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The homologies of the mammalian tarsal bones

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INTRODUCTION

Anatomists are in fairly general agreement that the primitive tarsal elements (Text-fig. 1A) have had the following fate in man (and other mammals): the talus represents a fused tibiale and intermedium, fibulare has become calcaneus, navicular is a derivative of the centrale (or centralia) and the primitive five tarsalia have given rise to the cuneiforms and cuboid. The anomalous os trigonum of the human foot is generally said to represent the intermedium tarsi; the commonly held belief that such a free intermedium, situated between tibia and fibula, is a normal feature of the marsupial foot, apparently affords valuable confirmation of this hypothesis.

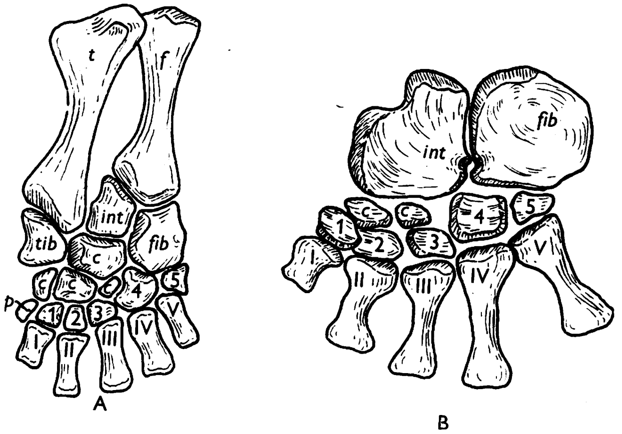
Gegenbaur (1864) initiated the above view. Noting the apparent fusion of tibiale and intermedium in certain of the Chelonia (e.g. *Chelydra*) to produce a tarsus resembling somewhat that of mammals, he reasoned that the same fusion must have occurred in mammals and that *Chelydra* represented a survivor of that reptilian stem which led to the mammals. Bardeleben (1883*a*, *b*, *c*), in search of support for this hypothesis, noted the occasionally separate posterior tubercle of the human talus (which he named os trigonum, and held to represent the intermedium tarsi, homologue of the carpal lunate) and maintained that such a free intermedium was a normal feature of the tarsus in a number of marsupials. This small bone in marsupials was first described by Owen (1841) in *Dasyurus macrourus* and later (1874) in *Phascolomys*; Owen, however, drew no conclusions regarding its morphological identity. Bardeleben seemed further to strengthen his case for a dual phylogenetic origin of the talus by reporting a separate anlage for the posterior tubercle of the talus in the 2-month human foetus.

Baur (1884, 1885*a*), however, raised a difficulty: in rodents there is an extra tarsal bone giving the appearance of a double navicular. Although this bone had long been known (even to Gegenbaur) it had been dismissed as an accessory element, a sesamoid, or the result of division of the navicular. Baur held that it was really the tibiale (as did Albrecht, 1884) and that in other mammals it fused to the centrale to form the navicular. He was also unable to verify Bardeleben's finding of a dual ontogenetic origin of the talus, which bone he held to be the intermedium; the extra element in marsupials he described as a 'Sehnenverknöcherung'. He saw the calcaneus as a derivative of the fibulare. This scheme of homologies was apparently irreconcilable with that of Bardeleben.

A compromise between the two views was next reached. Bardeleben (1885*a*) agreed with Baur's identification of the tibiale and even described a double developmental origin for the human navicular (tibiale and centrale). He persisted, however, in regarding the os trigonum as the intermedium, but decided that the remainder of the talus, since it could no longer be the tibiale, must represent a second centrale. Baur (1885*b*, *c*) agreed with these views.

Later, Bardeleben (1885*c*) rejected this compromise and returned to a modified version of his original view, again including the tibiale in the talus. Baur (1886) also, after a final detailed comparative and embryological study, favoured a return to his own original view with which Leboucq (1886) agreed.

Palaeontologists in general have agreed that the talus is the homologue of the intermedium. Broom (1901, 1904) at first supported Bardeleben's original hypothesis but later (1921, 1930) he considered the talus to be the intermedium alone and so suggested the navicular as the homologue of the tibiale. Most other authorities (Schaeffer, 1941*a*; Romer, 1955) have agreed on the homology of the talus, but have held that the tibiale is not represented in the mammalian tarsus, wherein the navicular is the homologue of the centrale.



Text-fig. 1. A. The crus, tarsus and metatarsus of the primitive amphibian *Trematops milleri* (after Schaeffer). B. The tarsus and metatarsus of the pelycosaur *Ophiacodon retroversus* (after Romer & Price). *c*, centrale; *f*, fibula; *fib*, fibulare; *int*, intermedium, *p*, prehallux; *t*, tibia; *tib*, tibiale; 1, 2, 3, 4, 5, tarsalia one to five; I, II, III, IV, V, metatarsals one to five.

Cope (1884, 1885), however, held there to be justification (partly palaeontological) for regarding the mammalian navicular as a fusion of the tibiale and the centrale, rather than as the one or the other alone. He drew attention to the belief that the bone bearing the horny perforated spur in the monotreme foot was a tibiale and further suggested the presence of such an element in pelycosaurs. Baur (1885*d*, 1886) welcomed this support for his view of a dual derivation of the navicular, established largely on conditions in the rodent tarsus. Unfortunately, Cope's views were based on a false assumption, since the monotreme spur-bearing bone (os calcaris) is not the tibiale. In fact, however, in the monotreme foot there is a true tibiale additional to the os calcaris (Lewis, 1963). Meckel (1826) confused this tibiale with the os calcaris and the former virtually disappeared from subsequent accounts. The figures in current text-books omit it entirely; it has occasionally been figured without comment, but only Emery (1901) seems to have clearly observed it and to have realized its significance. It thus transpires that Cope's conclusions as to the fate of the tibiale were apparently justified, though for the wrong reason. However, for the firm establishment of the homology of the monotreme and rodent tibiale with the navicular tuberosity of other mammals a more precise knowledge of the morphological relations of these elements is required, and establishment would leave little doubt that the talus represents the intermedium alone. The question thus arises as to the morphological nature of the metatherian 'intermedium tarsi' described by Bardeleben. His unillustrated descriptions give no very clear idea of its topographical relations, but he does state that when the bone is absent a meniscus takes its place. The possibility obviously exists that the ossicle is no more than a lunula, an ossification in a meniscus, such as is found in various mammalian joints.

There is in the mammalian tarsus an element, additional to those already considered, which takes the form of a single or double sesamoid on the tibial margin. Bardeleben (1885*b*, 1894) considered this the remnant of a sixth digit (prehallux). Whether or not this be so, there is no doubt that even the most primitive tetrapods had a pentadactyl foot and that this element therein was no more than a bony nodule (Text-fig. 1A). For a time, however, its presence occasioned some confusion concerning the homologies of the tarsalia in mammals (Baur, 1885*b*, *c*).

MATERIALS AND METHODS

Formalin-fixed wet specimens were used throughout this investigation; some of the feet were macerated in antiformin in order to facilitate examination of the skeletal details.

The tarsus was examined in the following Monotremata, attention being paid to the position and attachments of the tibiale, os calcaris and prehallux (tibial sesamoid): *Ornithorhynchus anatinus*, the platypus (1); *Tachyglossus aculeatus*, the Australian spiny anteater or echidna (3).

The feet of the following Marsupialia were examined: *Trichosurus vulpecula*, common brush-tailed possum (2); *Pseudochirus laniginosus*, ring-tailed possum (2), *Vombatus hirsutus*, common wombat (1); *Phascolarctos cinereus*, koala (1); *Sarcophilus harrisi*, Tasmanian devil (1); *Dasyurus quoll*, common Eastern native cat (1); *Perameles gunni*, Tasmanian barred bandicoot (1); *Macropus major*, great grey kangaroo (immature specimen, 1); *Macropus rufus*, red kangaroo (immature specimen, 1). Particular attention was paid to the morphological relations of the so-called intermedium tarsi (Bardeleben), the tibial sesamoid (prehallux) and the navicular.

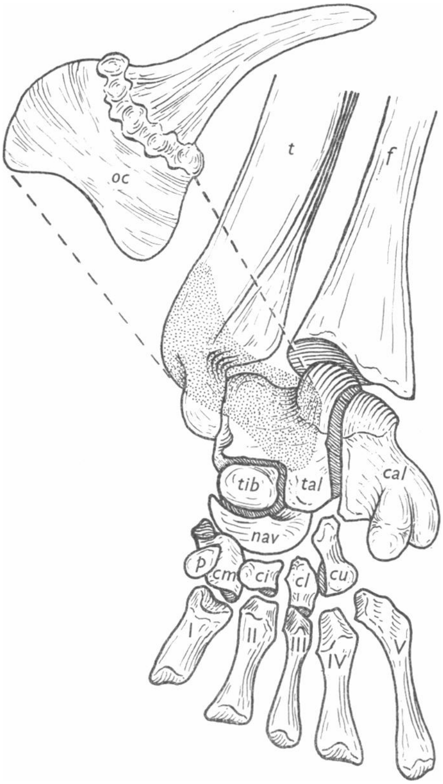
The feet of the following Rodentia were examined: *Protoxerus stangeri*, Stanger's squirrel (1); *Hydrochoerus hydrochoeris*, the capybara (1); *Cricetus cricetus*, hamster (1); *Coendou prehensilis*, Brazilian tree porcupine (1); *Mus norvegicus albinus*, white rat (7); Mystromys (? species) (1). Particular attention was paid to morphological relations of the tibial navicular (tibiale) and the prehallux.

In view of the fact that a prehallux has been reported in the feet of some monkey species, the following Primates were examined in a search for this ossicle: *Colobus polykomos*, black and white colobus monkey (1); *Procolobus verus*, olive colobus monkey (1); *Cercopithecus nictitans*, white-nosed monkey (1); *Cebus nigrivittatus*, weeper capuchin monkey (1); *Pan satyrus*, chimpanzee (1).

OBSERVATIONS

Monotremata

(*a*) *Ornithorhynchus anatinus*. The macerated tarsus of the platypus is shown in Text-figure 2. It manifests some very primitive features: both the L-shaped talus and the calcaneus articulate with the fibula; the tibia projects far distally to articulate with the talus; there is a free tibiale greatly resembling a separated navicular tuberosity. A small, flattened, plaque-like ossicle, the prehallux, articulates with the medial aspect of the medial cuneiform. The cuboid is a single bone (previous accounts have sometimes incorrectly accounted it double) bearing the articulations of the fourth and fifth metatarsals. The os calcaris is a flat bony mass formed about the base of the horny perforated spur which conveys to the exterior the secretion of the femoral (poison) gland. It is attached to the talus by a syndesmosis and it articulates through a small synovial joint with the tibia; between these attachments it bridges over the tibialis posterior and flexor tibialis tendons as they enter the foot.



Text-fig. 2. The flexor aspect of the right tarsus and metatarsus of *Ornithorhynchus anatinus*; the os calaris bearing the horny spur is shown lifted away from its site of articulation which is indicated by stippling. *cal*, Calcaneus; *ci*, intermediate cuneiform; *cl*, lateral cuneiform; *cm*, medial cuneiform; *cu*, cuboid; *f*, fibula; *nav*, navicular; *oc*, os calcaris; *p*, prehallux; *t*, tibia; *tal*, talus; *tib*, tibiale; I, II, III, IV, V, metatarsals one to five.

In the wet specimen it is seen that the distal terminal attachment of the tibialis posterior tendon is to the tibiale; to reach it, however, the tendon must cross the projecting talus to which a great part of it gains attachment and it is here deep to the os calcaris to which it has a minor insertion. It may be presumed that the tibiale was the primitive insertion, for it is not unusual for tendons crossing bony prominences to gain a partial attachment thereto, as has here happened in respect of the talus. The small bony plaque (prehallux) articulating with the medial cuneiform is found to be a sesamoid within the substance of the flexor tibialis tendon. The platypus foot contains another small sesamoid not shown in Text-fig. 2. This is a sesamoid within the flexor fibularis tendon in the sole. There is no intra-articular talo-fibular meniscus, such as is found in marsupials.

(*b*) *Tachyglossus aculeatus.* The basic arrangement is very like that in the platypus despite some minor differences: no true sesamoid bone, but a mere fibro-cartilaginous thickening occurs within the flexor tibialis tendon and there is no sesamoid within the flexor fibularis tendon.

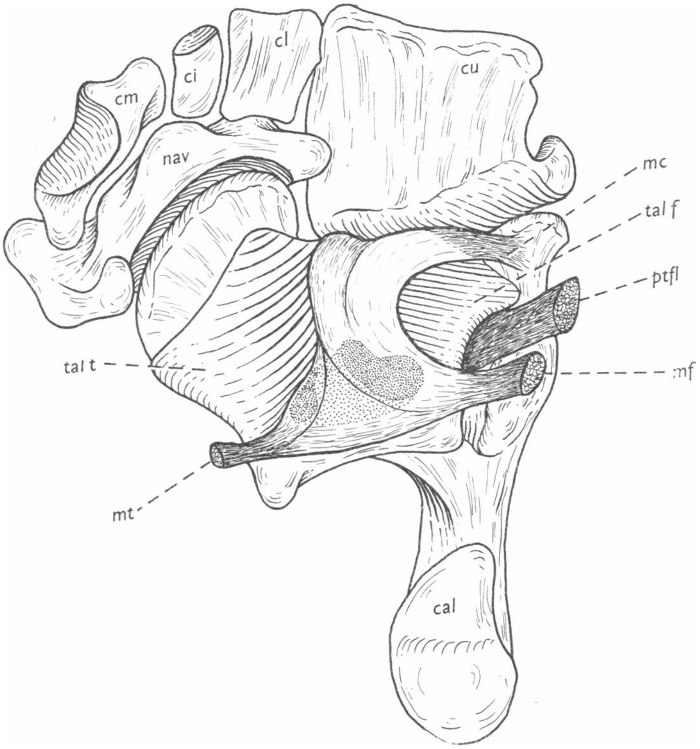
Marsupialia

(*a*) *Phascolarctos cinereus.* The skeleton of the foot of this species approximates the primitive marsupial type, except for the reduced and syndactylous character of the second and third digits. The fibula does not contact the calcaneus as in monotremes, but both tibia and fibula articulate with the upper surface of the talus; the talus has not yet been modified so as to bring the fibular facet on to its lateral surface as in the case of the somewhat cylindrical body of the human talus. There is a single navicular with a prominent tuberosity (not contacting the tibia) and into it is inserted the tibialis posterior tendon. There is no tibial sesamoid bone (prehallux) in the flexor tibialis tendon. A large intra-articular meniscus (Text-fig. 3) lies between the lower end of the fibula and the fibular facet on the talus. This meniscus has a thin extension upwards between tibia and fibula into the inferior tibio-fibular joint. Its attachments are as follows: behind it has a tough ligamentous attachment to the fibula (immediately behind a posterior talo-fibular ligament with position and attachments similar to that of human anatomy); from its posterior attachment the semilunar meniscus sweeps around between fibula and talus, here sending upwards its extension between tibia and fibula, and it terminates anteriorly in a tough fibrous attachment to the calcaneus. Posteriorly, in the interval between tibia, fibula and talus, the disc is very thick and has a small pyramidal ossicle (lunula) embedded within its substance. A ligamentous attachment passes from the thick posterior part of the disc to the tibia. There are thus three anchoring bands passing from the meniscus to the fibula, tibia and calcaneus, respectively.

(*b*) *Trichosurus vulpecula* and *Pseudochirus laniginosus* present an essentially similar arrangement. Both present a lunula, similar to that of the koala, within a similar meniscus in the ankle joint. In both these species, however, the navicular tuberosity articulates with the tibia within the ankle joint. Both also present a sesamoid (prehallux) within the flexor tibialis tendon where it lies adjacent to the medial cuneiform. The tendon here passes as a fascial sheet into the hallux superficial to the tibialis anterior insertion, but also gives another expansion joining the plantar aponeurosis.

(*c*) *Vombatus hirsutus* presents an arrangement very like that of the koala, and has an even larger lunula within the ankle joint meniscus.

(*d*) *Sarcophilus harrisi*. The intra-articular meniscus of the ankle joint is again very similar to those of the previous species and there is a corresponding lunula in the thick posterior part of the disc. The disc's tibial attachment is, however, particularly thick and presents within its substance a second ossicle. Thus, in this species, there are two lunulae within the disc. The hallux is greatly reduced and there is no sesamoid (prehallux) in relation to the medial cuneiform.



Text-fig. 3. The dorsal aspect of the right tarsus of *Phascolarctos cinereus* showing the intra-articular meniscus, the lunula of which is indicated by stippling. *cal*, Calcaneus; *ci*, intermediate cuneiform; *cl*, lateral cuneiform; *cm*, medial cuneiform; *cu*, cuboid; *mc*, calcaneal attachment of meniscus; *mf*, fibular attachment of meniscus; *mt*, tibial attachment of meniscus; *nav*, navicular; *ptfl*, posterior talo-fibular ligament; *tal f*, fibular facet on the talus; *tal t*, tibial facet on the talus.

(*e*) *Dasyurus quoll* presents features similar to those of the Tasmanian devil, but there is only one lunula within the ankle meniscus.

(*f*) *Macropus rufus* and *Macropus major* are essentially alike in foot structure: convergent evolution, however, has produced a talus not unlike the eutherian (and human) one having a superior trochlear surface for the tibia and a medial one for the tibial malleolus; as in man the facet for the fibula occupies the lateral surface of the bone. The posterior talo-fibular ligament has the usual attachments and in these species acts as an intra-articular disc between the articulating fibula and calcaneus.

There is an intra-articular meniscus homologous to those of the preceding species, with the usual fibular and calcaneal attachments, but no tibial. Semilunar in shape, it intervenes between talus and fibula, and thus occupies a vertical plane: it sends no extension between tibia and fibula and although thickened posteriorly it contains no lunula.

(*g*) *Perameles gunni*. The bony arrangements are very like those in the Macropodidae, but an ankle joint meniscus is entirely wanting.

(*h*) *Didelphys marsupialis*. A rather large sesamoid bone (prehallux) lies in the expansion of flexor tibialis to the hallux, and articulates with the medial cuneiform. The flexor tibialis tendon gives two other expansions—joining the flexor fibularis tendon and the plantar aponeurosis. The arrangements within the ankle joint are somewhat similar to those seen in Macropodidae. Although the fibular facet on the talus is not so vertical as in the latter, the disc is essentially similar, intervening between talus and fibula only, without upward extension between tibia and fibula, and presenting no lunula. There is a posterior talo-fibular ligament having the usual attachments.

Rodentia

A double navicular occurs in all the species examined herein. The medial element (identified by Baur as the tibiale) will, for the time being, be referred to as the tibial navicular, the other element as the fibular navicular, thus following the convention adopted by other authors.

(*a*) *Mus norvegicus albinus*. The tibialis posterior tendon inserts into the tibial navicular and into that bone alone. Greene (1955), in her monograph on the rat, erroneously states that it inserts into the fibular navicular and the medial cuneiform. A well-defined spring ligament passes from the calcaneal sustentaculum tali to the tibial navicular. The flexor tibialis tendon attaches in the sole to the plantar fascia alone—a specialization convergent with that occurring in some marsupials. The tendon has no connexion to the flexor fibularis, such as Greene describes. A tibial sesamoid lies on the medial cuneiform, embedded in a ligament bridging the tibialis anterior insertion. It is apparent that this ligament is the divorced representative of that part of the flexor tibialis tendon which proceeds to the hallux in the primitive condition (Lewis, 1962*b*) and that the sesamoid (the prehallux) is homologous with that found in the hallucial prolongation of flexor tibialis in many marsupials.

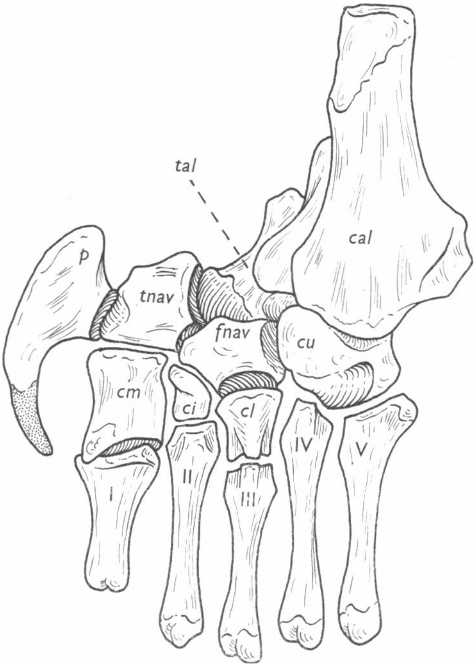
(*b*) *Mystromys* presents arrangements similar to those in the white rat.

(*c*) *Cricetus cricetus*. Arrangements again are similar, but no tibial sesamoid is identifiable.

(*d*) *Protoxerus stangeri*. Tibialis posterior and the spring ligament are attached to the tibial navicular. Flexor tibialis is attached in the sole to the plantar fascia, sends a strong expansion to the hallux, and presents a tibial sesamoid bone—an arrangement very like that of most Australian marsupials (e.g. *Trichosurus*).

(*e*) *Hydrochoerus hydrochoeris* has lost the fifth digit: the hallux is reduced, buried in the sole, and consists of a single bony element apparently inclusive of the medial cuneiform, which is not separately identifiable. The tibialis posterior tendon and a well-defined spring ligament are attached to the tibial navicular. The flexor tibialis tendon has its only attachment to that of flexor fibularis; there is no tibial sesamoid.

(*f*) *Coendou prehensilis.* The foot of this species shows a remarkable secondary specialization for arboreal life which has been fully described by Wood Jones (1953). Certain points relative to the present discussion, however, require amplification. There is a large hook-like tibial sesamoid (Text-fig. 4) articulating with the tibial navicular: this sesamoid forms the skeletal basis for a pad which may be opposed to the remainder of the sole, thus fulfilling a prehensile function. The flexor tibialis tendon is not attached to the sesamoid, but entirely joins the flexor fibularis tendon, spreading over the surface of the latter and being distributed especially to the marginal tendons in typical eutherian fashion (Lewis, 1962*b*). Both the tibialis posterior tendon and a well-defined spring ligament are attached to the tibial navicular. Wood Jones regarded the bipartite navicular as a specialization increasing the mobility of the prehensile pad and its contained sesamoid: there is, however, no foundation for this interpretation, for such a double navicular is a normal feature of the rodent foot, regardless of any functional modifications.



Text-fig. 4. The flexor aspect of the right tarsus and metatarsus of *Coendou prehensilis*. *cal*, Calcaneus; *ci*, intermediate cuneiform; *cl*, lateral cuneiform; *cm*, medial cuneiform; *cu*, cuboid; *fnav*, fibular navicular; *p*, prehallux; *tal*, talus; *tnav*, tibial navicular; I, II, III, IV, V, metatarsals one to five.

Primates

A prehallux was found in only one of the primates here examined—*Cebus nigrivittatus*. It was embedded in the distal attachment of a ligament, similar to that seen in the rat, passing between the navicular and first metatarsal and bridging the insertion of the tibialis anterior tendon. The ossicle entered into the cuneiform-metatarsal articulation in a manner reminiscent of that of the metatarso-phalangeal sesamoid bones. In other primates (e.g. the chimpanzee) wherein the prehallux is absent, the ligament alone is seen.

DISCUSSION

The literature reviewed herein, assessed in the light of recent knowledge, the observations recorded above, and evidence from palaeontological and embryological sources clearly point to the following conclusions: that the calcaneus is homologous with the fibulare, the talus with the intermedium, the navicular with the coalesced tibiale and centrale, the three cuneiforms with tarsalia one to three, and the cuboid with tarsalia four and five.

(*a*) *Morphological evidence.* As De Beer (1938, 1951) and Huxley (1955) point out, morphological relations provide the surest guide to homologies; homology carries with it the notion of continuity of structures in phylogeny but does not necessarily imply similarity of genetical control nor of ontogenetic processes.

The findings reported here clarify the nature of the so-called free 'intermedium tarsi' of the marsupial foot. It is no more than a lunula—an ossification within an intra-articular meniscus. These ossifications confer rigidity on the thickened parts of discs and may be expected when the angle between the surfaces exceeds 45° (Barnett, 1954); they are well shown in, for example, the knee joint menisci of the rat. (Had Bardeleben known of the two ossicles within the *Sarcophilus* disc his interpretation of their morphology would have proved interesting.) The disc with its lunula must be considered a primitive feature, lost in most higher mammals *pari passu* with the changed form and function of the bones comprising the ankle joint, although a disc somewhat similar to that of the kangaroo has been reported as an anomaly in man (Seymour Sewell, 1906). The marsupial meniscus is closely associated with the posterior talo-fibular ligament, which as noted, may intervene, disc-like, between an articulating fibula and calcaneus (fibulare). These structures together closely resemble the triangular articular disc at the wrist, especially with regard to the developmental stages (Leboucq, 1884; Corner, 1898) of the latter, for the developing wrist joint disc is attached to the lunate (intermedium) as well as to the radius, and it even presents a transient cartilaginous nodule within its substance (cf. the tarsal lunula). The basic plan of the carpus is clearly very similar to that of the tarsus. There is thus now little reason for regarding the anomalous human os trigonum as an intermedium tarsi. Perhaps it is not even the homologue of the marsupial lunula, and nothing more than an aberrant ossification of no morphological significance.

The insertion of the tibialis posterior tendon to the monotreme tibiale, to the rodent tibial navicular, and to the navicular tuberosity of other mammals (and also the attachment of the spring ligament to the latter two structures) suggests that these various bony elements are homologous. That they all represent the tibiale is supported by the finding (Schaeffer, 1941*a*) that the amphibian tibiale receives the insertion of the precursor of the tibialis posterior, the pronator profundus (plantaris profundus I of McMurrich, 1904). The phylogenetic continuity of the tibiale thus seems reasonably established. The insertion of tibialis posterior in higher primates to other tarsal and metatarsal bones is secondary, as will appear elsewhere.

These findings do not necessarily mean that rodents have here retained a very primitive tarsal feature. Probably the rodent condition represents an example of evolutionary reversal. Genetical studies (Muller, 1939) clearly demonstrate such a possibility. It is even likely that the genetical control differs from that of the primitive free tibiale, though this would not influence notions of homologization. Apparently a double navicular (i.e. free tibiale) is not confined to rodents. Cope (1884) reported a similar arrangement in certain fossil ungulates and Leche (1900) in *Galeopithecus*, *Hyrax* and the Dinocerata. A double navicular may also occur as an anomaly in man—the os tibiale externum or accessory scaphoid (Brailsford, 1953).

(*b*) *Embryological evidence.* The interpretation of embryological findings in the older literature has been biased by an uncompromising belief in a stereotyped recapitulation of phylogeny during development. De Beer (1938, 1951) has clarified the relationship of phylogeny and ontogeny by pointing out that embryological processes may be accelerated or retarded (even to disappearance) processes leading to progressive change in developmental history. The fairly well documented case of the phylogeny and embryology of the human carpal scaphoid serves to illustrate the processes at work in the evolution of the tarsus; for Primates (other than the Hominoidea) possess a separate bony centrale together with a radiale. In Asiatic anthropoid apes these may fuse together in old age; in African anthropoid apes they chondrify separately but fuse in late foetal or early juvenile life, the common mass then ossifying, although in some chimpanzees the centrale may begin ossification before the fusion (Schultz, 1936, 1944). In man centrale and radiale chondrify separately (Rosenberg, 1876), fusing together in the second month of foetal life (Leboucq, 1884), the fused mass later ossifying from one centre. (Rarely the centrale may not fuse and it then ossifies separately.) Persistence of this trend in human development would mean that the human scaphoid would ultimately chondrify, just as it ossifies, from one centre. Such an eventuality would not, however, mean that the carpal scaphoid should no longer be regarded as the homologue of both centrale and radiale. Usually the human pedal navicular chondrifies singly (O'Rahilly, Gray & Gardner, 1957); sometimes, however, it originates as two (tibiale and centrale) cartilaginous *Anlagen* (Emery, 1901). Certainly in most marsupials tibiale and centrale chondrify independently, thereafter fusing to form the navicular (Emery, 1897)—a course of events quite comparable to the development of the human carpal scaphoid. It is of significance that in the Macropodidae, with their digital reduction, no *Anlage* of the tibiale appears, and that in these marsupials the M. tibialis posterior, lacking its insertion, is also absent (Lewis, 1962*a*). Apparently also in some Eutheria (e.g. dog, cat, bear, gibbon) tibiale and centrale chondrify separately (Baur, 1884; Testut, 1904). Doubtless in those human cases where there is an os tibiale externum, this element chondrifies and ossifies separately. Thus, a particular developmental trend observable in the carpus is reflected in the tarsus; the incontrovertible embryological arguments for a dual origin of the carpal scaphoid are applicable with equal force to the tarsal navicular.

It is generally agreed that the human cuboid chondrifies and ossifies singly. In marsupials (Emery, 1897), however, there are two cartilaginous *Anlagen*. The inference is that the cuboid represents tarsalia four and five, regardless of its single developmental origin in man.

Most are now agreed that the talus normally chondrifies singly (Bardeen, 1905). Its developmental position between the tibia and fibula in marsupials (Emery, 1897) points to its homology with the intermedium and this is strongly supported by its relationship to the perforating artery of the tarsus. In the adult salamander in both carpus and tarsus there is a perforating artery between the intermedium on the one hand and fibulare or ulnare on the other; similar vessels appear in the development of the human carpus, between lunate and triquetral, and in the tarsus between talus and calcaneus, though only the latter vessel persists (Leboucq, 1886). The vessel clearly identifies intermedium and fibulare and their homologues in the mammalian carpus and tarsus. Thus the fundamental unity in plan between carpus and tarsus is again stressed.

(*c*) *Palaeontological evidence.* The facts of palaeontology appear to offer nothing conflicting with the view being presented, though commonly interpreted without reference to the evidence of comparative anatomy and embryology. The fossil record confirms the identity of talus and calcaneus with intermedium and fibulare, the canal for the perforating artery again providing a useful marker for these bones during their changes in position and form. The resemblance of the monotreme talus and calcaneus to the pelycosaur intermedium and fibulare bears this out.

Palaeontologists are prone to conclude that, when a particular bone occupies the position previously occupied by two, it is the functional equivalent of the two, but the homologue of one only, the other having disappeared. In pelycosaurs, two bones, identified as centralia (Text-fig. 1B), occupy the position of the mammalian navicular. It is held that the medial disappears, leaving the other to become the navicular. It seems more probable that, as Broom (1921) held, the medial one is the tibiale. It is therefore suggested that the tibiale persists through the therapsid line, either as an independent element or fused to the centrale. There appears a distinct possibility that a cartilaginous tibiale existed in the very mammal-like foot of *Bauria*. The fate of the other three centralia found in the labyrinthodont foot (Text-fig. 1A) remains problematic. They may have fused to other tarsal bones or all four centralia may have united to form the single reptilian centrale. Certainly it seems that at the time of attainment of the reptilian stage of evolution only a single free centrale existed.

Palaeontologists generally believe that the cuboid represents tarsale four alone. However, five tarsalia were present in pelycosaurs (Romer & Price, 1940) and in the therapsids *Ictidosuchoides* and probably *Bauria* (Schaeffer, 1941*a*, *b*). This supports the comparative embryological evidence favouring the view that the cuboid is homologous with tarsalia four and five.

The prehallux

There is often considerable confusion between this tibial sesamoid and the tibiale of rodents and monotremes (e.g. Flower, 1876; Schäfer & Thane, 1899). There is no evidence that it represents a true sixth tetrapod digit for even in the primitive pentadactyl amphibian *Trematops* (Text-fig. 1A) it is but a small bony nodule. It may, however, be the homologue of a pre-axial fin ray. In mammals it may appear as a sesamoid bone often associated with the flexor tibialis insertion. In the primitive mammalian condition (*Didelphys marsupialis*) this tendon has a triple insertion—to plantar aponeurosis, to hallux and to flexor fibularis tendon. The prehallux lies within the hallucial prolongation which bridges over the tibialis anterior insertion to the medial cuneiform. The varying fate of these three attachments within the mammalia (Lewis, 1962*a*) results in different topographical relations of the prehallux. In most marsupials and in some of the Rodentia, Insectivora and Edentata (Dobson, 1883*a*) the connexion to the flexor fibularis tendon is lost. The prehallux is then found (e.g. *Trichosurus vulpecula, Protoxerus stangeri*) within the hallucial continuation of the flexor tibialis tendon in the sole. In the rat, however, this hallucial continuation, severed from the flexor tibialis tendon (which is left attaching to the plantar aponeurosis only) constitutes a new ligament, which stretches from navicular to the first metatarsal across the tibialis anterior insertion, and contains the prehallux. In most Eutheria the connexion of flexor tibialis to the flexor fibularis tendon is alone retained. The remainder of the pedal portion of flexor tibialis persists as a ligament similar to that seen in the rat. The prehallux, when present, lies within this naviculo-metatarsal ligament. This same ligament is well marked in primates and a prehallux, when present (e.g. *Cebus*), lies within the distal part of this ligament, articulating with the medial cuneiform and first metatarsal rather in the manner of a metatarso-phalangeal sesamoid. This resemblance has been held to support the view that the medial cuneiform and first metatarsal of classical anatomy are in reality the homologues of hallucial metatarsal and first phalanx—a view no longer meriting serious consideration. The differing pedal terminations of flexor tibialis and the apparently abrupt phylogenetic appearance of an ossicle-containing ligament are not the major evolutionary novelties which they at first sight may seem. They represent quite minor variations of emphasis on a basic plan and are themselves presumably the result of relatively small genetic variations.

In the skeleton of some mammals—certain Rodentia and Edentata (Wood Jones, 1953), certain Insectivora (Dobson, 1883*b*) and even *Elephas africanus* (Leche, 1900)—the prehallux is enlarged and mimics an additional pre-axial digit. There is no doubt that this arrangement is a secondary specialization and not indicative of derivation from a true sixth digit.

CONCLUSIONS

The views presented herein stress the fundamental unity of plan, and perhaps some sharing of genetic control, between carpus and tarsus. Some of this was apparent even to Owen (1848, 1866). This similarity between the two is especially marked in man, for in other mammals reduction in the number of digits or varying fusions between individual carpal and tarsal bones may produce an overlay of difference. The similar basic plan represents an example of the polyisomerism of Gregory (1936); local differences (Gregory's anisomerism) between carpus and tarsus are the results of different emphasis due in turn to accelerations or retardations during development.

SUMMARY

1. No evidence is found for the common view that the mammalian talus represents a fusion of tibiale and intermedium.

2. Proponents of this view consider the anomalous human os trigonum as the homologue of the intermedium, a view gaining apparent support from the belief that

a normal 'os intermedium tarsi' occupies this position in the marsupial foot. It is shown that the so-called marsupial intermedium is merely a lunula within an intra-articular meniscus.

3. A free tibiale exists in the monotreme and in the rodent foot; the insertion into it of the tibialis posterior tendon indicates its homology with the tibial part of the navicular in other mammals.
4. It is concluded that the mammalian navicular is homologous with centrale plus tibiale, the talus with the intermedium, the calcaneus with the fibulare, and the cuboid with tarsalia four and five.
5. A fundamental unity of plan obtains between carpus and tarsus, even within the mammalia.

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