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PLIOCENE MAMMALS FROM INCHASI, BOLIVIA: THE ENDEMIC FAUNA JUST BEFORE THE GREAT AMERICAN INTERCHANGE

Federico Anaya[1] **and Bruce J. MacFadden**[2]

ABSTRACT

A new, high-elevation (3200 m) mammalian local fauna is described from Communidad Inchasi, ca. 50 km SE of Potosí, Bolivia. The fauna consists of 4 orders (Edentata, Rodentia, †Litopterna, and †Notoungulata), 9 families, 10 genera, and at least 11 species. Of these, one new genus and two new species of notoungulates are described. This fauna contains two genera endemic to the Bolivian altiplano, †*Posnanskytherium* and †*Hypsitherium* n. gen., whereas the remaining eight genera (†*Glossotheridium*, †*Proscelidodon*, †*Plaina*, †*Plohophorus*, †*Paraglyptodon*, †*Chapalmatherium*, †*Caviodon*, and †*Promacrauchenia*) are referable to previously described genera from the Pliocene of Argentina.

The biochronology of the Inchasi mammals indicates either a: (1) Montehermosan/ Chapadmalalan (undifferentiated) age because the included taxa are either restricted to the Montehermosan, Chapadmalalan, or span both mammal ages; or (2) Chapadmalalan age based on recent biostratigraphic redefinitions from classic localities in Argentina. Previous magneto- and biostratigraphic data indicate that the Inchasi beds and their contained mammalian fauna are middle Pliocene with an age range of between 3.3 and 4.0 myr ago. The Inchasi local fauna lacks any immigrant taxa and thus represents an endemic fauna that occurred about 1 myr before the beginning of the Great American Interchange.

RESUMEN

Una nueva fauna local de mamíferos es descripta para la Comunidad Inchasi, aproximadamente 50 kilometros al sudeste de Potosí, Bolivia, a una altura de 3200 m.s.n.m. Esta fauna comprende cuatro órdenes (Edentata, Rodentia, †Litopterna y †Notoungulata), nueve familias, 10 géneros y por lo menos 11 especies. Se describe un género nuevo y dos nuevas especies. Esta fauna tiene dos géneros endémicos del altiplano Boliviano, †*Posnanskytherium* y †*Hypsitherium* gen. n. y los ocho restantes (†*Glossotheridium*, †*Proscelidodon*, †*Plaina*, †*Plohophorus*, †*Paraglyptodon*, †*Chapalmatherium*, †*Caviodon* y †*Promacrauchenia*) pertenecen a géneros del Plioceno de Argentina.

Hay dos posibilidades para interpretar la biocronología de los mamíferos de Inchasi: o (1) los fósiles guía indican una edad Montehermosense/Chapadmalalense (no diferenciada) debido a que los taxones estan restringidos al Montehermosense, Chapadmalalense, o existieron durante las dos edades juntas; o (2) indican solo una edad Chapadmalalense en base a las investigaciones recientes en Argentina. Estudios previos de la magneto- y bioestratigrafía indican que los afloramientos de Inchasi pertenecen al Plioceno medio, con una edad entre 3.3 y 4 millones de años. La mastofauna de Inchasi carece de inmigrantes norteaméricanos y

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representa un intervalo aproximadamente de 1 millón de años antes del comienzo del Gran Intercambio Americano.

TABLE OF CONTENTS

INTRODUCTION

South America drifted as an island continent during most of the Cenozoic, carrying along with it an endemic biota. This isolation changed with the formation of the Panamanian Land Bridge and the consequent dry-land connection that allowed dispersal of many land mammals during the Great American Interchange (e.g. Stehli and Webb 1985). The main phase of this interchange began during the late Pliocene, about 2.5 myr ago, and continued through the Pleistocene until about 10,000 years ago when an extinction wave decimated the diversity of medium- to large-bodied mammals throughout the Americas.

The fossil record of late Pliocene and Pleistocene land mammals in South America is very rich, with many localities recorded from numerous regions on that continent (Marshall et al. 1983; 1984). In contrast, relatively little is known of the endemic mammalian faunas during the late Miocene and early Pliocene just before the interchange. Consequently, the paucity of these earlier faunas has led to confusion about the biochronological characterization and distinctness of the Montehermosan and Chapadmalalan land mammal ages. Several Pliocene, pre-interchange mammal localities have been reported from Bolivia, e.g. at Ayo Ayo-Viscachani south of La Paz (Hoffstetter et al. 1971; Hoffstetter 1986), and although certain taxa have been described in detail (e.g. Hoffstetter et al. 1984), in most cases these important faunas have never been fully described. Recently a rich Pliocene, pre-interchange mammalian fauna has been discovered at Inchasi, about 50 km south of Potosí. This fauna offers significant potential to: (1) better understand the endemic mammals just before the Great American Interchange; (2) provide a further understanding of the Montehermosan and Chapadmalalan land mammal ages; and (3) further constrain the timing of the beginning of the Great American Interchange.

The purpose of this study is to: (1) describe the mammalian fauna from Inchasi; (2) compare this fauna with other faunas of similar age in Bolivia and Argentina; (3) discuss the overall significance of this fauna with regard to faunal diversity, paleoecology, and land-mammal chronology. This report represents an amplification of a previous, preliminary description of this fauna (Anaya 1994).

ACKNOWLEDGEMENTS

The senior author gratefully acknowledges financial support from the Bryan Patterson Award of the Society of Vertebrate Paleontology in 1992. These funds allowed for one field trip to Inchasi and resulted in the collection of numerous important specimens that further increased the knowledge of this fauna. The authors thank Dr. Jaime Argollo of La Paz for showing us the Inchasi basin and for allowing us to pursue our studies there. Bernardino Mamani and Yuko Okamura assisted in the field and laboratory. Gary Morgan's expertise in specimen identification is gratefully acknowledged. Yuko Okamura skillfully photographed many of the specimens presented here or used to prepare the illustrations. Barbara Harmon prepared the line drawings and Linda Chandler assisted in the final preparation of the figures. Malcolm McKenna, Bruce Shockey, and Fred Thompson assisted with points about taxonomic nomenclature. The thorough and careful reviews of this manuscript provided by C. S. Churcher, G. DeIuliis, and J. J. Flynn are greatly appreciated. This research was also partially supported by a U.S. NSF grant EAR-8716207 and Fulbright Senior Research Fellowship to BJMacF. This is University of Florida Contribution to Paleobiology number 453.

GEOLOGICAL SETTING AND PREVIOUS STUDIES

Communidad Inchasi is located 8.5 km northeast of Puna and 50 km southeast of the city of Potosí in the Province of Linares, Department of Potosí, at an

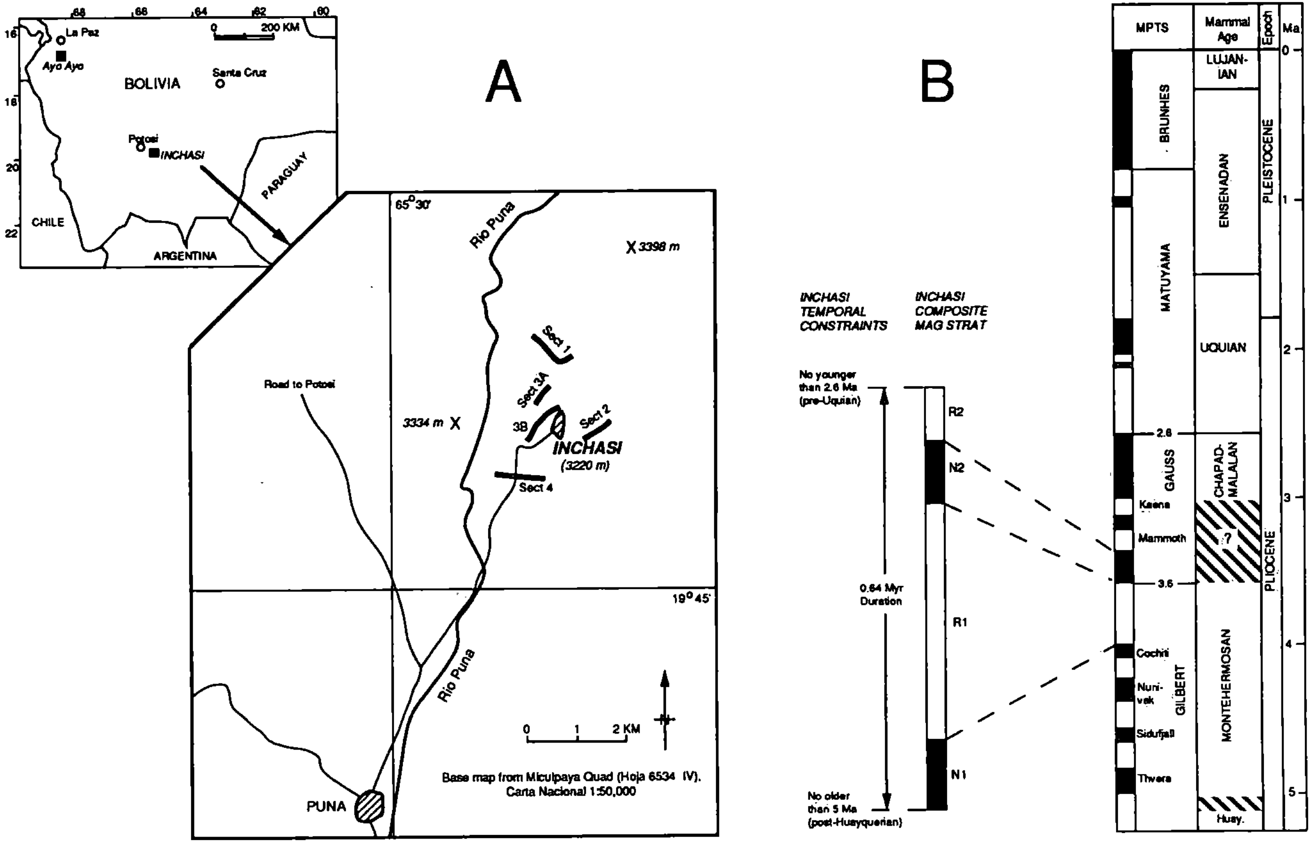

Figure 1. A. General location of Communidad Inchasi, about 50 km southeast of Potosi, and specific location of measured sections. B. Composite magnetostratigraphy of the Inchasi beds, absolute age constraints, and correlation to the Geomagnetic Polarity Time Scale and South American land mammal ages (modified from MacFadden et al., 1993).

elevation of 3220 m. Pliocene fossil mammals have been collected from around Inchasi between latitudes 19° 41' 20" -- 19° 44' 35" S and longitudes 65° 26' 30" -- 65° 29' 22" W (Fig. 1a) and can be located on the Miculpaya 1:50,000 quadrangle (Instituto Geográfico Militar Hoja 6534 IV).

The Pliocene Inchasi beds were deposited into a small basin with a topographic extent of about 30 km². The flanks of the basin consist of either undifferentiated Ordovician sediments or volcanic rocks of the prominent middle Miocene Kari Kari caldera. The Inchasi beds consist primarily of high-energy fluviatile gravels, fine grained-clays and silts, and several tuffaceous horizons of varied thicknesses.

The Inchasi beds were originally mapped as Quaternary Alluvium (Pareja et al. 1978). They were not known to contain fossils until the first specimens were discovered by Jaime Argollo in 1984. In 1988 a visit to Inchasi by Argollo, MacFadden, and Peter Friend yielded several fossil mammals indicating a probably late Pliocene age for these sediments. In 1990 Anaya and MacFadden spent one week at Inchasi measuring sections and collecting paleomagnetic samples and fossil mammals. Since 1990 the Inchasi beds have been prospected for fossils by Anaya and crews from the Museo Nacional de Historia Natural, La Paz. All fossils collected from there can be precisely located stratigraphically within the four principal sections that we measured (Fig. 1a). Although radioisotopic age determinations (analyzed by Carl Swisher of the Berkeley Geochronology Laboratory, California) on tuffaceous samples collected from within the Inchasi beds indicated middle Miocene detrital contamination (apparently from the Kari Kari volcanics), the magnetostratigraphic analysis yielded a calibration of the Inchasi beds. The composite section at Inchasi is dominantly of reversed polarity with two normal events (Fig. 1b). Using this polarity pattern and mammalian biochronology, the Inchasi beds and its contained fauna correlate to the late Gilbert and early Gauss chrons with an age range of about 4.0 to 3.3 myr (MacFadden et al. 1993). A minimum of 11 species of middle Pliocene mammals were reported in that study. Since the work published in MacFadden et al. (1993), Anaya and associates have greatly added to the number of specimens collected from Inchasi and revealed that two new species are contained in that fauna, as are described with the entire fauna below. The age of the Inchasi fauna with regard to the South American land mammal ages is within the problematic Montehermosan/ Chapadmalalan interval (see discussion below).

METHODS AND ABBREVIATIONS

All specimens from Inchasi described in this report are conserved in the Departamento de Paleontología, Museo Nacional de Historia Natural, La Paz (Cota Cota), Bolivia.

Although we were able to assign most of the material (except for some postcranial remains) to genus with reference to previous descriptions from either the classic material from Argentina or Bolivia, for several taxa we were unable to assign material to a particular genus. This resulted from either or both of the following situations: (1) our material was too poorly preserved for adequate characterization of diagnostic characters; or (2) the particular taxon originally described from Argentina consisted of several similar, relatively poorly characterized species *nomina*. In addition to our new descriptions, another taxon described below (*Chapalmatherium* cf. *saavedrai*) is almost certainly a new species, but the available sample is too fragmentary for a formal taxonomic description.

All measurements are presented in millimeters (mm) and were made using calipers. Dental terminology follows the convention of upper case for upper teeth (i.e. I, C, P, M) and lower case for lower teeth (i.e. i, c, p, m). The following abbreviations are used in the text:

@; measurement approximate (usually because of fragmentary specimen).
CF/cf; a caniniform tooth (upper/lower) of uncertain position and homology relative to eutherian canines.
GB; Vertebrate Paleontology collection, Servicio Geológico de Bolivia, now housed as part of the MNHN-Bol-V collection.
L; left side.
MF/mf; a molariform tooth (upper/lower) of uncertain position and homology relative to eutherian premolars and molars.
MNHN-Bol-V; Vertebrate Paleontology collection, Museo Nacional de Historia Natural, Bolivia,
R; right side.

Taxonomic nomenclature for higher categories follows Simpson (1945) and Pascual (1967), although with some minor revisions proposed by Mones (1994).

SYSTEMATIC PALEONTOLOGY

Class Mammalia Linnaeus, 1758
Order Edentata Cuvier, 1798
Infraorder Pilosa Flower, 1883
†Family Megatheridae, Owen, 1843
†Megatheriinae, indeterminate
Figure 2

Material.--MNHN-Bol-V 003354, R calcaneum.

Geographic and stratigraphic location.--350 m west of Communidad Inchasi, 17 m above the base of measured section 3B.

Description.--This large, robust calcaneum has a length of 240 mm. Dorsally, it contains a robust tuber calcis with rough surface for tendinous and muscular attachments (Fig. 2). The articular surface with the astragalus contains a

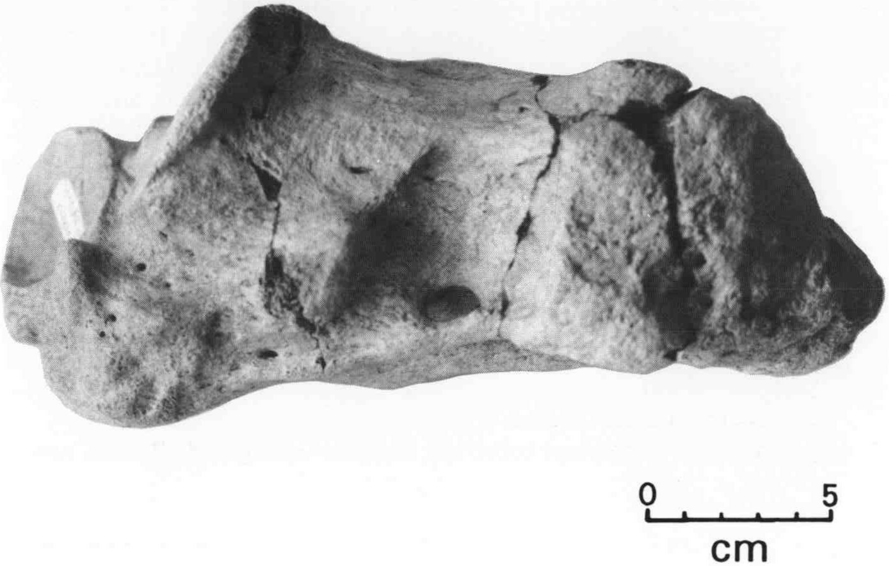

Figure 2. Medial view of right calcaneum of Megatheriinae, indeterminate, MNHN-Bol-V 003354.

lateral sustentacular facet with maximum dimension of 67 mm and a medial, convex ectal facet with a maximum dimension of 82 mm; these are distinctly separated by a sulcus talis. The sustentacular facet of the calcaneum forms an oblique angle with the cuboid articular surface. The main longitudinal sulcus in the center of the ventral part of the calcaneal shaft is wide and contains vascular foramina within its deeper part.

Discussion.--With the exception of Hoffstetter (1986; also see Marshall et al. 1983), who mentioned the presence of a possible ancestor (otherwise unspecified) of *Megatherium* in the Pliocene of Bolivia, the specimen from Inchasi is the first description of a pre-Pleistocene record of this subfamily in this country. Based on our comparisons with the large collection of megatheriines from Tarija in the MNHN-Bol, although of smaller size, the overall morphology and relative proportions of the calcaneum from Inchasi make it distinctly referable to Megatheriinae. However, without further, more diagnostic material, a more precise taxonomic allocation cannot be made at present. The occurrence from Inchasi extends the range of megatheres in Bolivia back into the middle Pliocene.

†Family Mylodontidae Ameghino, 1889
†Subfamily Mylodontinae Gill, 1872
†Genus *Glossotheridium* Kraglievich, 1934
†*Glossotheridium chapadmalense* (Kraglievich), 1925

Figures 3-5, Table 1

Material.--MNHN-Bol V 003358, partial mandible with Rcf, Rmf1-mf3, Lmf1-mf3; MNHN-Bol V 003359, L partial juvenile ramus with cf, mf1-mf3 (Fig. 5); MNHN-Bol V 003371; mandible with Rcf, mf3, Lcf, Lmf1-mf3 (Figs. 3-4).

Geographic and stratigraphic location.--750 m east and 1200 m southwest of Communidad Inchasi; stratigraphic position 56 m and 18 m, respectively, in measured sections 2 and 4.

Description.--The mandibles are laterally (i.e. labiolingually) compressed and have heavily fused symphyses (Fig. 3). The mandible is deepest ventral to mf3. The symphysial region extends anterior to the cf. The anterolingual part of the symphysis is relatively wide and the anteroventral region is spatulate. The dorsal surface of the symphysis exhibits rugose bone containing small pits. The anteroventral surface of the symphysis has a very well-developed convex crest in the sagittal plane of the chin which becomes less prominent as it approaches the dorsal surface. The mental foramina are large and well-developed, and one each is located on the right and left sides of a well-developed ventral sagittal ridge of the symphysis. In ventral view the anterior part of the mandible is very thin and forms a thin crest extending posteriorly to below the mf1.

The teeth are hypselodont with a thick, central pulp cavity surrounded by relatively thick dentine flanked by thinner orthodentine. The caniniforms are oval to elliptical in cross-section and separated from the mf1 by a small diastema with an anteroposterior length of about 5 mm. In MNHN-Bol-V 003358 (not illustrated) the cf is significantly more robust than in MNHN-Bol-V 003371. The cfs have two distinct wear surfaces forming an acute angle (Fig. 4). The cfs lie labially relative to the line of molariforms. In occlusal view all of the teeth contain a large central pulp cavity surrounded by a thick cap of dentine and thinner cap of orthodentine. Representative lower dental measurements are given in Table 1. The mf1 is triangular in cross-section; mf2 is trapezoidal in cross-section with the longitudinal axis aligned obliquely with respect to the mf1. The mf3 has a parallelogram or "figure-8" cross-section with a narrow constriction in the middle of the tooth that connects the larger anterior and smaller posterior lobes. MNHN-Bol V 003358 has a dentition with significantly greater wear than exhibited in MNHN-Bol V 003371; nevertheless they both present the same dental morphology. MNHN-Bol V 003359 (Fig. 5) represents a juvenile with essentially the same dental morphology, although at an earlier wear stage than that exhibited in the two adult specimens. The principal difference in the juvenile is the orientation of the teeth in the jaw; in medial view (Fig. 5B) the cf and mf1 are directed posterodorsally, whereas the mf2 and mf3 are directed anterodorsally.

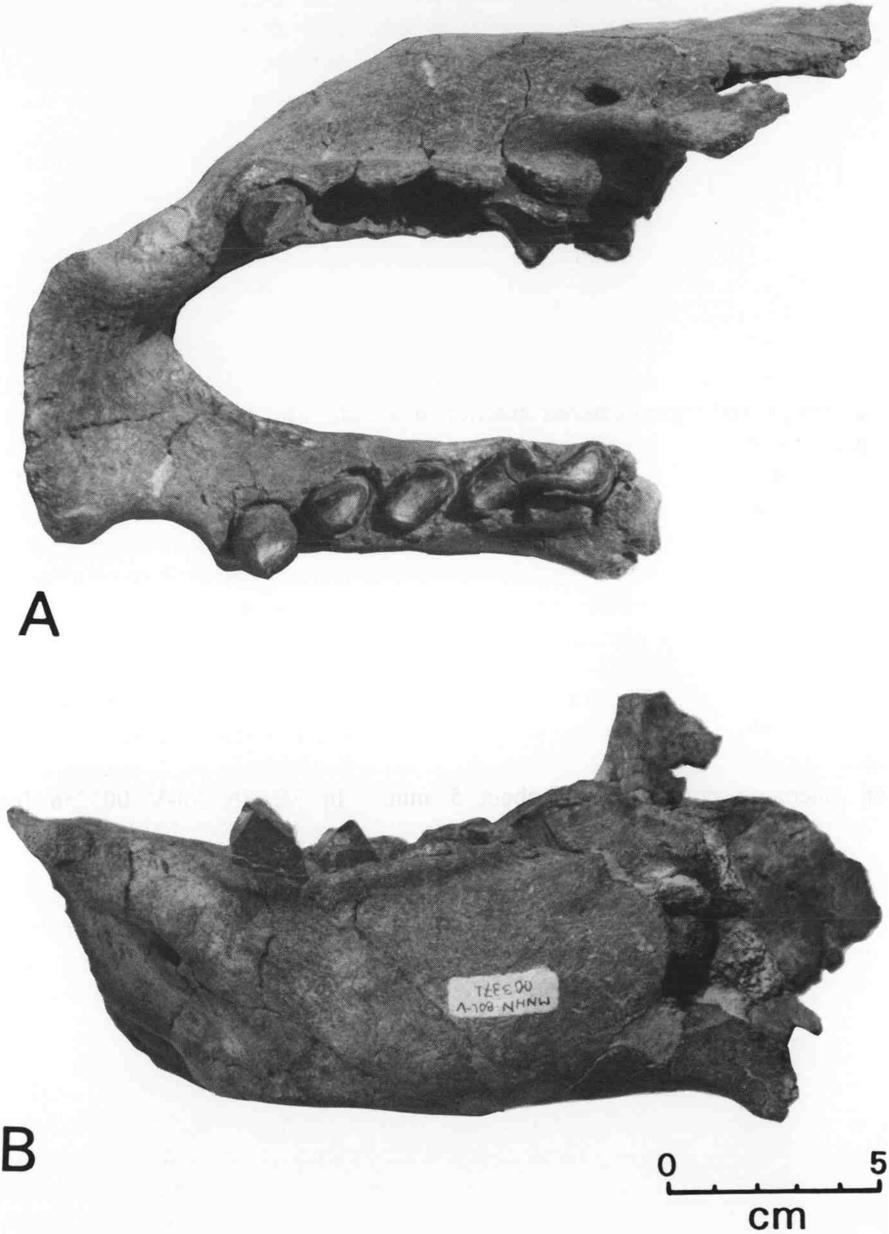

Figure 3. Occlusal (A) and left lateral (b) views of mandible of *Glossotheridium chapadmalense*, MNHN-Bol-V 003371.

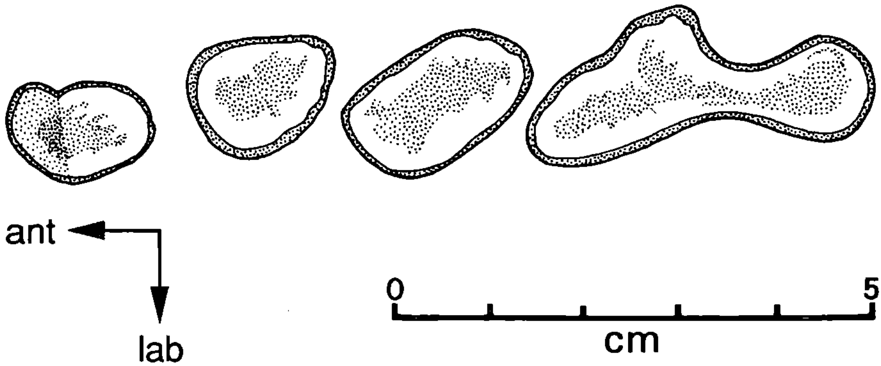

Figure 4. Occlusal view of left lower dentition (cf, mf1-mf3) of *Glossotheridium chapadmalense*, MNHN-Bol-V 003371. Abbreviations: ant, anterior; lab, labial.

Table 1. Dental measurements (mm) for mandibles of *Glossotheridium chapadmalense* (Kraglievich), 1925 from Inchasi, Pliocene of Bolivia.

Specimen	cf1		mf1		mf2		mf3	
Number	AP	T	AP	T	AP	T	AP	T
MNHN-Bol-V 003359	8.0	5.3	7.4	5.9	5.6	8.9	13.2	9.0
MNHN-Bol-V 003371	14.4	10.5	13.0	9.1	18.5	11.4	33.0	16.3

AP; anteroposterior length
cf; caniniform tooth
mf; molarifrom tooth
T; transverse width

Discussion.--Two Pliocene genera of closely related mylodont sloths, i.e. *Glossotherium* Owen, 1840 (*sensu* Simpson 1945), and *Glossotheridium* Kraglievich 1934, have been described in the literature. Some authors (e.g. Simpson 1945) consider *Glossotheridium* to be a junior synonym of *Glossotherium*, whereas others (e.g. Pascual 1967) consider the two genera to be distinct. We follow Pascual (1967) and relative to *Glossotherium*, *Glossotheridium* is smaller, has a narrower and less robust skull, and has a smaller caniniform. Both of these genera are characterized by having a bilobate posterior-most molariform (mf3),

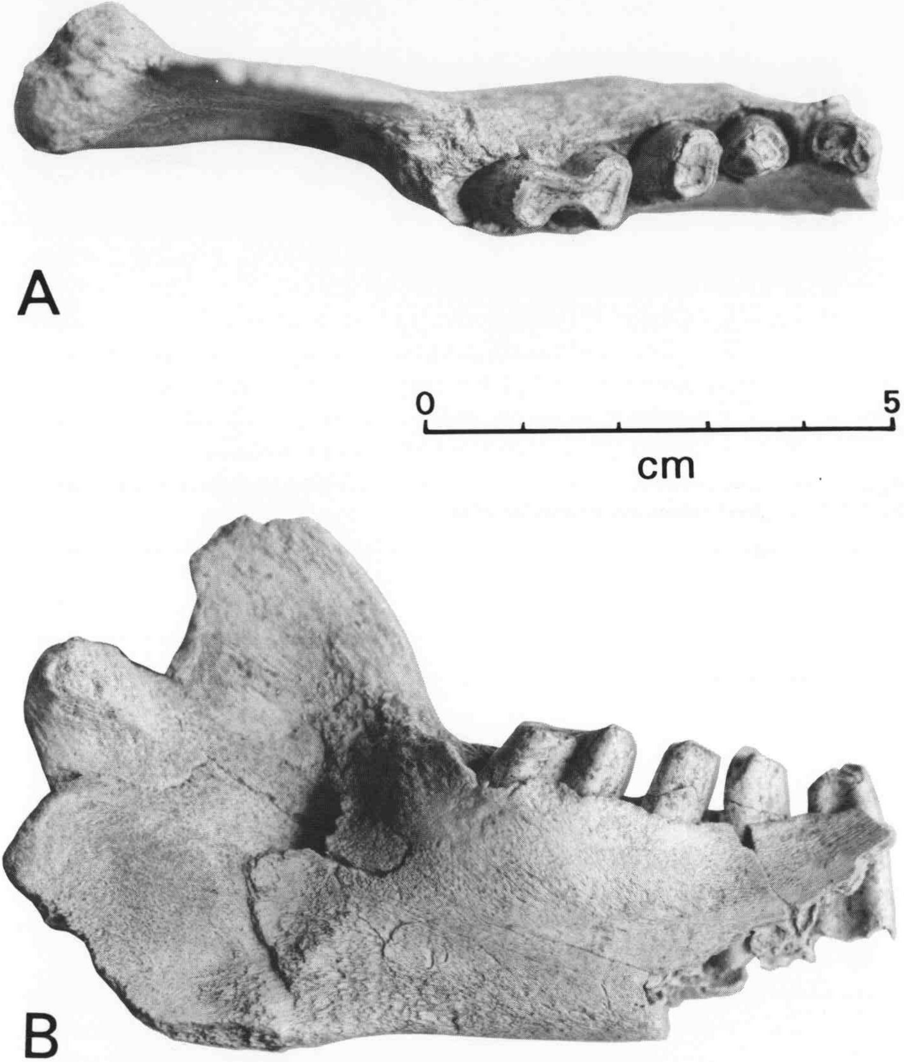

Figure 5. Occlusal (A) and medial (B) views of left mandible of juvenile specimen of *Glossotheridium chapadmalense*, MNHN-Bol-V 003359.

a character clearly developed in the Inchasi specimens described above. The available dental characters and general size preserved in the Inchasi mylodont justify allocation to the genus *Glossotheridium* and common species *G. chapadmalense* known from Argentina.

The genus *Glossotheridium* Kraglievich, 1934 was originally described from the Pliocene of Argentina. Hoffstetter (1986) mentioned the presence of *Glossotheridium* from Pliocene sediments of the northern altiplano of Bolivia. The only previously collected Bolivian material of *Glossotheridium* available in the GEOBOL collection (GB-078) was collected from Viscachani (some 10 km to the south of Ayo Ayo) by Villarroel in 1973. This specimen preserves the anterior region of the skull, but lacks the dentition. As such, it does not allow a detailed description of the important dental morphology of this genus. Its primary significance is to document the occurrence of this genus at another Pliocene site in Bolivia.

The original description of the type species of *Glossotheridium*, i. e. "*Eumylodon chapadmalensis*" Kraglievich (1925) is known from an associated skull and mandible. The illustrations from that description allow an identification of the most important characters of the dentition and mandible of the Bolivian specimens. The angular orientation, slight wear, and small size of the teeth in MNHN-Bol V 003359 clearly are evidence of juvenile morphology. However, the less robust caniniform of MNHN-Bol V 003371 relative to MNHN-Bol V 003358 could either be a result of ontogenetic differences in two adult specimens of different age or could be an example of sexual dimorphism. Because of the small sample from Inchasi, it is not possible to distinguish between these two possibilities for the adult specimens; nevertheless, if more specimens are collected from this or similar-aged localities in the future, perhaps this difference in dental morphology can be better explained.

†Mylodontinae, indeterminate
Figures 6, 7

Material.--MNHN-Bol-V 00365, R central and distal portion of a femur (Fig. 6) and MNHN-Bol-V 003355, distal (ungual) phalanx (Fig. 7).

Geographic and stratigraphic location.--Respectively, 1100 m north and 350 m west of Communidad Inchasi; 50 m above the base of measured section 1 and 17 m above the base of measured section 3B.

Description.--MNHN-Bol-V 003365 represents most of a R femur, including the central shaft and distal articular surface (Fig. 6). The shaft is anteroposteriorly compressed and bowed laterally so that it is concave medially. Distally, there are two condyles, a larger one medially and a smaller one laterally. There is a well-developed intercondylar fossa in the middle of the two distal condyles.

The proximal region of the ungual phalanx, MNHN-V-Bol 003355, is divided into two concave articular surfaces, one positioned laterally and the other medially. Ventrally there are two medium-sized foramina. The medial and distal portions of the phalanx are laterally compressed and claw-shaped (Fig. 7). Along the dorsal surface there is a groove running from the distal tip to midway up the claw.

Discussion.--Hoffstetter et al. (1971; 1972) first reported the presence of small mylodontines of an undescribed genus from Ayo Ayo, Viscachani, and Pomata. Later, Hoffstetter (1986) referred the mylodontine to an unspecified taxon different

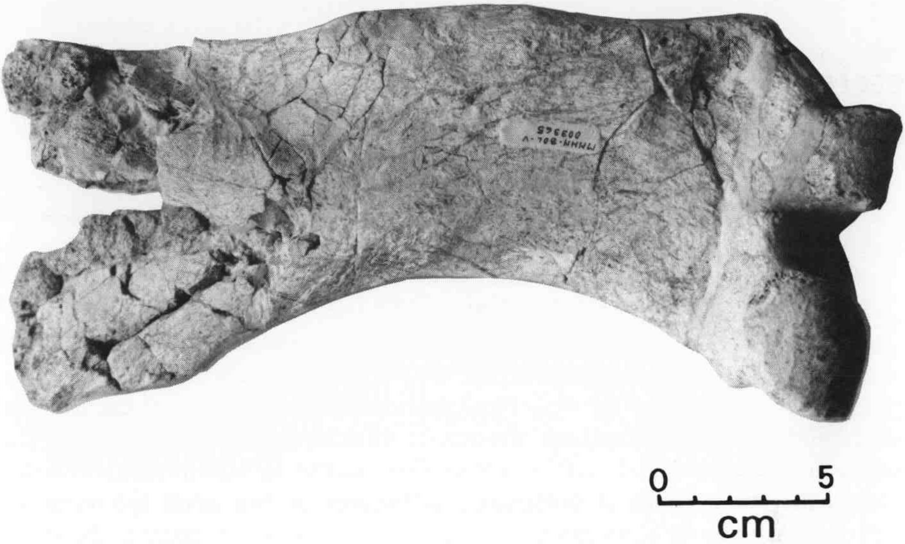

Figure 6. Posterior view of right femur of Mylodontinae, indeterminate, MNHN-Bol-V 003365.

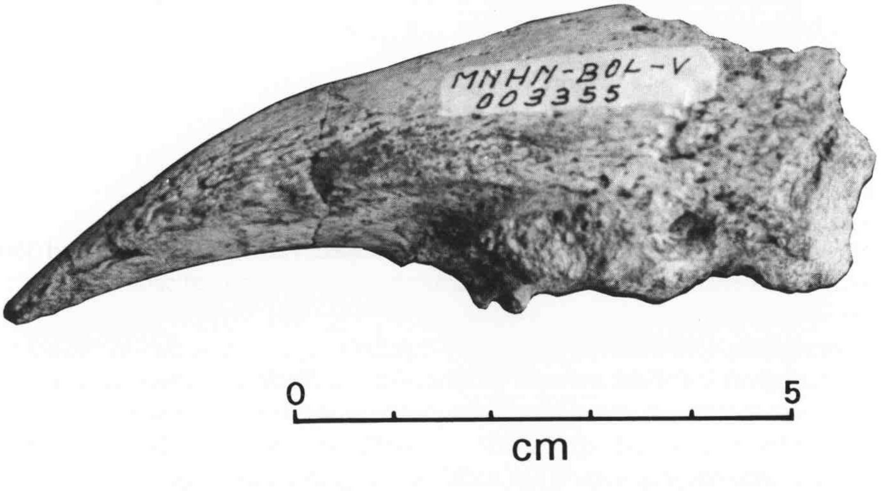

Figure 7. Lateral view of ungual phalanx of Mylodontinae, indeterminate, MNHN-Bol-V 003355.

from *Glossotheridium*. We refer these specimens to the Mylodontinae because they are relatively small and gracile and not Megatheriinae which would be larger and more robust. The specimens from Inchasi, as well as material contained in the GEOBOL collections from other Pliocene localities in Bolivia, are insufficient to make a more specific taxonomic identification, or to describe a new genus.

†Subfamily Scelidotheriinae Ameghino, 1909
†Genus *Proscelidodon* Bordas, 1935
†*Proscelidodon patrius* (Ameghino), 1888
Figures 8, 9

Material.--MNHN-Bol-V 003353, skull with fragmentary R and L molariforms MF1-MF5.

Geographic and stratigraphic location.--650 m northwest of Communidad Inchasi, 13 m above base of measured section 3A.

Description.--In dorsal view, the skull is of medium size and is laterally compressed from the anterior to medial regions; the posterior region forming the cranium is expanded (Fig. 8). The premaxilla is small and anteroventrally separated by two angular points. The nasals are fragmentary. In lateral view the frontals are slightly convex, and form an undulating surface with the parietal along the dorsal part of the skull. In dorsal view, the sagittal crest is weakly developed and the occipital crests are convex. The occipital condyles are well-developed. In ventral view the palatal suture is fused incompletely and there is a deep trough in the center of the palate. The basisphenoid, basioccipital, auditory, and right exoccipital regions are partially preserved. In the orbital region the skull is constricted and concave with respect to the zygomatic arch. In lateral view the zygomatic arches are positioned relatively high on the skull. The jugal is small, the lacrimal does not contact the nasal, and the pterygoids form obtuse angles with the posterior zygomatic processes. The auditory region is open and does not form a bulla. Posterior to the orbit the squamosal surrounds the posterior zygomatic arch, which is broken on both sides of this specimen.

Except for R MF4, the molariforms are fragmentary and broken at the level of the alveolar margin (Fig. 8). The broken cross-sections of the teeth show characteristic pulp, thick dentine, and a thinner, external rim of orthodentine. In cross-section the MF1 is elliptical, and MF2-MF5 are triangular with shallow lingual folds (Fig. 9).

Discussion.--The genus *Proscelidodon* was proposed by Bordas (1935) who used *Scelidotherium patrium* Ameghino, 1888 as the type species. The original material consists of a skull and left mandible, so the genus *Proscelidodon* is relatively well characterized by a suite of diagnostic characters, including the following: relative to *Scelidodon*, about one-third smaller; relative to Scelidotherium, anterior portion of palate and frontal-parietal regions broader; zygomatic arch more open, less flattened, and more dorsally positioned; and skull less laterally compressed.

P. patrius is reported from Argentina in the typical Monte Hermoso and Chapadmalal formations of Pliocene age (Pascual 1967). The presence of *P. patrius* from Inchasi is the first reported occurrence of this taxon from Bolivia.

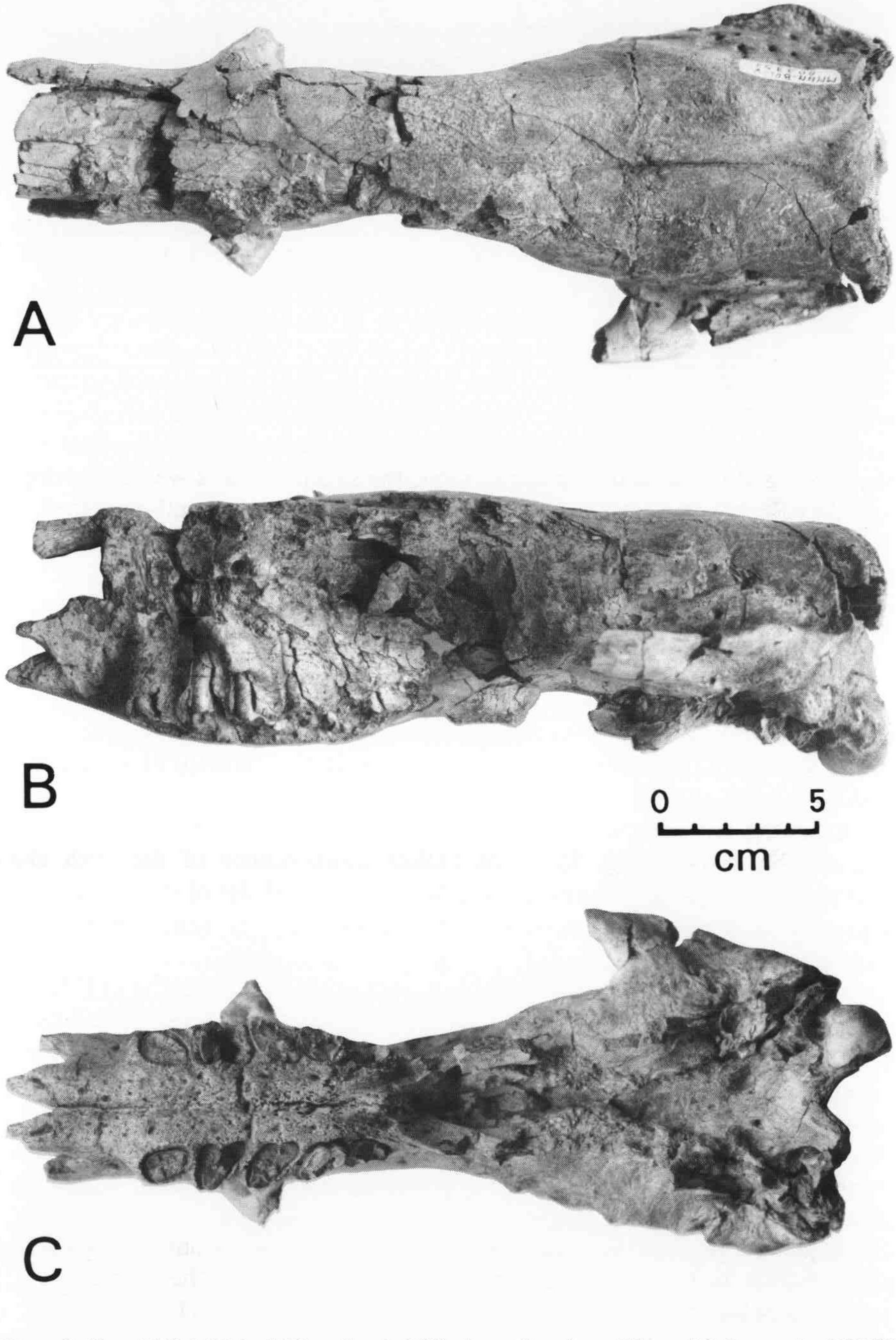

Figure 8. Dorsal (A), left lateral (B), and ventral (C) views of cranium of *Proscelidodon patrius*, MNHN-Bol-V 003353.

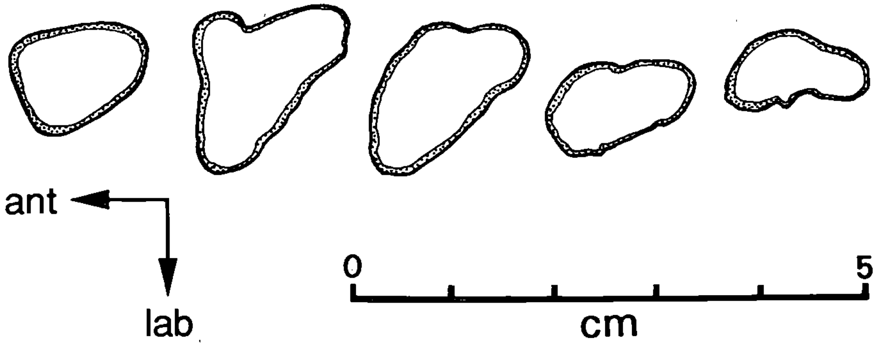

Figure 9. Occlusal view of right dentition (MF1-MF5, breakage below occlusal surface reconstructed) of *Proscelidodon patrius*, MNHN-Bol-V 003353. Abbreviations: ant, anterior; lab, labial.

Infraorder Cingulata Illiger, 1811
†Family Pampatheriidae Paula Couto 1954
†Genus *Plaina* Castellanos 1937
†*Plaina intermedia* (Ameghino), 1888

Figures 10-12

Material.--MNHN-Bol-V 003418, complete skull and mandible with anterior region of vertebral column, L scapula, most of L forelimb, fragment of R forelimb (Fig. 10); MNHN-Bol-V 003361 (Fig. 11), L mandibular fragment with partial mf5, mf 6-8, partial mf9; MNHN-Bol-V 003362, portion of carapace with articulated osteoderms; MNHN-Bol-V 003363 (Fig. 12a), rows of associated and partially articulated mobile osteoderms; MNHN-Bol-V 003364 (Fig. 12b), associated and partially articulated osteoderms.

Geographic and stratigraphic location.--MNHN-Bol-V 003418, 003362, 1100 m north of Communidad Inchasi, section 1, Unit A; MNHN-Bol-V 003361, 003363, 003364, 350 m west of Communidad Inchasi, section 3B, Unit A.

Description.--As represented in MNHN-Bol-V 003418 the skull is anteroposteriorly elongated (Fig. 10) and laterally compressed. The dorsal region of the skull was covered with oval to quadrate osteoderms during life, one of which remains attached in this specimen. The premaxilla is small, and although the sutures are difficult to distinguish in this region, this bone seems to house the CF1 (as represented by an alveolus) and CF2. The maxilla is relatively large and contains the CF3 and molariform teeth (MF1-MF5; the MF6, which presumably is present, is medial to, and hidden by, the ascending mandibular ramus). The nasal is relatively elongated. The anterior portion of the nasal is situated dorsal to the premaxilla and together they form the nasal opening. In the orbital region, the lacrimal is small, the jugal is fragmentary, and the frontal contains a prominent postorbital process. Dorsal to the anterior part of MF4 there is a well-developed infraorbital foramen. On the parietal, the sagittal crest is weakly developed and in

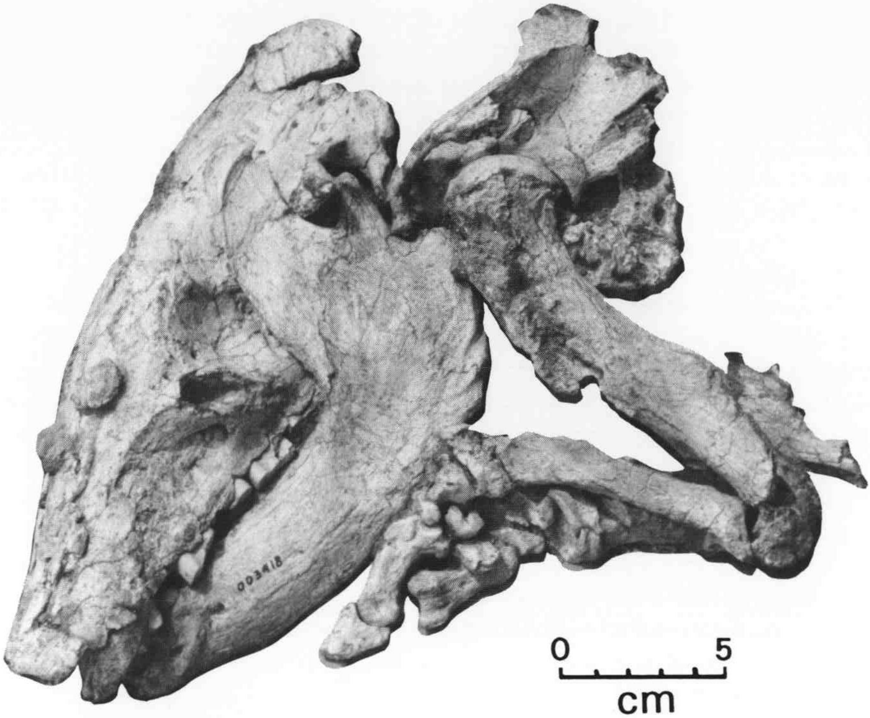

Figure 10. Left lateral view of cranium, mandible, anterior part of vertebral column, partial scapula, and left forelimb of *Plaina intermedia*, MNHN-Bol-V 003418.

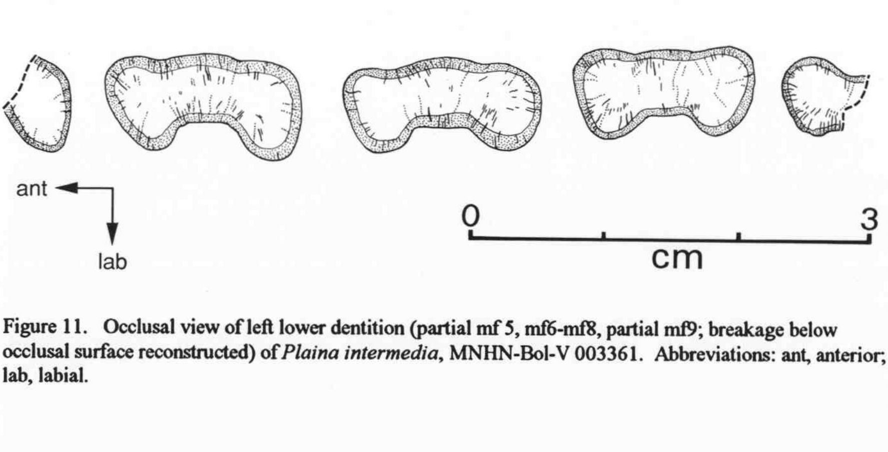

Figure 11. Occlusal view of left lower dentition (partial mf 5, mf6-mf8, partial mf9; breakage below occlusal surface reconstructed) of *Plaina intermedia*, MNHN-Bol-V 003361. Abbreviations: ant, anterior; lab, labial.

the ventral region of this bone (near the occipital crest) there are about nine small foramina on the left side (the right side is not prepared). The occipital crest is relatively thick and better-developed than the sagittal crest. The mandible consists of two well-fused rami. The left ascending ramus is complete and forms an angle of about 90° with respect to the horizontal portion of the ramus. The posteroventral gonion is rugose and forms a relatively shallow angle. Dorsal to the gonion there is a notch below the condyle. Dorsal to the condyle there is a well-developed sigmoid notch and a very high and delicate ascending coronoid process which extends dorsal to the upper tooth row.

In the upper and lower dentitions it is impossible to distinguish the exact tooth positions and homologies; therefore we refer to the teeth as caniniform if they are simple cones and molariforms if they are bilobate. In the upper dentition (not illustrated) there are positions for three anterior caniniforms, of which two are preserved, followed by positions for six molariforms, of which 5 are preserved. The preserved caniniforms are conical with CF2 being slightly smaller than CF3. The molariforms are bilobate with a larger, better-developed labial groove than the corresponding lingual structure, as is characteristic for this family.

Despite the fragmentary preservation of MNHN-Bol-V 003361, the general morphology of the lower dentition is preserved (Fig. 11). The cheek teeth are hypselodont with medium to high crowns and open roots. The internal dentine is surrounded by moderately thick external orthodentine. Although mf2-mf6 are only partially preserved and broken off at the top of the roots, the bilobulate occlusal surfaces (reniform, *sensu* Edmund 1985a; 1985b) are preserved in mf3-mf5. The teeth are strongly compressed labiolingually, with the long axis anteroposteriorly. There are moderately developed anterior and posterior lobes separated in each tooth by a large labial groove. As is characteristic for pampatheres (Edmund 1985b), and in addition to the characters described above, portions of the occlusal surface show transverse striations (Fig. 11), indicating lateral motion of the jaw during mastication.

With respect to the postcranial skeleton, the anterior portion of the vertebral column, scapula, and most of the forelimb are preserved in articulation (Fig. 10). In the proximal (anteromost) scapula there is a very large, recurved acromian process. As also described by Edmund (1985a 1985b), at least two, and perhaps three, cervical vertebrae are fused posterior to the atlas. The proximal articular surface of the humerus is rounded, smooth, and large. The distal half of the humeral shaft bears a well-developed deltoid crest. The radius and ulnae are separate bones. Many of the carpal and metacarpal bones are preserved; the phalanges are not preserved in this specimen.

The osteoderms of the scapular and pelvic bucklers of the carapace vary in outline from hexagonal to square and are of different sizes (Fig. 12). The external surface of these osteoderms are ornamented along the margins with numerous small fossettes, and the central region is relatively smooth. In the dorso-central

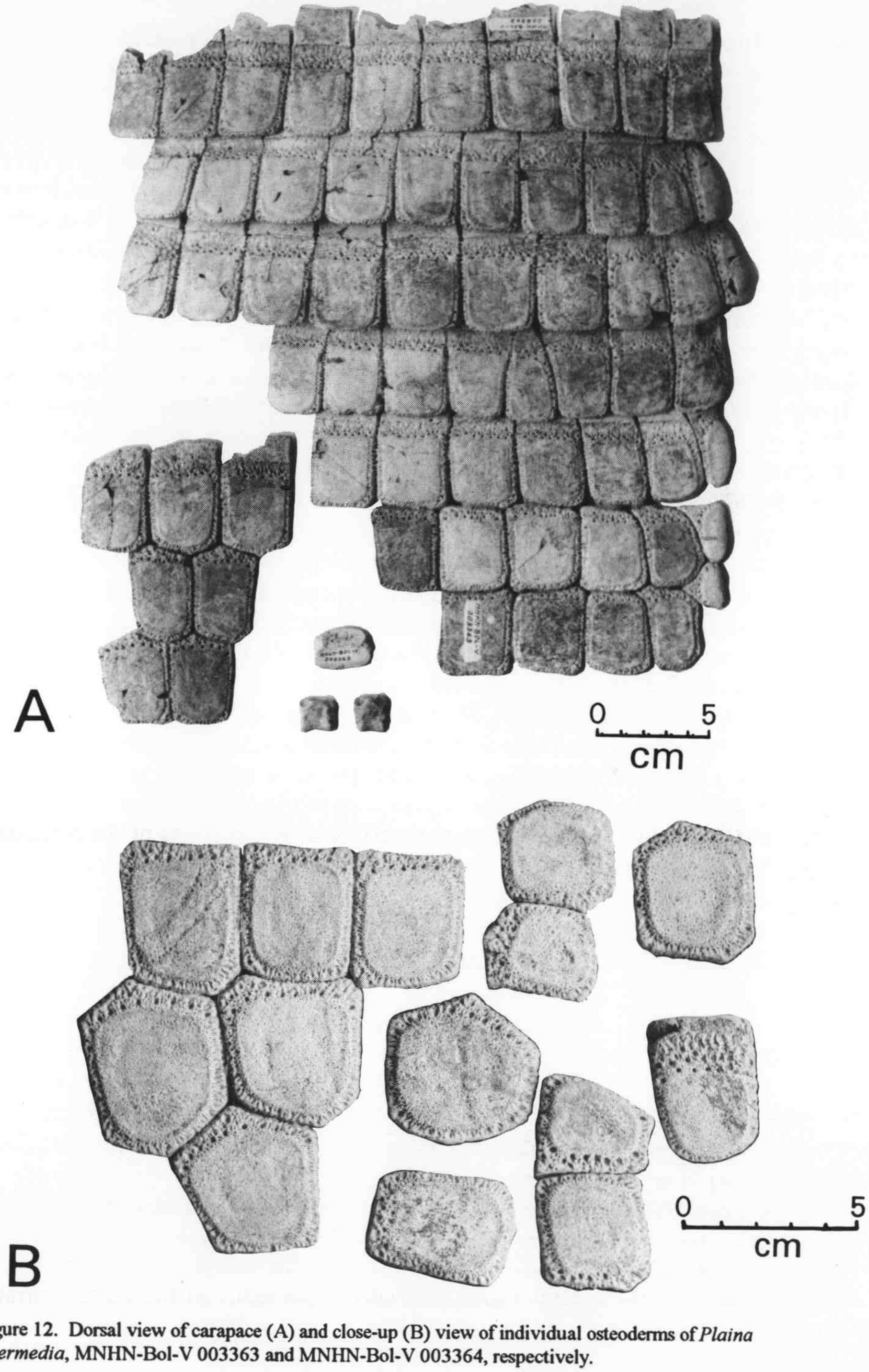

Figure 12. Dorsal view of carapace (A) and close-up (B) view of individual osteoderms of *Plaina intermedia*, MNHN-Bol-V 003363 and MNHN-Bol-V 003364, respectively.

region of the carapace there are movable bands composed of large, elongated osteoderms. The anterior one-third of each osteoderm has a raised region of imbrication with the adjoining osteoderm of the postero-adjacent band. Posterior to the raised region there is a slight transverse, concave depression with a line of small fossettes. The remaining posterior portion (about half the area of each osteoderm) consists of a small rugose periphery and a relatively large, internal part which is relatively smooth except for very tiny pitting on the surface.

Discussion.--The genus *Plaina* was originally described by Castellanos (1937) based on specimens collected from the Pliocene of Argentina. Edmund (1985b, p. 92) believes that: "The genus *Plaina* is based on inadequate material and will probably be relegated to synonomy." Until this is done, however, we have no choice but to rely upon this *nomen* for the most appropriate taxonomic assignment for the material from Inchasi. In Bolivia, the presence of *Plaina* was previously reported by Hoffstetter et al. (1971) and Hoffstetter (1986) from Pliocene sediments of the Umala Formation from Ayo Ayo and Viscachani.

Plaina and the other genera of the extinct armadillo family Pampatheriidae are characterized by large size, well developed and anteroposteriorly broad ascending mandibular ramus, teeth open-rooted (hypselodont), dental formula 9/9 with the anterior teeth conical (caniniform here) and posterior teeth bilobate or reniform (molariform here), occlusal surface of molariforms have transverse striations, presence of fused cervical vertebrae, and carapace with three imbricating bands of relatively large osteoderms (Edmund 1985b).

Based on the dental, postcranial, and dermal armor morphology described above, we are confident that the sample from Inchasi is clearly referable to *Plaina*, as this genus is presently recognized. Although we were unable to make direct comparisons with specimens from Argentina, we follow Paula Couto (1979) who indicates that this is a monotypic genus consisting of the species *P. intermedia* (Ameghino), 1888. Thus we are comparing the sample from Inchasi with the only valid, existing species within *Plaina*.

†Family Glyptodontidae Burmeister, 1879
†Genus *Plohophorus* Ameghino, 1887
†*Plohophorus* sp.
Figures 13-14

Material.--MNHN-Bol-V 003369, dorsal and lateral portion of a carapace.

Geographic and stratigraphic location.--1200 m southwest of Communidad Inchasi, about 18 m above the base of measured section 4.

Description.--The articulated osteoderms are of moderate thickness and either polygonal or hexagonal in shape (Figs. 13-14). The internal surfaces of these osteoderms are rugose with medium-sized fossettes distributed irregularly. In the central osteoderm the external surface is also rough, or rugose. Each of these

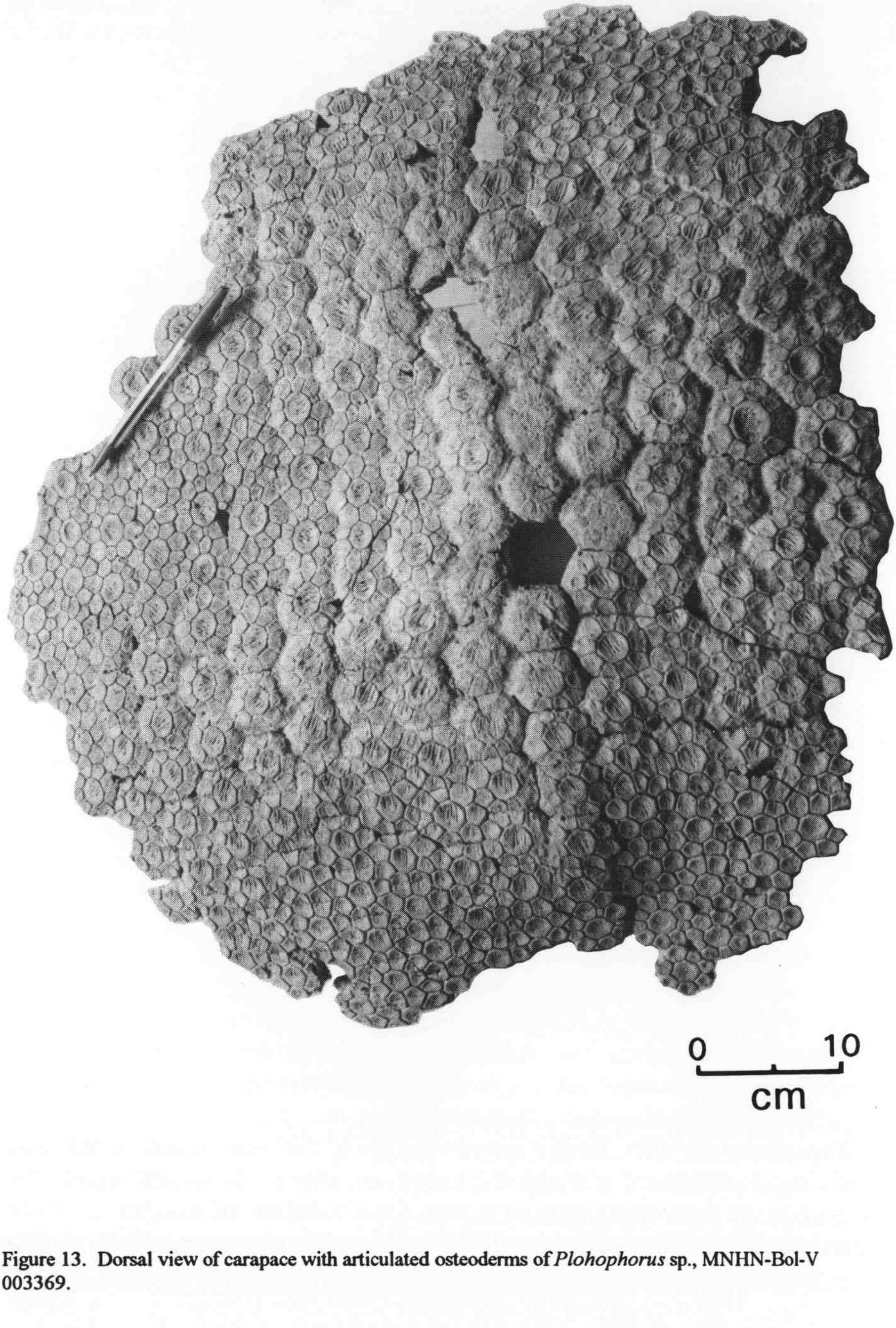

Figure 13. Dorsal view of carapace with articulated osteoderms of *Plohophorus* sp., MNHN-Bol-V 003369.

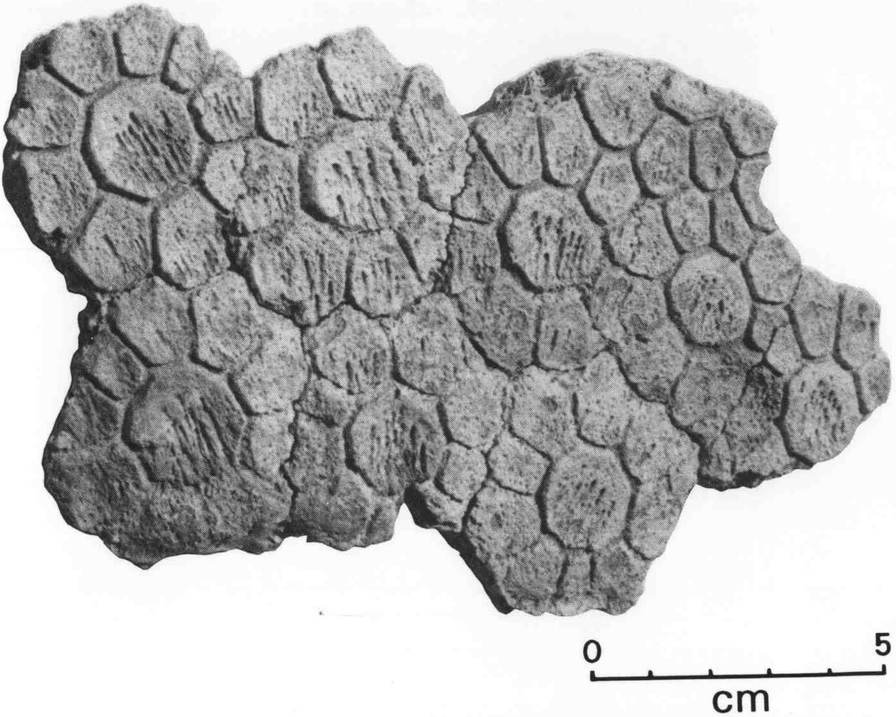

Figure 14. Close-up, dorsal view of articulated central osteoderms of *Plohophorus* sp., MNHN-Bol V 003369.

central osteoderms characteristically consists of a central, concave hexagon flanked by 9-10 surrounding smaller (approximately half the diameter of the central hexagon) sub-elements of either hexagonal, pentagonal, or irregular outline. The lateral osteoderms are smaller, more simple in design, and generally consist of a single, concave element with rugose surface of either pentagonal, hexagonal, or irregular shape. The rugosities are in the form of small fossettes or parallel lines. Slightly more than half of the portion of the preserved carapace consists of the central, more complex osteoderms and the remainder consists of the simpler lateral osteoderms. A notable characteristic of this carapace is that the boundary between the two types of osteoderms is relatively indistinct and undulates around the perimeter of central osteoderms.

Discussion.--As with almost all of the species of *Plohophorus* Ameghino (1887), our knowledge of this genus is based primarily on the caudal armor. An exception is *P. figuratus* which is known from carapace osteoderms from the Pliocene of Monte Hermoso in Argentina. As such, our knowledge of the morphology and specific differences within *Plohoporus* is quite incomplete. The relatively complete, although partial, carapace from Inchasi allows a better understanding of the morphological variation of individual osteoderms. We are able to assign this specimen to *Plohoporus* based on the presence of highly punctate plates of moderate thickness and of a general size similar to specimens assigned to this genus from Argentina.

There are numerous other specimens of osteoderms and fragmentary carapaces contained in the GB and MHNH-Bol collections attributable to *Plohophorus* from the Pliocene localities of Ayo Ayo, Viscachani, and Pomata on the altiplano near La Paz (also see Hoffstetter 1986). Although of generally similar morphology to the Inchasi specimen, the lack of relevant diagnostic material (i.e. caudal armor) and poor characterization of isolated osteoderms or partial carapaces from the various species of *Plohophorus* from Argentina prevents a more specific assignment. As such, this is the first description of portions of the carapace of this genus from the Pliocene of Bolivia. In Argentina, *Plohophorus* has a range from the middle to late Pliocene and it is characteristically found in Chapadmalalan-aged sediments (Pascual 1967). Given the available paleomagnetic correlations (MacFadden et al. 1993), the Inchasi occurrence is middle Pliocene in age.

†Genus *Paraglyptodon* Castellanos, 1932
†*Paraglyptodon* sp.
Figure 15

Material.--MNHN-Bol-V 003366, 7 articulated carapace osteoderms and 2 caudal plates.

Geographic and stratigraphic location.--1100 m north of Communidad Inchasi, approximately 36 m above the base of measured section 1.

Description.--The carapace osteoderms are relatively thin and hexagonal (Fig. 15). Each of these osteoderms consist of a surface covered with numerous tiny fossettes and a central region delimited by a circular depression. The lateral portions of each of these plates are separated by 6-9 shallow grooves radiating to the periphery. The caudal osteoderms are pentagonal, relatively flat, and with a rough external surface.

Discussion.--Hoffstetter et al. (1972) and Hoffstetter (1986) described the presence of glyptodonts related to, but different from, *Plohophorops* from north of Callapa and Anchocalla on the Bolivian altiplano. These forms, however, were not assigned to a particular glyptodont genus. With the material from Inchasi we are able to place on record the first-known occurrence of *Paraglyptodon* Castellanos (1932) from Bolivia based on the unique characters of this genus including: (1) size smaller than *Glyptodon*; (2) carapace osteoderms hexagonal; and (3) rugose osteoderms with large, well defined central figure. We are unable to assign these new specimens to either an existing species from Argentina, or to distinguish them as new. Given the paleomagnetic constraints for Inchasi, the Bolivian occurrence of *Paraglyptodon* sp. is middle Pliocene in age.

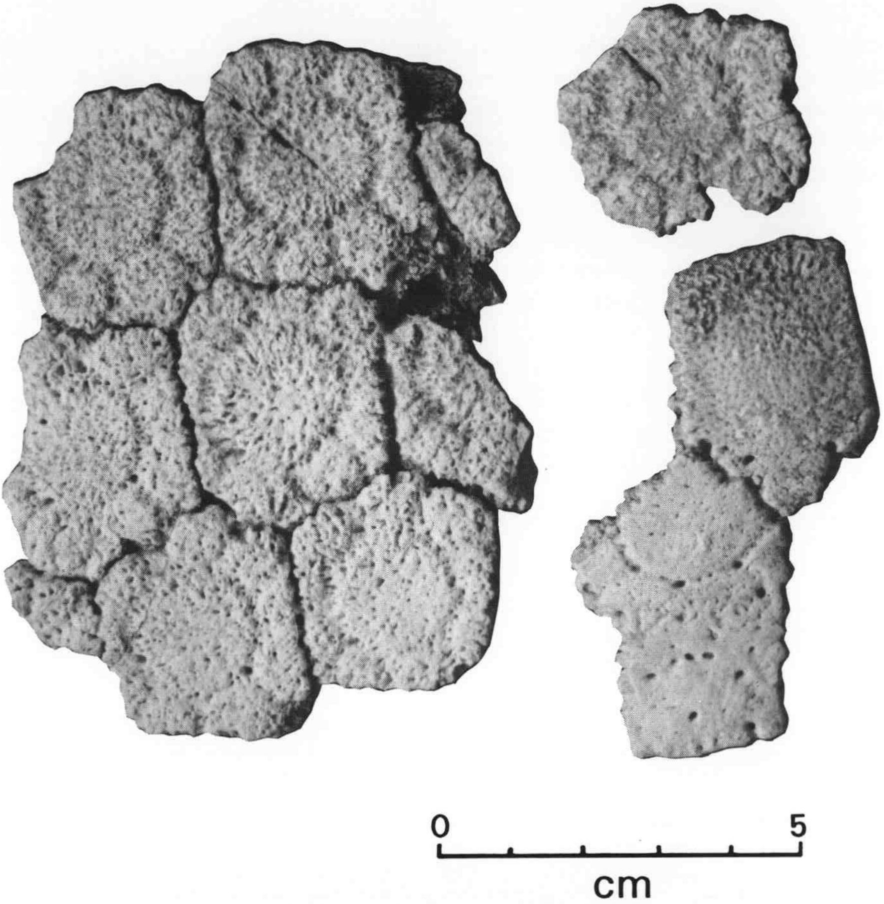

Figure 15. Articulated carapace osteoderms of *Paraglyptodon* sp., MNHN-Bol-V 003366.

Order Rodentia Bowdich, 1821
Suborder Caviomorpha Wood & Patterson, 1955
Family Caviidae Waterhouse, 1839
†Genus *Caviodon* Ameghino, 1885
†*Caviodon* sp.
Figure 16

Material.--MNHN-Bol-V 003367, fragmentary cheek teeth of uncertain position.

Geographic and stratigraphic location.--1100 m north of Communidad Inchasi, 59 m above the base of measured section 1.

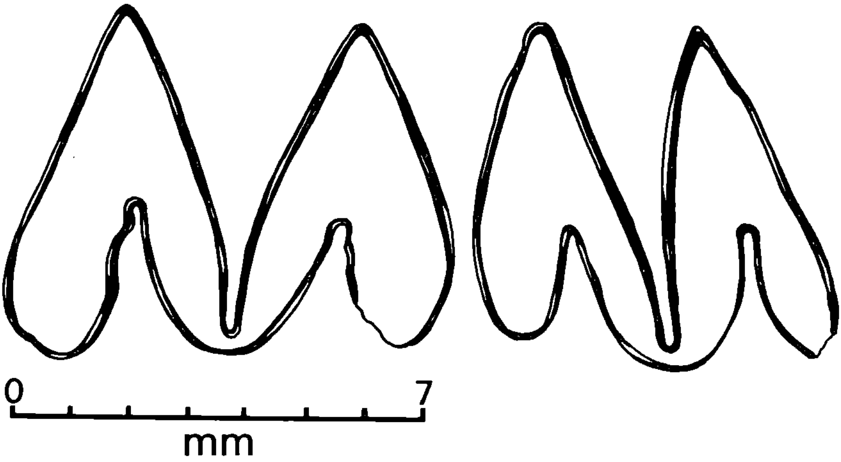

Figure 16. Occlusal view of cheek-tooth fragments (probably P4/p4, M1/m1, or M2/m2) of *Caviodon* sp., MNHN-Bol-V 003367.

Description.--These specimens have high-crowned, curved hypselodont teeth with open roots. Two of the teeth from Inchasi consist of a single prism. Another incomplete fragment consists of two small prisms. The better-preserved cheek teeth consist of two larger prisms forming an "M" shape (Fig. 16). The apices of each prism are anteroposteriorly compressed and are separated by a deep groove; each prism also contains a shallow groove, and there are three columns extending the height of the tooth. The crowns of all teeth are covered with enamel.

Discussion.--The genus *Caviodon* Ameghino (1885) was originally described from Argentina and is known to range from the middle to late Pliocene (Pascual 1967). Prior to this description, *Caviodon* had neither been reported in the literature nor was it present in any collections that we have examined from the Pliocene of Bolivia. Given the fragmentary nature of the available specimens from Inchasi, we cannot refer this sample to either an existing or new species, nor can we confidently identify the exact position of individual fragments within the toothrow. Following the illustrations in Pascual (1967) the two better-preserved specimens (Fig. 16) probably are either P4/p4, M1/m1, or M2/m2 (distinction between uppers and lowers are very difficult, if not impossible, in fragmentary specimens of this taxon). Despite the incomplete nature of the Inchasi specimens, they are confidently referred to *Caviodon* (rather that the closely related *Cardiomys*) because of the presence in the former genus of the very deep grooves (or, re-entrants) characterizing each lobe. The *Caviodon* sample from Inchasi is of similar size to representatives of this genus from Argentina (Pascual 1967). Given the paleomagnetic correlations for Inchasi (MacFadden et al. 1993), we assign the Bolivian occurrence of *Caviodon* sp. to the middle Pliocene.

Family Hydrochoeridae Gill, 1872
†Genus *Chapalmatherium* Ameghino, 1908
†*Chapalmatherium* cf. *saavedrai* Hoffstetter et al., 1984
Figure 17

Material.--MNHN-Bol-V 003368, incisor fragments, anterior prism of ?L m2, and fragmentary m3.

Geographic and stratigraphic location.--750 m east of Communidad Inchasi, about 56 m above base of measured section 2.

Description.--The lower portion of the anteromost part of an incisor (not illustrated here) shows diagnostic rodent-like enamel only on the anterior surface. The fragmentary cheek teeth consist of a portion of the anterior prism and a complete posterior prism which are separated by a deep groove (Fig. 17). The M3/m3? consists of fragments of isolated plates characteristically separated by cement. These teeth are relatively high-crowned. Although measurements are not possible because of the fragmentary nature of the specimens, general comparisons of the sample from Inchasi indicates that it is about 50% smaller than the previously described hypodigm of *Chapalmatherium saavedrai* from the Bolivian altiplano (Hoffstetter et al. 1984).

Discussion.--Ameghino (1908) originally proposed the genus *Chapalmatherium* from Pliocene sediments in Argentina. Hoffstetter et al. (1971) described the presence of this genus from Pliocene sediments of the Umala Formation at Ayo Ayo and Viscachani on the Bolivian altiplano south of La Paz. Hoffstetter et al. (1984) described the new species *C. saavedrai* based on a well-preserved lower ramus and corresponding dentition (GB 081). The diagnostic

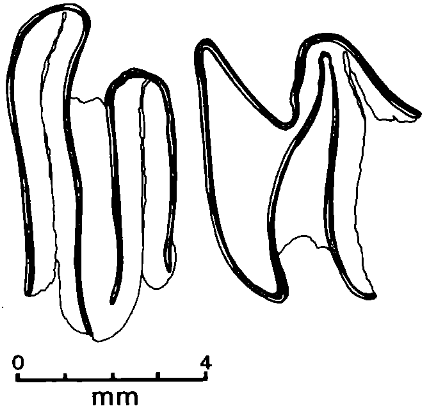

Figure 17. Occlusal view of cheek teeth of *Chapalmatherium* cf. *saavedrai*, MNHN-Bol-V 00338. Given the prism morphology, the specimen on the left is from a 3rd molar (upper/lower indeterminate); the specimen on the right is a more anterior tooth (P4/p4, M1/m1, or M2/m2).

generic and specific characters relate to the similar morphology of the enamel prisms. Despite the paucity of material from Inchasi and the difficulty in determining the exact position in the tooth row for individual fragments, we can confidently refer it to *Chapamaltherium* based on the presence of diagnostic characters, including: (1) cheek teeth (except M3/m3) consisting of triangular prisms with deep re-entrants surrounded by cement; and (2) the middle and posterior portions of M3/m3 consisting of a series of relatively flattened prisms alternating with vertical layers of cement. We note, however, that the sample from Inchasi is smaller than any of the species attributed to this genus from Argentina (Pascual 1967), and it is about 50% smaller than the hypodigm of *C. saavedrai* from Ayo Ayo and Viscachani (Hoffstetter et al. 1984). The Inchasi *Chapalmatherium* appears to be a new species, but the fragmentary material is insufficient upon which to formally describe it. Given the known range of this genus from Ayo Ayo-Viscachani and those of Argentina, this occurrence indicates a middle Pliocene age for Inchasi.

†Order Litopterna Ameghino, 1889
†Family Macraucheniidae Gill, 1872
†Genus *Promacrauchenia* Ameghino, 1904
†*Promacrauchenia* sp.
Figures 18-21, Tables 2, 3

Material.--MNHN-Bol-V 003351, L mandible with partial m2-m3 (Fig. 18a, b); MNHN-Bol-V 003352 (Fig. 18C, D; Fig. 19), partial ventral symphysis and R mandible with p2-m2; MNHN-Bol-V 003376, R mandibular fragment with m3 alveolus; MNHN-Bol-V 003372, R partial forearm (Fig. 20); MNHN-Bol-V 003374, partial R femur with shaft and distal articular surface (Fig. 21) and associated partial tibia with distal articular surface and shaft; MNHN-Bol-V 003377, partial tibia and fibula with distal articular surface; MNHN-Bol-V 003378, partial R tibia with proximal articular surface and fragments of distal articular surface.

Geographic and stratigraphic location.--The sample listed above was collected from two localities: 350 m west and 1200 m southwest of Communidad Inchasi, respectively, 17 m above base of measured section 3B and 18 m above base of measured section 4.

Description.--MNHN-Bol-V 003351 consists of fragmentary cheek teeth which are subhypsodont with a partial external cingulum located between the protolophid and metalophid (Fig. 18). The alveolus for m1 is double-rooted, only the posterior of which is preserved. In the better-preserved MNHN-Bol-V 003352 two mental foramina are present ventral to p3 and m1. The symphysial suture is well-fused, indicating an adult. The incisors and canine are not preserved, but their alveoli suggest teeth of moderate size relative to the cheek teeth. The lingual cingula are

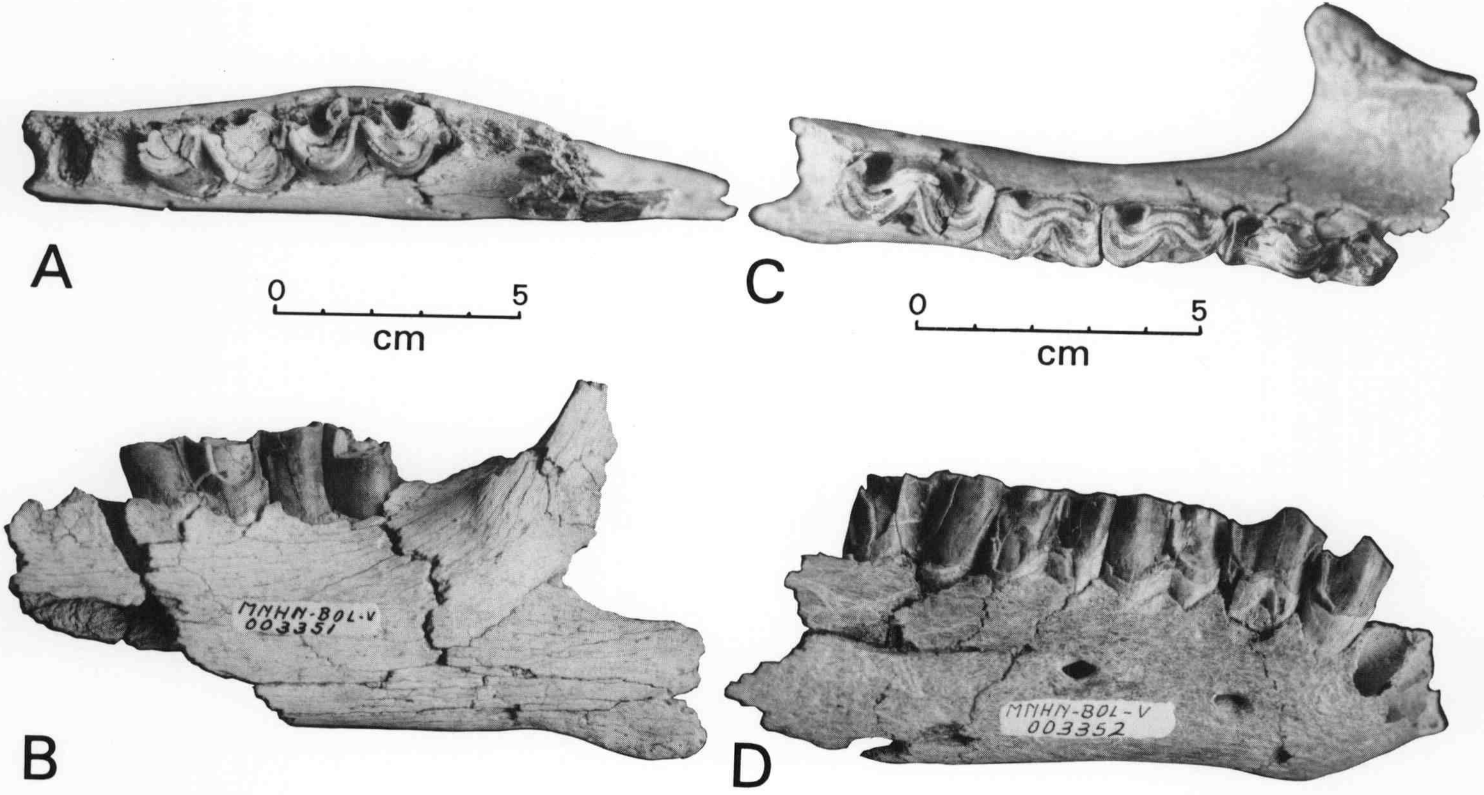

Figure 18. Occlusal (A, C) and lateral (B, D) views of mandibles of *Promacrauchenia* sp., MNHN-Bol-V 003351 and MNHN-Bol-V 003352, respectively.

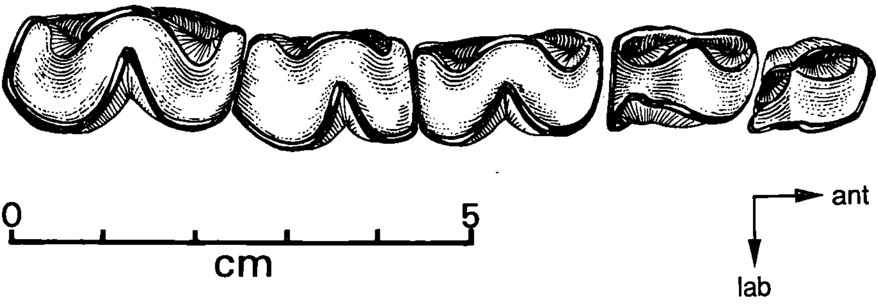

Figure 19. Occlusal view of right p2-m2 of *Promacrauchenia* sp., MNHN-Bol-V 003352. Abbreviations: ant, anterior; lab, labial.

Table 2. Mandibular measurements (mm) for *Promacrauchenia* sp. from Inchasi, Pliocene of Bolivia.

MNHN-Bol-V 003351	Length of series m2-m3	55.4
	Mandibular depth below m3	42.8
	Thickness of the mandible at position of m3	23.7
MNHN-Bol-V 003352	Length of the series p2-m2	96.7
	Length of the series p2-p4	52.0
	Length of the series m1-m2	46.6
	Mandibular depth below m2	36.2
	Mandibular depth below p3	30.6
	Thickness of the mandible at position of m2	22.6@

incomplete in p2-p3 and better developed in m1-m2. The p2 is relatively simple and lacks separate lophids (Fig. 19). In p3-p4 the protolophid is, respectively, smaller and slightly smaller than the metalophid. In m1-m2 the protolophids and metalophids are subequal in size. In occlusal view both specimens have well-developed pulp cavities (Fig. 18; not indicated in Fig. 19) surrounded by dentine and enamel. Representative mandibular and lower dental measurements are presented in Tables 2 and 3.

As represented in MNHN-Bol-V 003372, the right forelimb is partially preserved distal to the elbow (Fig. 20). The radius is anteroposteriorly compressed, exhibiting a well-developed medial crest on the proximal part of the shaft. The radius and ulnae are fused (indicated by dashed line in Fig. 20) for most of their lengths except for the distal articulation with the proximal carpals. The distal articular surface of the unfused portion of the ulnae articulates with the proximolateral carpal, i.e. cuneiform. The cuneiform is elongated proximodistally

Table 3. Measurements (mm) for lower dentitions of *Promacrauchenia* sp. from Inchasi, Pliocene of Bolivia.

Specimen Number	p2		p3		p4		m1		m2		m3	
	AP	T	AP	T	AP	T	AP	T	AP	T	AP	T
MNHN-Bol-V 003351									27.6	15.1	30.1	16.8
MNHN-Bol-V 003352	15.1	9.3	17.7	11.0	21.2	12.0	19.8	12.3	27.3	13.7		
GEOBOL s/n	28.2	11.7	21.0	13.0	24.2	14.3	34.1	17.7	40.2	10.2	40.0	18.7

AP = Anteroposterior length
s/n = unnumbered specimen
T = Transverse width

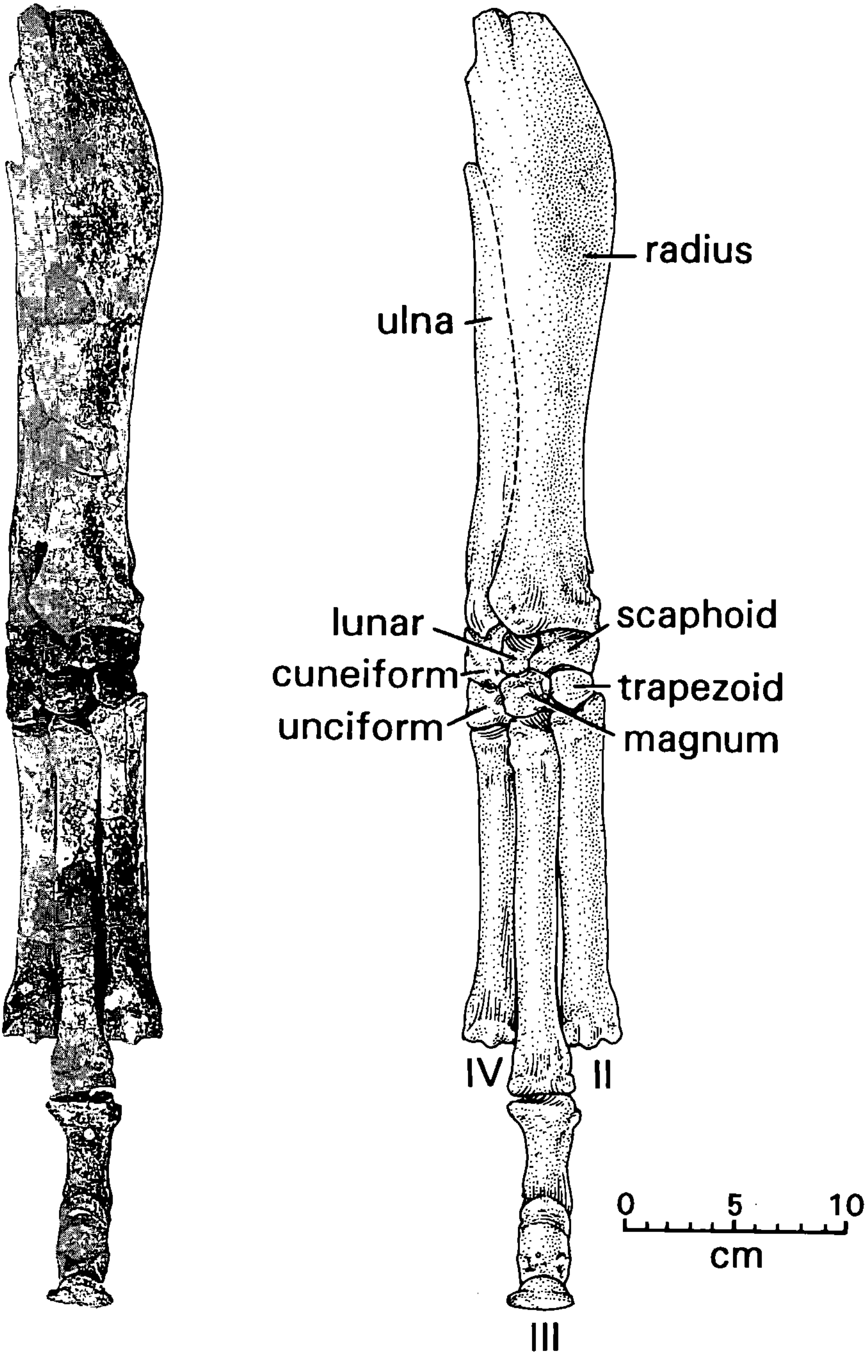

Figure 20. Anterior view of right forelimb of *Promacrauchenia* sp., MNHN-Bol-V 003372. Dashed line indicates fusion of radius and ulna.

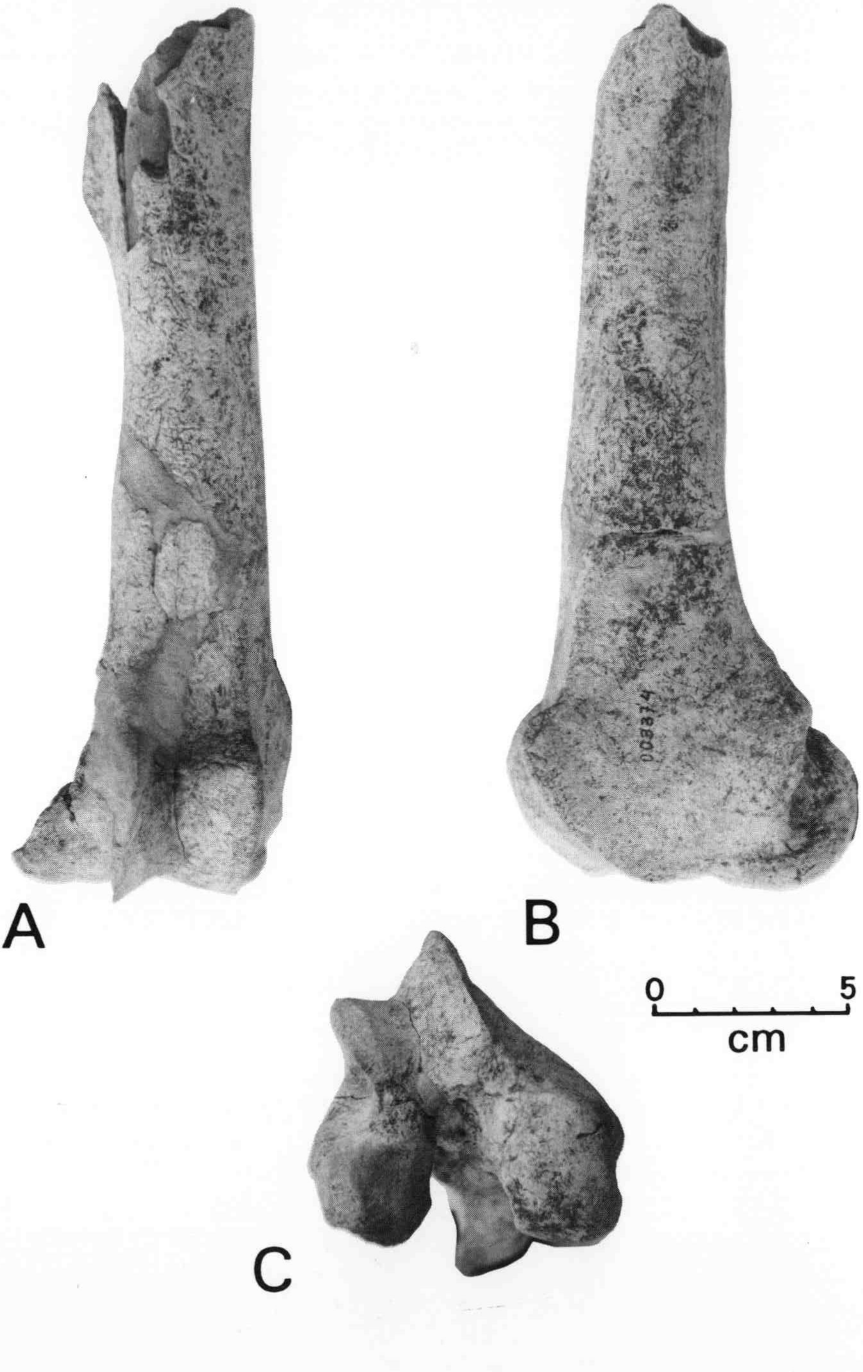

Figure 21. Anterior (A), medial (B), and distal (C) views of partial right femur of *Promacrauchenia* sp., MNHN-Bol-V 003374.

proximodistally and narrow mediolaterally. The posterior portion of the cuneiform has a well-developed facet for articulation with the pisiform (not illustrated). The carpals that articulate with the radius are the lunar medially and the scaphoid internally. The lunar is rectangular with an elongated proximodistal axis and is compressed mediolaterally. The scaphoid is also generally rectangular and elongated mediolaterally. The distal carpal series includes the unciform laterally, magnum medially, and trapezoid internally. These bones are generally square, with the unciform the largest, the magnum intermediate, and the trapezoid the smallest carpal of this series. These bones articulate with convex facets with the proximal carpal series. Distally the second carpal series articulates with metacarpals II, III, and IV. Metacarpal III is the longest (167 mm) and MC II and IV are of approximately equal length (151 mm and 140 mm, respectively). Distal to these metacarpals, only the phalanges of MC III are preserved. Of these elements, the proximal MC III is the longest (53 mm) and has widened proximal and distal articular surfaces. The medial MC III is subrectangular with a length of 29 mm. The distal-most (ungual) phalanx has a widened bony distal terminus forming a hoof.

As represented in MNHN-Bol-V 003374, the femur consists of a moderately developed shaft with a third trochanter developed proximolaterally (Fig. 21). The distal articular region consists of a fragmentary smaller lateral condyle and a larger well-developed medial condyle. In anterior view the external trochlear crest is smaller than the medial trochlear crest; these are separated by a deep intercondylar fossa. The proximal part of the medial trochlear crest has a moderately developed notch.

The tibia (not illustrated here) has a well-developed concave facet on the proximal articular surface for articulation with the medial condyle of the femur. There is a well-developed fossa for articulation with the patella. The posterolateral region is not preserved in MNHN-Bol-V 003377, but in MNHN-Bol-V 003378 there is a moderately developed surface for articulation with the lateral condyle. In anterior view the cnemial crest is well-developed. The central shaft is triangular in cross-section. The distal articular surface of MNHN-Bol-V 003377 exhibits the internal malleolus; the distolateral facet of the fibula is not preserved. The distal portion of the fibular shaft is gracile, mostly distinct, but also partially fused to the tibia.

Discussion.--The genus *Promacrauchenia* Ameghino (1904) was originally described from the late Pliocene of Argentina (Pascual 1967) and is based on the type species *P. antiqua* (=*Macrauchenia antiqua* Ameghino, 1887). This genus is distinctly macrauchenine in dental and postcranial morphology, including: (1) brachyodont cheek teeth with well-developed and distinct roots; (2) P2/p2 and P3/p3 relatively small and not molariform; (3) P4/p4 submolarifiorm; (4) relatively well-developed cingula; (5) shallow mandible; and (6) functionally tridactyl limbs with slightly larger MP III relative to MP II and IV (the latter character differentiates the family Macraucheniidae from their close relatives, the

Proterotheriidae). The basic difference between *Promacrauchenia* and the relatively well-known Pleistocene *Macrauchenia* is that the former genus is about one-third smaller in size (Pascual 1967).

In his thesis, Montaño (1968) cited the discovery of a femur and calcaneum of a small macrauchenine, which he referred to "*Microauchenia montañoi*" (currently a *nomen nudum*) from Quebrada Tijraska, which is an undescribed site located west of Anzaldo, Bolivia. Marshall et al. (1983) and Hoffstetter (1986) referred this material to cf. *Promacrauchenia* and assigned it a Pliocene age.

Hoffstetter et al. (1971) described two macrauchenid limb specimens from the Pliocene of Ayo Ayo, which they refer to a small macrauchenid, possibly *Promacrauchenia*. They also noted that this genus is present at other Pliocene sites in Bolivia. Our comparisons with available collections indicate that *Macrauchenia* is the common macrauchenine from the Pleistocene of Bolivia whereas *Promacrauchenia*, which is of generally similar morphology but about one-third the size of the former genus, is the correct taxonomic reference for Pliocene litopterns from Bolivia, as they are currently known. As such, the specimens from Inchasi represent the first definitive description of *Promacrauchenia* from Bolivia and indicate a middle Pliocene occurrence based on paleomagnetic calibrations at this site. This age is consistent with known occurrences of this genus from the middle and late Pliocene in Argentina (Pascual 1967).

†Order Notoungulata Roth, 1903
†Suborder Toxodonta Scott, 1904
†Family Toxodontidae Gervais, 1847
†Genus *Posnanskytherium* Liendo, 1943
Figures 22-25, Tables 4, 5

Genoholotype and locality.--GB 004, *P. desaguaderoi* Liendo, 1943, consisting of well-preserved skull and mandible. The exact locality is uncertain, but as the type species name indicates, Villarroel (1977) states that it was collected from Pliocene sediments along the Rio Desaguadero south of Lake Titicaca on the Bolivia-Peruvian border. Other referred specimens described in Villarroel (1977) come from the La Paz Valley and Ayo Ayo-Viscachani, both also known to be Pliocene localities.

Generic diagnosis.--Dental formula and skull morphology referable to toxodont subfamily Xotodontinae. Size smaller than *Xotodon* Ameghino. In lateral view, the cranial vault of *Posnanskytherium* is high, relatively flat, and has a weakly developed sagittal crest. Zygomatic arch less-well developed than in *Xotodon*. Mandibular rami posterior to the symphysis subparallel. Dental formula 2/3, 0/1, 4/3, 3/3, which is characteristic of the subfamily Xotodontinae. Upper and lower molariform teeth strongly compressed labiolingually. Incisors broad

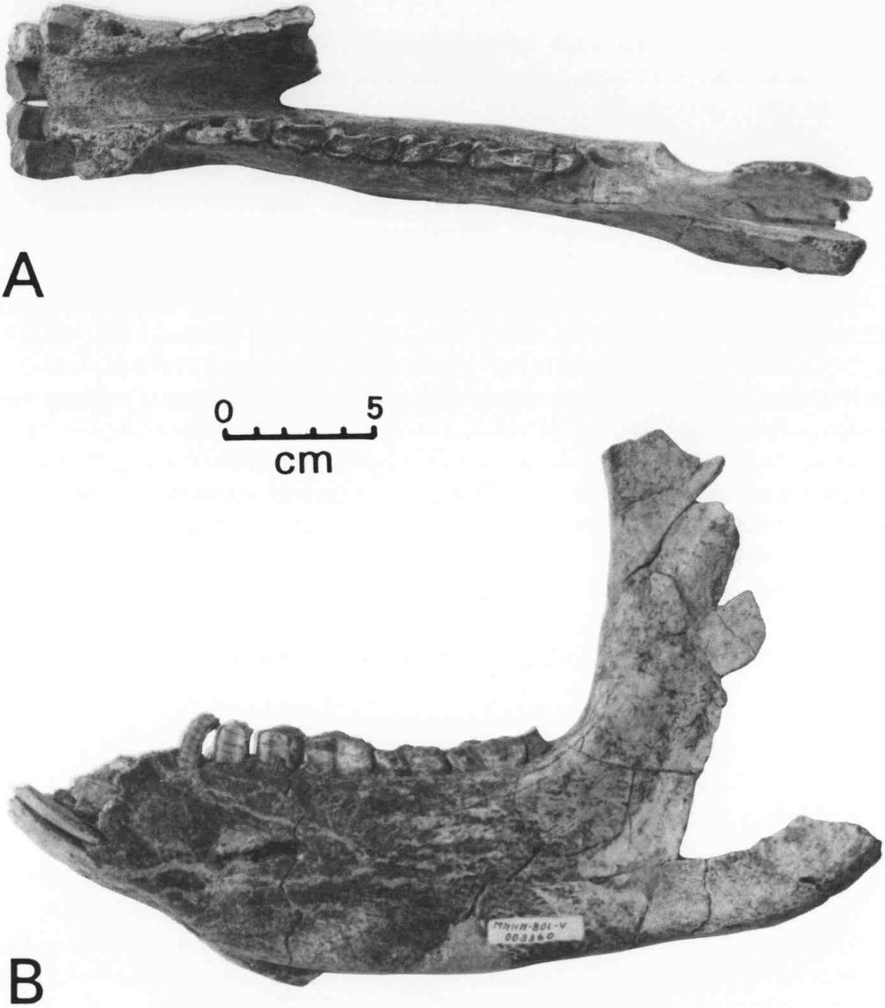

Figure 22. Dorsal (A) and left lateral (B) views of mandible of *Posnanskytherium desaguaderoi*, MNHN-Bol-V 003360.

transversely and slightly inclined posteromedially. P4 has a small posterolingual fold covered with enamel. M1-M2 each consist of one very deep lingual fold. M3 posterior to the main lingual fold has a weakly developed fold with poorly developed enamel. Lower molars with a single lingual fold; paraconid reduced, and much smaller than the protoconid (modified from Villarroel 1977).

Discussion.--The genus *Posnanskytherium* consists of one previously described species, *P. desaguaderoi*, and a new species described here, *P. inchasense*. This genus is only known from the Bolivian altiplano. Its exact affinities, other than being most closely related to xotodontine toxodonts, is otherwise unknown at present.

†*Posnanskytherium desaguaderoi* Liendo, 1943
Figures 22, 23, Tables 4, 5

Material.--From Inchasi: MNHN-Bol-V 003360, symphysis and L mandibular ramus with i1-m3 and R i1-p4 (Figs. 22, 23a); MNHN-Bol-V 003370, nearly complete mandible with L & R i1-i2, c, p2-p4, m1-m3; MNHN-Bol-V 003373, upper dental fragments; MNHN-Bol-V 003379, L mandibular fragment with m3; MNHN-Bol-V 003417, premaxilla with R and L i1-i2. (For referred material from other localities, see Villarroel 1977).

Geographic and stratigraphic location.--MNHN-Bol-V 003360, 750 m east of Communidad Inchasi, 56 m above base of measured section 2; MNHN-Bol-V 003370, 003373, 003379, 003417, 1200 m southwest of Communidad Inchasi, 18 m above base of section 4.

Diagnosis.--As for genus (above), with the following specific *differentia* relative to *P. inchasense*: *P. desaguaderoi* is larger, has a shallower mandibular ramus, and there are well-developed posterolabial grooves in the upper molars and anterolabial folds in the lower molars.

Description.--One fragmentary specimen, MNHN-Bol-V 003417 (not illustrated here), preserves the premaxillary region with a portion of the nasal crest. The I1 is very wide transversely; the I1s from the right and left sides form a linear cropping mechanism. I2 is positioned posterolabial to I1 and has a triangular cross-section.

As exemplified in MNHN-Bol-V 003360, the rami are robustly fused at the symphysis (Fig. 22). The symphysis is well-developed and extends posteriorly to a position ventral to p4-m1. The ramus is deep, with the maximum depth developed ventral to m3; it is laterally narrow extending anteriorly to the symphysis. The cheek tooth rows are subparallel and converge slightly anteriorly. There is a moderately well developed postcanine diastema. In MNHN-Bol-V 003360 the diastema is relatively shorter than in MNHN-Bol-V 003370 and the holotype, GB 004. The main body of the ramus is compressed labiolingually. The posterior region of the ascending ramus is preserved in MNHN-Bol-V 003370 but not in MNHN-Bol-V 003360 or the holotype. In MNHN-Bol-V 003370 the gonion (posteroventral surface of blade), coronoid, and sigmoid notch are all well-developed. There is a well-developed complex of mental foramina ventral to p4 and m1. Representative mandibular measurements are presented in Table 4.

The i1-i2 are anteroventrally compressed and form a distinctly linear cropping mechanism with the long axis oriented tranversely. The i3 is relatively small, triangular, and positioned posterolabial to i1-i2. In MNHN-Bol-V 003360 the

Table 4. Mandibular measurements (mm) of *Posnanskytherium desaguaderoi* and *P. inchasense* from the Pliocene of Bolivia.

Measurement	*P. desaguaderoi* Inchasi MNHN-Bol-V 003360	*P. desaguaderoi* Inchasi MNHN-Bol-V 003370	*P. desaguaderoi* holotype GEOBOL GB 004	*P. inchasense* holotype-Inchasi MNHN-Bol-V 003350
Mandibular height at m1	63.8	65.5	73.3	92.0
Mandibular height at m3	64.9	70.2	75.6	98.6
Length series p1-m3	114.6	114.1	122.3	129.6
Length series p1-p3	38.3	37.7	39.8	40.2
Length m1-m3	77.4	80.1	80.8	89.7
Length symphysis	77.9	111.2	106.2	117.8
Ant. symphysial width	22.0	27.9	33.1	33.8
Post. symphysial height	30.0	35.8	45.0	44.0

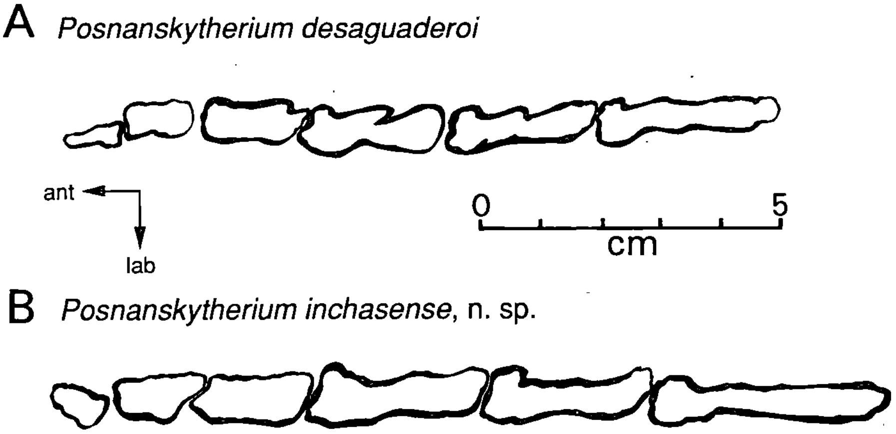

Figure 23. Occlusal views of left lower dentitions (p2-m3) of (A) *Posnanskytherium desaguaderoi*, MNHN-Bol-V 003360, and (B) *Posnanskytherium inchasense*, new species, MNHN-Bol-V 003350, holotype. Abbreviations: ant, anterior; lab, labial.

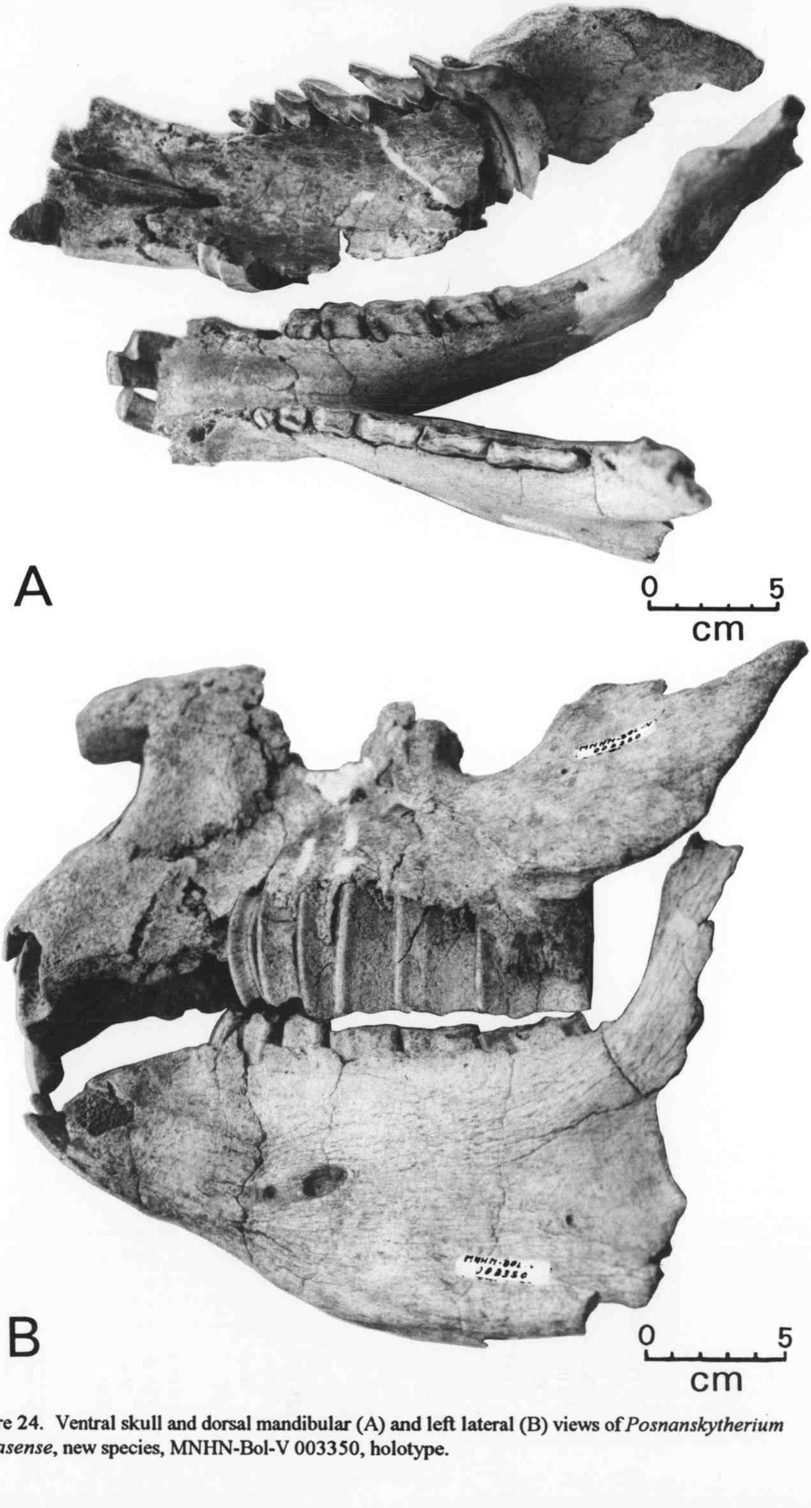

Figure 24. Ventral skull and dorsal mandibular (A) and left lateral (B) views of *Posnanskytherium inchasense*, new species, MNHN-Bol-V 003350, holotype.

Table 5. Measurements (mm) for upper and lower dentitions of *Posnanskytherium desaguaderoi* and *P. inchasense* from the Pliocene of Bolivia.

Upper Dentition	I1		I2		P1		P2		P3		P4		M1		M2		M3	
	AP	T	AP	T	AP	T	AP	T	AP	T	AP	T	AP	T	AP	T	AP	T
MNHN-Bol-V 003350, *P. inchasense* Holotype			13.2	18.4	8.1	5.4	13.5	8.5	19.0	10.5	21.6	11.1	34.6	11.8	41.8	11.7	41.0	11.9
GB 004, *P. desaguaderoi*, Holotype	26.2	8.5	13.6	18.4	6.1	5.2	13.8	9.6	17.1	9.9	22.4	9.3	30.7	12.4	33.0	11.6	35.5	12.2

Lower Dentition	i1		i2		i3		c1		p2		p3		p4		m1		m2		m3	
	AP	T	AP	T	AP	T	AP	T	AP	T	AP	T	AP	T	AP	T	AP	T	AP	T
MNHN-Bol-V 003350, *P.inchasense,* Holotype	7.5	14.5	6.8	14.2			3.6	3.1	8.3	6.0	12.1	8.3	16.3	9.2	26.7	9.8	27.4	10.2	37.7	9.2
MNHM-Bol-V 003360, *P. desaguaderoi*	5.8	13.5	5.6	12.7	9.8	14.8			8.2	5.0	11.5	6.6	15.5	7.8	22.8	8.8	24.0	8.7	32.1	8.4
GB 004, *P. desaguaderoi*, Holotype	7.3	14.9	6.1	14.2	9.6	14.8	4.7	3.0	9.6	5.6	11.3	7.3	16.9	8.4	23.6	9.0	24.0	9.3	33.0	8.6
MNHN-Bol-V 003370, *P. desaguaderoi*	7.0	14.0	6.0	13.6	10.7	16.3			7.7	4.9	11.3	6.3	16.1	8.0	23.9	7.9	26.1	8.0	33.0	7.4

AP; Anteroposterior length
T; Transverse width

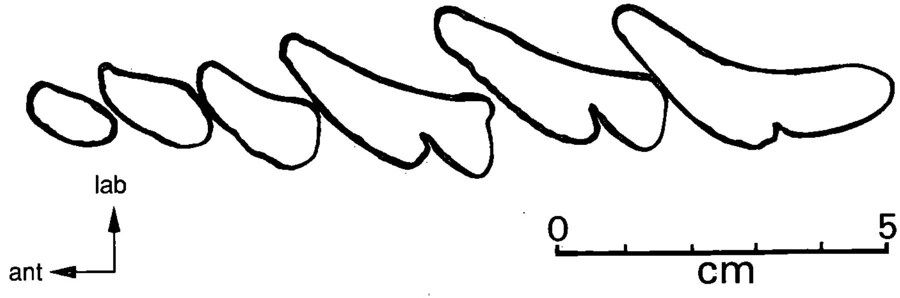

Figure 25. Occlusal view of left P2-M3 of *Posnanskytherium inchasense*, new species, MNHN-Bol-V 003350, holotype. Abbreviations: ant, anterior; lab, labial.

canine is small, elliptical in cross-section and positioned posterior to i3; there is a small precanine and larger postcanine diastema. The cheek teeth are very high-crowned (hypselodont), very laterally compressed, and in cross-section consist of a large pulp (not illustrated) and dentinal regions surrounded by relatively thin enamel (Fig. 23). The p2 is triangular, p3 is roughly rectangular; both of these teeth are relatively simple in cross-section; p4 is submolariform; p2-p4 have concave lingual borders covered with enamel; these are progressively larger and include double concavities in m1-m3; m1-m3 have well-developed, protolophids and metalophids; m3 has a well-developed, elongated posterior heel. Each molar has a single lingual fold between the protolophid and metalophid. In MNHN-Bol-V 003370 the molar protoconid lobes are better developed than in MNHN-Bol-V 003360 and the holotype. Representative dental measurements are presented in Table 5.

Discussion.--The genus and species *Posnanskytherium desaguaderoi* was originally proposed by Liendo (1943) based on a nearly complete skull and mandible from the Pliocene of Bolivia. The same material was later redescribed by Villarroel (1977), who also included several other referred specimens from other Pliocene localities on the Bolivian altiplano. The availability of the holotype (GB 004) and referred material (GB 098 and GB 099, also see Villarroel 1977) allow the direct comparisons with the Inchasi specimens.

The exact provenience, horizon, and geographic locality of the holotype of *P. desaguaderoi* is not certain at this time; various authors attribute different ages to this species. Liendo (1943) attributed this occurrence to middle Tertiary (but not a particular epoch), whereas Ortega (1970) considered it to be middle Pliocene and Villarroel (1977) and Hoffstetter et al. (1971) consider it upper Pliocene. Based on paleomagnetic data, MacFadden et al. (1993) correlate the Inchasi locality and its fauna to the middle Pliocene, thus essentially confirming the age assignments for this species of the previous authors.

The combination of morphological characters of the skull and dentition makes the Inchasi specimens indistinguishable from those previously referred to *P. desaguaderoi*. However, the Inchasi specimens differ in being slightly smaller than the holotype, (Table 5) but larger than the referred specimen from Alto Seqüencoma (GB 098), located in the La Paz Valley. We believe that this difference is not significant, and, as such, can be confidently assigned to this species. As mentioned above, these occurrences all appear to be middle Pliocene in age.

†*Posnanskytherium inchasense*, new species

Figures 23-25, Tables 4, 5

Holotype.--MNHN-Bol-V 003350, partial cranium and mandible with R I2, P2-P3; L P2-M3; R i1-i2, c, p3-m3; L i1-i2, p2-m3.

Etymology.--for Communidad Inchasi, location of the holotype.

Geographic and stratigraphic location.--1200 m southwest of Communidad Inchasi, 18 m above the base of measured section 4.

Generic diagnosis.--See above.

Specific Diagnosis.--Dental formula 2/3, 0/1, 4/3, 3/3. Lower tooth row length 130 mm. Very high-crowned, hypselodont teeth. Relative to *P. desaguaderoi*, shorter, deeper and more robust mandibular ramus, upper cheek teeth lacking well-developed posterolingual grooves, and the absence of anterolingual folds in the lower molars. P4 and M3 lack posterolingual folds seen in genoholotype. Lower molars with weaker lingual folds, and m3 longer than in *P. desaguaderoi*.

Description.--MNHN-Bol-V 003350 represents a relatively well preserved facial region and jaws of a mature individual in moderate wear (Fig. 24). The nasal notch is developed over the premaxillary/maxillary suture dorsal to the postcanine diastema. Only the anteromost portion of the nasals is preserved. Each premaxilla is relatively short; dorsally these bones have a rugose crest which is better developed than in *P. desaguaderoi*. The left maxilla is preserved up to the nasal suture. Although fragmentary, the lacrimal extends anterior to the orbit to a position lying above P2. The jugal extends to the same height as the squamosal suture. The zygomatic arch is well-developed and forms a distinct ventral crest; dorsally the zygomatic arch lacks the posterior orbital projection seen in the genoholotype. In ventral view there are several palatal foramina.

I1 is not preserved. I2 is triangular in cross-section. The alveoli for I3 indicate a large tooth positioned posterolabially to I1-I2. The upper canines are not preserved. A large diastema (ca. 60 mm) separates the C from the alveolus of P1. All of the cheek teeth are hypselodont and lack enamel on the antero- and posteromost part of the tooth. P1 is relatively small and elliptical. P2 and P3 are roughly oval (Fig. 25). P4 is the largest premolar and is submolariform; it lacks the well-developed posterolingual fold seen in *P. desaguaderoi*. In general morphology the M1-M2 are similar to the type species, consisting of a greatly expanded anterolabial region and two lingual lophs divided by a well-developed groove. The M3 of *P. inchasense* differs from that of *P. desaguaderoi* in that the former lacks a shallow posterolingual fold. Representative dental measurements are presented in Table 5.

The mandible has a heavily fused symphysis extending posteriorly to m1 similar to the genotypic species (Fig. 24). In general morphology, the mandible is very deep and laterally compressed. Representative mandibular measurements are presented in Table 4. The tooth row and sides of the mandible are subparallel in the symphysial region and slightly diverge posteriorly. The maximum mandibular depth is developed ventral to m3. Three mental foramina, which are partially confluent, are present on the lateral side of the mandible ventral to p3-m1 (Fig. 24B). The anterior portion of the ascending ramus rises at a steep angle (almost 90°) relative to the tooth row; the posterior portion of the ascending ramus is not preserved. The i1 and i2 are anteroposteriorly compressed and aligned to form a linear cropping mechanism. Although the i3s are not preserved, their alveoli are large and triangular. The canines are barely erupted and appear very small, conical, and positioned relatively close to the i1. There is a relatively large postcanine diastema. The p1 is absent. The p2 has a curved crown, is roughly conical in cross-section, and has a very small lingual fold (Fig. 23b); p3 is subrectangular; p4 is rectangular and submolariform. The p3-m3 are laterally compressed, and consist of a large pulp cavity, surrounded by dentine and relatively thin enamel, and exhibit lingual folds that are larger than the labial folds. The m1 and m2 consist of three principal lophids separated by folds. On the lingual side there are two shallow folds each on m1 and m2; these are less distinct than in *P. desaguaderoi*. The m1-m3 each have a weak labial fold. The m3 is the longest tooth and contains weak folds and an elongated posterior heel. The relative length of m3 is greater in *P. inchasense* than in *P. desaguaderoi*.

Discussion.--Leindo (1943) originally proposed the genus and species *Posnanskytherium desaguaderoi* based on a skull and mandible that was redescribed by Villarroel (1977). While the latter author confirmed the Pliocene age for this occurrence, the actual locality of the genoholotype is disputed (see discussion above). Hoffstetter et al. (1971) reported the presence of mandibular fragments of a xotodontine notoungulate comparable to *P. desaguaderoi* from Pliocene sediments of the Umala Formation at Ayo Ayo. Later, Hoffstetter (1986) recognized two species of *Posnanskytherium*, a larger one from Ayo Ayo, Viscachani, and Pomata and a smaller, undescribed species from Achocalla, both of Pliocene age from the Bolivian altiplano. It seems plausible that his second species is what we are calling here *P. inchasense*.

The holotype of the new species *P. inchasense*, MNHN-Bol-V 003350, differs in proportions from *P. desaguaderoi* in that it is larger and has a significantly deeper and more robust jaw (Table 4). Some of the most notable differences in *P. inchasense* include P4 and M3 that lack small posterolingual depressions and the absence of anterolingual folds in the lower molars, both of which are present in *P. desaguaderoi* (Fig. 22).

Based on the available sample of the genus *Posnanskytherium*, the differences in size and proportions described here cannot be attributed to sexual dimorphism, nor do they represent intraspecific variation. We therefore assert that the smaller taxon from Inchasi represents a new species, described here as *P. inchasense*.

†Family ?Mesotheriidae Alston, 1876
†Subfamily ?Mesotheriinae Alston, 1876
†*Hypsitherium bolivianum*, new genus and new species
Figures 26-28, Table 6

Holotype.--MNHN-Bol-V 003356, partial L mandible with p4-m2, m3 partially erupted (Figs. 26, 27a).

Referred Specimen.--MNHN-Bol-V 003357, fragmentary R maxilla with M1-M3 (Figs. 27b, 28).

Geographic and stratigraphic location.--For MNHN-Bol-V 003356 and 003357, respectively, 650 m north and 1200 m southwest of Communidad Inchasi, 13 and 18 m above the base of sections 3A and 4.

Etymology.--Generic: Gr., *hypsi-*, high, on high, or high place; *-therium*, mammal, beast, or wild animal; in reference to the discovery of this new genus from the eastern Andean Cordillera at a current elevation of 3,200 m; specific: *bolivianum*, for Bolivia.

Generic and specific (because of monotypy) diagnoses.--Small ?mesotheriid (also see Discussion below for family characters) with M1-M3 anteroposterior length about 36.5 mm; upper dentitions strongly curved hypselodont teeth with M1 crown height exceeding 29 mm. Ascending ramus of jaw forms an angle of about 45° relative to the horizontal ramus; upper cheek teeth lacking well-developed third (posterolingual) lobe distinctive of all other mesotheres; lower cheek teeth with well-developed lingual folds and labial grooves; size comparable with *Microtypotherium*; depth of mandible relatively deeper ventral to m1 than in *Plesiotypotherium*. Differs from other mesotheres in the presence of anterior lower premolars (p3 and possibly p2).

Description.--As represented in the holotype MNHN-Bol-V 003356, the mandible is relatively short and narrow with its greatest depth ventral to m1 (Fig. 26). There is a groove containing mental foramina ventral to p4-m1. Part of the symphysial region is preserved including the alveoli for p2-p3 (Fig. 26B). The symphysial suture extends posteriorly to beneath the p3-p4 junction. Posteriorly, only the anterior portion of the ascending ramus is preserved.

The lower cheek teeth are hypselodont. The dentine is covered with thin enamel; the crowns are compressed labiolingually with the anteroposterior axis being much longer than the transverse width (Figs. 26, 27a). Lingually there are

Table 6. Dental measurements (mm) for *Hypsitherium bolivianum* from Inchasi, Pliocene of Bolivia.

Upper dentition	M1		M2		M3	
	AP	T	AP	T	AP	T
MNHN-Bol-V 003357	12.4	6.9	14.5	6.2	11.8	6.2

Lower dentition	p4		m1		m2		m3	
	AP	T	AP	T	AP	T	AP	T
MNHN-Bol-V 003356, Holotype	11.2	4.2	11.6	4.15	12.7	3.8	unerupted	

AP; Anteroposterior length
T; Transverse width

relatively strong enamel folds situated about in the middle of each tooth; these are better developed in m1 and m2 than in p4. Labially, at about the position of the lingual folds, there are distinctive grooves. The m3 is only partially erupted, and therefore the characteristic dental pattern is not well exposed. Representative dental measurements are presented in Table 6.

As represented in the referred specimen, MNHN-Bol-V 003357, the upper molars are hypselodont, imbricate with one another, and have high, curved crowns (Figs. 27B, 28). In occlusal view the molars have dentine surrounded by thin enamel anterolingually and labially; posteriorly and posterolingually these teeth either lack, or have very thin, enamel. The molars have a roughly triangular cross-section consisting of large ectolophs with large, anterolabial projections; there also are moderately developed protolophs and smaller metalophs. Lingually a deep groove divides the protoloph and metaloph. Posterior to the metaloph there is a well-developed lingual groove in m2; this structure is poorly developed in m1 and the relevant region in m3 is fragmentary.

Discussion.--Several recent publications describe the presence of the family Mesotheriidae in South America. Francis (1960, 1965; *in* Pascual 1967) presented a revision of what have been considered to be the valid genera from the Miocene-Pleistocene of Argentina, including *Eutypotherium* Roth, 1901, *Typotheriopsis* Cabrera & Kraglievich, 1931; *Pseudotypotherium* Ameghino, 1904 and *Mesotherium* Serrés, 1867. To this list Villarroel (1974a; b) described the new

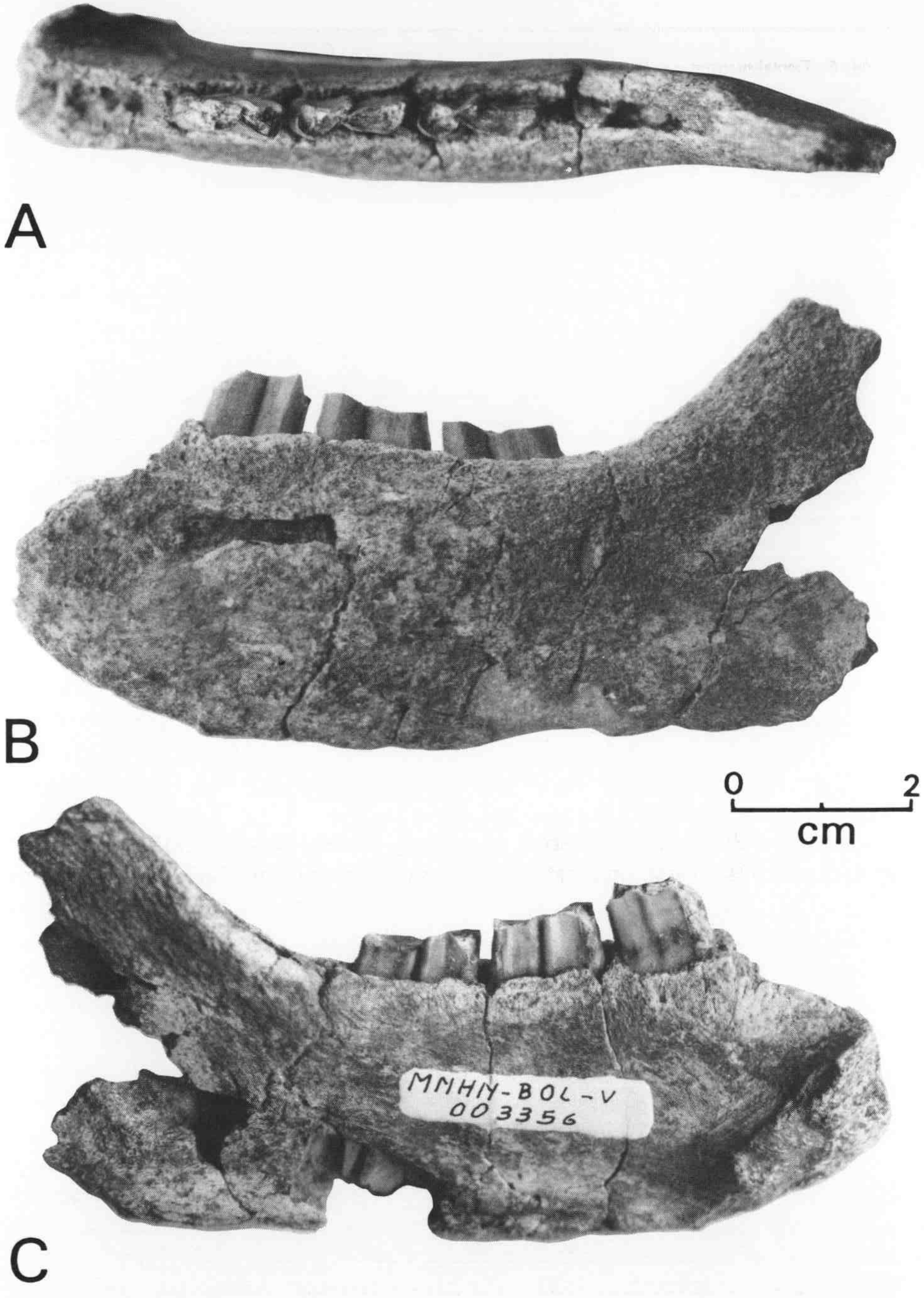

Figure 26. Dorsal (A), lateral (B), and medial (C) views of left mandible of *Hypsitherium bolivianum*, new genus and species, MNHN-Bol-V 003356, holotype.

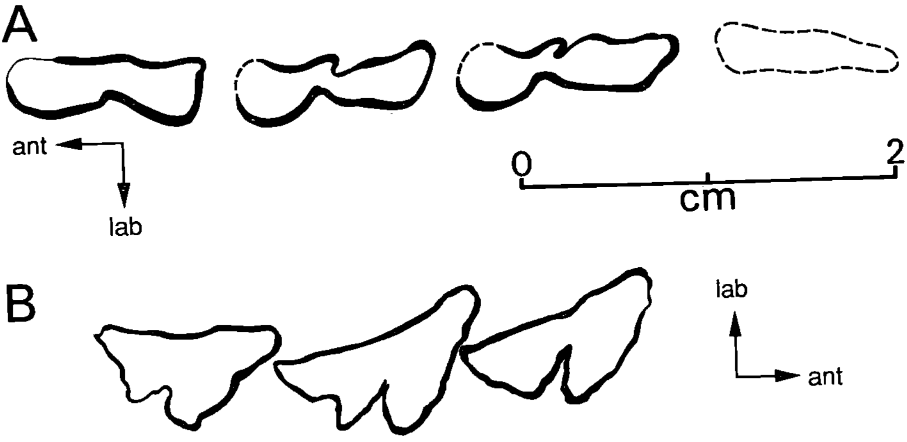

Figure 27. Occlusal views of (A) left lower (p4-m2; m3 unerupted) and (B) right upper dentitions (M1-M3) of *Hypsitherium bolivianum*, new genus and species, respectively, 003356 (holotype) and MNHN-Bol-V 003357. Abbreviations: ant, anterior; lab, labial.

genera *Plesiotypotherium* and *Microtypotherium* from the Miocene of the altiplano of Bolivia. Unlike the stratigraphic distribution of this family in Argentina, Villarroel (1974a; 1974b) indicated that the Mesotheriidae did not extend upwards into the Plio-Pleistocene (as currently calibrated) of Bolivia.

Many of the diagnostic characteristics that define this family and serve to separate the valid genera of mesotheres are based on the incisor and cranial morphologies, which are not represented in the sample from Inchasi. Nevertheless, there are several diagnostic characters that justify the new genus *Hypsitherium*. With respect to *Plesiotypotherium*, the mandible of *Hypsitherium* is relatively deeper beneath m1 and has an ascending ramus that forms an angle of about 45° relative to the horizontal ramus, in contrast to about 90° in the former genus. In the upper cheek teeth of *Hypsitherium*, the third, relatively well-developed posterior lobe seen in *Plesiotypotherium*, *Microtypotherium*, and the Argentine mesotheriines is absent. In the lower cheek teeth the lingual grooves and labial folds are significantly more pronounced in *Hypsitherium* than in *Plesiotypotherium*, *Microtypotherium*, and the Argentine mesotheriines.

We are confident that the two specimens from Inchasi represent a new genus and species of notoungulate. However, we are less confident about its allocation to an existing family. Taken together, the dental characters, in particular the molarized p4, and the number, position, and relative development of the lingual folds in the upper molars and lingual grooves and labial folds in the lower molars, are most similar to diagnostic mesothere characters (Francis *in* Pascual 1967; Villarroel 1974a, 1974b). There are, however, two seemingly important

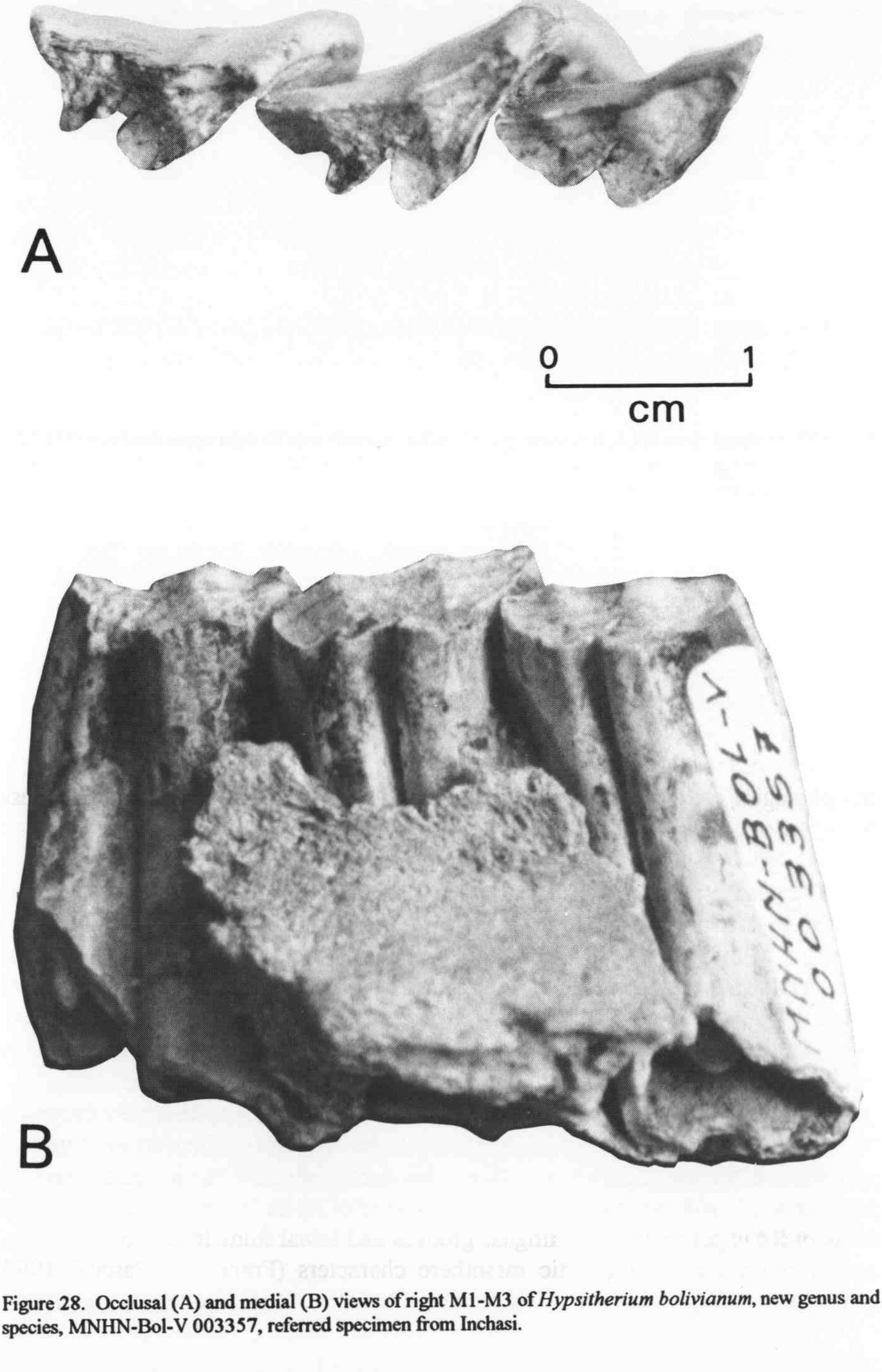

Figure 28. Occlusal (A) and medial (B) views of right M1-M3 of *Hypsitherium bolivianum*, new genus and species, MNHN-Bol-V 003357, referred specimen from Inchasi.

exceptions to the mesothere dentition found in *Hypsitherium*. Firstly, *Hypsitherium* lacks a well-developed third, posterolingual lobe in the upper molars. Secondly, the number of lower premolars in *Hypsitherium* differs from mesotheres. Previous descriptions of the dental formula for this family state that mesotheres lack the p1-p3 (Francis 1965; Pascual 1967; Villarroel 1974a, 1974b). In contrast, the lower jaw of *Hypsitherium* from Inchasi has alveoli for p2-p3 (the condition of the p1 is unknown). Despite these two morphological exceptions, in all other dental characters *Hypsitherium* is most similar to mesotheres. Taking into account the overall dental morphology, this genus differs significantly from that exhibited in the two other typothere notoungulate families, i.e. Interatheriidae and Hegetotheriidae (*sensu* Pascual 1967).

In summary, the specimens from Inchasi clearly represent a new genus and species, *Hypsitherium bolivianum*, which is most closely referable to the existing family Mesotheriidae. We cannot, however, rule out the possibility that *Hypsitherium* belongs to a new, currently undescribed family, but we are not prepared to propose one with the limited material available to us from Inchasi. If indeed *Hypsitherium* is a mesotheriid, then its occurrence at Inchasi extends the range of this family upward into the Pliocene of Bolivia, as the range of this family is also known from Argentina. Although the latest genus of this family, *Mesotherium*, is known from the Pleistocene of Argentina, no mesotherines are currently known from this epoch in Bolivia.

DISCUSSION

Faunal Composition, Diversity, and Alpha-level Taxonomy

The Inchasi local fauna consists of 4 orders, 9 families, 10 genera, and at least 11 species of mammals. The diversity within these orders is similar to other Pliocene sites from Bolivia (e.g. Ayo Ayo and Viscachani; Marshall et al. 1983; Hoffstetter 1986) and Argentina (e.g. Tonni et al. 1992). However, no Pliocene site from Bolivia has ever been as thoroughly sampled as, for example, the extensive fauna from the Pleistocene of Tarija (Boule and Thévenin 1920; Hoffstetter 1963) or some of the classic late Cenozoic localities from the Province of Buenos Aires and environs in Argentina (Marshall et al., 1984). There are some notable absences in the Inchasi fauna, including non-mammalian vertebrates and carnivorous mammals. In addition, micromammals are poorly represented. We believe that these absences are an artifact of the available sample and the underrepresentation results from the lack of screenwashing. Although four field trips (amounting to about 50 person-days) have been spent recovering fossils by surface prospecting at Inchasi, the discoveries to date must be viewed as preliminary (this is in contrast to four centuries of sporadic, sometimes intensive collecting at Tarija, for example). Given time for erosion to expose additional fossils in this limited collecting area, we anticipate that additional surface prospecting, and possibly screenwashing, for fossils will increase both the available samples of currently poorly known taxa (e.g. Megatheriinae and Mylodontinae), allowing more precise taxonomic allocations, and the recorded diversity both for other mammals (most notably, from the orders Marsupialia, Carnivora, and Rodentia) and probably the other vertebrate classes as well. The relatively low diversity of the herbivores from Inchasi is similar to the known diversity of modern mammalian faunas from the Bolivian altiplano (Anderson 1993; Teresa Tarifa, pers. comm. 1994).

Four of our taxonomic allocations have been made to the level of genus, with the species being indeterminant; these include *Plohophorus*, *Paraglyptodon*, *Caviodon*, and *Promacrauchenia*. The two main reasons for this level of allocation are either (1) there have been no comprehensive previous taxonomic studies of these genera and species allocations from other Bolivian Pliocene sites; and/or (2) the valid species for comparison from the classic, or better-known, sites in Argentina are poorly characterized, or consist of portions of the skeleton not present in the collections examined during this study. With regard to the latter, the original descriptions of many glyptodont taxa are based primarily on caudal morphology, whereas our specimens from Inchasi consist of carapace osteoderms. Two other allocations could only be made to subfamily, i.e. Megatheriinae and Mylodontinae, because the particular skeletal elements collected from Inchasi are non-diagnostic at a more specific taxonomic level. Undoubtedly, future discoveries of more characteristic elements, most notably teeth, and comparisons with descriptions from Argentina will further refine these subfamilial allocations.

In summary, the current description of the mammalian fauna from Inchasi is considered provisional. However, given the fact that all previous accounts of Pliocene mammals from Bolivia either consist of preliminary faunal lists (e.g. Hoffstetter et al. 1971), detailed descriptions of single taxa (e.g. Hoffstetter et al. 1984), or general taxonomic overviews (Marshall et al. 1983; Hoffstetter 1986), our current description of the entire fauna from Inchasi, as it currently is known, is therefore justified and of significance.

Paleoecology and Paleoenvironmental Reconstructions

A striking characteristic of middle Tertiary (Oligo-Miocene) mammalian faunas from Bolivia and Argentina is the abundance of numerous taxa with either very high-crowned (hypsodont), or ever-growing (hypselodont) teeth. This predominance of high-crowned, presumed grazers, suggests a period during the middle Tertiary of extensive grasslands as the predominant habitat and food resource for the endemic notoungulates.

The relative tooth crown heights and mix of medium- to large-bodied mammalian herbivores at Inchasi generally indicates local vegetation types and broad climatic parameters. Based on analogies with other members of their respective taxonomic groups, and/or the presence of short-crowned (brachyodont) teeth, the occurrence of Mylodontinae, Megatheriidae, and the litoptern

Promacrauchenia at Inchasi suggest browsing and hence, the presence of either scrub vegetation, woodlands, or forests. The diets and/or habitat preferences of the other edentates (i.e. glyptodonts and armadillos) from Inchasi are difficult to determine. At the other end of the spectrum, the presence of *Hypsiitherium bolivianum* and two species of *Posnanskytherium*, all with hypselodont teeth and the latter genus with a transversely linear cropping mechanism, suggest grazing to hyper-grazing adaptations (e.g. Janis and Ehrhardt 1988). MacFadden et al. (1994) has recently suggested from analysis of carbon isotopes of tooth enamel that *Posnanskytherium* from Inchasi fed upon C3 vegetation, in this case probably a predominance of montane grasses. Thus, so far as we know, the mammalian herbivores from Inchasi probably represent a diversity of feeding adaptations ranging from browsing to grazing. This balance and mixture of herbivores is in contrast to Oligocene and Miocene mammalian faunas from Bolivia and elsewhere in South America in which there usually is a strong predominance of grazers. The smaller proportion of grazers in the Pliocene of Bolivia seems related to the presence of different montane habitats resulting from Andean uplift.

Biogeography, Pliocene Regional and Continental Correlations, and the Problematic Montehermosan/Chapadmalalan Interval

The fauna from Inchasi consists of 10 genera of Pliocene mammals. Eight of these (*Plaina, Glossotheridium, Proscelidodon, Plohophorus, Paraglyptodon, Caviodon, Chapalmaltherium*, and *Promacrauchenia*) are relatively widespread in that they also are known from similar-aged deposits in Argentina. Only the genus *Posnanskytherium* and its two species, *P. desaguaderoi* and *P. inchasense*, and the new genus and species *Hypsitherium bolivianum* are unknown elsewhere and thus appear to be endemic to the Bolivian altiplano. At first glance this high degree of faunal similarity and low endemism is perhaps surprising. However, during the middle Pliocene about 3-4 myr ago when these mammals lived, Inchasi probably was at an elevation of about 2000 m and not 3200 m as it is today (MacFadden et al. 1994). While high elevations of 3000 m or greater can effectively act as biogeographic barriers to dispersal because of climatic effects and different vegetation, lower elevations are less of a hinderance to dispersal. Take for example, the middle Pleistocene mammalian fauna from Tarija in southern Bolivia (e.g. Hoffstetter 1963), which today is at about 2000 m elevation. With its position in the sub-Andean belt, the Tarija basin has probably experienced negligible uplift (MacFadden et al. 1994) within the past 1 myr (when the fossiliferous Tarija Formation was deposited). Its faunal composition both at the generic and in many cases, specific, levels is almost identical to similar-aged faunas from Argentina. This indicates an active dispersal corridor with regions at other latitudes in South America during the Pleistocene. A similar situation probably was in existence at Inchasi during the Pliocene.

The high degree of faunal similarity with classic and other well-known Pliocene sites from Argentina allows an opportunity to assess the age of Inchasi with regard to the Pliocene South American land-mammal ages (SALMAs). Two names are generally applied to Pliocene SALMAs, i.e. the early Pliocene Montehermosan and the middle Pliocene Chapadmalalan, both of which are based on faunas from Argentina. Although the beginning of the Montehermosan and end of the Chapadmalalan are fairly well accepted at, respectively, 5 and 2.5 Ma, the boundary between these two land mammal ages is very poorly characterized. There are two current hypotheses: (1) Some workers (e.g. Marshall et al. 1983) have challenged the biochronological distinctness of the Chapadmalalan and argue that both names should be included in an expanded concept of the Montehermosan than spans the early to early-late Pliocene from 5 to 2.5 Ma. Assuming that these two land mammal-ages are distinct, what can be said about the biochronological assemblage of widespread taxa at Inchasi? Following Marshall et al. (1983), the genera *Proscelidodon* and *Plohophorus* from Inchasi are restricted to the Montehermosan *s. s.* as it is known from Argentina. The genera *Glossotheridium* and *Paraglyptodon* are restricted to the Chapadmalalan. The longer-ranging genera *Plaina*, *Promacrauchenia*, *Chapalmatherium*, and possibly *Caviodon* are known from both the Montehermosan *s. s.* and Chapadmalalan. Based on these biochronological occurrences, the Inchasi local fauna suggests that the Monterhermosan *s. l.* is preferred over distinct Montehermosan *s. s.* and Chapadmalalan SALMAs. (2) In contrast, Cione and Tonni (1994) argue that, based on biochronological and magnetostratigraphic criteria, the Montehermosan and Chapadmalalan are distinct land-mammal ages. In their study they cite the importance of Inchasi to the resolution of these two biochrons. Their basic argument is that most of the widespread Chapadmalalan *s. s.* index genera, i.e. *Glossotheridium*, *Plaina*, *Plohophorus*, *Paraglyptodon*, and *Chapalmatherium*, are found at Inchasi. Furthermore, Inchasi is of prime importance to resolution of the definition of the land-mammal ages and Pliocene time in South America because this locality clarifies some of the problems with the discontinuous stratigraphic sections associated with the typical faunas from Argentina. Given their careful redefinition of these two SALMAs, we favor the conclusion of distinct Montehermosan and Chapadmalalan SALMAs proposed by Cione and Tonni (1994).

SUMMARY AND CONCLUSIONS

Prior to the discovery of fossil mammals at Inchasi, knowledge of Pliocene mammals of Bolivia was restricted to several sites in the northern altiplano, most notably from Ayo Ayo, Viscachani, and Umala, but also including the poorer known Alto Següencoma, Gualberto Villarroel, Achocalla, and Pomata (e.g. Marshall et al. 1983; Hoffstetter 1986). Furthermore, although preliminary faunal lists have been reported for these localities, only a few of the fossil mammals had been described in detail.

The mammalian fauna from Inchasi consists of 4 orders, 9 families, 10 genera, and at least 11 species of extinct mammals. Despite its somewhat fragmentary representation, and difficult taxonomic assignments for some of the specimens, description of this fauna represents a significant contribution to our knowledge of Pliocene mammals from Bolivia. In the interpretation of Marshall et al. (1983), the Inchasi mammals have faunal elements characteristic of both the Montehermosan and Chapadmalalan SALMAs and thus are referred to as Montehermosan *s. l.* In contrast, the preferred interpretation here follows the analysis of Cione and Tonni (1994), who recognize a distinct Chapadmalalan *s. s.* SALMA; it is therefore concluded that the Inchasi mammalian fauna is Chapadmalalan. In addition, previous magnetostratigraphic correlation of the Inchasi beds to the Geomagnetic Polarity Time Scale further refines the age of this fauna to middle Pliocene, between 4.0 and 3.3 myr ago (MacFadden et al. 1993).

We realize that the Inchasi fauna is only a first step in describing the interesting mammalian communities that existed in the Bolivian Andes just prior to the Great American Interchange. Further work at Inchasi and other high-elevation Pliocene sites will add to our knowledge of some of the more poorly represented taxa, allow further taxonomic refinements with respect to previous specimen descriptions from elsewhere in Bolivia as well as from classic Pliocene localities in Argentina, and provide further data relevant to refining the traditionally problematic Montehermosan and Chapadmalalan SALMAs.

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