J. Anat., Lond. (1963), 97, 1, pp. 55–63
With 2 text-figures
Printed in Great Britain

The monotreme cruro-pedal flexor musculature

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INTRODUCTION

Various theories have been proposed to explain the phylogenetic position of the Monotremata. Proponents of the diphyletic theory of the origin of mammals suggest that they represent a line of descent from the mammal-like reptiles independent of all other mammalian orders. Others consider them to be highly specialized survivors of the earliest mammals reflecting, in their more primitive features, a stage which was part of the heritage of all mammals. Gregory (1947, 1951) suggested a third possibility, the so-called palimpsest theory, deriving the monotremes from the arboreal Australian phalangeroid stem; this theory provides a possible basis for similarities both in distribution and in many structural features between the monotremes and the Australian marsupials.

The study of hind-limb structure has been important in charting the course of evolutionary change and Gregory, drawing on the classical studies of the nineteenth century, suggested that the monotreme cruro-pedal musculature showed clear similarities to that of other mammals. Yet the hind-limb, as depicted by Gregory, would seem most unlike that of non-monotreme mammals. The question therefore is posed as to whether indeed the monotreme hind-limb possesses a structure unlike that of other mammals or whether the classical studies were faulty, a question to be settled only by a critical re-study of the cruro-pedal musculature.

MATERIALS AND METHODS

The hind-limb of one male specimen of *Ornithorhynchus anatinus* (the platypus) and of two male specimens and one female of *Tachyglossus aculeatus* (the Australian spiny ant-eater or echidna) were dissected, using the dissecting microscope where necessary. The study included the muscles of the flexor aspect of the leg and their continuations into the foot, the m. flexor digitorum brevis and m. flexor accessorius, because of their intimate association with the long muscles, and the m. peroneus longus (strictly a member of the extensor group), because of its continuation across the sole.

OBSERVATIONS

Tachyglossus aculeatus (Figs. 1A, B, 2B)

(*a*) M. gastrocnemius is bicipital. Its lateral head arises from the most lateral part of the proximal border of that crest or process of the fibula which is prolonged proximally from the region of its articular head. The medial head, of similar size, arises from the femur above the medial condyle. The tendo Achillis, derived from these two heads, is inserted on the calcaneus where that bone projects distally into the sole. It is twisted in typical mammalian manner with the tendon of the medial head crossing superficially to that of the lateral head. No m. soleus is separable from the lateral head.

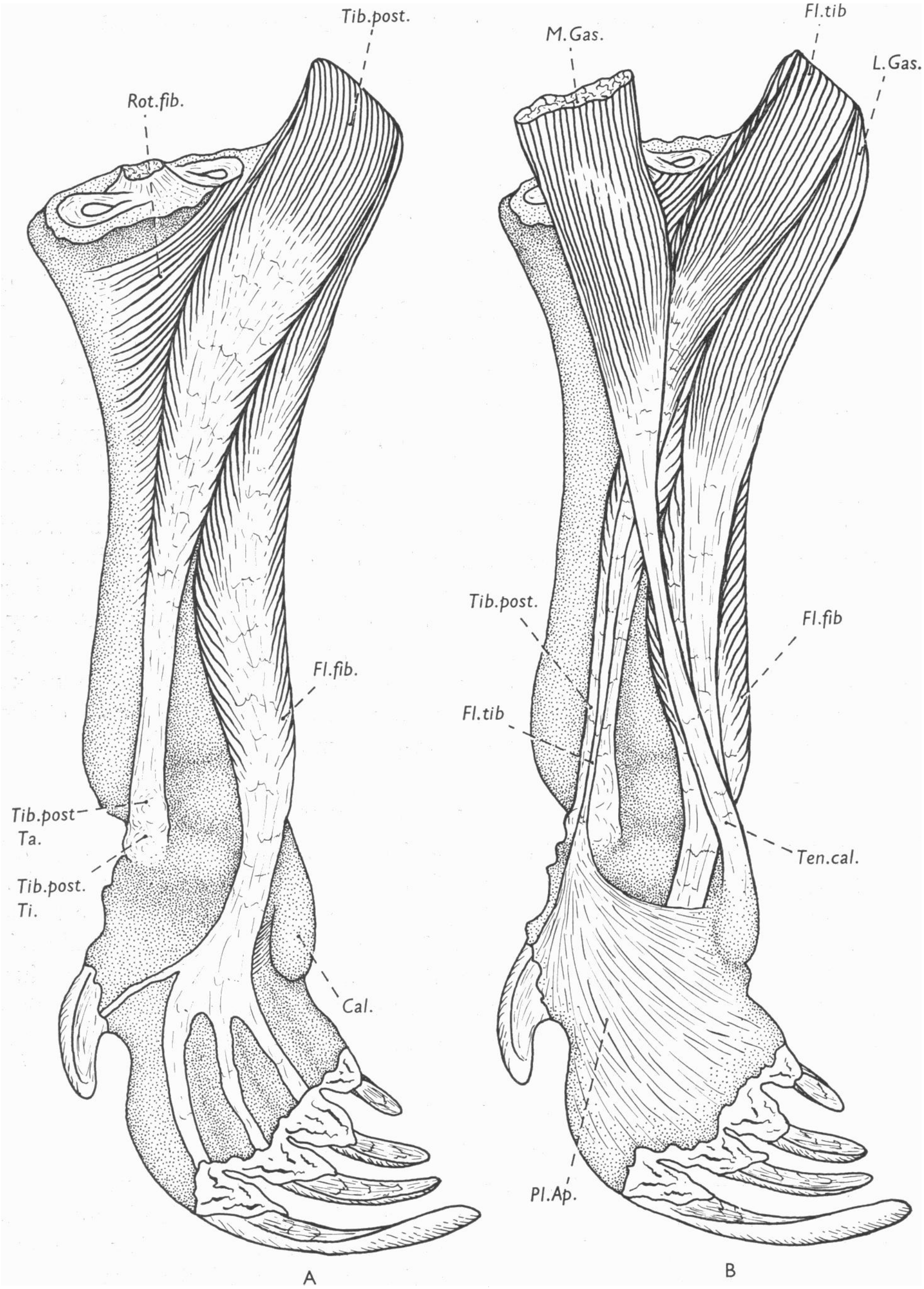

Fig. 1. (A) The deepest muscle layer in the flexor aspect of the right leg of *Tachyglossus aculeatus*. (B) the complete flexor musculature of the right leg of *T. aculeatus*.

(*b*) M. plantaris is not present.

(*c*) M. popliteus (rotator fibulae) occupies the upper three-quarters of the interosseous tibio-fibular space. Its origin from the fibula extends on to the crest and its highest fibres arise from the lateral meniscus of the knee joint. The muscle passes downwards and medially from this origin to an insertion on the tibia.

(*d*) M. flexor fibularis has an origin, anterolateral to that of M. tibialis posterior, from the upper two-thirds of the fibular shaft, extending above on to the lateral border of the shovel-shaped crest. It gives rise to a thick tendon which enters the sole between a rounded elevation formed by the talus and the plantar projection of the calcaneus. On entering the foot it supplies four tendons which are inserted on the distal phalanges of the hallux and second, third and fourth digits.

(*e*) M. flexor perforatus is not present.

(*f*) M. tibialis posterior is almost as massive as m. flexor fibularis and arises from the flexor aspect of the crest and upper two thirds of the shaft of the fibula, posterior to the latter muscle; its origin extends slightly on to the aponeurotic surface of m. rotator fibulae. Its fleshy belly, largely covered above by m. flexor tibialis and the lateral head of m. gastrocnemius, gives rise to a thick tendon which enters the foot behind the tibial medial malleolus; the slender tendon of m. flexor tibialis here lies on its superficial surface. It is largely inserted to the rounded prominence of the talus, but a considerable part skirts this prominence medially to reach a small bone, the os tibiale (see Discussion), articulating with the more distal part of the talus; the surface of the talar prominence is also clothed by a tendinous investment passing to the os tibiale.

Embedded in the soft tissues on the talar prominence is the base of the horny perforated spur of the male echidna. Around the base of this spur may be formed a small bony plaque, though in a young specimen this is apparently represented by a mere fibrocartilaginous thickening. This bony plaque is the better developed in *Ornithorhynchus*.

(*g*) M. flexor tibialis arises from the upper margin of the fibular crest, medial to the lateral head of m. gastrocnemius. About the middle of the leg it gives rise to a small flat tendon lying on the surface of m. tibialis posterior and maintaining this relationship as it enters the foot behind the medial malleolus. In the foot the tendon continues beyond the furthest insertion of m. tibialis posterior (i.e. it crosses the medial part of the os tibiale) and then presents a fibrocartilaginous thickening in relation to the medial cuneiform, a thickening which corresponds to the sesamoid bone found at the comparable site in *Ornithorhynchus* and in most marsupials. From this thickening one fascial expansion radiates laterally into the sole as the plantar aponeurosis; another tough fascial sheet continues down into the hallux.

(*h*) M. flexor accessorius arises from the plantar projection of the calcaneus and is attached to the lateral margin of the m. flexor fibularis tendon where it gives rise to the digital tendons.

(*i*) M. peroneus longus arises from the highest part of the extensor surface of the fibular crest, with also a tenuous origin from the upper half of the fibular shaft. Its tendon enters the sole through an aperture between the calcaneus and the cuboid. After establishing a slender attachment to the base of the fifth metatarsal, the major part of the tendon crosses the sole obliquely, as in other mammals, to be inserted on the flattened and disc-like first metatarsal.

Ornithorhynchus anatinus (Fig. 2A)

(*a*) M. gastrocnemius is similar in all respects to that of *Tachyglossus*, but here the lateral head is the larger.

(*b*) M. plantaris is not present.

(*c*) M. popliteus is similar to that of the echidna but occupies only about the upper quarter of the interosseous tibio-fibular space.

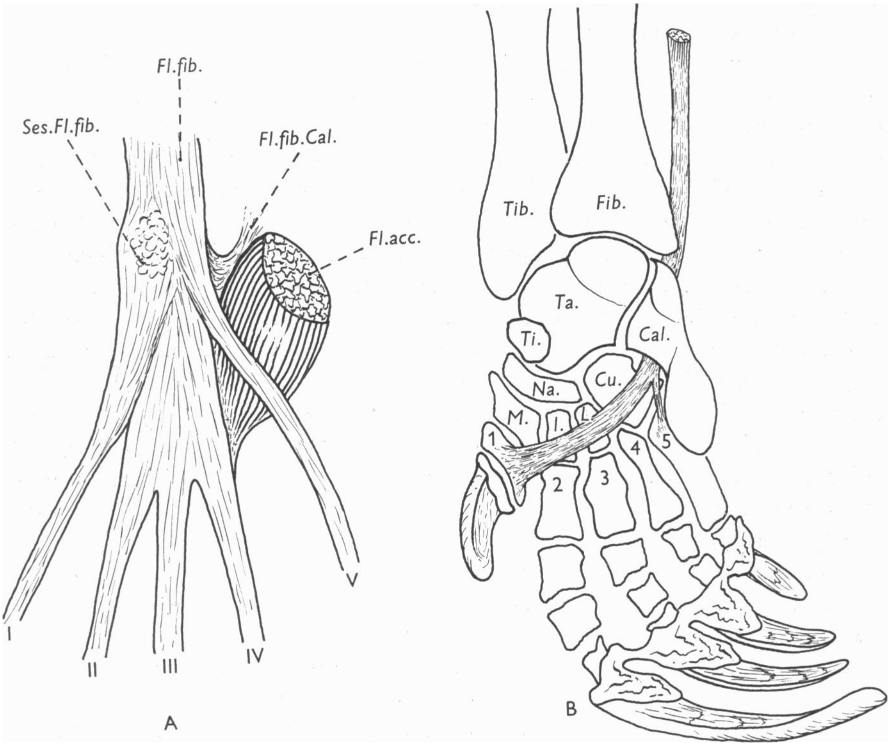

Fig. 2. (A) The relationship of m. flexor accessorius to the flexor fibularis tendons in the right foot of *Ornithorhynchus anatinus*. (B) The relationship of the right peroneus longus tendon to the tarsus in *Tachyglossus aculeatus*.

(*d*) M. flexor fibularis has essentially the same origin as in the echidna, but its muscle belly is more massive. Its tendon enters the foot as in *Tachyglossus* and therein expands somewhat, presenting a small sesamoid bone in its substance towards the tibial side. It supplies tendons to the five digits and is joined by m. flexor accessorius. The tendon before division shows the typically twisted mammalian arrangement (Lewis, 1962*b*), its superficial fibres diverging to form the tendons of digits 1 and 5, while the deeper fibres emerge to form the major part of the three central tendons.

(*e*) M. flexor perforatus (m. flexor digitorum brevis) consists of four fleshy bellies. Two arise from the m. flexor fibularis tendon in the region of its sesamoid and are destined for digits 2 and 3; the other two bellies, supplying tendons to digits 4 and 5, arise from the calcaneus. Each tendon lies superficial to the corresponding m. flexor fibularis tendon and is largely inserted to the strong looped ligaments which reinforce the fibrous flexor sheaths near the bases of the proximal phalanges. Portions of the tendon, however, enter the digital synovial sheath, proximal to the fibrous loop and either side of the flexor fibularis tendon, and pass distally deep thereto to be inserted on the glenoid ligament at the proximal interphalangeal joint. These latter prolongations show a variable degree of development in the different digits but their arrangement indicates clearly the homology of this muscle with the m. flexor perforatus of other mammals.

Table 1. *The identification of the individual flexor muscles in the classical and present accounts*

Present study	Meckel	Mivart	Coues	Westling	Manners-Smith
M. gastrocnemius, caput laterale	M. gastrocnemius, caput laterale	M. soleus	M. gastrocnemius, caput laterale	M. soleus	M. gastrocnemius, caput laterale
M. gastrocnemius, caput mediale	M. gastrocnemius, caput mediale	M. gastrocnemius	M. gastrocnemius, caput mediale	M. gastrocnemius	M. gastrocnemius, caput mediale
M. popliteus	—	M. popliteus	M. popliteus	M. popliteus	—
M. flexor fibularis	M. flexor digitorum	M. flexor digitorum longus	M. flexor digitorum longus	M. flexor digitorum longus	M. flexor digitorum longus
M. flexor perforatus	M. flexor perforatus + lumbricales	—	M. flexor digitorum brevis	—	M. flexor digitorum brevis
M. tibialis posterior	M. soleus	M.tibialis posterior	M. tibialis posticus	M. tibialis posticus	M. soleus
M. flexor tibialis	M. tibialis posterior	M. plantaris	M. plantaris	M. plantaris	M. tibialis posticus
M. flexor accessorius	—	M. flexor accessorius	Dismemberment of flexor fibularis	M. flexor accessorius	M. flexor accessorius
M. peroneus longus	M. peroneus longus	M. peroneus longus	M. peroneus longus	M. peroneus longus	M. peroneus longus

(*f*) M. tibialis posterior arises as in *Tachyglossus* and also enters the sole deep to the m. flexor tibialis tendon. It inserts both on to the talus and into an os tibiale which lies in a position similar to that in the echidna.

The bony plaque (os calcaris) formed around the base of the perforated spur in the male *Ornithorhynchus* is better developed than that of *Tachyglossus*. On the one hand it is attached by a fibrous union to the prominence of the talus and on the other it articulates by a small synovial joint with the tibial malleolus. Between these attachments it bridges over the tibialis posterior and flexor tibialis tendons, thus forming a tunnel by which they enter the sole. Some fibres of the m. tibialis posterior tendon are attached to the os calcaris.

(*g*) M. flexor tibialis has essentially the same attachments and disposition as in

Tachyglossus. In *Ornithorhynchus* there is a sesamoid bone in the tendon articulating with the medial cuneiform whereas *Tachyglossus* presents a fibrocartilaginous thickening only in this situation. Fascial expansions similar to those found in *Tachyglossus* pass from the region of this sesamoid.

(*h*) M. flexor accessorius has a thick fleshy belly arising from the calcaneus and inserting on the lateral border and dorsal surface of that part of the m. flexor fibularis tendon passing to digits 2, 3 and 4. The m. flexor accessorius is crossed superficially by the m. flexor fibularis tendon to digit 5. Just proximal to the attachment of m. flexor accessorius the flexor fibularis tendon is attached to the calcaneus by a fibrous band.

(*i*) M. peroneus longus arises and enters the sole as in *Tachyglossus*. However, the attachment to the base of the fifth metatarsal is relatively stronger, comprising about one-third of the tendon, the remainder of which crosses the sole to the first metatarsal.

DISCUSSION

The muscle group under consideration has been described in *Ornithorhynchus* by Meckel (1826), Coues (1871) and Manners-Smith (1894) and in *Tachyglossus* by Mivart (1866) and Westling (1889). The identification of the various muscles given by these authors is shown in Table 1. Clearly all these accounts are marred by the erroneous identification of certain of the muscles, the inevitable consequence of the current inadequate knowledge of the phylogeny of this muscle group. The identity of the two muscles passing behind the medial malleolus in monotremes and other mammals perplexed the nineteenth-century myologists; sometimes the pair was represented as a double m. tibialis posterior; sometimes the deeper (the true m. tibialis posterior) was identified as m. soleus and the more superficial (the true m. flexor tibialis) as m. tibialis posterior; sometimes m. tibialis posterior was correctly identified but m. flexor tibialis was incorrectly assumed to represent m. plantaris (this error presumably resulted from observing the attachment of the flexor tibialis tendon to the plantar aponeurosis, though this arrangement is, in fact, one of the normal attachments of the tendon in its primitive condition and is well shown in marsupials).

These authors were also unaware that the fibular crest of monotremes included a fused parafibula or lateral fabella. Indeed, the fabella of certain marsupials, with its attached m. plantaris and lateral head of m. gastrocnemius, may on some occasions fuse to the fibula. Thus, in monotremes the lateral head of m. gastrocnemius arises from the fibular crest, conferring on it a superficial resemblance to m. soleus as it exists in many mammals and leading to its incorrect identification as such by Mivart and by Westling.

If the interpretations of any of these authors are accepted the monotreme limb, would be unlike that of any other mammal. Especially the limb as depicted by Gregory (1947, 1951) would be strikingly dissimilar to the corresponding limb in other mammals. Gregory took his data from Mivart. He adopted the latter's figure but strangely gave the name m. peroneus longus to the muscle identified by Mivart as m. plantaris (the true m. flexor tibialis) and even added a broken line to give the impression of insertion of the tendon in that site typical of m. peroneus longus. The result was the remarkable and anomalous appearance of a leg with 'm. peroneus longus' on the tibial side and flexor aspect! Clearly such a description of the limb does little to substantiate Gregory's thesis of affinity between marsupials and monotremes. However, while some of the evidence used by him may have been faulty, the conclusions are to some extent justified. For the monotreme cruro-pedal flexor musculature, when the true nature of its components is realized, shows unmistakable relationship to the primitive marsupial pattern (for which see Lewis, 1962*a*). It is indeed a modified version of this type of limb, but specialized by the loss of m. plantaris and by the regression of m. perforatus in *Ornithorhynchus* and its absence in *Tachyglossus*.

The association of m. flexor accessorius and the m. flexor fibularis tendon has not previously been accurately described, but is clearly interpretable in the light of the history of these muscles (Lewis, 1962*b*). The sesamoid in the flexor fibularis tendon has not been described previously (its presence in monotremes is not, however, unique, for a similar structure is found in *Tupaia* and in *Ptilocercus*).

Apart from those of identification, minor discrepancies obtain between the descriptions given of the attachments of these muscles in the classical accounts and in the present descriptions, but in general these have little bearing on the broader question of the evolution of this muscle group. Surprisingly, however, none of the earlier authors noted the os tibiale as the ultimate and most distal attachment of the m. tibialis posterior tendon. Indeed this bone has had an unfortunate history in the literature. Meckel (1826), in his osteological description, had clearly noted it, but by the latter part of his monograph had apparently come to confuse it with the spur-bearing os calcaris, an entirely different entity. This unhappy confusion of the os tibiale with the os calcaris has persisted throughout the literature and the true os tibiale has virtually disappeared from consideration. It is of interest that m. tibialis posterior is attached to the os tibiale (by that portion which continues beyond the talus) as it is to the navicular tubercle in marsupials and higher mammals. This renders tempting the assumption that in most mammals the os tibiale has become incorporated in the navicular, much as the os radiale has become a part of the human carpal scaphoid, an hypothesis directly opposed to the common opinion that the os tibiale is the homologue of the whole talus save its os trigonum.

There can be little doubt that there exist similarities, unlikely to be merely convergent, between the hind-limb structure of the monotremes and that of the most primitive marsupials. This consideration does not, however, necessarily favour Greogry's palimpsest theory. Indeed, an alternative hypothesis seems more plausible in view of those primitive features which are manifested by the monotremes and which seem unlikely to result from neotony. Certainly it appears justifiable to hold that the monotremes were an early branch from the line leading from therapsids to Theria. Whatever general stage of organization (advanced therapsid or early mammal) had then been reached, the hind-limb had apparently already acquired the essential mammalian structure. There are indications that an essentially mammalian disposition of the hind-limb musculature had already been attained in the more advanced Therapsida (Parrington, 1961).

There are, also, indications that the predecessors of the Monotremata already possessed a somewhat divergent grasping hallux. In the primitive marsupial foot (e.g. *Trichosurus vulpecula*) m. peroneus longus clearly has the important function of approximating the divergent hallux to the rest of the foot. This tendon takes a similar course in the sole of the Monotremata and the obvious inference is that in the ancestors of both the Monotremata and the Marsupialia it had a similar action. The still considerable attachment to the fifth metatarsal in *Ornithorhynchus* is a more primitive feature than the marsupial arrangement. It may be suggested that the precursors of the monotremes enjoyed some degree of specialization of the hallux for grasping, and hence, perhaps, the potentialities for arboreal life.

SUMMARY

1. Classical accounts of the myology of the Monotremata erred in the identification of a number of hind-limb muscles.

2. Such accounts suggest dissimilarity between monotremes and other mammals, whereas, in fact, there exists close affinity in hind-limb structure.

3. Past and present findings are discussed in relation to the various theories of the origin of the Monotremata.

4. It is suggested that, in most mammals, the os tibiale has become incorporated in the pedal navicular.

5. It is concluded that the monotremes probably branched from the line leading from Therapsida to Theria after an essentially mammalian hind-limb had been acquired but before a total marsupial morphological pattern was attained.

I should like to thank Prof. A. J. E. Cave for valuable advice in the preparation of the manuscript.

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KEY TO THE LETTERING OF FIGURES

Cal.	Calcaneus	*Ten.cal.*	Tendo calcaneus
Cu.	Cuboid	*Ti.*	Tibiale
Fib.	Fibula	*Tib.*	Tibia
Fl.acc.	M. flexor accessorius	*Tib.post.*	M. tibialis posterior
Fl.fib.	M. flexor fibularis	*Tib.post.Ta.*	Insertion of tibialis posterior tendon to talus
Fl.fib.Cal.	Fibrous attachment of flexor fibularis tendon to calcaneus	*Tib.post.Ti.*	Insertion of tibialis posterior tendon to tibiale
Fl.tib.	M. flexor tibialis		
I	Intermediate cuneiform	1	First metatarsal
L	Lateral cuneiform	2	Second metatarsal
L.Gas.	M. gastrocnemius, caput laterale	3	Third metatarsal
M	Medial cuneiform	4	Fourth metatarsal
M.Gas.	M. gastrocnemius, caput mediale	5	Fifth metatarsal
Na.	Navicular	I	Flexor fibularis tendon to hallux
Pl.Ap.	Plantar aponeurosis	II	Flexor fibularis tendon to digit 2
Rot.fib.	M. rotator fibulae	III	Flexor fibularis tendon to digit 3
Ses.Fl.fib.	Sesamoid in flexor fibularis tendon	IV	Flexor fibularis tendon to digit 4
Ta.	Talus	V	Flexor fibularis tendon to digit 5