



The Palmar and Plantar Anatomy of *Dromiciops gliroides* Thomas, 1894 (Marsupialia, Microbiotheria) and its Relationship to Australian Marsupials

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Abstract The monito del monte *Dromiciops gliroides* Thomas, 1894, is a marsupial endemic to the temperate rainforests of Argentina and Chile. Studies on its phylogenetic relationships show the species is more closely related to Australian marsupials than to any other American taxon. The study of the palmar and plantar anatomy in this species through direct observation of more than 86 specimens and comparisons with American and Australian marsupials show the pattern of *D. gliroides* is derived from the ancestral mammalian pattern. *Dromiciops gliroides* show the presence of a single palmar/plantar pad in the position of interdigital pad 1 and the lack of a thenar pad (or the complete fusion between both pads), a pattern that appears closer to some Australian diprotodont marsupials. Also shared with several Australian marsupials is the transverse orientation of pad ridges, a condition that is not shared with most arboreal/scansorial American marsupials (e.g., *Caluromys* spp., *Marmosa* spp., *Marmosops* spp.).

Keywords Chiridia · Monito del monte · Ridges and volar areas

Introduction

Epidermal ridges or foot pads have been of interest to early mammal morphologists in late 1800s–early 1900s (Klaatsch 1888; Hepburn 1895) but have received little attention since, with few notable exceptions (e.g., Pocock 1921a, b, 1926 [and literature cited therein]; Ade 1993; Haffner 1998). Foot pads are the first locomotor contact between an individual and its environment, varying in size and disposition, and creating friction that assists in gripping and grasping (Hepburn 1895). The pattern of foot pads is therefore related to how feet function, their variability and variation being directly related to different locomotion types, with valuable morphological information that can be used in taxonomy.

The formation of foot pads and friction ridges was described by Whipple (1904) in a series of steps that include: 1) losing hair from scales located on the volar surfaces; 2) loss of hair causing sweat glands to become active, moistening the volar surface and improving grip; 3) fusion of volar scales into

rows, which enhance grip (the friction ridges); and 4) modification of these ridges when contact areas of the volar surface become specialized for grasping or locomotion. Further processes include the development of walking or prehension pads in the main areas of contact between volar areas with a surface, and an increase in friction ridges in these pads leading to the observed pattern. Associated with these friction ridges are three groups of flexion creases, the Major, Minor, and Secondary creases (Ashbaugh 1999). Flexion creases are “present where the volar skin is continually flexed through the movements of digits or the palms” and are “areas of firmer skin attachment to underlying structures” (Ashbaugh 1999). Interestingly, these areas where flexion creases are persistent within the friction ridge configuration remain without pads and ridges, and are relatively fixed during palmar/plantar movement. Studies in primates show friction ridges and flexion creases do not change from before birth and until death, showing a relatively constant pattern throughout each individual’s development (Ashbaugh 1999).

All mammals share the same morphological arrangement of volar pads on hands and feet, with modifications occurring at different stages of their intrauterine development, but remaining constant until death (Whipple 1904; Ashbaugh 1999). A typical arrangement as described by Whipple (1904), and Pocock (1921a, b, 1926) includes volar pads at each of the five fingers

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(the fingertips, digital or apical pads), in the four interdigital areas (interdigital pads 1, 2, 3, and 4 [hereafter i1, i2, i3, i4]), and on each side of the palm (the thenar and hypothenar pads). Therefore, specialized forms (e.g., cats, thylacines, dogs, lagomorphs) will have their palmar and plantar surfaces modified from this original pattern (Pocock 1926).

The anatomy of hands and feet in marsupials has been studied from an osteological point of view (see Szalay 1982, 1994; Szalay and Sargis 2001), but very little information is available on the chiridia and volar surfaces, with the exception of works by Pocock (1921a, 1926), Hamrick (2001), and a few other authors (e.g., Hershkovitz 1992; Lunde and Schutt 1999; Voss and Jansa 2003).

Living American marsupials are included in three orders: the highly diversified opossums (Didelphimorphia, with more than 100 species), the shrew opossums (Paucituberculata, with six species), and the monito del monte (Microbiotheria, with a single species) (Astúa 2015; Palma and Valladares-Gómez 2015; Patterson 2015). The monito del monte *Dromiciops gliroides* Thomas, 1894, is the only living representative of the order Microbiotheria (Valladares-Gómez et al. 2017; Martin 2017; but see D'Elía et al. 2016), and lives in the temperate rainforests of southern Chile and southwestern Argentina (Martin 2010). Despite being an American marsupial, the species has been recovered in phylogenetic analyses as closely related to the Australian marsupial radiation, instead of any American marsupial (Szalay 1994; Colgan 1999; Palma and Spotorno 1999; Asher et al. 2004; but see Hershkovitz 1999). Different studies (i.e., anatomical, molecular) have recovered the species as the sister taxon to Australian diprotodont marsupials (Kirsch et al. 1997; Springer et al. 1998; Horovitz and Sánchez-Villagra 2003), dasyurids + peramelids + *Notoryctes* (Nilsson et al. 2004), phalangerids and kangaroos (Temple-Smith 1987), or as the sister group to all the Australian radiation (Szalay 1994; Munemasa et al. 2006; Phillips et al. 2006). Recently, D'Elía et al. (2016) split *Dromiciops* in three species, an arrangement that has been recently questioned by Valladares-Gómez et al. (2017) and Martin (2017). Despite these different approaches and studies on the species locomotion (Pridmore 1994), the plantar anatomy of *Dromiciops* has not been studied in detail.

The objectives of this work are to describe and analyze the morphology of the chiridia (both plantar and palmar surfaces), pad disposition, and flexion creases in *D. gliroides*, and compare them, morphologically and through descriptions, with other American and Australian marsupials.

Material and Methods

The number, disposition and general morphology of plantar pads and flexion creases were analyzed following Ashbaugh

(1999), and literature cited therein. The general arrangement of hands and feet in mammals are characterized by digital/apical pads at the fingertips, interdigital pads numbered 1 to 4, and thenar and hypothenar pads. Flexion creases are grouped in Major and Minor Flexion creases, and Minor Digital creases (see Ashbaugh 1999: fig. 8.6). More than 170 specimens of every genera of American marsupials were studied (see Appendix 1), those of medium/large size (e.g., *Caluromys* spp., *Didelphis* spp., *Metachirus nudicaudatus*) were studied by direct observation, and small ones (e.g., *D. gliroides*, *Cryptonanus* spp., *Gracilinanus* spp., *Thylamys* spp.) through a stereoscope. When possible, males and females of different ages of all genera, and several species within non-monotypic genera were studied. Also, specimens from different localities were studied in genera with large distribution areas to account for intraspecific variability. A review of literature on Australian marsupials (e.g., Pocock 1921a, 1926; Archer 1981; Flannery 1994) was done, as well as direct observations of several species. A list of all studied specimens is presented in Appendix 1.

In order to test the occurrence of characters described/studied herein and analyze them within a phylogenetic framework, an optimization of character-states was performed using TNT (Goloboff et al. 2008). This procedure is intended to show how characters appear and change within a phylogeny, providing an opportunity to determine ancestral character-states, and map evolutionary information onto a phylogenetic tree (Flores et al. 2013). A set of six character-states were mapped on a phylogeny that included four placental genera as outgroups (*Cryptotis*, *Tupaia*, *Tenrec*, and *Geogale*), the data from Voss and Jansa (2009) for Didelphimorphia, and modifications of the cladograms presented by May-Collado et al. (2015) and Archer and Kirsch (2006). Characters mapped were the number of palmar and plantar pads, pad surface, and size of the largest pad in hands and feet; all characters were treated as unordered/non-additive. Character-states were coded as follows: Characters 1 and 4: Number of pads in the palmar and plantar surface, respectively; (0) six pads in the palmar/plantar surface; (1) without thenar pad; (2) without hypothenar pad; (3) without pads, and showing non-overlapping, thickened epidermal scales (see Hamrick 2001); (4) with a single unified pad; and (5) without pads, and epidermal scales covering all the palmar/plantar surface. Three character-states were added to the plantar surface to account for the observed variation: (6) with only three pads, i1, i2, and i3; (7) with a sub-hypothenar pad; and (8) with i1 and hypothenar pads united, lacking a thenar pad. Characters 2 and 5: Surface of the pads in hands and feet, respectively; (0) pads without ridges or epidermal scales; (1) pads with thickened epidermal scales; (2) pads with concentric ridges; and (3) pads with transversal ridges. Characters 3 and 6: Largest pad in hands and feet, respectively; (0) thenar pad is the largest; (1) i1 is the largest; (2) i2 is the largest; (3) i3 is the largest; (4) i4 is the largest; and (5) hypothenar is the largest.

All data generated or analyzed during this study are included in this published article.

Results and Discussion

A total of 86 specimens of *D. gliroides* from several localities throughout the species distribution were analyzed. Also, 15 embryos/fetuses of different stages of development and size were studied (i.e., five of 2.5 cm in length, four of 2 cm, two of 1.3–1.5 cm, two of 9 mm, and two of 6.5 mm). The pattern found in adult individuals of *D. gliroides* consisted of well-developed digital or apical pads, four interdigital (or three interdigital and the fused i1 + thenar pads), and a hypothenar pad in both manus and pes (Fig. 1). The species is characterized by long (anteroposteriorly) interdigital pads 2—3—4 (i2, i3, i4), a bean-shaped hypothenar pad in the manus, and a very long pad in the pes that could either be a very large i1 or the fusion of i1 with the thenar pad. This pattern was also found in

fetuses/embryos of at least 2 cm in length, the younger specimens showed no trace of pads in both manus and pes, even though the former were better developed than the latter. Fetuses/embryos of less than 1.5 cm showed an undifferentiated pattern of poorly developed scales (i.e., not prominent and without clear borders) in both palmar and plantar surfaces. Both males and females presented the same pattern, and size was not sexually variable. Also, throughout the species range, no differences were found in the overall pattern, adding support to consider *D. gliroides* as a single species. The crease pattern in the volar areas of *D. gliroides* is characterized by a lack of a Distal Transverse crease, a poorly developed Proximal Transverse crease, and no trace of a Little Finger crease. This lack of deeply developed creases implies the folding capacity of the volar surface of the hand and foot is very limited, remaining extended for (probably) locomotor purposes.

The fingertips of both hands and feet have ridges that are continuous, not closed, going around each fingertip in lateral view, with a U shape that opens posteriorly (\cap) in ventral view. Each fingertip is followed by scales along the fingers, which taper the surface of hands and feet to the wrist, including volar surfaces, with the exception of the interdigital and hypothenar pads. All pads are elongated and have transversal friction ridges, with the exception of the hypothenar pad in the hand, which is bean or kidney-like, and has ridges oriented in a radial pattern (Fig. 1). This pattern of transversal ridges was not observed in fetuses/embryos with developed (albeit poorly) palmar and plantar pads (see below). Despite size differences between hand and foot (the latter has a larger overall size and grasping surface than the hand), the pattern of pads in both hand and foot is similar, with large i1 pads, medium-sized interdigital pads, and smaller hypothenar pads. All pads are well developed, elevated from the volar area, which is covered by similar-sized scales. The hands have a large i1 (or thenar + i1) pad, interior to the pollex, which is more than half the size of i3 pad, the largest of the interdigital pads, followed in size by subequal i2—i4, and a shorter but broader hypothenar pad. Both i4 and hypothenar pads are located in the same line, exterior to the hand, but clearly separated from each other. The hypothenar pad is almost at the posterior end of the palmar surface, different from the pattern observed in the plantar surface. In the largest fetuses/embryos studied, the hypothenar pad is the largest in the hand, followed by similar-sized i1 and i4 (almost equal in size), which are larger than i2, and i3 as the smallest pad in the hand. The volar area of the hands has a short Proximal Transverse crease, between i1 and i2 pads, and a posteriorly bifurcated Middle Finger crease. Only poorly developed Middle Finger and Ring Finger creases were distinguishable in the hands of studied embryos/fetuses. The feet have a very well-developed i1 (or thenar + i1) pad, followed in size by a large i4, i2, i3, and a small hypothenar pad, even smaller than i3. The hypothenar pad

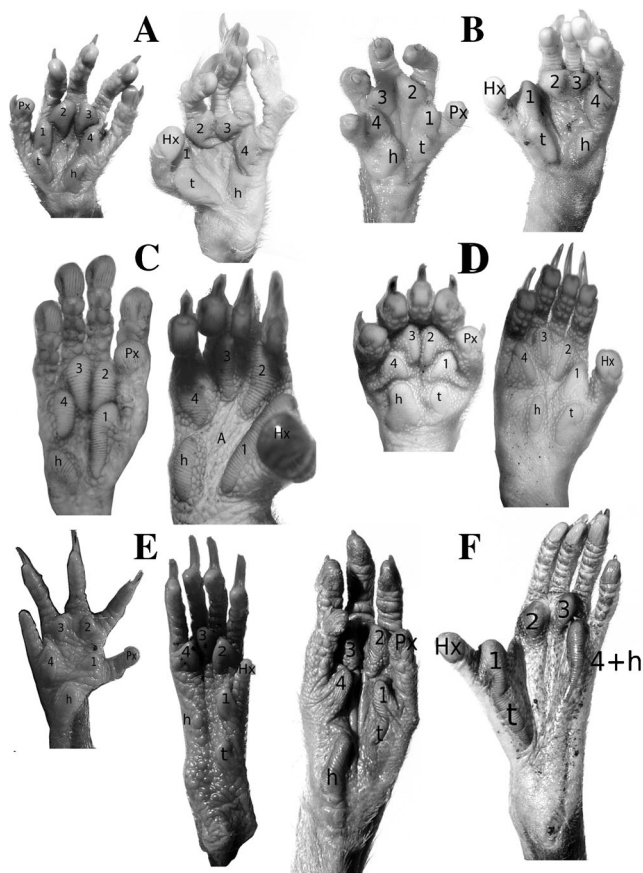


Fig. 1 Compared chiridia of several species of American marsupials with different locomotion. (A) *Marmosa murina*; (B) *Marmosops noctivagus*; (C) *Dromiciops gliroides*; (D) *Thylamys pallidior*; (E) *Lestoros inca*; and (F) *Metachirus nudicaudatus*. Pad terminology follows Whipple (1904) and Ashbaugh (1999). Numbers 1 to 4 indicate interdigital pads; t, thenar pad; h, hypothenar pad; Px, pollex; Hx, hallux; A, volar surface in the foot of *D. gliroides*

of the foot is smaller than its hand counterpart, and is straight as the other pads and not bean/kidney-like. The very large i1 (or thenar + i1) pad is visible in a dorsal view of the foot, extending as a finger-like projection between the hallux and the second finger. As in the hand, i4 and hypothenar pads are located in the same line, exterior to the hand, but clearly separated from each other. In the studied fetuses/embryos where pads were identifiable, i1 is the largest, followed by i4, which is larger than i3, a small i2, and a very small hypothenar pad. The foot has a Thenar crease which is absent in the hand, bordering i1 (or thenar + i1) pad. The Proximal Transverse crease in the foot is well developed, and has an accessory crease that posteriorly borders the i2 pad. The pattern of the Middle Finger crease is similar to that of the hand, but slightly more developed posteriorly. The foot also shows a well marked Ring Finger crease, which is not present in the hands. In fetuses/embryos, three creases were identified: the Thenar crease, a well marked Middle Finger crease, and a less developed Ring Finger crease.

Comparisons between *D. gliroides* and the majority of American marsupials showed most species have four interdigital pads, plus thenar and hypothenar pads, all separated (e.g., *Marmosa murina*, Fig. 1), which also represents the most common ancestral pattern (Whipple 1904). In some predominantly arboreal species like *Caluromys* spp., i1 and thenar pads are in contact but do not form a continuous or unique pad as in *D. gliroides*, allowing for an individual identification as separated pads (i.e., each pad has its own circular central ridge, followed by concentric ridges). In some specimens of *Caluromys* spp. (e.g., USNM 490227♀), a continuous pad is formed by the fusion of i4 with the hypothenar pad in both hands and feet, or only in the feet. In several specimens of *Caluromys* spp., the hypothenar pad doubles the thenar in size. A similar pattern was observed in *Marmosa* spp., in which i1 and thenar pads, and i4 and hypothenar pads are very close, sometimes even in contact (e.g., *M. regina* USNM 577748♂, USNM 577749♀), but do not form a continuous pad (Fig. 1). In *Marmosa* spp., i2 is the largest pad in the manus, while i1 is the largest in the pes. In *Marmosops* spp., i2 and i3 are the largest pads in the manus, followed by i1 and i4, which are similar. The thenar pad is small and rounded, while the hypothenar pad is kidney-shaped. In the pes, the volar surface is very large and pads are located around this central area; the size order is $i1 > i2 > i4 > i3$. The thenar and hypothenar pads are smaller, most of the time separated from i1 and i4, respectively (e.g., *M. fuscatus* USNM 496520♂, USNM 496517♂); sometimes the thenar is joined with i1 although still retaining individuality (e.g., *M. noctivagus* USNM 577755♂). In *Gracilinanus* spp., interdigital pads are larger than thenar and hypothenar pads in both manus and pes, which are not joined to i1 or i4, respectively. In some specimens (e.g., *Gracilinanus dryas* USNM 490248♂), i1 is very close or even joined to the thenar pad, but still retaining individuality. The pattern observed in the hand of *Tlacuatzin canescens* is of large i2-i3 pads,

followed by i1-i4 pads, a kidney-shaped hypothenar pad, and a small thenar pad. In the foot, i1 pad is the largest followed by i2-i4 pads, thenar pad, i3, and hypothenar pad, which is the smallest. The thenar and hypothenar pads are not joined to i1-i4, and remain posteriorly displaced, leaving a large area of the volar surface free of pads until the wrist. The pattern described above for a large sample of medium- to small-sized arboreal and scansorial species shows the arrangement of pads in hands and feet is varied, some species with large interdigital pads (e.g., *T. canescens*, *Gracilinanus* spp.), while others have large thenar or hypothenar pads (e.g., *Caluromys* spp., *Marmosa* spp.). These differences are probably related to the substrates in which animals move and the mechanical forces involved in providing the appropriate grip, but might also show some phylogenetic constraints (see below). Some terrestrial species (e.g., *Metachirus nudicaudatus*) present what appears to be the fusion of i4 and hypothenar pads in the pes, and i1 and thenar pads very close or even joined in the manus, although still retaining individuality (Fig. 1). Specimens of *M. nudicaudatus* also show a naked volar surface and well marked Flexion creases (i.e., a Thenar crease, Middle Finger crease, and Ring Finger crease). In all studied specimens of *M. nudicaudatus*, the interdigital pads had a circular ridge arrangement; thenar and hypothenar pads showed a transversal ridge pattern. In other species of predominantly terrestrial locomotion (e.g., *Lestoros inca*, *Monodelphis* spp.), the thenar or hypothenar pads can be missing, or are very much reduced in size, sometimes lacking structure (i.e., ridges) on their surface (Fig. 1). Specimens of *Monodelphis breviceaudata* (e.g., USNM 490247♂, USNM 490246♂, USNM 490242♂) showed a reduction in all pads in both hands and feet, a loss of the thenar pad, and a large hypothenar pad in the manus, and the loss of the hypothenar pad and a large thenar pad in the pes. In specimens of *L. inca*, all pads lack ridges; the thenar appears to be missing in the manus but is present and larger than the hypothenar in the pes (Fig. 1). A clear difference between *D. gliroides* and other American marsupials was found in the orientation of ridges in all the pads, which are supposed to maximize friction and minimize slipping, especially on uneven surfaces (Hepburn 1895; Whipple 1904). Ridges oriented transverse to the major axis of pads are therefore important in preventing animals from slipping backwards or forward during locomotion, and generating better traction, while concentric ridges are useful in preventing individuals from slipping in multiple directions, or when resulting forces are not oriented along the major axis of each pad. Ridges of all pads in *D. gliroides* with the exception of the hypothenar pad in the manus are transverse to the major pad extension (Fig. 1). In most arboreal and scansorial species of American marsupials, most pads are elevated, have a central circular ridge, and other ridges are arranged more or less concentrically from this central one (e.g., *Marmosa murina*, Fig. 1). More terrestrial species like *Thylamys pallidior* show transversal ridges, with the exception of the thenar and hypothenar pads

in the manus and thenar in the pes. A central circular ridge is also present in i1 to i4 pads in the manus, and i1 to i3 pads in the pes of *M. nudicaudatus* (Fig. 1).

Australian dasyurid marsupials show the typical arrangement of pads, with four interdigital, a thenar, and a hypothenar pad (Pocock 1926). Interestingly, these species have mostly transversal ridges similar to those observed in *D. gliroides*. Apart from this, the overall pattern observed in *D. gliroides* was found to be more similar to Australian diprotodont marsupials of the family Acrobatidae and Burramyidae than to any other American or Australian marsupial (Fig. 2). Comparisons with fluid preserved specimens and published descriptions of *Acrobates*, *Cercartetus*, and *Burramys* shows the same pattern as that of *D. gliroides*, where i1 is very well developed and the thenar pad does not occur, or i1 and thenar pads are fused (Turner and McKay 1989; Flannery 1994). Although convergence between the plantar anatomy of *D. gliroides* with these species cannot be ruled out, it is noteworthy that all of them (including *D. gliroides*) share the primitive $n = 14$ chromosome number, display deep torpor and/or true hibernation (instead of the torpor pattern described for other American and Australian marsupials), and live in what can be considered marginal areas for marsupials (i.e., regions with cool/cold winters and fluctuating food availability) (Tyndale-Biscoe 2005). [It would be interesting to explore

if *D. gliroides* has a pattern of embryonic diapause as that of Acrobatidae and Burramyidae, or other diprotodont marsupials (see Cockburn 1997, and literature cited therein)].

The information presented above for morphology, number, and pad shape described for *D. gliroides* might indicate the ancestral pattern of Microbiotheria + Diprotodontia (new Superorder Microbiodontia), adding support to the phylogenetic relationships proposed by Kirsch et al. (1997), May-Collado et al. (2015), and literature cited therein. Also, and despite extensive modification in finger lengths and general morphology (all Australian diprotodont marsupials are syndactylous), similarities in the number of plantar and palmar pads (but not in their development as per overall area) have been found between *D. gliroides* and some genera in the families Petauridae and Pseudocheiridae, particularly with the genera *Petaurus*, *Dactylopsila*, and especially *Pseudocheirus* (see McKay 1989: figs. 28.1 and 28.2; and also Pocock 1921a; Flannery 1994). All these genera have been recovered as part of the superfamily Petauroidea, which includes Acrobatidae (May-Collado et al. 2015). A similar pattern of very large i1 pad (or i1 + thenar pads) was observed in Phalangeridae, despite extensive modifications (see Flannery 1994: 154–159), which are grouped with Burramyidae in the superfamily Phalangerioidea.

Results of the character mapping show the condition described for hands and feet of *Dromiciops* are shared with Diprotodontia providing support for the Superorder Microbiodontia as proposed herein, and adding support to the placement of *Dromiciops* within Eometatheria sensu Kirsch et al. (1997) (Fig. 3, data matrix in Appendix 2). The occurrence of a large i1 pad (or i1 + thenar pads) in both hands and feet (characters 1 and 4) is shared with Diprotodontia, and appears derived from other marsupials, mammal outgroups used in this study, and other mammals not analyzed (e.g., Primates, Mustelidae, Rodentia; see Whipple 1904; Pocock 1921b, 1922), in which a pattern of four interdigital pads, thenar and hypothenar pads are the most common arrangement/configuration. Non-Microbiodontia marsupials share a pattern of six pads in both hands and feet, with some modifications as described above. It is interesting to note this pattern of a large i1 pad (or i1 + thenar pads) is also present in *Hypsiprymnodon*, considered the living most basal Macropodiformes (Burk et al. 1998), which otherwise show a highly derived pattern of hand and foot pads convergent with Peramelemorphia (Fig. 3). The pattern found in *Dromiciops* also appears in Vombatiformes and Phalangeriformes, giving support to consider *Dromiciops* at the base of the new Superorder Microbiodontia. Characters 2 and 5, which were used to describe the surface of hand and foot pads, show the same synapomorphic trend throughout Microbiodontia, being lost in Vombatiformes but persisting in most genera of Phalangeriformes. In some clades (e.g., Pseudocheiridae), the presence of circular and transversal ridges is probably related to more complex arboreal locomotion, where slipping in multiple directions must be prevented (see above). Despite the derived

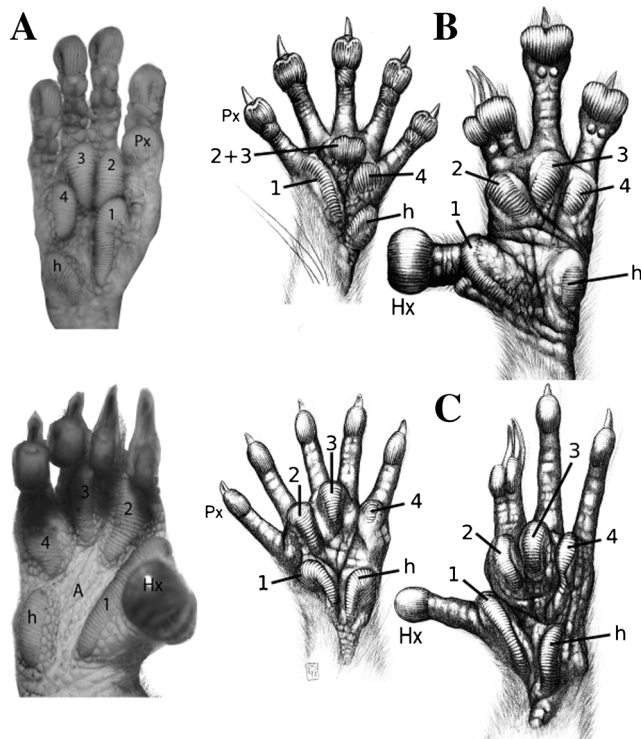
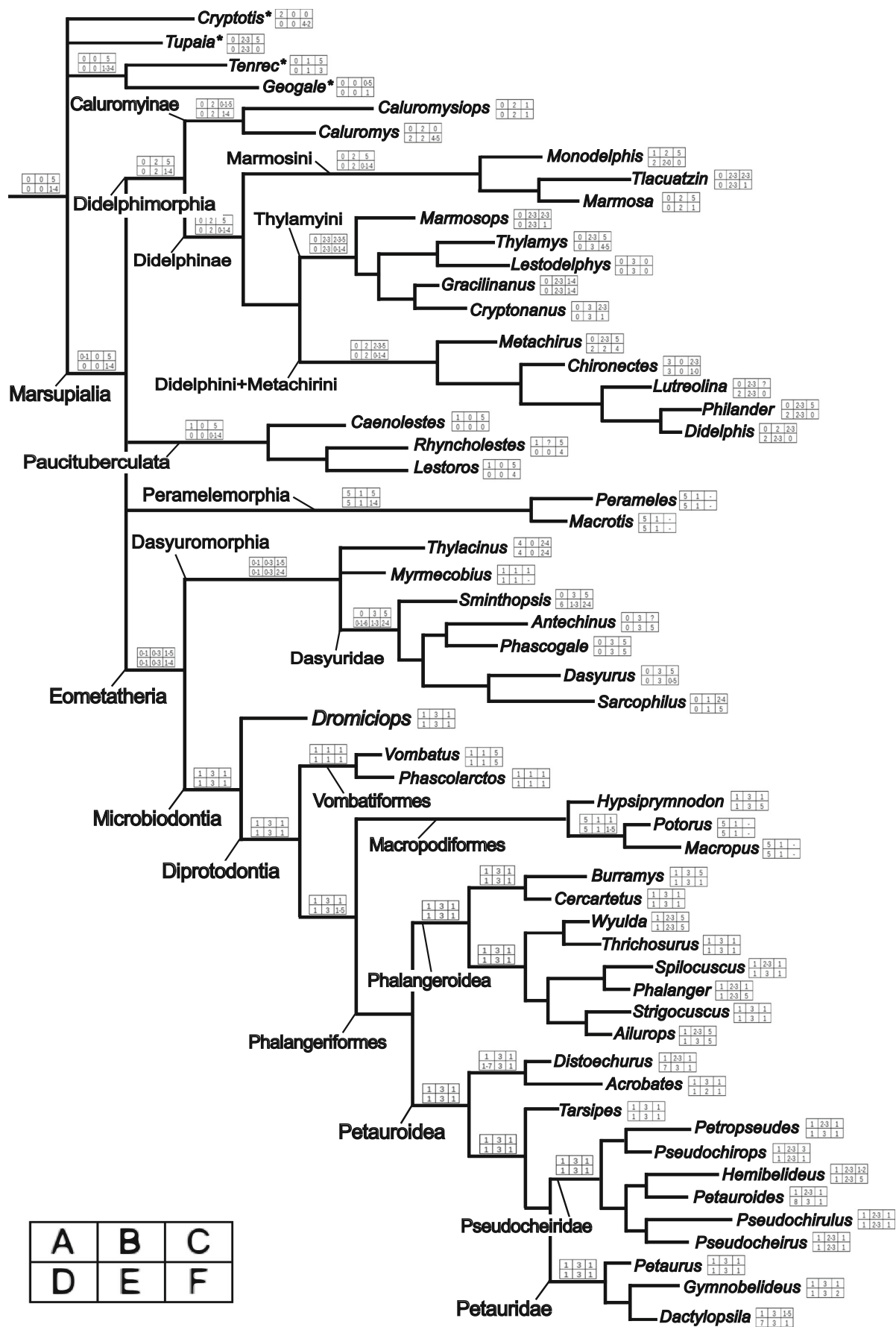


Fig. 2 Compared chiroidia of (A) *Dromiciops gliroides* with (B) *Acrobates pygmaeus* (Acrobatidae), and (C) *Burramys parvus* (Burramyidae). Drawings were modified from Flannery (1994). Pad terminology follows Whipple (1904) and Ashbaugh (1999). Numbers 1 to 4 indicate interdigital pads; h, hypothenar pad; Px, pollex; Hx, hallux; A, volar surface in the foot of *D. gliroides*



◀ **Fig. 3** Character-state mapping of the traits described in the palmar and plantar surface of marsupials and four selected outgroups. The combined phylogeny is based on Voss and Jansa (2009) for Didelphimorphia, and Archer and Kirsch (2006) and May-Collado et al. (2015) for the other groups. Characters-states in A-B-C are for hands, D-E-F for feet. (A) and (D) describe the number of pads in the palmar and plantar surface (characters 1 and 4), respectively; (B) and (E) describe the surface of the pads in hands and feet (characters 2 and 5), respectively; (C) and (F) describe the largest pad in hands and feet (characters 3 and 6), respectively. See text for other explanations

conditions of hand and foot in Macropodiformes, the presence of transversal ridges in palmar and plantar pads is also present in *Hypsiprymnodon* (Fig. 3). The pattern of transversal ridges also appears in the interdigital pads of some dasyurids (e.g., *Antechinus*, *Phascogale*, and *Dasyurus*), and appears combined with circular ridges in pads within some Didelphimorphia (e.g., *Didelphis*, *Gracilinanus*, *Metachirus*, *Philander*), but is not present in Caluromyinae. When analyzing the distribution of these character-states within the phylogenetic framework presented in Fig. 3, a lack of ridges appears to be the most plesiomorphic condition for therian mammals, which is also found in Paucituberculata. Peramelemorphia shows the surface of pads covered with scales and no ridges, a pattern convergent with that of *Myrmecobius* and Macropodidea, all of them with highly derived forms of locomotion. This type of surface also appears in the pads of the mostly terrestrial Vombatiformes, which also includes the arboreal *Phascolarctos*. The pattern of ridges found in Didelphimorphia and most Eometatheria (i.e., Dasyuromorphia and Microbiodontia) are already different at the base of each group, with predominantly circular ridges in the former (character-state 2 in characters 2 and 4), and predominantly transversal ridges in the latter (character-state 3 in characters 2 and 4) (Fig. 3). Despite this, convergence was found in some terminal taxa (e.g., several Didelphinae, Pseudocheiridae), which can be explained by two different evolutionary paths: one going from predominantly arboreal to more scansorial habits (i.e., Didelphinae), in which areas of the pads develop transversal ridges and the other by increasing arboreality and developing (few) circular ridges, added to the common pattern of transversal ones (i.e., Pseudocheiridae). It is also worth noting that despite their mostly arboreal habits (Astúa 2015), caluromyines predominantly show circular ridges, and lack transversal ridges. When characters 3 and 6 (i.e., size of pads in both hands and feet) are analyzed throughout the phylogeny of marsupials, the first interdigital pad (or i1 + thenar pad) is the largest in the palmar and plantar surface of Microbiodontia, with a few species showing a different derived pattern (e.g., *Ailurops*, *Vombatus*, *Wyulda*). The first interdigital pad is also the largest in some genera of Didelphimorphia (e.g., *Caluromysiops*, *Cryptonanus*, *Gracilinanus*), but all these genera also have a well-developed thenar pad, which is absent in *Dromiciops* and other Microbiodontia, as described above.

The information presented herein shows *D. gliroides* does not have an ancestral pattern of chiridia (i.e., hand and foot pads, flexion creases, volar surfaces), compared to other living marsupials. Also, the lack of overall variability in pads and flexion creases does not support the separation of *Dromiciops* into multiple species as proposed by D'Elia et al. (2016). Examination of several fetuses/embryos at different stages of development was important in showing the presence of a single i1 or i1 + thenar pad, a consistency between pads in adults and developed fetuses/embryos, and that the development of pads occurs at a later stage of development. The development of i1 pad closer to the area between the first and second fingers, and the lack of development of a thenar pad observed in fetuses/embryos, add support to considering the pad in that area of the hand and foot as i1, and not a fusion of i1 + thenar pads. The information discussed above also suggests that the formation of pads starts sometime late in the development of fetuses/embryos, probably in what Muñoz-Pedreros et al. (2005) defined as the Intra-marsupium Stage IV of development, a period in which pouched young apparently remain within the marsupium, while firmly attached to the teats. This stage is supposed to occur for about two months (November–December), consistent with the dates from the tags in the studied specimens. Based on the year-round cycle proposed by Muñoz-Pedreros et al. (2005) and the observations described above, it can be postulated that pads finish their development at Stage IV, while ridges develop during the Extra-marsupium Stage V of development, in which pouch young increase their motor capacities, abandon the marsupium for short excursions while they continue to suckle. This stage was previously defined by Hershkovitz (1999) as the nesting phase. This period of exploratory activities would benefit from well-developed pads and ridges, which would provide friction and better grasping for the young, while they learn to forage and move throughout the canopy by themselves.

The results of this work add support from a morphological point of view, for a relationship between *D. gliroides* and several (highly derived?) Australian marsupials, placing *D. gliroides* as nested within the Australian radiation as proposed by Kirsch et al. (1997), Springer et al. (1998), Burk et al. (1999), May-Collado et al. (2015), and literature cited therein. The new Superorder Microbiodontia would include all diprotodont marsupials and *D. gliroides*, in which the latter species would have the ancestral hand and foot pad pattern for the group.

Future research in pad formation and development, ridges and crease orientation could add more information to the affinities of both American and Australian marsupials, while improving our knowledge on the locomotor activities of marsupials in general.

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Compliance with Ethical Standards

Conflicts of Interest None

Appendix 1

List of specimens analyzed for this study. Acronyms are as follows: BMNH, British Museum of Natural History, London; CML, Colección “Miguel Lillo,” San Miguel de Tucumán; CRUB-M, Centro Regional Universitario Bariloche, Colección de Mamíferos, Universidad Nacional del Comahue, Bariloche; FMNH, Field Museum of Natural History, Chicago; LIEB-M, Laboratorio de Investigaciones en Evolución y Biodiversidad, Colección Mastozoología, Universidad Nacional de la Patagonia “San Juan Bosco,” Esquel; MACN, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia,” Buenos Aires; MMP, Museo de Mar del Plata “Lorenzo Scaglia,” Mar del Plata; NMW, Naturhistorisches Museum Wien, Vienna; OMNH, Sam Noble Oklahoma Museum of Natural History, Norman; RS, Richard Sage collection; UACH, Universidad Austral de Chile, Valdivia; USNM, United States National Museum – Smithsonian Institution, Washington, D.C.

Dromiciops gliroides: BMNH 22676; BMNH 35.11.10.49; BMNH 19.1.1.46–47; BMNH 92.5.9.3; CRUB-M-011; CRUB-M-013; CRUB-M-015-19; CRUB-M-028; CRUB-M-154; CRUB-M-177; CRUB-M-197-199; FMNH 129815; FMNH 22677; FMNH 127441, FMNH 127452; FMNH 134557; LIEB-M-1529-1531; MACN 48.26; CML 1869; UACH 687–90; UACH 836; UACH 986; UACH 1053; UACH 1056–57; UACH 1059; UACH 1731; UACH 1733–35; UACH 2144–57; UACH 2159–66; UACH 2565; UACH 3129; UACH 3131; UACH 3479–83; UACH 3655–56; UACH 4324; UACH 6161; UACH 6906; UACH 6997–7000; UACH 7027–28. Fetuses/Embryos: RS 18110 ($n = 2$); RS 18111 ($n = 2$); RS 18126 ($n = 4$); RS 18138 ($n = 5$); RS 18605 ($n = 2$).

Other marsupial species analyzed: *Acrobates pygmaeus*: USNM 221334, USNM 221346, USNM 223137, USNM 588353, USNM 588351. *Caenolestes* spp.: FMNH 72394, FMNH 72395, FMNH 72393, and see Martin (2008). *Caluromys* spp.: USNM 14812, USNM 4902289, USNM 490227, OMNH 10595, OMNH 9753–4, NMW 28622,

NMW 28624. *Caluromysiops irrupta*: OMNH 2838. *Cercartetus nanus*: NMW 63158. *Cryptonanus* spp.: USNM 236329, USNM 236677, USNM 19651. *Didelphis* spp.: USNM 8317, USNM 391488, USNM 391496, USNM 391500, USNM 391486, USNM 4947, USNM 490497, USNM 261389, USNM 261391, USNM 490528, USNM 522977, USNM 268736, USNM 399450, USNM 259851, USNM 60432, USNM 514482. *Gracilinaus* spp.: USNM 490248, USNM 490432, USNM 579272, USNM 385017, USNM 370047, OMNH 17359–61, OMNH 17373–74, NMW 28620. *Lestodelphys halli*: LIEB-M-1532-1533. *Lestoros inca*: USNM 194938, USNM 194942, USNM 194941, USNM 194943, FMNH 75587, FMNH 172034, FMNH 172036, FMNH 172038, FMNH 172040, FMNH 172041, FMNH 172043. *Lutreolina crassicaudata*: NMN 536832, USNM 536833, USNM 536834, USNM 536835. *Metachirus nudicaudatus*: MMP AN210, MMP 1255, MMP 1472, MMP 1475, USNM 391472, USNM 499760, USNM 57756, NMW 30651. *Marmosa* spp.: USNM 12888, USNM 14629, USNM 549604, USNM 549603, USNM 577748, USNM 577749, USNM 490259, USNM 496526, USNM 4900255, OMNH 37209, OMNH 9751, OMNH 37212–13, NMW 21682, NMW 21683, NMW 33857, NMW 23428, NMW 48888, NMW 48889, NMW 48891, NMW 29578–29,580. *Marmosops* spp.: USNM 496520, USNM 496517, USNM 577755, USNM 577752, USNM 551523, OMNH 37214, OMNH 37211, OMNH 37210, OMNH 37218, NMW 27464. *Monodelphis* spp.: USNM 490247, USNM 490246, USNM 490242, USNM 490240, OMNH 17380–81, OMNH 17387, OMNH 17377, OMNH 10596, OMNH 37221–24, NMW 28621. *Philander opossum*: MMP 57, MMP FN 591, MMP 3902, OMNH 17375. *Rhyncholestes raphanurus*: MMP 4055, FMNH 129825, FMNH 92832, FMNH 127476, and see Martin (2008). *Thylamys* spp.: MMP FN8291, MMP 16–7, MMP I10, MMP T33, MMP I397, MMP I399, MMP I404–6, MMP I410, MMP I412–3, MMP I416, MMP I446–9, MMP I451–3, MMP I620–2, MMP I766, MMP 836, MMP 844, MMP 859–63, MMP 875, MMP 2060, MMP 4072, MMP 4075–7, MMP 4079, and see Martin (2008, 2009). *Tlacuatzin canescens*: USNM 269980, USNM 512672, USNM 510080, OMNH 36199, OMNH 26640–42.

Appendix 2

The morphological data described and analyzed in this report is reproduced below. Missing data are indicated as “?”, and inapplicable characters are indicated as “-”. Square brackets enclose observed polymorphisms.

Geogale 0000[05]1

Tenrec 001153

Tupaia 00[23][23]50

Cryptotis 20000[42]

Caluromys 02220[45]
Caluromysiops 002211
Didelphis 022[23][23]0
Chironectes 3300[23][10]
Lutreolina 02[23][23]?0
Philander 02[23][23]50
Metachirus 00[23]25[45]
Marmosa (including *Micoureus*) 002251
Monodelphis 122[20]50
Tlacuatzin 00[23][23][23]1
Cryptonanus 0033[23]1
Gracilinanus 00[23][23][14][14]
Lestodelphys 003300
Marmosops 00[23][23][23]1
Thylamys 00[23]35[45]
Caenolestes 100050
Lestoros 100054
Rhyncholestes 10?054
Thylacinus 4400[24][24]
Myrmecobius 11111-
Sarcophilus 0011[24]5
Dasyurus 00335[05]
Phascogale 003355
Sminthopsis 063[13]5[24]
Antechinus 0033?5
Macrotis 5511--
Perameles 5511--
Dromiciops 113311
Phascolarctos 111111
Vombatus 111155
Cercartetus 113311
Burramys 113351
Ailurops 11[23]355
Strigocuscus 113311
Thrichosurus 113311
Wyulda 11[23][23]55
Phalanger 11[23][23]15
Spilocuscus 11[23]311
Hypsiprymnodon 113315
Macropus 5511--
Potorus 5511--
Acrobates 113211
Distoechurus 17[23]311
Tarsipes 113311
Pseudochirops 11[23][23]31
Petropseudes 11[23]311
Pseudocheirus 11[23][23]11
Pseudochirulus 11[23][23]11
Hemibelideus 11[23][23][12]5
Petauroides 18[23]311
Petaurus 113311
Gymnobelideus 113312
Dactylopsila 1733[15]1

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