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The evolutionary emergence and refinement of the mammalian pattern of foot architecture

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INTRODUCTION

There is little doubt that one of the major evolutionary assets of therian mammals was a complex foot architecture with subtly integrated articular complexes at the ankle, subtalar and transverse tarsal joints (Lewis, 1980*a*, *b*, *c*), producing a mobile pes easily orientated into a variety of grasping attitudes. The early therians, according to a plausible ecological scenario, were probably denizens of the spatially complex interface between arboreal and terrestrial habitats represented by the floor of the forest and its margins. Their basic foot architecture clearly proved to be highly adaptable because it must have equipped the emergent marsupials to become committed arborealists, and the retention of many of its essential attributes seems to have been a key feature in the origin of the basically arboreal primates from among the stem placentals. Moreover, this same morphological structure clearly possessed considerable evolutionary plasticity, and modifications catering for the invasion of a variety of exclusively terrestrial ecological niches occurred in parallel in both Metatheria and Eutheria.

The evolutionary roots of this complex suite of structural features are known in only the simplest anatomical terms.

Schaeffer (1941) rightly stressed that the therapsid foot was converted into a mammalian one by superposition of the talus upon the calcaneus, correlated with a loss of weight-bearing contact between fibula and calcaneus; but little is known about how the complex articular surfaces and ligamentous apparatus of the mammalian foot came into being.

Theoretically it might be expected that the living monotremes, usually thought of as extant relicts of the earliest (prototherian) phase of mammalian evolution, could provide valuable clues into the transitional phase towards therian mammals. It will be shown that a detailed analysis of the monotreme joints does indeed give excellent insights into the probable history of the complex structure of more advanced mammals.

On the basis of the condition in cynodonts and monotremes, it is usually assumed that any calcaneofibular contact in mammals is a persistence of the primitive condition. This notion has influenced a number of aspects of contemporary eutherian evolutionary theory, not the least being the controversial issue of the origin of the primates. The view has already been expressed (Lewis, 1980*a*, *b*, *c*) that a number of examples of calcaneofibular articulation, far from being primitive, in fact represent derived characters; this view point will be further explored in the present paper.

Apart from the vexed question of articulation with the fibula, the lateral aspect of the calcaneus of extant mammals presents a diversity of forms, often possessing prominently developed bony tubercles and shelves; the appearances in cynodonts and Triassic mammals are especially odd. These features, however, become readily interpretable in the light of morphological analysis.

As a preamble to what follows in the rest of this paper it is necessary to set the evolutionary perspective by giving a brief survey of current views on the early history of the mammals.

Origin and early evolution of the mammals

In recent years, the available fossil record covering the early so-called 'dark ages' of mammalian evolution – the first two thirds of their history (140 million years) from their origin in the latter part of the Triassic to their extensive radiation at the beginning of the Palaeocene – has been considerably augmented. To a large extent published interpretations rely on dental and cranial criteria even though it appears that quite a large range of postcranial fossils (even whole skeletons) has been recovered but remains largely undescribed.

Throughout the Triassic the predominant land vertebrates were mammal-like reptiles, in particular, therapsids, including both herbivorous and carnivorous varieties. In the latter part of the Triassic, the therapsids largely succumbed to the rise of the Archosauria, the ruling reptiles, the most conspicuous representatives being the Ornithischia and Saurischia (popularly lumped together as dinosaurs) which held sway until the end of the Cretaceous.

The first mammals were, by general consent, derived from one group of therapsids, the carnivorous cynodonts, in the late Triassic. They were tiny, from shrew to rat size, insectivorous and probably nocturnal, highly active in perhaps an arboreal/terrestrial habitat (Crompton & Jenkins, 1979) and presumably egg-laying, like their reptilian precursors; they were the first of the 'Prototheria'. They soon diversified into three orders, the Triconodonta, the Docodonta and the Multituberculata. The basal order from which the others were derived was seemingly the Triconodonta, and in particular the family Morganucodontidae (Jenkins & Crompton, 1979).

These 'Prototheria' formed the major part of the mammalian fauna (although completely overshadowed by the dinosaurs) until the late Cretaceous, when 'Theria' started to become the dominant mammals. The docodonts died out at the end of the Jurassic (Kron, 1979). The multituberculates, however, flourished (Clemens & Kielan-Jaworowska, 1979) in their predominant role as herbivores (the 'rodents of the Mesozoic'), and showed a considerable expansion in the middle Cretaceous with the origin and spread of the flowering plants (angiosperms), reaching their greatest diversity in the Palaeocene and succumbing at last in the Eocene to the competition provided by placental herbivores.

Almost at the same time as the Morganucodontidae appear in the fossil record so do the first of the 'Theria' (*Kuehneotherium*), which were the earliest representatives of the pantotheres, the Symmetrodonta. It has been suggested that they were derived from early morganucodontids (Cassiliano & Clemens, 1979) and it is generally believed that they were viviparous, producing altricial young. Thus, there seems to have been a very early dichotomy in mammalian evolution into these basic two lineages, but it is now widely held (Crompton & Jenkins, 1979) that mammalian origin was monophyletic, as stated here, although in the recent past it was fashionable to postulate a polyphyletic origin of different mammalian groups from the cynodonts. Yet the early stages of the dichotomy are blurred and the terms 'Prototheria' and 'Theria' are used in only an informal taxonomic sense (Lillegraven, 1979*a*). This blurring is emphasized by the way in which certain 'Prototheria' without surviving descendants showed a shared potentiality to evolve what are usually thought of as therian features (Jenkins & Crompton, 1979). The living monotremes (*Ornithorhynchus* and *Tachyglossus*) are generally considered to be surviving prototherians, but their fossil record is shrouded in mystery (Clemens, 1979*a*).

By the mid-Jurassic the Symmetrodonta, destined to die out at the end of the Cretaceous, had given rise to the more advanced, and possibly arboreal (Kraus, 1979), Eupantotheria. The Theria of metatherian–eutherian grade, characterized by a tribosphenic dentition suited to an insectivorous diet (Bown & Kraus, 1979) were derived from the Eupantotheria during the so-called 'Middle' Cretaceous – the period of spread of the flowering angiosperm flora with its attendant pollinating insects. There is little doubt that the Theria of metatherian–eutherian grade already possessed many of the characters usually considered as diagnostic of marsupials (Clemens, 1979*b*) and that they, in turn, were the source of the Metatheria and the Eutheria. The earliest placentals, grouped in the families Leptictidae, Palaeoryctidae and Zalambdalestidae retained a number of features usually considered as metatherian and are often included in the 'wastebasket' Order Insectivora (Kielan-Jaworowska, Bown & Lillegraven, 1979).

There are thus fairly sound palaeontological grounds for believing that modern monotremes, marsupials and placentals should present, in many anatomical features, an ascending scale of specialization.

MATERIAL AND METHODS

The feet of all the extant mammals specifically mentioned are in the author's collection and were initially dissected as formalin-fixed wet specimens and subsequently preserved as either macerated skeletons or as ligamentous preparations, using the technique of Krahl & Mueller (1947). Included were four hindlimbs of the echidna (*Tachyglossus aculeatus*). The fossil material included the complete pes of a small unidentified cynodont (TR. 8) from the middle Triassic Manda Formation of Tanzania and now held in the collection of the British Museum (Natural History), and the calcaneus (DMSW R. 191) of a larger cynodont, possibly referable to *Diademodon*, held in the University Museum of Zoology, Cambridge. Five tali and five calcanei of the Triassic mammal *Eozostrodon* (*Morganucodon*), recovered from the Port Alun quarry in Wales, and held in the University Museum of Zoology, Cambridge, were also available for study. All illustrations of the fossils were made using a drawing tube on a stereoscopic microscope.

OBSERVATIONS

The monotreme foot: morphology

To casual examination the foot architecture of monotremes seems far removed from the therian condition and superficially seems to show much more affinity with that of the reptilian precursors. As will appear, however, critical examination uncovers revealing insights into the ancestry of form and function in the more advanced mammals. For this purpose the foot of the echidna is most informative, for although it possesses obviously aberrant specializations, these are less extreme than those of the platypus.

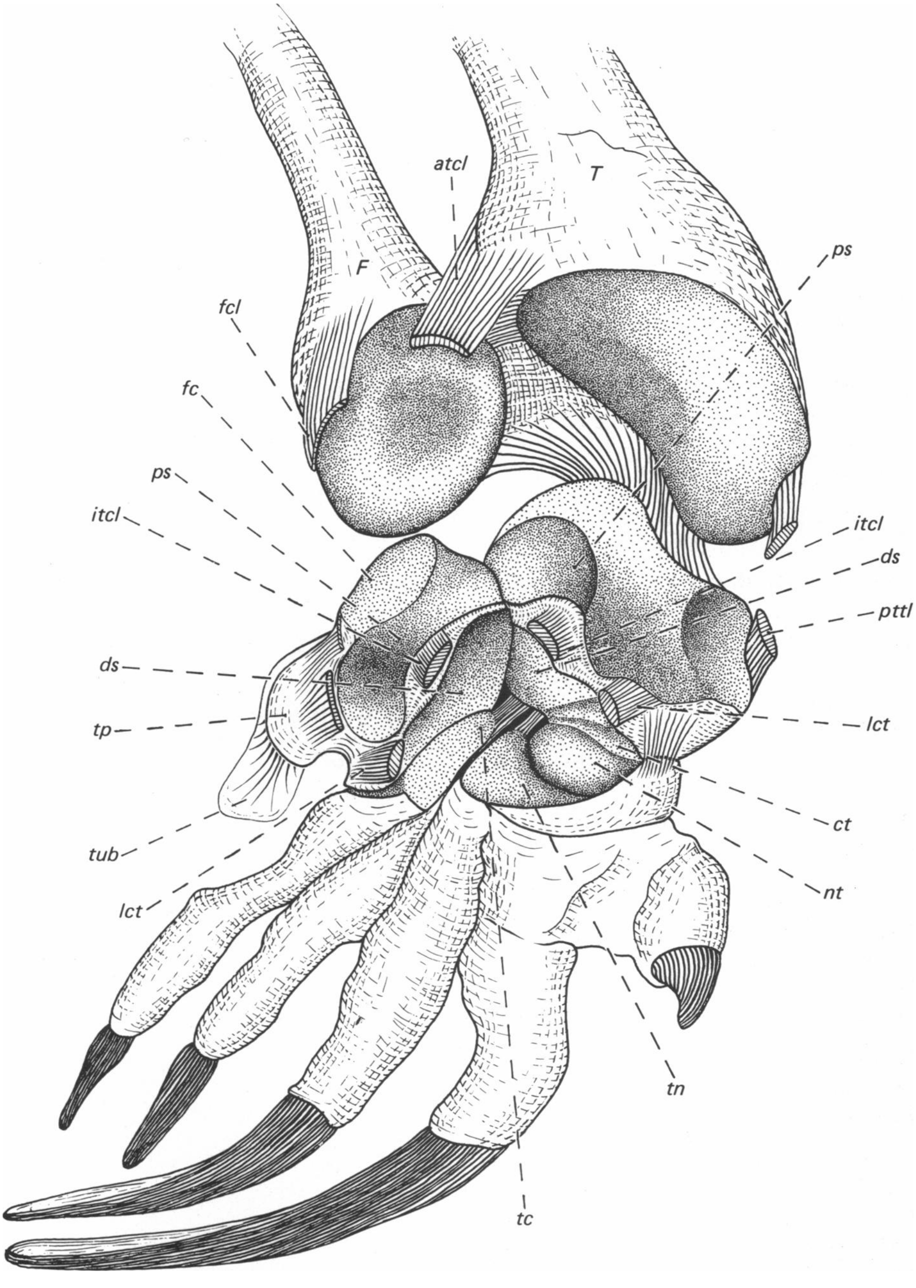

Fig. 1. The right ankle and foot of the echidna, *Tachyglossus aculeatus*, viewed from dorsally with tibia (*T*) and fibula (*F*) partially detached and folded back to reveal the articular surfaces of the ankle joint including the fibular facet on the calcaneus (*fc*), the posterior ligament, the medial ligament (posterior tibiotalar ligament, *pttl*), and the anterior tibiocalcaneal ligament (*atcl*) and the lateral fibulocalcaneal ligament (*fcl*), both attaching distally to the trochlear process (*tp*) of the calcaneus which lies dorsal to the calcaneal tuber (*tub*). The talus and calcaneus are shown partially disarticulated and separated anteriorly revealing: *ps*, proximal articular surfaces on calcaneus and talus; *itcl*, interosseous talocalcaneal ligament; *ds*, distal articular surfaces on calcaneus and talus; *lct*, ligamentum cervicis tali; *nt*, navicular articular surface on talus; *ct*, cuboid facet on talus. The talar articular surface on the navicular (*tn*) and the talar surface on the cuboid (*tc*) are joined posteriorly by ligaments to the talus, embracing between them a further ligament from the lateral cuneiform.

The ankle joint (Fig. 1)

Tibia and fibula both participate in the joint, as do the calcaneus and talus. The articulation of the shallowly concave lower extremity of the fibula is with both talus and calcaneus, and no meniscus is present as in marsupials; there can be little doubt that the fibular articulation with the calcaneus is a primitive inheritance from the cynodont ancestors. The tibia has a rather hook-like articular surface, prolonged dorsally and medially into a prominent knob, the whole presenting a remarkable resemblance to the comparable surface in generalized marsupials, such as *Caluromys lanatus* or *Pseudochirus laniginosus.* The conarticular surface on the talus terminates medially in a concave depression (most clearly demarcated from the remaining convex part of the surface in fresh specimens) which accommodates the terminal protuberance on the tibia. Medially the bones are united by a strong ligament, clearly the homologue of the higher mammalian posterior tibiotalar ligament. The joint is walled posteriorly by another strong ligament passing from the crural bones to attach to the talus, largely into a posterior cleft or groove in that bone. Anteriorly there is a strong anterior tibiocalcaneal ligament passing obliquely across the joint and laterally is a less well defined fibulocalcaneal ligament.

The form of the tibial articular surface and its attached posterior tibiotalar ligament proclaims ancestry to the marsupial condition, which, in turn, foreshadows the architecture characteristic of the prosimian and higher primates (Lewis, 1980*a*). The articular surface on the talus similarly represents a reasonable precursor form to the marsupial pattern. The oblique anterior ligament may well have furnished the basis of the fibrous anterior horn of the marsupial meniscus when that structure became elaborated, but the remainder of the therian ligamentous apparatus (Lewis, 1980*a*) is not recognizable at the monotreme grade.

The subtalar joint complex (Figs. 1, 2)

The somewhat hemispherical talus lies effectively alongside the calcaneus and is thus not substantially supported upon it. Dual articulations separated by a non-articular canalis tarsi unite the bones. The proximal articular surfaces are basically concave on the talus and convex on the calcaneus, although the latter is hollowed out at its two extremities, whilst the distal surfaces are curved in the opposite sense. The distal facet on the calcaneus forms the posterolateral margin of a complex cup-shaped cavity (rudimentary acetabulum pedis) for the talus. The navicular and a separate bony tibiale form additional components of this complex articular surface and are united by a plantar calcaneonavicular ligament to the calcaneus below its distal facet. This distal calcaneal facet is in continuity with the articulation for the cuboid, and here the latter bone intrudes into the acetabulum pedis, thereby forming a component of its wall.

Three ligaments – anterior, middle and posterior – bind talus to calcaneus and all have persistent homologues in therian mammals. The anterior ligament is clearly the homologue of the ligamentum cervicis tali and is so named here, even if the term is not entirely appropriate because the talus has no discernible neck. The middle ligament lies in the canalis tarsi, and is the interosseous talocalcaneal ligament. The posterior talocalcaneal ligament at its calcaneal origin lines the quite deep channel for the flexor fibularis tendon, and is continued to attach into the posterior inflection or cleft on the talus. Merging on to its surface here is the posterior ligament of the ankle joint, and the ligamentous-lined groove directs the flexor fibularis down, medial to the tuber calcanei, into the sole. It will become apparent that this ligament also has clear, frequently overlooked, therian homologues.

The distal calcaneal surface on the talus is continued in a semicircular arc (Fig. 2 A) as articulations for the cuboid and navicular, and beyond that is a small independent facet for the tibiale. The non-articular area encircled by these facets carries the attachments of strong ligaments intruding into the acetabulum pedis from the cuboid and the navicular. Insinuating itself between these latter two bones and their ligamentous continuations is another flattened ligament uniting the lateral cuneiform to the talus.

The monotreme foot: phylogenetic implications

At first sight the echidna foot seems structurally far removed from that of therian mammals, a false impression that is largely created by the unfamiliar disposition of the tuber calcanei. This is directed downwards towards the ground, with some distal declination, and its projection into the sole carries with it the attached tendo calcaneus (Lewis, 1963); it here forms the lateral boundary of a deep channel for the entry of the massive flexor fibularis tendon into the sole. If the tuber could be imagined as deflected backwards to form a true heel it would soon become apparent that the topography of the articular surfaces and associated ligaments corresponds closely to the arrangement in therians (Fig. 2D).

The resemblance can be appreciated most easily by comparison with the marsupial generalized condition, where the heel is incompletely bent backwards, thus providing a transitional link to the characteristic eutherian pattern. In the majority of marsupials the similarity is obscured by confluence of proximal (posterior) and distal (sustentacular) talocalcaneal conarticular surfaces. Yet this is undoubtedly a derived character of certain marsupials, particularly those of Australia. In *Didelphys marsupialis* (Fig. 2D), fibrous and synovial tissue represents the site of the regressed canalis tarsi which, if complete, would have occupied the site shown by the broken line. Moreover, in *Caluromys lanatus* (Fig. 7A), the subdivision by a complete canalis tarsi is retained and the correspondence to the echidna is accentuated.

The marsupial talus (Fig. 2C), which lacks a really clear-cut head and neck, also represents an ideal transitional form between the hemispherical echidna bone and the typical eutherian condition. The talus in *Didelphys marsupialis* even retains synovial remnants representing the ligaments joining navicular, cuboid and lateral cuneiform to talus, which are destined to disappear in more advanced mammals. Where there is a posterior cleft on the echidna talus the marsupial bone presents a broad groove, still for the flexor fibularis tendon, but in the marsupial bracketed by emergent posterior and medial talar tubercles. Groove and tubercles are strongly united to the calcaneus by the posterior talocalcaneal ligament. This often massive attachment of the talar tubercles to the calcaneus, including the posterior part of its sustentaculum, is a characteristic, but seldom appreciated, feature of the eutherian

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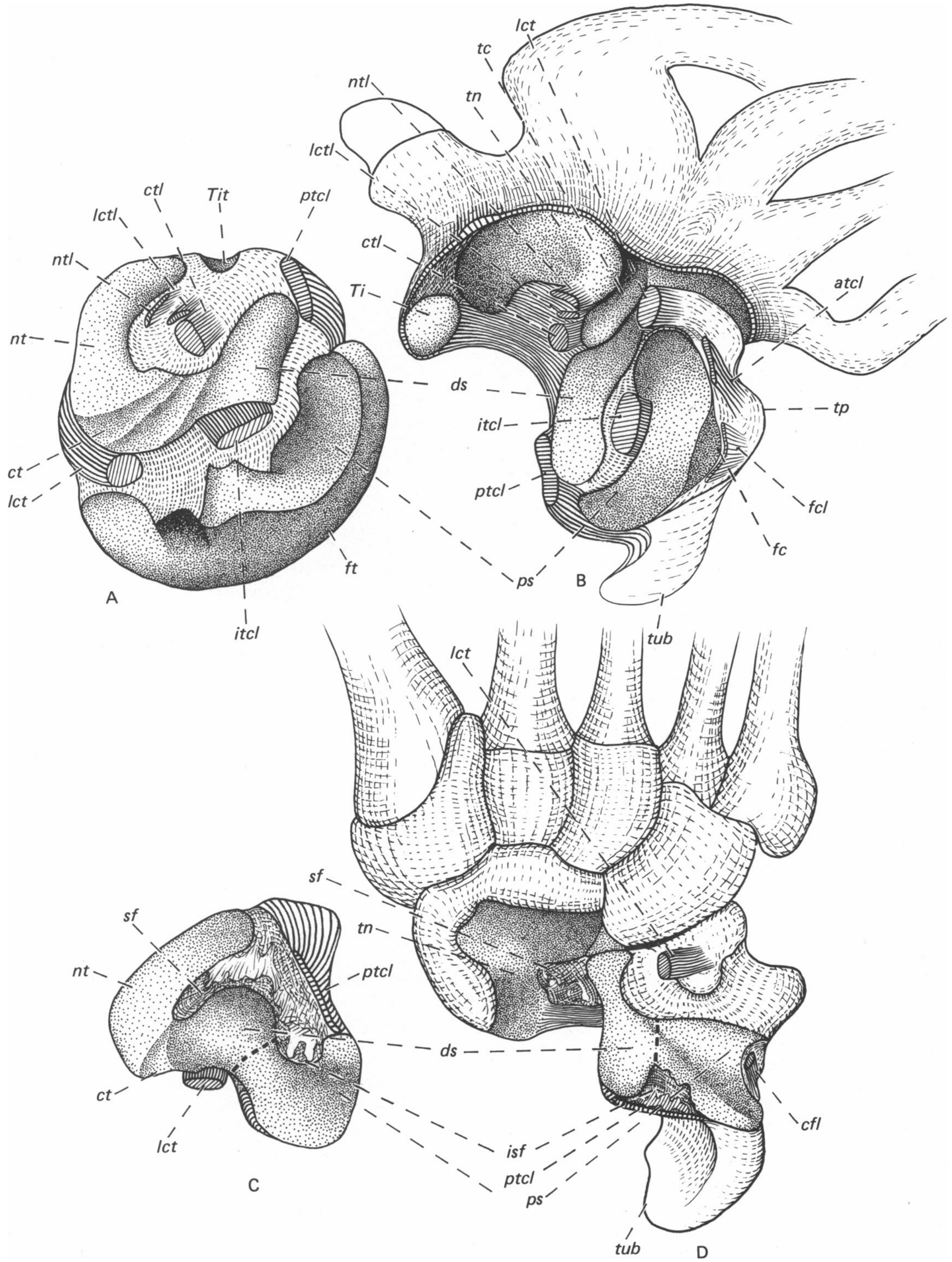
Fig. 2. Above, a dorsal view of the right lamina pedis (B) of *Tachyglossus aculeatus* with the talus (A) rolled away to reveal the under surface. Below, comparable views of the right lamina pedis (D) and talus (C) of *Didelphys marsupialis*. *cfl*, calcaneofibular ligament; *ctl*, talocuboid ligament; *ft*, fibular articular surface on talus; *isf*, synovial folds representing the site of the interosseous talocalcaneal ligament (the broken line represents the site where, in other marsupials, proximal (*ps*) and distal (*ds*) talocalcaneal surfaces are completely separated); *lctl*, talus-lateral cuneiform ligament; *ntl*, naviculotalar ligament; *ptcl*, posterior talocalcaneal ligament; *sf*, synovial fold representing the site of ligaments from cuboid, lateral cuneiform and navicular to talus; *Ti*, tibiale; *Tit*, tibiale facet on talus.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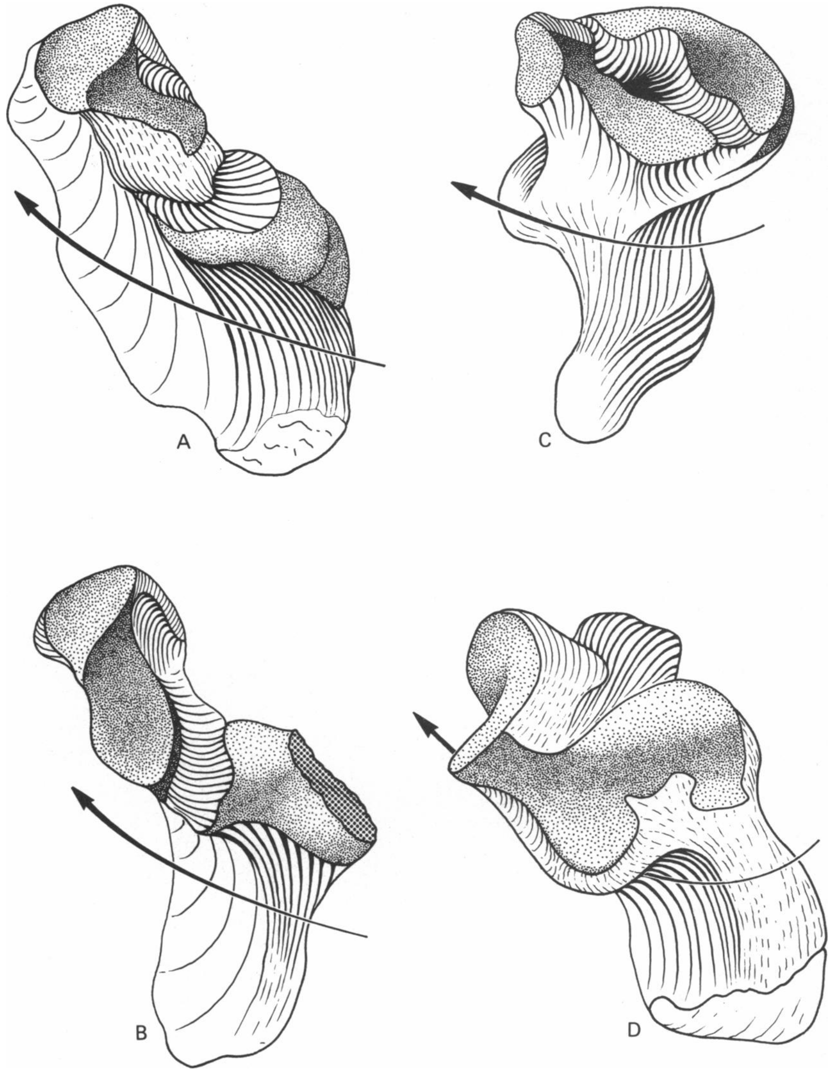

Fig. 3. The right calcanei of a cynodont, TR. 8 (A); the Triassic morganucodontid *Eozostrodon* (B); *Tachyglossus aculeatus* (C); *Didelphys marsupialis* (D); all viewed from medially and somewhat towards the plantar aspect; in all the diagrams the cuboid facet faces upwards and to the left and, like other articular surfaces, is stippled (that for the fibula in (B) is partially broken off). The arrow in all the diagrams represents the known, or presumed, course of entry of the flexor fibularis tendon into the sole. The various articular areas and ligamentous attachments in (C) and (D) may be identified from Figs. 1 and 2; corresponding features may be identified with some confidence in the fossils despite their different relative positions, as described in the text.

tarsus, even including that of primates. The ligament tends to be subdivided in, for example, the hominoids, into medial and posterior talocalcaneal ligaments attaching to the twin tubercles.

The cynodont foot

The consensus of palaeontological opinion would have us believe that cynodonts were already well on the way to achieving the essential characteristics of mammalian

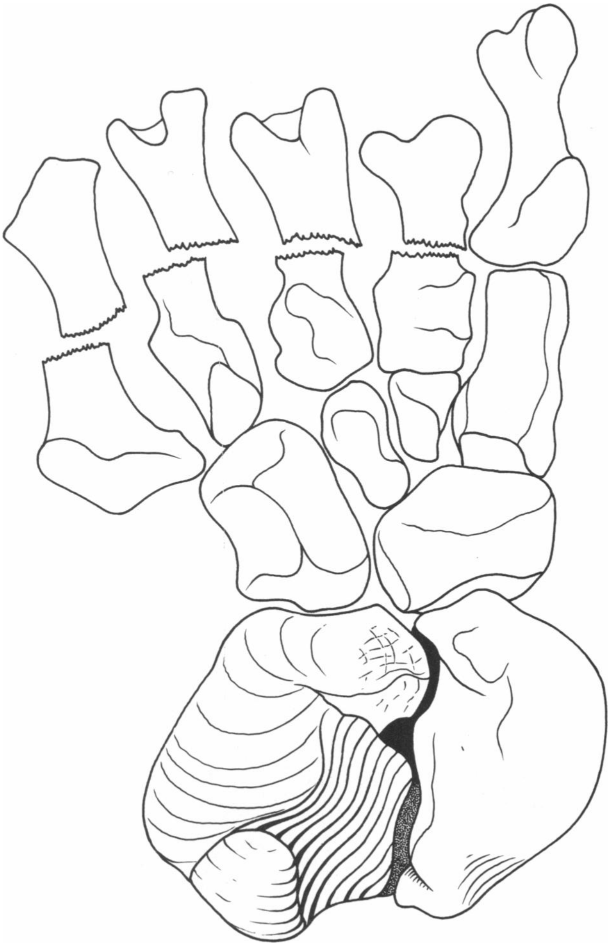

Fig. 4. The right pes (tarsus and metatarsus) of the small cynodont TR. 8, viewed from the plantar aspect, with the bones in what is believed to be the correct articular relationships.

foot structure. Indeed, published illustrations and museum exhibits often portray these reptiles with hindfeet apparently not so very different from those of plantigrade therian mammals. This view is, in fact, based on only the most general level of osteological analysis. Reference is made to such characteristics as the elaboration of a sustentaculum tali leading to 'astragalar superposition', and to the acquisition of a backwardly directed tuber calcaneus (Jenkins, 1970*b*, 1971*a*). The morphological background needed for a more subtle and detailed analysis has simply not been adequately explored.

Probably most mammalian morphologists when confronted for the first time with a cynodont talus and calcaneus would be rather perplexed, and would tend to reject any notion of particular affinity with extant mammals. In fact, familiarity with monotreme foot structure, and not merely osteology, provides the conceptual link which clarifies the cynodont arrangements. Even to the relatively inexpert observer the roughly hemispherical cynodont talus (Figs. 4, 5A) is reminiscent of that of the echidna; the flattened semidiscoidal calcaneus, however, seems to belie any such affinity. The core of this odd looking tarsal (Fig. 3A) is a thickened bony column

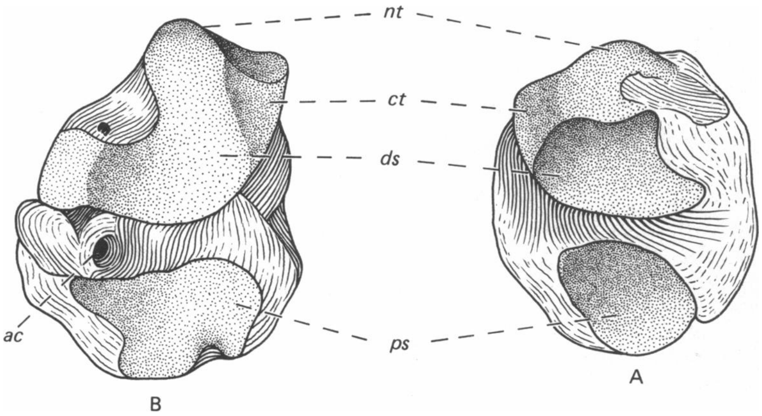

Fig. 5. The right talus of a cynodont TR. 8 (A) and the left talus of *Eozostrodon* (B) shown in positions similar to that of the echidna talus in Fig. 2 A. The features labelled may be identified with confidence; related areas were probably comparable in function to those shown in Fig. 2 A. *ac*, astragalar canal.

forming its medial aspect and bearing the articular apparatus. Laterally is attached a thin lateral flange which is, however, reduced in the large cynodont (DMSW R. 191), and as will be seen, is largely but not entirely eliminated in extant mammals.

When the cynodont calcaneus is so orientated as to highlight the functionally important articular features, and is compared with an echidna calcaneus in comparable position (Fig. 3 A, C), it is apparent that the basic topography of the articular surfaces is not all that dissimilar. The most striking difference, which at first sight obscures the resemblance, is that in the cynodont the distal and proximal talar facets are linearly arranged along the length of the bone. If the distal prolongation could be imagined as compacted into the main mass of the bone, so that the distal talar facet were in a more mediolateral relationship to the posterior talar facet, then something very similar to the monotreme arrangement would be realized. As noted above, the morphological features of the monotreme can readily be conceived as pre-adaptive to the typical therian condition.

There are also distinct resemblances between the orientation of the tuber calcaneus in cynodonts and monotremes. This tuberosity is the insertion of the tendo calcaneus, but the bone bearing it is moulded around the large flexor fibularis, the primary flexor of the toes, forming an obvious groove for this tendon. In the weight-bearing foot of the echidna this heel-like prominence is directed downwards towards the ground, but is also directed somewhat distally towards the toes, an appearance which is exaggerated by the lateral deviation of the postaxial digits in this monotreme (Fig. 1). When the pes of the small cynodont (TR. 8) is accurately articulated (Fig. 4), using the experience derived from knowledge of the articular and muscular arrangements in echidna, it is clear that the cynodont tuber is also directed downwards in the plantigrade position, though lacking the distal deflection seen in echidna. There can be little doubt that the published reconstruction of the pes, showing a backwardly projecting tuber (Jenkins, 1971 *a*), represents an unnatural position, apparently the result of deformation during fossilization, which has moved the bones out of articular contact, flattening the natural arched conformation of the foot.

It has already been noted above how the transition from a monotreme to a therian foot architecture has, as its essence, the bending outward and backward of the primitively downwardly projecting heel. A consequence of this re-alignment is that the massive flexor fibularis tendon now enters the sole by undercutting the distal talar facet. Only when this structural grade is reached is it truly accurate to speak of a sustentaculum tali and sustentacular facet; attribution of these terms to the cynodont condition is not, therefore, strictly appropriate.

Where the echidna flexor fibularis tendon enters the sole through its calcaneal furrow (Figs. 2B, 3C) it is flanked laterally by a bony prominence on that bone to which the tendon is held by the substantial m. flexor accessorius. The same bony tuberosity is crossed on its dorsal surface by the peroneal tendons, with peroneus longus entering the sole in the groove between tuberosity and the cuboid articulation. These myological relationships proclaim this feature as the homologue of the trochlear process of therian mammals. Although this stubby protuberance contrasts in form with the shelf-like therian trochlear process (to be considered later) there can be little doubt that both structures are remnants of the projecting semicircular flange on the cynodont calcaneus. It is a reasonable assumption, therefore, that probably the cupped lower surface of this bony therapsid structure gave rise to a m. flexor accessorius, and its disposition in relationship to the flexor fibularis groove is precisely as would be expected (Fig. 4). Similarly, its upper surface presumably supported the bundle of peroneal tendons entering the foot; indeed, the large cynodont calcaneus (DMSW R. 191) shows a clear-cut groove here for these tendons, and especially for the entry of peroneus longus.

The cynodont talus (TR. 8) has been figured and described (Jenkins, 1971*a*) in only the most general terms, such as recognition of the duality of facets for the calcaneus. Its resemblance in overall form to that of echidna has already been noted. With the benefit of the hindsight provided by knowledge of the anatomy of the soft parts in monotremes it seems possible to go further and to propose that a considerable approximation to the basic structure exhibited by echidna had already been achieved in cynodonts. Recognition of articular areas and ligamentous attachments is necessarily somewhat speculative, but the interpretations given (Fig. 5A) seem plausible and no liberties have been taken with the details of anatomical form.

The tarsus of Triassic mammals

The talus and calcaneus of the Triassic triconodont *Eozostrodon* (*Morganucodon*) have been described and figured by Jenkins & Parrington (1976) but only in quite general terms. In the light of the descriptions already given above it seems that some new structural insights are now possible. The hemispherical talus is again reminiscent of those of monotremes and cynodonts, and a plausible interpretation of its various features is shown in Figure 5B. Its main distinction is that the medial extremity of the groove between the two calcaneal facets is walled over to create an 'astragalar canal'.

The calcaneus (Fig. 3B) also is not unlike that of cynodonts, bearing a similar thin semicircular lateral flange, and its articular apparatus seems to have been essentially cynodont in form. The same basic suite of articular surfaces and presumptive ligamentous areas is identifiable, and there are clear indications that the tuber was also directed towards the ground as it appears to have been in cynodonts.

The mammalian calcaneofibular articulation

There can be no doubt that the earliest mammals possessed a calcaneofibular articulation as part of their reptilian inheritance. In mammal-like reptiles, from pelycosaurs to cynodonts, the fibula participates in the ankle joint as a significant weight-bearing component, articulating with the calcaneus and often with the talus also. *Eozostrodon* and the monotremes retain similar morphological features. It has therefore become an automatic assumption that any calcaneofibular contact in extant or fossil mammals represents a persistence of this primitive condition. In fact, it seems clear that calcaneofibular contact in various extant mammals, and by analogy in certain fossils, is a secondarily derived condition, utilizing even a quite different part of the calcaneus, and having arisen in parallel a number of times in response to new functional requirements.

Lewis (1980*a*) has suggested that the study of the arboreal Australian marsupial phalangers gives very plausible insights into the probable morphological features of the emergent therian ankle joint. In contrast to monotremes, with increased superposition of talus upon calcaneus, the fibula is withdrawn from direct contact with the calcaneus and a neomorphic meniscus has been elaborated between fibula and talus, greatly amplifying the capacity for rotatory movement between the bones. Apparently correlated with the relative retreat of the fibula a massive new ligament, the posterior talofibular ligament, which has no apparent monotreme homologue, has emerged. This ligament is essentially intracapsular, and intervenes between the lower extremity of the fibula and a lateral projection of the proximal facet on the calcaneus, which emerges from under cover of the conarticular talus, bringing subtalar and ankle joints here into continuity. There is thus only an indirect relationship between fibula and calcaneus, and no articular contact. It is to be noted that the calcaneal articular surface underlying the ligament is the homologue of part of the proximal articular surface of the calcaneus for the talus in echidna and is not homologous with the calcaneal facet for the monotreme fibula. It is also apparent that continuity between talocalcaneal and ankle joints is no new acquisition – it is merely a retention of the monotreme condition. Essentially similar relationships, although with modification to the ankle meniscus, are found in the American opossums *Didelphys marsupialis* and *Caluromys lanatus*.

A lateral communication between the ankle joint and the posterior talocalcaneal joint is not restricted to marsupials but persists as a common eutherian feature, being found in *Tupaia sp.*, prosimian primates, and New and Old World monkeys; to a varying extent an indirect approximation of calcaneus (posterior talar facet) to fibula then may occur, the interposed thick posterior talofibular ligament preventing direct articulation.

This basic form seems to have included a ready potentiality for modification in response to new functional needs. The saltatory kangaroos, derived from phalanger-like ancestors, neatly demonstrate such a progressive change. The subtalar joint in the grey kangaroo, *Macropus major*, for instance, is drastically remodelled into what is effectively a 'lower ankle joint' (Fig. 6A) with an almost transverse axis and an overall form converging on that described for artiodactyls by Schaeffer (1947). The ankle joint is also remodelled into a complementary hinge, with a talus of trochlear shape and a splint-like fibula expanded below into a lateral malleolus for articulation with the side of the talus. Here lies a reduced marsupial meniscus, but significantly the fibula here is in intimate relationship with the talar calcaneal facet, being only partially separated from it by a flattened posterior talofibular ligament which has the form almost of an intra-articular meniscus.

This combination of conversion of the subtalar joint to a 'lower ankle joint' associated with substantial calcaneofibular articulation, and often with progressive degrees of amalgamation of fibula with tibia, seems to have been realized con-

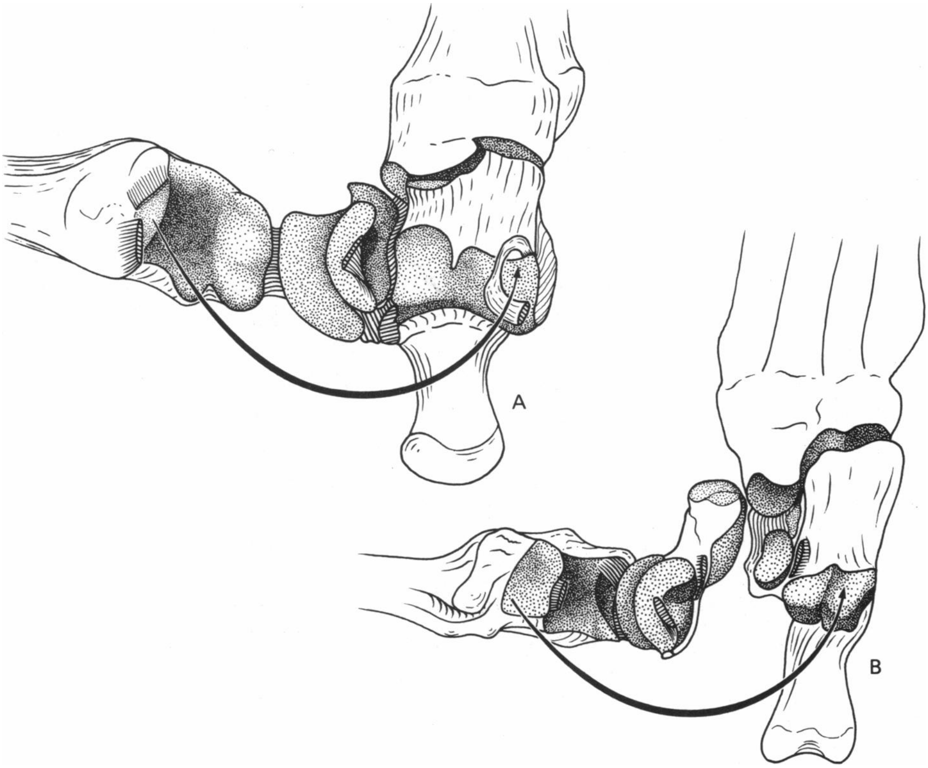

Fig. 6. Right feet of *Macropus major* (A) and *Oryctolagus cuniculus* (B). In each case the talus and fibula have been cut from their attachments laterally, and rolled away medially. The arrows represent how the conarticular fibular and calcaneal articular surfaces may be brought back into contact.

vergently a number of times in mammalian evolution, apparently as an adaptation to saltatory or cursorial locomotion. No attempt will be made here to give a comprehensive survey of the Eutheria for evidence of this adaptation, but certain clear-cut examples will illustrate the main features of the derived morphological structures. These examples are largely chosen because of the way in which misconceptions about their nature have influenced cladistic reasoning.

The rabbit, *Oryctolagus cuniculus* (Fig. 6B), shows clearly the manner in which calcaneofibular contact may be realized in eutherian mammals. The talus is effectively displaced medially, freeing the lateral part of the posterior calcaneal facet for articulation with the fibula. Furthermore, the residual surface for the talus is remodelled so that its anterior slope is concave, forming with the talocalcaneonavicular joint a concave trough for the talus – a lower ankle joint. To accommodate the remodelled calcaneal facet, which retains its convex posterior rim, the talus is laterally excavated by a wedge-shaped articular notch. The large exposed lateral portion of the calcaneal facet has a broad articular contact with the distal extremity of the fibular component of the fused tibiofibula. Unlike *Macropus major* this considerable contact is extensive and direct, because it lies lateral to the posterior talofibular ligament.

Certain shrews (*Suncus caeruleus*) and elephant shrews (*Elephantulus sp.*) show similar calcaneofibular articulation, again correlated with a fused tibiofibula. In contrast, in *Tenrec ecaudatus* and the treeshrew, *Tupaia sp.*, there is no calcaneofibular articulation, and the tibia and fibula are not united.

All those species described which do show unequivocal direct calcaneofibular articulation are characterized by a lengthened pes, fusion of the tibia and fibula, and remodelling of the subtalar joint complex comparable to the transitional stages described by Schaeffer (1947) for the emergence of the fully elaborated 'lower ankle joint' of artiodactyls.

Clearly this derived type of calcaneofibular articulation is not a completely new acquisition but rather results from a redeployment of pre-existing morphological features. The primitive lateral continuity between ankle and posterior talocalcaneal joint presupposes that there is here the potential for articular contact between fibula and calcaneus, only the posterior talofibular ligament presenting an effective barrier. Modification of the subtalar joint complex into a transversely disposed 'lower ankle joint' seems often to be associated with a bodily medial shift of the talus. The exposed lateral portion of the posterior talar surface on the calcaneus is then usurped by the fibula, which thus establishes a major direct weight-bearing articulation lateral to the posterior talofibular ligament. Because the fibula in therian mammals (and particularly Eutheria) has relinquished weight-bearing contact with the femur, it is not surprising that a correlated morphological change should involve varying degrees of amalgamation of the shaft of the fibula with that of the tibia.

The very nature of the gradual transition from mere contiguity to substantial direct articulation between fibula and calcaneus means that a study restricted to osteological material may yield equivocal or even frankly misleading results.

Calcaneal form: Mesozoic mammal to man (Fig. 7)

Many mammals show a striking lateral calcaneal projection, usually described as the trochlear process or peroneal tubercle. The existence of this process, and whether it is distally located, adjoining the cuboid facet, or posteriorly retracted on the lateral surface, has proved to be a useful taxonomic feature (Stains, 1959). Its derivation, however, is uncertain, although Jenkins (1971*a*) has suggested that the lateral flange of cynodonts is lost to produce calcaneal proportions similar to those of mammals, "although some mammals (e.g. *Didelphys*) retain a slight lateral shelf on the calcaneum".

Laidlaw (1904) has given an instructive and largely disregarded account of the surface features of the lateral aspect of the human calcaneus. He noted the presence of a processus trochlearis (peroneal tubercle) in 40 %, and further noted that behind it lay an eminentia trochlearis connected by a faint ridge to the lateral process of the tuber. Furthermore, Laidlaw (1905) made some significant comparative observations, suggesting that the processus lateralis of the tuber calcanei is peculiar to man, and that it was derived by downward and backward migration of the posterior part of the retrotrochlear eminence. This posterior displacement is manifested to varying degrees in different human bones.

No attempt will be made to describe exhaustively the varied form of the calcaneus in therian mammals but examples will be selected illustrating the general principles involved. A marsupial such as *Caluromys lanatus* (Fig. 7A), which seems to possess a foot form close to the basal pattern for the Metatheria (and 'Theria' as a whole), shows what may reasonably be considered the primitive therian form of trochlear process. A broad flattened flange, dished into a concave form on the plantar aspect,

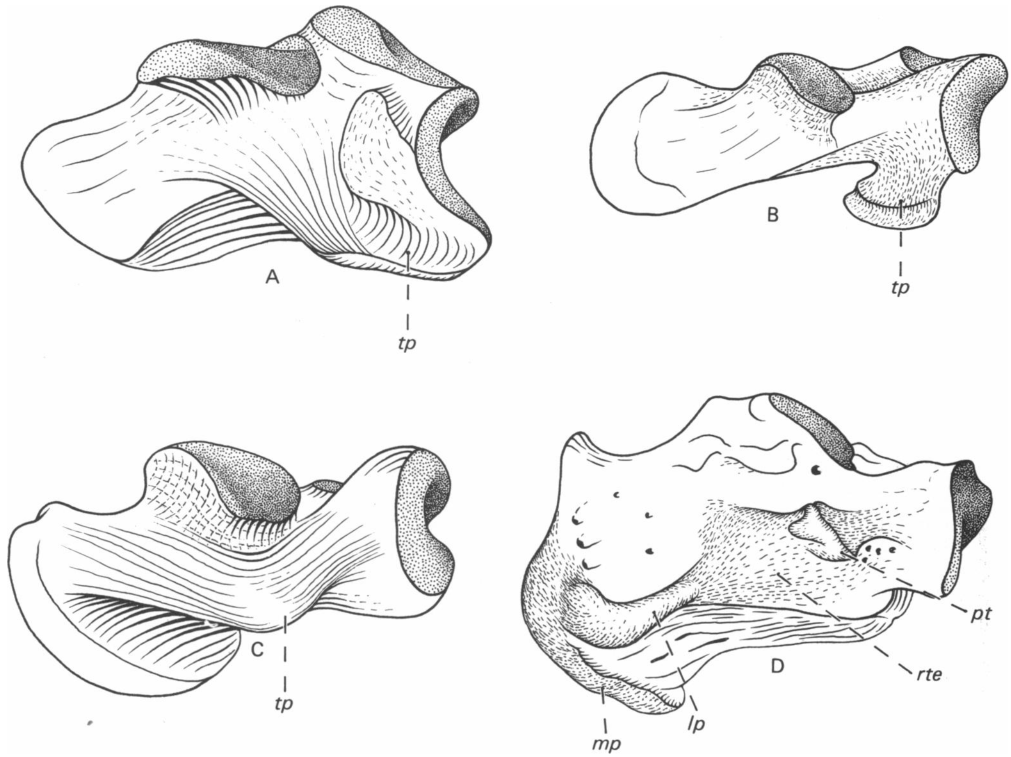

Fig. 7. The lateral aspects of the right calcanei of *Caluromys lanatus* (A); *Tenrec ecaudatus* (B); *Pan troglodytes* (C); and *Homo sapiens* (D). The human calcaneus is tilted up somewhat to reveal the plantar aspect, and this particular specimen shows the lateral process of the tuber still associated with the other components of the trochlear process – the peroneal trochlea and the retrotrochlear eminence. *tp*, trochlear process; *pt*, peroneal trochlea; *rte*, retrotrochlear eminence; *lp*, lateral process of tuber calcanei; *mp*, medial process of tuber calcanei.

projects laterally from the calcaneus. Distally the margin of this flange extends to the lateral edge of the calcaneocuboid articular surface. Posteriorly, the thickened rim blends on to the lateral surface of the calcaneus below the talocalcaneal joint surface, and fades away indeterminately towards the lateral surface of the calcaneal tuber. In generalized Australian marsupials (*Trichosurus vulpecula* or *Pseudochirus laniginosus*) the trochlear process is similarly distally located but is condensed into a thick stubby projection overlapping the lateral aspect of the calcaneocuboid joint. *Didelphys marsupialis* retains a trochlear process with a shelf-like character (Figs. 2D, 3D), but here it is retracted behind the lateral aspect of the calcaneocuboid joint. As will be seen, a similar posterior displacement of the trochlear process has occurred in parallel in a number of mammalian orders.

In insectivores such as *Tenrec ecaudatus* (Fig. 7B) or *Suncus caeruleus*, the trochlear process is a prominent, laterally projecting shelf distally located so that anteriorly it adjoins the margin of the calcaneocuboid joint. In elephant shrews, (*Elephantulus sp.*), it is rather reduced and somewhat posteriorly located. In *Tupaia sp.* it is again a prominent shelf, but is markedly retracted along the lateral aspect of the calcaneus.

Rodents invariably show a well marked trochlear process (Stains, 1959), which may be distally located, or quite posteriorly displaced, as in *Sciurus carolinensis*.

The morphological significance of the trochlear process, when well developed as in the above species, becomes apparent only when soft tissue anatomy is examined. The under surface provides a platform for the broad fleshy origin of the muscle flexor accessorius. This muscle, the homologue of the lateral head of the human flexor accessorius, is a prominent part of the primitive myological apparatus in the therian foot (Lewis, 1962) and, via its connections with deep flexor tendons, or common tendon plate, apparently re-aligns the pull along the variably divergent hallux. The upper surface of the process forms a shelf underlying the bundle of peroneal tendons which are here often bound down by a peroneal retinaculum. The peroneus longus usually lies along the margin of the shelf, and is thus directed in a smooth curve into the sole towards its insertion at the base of the hallucial metatarsal. The other tendons are variable in number, because, besides the peroneus brevis, they include tendons of bellies of the deep extensor stratum – extensor brevis digitorum – which are located in the peroneal region of the leg (Lewis, 1966). In *Didelphys marsupialis*, for instance, they include the tendons for digits two to five; commonly, in other mammals, some of these bellies have descended to arise in the foot medial to the trochlear process, but usually that for the fifth digit (peroneus digiti quinti) retains a crural origin.

These myological relationships confirm the assumption that the tubercle lying adjacent to the calcaneal tuber in echidna is the homologue of the trochlear process, because flexor accessorius arises from its plantar surface and the peroneus longus and brevis course over its dorsal aspect.

There can also be little doubt that the trochlear process is a therian remnant of the flattened lateral flange on the calcaneus of cynodonts and Mesozoic mammals, and it follows that probably this bony plate had similar myological relationships. Its under surface is strategically located to provide origin for flexor accessorius, lying as it does adjacent to the entry of the flexor fibularis tendon into the sole. Its upper surface may well, however, be more than just a bony shelf supporting the peroneal tendons. The deep extensor layer of reptiles, the homologue, in part, of the accessory peroneal bellies in many mammals, is essentially pedal in origin (Lewis, 1966) – the upper surface of this broad flange may have provided such an origin.

There is ample evidence to suggest that a prominent trochlear process, well retracted back along the lateral aspect of the calcaneus, was an ancestral primate feature. This is despite the fact that in one part of the extant primate radiation (prosimians) it is almost totally suppressed, and in another (*Homo sapiens*) the process is fragmented into several parts. No attempt will be made to give a comprehensive survey of this feature in extant primates, but selected examples will illustrate the main morphological trends.

In prosimians (*Lemur catta*, *Galago senegalensis*, *Perodicticus potto*) there is virtually no apparent trochlear process, merely a slight residual roughened elevation situated far posteriorly below the posterior talocalcaneal joint.

New World monkeys (*Cebus nigrivittatus*, *Pithecia monachus*) show the trochlear process in well developed form and the morphological arrangements may be taken as a model for the Anthropoidea as a whole. The process is a prominent shelf projecting laterally from the calcaneus, with its summit lying below the anterior part of the posterior talocalcaneal joint. Its lower aspect gives origin to the m. flexor accessorius. The grooved upper aspect of the shelf supports the bundle of peroneal tendons – peroneus longus, peroneus brevis and m. extensor digitorum brevis V (peroneus digiti quinti). The remaining extensor brevis bellies, having descended to the foot (Lewis, 1966), arise under cover of these tendons from the medial part of the shelf.

A trochlear process of essentially similar form and relationships is a common attribute also of Old World monkeys (*Procolobus verus*, *Cercopithecus nictitans*). In other genera (*Papio sp*., *Erythrocebus patas*) this feature may be rather poorly expressed, and the process may be reduced to a quite rudimentary tubercle.

It is clear that living monkeys have conserved a character lost in extant prosimians. Regardless of controversy about the precise origin of the higher primates, it is of interest that the fossil prosimian Adapidae (in particular notharctines) present a well developed retracted trochlear process (Decker & Szalay, 1974).

The apes (*Hylobates lar*, *Pan troglodytes*, *Pongo pygmaeus*) all show a well developed trochlear process resembling that of New World monkeys. A description of the situation in *Pan* has perhaps most relevance to the situation in that other family of the Hominoidea, the Hominidae. The chimpanzee has a prominent trochlear process (Fig. 7C) with the usual morphological relationships: the peroneal tendons run above it and m. flexor accessorius (not always present) arises from its plantar aspect. It is apparent that during terrestrial locomotion, with the foot held in its habitually inverted posture, the trochlear process is one of the main weight-bearing points of the foot, sharing this function with the tuber calcanei. This seems to be the key to the rather strange derivative condition of the trochlear process in man.

If a series of human calcanei is examined many transitional forms can be found, ranging from a pattern not far removed from the chimpanzee type of trochlear process (Fig. 7D), to the classically described type of human anatomy. Laidlaw (1905), notwithstanding the limited morphological material at his disposal, and the lack of any fossil data, came very close to a clear insight into these morphological features. It now seems clear that all three of the main features recognized by Laidlaw (1904, 1905) from before back on the lateral aspect of the human calcaneus – his trochlear process, retrotrochlear eminence, and lateral process of the tuber calcanei – are, in fact, homologous with the trochlear process proper of *Pan* and other mammals. The commonly used term 'peroneal tubercle' (P.N.A. trochlea peronealis) is most appropriate for the anterior of these elements, which lies between the two peroneal tendons, because it represents only a small part of the whole trochlear process of monkeys and apes. The retrotrochlear eminence also should not be confused, as is often done in textbooks, with the attachment of the calcaneofibular ligament which lies higher, as Laidlaw (1904) emphasized. The uniquely human lateral tuber of the human calcaneus is obviously derived by what is effectively a migration of the posterior part of the ape trochlear process to the heel, an elaboration of its weight-bearing function already foreshadowed in *Pan*. The origin of the lateral head of flexor accessorius in man, by a flattened tendon from the lateral tubercle of the tuber, supports this view of the derivation of the tubercle.

It seems that these derived morphological features constitute a quite recent hominid acquisition. Three partial calcanei are known now from the central Afar of Ethiopia, dated at between 3·0 and 4·0 m.y. and referred to the hominid taxon *Australopithecus afarensis*. One in particular, a right calcaneus A.L. 338–8, preserves those features relevant to the present discussion and it has recently been described, with accompanying photographs, by Latimer, Lovejoy, Johansen & Coppens (1982). It is quite evident that the calcaneus is much more ape-like in form than even such variants of *Homo sapiens* as that shown in Figure 7D, and closely resembles that of

Pan troglodytes shown in Figure 7C; it clearly exhibits a trochlear process in similar position, not yet disrupted into the various elements characteristic of the human condition and described above.

DISCUSSION

Origin and early radiation of the mammals

Belief in the polyphyletic derivation of mammals from the mammal-like reptiles, which held sway for many years, has now effectively been rebutted by increased knowledge of the fossil record. Few would now quarrel with the concept of monophyly (Crompton & Jenkins, 1979). Yet a belief in a fundamental dichotomy between prototherians (including fossils such as the morganucodontids and also the extant monotremes) and therians has persisted. The main stumbling block preventing ideas of an ancestor–descendant relationship between these two groups has been the apparently divergent ways in which the cavum epiptericum has been enclosed in the two groups, leading to apparently irreconcilable differences in the form of the side wall of the braincase. The essence of this conflict has now been resolved (Presley, 1981; Kemp, 1982) and no valid argument preventing consideration of a prototherian origin for the therians remains.

Jenkins (1970*b*), in a wide-ranging review of the anatomical and physiological characteristics of monotremes, convincingly argued that they possess a wide array of characteristics which are shared with the theria and which, in all probability, must have been inherited from a common ancestor – his 'prototherian level of organisation'! On the face of it, this would perhaps seem quite consistent with a Late Triassic derivation of the Theria from morganucodontids, assuming, of course, that the mammalian characteristics of these early prototherians were as advanced as is commonly supposed.

The many therian characters present in monotremes prompted Gregory (1947, 1951) to suggest a much more radical theory – his so-called palimpsest theory – which proposed that the monotremes were, in effect, back-sliding derivatives of the Australian marsupial phalangeroid stem. This idea has been resurrected by Kuhne (1973), who, on the strength of a cladistic analysis using only a single apomorphic character, maintained that monotremes have their nearest relationship with marsupials and that the dichotomy of these two lines must have occurred after the cladistic separation of placentals and marsupials – therefore not earlier than 'middle' Cretaceous. A less extreme view is the proposal by Kemp (1982) that the monotremes diverged from an early (eupantothere) part of the therian stock. This suggestion circumvents a major difficulty with the notion of an earlier prototherian derivation: monotremes possess ear ossicles closely resembling those of therians, yet in the Mesozoic prototherians and the earliest therians (e.g. the pantothere *Kuehneotherium*) both reptilian and mammalian jaw joints were present, and the postdentary bones had not realized their new sound-conducting role in the middle ear (Crompton & Jenkins, 1979). Those who argue for a prototherian origin of monotremes invoke parallel evolution to explain this.

The data on foot structure presented in this paper seem to have the potential for largely resolving this impasse on therian origins and the phylogenetic grade of the monotremes.

Foot structure and function and the early evolution of mammals

Enthusiasm for documenting the emergence of a new class, the mammals, seems to have caused palaeontologists to over-emphasize the evidence for relatively advanced mammal-like form and function in Triassic fossils. This applies particularly to analyses of the hindlimb and interpretations of mechanisms of gait in cynodonts and early mammals (Kemp, 1982) where undue emphasis is laid upon a major structural advance from the sprawling reptilian gait towards a more erect and 'fully mammalian' posture with parasagittal femoral movements and feet placed close to the mid-line. This scenario fails adequately to take account of Jenkins' (1971*b*) important cineradiographic study which showed that vertical limb orientation and parasagittal excursion, the traditional concept of the 'fully mammalian' type, are in fact characteristic of the specialized cursorial mammals; more generalized therians conserve many aspects of the primitive sprawling attitude. Advanced cynodonts and early mammals could scarcely have forsaken this mode of locomotion entirely even if they did have a facultative capacity for more erect running. This over-riding notion of a dramatic conversion to a more erect gait has had a profound effect on interpretations of therapsid foot structure. It is generally acknowledged that therapsids must have retained that rotatory capacity of tibia and fibula, both about their long axes and in the same direction, which is typical of reptiles (Haines, 1942) and which is a necessary concomitant of the femoral retraction and rotation of the sprawling gait (Rewcastle, 1981). The ankle provides for such rotatory motion, but it is argued that this is the only movement accommodated here. Foot extension providing thrust at the end of the stride is said to be effected by a new rotatory capacity at the talocalcaneal joints about a more or less transverse axis; this has been described for gorgonopsids (Kemp, 1982) and therocephalians (Kemp, 1978) but is suggested to be of quite general application, the mechanism in therapsids being made particularly effective by the supposed backwardly projecting lever arm of the tuber calcaneus. Interestingly, the whole forefoot is envisaged as moving with the calcaneus (in a manner analogous to the lamina pedis of therian mammals) whilst the talus effectively acts as part of the crus. Yet there seem to be no sound morphological grounds for this assumption. Indeed, in monotremes (Fig. 1) it is primarily the talus which is functionally anchored to the forefoot, and made an integral part of it, by the ligaments uniting it to cuboid, lateral cuneiform and navicular. Although foot movements are not specifically considered by Jenkins (1970*a*) in his cineradiographic study of locomotion in the echidna, they may be deduced with confidence from his informative illustrations of the phases of gait in the hindlimb. As would be expected, femoral retraction and rotation are accompanied by the reptilian type of rotation on the long bones of the crus, clearly involving movement of these bones at the ankle. However, it is also apparent that as the body moves forward over the implanted pes there is both an effective dorsiflexion at the ankle accompanied by medial angulation of crus in relation to foot. Whilst the ankle would seem to be fitted to cope with a proportion of the sideways movement, it is obvious that, if the sole is to remain applied to the ground, then a longitudinal torsion of the whole foot must occur. This is effected by rotational movement between talus and calcaneus which in effect 'raises' the inner border of the foot at the end of propulsion – this is analogous to supination or inversion in the therian foot. Barnett (1970) appreciated something of this when he suggested that talocalcaneal movements in monotremes produced cupping and flattening of the sole.

This whole mechanism seems to have been remarkably pre-adaptive to the more refined structure found in unspecialized therians, and characteristically in arboreal marsupials. Although not specifically commented upon, it is clear from the excellent illustrations of the phases of the gait in the Virginia opossum illustrating Jenkins' (1971*b*) cineradiographic study, that comparable important adjustments between crus and pes are obligatory. Rotatory movement at the ankle, particularly of the fibula, is greatly facilitated here by the presence of a meniscus (Lewis, 1980*a*). Adjustments of lateral angulation between leg and foot are clearly realized at the subtalar joint complex whose axis (Lewis, 1980*b*) is admirably disposed to accommodate them. The notable advance over monotremes is the freeing of the talus from restrictive ligamentous attachments to the forefoot within the acetabulum pedis, even though flimsy remnants of these attachments may persist in marsupials (Fig. 2C, D). These metatherian modifications have refined the gait even though it retains clear echoes of its reptilian sprawling ancestry. The mobility of the leg bones in relationship to the ankle, providing for movements analogous to pronation and supination in the forearm, but utilizing a different biomechanical solution, coupled with subtalar inversion and eversion produce a highly mobile foot admirably adapted to clambering and climbing in a three dimensional environment.

It seems highly probable that cynodont and morganucodontid locomotion had much in common with that of the echidna, and presumably required rather similar mechanical solutions for making adjustments between the planes of the sole of the foot and the crus. Whereas the axis of talocalcaneal movement in echidna is approximately transverse, however, it is apparent that in cynodonts and morganucodontids it must have been more longitudinally orientated. Moreover, the distal talar facet on the calcaneus, like the proximal one, was convex and had not elaborated the cup-like concavity characteristic of therians and even already apparent in echidna. It seems that the movement must have been a rocking one between calcaneus and talus, with the latter bone nevertheless transmitting its movement to its related part of the forefoot. This torsional movement then would adjust the plane of the sole of the foot, essentially as in echidna.

It is clear that in foot structure the monotremes were further along the path to a therian pattern than either cynodonts or Triassic prototherians. This strongly indicates that monotremes were derived from eupantotheres; essentially this agrees with the proposal by Kemp (1982) based on other criteria. The only real conflict is with current taxonomy which is, in any case, in a state of flux. It is clear that the earliest members of the 'Theria', before the branching off of the monotremes, must then have had an oviparous mode of reproduction making their present therian designation (which is based entirely on cranial and dental criteria) inappropriate.

After the dichotomy, a marsupial pattern of development, which retains relics of the oviparous habit in a persistent eggshell and egg tooth (Lillegraven, 1979*b*), must have been established by the time of the emergence of Theria of metatherian–eutherian grade. Confirmation of this view should be given when eupantothere post-cranial material becomes known, and apparently a complete skeleton has been recovered (Kraus, 1979). The monotremes, of course, possess their own quota of derived characters, such as the bulbous enlargement of the talocalcaneal articular regions, the distal deflection of the tuber calcaneus, and the lateral deviation of the postaxial digits.

Cladistic analysis and the foot

Following the English translations of the works of Hennig (1965, 1966) 'cladism' has emerged in the last decade as the dominant theme of much of the writing on phylogeny and taxonomy. The essence of cladistics lies in the recognition of specialized, derived, or apomorphic characters, and their distinction from primitive or plesiomorphic ones. The emergence of new apomorphic characters coupled with the branching of lineages, or clades, which as a methodological device (Panchen, 1982) is always considered as dichotomous (although in nature it may not always be so), gives rise to sister groups sharing the derived characters or synapomorphies. Thus is derived a branching hierarchy, consisting of a nested set of synapomorphies uniting sister groups – a cladogram. A consequence of this methodology is that all known species, including fossils, are located on terminal branches, never at nodal points which represent hypothetical ancestral morphotypes. The rationale of this is that it is never fully possible to exclude that an often fragmentary fossil might not possess some unrecognized apomorphic character which would exclude it from ancestral status. Theoretically then, cladograms are rigorously objective and falsifiable.

Cladograms, however, may be considered as a step in constructing phylogenetic trees (Eldredge & Tattersall, 1975; Tattersall & Eldredge, 1977; Delson, 1977*a*, *b*). These may include more speculative information, such as stratigraphic order and postulated ancestor–descendant relationships. New taxonomies may also be deduced from cladograms, which often differ radically from the traditional ones based not only upon phylogenetic branching but also on overall phenetic resemblance, and which act as an acceptable and stable information-retrieval system, not necessarily completely mirroring phylogeny (which may be quite impracticable) but not conflicting with it.

The more doctrinaire application of cladistics, particularly in the realm of taxonomy where branching points irrevocably determine the categorical rank of subsequently evolving taxa, has generated an extraordinarily acrimonious debate. There is little doubt that cladistic-based classifications are often revolutionary and seem to offend commonsense. If this controversial aspect of cladistics is set aside then there is widespread agreement that the method has had a beneficial catalytic effect on phylogenetic studies by concentrating attention in a disciplined way on apomorphic characters (Mayr, 1974). Yet this really only represents the culmination of a changing emphasis in evolutionary studies. It used to be fashionable to stress the phylogenetic value of non-adaptive, 'sheltered' or 'palaeotelic' characters (Gregory, 1910). Many morphologists, however, have become increasingly aware of the significance of adaptive characters (Clark, 1959) or evolutionary novelties (Mayr, 1960).

Cladistic methods are not, however, a panacea for the problems of evolutionary morphologists, and may sometimes give no more than a veneer of scientific impartiality. Thus, Gardiner (1982) applied this method to tetrapod relationships and came up with the startling conclusion that birds are the sister group of mammals and cynodonts are only distantly related to the latter, and more distantly than crocodiles and dinosaurs. As Cox (1982) has pointed out, the flaw in this analysis is the inadequacy of the morphological data used. A similar notorious example is that cited above (Kuhne, 1973) where, on the basis of one synapomorphy – in tooth replacement – monotremes were linked with marsupials and for the author this represented "the end of the argument"; Panchen (1982) has trenchantly criticized this approach.

Pitfalls other than relying on the vagaries of too few characters await the unwary. In a transitional series of states of one character complex it is of fundamental importance to determine which state is primitive and which derived – the morphocline polarity. Also, failure to recognize parallelism or convergence may give rise to false indications of affinity. Szalay (1981) properly stressed that the most potentially useful characters are those complex ones which can be related to some major function, such as feeding or locomotion, and which have been subjected to detailed functional analysis. Attempts to devise methods for weighting such characters and establishing correlations are clearly desirable. This approach contrasts with the view of post-Hennigean purists who scorn any attempt to incorporate functional analysis or weighting.

Recent studies (Lewis, 1980*a*, *b*, *c*), and the present paper indicate that evolving foot form is replete with apomorphic characters, and moreover, that these can be keyed to reasonable functional and adaptive roles. Gregory (1910) perceptively recognized the potential importance of characters of the feet, particularly tarsals, even ranking them above teeth! Certain pedal characters have already figured in phylogenetic analysis but these illustrate the pitfalls cited above. Under the misapprehension that calcaneofibular contact is necessarily primitive, Szalay & Decker (1974) postulated that the condylarth tarsus was an appropriate model for that of the precursors of the primates. The ungulate orders of course arose from the condylarths and, as described above, calcaneofibular contact in therians is apomorphic and has been evolved independently a number of times – in kangaroos, rabbits, elephant shrews and artiodactyls. Luckett (1980) and Novacek (1980) also misunderstood the true nature of the morphocline polarity of calcaneofibular contact, and of its correlation with tibiofibular fusion, in cladistic-based studies aimed at assessing the relationships of treeshrews; Novacek (1980), moreover, incorrectly denied calcaneofibular contact in Macroscelidae but asserted its presence in Tenrecidae. Inadequately researched use of the trochlear process (peroneal tubercle) has also figured in the above studies and certain others on primate (Szalay, Tattersall & Decker, 1975; Szalay, 1977) and tupaiid relationships (Szalay & Drawhorn, 1980).

It is clear that any cladistic analysis stands or falls on the validity of the apomorphic characters used. When practised as an armchair exercise, juggling data culled from the literature, a quite spurious impression of precision may be given. The plea is that such studies must go in tandem with more informed investigation of functional morphology.

SUMMARY

It is shown that in form and function the articular complexes of the monotreme foot are pre-adaptive to the therian condition, but the echidna differs by having a tuber calcaneus which is directed downward and distally.

The cynodont foot (TR. 8) and that of the Triassic mammal *Eozostrodon* seem to possess the essential articular features present in monotremes, but they are assembled rather differently. In both, tuber calcaneus was apparently directed downwards.

It follows that monotremes were probably derived from some way along the lineage usually, but inappropriately, termed 'Theria'.

A calcaneofibular articulation is present in kangaroos, certain shrews, elephant shrews, rabbits and artiodactyls. In all of them it is an apomorphic condition in-

volving annexation of part of the posterior talar facet on the calcaneus by the fibula, which invariably shows some degree of amalgamation with the tibia.

It is shown that the trochlear process of the mammalian calcaneus has the dual function of providing origin for the m. flexor accessorius and acting as a supporting shelf for the bundle of peroneal tendons. It is almost certainly a derivative of the lateral flange on the cynodont calcaneus, which presumably had a comparable function. In man, the process is fragmented, one of its derivatives being the lateral process of the calcaneal tuber which shows varying degrees of migration towards the medial process and amalgamation with it.

The importance of these morphological features is discussed in relation to their use in cladistic analysis and their relevance to theories of the early evolution of the mammals.

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