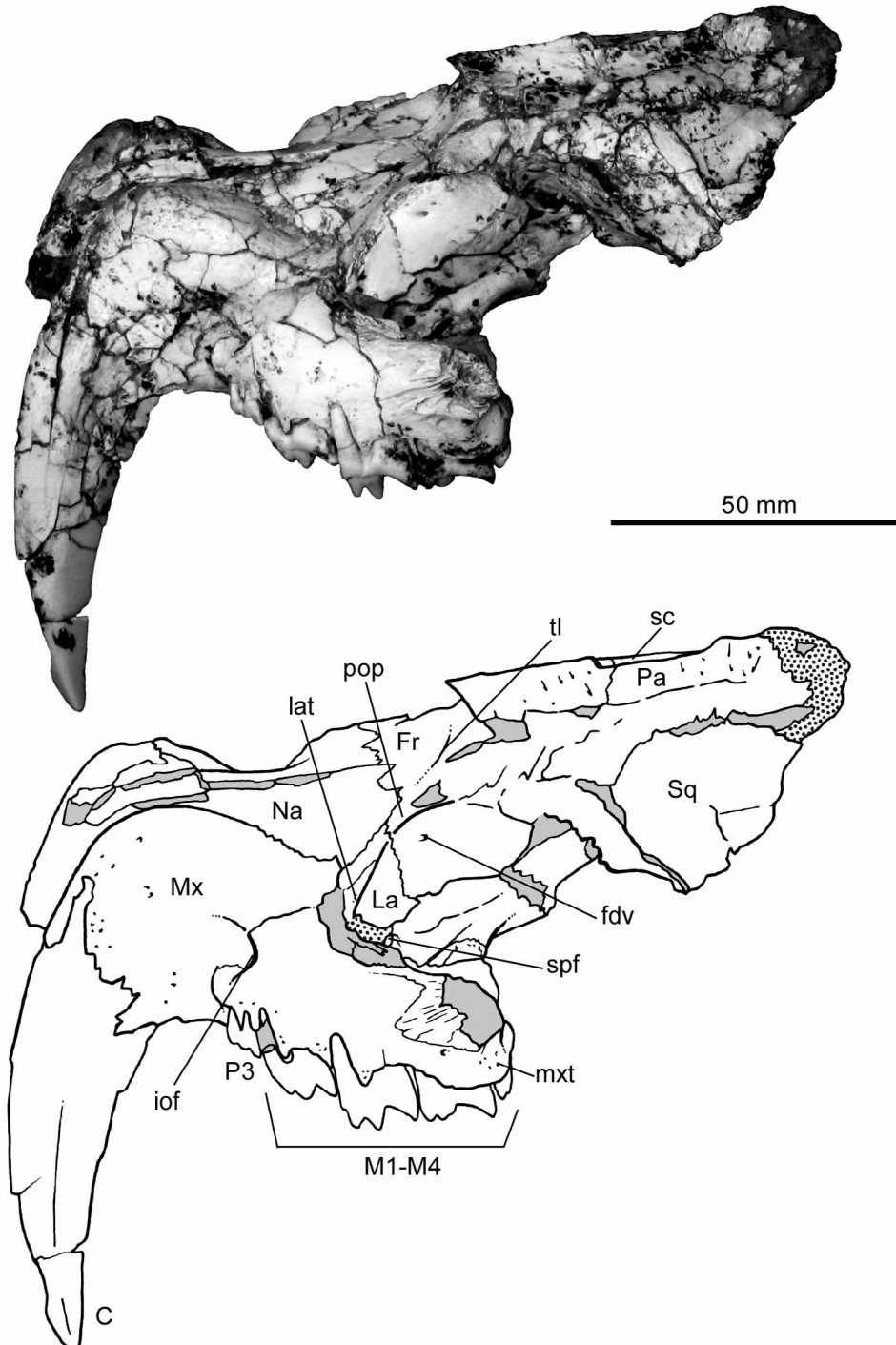


FIGURE 2. Skull of *Patagosmilus goini*, specimen MLP 07-VII-1-1 in lateral view. Abbreviations: **C**, upper canine; **fdv**, foramen for the frontal diploic vein **Fr**, frontal; **iof**, infraorbital foramen; **La**, lacrimal; **lat**, lacrimal tuberosity; **M1-M4**, upper molars, from the first to the fourth; **Mx**, maxilla; **mxt**, maxillary tuberosity; **Na**, nasal; **P3**, third upper premolar; **Pa**, parietal; **pop**, postorbital process of frontal; **sc**, sagittal crest; **Sq**, squamosal; **tl** temporal line; **spf**, sphenopalatine foramen.

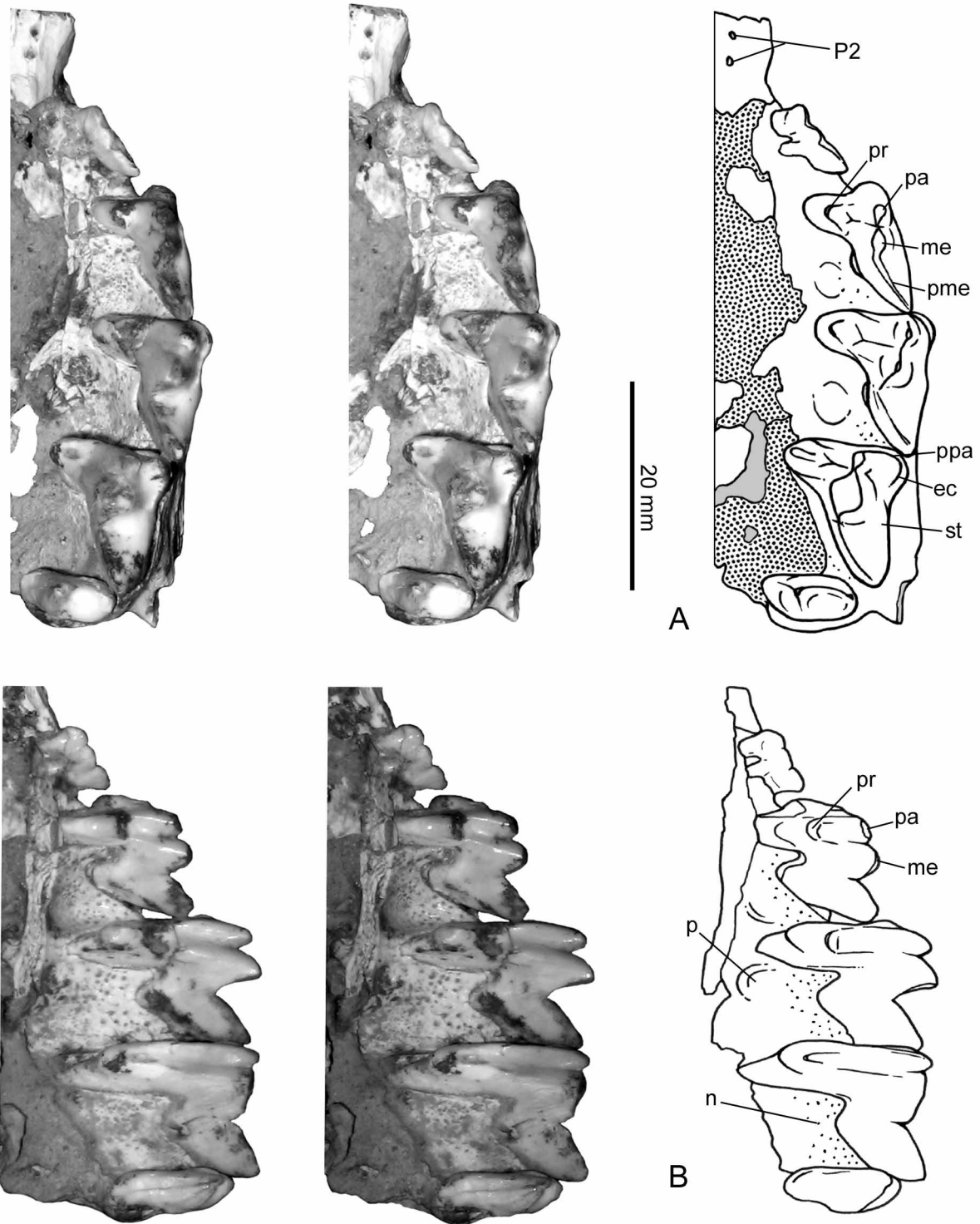


FIGURE 3. Stereographic photographs and line drawing of the upper dentition of *Patagosmilus goini*, specimen MLP 07-VII-1-1 in occlusal (A) and lingual (B) views. Abbreviations: **ec**, ectocingulum; **me**, metacone; **n**, nutrient foramina; **P2**, alveoli for the anterior and posterior roots of second upper premolar; **p**, pit for housing the protoconid; **pa**, paracone; **pme**, postmetacrista; **pr**, protocone; **ppa**, preparacrista; **st**, styelar shelf.

The frontals contact the parietals by means of a transverse suture visible in dorsal view (Fig. 2). The entire fronto-parietal portion of the temporal fossa displays shallow scars for attachment of the temporal musculature. These scars are deeper in *Thylacosmilus*. In lateral view, the frontal and parietal contact the squamous portion of the temporal, which, in turn, is the only portion of this bone that is preserved (Fig. 2).

Similar to other sparassodonts, including *Thylacosmilus*, the squamous portion in *Patagosmilus* is tall, nearly reaching the dorsal surface of the skull (Sinclair 1906; Riggs 1934; Forasiepi 2009). The most ventral portion of the squamosal that is preserved is slightly flatter to laterally concave, suggesting that this area would correspond to the posterior base of the zygomatic process. If so, then the distance between the glenoid cavity and the last molar is very short, resembling *Thylacosmilus* more so than any other sparassodont (Riggs 1933, 1934).

Dentition. The upper dentition is represented by one hyperdeveloped canine, one premolar (and the alveolus of a second), and four molars. This upper tooth count is also observed in *Thylacosmilus* and probably *Anachlysictis* as judged by its lower dentition (Riggs 1933, 1934; Marshall 1976; Goin & Pascual 1987; Goin 1997). The incisors, if present, are unknown in *Patagosmilus*. In *Thylacosmilus*, upper incisors are unknown, while there are two lower incisors (Goin & Pascual 1987). Based on wear surfaces on the lower canines, *Thylacosmilus* possessed at least one pair of upper incisors (Churcher 1985). *Thylacosmilus* and *Anachlysictis* have two lower premolars. In the dentary of *Thylacosmilus* both premolars are similar in size and located closer to the molars than the canine. In the thylacosmilid-like taxon from La Venta (IGM 251108; Goin 1997), there are three lower premolars (the upper dentition is unknown); p1 is very small and p2-p3 are larger and similar in size. If the Colombian form in fact corresponds to a thylacosmilid, then the two lower premolars present in *Thylacosmilus* and *Anachlysictis* would correspond to p2-p3 (p1 is lost; Forasiepi 2009), and by extension, the upper premolars of *Thylacosmilus* and *Patagosmilus* would likely correspond to P2-P3 (Fig. 3).

Such as other thylacosmilids, the most outstanding feature of the upper dentition of *Patagosmilus* is the canine. This tooth is large, narrow, and saber-like, with a pointed tip (Fig. 2). Both anterior and posterior edges are posteriorly concave, the anterior is the most curved. The anterior border is blunt and slightly thick, whereas the posterior is sharp. In macroscopic view, the surface of the tooth is smooth, lacking grooves and crests such as those found in some sparassodonts (e.g., *Arminiheringia*, *Callistoe*, *Proborhyaena*, *Paraborhyaena*, *Pharsophorus*, *Arctodictis*, among others; Babot *et al.* 2002; Forasiepi 2009). The enamel is thin and restricted to the labial face of the tooth, and covers the tip and the posterior part of the blade, close to the posterior border of the tooth. The surface of the enamel has shallow wrinkles (i.e., ridges and valleys), even more conspicuous than those seen in *Thylacosmilus* (Koenigswald & Goin 2000). In lingual view, the tip of the canine of *Patagosmilus* has two main wear surfaces: one adjacent to the anterior border of the tooth and the other closer to the posterior one. A similar wear pattern was described for *Thylacosmilus* (Goin & Pascual 1997), suggesting a similar functional significance. The root of the canine is deeply inserted in the alveolus and it widens toward the base, suggesting that in *Patagosmilus* the tooth was likely hypsodont similar to *Thylacosmilus*, *Arminiheringia*, *Callistoe*, and probably *Proborhyaena* among the sparassodonts (Simpson 1948; Marshall 1978; Babot *et al.* 2002; but see also Bond & Pascual 1983).

The first premolar (i.e., P2) is not preserved. There are only vestiges of what is interpreted here as the alveoli for two roots in the ventral margin of the maxilla (Fig. 3). The alveoli are minute and almost closed, suggesting that the tooth was lost in life and the bone was reabsorbed. The alveoli of P2 is set parallel to the margin of the maxilla and equidistantly separated from the canine and the following premolar (i.e., P3). In *Thylacosmilus*, the first upper premolar (P2) is single-rooted and set closer to other cheek teeth than the canine (Riggs 1933, 1934; Marshall 1978; Goin & Pascual 1987). In *Patagosmilus*, P3 is the only premolar whose crown is known (Fig. 4). Its morphology is complex, resembling the deciduous premolar of other sparassodonts (Sinclair 1906; Marshall 1978; Forasiepi 2009). This premolar is small compared to the molars (measurements in table 1), with three roots: one lingual and two labials, such as previously described for some specimens of *Thylacosmilus* (Riggs 1933; Goin & Pascual 1997; see also MNHNA 1636, Mones & Rinderknecht 2004). The lingual root is the smallest and the posterolabial is the largest. The morphology of the crown consists of three aligned main structures, interpreted here as paracone, metacone, and postmetacrista, and a lower swelling on the lingual root that is probably homologous to the protocone. The paracone and the metacone are oval in cross section. The metacone is slightly larger than the paracone. The postmetacrista is tall and blunt. There are two notches: one between the paracone and the metacone and the other between the metacone and the postmetacrista.

The four upper molars are preserved, completely erupted in the maxilla. The wear facets are poorly defined, suggesting that specimen MLP 07-VII-1-1 is a young adult. The molars have conspicuous carnassial features, which are roughly summarized as possessing reduced crushing surfaces in favor of cutting blades (Butler 1946; Muizon & Lange-Badré 1997). The size of the molars increases from M1 to M3, whereas M4 is small (measurements in table 1). With the exception of M4, whose morphology is simpler, the aspect of M1-M3 is largely similar among them, differing in the relative development of cusps and crests. The protocone is very narrow and considerably low, positioned at the base of the crown, while in *Thylacosmilus*, this cusp is absent in all upper molars and the lingual surface of the teeth is nearly vertical (Goin & Pascual 1987). The paracone and the metacone are tall and conical. The metacone is the tallest cusp in all the molars and is more prominent in the posterior molars (except for M4). In lingual view (Fig. 3B), the paracone and the metacone have two crests that descend towards the protocone. The paracone and the metacone sit very close to each other and are adjoined at their base, and for this reason the centrocrista, as such, is not identified. The postmetacrista is long and oblique in all molars, with a deep carnassial notch at the base of the metacone. In *Thylacosmilus*, the postmetacrista is even longer, and in M1-M3, it is half the length of the anteroposterior length of the teeth (Goin & Pascual 1987). In *Patagosmilus*, there is no styler shelf in M1; the labial face of the tooth is nearly vertical. On M2, the labial face is slightly oblique, whereas on M3, there is a narrow styler surface. In *Thylacosmilus*, the styler shelf is absent in all molars (Goin & Pascual 1987). On M1 of *Patagosmilus*, there is a tiny, blunt cusp located almost at the same level as the protocone and nearly aligned with the paracone and the metacone, and this would be homologous to the parastyle. On M2, the parastyle connects with a very short cingulum that descends towards the labial side of the tooth, forming a small ectocingulum (*sensu* Marshall 1978). This structure is better defined in M3. The anterior cingulum is virtually absent in the molars, being only weakly present in M3. There is no preparacrista in M1-M2 and it is present only in M3, where it runs transverse to the labial border of the tooth. M4 has a simpler morphology than previous molars: it is labiolingually wide and anteroposteriorly short with only one tall cusp, the paracone. The protocone is represented by a short cingulum, whereas the metacone is absent. Differing from previous molars, the styler region is well-developed and labial to the paracone. There is, in addition, a long and narrow anterior cingulum that descends from the anterolabial angle of the tooth to the base of the paracone. In this tooth, the preparacrista is twice larger than in M3 and nearly transversal. There is a very short postparacrista that descends from the tip of the paracone to the posterior border of the tooth.

Postcranium. The right magnum and a small proximal fragment of an ungual phalanx are the only postcranial elements preserved (Fig. 5). The magnum is a small piece, very similar to the homologous element in *Prothylacynus* (Sinclair 1906; Argot 2003), with a roughly rectangular outline in lateral and medial views. The lateral surface is nearly vertical and bears an elongated, articular facet adjacent to the anterior border of the bone, for articulation with the unciform. The medial surface is slightly oblique, apparently less so than in *Thylacosmilus* (Riggs 1934), and proximally convex. The proximal portion of this bone is head-like, and bears two facets: one for the semilunar in the most proximal part of the bone and one for the scaphoid, facing medially. The distal portion is massive and with straight borders. There are also two facets, one developed in medial view for articulation with the trapezoid, and the other on the distal face for articulation with the metacarpal III. The later is nearly trapezoidal in shape and slightly concave. The palmar tubercle is relatively poorly defined. Among the sparassodonts, the morphology of the magnum of *Patagosmilus* closely resembles that of *Prothylacynus* (Sinclair 1906; Argot 2003). In *Thylacosmilus*, *Arctodictis*, and *Borhyaena* (Sinclair 1906; Riggs 1934; Argot 2003, 2004; Forasiepi 2009), this bone is more pyramidal, with triangular lateral and medial surfaces, and stronger palmar tuberosities.

The ungual phalanx is very fragmentary and the preserved portion resembles that of *Prothylacynus*. The blade was apparently sharp dorsally, rather than blunt as in *Borhyaena* and *Arctodictis* (Sinclair 1906; Forasiepi 2009). The articular surface is nearly circular in outline, and in this regard, it is similar to *Borhyaena* (Argot 2003). In *Thylacosmilus*, the articular surface is wider than tall, while in *Prothylacynus*, it is higher than wide (Argot 2003, 2004). The flexor and extensor processes are subtly defined, the subungual process is small, and the ungual foramen is minute. In *Thylacosmilus*, in turn, the processes are stronger than in *Patagosmilus*.

After a broad analysis of the postcranial skeletons of several sparassodonts, Argot (2003, 2004) suggested that among large-sized forms, *Prothylacynus* was the most arboreally adapted taxon, whereas *Borhyaena* and *Thylacosmilus* were the most terrestrial. Because of close resemblances in the elements of the postcranium between *Patagosmilus* and *Prothylacynus*, and if the morphology of the magnum and unguinal phalanx in fact reflects functional capabilities, then it is probable that *Patagosmilus* was able to climb.

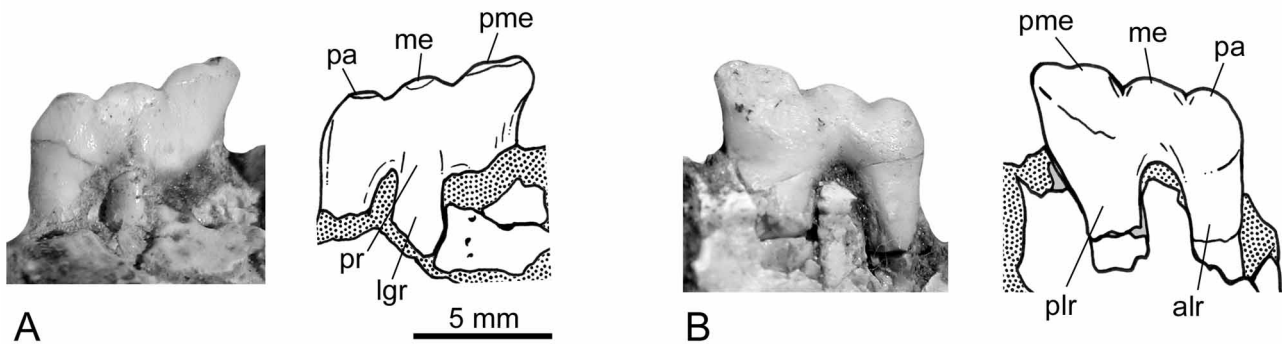


FIGURE 4. Third upper premolar of *Patagosmilus goini*, specimen MLP 07-VII-1-1 in lingual (A) and labial (B) views. Abbreviations: **alr**, anterior labial root; **lgr**, lingual root; **me**, metacone; **pa**, paracone; **pme**, postmetacrista; **pr**, protocone; **plr**, posterior labial root;

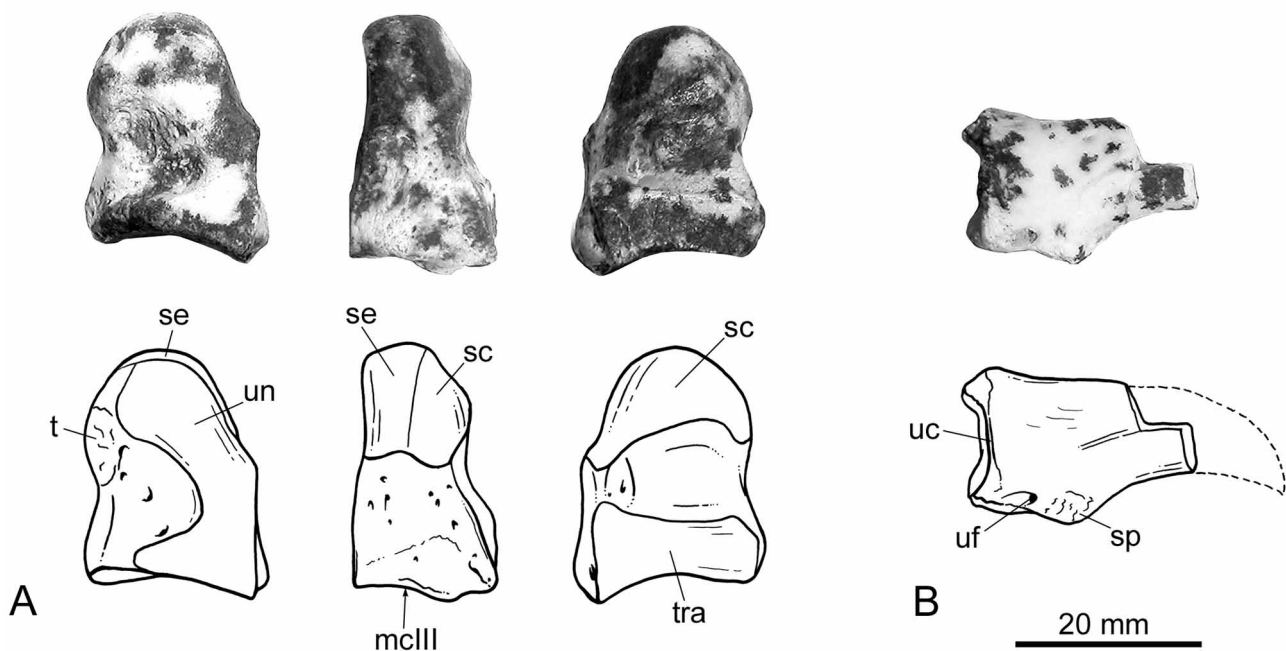


FIGURE 5. *Patagosmilus goini* specimen MLP 07-VII-1-1. Magnum in lateral, anterior, and medial views from left to right (A), and proximal portion of an unguinal phalanx in lateral view (B). Abbreviations: **mclIII**, facet for articulation with the third metacarpal; **sc**, facet for scaphoid; **se**, facet for semilunar; **sp**, subungual process; **t**, palmar tubercle; **tra**, facet for trapezoid; **uc**, unguicular crest; **uf**, unguinal foramen; **un**, facet for unciform.

Discussion

With the recognition of the new Patagonian taxon described here, the family Thylacosmilidae encompasses three formally recognized species: *Thylacosmilus atrox* from the late Miocene to the late Pliocene (Huayquerian to Chapadmalalan SALMAs) of Argentina (Riggs 1933, 1934; Marshall 1976; Goin & Pascual 1987), *Anachlysictis gracilis* from the middle Miocene (Laventan SALMA) of Colombia (Goin 1997), and

Patagosmilus goini from the middle Miocene (Colloncuran SALMA) of Argentina. Concerning the age, the new Patagonian species is older than the other recognized species, but probably not the oldest known thylacosmilid (see Goin *et al.* 2007). The discovery of new and more antique forms with more plesiomorphic morphologies is crucial for understanding the evolution of this peculiar family of sparassodontan metatherians.

Affinities. The morphology of *Patagosmilus goini* is clearly more generalized than that of *Thylacosmilus atrox*. The latter has the following derived features compared to the plesiomorphic states exhibited by *Patagosmilus*: a shorter skull and higher snout, an extended process of the maxilla covering the nasals in dorsal view, the presence of an anteorbital fossa and a notch at the anterior border of the orbit, a stronger lacrimal process, an osseous postorbital bar separating the orbit from the temporal fossa, a shorter and stronger sagittal crest, larger upper and more posteriorly concave canines, a single rooted P2, molars lacking the protocone and the styler shelf, and a larger and sharper postmetacrista.

The Colombian taxon *Anachlysictis gracilis*, unfortunately, does not preserve any homologous structures with *Patagosmilus*, with the exception of a small piece of the frontal bone. This portion of the skull is similar in *Anachlysictis*, *Patagosmilus*, and other generalized sparassodonts (Goin 1997), but plesiomorphic with regard to *Thylacosmilus*. Some cranial features of *Anachlysictis* inferred from the morphology of the dentary suggest that *Patagosmilus* shares with *Thylacosmilus* at least three derived features, which were apparently absent in the Colombian taxon. *Patagosmilus* and *Thylacosmilus* have a conspicuously bowed upper postcanine tooth row. In *Anachlysictis*, in contrast, based on the morphology of the lower tooth row and the more widespread disposition of the teeth (Goin 1997), the upper arcade was somewhat less bowed. The distance between the glenoid cavity and the end of the postmetacrista of M3 is shorter in *Patagosmilus* and *Thylacosmilus* than in any other sparassodont. In *Anachlysictis*, as evidenced by the distance between the condyle of the dentary and the preprotocristid of M4, the distance between the glenoid cavity and the M3 is greater than in the aforementioned thylacosmilids, and more similar to other sparassodonts. Finally, assuming that the hypertrophied upper canine is accompanied by a descending bony flange on the dentary in all thylacosmilid taxa, the upper canine of *Anachlysictis* would be smaller than that of *Patagosmilus* and *Thylacosmilus*. In summary, the analysis of the overall morphology and comparisons with other sparassodonts suggest that *Patagosmilus goini* is probably more closely related to *Thylacosmilus atrox* (Riggs, 1933, 1934) than to *Anachlysictis gracilis* (Goin 1997). In addition, *Patagosmilus* has the autopomorphic features of P2 equidistantly separated from the canine and P3, the sphenopalatine foramen more anteriorly located than in the other members of the family, and the nasals extremely narrow at the anterior half and conspicuously wide at the level of the orbits, which differs from any other known sparassodont. These characteristics support the recognition of a new species. The recognition of this new, more generalized taxon, in turn, provides new anatomical data, which should be included in future phylogenetic analyses of a broad sample of sparassodonts.

Last upper premolar. One peculiar feature of the anatomy of *Patagosmilus*, which is shared with *Thylacosmilus*, is the complex morphology of the last premolar. In most metatherians, including sparassodonts, the P3/p3 predecessor (i.e., DP3/dp3) is three-rooted and with a morphology more complex than that of P3/p3 (e.g., Lockett 1993; Cifelli *et al.* 1996; Voss & Jansa 2003; Marshall 1978; Forasiepi 2009). In sparassodonts, however, the deciduous tooth is simpler than in basal metatherians (e.g., *Alphadon*; Cifelli *et al.* 1996) or didelphids (Lockett 1993; Voss & Jansa 2003), and this trait is in accordance with the simpler overall morphology of the cheek teeth of these carnivorous species (Marshall 1978; Forasiepi 2009). Under this framework and based on the morphology of the last premolar of *Thylacosmilus*, Goin & Pascual (1987) suggested that the tooth in this species should be regarded as DP3.

In specimens MLP 07-VII-1-1 of *Patagosmilus goini* and MLP 35-X-41-1 and MMP 1443 of *Thylacosmilus atrox*, all the molars are fully erupted, including M4. Furthermore, MLP 07-VII-1-1 shows no evidence of a successor premolar, as seen through the fractured skull. In other sparassodonts, the timing of the origin of cheek teeth is such that P3/p3 erupts almost simultaneous with M4/m4. Moreover, the complete eruption of P3/p3 apparently slightly precedes that of M4/m4, as evidenced by specimens UCMF 38061 of *Lycopsis longirostris* and MACN-A 5931-5932 of *Prothylacynus patagonicus* (Forasiepi 2009). This pattern

of eruption sequence appears to be ancestral in didelphids and fossil outgroups (Cifelli *et al.* 1996; Van Nielvet & Smith 2005; Astúa & Leiner 2008), including sparassodonts (Forasiepi 2009).

Because M4 is completely erupted in both thylacosmilid species, two hypotheses can be advanced: A) the timing of the eruption of P3 is delayed in thylacosmilids with regard to other sparassodonts, and DP3 is replaced in later ontogenetic stages; or B) the permanent last premolar in thylacosmilids corresponds to DP3, which is never replaced. Specimen MLP 07-VII-1-1 of *Patagosmilus goini* should be regarded as a young adult (all molars have only incipient wear surfaces), but specimen MMP 1443 of *Thylacosmilus atrox* has strong wear facets affecting the cusps, especially on M1-M2, and MLP 35-X-41-1 has the molar crowns completely worn, suggesting a very advanced age. Assuming that both thylacosmilid species possessed the same timing of tooth eruption, the second hypothesis is apparently more likely, that is, the deciduous tooth is never replaced. The retention of DP3 in the adult dentition would be regarded as an example of a paedomorphic process, in which juvenile features are retained in the adult stage of descendant taxa of the same lineage (e.g., McKinney & McNamara 1991). The recognition of heterochronic processes in metatherian lineages could provide new insights for understanding patterns of evolution. A broader sample of metatherians and the ontogenetic series of living species should be analyzed more carefully in future studies.

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References

- Álvarez, D. & Tauber, A. (2004) Vertebrados de la Formación Brochero (Mioceno Tardío-Plioceno) de Córdoba, Argentina. *Ameghiniana*, 41, 32R–33R.
- Ameghino, F. (1891) Caracteres diagnósticos de cincuenta especies nuevas de mamíferos fósiles argentinos. *Revista Argentina de Historia Natural*, 1, 240–259.
- Ameghino, F. (1894) Enumération synoptique des espèces de mammifères fossiles des formations éocènes de Patagonie. *Boletín de la Academia Nacional de Ciencias de Córdoba*, 13, 259–452.
- Argot, C. (2003) Functional adaptations of the postcranial skeleton of two Miocene borhyaenoids (Mammalia, Metatheria) *Borhyaena* and *Prothylacynus*, from South America. *Palaeontology*, 46, 1213–1267.
- Argot, C. (2004) Functional-adaptive features and paleobiologic implications of the postcranial skeleton of the late Miocene sabretooth borhyaenoid, *Thylacosmilus atrox* (Metatheria). *Alcheringa*, 28, 229–266.
- Astúa, D. & Leiner, N.O. (2008) Tooth eruption sequence and replacement pattern in woolly opossums, genus *Caluromys* (Didelphimorphia: Didelphidae). *Journal of Mammalogy*, 89, 244–251.
- Babot, M.J., Powell, J.E. & Muizon, C. (2002) *Callistoe vincei*, a new Proborhyaenidae (Borhyaenoidea, Metatheria, Mammalia) from the early Eocene of Argentina. *Geobios*, 35, 615–629.
- Bond, M. & Pascual, R. (1983) Nuevos y elocuentes restos craneanos de *Proborhyaena gigantea* Ameghino, 1897 (Marsupialia, Borhyaenidae, Proborhyaeninae) de la edad Deseadense -un ejemplo de coevolución. *Ameghiniana*, 20, 47–60.
- Butler, P.M. (1946) The evolution of carnassial dentitions in the Mammalia. *Journal of Zoology*, 116, 198–220.
- Churcher, C.S. (1985) Dental functional morphology in the marsupial sabre-tooth *Thylacosmilus atrox* (Thylacosmilidae) compared to that of felid sabre-tooths. *Australian Mammalogy*, 8, 201–220.
- Cifelli, R.L., Rowe, T.B., Lueckert, W.P., Banta, J., Reyes, R. & Howes, R.I. (1996) Origin of marsupial pattern of tooth replacement: fossil evidence revealed by high resolution X-ray CT. *Nature*, 379, 715–718.
- Cione, A.L., Azpelicueta, M.M., Bond, M., Carlini, A.A., Casciotta, J.R., Cozzuol, M.A., de la Fuente, M.S., Gasparini, Z., Goin, F.J., Noriega, J., Scillato-Yané, G.J., Soibelzon, L., Tonni, E.P., Verzi, D. & Vucetich, M.G. (2000) Miocene vertebrates from Entre Ríos Province, eastern Argentina. In: Acenolaza, F.G. & Herbst, R. (Eds.), *El Neógeno de*

- Argentina. Serie Correlación Geológica 14, San Miguel de Tucumán, pp. 191–237.
- Feruglio, E. (1949) Descripción geológica de la Patagonia. *Yacimientos Petrolíferos Fiscales*, 2, 1–349.
- Forasiepi, A.M. (2009) Osteology of *Arctodictis sinclairi* (Mammalia, Metatheria, Sparassodonta) and phylogeny of Cenozoic metatherian carnivores from South America. *Monografías del Museo Argentino de Ciencias Naturales n.s.*, 6, 1–174.
- Forasiepi, A.M., Martinelli, A.G. & Goin, F.J. (2007) Revisión taxonómica de *Parahyaenodon argentinus* Ameghino y sus implicancias en el conocimiento de los grandes mamíferos carnívoros del Mio-Plioceno de América del Sur. *Ameghiniana*, 44, 143–159.
- Goin, F.J. (1995) Los marsupiales. In: Alberdi, M.T., Leone, G. & Tonni, E.P. (Eds.), *Evolución Biológica y Climática de la Región Pampeana durante los Últimos Cinco Millones de Años. Un ensayo de Correlación con el Mediterráneo Occidental*. Monografías del Museo Nacional de Ciencias Naturales, Madrid, pp. 165–179.
- Goin, F.J. (1997) New clues for understanding Neogene marsupial radiations. In: Kay, R.F., Madden, R.H., Cifelli, R.L. & Flynn, J. (Eds.), *A History of the Neotropical Fauna -Vertebrate Paleobiology of the Miocene in Colombia*. Smithsonian Institution Press, Washington, pp. 185–204.
- Goin, F.J. & Carlini, A.A. (1993a) Un primitivo Thylacosmilidae (Marsupialia, Sparassodonta) del Mioceno medio de Patagonia. *Ameghiniana*, 30, 107–108.
- Goin, F.J. & Carlini, A.A. (1993b) The most primitive South American sabretooth marsupials: their significance in the reassessment of sparassodont phylogeny. *Sixth International Theriological Congress (Sydney)*, 113.
- Goin, F.J. & Pascual, R. (1987) News on the biology and taxonomy of the marsupials Thylacosmilidae (late Tertiary of Argentina). *Anales de la Academia Nacional de Ciencias Exactas Físicas y Naturales de Buenos Aires*, 39, 219–246.
- Goin, F.J., Montalvo, C.I. & Visconti, G. (2000) Los marsupiales (Mammalia) del Mioceno Superior de la Formación Cerro Azul (Provincia de La Pampa, Argentina). *Estudios Geológicos*, 56, 101–126.
- Goin, F.J., Abello, A., Bellosi, E., Kay, R., Madden, R. & Carlini, A.A. (2007) Los Metatheria sudamericanos de comienzos del Neógeno (Mioceno Temprano, edad-mamífero Colhuehuapense). Parte I: Introducción, Didelphimorphia y Sparassodonta. *Ameghiniana*, 44, 29–71.
- González Díaz, E.F. (1990) Las relaciones entre las formaciones Campana y Collón Curá en el valle del Río Chico (paralelo 42°00'), provincias de Río Negro y Chubut: Reconocimiento de dos unidades diferenciables temporalmente en la definición de la Fm. Campana. *Actas del XI Congreso Geológico Argentino (San Juan)*, 2, 93–96.
- Huxley, J.S. (1880) On the application of the law of evolution to the arrangement of the Vertebrata, and more particular to the Mammalia. *Proceedings of the Zoological Society of London*, 43, 649–662.
- Koenigswald, W.V. & Goin, F.J. (2000) Enamel differentiation in South American marsupials and a comparison of placental and marsupial enamel. *Palaeontographica*, 255, 129–168.
- Kraglievich, J.L. (1960) Marsupiales tilacosmilinos de la fauna de Chapadmalal. *Publicaciones del Museo Municipal de Ciencias Naturales y Tradicional de Mar del Plata*, 1, 53–72.
- Luckett, W.P. (1993) An ontogenetic assessment of dental homologies in therian mammals. In: Szalay, F.S., Novacek, M.J. & McKenna, M.C. (Eds.), *Mammal Phylogeny: Mesozoic Differentiation, Multituberculates, Monotremes, Early Therians, and Marsupials*. Springer-Verlag, New York, pp. 182–204.
- Marshall, L.G. (1976) Evolution of the Thylacosmilidae, extinct saber-tooth marsupials of South America. *PaleoBios*, 23, 1–30.
- Marshall, L.G. (1977) Evolution of the carnivorous adaptative zone in South America. In: Hecht, M.K., Goody, P.C. & Hecht, B.M. (Eds.), *Major Patterns in Vertebrate Evolution*. Plenum Press, New York, pp. 709–722.
- Marshall, L.G. (1978) Evolution of the Borhyaenidae, extinct South American predaceous marsupials. *University of California Publications in Geological Sciences*, 117, 1–89.
- Marshall, L.G. (1981) Review of the Hathlyacyninae, an extinct subfamily of South American “dog-like” marsupials. *Fieldiana Geology, n.s.*, 7, 1–120.
- Marshall, L.G., Case, J.A. & Woodburne, M.O. (1990) Phylogenetic relationships of the families of marsupials. *Current Mammalogy*, 2, 433–502.
- McKenna, M.C. & Bell, S.K. (1997) *Classification of Mammals above the Species Level*. Columbia University Press, New York, 631 pp.
- McKinney, M.L. & McNamara, K.J. (1991) *Heterochrony. The Evolution of Ontogeny*. Plenum Press, New York, 437 pp.
- Mones, A. & Rinderknecht, A. (2004) Primer registro de Thylacosmilidae en el Uruguay (Mammalia: Marsupialia: Sparassodonta). *Comunicaciones Paleontológicas del Museo Nacional de Historia Natural y Antropología*, 34, 193–200.
- Muizon, C. de (1999) Marsupial skulls from the Deseadean (late Oligocene) of Bolivia and phylogenetic analysis of the Borhyaenoidea (Marsupialia, Mammalia). *Geobios*, 32, 483–509.
- Muizon, C. de & Lange-Badré, B. (1997) Carnivorous dental adaptations in tribosphenic mammals and phylogenetic reconstruction. *Lethaia*, 30, 351–366.
- Ravazzoli, I.A. & Sesana, F. (1977) Descripción geológica de la Hoja 41c, Río Chico, Provincia de Río Negro. *Boletín del Servicio Geológico Nacional*, 148, 1–90.

- Reig, O.A. (1958) Notas para la actualización del conocimiento de la fauna de la Formación Chapadmalal. II Amphibia, Reptilia, Aves, Mammalia (Marsupialia: Didelphidae, Borhyaenidae). *Acta Geologica Lilloana*, 2, 255–283.
- Riggs, E.S. (1929) New family of South American Pliocene mammals. *Bulletin of the Geological Society of America*, 40, 117.
- Riggs, E.S. (1933) Preliminary description of a new marsupial saber-tooth from the Pliocene of Argentina. *Field Museum of Natural History, Geological Series*, 6, 61–66.
- Riggs, E.S. (1934) A new marsupial saber-tooth from the Pliocene of Argentina and its relationships to other South American predaceous marsupials. *Transactions of the American Philosophical Society, n.s.*, 24, 1–31.
- Riggs, E.S. & Patterson, B. (1939) Stratigraphy of late Miocene and Pliocene deposits of the Province of Catamarca (Argentina). *Physis*, 14, 143–162.
- Ringuelet, A.B. (1966) Marsupialia. In: Borrello A.V. (Ed.), *Paleontografía Bonaerense*. Comisión de Investigaciones Científicas de la Provincia de Buenos Aires, La Plata, pp. 46–59.
- Simpson, G.G. (1948) The beginning of the age of mammals in South America. *Bulletin of the American Museum of Natural History*, 91, 1–232.
- Simpson, G.G. (1971) The evolution of marsupials in South America. *Anais da Academia Brasileira de Ciências*, 43, 103–118.
- Sinclair, W.J. (1906) Mammalia of the Santa Cruz beds: Marsupialia. *Reports of the Princeton University, Expedition to Patagonia*, 4(3), 333–460.
- Turnbull, W.D. (1978) Another look at dental specialization in the extinct saber-toothed marsupial, *Thylacosmilus*, compared with its placental counterparts. In: Butler, P.M. & Joysey, K.A. (Eds.), *Development, Function and Evolution of Teeth*. Academic Press, London, pp. 399–414.
- Turnbull, W.D. & Segall, W. (1984) The ear region of the marsupial sabertooth, *Thylacosmilus*: influence of the sabertooth lifestyle upon it, and convergence with placental sabertooths. *Journal of Morphology*, 181, 239–270.
- Van Nievelt, A.F.H. & Smith, K.K. (2005) Tooth eruption in *Monodelphis domestica* and its significance for phylogeny and natural history. *Journal of Mammalogy*, 86, 333–341.
- Voss, R.S. & Jansa, S.A. (2003) Phylogenetic studies on didelphid marsupials II. Non molecular data and new IRBP sequences: separate and combined analyses of didelphine relationships with denser taxon sampling. *Bulletin of the American Museum of Natural History*, 276, 1–82.
- Wible, J.R. (2003) On the cranial osteology of the short-tailed opossum *Monodelphis brevicaudata* (Didelphidae, Marsupialia). *Annals of the Carnegie Museum*, 72, 137–202.