

# A NEW GENERALIZED PAUCITUBERCULATAN MARSUPIAL FROM THE OLIGOCENE OF BOLIVIA AND THE ORIGIN OF ‘SHREW-LIKE’ OPOSSUMS

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**Abstract:** Insights into the origin of ‘shrew-like’ opossums of South America are gained thanks to a new fossil from the Oligocene Salla Beds in Bolivia. The specimen described here consists of a partial rostrum, palate and postcanine teeth, and shows several generalized features (cranial and dental) in the context of the Paucituberculata. On this basis we recognize *Evolestes hadrommatos* gen. et sp. nov. In order to evaluate the affinities of the new taxon, we performed a phylogenetic ana-

lysis including representatives of the Caenolestidae, *Pichipilus* and allies (not regarded here as caenolestids), Palaeothentidae, and Abderitidae, with three outgroups. *Evolestes* is the basal-most ‘caenolestoid’, and provides clues to the morphological changes involved in the origin of caenolestids.

**Key words:** Metatheria, Marsupialia, Caenolestidae, Abderitidae, Palaeothentidae, South America, anatomy.

MOST of the fossil record of paucituberculatan marsupials consists of highly derived forms that illustrate the great extent of ecomorphological diversity attained by this clade in the Cenozoic of South America (Bown and Fleagle 1993; Rae *et al.* 1996; Goin *et al.* 2003). Such richness contrasts with the diversity and distribution of living paucituberculatans (Caenolestidae), of which two or three genera and a handful of species of restricted Andean distribution exist (Bublitz 1987). These are the ‘shrew-like’ opossums, so-called because of their small size and insectivorous-faunivorous habits. The position of Caenolestidae in marsupial phylogeny has been a matter of long debate (Kirsch *et al.* 1997), but there is a growing consensus that they represent a clade second to South American opossums (didelphids) in a pectinate phylogeny, being the sister group to the diverse australidelphian radiation. This consensus is supported by both morphological (Horovitz and Sánchez-Villagra 2003) and molecular data (Amrine-Madsen *et al.* 2003; Nilsson *et al.* 2004; Phillips *et al.* 2006), as well as by combined analyses of the two (Asher *et al.* 2004).

Here we describe a fossil representing a new genus and species of a ‘caenolestoid’, which provides insights into the phylogeny of the group and the origin of some of the morphological specializations of shrew-like opossums. This

fossil provides important information for reconstructing the last common ancestor of the Paucituberculata, the sister group to the Australidelphia. The stratigraphical distribution of the genera considered in the phylogenetic analysis conducted in this study, and mentioned in comparisons, is listed in Table 1. Molar nomenclature follows Goin *et al.* (2003). The generalized metatherian dental formula is assumed to be:  $L/i\ 5/4$ ,  $C/c\ 1/1$ ,  $P/p\ 3/3$ ,  $M/m\ 4/4$ . The new specimen is housed in the Museo Nacional de Historia Natural, La Paz, Bolivia (MNHN-Bol).

## SYSTEMATIC PALAEOLOGY

MARSUPIALIA Illiger, 1811

PAUCITUBERCULATA Ameghino, 1894

Genus *EVOLESTES* gen. nov.

*Derivation of name.* Evo, referring to evolution, because of the importance of this fossil in showing the morphological changes involving the origin of a marsupial clade; Latin, *lestes*, thief, pirate and, by extension, carnivorous (Greek, *lestikos*), a term that characterizes the generic name of several fossil and living Paucituberculata.

**TABLE 1.** Stratigraphical distribution of the genera considered in the phylogenetic analysis conducted in this study and mentioned in comparisons.

Taxon	Age	Reference
<i>Turgidodon</i>	Lancian NALMA (Late Cretaceous)	Case <i>et al.</i> (2005)
<i>Pucadelphys</i>	Tiupampan SALMA (Early Palaeocene)	Muizon (1991)
<i>Derorhynchus</i>	Itaboraian SALMA (Late Palaeocene)	Marshall (1987)
<i>Stilotherium</i>	Santacrucian SALMA (Middle Miocene)	Marshall (1980)
<i>Pliolestes</i>	Montehermosan SALMA (Early Pliocene)	Marshall (1980)
<i>Pichipilus</i>	Colhuehuapian–Santacrucian SALMA	Marshall (1980)
<i>Phonocdromus</i>	Colhuehuapian–Santacrucian SALMA	Marshall (1980)
<i>Palaeothentes</i>	Colhuehuapian–Santacrucian SALMA	Bown and Fleagle (1993)
<i>Acdestis</i>	Santacrucian SALMA	Marshall (1980)
<i>Abderites</i>	Colhuehuapian–Santacrucian SALMA	Marshall (1980)
<i>Rhyncholestes</i>	Recent	Patterson and Gallardo (1987)
<i>Lestoros</i>	Recent	Marshall (1977)
<i>Caenolestes</i>	Recent	Bublitz (1987)

*Type species.* *Evolestes hadrommatos* sp. nov.

*Diagnosis.* As for the type and only known species.

*Evolestes hadrommatos* sp. nov.

Text-figures 1–3

*Derivation of name.* Greek, *hadros*, well developed, strong, and *ommatos*, eye, implying that the type species has larger orbits than those of living caenolestids.

*Type.* MNHN-Bol 96-400, a fragment of a skull preserving part of the rostrum, palate and skull roof; on the left side alveoli and roots of the canine of P1 and of M4, fragmentary P2–M1 and complete M2–3; alveoli and roots of the right C–P1 (Text-figs 1–2).

*Hypodigm.* The type only.

*Occurrence.* Salla Beds, an alluvial fill of a basin cut into deformed Palaeozoic strata at the edge of the eastern Andean Cordillera of northern Bolivia (Sempere *et al.* 1990); stratigraphic level 6 at Tapial Pampa. Kay *et al.* (1995) reported Ar<sup>40</sup>/Ar<sup>39</sup> dates bracketing stratigraphic levels 5 and 6 at between 24.93 ± 0.50 and 24.79 ± 0.27 Ma (late Oligocene), confirming previous age estimates of MacFadden *et al.* (1985) and Naeser *et al.* (1987).

*Measurements* (in mm); \* = estimated value.

Maximum width of nasals, 5.23\*

Skull height at the level of M3, 4.81

Rostral width at the level of canines, 4.47

Rostral width at the level of M3, 9.53

Palatal width at the level of M3, 5.10\*

Length of the left maxillary fenestra, 5.44

Width of the left maxillary fenestra, 0.86

Length C–M3, 11.54

Length M1–M3, 5.06

Length M1–M4, 5.98\*

Length M1, 1.84

Width M1, 1.72\*

Length M2, 1.95

Width M2, 2.12

Length M3, 1.19

Width M3, 1.71

Length P3, 1.75

Width P3, 0.62

Length P2 (alveolus), 1.54\*

Length P1 (alveolus), 0.97\*

*Diagnosis.* Differs from all other Paucituberculata in that the upper molars have a less-developed, ‘hypocone-like’ metaconule. Differs from the Caenolestidae in having a shorter rostrum, larger orbits that are more dorsally placed; upper molars have a well-developed postmetacrista, smaller stylar cusp D (StD), and the paracone and metacone are proportionally less coupled to stylar cusp B (StB) and stylar cusp D (StD), respectively. Differs from the Pichipilinae in that the nasals end more anteriorly; in pichipilines the protocone and metaconule are placed more posteriorly in relation to StB and StD, making the molar more quadrangular in occlusal view. The metacone in *Evolestes* is twinned with StD whereas in pichipilines (and some caenolestines) the metacone has moved anteriorly with respect to the stylar region. M1–2 of pichipilines have the occlusal surface of the metaconule proportionally smaller in relation to that of the whole tooth than in *Evolestes*. Differs from Palaeothentidae and Abderitidae in the anterior extension of the maxillary fenestrae (in palaeothentids the maxillary fenestrae of the palatal process of the maxilla end anteriorly at the level of M1 whereas in *Evolestes* they do this at the level of P2; Abderitidae lack maxillary fenestrae); P3 is labiolingually compressed (not

reaching the posterior widening typical of palaeothentids and abderitids); M1–2 have the occlusal surface of the metaconule barely above the occlusal surface of the trigon (in palaeothentids and abderitids the metaconule surface is relatively higher); StB and StD are less labiolingually compressed.

#### Description

**Skull.** *Evolestes* is slightly larger and more robust than *Caenolestes fuliginosus*. The rostrum was long, although shorter than in living caenolestids, and narrow in its anterior portion. There is a marked constriction in the lateral expansion of the maxilla, just anterior to the level of P2. Posterior to this point, the rostrum expands laterally. Orbits are relatively large and their upper borders are not parallel to the sagittal plane but instead slightly

oblique, i.e. more frontal. As can be seen on the left side of the skull, the anterior border of the orbit is not round, forming instead a crest at an angle of almost 90 degrees with the distal portion of the jugal bone. In the vertex of this angle at least a single lacrimal foramen can be seen, internal to the orbit.

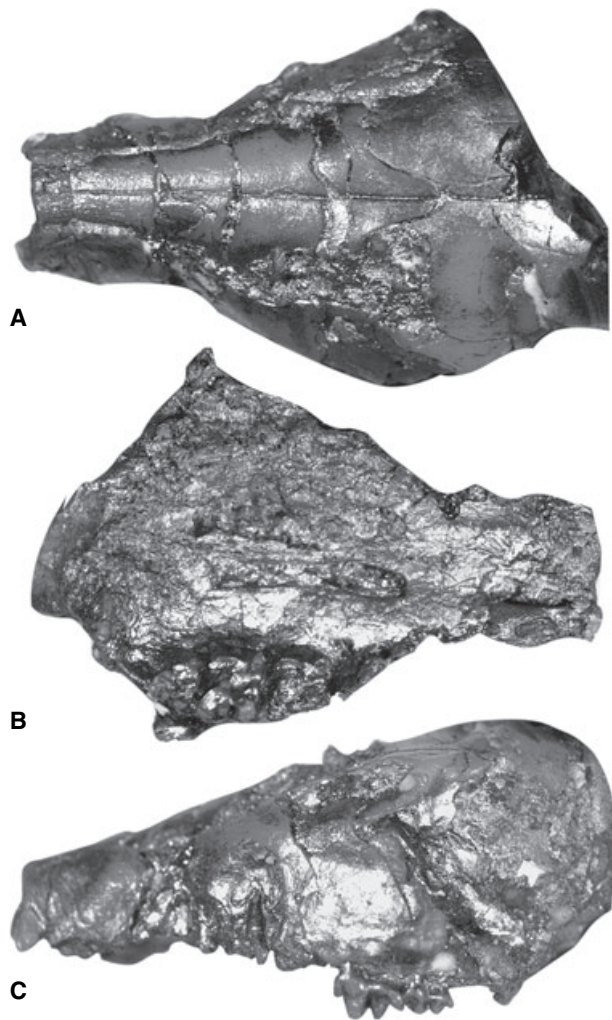
The nasals are relatively narrow in their anterior portion and have subparallel lateral borders. Starting at the maxillary constriction, the nasals expand laterally, reaching their maximum width at the level of the M1. Posterior to this point, the nasals join in the middle of the dorsal skull at the level just behind the anterior border of the orbits. They expand in the skull roof more than in any other known Paucituberculata. The suture between the nasal and the maxilla is more or less round in its anterior portion. Dorsally, the contact between the frontal and the lacrimal is parallel to the sagittal plane of the skull.

The frontal-maxilla contact is wide, much wider than in the *Didelphimorphia* and similar to that of other Paucituberculata. In contrast to caenolestids there is no anteorbital vacuity in the contact of the nasal, frontal and maxilla. Frontals are relatively flat and in their anterior portion are wedge-like, within which the posterior border of the pointed nasals is in contact. In lateral view, the maxilla shows two well-defined planes: one posterior to P2, in which the rostrum expands laterally, and another, shorter plane, corresponding to the rostral anterior projection. Dorsal to the posterior root of P3 there is a well-developed infraorbital foramen.

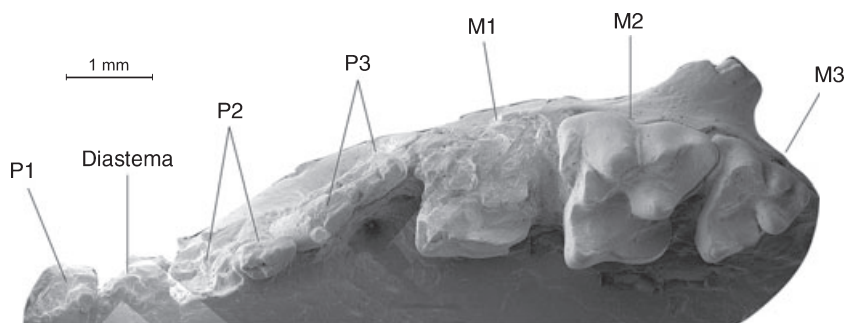
Owing to the fragmentary anterior end of the skull, only the posterior portion of the left premaxilla and the suture between the premaxilla and maxilla suture, of vertical orientation, can be seen. Posterior to the P2, the palate is proportionally wider than in living caenolestids. The incisive fenestrae reach posteriorly to a point posterior to the canines; the maxillary fenestra (preserved on the right side) is thin and elongated, extending from P2 almost to the border M2–3.

**Dentition.** Based on what is preserved on the left side, we conclude that the postincisor dental formula of *Evolestes* includes a canine, three premolars and four molars. The canine is larger and more robust than in living caenolestids and *Stilotherium*. As in the latter, the canine is suboval in section, i.e. less compressed laterally than in living caenolestids. Two very small roots of the P1 are located posterior to the canine. P1 is separated from C and P2 by very short diastemata; in fact, on the right side there is apparently no diastema between C and P1. Only the posterior root of P2 is preserved, which shows an apparently unicuspid talonid. Judging by the relative size of the alveoli, the anterior root was larger than the posterior one. P3 is better preserved, although its crown is partially broken. This tooth was longer than the P1–P2 and probably much larger. In contrast to living caenolestids, P3 shows a well-developed unicuspid talon.

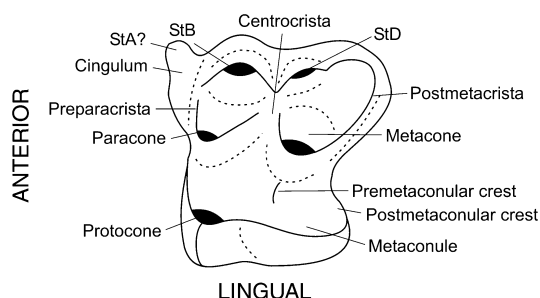
M1–2 are the largest of the molar series; they are subequal in length, but M2 is wider than M1. M3 is much smaller than M2; only alveoli of M4 are preserved, showing that this tooth was smaller than M3. M2 is quadrangular in shape. The highest cuspid of M2 is the StB, which is more robust than the metacone. The paracone is relatively small and joins lingually the base of



**TEXT-FIG. 1.** *Evolestes hadrommatos* gen. et sp. nov., MNHN-Bol 96-400. Partial skull in A, dorsal, B, ventral and C, left lateral views. Estimated maximum width of nasals is 5.2 mm.



**TEXT-FIG. 2.** *Evolestes hadrommatos* gen. et sp. nov., MNHN-Bol 96-400. Detail of palate with left postcanine dentition.



**TEXT-FIG. 3.** *Evolestes hadrommatos* gen. et sp. nov., MNHN-Bol 96-400. Schematic drawing of left M2.

StB; a short preparacrista ends in the anterolingual base of StB. The cuspid of the paracone is located more to the anterior than that of the StB. The postparacrista is not connected to the premetacrista and ends at the base of the lingual face of StB. The metacone is much higher, larger and more robust than the paracone. Although the premetacrista is barely developed, the postmetacrista is large and reaches the metastylar corner, where a cuspid (?StE) may have been present. StD is much smaller than StB and faces labially the metacone. StB and StD are connected by crests; posterior to this, the StD also projects a short crest. Labially, StB and StD are separated by a deep but short ectoflexus.

The protocone is located in the anterolingual corner of the tooth and aligned with the StB and the paracone. In occlusal view, the pre- and postprotocrista join at an acute angle; thus, the anterolingual edge of the protocone is keel-shaped. The paraconule is absent. Posterior to the protocone there is a very worn metaconule. Despite this wear, it is clear that the tip of the metaconule was lower than that of the protocone. The premetaconule crista is barely marked and ends labially at the base of the metacone. Because of wear of both the metaconule and the postmetaconular crest, it is difficult to establish the precise trajectory of the latter. However, it is clear that this crest was relatively long and extended labially up to the posterolabial corner of the tooth, resembling a cingulum running below and posterior to the postmetacrista. In the anterolabial corner of M2 there is a short but wide anterobasal cingulum. This is at the base of the paracone and it rises towards the anterolabial corner of the tooth (possibly supported by an StA).

In contrast to M1–2, the M3 is triangular, as it does not have an expanded metaconule at its posterolingual corner. StB and StD have similar size relations to each other as in M2. Only the base of the paracone is preserved; it was smaller than the metacone and proportionally larger than that of M2. The postparacrista and premetacrista join at a point below the joining of the anterior crest of the StD and the posterior crest of the StB. The postmetacrista is shorter and more perpendicular to the dental axis than in M2; it ends in the metastylar corner, showing a small cuspid (StE?). The paraconule is absent. The metaconule is small, and supports a short premetacone crista ending anterior to the metacone. There is no postmetacone crista. A deep sulcus separates the metaconule from the metacone. In relation to its size, the trigon basin in M3 is wider than that of M2. The protocone is located more posteriorly than in M2. The anterobasal cingulum is proportionally more developed than the M2. The ectoflexus is short and deep, as in M2.

*Comparisons and comments.* Paucituberculatan features of *Evolestes* include having a long rostrum; a wide contact between the frontal and the maxilla; the posterior end of the nasals end at the same level as, or rostral to, the anterior border of the orbits; upper molars with very large StBs, winged and lingually expanded metaconules, not reaching the level of the protocones; labially extended postmetacristae; and protocones and metacones reduced in relation to StB; and in lacking paraconules. Some of these features deserve further comment.

In the Didelphimorphia the nasals end caudally well behind the anterior border of the orbits. In the Paucituberculata, on the other hand, these bones end more cranially. However, there is some variation: in *Evolestes* and living caenolestids the posterior limit of the nasals coincides with a point located above the anterior border of the orbits. In the palaeothentid *Acestis* the nasals extend posteriorly beyond this point, whereas in the pichipiline *Pichipilus centinelus* the nasals end well to the anterior of it.

The size of the orbits differs from that of living Caenolestidae, in which the orbits are relatively small and low in relation to the skull roof. In *Evolestes*, by contrast, the orbits are high, reaching dorsally almost to the skull roof.

On the right side of specimen MNHN-Bol 96-400, a portion of the maxilla forming the boundary of the frontal is preserved; it is clear that an antorbital vacuity is present. Ventral and anterior to this portion of the maxilla, a smooth surface corresponds to the area over which the maxilla was present. In its most anterior and dorsal extension, this surface is in contact with the nasal bone; also, no antorbital vacuity is present. Osgood (1921, pl. 22, fig. 2, for *Caenolestes fuliginosus*) and Patterson and Gallardo (1987, fig. 1, for *Rhyncholestes raphanurus*) showed that these two species exhibit the greatest development of the antorbital vacuity, but they are clearly absent in *Evolestes*. Anterior to the greatest expansion of the nasals, the border with the maxilla is not preserved, so it is uncertain whether in this area (in which the most anterior extension of the vacuity is present in extant forms) the antorbital vacuity was also absent.

The infraorbital foramen is much larger in *Evolestes* than in living caenolestids, and whereas in the latter the incisive fenestrae extend posteriorly to a point located at the level of the anterior root of the P2, in *Evolestes* they extend just to the P1. The maxillary fenestrae of *Evolestes* extend from the posterior root of P2 up to the boundary of M2–3. In *Lestoros* they extend from the anterior root of P3 up to the protocone of M2 or M3; in *Rhyncholestes* and *Caenolestes* they are longer, as they extend from P3 up to M4.

In *Evolestes*, C, P1 and P2 are more closely packed, i.e. they show narrower interdental diastemata than those of living Caenolestidae, especially *Rhyncholestes*. Although the most anterior portion of the skull of *Evolestes* is not preserved, it is clear that this animal had a shorter rostrum than living Caenolestidae.

Despite being more generalized than any other known paucituberculatan, the upper molar pattern of *Evolestes* resembles that of the caenolestid *Stilotherium* in several respects. First, there is a marked difference in height of the metaconule and the protocone. This feature differentiates both *Evolestes* and *Stilotherium* from all other 'caenolestoids'. A second feature of *Evolestes* shared exclusively with *Stilotherium* is the presence of an elongate postmetaconule crista that is not continuous but rather interrupted at the midpoint of the posterior face of the molar leaving two cingulum-like structures at the posterior face of the upper molars (especially M1–2). In most paucituberculatans, the postmetaconule crista extends labially up to the metastylar corner of the tooth, forming a continuous, cingulum-like structure below the postmetacrista.

A noteworthy feature of the upper molars of *Evolestes hadrommatus* is the morphology, position and relative size of the stylar cusps. The StB is very large, high and clearly

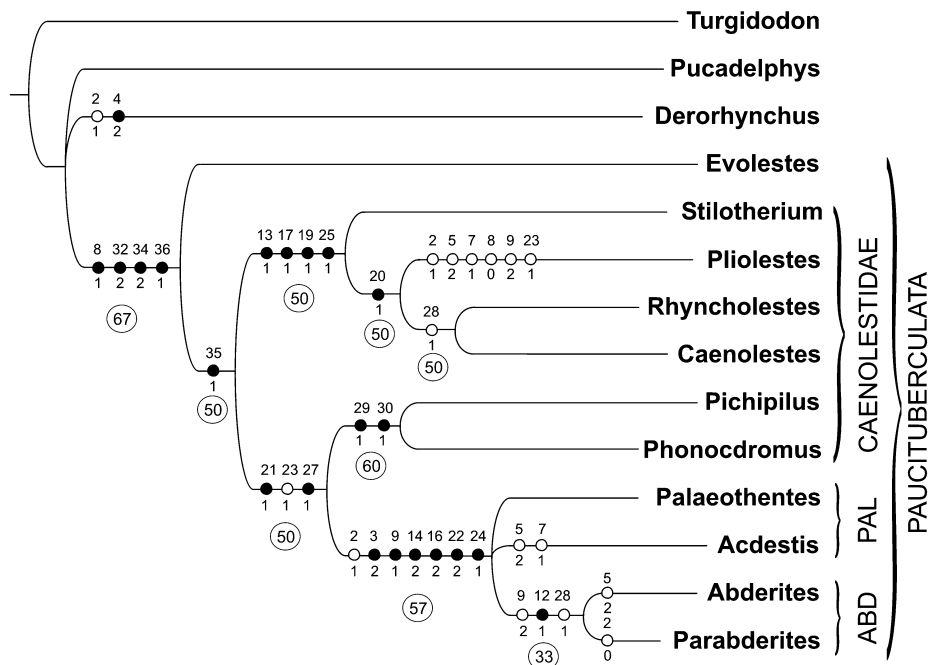
facing the paracone, though slightly 'shifted' posteriorly compared with other South American marsupials.

## PHYLOGENETIC ANALYSIS

A parsimony analysis was conducted using PAUP (Swoford 2002). This matrix (see Appendix) includes a total of 36 characters, ten caenolestid species, *Evolestes*, and *Turgidodon*, *Pucadelphys* and *Derorhyncus* as outgroups (Marshall *et al.* 1990). Multistate characters were treated as unordered. A heuristic search was applied using TBR (tree bisection-reconnection) to find the most parsimonious trees. Support for the clades was measured by means of the relative Bremer support (Goloboff and Farris 2001). A preliminary report of results of a more extensive phylogenetic analysis of the Paucituberculata was given by Abello *et al.* (2004). It is worth mentioning that only one-third of the total number of characters coded (12 out of 36) are known for *Evolestes*, the rest being missing data.

## RESULTS AND DISCUSSION

As a result of the phylogenetic analysis, *Evolestes* appears as the basalmost 'caenolestoid' (Paucituberculata, *sensu* Abello *et al.* 2004), sister to two major clades: one consists of living caenolestids plus two extinct forms; the other includes the Pichillipinae as sister group of palaeothenitids and abderitids (Text-fig. 4). Concerning the phylogeny of caenolestoids, the most noteworthy results are: (1) the exclusion of *Pliolestes* from the 'Pichipilinae' (*sensu* Marshall *et al.* 1990; Abello *et al.* 2004) and their grouping together with the Caenolestidae *Stilotherium*, *Caenolestes* and *Rhyncholestes*, and (2) the exclusion of *Pichipilus* and *Phonocdromus* from the Caenolestidae and their consideration as sister group to Palaeothenitidae plus Abderitidae (Abello *et al.* 2004). Concerning this second point, it is worth mentioning that Marshall (1980, p. 127) stated that '... The common possession of an antorbital vacuity between the nasal, frontal and maxilla in both Caenolestini and Pichipilini is a unique apomorphy that establishes the Caenolestinae as a monophyletic group'. We have examined the *Pichipilus* specimen MLP 66-V-17-204, the only known cranial remain assignable to a 'Pichipilini' *sensu* Marshall (1980). Owing to the damaged state of the dorsum of the skull, it is impossible to determine whether it had such vacuities. Although, as Marshall and Pascual (1977) pointed out, the area of the antorbital vacuities is 'sunken', this does not by itself indicate vacuities, as the whole side of the skull is broken with respect to the naso-frontal plane.



**TEXT-FIG. 4.** Strict consensus of nine equally most-parsimonious trees (TL = 56). Numbers above each branch indicate character number; those below are the character-states; encircled are relative Bremer support values for each branch.

Consequently, the state of this character in *Pichipilus* was scored as unknown.

The dental anatomy of palaeothentids and abderitids is more derived than that of caenolestids (see Marshall 1980; Bown and Fleagle 1993). In the former there is a simplification of molar morphology in favour of the development of buccolingually transverse lophs. The reduction in incisor number is moderate in the Caenolestidae (three or four) and greater in palaeothentids and abderitids (only two incisors). As described above, most features of *Evolestes* are quite generalized and plesiomorphic when compared with the Caenolestinae. On the other hand, features of the metaconule and postmetaconule crista resemble *Stilotherium*.

The specialized dental anatomy of the extinct palaeothentids and abderitids could suggest that the living Caenolestidae are the most generalized Paucituberculata, as has been stated in the literature (Marshall 1980). However, organisms are mosaics of plesiomorphic and derived features, and *Evolestes* serves to reconstruct the last common ancestor of these clades and clarify the polarity of several cranial features. Optimization in the resulting phylogeny and outgroup comparison suggest that *Evolestes* has several features in common with palaeothentids and abderitids that are plesiomorphic for Paucituberculata. Various aspects of the cranial anatomy of *Evolestes* provide insights into what aspects of the mosaic of features characterizing living caenolestids are plesiomorphic and which are derived:

1. The dorsal position of the orbits and their relatively large size in *Evolestes* resembles the condition of palaeothentids and abderitids and is more plesiomorphic than that of living caenolestids.

2. The rostrum of *Evolestes* is clearly elongated, but not to the extent seen in living caenolestids. The diastemata surrounding P1 characterizing living caenolestids are not as prominent in *Evolestes*. Besides the Caenolestidae, another group of marsupials is characterized by a long rostrum, namely the Peramelina, a clade of Australidelphia. The phylogenetic placement of the Peramelina implies that its last common ancestor did not have an elongate rostrum, suggesting a convergent evolution of this feature with caenolestids. The very elongate rostrum of caenolestids is possibly correlated with the presence of antorbital vacuities and laterally expanded olfactory bulbs (Herrick 1921). At least the first of these features is lacking in *Evolestes* or in known skulls of palaeothentids (Goin *et al.* 2003).

3. The basicranial anatomy of *Evolestes* is unknown, but we expect that in this or in other basal caenolestoid taxa, features in common with palaeothentids will be found once these parts become known. Some basicranial features in the holotype of the palaeothentid *Adestis maddeni* (Goin *et al.* 2003) are more primitive than those of living caenolestids. In particular, the paroccipital processes are less compressed against the mastoid part of the petrosal, the alisphenoid bullae is posterior to the foramen of the transverse canal and the carotid foramen, and the groove

at the opening of the transverse canal is posterolaterally orientated, instead of the (rare among living South American marsupials) anterolateral orientation recorded in caenolestids.

One of the most distinctive features of the skull in living caenolestids is the notable elongation of the rostral part as compared with other living and extinct marsupials. In *Evolestes* the rostrum is already antero-posteriorly elongate, but without approaching the extreme of caenolestids. For instance, there is an extensive diastema between P1 and P2, but not between P2 and P3 or between C and P1. This is precisely the condition that characterizes living caenolestids (*Rhyncholestes*, *Caenolestes*, *Lestoros*). An interesting hypothesis for future testing postulates that the extreme snout elongation in living caenolestids involved developmental processes that were especially active at the posterior part of the rostrum (i.e. between the canine and the first molar regions). Heterochronic processes in this part of the skull may have been involved. Additionally, this could explain the lack of ossifications in the nasal-maxilla-frontal region (i.e. the antorbital vacuities), a feature found in caenolestids but not in other paucituberculatans, including *Evolestes*.

*Evolestes hadrommatos* already shows the basic synapomorphies characteristic of the upper molar pattern of paucituberculatans, and helps understanding of the contrast between this group and polydolopimorphians. Goin (2003), Goin and Candela (2004) and Case *et al.* (2005) stressed the distinctness of the molar patterns of representatives of these two clades. The upper molar pattern of polydolopimorphians involved the progressive 'labialization' and twinning of the paracone and metacone with the stylar cusps B and D, respectively. All four cusps decrease in relative size and are subequal in height very early in the evolution of the polydolopimorphian clade. Finally, in polydolopimorphians, the expanded, 'hypocone-like' metaconule has its base set at the same level of the trigon basin. None of these features occurs in the Paucituberculata (including *Evolestes*), which in contrast, exhibit the following features: the metacone is much larger than the paracone; even though the paracone and metacone are close to stylar cusps B and D, these cusps (especially StB) increase in size dramatically compared with other molar cusps, and the base of the metaconule is higher than that of the trigon basin. It is also clear from *Evolestes* that StD is smaller than StB (whereas they are subequal in polydolopimorphians), and that this cusp evolved to a much larger size in other paucituberculatans. Finally, in polydolopimorphians the process undergone by the labial cusps (paracone, metacone, StB, StD) implies a reduction in their relative sizes on the stylar shelf, whereas in paucituberculatans this did not happen: even though there is a net reduction of the paracone and

metacone (a feature that is already present in basal caenolestids such as *Stilotherium*), the proportionally enormous size of the stylar cusps occupy almost all the area of the original stylar shelf.

In order to reconstruct the palaeobiology, studies of adaptations and constraints for the group in which phylogenetic aspects are controlled are needed. However, some preliminary observations can be made. The relatively large size of the orbits, as well as their orientation (more frontated than in the Caenolestidae), could suggest more nocturnal and/or arboreal habits than for living caenolestids. On the other hand, the infraorbital foramen is larger in *Evolestes*. The apparently plesiomorphic arboreality of metatherians and most probable didelphimorphs (Springer *et al.* 1997; Luo *et al.* 2003) is likely to have characterized the last common ancestor of Paucituberculata, a basal group in marsupial phylogeny (Asher *et al.* 2004), and probably also *Evolestes*. The large infraorbital foramen of *Evolestes* implies a rich innervation and vascularization of the snout, a feature perhaps related to acquisition of prey and negotiating through complex substrates by touch rather than vision (Kay and Cartmill 1977). Finally, the molar morphology of *Evolestes* suggests an insectivorous-omnivorous diet, as for numerous living marsupials with arboreal or semi-arboreal habits.

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## APPENDIX

## Data matrix and character list used in the cladistic analysis

	1	2	3
<i>Turgidodon</i>	-000000000000000000	0000000000	0000000
<i>Pucadelphys</i>	0000000000000100000	0000000000	0101100
<i>Derorhynchus</i>	-10200-00-----00000	0000000000	0201100
<i>Stilotherium</i>	-011000100101111111	0010011000	0321211
<i>Rhyncholestes</i>	1011000102101111111	1010011010	0321211
<i>Caenolestes</i>	1011000102101111111	1010011010	0321211
<i>Pliolestes</i>	-1112-1022101111111	1011011000	0-----
<i>Pichipilus</i>	-011000102100111010	0111001101	1321211
<i>Phonocromus</i>	-0110--102100111010	0110011011	1321211
<i>Palaeothentes</i>	0121000111100202010	0121101100	--21211
<i>Aclestis</i>	0121201111100202010	0121101100	0-21211
<i>Abderites</i>	-121220121-1--02010	0121101110	0-21211
<i>Parabderites</i>	-0210--121-1-002010	0121101110	0-21211
<i>Evolestes</i>	0----0010-----	-----0---	-321201

## Character description

- Antorbital vacuities: absent (0), present (1).
- Relative height of the dentary: moderate to low (0), high (1). The height of the dentary was measured with respect to the length of m2–3. Because in some taxa the m1 is often large and the m4 is very reduced, the chosen measure is the length of the intermediate molars of the series. The m2–3 length was divided by the height of the mandibular body measured below the contact between these two molars. Two states were considered for this character: above the mean value 1.11 (0) and below this value (1).
- Number of incisors: 4 (0), 3 (1), 2 (2).
- Size and orientation of the first incisor: small and subvertical (0), hypertrophied and procumbent (1), large but not hypertrophied and procumbent (2).
- Size of p3: p3 similar in relative size to molars to the condition in *Turgidodon* or moderately larger than p2 and m1 (0), hypertrophied (1), reduced in comparison with the condition in *Turgidodon* (2).
- Size of P3: moderately developed, as in *Turgidodon* (0), reduced (1), enormous (2).
- Length-width ratio of P3: more than 1.5 (0), less than 1.5 (1).
- Size of the canine: normally developed (0), reduced or absent (1). The canine is well developed in peradectians and didelphimorphians. In some, but not all, microbiotherians, it is somewhat reduced. In prepodolopids and bonapartheriids the canine is moderately to well developed. The canine is certainly present in *Evolestes*, but proportionally in size to the molars, it is similar to the condition in *Stilotherium*, coded as 'reduced'. Therefore, we coded this character as 1 in *Evolestes*.
- Presence/absence of transverse lophs: upper and molars without transverse lophs (0), with incipient transverse lophs (1), with well-developed transverse lophs (2).
- Relative length of trigonid and talonid of m1: subequal (0), long trigonid (1), short trigonid (2). The length relationship between the trigonid and the talonid (limited by the metacristid) can be expressed as an index: length of m1 trigonid/length of m1 talonid. The generalized condition corresponds to the range of index values between 0.9 and 1.2 (state 0).
- Form of the paracristid in m1: m1 paracristid normal (0), without notch, forming a continuous blade between proto- and paraconid (1). In most marsupials the paracristid does not form a continuous blade between proto- and paraconid; instead, it develops a notch between both cusps (0). But in most paucituberculatans, both cusps are joined by a continuous blade that lacks a notch (state 1).
- Presence of ribs in the trigonid of m1: ribs absent (0), ribs present (1). In abderitids the trigonid reaches significant development and is traversed by ribs or crenulations that extend from the base of the crown to the trigonid edge. In the case of *Abderites* these ribs or crenulations also occur on the lingual side of the m1 trigonid, although in smaller numbers than the labial ribs.
- Notch in the metacristid of m1: metacristid with a deep or moderate notch (0), metacristid notch poorly or not developed (1).
- Orientation of the cristid obliqua in m1: toward the protoconid or slightly labial with respect to the metacristid notch (0), toward the notch or at midpoint between the protoconid and metaconid (1), in contact with the metaconid (2).
- Development of the hypoconid in m1–2: poorly developed (0), quite developed and labially salient (1). The derived character is a hypoconid quite prominent labially, so the talonid is clearly broader than the trigonid (state 1).
- Hypoconulid shape in m1–3: well developed (0), somewhat reduced, with certain anteroposterior compression (1), disc-shaped, very broad, occupying most of the posthypocristid edge (2), forming a cingulum posterior to the talonid (3).
- Distal height of the entocristid in m1–3: low (0), high (1). In most marsupials the entocristid is a relatively low cusp that extends along the anterior slope of the entoconid, disappearing at the level of the base of this cusp. In the caenolestids, by contrast, the anterior part of this crest is clearly raised above the talonid floor, thus contacting with the posterior face of the metaconid.
- Shape of the entoconids of m1–3: conical (0), laterally compressed (1).
- Orientation of the entocristid in m1–3: straight (0), curved (1).
- Position of the entoconid: normally placed, opposed to the hypoconid at the lingual edge of the talonid (0), more posteriorly located, at least in the m1 (1), more anteriorly located (2).
- Crest-like expansion posterior to the metaconid in m1–3: absent (0), present (1).
- Height of the protoconid in m2–3: protoconid higher than the para- and metaconid (0), subequal in height to the para- and metaconid (1), lower than the para- and metaconid (2). The protoconid is usually higher than the para- and metaconid (state 0).

23. Position of the metaconid in m3: at the same level of the protoconid (0), anteriorly placed and frequently twinned or fused to the paraconid (1).
24. Development of the anterobasal cingulum in m2–4: normally developed (0), vestigial or absent (1). The generalized condition in marsupials is an anterobasal cingulum moderately developed below the paracristid (state 0). In palaeotheriids and abderitids the anterobasal cingulum is vestigial or absent (state 1).
25. Size and roots of m4: m4 double-rooted and subequal in size to m3 (or, if smaller, representing the extreme size of a gradient from m1 to m4) (0), m4 single-rooted and greatly reduced in relation to m3 (1).
26. p3–m1 contact: mostly contiguous (0), p3 talonid supports most or all of the m1 trigonid (1).
27. Enamel thickness in the molars: uniform throughout the entire surface of the tooth (0), markedly different thickness between the lateral and occlusal faces (1).
28. Depth of the metacristid in m2–3: relatively deep (0), little or not developed (1).
29. Crest posterior to the protoconid in m1–3: absent (0), present (1).
30. Posterior entoconid crest: absent (0), present (1).
31. Shape of the centrocrista in M2: straight (0), slightly V-shaped (1), deeply V-shaped (2), open, with the premetacrista and postparacrista basally fused to the lingual slopes of StD and StB, respectively (3), open, with the premetacrista and postparacrista connected to the anterior edge of StD and posterior edge of StB, respectively (4). In *Evolestes*, M2 shows condition 3 and M3 shows condition 2.
32. Relative sizes of the paracone and metacone with respect to styler cusps B and D: para- and metacone larger (0), approximately subequal (1), StB, or StB and StD, much larger (2).
33. Relative size of paracone and metacone: subequal (0), metacone larger (1).
34. Relative size of the metaconule in M2: subequal to the paraconule (0), larger than the paraconule (1), very large, 'hypocone'-like, but without reaching lingually to the level of the protocone (2), very large, 'hypocone'-like, lingually reaching the protocone (3). In *Evolestes*, condition 2 is present, although the tooth is worn. If we were to code M3, *Evolestes* would show condition 1.
35. Degree of labiolingual compression of StB and StD: not compressed (0), compressed (1). In *Evolestes* cusp B is clearly not compressed, cusp D is slightly labiolingually compressed in both M2 and M3. However, this compression does not reach the level seen in the other taxa coded 1 for this character.
36. Styler cusp C: present (0), absent (1).