

Limb reconstruction of *Eutatus seguini* (Mammalia: Xenarthra: Dasypodidae). Paleobiological implications

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Abstract. *Eutatus seguini* Gervais is one of the largest members of the family Dasypodidae. It was very common during the Late Pliocene-Early Holocene in Uruguay and central-eastern Argentina. Some specimens that include well preserved and complete endoskeletal elements allowed to perform morpho-functional and biomechanical studies in order to infer locomotory adaptations. Comparative anatomical descriptions of *Eutatus seguini* Gervais with the recent armadillos *Chaetophractus villosus* (Desmarest), *Dasypus hybridus* (Desmarest), and the only living species of similar size *Priodontes maximus* (Kerr), were made. Its body mass was estimated through allometric equations. Different indices were calculated in order to analyse its limb proportions and their correlation with digging habits. The indices were compared with the values recorded for all living armadillo tribes, from mostly cursorial through subterranean. The general architecture and proportions of the limbs of *E. seguini*, and therefore its digging habits, are similar to those of the Euphractini and Dasypodini. *Eutatus seguini* shows unique features, for it reaches the size of the hyperspecialised digger and mirmecophagous *Priodontes maximus*, but with less fossorial specialisation and markedly herbivorous feeding habits.

Resumen. RECONSTRUCCIÓN DE LOS MIEMBROS DE *EUTATUS SEGUINI* (MAMMALIA: XENARTHRA: DASYPODIDAE). IMPLICACIONES PALEOBIOLÓGICAS. *Eutatus seguini* Gervais es uno de los representantes de mayor tamaño de la familia Dasypodidae. Su registro es muy abundante durante el Plioceno tardío-Holoceno temprano del centro oeste de la Argentina y Uruguay y está representado principalmente por placas de la coraza. Se conocen algunos esqueletos bastante completos y otros huesos aislados que permitieron realizar estudios morfofuncionales y biomecánicos con el objeto de inferir las adaptaciones del aparato locomotor. Se realizaron descripciones anatómicas comparadas de *E. seguini* con los armadillos actuales *Chaetophractus villosus* (Desmarest), *Dasypus hybridus* (Desmarest) y la única especie viviente de tamaño similar *Priodontes maximus* (Kerr) y se estimó su masa corporal mediante ecuaciones alométricas. Se calcularon diferentes índices para analizar las proporciones de los miembros y su correlación con los hábitos cavadores. Se comparó con los valores registrados para representantes de todas las tribus actuales, desde mayormente cursoriales hasta subterráneas. La arquitectura general y las proporciones de los miembros de *E. seguini*, y por lo tanto sus hábitos cavadores, son similares a los Euphractini y Dasypodini. *Eutatus seguini* presenta características únicas, por cuanto alcanza un tamaño comparable al del hiperespecializado cavador y mirmecófago *Priodontes maximus*, aunque con menor especialización fosorial y hábitos alimentarios marcadamente herbívoros.

Key words. Mammalia. Dasypodidae. *Eutatus seguini*. Limb bones. Paleobiology.

Palabras clave. Mammalia. Dasypodidae. *Eutatus seguini*. Esqueleto apendicular. Paleobiología.

Introduction

Eutatus seguini Gervais (figure 1) is one of the largest armadillos of the family Dasypodidae. Its body size was similar to that of the living giant armadillo *Priodontes maximus* Kerr, approximately 50 kg (see Fariña and Vizcaíno, 1997). Other peculiarities are the very conspicuous piliferous foramina on the posterior margin of the dorsal carapace scutes, and the structure and arrangement of the tooth dentine.

Eutatus seguini was very common during the Late Pliocene-Early Holocene in Uruguay and central-eastern Argentina. Although several species of the genus were named, Scillato-Yané (1980, 1982, 1986) recognised them as single species and included it, with species of twelve other genera, in the Tribe Eutatini of the Subfamily Euphractinae. Engelmann (1985) united eutatine armadillos, glyptodonts and pampatheres as Glyptodonta, separated from all remaining armadillos (Dasypoda). More recently, Vizcaíno and Bargo (1998) considered Engelmann's grouping as plausible but indicated that further studies are necessary to establish unambiguous synapomorphies.

Despite the already mentioned fact that it is well recorded, mainly by dermal scutes, very few speci-

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Figure 1. Reconstruction of *Eutatus seguini*. Total length approximately 1 m. / *Reconstrucción de Eutatus seguini*. Largo total aproximado 1 m.

mens including well preserved endoskeletal elements are known. One of them is the type specimen described by Gervais (1873), deposited in the Muséum National d'Histoire Naturelle, Paris. It consists of skull, mandible, and almost complete limbs. A second one, better specimen is housed at the Museo de Paleontología Rodrigo Botet (= Museo de Ciencias Naturales), Valencia, Spain. It is a complete, articulated specimen, including both carapace and endoskeleton, and was described and figured by Boscá y Casanoves (1920). Unfortunately, this display specimen was not available for analysis.

The new record of two other well-preserved specimens allowed us to perform a study of proportions of the bones of the proximal and middle segments of the limbs and a reconstruction of limb musculature. One of the specimens is an almost complete skeleton, including skull and mandible, which belongs to the Centro de Investigaciones Paleontológicas de Salto, Argentina. The other belongs to the collections of the Museo de La Plata and consists of incomplete fore and hind limbs.

Only general interpretations on the paleobiology of *Eutatus seguini* have been done (Winge, 1941; Scillato-Yané 1982, 1986). Except for the study on the masticatory apparatus by Vizcaíno and Bargo (1998), it has never been the subject of detailed morpho-functional or biomechanical analysis.

The aim of this contribution is to provide information on the adaptations of the locomotory apparatus of *Eutatus seguini*. This information will be considered together with that from the masticatory apparatus (Vizcaíno and Bargo, 1998) to improve our knowledge of the paleoautoecology of this species.

Material and methods

Acronyms

MACN: Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina.

MLP: Museo de La Plata, La Plata, Argentina.

MMCIPAS: Museo y Centro de Investigaciones Paleontológicas de Salto, Salto, Buenos Aires Province, Argentina.

MNHN: Muséum National d'Histoire Naturelle, Paris, France.

Material

The nearly complete specimens of *Eutatus seguini* analysed were:

MMCIPAS 2901-3068. Almost complete skeleton very well preserved, lacking carapace. Lujanian (Late Pleistocene), Lobos, Buenos Aires Province, Argentina.

MNHN PAM 273. Holotype. Skull, mandible, and almost complete fore and hindlimbs. "Pampean", Río Salado, Buenos Aires Province, Argentina. Coll. M.F. Seguin.

MLP 00-VIII-5-1. Humerii, ulnae, radii, left femur, several bones from fore and hind feet, and several scutes. Pleistocene, Chascomús, Buenos Aires Province, Argentina.

Other partial specimens were measured:

MACN 5697. Incomplete left ulna, femora, tibiae, patellae, tarsals, phalanges, incomplete pelvis, some vertebrae, ribs and other fragments of the skeleton; two teeth. "Pampean", Buenos Aires Province, Argentina.

MACN 14080. Left tibia-fibula. "Pampean", Buenos Aires Province, Argentina.

MACN 2436. Right femur. "Pampean", Buenos Aires Province, Argentina.

MACN 1636. Incomplete skull with some teeth and cephalic scutes, fragments of ribs, right ulna, radius and hand articulated, right tibia-fibula, some metatarsals, sesamoid, and several scutes of the carapace. Provenance unknown.

MACN 5121. Left humerus. Provenance unknown.

MLP 38-X-2-1. Carapace, right humerus, left femur, left tibia, left calcaneum, metatarsal, and caudal vertebrae. "Upper pampean", Mar del Sur, Buenos Aires Province, Argentina.

MLP 42-IX-1-2. Left tibia, left astragalus, metatarsals, etc. Pleistocene, Villa Estación Ramallo, Buenos Aires Province, Argentina.

MLP 69-VIII-4-1. Right femur. Provenance unknown.

MLP 69-VIII-5-5. Left femur, left humerus and right radius. "Pampean", Mar del Plata, Buenos Aires Province, Argentina.

MLP 69-IX-8-15. Left humerus. Provenance unknown.

MLP 69-IX-8-17. Right femur. Pleistocene, Buenos Aires Province, Argentina.

MLP 69-IX-9-7. Right femur, right tibia, and both ulnae. Pleistocene.

MLP w/n. Incomplete femur. Provenance unknown.

Methods

Comparative descriptions were made with the more generalised living armadillos *Chaetophractus villosus* (Desmarest) (Euphractinae, Euphractini), *Dasypus hybridus* (Desmarest) (Dasypodinae, Dasypodini), and the only living species of similar size *Priodontes maximus* (Kerr) (Priodontinae). The muscular reconstructions described in the results were based on detailed dissections of the living species *Chaetophractus vellerosus* (Gray) (Euphractinae, Euphractini), *Dasypus hybridus* (Desmarest) (Dasypodinae, Dasypodini), *Tolypeutes matacus* (Desmarest) (Tolypeutinae) and *Cabassous chacoensis* Wetzel (Priodontinae).

Table 1. Allometric equations used for body mass estimations from Fariña and Vizcaíno (1997). / *Ecuaciones alométricas utilizadas para las estimaciones de masa corporal (Fariña y Vizcaíno, 1997).*

Measurement	Equation
Humeral length (HL)	$\text{Log mass} = (\log \text{HL} - 1.5865) / 0.3155$
Humeral anteroposterior diameter (HD)	$\text{Log mass} = (\log \text{HD} - 0.6314) / 0.4195$
Ulnar length (UL)	$\text{Log mass} = (\log \text{UL} - 1.6313) / 0.3089$
Ulnar anteroposterior diameter (UD)	$\text{Log mass} = (\log \text{UD} - 0.7037) / 0.374$
Femoral length (FL)	$\text{Log mass} = (\log \text{FL} - 1.6886) / 0.391$
Femoral anteroposterior diameter (FD)	$\text{Log mass} = (\log \text{FD} - 0.7146) / 0.3795$
Leg length (LL)	$\text{Log mass} = (\log \text{LL} - 1.636) / 0.3134$

Body masses were estimated based on specific allometric equations from long bones of living dasypodids (Fariña and Vizcaíno, 1997) (Table 1).

Locomotor habits of *Eutatus sequini* were characterised based on the morphology and proportions of the bones of the proximal and middle segments of the limbs. The following measurements were taken with digital callipers to the nearest tenth of a millimetre.

a) Humeral length (HL) is the maximum length measured along the long axis of the humerus.

b) Proximal humeral length (PH) is the distance from the distal end of the deltoid tuberosity to the proximal point of the humeral head.

c) Ulnar length (UL) is the maximum length of the ulna.

d) Olecranon length (OL) is the distance, measured along the long axis of the ulna, from the centre of the trochlear notch to the tip of the olecranon process.

e) Functional femoral length (FL) is the distance from the femoral condyles to the proximal point of the femoral head.

f) Proximal femoral length (PF) is the distance from the distal end of the third trochanter to the proximal point of the femoral head.

g) Leg length (LL) is the distance between the proximal and distal articular surfaces of the tibia-fibula.

h) Mid-leg width (LW) is the width of the tibia-fibula measured half way along their length.

i) Anteroposterior diameter, measured at diaphyseal midshaft (FD, HD and UD) for femur, humerus and ulna.

The following indices multiplied by 100, previously studied in living armadillos by Vizcaíno and Milne (2002), were calculated from the measurements (Figure 2):

1. Shoulder Moment Index (SMI) is the proximal humeral length divided by the humeral length [PH/HL]. This index is an indication of the mechanical advantage of the posterior deltoid muscle acting across the shoulder joint.

2. Brachial Index (BI) is the functional forearm length (difference between ulnar length and olecranon length) divided by the humerus length [(UL-OL)/HL]. It gives an indication of the extent to which the forelimb is adapted for fast movement (Howell, 1944; Fleagle, 1979).

3. Index of Fossorial Ability (IFA) is the olecranon length divided by the difference between ulnar length and the olecranon length [OL/(UL-OL)]. This index gives a measure of the mechanical ad-

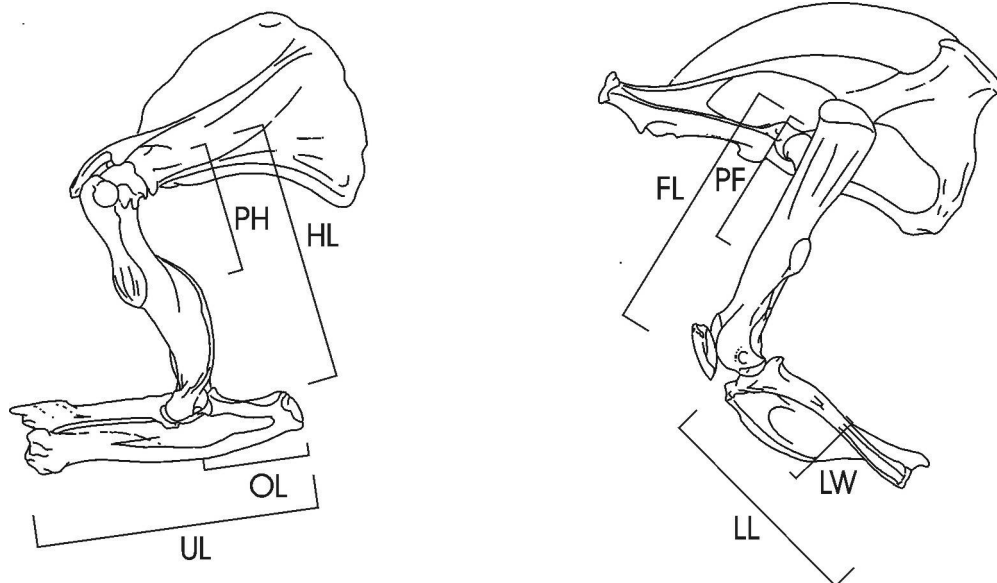


Figure 2. Measurements of the limb bones (from Vizcaíno and Milne, 2002). HL: humeral length. PH: proximal humeral length. UL: ulnar length. OL: olecranon length. FL: functional femoral length. PF: proximal femoral length. LL: leg length. LW: Mid-leg width. / *Medidas de los huesos de los miembros (tomado de Vizcaíno y Milne, 2002). HL: largo del húmero. PH: largo proximal del húmero. UL: largo de la ulna. OL: largo del olécranon. FL: largo funcional del fémur. PF: largo proximal del fémur. LL: largo de la pierna. LW: ancho tomado a la mitad de la pierna.*

vantage of the triceps muscle in elbow extension. This index was defined by Vizcaíno *et al.* (1999), but presented as a simple ratio. In the present study it is multiplied by 100 to conform with the other indices used here.

4. The Hip Moment Index (HMI) is the proximal femoral length divided by the functional femoral length [PF/FL]. It gives an indication of the mechanical advantage of the gluteus maximus muscle in hip extension.

5. Leg Robusticity Index (LRI) is the mid-leg

width divided by the leg length [LW/LL]. It gives an indication of the strength of the leg and also the relative width available for the origin of the muscles acting across the ankle.

6. The Crural Index (CI) is the leg length divided by the functional femoral length [LL/FL]. It gives a measure of the extent to which the hind limb is built for speed (Howell, 1944; Fleagle, 1979).

7. Intermembral index (IMI) is the forelimb length divided by the hindlimb length [(HL+UL-OL)/(FL+LL)] (Howell, 1944; Fleagle, 1979).

Figure 3. Limb bones of *Eutatus seguini* (MMCIPAS 2901-3068). **A**, anterior and **B**, posterior views of left humerus. **C**, lateral views of right ulna and radius. **D**, medial view of left ulna and radius. **E**, anterior view of right femur. **F**, posterior view of left femur. **G**, anterior view of right tibia-fibula. **H**, posterior view of left tibia-fibula. / *Huesos de los miembros de Eutatus seguini* (MMCIPAS 2901-3068). **A**, vista anterior y **B**, vista posterior del húmero izquierdo. **C**, vista lateral externa de la ulna y radio derechos. **D**, vista lateral interna de la ulna y radio izquierdos. **E**, vista anterior del femur derecho. **F**, vista posterior del femur izquierdo. **G**, vista anterior de la tibia-fíbula derecha. **H**, vista posterior de la tibia-fíbula izquierda.

Principal components analyses applied to the indices were conducted using GenStat (GenStat Release 4.21 Lawes Agricultural Trust - Rothamsted Experimental Station). These analyses were carried out to further explore how *Eutatus seguini* fits the patterns of structure and function already observed in the limbs of living armadillos by Vizcaíno and Milne (2002).

Results

Eutatus seguini limb bones in relation to living armadillos

Scapula. Only the glenoid side of the scapula and the acromion and coracoid processes are preserved in the available *Eutatus seguini* specimens. However, they are much more similar to *Chaetophractus villosus* than to *Dasypus hybridus*.

The coracoid process is long and hooked towards the ventral side in both *E. seguini* and *Ch. villosus*, which also have a well-marked supraglenoid tubercle. However, in *D. hybridus* and *Priodontes maximus* the supraglenoid tubercle is not clearly distinguished from the short coracoid process, possibly indicating that *E. seguini* had the typical mammalian biceps muscle with long and short heads (see Miles, 1941). The acromion is less curved in *E. seguini* and *Ch. villosus* than in *D. hybridus* and *P. maximus*. The suprascapula notch is not complete in *E. seguini* but its lateral part is quite curved and more like that of *Ch. villosus* than the smooth upper border of the *D. hybridus* or *P. maximus* scapula. On the other hand the *Ch. villosus* scapula has a large and prominent infraglenoid tuberosity on the caudal border just dorsal the glenoid fossa but *E. seguini*, *P. maximus*, and *D. hybridus* have similar but smaller rugosities in that region. This is the site for the attachment of the long head of triceps (or the lateral part of the scapular head).

Humerus. The overall shape of the humerus of *Eutatus seguini* is more like that of *Chaetophractus villosus* and *Priodontes maximus*, than of *Dasypus hybridus* (figures 3.A and B; 4.A, E, I and M; 5.A and E). The distal end of the humerus is very broad and robust. This breadth is mainly due to the large trochlea and medial epicondyle. On the lateral side the *E. seguini* humerus has a modest supinator plate/lateral supracondylar crest. The proportions of the medial epicondyle are larger than, but more like those of the euphractines and priodontines than of the dasyrodines. The supinator crest of *E. seguini*, while still very prominent and larger than that seen in the dasyrodines, does not have the same proportions as that found in *P. maximus* and *Cabassous* and is more like that seen in the euphractines.

The position of the deltoid tuberosity is described numerically (SMI), but it is worth noting that the tuberosity in *E. seguini* is marked with a vertical ridge in the middle as well as anterior and posterior ridges. This condition is much more similar to that of *P. maximus* and *Ch. villosus* than to that of the more gracile *D. hybridus*, and suggests that the middle (acromial) part of deltoid is more powerful with larger intramuscular tendons. The *P. maximus* and *E. seguini* humeri are of similar size, but the deltoid tuberosity in *E. seguini* is twice as wide, and much more similar in shape to that of *Ch. villosus*.

Both the *E. seguini* and the *Ch. villosus* humeri have a deep fossa on the anterior surface above the medial part of the trochlea that merges into the epitrochlear foramen. This feature, absent in either *P. maximus* and *D. hybridus*, is not related to the coronoid fossa for elbow flexion. In *D. hybridus* the trochlea is set quite obliquely to the long axis of the shaft, but in *E. seguini*, *P. maximus*, and *Ch. villosus* it is more nearly perpendicular. The absolute diameter of the trochlea is larger in *Ch. villosus* than in *D. hybridus* humeri (the humeri are of similar size overall) and more similar to the proportions seen in *E. seguini* and *P. maximus*. In *D. hybridus* the lesser tubercle is considerably smaller than the greater tubercle and the head itself. The lesser tubercles in *E. seguini*, *P. maximus*, and *Ch. villosus* are larger and approach the size of the greater tubercle. This suggests a stronger subscapularis muscle with greater leverage producing more powerful medial (internal) rotation of the humerus in *E. seguini*, *Ch. villosus* and *P. maximus* than in *D. hybridus*.

Reconstruction of the origin and insertion areas of the *E. seguini* humerus muscles is shown in figures 6.A and B.

Radius and ulna. The overall shapes of the radius and ulna of *Eutatus seguini* are more like those of *Priodontes maximus* and *Chaetophractus villosus* than of *Dasypus hybridus* (figures 3.C and D; 4.B, F, J and N; 5.B and F). The ulnae are quite robust and have similar proportions (thickness versus length). Reconstruction of the origin and insertion areas of the radius and ulna musculature of *E. seguini* is shown in figure 6.C and D.

In flexor view *D. hybridus* has a quite narrow trochlear notch compared with either *Ch. villosus* or *E. seguini* (as mentioned earlier in relation to the humeral trochlea).

The ulnae of *E. seguini*, *Ch. villosus* and *P. maximus* are markedly curved in lateral or anterior views, while that of *D. hybridus* is straight. The curve seen in the anterior view is largely due to the medial flexion of the olecranon process. In addition, both *E. seguini* and *Ch. villosus* have a distinct hook on the medial

Figure 4. Limb bones of extant armadillos. *ChaetophRACTUS villosus* (MLP 911): **A**, anterior view of right humerus. **B**, lateral view of right ulna. **C**, anterior view of right femur. **D**, anterior view of right tibia-fibula. **E**, posterior view of right humerus. **F**, medial view of right ulna. **G**, posterior view of right femur. **H**, posterior view of right tibia-fibula. *Dasypus yepesi* (MLP 30-III-90-2): **I**, anterior view of right humerus. **J**, lateral view of right ulna. **K**, anterior view of right femur. **L**, anterior view of right tibia-fibula. **M**, posterior view of right humerus. **N**, medial view of right ulna. **O**, posterior view of right femur. **P**, posterior view of right tibia-fibula. / *Huesos de los miembros de armadillos vivientes*. *ChaetophRACTUS villosus* (MLP 911): **A**, vista anterior del húmero derecho. **B**, vista lateral externa de la ulna derecha. **C**, vista anterior del fémur derecho. **D**, vista anterior de la tibia-fibula derecha. **E**, vista posterior view del húmero derecho. **F**, vista lateral interna de la ulna derecha. **G**, vista posterior del fémur derecho. **H**, vista posterior de la tibia-fibula derecha. *Dasypus yepesi* (MLP 30-III-90-2): **I**, vista anterior del húmero derecho. **J**, vista lateral externa de la ulna derecha. **K**, vista anterior del fémur derecho. **L**, vista anterior de la tibia-fibula derecha. **M**, vista posterior del húmero derecho. **N**, vista lateral interna de la ulna derecha. **O**, vista posterior del fémur derecho. **P**, vista posterior de la tibia-fibula derecha.

side of the olecranon process for the proximal origin of the flexor carpi ulnaris. *Dasypus hybridus* does not have and *P. maximus* has a broader area on the medi-

al side of the olecranon process for this muscle attachment. On the medial surface of the proximal end of the ulna lie fossae for the origins of the flexor digitorum superficialis and profundus. Thus it appears that *E. seguini*, *Ch. villosus*, and *P. maximus* have improved lines of action and power for their carpal and digital flexors.

The lateral aspect of the proximal end of the ulna bears a deep fossa for insertion of the anconeus, which is important in providing support for the elbow joint in powerful actions of the forearm. This fossa is very similar to that of *Ch. villosus*, while the fossa in *P. maximus* and *D. hybridus* is shallower (in *Tolypeutes* the fossa does not extend beyond the trochlea).

At the distal end of the extensor surface *E. seguini* and *Ch. villosus* have a large triangular area for the deep group of extensor muscles. This area is larger than that in *D. hybridus*.

On anterior surface of the distal end of the radius both *E. seguini* and *Ch. villosus* have a well-marked, raised, triangular area for the insertion of pronator teres and brachioradialis. This area occupies the whole distal edge and extends 1/3 of the way proximally along the lateral edge. *Dasypus hybridus* and *Prionodontes maximus* have a homologous area, though (especially in *D. hybridus*) it is less raised and prominent, but extends more than halfway towards the proximal end of the radius.

Pelvis. In some ways the pelvis of *Eutatus seguini* is more similar to that of *Dasypus hybridus* than that of *ChaetophRACTUS villosus*. They both have a better-marked anterior inferior iliac spine for the origin of the rectus femoris muscle. However the ischial tuberosities of *E. seguini* and *Ch. villosus* have a much more similar shape, facing dorsally and lying approximately in the sagittal plane.

Femur. Reconstruction of the origin and insertion areas of the *Eutatus seguini* femur muscles is shown in figure 6.E and F. The affinities of the *E. seguini* femur are not as clear as those seen in the forelimb bones. The lesser trochanter in *E. seguini* is similar to that of *Ch. villosus* and *P. maximus* in that it is more flat and plate like and flexed somewhat anteriorly (figures 3.E and F; 4.C and G; 5.C and G). However the greater trochanter of *E. seguini* is much longer and larger (of the three living forms examined *Dasypus hybridus* has the longest greater trochanter). The third trochanter of *E. seguini* is more similar to *Ch. villosus* and *P. maximus* in that it has a more expanded extremity for the attachment of the superficial hip muscle group consisting of tensor fascia lata and gluteus maximus. The third trochanter also provides attachment for the powerful adductor magnus, the vastus lateralis and the

Figure 5. Limb bones of *Priodontes maximus* (MLP s/n). **A**, anterior view of right humerus. **B**, lateral view of right ulna. **C**, anterior view of left femur. **D**, anterior view of left tibia-fibula. **E**, posterior view of right humerus. **F**, medial view of right ulna. **G**, posterior view of left femur. **H**, posterior view of left tibia-fibula. / *Huesos de los miembros de Priodontes maximus (MLP s/n)*. **A**, vista anterior del húmero derecho. **B**, vista lateral externa de la ulna derecha. **C**, vista anterior del fémur derecho. **D**, vista anterior de la tibia-fíbula izquierda. **E**, vista posterior del húmero derecho. **F**, vista lateral interna de la ulna derecha. **G**, vista posterior del fémur derecho. **H**, vista posterior de la tibia-fíbula izquierda.

proximal end of the lateral head of gastrocnemius (figures 6.E and F). The ridge above the medial condyle that gives attachment to the medial head of gastrocnemius is larger in *E. seguini* than any of the

living forms, among which *D. hybridus* has the least developed. The tubercle for the distal end of adductor longus on the posterior aspect is quite separate in *E. seguini* but in the three living forms it ap-

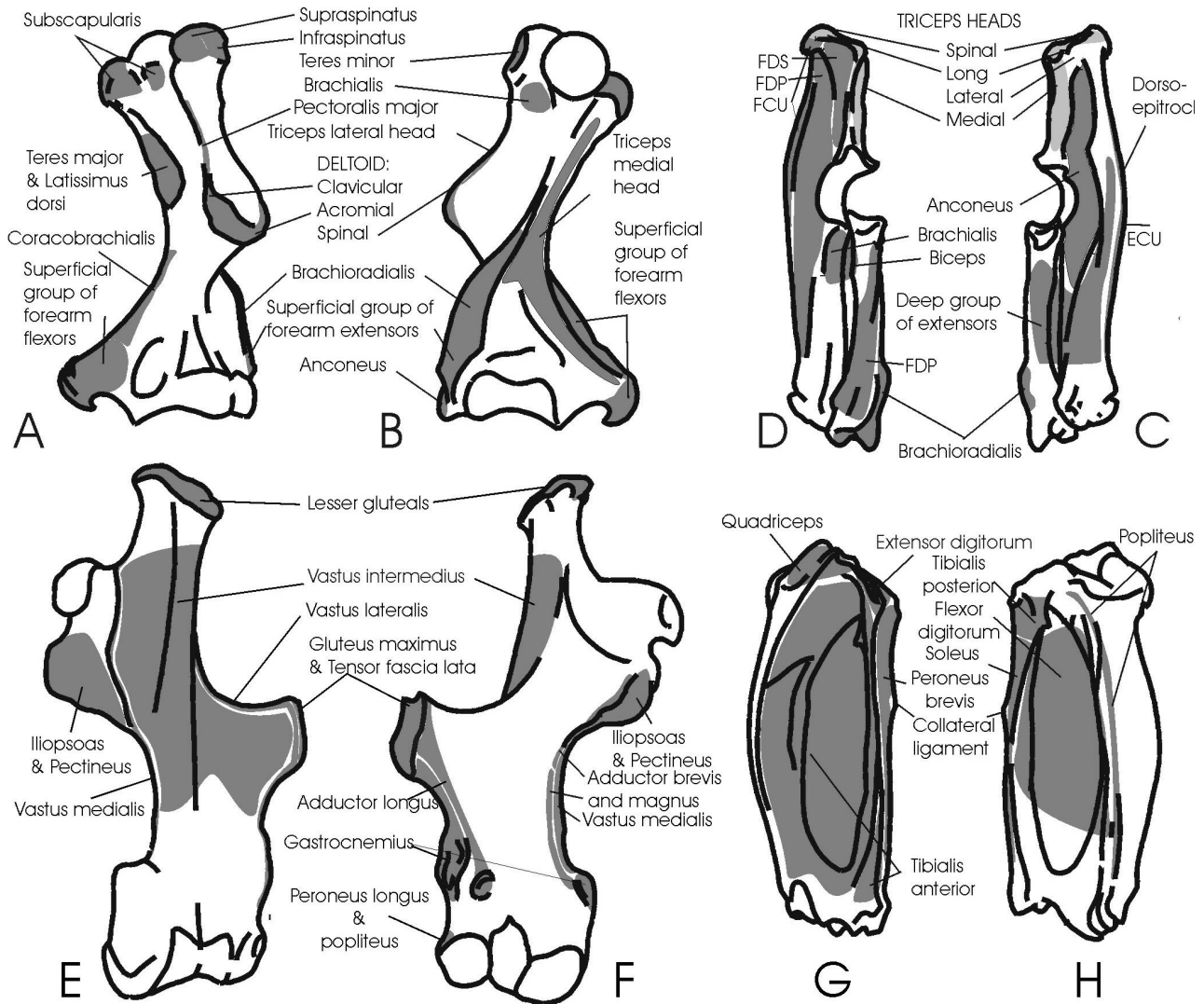


Figure 6. Reconstruction of the origin and insertion areas of the limb muscles of *Eutatus seguini*. **A**, anterior and **B**, posterior surface of humerus. **C**, lateral and **D**, medial surface of radius and ulna. **E**, anterior and **F**, posterior surface of femur. **G**, anterior and **H**, posterior surface of tibia-fibula. FDS, flexor digitorum superficialis. FDP, flexor digitorum profundus. FCU, flexor carpi ulnaris. ECU, extensor carpi ulnaris. / *Reconstrucción de las áreas de origen e inserción de los músculos de los miembros de Eutatus seguini*. **A**, superficies anterior y **B**, posterior del húmero. **C**, superficies lateral externa y **D**, lateral interna del radio y ulna. **E**, superficies anterior y **F**, posterior del fémur. **G**, superficies anterior y **H**, posterior de la tibia-fibula. FDS, flexor digitorum superficialis. FDP, flexor digitorum profundus. FCU, flexor carpi ulnaris. ECU, extensor carpi ulnaris.

pears to merge with the area for the medial head of gastrocnemius. Proximal to the lateral condyle in *E. seguini* and *Ch. villosus* the expanded area for the lateral head of gastrocnemius is large and set quite high above the condyle, unlike in *P. maximus* where it is large but close to the condyle and *D. hybridus* where it is smaller but also set quite high. The lateral epicondyle of the femur has well marked sites for the lateral collateral ligament as well as the peroneus longus and popliteus muscles.

Tibiafibula. Reconstruction of the origin and insertion areas of the *Eutatus seguini* tibia-fibula muscles is shown in figures 6.G and H. The tibia has a deep fossa on the lateral side for the origin of the tibialis an-

terior muscle, which is deeper than in all the living forms. This part of the tibia of *D. hybridus* is most similar to that of *E. seguini* both in the depth of the fossa and the shape of the anterior border of the tibia (figures 3.G and H; 4.L and P). At the proximal edge of the deep fossa the extensor digitorum (longus?) muscle arose from the tibia and fibula lateral to the quadriceps insertion. The peroneus brevis muscle arose along the anterior aspect of the fibula. There is a small tubercle midway down the lateral surface of all the fibulae for the superficial part of the lateral collateral ligament of the knee (there is also a corresponding tubercle for the long ligament on the medial side).

Table 2. Limb bone measurements (in mm) of *Eutatus seguini* / Medidas de los huesos de los miembros (en mm) de *Eutatus seguini*.

SPECIMENS	HUMERUS			ULNA			FEMUR			TIBIA	
	HL	PH	HD	UL	OL	UD	FL	PF	FD	LL	LW
CIPAS 2901-3068	131.7	77	21.7	149	61.1	23.8	165	91	25.3	159	52.7
MLP 69-IX-9-7	—	—	—	153	60.5	22.7	164	87	23.7	150	52
MLP 38-X-2-1	—	—	—	—	—	—	—	—	20.9	—	—
MLP 69-X-8-17	—	—	—	—	—	—	—	—	24.6	—	—
MLP 69-IX-8-15	130.6	75.2	22.4	—	—	—	—	—	—	—	—
MLP 69-VIII-5-5	—	—	21	—	—	—	—	—	—	—	—
MLP 69-VIII-4-1	—	—	—	—	—	—	—	—	23.3	—	—
MLP 42-IX-1-2	—	—	—	—	—	—	—	—	—	164	58.5
MLP w / n	—	—	—	—	—	—	—	—	25.7	—	—
MLP 00-VIII-5-1	129.6	74	20.1	143.6	57.8	22.0	—	—	23.4	—	—
MACN 5697	—	—	—	—	—	—	160	83	—	142	51
MACN 14080	—	—	—	—	—	—	—	—	—	155	52
MACN 2436	—	—	—	—	—	—	173	95	—	—	—
MACN 1636	—	—	—	149	58	—	—	—	—	165	57
MACN 5121	145	85	—	—	—	—	—	—	—	—	—
MNHN PAM 273	129.3	78.5	22.4	149.5	60.7	—	181	91.4	25.5	134.2	56.9

A distinct area for the insertion of popliteus muscle lies on the posterior surface of the tibia of all species. This area is very large and extends along the posterior border of the tibia almost to the distal end. There is a wide corresponding groove on the posteromedial surface of the lateral tibial condyle for the tendon of the popliteus muscle acting on the lateral femoral condyle. The lower end of the tibia is marked by grooves for the tendons of the deep flexor muscles (tibialis posterior and flexor digitorum). *Eutatus seguini* and *Ch. villosus* have two distinct grooves, while *P. maximus* and *D. hybridus* have only one wide groove. The deep flexor muscles arise from the large tubercle on the posterior surface of the fibular head, while the soleus appears to be confined to the posterior border of the fibula. All four specimens have well-developed extensions of the tibia behind the astragalar trochlea to prevent forward displacement of the pes.

Body size and limb proportions

Measurements of the humerus, ulna, femur and tibia-fibula of the *Eutatus seguini* specimens are provided in Table 2.

Table 3 presents body mass estimations of the *E. seguini* specimens obtained using allometric equations of living armadillos (Fariña and Vizcaíno, 1997). Values range from 36.8 to 71.7 kg. The FL provides the lowest estimations, and the FD and LL the highest, with averages close to 60 kg. The total average is 49.9 kg.

Table 4 shows the indices of *E. seguini* calculated for eleven specimens. Only two specimens (MMCI-PAS 2901-3068 and MLP 00-VIII-5-1) are complete enough to provide measurements to calculate all the indices. With the exception of IFA, the calculated means for the *Eutatus* indices lie between those of the two complete specimens.

Table 3. Body mass estimations (in kg) using allometric equations of living armadillos (Fariña and Vizcaíno, 1997) / Estimaciones de la masa corporal (en kg) utilizando ecuaciones alométricas de armadillos vivientes (Fariña y Vizcaíno, 1997).

SPECIMENS	HUMERUS				ULNA				FEMUR				TIBIA	
	HL	mass	HD	mass	UL	mass	UD	mass	FL	mass	FD	mass	LL	mass
CIPAS 2901-3068	131.7	48.9	21.7	47.9	149	56.8	23.8	63.0	165	22.5	25.3	65.2	150.8	53.8
MLP 69-IX-9-7	—	—	—	—	153	61.9	22.7	55.5	164	22.2	23.7	54.9	150	52.9
MLP 38-X-2-1	—	—	—	—	—	—	—	—	—	—	20.9	39.4	—	—
MLP 69-X-8-17	—	—	—	—	—	—	—	—	—	—	24.6	60.6	—	—
MLP 69-IX-8-15	130.6	47.7	22.4	51.7	—	—	—	—	—	—	—	—	—	—
MLP 69-VIII-5-5	—	—	21	44.3	—	—	—	—	—	—	—	—	—	—
MLP 69-VIII-4-1	—	—	—	—	—	—	—	—	—	—	23.3	52.5	—	—
MLP 42-IX-1-2	—	—	—	—	—	—	—	—	—	—	—	—	164	70.3
MLP w / n	—	—	—	—	—	—	—	—	—	—	25.7	68.0	—	—
MLP 00-VIII-5-1	129.6	46.5	20.1	39.9	143.6	50.4	22.0	51.0	—	—	23.4	53.1	—	—
MACN 5697	—	—	—	—	—	—	—	—	160	20.8	—	—	142	44.4
MACN 14080	—	—	—	—	—	—	—	—	—	—	—	—	155	58.7
MACN 2436	—	—	—	—	—	—	—	—	173	25.4	—	—	—	—
MACN 1636	—	—	—	—	149	56.8	—	—	—	—	—	—	165	71.7
MACN 5121	145	66.4	—	—	—	—	—	—	—	—	—	—	—	—
MNHN PAM 273	129.3	46.2	22.4	51.7	149.5	57.4	—	—	181	28.5	25.5	66.6	144.2	46.6
Partial averages	—	51.1	—	47.1	—	56.6	—	56.5	—	23.9	—	57.5	—	56.9
TOTAL AVERAGE						49.9								

Table 4. Indices of *Eutatus seguini* / Índices de *Eutatus seguini*.

SPECIMENS	IFA	SMI	BI	HMI	LRI	CI	IMI
CIPAS 2901-3068	69.51	58.47	66.74	55.15	33.14	96.37	67.78
MLP 69-IX-9-7	65.40	—	—	53.04	34.66	91.46	—
MLP 69-IX-8-15	—	57.58	—	—	—	—	—
MLP 42-IX-1-2	—	—	—	—	35.67	—	—
MLP 00-VIII-5-1	67.36	57.09	66.20	—	—	—	—
MACN 5697	—	—	—	51.87	35.91	88.75	—
MACN 14080	—	—	—	—	33.54	—	—
MACN 2436	—	—	—	54.91	—	—	—
MACN 1636	63.73	—	—	—	34.54	—	—
MACN 5121	—	58.62	—	—	—	—	—
MNHN PAM 273	68.35	60.71	68.67	50.49	42.39	74.14	69.19
AVERAGES	66.87	58.49	67.20	53.09	35.69	87.68	68.48

Table 5 shows the means for the calculated indices for species and tribes (Vizcaíno and Milne, 2002). Among the living taxa, the Tolypeutini and Chlamyphorini are represented, in the present, by one species each. In the forelimb, the IFA of *Eutatus seguini* overlaps the values of the living euphractines and dasypodines, the BI overlaps that of the dasypodines; but the SMI is somewhat higher than that of both the euphractines and dasypodines, and is more similar to that of *Tolypeutes matacus*, but not as large as seen in the priodontines. In the hindlimb, the LRI, HMI and CI overlap the values seen among the priodontines, euphractines and dasypodines. The IMI is similar to that of *T. matacus*.

Figure 7 is a plot of the first two principal components resulting from an analysis of the data of *E. seguini* plus the species means from Vizcaíno and Milne (2002). *Eutatus seguini*, the euphractines, and the dasypodines all lie close together and are well separated from the other tribes. The IFA and SMI seem to be the important indices separating *E. seguini* from the priodontines, while BI and CI contribute strongly to the separation of *E. seguini* from *Tolypeutes matacus* and *Chlamyphorus truncatus* Harlan.

Discussion

Body mass values obtained for *Eutatus seguini* are similar to those known for the living species *Priodontes maximus* which is of nearly equivalent overall size and has been recorded to weigh from 30 (Wetzel, 1985) to 60 kg (Nowak, 1991). Another dasy-

podid of similar size is the Pleistocene dasypodine *Propaopus grandis* (Fariña and Vizcaíno, 1997). Many life traits are influenced or correlated with body size, such as autoecology, physiology, and bone dimensions, among others.

McNab (1985) proposed that the combination of large mass and burrowing habits in armadillos is allowed by the possession of a nearly naked body in association with high thermal conductance. These prevent most armadillos from extensively penetrating temperate climates. Living armadillos “often face environmental temperatures that require increase in metabolism to maintain body temperature, even in the tropics” (McNab, 1985: 223). The presence of large piliferous foramina on the posterior margin of the carapace scutes suggests the presence of relatively abundant hair (figure 1). The fetures of its coat are unknown but as *Eutatus seguini* must have been a good burrower (see below), it is improbable that it had a thick coat of fur.

The structure of the forelimb in armadillos is much more specialised for digging than the hindlimb, whereas the latter is more specialised for weight bearing. Vizcaíno and Milne (2002) demonstrated that the forelimb indices of living armadillos do not show significant correlations with body mass, as had been previously concluded by Vizcaíno *et al.* (1999) based on the IFA. Fariña and Vizcaíno (1997) stated that the humeri and ulnae of armadillos scale similarly to those of other digging mammals (i.e., unlike in generalized mammals).

For the IFA there is a steady increase from the most cursorial tribe Tolypeutini through the Dasypodini,

Table 5. Mean value of the indices of *Eutatus seguini* compared with those of living armadillos (Vizcaíno and Milne, 2002) / Valores promedio de los índices de *Eutatus seguini* comparados con los de armadillos vivientes (Vizcaíno y Milne, 2002).

TAXA	IFA	SMI	BI	HMI	LRI	CI	IMI
<i>T. matacus</i>	58.02±9.16	58.78±1.28	80.17±5.30	46.05±4.11	18.91±6.85	101.5±4.48	68.29±2.32
Dasypodini	66.85±3.11	48.44±1.56	69.29±3.32	54.49±1.52	36.75±0.76	81.93±2.33	70.93±2.33
Euphractini	69.44±3.61	56.07±0.74	63.21±1.00	50.40±1.06	36.48±1.74	85.48±3.58	84.71±1.91
Priodontini	92.86±6.04	68.67±3.86	55.92±1.98	51.08±6.51	42.35±7.59	81.22±4.01	77.11±9.63
<i>C. truncatus</i>	112.68±5.99	77.40±0.44	61.54±5.41	42.24±4.62	22.13±1.44	105.02±4.20	70.60±0.78
<i>E. seguini</i>	66.87	58.49	67.20	53.09	35.69	87.68	68.48

IFA: index of fossorial ability. SMI: shoulder moment index. BI: brachial index. HMI: hip moment index. LRI: leg robusticity index. CI: crural index. IMI: intermembral index.

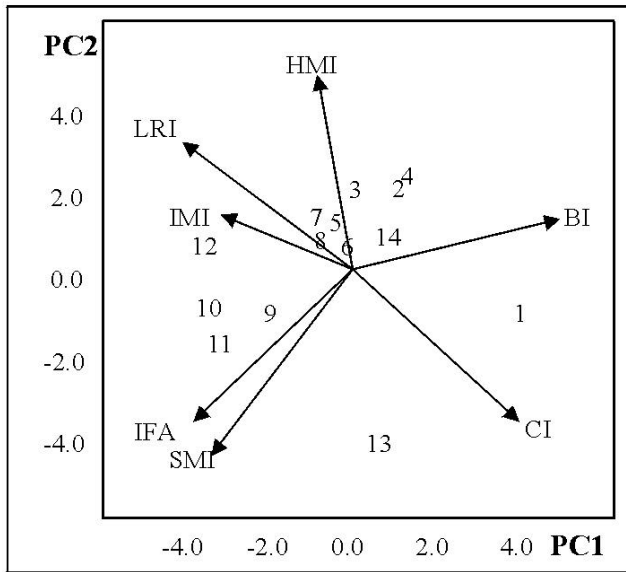


Figure 7. A biplot of principal components one and two based on the indices. The numbers indicate the species studied in Vizcaíno and Milne (2002): *Análisis de componentes principales uno y dos basado en los índices. Los números indican la especie estudiada en Vizcaíno y Milne (2002):* 1. *Tolypeutes matacus*, 2. *Dasypus novemcinctus*, 3. *Dasypus hybridus*, 5. *Euphractus sexcinctus*, 6. *ChaetophRACTUS vellerosus*, 7. *ChaetophRACTUS villosus*, 8. *Zaedyus pichiy*, 9. *Priodontes maximus*, 10. *Cabassous unicinctus*, 11. *Cabassous centralis*, 12. *Cabassous chacoensis*, 13. *Chlamyphorus truncatus*, 14. *Eutatus seguini*. The size and direction of the arrows gives an indication of the extent to which each index contributed to the Principal Components (PC) / El tamaño y dirección de las flechas brinda una idea de cuánto contribuye cada índice a los Componentes Principales (PC).

Euphractini and Priodontini to the Chlamyphorini, which is the most fossorial tribe. The SMI shows a similar pattern to that of the IFA, with *Chlamyphorus truncatus* having the highest values, followed by the Priodontini and the other tribes. The exception is that *Tolypeutes matacus* has a higher SMI than expected, but nearly as high as that of the most fossorial dasypodines. *T. matacus* has the ability to roll into a tight ball, and Vizcaíno and Milne (2002) suggested that perhaps the relatively more powerful shoulder also has a role in this function. The BI gives an indication of the extent to which the forelimb is adapted for fast movement, which is more prominent in cursorial mammals. It shows the expected pattern with *T. matacus* having the highest values followed progressively by the more fossorial tribes (Dasypodini, Euphractini, and Priodontini). The exception is *C. truncatus* with a higher BI than expected, but its digging strategies are much less well known than for the other representatives of the family. Additionally, the possibility exists that the Priodontini has a somewhat lower than expected BI, which could exacerbate the impression of a high BI for *C. truncatus*.

We have noted above that in the forelimb of *Eutatus seguini* the IFA and the BI values are between those of the living euphractines and dasypodines, and the SMI is somewhat higher than that of the eu-

phractines and similar to that of *T. matacus*. These results suggest that *E. seguini* was at least as good a digger as living euphractines and dasypodines. These two taxa have the typical fossorial habits expected for the members of the group belonging to the second category of fossoriality proposed by Vizcaíno *et al.* (1999), who divided the fossorial habits of the armadillos into three categories: 1) species that are mainly cursorial (Jenkins 1971, Stein and Casinos 1997); 2) species that often dig, but for which digging plays no essential part in their alimentary strategy; and, 3) species that are burrowers or that feed on termites or ants. The three-banded armadillo *T. matacus* is the most cursorial within the family and apparently does not dig burrows (Nowak, 1991). The third category includes the naked tailed armadillo *Cabassous* spp. and the pygmy armadillo *Chlamyphorus truncatus*, both of which have extremely fossorial habits (Nowak, 1991), and the giant armadillo *Priodontes maximus* which is considered a powerful and rapid digger, and shelters in burrows of its own construction (Nowak, 1991).

In the hindlimbs, the correlation of body mass with HMI and the positive relationship between HMI and LRI (Vizcaíno and Milne, 2002) suggest that the high leverage at the hip and the relatively short robust tibia-fibula, which are features of the larger armadillos, do not relate to fossoriality but to body support. The correlation of the hindlimb indices with body mass may reflect the habit of armadillos of supporting most of their weight on their hindlimbs (Frechkop, 1949). This agrees with the findings of the previous study mentioned above (Fariña and Vizcaíno, 1997), which showed that the femur and, partially, the tibia of armadillos scale more like those of generalized mammals than of specialized diggers such as the ctenomyd rodents (Casinos *et al.*, 1993).

Eutatus seguini has a high HMI, similar to that of dasypodines and priodontines, and relatively high CI and low LRI when compared with the more generalized diggers, the dasypodines and euphractines (Vizcaíno and Milne, 2002). While the high leverage at the hip would be interpreted in the context of the large body size of *E. seguini*, the high CI and low LRI might suggest adaptation to cursoriality.

The values obtained by Vizcaíno and Milne (2002) indicate that in living armadillos the combination of a high BI and CI and low LRI correlates with cursoriality, as it is apparent in *T. matacus*. There is a clear tendency for increased fossorial adaptations from the tolpeutines to the priodontines, with the dasypodines and euphractines falling in an intermediate position. On the other hand, *C. truncatus* which leads a completely subterranean life and has an extremely reduced size does not follow the general for most of the indices, including CI and LRI, almost as though a

subterranean lifestyle imposes different functional solutions than available to most other mammals.

In living armadillos, comparisons of proportions between fore and hindlimbs (IMI) indicate that larger-sized species have increased hindlimb dominance related to supporting most of their weight on their hindlimbs (Vizcaíno and Milne, 2002). Hindlimb values, indicating hindlimb dominance in *Eutatus sequini*, are similar to those of the similarly sized *Priodontes maximus*, in which the hindlimbs are suited for supporting body weight. However, the former has quite different forelimb adaptations that clearly suggests digging abilities closely similar to those of group 2 armadillos. The combination of these features in *E. sequini* might thus suggest selection for modifications favouring a somewhat intermediate locomotory mode between the more extreme fossorial and cursorial armadillo modes.

Based on the results of the analyses discussed above, *Eutatus sequini* falls most probably in the second category of fossoriality proposed by Vizcaíno *et al.* (1999); that is, to the group of species that often dig, but for which digging plays no essential part in their alimentary strategy. The principal components analysis shown in figure 7 clearly demonstrates that *E. sequini* was a generalised armadillo with similar limb proportions to the Dasypodini and Euphractini.

On the one hand, it is easily recognised from the general morphology and the analysis of the limb proportions performed here that the limbs, especially the forelimbs, were well adapted for digging. It is well known that most living armadillos dig their own burrows for shelter and nesting. Mammalian burrows of different sizes are commonly mentioned, but not specifically described, in the literature on the late Cenozoic deposits of South America, especially in the coastal region of Buenos Aires Province, Argentina (Ameghino, 1908; Frenguelli, 1921, 1928; Kraglievich, 1952). Although it was recently demonstrated that some of the largest structures of this kind must have been built by mylodontid ground sloths (Zárate *et al.*, 1998; Bargo *et al.*, 2000; Vizcaíno *et al.*, 2001), there is no doubt that the largest armadillos were the builders of many of the paleoburrows recorded in several localities in South America. The transverse diameters of the bodies of these armadillos are consistent with the diameters recorded (approximately between 40 and 80 cm) in many of these burrows. Some proposed candidates as builders are *Eutatus sequini*, the dasypodine *Propaopus grandis*, and the pampatherid *Pampatherium typum* (Imbellone and Teruggi, 1988; Imbellone *et al.*, 1990; Quintana, 1992; Bergqvist and Maciel, 1994).

On the other hand, digging must have played no essential part in the alimentary strategy of *E. sequini*. It

is well known that most living armadillo species dig to search for invertebrate prey (Redford, 1985) and the extinct peltephilines, at least, have been proposed as specialised to feed on underground plant matter (Vizcaíno and Fariña, 1997). The analysis of the masticatory apparatus of the eutatines performed by Vizcaíno and Bargo (1998) noted that *E. sequini* is one of the eutatines that exhibit the most specialized morphology known for a herbivore with an armadillo-like skull pattern. The general morphology of its masticatory apparatus resembles that of browser ungulates of moderate to small size, such as some deer and antelopes adapted to feeding on a variety of plant material, such as leaves and buds, and possibly also including some proportion of grasses. The long snout and the absence of anterior teeth in *E. sequini* indicate that items such as nuts, twigs, roots, and tubers were not part of its diet. In this context, it differs from other giant dasypodid armadillos. While the Pleistocene Dasypodinae *Propaopus grandis* retained the generalised habits of the subfamily, the sole armadillo species attaining this size in the Recent is *Priodontes maximus*, in association with a high specialisation in a trophic niche as a termites or ants feeder (Fariña and Vizcaíno, 1997). It seems that increase in size in armadillos would probably lead to divergent trophic specializations.

Conclusions

The analyses conducted here provide useful information in characterising some functional aspects of the locomotory apparatus and the paleobiology of *Eutatus sequini*. The limb proportions of this fossil armadillo indicate digging behaviour similar to that of the living euphractines and dasypodines, although more restricted to building burrows and less specialised in searching for food. When compared with living dasypodids *Eutatus sequini* shows exclusive features: it reaches a body size comparable to that of the hyperspecialised digger and myrmecophagous *Priodontes maximus*, but is less specialised for digging and has completely different dietary habits.

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