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The phylogeny of the cruropedal extensor musculature, with special reference to the primates

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INTRODUCTION

Comprehensive accounts by Ruge (1878*a*), Frets (1908), Ribbing (1909) and Hunter (1925), incorporating the findings of many other, more limited studies, have adequately documented the anatomy of the cruropedal extensors in a wide variety of mammals. Yet, despite this wealth of data, the phylogenetic picture remains confused, for wholly contradictory hypotheses have been proposed by St John Brooks (1889), Ruge (1878*a*), Frets (1908) and Ribbing (1909). St John Brooks established the relatively simple bilaminar arrangement of this musculature in the primitive tetrapod limb (Fig. 1). The crural superficial muscle layer of Amphibia and Reptilia is subdivisible into a tibial component (inserting into the preaxial border of the foot), a fibular component (inserting into the postaxial border of the foot), and an intermediate component (inserting into the bases of the second to fifth metatarsals); the deep layer, arising from both fibula and tarsus, traverses the foot obliquely to insert into its preaxial border and to provide extensor tendons (reinforced by additional metatarsal capitular slips) to all five digits. St John Brooks' identification of the human homologues of these various components is indicated in Table 1; it is noteworthy that no contribution from the deep layer to the human fifth digit is recognized and that the common peroneus digiti quinti tendon is simply interpreted as a supernumerary attachment of m. peroneus brevis.

Ruge (1878*a*) proposed an entirely different derivation for the mammalian m. extensor digitorum brevis. He was impressed by his observation that a number of mammalian orders exhibit additional muscle bellies in the peroneal region, furnishing pedal tendons with topographical relationships similar to those of the m. extensor digitorum brevis of *Homo*. These bellies received no notice from St John Brooks: Ruge regarded them as initially derived from the mm. peronei, as homologous with m. extensor digitorum brevis, and as prone to undergo a progressive descent to the foot.

Frets (1908), freshly scrutinizing Ruge's view, denied the peroneal derivation of m. extensor digitorum brevis and concluded that the supernumerary muscle bellies associated with the mm. peronei, although inserting in the manner typical of m. extensor digitorum brevis, were of a totally different nature. Denying their phylogenetic descent to the foot, he postulated that they regressed and were subsequently replaced by a lateral enlargement of the true extensor brevis, annexing the territory of the more lateral toes. The basis of Frets' hypothesis was the concept of nerve-muscle specificity. He reasoned that, since the superficial peroneal nerve supplies the mm. peronei, together with their associated supernumerary bellies

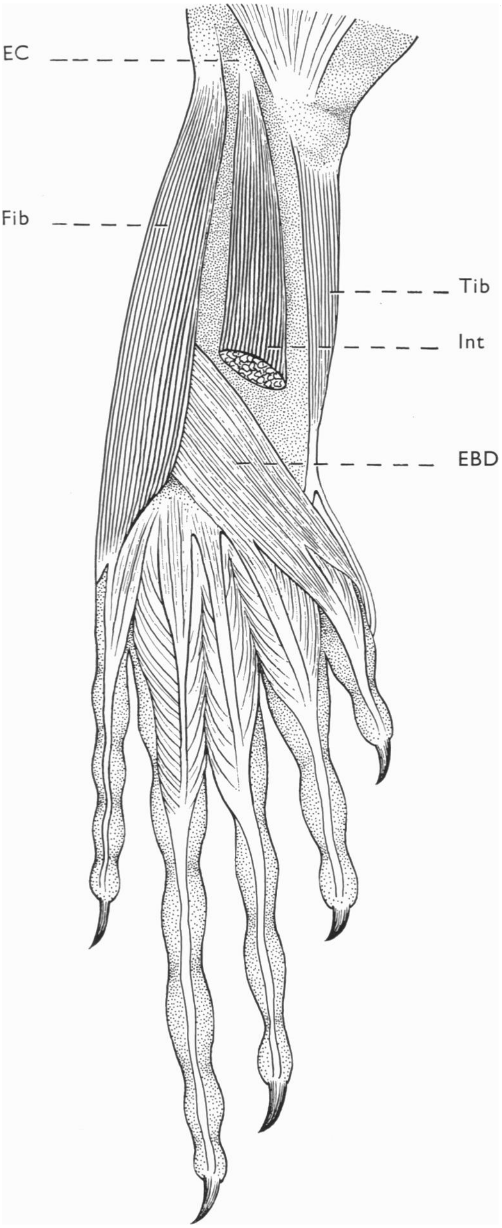

Fig. 1. The extensor aspect of the right hind limb of *Hatteria* (*Sphenodon*), after St John Brooks (1889). EC, external condyle of femur; Tib, tibial sector of superficial stratum; Int, intermediate sector of superficial stratum; Fib, fibular sector of superficial stratum. EBD, deep stratum (extensor digitorum brevis); the part labelled arises from the fibula, but the more postaxial heads arise lower from the tarsus; each of the central three tendons is joined by a pair of metatarsal heads and that for the hallux by a single metatarsal head on the tibial side; no metatarsal heads join the tendon to the minimus.

(which he called mm. peronei digitorum), and since the deep peroneal nerve supplies the true short extensor, then a m. extensor brevis innervated entirely by the latter nerve (e.g. in *Homo*) cannot include descended 'mm. peronei digitorum'. He admitted, however, that the pedal extensor brevis of a few carnivore and edentate forms included a lateral component of peroneal affinity, for in these forms he demonstrated that the superficial peroneal nerve descended behind the lateral malleolus to innervate the lateral part of the extensor brevis. The notion of nerve supply as an infallible guide to muscle homologies is, however, now discredited (Haines, 1935; Straus, 1946*a*) and Frets' conclusions are therefore suspect.

Table 1. *Muscle homologies in the forelimb and hind limb according to St John Brooks* (1889)*; inconstant muscles are indicated in parentheses*

Hind limb		Forelimb	
Primitive tetrapod (*Hatteria*)	Man	Man	Primitive tetrapod (*Hatteria*)
Superficial layer			
Tibial sector	Tibialis anterior	Brachioradialis Supinator Extensor carpi radialis longus Extensor carpi radialis brevis	Radial sector
Intermediate sector	Extensor digitorum longus Peroneus tertius	Extensor digitorum longus	Intermediate sector
Fibular sector	Peroneus longus Peroneus brevis (Peroneus quinti digiti)	Extensor carpi ulnaris Anconeus	Ulnar sector
Deep layer			
Extensor digitorum brevis	Extensor hallucis longus Extensor digitorum brevis (Extensor hallucis brevis)	Abductor pollicis longus Extensor pollicis brevis Extensor pollicis longus Extensor indicis (Extensor medii digiti) (Extensor annularis) Extensor minimi digiti	Extensor digitorum brevis

Ribbing (1909) also maintained that the additional muscle bellies (which he called collectively m. extensor digitorum lateralis) associated with the mm. peronei were not homologous with the lateral bellies of m. extensor digitorum brevis. Unlike Frets, however, he maintained that the m. extensor digitorum lateralis was a specialized development, replacing the lateral part of a primitively complete m. extensor digitorum brevis in certain mammals.

Both Ruge and St John Brooks based their respective hypotheses on inadequate data: Ruge, restricting his studies to mammals, took no cognizance of the primitive tetrapod deep layer, while St John Brooks, working only on an amphibian, a reptile and a monotreme, omitted consideration of the common supernumerary muscles associated with the true mm. peronei. It would seem that the truth must include something of both views and the following hypothesis is therefore proposed: (1) The fate of the primitive three subdivisions of the superficial layer, as recounted by St John Brooks (Table 1), may be accepted; (2) it appears certain that part of the deep layer has extended proximally on the fibula as the m. extensor hallucis longus; (3) it is suggested, however, that early in mammalian evolution the more lateral part of the deep lamina migrated proximally into the territory of the peronei, the digital tendons of these bellies becoming segregated with those of the peronei behind the emergent lateral malleolus; (4) it is suggested that subsequently these bellies have undergone a progressive return to the dorsum of the foot, that for the fifth digit, however, achieving this in certain Prosimii only. The anatomical findings presented below, considered in the light of current knowledge of embryological mechanisms and basic principles, support this hypothesis, and there emerges a better understanding of hind limb evolution which can be instructively compared with parallel changes in the forelimb.

MATERIAL AND METHODS

The cruropedal extensor musculature was dissected in one specimen of each of the following species: Virginian opossum (*Didelphys marsupialis*), common brush-tailed possum (*Trichosurus vulpecula*), ring-tailed lemur (*Lemur catta*), Moholi bush-baby (*Galago moholi*), Humboldt's saki (*Pithecia monachus*), red-handed tamarin monkey (*Mystax midas*), weeper capuchin monkey (*Cebus nigrivittatus*), black and white colobus monkey (*Colobus polykomos*), olive colobus monkey (*Procolobus verus*), white-nosed monkey (*Cercopithecus nictitans*), lar gibbon (*Hylobates lar*), silvery gibbon (*Hylobates lar leuciscus*), chimpanzee (*Pan satyrus*).

OBSERVATIONS

Didelphys marsupialis (*Fig.* 2)

The cruropedal extensors of this species retain clear indications of their reptilian derivation, yet in turn provide a sound basis for the consideration of arrangements in other therian mammals. Only a rudimentary lateral malleolus is present, and those tendons destined to be trapped behind it in the Eutheria here merely occupy a lateral groove in the expanded lower end of the fibula.

(*a*) m. tibialis anterior, representing the tibial sector of the superficial stratum, arises from the upper quarter of the tibial lateral surface and gives rise to a single thick tendon passing anterior to the medial malleolus. (The tendons on the front of the ankle are related in this species to the complex and very strong extensor retinaculum which in marsupials is very similar to that described in monkeys by Stamm, 1931.) The tendon inserts into the medial cuneiform bone. A fascial expansion from the flexor tibialis tendon to the hallux, containing a sesamoid bone (the prehallux), bridges this insertion. Divorce of this ossicle-containing expansion from the remainder of the flexor tibialis tendon created the naviculo-metatarsal ligament found at this site in many mammals, most notably Primates (Lewis, 1964*b*).

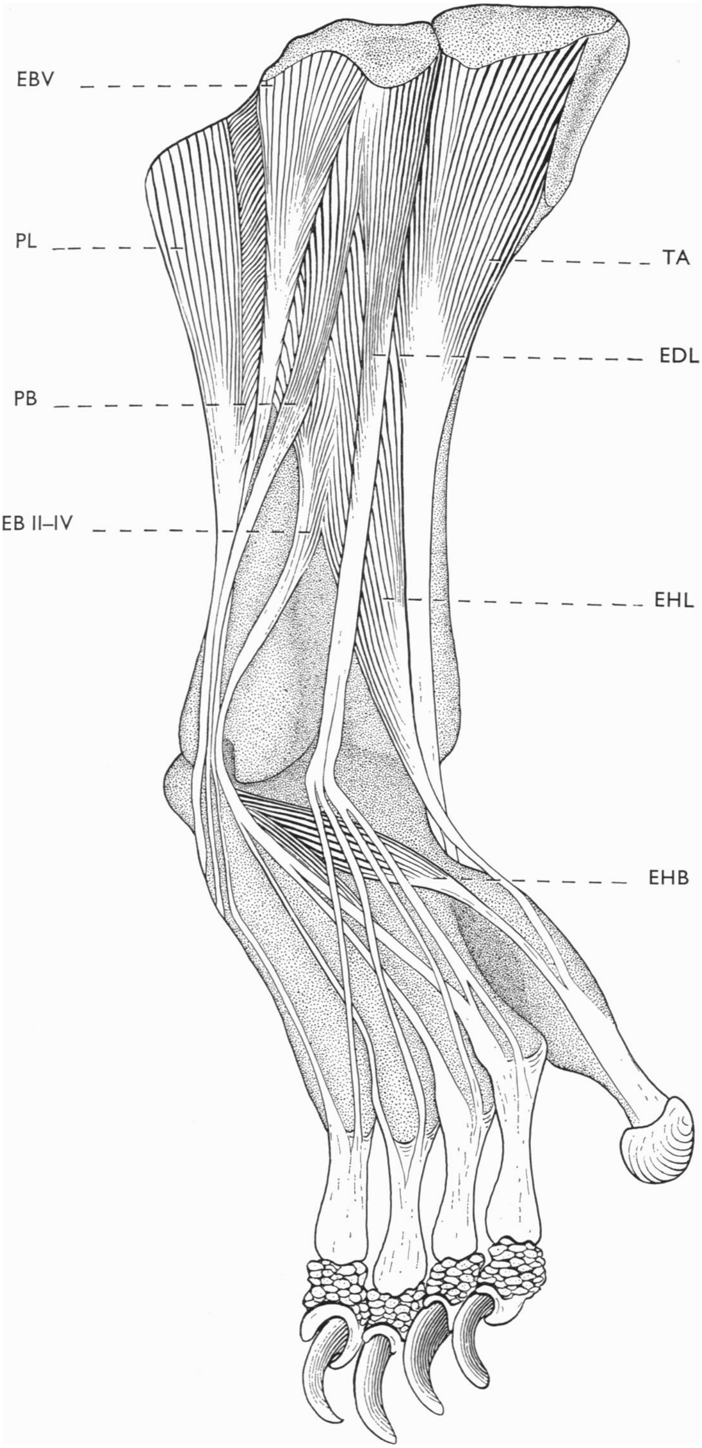

Fig. 2. The extensor aspect of the right leg and foot of *Didelphys marsupialis*, showing the complete musculature; mm. peroneus longus et brevis have been parted to display the m. extensor digitorum brevis V. EB II–IV, m. extensor digitorum brevis II–IV; EBV, m. extensor digitorum brevis V; EDL, m. extensor digitorum longus; EHB, m. extensor hallucis brevis; EHL, m. extensor hallucis longus; PB, m. peroneus brevis; PL, m. peroneus longus; TA, m. tibialis anterior.

(*b*) m. extensor digitorum longus, the mammalian representative of the intermediate component of the superficial stratum, arises from the fibular head, and from an intermuscular septum shared with the adjoining m. peroneus brevis. The muscle belly overlies the deep peroneal nerve as it winds around the fibula into the front of the leg, and furnishes tendons terminating as the extensor expansions on all the digits save the hallux.

(*c*) Mm. peronei longus et brevis comprise the fibular component of the superficial stratum. M. peroneus brevis arises high in the leg from the intermuscular septum between it and m. extensor digitorum longus, and by a few fibres from the anterior aspect of the fibula just below the passage of the deep peroneal nerve to the front of the leg. Its tendon is moulded on to the outer aspect of a bony prominence, proximal to the lateral malleolus, produced by lateral bowing of the fibular shaft in this species. Below this the tendon lies within the groove on the lateral aspect of the fibular lower extremity, then passes to an insertion into the fifth metatarsal base. M. peroneus longus arises from the fibular head and upper half of the lateral aspect of the shaft. Its tendon runs with that of peroneus brevis to the foot where it gives a slip to the fifth metatarsal base and traverses a groove in the cuboid to reach its major insertion into the base of the first metatarsal.

(*d*) M. extensor hallucis longus here unmistakably shows its derivation from the deep stratum, and retains some association with the modified remainder of this layer. It arises from the middle third of the fibula, and its unipennate belly terminates in a tendon closely related to that of tibialis anterior in front of the medial malleolus. It inserts by means of an expansion into the terminal phalanx of the hallux.

(*e*) Mm. extensores breves II–V. The imperfectly separated bellies furnishing tendons to digits II, III and IV arise from the middle third of the fibula, where they are in close association with m. extensor hallucis longus; distally they are separated from the latter by the emergent lateral malleolus. The belly for digit V (a more proximal extension of the same layer as the other bellies) arises deeply between the peroneus longus and brevis from the proximal third of the fibula. Its tendon, associated with those of the two peronei, is separated in the lower leg from the tendons of the extensores breves II–IV by that bony prominence produced by the angulation of the fibular shaft. Finally all the extensor brevis tendons come to lie deeply to those of the peronei in the lateral groove on the distal fibular extremity. Thus entering the foot they radiate across its dorsum, deeply to those of m. extensor digitorum longus, to reach insertions into the lateral wings of the extensor expansions on the lateral four digits. The arrangements in this species leave little doubt that the extensor hallucis longus and the extensores breves II–V are ascended segments of the same muscle sheet—the oblique deep lamina of Amphibia and Reptilia. The elaboration of the lateral malleolus, and the seclusion behind it of part of this sheet, have not progressed to the point where this affinity is greatly obscured.

(*f*) M. extensor hallucis brevis arises from the calcaneus immediately below the lateral malleolus, under cover of the peroneal and extensor brevis tendons as these enter the foot. In reality the muscle consists of two closely associated bellies. The larger and deeper portion provides a tendon passing to the hallux, where it enters the extensor expansion common to it and extensor hallucis longus; the smaller and more superficial belly is closely associated with the tendon of extensor digitorum brevis II, which overlies it and which is reinforced by its tendon.

This species provides an instructive insight into what may be assumed to be the primitive therian arrangement. Subsequent descriptions of individual species need only note significant departures from this basic pattern.

Trichosurus vulpecula

The modifications seen here are partly imposed by the reduced and syndactylous nature of the second and third digits. Close to its insertion the tibialis anterior tendon divides, for it has a dual insertion, into both the medial cuneiform and the overlying prehallux. M. extensor digitorum longus has extended its origin half-way down the fibular shaft, bridging over the passage of the deep peroneal nerve; the muscle provides but a slender, distally divided tendon to the reduced second and third toes, and the tendons for the fourth and fifth digits are united by a junctura intertendinea. M. peroneus longus inserts entirely into the hallucial metatarsal, and the tendon of M. peroneus brevis, at its insertion into the fifth metatarsal, is pierced by the tendon of extensor brevis V. M. extensor hallucis longus has extended its origin higher on the fibula. Modifications to the Mm. extensores breves are particularly noteworthy for they present a trend paralleled among the Primates. The mm, extensores breves II and III have descended to the dorsum of the foot where they arise, below and behind the lateral malleolus, by a slender tendon of origin from the surface of the calcaneo-fibular ligament. The mm. extensores breves IV and V retain a fibular origin between the two mm. peronei. M. extensor hallucis brevis is lacking.

Lemur catta

Certain of the modifications observed in *Trichosurus* are here paralleled and accentuated, and the lateral malleolus is well developed. Minor changes only have occurred in the superficial layer. M. extensor digitorum longus and m. peroneus longus have extended their origins proximally on to the lateral tibial condyle. The extensor longus tendon in the foot expands into an aponeurotic sheet from which the tendons to the lateral four digits are derived. M. tibialis anterior has a single insertion into the medial cuneiform. M. peroneus brevis inserts into the fifth metatarsal and M. peroneus longus into the first (with a mere fascial attachment to the fifth). M. extensor hallucis longus also has extended its origin to the lateral tibial condyle, and its tendon, passing to the usual insertion, is closely bound to that of tibialis anterior by the naviculo-metatarsal ligament. No prehallux is present. The most noteworthy changes concern m. extensor digitorum brevis. Only the belly for the fifth digit retains a fibular origin, between the mm. peronei, and its tendon as usual enters the foot behind the lateral malleolus. The bellies serving the remaining four digits arise from the calcaneus, those for the fourth and third digit being most superficial and arising most posteriorly, below the lateral malleolus, where they are overlaid by the peroneal tendons. All the extensor brevis tendons take their usual deep course to their insertions, that for the hallux being very tenuous.

Fig. 3. The bones of the right leg and the foot of (A) *Cebus nigrivittatus*, (B) *Procolobus verus*. The m. extensor digitorum brevis is shown in each case; the m. extensor digitorum brevis V arises from high on the fibula in (B) and from the lower part of the fibula in (A). In each case the origin of m. peroneus longus is shown in dark stipple and that of m. peroneus brevis in light stipple.

Galago moholi

The striking specialization of the foot of this species—great elongation of the navicular and distal part of the calcaneus—has imposed relatively few modifications upon the musculature in question. Indeed, the pattern differs little from that of *Lemur catta*. The insertions of m. tibialis anterior and m. peroneus brevis (which are unchanged) are carried expectedly far forward in the foot, as is the passage of the peroneus longus tendon to the sole. Again m. extensor brevis V has a high fibular origin between the mm. peronei, and its tiny belly terminates in a thread-like tendon which passes with those of the peronei behind the lateral malleolus. The mm. extensores breves I–IV arise from the calcaneus.

Pithecia monachus

Only m. tibialis anterior and m. extensor digitorum brevis merit special description. Two tendons are derived from m. tibialis anterior about half-way down the leg. The more slender tendon inserts into the prehallux, which has moved forward from its marsupial position to be incorporated in the first tarso-metatarsal joint: the thicker tendon inserts as usual into the medial cuneiform. These two tendons, together with that of m. extensor hallucis longus, are bound in typical primate fashion to the medial border of the foot by the naviculo-metatarsal ligament. Again those bellies of m. extensor digitorum brevis serving the hallux and digits II, III and IV arise from the calcaneus under cover of the peroneal tendons. Only the belly for the fifth digit arises in the leg (extending about halfway up the fibula between the peronei) and its tendon closely accompanies that of peroneus brevis behind the lateral malleolus, parting company from it at the base of the fifth metatarsal to reach the usual insertion.

Mystax midas

Arrangements in this species are essentially similar to those in *Pithecia monachus*.

Cebus nigrivittatus

Arrangements are comparable to those in the preceding two species, but certain trends are accentuated. M. tibialis anterior shows even greater sub-division, for duplication affects a considerable part of its belly; its tendons insert as in the other New World monkeys (Fig. 4A). M. extensor brevis V has descended further towards the foot (Fig. 3A), and arises solely from the lower fifth of the fibula and the adjacent sheath of m. peroneus brevis. The muscular belly extends into the foot and where compressed behind the lateral malleolus by the peroneal tendons it manifests an intermediate tendon, so that the muscle is, effectively, digastric.

Colobus polykomos

This species differs from the platyrrhine monkeys in two important respects. M. tibialis anterior again has dual tendons, arising from partially separate muscle bellies. The larger tendon again inserts into the medial cuneiform, but the smaller now inserts directly into the first metatarsal base, for no separate prehallux is present. The bellies of mm. extensores breves I–IV have a pedal origin from the calcaneus. There is no muscle belly, neither crural nor pedal, for digit V: a tendon with the typical insertion is, however, present, separating from that of peroneus brevis just below the lateral malleolus—but the muscle belly itself is either suppressed or amalgamated with that of peroneus brevis.

Procolobus verus

The arrangements are not unlike those in *Colobus polykomos*, with only one significant difference: an independent m. extensor digitorum brevis V arises from the fibula (Fig. 3B), its tendon accompanying those of the peronei to the foot, where it reaches the usual digital insertion. Mm. extensores breves I–IV are confined to the dorsum of the foot. M. tibialis anterior again inserts by two tendons, arising from a partially double muscle belly, into the medial cuneiform and the first metatarsal base; there is no separate prehallux (Fig. 4B).

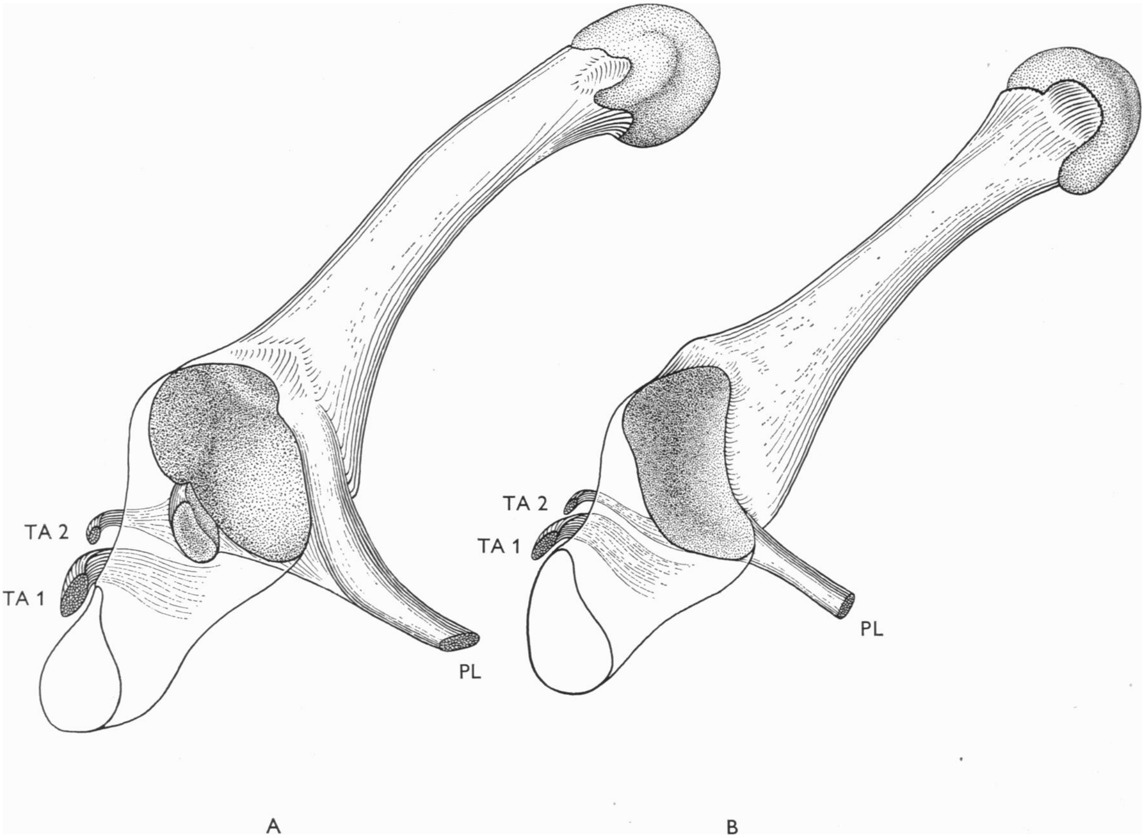

Fig. 4. The right first metatarsal of (A) *Cebus nigrivittatus* and (B) *Procolobus verus*, showing its articulation with the medial cuneiform, which is indicated in outline. PL, tendon of peroneus longus; TA 1, main tendon of tibialis anterior inserting into the medial cuneiform in each case; TA 2, second tendon of tibialis anterior inserting into the separate prehallux in (A), and into the base of the first metatarsal in (B).

Cercopithecus nictitans

In essentials the arrangement is comparable to that shown by *Procolobus verus*; the m. extensor digitorum brevis V again has a high origin from the fibula.

Hylobates lar

(This is a young specimen at the commencement of the juvenile II period, according to the criteria of Schultz, 1944.) Only m. tibialis anterior and the extensor brevis complex warrant special description, the rest of the muscle group conforming to the now well-established pattern. M. tibialis anterior is again bifid in its lower part, and of its two derivative tendons the larger inserts as usual into the medial cuneiform but the smaller terminates on a separate cartilaginous prehallux lying in a comparable position to those described above in the platyrrhine monkeys. These tendons, together with that of m. extensor hallucis longus, are bound down by a typical primate naviculo-metatarsal ligament. M. extensor digitorum brevis I–IV is restricted to the dorsum of the foot, but M. extensor brevis V arises from the fibula between the peronei. Its tendon, having entered the foot with those of the peronei, fails to reach its usual digital insertion and merges with that of peroneus brevis close to the latter's insertion. M. peroneus longus inserts into the first metatarsal but also has a fibrous attachment to the base of the fifth metatarsal.

Hylobates lar leuciscus

Again in this adult specimen there is a separate prehallux, but here it is ossified. The muscular arrangements differ from the preceding gibbon specimen only in the complete absence of m. extensor brevis V, neither muscle belly nor terminal tendon being present.

Pan satyrus

The muscles in this species retain the usual pattern, but origins are more extensive, freely utilizing the deep fascia and intermuscular septa. M. tibialis anterior is again split in its lower portion and its two tendons insert into the medial cuneiform and the first metatarsal base. There is no separate prehallux. M. extensor digitorum brevis I–IV is restricted to the dorsum of the foot and the only relic of m. extensor brevis V is a tendon, having the usual digital insertion, separating from that of peroneus brevis near its insertion. The belly of m. extensor digitorum brevis providing the hallucial tendon is largely separate, and the tendon terminates on the base of the hallucial proximal phalanx. In addition to its primary insertion into the base of the first metatarsal, m. peroneus longus has a fibrous attachment to the fifth metatarsal.

This arrangement described for *Pan*, whose phylogenetic history is so abundantly clear, differs from the corresponding arrangement in *Homo* in but minor details. Thus any splitting of the human M. tibialis anterior is generally confined to the terminal portion of the tendon (although occasionally indeed the muscle belly itself may show duplication): and an extensor brevis V tendon separating from that of M. peroneus brevis is a common, though inconstant, finding in the human subject. Otherwise, indeed, the pattern of the cruropedal extensor musculature in *Pan* and in *Homo* is virtually identical.

DISCUSSION

The findings recorded here are rendered readily intelligible by the hypothesis outlined in the Introduction and permit the development of certain aspects of this view.

The intermediate component of the superficial muscle layer in Amphibia and Reptilia inserts into the metatarsal bases: its mammalian homologue (m. extensor digitorum longus) inserts into the dorsal digital expansions of all the digits save the hallux. It is suggested that this distal prolongation has been effected by a specialization of the investing fascia of the dorsum of the foot. Indeed in *Homo*, and in other Primates, these tendons are still incorporated in this fascial sheet, and embryological evidence supports this view. Thus Bardeen (1906) showed that m. extensor digitorum longus is early attached to the metatarsals, later extending towards the digits as an initially undivided tendon plate. Variation in the subdivision of this aponeurotic sheet into discrete tendons is not surprising: in *Lemur catta* the whole sheet persists and in *Trichosurus*, and occasionally in man (Testut, 1884; Le Double, 1897), juncturae intertendineae, comparable to those of the hand, are found. On the other hand a metatarsal insertion may be retained in a mammal (sloth). The m. peroneus tertius doubtless represents a partial retention of this early attachment and there are no grounds for Wood Jones's (1944) speculation that this muscle represents the apparently missing short extensor of the fifth digit. Extension of this same mechanism may give rise to a hallucial tendon from m. extensor digitorum longus, occurring normally in the seal and anomalously in man. This progressive specialization cannot be interpreted as support for the view of Ribbing (1909), of Wood Jones (1944) and of Howell & Straus (1961) that the m. extensor hallucis longus is a derivative of the superficial extensor. If this mechanism operates in the hind limb it is reasonable to expect it to be active in the forelimb where the primitive insertion of the common extensor is similar, and such a mechanism was indeed suggested by Howell (1936). The alternative hypothesis, that the distal prolongation is achieved by utilizing the digital tendons of the short extensor (Straus, 1941), affords no explanation for the bilaminar arrangement of tendons on the dorsum of the hand and foot. The mechanism whereby a muscle may effect distal prolongation of its insertion by utilizing fascia or ligaments is of widespread occurrence. The ontogenetic and phylogenetic shift in insertion of m. peroneus longus from the fifth to the first metatarsal (Ruge, 1878*a*) is sufficiently established. M. tibialis posterior in the foot (Lewis, 1964*a*) and the mm. interossei in the hand (Lewis, 1965) show comparable evolutionary changes.

The factors initiating subdivision of the primate m. tibialis anterior now become apparent. Even in *Trichosurus* a duplication of the tendon is found, with the supernumerary tendon attaching to the prehallux. In the platyrrhine monkeys examined (and oddly enough in gibbons) the same change is paralleled and emphasized, but in these forms the prehallux has become closely related to the base of the first metatarsal, and has entered into the composition of the first tarso-metatarsal joint. With the disappearance of a separate prehallux (Old World monkeys, *Pan*, *Homo*), either by its suppression or its incorporation into the first metatarsal base, the supernumerary tibialis anterior tendon comes to insert into the first metatarsal base. The functional importance of this extra tendon in the prehensile foot is obvious, for it is the antagonist of that of m. peroneus longus (Fig. 4). Changes in the joint at the base of the hallucial metatarsal have played an important role in primate evolution and have been exhaustively studied, yet the evidence herein submitted has not previously received due consideration. The fate of the prehallux in Old World monkeys and the Hominoidea merits further examination. Superficial similarities between the insertions of m. tibialis anterior and that of m. abductor pollicis longus have prompted the view that these are serial homologues (Le Double, 1897); such an interpretation (still to be found in certain textbooks) is, however, invalid for the muscles are demonstrably derivatives of different primitive layers.

Supernumerary muscle bellies located with the mm. peronei have provided a source of controversy, for their true nature has been obscured by the elaboration of the lateral malleolus. The arrangement in *Didelphys*, where the lateral malleolus is only rudimentary (as it is early in human development), indicates that the deep extensors of digits II–V have undergone a proximal migration early in mammalian history. Comparably in Monotremata, which possess no lateral malleolus, the whole deep muscular lamina has migrated proximally. (St John Brooks' description of the arrangement in *Ornithorhynchus* has been confirmed by the present author and a comparable pattern, modified by the loss of certain digital tendons, has been observed in *Tachyglossus aculeatus*.) In the Theria proximal migration of the medial and lateral portions of the deep lamina (m. extensor hallucis longus and m. extensor brevis II-V) either side of the lateral malleolus contrasts with the proximal encroachment of the undivided sheet in Monotremata. This suggests that the process has occurred independently in the two groups, as might be expected if the now commonly held view of the diphyletic origin of these two mammalian groups be true.

The sequence of descent of the bellies of m. extensor brevis II–V from a primitive therian peroneal situation to the dorsum of the foot is clearly demonstrated by the observations recorded here and by those in the literature reviewed above; this trend of descent seems to have occurred convergently several times. Marsupials primitively have crural bellies for the tendons to digits II–V, but *Trichosurus* preserves crural bellies for the lateral two digits only. This latter arrangement has also been acquired in rodents, whilst in carnivores the belly for digit V only has retained a fibular origin. Generally among the Primates the m. extensor digitorum brevis V alone (but occasionally also the belly for digit IV) arises in the leg; in platyrrhine monkeys, however, it may lie just above the lateral malleolus and in *Loris* it may arise on the dorsum of the foot. The Hominoidea but rarely manifest a belly (usually crural, but sometimes pedal) for extensor digitorum brevis V, but the digital tendon, separating from the termination of the peroneus brevis tendon, is commonly present. Its identity is ill understood, as is indicated by the variety of names given to it—peroneus quinti digiti, extensor proprius quinti digiti, peroneus medius, peroneus accessorius, peroneus parvus, and even peroneus tertius.

The 'ascent' and 'descent' of these muscle bellies is a terminological convention which implies the conversion of one adult pattern into another, but conveys little information regarding the precise embryological mechanism involved. It is clear that the m. extensor brevis can only have encroached proximally at the expense of the peronei, i.e. by annexing some of the limb anlage at this site. The muscular pattern then has changed only in the relative proportions of its component muscles. There is, however, no logical basis for homologizing these bellies, in their new crural situation, with the mm. peronei although in a sense they are so derived ontogenetically. Comparative embryology abounds with examples of structures changing their ontogenetic derivation, but nevertheless accepted as homologues, for the concept of homology has implicit within it the notion of phylogenetic continuity. In fact the available terminology lacks the precision necessary to convey all the ideas involved (Szarski, 1949) and this has resulted in much confusion in comparative myology. Thus, McMurrich (1903) compared the mammalian forearm muscles, which show great specific variations in mass and relative extent, with those of a remote ancestor. He then attributed different 'homologies' (in terms of the components of the primitive forearm) to any one muscle (e.g. flexor digitorum superficialis) according to the subdivision of the limb anlage in a given mammal. Such work can clearly prompt the speculation (e.g. Straus, 1946*b*) that it is fruitless to attempt muscle homologies beyond single vertebrate classes.

The mechanism extending the territory of any one muscle is of common application and provides the logical basis for the assertion that, in attributing homologies, muscle insertions are more important than muscle origins. Other examples of the operation of this principle may be found among the cruropedal extensors. The proximal migration of m. extensor hallucis longus has occurred at the expense of m. extensor digitorum longus, though Bardeen's (1906) demonstration that it develops from the deep surface of the anlage of the latter is no indication of its phylogenetic derivation therefrom.

Awareness of this same principle provides the solution to a major conflict concerning the evolution of the corresponding forearm muscles, and demonstrates instructive parallels between the evolution of the corresponding muscle groups in the two limbs, from a basically similar primitive pattern. St John Brooks (1889) suggested that the primitive deep layer in the forearm migrated proximally, the most ulnar portion extending furthest to become the extensor digiti minimi (Table 1). This is comparable to the process suggested here for the hind limb. Haines (1939) and Straus (1941), however, derived m. extensor digiti minimi from the superficial sheet—from extensor carpi ulnaris. Earlier Ribbing (1907) and Howell (1936) had derived it from extensor digitorum longus. Straus argued that his own (commonly accepted) view was supported by the superficial position of the muscle belly and by its development from the anlage of the superficial layer (Lewis, 1910). But m. extensor digiti minimi does not always occupy a superficial position: indeed in *Hylobates* (and sometimes in other anthropoid apes) it arises, with the other representatives of the deep layer, from the ulna. All the arguments proposed above for the leg may be applied here and confirm St John Brooks's (1889) view.

Interesting parallels between the musculature of the forearm and leg thus result, but the crural pattern is somewhat obscured by the more distal origin of the derivatives of the three subdivisions of the superficial stratum. However, all of these (m. peroneus longus, m. extensor digitorum longus, and m. tibialis anterior) may be observed to retain a femoral origin in certain mammals.

Comparison of the musculature of the two limbs, and interpretation of the great range of mammalian variations, may best be understood by application of the above principles to a relatively simple primitive pattern, basically identical in fore-limb and hind limb. The relatively limited evolutionary alternatives available to individual muscles often (but not invariably) compel and determine serial homologues between the limbs: the recognition of such homologues depends for its accuracy upon the application of the principles enunciated.

SUMMARY

1. The cruropedal extensor musculature is described in the marsupials *Didelphys marsupialis* and *Trichosurus vulpecula* and compared with the arrangement in a representative series of Primates.

2. *Didelphys* preserves a primitive mammalian pattern, still bearing the hall-marks of its reptilian derivation.

3. The mammalian homologues of the three subdivisions of the reptilian superficial layer are m. tibialis anterior, m. extensor digitorum longus, and the mm. peronei.

4. In *Didelphys* the marginal portions of the reptilian deep lamina have migrated proximally either side of an emergent lateral malleolus to form m. extensor hallucis longus and crural bellies of mm. extensores digitorum breves II–V; m. extensor brevis I remains confined to the foot.

5. Primates, and other mammalian orders, show a progressive return of the crural m. extensor brevis bellies to the dorsum of the foot.

6. The mechanisms effecting migration in muscle origins and insertions are discussed.

7. Parallels are drawn between the evolution of the cruropedal and forearm extensor musculature.

8. It is shown that the common primate duplication of the m. tibialis anterior results from the acquisition of a secondary insertion to the prehallux; this bone, incorporated in the first tarso-metatarsal joint, is a separate entity in platyrrhine monkeys and gibbons.

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