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POSTCRANIAL SKELETON OF THE MIOCENE MARSUPIAL *PALAEOTHENTES* (PAUCITUBERCULATA, PALAEOTHENTIDAE): PALEOBIOLOGY AND PHYLOGENY

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ABSTRACT—This contribution presents a morphofunctional analysis of the previously unknown appendicular skeleton of the paucituberculatans *Palaeothenes minutus* and *Palaeothenes lemoinei* from the Santa Cruz Formation (late early Miocene, Santa Cruz province, Argentina), performed in order to infer their locomotor behavior. In addition, a cladistic analysis was conducted to explore the phylogenetic information of postcranial features of *Palaeothenes* in the context of Marsupialia. The results indicate that *Palaeothenes* would have been an agile cursorial dweller, with leaping ability, similar to the extant paucituberculatan *Caenolestes fuliginosus* and the didelphid *Metachirus nudicaudatus*. This mode of locomotion is evidenced mainly by the following features: proximal location of the deltopectoral crest and bicipital tuberosity, reflecting rapid flexion at the gleno-humeral and elbow joints, respectively; shape of the humero-ulnar and humero-radial joints (deep and high humeral trochlea, deep olecranon fossa, deep trochlear notch, mediolaterally broad proximal trochlear crest), denoting a marked stability for flexion and extension; restrictive acetabulum, showing emphasized congruence at the hip joint; lengthened ischium and prominent femoral tubercle and ischial tuberosity, indicating an increased mechanical advantage of the rectus femoris and hamstring muscles; proximally projected greater trochanter, demonstrating a relatively great mechanical advantage of the gluteal muscles; and configuration of the upper ankle, lower ankle, and transverse tarsal joints, indicative of restrictive rotational movements (right angle between the medial and lateral astragalotibial facets, distal and proximal calcaneo-cuboid facet halves forming a right angle). A cladistic analysis positions *Palaeothenes* as the sister taxon to the extant *Caenolestes*, demonstrating that postcranial features support the monophyly of Paucituberculata.

INTRODUCTION

Paucituberculata constitute a clade of marsupials endemic to South America. The earliest records of the clade are from the late Paleocene of Brazil and Argentina (Goin et al., 2009). Extant paucituberculatans are represented by six species in the genera *Caenolestes*, *Lestoros*, and *Rhyncholestes*, all of them belonging to the family Caenolestidae (Albuja and Patterson, 1996). These species occur in diverse environments, as the Páramo, Montane forest, and Valdivian forest, in Colombia, Ecuador, Venezuela, Perú, Bolivia, Chile, and Argentina. The scarce available data on their locomotor habits indicate that living species are cursorial, typically showing a symmetric gait. At high velocity, they can leap using the fore- and hind legs nearly or exactly together (Kirsch and Waller, 1979).

Extinct paucituberculatans had a wider distribution than the extant representatives of this order, and their well-documented fossil record shows that they reached their highest taxonomic diversity during early and middle Miocene (Abello, 2007). Traditionally, three main groups of paucituberculatans have been recognized: Caenolestidae and the extinct Abderitidae and Palaeothenidae (but see Abello, 2007; Goin et al., 2009). Palaeothenidae include several genera and species and are particularly abundant during the Miocene in Patagonia (Abello, 2007). Among Palaeothenidae, *Palaeothenes* is the most diverse genus and a typical member of the Miocene marsupial assemblages. Until now, palaeothenids were known exclusively from dental and cranial remains. In this contribution, we present the first comparative description and morphofunctional analysis of the postcranial skeleton of two species of *Palaeothenes*:

Palaeothenes minutus, the most abundant palaeothenid of the late early Miocene of Patagonia, and *P. lemoinei*, one of the largest species of the genus. Both species are represented by well-preserved and associated postcranial remains from the Santa Cruz Formation (late early to early middle Miocene, Santa Cruz province, Patagonia, Argentina; Kay et al., 2008). In addition, to investigate the phylogenetic implications of the previously unknown postcranial features of *Palaeothenes* in the context of Marsupialia, a cladistic analysis is included.

MATERIALS AND METHODS

To assess the functional adaptive significance of the postcranial features in *Palaeothenes minutus* and *P. lemoinei*, we conducted a comparative analysis with living South American marsupials exhibiting a wide range of locomotor behaviors. Specifically, comparisons were made with the extant paucituberculatan *Caenolestes fuliginosus*, an agile terrestrial species with saltatory ability; the microbiotherian *Dromiciops gliroides*, a mostly arboreal species; and the didelphimorphians *Didelphis aurita* (a scansorial form), *Metachirus nudicaudatus* (an agile, cursorial to saltatory species), and *Monodelphis dimidiata* (a cursorial form). The comparisons with *Caenolestes* were based on detailed information provided by Osgood (1921) and Szalay and Sargis (2001).

Because no observations on the locomotor behavior of *Rhyncholestes raphanurus* have been reported, we do not employ this species as a comparative model to infer the locomotor behavior of *Palaeothenes*. However, we did incorporate postcranial features of *R. raphanurus* in the comparative description of *Palaeothenes* in order to increase the comparative sample of living Paucituberculata. Postcranial features and information on locomotor habits of the species listed above and other living South

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TABLE 1. Measurements (in millimeters) of the forelimb of *Palaeotheres minutus* and *P. lemoinei*.

	Humerus							Entepicondyle width
	Humeral trochlea width	Humeral capitulum width	Humeral trochlea length	Humeral capitulum length	Humeral trochlea depth	Humeral distal articular surface width	Humeral distal end width	
<i>P. minutus</i> MACN 5619–5639c	1	2.1	1.9	0.8	2.2	3.1	4.5	1.5
	Ulna							
	Ulnar olecranon process length	Ulnar trochlear notch width	Ulnar radial facet length	Ulnar radial facet width	Ulnar trochlear notch depth	Ulnar trochlear notch length		
<i>P. minutus</i> MACN 5619–5639e	2.5	1.8	0.7	2	1.2	2.6		
<i>P. lemoinei</i> MPM-PV 3494		4.3	1.7	3.6	2.4	5.2		
	Radius							
	Radial neck length	Radial head width	Radial head rim length	Radial head length	1: Length of the preserved radius shaft	2: Distance between the proximal tip of the radius and the bicipital tuberosity	2/1 (%)	
<i>P. minutus</i> MACN 5619–5639d	1.4	1.7	0.8	1.3	19	2.1	11	

American marsupials, such as the arboreal didelphid *Caluromys philander*, were also evaluated from bibliographic data (Szalay, 1994; Argot, 2001, 2002; Szalay and Sargis, 2001; Flores, 2009). Major osteological postcranial features functionally associated with different locomotor habits (including the capacity to climb, run, and leap) were identified in living marsupials and used as a model to infer the functional significance of those attributes preserved in the *Palaeotheres* species. Areas of articulation and muscular attachment were emphasized in our analysis. Information on the postcranial myology of living South American marsupials was obtained from Osgood (1921) and Argot (2001, 2002). Because of the resemblance found in the tarsus of the Caenolestidae and Sparassodonta (Szalay, 1982), extensive comparisons also were made between *Palaeotheres* and some sparassodonts.

The specimen of *Palaeotheres minutus* studied herein is housed in the Ameghino Collection of the Museo Argentino de Ciencias Naturales ‘Bernardino Rivadavia’ (MACN), Buenos Aires, Argentina. This specimen (MACN 5619–5639a–i) is represented by right and left mandibular rami bearing m3–4 (MACN 5619–5639a and MACN 5619–5639b) and several associated postcranial remains: distal portion of right humerus (MACN 5619–5639c), right radius (MACN 5619–5639d), proximal portion of the right ulna (MACN 5619–5639e), partially complete pelvis (MACN 5619–5639f), proximal portion of right femur (MACN 5619–5639g), proximal portion of left femur (MACN 5619–5639h), and right calcaneum (MACN 5619–5639i). MACN 8319–22, a distal fragment of left humerus, is here assigned to *P. minutus*. The specimen of *P. lemoinei* belongs to the Museo Regional Provincial Padre ‘M. J. Molina’ (MPM), Rio Gallegos, Santa Cruz province, and was recovered between 2003 and 2008 by a joint team from the Museo de La Plata (Argentina) and Duke University (U.S.A.). This specimen (MPM-PV 3494) is represented by the following associated materials: right mandibular fragment with m2–4 and left edentulous mandibular fragment, left humerus, left ulna, left fragment of pelvis, fragment of right tibia, fragment of left tibia, and right astragalus. All fossil specimens come from the Santa Cruz Formation (late early Miocene, Santa Cruz province, Patagonia, Argentina).

Specimens of the living marsupials examined are housed in the Museo de La Plata, La Plata, Argentina (MLP), and the

Museo Municipal de Ciencias Naturales ‘Lorenzo Scaglia,’ Mar del Plata, Argentina (MMP).

Measurements of limb bones are compiled in Tables 1 and 2. Following previous studies (Sargis, 2002a, 2002b; Basarova et al., 2009), they were selected because they either represent standard postcranial measurements, or have functional significance and hence can be utilized in future morphometric and biomechanical studies. Measurements were taken using an ocular micrometer in a Nikon SMZ 1000 stereo microscope. Terminology of the postcranial features of *Palaeotheres* mainly follows Argot (2001, 2002) and Szalay and Sargis (2001), providing, whenever necessary, the equivalence among the terms used by the different authors. Analyses of the forelimb and hind limb of *Palaeotheres* are provided separately.

To investigate the phylogenetic implications of the previously unknown postcranial features of *Palaeotheres* in the context of Marsupialia, we performed a parsimony analysis mainly based on the data set of Horovitz and Sánchez-Villagra (2003). Their data matrix consisted of 230 morphological characters (postcranial, craniodental, and soft tissue) and 31 terminal taxa representing all major clades of marsupials. The new data matrix here analyzed, including 231 characters and 32 terminal taxa, was modified with respect to the original data through modifications to the scoring of *Caenolestes* and the addition of one postcranial character (character 231: presence/absence of third trochanter). This latter was added to the original matrix to test its phylogenetic information in the context of the marsupials. With respect to the dental features of *Palaeotheres* and *Caenolestes*, we followed the dental homology hypothesis for Paucituberculata proposed by Abello (2007). This resulted in seven state changes of dental characters in *Caenolestes* (Supplementary Data, Table 1S). Postcranial features of *Caenolestes* were not recoded with respect to the original data. For *Palaeotheres*, 59 postcranial and 25 dental characters were coded based on the new materials studied here (see Supplementary Data, Table 1S). Cranial features of *Palaeotheres* were not included in this analysis because an exhaustive anatomical study of the skull of this genus is necessary to establish character homologies with confidence (M. A. Abello, unpubl. data).

TABLE 2. Measurements (in millimeters) of the hind limb and pelvis of *Palaeotheres minutus* and *P. lemoinei*.

	Pelvis			Femur								
	Acetabulum length	Acetabulum width	Ischium length	Femoral head length	Femoral head width	Proximal extension of great trochanter	Medial extension of lesser trochanter	Lateral extension of third trochanter	Femoral mid-shaft mediolateral length	Distal extent of lesser trochanter	Distal extent of third trochanter	
<i>P. minutus</i> MACN 5619–5639f	3.1	2.7	6.5									
<i>P. lemoinei</i> MPM-PV 3494	6	5										
	Tibia					Calcaneum						
	Tibial distal end width	Tibial medial malleolus length	Tibial medial malleolus width	Lateral astragalar facet width	Lateral astragalar facet length	Tuber length	Tuber width	Calcaneal head length	Calcaneal head width	Entire calcaneal length		
<i>P. lemoinei</i> MPM-PV 3494	4.1	2.1	2.4	2	3.5	2	1.4	3.4	2.5	5.4		
<i>P. minutus</i> MACN 5619–5639i												

The data set was analyzed by performing a heuristic search with parsimony under equal weights with TNT 1.0 (Goloboff et al., 2003). Multistate characters were treated as in the original analyses of Horovitz and Sánchez-Villagra (2003). The shortest trees were found by generating 500 Wagner trees, and then submitting them to the tree bisection reconnection branch-swapping method, retaining 10 trees per replication. State transformations were considered synapomorphies for a given node only if they were unambiguous. Relative and absolute Bremer support (Goloboff and Farris, 2001) were calculated using heuristic searches in TNT (Goloboff, et al., 2003) in order to assess clade support. Unambiguous character state optimizations and the obtained tree were edited with the program WINCLADA (Nixon, 1999).

COMPARATIVE DESCRIPTION

Humerus

Like *Caenolestes* (Osgood, 1921:fig. 15.1), the humeral shaft in *Palaeotheres minutus* (Fig. 1A–B) is relatively slender compared with that of *Rhyncholestes*, *Dromiciops*, *Monodelphis*, and *Didelphis* (Fig. 3A–B). Based on the preserved portion of the humerus, it is possible to observe that, as in *Caenolestes*, the deltopectoral crest, which provides the area of insertion for the pectoralis major and minor, acromiodeltoideus, clavodeltoideus, and spinodeltoideus muscles in living marsupials, is less distally extended than that of *Rhyncholestes* and other examined marsupials (e.g., *Didelphis*, *Monodelphis*). In *Rhyncholestes* the deltopectoral crest is very salient, and extends distally to near the distal end of the humerus. The lateral epicondylar crest (Fig. 1A–B), area of origin of the brachioradialis (elbow flexor and forearm supinator), and the extensors extensor carpi radialis (anteriorly), anconeus, and triceps brachii caput laterale (posteriorly), is much less salient than that of most of the examined didelphids, *Dromiciops*, and

Rhyncholestes (Fig. 3A–B), resembling that of *Caenolestes* (Osgood, 1921:fig. 15.1) and *Metachirus* (Argot, 2001:fig. 8F). Thus, it is possible that these muscles would have not achieved the great development characteristic of arboreal marsupials and others arboreal mammals (e.g., Argot, 2001; Candela and Picasso, 2008). The medial epicondyle in *Palaeotheres* extends medially less than that of *Rhyncholestes*, *Dromiciops*, *Monodelphis*, and *Didelphis* (Fig. 1A–C; Fig. 3A–C). This condition indicates relatively less developed wrist and digit flexors (flexor digitorum profundus and superficialis, pronator teres, and flexor carpi radialis muscles). Note that in *Palaeotheres* the medial epicondyle is even more reduced than that of *Caenolestes* (Osgood, 1921:fig. 15.1), resembling that of *Metachirus* (Szalay and Sargis, 2001:fig. 9).

The distal humerus is slender relative to the examined marsupials, resembling that of *Metachirus* and *Caenolestes*. In *Palaeotheres*, the radial and coronoid fossae are very deep, much more so than any examined marsupials (Fig. 1A; Fig. 3A). Both fossae form a confluent depression that extends from the proximal border of the articular joint to approximately the level of the supracondyloid foramen. Note that in *Rhyncholestes* the radial and coronoid fossae are deep but less so than in *Palaeotheres*. A deep coronoid fossa is observed in *Metachirus* (Argot, 2001). The supracondyloid crest (=medial epicondylar crest) is very robust. The supracondyloid foramen (=entepicondylar foramen sensu Flores, 2009) opens at the medial border of the coronoid fossa, so this foramen cannot wholly be seen in anterior view. In *Rhyncholestes*, *Dromiciops*, *Didelphis*, and *Monodelphis*, the supracondyloid foramen is open anteriorly.

In *Palaeotheres* the distal articulation of the humerus is more extended proximodistally relative to that of most of the didelphids, *Rhyncholestes*, and *Dromiciops* (Fig. 3A–B), similar to that of *Metachirus* (Argot, 2001:fig. 8F) and *Caenolestes*. In distal view the humerus is very deep (anteroposteriorly extended), more so

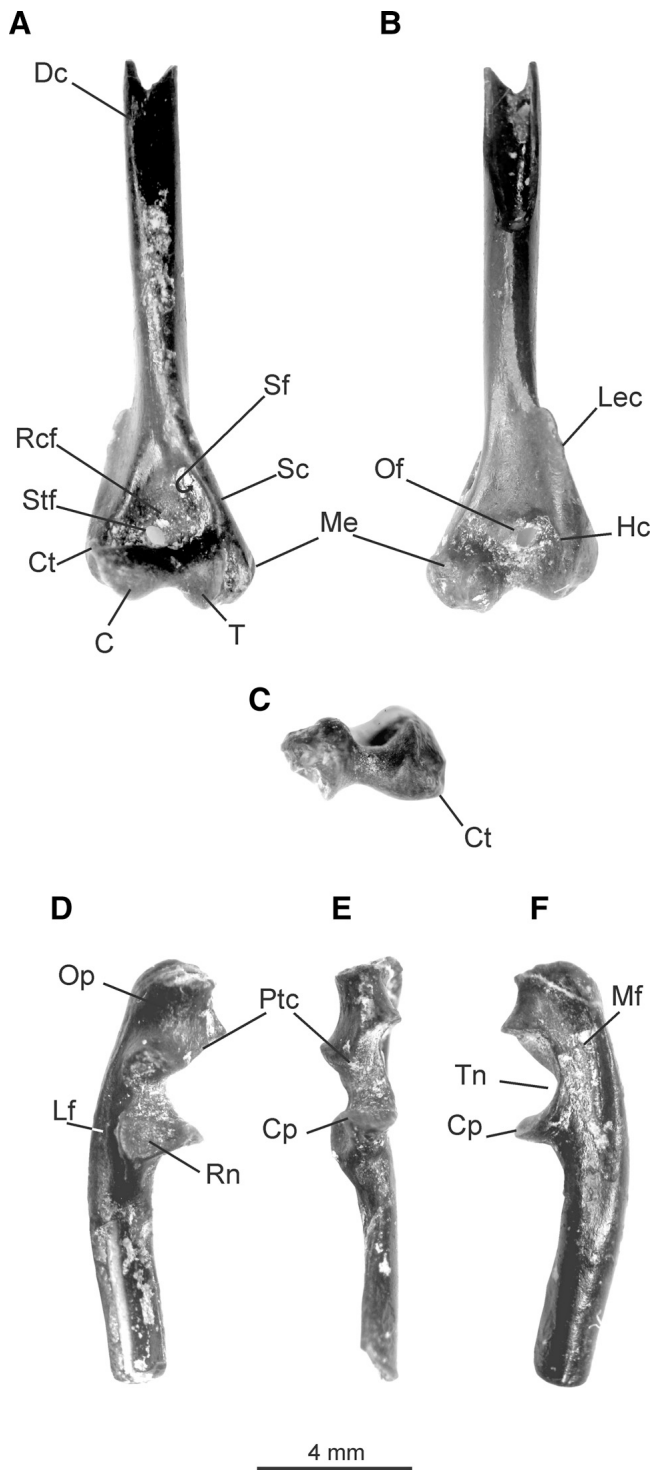


FIGURE 1. *Palaeothenes minutus*; A–C, right humerus (MACN 5619–5639c) in anterior (A), posterior (B) and distal (C) views; D–F, right ulna (MACN 5619–5639e) in lateral (D), anterior (E), and medial (F) views. **Abbreviations:** C, capitulum; Cp, coronoid process; Ct, capitular tail; Dc, deltopectoral crest; Lec, lateral epicondylar crest; Lf, lateral fossa; Me, medial epicondyle; Mf, medial fossa; Of, olecranon fossa; Op, olecranon process; Ptc, proximal trochlear crest; Rcf, radial + coronoid fossae; Rn, radial notch; Sc, supracondyloid crest; Sf, supracondyloid foramen; Stf, supratrochlear foramen; T, trochlea; Tn, trochlear notch.

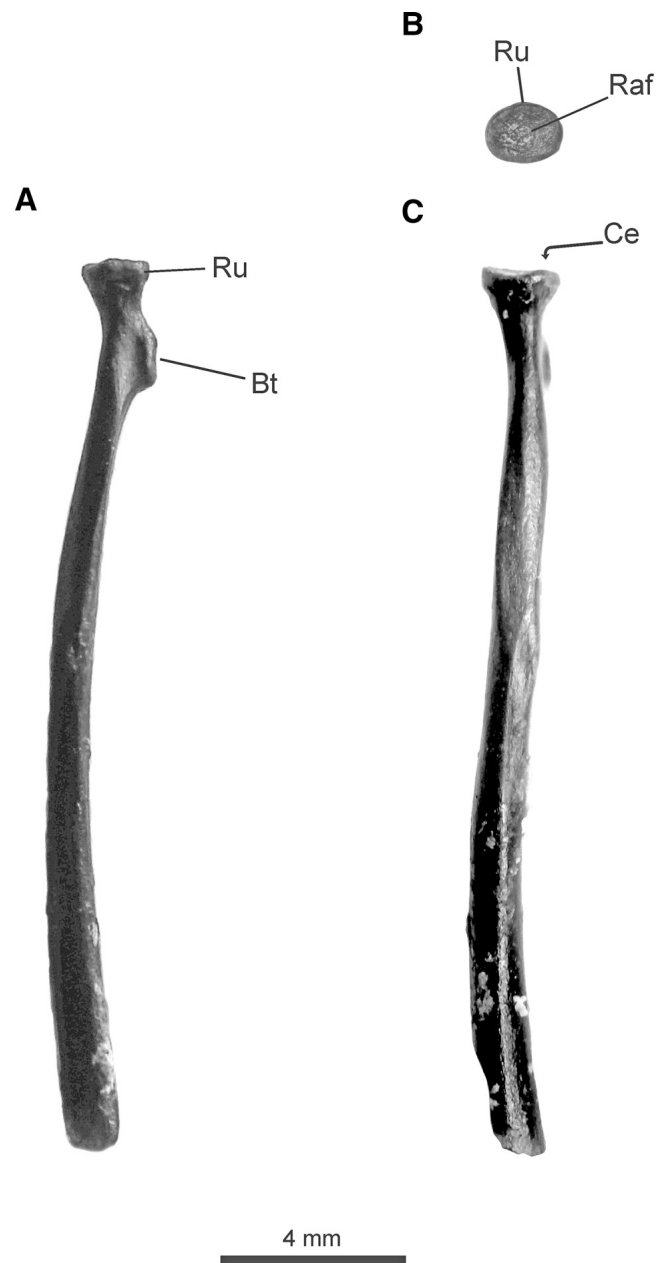


FIGURE 2. *Palaeothenes minutus*; A–C, right radius (MACN 5619–5639d) in medial (A) proximal (B), and anterior (C) views. **Abbreviations:** Bt, bicipital tuberosity; Ce, capitular eminence; Raf, radial articular facet for the capitulum; Ru, radio-ular facet.

than in the most of the examined marsupials (Fig. 1C; Fig. 3C), a condition comparable to that of *Metachirus* (Argot, 2001:fig. 8F). In anterior view the height of the trochlea is sub-equal to that of the capitulum, and their anteromedial border (or medial lip) is very salient. The trochlea is relatively more concave posteriorly than in *Rhyncholestes*, *Dromiciops*, and most of the didelphids examined, with exception of *Metachirus*. In posterior view it extends medially forming a posteromedial convexity (Fig. 1B–C), as occurs in *Metachirus* (Argot, 2001). The capitulum is well developed and subcylindrical. The capitular tail is moderately developed. Between the trochlea and the medial epicondyle is a deep sulcus. Like *Rhyncholestes* and *Metachirus*, the olecranon

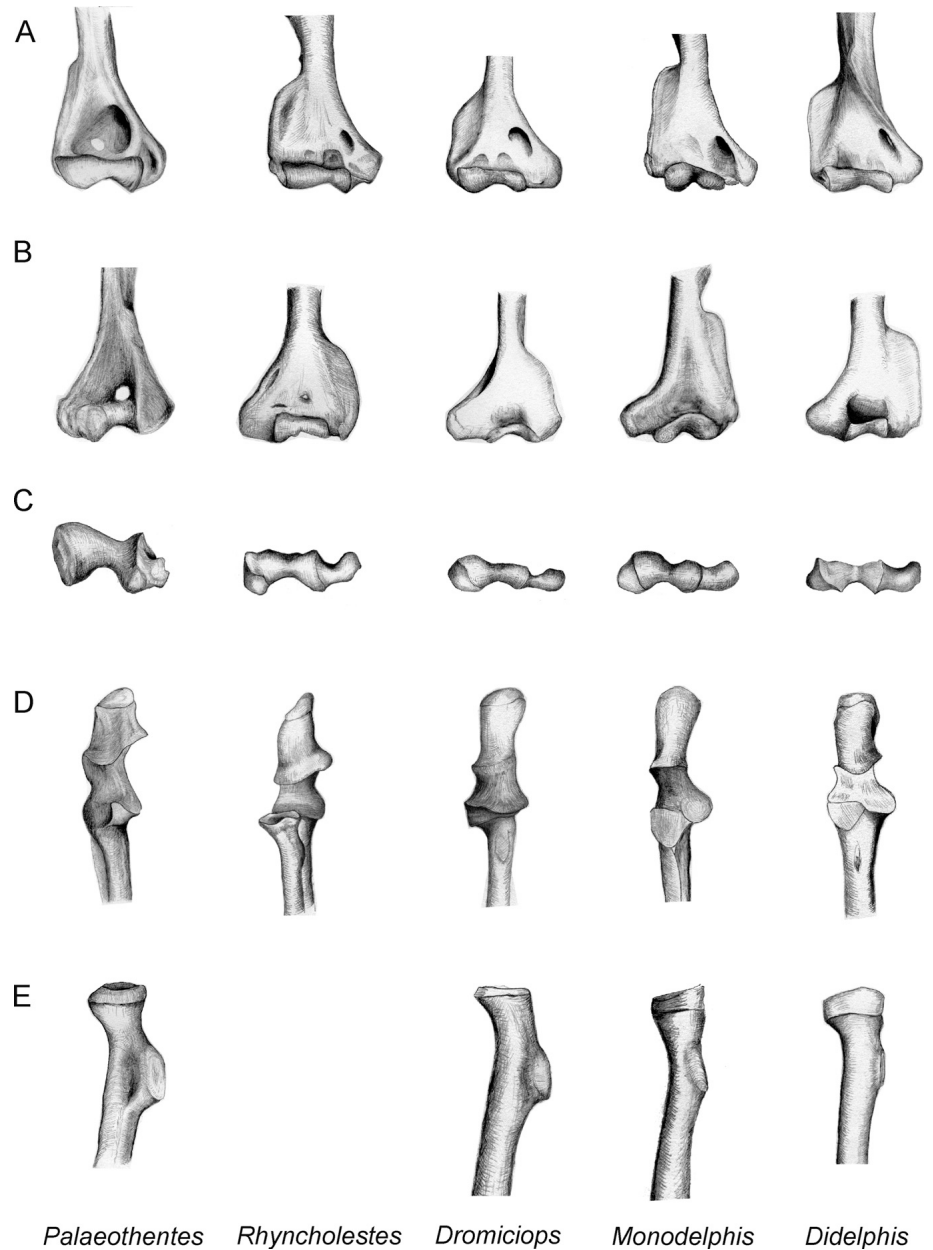


FIGURE 3. Forelimb in *Palaeothenes* and several marsupials. Distal end of right humerus in anterior (A), posterior (B), and distal (C) views. Proximal end of right ulna in anterior view (D). Proximal end of right radius in lateral view (E). Not to scale.

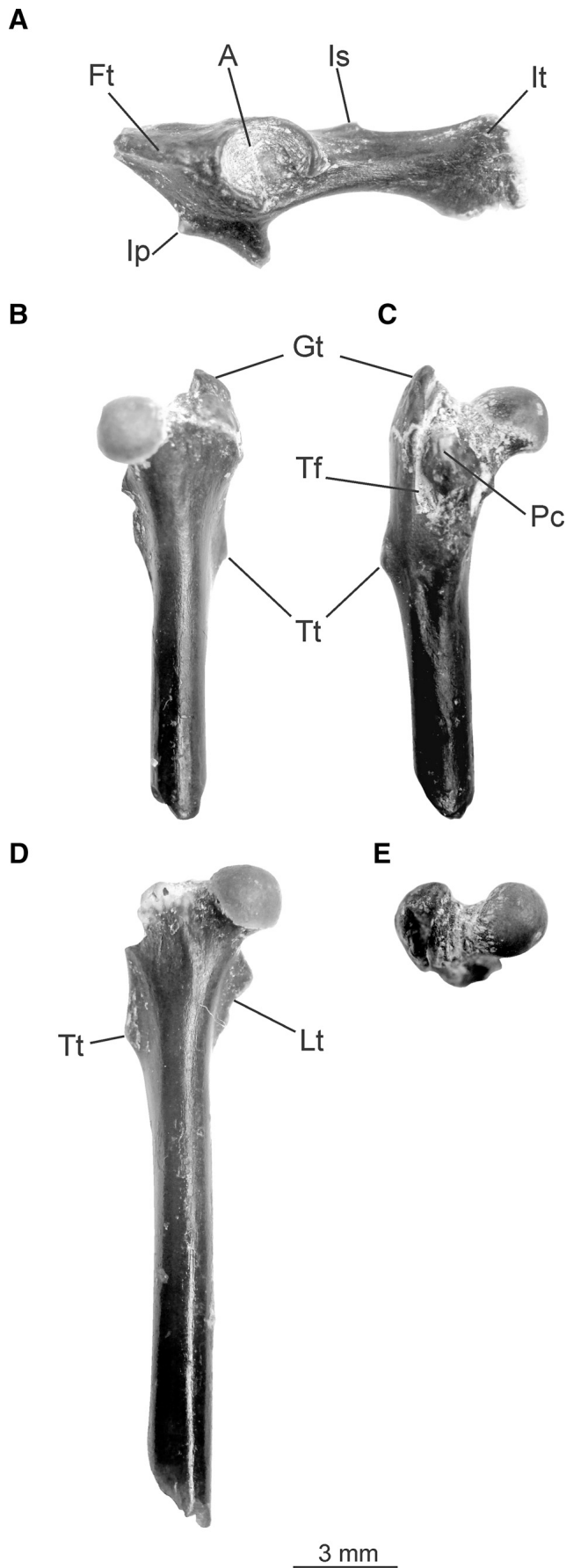
fossa is broad and very deep, being perforated (=supratrochlear foramen) in *Palaeothenes*. On the posterior facet of the distal humeral joint, the humeral posterolateral crest (=hplcr sensu Szalay and Sargis, 2001), which is sharp and robust, is continuous with the lateral crest bordering the olecranon fossa.

The humerus of *Palaeothenes lemoinei*, represented by a very fragmentary specimen (MPM-PV 3494), is similar to that of *P. minutus* in most features. The preserved portion of the entepicondyle seems to be relatively larger than that of *P. minutus*.

Ulna

In several features, the ulna of *Palaeothenes* (Fig. 1D–F) is similar to that of living caenolestids and *Metachirus*. As in *Metachirus* (Flores, 2009), the olecranon process is shorter than that of *Dromiciops* and most of the didelphids examined (Fig. 3D). Like living caenolestids (Szalay and Sargis, 2001:fig. 12G–L),

it is very robust and markedly extended anteroposteriorly. The trochlear notch is proximally very wide (Fig. 1D–E), a feature that is expressed in a mediolaterally extended proximal trochlear crest (ulptc sensu Szalay and Sargis, 2001). This crest is prominent and, compared with the distal trochlear crest, is relatively wider than that of *Dromiciops* and most of the examined didelphids (Fig. 3D). It resembles *Metachirus* (Argot, 2001:fig. 10F) and living caenolestids. In addition to the very wide trochlear notch, one of the most distinctive ulnar features in *Palaeothenes* is the sinuous shape of the proximal trochlear crest. In *Rhyncholestes* and *Caenolestes* the proximal crest of the trochlear notch is wider and less sinuous than in *Palaeothenes* (Fig. 3D; Szalay and Sargis, 2001:fig. 12G–L). The cranial projection of the coronoid process (=ulco, anterior extension of the coronoid process, sensu Szalay and Sargis, 2001) is prominent, more so than in the other examined marsupials (Fig. 3D). The trochlear notch is more closed than in the arboreal didelphids and *Dromiciops*. The Trochlea



Notch Index (see Szalay and Sargis, 2001) in *Palaeothenes* (46) is larger than that of arboreal *Dromiciops* and *Caluromys* (36). The radial notch of the ulna is concave, consistent with the convex and mediolaterally extended radio-ulnar facet of the radial head (RaUlp sensu Szalay and Sargis, 2001). The angle between radial notch and the coronoid process is nearly 90°, as in *Metachirus* (Argot, 2001). It is more open in the other marsupials examined. Distal to the coronoid process is a depression that corresponds to the insertion area for the flexors of the forearm (brachialis and the ulnar head of biceps brachii). The posterior border of the proximal portion of the ulna is relatively straight (Fig. 1D, F), but bears a slight convexity, as in living caenolestids and *Metachirus* (Szalay and Sargis, 2001:figs. 11F–J, 12G–L; Flores, 2009). On the proximal portion of the ulna, the medial fossa is shallower than that of *Rhyncholestes*. This fossa seems to correspond to the area of origin of the flexor digitorum profundus muscle that is involved in the prehensibility of the manus. The lateral fossa, on the proximal portion of the ulna, is shallower than that of *Rhyncholestes*, probably representing the insertion area for the anconeus muscle.

The ulna of *Palaeothenes lemoinei* (better preserved than that of *P. minutus*, conserving the more distal portion of the shaft), is very similar to that of *P. minutus*, but the lateral fossa is shallower.

Radius

The radius (Fig. 2) is relatively more slender and less anteroposteriorly bowed than in *Rhyncholestes* and some didelphids (e.g., *Caluromys*; see Argot, 2001:fig. 16). Proximally, the shaft is relatively anteroposteriorly compressed (Fig. 2A); at the preserved portion of the distal shaft there is a markedly sharp posterolateral border. The relatively straight radius indicates that flexor digitorum profundus and abductor pollicis longus muscles would have been less developed than in arboreal didelphids (Argot, 2001; see also Flores, 2009). In proximal view, the radial head is suboval, not circular as in arboreal forms, with the mediolateral diameter larger than the anteroposterior one (Fig. 2B). The articular facet for the capitulum (=radial central fossa sensu Szalay and Sargis, 2001) is shallow, as in *Metachirus*. The radio-ulnar facet extends from the posterolateral to the anteromedial margin of the radial head, where it is interrupted by the capitular eminence (=central process, repr sensu Szalay and Sargis, 2001). The bicapital tuberosity, the insertion of the radial head of biceps brachii, is very robust (Fig. 2A), more so than other examined marsupials (Fig. 3E). This tuberosity is relatively more proximally positioned than in the arboreal marsupials (Table 1; cf. Argot 2001:table 3). Note that, as in *Palaeothenes*, the bicapital tuberosity in *Metachirus* is both more proximal and more sharply delineated distally than in the arboreal *Caluromys* (Argot, 2001).

Pelvis

The preserved portion of the pelvis (Fig. 4A) is robust in relation to that of the examined marsupials. The dorsal ramus of the ischium is relatively long compared with the anteroposterior diameter of the acetabulum relative to that of *Dromiciops* and most of the examined didelphids (Fig. 5), as occurs in *Caenolestes*, *Rhyncholestes*, and *Metachirus* (Argot, 2001). The

← FIGURE 4. *Palaeothenes minutus*; **A**, left pelvis (MACN 5619–5639f) in lateral view; **B–C**, left femur (MACN 5619–5639h) in anterior (**B**) and posterior (**C**) views; **D–E**, right femur (MACN 5619–5639g) in anterior (**D**) and proximal (**E**) views. **Abbreviations:** Ft, femoral tubercle; Gt, great trochanter; Ip, iliopectineal process; Is, ischial spine; It, ischial tuberosity; Lt, lesser trochanter; Pc, paratrochanteric crest; Tf, trochanteric fossa; Tt, third trochanter.

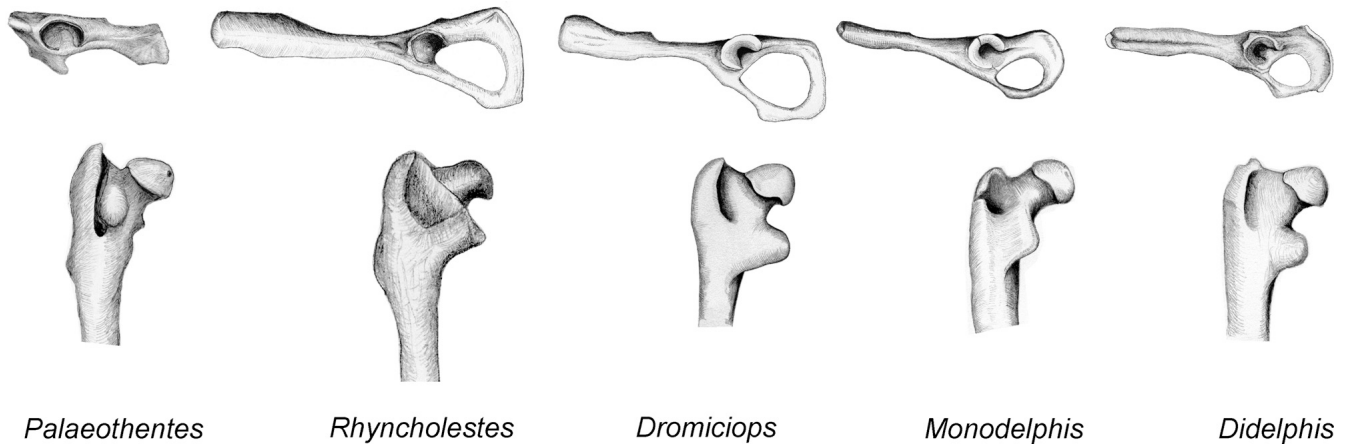


FIGURE 5. Pelvis and femur of *Palaeothenes* and several marsupials. Upper, left pelvis in lateral view; lower, left femur in posterior view. Not to scale.

ischial tuberosity, the origin of the hamstring muscles, is well developed. Like *Caenolestes* and *Metachirus*, the ischial spine is posteriorly located relative to the posterior border of the acetabulum. The iliopectineal process, the area of attachment of *psaos minor* muscle, is well developed and anteriorly positioned relative to the anterior border of the acetabulum. Like *Rhyncholestes*, the femoral tubercle (area of attachment of the *rectus femoris* muscle) is salient, forming an elongated protuberance, more developed than in didelphids and *Dromiciops*. The acetabular cavity is slightly oblong and deep, with the anterior and dorsal surfaces extended, indicating a restrictive articulation as in *Metachirus* (Flores, 2009). The pelvis of *Palaeothenes lemoinei* is essentially identical to that of *P. minutus*.

Femur

Unlike arboreal species (e.g., *Caluromys* and *Dromiciops*), the great trochanter in *Palaeothenes* projects beyond the ar-

ticular surface of the femoral head, resembling the condition in *Rhyncholestes*, *Caenolestes*, and *Metachirus* (Fig. 4B–C; Fig. 5). Like *Caenolestes* and *Rhyncholestes*, the articular surface of the femoral head is not laterally extended (Fig. 4E), in contrast to the condition in arboreal *Dromiciops* and *Caluromys*. The trochanteric fossa is straight and limited medially by a strong paratrochanteric crest (the area of attachment for the ischiofemoral ligament). Like *Caenolestes* and *Rhyncholestes*,

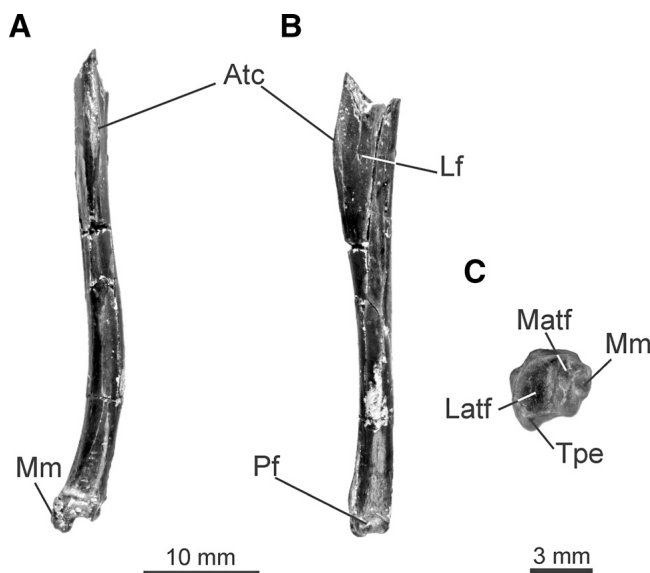


FIGURE 6. *Palaeothenes lemoinei* (MPM-PV 3494); **A–B**, left tibia in anterior (**A**) and lateral (**B**) views; **C**, right tibia in distal view. **Abbreviations:** **Atc**, anterior tibial crest; **Latf**, lateral astragalotibial facet; **Lf**, lateral fossa; **Matf**, medial astragalotibial facet; **Mm**, medial malleolus; **Pf**, peroneal facet; **Tpe**, tibial posterior extension.

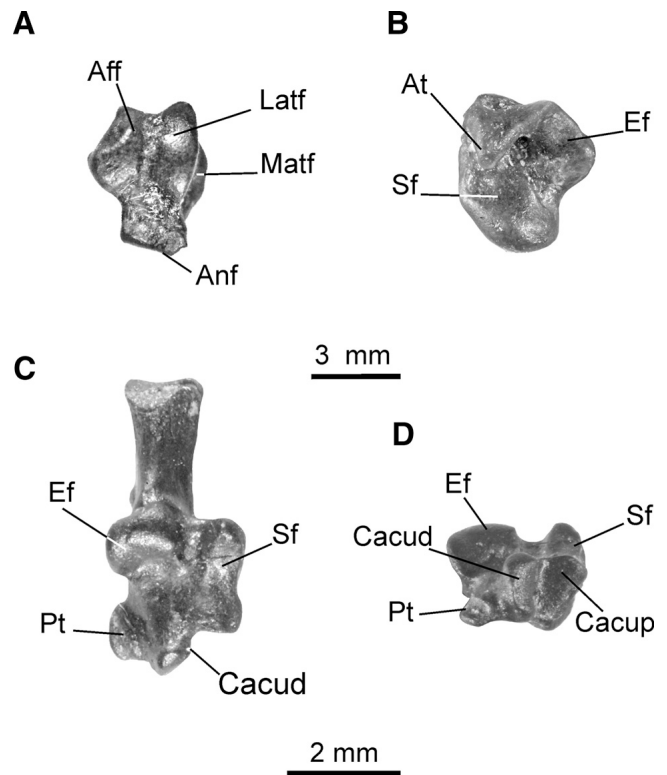


FIGURE 7. *Palaeothenes lemoinei* (MPM-PV 3494); **A–B**, right astragalus in dorsal (**A**) and ventral (**B**) views; *Palaeothenes minutus* (MACN 5619–5639i); **C–D**, right calcaneum in dorsal (**C**) and anterior (**D**) views. **Abbreviations:** **Aff**, astragalofibular facet; **Anf**, astragalonavicular facet; **At**, medial astragal plantar tuberosity; **Cacud**, cuboid facet distal half; **Cacup**, cuboid facet proximal half; **Ef**, ectal facet; **Latf**, lateral astragalotibial facet; **Matf**, medial astragalotibial facet; **Pt**, peroneal tubercle; **Sf**, sustentacular facet.

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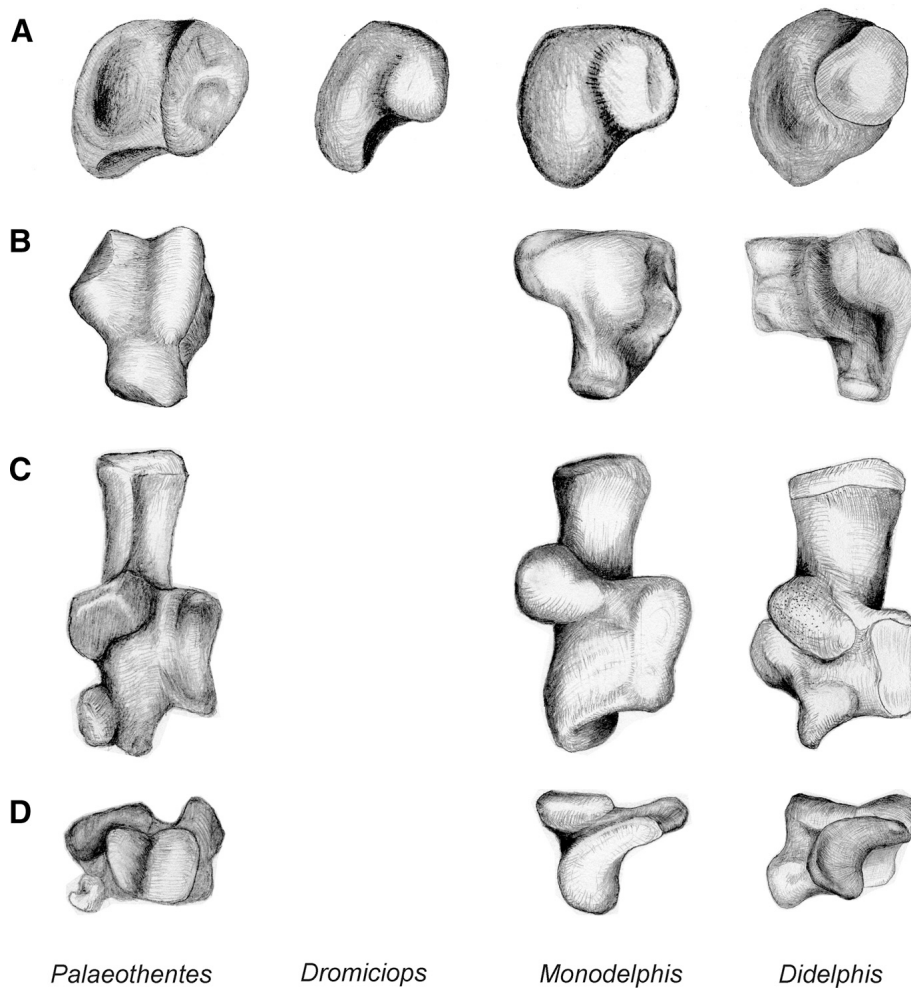


FIGURE 8. Tibia, astragalus and calcaneum of *Palaeothenes* and several marsupials. Distal end of the tibia in distal view (A). Astragalus in dorsal view (B). Calcaneum in dorsal (C) and anterior (D) views. Not to scale.

the trochanteric fossa extends distally to the level of the lesser trochanter (are of insertion of iliopsoas complex). As in *Metachirus*, the lesser trochanter of *Palaeothenes* is relatively more reduced than in the other didelphids, *Dromiciops*, and *Rhyncholestes*. It is compressed craneocaudally and is continuous with a crest that extends distally to the level of the third trochanter. This latter structure is absent in didelphids and *Dromiciops* but is well developed in *Caenolestes* and *Rhyncholestes*. The third trochanter is one of the most characteristic femoral traits of Paucituberculata.

Tibia

The tibia is only represented in *Palaeothenes lemoinei* (Fig. 6). The preserved portion resembles that of *Caenolestes*, being convex proximally and concave distally (Osgood, 1921:fig. 12). The anteriorly projecting anterior tibial crest is very distinctive. Although it is evident in *Rhyncholestes*, it is less salient than in *Palaeothenes*. The lateral fossa, the origin of tibialis anterior muscle, is clearly evident on the lateral face of the anterior tibial crest (Fig. 6B). In the examined didelphids, the anterior tibial crest and lateral fossa are not clearly distinguishable.

The distal portion of the shaft is nearly subcircular. The peroneal facet is larger than any other examined marsupial. As in living caenolestids (see Szalay, 1994), the lateral astragalotibial facet of the distal tibial joint is relatively anteroposteriorly narrow and subrectangular, not suboval as in didelphids (Fig. 8A).

It bears a reduced tibial posterior extension (astragalotibial posterior facet, Atip sensu Szalay, 1994), characteristic of didelphids (Fig. 6C; Fig. 8A). Unlike most of the didelphids and *Dromiciops*, the medial and lateral astragalotibial facets form a fairly sharp angle, a condition similar to that of sparassodonts (Argot, 2004). The medial astragalotibial facet extends on the medial surface of the medial malleolus, which is very prominent, projecting beyond the lateral astragalotibial facet, as in *Caenolestes* (Fig. 6B; see also Osgood, 1921). Unlike other marsupials, the medial malleolus extends near the posterior border of the tibial distal joint in distal view (Fig. 6C; see also Szalay, 1994; Argot, 2002:fig. 131).

Astragalus

The astragalus is only represented in *Palaeothenes lemoinei* (Fig. 7A–B). As in living caenolestids (Szalay, 1994:201) and sparassodonts (Szalay, 1994:208–209; Argot, 2004:500), and in contrast to didelphids and *Dromiciops* (Fig. 8B; see also Szalay, 1994:189–199, 217), the astragalofibular facet is relatively narrow. The angle between the medial and lateral astragalotibial facets is very sharp, in agreement with the sharp angle formed by the tibial distal facets (see above), one of the most distinguishing astragalotibial features. Like sparassodonts, the astragalotibial medial facet is extensive. As in *Metachirus* and Sparassodonta, the astragalonavicular facet is mainly vertically orientated (see Szalay, 1994; Argot, 2002; Flores, 2009). As in living caenolestids, the sustentacular facet is confluent with the astragalonavicular

facet. The sustentacular facet is proximodistally long, ribbon-like in shape, and distally very broad and convex, having its proximal end narrow and very concave. The ectal facet is concave and elongate with its major axis oriented slightly obliquely (postero-medial to anterolateral). The medial astragalar plantar tuberosity for the posterior astragalocalcaneal ligament (ampt sensu Szalay, 1994) is very large and robust and extends posteriorly over the sustentacular facet (Fig. 7B).

Calcaneum

The calcaneum (Fig. 7C–D) resembles that of living caenolestids (Szalay, 1994:fig. 7.14). There is no continuity between the ectal (=lateral calcaneoastagalar) and sustentacular facets, as occurs in *Dromiciops* and remaining Australidelphia (Szalay, 1982, 1994). The sustentacular facet is narrow and proximodistally elongate, with its major axis parallel to the long axis of the bone. It is slightly concave and extends to the cuboid facet. The ectal facet is anteroposteriorly convex and dorsally orientated, with its major axis slightly oblique relative to the long axis of the bone (proximomedial to distolateral). Unlike didelphids and *Dromiciops*, the calcaneofibular facet is well developed, as occurs in *Caenolestes* (Szalay, 1994:201) and some sparassodonts (Argot, 2004:500). The peroneal tubercle (Fig. 7C–D) is large (as in living Caenolestidae; Szalay, 1994:201) and grooved (gtpl, groove for tendon of peroneus longus). The calcaneocuboid facet (Fig. 7D; Fig. 8D) is dorsoventrally deep and is clearly divided into distal and proximal halves, which form a sharp angle of nearly 90°, one of the most distinctive calcaneal features. The distal half faces medially whereas the proximal one is flat and faces anteriorly. There is no medial ventral recess for the cuboid process (cacup sensu Szalay, 1994), as occur in the didelphids. At the medial end of the plantar surface of the calcaneocuboid facet is a moderately developed plantar tubercle.

FUNCTIONAL ANALYSES

Humeral Features

In the framework of this comparative sample, the humeral features of *Palaeothentes* are more similar to those of the *Metachirus* and *Caenolestes*. The proximal location of the deltopectoral crest (Fig. 1A) indicates that the pectoralis muscle, an adductor of the forelimb and flexor of the glenohumeral joint, would have had a lesser mechanical advantage than in the most of examined marsupials, where this crest is more distally extended (e.g., *Didelphis*, *Monodelphis*). The position of the deltopectoral crest in *Palaeothentes* appears to be linked to dorsoventral shortening of pectoralis. This may reduce the weight of the limb without limiting its strength, thus resulting in more agile movements of the limb. Rapid rather than powerful flexion of the glenohumeral joint appears to have been emphasized in species of *Palaeothentes*, consistent with agile locomotor habits, similar to those of *Caenolestes*. It should be pointed out that unlike *Palaeothentes*, *Rhyncholestes* has a very salient and distally extended deltopectoral crest. This reflects a marked development of pectoral muscles, as occurs in arboreal didelphids, in which it is particularly used when climbing (Argot, 2001). However, the biology of *Rhyncholestes* is unknown and more information is necessary to establish the possible association between locomotor behavior and humeral features.

The little-developed lateral epicondylar crest of *Palaeothentes* (Fig. 1A–B; Fig. 3A–B) indicates scarce development of the brachioradialis muscle, especially with respect to that of the arboreal species. This muscle is mainly a flexor of the elbow joint and acts partly as a supinator in arboreal forms, a role particularly emphasized when climbing (McEvoy, 1982; Argot, 2001). The proximal location and prominent development of this crest, as are seen in arboreal didelphids, accentuate the action

of brachioradialis (Szalay and Sargis, 2001). Unlike in arboreal didelphids and *Dromiciops*, in *Palaeothentes* the short and subtle lateral epicondylar crest is similar to the condition of *Metachirus* and *Caenolestes*.

One of the more distinctive humeral features of *Palaeothentes* is the scarcely protruding medial epicondyle (Fig. 1A–B), a condition similar to that of *Metachirus* and *Caenolestes* (Osgood, 1921; Argot, 2001; see also Szalay and Sargis, 2001). A medially protruding medial epicondyle occurs in *Dromiciops* and arboreal didelphids (Fig. 3A–C), which have well-developed flexors of the digits (Argot, 2001:fig. 8; Table 2). This protrusion is correlated with the power of contraction of the flexors, which exert a medial torque at the elbow joint (Jenkins, 1973; Argot, 2001). The diminution of the medial epicondyle of *Palaeothentes*, and almost certainly of the flexor musculature (as has been noted in *Metachirus*; Argot, 2001), reflects the reduction of the medial torque exerted by these muscles at the elbow joint during the propulsion phase of locomotion (Jenkins, 1973). A reduced medial epicondyle is present in some living terrestrial marsupials and others mammals that exhibit reduced manipulative capabilities of the manus (Argot, 2004). Thus it is possible to infer that *Palaeothentes* would have had more reduced controlling capabilities of the manus than arboreal didelphids. A reduced medial epicondyle is found in at least some borhyaenoids (Argot, 2003a) and in several terrestrial species of others groups of mammals (e.g., Jenkins, 1973; Taylor, 1974; Rose and Chinnery, 2004; Candela and Picasso, 2008).

Humero-Radial, Humero-Ulnar, and Radio-Ulnar Joints

The features of the elbow joint of *Palaeothentes* (Figs. 1–2) reflect marked congruence and stability, conditions related to the ability to resist high-impact loading during running or leaping, as has been observed in terrestrial marsupials (Szalay and Sargis, 2001). The shape of the distal humeral joint in *Palaeothentes* is related to an increase of the surface during close packing of the elbow joint. Unlike most of the examined marsupials (Fig. 3; see also Comparative Description, above), the very proximodistally (high) and anteroposteriorly (deep) extended humeral trochlea of *Palaeothentes* conforms with a deep and close trochlear notch of the ulna. This arrangement, similar to that of *Metachirus* (Argot, 2001), improves parasagittal movements, as also occurs in other terrestrial mammals (Candela and Picasso, 2008). The prominent medial lip of the humeral trochlea maximizes the congruence at this joint. Some features in *Palaeothentes* (higher, narrower, and deeper humeral trochlea) are indicative of a more stabilized elbow joint than in *Rhyncholestes*. As in *Metachirus* and other terrestrial mammals (e.g., Taylor, 1974; Szalay and Dagosto, 1980; Sargis, 2002a; Candela and Picasso, 2008), the deep olecranon fossa, which corresponds on the ulna to a prominent proximal ulnar trochlear crest, allows the olecranon process to pass through this fossa during complete extension (Szalay and Sargis, 2001). Like *Metachirus* and *Caenolestes*, the widened and deep olecranon fossa is in agreement with the closely fitting and mediolaterally spread proximal trochlear crest of the trochlear notch. The sinuous shape of this crest is congruent with the posteromedial convexity of the humeral trochlea (see description). The prominent and anteriorly protruding coronoid process matches the deep coronoid fossa. These features emphasize the stability of the elbow and increase the range of extension during locomotion (Szalay and Sargis, 2001).

Note that several features of the elbow joint of *Palaeothentes* are present in some borhyaenoids, such as *Borhyaena*, which were associated with stabilized movements, compatible with terrestrial habits (Argot, 2003b). Some of the mentioned features of *Palaeothentes* are characteristic of living terrestrial marsupials, rodents, and scandentians (Argot, 2001; Szalay and Sargis,

2001; Sargis, 2002a; Rose and Chinnery, 2004; Candela and Picasso, 2008).

The subcylindrical humeral capitulum is in agreement with the suboval radial head of the radius, not circular as in arboreal forms (Argot, 2001). The evident capitular tail, and the presence of the capitular eminence of the radius, implies stabilized flexions through radio-capitular contact. The nearly right angle subtended by the radial notch of the ulna and the coronoid process, as in *Metachirus*, is also indicative of stabilized movements (Argot, 2001). The radial notch is concave, consistent with the convex and lateromedially extended radio-ulnar facet of the radial head, which facilitates rotation of the radius during supination. The radio-ulnar facet of *Palaeotheres* is less convex than that of arboreal didelphids, suggesting a lesser range of pronation-supination in *Palaeotheres*. The features of the elbow joint shared by *Palaeotheres*, *Metachirus*, and *Caenolestes* probably reflect similar stabilized movements at this joint associated with an agile mode of locomotion.

Ulnar Features

The short and deep olecranon process in *Palaeotheres* (Fig. 1D–F; Fig. 3D) implies a strong insertion area for the triceps brachii complex, emphasizing the traction exerted by these muscles. It is possible that the relatively short moment arm of the triceps is compensated by increased volume of this muscle. The short and robust olecranon, mirroring the well-developed triceps complex, is consistent with a powerful and fast extension of the elbow at the beginning of propulsive phase. A relatively short and robust olecranon process is also present in *Metachirus* and living caenolestids (Argot, 2001; Szalay and Sargis, 2001; Flores, 2009). As in *Metachirus* and other terrestrial marsupials (Argot, 2001:fig. 10F; Argot, 2004), the nearly straight posterior edge of the proximal ulna in *Palaeotheres* would have allowed greater extension of the elbow joint relative to arboreal marsupials and other arboreal mammals (Taylor, 1974; Argot, 2001; Szalay and Sargis, 2001; Rose and Chinnery, 2004; Candela and Picasso, 2008). In such arboreal mammals, the posterior border of the proximal ulna is convex, with the triceps being more efficient at flexed positions of the elbow (Sargis, 2002a).

Radial Features

The very robust bicipital tuberosity would provide a strong insertion area for the biceps brachii (radial head), more so than in *Rhyncholestes* and *Dromiciops*. The tuberosity also is more proximally located than in arboreal marsupials. These conditions are consistent with fast and powerful flexion movements of the elbow joint. Note that, as in *Palaeotheres*, the bicipital tuberosity in *Metachirus* is both more proximal and more sharply delineated distally than in the arboreal *Caluromys* (Argot, 2001). The straighter radial diaphysis of *Palaeotheres* relative to those of the arboreal didelphids indicates that the muscles involved in the mobility of the manus or climbing (flexor digitorum profundus and abductor pollicis longus) may have been less developed than in extant arboreal species (Argot, 2001). It is possible to infer that in *Palaeotheres* the manus was less prehensile than in living arboreal species.

Pelvic Features

Like *Caenolestes* and *Metachirus*, the prominent ischial tuberosity and elongate ischium (Fig. 4A; Fig. 5) indicate marked development and relatively high mechanical advantage of the hamstring muscles (i.e., biceps femoris, semitendinosus, semimembranosus). These muscles act at the beginning of the propulsive phase of locomotion, providing the acceleration needed for leaping (Maynard Smith and Savage, 1956; Argot, 2002). As in *Metachirus*, the development of these extensors

in *Palaeotheres* could be related to cursorial to saltatory habits. It is noteworthy that the elongated ischium, providing leverage to the hamstrings, is typical of macropodoids (Kear et al., 2007). The prominent femoral tubercle reflects a well-developed rectus femoris muscle, an extensor of the knee and flexor of the hip (Sargis, 2002b). A rapid extension of the knee is necessary in species with agile movements (Szalay and Sargis, 2001).

Hip Joint

Features of the hip joint restrict rotational movements of the femur by limiting them to a parasagittal plane. The deep acetabulum, with extended dorsal and anterior surfaces, limits rotational movements of the femur, increasing congruence at this joint. A restrictive hip joint is found in the agile cursorsaltatorial *Metachirus* (Argot, 2002; Flores, 2009). In *Palaeotheres*, the femoral head articulation does not extend laterally, a condition that reflects an exclusive contact during extension and flexion (Szalay and Sargis, 2001). The proximally extended greater trochanter of the femur (see below) would have restricted mobility at this joint, limiting abduction of the femur, as in other terrestrial mammals (Sargis, 2002b; Candela and Picasso, 2008).

Femoral Features

Like *Caenolestes* and *Metachirus* (Argot, 2002:fig. 8B), a greater trochanter that projects beyond the proximal surface of the femoral head expresses a markedly developed and relatively high mechanical advantage of the gluteus medius, profundus, and minimus (Argot, 2002). This condition indicates fast extension of the hip joint during the second phase of propulsion, characteristic of agile terrestrial and leaping species (Taylor, 1976; Argot, 2002). As in *Metachirus*, the lesser trochanter is relatively reduced in *Palaeotheres* compared with the examined marsupials. Because this area is the insertion for the iliopsoas complex, a flexor, protactor, and lateral rotator of the femur, its reduction suggests relatively more rapid flexion of the hip joint than in arboreal species, where abduction of the femur is emphasized (Szalay and Sargis, 2001). In *Rhyncholestes*, the lesser trochanter is more medially protruding and larger than that of *Palaeotheres*, as in arboreal species. The third trochanter in *Palaeotheres*, the insertion area for the gluteus superficialis (Osgood, 1921), an extensor and abductor of the femur, is well developed, as in *Caenolestes* and *Rhyncholestes*. The relatively proximal location of third trochanter suggests that this muscle as acted more as an extensor than an abductor (Candela and Picasso, 2008). In *Palaeotheres*, the third trochanter is at approximately the same level as the lesser trochanter (where gluteus maximus/superficialis inserts), as occurs in primates. This feature has been interpreted as having the “likely effect of decreasing the mechanical advantage of the hip extensors, but increasing their speed of action, and is a morphology typical of leaping primates . . .” (Dagosto, 2007:514). However, more information is necessary to evaluate the functional significance of the third trochanter in Paucituberculata.

Tibial Features

The noticeable curvature of the tibial shaft is difficult to analyze from functional point of view (see Szalay and Sargis, 2001; Argot, 2002, and references therein). The prominent anterior tibial crest (Fig. 6B) seems to reflect marked development of the hamstring muscles, as is indicated by the salient ischial tuberosity (see above). The distinctive lateral fossa is associated with a well-developed tibialis anterior muscle. This would have had an important function as an extensor (=dorsiflexor) rather than as an inverter of the pes, in agreement with the limited rotational movements at upper ankle joint (see below).

Upper Ankle Joint

The features of the upper ankle joint in *Palaeotheres* (the sharp angle formed by the medial and lateral astragalotibial facets, the extensive medial astragalotibial facet and prominent medial tibial malleolus, the anteroposteriorly short and subrectangular lateral astragalotibial facet of the tibia, and the reduced tibial posterior facet) constitute an arrangement better suited for flexion-extension than rotational movements. These features indicate that the upper ankle joint in *Palaeotheres* would have been more stable relative to that of the arboreal marsupials. In fact, the Tibial Medial Malleolar Index (TMMI; see Szalay and Sargis, 2001), which reflects the relative degree of medial stabilization of the upper ankle joint, is much greater in *Palaeotheres* (TMMI = 52.5) than in *Caluromys* (TMMI = 11.7) and *Metachirus* (TMMI = 28.8). A sharp angle between the lateral and medial astragalotibial facets is also observed in borhyaenoids (Argot, 2003a). In didelphids, the lateral astragalotibial facet of the tibia is suboval and alongate, especially posteriorly (Argot, 2002); the medial malleolus is not very prominent distally, and not sharply angled from the lateral facet. In *Metachirus* the angle made by the medial astragalotibial facet and the lateral astragalotibial facet is sharper compared with arboreal didelphids, and the tibial malleolus is more prominent than in *Caluromys* (Szalay, 1994; Argot, 2002; Flores, 2009), but not to the degree seen in *Palaeotheres*. The reduced tibial posterior facet, which "... mirrors the extreme of conjunct rotation of the tibia during foot inversion and dorsiflexion at the upper ankle joint ..." (Szalay, 1994:203), is reduced in *Palaeotheres*, showing that the rotation of the tibia at this joint was limited. In short, the upper ankle joint in *Palaeotheres* was much more restrictive than in any examined didelphid and *Dromiciops*, allowing only parasagittal movements.

Lower Ankle Joint

Several features of *Palaeotheres* provide evidence that inversion-eversion of the foot were restricted. The ectal facet of the calcaneus, which is anteroposteriorly convex and dorsally orientated, is in agreement with the concave and anteroposteriorly oriented ectal astragalal facet; the sustentacular facet of the calcaneum proximodistally long, slightly concave, and extended towards the cuboid facet, is congruent with the proximodistally long and distally convex sustentacular astragalal facet (Fig. 7B–C). This configuration improves movements in the parasagittal plane (Szalay, 1994). As was inferred for the terrestrial *Borhyaena*, the dorsally orientated ectal facet of the calcaneum suggests that in a resting posture the plantar side of the foot would have lain on a horizontal support (Argot, 2003b). Accepting this functional interpretation, it is not possible that the foot of *Palaeotheres* would have had inversion capacity. The well-developed calcaneofibular facet (reduced in didelphids; see Szalay, 1994; absent in didelphids with the exception of *Metachirus*; see Argot, 2002) and relatively reduced astragalofibular facet of *Palaeotheres* (larger in didelphids) would indicate the weight-bearing contact with the fibula is mainly distributed on the calcaneum, unlike the condition of the didelphids (Szalay, 1994). Both astragalus and calcaneum would have acted to support of the forces generated during locomotion (Szalay, 1994). The calcaneofibular and astragalofibular contacts in *Palaeotheres* expresses a restrictive joint, with the fibula embracing laterally the both calcaneum and astragalus.

Transverse Tarsal Joint

As in *Metachirus*, living caenolestids, and Sparassodonta (see Szalay, 1994:201, 203; Argot, 2002:94), the astragalonavicular facet of *Palaeotheres* is mainly vertically orientated. This morphology would have facilitated flexion and extension more

than supination-pronation of the pes. The pattern of the calcaneocuboid facet, without a medial recess and with a very different orientation of the distal and proximal halves of this facet (Fig. 7C–D), restricts the eversion-inversion of the foot, being compatible with flexion-extension movements. Calcaneocuboid and the astragalonavicular joints reflect a limited rotational ability in comparison with most of the didelphids and *Dromiciops* (Fig. 8D). Compared with the didelphids, the pattern of *Palaeotheres* is more similar to that of the *Metachirus*. Therefore the pattern of the transverse joint of *Palaeotheres* expresses a limited capacity of inversion of the pes, as is seen in agile terrestrial and leaping species.

PHYLOGENETIC ANALYSIS

One most parsimonious tree of 912 steps in length was obtained. The phylogeny acquired is fully consistent with the previously established hypothesis of Horovitz and Sánchez-Villagra (2003). All currently accepted marsupial orders are recovered by our analysis. Paucituberculata is the sister group of Australidelphia (i.e., the 'monito del monte' *Dromiciops* plus Australasian marsupials). The nesting of the *Caenolestes-Palaeotheres* clade with australidelphians rather than with South American didelphimorphians is supported by the same shared character states as those obtained by Horovitz and Sánchez-Villagra (2003). *Palaeotheres* is the sister taxon of the extant *Caenolestes*. This clade is supported by 13 unambiguous synapomorphies (see below) and high values of absolute and relative Bremer support (Supplementary Data, Figure 1S).

Synapomorphies of Paucituberculata

This analysis shows that the postcranial features are informative to support the closer affinities of *Palaeotheres* with the living *Caenolestes*, such as was indicated by previous studies based on cranial and dental features (e.g., Abello, 2007; Goin et al., 2009). Eight unambiguous postcranial synapomorphies support the *Palaeotheres-Caenolestes* clade (discussed below). Character numbers in this analysis are retained from the primary data matrix so as to facilitate comparisons of results and scoring between the study of Horovitz and Sánchez-Villagra (2003) and ours.

Character 47—Humerus, olecranon fossa or foramen: 0 = absent; 1 = fossa; 2 = large fossa; 3 = foramen. Ordered. A large fossa (coding 2) emerges as a synapomorphy of Paucituberculata. This character was coded as 3 for *Palaeotheres*. State 2 occurs also in Australidelphian peramelids and *Phascogale*.

Character 79—Relative height of greater trochanter/femoral head: 0 = greater trochanter is lower or equal; 1 = higher. A proximally extended greater trochanter (state 1) groups *Caenolestes* and *Palaeotheres*. Peramelids and some diprotodonts also show this character state.

Character 93—Tibia, posterior shelf articulation: 0 = not articular; 1 = articular. The posterior shelf may or may not participate in the distal contact of the tibia with the astragalus. The absence of this articulation supports the *Caenolestes-Palaeotheres* clade and occurs as an autapomorphy of the Australian *Dasyuroides*.

Character 94—Astragalus, angle between medial and lateral facets for tibia: 0 = 90°; 1 = intermediate; 2 = 180°. The presence of the right angle between both facets of the distal articulation joint of the tibia supports the Paucituberculata clade. This character is present in some Australidelphian taxa (e.g., *Macropus*).

Character 116—Calcaneal anterior peroneal tubercle shape: 0 = protuberance; 1 = laminar; 2 = process. Character state 1 supports the monophyly of *Caenolestes-Palaeotheres* clade. A laminar shape of calcaneal peroneal tubercle is an autapomorphy in *Didelphis* and *Cercartetus*.

Character 117—Calcaneal anterior peroneal tubercle position: 0 = protruding anteriorly beyond calcaneocuboid facet; 1 = anterior, nonprotruding; 2 = at a distance from

anterior end of calcaneum. Character state 2 is a synapomorphy of Paucituberculata and occurs in several marsupial taxa (*Didelphis*, *Cercartetus*, *Dromiciops*, and some diprotodontians).

Character 126—Calcaneal facet for fibula orientation: 0 = lateral; 1 = dorsal. In the context of Metatheria analyzed here, lateral orientation of the calcaneal facet for fibula (=calcaneofibular facet) is exclusive of Paucituberculata.

Character 231—Third trochanter: 0 = present; 1 = absent. In the context of Metatheria analyzed here, the presence of the third trochanter is exclusive of Paucituberculata.

As noted above, affinity of *Palaeothenes* with the living *Caenolestes* based on dental and cranial characters was previously proposed (Thomas, 1895; Abello, 2007; Goin et al., 2009). Consistently, in this study several dental characters emerge as synapomorphies of Paucituberculata: absence of centrocrita (character 156, state 2); upper incisor arcade V-shaped and narrow (character 161, state 2); I3 smaller than I2 (character 166, state 2); greatly reduced lower canine (character 169, state 1) and caniniform upper canine (character 170, state 1). Homologies of these characters are exhaustively discussed in Abello (2007).

DISCUSSION AND CONCLUSIONS

Paleobiological Implications

The ecology, behavior, and adaptations of extant caenolestids are poorly known (Kirsh and Waller, 1979; Meserve et al., 1982). Locomotor data are only available for *Caenolestes fuliginosus* and *Lestoros inca*, and indicate that these species are typically terrestrial and show the capacity to leap at high velocities simultaneously using anterior and posterior limbs (Kirsh and Waller, 1979). Although leaping is an important part of the locomotor behavior of these species, it probably is not the only way used to move from one location to another, nor does it imply the inability to dig or climb. The postcranial morphology of *Palaeothenes*, characterized by marked joint stability, lengthened ischium, prominent femoral tubercle and ischiatal tuberosity, proximally third trochanter, among other features, suggests that selective factors operated on the evolution of this paucituberculatan in favor of an agile mode of locomotion. Results from our comparative study support *Palaeothenes* being a cursorial mammal with leaping capacity, resembling *Caenolestes fuliginosus* and *Metachirus nudicaudatus*. The temporal record of *Palaeothenes* reveals that some of these features originated at least by the late early Miocene.

Numerous fossil mammals of many lineages, including primates, xenarthrans, metatherians, ungulates, and rodents, have been reported from the Santa Cruz Formation (e.g., Ameghino, 1891; Scott, 1932; Marshall, 1981; Tauber, 1997; Tejedor et al., 2006; Abello, 2007; Kay et al., 2008). More recent contributions focused on the study of this important mammalian diversity from a palaeobiological perspective (e.g., Vizcaíno, 1994; Vizcaíno and Fariña, 1994; Vizcaíno et al., 2006a, 2006b). The available studies pointed out that Santacrucian mammals developed varied modes of locomotion: arboreal or scansorial, represented by the porcupine *Steiromys duplicatus* (Candela and Picasso, 2008); relatively large cursorial, represented by the dasyproctid *Neoreomys australis* (Candela and Vizcaíno, 2007) and some sparassodonts (Argot, 2004); and agile curso-saltatorial forms, represented by *Palaeothenes minutus* and *P. lemoinei*. It is possible that the numerous Patagonian species of Paucituberculata had also developed several styles of life, as expressed by their wide range of body sizes (e.g., *Palaeothenes pascuali*-*Palaeothenes aratae*; Dumont et al., 2003; Abello and Ortiz Jaureguizar, 2009) and dental patterns (*Stilotherium dissimile*, *Abderites meridionalis*; Abello, 2007). *Palaeothenes minutus* and *P. lemoinei*, with body masses of about 83 g and 300 g, respectively (Dumont et al., 2003), represent some of the smallest Santacrucian mammals and, along with the tyotherians hegetotheriids (Sinclair, 1909), the only with inferred leaping ability. These small species were coeval with di-

verse carnivorous metatherians (Argot, 2004). In conformity with their skillful manipulative ability and predatory activities, Santacrucian sparassodonts *Sipalocyon*, the small marten-like *Cladosictis* (3.5–8 kg), and the large wolverine-size *Prothylacinus* (30 kg) (Argot, 2003a, 2003b, 2004) may have commonly preyed on *Palaeothenes* species. According to this scenario, carnivorous metatherians may have acted as important selective pressures favoring the evolution of an agile mode of locomotion in *Palaeothenes*. The integrative study of the well-preserved specimens of Palaeothenidae and Abderitidae (M. A. Abello, unpubl. data) should help clarify the paleoecology of Miocene Patagonian marsupials and their paleohabitats.

Phylogenetic Implications

Our study demonstrates that postcranial features support the monophyly of the Paucituberculata, showing that *Palaeothenes* is closely allied to living *Caenolestes*. Several features appear as apomorphies of this clade, including large olecranon fossa; greater trochanter higher than femoral head; angle between medial and lateral facets for tibia forming a 90° angle; and presence of third trochanter. Most of these characters appear to be related to leaping capability (see above). *Palaeothenes* is the oldest paucituberculatan known from postcranial material and provides evidence that a leaping ability appeared early in the evolutionary history of this group.

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