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Hind limb myology of the southern brown bandicoot *Isoodon obesulus* and greater bilby *Macrotis lagotis* (Marsupialia: Peramelemorphia)

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Abstract

Bandicoots and bilbies (order Peramelemorphia) represent the principle group of omnivorous marsupials from a range of habitats across Australia and New Guinea. Bandicoots and bilbies most commonly use quadrupedal, asymmetrical half-bounding or bounding gaits and present an unusual combination of hind limb morphological features, including an ossified patella, a modified tibiofibular joint, and syndactylous morphology of the pes. We performed comparative dissections of the hind limb of the southern brown bandicoot (*Isoodon obesulus fusciventer*; n = 13) and greater bilby (*Macrotis lagotis*; n=4) providing detailed descriptions of the muscular anatomy. These species displayed significant modification of the hind limb muscular anatomy and associated connective tissues, including emphasis on multi-articular muscles, such as the hamstrings, and extreme development of fascial structures. These patterns were more extreme in *I. obesulus* than in *M. lagotis*. Differences between the hind limb anatomy of the *I. obesulus* and *M. lagotis* reflect the different ecological and environmental pressures on their locomotion and digging behaviours.
Introduction

Bandicoots and bilbies (order Peramelemorphia) represent the principle group of omnivorous marsupials from a range of habitats across Australia and New Guinea (Gordon and Hulbert 1989). Bandicoots and bilbies most commonly use quadrupedal, asymmetrical half-bounding or bounding gaits (Bennett and Garden 2004). Within the monophyletic cohort Australidelphia (Szalay 1982), peramelemorphs present an unusual combination of skeletal features of the hind limb. Firstly, as marsupials, they possess bilateral epipubic bones, which serve as an attachment point for muscles of both the abdomen and the hind limb. Secondly, peramelemorphs are unusual among marsupials in that they possess an ossified patella. Typically only a cartilaginous patelloid is present in marsupials (Szalay 1994; Reese, Pfuderer et al. 2001), although there are exceptions (Notoryctes; Warburton 2006). Thirdly, the fibula does not articulate with the femur at the knee, as it does in almost all other marsupials, and consequently there is no femoro-fibular disc (Barnett and Napier 1953). The distal fusion of the tibia and fibula in the greater bilby (Macrotis lagotis) and pig-footed bandicoot (Chaeropus ecaudatus) is also uncommon (Barnett and Napier 1953). Finally, peramelemorphs possess a syndactylous morphology of the pes, in which the second and third digits are developmentally and anatomically bound together and relatively diminutive in comparison to the weight-bearing fourth and fifth digits. The syndactylous pes is similar to the pedal morphology of diprotodontian marsupials (Szalay 1982; Szalay 1994; Archer and Hand 2006), however, molecular studies do not support a close affinity of these two groups, but rather suggest convergent evolution of this trait (Kirsch, Lapointe et al. 1997; Amrine-Madsen, Scally et al. 2003).

Despite their phylogenetic placement and distinctive morphology, relatively few descriptions of bandicoot musculature are available (Parsons 1903; Elftman 1929; Horiguchi 1981; Filan 1990). In terms of comparative anatomy, little attention has been given to morphological diversity between different groups of ‘bandicoots’, though there are obvious differences between the major lineages and highly specialised forms have evolved (e.g. C. ecaudatus and Macrotis spp.). From the standpoint of palaeontology and paleoecology, species specific data of the relationship between the morphology of the bones and the related patterns of myology will contribute to the development of ecological and evolutionary hypotheses within fossil bandicoots and among marsupials more broadly.
Following the recent description of the forelimb muscular anatomy (Warburton, Gregoire et al. 2013), the current study provides detailed myological descriptions of the hind limb of the southern brown bandicoot (Isoodon obesulus) and greater bilby (M. lagotis). The descriptions, muscle maps and comparative notes reported here provide baseline morphological data for an examination of the musculoskeletal basis of bandicoot locomotion, and for palaeontologists and neontologists investigating morphological evolution in living and fossil bandicoots. This work also represents a contribution to our understanding of the comparative morphology of marsupials and synonymises the nomenclature of the muscles described here with terms given by previous workers.

Methods
Ethically sourced cadaver specimens of southern brown bandicoots I. obesulus fusciventer were obtained from the Perth metropolitan area with approval of the Murdoch University Animal Ethics Committee. Specimens were predominantly victims of road incidents and were sourced from frozen collections at Kanyana Wildlife Rehabilitation Centre (Western Australia; n = 7), the Department of Parks and Wildlife (DPaW; n = 1) and directly under licence (Reg. 17 SF006788; n = 1 and SF009640; n = 4). Cadavers of captive-bred greater bilbies M. lagotis, euthanized for humane reasons, were donated by Kanyana Wildlife Rehabilitation Centre (n = 3), and DPaW (n = 1) for dissection.

Frozen specimens were thawed, skinned, eviscerated and embalmed using a solution of 10% formalin and 4% glycerol solution for one week, before being stored in 70% ethanol (n=8). Standard dissecting techniques were used. Muscles were identified, their attachments recorded, and then removed from the skeleton. After muscle removal, skeletal material was boiled to remove any traces of flesh to allow observation of the bones for muscle attachment processes and scars. As far as possible, the anatomical terminology follows the Nomina Anatomica Veterinaria.

In order to obtain data on wet muscle weights, five additional specimens of I. obesulus were dissected immediately after thawing (unfixed). Individual muscles were dissected away from the limb and weighed immediately on a Mettler BasBal digital scale (2006). Raw muscle data are presented in appendix 1. The proportional length of the muscle bellies of the plantar flexor muscles was calculated as the ratio of total muscle length (from origin to insertion) to
muscle belly length (after dissection away from the tendon). Lengths were measured using a standard dress-maker’s measuring tape.

To facilitate anatomical comparison and interpretation of the literature, unfixed non-peramelemorphian specimens were dissected following the technique described above: western grey kangaroo *Macropus fuliginosus* (King River International Abattoir; n = 3), brush wallaby *Macropus irma* (DPaW; n = 1), quokka *Setonix brachyurus* (DPaW; n = 3) and brush tail possum *Trichosurus vulpecula* (Reg. 17 SF009640; n = 3). Comparative anatomical and nomenclatorial remarks from the published literature (Table 1) are included within the results, in order to avoid unnecessarily repetition.

**Results**

The hind limb bones of *I. obesulus* are relatively shorter and more robust than those of *M. lagotis* (Figure 1). The difference in length is principally a function of relatively shorter tibia compared to femur length (crural index). The metatarsal length relative to femur length is also shorter in *I. obesulus*. At rest and whilst digging, both species take on a highly flexed, plantigrade hind limb posture as illustrated in Fig. 1B for *M. lagotis*. During locomotion, *M. lagotis* exhibits a more extended, digitigrade posture of the hind limb with hind quarters raised in comparison to the more strongly flexed posture in *I. obesulus*. The first digit of the pes is highly reduced in *I. obesulus*; in *M. lagotis* the first digit and metatarsal is absent. In both species, the syndactylous second and third digits are relatively short and gracile, in comparison to the long, robust fourth digit, and slightly shorter fifth digit.

**Extrinsic muscle of the pelvic limb**

*M. iliopsoas*

*M. iliopsoas* is a long deep flexor of the hip joint formed by the fusion of the m. iliacus and m. psoas major. It arose from the ventrolateral surface of the body of the ilium (m. iliacus; Fig. 2b, d), the ventral surface of the body and the transverse processes of the lumbar vertebrae (M. psoas). The two portions fused into one belly at the level of the lumbosacral junction and inserted together onto the lesser trochanter of the femur (Fig. 3a,b,c,e,f). In *I. obesulus* the insertion also extended onto the neck of the femur (Fig. 3 a-c). In both *I. obesulus* and *M. lagotis* the iliopsoas appeared to be a relatively long and strongly developed muscle.
Gluteal region

*M. tensor fascia latae*

*M. tensor fascia latae* was identified in *I. obesus* as a broad, thin triangular muscle sheet covering the caudal gluteal region and lateral thigh, and connecting to the fascia lata passing cranially to meet the sartorius, and on its caudal margin penetrating to insert along the two-thirds of the lateral edge of the femur (Figs. 3a,c,d; 4a). In *M. lagotis* the muscle was exceedingly thin, and the insertion limited to the middle third of the lateral femur via the deep fascia.

This muscle is generally regarded as absent, or at least not recorded, in most marsupials (Barbour 1963). A distinct tensor faciae latae has been reported in *Sarcophilus* (Macalister 1872) and in macropods (Hopwood and Butterfield 1976; Warburton, Yakovleff et al. 2012).

*M. gluteus superficialis* (*M. ectogluteus*) and *M. gluteofemoralis* (*M. caudofemoralis*, *M. agitator caudae*)

The superficial gluteal region comprised a number of muscle portions which arose from the gluteal fascia, lumbosacral fascia and sacrocaudal vertebral column which function primarily for extension of the hip joint. These muscle portions were separable into a number of thin laminae, in which the caudal (posterior) laminae overlapped the more cranial sheets, such that the whole resembled overlapping tiles or scales (Fig. 4b). The most superficial caudal portion comprising the *m. gluteofemoralis* (*m. caudofemoralis* or *m. agitator caudae*) was itself subdivided into two portions; a caudal strap muscle from the transverse processes of the last sacral and first caudal vertebrae inserted most distally to the lateral femur below the greater trochanter, and a broader triangular sheet from the thick sacral fascia, which had an aponeurotic insertion to the cranilateral aspect of the greater trochanter of the femur and most proximal part of the lateral femur. In some specimens an additional distinct tendon, passing to the lateral aspect of the knee, was also observed. The caudal aspect of the sheet lay deep to the cranial margin of the biceps femoris. *M. gluteus superficialis* arose mostly from the thick gluteal fascia from spinous processes of the S1-3 and was present as a thin fan-shaped muscle and inserted obliquely to the base of the greater trochanter (Figs. 3a, d, h). Each of the preceding muscle portions was quite thick at its origin, but very thin at the site of insertion, and very difficult to dissect. Parsons (1903) describes a similar arrangement in *C. ecaudatus*, including a narrow tendon of the gluteofemoralis (caudofemoralis) inserting to the cranilateral aspect of the patella.
**M. gluteus medius**

M. gluteus medius was a thick, broad and fleshy muscle from the lateral surface of the iliac crest and the deep lumbar fascia and aponeurosis of the m. sacrocaudalis (Figs. 2a, d 4b). The sciatic nerve passed over its deep surface. The medial gluteal muscle was inserted by both fleshy fibres and strong aponeurotic sheets to the crest and caudal margin of greater trochanter of the femur (Figs. 3d, h). M. gluteus medius acts to extend the hip joint. This muscle is often quite complex in internal architecture, particularly in macropodids (Hopwood and Butterfield 1976; Warburton, Yakovleff et al. 2012).

**M. gluteus profundus**

M. gluteus profundus was observed as a discrete muscle belly which arose from the common aponeurosis on the deep surface of the m. gluteus medius, from cranial half of the dorsolateral aspect of the ilium, and from the iliac tuberosity to level with the first sacral spine. The insertion was to the apex of the greater trochanter (Figs. 2a, c, 3, 4c). Action: extension of the hip joint.

**M. gluteus minimus and M. gluteus quartus**

M. gluteus minimus arose from the caudolateral aspect of the ilium (Figs. 2a, c, 3, 4c). In *M. lagotis* the origin was from the body of the ilium, taking an arc from the mid-ventral crest to the mid-dorsal border, at the level of the caudal margin of the acetabulum. In *I. obesulus* the origin was broader and extended more cranially. The fleshy belly converged to a broad tendon that inserted to the lateral aspect of the greater trochanter. An additional small portion of short muscle fibres was separable, arising from the ilium close to the hip joint and inserting into the medial aspect of the greater trochanter corresponded to the gluteus quartus observed in *D. viverrinus* (MacCormick 1886) and *C. ecaudatus* (Parsons 1903). Action: extension of the hip joint.

As is common in marsupials, the muscles of the gluteal region and deep hip region were particularly complex, with a highly laminated arrangement, extremely thin superficial portions and thick fascial connections. This region in marsupials does not conform to the arrangement of muscles in the typical eutherian models and poses particular challenges when trying to apply standard nomenclature.
Two muscles lying in the same plane were found, deep to the gluteal muscle group and sciatic nerve but superficial to the gemellus, (Fig. 4b). These appear to correspond to the muscles variably identified as ischiofemoralis and/or piriformis among various marsupials. The more caudal muscle, m. ischiofemoralis, originated from the transverse processes of sacral vertebrae (S2-3), the deep dorsal fascia and the sacroiliac ligament passing between ischiatic spine and sacrum. The muscle consisted of long fleshy fibres throughout, and inserted along the caudolateral aspect of the femoral shaft from the base of greater trochanter for approximately two-fifth the length of the bone in I. obesulus (Fig. 3c, g). The insertion was less extended along the proximal third of caudolateral aspect of femur in M. lagotis. The more cranial m. piriformis was triangular in shape, and originated from the first two caudal transverse processes and inserted via aponeurotic fibres to the tip of the greater trochanter. Action: extension of the hip joint.

The muscles herein referred to as mm. ischiofemoralis and piriformis, lying deep to the sciatic nerve and superficial to the mm. quadratus femoris, gemelli and obturator internus, do not appear homologous with any muscles typically found within eutherian mammals. The cranial portion represents the muscle that in many marsupials has been given the name m. piriformis, arising from the sacral and first caudal vertebrae (see Barbour 1963 for review). While the origin roughly corresponds to the m. piriformis, the eutherian piriformis lies superficial to the sciatic nerve as illustrated in the dog (Miller 1988). The name m. ischiofemoralis has sometimes been applied to muscles of similar description in marsupials, though the name does not reflect the anatomical origin from the caudal vertebrae. We observed two distinct muscles in this region and for consistency with the marsupial literature we have maintained both names, though we acknowledge that this nomenclature is not ideal.

M. obturatorius internus
The internal obturator muscle arose from the dorsal rim of the obturator foramen (Fig. 2a, c). The thin, fleshy sheet of muscle fibres converged to a short tendon that passed over the ischiatic spine and superficial surface of the mm. gemelii to insert into the proximal part of the trochanteric fossa of the femur (Figs. 3c,g). The internal obturator acts as a lateral rotator of the hip joint.
**Mm. gemelli**

Mm. gemelli arose from a relatively large area on the body of the ischium, caudolateral to the obturator foramen (Fig. 2a,c) and inserted into the proximal trochanteric fossa together with the tendon of the internal obturator (Fig. 3 c,g). The separation of the two heads was not always clear, though there was an appearance of two portions. Action: lateral rotation of the hip joint.

**M. quadratus femoris**

The strongly developed m. quadratus femoris arose from the ischiatic table, caudal to the obturator foramen (Fig. 2b,d). In *M. lagotis*, two distinct portions were obvious, while in *I. obesulus* the two portions were combined into one large fleshy mass. In *I. obesulus*, the insertion was via a strong tendon to the rugose surface on the mid-caudal femoral shaft (Fig. 3b-d). In *M. lagotis*, the medial portion inserted to the mid-caudal tuberosity while the lateral portion inserted some distance away to the caudal aspect of the lesser trochanter (Fig. 3g). Action: extension of the hip joint.

This muscle is generally present in marsupials, though the nomenclature has been problematic (“caudofemoralis” Thompson & Hillier 1905, “glutofemoralis” Warburton 2006). Parsons (1903) describes a similar muscle as “presemimembranosus” in *C. ecaudatus*. The separation into two portions is not typical; the muscle is apparently single in *Di. virginiana* (Coues 1871), takes a broad continuous origin along the ischiatic ramus in macropods (Hopwood and Butterfield 1976; Warburton, Yakovleff et al. 2012) but has a double origin in *Da. viverrinus* (MacCormick 1886).

**Cranial thigh**

**M. sartorius**

In *M. lagotis*, m. sartorius arose from the cranial ventral iliac spine and inserted to the medial crural fascia over the proximal tibial crest (figs 2a-d, 4a). In *I. obesulus*, the sartorius was divisible into a cranial portion from the cranial ventral iliac spine and a caudal portion from the gluteal fascia over the m. iliacus. On the lateral aspect of the thigh, the caudal margin of the sartorius fused with the thick fascia lata. The insertion was to the medial aspect of the patella and distal fascia of the vastus medialis. Action: flexion of the hip joint to protract the free limb.
Mm. quadriceps femoris

The quadriceps femoris group consists of four muscles that are responsible for extension of the knee joint. M. rectus femoris deep to m. sartorius was very large. The origin extended from the rectus tubercle on the lateral spine of the ilium, immediately cranial to the acetabulum, cranially to roughly the midpoint of the lateral border of the ilium in M. lagotis, and more than two-thirds along the length of the ilium in I. obesusulus (figs 2b, d, 3, 4a). In addition to extension of the knee joint, m. rectus femoris also contributes to flexion of the hip joint. M. vastus lateralis arose from the lateral aspect more than half of the femoral shaft in I. obesusulus. In M. lagotis the origin was restricted to the base of the greater trochanter. M. vastus medialis arose from the proximal medial aspect of the femoral neck. M. vastus intermedius arose from entire length of the cranial aspect of the femoral shaft in M. lagotis, and the distal two-thirds of the cranial aspect of the shaft of the femur in I. obesusulus, deep to m. rectus femoris. The medial vastus muscle was the smallest portion of the quadriceps and in Isoodon it was difficult to separate the medial and internal bellies. The four muscles of the quadriceps group converge to insert to the cranial, lateral and medial borders of the patella and via the patellar tendon to the crest of the tibia.

Medial thigh

M. gracilis

In M. lagotis, m. gracilis was a small muscle, passing from the caudal third of the pubic symphysis (Fig. 2d) to the crural fascia, level with the distal portion of tibia crest, and immediately proximal to the insertion of the m. semitendinosus. In I. obesusulus the gracilis was much broader and covered almost the entire medial aspect of the thigh. It arose from the caudal two-thirds of the pubic symphysis (Fig. 2b) and inserted via the thick crural fascia to the medial surface of the tibia and the tibial crest. The gracilis contributes to extension and adduction of the hip joint.

M. pectineus

M. pectineus arose from the iliopectineal eminence of the pubis and inserted by fleshy fibres to the medial aspect of the femur, at approximately the junction of the proximal and middle thirds of the shaft (Fig. 2b). In M. lagotis the insertion is slightly more distal than in I. obesusulus. M. pectineus contributes to adduction of the hip joint.
**Mm. adductores**

In *I. obesusulus*, the adductors arose along the ventral surface of the pubis and the ventral half of the greater ischiatic arch (Fig. 2b). The insertion was to the distal two-thirds of the caudomedial aspect of the femur to almost the level of the medial epicondyle. The muscle mass was roughly separable into two portions. In *M. lagotis* a greater degree of internal separation was evident; one portion passed from ischiatic table to the distal half of caudal line of the femur; a strap from the ischiatic table to the distal caudal aspect of femur; a triangular portion from along the ramus of the ischium to the distal half of medial shaft of the femur; a small portion from the cranial end of the pubic ramus to the rugose surface on the medial aspect of the shaft of the femur, immediately distal to the lesser trochanter (Fig. 2d). The adductors act to adduct the thigh and extend the hip joint.

**M. obturatorius externus**

The fleshy fibres of *m. obturatorius externus* took a broad origin from the ventral aspect of the ischium and pubis, encircling the obturator foramen (Fig. 2b,d). The insertion filled all but the most proximal part of the trochanteric fossa of the femur, immediately distal to the much smaller tendons of the mm. gemelli and internal obturator (Fig. 3). Action: lateral rotation of the femur at the hip joint.

**Caudal thigh**

**M. biceps femoris**

*M. biceps femoris* was a thick muscle on the lateral aspect of the thigh and was incompletely separable into two heads. In *I. obesusulus*, the caudal head (biceps caudalis) originated from the sacrum via the lumbo-dorsal fascia, and the cranial head (biceps proprius) arose from the ischiatic tuberosity (Fig. 2b). In *M. lagotis*, the caudal head more distinctly arose from the second sacral to the first caudal vertebra, with only a small connection to the ischiatic tubercle (Fig. 2d). The insertion was to the lateral surface of the patella and the lateral part of the crural fascia in the proximal half to two-thirds of the leg via a thick fascial sheet (Fig. 5b,c,e). *M. biceps femoris* acts to extend the hip, knee and tarsus (via the fascial sheath of the common calcaneal tendon) of the weight-bearing limb. In the non-weight-bearing limb this muscle will also contribute to flexion on the knee joint.
**M. abductor cruris caudalis (M. tenuissimus)**

The caudal crural abductor was a very long strap muscle, lying between the deep surface of the m. biceps femoris, and the lateral aspect of m. semitendinosus. It arose from the transverse process of the second caudal vertebrae (Ca2) and inserted to the lateral distal crural fascia, and fascial sheath for the common calcaneal tendon in the distal third of the tibia. In one specimen, there was an additional medial slip from a tendinous intersection inserting in to the distomedial crural fascia. This muscle was relatively strongly developed in *I. obesulus* and *M. lagotis*. Action: contributes to extension of the hip and knee joints in the weight-bearing limb. (Abduction of the hind limb at the hip joint is limited.)

In many marsupials, including *Didelphis* (Coues 1871), *Trichosurus* (Barbour 1963) and *Dasyurus* (Macormick), the caudal head (m. cruro-coccygeus) has a tendinous intersection, midway along it’s length, which gives rise to a medially inserting portion, as well as the lateral insertion to the crus of the main belly. Parsons (1903) describes the biceps femoris as a single muscle in *C. ecaudatus*, however he describes a muscle belly splitting into medial and lateral as the semitendinosus, which may represent in part what we have referred to here as the caudal head of the biceps.

**M. semitendinosus**

M. semitendinosus arose from the caudoventral aspect of ischial tuberosity (Fig. 2b, d), and inserted to the middle third of the medial aspect of crural fascia, distal to the tibial crest. This muscle was incompletely separable into two portions. Action: extension of the hip, knee and tarsus joints in the weight-bearing limb; knee flexion in the free limb.

**M. semimembranosus**

In *M. lagotis* the semimembranosus arose from the caudal border of the ischium (fig, 2b, d) and inserted to the medial fascia of the knee, covering the medial epicondyle of the femur and the medial border of the tibial plateau. In *I. obesulus* this very large muscle arose from the ischiatic tuberosity and ventral surface of the ischiatic arch, and inserted to the medial aspect of the fascia of the crus. Action: extension of the hip, knee and tarsus in the weight-bearing limb; knee flexion in the free limb.

Occasionally, two distinct portions (semimembranosus and presemimembranosus) have been recorded in marsupials, including *T. vulpecula* (Barbour 1963), though Hopwood and
Butterfield (1976) consider the partial to complete separation of the muscle belly to be variable, at least within *Macropus giganteus*.

**Muscles of the leg**

*M. tensor of the crural fascia*

The tensor of the crural fascia was a thin sheet of muscle that arises from the lateral head of the m. gastrocnemius and lateral fibular fascia (Fig. 4a). It inserted into the crural fascia from the level of the tibial crest proximally to the sheath of the common calcaneal tendon distally. The crural fascia was very thick in the both species and enclosed the crus, from the knee to the common calcaneal tendon. A number of muscles, including the *m. semimembranosus*, *m. semitendinosus*, and *m. biceps femoris*, contributed to the fascia via their aponeurotic insertions. A distinct tensor muscle of the crural fascia is very unusual, and has not been reported in any other marsupials.

**Cranial leg**

*M. tibialis cranialis*

The cranial tibial muscle arose from the proximal third of the cranial border of the tibia, immediately below the lateral tibial condyle, and filled the depression on the lateral aspect of the tibial crest (Fig. 5b,e, 6a-b). In *I. obesus*, the belly remained fleshy to the upper ankle joint before giving rise to a tendon that was inserted to the tubercle on the plantar-medial aspect of the base of the first metatarsal. In *M. lagotis* the muscle gave rise to a tendon in the distal third of the crus that was traced to the medial cuneiform. Parsons (1903) gives the insertion of the ‘tibialis anticus’ to the base of metatarsals II and III in *C. ecaudatus*, which corresponds to the absence of the first metatarsal in that species. Action: extension (dorsiflexion) of the tarsus.

*M. extensor digitorum longus (EDL)*

Two muscle portions were found to correspond to the long digital extensors. The more proximal origin from the head of the fibula (Fig. 5a-c,e) gave rise to a broad tendon that inserted to the dorsal aspect of the distal phalanx IV. The second portion originated from the lateral aspect of the tibial shaft adjacent to the head of the fibula and proximal interosseous membrane. In the distal third of the crus, the small muscle belly gave rise to two thin tendons, which passed under the tarsal retinaculum and dorsally over the foot to insert to
the extensor facia of digits II and III as far as the distal phalanx. Parsons (1903) reports insertions of two tendons to digit IV only in *C. ecaudatus*.

*M. extensor digitorum lateralis*

The lateral extensor of the digits originated from the proximal lateral aspect of the tibia and cranial border of the fibula and the interosseous membrane, lateral to the two heads of the m. extensor digitorum longus (fig 5a-c,e). The tendon passed alongside that of the long digital extensor to the extensor fascia over the middle and distal phalanges of digits IV and V. The belly and tendon were relatively larger than the preceding muscle.

No long extensor muscle of the first digit (m. extensor hallucis longus) as found in *Trichosurus* (Barbour 1963) and other arboreal marsupials (*e.g.* “Extensor proprius pollicis longus” *D. virginiana* (Coues 1871)) was identified in either the *I. obesulus* or the *M. lagotis*. This muscle is reportedly absent in *C. ecaudatus* (Parsons 1903) and some dasyurids corresponding to the reduction or absence of the first digit (Barbour 1963).

**Lateral leg**

*M. fibularis [peroneus] longus*

M. fibularis longus was a fusiform muscle, which arose by a flat tendon from the lateral aspect of the fibular head (Fig. 5). The distinct belly gave rise to a tendon that passed on the lateral aspect of the tarsus, and under the process of the cuboid via a fibrous sheath to the plantar aspect of pes. In *I. obesulus*, the tendon could be traced to the medial cuneiform, with a small slip to the base of the first metatarsal. In *M. lagotis*, the tendon could not be traced more medially than the level of the cuboid metatarsal articulation. In *I. obesulus*, the belly extended for the length of the fibula and became tendinous at the level of the lateral malleolus. In *M. lagotis* the tendon arises in the distal third of the leg. An additional, very small but separate muscle belly approximately one cm long was observed within the distolateral crus in *I. obesulus*, arising from the aponeurosis of the fibularis longus; its tendon was extremely thin and could not be traced beyond the dorsolateral aspect of the tarsus. Action: eversion of the pes.

*M. fibularis [peroneus] brevis*

M. fibularis brevis arose from the lateral aspect of the fibular head and proximal shaft, cranial to the fibularis longus (Fig. 5). In *I. obesulus* the origin extended more proximally than
in *M. lagotis*. The tendon passed under the lateral malleolus to insert to the base of metatarsal V in *I. obesulus* and to metatarsals IV and V in *M. lagotis*. As with the previous muscle, the fleshy portion of the muscle was much longer in *I. obesulus* than in *M. lagotis*. Action: extension of the lateral digits and dorsi-flexion of the tarsus.

*M. peroneus digiti quinti*

*M. peroneus digiti quinti* arose from the craniolateral aspect of the fibular shaft, distal to the peroneus longus and proximal to the brevis (Fig. 5e). The tendon passed along the lateral aspect of the pes and perforates the tendon of the peroneus brevis near the malleolus to insert to the middle phalanx of digit V. Action: abduction of digit V.

**Caudal leg**

*Mm. triceps surae*

The two heads of the m. gastrocnemius together with m. soleus comprise the mm. triceps surae, which act to plantar-flex the pes. In both species, the broad lateral head of m. gastrocnemius has complex muscle architecture. Superficially, muscle fibres arose from the anterior arch of the lateral epicondyle of the femur (Fig 3d,h) and from the dense fascia lateral aspect of the patella. Deep to these, a strong, flat tendon arose from the lateral epicondyle that connected to an unusually large and irregularly shaped sesamoid bone (fabellum). An additional portion of the lateral gastrocnemius arose aponeurotic fibres from the superficial, anterior aspect of this sesamoid. M. soleus was found on the deep surface of the lateral gastrocnemius (Fig. 6a), and arose from the superficial caudal aspect of the lateral sesamoid. While the separate muscle bellies were distinguished, the tendons of the soleus blended into that of the lateral gastrocnemius. The medial head arose from the medial supracondylar fossa of the femur; there was no medial sesamoid. Each muscle belly gave rise to a strong tendon in the distal third of the crus to insert to the tuberosity and plantar aspect of the calcaneus. In *I. obesulus* the tendons appeared to fuse into a single entity. In *M. lagotis*, the medial tendon remained distinct and passed caudally around the lateral tendon to insert into the caudolateral aspect of the calcaneal tuberosity.

*M. flexor digitorum superficialis (M. plantaris + M. flexor digitorum brevis)*

The superficial digital flexor arose from the mesial part of the inferior edge of the large lateral sesamoid bone (Fig. 6a-b). The long, fleshy belly gave rise to two thick tendons in the distal crus which passed over the plantar surface of the pes to the sesamoid bones at the
metatarsoplanangetal joints and, from there, into the flexor fascia of digits IV and V. Parsons (1903) gave the insertion of this muscle (‘plantaris’) as superficial tendons to the middle phalanges II, III and IV in *C. ecaudatus*.

It is easy to become confused by the nomenclature of this muscle, thus some remarks here are useful. Typically, a muscle referred to as m. plantaris is a large and obvious muscle in marsupials, from the lateral sesamoid (fabella) or distal femur and inserting into the plantar aponeurosis. More broadly in mammals, the plantaris typically has a femoral origin and inserts onto the calcaneal tuberosity and or plantar aponeurosis (e.g. Human (Gray 1858)). Where this is the case, a separate m. flexor digitorum breves/brevis is generally present, extending from the plantar fascia to insert bilaterally to the middle phalanx of the digits, e.g. pandas (Davis 1964); rodents (Stein 1986). The bilateral insertion giving a perforated appearance (thus sometimes “flexor perforatus”) allows the passage of the deep digital flexor to the distal phalanx. Among marsupials, the flexor digitorum brevis may arise more proximally, from the tendon of the m. flexor digitorum profundus (e.g. *Da. viverrinus* (MacCormick 1886)), or from the superficial aponeurosis of the deep flexor muscle belly within the distal half of the crus (e.g. *T. vulpecula* (Barbour 1963) and *Phascolarctos cinereus* (Young 1882)). M. flexor digitorum superficialis apparently results from the union of the plantaris and flexor digitorum brevis (Chauveau 1891), and this muscle is common in the veterinary literature (Sisson and Grossman 1975; Miller 1979), presumably reflecting the digitigrade or unguligrade adaptations of the foot of most domestic species. Among marsupials, we consider the name m. flexor digitorum superficialis to be appropriate for taxa in which there is continuity between the muscle belly of femoral origin and the insertion to the digits, i.e. macropodoids (Parsons 1896; Windle and Parsons 1898; Hopwood and Butterfield 1990; Warburton, Yakovleff *et al.* 2012), *C. ecaudatus* (Parsons 1903) and here in *I. obesulus* and *M. lagotis*.

*M. flexor digitorum profundus (M. flexor digitorum longus)*

In both species, the deep digital flexor was incompletely separable into lateral and medial portions that arose from the caudomedial aspect of the head of the fibula, the proximal half of the caudal fibular diaphysis and the caudolateral aspect of the tibia respectively (figs, 5a,d, 6b). At the distal end of the crus, the fleshy muscle gave rise to a flattened tendon that split into three portions; the medial tendon passed to the distal phalanx of digits II and III, the large mesial tendon split terminally to insert on either side of the distal phalanx of digit
IV, and the lateral tendon to digit IV. In one specimen of *I. obesulus*, a small tendon was also traced to digit I. In some specimens of *I. obesulus*, a small superficial medial head was also observed, which may correspond to the M. flexor digitorum superficialis, but generally, the distinction is lacking (see note above). A similar arrangement was described for *C. ecaudatus* (Parsons 1903; ‘flexor tibialis and flexor fibularis’).

*M. popliteus*

M. popliteus arose by a strong tendon from the popliteal fossa on the lateral margin of the lateral femoral condyle. In *I. obesulus* the origin extended onto the caudolateral aspect of the fibula. The insertion was to the medial condyle and proximal third of the medial aspect of the tibia (Figs. 3d,h, 5a,d, 6b). In *M. lagotis*, the tibia is marked by a strong medial crest for the insertion of the popliteus. The popliteus is a flexor of the knee and also acts to stabilise against medial rotation of the tibia at the knee joint. Parsons (1903) describes the popliteus as reduced in *C. ecaudatus*.

*M. tibialis caudalis (M. tibialis posterior)*

In *M. lagotis*, the very small m. tibialis caudalis passed from the proximal caudal tibia to the lateral aspect of the tarsus near the base of metatarsal I (Fig. 5d). M. tibialis caudalis was not identified in *I. obesulus*.

**Intrinsic muscles of the foot for *I. obesulus* and *M. lagotis***

*M. extensor digitorum brevis*

M. extensor digitorum brevis arose by mostly aponeurotic fibres from the medial and lateral collateral ligaments of the tarsus, deep to the tendons of the mm. extensor digitorum longus and lateralis. Fibres from the bipartite origin unite to form a short fleshy mass and thick tendon on dorsal surface of fourth metatarsal that insert to the base of middle phalanx of the fourth toe.

*Mm. interflexorii*

Two fleshy bundles of muscle fibres passed from the plantar surface of the m. flexor digitalis profundus (from between the divisions of the deep tendon) to the deep surface of m. flexor digitalis superficialis.
Mm. flexor breves and adductores digitii
(M. adductor digiti I [hallucis], M. adductor digiti II, M. abductor digiti II, M. abductor digiti V, M. adductor digiti V, M. flexor digitorum [digitalis] brevis)
The intrinsic flexors and adductors lying deep to the m. flexor digitorum profundus pass from the metatarsals to the digits. Both a flexor and an adductor muscle were present for each of the digits I-V, but they were difficult to isolate. The adductors for digits II and III appeared to be fused.

Mm. lumbricales
Two lumbricals were found passing from the tendon of the deep digital flexor to either side of the large IV digit.

Mm. interossei
Two large interossei inserted to the flexor sesamoids of digit IV, and a smaller pair to the flexor sesamoids of digit V.

To provide broad comparisons in hind limb muscle distribution, wet muscle data of I. obesulus, T. vulpecula (generalist arboreal diprotodont marsupial) and S. brachyurus (small macropodine marsupial), mean muscle proportions, grouped by muscle action, were calculated and are presented in graphical form in Figure 7. The hamstring muscle group (combined m. biceps femoris, m. semitendinosus and m. semimembranosus) in all species comprised the greatest component of hind limb musculature, but was proportionately much larger in I. obesulus than in either T. vulpecula or S. brachyurus. The hip flexor group was relatively large in I. obesulus, while the adductor mass was relatively smaller in comparison to the other two species. In S. brachyurus, the gluteal muscle group almost equalled the relative size of the hamstring group, and the adductors are also relatively large compared to the other two species.

Discussion
In general, the hind limb musculature of I. obesulus and M. lagotis followed the typical arrangement of marsupials, including complex gluteal, adductor and hamstring groups, and a distinct ischiofemoral muscle, large m. quadratus femoris, reduced m. soleus, complex fibularis (peroneus) muscle group, and a modified arrangement of insertions of the digital extensor and flexor musculature corresponding with the unequal proportions of the
syndactylous digits (Macalister 1865; MacAlister 1870; MacCormick 1886; Sonntag 1922; Barbour 1963; Hopwood and Butterfield 1976; Hopwood and Butterfield 1990; Warburton 2006; Warburton, Yakovleff et al. 2012). While conforming to general marsupial patterns, there are subtle differences in the sites of origin and insertion, and differences in the relative muscle development in these two species, when compared both with each other and also when compared to other marsupials.

Differences of hind limb myology among peramelemorphians
The muscular descriptions of *I. obesulus* and *M. lagotis* provided herein, together with the published description of *C. ecaudatus* (Parsons 1903), provide a framework for advancing hypotheses regarding the relationship between myology and lifestyles in peramelemorphians. Three distinct ecomorphs are represented (i) a semi-fossorial lineage (represented by *M. lagotis*), (ii) a surface-digging, terrestrial lineage (represented by *I. obesulus*), and (iii) a non-digging, cursorial lineage (represented by *C. ecaudatus*). As patterns of muscle anatomy tend to be conservative within clades (Taylor 1974; Argot 2002; Fisher, Brent et al. 2008; Fisher, Brent et al. 2009; Harvey and Warburton 2010; Julik, Zack et al. 2012; Warburton, Yakovleff et al. 2012), the observed differences in the muscle attachments and relative development between these three species may provide clues to the functional adaptation of limb muscles related to behaviour.

In comparison to *M. lagotis*, *I. obesulus* had a relatively broader, larger m. gracilis, more massive and less differentiated mm. adductores, more distal insertion of the m. ischiofemoralis, extended origin of m. rectus femoris, and within the hamstrings a larger biceps femoris and semimembranosus in comparison to semitendinosus. *M. lagotis*, in contrast, has relatively thinner m. gracilis, highly differentiated m. adductors with three distinct portions, relatively larger area of origin of m. semitendinosus and m. quadratus femoris on the ischium, and two distinct muscular bellies of the latter muscle. The shape of the proximal femur of *M. lagotis* also provides a more medially extended lesser trochanter for the insertion of the m. iliopsoas, and a more laterally expanded greater trochanter for the insertion of the mm. gluteus medius and minimus.

The hindlimb anatomy of *I. obesulus* appears to be adapted for strong propulsion; massive muscle development on the medial aspect of the thigh (mm. adductores and m. gracilis) contributes to hip extension while at the same time drawing the limbs under the body and maintaining a parasagittal alignment for forward propulsion. The more distal insertion of the
m. ischiofemoralis and proximally extended origin of m. rectus femoris, gives greater mechanical advantage to these muscles which may also contribute to strong propulsion in \textit{l. obesulus}. The hamstring muscle group, which formed almost 30\% of the total hind limb muscle mass, also contributes to hip extension for propulsion in a parasagittal alignment. The hamstring muscles are significant in that they act over more than one joint – hip extension, knee flexion and also plantar flexion; the latter as a consequence of the contribution to the distal crural fascia and the common calcaneal tendon. Multi-articular muscles, those muscles that cross more than one joint, such as the hamstrings, may reduce the metabolic energy necessary for movement by providing force at two joints by the contraction of only one muscle (Sacks and Roy 1982; Lieber and Blevins 1989; Ingen Schenau 1994; Alexander 2003). In contrast, the hamstring muscle group in the macropodid \textit{S. brachyurus} account for roughly 21\% of total muscle mass. \textit{S. brachyurus} had relatively larger development of m. gluteofemoralis (superficial gluteal group comprised more than 17\% of hind limb muscles; \textit{c.f.} 11.4\% in \textit{l. obesulus}) and adductor muscles (adductor group 12.8\% in \textit{S. brachyurus} \textit{c.f.} 6.4\% in \textit{l. obesulus}); a muscular arrangement shared with other macropodoids (Alexander and Vernon 1975; Hopwood and Butterfield 1976; Lodder 1991). This reflects the tendency among cursorial mammals to decrease rotational inertia within the hind limb by concentrating the muscle mass more proximally (Lieber and Blevins 1989; Hildebrand and Goslow 2001).

\textit{M. lagotis}, in contrast to \textit{l. obesulus}, had more highly differentiated mm. adductores and m. quadratus femoris. The subdivision into numerous, distinct bellies suggest that these muscles (muscle groups) contribute contractile force through a wider range of movement or act through a greater range of positions in \textit{M. lagotis}, a hypothesis that may reflect a greater role of hind limbs during digging in this species. Though digging principally employs the forelimbs, successful digging requires the forequarters to be stabilised; if the hind limbs (and trunk) do not stabilize the forequarters then digging strokes with the forelimbs will tend to propel the animal forward instead of drawing soil backwards. Thus, both species must employ the hindlimbs to help stabilise the body during digging. \textit{l. obesulus} dig small, conical feeding holes and during digging the fore- and hindlimbs appear to be maintained in an adducted, parasagittal alignment. \textit{M. lagotis} construct large burrows and appear to adopt a more abducted and laterally rotated limb position during digging than \textit{l. obesulus}. \textit{M. lagotis} also use their hind limbs together to push back the spoil excavated by the forelimbs during
digging (Johnson 1989). This requires hip extensor and stabiliser muscles that are able to apply force through a range of abducted and rotated positions of the limb. The myological differences between these two species reflect, on the one hand, adaptation for parasagittal movements for locomotion in *I. obesulus*, and on the other hand, a compromise between the requirements of use of the hind limb for bracing and removing soil during digging as well as over-ground locomotion in *M. lagotis*. Future analysis of the axial skeleton, sacrum and pelvis will help to clarify the differential demands of digging and bounding locomotion in these species.

In the lower hind limb we observed a difference in the relative length of the muscle bellies and tendons in the crus between *I. obesulus* and *M. lagotis*. The muscles bellies of the plantar flexor muscles (especially mm. gastrocnemii) appeared to be relatively long in *I. obesulus*, with shorter tendons. In comparison, we observed that *M. lagotis* had shorter muscle bellies with longer tendons. Quantitative data of muscle belly length as a proportion of total muscle length provide a comparison between *I. obesulus*, *S. brachyurus* and *T. vulpecula* (Table 2). The bellies of the mm. gastrocnemii and plantaris are proportionately longer in *I. obesulus* than in *S. brachyurus*, and roughly comparable to those of the generalist *T. vulpecula*. The long muscle bellies and short tendons in *I. obesulus* may provide greater fidelity in the transmission of muscle force across a joint (Bennett 2000; Biewener and Roberts 2000), and thus may represent another adaptation for more rapid and/or forceful limb extension for rapid locomotion in *I. obesulus* in comparison to the longer tendons of *M. lagotis*.

**Shared features of hind limb myology among peramelemorphians**

Principally, the arrangement of the hind limb muscles in *I. obesulus* and *M. lagotis* follow the typical arrangement in marsupials, but are there hind limb myological features that are distinctive to peramelemorphians as a group? One striking feature of the hind limb of both *I. obesulus* and *M. lagotis*, in comparison to other marsupials observed, was the great quantity and extensive distribution of very tough deep fascia surrounding the muscle compartments in the hind limb. Connective tissues such as fascia may provide a soft tissue skeleton for extensive muscle attachment (e.g. mm. biceps femoris and m. sartorius), help to coordinate muscle activity, and are capable of transmitting substantial force (Benjamin 2009; Maas and Sandercock 2010). For example, the thick fascia within the crus of *I. obesulus* and *M. lagotis* receives contributions from the hamstring muscles. A similar arrangement of hamstrings in
cats has been suggested to contribute to propulsion via limb retraction (Stahl and Nichols 2011). In addition to such connections between the fascia and muscles of the limb, distinct tensor muscles inserting onto the deep fascia (m. tensor fasciae latae and m. tensor fasciae cruralis) were observed. M. tensor fasciae latae is uncommon in marsupials (see Barbour 1963), though present in macropods (Hopwood and Butterfield 1976; Warburton, Yakovleff et al. 2012), while the distinct tensor muscle of the crural fascia we have described in I. obesulus has not previously been recorded in marsupials or eutherian mammals. The tensor fasciae muscles appear likely to increase the potential transmission of forces through the fascia to surrounding tissue. The additional tension generated in the fascia of the thigh and crus by the tensor muscles would further enhance the coupling of muscle chains across multiple joints, in a similar manner to that discussed above for the hamstrings. Finally, the tensor muscles may serve to dissipate the mechanical shock of ground reaction forces during locomotion. In larger cursors (e.g. horses), the long tendons of the distal limbs absorb reaction forces and are supported by small muscle bellies that serve to reduce unwanted vibrations within the tendons (Alexander 2001). While tendons themselves are passive structures that tend to vibrate with a resonant frequency, the small muscles associated with the tendons dissipate these vibrations by absorbing energy and influencing the stiffness of the tendon. In this way, the attached muscles help to mitigate shock and vibration. The unique tensor muscle of the crural fascia, together with the relatively strong tensor muscle of the thigh in I. obesulus, may function to reduce or dissipate unwanted vibrations in the tendons and fascia. The deep fascia and connective tissues are a hitherto little studied area of marsupial biology that warrants future investigation.

The other major pattern in hind limb myology among peramelemorphians corresponds to the adaptive skeleton morphology of the tarsus and pes; the progressive reduction of non-weight-bearing digits, and elongation of the weight-bearing digits from the presumably plesiomorphic condition in Isodon, to a more derived pedal condition in M. lagotis and especially C. ecaudatus (Marshall 1972). As a group, the peramelemorphs exhibit changes to many of the muscles of the lower leg and foot related to these skeletal modification including: reduction in the size of the tibialis caudalis, modification of the number or location of tendinous insertions of the extrinsic muscles of the pes (m. extensor digitorum longus, m. tibialis cranialis, m. fibularis longus, m. flexor digitorum superficialis, and m. flexor digitorum profundus) and reduction in the number of the intrinsic muscles of the pes (mm. interflexorii, mm. lumbricales, and mm. interossei).
Conclusion

The two species investigated in this anatomical study are essentially half-bounding, terrestrial insectivores. Interspecific differences in hind limb myology that reflect behavioural patterns related to locomotion and digging. Where as I. obesulus prefers close cover and scrubby vegetation in mesic environments (Braithwaite 1995), bilbies forage in areas with sparse ground cover through the arid and semi-arid zones of Australia (Johnson 2008). The hind limb anatomy of I. obesulus is indicative of an animal capable for fast powerful limb movements. Indeed, field observations of other bandicoots attest to their abilities, with their “powers of jumping… habit of rising vertically into the air…” when alarmed (Wood-Jones 1923-1925, p.150 describing Perameles myosura). When taken together with the compact, torpedo shaped body, thick skin and cutaneous muscle layers, reduced ear pinnae and highly flexed limb posture of I. obesulus (Gordon and Hulbert 1989), this animal appears to be very well-suited to an explosive escape behaviour through dense habitat (Gordon and Hulbert 1989; Braithwaite 1995). Though quantitative data on the M. lagotis are not presented, due to the dehydration of muscle tissues in the fixed specimens, the descriptive anatomy demonstrates numerous subtle points of difference in comparison to I. obesulus with regard to the placement of muscle attachments. These differences appear to be linked to different postural and functional use of the hind limb to support and contribute to burrowing. The relatively longer limbed, less-flexed limb posture of the hind limb in this species during locomotion would seem likely to represent a compromise between the requirements of digging and quadrupedal locomotion though open, arid country for foraging and in order to retreat to the shelter of their burrow when threatened (Johnson 1989; Szalay 1994). The descriptive muscular anatomy presented here, provides baseline data for more detailed studies of evolutionary functional morphology in this very interesting but little-studied group of mammals.

Acknowledgements

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Table 1. The sources of data for the Subclass Marsupialia
Taxonomy after Aplin and Archer (1987) and Szalay (1994)

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Table 2. Mean muscle belly length as a proportion of total muscle length
Standard deviations are shown in parentheses

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Appendix 1. Raw data of wet muscle masses for individual specimens used in the analyses. All masses are present in grams (g).

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<td>0.6</td>
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<tr>
<td>xor digitorum profundus (+ superficialis)</td>
<td>4.0</td>
<td>3.5</td>
</tr>
</tbody>
</table>
Fig. 1. Comparative body form and hind limb skeleton of (a) *Isoodon obesulus* (drawn from X-ray) and (b) *Macrotris lagotis* (drawn from mounted skeleton).

Fig. 2. *Left os coxa* (innominate) of *Isoodon obesulus* (a, b) and *Macrotris lagotis* (c, d), showing areas of muscle origin and insertion. (a, c) Dorsal view; (b, d) ventral view.
Fig. 3. Left femur of *Hsodosum obesus* (a-d) and *Macrolopus lagalis* (e-h), showing areas of muscle origin and insertion. (a, c) Cranial view; (b, f) medial view; (c, g) caudal view; (d, h) lateral view. Abbreviations: Add, mm. adductores; GaL, m. gastrocnemius lateralis; GaM, m. gastrocnemius medialis; Gem, mm. gemelli; GIMd, m. gluteus medius; GIMn, m. gluteus minimus; GIPr, m. gluteus profundus; GISp, m. gluteus superficialis + gluteofemoralis; Gra, m. gracilis; IIPs, m. iliofemoris superficialis; IsFe, m. ischiofemoralis; ObEx, m. obturatorius externus; ObIn, m. obturatorius internus; Pec, m. pectineus; Pir, m. piriformis; Pop, m. popliteus; QFe, m. quadratus femoris; TFL, m. tensor fasciae latae; Val, m. vastus intermedius; VaL, m. vastus lateralis; VaM, m. vastus medialis.
Fig. 4. Left lateral view of the thigh and hip muscles of *A. ocellata*. (a) Superficial muscles, m. biceps femoris and fascia lata reflected; (b) superficial view of gluteal muscle group, m. biceps femoris removed; (c) deep gluteal muscles.
Fig. 5. Left tibia and fibula of *I. o. oberdorfer* (a–c) and *M. lugosi* (d–f), showing areas of muscle origin and insertion. (a, d) Caudal view; (b, e) lateral view; (c, f) cranial view.
Fig. 6. Muscles of the left lower leg of *Isoodon obesulus*. (a) Lateral and (b) medial view.

Fig. 7. Mean hind limb muscle proportions grouped by muscle actions calculated from wet muscle weights for *Isoodon obesulus*, *Trichosurus vulpecula* (generalist arboreal diprotodont marsupial) and *Setonix brachyurus* (small macropodine marsupial).