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New Palaeothentid Marsupials (Caenolestoidea) from the Early Miocene of Patagonian Argentina

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ABSTRACT

Recent fieldwork in Argentina has resulted in the recovery of numerous new specimens of palaeothentid marsupials, an important component of the Deseadan-Santacrucian (Oligocene–middle Miocene) mammalian fauna of Patagonia. The 1994 collections include a new genus and species from the early Miocene Pinturas Formation at Estancia La Cañada and the first complete lower dentition of *Acdestis oweni* from a locality in the Santa Cruz Formation along the Río Chalia.

Specimens from the La Cañada locality, an isolated m1 and two dentary fragments, represent a new genus and species of a very large palaeothentine, here named *Titanothentes simpsoni,* new genus and species. Several dental features distinguish the new form from its closest relatives. Chief among these is the length of the m1 paracristid, which is nearly twice the size of that seen in the largest palaeothentine known previously (*Palaeothentes aratae*). Details of the molar structure indicate that the phylogenetic affinities of the new form probably lie with *P. aratae* and *P. primus.*

The new dentary of *Acdestis* contains the complete lower dentition, including many previously unknown anterior teeth. This specimen confirms that the lower dental formula of *A. oweni* is 2.1.3.4. The central incisor is large and procumbent. The previously unknown i2-p2 are minute, single-rooted, and resemble those of other palaeothentids and even abderitids in having an elongated mesial extension of the enamel, giving the teeth a "bent" appearance in lateral view.

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INTRODUCTION

Palaeothentid marsupials have been known from Tertiary deposits in South America since the 19th century (Ameghino, 1887). Remains of this extinct family of small caenolestoids, related to extant rat opossums, occur in Oligocene through Miocene rocks from Colombia to the southern portion of mainland Argentina (Marshall, 1980; Bown and Fleagle, 1993; Dumont and Bown, in press). The family Palaeothentidae was recently revised by Bown and Fleagle (1993) on the basis of hundreds of new specimens recovered since 1982. The authors recognized 9 genera and 19 species of palaeothentids, contained primarily in two subfamilies, the Palaeothentinae and the Acdestinae. The new late Miocene form from Colombia (Dumont and Bown, in press) is considered a separate lineage from the remaining palaeothentids. Collections made in 1994 include several new specimens that shed additional light on this unusual group of small fossil marsupials (Rae et al., 1994). In this communication we report the first complete dentition of *Acdestis oweni* and a new genus and species of palaeothentid from central Santa Cruz Province, Argentina.

Fig. 1. Geographic position of La Cañada and Río Chalia (*). Collections were made by an international team from the State University of New York at Stony Brook, U.S. Geological Survey, American Museum of Natural History, Museo Argentino Ciencias Naturales "Bernardino Rivadavia," and Central Patagonian Research Center.

ACKNOWLEDGMENTS

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SYSTEMATIC PALEONTOLOGY

SUPERORDER MARSUPIALIA
ILLIGER, 1811

ORDER PAUCITUBERCULATA
AMEGHINO, 1894

FAMILY PALAEOTHENTIDAE
(SINCLAIR, 1906) OSGOOD, 1921

SUBFAMILY PALAEOTHENTINAE
SINCLAIR, 1906

Titanothentes, new genus

TYPE SPECIES: *Titanothentes simpsoni,* new and only known species.

ETYMOLOGY: Greek *titan-*, of enormous size, strength, power; and ?Tehuelche *-thentes* (see Marshall, 1980, for a discussion of the possible etymology), a common suffix for palaeothentids.

TYPE LOCALITY: Estancia La Cañada, cen-

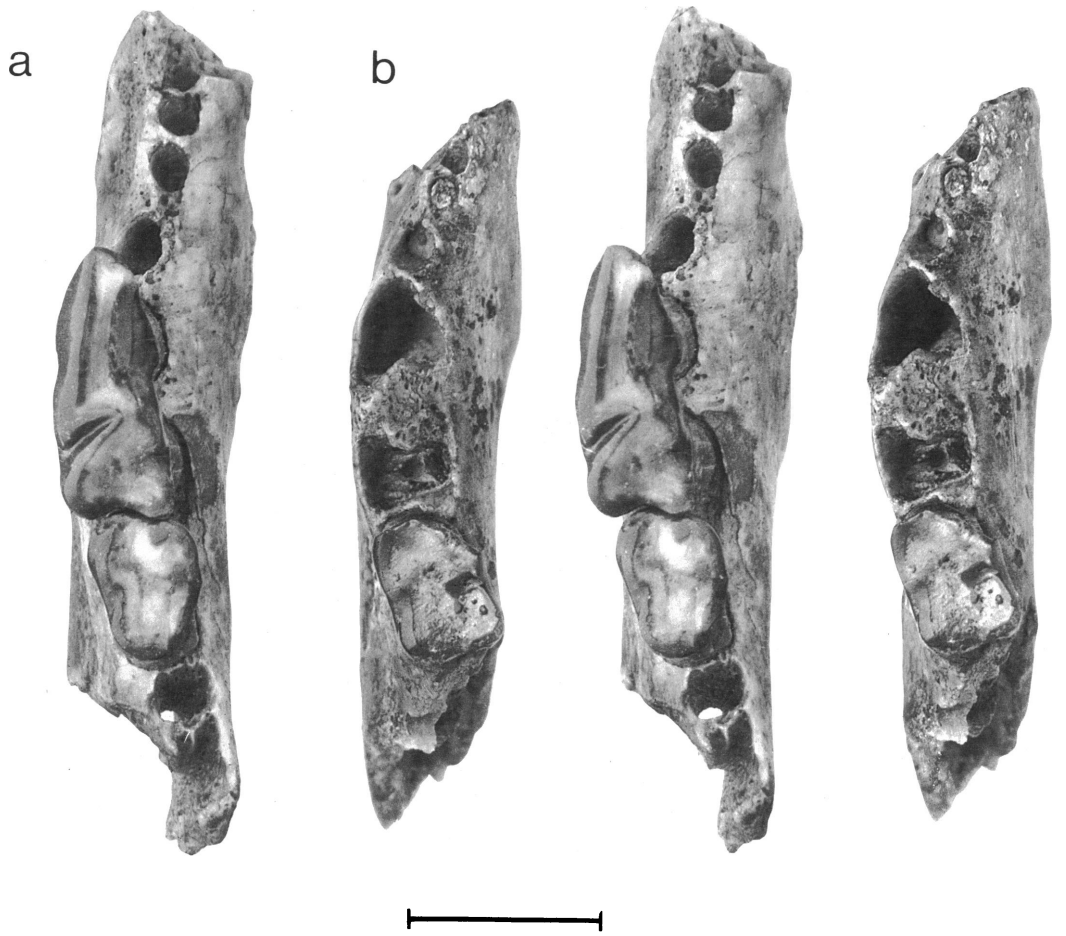

Fig. 2. **(a)** Stereopair (occlusal view) of the holotype of *Titanothentes simpsoni* (MACN SC-3157a), a left dentary with m1-2. Note especially the elongated paracristid of m1. **(b)** Stereopair (occlusal view) of MACN SC-3156 (*T. simpsoni*), a right dentary with m2. In this and all subsequent photographs, the scale bar = 5 mm.

tral Santa Cruz Province, Argentina. The geology and stratigraphy of the Miocene palaeothentid sites in southern Argentina are summarized in Bown and Larriestra (1990) and Bown and Fleagle (1993). This site is located in north-central Santa Cruz Province, southern Argentina, between the Río Deseado to the north and the Río Chico to the south (47°58.85′S latitude, 70°09.81′W longitude: see fig. 1). The outcrop is a small amphitheater about 4.5 km north of the estancia house. Fossils occur in a paleosol developed on an erosion surface that bordered a small lake or pond. Paleosol development and the erosional unconformity at the site indicate a stratigraphic position similar to that at Cauce Seca in the upper-middle Pinturas Formation of the Río Pinturas area further north (Bown and Fleagle, 1993).

DIAGNOSIS: Largest known palaeothentine, m1 about 25% longer MD (mesiodistally) than mean of m1 in *Palaeothentes aratae*. Differs from all palaeothentids in having a very short m1 talonid, an extremely long m1 paracristid, and a pronounced size discrepancy between m1 and m2; differs from palaeothentids other than *P. aratae* and *P. primus* in having an anterior extension (or mure) on the entoconid of m1; differs from palaeothentids other than *P. aratae, P. primus, P. boliviensis,*

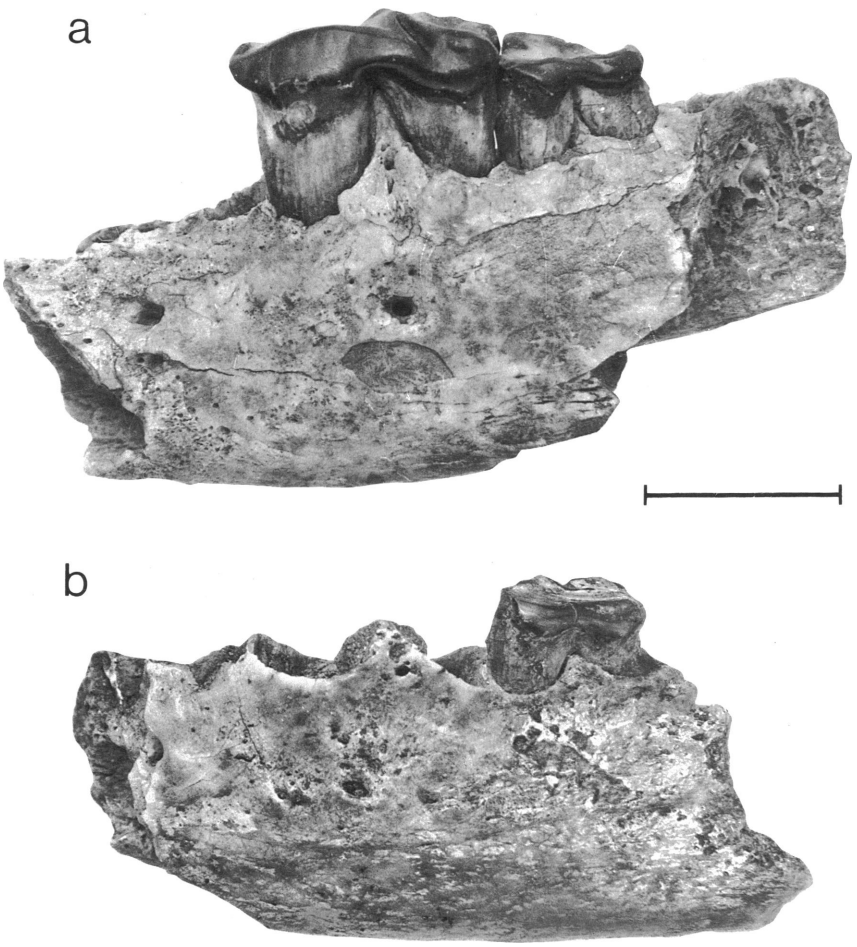

Fig. 3. Dentaries of *T. simpsoni* (lateral view). **(a)** MACN SC-3157a (holotype); **(b)** MACN SC-3156.

and *Carlothentes* in possessing a shallowly bifurcated m1 paraconid.

Titanothentes simpsoni, new species

HOLOTYPE: MACN SC-3157a, left dentary with m1-2 and alveoli of p1-3 and m3 (figs. 2a, 3a).

DIAGNOSIS: Only known species; as for genus.

HYPODIGM: The holotype; a right dentary with m2 and alveolus of m1 (MACN SC-3156; figs. 2b and 3b); and an isolated right m1 (MACN SC-1613; fig. 4).

DISTRIBUTION: Upper part of the middle Pinturas Formation; Santacrucian (early-middle Miocene); Estancia La Cañada, Provincia de Santa Cruz, Argentina.

ETYMOLOGY: Named for G. G. Simpson, a pioneer in South American paleontology.

DISCUSSION: *Titanothentes simpsoni* is among the largest species of palaeothentids, equaling the size of the largest palaeothentine species known previously (*P. aratae*) in the depth of the corpus and exceeding all other palaeothentines in m1 MD length. Only the dentary and lower first and second molars of the taxon are known (two examples of each).

Both the holotype (fig. 2a) and MACN SC-3156 (fig. 2b) preserve portions of the dentary. The holotype is a fragmentary left dentary, broken through the alveoli for p1 anteriorly and m3 posteriorly. The corpus of

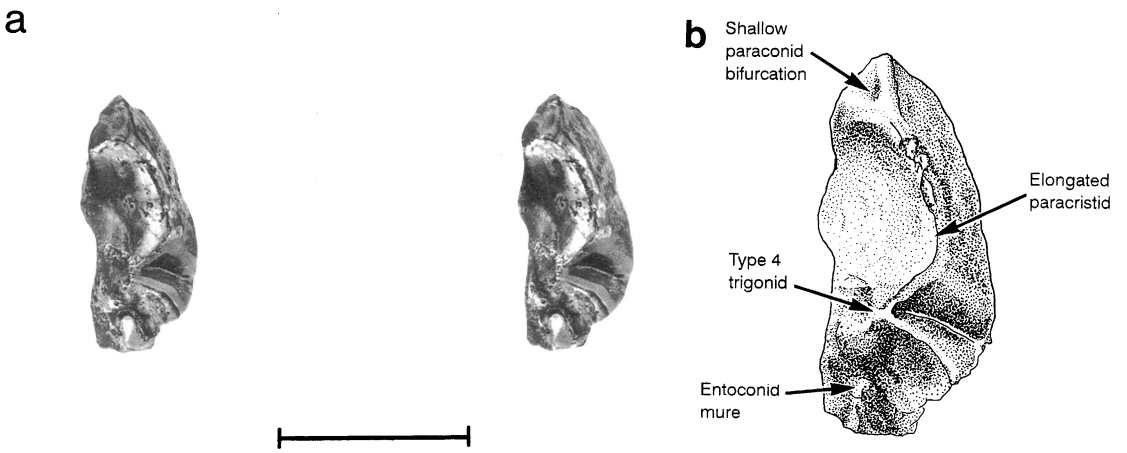

Fig. 4. MACN SC-1613 (*Titanothentes simpsoni*), a right m1. **(a)** Stereopair (occlusal view) of specimen; **(b)** schematic drawing (not to scale) with the major characteristics highlighted.

SC-3156 is nearly identical in preservation, although it is broken anteriorly through the alveolus of p2. The corpus of *Titanothentes* is relatively deep and gracile (fig. 3a, b). There is a mental foramen below m1 that is situated just superior to midcorpus. There are two additional foramina in the holotype (one in SC-3156) that lie beneath the alveolus of p2

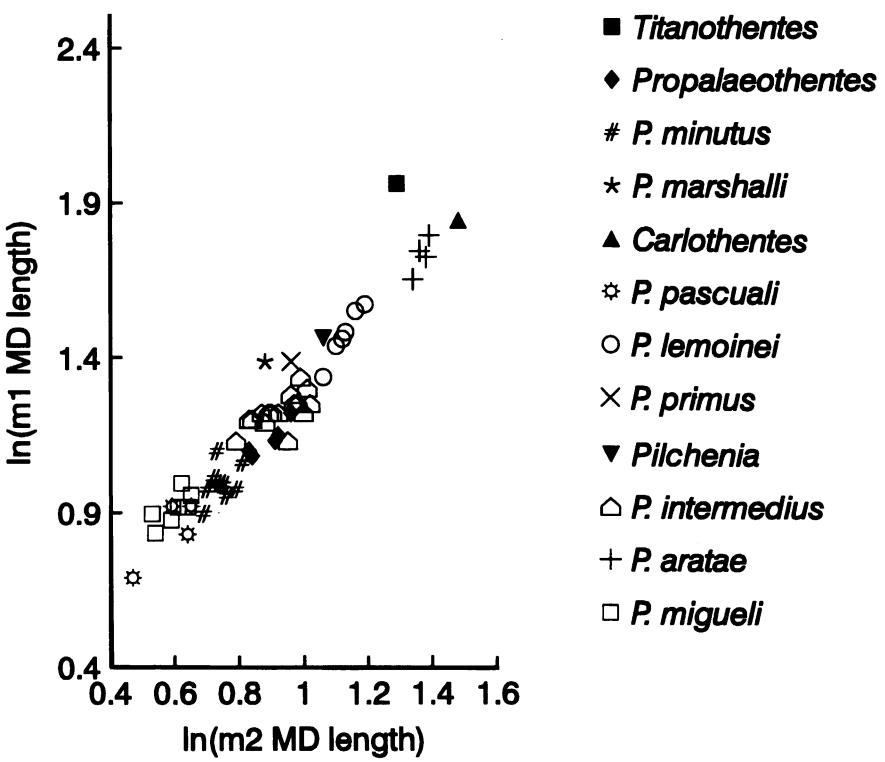

Fig. 5. Natural log (ln) of MD length for m1 plotted against (ln) MD length of m2 for palaeothentids. *Titanothentes* (filled square) possesses an m1 that is longer than that of any other known palaeothentid.

and open anteriorly. The lower of the two foramina is about half the size of the upper and is situated at midcorpus. An alveolus for a large, procumbent incisor is clearly visible at the inferior margin of the mesial break in both specimens. The inferior and superior margins of the dentary are parallel under the molar teeth, but the corpus becomes shallower under the premolars (fig. 3) as in some other palaeothentids (see fig. 10).

Both the first and second lower molars are represented, but one specimen of m1 and both specimens of m2 are heavily worn. SC-1613 (an isolated m1) is relatively unworn, but the distal portion of the talonid is missing; a shallow bifurcation of the paraconid can be seen clearly (fig. 4). There is a mure, or anterior shelflike extension (Bown and Fleagle, 1993; see fig. 4b), on the entoconid. The first molar also possesses a trigonid on which the metaconid is twinned into a large talonid moiety and much smaller trigonid moiety (trigonid pattern 4 of Bown and Fleagle, 1993).

The first lower molar in *Titanothentes* is extremely long mesiodistally. Even though it is severely worn in SC-3157a, the m1 of this specimen is, in fact, longer than all other palaeothentid m1s (fig. 5). In addition to possessing a long m1, *Titanothentes* also has a uniquely elongated m1 paracristid, nearly twice the size of that seen in any other palaeothentid (fig. 6). The great length of this tooth may not be attributable to larger overall body size in *Titanothentes,* as the m2 of the new genus is *shorter* mesiodistally than in some other palaeothentids (see fig. 5) and the depth of the dentary at m1 is indistinguishable from that in *P. aratae,* formerly the largest known member of the Palaeothentinae (fig. 7).

The m2 is broad, short, and heavily worn in both the holotype and SC-3156. Measurements of the holotype indicate that this tooth is smaller than the average m2 of *P. aratae* in terms of mesiodistal (MD) length (see fig. 5), although the buccolingual (BL) width of the tooth is exceeded by only two specimens of *P. aratae.* The ratio of m1/m2 MD length in *T. simpsoni* is also unique among palaeothentids, as m1 is 195% the MD length of m2. This value falls well outside the range of the m1/m2 length ratio for all other palaeothentines (fig. 8). It is possible that some portion of the reduced length of m2 in the holotype may be an artifact of damage (a small portion of the distolingual margin of the tooth enamel is missing) or of interstitial wear against m1, which appears to be advanced. There is, however, interstitial wear on m1 as well, which suggests that the m1/m2 ratio reported probably corresponds closely to the

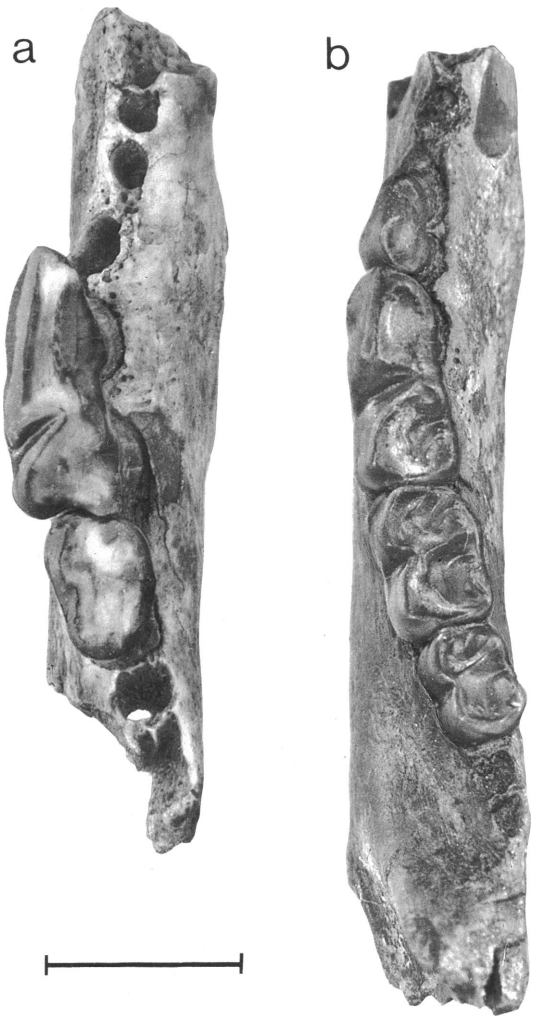

Fig. 6. *Titanothentes* compared to the largest previously known palaeothentid, *Palaeothentes aratae.* **(a)** Holotype of *T. simpsoni* (MACN SC-3157a); **(b)** right dentary of *P. aratae* (MACN SC-1302: image reversed) in occlusal view. Note increased MD length of m1 and relative elongation of m1 paracristid in *T. simpsoni.*

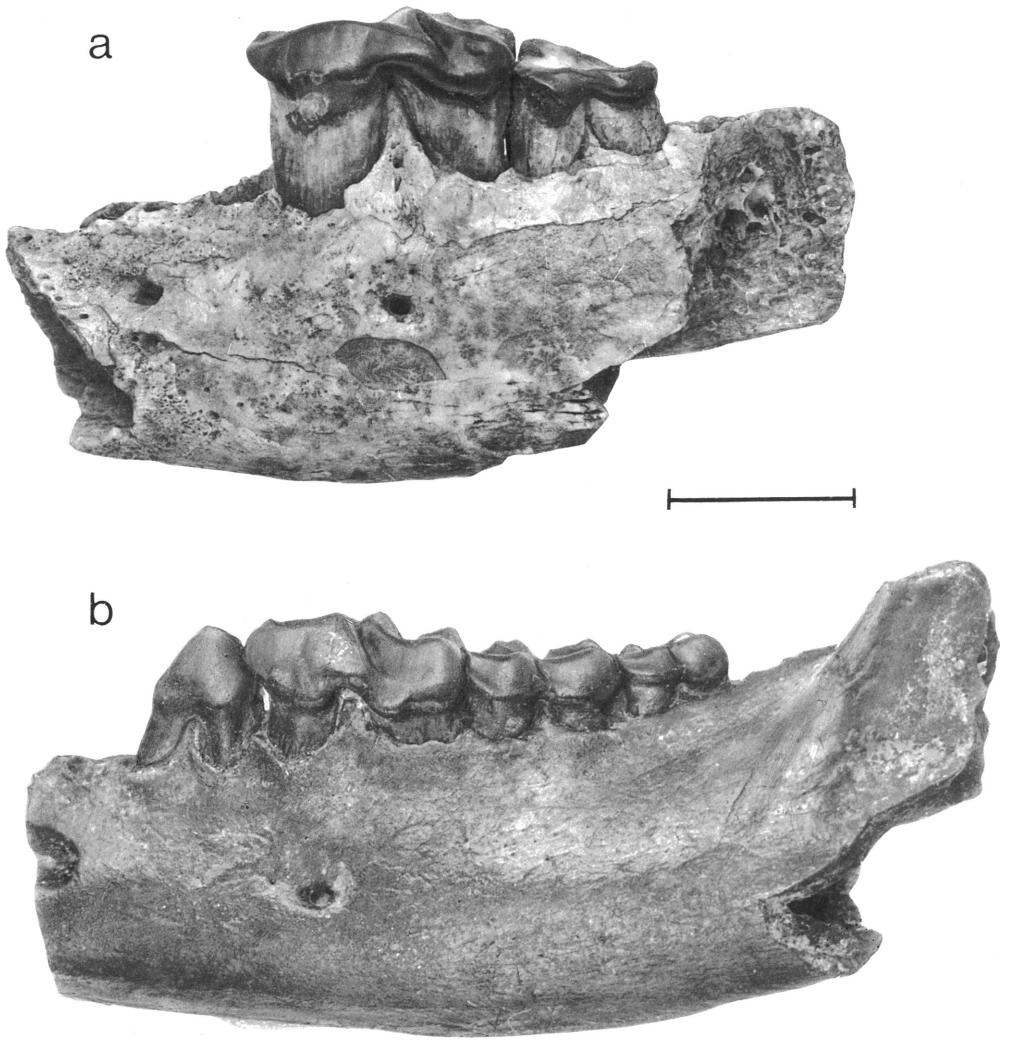

Fig. 7. *Titanothentes* compared to the largest previously known palaeothentid, *Palaeothentes aratae*. **(a)** *T. simpsoni* (MACN SC-3157a); **(b)** *P. aratae* (MACN SC-1302: image reversed) in lateral view. These taxa are indistinguishable in the depth of the corpus below m1.

value that would be expected if the specimens were unworn.

T. simpsoni shares several characters with other palaeothentines. In particular, the shallowly bifurcated paraconid and the entoconid mure are seen primarily in *P. aratae* and *P. primus*. Bown and Fleagle (1993) proposed that these characteristics of m1 link *P. aratae* and *P. primus* deep within the palaeothentine clade. Phylogenetic analysis of *Palaeothentes* and *Titanothentes*, using the characters and polarities of Bown and Fleagle (1993) and the maximum parsimony algorithm of the computer program Hennig86 (Farris, 1988), confirms this arrangement and suggests that *P. aratae, P. primus,* and *T. simpsoni* are the most derived of the palaeothentines. The data at hand are not sufficient, however, to resolve the trichotomy between these three species and additional data are needed to clarify the phylogenetic relationships within this clade of advanced palaeothentids.

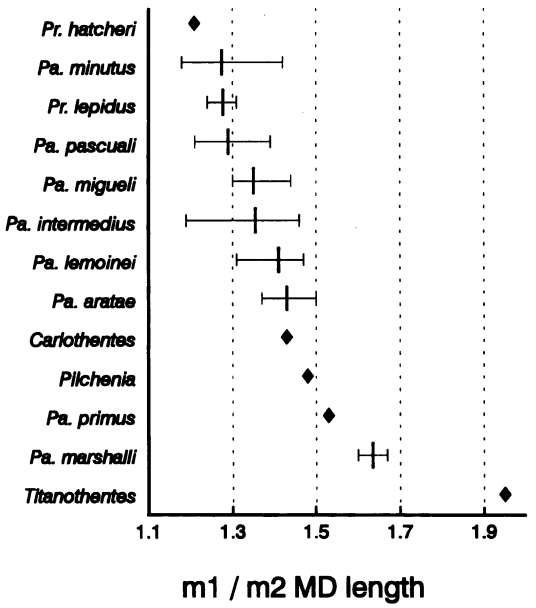

Fig. 8. Ratio of m1 MD length over m2 MD length in palaeothentids. *T. simpsoni* falls outside the range of all previously known taxa for this variable.

SUBFAMILY ACDESTINAE
BOWN AND FLEAGLE, 1993

Acdestis oweni Ameghino, 1887

NEW MATERIAL: MACN SC-3649, a left dentary with complete dentition (fig. 9).

LOCALITY: The specimen was collected from locality 94d-2 (49°37.65'S latitude, 70°06.21'W longitude; see fig. 1), south of Estancia La Ensenada. This site is located in extensive exposures of the Santa Cruz Formation that are developed along the south side of the Río Chalia, south of Laguna Grande and about 125 km northwest of Cmte. Luis Piedrabuena. These exposures almost certainly include the "Sehuen" locality described by Ameghino (1891) and Hatcher (1903). 94d-2 is in the basal Santa Cruz Formation, about 50 m above the local contact with marine rocks of the underlying Grupo Patagonia.

DESCRIPTION: The new specimen of the acdestine *Acdestis oweni* is a nearly complete left dentary with complete dentition (fig. 9). This is the first known specimen of the species with associated anterior and posterior teeth.

The corpus is complete anteriorly; posteriorly it is broken obliquely from the anterior root of the ramus inferiorly to the base of the corpus. There is a slight medial inflection of the base of the dentary. The corpus is relatively shallow and gracile, but lies within the range of depth (5.43 mm) at m1 of *A. oweni* specimens known previously. The dentary is uniformly deep under the molars, but is significantly shallower anterior to p3. There is a mental foramen between the roots of m1 at midcorpus and a second foramen between c and p1 that opens anteriorly. The symphyseal surface is a nearly horizontal, oval structure that is concave and rugose. Although it is broken superiorly, it is clear that the root

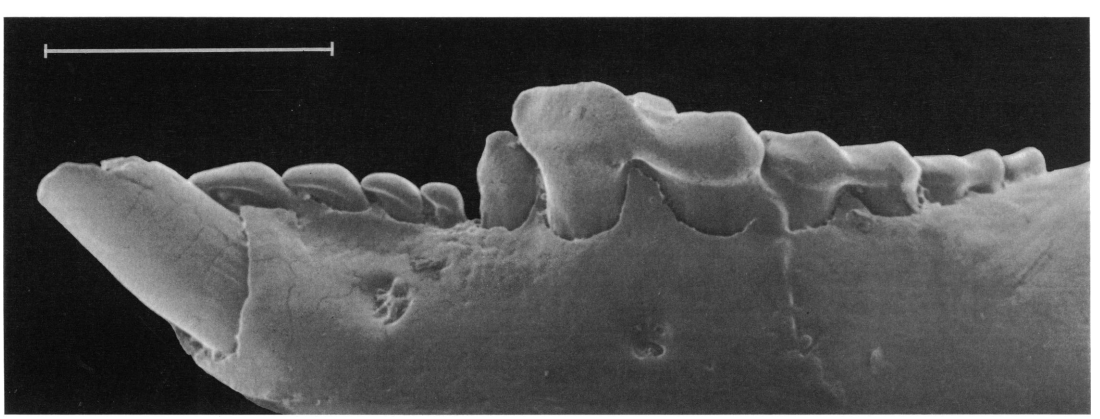

Fig. 9. Scanning electron micrograph of *Acdestis oweni* dentary MACN SC-3649 (lateral view). Note the unusual conformation of the crowns of i1-p2.

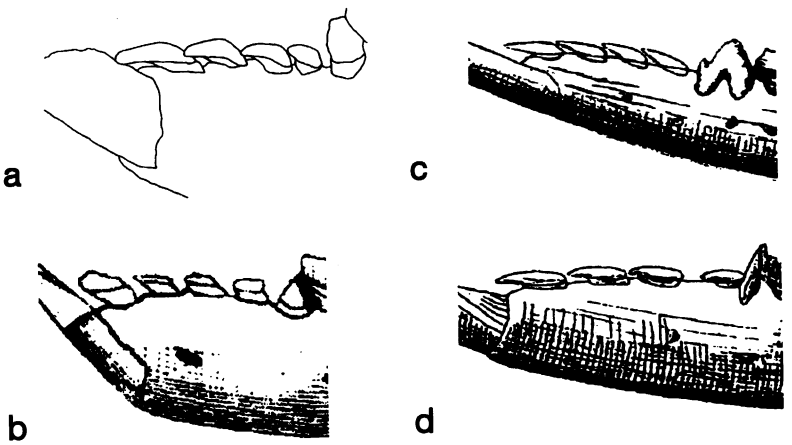

Fig. 10. Mandibular dentition of *A. oweni* and other caenolestoids (lateral view: not to scale). **(a)** New specimen of *A. oweni* (MACN SC-3649) showing the "bent" appearance of i2-p2; **(b)** *A. oweni* as originally reconstructed (the crowns of i1-p2 were unknown); **(c)** *Palaeothentes*; **(d)** *Abderites* (Abderitidae). [b-d after Ameghino]

of the ascending ramus did not overlap the molar row in lateral view and that the ramus was deeply excavated for the insertion of the masseter muscle.

The central incisor is a large, procumbent tooth. The bone is formed closely about the root, which can be seen (on the lingual surface of the dentary) to extend posteriorly to below m1. Most of the tip of the crown is missing, but it appears to have been bilaterally compressed. The anteriormost part of the remaining crown is smooth, as if from wear, and a small dentine island is exposed. More posteriorly, the surface of the crown enamel is cracked.

There are four teeth between the enlarged incisor and p3. They are minute and single rooted. On each, the enamel cap extends posteriorly down the root on the distal side, is flat occlusally, and is elongated anteriorly, overlapping the root and giving the teeth a "bent" appearance in lateral view (figs. 9 and 10a). The tooth nearest the incisor is the largest and the tooth crowns decrease posteriorly in both size and in the degree of anterior extension. The anterior extension of each tooth contacts the back of the crown of the next anterior tooth.

The p3 in SC-3649 is a moderately tall, pointed tooth, closely approximated against the anteroinferior edge of m1. It resembles the p3 in SC-972 (see fig. 13 of Bown and Fleagle, 1993). A single cusp is situated mesially on the crown. There are two roots lingually, but they appear fused on the buccal side; the alveolus is "figure 8-shaped" as in MACN 2038 (Marshall, 1980). The cusp tip is slightly damaged.

The heavily worn molars, which decrease in size posteriorly, conform to the pattern seen in all other acdestines; the paraconid is not bifurcated, and m2-4 are not constricted in the region of the hypoflexid and talonid notch as in many palaeothentines. The new dentary closely resembles other specimens of *A. oweni* in its molar teeth. The m1 displays a trigonid pattern, found in 61% of previously known specimens of the species, in which the protocristid is more or less transversely aligned and the metaconid is not twinned (type 1 trigonid pattern of Bown and Fleagle, 1993). The m4 is greatly reduced (about the size of p3) and lacks cusp definition, another hallmark of the species.

DISCUSSION: This uniquely complete dentary provides answers to some lingering questions about the dental morphology of *Acdestis oweni*. Initially, the anteriormost tooth of *A. oweni* was reconstructed as a large, procumbent incisor by Ameghino (1887; see fig. 10b). Indeed, the anterior incisor in the new specimen is also large and procumbent, a condition similar to that seen in other palaeothentids from the Patagonian Miocene.

The nature of the other antemolar teeth of *A. oweni* was unclear previously. In the first illustrations of the species, Ameghino (1891) reconstructed four teeth between the central incisor and p3, with crowns that were low and relatively flat (c-p2) or faintly caniniform (i2: see fig. 10b). As more specimens were discovered, the number of teeth anterior to p3 (judged from alveoli) was shown to vary; in at least three specimens that are complete between the p3 and the enlarged incisor, there are only three alveoli in this area (Marshall, 1980). Marshall (1980) hypothesized that p2 was lost in these individuals, on the basis of a space between p3 and the alveolus of the next anterior tooth on one dentary (MACN 5693) and a small depression in this area in another (MACN 8254). The alveolus immediately posterior to the enlarged incisor of some incomplete *A. oweni* dentaries (e.g., MACN SC-578 and SC-1473) had suggested that the "penultimate anterior" tooth was small and implanted vertically (Bown and Fleagle, 1993).

The new specimen contains four teeth between i1 and p3 and demonstrates that Ameghino's reconstruction of the shapes of the i2-p2 crowns was inaccurate. Rather than the flat or caniniform appearance hypothesized, these teeth have "bent" crowns when seen in lateral views (figs. 9 and 10a). In fact, their shape is similar to that seen in other palaeothentids and even abderitids (figs. 10c, d). The antemolar teeth are also similar to those seen in some living shrews and their shape may be related to insectivory, although the dietary pattern inferred for *A. oweni,* based on body weight and dental shearing crests, also includes a high proportion of fruit (Strait et al., 1990; Bown and Fleagle, 1993). Further work, including microwear analysis, should help to clarify the dietary preferences of this interesting Miocene marsupial.

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