

Postcranial Skeleton of *Glironia venusta* (Didelphimorphia, Didelphidae, Caluromyinae): Description and Functional Morphology

David A. Flores^{*, 1, 2} and M. Mónica Díaz^{2, 3}

¹ Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, División Mastozoología, Av. Angel Gallardo 470, CP 1405, Ciudad de Buenos Aires, Argentina

² CONICET. Consejo Nacional de Investigaciones Científicas y Técnicas, Argentina

³ PIDBA. Programa de Investigaciones de Biodiversidad Argentina, Facultad de Ciencias Naturales e Instituto Miguel Lillo, Universidad Nacional de Tucumán, Argentina

Abstract

Received 16 September 2008

Accepted 14 May 2009

Published 24 September 2009

The postcranial skeleton of the neotropical living marsupial *Glironia venusta* is described and compared in a functional framework. Osteological and myological characters of 19 species of living didelphids and some additional placentals were consulted as models to explain functional implications from the morphology. The skeleton of *G. venusta* provides evidence about locomotory behavior and specific capacities of movements, and reveals patterns comparable to arboreal didelphids and placentals with high capacity to climb. In general terms, *G. venusta* has few diagnostic characters in the context of the didelphid sample analyzed, which includes representatives of all recognized clades in the family (second sacral not fused to the ilium, humeral greater trochanter well developed, tibia shorter than femur). Most of the postcranial pattern in *G. venusta* is consistent with arboreal locomotion, but unlike *Caluromys* and *Caluromysiops*, it seems to have faster locomotion. The morphology of the vertebral column, at the thoracic and lumbar portions, shows features that allow powerful lateral and sagittal movements during different phases of locomotion. The patterns evidenced in the forelimbs, pelvic girdle, and hindlimbs point to arboreal habits as well, except for some features on the humerus, ilium and fibula. Even if most didelphids have been cataloged as generalized with respect to their mode of gait, the skeletal morphology of *G. venusta* and the high variation existent in further neotropical marsupials with a variety of body sizes, reveal a diverse combination of features associated to specialized capacities of movements. This indicates a diversity of locomotory modes and postures in didelphids.

Key Words

marsupials
comparative anatomy
locomotor system

Introduction

The genus *Glironia* includes a single species, *G. venusta*, distributed in the amazonian rainforests of Bolivia, Ecuador, Peru, Brazil, and Colombia (Barkley 2007; Díaz & Willig 2004). This species represents one of the most enigmatic and least known living marsupials of the New World (Marshall 1978). Simpson (1945) included the genus in the subfamily Didelphinae, but later Reig (1955) considered this, together with *Caluromys*, *Caluromysiops*, and *Dromiciops*, as Microbiotheriinae, based on

dental and basicranial morphology. Nonetheless, the basicranial resemblance among microbiotherids with *Glironia*, *Caluromys*, and *Caluromysiops* were argued by Segall (1969). Kirsch (1977) created the subfamily Caluromyinae to include these genera. At present, the similarities of the dentary between Caluromyinae and *Dromiciops* are recognized as convergencies, and thus are not the result of common ancestry (e.g. Kirsch 1977; Reig et al. 1987).

In the morphological pattern exhibited by caluromyines, the cranio-dental morphology and some tegu-

* Corresponding author, e-mail: dflores@macn.gov.ar

mentary characters are mostly shared between *Caluromys* and *Caluromysiops* (see Marshall 1978; Voss & Jansa 2003). Hershkovitz (1992) created the family Glironiidae (including only *Glironia venusta*), defined by cranio-dental morphology and some external and tegumentary features, but the name is unavailable. The phylogenetic analysis performed by Voss & Jansa (2003), includes several diagnostic conditions for *G. venusta* in the context of caluromyine group: manual digit III and IV subequal and longer than other manual digit, absence of pouch, tail morphology, premaxillae extended to upper canine alveoli, transverse canal present, anterior limb of ectotympanic directly attached via malleus, fenestra cochleae of petrosal exposed in lateral view, angular process acute and strongly inflected, first premolar large, second and third premolars subequal in size, M4 wider than M1, and upper molars with a distinct ectoflexus. Although those cranio-dental and external features have been properly defined and described in previous papers, its postcranial morphology is scarcely known, except for some details of tarsal morphology (see Szalay 1994; but see Flores 2009). To date, the skeletal material of *G. venusta* deposited in systematic collections is quite scarce, and just one specimen with complete cleaned postcranial skeleton is known, on which our description and comparisons are based. Detailed information of the postcranial morphology of *G. venusta* is significant in order to add new evidence on a functional background of this scarcely known marsupial. We focused our study on two main purposes: 1) to provide a comprehensive description of the skeleton of *G. venusta*, and 2) to draw conclusions about its functional morphology through comparison with models developed from better known didelphids, and thereby understand its locomotory mode and substrate use in the rainforest.

Material and methods

Our description of the postcranial morphology of *Glironia venusta* is based on one cleaned skeleton of an adult lactating female collected by M. Mónica Díaz (collection catalogue MMD 607, deposited in the Museo de Historia Natural de San Marcos, Peru; not cataloged). The specimen was captured at Puerto Almendra, km 6 de la carretera Iquitos-Nauta, 6.5 km al W del camino a Zungarococha, Maynas Province, Loreto Department, Perú (3°50.039' S, 73°22.633' W). Even when few specimens of this taxon are deposited in several museums (see Díaz & Willig 2004), most of them are preserved in alcohol or skin-skull preparations. Although at present it is not possible to analyze the individual or sexual variations, the collection of more specimens with complete skeletons will facilitate descriptions and comparisons. We compared the skeletal morphology of *G. venusta* with 19 other species of arboreal, generalized, and terrestrial didelphid species, essential in order to deduce about its ecological habits and locomotory abilities. Several inferences on locomotion are based on specific models linked with precise functional capacities in the postcranium of living and fossil marsupials and some placental mammals (e.g. Slijper 1946; Oxnard 1963; Yalden 1972; Taylor 1974, 1976; Jenkins & Camazine 1977; Jenkins & Weijjs 1979; Gebo 1989; Larson 1993; Curtis 1995; Johnson & Shapiro 1998; Szalay & Sargis 2001; Argot 2001, 2002, 2003; Sargis 2001a, 2001b, 2002a, 2002b;

Muizon & Argot 2003; Weisbecker & Warton 2006; Candela & Picaso 2008; Weisbecker & Archer 2008; Flores 2009). In agreement with the variety of locomotory habits exhibited by didelphids, the postcranial skeleton shows important anatomical variability whose phylogenetic interpretations were recently incorporated (Flores 2009). Thus, although the descriptions and comparisons include the morphology of each skeletal element, only the major, functionally important postcranial features are discussed and illustrated, to understand the functional compromise of the skeleton of *G. venusta*.

Study specimens (Appendix). For comparisons, we analyzed a sample of the arboreal *Caluromys* and *Caluromysiops* skeletons among caluromyines, and postcranial material of some didelphines with diverse habits of posture and locomotion (*Didelphis*, *Chironectes*, *Cryptonanus*, *Metachirus*, *Micoureus*, *Philander*, *Lestodelphys*, *Monodelphis*, *Marmosa*, *Marmosops*, and *Thylamys*), including representatives of all recognized clades in Didelphidae (Voss & Jansa 2003; Flores 2009).

For terminology of bones, foramina, processes, and muscles we follow complete descriptions of marsupial and placental mammals (e.g. Evans 1993; Szalay 1994; Marshall & Sigogneau Rusell 1995; Szalay & Sargis 2001; Bezuidenhout & Evans 2005; Flores 2009).

Results

The postcranial morphology of *G. venusta* differs in some characters from the morphology described in other didelphids. Important differences with the remaining caluromyines were also detected in most of the postcranial elements. However, some characters are highly conservative across our caluromyine sample, and in some cases, *G. venusta* is autapomorphic in the context of living didelphids. We offer a meticulous description of the morphology of each element of the postcranial skeleton of *G. venusta*, and comparisons with other didelphids.

Vertebral Morphology

In *Glironia venusta*, as in the remaining didelphids, the column is formed by 7 cervical, 13 thoracic, 6 lumbar, 2 sacral, and 24 caudal elements. However, the general vertebral morphology shows some remarkable differences compared with other analyzed didelphids.

Atlas. The general morphology of the atlas of *Glironia venusta* (Figs 1a–b) is essentially similar to other didelphids. It is a small element, with neural arches dorsally convergent and cranio-caudally extended in relation to the intercentrum I. Behind the cranial articular fovea a small atlantal foramen for the cranial nerve I is present (Fig. 1b). In dorsal view, the neural arches are similar to the cranio-caudal extension of the transverse processes, being longer in *Caluromys* and *Caluromysiops*. The transverse processes are not caudally extended, but reaching the same level than the caudal articulation. In ventral plane, the processes are oblique with respect to the vertebral body as in other caluromyines, but the contact to this (Fig. 1b) is comparatively thinner than in *Caluromys* (Fig. 1d) and *Caluromysiops*. The transverse foramina are incompletely closed, forming a canal (Figs 1a–b), whereas in adult specimens of *Caluromys*

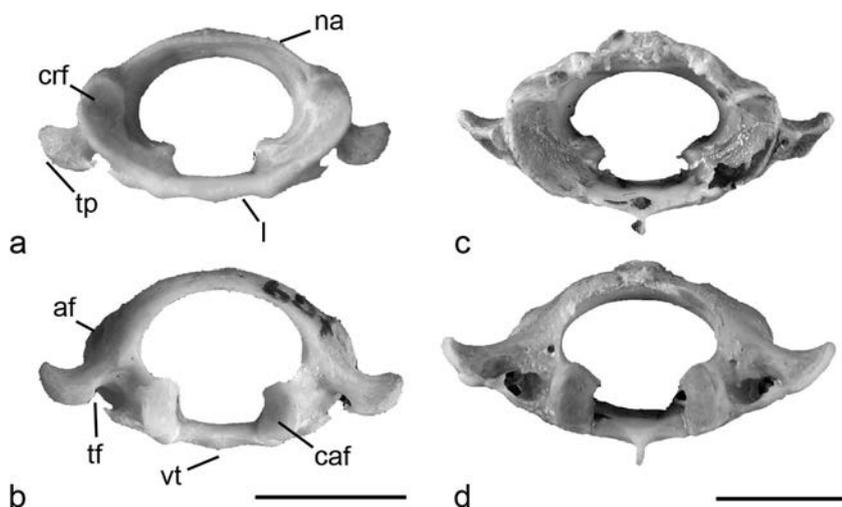


Figure 1. Atlas of *Glirionia venusta* MMD 607 (a–b) and *Caluromys philander* AMNH 267337 (c–d). **a, c.** Cranial view; **b, d.** Caudal view. **af** – atlantal foramen; **caf** – caudal articular fovea; **crf** – cranial articular fovea; **I** – intercentrum; **na** – neural arch; **tf** – transverse foramen; **tp** – transverse process; **vt** – ventral tubercle. Scale bars: 5 mm.

(Figs 1c–d) and *Caluromysiops* the foramina are completely closed. However, ontogenetic variations were evidenced in some taxa, as in *Caluromys philander*, where the foramina are incompletely closed in young specimens, showing asymmetry in some cases.

As in *Caluromys*, *Caluromysiops*, and most of didelphines analyzed, the cranial facets of the atlas have the dorsal borders curved, although in lesser degree than other caluromyines (Figs 1a, c). The ventral arches are in contact and the sutures with the intercentrum I are slightly evident. The ventral tubercle is scarcely developed (Figs 1a–b), whereas in *Caluromys* (Figs c–d) and *Caluromysiops* it is evident. In caudal view, the caudal articular foveae are rounded (Fig. 1b), and the trans-

verse canal is well developed. Compared to *Caluromys* and *Caluromysiops*, the articular foveae of *G. venusta* are more caudally oriented.

Axis. The axis (Figs 2a–c) of *G. venusta* is structurally similar to those of *Caluromys* and *Caluromysiops*. The sutures among its different components are absent, although an almost imperceptible suture is present between the centrum I and II (Fig. 2c). The sutures among its remaining components are clearly evident in young or subadult specimens of other didelphines analyzed (e.g. *Didelphis*, *Philander*). The transverse foramen is completely closed, and the spinous process is well developed cranially and caudally extended beyond the

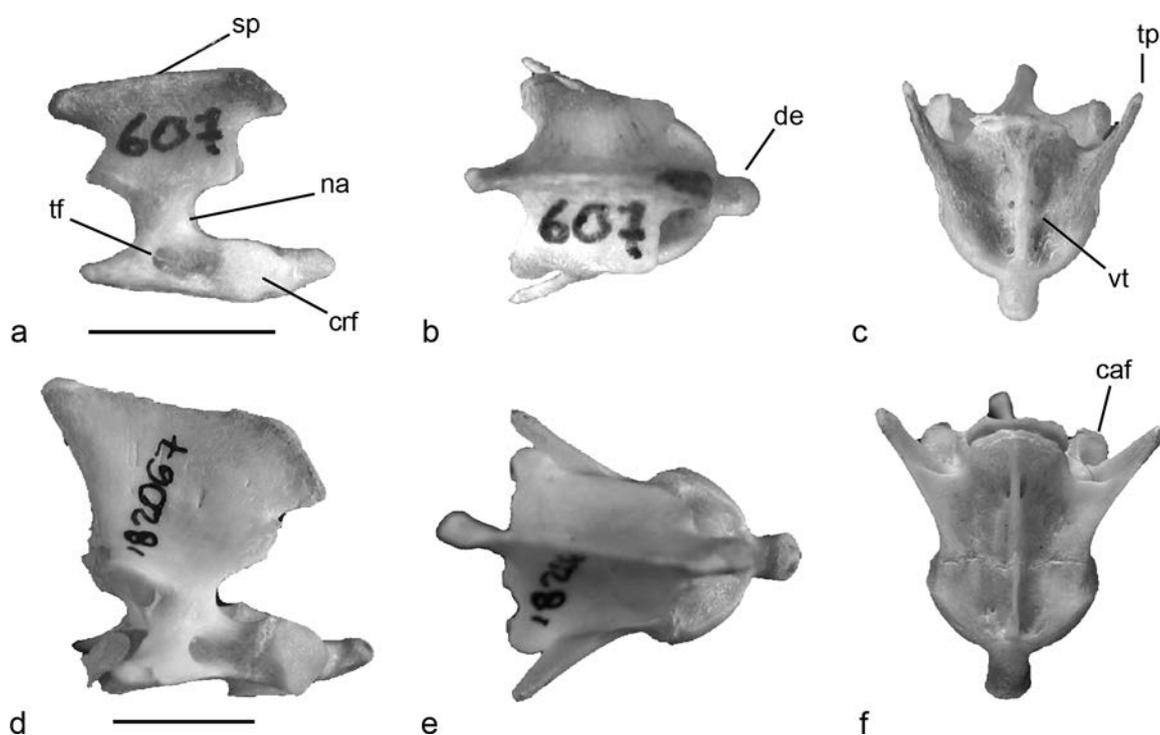


Figure 2. Axis of *Glirionia venusta* MMD 607 (a–c) and *Philander frenatus* MVZ 182067 (d–f). **a, d.** Lateral view; **b, e.** Dorsal view; **c, f.** Ventral view. **caf** – caudal articular fovea; **crf** – cranial articular fovea; **de** – dens; **na** – neural arch; **sp** – spinous process; **tf** – transverse foramen; **tp** – transverse process; **vt** – ventral tubercle. Scale bars: 5 mm.

neural arches (Fig. 2a) forming a sagittal crest, as in all analyzed groups, except *Didelphis*, which lacks of such caudal extension (see Coues 1869). The crest is taller and more robust in *Caluromys* and *Caluromysiops*, being almost parallel to the ventral plane, whereas it is anteroventrally inclined in *G. venusta* (Fig. 2a). The dens is anterodorsally oriented, cranially extended with respect to the anterior tip of the spinous process (Figs 2a–b), a condition observed also in the remaining caluromyines and some didelphines (e.g. *Didelphis*, *Marmosops*, *Thylamys*). The transverse process is caudally oriented (Figs 2b–c) but not enlarged, reaching just the half of the C3 body (as in *Caluromysiops*), whereas in some specimens of *Caluromys* it is more caudally extended, reaching the posterior border of C3 body.

The cranial articular foveae are almost rounded and cranio-laterally oriented (Fig. 2a). Similarly to *Caluromys* and *Caluromysiops*, the caudal articular foveae of *G. venusta* are oval shape and caudo-ventrally oriented. In

other taxa, as *Didelphis*, *Metachirus*, and *Philander*, the caudal articular foveae are rounded and almost ventrally oriented. In lateral view, the inferior part of the neural arch is thin (Fig. 2a), as evidenced in some mouse opossums (e.g. *Thylamys*, *Marmosa*, *Marmosops*, *Lestodelphys*). On the ventral surface, 3 pairs of small foramina are present, one posterior to the dens, one medial (which is also observed on the interior floor), and one posterior (Fig. 2c). The ventral tubercle is formed by two weak separated lobes (Fig. 2c), which is also shown in some didelphines, as *Lestodelphys*, *Marmosops*, *Metachirus*, some species of *Thylamys*, and *Cryptonanus unduaviensis*. The anterior notch of the neural arches is wide (Fig. 2a), a condition widely spread among mouse opossums, and present also in *Chironectes* and *Lutreolina*.

Posterior Cervical Vertebrae (C3–C7). In *G. venusta* the spinous process is tiny in C3, and gradually become more developed from C4 to C7 (Fig. 3a). This condi-

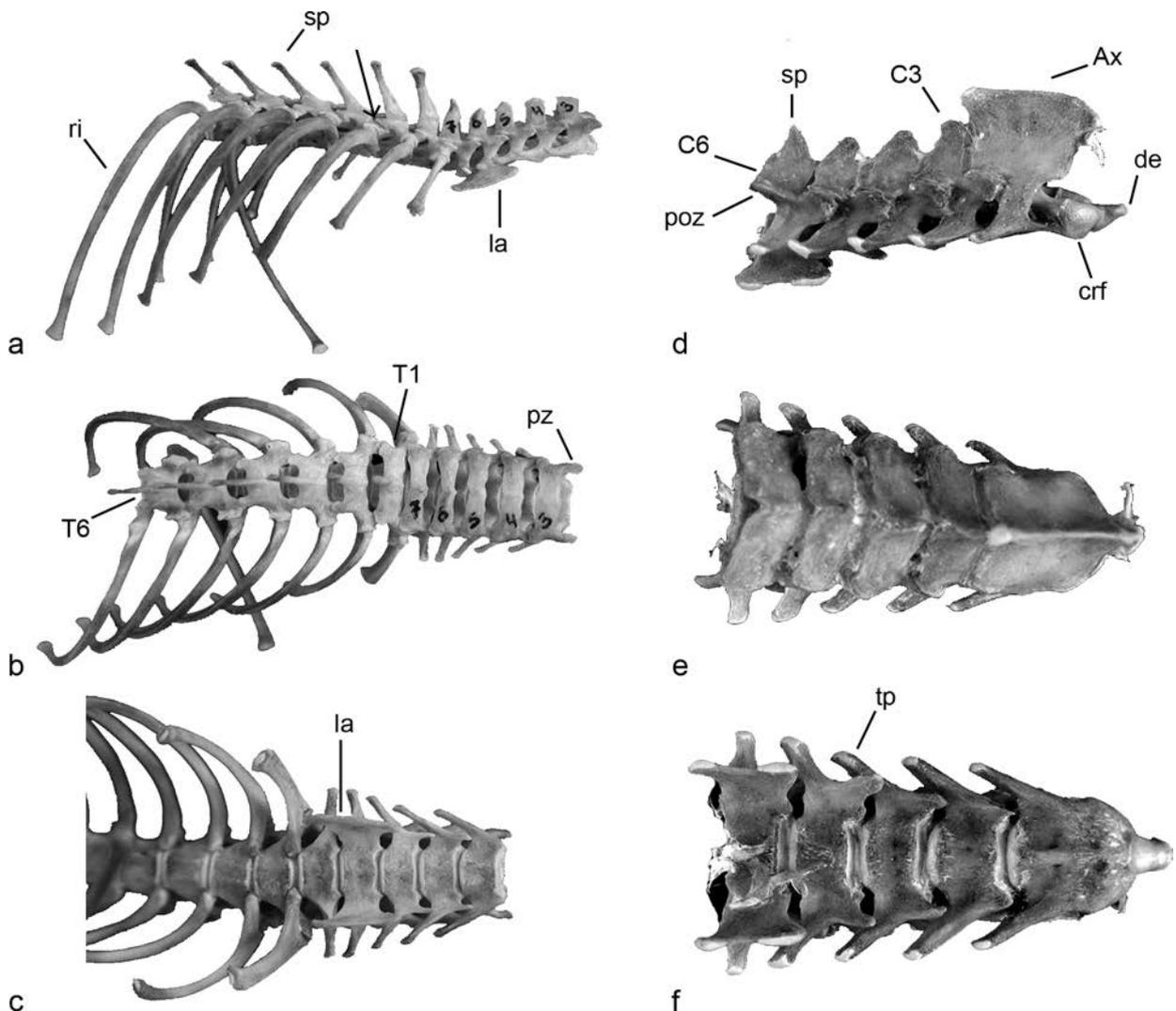


Figure 3. Posterior cervical and anterior thoracic vertebrae of *Glironia venusta* MMD 607 (a–c) and cervical vertebrae of *Caluromys philander* AMNH 267337 (d–f). a, d. Lateral view; b, e. Dorsal view; c, f. Ventral view. Ax – axis; C3 – third cervical vertebra; C6 – sixth cervical vertebra; crf – cranial articular fovea; de – dens; la – lamellae; poz – postzygapophysis; pz – prezygapophysis; ri – rib; sp – spinous process; T1 – first thoracic vertebra; T6 – sixth thoracic vertebra; tp – transverse process. Arrow indicates the different orientation of prezygapophysis. Not in scale.

tion is a significant difference with *Caluromys* and *Caluromysiops* in which the spinous process is well developed and lamina shape in all post-axis cervical vertebrae. The transverse process on C3 has one head (Fig. 3c), as in most of mouse opossums, whereas in *Caluromys*, *Caluromysiops*, *Metachirus*, and the 2n = 22 large opossums, it has two heads. The prezygapophysis is dorso-mesially oriented, and the postzygapophysis is ventro-laterally oriented from (Fig. 3a). In C6 a well developed lamella is observed as in all taxa analyzed (Figs 3a, c). The transverse foramen is present in C7, and the transverse processes are caudally oriented from C3 to C5, almost perpendicular to the vertebral body in C6, and slightly anterior and ventro-laterally oriented in C7 (Figs 3a–c), as in *Caluromys*, *Caluromysiops*, *Didelphis*, and some mouse opossums.

Thoracic Vertebrae (T1–13). The thoracic vertebrae of *G. venusta* show some remarkable differences with respect to *Caluromys* and *Caluromysiops*. The spinous process of T1 is scarcely lower than in T2 and T3 (although not as in *Monodelphis*, see Flores 2009: fig. 3) and slightly wider cranio-caudally. The spinous processes become more caudally oriented starting from T3 (Fig. 3a). In *Caluromys* and *Caluromysiops* the processes from T1 to T3 are similar in size and orientation, being in T3 slightly caudal. In didelphines, the process of T1 is taller or equal than in T2, except in *Monodelphis*, where it is notably shorter.

In *G. venusta*, as in all studied didelphines, the first thoracic vertebra with the prezygapophysis facing laterally is placed on the third element (Fig. 3a), whereas in *Caluromys* and *Caluromysiops* it is placed on the second position. From the eighth vertebra, the accessory process is completely separated from the transverse process (Fig. 4), whereas in *Caluromys* this condition occurs in the ninth thoracic vertebra; and in the seventh in *Caluromysiops*. The accessory processes are small (Fig. 4) if compared with those of *Caluromys*, *Caluromysiops* or *Metachirus*.

From T10 to T13, the spinous processes become notably shorter and cranio-caudally enlarged, and the general vertebral morphology resembles to anterior lumbar

elements (Fig. 4). Until T9 or T10 the facets for vertebral articulation are parallel with respect to the ventral plane, but from T11 a change in orientation occurs, becoming it more oblique (Fig. 4). In this sense, T11 is identified as diaphragmatic vertebra in *G. venusta* (Flores 2009). In the same way, T11 is the first element that shows the mammillary process notably developed (Fig. 4), as in *Caluromysiops* and *Caluromys philander*. Both *G. venusta* and *Caluromys* display the T11 spinous process almost vertical respect to the long axis of vertebral body, whereas in T12–13 they are caudally oriented.

Lumbar Vertebrae (L1–6). The lumbar vertebrae of *G. venusta* show both the spinous and mammillary processes well developed (Fig. 5a). Starting from the third lumbar element, the mammillary process surpasses slightly the level of articulation with the anterior vertebra (Fig. 5a). This condition is shared with *Caluromys*, *Caluromysiops*, and several didelphines, such as *Metachirus*, *Chironectes*, *Micoureus*, *Marmosa robinsoni*, and *Cryptonanus unduaviensis*. Small accessory processes are present in L1–4 (Fig. 5a), contrasting with *Caluromys* and *Caluromysiops*, where those are well developed and present in all lumbar vertebrae. In dorsal view, an evident intervertebral space is observed (Fig. 5b), a state shared with mouse opossums, but absent in the remaining caluromyines and large didelphines. A small foramen on the base of the neural arches in the last lumbar element is present, as in all other taxa analyzed.

Caudally, the spinous process becomes taller and cranio-caudally expanded (Figs 5a–c). The process at L4 is more expanded and vertically oriented, whereas in posterior lumbar vertebrae they are cranially oriented, being taller and thinner in L6 (Figs 5a, c). In this sense, the anticlinal vertebra in *G. venusta* is located at L4, whereas in other taxa its position shows notable variation. For instance, in *Caluromys* the process is vertical in L4 and L5 but in L6 it is cranially oriented (Fig. 5d), whereas in *Caluromysiops* and *Micoureus* the vertical process is placed on L6. On the other hand, in *Metachirus* this element is placed at L3, and at L4 in *Philander*.

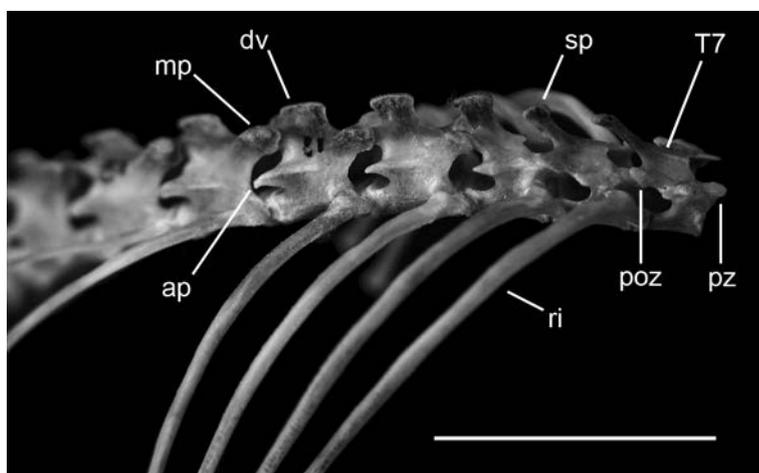


Figure 4. Lateral view of posterior thoracic vertebrae of *Glironia venusta* MMD 607. **ap** – accessory process; **dv** – diaphragmatic vertebra; **mp** – mammillary process; **poz** – postzygapophysis; **pz** – prezygapophysis; **ri** – rib; **sp** – spinous process; **T7** – seventh thoracic vertebra. Scale bar: 10 mm.

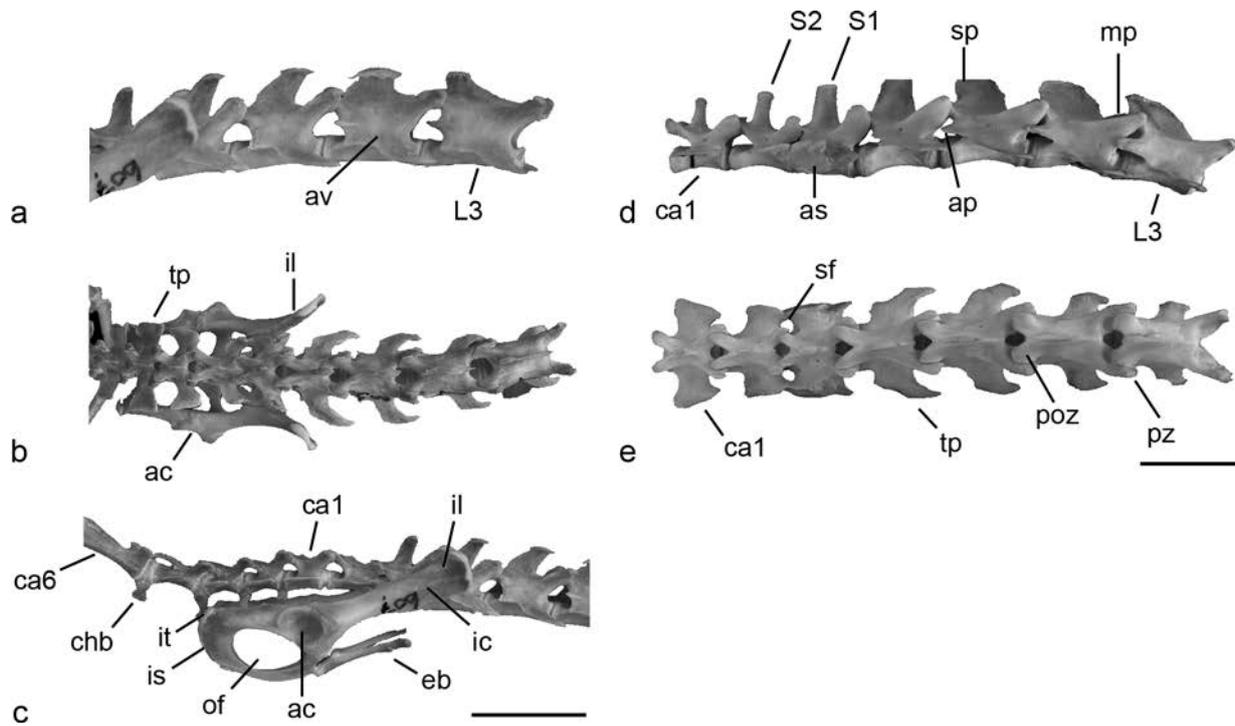


Figure 5. Os coxae, lumbar, sacral, and anterior caudal vertebrae of *Glironia venusta* MMD 607 (a–c), and *Caluromys lanatus* AMNH 215001 (d–e). The os coxae in *C. lanatus* were removed. **a.** Lateral view of thoracic vertebrae; **b.** Dorsal view; **c.** Lateral view of os coxae, sacral, and anterior caudal vertebrae of *G. venusta*; **d.** Lateral view; **e.** Dorsal view of lumbar, sacral and first caudal vertebrae of *C. lanatus*. **ac** – acetabulum; **ap** – accessory process; **as** – articular surface; **av** – anticlinal vertebra (L4 in *G. venusta*); **ca1** – first caudal vertebra; **ca6** – sixth caudal vertebra; **chb** – chevrons bones; **eb** – epipubic bones; **ic** – iliac crest; **il** – Ilium; **is** – Ischium; **it** – ischiastic tuberosity; **L3** – third lumbar vertebra; **mp** – mammillary process; **of** – obturator foramen; **poz** – postzygapophysis; **pz** – prezygapophysis; **S1** – first sacral vertebra; **S2** – second sacral vertebra; **sf** – sacral foramen; **sp** – spinous process; **tp** – transverse process. Scale bars: 10 mm.

The transverse processes are cranially oriented, becoming larger caudally, and reaching its maximum development on L6, where they are also laterally expanded (Figs 5a–b). The processes are not ventrally extended beyond the ventral plane of the vertebral body, whereas in *Chironectes* and *Metachirus* the processes are relatively more lateral and ventrally expanded.

Sacrum (S1–2). As in all didelphids analyzed, two vertebrae are involved in the organization of the sacrum in *G. venusta* (Fig. 5b). However, whereas in all species both vertebrae are completely (e.g. *Metachirus*), or partially (e.g. *Caluromys*, *Micoureus*) fused to the ilium (Figs 5d–e), only the first sacral vertebra is fused to the ilium in *G. venusta* (Fig. 5b), which is interpreted as an autapomorphic feature in the context of our sample. The spinous process of the first sacral vertebra is tall, but it is absent in the second one (Fig. 5c). This unusual pattern was just evidenced in some species of *Marmosops* (*M. incanus* and *M. parvidens*, Flores 2009) among didelphids. In most didelphids analyzed, the transverse process of the S2 is cranio-caudally expanded in dorsal view (Fig. 5e), but this condition is absent in *G. venusta* (Fig. 5b), as well as in *Lestodelphys* and *Marmosa rubra* (Flores 2009). The dorsal sacral foramen is rounded (Figs 5b, e), and the ventral

foramen on the first sacral element is absent, as in *Caluromys* and *Caluromysiops*.

Caudal Vertebrae (Ca1–24). In *G. venusta*, as in most of didelphids (excluding the short-tailed *Monodelphis*), the tail is longer than head–body. The caudal vertebrae display two different morphological patterns for articulation: the anterior portion (including to the fourth or fifth caudal element), similar to lumbar and sacral vertebrae (i.e. articulation via pre- and postzygapophysis; Figs 5b–e), and the posterior portion, with vertebral body longer, thin and reduced processes, articulating directly via vertebral body (Fig. 5c). The articulation through vertebral body begins between fourth and fifth caudal vertebrae in *G. venusta*, whereas in *Caluromys* and *Caluromysiops* it occurs between caudal sixth and seventh element. The condition showed by *G. venusta* is observed also in some mouse opossums, such as *Thylamys macrurus*, *Monodelphis adusta*, *M. theresa*, and *Cryptonanus unduaviensis*.

Compared with those of *Caluromys* and *Caluromysiops*, the mammillary processes of the first three caudal vertebrae of *Glironia venusta* are reduced. The spinous processes of the anterior caudal vertebrae are absent (Fig. 5c), but well developed in *Caluromys* (Fig. 5d), *Caluromysiops*, and *Micoureus*. The transverse processes of the first four vertebrae are laterally well de-

veloped and cranio-caudally extended (Fig. 5b), being reduced to just one anterior and one posterior prominences on the fifth element. The same reduction is observed at the seventh element in *Caluromys* and *Caluromysiops*. In most didelphids, there is a caudal element where the transverse process is cranio-caudally lengthened as the vertebral body (see Argot 2003: fig. 10a), which is absent in *G. venusta*. The chevrons bones are well developed on the first caudal vertebrae (Fig. 5c), becoming smaller and weaker between the fourth and fifth elements.

Pectoral Girdle and Forelimb Morphology

Ribs and Sternum. In *Glironia venusta* the ribs are cylindrical, as in all didelphines (Figs 3–4), being cranio-caudally enlarged in *Caluromys* (see Argot 2003: fig. 8a) and *Caluromysiops*. The first rib is thin and notably less curved in (Fig. 3c), even when compared with that of the arboreal *Micoureus*, whereas in *Caluromys* and *Caluromysiops* they are notably robust and curved. In old specimens of *Caluromys* and *Caluromysiops*, the costal cartilages are almost completely ossified, with only small portions without ossification. Such a condition is not observed in *G. venusta*.

The sternum is formed by 6 sternbrae (including manubrium and xiphoides), although some occasional

individual variation is evidenced in *Caluromys philander*, where 5 or 7 elements were occasionally detected (e.g. AMNH 267002, RMNH 19646). The manubrium of *Glironia venusta* is less robust compared with *Caluromys*, slightly keeled, and the cranial section less enlarged anteriorly. The second sternbrae is compressed, and the remainings are flattened. From third to fifth element, the morphology is basically similar. The xiphoid is enlarged with a small medial compression. Alternatively, in *Caluromysiops* and *Caluromys* all sternbrae are laterally compressed and caudally expanded, becoming posteriorly smaller.

Clavicle. The clavicles of *Glironia venusta* are thin and slightly concave, with the sternal tip notably expanded compared with the scapular tip, and proportionally thin compared with that of *Metachirus*, *Didelphis*, *Micoureus*, and *Philander*. In *Caluromys* and *Caluromysiops*, the clavicles are also curved but with both tips of similar size.

Scapula. The general morphology of the scapula of *Glironia venusta* (Figs 6a–c) is comparable to generalized forms (see Argot 2001: fig. 2), being longer and less expanded than arboreal forms, as *Caluromys*, *Caluromysiops*, and *Micoureus* (total width/length = 0.439 in *G. venusta*; compare values in Argot 2001: tab. 1). In other generalized didelphids, as *Didelphis* and *Chiro-*

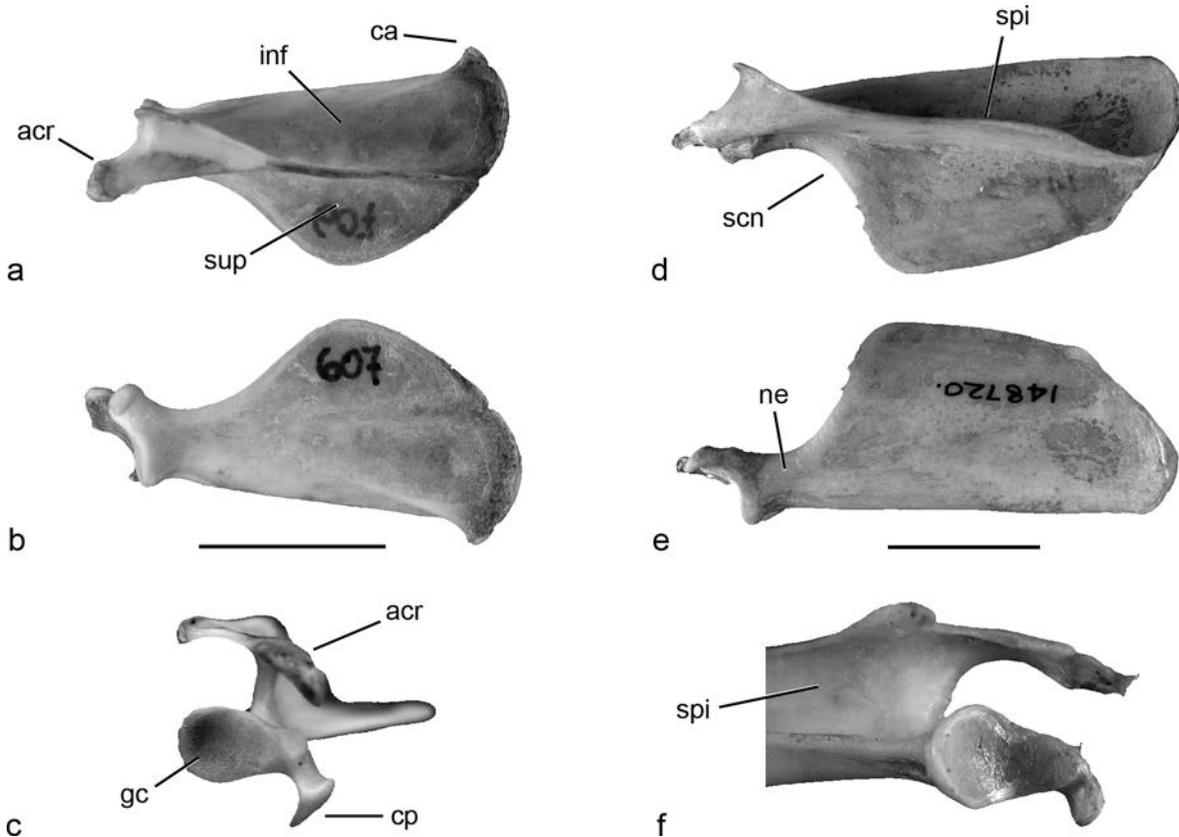


Figure 6. Left scapula of *Glironia venusta* MMD 607 (a–c) and *Chironectes minimus* AMNH 148720 (d–f). **a, d.** Lateral view; **b, e.** Mesial view; **c, f.** Cranial view. **acr** – acromion; **ca** – caudal angle; **cp** – coracoid process; **gc** – glenoid cavity; **inf** – infraspinous fossa; **ne** – neck; **scn** – scapular notch; **spi** – spine; **sup** – supraspinous fossa. Scale bars: 5 mm. **c** and **f** not in scale.

nectes, the scapula is rectangular (Fig. 6d), being wider in terrestrial taxa as *Metachirus* or *Monodelphis*. The suprascapular fossa is wider and larger than the infraspinous one, as in *Metachirus*, *Philander*, and *Marmosa*. Similarly to arboreal forms, the caudal angle is acute and the scapular notch is extended to the half of the scapula (Figs 6a–b). The coracoid process is well developed (Fig. 6c), being highly variable across the didelphines. For instance, in *Philander* and *Chironectes* it is small (Fig. 6f), whereas in *Metachirus* and *Didelphis* it is notably wide. The acromion is strong and extends beyond the glenoid fossa of the scapula (Fig. 6b); in general, it is more developed in caluromyines than didelphines. The glenoid fossa is piriform shape (Fig. 6c) and anteroventrally oriented, as in all groups analyzed. The scapular spine is well developed (Figs 6a, c) in *G. venusta*, as wide as the infraspinous fossa at the neck level, a condition shared with *Caluromysiops* and *Caluromys*. In contrast, the spine is proportionally lower in *Metachirus*, *Philander*, *Didelphis*, and *Chironectes* (Fig. 6f), descending more abruptly compared with strongly arboreal forms.

Humerus. The body is robust, with the diaphysis almost straight (Figs 7a–c). The humeral head is slightly oval (Fig. 7b), being proportionally lesser in *G. venusta* compared with those of *Caluromys* and *Caluromysiops*, where it is more rounded. As in *Caluromys* and *Caluromysiops*, the neck is not strongly marked in *G. venusta*, whereas it is more evident in some didelphines, as *Metachirus*, *Micoureus* and *Philander* (Fig. 7f). In the proximal section, the humeral greater and lesser tuber-

osities are well developed (Fig. 7b) and the greater one slightly surpasses the level of the head. Among didelphids, this condition was detected only in *Glironia* (compare with *Philander*; Fig. 7e), and additionally in some Australasian groups, as *Dasyurus* and *Vombatus* (Horovitz & Sánchez-Villagra 2003). The deltopectoral crest is well developed, extending to the proximal half of the diaphysis and determining a deep bicapital groove (Figs 7a, c), as in *Caluromys*, *Caluromysiops*, and some mouse opossums. Instead, in *Philander* (Fig. 7f) and *Metachirus* the crest is low, but extending beyond the proximal half of the humerus, and the bicapital groove is comparatively shallow.

In mesial view, a medial relief for the insertion of the M. teres major is observed, which is also present in *Caluromys* and *Caluromysiops*. The relief is less evident in *Didelphis*, *Micoureus*, *Metachirus*, and *Philander*, and well developed in the terrestrial *Monodelphis*. In lateral view, the tuberosity for the insertion of M. teres minor is evident (Fig. 7c), as in *Monodelphis*, *Metachirus*, and *Philander*. On the distal portion of the humerus, the ectepicondylar crest (or supinator ridge) is well developed and laterally expanded in *G. venusta*, showing a small proximal process (Figs 7a–c). The trochlea is evident, and clearly separated from the capitulum (Fig. 7c), although in *Caluromys*, *Caluromysiops*, and *Micoureus* both structures are comparatively more separated by a wider zone for the humero-ulnar articulation. The capitulum is spherical, more proximally extended than the trochlea, showing a clear lateral projection (Fig. 7a) as in the large opossums. The entepicondyle is well developed protruding mesially

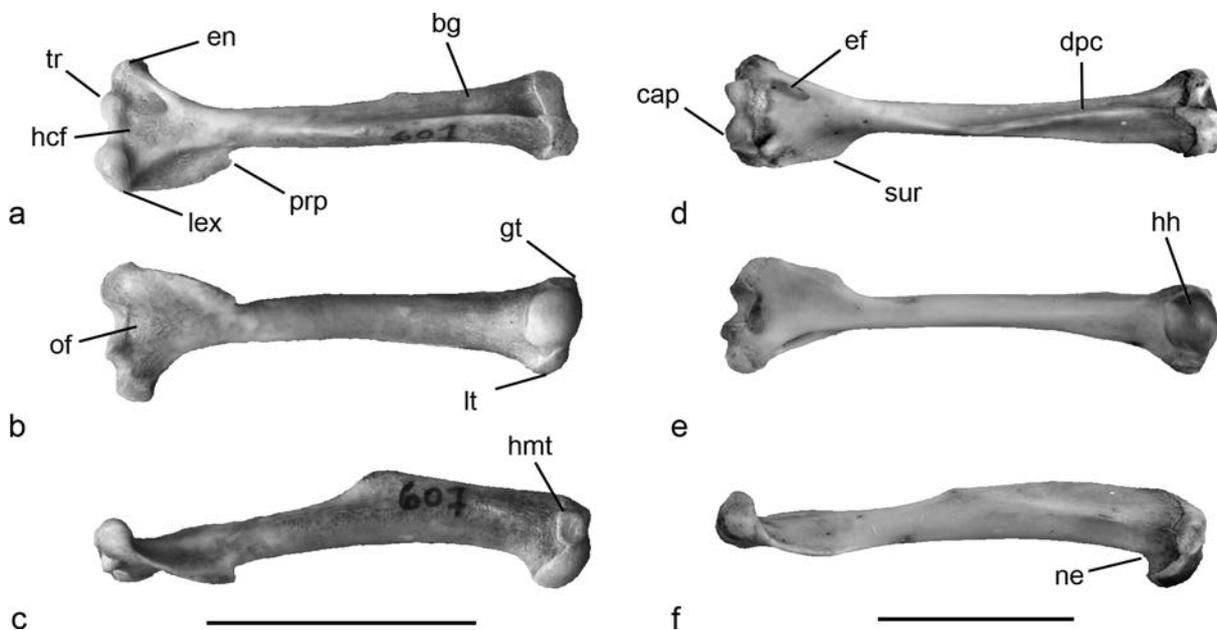


Figure 7. Left humerus of *Glironia venusta* MMD 607 (a–c) and *Philander opossum* AMNH 190446 (d–f). **a, d.** Cranial view; **b, e.** Caudal view; **c, f.** Lateral view. **bg** – bicapital groove; **cap** – capitulum; **dpc** – deltopectoral crest; **ef** – entepicondylar foramen; **en** – entepicondyle; **gt** – greater tuberosity; **hcf** – humeral coronoid fossa; **hh** – humeral head; **hmt** – humeral lateral tuberosity; **lex** – lateral extension of the capitulum; **lt** – lesser tuberosity; **ne** – neck; **of** – olecranon fossa; **prp** – proximal process of the supinator ridge; **sur** – supinator ridge; **tr** – trochlea. Scale bars: 10 mm.

and separated from the trochlea by a small groove (Figs 7a–b). The separation of both structures is variable in different groups. For instance, in *Micoureus* the groove is wide, whereas in *Didelphis*, *Philander* (Fig. 7e), and *Metachirus* it is almost absent. The entepicondylar or humeral supracondyloid foramen is well developed and oval shape (Fig. 7a), as in most the groups analyzed, although it is rounded and relatively smaller in *Metachirus* and *Micoureus*. As in *Caluromys*, *Micoureus* and *Philander* (Fig. 7e), the olecranon fossa is visible but shallow in *G. venusta* (Fig. 7b), and the humeral coronoid fossa is also shallow (Fig. 7a).

Ulna and Radius. In *Glironia* the ulna and radius are strong bones (Figs 8a, 9). The diaphysis of the ulna is laterally compressed as in arboreal forms, but in larger didelphines (as *Didelphis*, *Metachirus*, and *Philander*), it is rather cylindrical. The olecranon is short and robust (Fig. 8a), with its proximal tip slightly curved cranially. Such pattern was also seen in didelphids as *Caluromys*, *Caluromysiops*, *Micoureus*, and *Marmosa* (Flores 2009). In *Monodelphis* (Fig. 8b) and *Didelphis*, the olecranon is longer, whereas in *Metachirus*, *Hyladelphys*, and *Marmosops parvidens* it is shorter and robust (see Flores 2009: fig. 19). The anconeal process is poorly developed in *G. venusta*, being defined by two small crests (Fig. 8a): the ulnar lateral proximal trochlear (ulptcl) and the ulnar medial proximal trochlear (ulptcm). Both crests are about the same size, and the ulptcm is less extended proximally than the ulptcl, a feature also observed in *Didelphis*, *Caluromys*, *Caluro-*

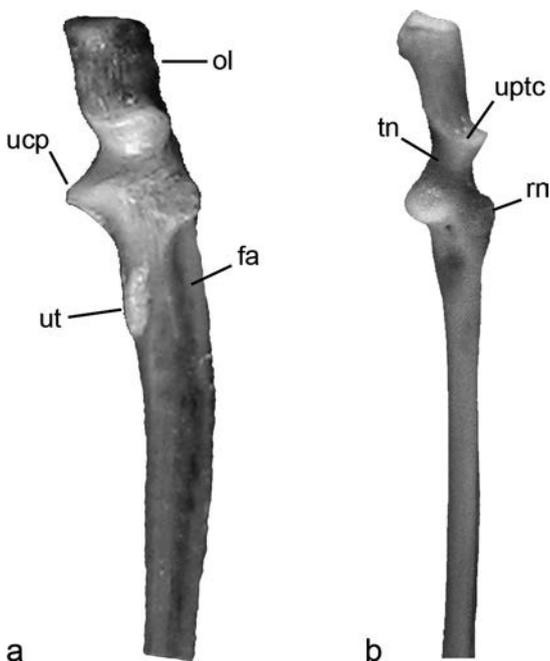


Figure 8. Cranial view of left ulna of *Glironia venusta* MMD 607 (a) and *Monodelphis domestica* AMNH 261241 (b). **fa** – fossa for *anconeus* muscle; **ol** – olecranon; **rn** – radial notch; **tn** – trochlear notch; **ucp** – ulnar coronoid process; **uptc** – ulnar proximal trochlear crest; **ut** – ulnar tuberosity. Not in scale.

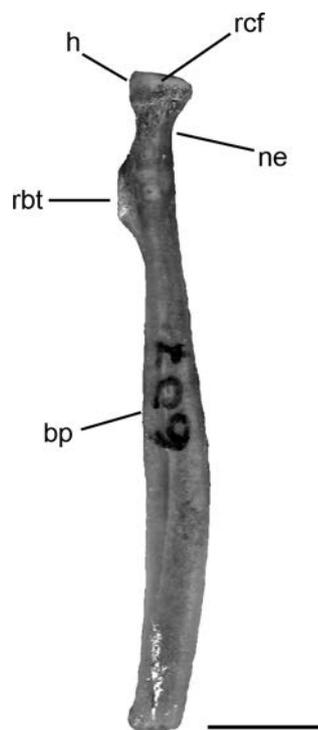


Figure 9. Lateral view of left radius of *Glironia venusta* MMD 607. **bp** – bony plate for insertion of the *flexor digitorum profundus*; **h** – head, **ne** – neck; **rbt** – radial bicipital tuberosity; **rcf** – radial central fossa. Scale bar: 5 mm.

mysiops, and *Micoureus*. Alternatively, the anconeal process is more developed in *Metachirus* than in *Philander*, although in both genera the ulptcm is longer and more proximally extended than ulptcl. The angle formed by the small radial notch and the border of the coronoid process is obtuse in *G. venusta* (Fig. 8a), *Caluromys*, and *Caluromysiops*. The coronoid process and the greater sigmoid cavity are well developed, oriented perpendicular respect to the ulnar diaphysis (Fig. 8a), as in arboreal forms. On the diaphysis, the ulnar fossa for *M. flexor digitorum profundus* is deep, extending beyond the trochlear notch (Flores 2009) and a weak groove for the *M. abductor pollicis longus* is present. The fossa for the insertion of *M. anconeus* is evident on the lateral side (Fig. 8a), although in lesser degree than observed in *Caluromysiops* (Flores 2009: fig. 19). On the cranial side, there is a marked crest for the origin of *M. pronator quadratus* and *M. flexor digitorum profundus*. Distally, the ulna is cylindrical in transverse plane, with an anterior sulcus. The ulnar styloid process is well developed, and articulates with the cuneiform and pisiform through the ulnar-cuneiform facet.

The radius is transversally compressed and antero-posteriorly arched (Fig. 9), although in *G. venusta* and *Micoureus* this outline is less evident than in other arboreal forms. The radial central fossa is circular and concave as in *Caluromys* and *Caluromysiops*, but its morphology is highly variable in didelphids. For instance, in some specimens of *Didelphis* and *Philander* it is oval, in *Chironectes* it is strongly oval and notably

concave, whereas in *Metachirus* it is circular and less concave than in caluromyines. As in all didelphids, the radial bicapital tuberosity is well developed in *G. venusta* (Fig. 9), although it is particularly large and strong in arboreal forms. On the caudal surface, a thin bony plate (Fig. 9) increases the area for origin of the *M. flexor digitorum profundus*. The distal section of the radius is flattened, without any sulcus, and the articular surface exhibits a lateral tubercle (the radial distal malleolus) more distally extended than the medial radio-scaphocentrale facet, where the scaphoid and lunatum articulates.

Carpus and Manus. In didelphids, the carpal and metacarpal morphology has been scarcely studied compared to tarsal morphology. Here, we offer a detailed description of the morphology and position of the carpal bones of *G. venusta*. The general location of the carpal bones is similar to that proposed for didelphids (see Szalay 1994: fig. 3.2). The carpus is composed by eight bones: pisiform, cuneiform, lunatum, scaphoid, unciform, magnum, trapezium, and trapezoid.

The articulation of the scaphoid and radius is transversally wide in *Glironia venusta*, similar to arboreal forms, whereas in the terrestrial *Metachirus* it is transversally restricted. The scaphoid shows a well developed cranial process separating the lunatum from the trapezoid. The lunatum is relatively well developed, and in cranial view it shows the typical didelphid pattern: saddle shape articulating with the radius, scaphoid, and magnum. The proximal tip is thinner than the distal one, contacting with the cuneiform. In *G. venusta* this is a small bone that articulates through concave facets with the distal tip of the ulna proximally, and distally with the pisiform, which is small and expanded, as observed in *Caluromys* and *Caluromysiops*. Although sexual dimorphism was reported in the pisiform and prepollex morphology of several didelphids (in males of some species of *Marmosa* and *Marmosops*, both elements become hyperdeveloped, see Lunde & Shutt 1999), both elements are just somewhat more developed in males of *Caluromys* and *Caluromysiops*. However, it was not possible to observe this condition in *G. venusta* since our single specimen is a female.

The articulation between unciform and cuneiform is helicoidal shape in *Glironia venusta*, as in all analyzed groups. The unciform is dorsally thinner than in *Caluromys*, and ventrally protrudes to the palmar side through a rounded process but proportionally smaller than in *Caluromys* and *Caluromysiops*. The articulations with the Mc IV and V are strongly concave, as occur in all analyzed groups. The unciform shows a lateral notch, like the other didelphids, and it extends proximally to the same level than the magnum. This pattern is similar in *Caluromys* and *Caluromysiops*, but in *Metachirus* the unciform extends proximally beyond the magnum. The magnum has one proximal head, distally articulated with Mc III through a strongly concave facet. Mesially, it articulates on a lateral notch of the

unciform, and laterally it extends to the level where the trapezoid lies down. In this way, the Mc II articulates with the trapezoid mesially, and with the magnum laterally. In proximal view, the trapezoid shows a facet articulating with the process of the scaphoid, and a cranial concavity. The trapezium of *G. venusta* has two distal heads, as in all analyzed didelphids, being somewhat more enlarged than *Caluromys* and *Caluromysiops*, and without the dorsal depression observed in those and *Micoureus*. The plane of articular surface between trapezium and metacarpal I is not parallel with respect to other articulations. The prepollex is small and proportionally shorter than *Caluromys* and *Caluromysiops*.

The metacarpals of *G. venusta* are similar to those of *Caluromys* and *Caluromysiops*: cylindrical but barely flattened. The Mc I is wide and slightly flattened, with a mesial and proximal projection; the Mc I and Mc V are shorter than the other elements. On the cranial side of Mc V, a proximal depression for insertion of the extensor tendons is present. The proximal tip of the metacarpals has two heads articulating with carpal bones.

The proximal phalanges are flattened and laterally convex. Ventrally, a deep palmar sulcus for insertion of flexor tendons is observed. In all caluromyines analyzed, the proximal phalanges are about the same length of metacarpals, unlike *Micoureus*, whose proximal phalanges are longer than metacarpals, and *Metachirus*, where the proximal phalanges are shorter than metacarpals. The medial phalanges are shorter than the proximal ones, as in all analyzed groups. Finally, the ungual phalanges are short, pointed, and strongly curved in lateral view, as in *Caluromys* and *Caluromysiops*, whereas in terrestrial forms as *Metachirus* and *Philander*, they are just slightly curved.

Pelvic Girdle and Hindlimb Morphology

Pelvis. The ilium of *G. venusta* is longer than the ischium (Fig. 5c), with an evident suture between both bones, whereas the ischium and pubis are completely fused. The anterior tip of the ilium is laterodorsally curved (Fig. 5b), while in *Caluromys* (see Argot 2002: fig. 7a), *Caluromysiops*, *Didelphis*, and *Micoureus* it is almost straight. The iliac and gluteal fossae are similar in size and separated by a well developed iliac crest (Fig. 5c). This pattern is also observed in *Caluromys* and *Caluromysiops*, but in the terrestrial *Metachirus* the gluteal fossa is notably larger. The ischiatic spine is not laterally expanded as observed in *Caluromys*, *Caluromysiops*, and *Micoureus*, being strongly extended laterally only in *Metachirus*. In caudal view, the ischiatic arch determines a not strongly acute angle in *G. venusta*, which is accentuated in *Caluromys* and *Caluromysiops*, and wide in *Metachirus*, *Didelphis*, and *Philander* (even more than in *Glironia*; see Argot 2002: fig. 7; Flores 2009). In *G. venusta* and *Caluromysiops* the dorsal border of the ischium (caudal to the acetabu-

lum) is straight, but laterally oriented in *Caluromys*, *Didelphis*, and *Metachirus*. The ischiatic tuberosity is enlarged in *Glironia* (Fig. 5c) and arboreal forms as *Caluromys*, *Caluromysiops*, and *Micoureus*, but less than *Didelphis*, *Metachirus*, or *Philander*.

The iliopubic process is scarcely developed in *Glironia*, although in some specimens of *Caluromys* and *Caluromysiops* it is well developed. In caluromyines and *Micoureus*, the symphysis pubis is as large as the cranio-caudal length of the obturator foramen (Fig. 5c), being shorter in *Didelphis* and *Philander*. The obturator foramen is rounded (Fig. 5c) and proportionally wider than in *Micoureus*, *Caluromys*, or *Caluromysiops*. The acetabulum is opened, oval shape, and with a well marked and concave dorsal border (Figs 5b–c). This morphology is common in all analyzed taxa, except in *Metachirus* where the acetabulum is notably deep and rounded.

Epipubic bones. The epipubic bones of *Glironia venusta* are robust, wider on its proximal section, becoming thinner and slightly curved laterally at the distal tip, and extending approximately to half of the ilium (Fig. 5c). This pattern is also observed in our entire sample, although some variation is found in *Caluromys*, *Caluromysiops*, and *Metachirus*. Flores (2009: fig. 24) report epipubic bones notably elongated and strongly curved ventrally in *Caluromysiops*, *Caluromys*, *Marmosops parvidens*, *Chironectes*, and *Marmosa rubra*.

Femur. The general morphology of the femur in *Glironia* is basically similar to those observed in arboreal didelphids. The head is well developed and dorso-medially oriented (Fig. 10a), whereas it is more horizontal

and mesially oriented in *Caluromys* and *Caluromysiops* (Fig. 10c). The femoral head in *Glironia* and *Caluromys* shows a lateral and posterior extension, whereas it is spherical and mesially oriented in the terrestrial *Metachirus*. The neck is short (Figs 10a–b), being longer compared with *Metachirus*. A notable protuberance (called femoral paratrochanteric crest; Fig. 10a) is present between the well developed trochanteric fossa and the femoral head. The greater trochanter is not well developed, reaching almost the level of the head, as in *Caluromys* and *Caluromysiops* (Figs 10a–d), while it clearly surpasses the femoral head in *Metachirus* (see Flores 2009: fig. 27). The lesser trochanter is well developed, almost aligned to the sagittal plane of the femur (Fig. 10b). In terrestrial forms as *Metachirus*, *Lestodelphys* or *Monodelphis*, the lesser trochanter is smaller and more caudally oriented.

On the distal epiphysis of the femur of *Glironia*, the lateral condyle is cranio-caudally compressed, conical-shaped, with a remarkable lateral extension (Fig. 10b), which is not observed in other analyzed taxa. The lateral condyle is notably broader than the mesial one and distally extended at the same level (Fig. 10b), whereas in *Caluromysiops* the mesial condyle is more distally projected (Figs 10c–d). The difference in size of both condyles is greater in caluromyines and *Micoureus* than in some terrestrial and generalized didelphines, such as *Metachirus*, *Didelphis*, and *Philander*. The posterior surface of the mesial condyle is concave, and separated from the lateral one by a broad and shallow intercondyloid fossa (Fig. 10b), which is narrower in *Metachirus*. The femoral or trochlear groove for the M. quadriceps femoris is wide and flat in *G. venusta* (Fig. 10a) and

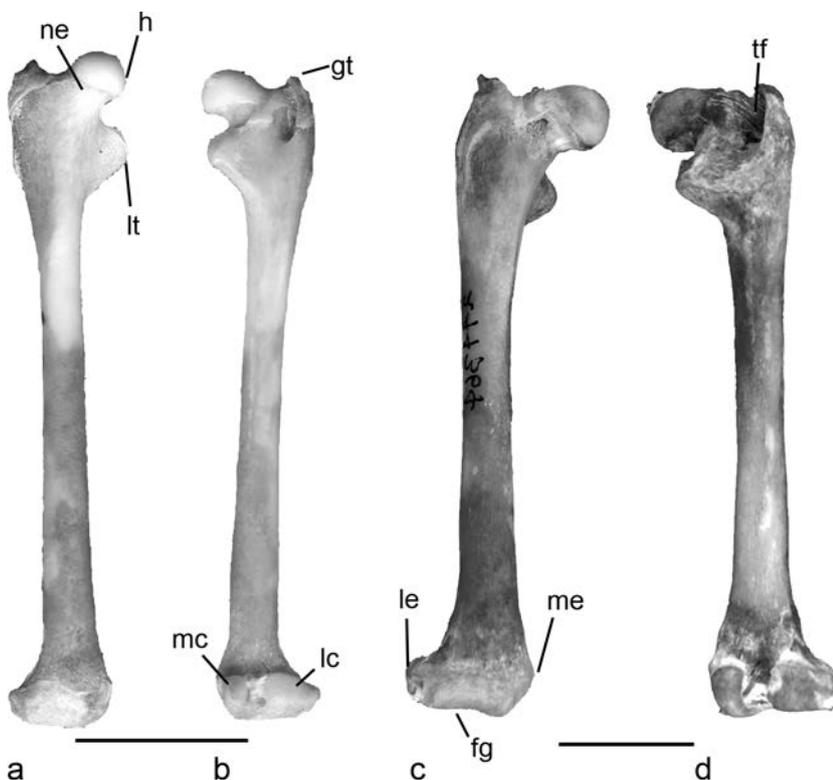


Figure 10. Right femur of *Glironia venusta* MMD 607 (a–b) and *Caluromysiops irrupta* AMNH 244364 (c–d). **a, c.** Anterior view; **b, d.** Posterior view. **fg** – femoral groove for *quadriceps femoris*; **gt** – greater trochanter; **h** – head; **lc** – lateral condyle; **le** – lateral epicondyle; **lt** – lesser trochanter; **mc** – medial condyle; **me** – medial epicondyle; **ne** – neck; **tf** – trochanteric fossa. Scale bars: 10 mm.

Micoureus, whereas it is slightly concave in *Caluromys* and *Caluromysiops* (Fig. 10c), and narrow and concave in the terrestrials *Metachirus* and *Monodelphis*.

Fibular fabella. The fabella or parafibula (Szalay & Sargis 2001) is an ossification fixed on the proximolateral surface of the fibula. In *Glironia*, it is basically similar to all analyzed taxa: the distal tip, which articulates to the fibula, is wider and flattened, and the proximal tip is thinner and curved. However, the fabella of *G. venusta* shows the proximal tip rounded with a strong ventral curvature, compared to the oval shape and less curved structure observed in *Caluromys* and *Caluromysiops*.

Tibia and fibula. In *Glironia venusta*, both bones contact only at the proximal and distal sections, with the epiphyses broadly separated, as in *Caluromys* and *Caluromysiops*; while in *Metachirus* both bones are contacting in about 1/3 of its length. In *G. venusta*, the tibia is shorter than the femur. This condition is unique among didelphids analyzed, since it was evidenced only in some Australasian groups such as *Vombatus*, *Phascolarctos*, *Phalanger*, and *Pseudochirops* (Horovitz & Sanchez-Villagra 2003), and the fossils *Mayulestes* (Argot 2002) and *Thylacoleo* (Finch & Freedman 1988) among marsupials. The tibia of *G. venusta* (Fig. 11a) is sigmoid shape in anterior view and laterally convex, as in all taxa analyzed, although in *Chironectes* or *Tlacuatzin* it is strongly sigmoid (see Flores 2009: fig. 28). The lateral condyle is extended caudally, convex, and wider than the concave medial condyle (Fig. 11a). A small posterior extension on the caudal side of the lateral condyle is observed, which is more developed in *Metachirus* but absent in *Micoureus*. Below the mesial condyle, there is a shallow fossa proximally restricted (Fig. 11a), which is deeper and more extended distally in *Philander* (Fig. 11b), *Micoureus*, *Caluromys*, and

Caluromysiops. The tibial lateral intercondylar tubercle is evident, but less developed than *Metachirus*. The cranial intercondylar area is concave and shallow, with a well developed intercondyloid eminence (Fig. 11a), similar to *Caluromys* and *Caluromysiops*. The polieptal notch of *G. venusta* is wide, with a shallow fossa below (Fig. 11a), as in arboreal forms, whereas in *Metachirus* and *Philander* (Fig. 11b) it is narrow with a deeper fossa. The tibial tuberosity is anteriorly flattened as in other arboreal didelphids, whereas in *Metachirus* it is cranially prominent. The distally extended anterior tibial crest is convex and relatively wider proximally, and distally thinner and sharp, as in *Micoureus*. Alternatively, the crest is wide but not sharp in *Caluromys* and *Caluromysiops*, being more distally extended compared with *G. venusta*. On the posterior side, the crest for the insertion of the M. flexor digitorum tibialis is poorly developed if compared with *Hyladelphys*, *Marmosops* or *Lestodelphys* (Flores 2009: fig. 29). Lateral to this crest, the extensive area for origin of the M. tibialis anterior is remarkable.

On the tibial distal epiphysis of *Glironia*, the area of contact between tibia and astragalus is broad. The medial malleolus is the most prominent structure on the distal portion of the tibia, being similarly developed in other caluromyines, but not as *Metachirus*. The lateral astragalotibial facet is flat, elongated and crescent shape, caudally contacting with the well developed posterior astragalotibial facet, which is located between the lateral astragalotibial facet and the tibial medial malleolus, on the inner side of the medial malleolus. This facet is also flat and craniocaudally shorter than the lateral one. Contrasting with *Metachirus*, the sulcus between the lateral and medial facets is absent in *G. venusta*.

The fibula of *Glironia* articulates with the tibia, femur, and the fibular fabella. It is thinner than the tibia, cylindrical in transverse plane, and slightly curved near the proximal tip. The curvature is more pronounced in *Micoureus*, whereas the diaphysis is almost straight in *Caluromys* and *Caluromysiops*. The proximal tip is compressed and the head is cranio-caudally well developed in *G. venusta* (Fig. 12), as in all analyzed taxa. However, the cranio-caudal extension of the fibular head is proportionally lesser in *G. venusta* than in *Caluromys*, *Caluromysiops*, and *Micoureus*, but greater if compared with terrestrial forms as *Metachirus*, *Lestodelphys*, and *Monodelphis*. The lateral side of the fibular head (Fig. 12a) is slightly concave, as in most analyzed taxa, except *Metachirus*, where it is strongly concave. On mesial side (Fig. 12b), the fibular head is plane and without crests, whereas two crests are evidenced in *Metachirus* (one below the femoro-fibular facet and other below the parafibular facet). The parafibular facet of *G. venusta* is well developed, oval shape, flattened, and almost vertically oriented in sagittal plane (Fig. 12a). This is a common pattern observed in arboreal forms, whereas it is rounded in *Didelphis* and strongly rounded and concave in *Metachirus*. Below the

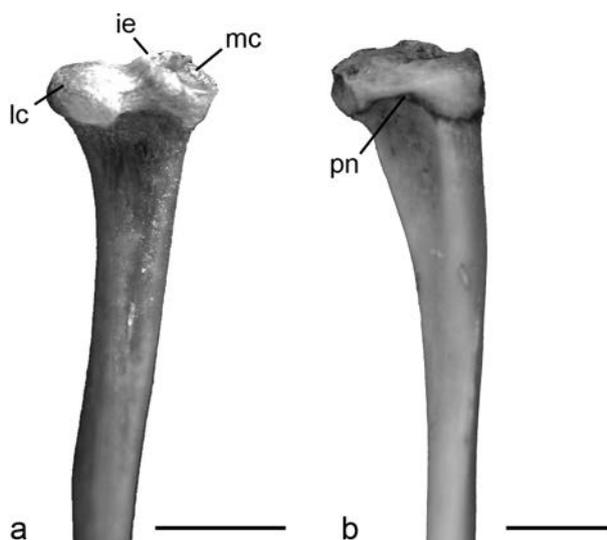


Figure 11. Caudal view of left tibia of *Glironia venusta* MMD 607 (a) and *Philander opossum* AMNH 190446 (b). **ie** – intercondyloid eminence; **lc** – lateral condyle; **mc** – medial condyle; **pn** – polieptal notch. Scale bars: 5 mm.

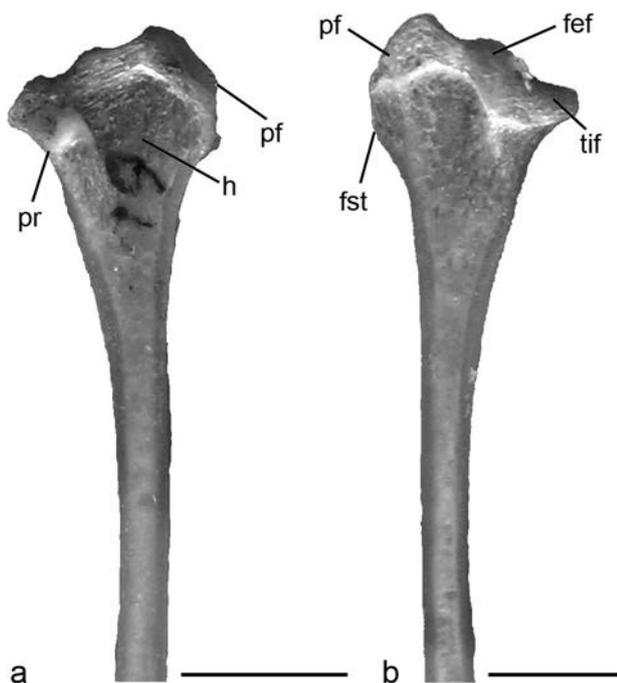


Figure 12. Fibula of *Glironia venusta* MMD 607. **a.** Lateral view; **b.** Mesial view. **fef** – femorofibular facet; **fst** – fibular soleus tuberosity; **h** – head; **pf** – parafibular facet; **pr** – process; **tif** – tibiofibular facet. Scale bars: 5mm.

parafibular facet, a fairly developed fibular soleus tuberosity is present (Fig. 12b), as in *Caluromys* and *Caluromysiops*. This tuberosity is laterally extended in *Metachirus*, whereas the extension is caudally oriented in *Micoureus*. The tibiofibular facet is concave and the femorofibular facet is convex and mesially slender in *G. venusta* (Fig. 12b); both facets are well differentiated, mesially oriented, and separated from the parafibular facet by a small groove (Fig. 12b). *Caluromys* and *Caluromysiops* exhibit a similar morphology, but in *Micoureus* these are smaller and widely separated from the parafibular facet. Below the tibiofibular facet, on lateral side, a notorious process is present in *G. venusta* (Fig. 12a), also well developed in *Micoureus* and *Metachirus*. At the distal epiphysis of the fibula, the astragalofibular facet is slightly concave and well developed. On the posterolateral portion of the fibula a deep groove for extensors muscles is present (see Szalay 1994).

Astragalus, calcaneus and foot. The astragalus of *Glironia venusta* basically shows a similar pattern to that of *Caluromys*. In dorsal view, the lateral astragalotibial facet is wider than the medial astragalotibial facet, forming an obtuse angle (Fig. 13a). A thin ridge between medial and lateral astragalotibial facets is present, but absent between the lateral astragalotibial and astragalofibular facets (Fig. 13a), being better defined in *Metachirus*. The astragalofibular facet is well developed in *G. venusta* (but lesser than the lateral astragalotibial), which reveals the wide contact between fibula and astragalus. A relatively deep fossa is observed between

the medial astragalotibial and the astragalonavicular facets (Fig. 13a). In plantar view, the tip of the astragal medial plantar tuberosity is well developed and mesially extended beyond the level of the astragalonavicular facet (Fig. 13b), unlike *Caluromys*, where the tuberosity is not mesially extended. The astragalonavicular facet is transversally wide in distal view, although not laterally extended beyond the calcaneoastragal facet (Fig. 13b). The sulcus astragali is shallow and located between the calcaneoastragal and sustentacular facets, being continuous with a deep fossa, mesial to the sustentacular facet (Fig. 13b). The sustentacular facet is oval shape and slightly convex, while the calcaneoastragal facet is concave and transversally developed. In *G. venusta*, the astragalonavicular and sustentacular facets are contacting (Fig. 13b), as in *Caluromys* and *Caluromysiops*.

In the calcaneus, the tuber represents approximately 40% of its total length; it is laterally compressed, straight, and the distal tip is slightly mesially oriented. The tuber is relatively more compressed in *Caluromys* and *Micoureus*, while it is almost straight and cylindrical in *Caluromysiops*. The calcaneoastragal facet is convex and transversally wider than the sustentacular one, as in *Caluromys* and *Caluromysiops*, while both facets are similarly developed in *Metachirus* and *Monodelphis*. The facet for the calcaneofibular ligament is well developed, and the calcaneofibular facet is absent, which is also observed in *Caluromys* and *Caluromysiops*. On the other hand, in some terrestrial and generalized forms as *Metachirus*, *Philander*, or *Didelphis*, this facet is secondary acquired (Szalay 1994). The sustentacular facet is more cranially placed than the calcaneo-astragal one; its proximal half is slightly concave and oval shaped, whereas the distal half is narrower and mesially faced. Unlike *Caluromys* and *Caluromysiops*, the different size between both facets is not so emphasized in *G. venusta*. Although the sulcus calcanei is present, the separation between both facets is not especially clear. The peroneal process is well developed in *G. venusta*, as in other arboreal taxa. The groove for

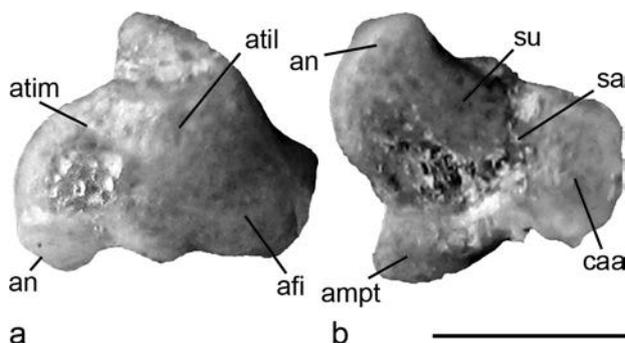


Figure 13. Astragalus of *Glironia venusta* MMD 607. **a.** Dorsal view; **b.** Plantar view. **afi** – astragalofibular facet; **ampt** – astragal medial plantar tuberosity; **an** – astragalonavicular facet; **atil** – lateral astragalotibial facet; **atim** – medial astragalotibial facet; **caa** – calcaneoastragal facet; **sa** – sulcus astragali; **su** – sustentacular facet. Scale bar: 3 mm.

the tendon of the *M. peroneus longus* is terminal and deep, as in *Caluromys* and *Caluromysiops*, whereas it is proximally located in *Didelphis* or *Philander*. In all analyzed taxa, the calcaneocuboid facet is subdivided in a distal and proximal portion, both slightly flat. The distal portion is semicircular and the proximal one is proximally projecting, conical, and articulated to the projecting conical facet of the cuboid, as described by Szalay (1994) for *Caluromys*. According to Argot (2002), the calcaneum-cuboid contact is a derived condition in didelphids.

The cuboid is a robust bone in *Glironia*, slightly wider than the navicular in dorsal view (Fig. 14), whereas in *Caluromys* and *Micoureus* both bones are about the same size. The more evident feature of the cuboid is the cuboidal proximal process, which determines two facets, the proximal and distal calcaneocuboid facets (see Szalay 1994: figs 7–3). This process is well developed in *Glironia*, *Caluromys*, *Caluromysiops*, and *Micoureus*, but thinner in *Metachirus*. The sulcus for the tendon of the *M. peroneus longus* is deep, latero-plantar and transversally located, while in *Metachirus* it is plantar, superficial, and oblique. The cuboid-ectocuneiform facet is larger than the cuboid-navicular facet (Fig. 14). The mesial border of the cuboid of *Glironia* is less concave compared with those of *Caluromys* or *Micoureus*, where the proximal portion of the border is notably extended behind the ectocuneiform. The articulation with the metatarsals IV and V is concave and stepped (Fig. 14).

The navicular of *Glironia* is cradle shape, and the astragalonavicular facet is the largest structure in the bone, as in arboreal forms (e.g. *Caluromys*, *Caluromysiops*, and *Micoureus*), but in terrestrial and generalized

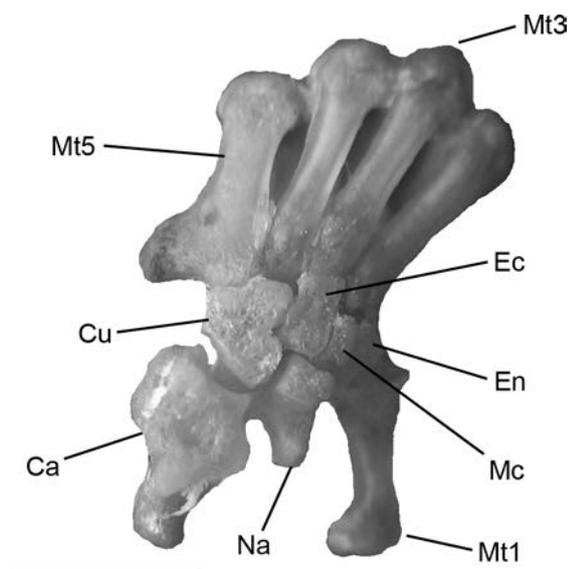


Figure 14. Dorsal view of left tarsus and first metatarsals of *Glironia venusta* MMD 607. **Ca** – calcaneus; **Cu** – cuboid; **Ec** – ectocuneiform; **En** – entocuneiform; **Mc** – mesocuneiform; **Mt1** – first metatarsus; **Mt3** – third metatarsus; **Mt5** – fifth metatarsus; **Na** – navicular. Scale bar: 5 mm.

taxa (e.g. *Metachirus*, *Philander*, *Didelphis*), it is laterally broader and proximally extended. Laterally, it articulates with the cuboid through a slightly concave facet (Fig. 14). The articulation with the ectocuneiform is small, convex, with latero-distal position (Fig. 14). The navicular-mesocuneiform facet is slightly concave and distal, and the navicular-entocuneiform facet is mesial and larger than the ecto- and mesocuneiform facets.

In dorsal view, the ectocuneiform is rectangular shape and distally extended beyond the other cuneiform bones, articulating to the metatarsal III (Fig. 14). This morphology is similar to that of *Philander*, while the ectocuneiform is square shape in *Caluromys* and *Micoureus*. The articulation with the cuboid is split in a concave distal and proximal facet, the latter with a well developed projection, latero-plantar oriented. Mesially, it articulates proximally with the mesocuneiform and distally with the metatarsal III (Fig. 14).

The mesocuneiform is the smallest bone of the foot, located in a central area. It articulates laterally with the ectocuneiform through a concave facet, and mesially with the entocuneiform through a flat facet (Fig. 14). The facet contacting the navicular is slightly convex, whereas that for the metatarsal II is concave with a small mesial projection, distally oriented. This projection is similarly developed in *Caluromys*, *Caluromysiops*, and *Micoureus*, but well marked in generalized forms as *Philander* or *Didelphis*.

The entocuneiform of *Glironia* (Fig. 14) is a strong bone, anteroposteriorly elongated, displaying a singular morphology. Laterally, it exhibits two contiguous facets: the entocuneiform-mesocuneiform, flat and larger (slightly visible also in mesial view), and the entocuneiform-metacarpal II, which is concave and very small. Mesially, there is a slightly concave facet articulating with the navicular, and a very small facet articulating with the reduced prehallux, which according to Szalay (1994) is not a true facet. Distally, a wider and saddle shape facet contacting the metatarsal I is present, subdivided by a very low ridge in a larger lateral portion and a smaller mesial one.

In *Glironia*, as in *Caluromys* and *Caluromysiops*, the metatarsals I and V are more robust compared with other elements, being concaves, broad, and with well developed heads (Fig. 14). In contrast, both bones are straight and relatively longer in the terrestrial *Metachirus*. The lateral process of the metatarsal V is prominent (Fig. 14), more anteroposteriorly expanded if compared with *Micoureus*, and well separated from the proximal facet which articulates the cuboid. Alternatively, the process is proximally developed in *Metachirus*, and the facet contacting the cuboid is slightly extended on the internal side of the process. The metatarsal I is mesially oriented in *G. venusta* (Fig. 14), with the proximal epiphysis (in the conarticular surface of the entocuneiform-metatarsal I) globular, with a conspicuous ridge subdividing a well developed lateral facet and a smaller mesial one. The proximal phalanges are long and curved, with the phalanx of the third digit

as long as the metatarsal. The proximal facets, articulating the metatarsals, are transversely wider. The medial phalanges represent almost two-thirds of the length of the proximal ones, and the ungual phalanges are robust and long, with the proximal articular facet dorsoventrally deep.

Discussion

Regarding to other didelphid species the postcranial morphology of *Glironia venusta* shows different and similar characters and a few autapomorphies (see Flores 2009). Although according to several authors *G. venusta* is mostly arboreal (e.g. Marshall 1978; Redford & Eisenberg 1989; Emmons & Feer 1990), this supposition is certainly an extrapolation from other closely related groups (principally *Caluromys*, see Rasmussen 1990; Lemelin 1999), since direct studies on locomotory habits or substrate use were not performed in *G. venusta* to date. However, alternative neotropical marsupials, which were well-studied in this sense, show different patterns of substrate preferences and locomotion (e.g. *Caluromys* [Rasmussen 1990; Lemelin 1999]; *Monodelphis* [Pridmore 1992]; *Dromiciops* [Pridmore 1994]; *Didelphis* [Jenkins 1971]). Even when part of the postcranial morphology of *G. venusta* is consistent with high capacity for arboreal locomotion, our results indicate that its skeletal pattern is better adjusted for a fast generalist in the use of substrate. This is also supported by records of captured specimens of the species in the forest canopy (Emmons & Feer 1990) as well as on the ground (Bernardé & Rocha 2003; Díaz & Willig 2004; Santos Filho et al. 2007).

Below, we discuss the postcranial morphology of *Glironia* in a comparative and functional framework, essential to determine precise locomotory specializations of this uncommon species. With respect to tarsal bones, the topics discussed are complementary to the extensive analysis for the didelphid tarsal morphology performed by Szalay (1994), and Szalay & Sargis (2001).

Functional Morphology of the Vertebral Features

The similar cranio-caudal extension of the transverse process with respect to the cranio-caudal extension of the hemal arches in the atlas of *Glironia*, have functional significance since origin and insertion of important muscles involved in head movements (as *Mm. obliquus capitis caudalis*, *splenius* and *rectus capitis dorsalis minor*), are related with the transverse process and the dorsal portion of hemal arches of the atlas (Coues 1869; Filan 1990; Evans 1993; Argot 2003). In this way, the little cranio-caudal development of the transverse process in the atlas of *G. venusta* (as in most didelphids, except *Didelphis* and *Philander*; see also Flores 2009) indicates some limitation of power in some head movements. In addition, the weakly developed ventral tubercle of the atlas (Figs 1a–b), limits

the strength of neck flexion in sagittal plane, since muscles associated to this movement (e.g. *Mm. longus colli* and *longus capitis*) are inserted in this structure (see Evans 1993: figs 6–31; Argot 2003). However, according to the observations in tupaiids of Sargis (2001a, 2001b), a proportionally short atlas (as observed in *G. venusta*) is associated with a freest capacity of movement in this section of the neck. In addition, the slightly curved dorsal portion of the cranial facets (Fig. 1a) permits wider range of movement in the atlas-occipital articulation.

On the axis, the cranial extension of the spinous process (Fig. 2a) restricts neck mobility, by the contact between this extension and the atlas (Sargis 2001a). However, the spinous process is also caudally extended in *G. venusta* (Figs 2a–c), as in the remaining analyzed groups (except for *Didelphis*; see Coues 1869: fig. 13; Flores 2009: fig. 1). This pattern is directly associated with head movements, as important muscles implied in such function (e.g. *Mm. rectus capitis posterior*, *obliquus capitis caudalis* and *spinalis capitis*), originates on the axis spinous process (Coues 1869; Evans 1993; Filan 1990; Sargis 2001a; Muizon & Argot 2003). According to some authors (e.g. Finch & Freedman 1986; Muizon 1998; Muizon & Argot 2003), the development of the occipital crest in the skull, and the caudal extension of the axis spinous process, indicates strong neck musculatures, which were related with predaceous habits in some fossils marsupials.

The spinous process of the posterior cervical vertebrae provides attachment for deep musculature of the neck, such as *Mm. spinalis cervicis* and *multifidus cervicis* (Mann Fisher 1956; Finch & Freedman 1986; Evans 1993; Argot 2003; Flores 2009). In this sense, the weak development of the spinous process on medial and posterior cervical vertebrae (Fig. 3a) in *G. venusta*, restricts the area for attachment for part of deep musculature. Similarly, the small anterior head of the transverse process (Figs 3a–c), indicates a limited strength of neck movements, since on that process originate muscles essential for neck flexion too (i.e. *Mm. longus colli* [pars cervicalis], *longissimus cervicis*, *intertransversarii dorsalis cervicis*, and *intertransversarii ventralis cervicis*; see Evans 1993: figs 6–28, 6–30; Argot 2003: fig. 4a; Flores 2009: figs 2–4). According to Argot (2003), the C7 transverse process of some taxa (as *Metachirus*) is cranially oriented. However, our observations in *G. venusta* also indicate ventro-lateral orientation of C7 transverse process (Fig. 3c), where inserts the *M. ilio-costalis thoracis*.

The muscular system affecting the first two thoracic vertebrae is complex, because nuchal musculature and *M. splenius* attach in this region (Mann Fisher 1956; Finch & Freedman 1986; Filan 1990). The slightly lower size of the spinous process in the first thoracic vertebra of *Glironia* (Fig. 3a), a condition strongly marked in some species of *Monodelphis* (Flores 2009: fig. 3), affects the area for origin of the *M. splenius*, implicated in the support and movements of the head (see Slijper

1946; Finch & Freedman 1986; Evans 1993; Argot 2003: fig. 4a). In this way, the morphological pattern of cervical and anterior thoracic vertebrae evidenced in *G. venusta*, shows a combination of features that functionally allow a quick and agile head movements and neck flexion (i.e. the proportionally low cranio-caudal extension of the dorsal part of the hemal arches of the atlas, the dorsal part of the cranial facets slightly curved, and caudal extension of the axis spinous process), and other conditions that indicate limitation of the capacity for some neck and head movements (i.e. the scarce development of the atlas ventral tubercle, low C3 spinous process, posterior cervical vertebrae with the anterior head of transverse process absent, and low spinous process on T1).

Caudally, the mammillary process of the thoracic vertebrae of *Glironia* becomes more developed (Fig. 4), starting from the diaphragmatic vertebra. It represents a transitional point in the column, where the articulation displays a different articular mode, and therefore functionally distinct (Argot 2003). Posterior to this, the thoracic elements are morphologically lumbar-like (Fig. 4). From this point the contact between facets become oblique, reducing the lateral bending and the long-axis rotation of the vertebral column (Pridmore 1992; Shapiro & Jungers 1994; Flores 2009). The oblique orientation of the facets in postdiaphragmatic vertebrae (Fig. 4) permits sagittal flexion-extension of the spine, being restrictive for lateral bending (Rockwell et al. 1938; Washburn & Buettner-Janush 1952). Contrarily, the horizontal orientation of the zygapophysis in the anterior trunk (Fig. 4) allows the lateral bending, but is restrictive respect to sagittal movements. On the mammillary process of the diaphragmatic and post-diaphragmatic vertebrae originate tendons for the *Mm. longissimus dorsi* (the powerful extensor of the back, see Argot 2003), and *multifidus thoracis*, which together with others dorsal back muscles, fixes the vertebral column, especially in bilateral action (see Evans 1993: fig. 6–30). In consequence, the position of the diaphragmatic vertebra has important functional significances (Flores 2009). As in terrestrial forms (e.g. *Metachirus*), the diaphragmatic vertebra of *G. venusta* is anteriorly located, which implies an anteriormost point for the origin of the *M. multifidus thoracis* and sagittal mobility, although from the diaphragmatic vertebra the spinous process become shorter and cranio-caudally expanded, restricting the spinal mobility (Gambaryan 1974; Sargis 2001a). Nevertheless, the sagittal mobility of the spine is still highly viable in *G. venusta*, because a wide space between lumbar and posterior thoracic vertebrae is noteworthy in dorsal view (Fig. 5b), which is absent in *Caluromys* and *Caluromysiops*, but present in most of the mouse opossums. Although there are no studies of trunk movements or gait selection during locomotion in *G. venusta*, its spinal morphology suggests in a general sense, the option of both kind of movements (i.e. lateral and sagittal) during the different phases of locomotion.

For some authors (e.g. Slijper 1946; Mann Fisher 1953; Shapiro 1995; Muizon & Argot 2003; Kurz 2005), the anticlinal vertebra is the element in which the spinous process reverses from posterior to anterior orientation, product of the tractions exerted for the common epaxial musculature. This pattern is part of a functional complex that allows the sagittal flexibility required for quadrupedal locomotion (Rockwell et al. 1938; Slijper 1946; Howell 1965; Shapiro 1995). According to Argot (2003), there is no anticlinal vertebra in *Caluromys* and *Philander*, because the orientation of the spinous process does not reverse; a common pattern evidenced in most didelphines (except in *Metachirus*, Flores 2009). However, and following the criterion of Evans (1993), we consider the anticlinal vertebra as the element in which the spinous process is almost perpendicular to the long axis of the vertebral body. In this way, an anticlinal vertebra is present in caluromyines (also indicated by Kurz (2005) for *Caluromys*). In *Glironia*, the spinous processes of the first lumbar vertebrae are caudally oriented, becoming posteriorly stronger, taller, and slightly cranially oriented (L4 is identified here as the anticlinal element; Figs 5a, c). Such changes in orientation are functionally significant, since the cranial orientation favors extension of the spine, whereas caudal orientation favors its rotation (Curtis 1995). The anterior location of the anticlinal vertebra in *Metachirus*, with respect to *Glironia*, *Caluromys* and *Caluromysiops*, allows an increased power of epaxial musculature, as consequence of changes in position of the muscular insertion on the apex of the spinous process (Muizon 1998; Muizon & Argot 2003). On the other hand, the posterior location of the anticlinal vertebra in caluromyines, suggest a more scansorial-arboreal locomotion (Kurz 2005), which is coherent with the fragmentary knowledge of the habits of *G. venusta* (Marshall 1978; Emmons & Feer 1990). Furthermore, the well developed spinous process in lumbar vertebrae of *G. venusta* (Figs 5a, c), *Caluromys* (Fig. 5d) and *Caluromysiops*, act as levers for the vertebral extensor muscles, as *Mm. multifidus* and *semispinalis dorsi* (Le Gros Clark 1924, 1926; Shapiro 1993, 1995; Sargis 2001a).

On lumbar and posterior thoracic sections, the accessory process become more evident (Figs 4, 5a), causing restriction for lateral movements, because the processes protrude posteriorly and partially lock the articulation with the next vertebra. We assume that *Glironia venusta* exhibit a less marked restriction for lateral movements if compared with *Caluromys* and *Caluromysiops*, because the lesser development of accessory processes on posterior lumbar elements (Fig. 5a).

The transverse processes on the lumbar vertebrae are well developed, cranially and ventrally oriented (Figs 5a–c), but not extending beyond the vertebral body. The morphology of lumbar transverse process is associated with the ventral flexion of the column and body posture: a notable ventral extension indicates powerful sagittal extension/flexion of the spine (Johnson & Shapiro 1998; Shapiro 1995; Shapiro et al. 2005; Flores

2009), since it improves the mechanical advantage of spinal flexor muscles (i.e. Mm. psoas major and quadratus lumborum), which attach in the ventral surface of the transverse processes (Gambaryan 1974; Stein 1981; Currey 1984; Shapiro 1995; Sargis 2001a). Furthermore, the ventral extension of the transverse process in lumbar vertebrae, increase the space for the attachment of erector spinae muscles, which extend the vertebral column (Sanders & Bodenbender 1994; Shapiro 1995; Sargis 2001b). On the other hand, the transverse process cranially oriented in *Glironia* (Figs 5b, e), improve the leverage for lateral flexion (Gambaryan 1974), and the leverage for spinal extensor muscles, which attach on its dorsal surfaces (Sanders & Bodenbender 1994; Sanders 1995). Among living didelphids, *Metachirus* is the only taxon with extremely developed transverse process, because its saltatorial locomotion habits (Grand 1983; Muizon & Argot 2003; Flores 2009: fig. 7), although other taxa as *Lutreolina* and *Chironectes* show large transverse processes as well. However, the morphology of the lumbar vertebrae of *G. venusta* is consistent with high capacity for flexion and extension of the column. Additionally, the flexion of the spine in this species is facilitated by the low rigidity of the rib cage, since the ribs does not show the cranio-caudal extension observed in *Caluromys* and *Caluromysiops* (Figs 3a–c; see discussion below). According to Vázquez Molinero et al. (2001), the characteristic flexion of the vertebral column, as observed in small therian taxa of Didelphidae and Tupaiidae (e.g. Jenkins 1974; Sargis 2001a) may have been retained from an ancestral therian mode of locomotion, since it was detected in the jurassic *Henkelotherium*.

The structure of caudal vertebrae in small mammals reflects types of dynamic use; prehensile tails are characterized by short and wide caudal vertebrae (Vázquez Molinero et al. 2001). A tail formed by short vertebrae (as the anterior caudal elements in *Glironia*) is able to fix the tail efficiently around a substrate, and the width and robusticity of the caudal vertebrae provide a larger area for the insertions of the Mm. sacrococcygei as flexors and extensors of the tail. On the anterior caudal vertebrae, the transverse process form a strong structure that protrudes laterally and expand cranio-caudally (Fig. 5b), where insert the Mm. ischio-caudalis and abductor caudae dorsalis (Argot 2003), which move the tail in transverse plane. Furthermore, some muscles related with hindlimb movements (i.e. Mm. caudofemoralis, femoro-coccygus, and semitendinosus caput dorsalis) are originated on the transverse processes of the anterior caudal elements. The absence of spinous process on the anterior caudal vertebrae (Fig. 5c) indicates a restricted capacity for vertical movements of the tail. In this sense, the morphology of the anterior caudal vertebrae of *Glironia* is associated to high mobility of the tail in lateral plane and limited movements in vertical plane.

The two types of caudal articulation found in *Glironia* (see Fig. 5c), are product of morphological modifi-

cations in the vertebral body (i.e. the vertebrae become long, slender, with reduced apophysis). The articulation through intervertebral discs increases the flexibility of the middle and posterior portion of the tail (Argot 2003). In *G. venusta*, the presence of this articulation among caudal vertebrae 4–5 (Fig. 5c) increases the flexibility in an anterior position, compared with *Caluromys* and *Caluromysiops*. In this way, the tail of *G. venusta* shows high capacity for lateral movements, and high faculty for flexibility, which allows a significant competence for tail prehensility.

Functional Morphology of the Pectoral Girdle and Forelimb Features

The function of the vertebral column is indirectly influenced by the rib morphology (Jenkins 1970). The cranio-caudal extension of the ribs of *Caluromys* and *Caluromysiops*, reduces the space filled up by intercostal muscles, increasing the rigidity of the rib cage and reducing the flexibility provided by muscles and ligaments (Jenkins 1970, Sargis 2001b; Argot 2003). This morphology was also evidenced in bats, some primates, and arboreal myrmecophagids (Jenkins 1970; MacPhee & Jacobs 1986; Gebo 1989). Jenkins (1970) concludes that the cranio-caudally expanded ribs increase the stability in the rib cage, and the vertebral column as whole, connecting forequarters and hindquarters. In some medium sized taxa as *Caluromys* and *Caluromysiops*, this stability is necessary during arboreal locomotion (see Flores 2009: fig. 5). However, in *Glironia* and other arboreal opossums (e.g. *Micoureus*) this pattern is absent (Figs 3a–c, 4). Although *G. venusta* presents several arboreal attributes in its skeletal morphology, the different configuration of the ribs compared with *Caluromys* and *Caluromysiops*, likely is a consequence of their lesser body size and weight. The short and robust first pair of ribs of *G. venusta* (Figs 3a–c), as in the remaining taxa analyzed, develops a particularly strong connection with the sternal complex (Klima 1987). Some important muscles (e.g. Mm. pectoralis, scalenus, subclavius, and serratus ventralis thorcis) implied in the support of the head and forequarters, and transmission of forces between forelimb and trunk (Argot 2003), are inserted on the anterior section of the first pair of ribs (Bezuidenhout & Evans 2005), which supports high mechanical demands.

The morphology of the breast-shoulder apparatus evidenced in *Glironia* is similarly arranged as the general pattern described by Klima (1987) for adult marsupials (i.e. scapula and sternum connected via clavicle). On the sternum, the well keeled manubrium and the laterally compressed sternbrae post-manubrium of *Caluromys* and *Caluromysiops*, suggests important function of the M. pectoralis (Cheng 1955; Jenkins & Weijs 1979; Argot 2003), which move the trunk cranially over the advanced limb, and extend the shoulder joint during locomotion (Evans 1993; Bezuidenhout & Evans 2005). The weakly keeled manubrium and the flattened ster-

nebrae in *G. venusta*, likely is indicative of the lesser development of the M. pectoralis, and consequently a proportionally reduced power of those trunk movements.

On the scapula, the well developed coracoid process observed in *Glironia* (Fig. 6c) suggests a powerful action of the Mm. coracobrachialis and biceps brachii. The coracobrachialis is involved in the extension and adduction of the shoulder joint (McEvoy 1982; Evans 1993; Sargis 2002a), and according to Argot (2001), its structure is associated to locomotory habits. The functional study of Sargis (2002a) on forelimb morphology in tupaiids, states that a long coracoid process increases the lever arm of the Mm. coracobrachialis and biceps brachii, giving some advantage in adduction during arboreal locomotion. However, although all caluromyines show a well developed coracoid process, this is lesser than *Ptilocercus* or *Tupaia* (see Sargis 2002a: fig. 6). On the other hand, the M. biceps brachii is implied in the flexion of the elbow, and the large coracoid process provides a longer lever arm for it, which is crucial during climbing in arboreal locomotion (Argot 2001; Sargis 2002a).

The scapular caudal angle acute of *Glironia* (Figs 6a–b) and *Caluromys*, is clearly related with active function of some muscles associated to scapular rotation and flexion of the shoulder joint. The Mm. serratus and rhomboideus rotate the scapula such a way that the vertebral border is pulled posteroventrally, and the glenoid cavity is forced craniodorsally, by the action of the M. omotransversarius (Smith & Savage 1956; Taylor 1974; Jenkins & Weijjs 1979; Larson 1993; Argot 2001; Muizon & Argot 2003). Moreover, the caudal angle is part of the attachment of M. teres major (Mann-Fisher 1956; Jenkins 1970; Taylor 1974; Jenkins & Weijjs 1979; Stein 1981), whose function is flexionate the shoulder joint, to move the humerus backward (Taylor 1974; Evans 1993).

The supraspinous fossa (which is well developed in *Glironia*; see fig. 6a) is filled up by the M. supraspinatus (Jenkins & Weijjs 1979), whose origin is on the greater tubercle of the humerus (see Argot 2001: fig 3a; Evans 1993: fig. 6–45). The function of the M. supraspinatus is to extend the shoulder joint for the advancement of the limb, and elevation of the arm (Evans 1993; Larson 1993). Additionally, this muscle is important to stabilize and prevent collapse in the shoulder joint (Goslow et al. 1981), and to absorb part of the kinetic energy generated when the forelimbs contact the substrate at the end of the lips (Smith & Savage 1956; Roberts 1974). According to Endo et al. (1999), a narrow supraspinous fossa is indicative of arboreal habits. However, as is stated by Sargis (2002a), such pattern as an arboreal feature is contradictory with previous evidence, since in terrestrial forms of tupaiids (Sargis 2002a), cercopithecids (Jolly 1967), others eutherians (Smith & Savage 1956; Roberts 1974), and marsupials (Argot 2001) a narrow scapula was observed. Contrarily, a short and wide scapula is observed in slow

climbing and suspensory dermopterans and chiropterans (Simmons 1994). Nonetheless, notably broader scapula in the terrestrial *Metachirus*, probably is associated to the particular mode of locomotion. A wide area for the attachment of the M. supraspinatus, increased in *G. venusta* by a cranial expansion of the supraspinous fossa (as in *Ptilocercus*; see Sargis 2002a), is required for the high demands of this muscle during the arboreal locomotion.

The well developed scapular spine in *Glironia venusta* (Figs 6a, c) indicates the importance of the Mm. omo-transversarius and pars acromialis of the trapezius, since those muscles insert at this area (Jenkins & Weijjs 1979), and exert an anteriorly directed force to move the glenoid cavity craniodorsally, and elevate the limb and draw it forward (Evans 1993; Larson 1993; Argot 2001). In this way, the posterodorsal extension of the caudal angle, the well developed supraspinous fossa and scapular spine, and the well developed coracoid process (all characters present in *G. venusta*), increase the stability of the articulation, which is consistent with an elevated capacity for arboreal locomotion (Muizon 1998; Muizon & Argot 2003). However, according to the model proposed by Argot (2001: fig. 2d), the general shape of the scapula of *G. venusta* is more compatible with generalized forms.

On the humerus, the well developed greater tuberosity (Fig. 7b) is an autapomorphic condition of *Glironia venusta* among didelphids analyzed. The development of the greater tuberosity is related with a better stabilization at the humero-scapular articulation, since in this structure inserts the tendons of the Mm. supraspinatus and infraspinatus. The oval shape of the head and the well developed greater tuberosity are associated to lower capacity for arm rotation (Argot 2001), compared with the arboreal *Caluromys*, *Caluromysiops* and *Micoureus*, where the tuberosity is low and the head is rounded, permitting better rotational movements at the gleno-humeral joint, a pattern detected in other arboreal mammals as well (e.g., Taylor 1974; Szalay & Sargis 2001; Candela & Picasso 2008). The humeral trochlea, capitulum, radial central fossa, and the trochlear notch of the ulna, are structures involved in movements of flexion/extension of the elbow joint (Argot 2001; Muizon & Argot 2003), being indicative of the nature of movement that the limb is able to perform (e.g., Jenkins 1973; Szalay & Sargis 2001; Sargis 2002a). On the distal articular surface of the humerus, the capitulum shape is related to arm movements since distally it lies on the radial central fossa. In *G. venusta*, the globular shape of the capitulum (Fig. 7a) permits free rotational movement on the radial central fossa during pronation-supination of the arm, essential in arboreal locomotion (Sargis 2002a; Candela & Picasso 2008). Additionally, the capitulum proximally extended (Fig. 7a) permits a narrower angle for flexion of the elbow joint. On the well marked lateral extension of the capitulum of *G. venusta* (Fig. 7a), originates the M. supinator brevis (see Argot 2001: figs 4a, 13d),

which inserts on the proximal portion of the anterior side of the radius, and produces the supination of the paw, so the palmar surface faces medially (Evans 1993). Furthermore, the separation between capitulum and trochlea (conformed by a deep “zona conoidea” sensu Candela & Picasso 2008: see figs 7a–b) provides additional joint stability (Jenkins 1973). Therefore, as observed for arboreal erethizontids (Candela & Picasso 2008), the elbow joint of *G. venusta* shows features that permit high capacities for pronation-supination movements and simultaneously provide stability.

In the arm movement, the depth and extension of the olecranon fossa is functionally important for arm extension at the elbow joint. Although the olecranon fossa is not perforated in *Glironia venusta* (as in all living didelphids; Flores 2009), it is relatively deep (Fig. 7a) permitting notable extension of the ulna, as the superior edge of the ulnar trochlear notch contacts the floor of the fossa when the arm is fully extended. A relatively shallower olecranon fossa, as observed in *Caluromysiops* and other arboreal mammals, reflects an incomplete extension of the ulna and limited stability during extension of the antebrachium (Candela & Picasso 2008). This would be associated with a mobile elbow joint and a frequently flexed posture, characteristic of strongly arboreal species (e.g. Argot 2001; Szalay & Sargis 2001; Sargis 2002a; Candela & Picasso 2008). The distal extension of the deltoid crest observed in *G. venusta* (Figs 7a, c), increase the length of the M. deltoideus, emphasizing the function of flexion on the shoulder joint (Jenkins & Weijs 1979; Argot 2001); and also indicates a large M. pectoralis major, which inserts in the medial surface of the crest (McEvoy 1982; Bezuidenhout & Evans 2005), rotating the humerus as it is adducted, and aid to locate the distal part of the forelimb in medial position when the elbow is flexed (McEvoy 1982). Then, functional interpretations associated with length of deltoid crest are complicated by the fact that muscles with different functions insert on it; the deltoid muscle is both a shoulder stabilizer and flexor of the arm and the pectoralis major acts as a limb protractor during locomotion (Elissamburu & Vizcaíno, 2004).

In *Glironia*, the proximal process in the supinator ridge (Figs 7a, c) increases the area for the origin of the Mm. triceps brachii caput laterale and brachioradialis. The former (inserted on the olecranon of the ulna) generates the extension of elbow joint, and the M. brachioradialis (inserted on the distal portion in the medial side of radius) produces the dorsolateral rotation of the arm (Evans 1993). Most muscles moving the wrist and hand originate in the humeral epicondyles (Argot 2001; Muizon & Argot 2003). On the medial epicondyle originates part of the Mm. flexor carpi radialis, flexor digitorum profundus and superficialis (Abdala et al. 2006; Flores 2009); the former inserts in the palmar side of metacarpals II and III, and the others produce the synchronized phalangeal flexion (McEvoy 1982; Abdala et al. 2006; Candela & Picasso 2008). In this

way, the well developed entepicondyle observed in *G. venusta* (Figs 7a–b), and some mouse opossums not strictly arboreal (e.g. *Lestodelphys*, *Marmosa murina*, *Gracilinanus agilis*, Flores 2009) evidences high capacity for hand and wrist movements. However, some mouse opossums not directly associated with arboreal habits (e.g. *Lestodelphys*, *Marmosa murina*, *Gracilinanus agilis*) exhibit this structure highly developed (Flores 2009). Is possible that the arrangement of the M. flexor digitorum superficialis of *G. venusta* looks like the pattern described for *Chironectes* by Stein (1981), i.e. consisting in a short belly with strong insertion through tendons in a pinnate structure, which confers an amount of the force exerted by the muscle. A similar pattern was also reported by Abdala et al. (2006) for *Thylamys*, *Cryptonanus*, *Marmosops*, and some arboreal Australasian marsupials. Lastly, the deep bicipital groove (Fig. 7a) and the large bicipital tuberosity of the radius are indicative of a well-developed M. biceps brachii, deeply implied in pulling the body up when climbing (McEvoy 1982; Argot 2001).

On the well developed crest at the anterior side of the ulna of *Glironia venusta*, originates the Mm. flexor digitorum profundus and pronator quadratus, which are implied in grasp ability and maintaining the integrity of the antebrachium near the carpus. The extended fossa for the exterior ligament is also part of the extensive surface for the origin of the M. flexor digitorum profundus (Muizon & Argot 2003; Abdala et al. 2006). This fossa has been associated with arboreal locomotion, because the role of this muscle for grasping (Muizon & Argot 2003; Abdala et al. 2006; Flores 2009). The short olecranon in the ulna of *G. venusta* (Fig. 8a), *Caluromys* and *Caluromysiops*, shows biomechanics consequences, since a short olecranon generates a reduction of the power, but increment of the speed of movement, which is interpreted as an adaptation for arboreal habits, because the extension of the elbow does not require power but rapidity to grasp a support in arboreal forms (Szalay & Sargis 2001; Sargis 2002a; Muizon & Argot 2003). Furthermore, the cranially curved posterior border of the olecranon in *G. venusta*, could be associated to arboreal habits as well (Walker 1974; Argot 2001), since such curvature is product of combinations of tractions caused by flexors and extensors of the elbow joint, as the M. triceps brachii, whose function is to extend the elbow joint (Evans 1993; Muizon & Argot 2003; see Flores 2009: fig. 19). Additionally, this curvature limits the degree for arm extension and provides the triceps with a mechanical advantage when the forearm is flexed, as observed in others mammals (Argot 2001; Sargis 2002a; Candela & Picasso 2008).

The prominent mesial extension of the greater sigmoid cavity in *Glironia venusta*, (called ulnar coracoid process; see fig. 8a) if compared with terrestrial forms as *Monodelphis* (Fig. 8b), implies higher stability at the elbow joint and ability for arm flexion and pronation-supination movements. In this structure rests the hum-

eral trochlea, and serves like a pivot during the flexion-extension movements on the elbow joint. The wider trochlea-ulnar coronoid process contact seems to have an important function in supporting body weight during the propulsive phase of climbing, and probably it assumes a large load-bearing role during the flexed and abducted forelimb postures used on arboreal substrates (Argot 2001; Sargis 2002a; Candela & Picasso 2008). In this sense, the relatively small radial notch with respect to the well developed ulnar coronoid process of *G. venusta* is consistent with arboreal habits, as evidenced for Hystricognathi rodents (Candela & Picasso 2008) and squirrels (Rose & Chinnery 2004). The longitudinal groove on the lateral surface of the ulna (Fig. 8a) is indicative of strong insertion of the *M. anconeus* (implied in the extension of the elbow joint, Jenkins & Weijs 1979; Evans 1993), as well as origin of the *M. abductor pollicis longus*. According to Argot (2001), this muscle is well developed in arboreal forms. However, some arboreal taxa such as *Caluromys* have not a well developed groove, being deeper in the arboreal *Caluromysiops* and *Marmosops parvidens* (Flores 2009: fig. 19), as well as in the terrestrial *Metachirus* and the swimmer *Chironectes* (Stein 1981).

The radius transversally compressed has been associated with major flexibility for pronation-supination movements (Oxnard 1963; Walker 1974; Argot 2001). In *Glironia*, the slighter compression of the radius (Fig. 9), if compared with *Caluromys* and *Caluromysiops*, seems to prevent certain flexibility in the forearm. However, the thin bony plate posterolaterally extended (Fig. 9), reinforces the wide area for the origin of the flexor *M. digitorum profundus* (Argot 2001), indicating high capacity for grasping, although the development of the radial bony plate in *Glironia* is scarce if compared with those of *Caluromys*, *Caluromysiops* or *Lestodelphys* (Flores 2009: fig. 22). Moreover, the circular shape of the radial central fossa allows potentially a wide range for pronation-supination movements. The radial central fossa antero-posteriorly compressed indicates a more stable radio-capitulum joint and improved capacity for movements along the parasagittal axis, as in scansorial and swimmer forms, and different to the circular shape evidenced in highly arboreal forms (Taylor 1974; MacLeod & Rose 1993; Szalay & Sargis 2001; Rose & Chinnery 2004; Candela & Picasso 2008; Flores 2009). In this sense, the oval shape detected in *Chironectes* (Flores 2009) improves the mobility on parasagittal axis, which could be interpreted as an adaptation to swim. The radial bicipital tuberosity well developed and distally located in *G. venusta* (Fig. 9) is also consistent with arboreal habits (McEvoy 1982; Argot 2001). The distal location improves the mechanical advantage of the biceps brachii, by increasing its lever arm (McEvoy 1982; Candela & Picasso 2008). Thus, the general morphology of the radius in *G. venusta* indicates powerful pronation and supination of the antebrachium, in spite of the slighter compression of the diaphysis, which is functionally optimal to climb.

The anatomy of the mammalian hand is a postcranial skeletal complex informative of locomotor behaviour, and a source of phylogenetic characters (e.g. Horovitz & Sanchez-Villagra 2003; Weisbecker & Sanchez-Villagra 2006; Weisbecker & Archer 2008; Flores 2009). The consideration of the skeletal wrist anatomy related with locomotor habits is supported by a range of comparative and mechanical studies (e.g. Yalden 1972; Stafford & Thorington 1998; Weisbecker & Sanchez-Villagra 2006; Weisbecker & Archer 2008). The carpal bones of *Glironia* exhibit facets that in general allow considerable flexibility on the wrist without any reduction or fusion of bones, different to the limited joint mobility detected in the larger and more derived macropodoids and vombatiforms (Weisbecker & Sanchez-Villagra 2006; Weisbecker & Archer 2008). Although the lunatum is small in some didelphids, it is always present (Flores 2009). The broad facet for articulation between scaphoid and distal epiphysis of the radius observed in *G. venusta* suggest an extensive range for flexion, or possible fully palmigrade position, as observed in *Caluromys* (Argot 2001). The well developed palmar protrusion of the unciform of *Glironia*, *Caluromys*, and *Caluromysiops*, determines the lateral wall of the deep carpal tunnel, where the common tendon of the *M. flexor digitorum profundus* crosses toward the ungual phalanges (Abdala et al. 2006). The length of this process is a measure of digital flexor muscle power, usually well developed in arboreal mammals (Napier 1961; Argot 2001; Weisbecker & Sanchez-Villagra 2006; Weisbecker & Archer 2008). The concave ulnar-cuneiform facet of *Glironia* and most didelphids (see Flores 2009: fig. 30) is not particularly suitable for arboreal locomotion, since it appears obstruct flexibility, and several arboreal mammals (e.g. *Dromiciops gliroides*) display a proximally flattened cuneiform (Yalden 1972; Szalay & Sargis 2001). In the arboreal tree shrew *Ptilocercus*, Stafford & Thorington (1998) found that a cuneiform with a concave facet around the ulna might stabilize this joint during strong ulnar deviation. Cuneiform shape is convergent in macropodoids and vombatiforms, sharing an ulnarly flattened surface of the ulnar-cuneiform facet, probably related to lack of rotational ability (Yalden 1972; Weisbecker & Sanchez-Villagra 2006).

The similar proximal extension of the unciform and magnum in *G. venusta*, also observed for arboreal primates (Jenkins 1981), is significant for the hand ability to perform movements of deviation (Yalden 1972). The unciform is more proximally extended than the magnum in secondarily arboreal diprotodontians, in the terrestrial *Metachirus* among didelphids, and in macropodoids, where the magnum and unciform interlock firmly with the proximal carpal row by several straight articulation surfaces (Weisbecker & Sanchez-Villagra 2006). In *Caluromys* and *Caluromysiops* the *M. abductor pollicis longus* (involved in the abduction and flexion of the first digit) inserts on the lateral depression observed in the trapezium. However, the absence of such depression

in *Glironia* suggests reduced grasping ability compared with other *Caluromyines*. In *Glironia* the deep lateral fossa on the metacarpal V where the tendon of the M. extensor carpi ulnaris inserts (implied in the extension of the carpal joint), the particular shape of the metacarpal V, and the general morphology of metacarpals are also associated with arboreal habits (Argot 2001; Weisbecker & Warton 2006). The wide space among contiguous metacarpals filled up by the M. interossei, is important in the flexion of the metacarpal-phalangeal joints (Young 1879; Evans 1993; Argot 2001) and were related with arboreal locomotion (Argot 2001). However, Weisbecker & Warton (2006) found that metacarpal slenderness is not a good indicator of locomotor habits in diprotodontians marsupials.

The strong convexity of the proximal phalanges and the proximal phalanges as long as metacarpals observed in *Glironia* suggests high ability for arboreal locomotion (e.g. *Caluromys*, Lemelin 1999; Argot 2001; arboreal Primates: Oxnard 1963, Jolly 1967; viverrids: Taylor 1974; australasian marsupials: Weisbecker & Warton 2006). Functionally, wider hands combined with elongated phalanges facilitate grasping during climbing and provide broad circumference of the limbs around large vertical supports (Jolly 1967; Weisbecker & Archer 2008). In addition, the marked medial groove on the palmar surface of proximal phalanges emphasizes the development of the tendons of the M. flexor digitorum profundus. Finally, the small ungual phalanges of *Glironia* shows morphology typically associated with arboreal mode of locomotion. The flexor tubercle on the palmar face notably developed (as in *Caluromys*, *Caluromysiops* and arboreal didelphines), suggests powerful traction exerted by the tendons of the M. flexor digitorum profundus during the grasp.

Functional Morphology of the Pelvic Girdle and Hindlimb Features

The pelvic girdle of *Glironia venusta* does not exhibit noteworthy specializations, although some traits are clearly related with arboreal habits. The acetabulum morphology is highly conservative in most didelphids analyzed (Flores 2009): opened, with the dorsal component of the acetabular fossa not laterally expanded (Figs 5b, c). This morphology improves the flexion of the femur, as it allows a wide range of movements, especially in its abduction (Argot 2002; Muizon & Argot 2003). However, this pattern also generates reduction of the stability of the joint, as stated for *Caluromys* (Muizon & Argot 2003), which suggests slow climbing habits. Among didelphids, only *Metachirus* shows the acetabular fossa with the dorsal portion laterally extended (Argot 2003; Flores 2009), which is a specialized morphology for its cursorsaltatorial mode of locomotion. Whatever, the forelimb mobility is always higher than the hindlimb mobility, because the glenohumeral joint is notably more mobile than the hip joint (Larson et al. 2001; Lammers 2007).

In caudal view, the sharp angle conformed by the two rami of the ischium (as in *Caluromys* and *Caluromysiops*), were associated with higher range for abduction (Jenkins & Camazine 1977), whereas the slightly opened angle observed in *Glironia* suggests some reduction for the range of abduction. The morphology of the distal portion of the ilium is related with movements of the hip joint, as on this area originates the M. glutei and epaxial musculature (Eftman 1929; Smith & Savage 1956; Grand 1983). In *G. venusta*, this section is laterodorsally curved (Fig. 5b), increasing the area for the origin of the aforementioned muscles, conferring stability to the hip joint. The ilium is straight in most didelphid groups, except in *Metachirus* (Argot 2002; Muizon & Argot 2003), *Chironectes* and *Tlacuatzin* (see Flores 2009: fig. 25), where the laterally curved distal portion of the ilium favors the mechanical of the M. glutei (a thigh extensor Smith & Savage 1956), necessary for climbing (*Glironia*), swimming (*Chironectes*) or leaping (*Metachirus*). Indeed, the M. glutei is strongly developed in *Chironectes* (Stein 1981).

In the context of the sample analyzed, the femur longer than tibia is an autapomorphic condition of *Glironia venusta* as this feature was evidenced just in some Australasian and fossil marsupials (see results). In all living neotropical marsupials the tibia is longer than femur (Hershkovitz 1999: tab. 3; Stein 1981: tab. 1). However, Smith & Savage (1956) found similar proportions in large mammals, such as *Rhinoceros*, *Mastodon*, and horses. In marsupials, this condition is associated to slow-medium locomotory habits (Finch & Freedman 1988; Argot 2002), which is consistent with the pelvic morphology exhibited by *G. venusta* (e.g. acetabular fossa opened). In addition, Candela & Picasso (2008) reported the same proportions in arboreal porcupines, showing high variation on the crural index in some rodents, indicating that low values of index correspond to the generalized condition present in arboreal and large terrestrial taxa, while higher values correspond to more cursorial, digging or leaping taxa. According to Stein (1981), the femoral length is also associated with the forces exerted by specific muscles as Mm. vastus internus, vastus externus, and rectus femoris.

On the femur, the cylindrical femoral head, the low greater trochanter, and the well developed lesser trochanter (Figs 10a–b), are characters consistent with arboreal habits as well (Szalay & Sargis 2001; Argot 2002). The last condition reflects the importance of some muscles, such as the iliacus and psoas major, implied in several functions as the flexion of the hip joint, flexion and fixation of the vertebral column (Evans 1993), and external rotation and adduction of the leg (Stein 1981; Muizon & Argot 2003). Although the proximal extension of the greater trochanter does not seem to have relationship with locomotory habits in rodents (Candela & Picasso 2008); the particular extension of this structure in *Metachirus* (see Flores 2009: fig. 27) is clearly related with its leaping mode of loco-

motion. The greater trochanter proximally more projected than the head increases the moment arm and the mechanical advantage of the *M. glutei* (Smith & Savage 1956). Such condition is consistent with a powerful and fast extension of the leg for propulsion during terrestrial locomotion, as found in cursorial Hystricognathi, such as *Agouti*, *Dasyprocta*, *Dolichotis* (Candela & Picasso 2008), and digging caviomorph rodents (Elisamburu & Vizcaino 2004) in which parasagittal movements are emphasized. However, the proximal projection of the greater trochanter also restricts the mobility of the hip joint, limiting the abduction of the femur (emphasized in *Metachirus* by the closed acetabular fossa), as observed in some tupaiids (Sargis 2002b). Alternatively, the slightly projected greater trochanter in most of living didelphids (Flores 2009), allow an improved mobility at the hip joint, especially for abduction of the femur during climbing (McEvoy 1982). As pointed for arboreal viverrids (Taylor 1976), when the *M. glutei* is inserted on a greater trochanter located at the level or distal to the center of rotation, the muscle tend to act as an abductor. Therefore, as detected in erethizontid rodents (Candela & Picasso 2008) it is possible that the relative low position of the greater trochanter in *G. venusta* enhances the abduction function of the *M. glutei* to reach an effective position of the hindlimb during the propulsion phase of climbing (McEvoy 1982).

The robust femoral lesser trochanter almost aligned to the sagittal plane of the femur evidenced in *Glironia* is consistent with the pattern showed in arboreal forms as well. On the lesser trochanter insert the *Mm. iliacus* and *psoas major* (McEvoy 1982; Evans 1993), which acts as flexor, external rotator, and protractor of the femur, producing the recovery phase during the locomotion, when the leg is carried forwards (Elftman 1929); and its mesial position emphasizes the external rotation and flexion functions of the muscles during the recovery phase of climbing in the arboreal substrate (Taylor 1976; McEvoy 1982; Argot 2002; Candela & Picasso 2008). Then, in *G. venusta*, the rotation of the femur is highly viable during locomotion. In terrestrial didelphids (e.g. *Metachirus* or *Monodelphis*), the lesser trochanter is more caudally positioned and smaller suggesting greater speed; this pattern is widely evidenced in an array of mammals with a variety of locomotory modes (Taylor 1976; Szalay & Sargis 2001; Argot 2002; Candela & Picasso 2008). The caudal position of the lesser trochanter indicates an anteroposterior orientation of the fibers of the iliopsoas complex, which act principally as protractor of the femur, facilitating parasagittal movements.

The shape of the femoral distal epiphysis, at the knee joint, indicates the amount and types of movements to which the joint is able to carry out. The distal femoral epiphysis craniocaudally compressed and rectangular shape of *Glironia* (Fig. 10b) is product of the wide and shallow intercondyloid fossa, and the small diameter of the condyles. The shallower distal femoral epiphysis in-

dicates more habitually flexed hindlimb, as observed for other arboreal mammals (Sargis 2002b). Moreover, the posterior orientation of the condylar facets also indicates a usually flexed limb (Argot 2002; Candela & Picasso 2008), which was observed in didelphids (Szalay & Sargis 2001; Argot 2002), viverrids (Taylor 1976), tupaiids (Sargis 2002b), primates (Tardieu 1983), and cavioid rodents (Candela & Picasso 2008), with well developed arboreal habits. The strong asymmetry of both femoral condyles as observed in *G. venusta* (i.e the lateral condyle wider than the medial one; Fig. 10b) has been associated with arboreal habits (Argot 2002), and was also observed in extremely agile arboreal mammals (e.g. *Sciurus*, *Tupaia*). However, such asymmetry is also present in terrestrial didelphids (e.g. *Lestodelphys* and *Metachirus*; Flores 2009), and some terrestrial echimyids (Candela & Picasso 2008). In the arboreal scandentian *Ptilocercus* the medial condyle is slightly wider than the lateral one, while in more terrestrial tupines the lateral condyle is wider than the medial one (Sargis 2002b), this condition was interpreted as reflecting the support of greater loads medially in the knee, during the flexed and abducted hindlimb postures used in arboreal locomotion (Sargis 2002b). This pattern, which is in clear contrast with the asymmetry found in femoral condyles of *G. venusta* and didelphids in general, can be explained in the same way than *Ptilocercus*, but with the lateral side supporting the greater loads. In *Caluromys*, *Caluromysiops* (Figs 10c, d) and other arboreal didelphids (Argot 2002) the more distally projected medial femoral condyle with respect to the lateral condyle favors the stability of the knee joint, precluding dislocation and improving abduction of the thigh while the knee is flexed, and the foot is medially located against the arboreal substrate (McEvoy 1982; Candela & Picasso 2008), but does not preclude the rotational capacity of the tibia in relation to the femur. As indicated for *Trichosurus*, this condition seems to be related to rotational movements of the tibia during climbing (Argot 2002). According to Argot (2002), the external rotation of the tibia during the extension of the leg and its medial rotation during flexion, would occur on a longer trajectory for rotation, provided by the longer medial condyle. In *Glironia* and in terrestrial Hystricognathi (e.g. *Dolichotis*, *Lagostomus*, *Dasyprocta*; Candela & Picasso 2008), the medial and lateral condyles are extended distally to the same level (Fig. 10b), indicating lower capacity for femur abduction. In spite of the asymmetry and morphology of the tibial facets of *Glironia*, rotational movements at the knee joint are still possible, which is also allowed by the low intercondylar tubercles on the tibia (Fig. 11a). Therefore, in *G. venusta*, the similar height of the femoral condyles and the low tibial spines, facilitate the rotational capacity of the tibia. Several characters, such as the morphology of the intercondyloid fossa of the femur, the tibial tuberosity, the femoral groove, and the proximal shape of the anterior tibial crest, are highly related to the function of *M. quadri-*

ceps femoris during the locomotion (Muizon 1998; Szalay & Sargis 2001; Argot 2002). The femoral groove for the *M. quadriceps femoris* (a powerful extensor of the knee) is notably flat in *G. venusta* (Fig. 10a), which is typical of fast running forms, being more concave in slower arboreal species (e.g. *Caluromys* and *Caluromysiops*; see Fig. 10c). This demonstrates that, as stated by Muizon & Argot (2003), the morphology of the femoral distal epiphysis is more related to the activity (slow vs. fast) than behavioral locomotion (terrestrial vs arboreal; Tardieu 1983).

The sigmoid shape of the tibia is a state shared among most didelphids, and according to Szalay & Sargis (2001) it is a plesiomorphic condition in marsupials. Even when the curvature observed in *G. venusta* is less conspicuous than the aquatic *Chironectes* (see Flores 2009: fig. 28), the contact between tibia and fibula is restricted to the proximal and distal portion of the diaphyses, which confers some capacity for rotation between both bones, necessary during arboreal locomotion. However, both bones are provided by strong ligaments that reinforce their interconnection (Stein 1981; Argot 2002). The wide space between tibia and fibula relates to the development of the *M. flexor digitorum fibularis* (Stein 1981), important in arboreal forms, since the digital flexion on the hindlimb is steadily used to force the claws into irregularities in the substrate during climbing and to grasp branches (McEvoy 1982). The weak tibial tuberosity observed in *G. venusta* seems to indicate arboreal habits, since other arboreal caluromyines and didelphines (e.g. *Caluromys*, *Caluromysiops*, *Micoureus*), exhibit this structure flat and not cranially expanded and in terrestrial forms the tuberosity is prominent (Muizon & Argot 2003; Flores 2009). The tendon for the *M. quadriceps femoris* inserts directly on the tibial tuberosity, as the patella is absent in didelphids (Szalay & Sargis 2001; Argot 2002). Equally to the asymmetry exhibited by femoral condyles, the tibial condyles of *G. venusta* show strong asymmetry in shape and size (Fig. 11a). The most pronounced difference between both tibial condyles is observed in *Metachirus* implying increment of the stability on the articulation in the terrestrial form. In this sense, the lesser stabilized joint between femur and tibia of *G. venusta*, permits independent rotation of the tibia in relation to the femur, which is necessary for changes of position, whereas the foot is fixed (see above). Additionally, an evident triangular area on the medial side of the tibia is present in *Caluromys* and *Caluromysiops*, where inserts strong ligaments coming from the medial femoral condyle, fixing the tibia to femur during the rotation. The development and extension of this structure in *G. venusta* is less than in *Caluromys* and *Caluromysiops*, suggesting reduced mechanical stress likely because the lesser body size of *G. venusta*. Such ligaments are also present in other arboreal mammals, as primates (Tardieu 1983), and Sciuridae (Haines 1942). According to Argot (2002), the rotation between tibia and femur is emphasized by

the slight lateral torsion of the distal epiphysis of the femur in *Caluromys*. However, we did not observe such torsion in Caluromyines.

The *M. gracilis*, one of the main adductors of the hip and a powerful flexor of the knee, is inserted on the tibial crest (McEvoy 1982; Evans 1993). In arboreal mammals, as extant Erethizontidae, the well developed *gracilis* is associated with a powerful adduction of the hindlimb during climbing (McEvoy 1982; Candela & Picasso 2008). The long moment arm of the *gracilis*, as consequence of its distal insertion on the tibial crest, increases the mechanical advantage of this muscle (Candela & Picasso 2008). The well developed anterior tibial crest in *Glironia* is indicative of faster mode of locomotion (Muizon 1998; Szalay & Sargis 2001). In *Caluromys* and *Caluromysiops*, the area for insertion of *M. gracilis* seems to be more distally located than in *G. venusta*, and this apparent well developed muscle is consistent with the larger body size of those species compared with *G. venusta*. In addition, the distal extension of the tibial crest indicates distal insertion of hamstring muscles, which implies long moment arms, generating powerful movement of the leg at the beginning of propulsion (Elftman 1929; Smith & Savage 1956; Candela & Picasso 2008). The more proximal insertion of the *M. semitendinosus* on the tibia is associated to greater speed of the initial phase of step in caviomorph rodents (Elissamburu & Vizcaino 2004) and marsupials (Elftman 1929). In agreement with the relatively well developed and distally projected tibial crest of *G. venusta*, the extensive lateral area for the origin of the tibial portion of the *M. tibialis anterior* is evident, suggesting high importance of this muscle inverting the foot to locate its plantar side against the arboreal substrate (McEvoy 1982; Evans 1993). However, the grasp capacity of the foot seems to be partially limited in *G. venusta*, which is inferred by the poorly developed area for the origin of the *M. flexor digitorum tibialis*, although this function could be substituted by the well developed *M. flexor digitorum fibularis* (see above). In agreement with the broad contact between tibia and astragalus, the cruro-astragalar joint of *G. venusta* is highly mobile, as in most of arboreal marsupials (Szalay 1994). The elongated and crescent shaped lateral astragalotibial facet of *G. venusta* facilitates the rotational movement of the foot during dorsiflexion-plantarflexion movements, a condition also evidenced in arboreal rodents (e.g. *Coendou*, Candela & Picasso 2008). The well developed and flattened posterior and medial astragalotibial facets of the tibia, permits a wide range of movements at the cruro-astragalar joint. Moreover, intercondylar ridges between the facets are not evidenced, which add mobility to the joint, as observed in arboreal marsupials (Szalay 1994; Szalay & Sargis 2001; Argot 2002) and rodents (Candela & Picasso 2008). Alternatively, the slightly concave shape of the cruro-astragalar facets of some terrestrial didelphids (e.g. *Metachirus*, *Lestodelphys*) limits the lateral movements, because the articular surface of the tibia shows

a deeper and more concave lateral facet, separated from the medial facet by a sharp but not prominent intercondylar ridge. This pattern of cruro-astragalar morphology and their relation with locomotor habits were detected also in cavioid rodents (Candela & Picasso 2008).

Although less evident than *Caluromys* and *Caluromysiosps*, the fibular head anteroposteriorly developed in *Glironia* (Fig. 12), is associated with an increased area for the origin of the *M. peroneus longus*, involved in the flexion of tarsus (Evans 1993) and the opposability of the hallux, since it inserts on the proximal portion of the first metatarsal, and consequently related to grasp and arboreal habits (Argot 2002; Muizon & Argot 2003). The slightly curved fibular diaphysis of *G. venusta* (compared for instance with *Chironectes*) differs from the straighter fibula of *Caluromys* and *Caluromysiosps*. According to Lanyon (1980), the straight shape in long bones is adequate to transmit longitudinal loads, apart of areas where special muscular attachment is required. In this sense, the curved shape of the proximal portion of the fibula, suggests an important function of flexors and extensors muscles (e.g. *Mm. gastrocnemii* and *plantaris*) originating in the curved regions of the diaphysis. Although the diaphyses of the tibia and fibula are notably separated (indicating a well developed *M. flexor digitorum fibularis*), there are no traces of the origin of this muscle on the fibular diaphysis, and the fibula is, in general terms, notably slender in *G. venusta*, compared with the robust fibular diaphysis observed in *Caluromys* and *Caluromysiosps*.

The general morphology of the tarsal bones of *Glironia* is comparable to arboreal didelphids, as *Caluromys*, *Caluromysiosps*, and *Micoureus* (see Szalay 1994). In agreement with the morphology of the distal articular facets of the tibia of *G. venusta*, the astragalar features are indicative of lateral and rotational movements at the cruro-astragalar joint. The three dorsal astragalar facets are flat but well defined, and limited just by very thin ridges (Fig. 13a), suggesting a stabilized articulation with high capacity of movements, as observed for the agile arboreal *Micoureus* (Argot 2002; Flores 2009). The lateral astragalotibial facet wider than the medial one (as observed in *G. venusta*) allows the foot some lateral movements during dorsiflexion-plantarflexion (Candela & Picasso 2008). As was examined in arboreal mammals, the wide contact between the astragalus and navicular indicates the importance of the medial region of the foot both for mobility and supporting stress during climbing (Szalay 1994; Argot 2002; Candela & Picasso 2008). In addition, the astragalonavicular facet of *G. venusta* (well developed transversally; Fig. 13b) is consistent with arboreal habits as well, since such orientation facilitates pronation-supination movements on the medial part of the foot (Szalay 1994; Argot 2002). Contrarily, in the terrestrial *Metachirus* and terrestrial cavioids, such as *Dolichotis* (Candela & Picasso 2008), the astragalonavicular facet is more parasagittally oriented, showing a condition more

restrictive for the aforementioned movements (Szalay 1994; Argot 2002; Flores 2009).

In plantar view (Fig. 13b), the size and shape of the calcaneo-astragalar and sustentacular facets are consistent with the morphology exhibited by arboreal forms as well (i.e. calcaneo-astragalar facet well developed, and sustentacular facet more or less flat and less developed; Szalay 1994). However, although both facets are different sized in *Glironia*, the differences in shape and size are not so conspicuous as in *Caluromys*, *Caluromysiosps* or *Micoureus*. The sustentacular facet medially oriented towards the astragalonavicular facet (Fig. 13b) is indicative of transverse movements. Although the sustentacular and calcaneo-astragalar facets are not confluent, the clear contact between these facets (Fig. 13b; see also Flores 2009: fig. 31) suggests that the medio-lateral movements at the lower astragalar joint are extensive. Consequently, the orientation and morphology of the plantar facets in the astragalus in *G. venusta* facilitate transverse movements, permitting the inversion of the foot, which represents a particularly important movement for arboreal locomotion.

On the calcaneum of *Glironia*, the sustentacular facet flat and barely separated of the calcaneo-astragalar facet by the weak sulcus calcanei, facilitate the lateral movements at the calcaneo-astragalar joint, which is highly related to grasping ability and foot inversion (Candela & Picasso 2008). The calcaneocuboid facet is subdivided in a distal and proximal portion by a deep recess that receives the projected conial process of the cuboid, indicating that *G. venusta* exhibits the derived pattern (see Argot 2002). This morphology facilitates the rotation of the cuboid, such a way that the plantar side of the digits IV and V is turned medially (Jenkins & McLearn 1984; Argot 2002), which helps to adjust the pes to diverse arboreal substrates (Argot 2002). The transversely wider calcaneo-astragalar facet of *G. venusta* (as in arboreal forms) permits an additional range of inversion of the calcaneus. Additionally, the well developed peroneal process of *G. venusta*, as well as its associated groove, are also consistent with arboreal habits, as argued by Szalay (1994), and seemingly exhibited in arboreal echimyids as well (Candela & Picasso 2008).

Contrasting with strongly arboreal forms, the cuboid of *Glironia venusta* is slightly wider than the navicular (Fig. 14), which is related to terrestrial locomotion (Szalay 1994). However, the well developed cuboidal process permits the attachment of ligaments that resists the bending moment that would open the calcaneocuboid joint plantarly (Szalay 1994; Argot 2002). On the navicular, the extensive astragalonavicular facet (Fig. 14) is indicative of the importance of the medial part of the foot, both in terms of mobility and loading (Szalay 1994), increasing the functional importance of pronation-supination movements rather than flexion-extension of the hindfoot, as occurs in *Metachirus* (Szalay 1994; Argot 2002). Such morphology is in clear agreement with the development and orientation of the astragalonavicular facet of the astragalus (see above).

The lateral process on the proximal portion of the metatarsal V (Fig. 14) emphasizes the abductive role of the tendon of the *M. peroneus brevis*, increasing the mobility of the lateral part of the foot (Argot 2002). In addition, the spherical shape of the proximal portion of the metatarsal I, as well as its distal tip dorsoventrally flattened (Fig. 14) is also similar to the pattern exhibited by arboreal forms.

The phalangeal morphology of the hindlimb of *Glironia* is consistent with arboreal habits as well. On the third digit, the similar length between metatarsal III and proximal phalanx is indicative of an important capacity for prehensibility of the foot. The proximal facets transversely wider also emphasize the lateral stabilization in the articulation with metatarsals (Argot 2002), a pattern detected in arboreal viverrids as well (Taylor 1976). The mesial orientation of the metatarsal I improves the grasping ability of the foot during adduction movements, which was found in additional arboreal mammals (e.g. Sargis 2002b; Candela & Picasso 2008). Finally, the ungual phalanx in the foot of *G. venusta* has basically the same morphology as *Caluromys* and *Caluromysiops* (i.e. dorsoventrally deeper), increasing the range for dorsiflexion-plantarflexion (Argot 2002), which is essential for grasping during arboreal locomotion.

Summary and conclusions

The stability of character distribution in the terrestrial, generalized and arboreal marsupial groups, and the amount of convergence indicate a strong influence of lifestyle on skeletal anatomy in didelphids (e.g. Szalay 1994; Argot 2001, 2002, 2003, Szalay & Sargis 2001; Flores 2009) and Australasian groups (e.g. Weisbecker & Sanchez-Villagra 2006; Weisbecker & Warton 2006; Weisbecker & Archer 2008). However, the strong functional component detected in several studies on didelphid anatomy, does not reduce the value of the postcranial anatomy for phylogenetic conclusions, as shown by the coincidence of clade distinctions with specific differences in postcranial anatomy and functional patterns (e.g. Abdala et al. 2006; Flores 2009). As observed in Diprotodontia (e.g. Weisbecker & Sanchez-Villagra 2006; Weisbecker & Archer 2008), postcranial anatomy is useful to resolve subordinal relationships of Didelphimorphia (Flores 2009).

The three genera in the Subfamily Caluromyinae (*Caluromys*, *Caluromysiops* and *Glironia*) exhibit strong morphological correlations with arboreal habits in the postcranial skeleton. However, the morphological diversity and types of locomotion in their sister group Didelphinae are remarkably higher, including terrestrial, arboreal, and aquatic (or semiaquatic) species. In an evolutive framework, the morphological adaptation to terrestrial or cursorial locomotion seems to be derived in the didelphid radiation (Flores 2009), since potential outgroups are predominantly arboreal (e.g. Caluromyi-

nae, *Pucadelphys*). Nonetheless, some terrestrial or semiterrestrial species, as *Thylamys*, *Lestodelphys* or *Monodelphis*, actually keep some postcranial and muscular characters associated with good capacities for arboreal locomotion as well. Indeed, similarities in morphological patterns in flexor muscles (specialized to grasp) were evidenced both in arboreal and in terrestrial small didelphids (Abdala et al. 2006), although the current geographical distribution of such terrestrial or semiterrestrial taxa includes predominantly open and xeric environments of low complexity (Flores et al. 2007; Gardner 2007), if compared with tropical and subtropical humid rainforests. Small mammals are frequently confronted with surface irregularities that require certain abilities for climbing (Jenkins 1974), independent of the landscape, taxonomy or lifestyle. Below a critical body size, differences between the locomotory modes of arboreal and terrestrial species are not significant (Schilling & Fischer 1999; Vázquez-Molinero et al. 2001). Most small mammals demonstrate high locomotory versatility and capacity to climb (e.g. Jenkins 1974; Abdala et al. 2006). Distinctive characters of *Glironia* represent adaptations for climbing, indicating abilities to move over irregular or inclined substrates. Furthermore, the method of climbing generally used by small mammals requires that the limbs can perform a wide range of postures (Jenkins 1974; Vázquez Molinero et al. 2001), and the shoulder and hip morphology of *G. venusta* is consistent with postural and locomotor flexibility. Moreover, small and medium sized mammals (as *Glironia*) have a partial advantage in moving on steeper vertical surfaces because they expend less energy in climbing than larger ones (Taylor et al. 1972). Such strategy provides access to varied nutritional resources and refuge from predators. The postcranial adaptations for this range of locomotor abilities were subsequently inherited by metatherians and eutherians of the Early Cretaceous (Vázquez Molinero et al. 2001).

The skeletal morphology *Glironia* exhibits features consistent with notorious abilities for arboreal locomotion in all elements of the postcranium, with some capacities coherent with terrestrial habits as well. The fact that *G. venusta* was captured both on the canopy and the ground indicates that the species makes diverse substrate use in a complex ecosystem as neotropical rainforests, which is supported by its skeletal morphology. The morphology of the vertebral column shows attributes that permit powerful lateral and sagittal movements on thoracic and lumbar sections during different phases of locomotion. Then, the anterior position of the diaphragmatic vertebra, the presence of a space between elements on the posterior thoracic and lumbar vertebrae, and the slightly developed accessory process on lumbar region, indicate patterns for vertebral movements comparable with arboreal mouse opossums, which probably is a functional outcome for the smaller body weight of *G. venusta* if compared with other caluromyines. Additional characters, as the absence of a

cranio-caudal extension of the ribs, and the weakly keeled manubrium and flattened sternbrae, possibly are features also related with differences in body weight. According to the morphology exhibited by caudal vertebrae, *G. venusta* shows high capacity for lateral movements and flexibility, although limited movements on vertical plane.

Albeit several characters of scapular morphology point to a highly stabilized shoulder articulation, consistent with arboreal locomotion, its general shape resembles generalized forms. Most of the morphological patterns of the forelimb have functional significance for arboreal capacities, except the oval shape of the humeral head and the well developed greater trochanter, which limits the ability for humeral rotational movements in the humero-scapular articulation.

The pelvic girdle and hindlimb morphology reflect good capacities for arboreal and fast locomotory habits. In a general sense, *Glironia* seems to be faster than *Caluromys* and *Caluromysiops*, which probably is also associated to its smaller body weight. Some distinctive features, as the distal portion of the ilium laterodorsally curved, femur with flat femoral groove, and the wider proximal shape of the anterior tibial crest, are conditions linked to fast running capacities, in spite of the widespread low stability in the acetabulum joint, and the femur slightly longer than tibia. Additionally, several traits resemble clear aptitudes for movements related to arboreal habits (e.g. cylindrical femoral head, low greater trochanter on femur, well developed lesser trochanter, weak tibial tuberosity, low stabilized joint between femur and tibia, and tarsal, metacarpal, and phalangeal morphology). However, as observed in vertebral spine and forelimb, some punctual conditions are associated with limited abilities for hindlimb movements (e.g. sharp angle conformed by both rami of the ilium, absence of traces of the origin of *M. flexor digitorum fibularis*, and fibula slender). The foot of *G. venusta* is characterized by a set of specialized features functionally related to grasping ability and inversion movements.

Finally, the skeletal morphology of *Glironia venusta* and other didelphid species, offer clear evidence of high variation indicating diverse abilities for specific movements, even if most of didelphid species have been cataloged as generalized with respect to locomotory habits. Although the functional context of the complete postcranial morphology were already explored in some crucial metatherian fossils (e.g. *Pucadelphys*, *Mayulestes*, some borhyaenoids, and marsupials from the Paleocene of Itaboraí), detailed descriptions and a functional interpretation of specific components of the marsupial postcranial skeleton are still highly required in other didelphid and non-didelphid living species. Such studies could reveal morphological adaptations for particular movements in taxa with varied locomotory habits and posture, explained as convergencies, apomorphies or plesiomorphies in a phylogenetic frame, assessing the evolution of locomotory abilities in marsupials and its fit to current ecosystems.

Acknowledgements

Our thanks are due to the staff and curators of museums who permitted the access to the postcranial material deposited at Systematic Collections: Robert Voss (AMNH), Daphne Hills (BNHN), Ruben Barquez (CML), Jim Patton (MVZ), Hein Van Grow (RMNH), and Phil Myers (UMMZ). This work was partially supported by a Kalbfleisch Postdoctoral Research Fellowship from the American Museum of Natural History to DAF, and the Consejo de Nacional de Investigaciones Científicas y Técnicas, Argentina (CONICET). We thank Christine Argot, Vera Weisbecker, Ruben Barquez and an anonymous reviewer for their valuable comments and criticism that improved the quality of this work. Our thanks are also due to Joseph Vinetz, the principal investigator of the grants (Grant no. 1R01TW005860; United States Public Health Service National Institute of Allergy and Infectious Diseases, USA), who supported the fieldwork in Peru. The Instituto Nacional de Recursos Naturales (INRENA), Ministerio de Agricultura of Peru and its fieldworkers are acknowledged for permits and practical help to capture and collect specimens.

References

- Abdala, V., Moro, S. & Flores, D. 2006. The flexor tendons in the didelphid manus. – *Mastozoología Neotropical* 13: 193–204.
- Argot, C. 2001. Functional-Adaptive anatomy of the forelimb in the Didelphidae, and the paleobiology of the Paleocene Marsupials *Mayulestes ferox* and *Pucadelphys andinus*. – *Journal of Morphology* 247: 51–79.
- Argot, C. 2002. Functional-Adaptive analysis of the hindlimb anatomy of extant Marsupials and Paleobiology of the Paleocene Marsupials *Mayulestes ferox* and *Pucadelphys andinus*. – *Journal of Morphology* 253: 76–108.
- Argot, C. 2003. Functional-adaptative anatomy of the axial skeleton of some extant marsupials and the paleobiology of the Paleocene marsupials *Mayulestes ferox* and *Pucadelphys andinus*. – *Journal of Morphology* 255: 279–300.
- Barkley, L. J. 2007. Genus *Glironia* Thomas, 1912. In Gardner A. L. (ed.). *Mammals of South America. Volume 1. Marsupials, xenarthrans, shrews, and bats.* The University of Chicago Press, Chicago: pp. 12–14.
- Bernardé, P. S. & Rocha, V. A. 2003. New record of *Glironia venusta* Thomas, 1912 (bushy-tailed opossum) (Mammalia: Glironiidae) for the State of Rondônia–Brazil. – *Biociências* 11: 183–184.
- Bezuidenhout, A. J. & Evans H. E. 2005. Anatomy of the Woodchuck (*Marmota monax*). – *Special Publications of The American Society of Mammalogist*: 180 pp.
- Candela, A. & Picasso, M. B. J. 2008. Functional Anatomy of the Limbs of Erethizontidae (Rodentia, Caviomorpha): Indicators of Locomotor Behavior in Miocene Porcupines. – *Journal of Morphology* 269: 552–593
- Cheng, C. C. 1955. The development of the shoulder region of the opossum, *Didelphys virginiana*, with special reference to the musculature. – *Journal of Morphology* 97: 415–471.
- Coues, E. 1869. The osteology and myology of *Didelphis virginiana*. – *Memories of the Boston Society of Natural History* 2: 41–154.
- Currey, J. D. 1984. The mechanical properties of materials and the structure of bone. In Currey, J. D. (ed.). *The mechanical adaptation of bones.* University Press, Princeton: pp. 3–37.
- Curtis, D. J. 1995. Functional anatomy of the trunk musculature in the slow loris (*Nycticebus coucang*). – *American Journal of Physical Anthropology* 97: 367–379.
- Díaz, M. M. & Willig, M. 2004. Nuevos registros de *Glironia venusta* y *Didelphis albiventris* (Didelphimorphia) para Perú. – *Mastozoología Neotropical* 11: 185–192.

- Elftman, H. O. 1929. Functional adaptations of the pelvis in marsupials. – *Bulletin of the American Museum of Natural History* 58: 189–232.
- Elissamburu, A. & Vizcaíno, S. F. 2004. Limb proportions and adaptations in caviomorph rodents (Rodentia: Caviomorpha). – *Journal of Zoology* 262: 145–159.
- Emmons, L. H. & Feer, F. 1990. *Neotropical Rainforest Mammals: A Field Guide*. University of Chicago Press, Chicago, Illinois.
- Endo, H., Rerkamuychoke, W., Kimura, J., Sasaki, M., Kurohmaru, M. & Yamada, J. 1999. Functional Morphology of the locomotor system in the northern smooth-tailed shrew (*Dendrogale murina*). – *Annals of Anatomy* 181: 397–402.
- Evans, H. E. 1993. *Miller's Anatomy of the Dog*. Third Edition. W.B Saunders Company, Philadelphia.
- Filan, S. L. 1990. Myology of the head and neck of the bandicoot (Marsupialia: Peramelemorphia). – *Australian Journal of Zoology* 38: 617–634.
- Finch, M. E. & Freedman, L. 1986. Functional-Morphology of the Vertebral Column of *Thylacoleo carnifex* Owen (Thylacoleonidae, Marsupialia). – *Australian Journal of Zoology* 34: 1–16.
- Finch, M. E. & Freedman, L. 1988. Functional morphology of the limbs of *Thylacoleo carnifex* Owen (Thylacoleonidae: Marsupialia). – *Australian Journal of Zoology* 36: 251–272.
- Flores, D. A. 2009. Phylogenetic Analyses of Postcranial Skeletal Morphology in Didelphid Marsupials. – *Bulletin of The American Museum of Natural History* 320: 1–81.
- Flores, D., Díaz, M. M. & Barquez, R. M. 2007. Marsupials of Argentina: an update of their Systematics and Distribution. In Kelt, D., Lessa, E., Salazar-Bravo, J. & Patton, J. (eds). *Essay in Honor of Oliver Pearson*. University of California, Publications in Zoology Series 134: 579–670.
- Gambaryan, P. P. 1974. How mammals run: Anatomical adaptations. Transl. from Russian ed. (Leningrad, 1972) by Hilary Hradin. Halsted (Wiley), Program for Scientific Translations, New York, and Israel, Jerusalem.
- Gardner, A. 2007. Order Didelphimorphia. In Gardner, A. (ed.). *Mammals of South America*. Vol 1. University of Chicago Press: pp. 1–124.
- Gebo, D. L. 1989. Locomotor and pylogenetic consideration in anthropoid evolution. – *Journal of Human Evolution* 18: 201–233.
- Goslow, G. E., Seeherman, H. J., Taylor, C. R., McCutchin, M. N. & Heglund, N. C. 1981. Electrical-activity and relative length changes of dog limb muscles as a function of speed and gait. – *Journal of Experimental Biology* 94: 15–42.
- Grand, T. I. 1983. Body weight: its relationships to tissue composition, segmental distribution of mass, and motor function. III. The Didelphidae of French Guyana. – *Australian Journal of Zoology* 31: 299–312.
- Haines, R. W. 1942. The tetrapod knee joint. – *Journal of Anatomy* 76: 270–301.
- Herskovitz, P. 1992. The South American gracile mouse opossums, genus *Gracilinanus* Gardner and Creighton, 1989 (Marmosidae, Marsupialia): a taxonomic review with notes on general morphology and relationships. – *Fieldiana Zoology, new series* 70: 1–56.
- Herskovitz, P. 1999. *Dromiciops gliroides* Thomas, 1894, last of the Microbiotheria (Marsupialia), with a review of the Family Microbiotheriidae. – *Fieldiana Zoology, new series* 93: 1–60.
- Horowitz, I. & Sánchez-Villagra, M. R. 2003. A morphological analysis of marsupial mammal higher-level phylogenetic relationships. – *Cladistics* 19:181–212.
- Howell, A. B. 1965. *Speed in animals: their specialization for running and leaping*. Hafner Publishing Company, New York.
- Jenkins, F. A., Jr. 1970. Anatomy and Function of expanded ribs in certain edentates and primates. – *Journal of Mammalogy* 51: 288–301.
- Jenkins, F. A., Jr. 1971. Limb posture and locomotion in the Virginia opossum (*Didelphis marsupialis*) and in other non-cursorial mammals. – *Journal of Zoology* 165: 303–315.
- Jenkins, F. A., Jr. 1973. The functional anatomy and evolution of the mammalian humero-ulnar articulation. – *American Journal of Anatomy* 137: 281–298.
- Jenkins, F. A., Jr. 1974. Tree shrew locomotion and the origin of primate arborealism. In Jenkins, F. A., Jr. (ed.). *Primate Locomotion*. Academic Press, New York: pp. 85–115.
- Jenkins, F. A., Jr. 1981. Wrist rotation in primates: a critical adaptation for brachiators. – *Symposium of the Zoological Society, London* 48: 429–451.
- Jenkins, F. A., Jr. & Camazine, S.M. 1977. Hip structure and locomotion in ambulatory and cursorial carnivores. – *Journal of Zoology* 181: 351–370.
- Jenkins, F. A., Jr. & McClearn, D. 1984. Mechanisms of hind foot reversal in climbing mammals. – *Journal of Morphology* 182: 197–219.
- Jenkins, F. A. Jr. & Weijs, W. A. 1979. The functional anatomy of the shoulder in the Virginia opossum (*Didelphis virginiana*). – *Journal of Zoology* 188: 379–410.
- Johnson, S. E. & Shapiro, L. J. 1998. Positional behavior and vertebral morphology in atelines and cebines. – *American Journal of Physical Anthropology* 105: 333–354.
- Jolly, C. J. 1967. The evolution of the baboons. In Vagtberg, H. (ed.). *The baboon in medical research*. University of Texas Press, Austin: pp. 23–50.
- Kirsch, J. A. W. 1977. The comparative serology of marsupialia, and a classification of Marsupialia. – *Australian Journal of Zoology* 52: 1–152.
- Klima, M. 1987. Early development of the shoulder girdle and sternum in marsupials (Mammalia, Metatheria). – *Advances in Anatomy, Embriology and Cell Biology* 109: 1–91.
- Kurz, C. 2005. Ecomorphology of opossum-like marsupials from the Tertiary of Europe and a comparison with selected taxa – *Kaupia, Darmstädter Beiträge zur Naturgeschichte* 14: 21–26.
- Lammers, A. R. 2007. Locomotor kinetics on sloped arboreal and terrestrial substrates in a small quadrupedal mammal. – *Zoology* 110: 93–103.
- Lanyon, L. E. 1980. The influence of function on the development of bone curvature. An experimental study on the tibia rat. – *Journal of Zoology* 192: 457–466.
- Larson, S. G. 1993. Functional morphology of the shoulder in primates. In Gebo, D. L. (ed.). *Postcranial adaptation in nonhumans primates*. DeKalb, Northern Illinois University Press: pp. 45–69.
- Larson, S. G., Schmitt, D., Lemelin, P. & Hamrick, M. 2001. Limb excursion during quadrupedal walking: how do primates compare with other mammals? – *Journal of Zoology* 255: 353–365.
- Le Gros Clark, W. E. 1924. The myology of the Tree-Shrew (*Tupaia minor*). – *Proceedings of the Zoological Society* 31: 461–497.
- Le Gros Clark, W. E. 1926. On the anatomy of the pen-tailed Tree-Shrew (*Ptilocercus lowii*). – *Proceedings of the Zoological Society* 35: 1179–1309.
- Lemelin, P. 1999. Morphological correlates of substrate use in didelphid marsupials: implications for primate origins. – *Journal of Zoology* 247: 165–175.
- Lunde, D. P. & Shutt, W. A. 1999. The peculiar carpal tubercles of male *Marmosops parvidens* and *Marmosa robinsoni* (Didelphidae: Didelphinae). – *Mammalia* 63: 495–504.
- MacLeod, N. & Rose, K. D. 1993. Inferring locomotor behavior in Paleogene mammals via eigenshape analysis. – *American Journal of Science* 293 A: 300–355.
- MacPhee, R. D. E. & Jacobs, L. L. 1986. *Nycticeboides simpsoni* and the morphology, adaptations, and relationships of Miocene Siwalik Lorissidae. In Flanagan, K. M. & Lillegraven, J. A. (eds). *Contributions to Geology*. University of Wyoming Press, Laramie: pp. 131–161.
- Mann Fisher, G. 1953. Filogenia y función de la musculatura en *Marmosa elegans* (Marsupialia, Didelphidae). – *Investigaciones Zoológicas Chilenas* 1: 3–15.

- Mann Fisher, G. 1956. Filogenia y función de la musculatura en *Marmosa elegans* (Marsupialia, Didelphidae). 2 da. Parte. – Investigaciones Zoológicas Chilenas 3: 3–28.
- Marshall, L. G. 1978. *Glironia venusta*. – Mammalian Species 107: 1–3.
- Marshall, L. G. & Sigogneau Rusell, D. 1995. Postcranial skeleton. In Marshall, L., Muizon, C. & Sigogneau–Russell, D. (eds). *Pucadelphys andinus* (Marsupialia, Mammalia) from the early Paleocene of Bolivia. Mémoires du Muséum National d'histoire Naturelle, Paris: pp. 91–164.
- McEvoy, J. S. 1982. Comparative myology of the pectoral and pelvic appendages of the North American porcupine (*Erethizon dorsatum*) and the prehensile-tailed porcupine (*Coendou prehensilis*). – Bulletin of the American Museum of Natural History 173: 337–421.
- Muizon, C. 1998. *Mayulestes ferox*, a borhyaenoid (Metatheria, Mammalia) from the early Paleocene of Bolivia. Phylogenetic and paleobiologic implications. – Geodiversitas 20: 19–142.
- Muizon, C. & Argot, C. 2003. Comparative anatomy of the Tiupampa didelphimorphs; an approach to locomotory habits of early marsupials. In Jones, M. E., Dickman, C. R. & Archer, M. (eds). Predators with pouches: the biology of carnivorous marsupials. Csiro publishing, Australia: pp. 43–62.
- Napier, J. R. 1961. Prehensibility and opposability in the hands of primates. – Symposium of the Zoological Society, London 5: 115–133.
- Oxnard, C. E. 1963. Locomotor adaptations in the primate forelimb. In Napier, J. & Barnicot, N. A. (eds). The primates. Elsevier, Amsterdam: pp. 165–182.
- Pridmore, P. A. 1992. Trunk movements during locomotion in the Marsupial *Monodelphis domestica* (Didelphidae). – Journal of Morphology 211: 137–146.
- Pridmore, P. A. 1994. Locomotion in *Dromiciops australis* (Marsupialia: Microbiotheriidae). – Australian Journal of Zoology 42: 679–699.
- Rasmussen, D. T. 1990. Primate origins: Lessons from a neotropical marsupial. – American Journal of Primatology 22: 263–277.
- Redford, K. & Eisenberg, J. F. 1989. Mammals of the Neotropics. Vol. 2, The Southern Cone: Chile, Argentina, Uruguay, Paraguay. University of Chicago Press, Chicago, Illinois, USA: 430 pp.
- Reig, O. A. 1955. Noticia preliminar sobre la presencia de microbio-terinos vivientes en la fauna sudamericana. – Investigaciones Zoológicas Chilenas 2: 127–130.
- Reig, O. A., Kirsch, J. A. W. & Marshall, L. G. 1987. Systematic relationships of the living and neocenoic American “opossum-like” marsupials (Suborder Didelphimorphia), with comments on the classification of these and of the Cretaceous and Paleogene New World and European metatherians. In Archer, M. (ed.). Possums and opossums: studies in evolution. Vol. 1. Surrey Beatty, Sydney: pp. 1–89.
- Roberts, D. 1974. Structure and function of the primate scapula. In Jenkins, F. A. (ed.). Primate locomotion. Academic Press, New York: pp. 171–200.
- Rockwell, H., Gaynor Evans, F. & Pheasant, H. 1938. The comparative morphology of the vertebrate spinal column. Its form as related to function. – Journal of Morphology 63: 87–117.
- Rose, K. D. & Chinnery, B. J. 2004. The postcranial skeleton of early Eocene rodents. – Bulletin of the Carnegie Museum of Natural History 36: 211–244.
- Sanders, W. 1995. Function, allometry, and evolution of the australopithecine lower precaudal spine. Doctoral Dissertation, New York University.
- Sanders, W. & Bodenbender, B. 1994. Morphometric analysis of lumbar vertebra UMP 67–28: implications for spinal function and phylogeny of the Miocene Moroto hominid. – Journal of Human Evolution 26: 203–237.
- Santos Filho, M., da Silva, M. N. F., Costa, B. A., Bantel, C. G., Vieira, C. L. G., Silva, D. J. & Franco, A. M. R. 2007. News records of *Glironia venusta*, Thomas, 1912 (Mammalia, Didelphidae), from the Amazon and Paraguay basins, Brazil. – Mastozoología Neotropical 14: 103–105.
- Sargis, E. J. 2001a. A preliminary qualitative analysis of the axial skeleton of tupaiids (Mammalia, Scandentia): functional morphology and phylogenetic implications. – Journal of Zoology 253: 473–483.
- Sargis, E. J. 2001b. The grasping behaviour, locomotion and substrate use of the tree shrews *Tupaia minor* and *T. tana* (Mammalia, Scandentia). – Journal of Zoology 253: 485–490.
- Sargis, E. J. 2002a. Functional morphology of the forelimb of tupaiids (Mammalia, Scandentia) and its phylogenetic implications. – Journal of Morphology 253: 10–42.
- Sargis, E. J. 2002b. Functional morphology of the hindlimb of tupaiids (Mammalia, Scandentia) and its phylogenetic implications. – Journal of Morphology 254: 149–185.
- Schilling, N. & Fischer, M. S. 1999. Kinematic analysis of treadmill locomotion of Tree shrew. *Tupaia glis* (Scandentia: Tupaiidae). – Zeitschrift für Säugetierkunde 64: 129–153
- Segall, W. 1969. The middle ear region of *Dromiciops*. – Acta Anatomica 72: 489–501.
- Shapiro, L. J. & Jungers, W. J. 1994. Electromyography of back muscles during quadrupedal and bipedal walking in Primates. – American Journal of Physical Anthropology 93: 491–504.
- Shapiro, L. J. 1993. Functional morphology of the vertebral column in primates. In Gebo, D. (ed.). Postcranial adaptation in nonhuman primates. Northern Illinois University Press, Illinois: pp. 121–149.
- Shapiro, L. J. 1995. Functional morphology of indrid lumbar vertebrae. – American Journal of Physical Anthropology 98: 323–342.
- Shapiro, L. J., Seiffert, C. V., Godfrey, L. R., Jungers, W. L., Simons, E. L. & Randria, G. F. 2005. Morphometric analysis of lumbar vertebrae in extinct Malagasy strepsirrhines. – American Journal of Physical Anthropology 128: 823–839.
- Simmons, N. B. 1994. The case for Chiropteran monophyly. – American Museum Novitates 3103: 1–54.
- Simpson, G. G. 1945. The principles of Classification and a Classification of Mammals. – Bulletin of the American Museum of Natural History 85: 1–350.
- Slijper, E. J. 1946. Comparative biologic–anatomical investigations on the vertebral column and spinal musculature in Mammals. – Koninklijke Nederlandsche Akademie van Wetenschappen 5: 1–128
- Smith, M. J. & Savage, R. J. G. 1956. Some locomotory adaptations in Mammals. – Zoological Journal of the Linnean Society 42: 603–622.
- Stafford, B. J. & Thorington, R. W. 1998. Carpal development and morphology in archontan mammals. – Journal of Morphology 235: 135–155.
- Stein, B. R. 1981. Comparative limb myology of two opossums, *Didelphis* and *Chironectes*. – Journal of Morphology 169: 113–140.
- Szalay, F. S. 1994. Evolutionary History of the marsupials and an analysis of osteological characters. Cambridge University Press, New York.
- Szalay, F. S. & Sargis, E. J. 2001. Model–based analysis of postcranial osteology of marsupials of Palaeocene of Itaboraí (Brazil) and the phylogenetics and biogeography of Metatheria. – Geodiversitas 23: 139–302.
- Tardieu, C. 1983. L'articulation du genou. Analyse morphofonctionnelle chez les primates, application aux hominidés fossiles. Paris: Cahiers de Paléanthropologie, CNRS.
- Taylor, M. E. 1974. The functional anatomy of the forelimbs of some African Viverridae (Carnivora). – Journal of Morphology 143: 307–336.
- Taylor, M. E. 1976. The functional anatomy of the hindlimbs of some African Viverridae (Carnivora). – Journal of Morphology 148: 227–254.

- Taylor, C. R., Caldwell, S. L. & Rowntree, V. J. 1972. Running up and down hills: some consequences of size. – *Science* 178: 1096–1097.
- Vázquez-Moliner, R., Martín, T., Fischer, M. S. & Frey, R. 2001. Comparative anatomical investigations of the postcranial skeleton of *Henkelotherium guimarotae* Krebs, 1991 (Eupantotheria, Mammalia) and their implications for its locomotion. – *Mitteilungen aus dem Museum für Naturkunde in Berlin. Zoologische Reihe* 77: 207–216.
- Voss, R. S. & Jansa, S. A. 2003. Phylogenetic studies on Didelphid marsupials II. Nonmolecular data and new IRBP sequences: separate and combined analyses of Didelphine relationships with denser taxon sampling. – *Bulletin of the American Museum of Natural History* 276: 1–82.
- Walker, A. 1974. Locomotor adaptations in past and present prosimian primates. In Jenkins, F. A. (ed.). *Primate Locomotion*. Academic Press, New York: pp. 349–381.
- Washburn, S. & Buettner-Janush, J. 1952. The definition of thoracic and lumbar vertebrae. – *American Journal of Physical Anthropology* 10: 251–252.
- Weisbecker V. & Archer, M. 2008. Parallel evolution of hand anatomy in kangaroos and vombatiform marsupials: functional and evolutionary implications. – *Palaeontology* 51: 321–338.
- Weisbecker, V. & Sanchez-Villagra, M. R. 2006. Carpal evolution in diprotodontian marsupials. – *Zoological Journal of the Linnean Society* 146: 369–384.
- Weisbecker, V. & Warton, D. I. 2006. Evidence at hand: diversity, functional implications, and locomotory prediction in intrinsic hand proportions of diprotodontian marsupials. – *Journal of Morphology* 267: 1469–1485.
- Yalden, D. W. 1972. The form and function of the carpal bones in some arboreally adapted mammals. – *Acta Anatomica* 82: 383–406.
- Young, A. H. 1879. The intrinsic muscles of the marsupial hand. – *Journal of Anatomy and Physiology* 14: 149–165.
- RMNH Rijksmuseum van Natuurlijke Historie, Leiden
- UWZM University of Wisconsin Zoological Museum (Madison)
- MMD Personal catalog of M. Mónica Díaz (deposited at CML and Museo de Historia Natural de San Marcos, Peru uncataloged)
- Caluromys lanatus*: MMD 2973, 4508; CML 7573, 7574; AMNH 133199, 133200, 215001.
- Caluromys philander*: AMNH 95761, 267001, 267002, 267337, 95974; RMNH uncataloged, 12866, 10790, 19646, 20664.
- Caluromysiops irrupta*: AMNH 208101, 244364.
- Chironectes minimus*: AMNH 97319, 148720, 212909, 264571; RMNH uncataloged.
- Cryptonanus unduaviensis*: AMNH 210369, 262401.
- Didelphis albiventris*: AMNH 13102, 148320, 170653, 170654, 170664, 204406, 205301, 205382, 238006.
- Didelphis marsupialis*: MMD 3313; CML 7575; AMNH 13448, 97318, 132784, 209164, 210427, 210428, 210439, 210447, 255854
- Glironia venusta*: MMD 607 (deposited at the Museo de Historia Natural de San Marcos, Peru uncataloged).
- Lestodelphys halli*: UWZM 224223; BMNH 21.6.7.19.
- Marmosa robinsoni*: AMNH 206596, 206597, 206766, 207766, 257209, 257210.
- Marmosops bishopi*: CML 7564, 7565.
- Marmosops noctivagus*: AMNH 136157, 231952; MMD 2201, 3503, 3520, 4663, 4776, 4789.
- Metachirus nudicaudatus*: MMD 785, 801; CML 7579, 7580, 7342; AMNH 97320, 136151, 136155, 244617, 267009.
- Micoureus regina*: AMNH 61391, 148757.
- Micoureus demerarae*: AMNH 257211, 257212; RMNH 12871, 998, 18228.
- Micoureus* sp.: MMD 556, 613, 1252, 1984, 2203, 2206, 2586, 2590, 3458, 4617.
- Monodelphis adusta*: MMD 4305; CML 7591; AMNH 136158, 139227.
- Monodelphis breviceaudata*: AMNH 48133, 257203; RMNH 18079, 12851, 17907.
- Monodelphis theresa*: MVZ 182775.
- P. opossum*: MMD 581, 1033, 1046, 1255, 1973, 2214, 2972, 3314, 3379, 3735, 3398, 3737, 4294; CML 7583, 7585; AMNH 61396, 61864, 97332, 133074, 190446, 210406, 210410, 248703, 254509, 261273, 261276, 262415; RMNH 12835, 12838, 12834.
- Philander andersoni*: MMD 4621, 4652.
- Thylamys pallidior*: AMNH 262405, 262406, 262408; CML 3189, 3192, 3574, 3575.

Appendix

Specimens examined

The skeletons analyzed for this study are deposited in the following systematics collections, listed in alphabetical order by their acronyms:

- AMNH American Museum of Natural History, New York
- BMNH British Museum (Natural History), London
- CML Colección Mamíferos Lillo, Universidad Nacional de Tucumán, Tucumán, Argentina
- MVZ Museum of Vertebrate Zoology, University of California, Berkeley

