

NEW PALAEOThENTID MARSUPIAL FROM THE MIDDLE MIOCENE OF BOLIVIA

by FRANCISCO J. GOIN, MARCELO R. SÁNCHEZ-VILLAGRA, RICHARD F. KAY,
FEDERICO ANAYA-DAZA *and* MASANARU TAKAI

ABSTRACT. The new species *Acestis maddeni* is described based on the most complete skull of a palaeothentid marsupial known so far. The skull preserves most of the upper dentition and of the ear region, the latter an anatomical region previously unknown in this extinct family. A right maxillary fragment including C-M2 also belongs to the new species. The specimens come from the middle Miocene localities of Rosario and Quebrada Honda in southernmost Bolivia. The generic allocation of the new species is somewhat problematic, given that most of the taxonomy of fossil palaeothentids is based on lower dentitions. Compared to that of caenolestids, the skull of *A. maddeni* is much larger, with a shorter and broader snout, a proportionally narrower interorbital constriction, and a less globular, more triangular-shaped braincase in dorsal view.

KEY WORDS: Marsupialia, Palaeothentidae, Caenolestidae, Bolivia, Miocene, anatomy.

MARSUPIALS of the order Paucituberculata have had a long Cenozoic history in South America, their earliest record being in the mid Palaeocene (Itaboraian Age) of Brazil and southern Argentina (Oliveira *et al.* 1996). All extant representatives of this order belong to the family Caenolestidae, with only two genera and seven species with a restricted distribution in Andean South America (Bublitz 1987). By contrast, the fossil record of caenolestoids (*sensu* Kirsch *et al.* 1997, excluding Kollpaniinae) is very rich. Three major groups have been recognized: the Caenolestidae, and the more derived and extinct Abderitidae and Palaeothentidae. Palaeothentids occur in Oligocene through Miocene rocks from Colombia to southern Argentina and Chile (Marshall 1980; Bown and Fleagle 1993). Most species are known only from dental remains and/or jaw fragments. Bown and Fleagle (1993) recognized two subfamilies of palaeothentids: the herbivorous to frugivorous Acestinae and the largely carnivorous Palaeothentinae. Following the revision of Bown and Fleagle (1993) and the addition of Rae *et al.* (1996), we recognize ten genera and 20 species of palaeothentids.

Here we describe the most complete skull so far known of a palaeothentid, belonging to a new species of *Acestis*. The skull preserves not only the molars but also the anterior dentition, as well as detailed aspects of the ear region, the latter an anatomical region previously unknown in this extinct family of marsupials.

Abbreviations used in this paper are as follows: MNHN-Pal-Bol-V, Museo Nacional de Historia Natural, Paleontologie, La Paz, Bolivia; MACN, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Buenos Aires, Argentina; MLP, Museo de Ciencias Naturales de La Plata, Argentina; PU, Princeton University collections at Yale University, USA; FMNH, Field Museum of Natural History, Chicago, USA. Ma, million years before present; I, C, P, M, upper incisors, canine, premolars, and molars, respectively; StB, StD, stylar cusps B and D, respectively. All measurements are in mm.

SYSTEMATIC PALAEOONTOLOGY

Supercohort MARSUPIALIA Illiger, 1811

Order PAUCITUBERCULATA Ameghino, 1894

Family PALAEOThENTIDAE (Sinclair, 1906) Osgood, 1921

Subfamily ACDESTINAE Bown and Fleagle, 1993

Genus ACDESTIS Ameghino, 1887



TEXT-FIG. 1. *Adestis maddenii* sp. nov. Holotype, MNHN-Pal-Bol-V-4000 in lateral (top), dorsal (middle), and ventral (bottom) views. Scale bar represents 10 mm.

Adestis maddenii sp. nov.

Text-figures 1–3

Derivation of name. The species is named after Dr Richard H. Madden, in recognition of his contributions to the collection and study of South American mammals.

Holotype. MNHN-Pal-Bol-V-4000, a fragmentary skull including most of the tooth series on both sides, the palatal region, the basicranial region, and part of the sidewall and roof of the braincase (Text-figs 1, 3).



TEXT-FIG. 2. *Acestis maddeni* sp. nov. Specimen MNHN-Pal-Bol-V-003689. Occlusal (top) and lingual (bottom) views. Scale bar represents 3 mm.

Referred specimen. MNHN-Pal-Bol-V-003689, a right maxillary fragment including C-M2 (Text-fig. 2).

Diagnosis. Known skull dimensions about one third larger than *Acestis oweni* and dental dimensions 30–50 per cent larger than those of *A. lemairei*; in comparison with *A. lemairei* the decrease in size from M1 to M2 is more marked; in comparison with both *A. oweni* and *A. lemairei* the P3 is more laterally compressed and penetrates more deeply in the anterolabial notch of M1.

Measurements. For dental measurements, see Table 1. Skull measurements (in mm) of the holotype are as follows: total (condylobasal) length, 53.8; palatal length, 28.8*; interorbital constriction width, 8.7*; intercondylar width, 13.6; maximum palate width (between M1s), 11.3; intersquamosal width, 21.0; skull height at occipital, 14.2. *indicates that the measurement is approximate, accounting for breakage and distortion.

Distribution and age. The type specimen comes from Rosario, 6 km north of Quebrada Honda, on the physiographic boundary between the eastern Cordillera and Altiplano in southernmost Bolivia (Hoffstetter 1977; MacFadden *et al.* 1990). It was collected by Yuko Okamura on August 12, 1994, from 'Nivel I–II' of Río Rosario (MacFadden *et al.* 1990). The rocks of Río Rosario are roughly equivalent in age to those of Quebrada Honda, and palaeomagnetic and $^{40}\text{K}/^{40}\text{Ar}$ data suggest an age between 11.9 and 15.4 Ma (MacFadden *et al.* 1990), i.e. approximately mid Miocene. Specimen MNHN-Pal-Bol-V-003689 was collected on August 8, 1994, from the locality of Willajara, 'Nivel I' of Quebrada Honda.

Description

Upper dentition. The upper dental formula is I3.C1.P3.M4/. I1 is the largest upper incisor, with its tip projecting far below that of I2–3. It is mesio-laterally compressed, with its roots very deeply implanted, and its tip slightly recumbent. I2–3 are much shorter and are set in line, behind and labially to I1; I2 is more laterally compressed than I3. Behind I3 there is a short diastema.

Judging by the left and right alveoli in the holotype of *A. maddeni*, the canine was moderately developed and laterally compressed. Specimen MNHN-Pal-Bol-V-003689 preserves the root of the right canine, which is quite short and points backwards in the maxillary. Between the canine and the first upper premolar there is a short diastema.

TABLE 1. Dental measurements (mm) of *Acelestis maddeni* sp. nov. (MNHN-Pal-Bol) and other aclestine palaeo-
 thetids with known upper dentitions. Mean values for *A. oweni* were taken from Marshall (1980, table 18); those for
A. lemairei and *Trelewthentes rothi* were averaged from raw data in Bown and Fleagle (1993, tables 4, 6).
 Abbreviations: L, length; W, width.

	LP1– M4	LP3– M4	LM 1–4	L P3	W P3	L M1	W M1	L M2	W M2	L M3	W M3	L M4	W M4
<i>Acelestis maddeni</i> :													
V-4000 (type, left)	29.6	13.7	9.6	5.2	2.4	4.4	4.2	2.8	3.8	1.8	2.7	1.4	1.7
<i>A. maddeni</i>													
V-4000 (type, right)	29.5	13.2	9.6	4.3	2.4	4.3	4.0	2.8	3.6	1.6	2.2	1.3	1.7
<i>A. maddeni</i>													
V-003689				3.8	2.8	4.4	4.1	2.9	3.7				
<i>Acelestis oweni</i>		10.9	8.49	3.03	2.20	3.55	3.33	2.49	3.14	1.26	1.96	0.87	1.28
<i>Acelestis lemairei</i>						3.28	2.85	2.52	2.84				
<i>Trelewthentes rothi</i>						3.28	2.92	2.38	2.83				

P1–3 are two-rooted and closely set. P1–2 are small and anteroposteriorly aligned. Specimen MNHN-Pal-Bol-V-003689 has a well-preserved P2; it has three cusps, of which the central one is the largest and is aligned with two accessory, much smaller cusps, one anterior and one posterior to it. P3 is comparatively enormous and is placed slightly labial to P1–P2. The anterior root of P3 is much larger than the posterior one, and is not straight but curved backwards. The P3 crown is wider in its posterior half. Lingually, it has a well-developed ‘talon’, which in both specimens examined is heavily worn. Labially the P3 develops a high, subhorizontal edge of trenchant aspect.

Molars decrease rapidly in size from M1 to M4, and especially between M1 and M2, and M2 and M3 (see Table 1). In occlusal view M1–2 are subquadrate, while M3–4 are subtriangular. The ‘hypocone’ (metaconule) in M1 is clearly higher than the protocone in M1, while both structures are subequal in height in M2. Styler cusps in M1–3 are large and labio-lingually compressed. In M1 the styler cusp D (StD) seems to be larger, or at least taller, than the styler cusp B (StB), while in M2–3 the StB is larger and taller than the StD. The crown of M4 in the holotype is completely worn (Text-fig. 1). In the M2 of specimen MNHN-Pal-Bol-V-003689 (Text-fig. 2), a very small cusp, the metacone (‘intermediate cuspule’ of Marshall 1980; Bown and Fleagle 1993; but see Marshall 1987 and Oliveira and Goin, in press) is visible, firmly attached to the lingual face of the StD, as in other palaeo-*the*tids and as in caenolestids. Each successive molar is in full contact with the contiguous one, as indicated by interstitial facets. M3 has its ‘hypocone’ highly reduced, while in M4 it is most probably absent. The posterior border of P3 fits deeply in the anterolabial portion of the M1 in a ‘tongue and groove’ structure, which in the holotype of *A. maddeni* is particularly deep as compared to other species of the genus.

Skull. Compared to that of caenolestids, the skull of *A. maddeni* is much larger, with a shorter and broader snout, a proportionately narrower interorbital constriction, and a less globular, more triangular-shaped braincase in dorsal view. Judging by the lateral expansion of the maxillae, the zygomatic arches must have been quite strong. The infraorbital foramen opens in a point above the posterior root of the P3. The contact area between nasals, frontals, and maxillae has not been preserved, neither have the lacrimals nor the anterior part of the frontals. Frontal cristae are present although weakly developed; they almost join in the midline of the skull well behind the interorbital constriction. The sagittal crest is absent; only slightly marked temporal cristae are present. Even though moderately developed, the lambdoid cristae are much stronger than those of caenolestids.

On the left side of the skull roof, a sedimentary cast of the anterior portion of the olfactory bulb is preserved. It is shaped as that in living didelphids and does not show the strong lateral expansion present in long-snouted marsupials, as in the caenolestid *Caenolestes* (Herrick 1921) and the peramelid *Isodon obesulus* (Haight and Murray 1981).

A large posterior palatal vacuity, which extends up to the level of the anteriormost edge of M1 is visible in ventral view. The anterior palatal vacuity extends posteriorly up to the posterior border of P1. This is within the range of variation of size of this feature in extant species of caenolestids (Osgood 1921; Patterson and Gallardo 1987). In MNHN-Pal-Bol-V-003689 there is a small foramen lingual to the anterior root of the P1. This foramen is not present in the holotype of *A. maddeni*.

The basicranial portion of the skull is well preserved. There is a raised central stem on the basioccipital. As in other caenolestids, the pars mastoidea of the petrosal is smooth, almost vertical, and interrupts the lambdoid crest dorsally.

The ventralmost portion of the mastoid has not been preserved, but it seems clear that the paroccipital process of the exoccipital ran parallel and close to it, even though not so close as in *Caenolestes*. There are two large hypoglossal foramina on each side of the skull. The paroccipital processes, partially broken in the specimen, were prominent.

The carotid foramen is in the basisphenoid, anterior to the suture with the basioccipital. The transverse canal foramen is situated just anterior to the carotid foramen. In extant caenolestids, the transverse canal foramen is anterior to the carotid foramen, and there is no intramural connection between the openings of each side (Sánchez-Villagra and Wible 2001). Also, the groove beside the opening of the transverse canal in *A. maddeni* points posterolaterally, not anterolaterally as in caenolestids.

Judging from a small portion preserved in the left side of the skull, the alisphenoid tympanic wing was located more posteriorly than in extant caenolestids; in the latter, the anterior wall of the alisphenoid bulla reaches as far anteriorly as the opening of the transverse canal. Neither the ectotympanic nor most of the alisphenoid are preserved in the holotype of *A. maddeni*. The rostral tympanic process of the petrosal (hereafter RTPP) is of similar size and shape as in extant caenolestids. Because of breakage of the alisphenoid, it is not possible to determine whether the foramen ovale is surrounded by both the alisphenoid and the petrosal, as in most marsupials including extant caenolestids, or by just the alisphenoid as in *Dromiciops* and most Diprotodontia (Sánchez-Villagra 2001). The foramen medial to the petrosal (just medial to the RTPP; see Text-fig. 3) is identified as the inferior petrosal sinus foramen (*sensu* Wible 1984), a structure universally present among extant marsupials with the exception of *Dromiciops*, *Phascolarctos*, and *Acrobates* (Marshall and Muizon 1995; Sánchez-Villagra 1998). This foramen is very large in *A. maddeni*.

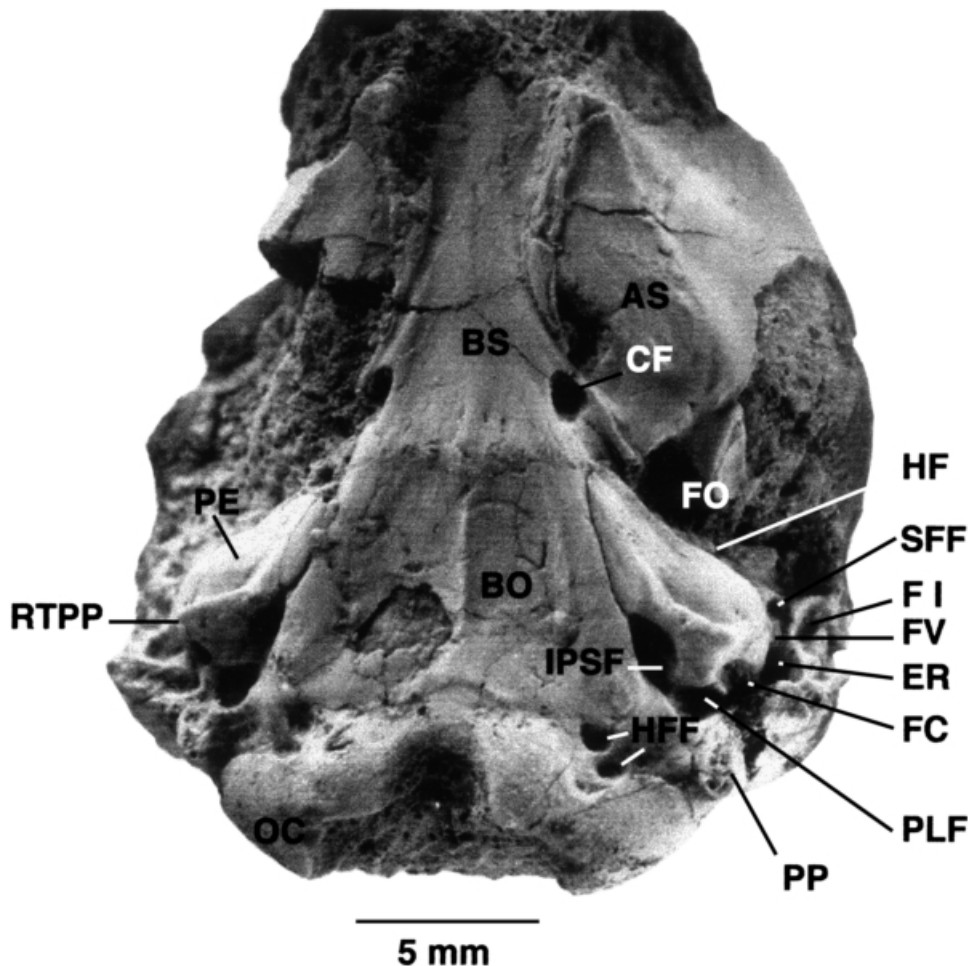
The hiatus fallopii (an anterior opening in the petrosal for the greater petrosal nerve, a branch of the facial nerve) is situated ventrally instead of dorsally as in *Caenolestes fuliginosus* (Sánchez-Villagra and Wible 2001). The stapedial ratio (obtained by dividing the maximum length of the fenestra vestibuli by its perpendicular) is approximately 1.4, similar to that of *Didelphis* (Segall 1971).

DISCUSSION

Taxonomy

In spite of the completeness of the type specimen described here, its generic allocation is somewhat problematic, given that most of the taxonomy of fossil palaeothentids is based on lower dentitions (Marshall 1980; Bown and Fleagle 1993). According to Marshall (1980, p. 52), palaeothentids include a primitive dental formula of I3/2, C1/1, P3/(2–3), M4/4, and their upper dentition and skull is characterized by the following features: (1) 'P2 laterally compressed with prominent central cusp and smaller anterior and posterior accessory cuspules'; (2) 'P3 enormous, rivalling M1 in size in some taxa, and with crown height equal to or greater than that of M1'; (3) 'posterior end of P3 crown much broader than anterior and with posterolingual cingular shelf'; (4) 'anterior root of P3 is much narrower transversally than posterior root'; (5) 'sharp cutting edge formed along labial sides of M1–2 and extending onto P3'; (6) 'M1 with cingular shelf along anterior edge of paracone'; (7) 'intermediate conule' (metacone) weakly developed in unworn M1–3 only in *P. minutus*'; (8) 'anterior ends of M1–3 much broader than posterior ends'; (9) 'sectorial-posterointernal surface of P3 shears against labial surface of m1 trigonid'; (10) 'no trace of antorbital vacuity as in Caenolestinae (= Caenolestidae)'. According to Bown and Fleagle (1993, p. 17), palaeothentids also differ from caenolestids (in upper dental features) in having (11) 'P1–2 very reduced', and (12) 'M1 with elevated hypocone platform (unworn teeth), invariably separated from trigon at lingual midline of tooth by a deep fissure'. In turn, they differ from abderitids in having (13) 'M1–3 tribosphenic, unsquared, and divided into distinct elevated hypocone platform and lower trigon basin', and (14) 'M1–3 lacking lophs connecting primary labial and lingual cusps'.

With the exception of characters 9 and 10, which are impossible to verify in the specimens studied, all other features, including the dental formula, agree well with the upper dental form of the new palaeothentid. According to Marshall (1980, p. 54), the only feature involving upper dentitions that could distinguish *Palaeothentes* from *Acdestis* was, in the former (15) a more gradual size decrease from M2 to M4. Bown and Fleagle (1993) diagnosed the subfamily Acdestinae as having, in the upper dentition, (16) 'more triangular M2–4', and (17) more reduced M4, generally lacking distinct cusps. An additional feature of the dentary of acdestines, the foreshortened ramus, possibly implies (18) a relatively shortened upper dental row in relation to palaeothentines. While feature 16 is somewhat ambiguous (compare Marshall 1980, figs 16, 19, 23, 26, 30, and Bown and Fleagle 1993, figs 24–25, with Marshall 1980, fig. 34, and Bown and Fleagle 1993, fig. 15), all other features are not, and suggest the placement of the new



TEXT-FIG. 3. *Acestis maddeni* sp. nov. Holotype, MNHN-Pal-Bol-V-4000. Detail of basicranial region. Scale bar represents 5 mm. Abbreviations: AS, alisphenoid; BO, basioccipital; BS, basisphenoid; CF, carotid foramen; ER, epitympanic recess; FC, fenestra cochleae; FI, fossa incudis; FO, foramen ovale; FV, fenestra vestibuli; HFA, hiatus fallopii; HFF, hypoglossal foramina; IPSF, inferior petrosal sinus foramen; OC, occipital condyles; PE, petrosal; PLF, posterior lacerate foramen; PP, paroccipital process; RTHP, rostral tympanic process of the petrosal; SFF, secondary facial foramen.

palaeoentid in the Acestorinae. Regarding feature 18, it is interesting to note that *Palaeoenthes aratae* (a relatively large palaeoentine) has small diastemata between the upper canine and P1, P1 and P2, and P2 and P3 (the premolar diastemata in *P. minutus* seem to be even larger). The holotype of *A. maddeni* shows only a short diastema between the canine and P1, but not between the premolars (see also *Acestis oweni*; Marshall 1980, fig. 34a–c; Bown and Fleagle 1993, fig. 15).

Taxonomy among acestine palaeoentids is mainly based on features of the lower dentition; as such, it precludes any confident generic assignment of the materials studied here. A recent review by Bown and Fleagle (1993) led to the recognition of four genera: *Acestis*, *Acestoides*, *Acestodon*, and *Trelewthentes*. *Acestoides* and *Acestodon* are known only from lower dentitions. *Trelewthentes* includes a few M1 and M2; they differ from the new specimens, especially from MNHN-Pal-Bol-V-003689, in which the upper molar crowns are not worn away, in that the protocone and ‘hypocone’ are more widely

separated by a deep valley. Finally, both known species of *Acelestis*, *A. oweni* and *A. lemairei*, include upper dentitions among their referred specimens. Upper molars of the Rosario skull are more similar to those of *A. oweni* in that there is a more drastic decrease in size from M1 to M4 and in the comparatively larger size of P3. However, it differs dentally from *A. oweni* and *A. lemairei* in its larger size, and in that the P3 is relatively longer, or more laterally compressed, and ‘penetrates’ deeper in the anterolabial notch of M1 (see Text-figs 1–2). *A. maddeni* also differs from *A. lemairei* in that it shows a more rapid decrease in size from M1 to M2 (see Table 1). Finally, it differs from *A. oweni* in several cranial features (see below). In brief, the evidence at hand suggests that the new specimens represent a new species of palaeothentid, most probably belonging to the genus *Acelestis*.

Skull morphology

Including the holotype of *Acelestis maddeni*, up to four skulls of palaeothentid paucituberculatans are known. One of them, MACN 8271, belongs to the Palaeothentinae *Palaeothentes minutus*, from the lower–middle Miocene of Patagonia (Santacrucian Age), and was damaged subsequent to its illustration by Ameghino (1887, p. 6; see also Marshall 1980, fig. 20). Two other partial skulls are assignable to the accestine *Acelestis oweni*, also from the lower–middle Miocene of Patagonia: specimen PU 15225, and specimen FMNH 13160, the former described by Sinclair (1906) as *Palaeothentes intermedius* (Marshall 1980, p. 93). The fourth skull known to date is MNHN-Pal-Bol-V-4000, described here. We compare below some features of the skull of *A. maddeni* with those of other fossil and extant caenolestoids.

A. oweni (PU 15225) is approximately one-third smaller than *A. maddeni*. The most marked difference between the two skulls is that *A. maddeni* is more slender, while *A. oweni* is stouter and proportionally wider. The sagittal and frontal cristae are much more marked in *A. oweni* than in *A. maddeni*. Frontal cristae in *A. oweni* merge into a sagittal crest more anteriorly than the point at which the frontal cristae almost join in *A. maddeni*. The incisive foramina are much larger in *A. maddeni*. In *A. oweni* they expand posteriorly just behind the canine, while in *A. maddeni* they expand well behind P1. The nasals in *A. maddeni* are also expanded posteriorly, but not so markedly as in *A. oweni*. The floor of the orbit is equally expanded in both species. In *A. maddeni* the aperture of the infraorbital foramen is located at the level of the posterior root of P3, while in *A. oweni* it is located more anteriorly, at the level of the anterior root of the same tooth. The orbits in *A. oweni* are, relative to skull length, larger than those of *A. maddeni*. In *A. maddeni* there is a marked lateral expansion of the braincase. The width of the maxillary vacuities is also larger in *A. maddeni* in contrast to *A. oweni*.

Some of the observed differences between the skulls of *A. oweni* and *A. maddeni* might be related in part to scaling or to sexual dimorphism. Among living didelphids, *Monodelphis dimidiata* shows such extreme differences in skull form between males and females that both sexes should be treated separately in taxonomic analysis according to Pine *et al.* (1986). Some of these differences in *Monodelphis* refer, as it happens in both species of *Acelestis*, to the relative development of the frontal and sagittal cristae.

Marshall and Pascual (1977) described *Pichipilus centinelus* from the Miocene (Santacrucian Age) of southern Patagonia. They suggested the presence of antorbital vacuities in this species; however, a recent examination of the same type material could not confirm this inference, owing to the poor state of preservation of the specimen (Goin, pers. obs.). The infraorbital foramen is much larger in *Pichipilus* than in *A. maddeni*, the nasals are also posteriorly expanded, and the maxillary and especially incisive palatine foramina are not as expanded in *Pichipilus* as they are in *A. maddeni*.

The dental anatomy of palaeothentids is more derived than that of caenolestids (see Marshall 1980; Bown and Fleagle 1993). However, their cranial anatomy shows several features in more plesiomorphic states than those of caenolestids, including the following:

1. Caenolestids have a very elongated rostrum, a feature possibly correlated with the presence of antorbital vacuities and laterally expanded olfactory bulbs (Herrick 1921). None of these features is present in known skulls of palaeothentids. In *Acelestis maddeni* olfactory bulbs are not laterally expanded (see above), a feature that corresponds well with the relatively compressed interorbital constriction (in caenolestids the interorbital constriction is wider relative to skull length); judging from specimen PU 15225 of *Acelestis oweni*, antorbital vacuities were not present in representatives of this genus.

2. General basicranial features in the holotype of *Acelestis maddeni* are as generalized as those of caenolestids. Some features seem, however, to be even more primitive in the former: the paroccipital processes are less compressed against the mastoid part of the petrosal, the location of the alisphenoid bullae is posterior to the transverse canal foramen and the carotid foramen, and the groove at the opening of the transverse canal is posterolaterally oriented, instead of the (rare among living South American marsupials) anterolateral orientation recorded in caenolestids.

Acknowledgements. This work was financed by the US National Science Foundation to RFK and to Dr R. H. Madden. MRSV thanks the support of the Lehrstuhl für Spezielle Zoologie, Universität Tübingen. FJG thanks the logistic support of the Alexander Humboldt-Stiftung. We both thank J. A. Clack and J. R. Wible for useful suggestions to improve the manuscript.

REFERENCES

- AMEGHINO, F. 1887. Enumeración sistemática de las especies de mamíferos fósiles coleccionados por Carlos Ameghino en los terrenos eocenos de la Patagonia austral y depositados en el Museo de La Plata. *Boletín del Museo de La Plata*, **1**, 1–26.
- 1894. Énumération synoptique des espèces de mammifères fossiles des formations éocènes de Patagonie. *Boletín de la Academia de Ciencias de Córdoba*, **13**, 259–452.
- BOWN, T. M. and FLEAGLE, J. G. 1993. Systematics, biostratigraphy, and dental evolution of the Palaeothentidae, late Oligocene to early–middle Miocene (Deseadan–Santacrucian) caenolestoid marsupials of South America. *Journal of Paleontology*, **67**, 1–76.
- BUBLITZ, J. 1987. Untersuchungen zur Systematik der Rezenten Caenolestidae Trouessart, 1898. *Bonner Zoologische Monographien*, **23**, 1–96.
- HAIGHT, J. R. and MURRAY, P. F. 1981. The cranial endocast of the early Miocene marsupial, *Wynardia bassiana*: an assessment of taxonomic relationships based upon comparisons with recent forms. *Brain, Behavior and Evolution*, **19**, 17–36.
- HERRICK, C. J. 1921. The brain of *Caenolestes obscurus*. *Field Museum of Natural History, Zoological Series*, **14**, 157–162.
- HOFFSTETTER, R. 1977. Un gisement de mammifères miocènes Quebrada Honda (Sud Bolivien). *Comptes Rendus Hebdomadaires des Seances de l'Académie des Sciences, Paris*, **284**, 1517–1520.
- KIRSCH, J. A. W., LAPOINTE, F.-J. and SPRINGER, M. S. 1997. DNA-hybridisation studies of marsupials and their implications for metatherian classification. *Australian Journal of Zoology*, **45**, 211–280.
- MACFADDEN, B. J., ANAYA, F., PEREZ, H., NAESER, C. W., ZEITLER, P. K. and CAMPBELL, K. E. J. 1990. Late Cenozoic paleomagnetism and chronology of Andean basins of Bolivia: evidence for possible oroclinal bending. *Journal of Geology*, **98**, 541–555.
- MARSHALL, L. G. 1980. Systematics of the South American marsupial family Caenolestidae. *Fieldiana Geology*, **5**, 1–145.
- 1987. Systematics of Itaboraian (middle Paleocene) age 'opossum like' marsupials from the limestone quarry at Sao José de Itaboraí, Brazil. 91–160. In ARCHER, M. (ed.). *Possums and opossums. Studies in evolution*. Surrey Beatty and Sons Pty Ltd, Sydney, 400 pp.
- and MUIZON, C. D. 1995. Part II: The skull. In MUIZON, C. D. (ed.). *Pucadelphys andinus* (Marsupialia, Mammalia) from the early Paleocene of Bolivia. *Mémoires du Muséum National d'Histoire Naturelle*, **165**, 21–90.
- and PASCUAL, R. 1977. Nuevos marsupiales Caenolestidae del 'Piso Notohipidense' (SW de Santa Cruz, Patagonia) de Ameghino. Sus aportaciones a la cronología y evolución de las comunidades de mamíferos sudamericanos. *Publicaciones del Museo Municipal de Ciencias Naturales de Mar del Plata 'Lorenzo Scaglia'*, **2**, 91–122.
- OLIVEIRA, E. V. and GOIN, F. J. in press. Marsupiais fósseis do Paleoceno de Itaboraí: origem, irradiação e história biogeográfica. In CACERES, N. C. (ed.) *Marsupiais do Brasil*. Universidade Federal do Rio de Janeiro, Rio de Janeiro.
- and CANDELA, A. M. 1996. Un nuevo marsupial 'pseudodiprotodonte' del Paleoceno medio de Itaboraí (Brasil). Consideraciones sobre el origen, radiación y heterocronía en los Paucituberculata. *Ameghiniana*, **33**, 468.
- OSGOOD, W. H. 1921. A monographic study of the American marsupial, *Caenolestes*. *Publications of the Field Museum of Natural History, Zoological Series*, **14**, 1–156.
- PATTERSON, B. D. and GALLARDO, M. H. 1987. *Ryncholestes raphanurus*. *Mammalian Species*, **286**, 1–5.
- PINE, R. H., DALBY, P. L. and MATSON, J. O. 1985. Ecology, postnatal development, morphometrics, and taxonomic status

- of the short-tailed opossum, *Monodelphis dimidiata*, an apparently semelparous annual marsupial. *Annals of the Carnegie Museum of Natural History*, **54**, 195–231.
- RAE, T. C., BOWN, T. M. and FLEAGLE, J. G. 1994. New palaeotheriid marsupials (Caenolestoidea) from the early Miocene of Patagonian Argentina. *American Museum Novitates*, **3165**, 1–10.
- SÁNCHEZ-VILLAGRA, M. R. 1998. Patterns of morphological change in the ontogeny and phylogeny of the marsupial skull. Unpublished PhD thesis, Duke University, Durham, North Carolina, 535 pp.
- 2001. The phylogenetic relationships of argyrolagid marsupials. *Zoological Journal of the Linnean Society*, **131**, 481–496.
- and WIBLE, J. R. 2001. Patterns of evolutionary transformation in the petrosal bone and some basicranial features in marsupial mammals, with special reference to didelphids. *Journal of Zoological Systematics and Evolutionary Research*, **39**, 26–45.
- SEGALL, W. 1971. The auditory region (ossicles, sinuses) in gliding mammals and selected representatives of non-gliding genera. *Fieldiana Zoology*, **58**, 27–59.
- SINCLAIR, W. J. 1906. Mammalia of the Santa Cruz beds. Marsupialia. *Reports of the Princeton University Expedition to Patagonia*, **4**, 333–460.
- WIBLE, J. R. 1984. The ontogeny and phylogeny of the mammalian cranial arterial pattern. Unpublished PhD thesis, Duke University, Durham, North Carolina, 705 pp.

FRANCISCO J. GOIN

Departamento Paleontología de Vertebrados
Museo de La Plata, Paseo del Bosque s/n, 6
1900 La Plata, Argentina
e-mail fgoin@museo.fcngm.unlp.edu.ar

MARCELO R. SÁNCHEZ-VILLAGRA

Zoologisches Institut, Universität Tübingen
Auf der Morgenstelle 28
D-72706 Tübingen, Germany
e-mail marcelo.sanchez@uni-tuebingen.de

RICHARD F. KAY

Department of Biological Anthropology and Anatomy
Duke University Medical Center, Box 3170
Durham, NC 27710, USA

FEDERICO ANAYA-DAZA

Universidad Autónoma 'Tomás Frías'
Facultad de Ingeniería Geológica
Casilla No. 5
Potosí, Bolivia

MASANARU TAKAI

Primate Research Institute
Kyoto University, Inuyama
Aichi 484, Japan

Typescript received 23 May 2001
Revised typescript received 26 November 2001