

The joints of the evolving foot. Part II. The intrinsic joints

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INTRODUCTION

In the previous paper (Lewis, 1980*a*) an attempt was made to outline a scenario for the evolutionary history of the mammals, with particular reference to the primates, using mainly the criteria of ankle joint morphology as an indicator of locomotor habit and habitat. It was suggested that the last common ancestors of the marsupials and placentals, the advanced therians of the early Cretaceous, were already well adapted to life in a spatially complex arboreal environment, possessing a grasping opposable hallux and an ankle joint, such as that found in extant marsupials, which permitted movements of the foot and leg bones in a manner analogous (though biomechanically different) to pronation–supination in the forelimb. From such a stock the first marsupials were probably derived as committed arborealists. It is likely that the first placentals evolved from this same stock but as occupants of a niche in the complex uneven terrain of the undergrowth where they lost the talocrural features permitting ‘pronation–supination’ but retained a useful degree of opposability of the hallux. From among such placentals we can infer that the primates arose as arboreal specialists; other placental lineages presumably explored, and adapted to, the more terrestrial environment. The arboreal primates, as will be shown in this paper, appear to have evolved specializations in the intrinsic foot joints compensating for the lost capacity for talocrural ‘pronation–supination’. The present paper will also deal with the further modifications of these arboreal specializations necessitated by the terrestrial bipedal demands of man. A preliminary report of some of these findings has been presented by Lewis (1980*b*).

MATERIALS AND METHODS

The following formalin-fixed wet specimens from the author's collection were utilized: *Trichosurus vulpecula* (brush-tailed possum or phalanger); *Pseudocheirus laniginosus* (ring-tailed possum or phalanger); *Phascolarctos cinereus* (koala); *Macropus major* (great grey kangaroo); *Sarcophilus harrisi* (Tasmanian devil); *Tupaia sp.* (treeshrew); *Tenrec ecaudatus* (tailless tenrec); *Suncus caeruleus* (Ceylon musk shrew); *Lemur catta* (ring-tailed lemur); *Galago senegalensis moholi* (Moholi galago); *Pithecia monachus* (Humboldt's saki); *Cebus nigrivittatus* (weeper capuchin monkey); *Saimiri sciureus* (squirrel monkey); *Procolobus verus* (olive colobus monkey); *Colobus polykomos* (black and white colobus monkey); *Cercopithecus nictitans* (spot-nosed guenon); *Hylobates lar leuciscus* (silvery gibbon); *Pan troglodytes* (young male chimpanzee); *Pan troglodytes* (two years old chimpanzee); *Pongo pygmaeus* (juvenile orang-utan). In addition feet from a number of dissecting room cadavers were available for study. The foot of a wet specimen of *Gorilla gorilla*

gorilla (Western lowland gorilla) was also dissected; the skeleton of this specimen ('Guy', which died in London Zoo in 1978) is now deposited in the British Museum (Natural History) with the catalogue number 1978-1226.

The compromise axis of movement of the subtalar joint complex was determined by a modification of the method devised by Hicks (1953). This axis, although only an abstraction, provides a useful aid to the visualization of the movements occurring at this complex system of joints.

Movements at the transverse tarsal joint complex were analysed by superimposing serial radiographs of ligamentous preparations with appropriate metal markers inserted.

OBSERVATIONS AND COMMENTS

The subtalar joint complex – morphology and function

The nomenclature of the joints involved here has been bedevilled by varying usage and changes in terminology. This confusion applies even more to the definition of the movements involved and becomes especially troublesome in the comparative context. It is, of course, well recognized that the talus articulates with the remainder of the foot – the lamina pedis (footplate) as it was aptly termed by MacConaill & Basmajian (1969) – by two anatomically distinct articulations involving its under surface. These are a posterior talocalcaneal joint and anteriorly the talocalcaneo-navicular joint. Movement, however, of lamina pedis upon talus involves both joints simultaneously and this functional composite has frequently been termed the subtalar joint (Manter, 1941). In deference to the common clinical usage this term was incorporated in the official anatomical nomenclature, but, curiously and inappropriately, was applied only to the posterior of the two functionally interacting joints. The term 'subtalar joint' was also used restrictively by Shephard (1951) for the posterior talocalcaneal joint together with only part (the talocalcaneal part) of the anterior joint, the remainder of this latter articulation being included as part of the midtarsal joint; Shephard (1951) then introduced the term 'peritalar joint' for the whole of the two joints. The articulations underlying the talus have commonly been described as 'the lower ankle joint' in comparative anatomy but this term is really only an apt one in cursorial or saltatory forms where the axis of movement tends to be transverse and complements, and amplifies, movement at the talocrural joint (Barnett, 1970); it is particularly appropriate in the highly modified subtalar joints of artiodactyls (Schaeffer, 1947). In this paper the term 'subtalar joint complex' will be used for the articulations (or single articulation in marsupials) between the talus and the lamina pedis. In the human foot then this complex is represented by the talocalcaneal and talocalcaneo-navicular joints.

The movements occurring at this joint complex about an oblique compromise axis are usually defined as 'inversion' and 'eversion'. These movements can be artificially resolved into two components: a rotation of the foot about its long axis (supination-pronation) and a rotation of the whole foot about a vertical axis (adduction-abduction). Thus inversion can be seen as a combination of adduction of the front part of the foot plus partial supination. It should be noted that Shephard (1951) and Manter (1941) used the terms in a quite contrary sense; for them the composite movements were supination-pronation, supination, for instance, in their usage, consisting of inversion and adduction. In the present paper the term inversion-eversion will be used for the composite movements at the subtalar joint

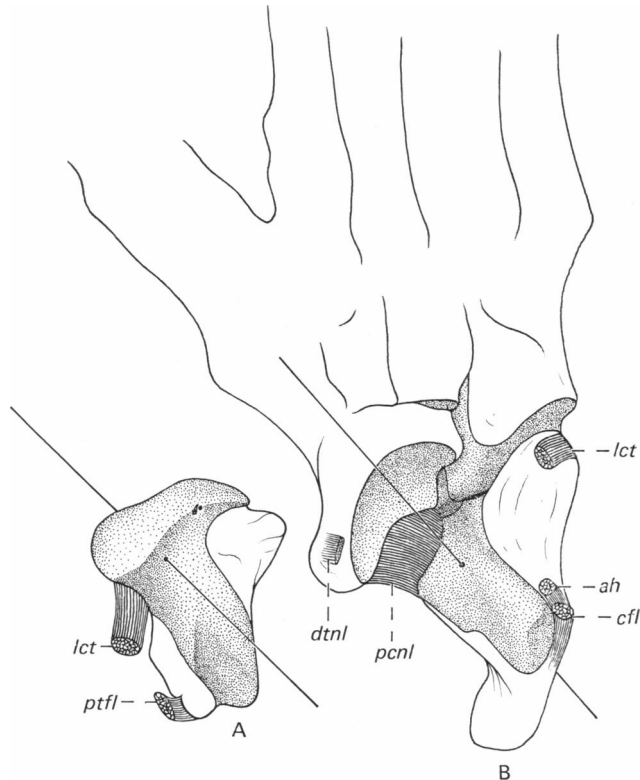


Fig. 1. A dorsal view of the right lamina pedis (B) of *Trichosurus vulpecula* with the talus (A) rolled away medially from its articulations. In each case the compromise subtalar axis is shown. *lct*, ligamentum cervicis tali; *ptfl*, posterior talofibular ligament; *pcnl*, plantar calcaneonavicular (spring) ligament; *ah*, anterior fibrous horn of ankle meniscus; *cfl*, calcaneofibular ligament; *dtnl*, dorsal talonavicular ligament.

complex. The terms supination–pronation will be restricted to movements at the midtarsal joint complex, as will be described later.

The marsupial joint

Trichosurus vulpecula (Fig. 1). The lamina pedis bears a single compound articular surface for the talus. Behind, this surface is formed by a cylindrical articular convexity which reverses its curvature when traced anteriorly, becoming concave and continuous with an articular cup for the reception of the head of the talus. This cup is formed largely by the navicular and the sustentaculum tali of the calcaneus, joined together by the plantar calcaneonavicular (spring) ligament, but the cuboid also intervenes laterally and so participates in the joint. The tarsus is thus of the so-called ‘alternating’ type. It seems likely that an alternating tarsus is the primitive therian arrangement and it is also widely considered that a similar arrangement is the primitive eutherian condition (Schaeffer, 1947). Noteworthy is the fact that in marsupials there is no interosseous talocalcaneal ligament, no tarsal canal, and thus no subdivision of the subtalar joint complex into anterior and posterior components. It could be reasoned that this represents the basic therian condition and would therefore also have been the ancestral morphology of the placentals. It appears more likely, however, that the Metatheria have secondarily eliminated the ancestral inter-

osseous ligament since the echidna (*Tachyglossus*) possesses one, together with dual articulations (Barnett, 1970). There are also dual articulations in the therocephalian mammal-like reptiles (Kemp, 1978).

The compromise axis for inversion–eversion lies very obliquely, being almost in line with the widely divergent hallux and in a quite flat plane, rising relatively little when traced anteriorly. The correspondence of the axis with the divergent hallux may be mechanically advantageous, for the grasping hallux thus remains relatively stationary as the remainder of the foot inverts into gripping posture. A strong ligamentum cervicis tali is advantageously disposed to limit inversion, and a very tough dorsal talonavicular ligament retains the head of the talus within its articular cup. There is at least a suggestion of a screwing action being involved in movements, with inversion being accompanied by slight forward advance of the lamina pedis.

Pseudocheirus laniginosus, *Phascolarctos cinereus* and *Sarcophilus harrisi*. In all these marsupial species the form and function are similar to *Trichosurus*.

Macropus major. Drastic remodelling has occurred in the joint in this species so that it is truly a 'lower ankle joint', yet its derivation from a morphology such as that of *Trichosurus* is still readily apparent. The joint axis has been re-orientated so that it is almost transverse and the morphology thus shows a quite striking convergence towards that described for the precursors of the artiodactyls by Schaeffer (1947). Significantly the joint shows a partial subdivision into two components, perhaps indicative of the fact that the marsupial joint was primitively double.

The insectivore joint

Tupaia sp. The most noteworthy difference from the marsupials is the presence here of an interosseous talocalcaneal ligament in a tarsal canal, subdividing the subtalar joint complex into a posterior talocalcaneal and an anterior talocalcaneonavicular joint. This latter, however, partially retains the pattern of an alternating tarsus for, although in the floor of the articular cup for the talar head the calcaneus is extended forward to meet the navicular, more dorsally the cuboid participates in the joint and contacts the talus in eversion. A ligamentum cervicis tali and a dorsal talonavicular ligament are present.

Tenrec ecaudatus. The morphology is basically similar to the preceding species, with an interosseous talocalcaneal ligament and a partial participation of the cuboid in the talocalcaneonavicular joint.

Suncus caeruleus. In this species the tarsus is no longer of alternating type for the calcaneus is prolonged forward to articulate with the navicular, completely excluding the cuboid from contact with the talus.

The primate joint

The basic aspects of morphology and function are fairly constant throughout the primates, with the noteworthy exception of *Homo sapiens* which will be considered separately. There are variations in emphasis of certain features, and some extreme exaggerations but the underlying pattern seems to be a basic primate heritage. It may be helpful to commence by describing a primate showing the total morphology in very clear-cut fashion, and this is best exhibited in arboreal New World monkeys.

Pithecia monachus (Fig. 2). An interosseous talocalcaneal ligament and a canalis tarsi are present, subdividing the subtalar joint complex into the typical eutherian posterior and anterior components. Posteriorly the calcaneus bears a convex facet, which is markedly prolonged backwards and medially, for the body of the talus.

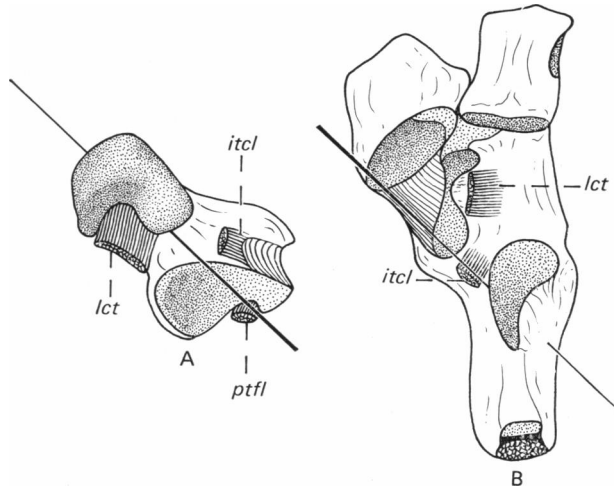


Fig. 2. A dorsal view of the right lamina pedis (B) of *Pithecia monachus* with the talus (A) rolled away. In each case the compromise subtalar axis is shown. *itcl*, interosseous talocalcaneal ligament. Other labels as in Fig. 1.

Anteriorly is the receptive surface on the lamina pedis for the head and neck of the talus, which together are essentially cylindrical and terminate in a convexity for articulation with the navicular. On the surface of this cylinder is an L-shaped area for articulation with facets, joined by a narrow articular isthmus, on the body and sustentaculum tali of the calcaneus; the L-shaped articulation encloses the attachment of the ligamentum cervicis tali. The receptive cup for the head of the talus is completed by the plantar calcaneonavicular ligament. The calcaneus extends forwards and achieves a considerable articulation with the navicular thus excluding the cuboid from the talocalcaneonavicular joint.

The compromise subtalar axis of movement occupies a quite flat plane rising comparatively little when followed anteriorly. It is markedly deviated from the long axis of the foot, traversing the cylindrical talar neck whose angulation to the body of the bone is thus an expression of the obliquity of the axis. Its relationship to the posterior part of the tarsus is not unlike that in *Trichosurus*, but the overall relationship to the foot is rather different because of the lengthening of the pes in the monkey. The lamina pedis inverts and everts upon the talus about this axis just as it does in marsupials. But whereas in the latter there is only a poorly defined screwing motion, in the monkey this has become a major component of the movement. The posterior talocalcaneal articulation has a helical orientation in relationship to the subtalar axis – in a right foot it is a segment of a right-handed screw. Thus, as the lamina pedis moves into inversion the calcaneus is screwed forward beneath the talus; conversely, in eversion it is retracted. The biomechanical advantages of this will be considered later.

Cebus nigrivittatus. In morphology and function this species is similar to the preceding one.

Colobus polykomos (Figs. 3, 4). In all essentials the arrangements are similar to the preceding species. However, the two facets on the body and sustentaculum tali of the calcaneus are discontinuous but the interval between them is bridged by smoothly surfaced ligamentous tissue, continuous with the plantar calcaneonavicular ligament; whether or not dry bones exhibit two separate facets, or a single confluent

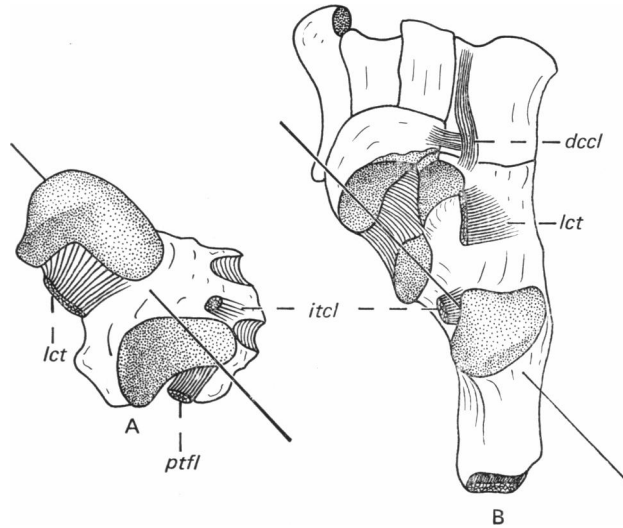


Fig. 3. A dorsal view of the right lamina pedis (B) of *Colobus polykomos* with the talus (A) rolled away from its articulations. In each case the compromise subtalar axis is shown. *dccl*, dorsal calcaneocuboid ligament. Other labels as in Figs. 1-2.

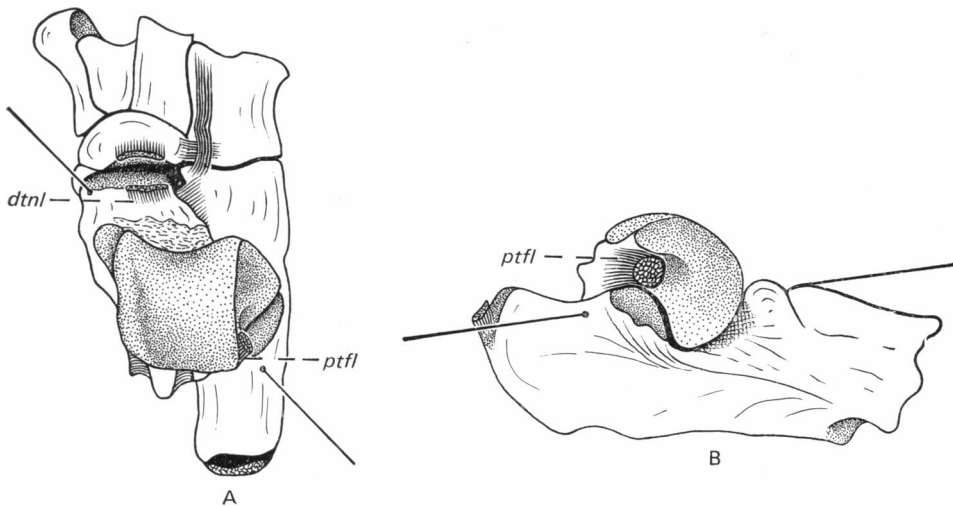


Fig. 4. The right foot of *Colobus polykomos* viewed from dorsally (A) and laterally (B) showing the compromise axis of the subtalar joint complex. Labels as in Fig. 1.

one, appears to have little relevance to function in the living. The calcaneus is less prolonged anteriorly than in *Pithecia monachus* and thus has a more limited articulation with the navicular. The orientation of the posterior talocalcaneal facet with respect to the subtalar axis is less obviously helical than in the previous species, but manipulation of a ligamentous specimen reveals that a comparable screwing motion occurs although of more limited amplitude.

Cercopithecus nictitans. As in *Colobus polykomos* there is only a very limited area of contact between the calcaneus and navicular and there is only a minimal amount of 'screwing' action at the subtalar joint complex. There is the usual ligamentum cervicis tali and interosseous talocalcaneal ligament; there is the usual dorsal

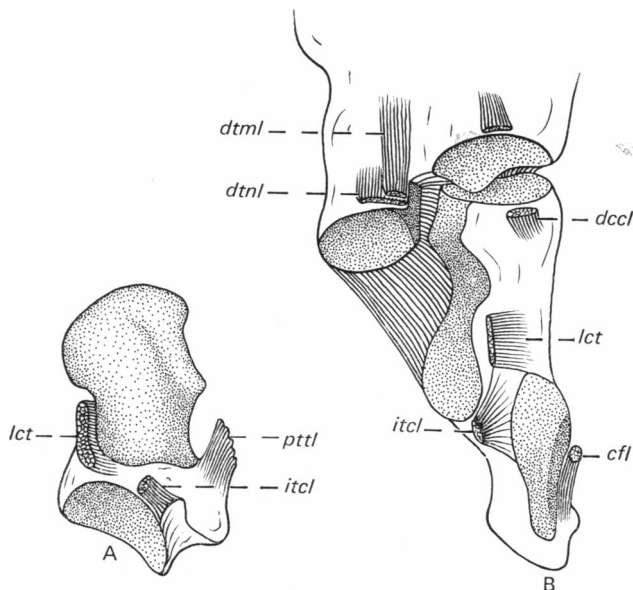


Fig. 5. A dorsal view of the right lamina pedis (B) of *Lemur catta* with the talus (A) rolled away. *dtml*, dorsal talometatarsal ligament; *pttl*, posterior tibiotalar ligament. Other labels as in Figs. 1-3.

talonavicular ligament, also, and associated with it is a band prolonged forwards towards the metatarsal bases – a dorsal talometatarsal ligament.

Lemur catta (Fig. 5). The essence of the morphology shown in, for example, *Pithecia monachus* is also demonstrated here, but the calcaneus is even further prolonged forward, achieving a considerable articular contact with the navicular. There is the usual ligamentous apparatus – ligamentum cervicis tali and interosseous talocalcaneal, dorsal talonavicular and talometatarsal ligaments. In function, also, the subtalar complex is like *Pithecia monachus* with a marked ‘screwing’ action.

Galago senegalensis moholi (Fig. 6). The arrangements represent a gross caricature of the sort of morphology shown by *Lemur catta* and this is realized by an enormously exaggerated and disproportionate anterior elongation of the calcaneus, which is matched by a comparable elongation of the navicular. If consideration is, however, restricted to the subtalar joint complex the morphology and function are not unlike *Lemur catta*. In this case, however, subtalar movement is a mere minor adjunct to the more extensive movement occurring at the calcaneocuboid joint which will be considered later.

Hylobates lar leuciscus. Again the essence of the arboreal primate heritage, as is well shown in *Pithecia monachus*, is exhibited here, although contact between the calcaneus and the navicular is limited to a narrow articular strip. The head and neck of the talus conserve an essentially cylindrical form, bearing an L-shaped calcaneal articular surface, as seen in monkeys. The posterior articular surface has a helical orientation about the oblique subtalar axis, which imparts a marked ‘screwing’ action to the movements of inversion and eversion.

Pongo pygmaeus. A quite conservative anthropoid structure and function is presented here as in the preceding higher primate species. Again the obliquely set talar neck is elongated and cylindrical, bearing the usual L-shaped calcaneal facet.

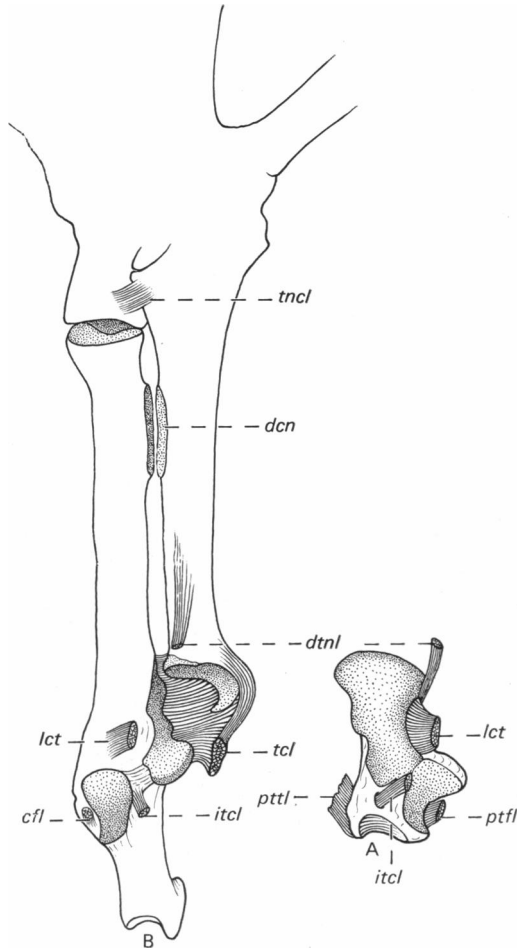


Fig. 6. A dorsal view of the left lamina pedis (A) of *Galago senegalensis moholi* with the talus (A) rolled away. *tncl*, transverse naviculocuboid ligament; *dcn*, diarthrosis between calcaneus and navicular. Other labelling as in Figs. 1-5.

Pan troglodytes (Figs. 7, 8A, 8B). The chimpanzee shows certain derived features which are with little doubt grafted onto the morphology typical of the higher primates described above. The subtalar axis is still markedly oblique and more or less in line with the abducted hallux but it is rather more elevated when traced anteriorly. This is seemingly a consequence of the fact that the talus has become rather foreshortened with a broadened head and shortened neck. The calcaneal facets on the head and neck no longer show such an obvious L-shaped configuration since the two limbs show a tendency to blend into one continuous surface. The posterior talocalcaneal joint retains an obvious helical disposition in relation to the subtalar axis and during the screwing motion accompanying inversion the calcaneus attains a small articular contact with the navicular. Rather surprisingly in the juvenile specimen the cuboid intruded slightly into the talocalcaneonavicular joint – the tarsus thus retained a semblance of the ancestral alternating character.

Gorilla gorilla gorilla. In the essentials of structure and function this species resembled the chimpanzee.

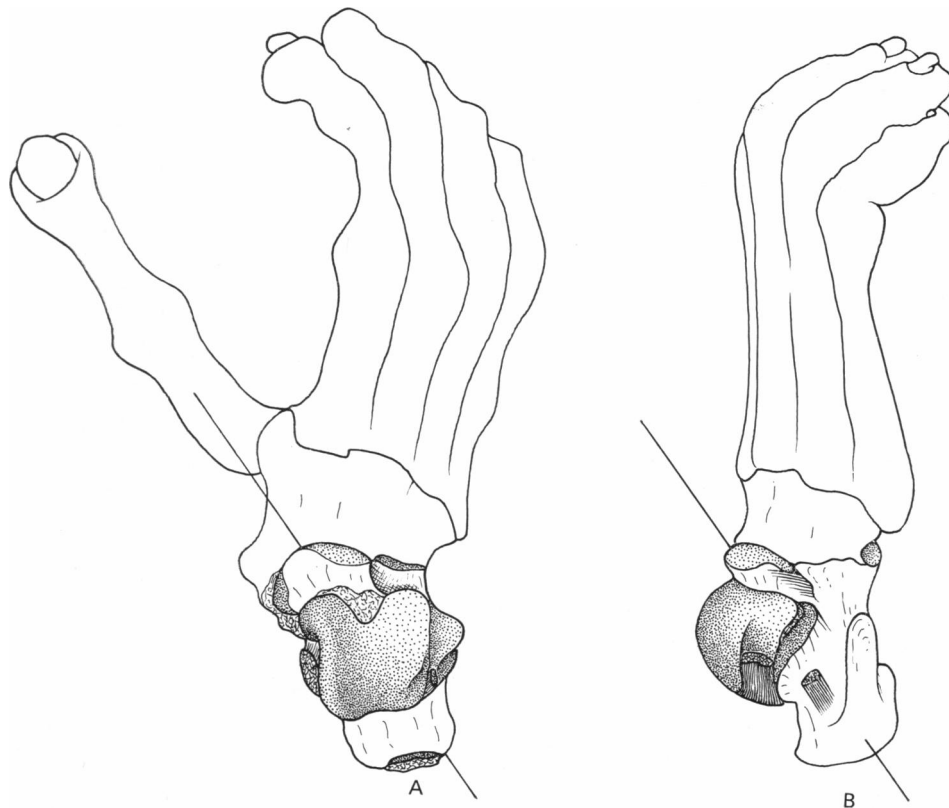


Fig. 7. The right foot of *Pan troglodytes* viewed from dorsally (A) and laterally (B), with the foot in inversion, showing the compromise subtalar axis.

Homo sapiens (Figs. 8C, 8D, 9, 10). The subtalar joint complex of man is quite clearly derived from the basic primate pattern, and in particular its unique structural attributes seem to have resulted from the accentuation of trends already incipient in *Pan* and *Gorilla*. Quite subtle and easily overlooked morphological changes have drastically modified the function. Contact between the calcaneus and navicular has been lost and the joint complex is separated into distinct posterior talocalcaneal and talocalcaneonavicular joints. The usual interosseous talocalcaneal ligament and the ligamentum cervicis tali are present and these have been described in detail by Smith (1896) and more recently by Cahill (1965). A strong dorsal talonavicular ligament is present attached to a rough arcuate tubercular ridge on the dorsum of the talar neck; to the ridge also attaches the anterior capsule of the ankle joint (as noted by Jones, 1944) but it is clear that the former ligament is the significant structure producing the ridge. Ossification may extend into the ligament producing the radiological image of a 'talar beak' (Meschan, 1975). The calcaneus can exhibit two articular facets – on sustentaculum tali and body – entering into the talocalcaneonavicular joint (as can also occur in monkeys, Fig. 3) or these can be united into a single confluent facet; the distribution of these two types has been documented in different races (Bunning & Barnett, 1965) and presumably has little functional significance. Rarely (except apparently in the Veddah where it is quite common) the confluent anterior facets may also be united with the posterior talar facet, convergently resembling then the morphology of *Trichosurus vulpecula*.

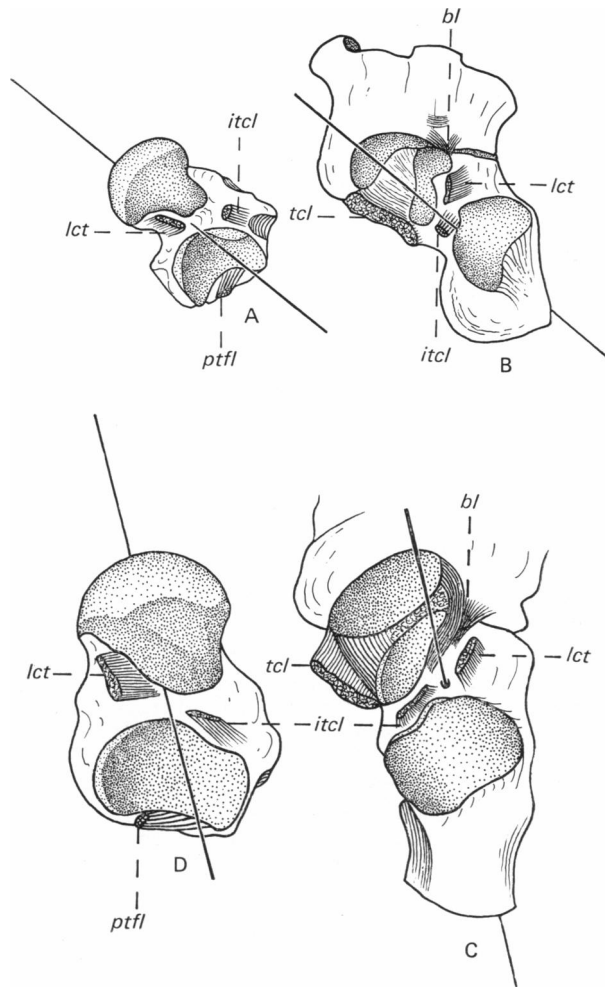


Fig. 8. Above, a dorsal view of the right lamina pedis (B) of *Pan troglodytes*, with the talus (A) rolled away. Below, a dorsal view of the right lamina pedis (C) of *Homo sapiens* with the talus (D) rolled away. In each case the compromise subtalar axis is shown. *tcl*, talocalcaneal part of deltoid ligament; *bl*, bifurcated ligament. Other labels as in Figs. 1-2.

It has been customary to describe the human subtalar axis as running upwards, forwards and medially through calcaneus and talus from the lateral side of the heel (Shephard, 1951). In its exaggerated upwards inclination it thus differs markedly from that of other primates, and the morphological remodelling underlying this change must be of considerable evolutionary and functional importance. The posterior calcaneal surface is inclined to this axis and in the right foot forms a segment of right-handed screw. This was recognized by Manter (1941) for the human foot, and in the light of the primate heritage described above should occasion no surprise. Another feature of obvious functional significance in the human foot is, however, highlighted by the comparative observations recorded above. The calcaneal surface (or surfaces) entering into the talocalcaneonavicular joint no longer forms an L-shaped arrangement, each segment having its own curvature related to the subtalar axis. They have become smoothly confluent to form also a segment of a screw,



Fig. 8. The right foot of *Homo sapiens* viewed from dorsally showing the compromise subtalar axis.

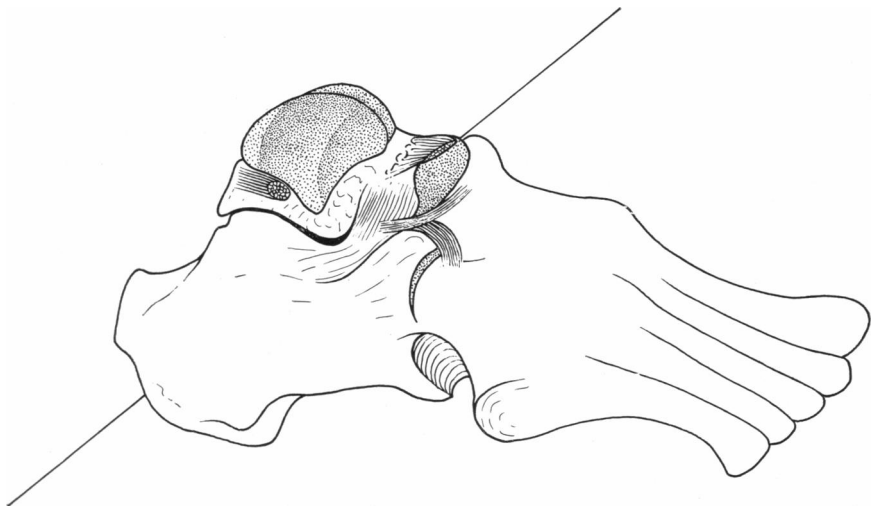


Fig. 10. The right foot of *Homo sapiens* (the same foot as shown in Fig. 9) viewed from laterally showing the compromise subtalar axis.

left-handed in the right foot; this is also clearly revealed by observing the corresponding articular surface on the underside of the talus. This helical calcaneal surface then contributes to the articular cup – aptly termed ‘acetabulum pedis’ by MacConaill (1945) – which receives the head of the talus. The combination of these screwing movements on the talus – forwards from behind and backwards on the head – means that in effect the whole bone is bodily rotated medially about a vertical axis. This vertical component is reflected in the much more upright disposition of the compromise subtalar axis of man, compared to that of other primates. Another feature elevating the axis has been that the anterior articular platform on the human calcaneus has been built up and effectively raised (Morton, 1924). The movements of inversion and eversion are of course significant in adjusting the attitude of the human foot to inclined surfaces, a function not unlike that in other primates. In bipedally walking man it is even more instructive to visualize the movements of the talus, and with it the leg, on the foot. Jones (1945) has noted that the extreme declination of the human subtalar axis has added an element of rotational torque of leg (with talus) on the foot: as the foot is inverted the leg is externally rotated; as the foot everts the leg internally rotates. This can be seen in one leg balancing, for the supporting leg laterally rotates as its foot inverts and the whole body then turns medially with respect to that foot (Jones, 1945; Hicks, 1953). The importance of this torque of leg (with talus) on the foot during walking will be considered later. With its new role as a pivotal link between leg and foot, providing for torque about an increasingly vertical axis, the talus has taken on a squat, dumpy character compared with other primates. As noted above, however, a trend in this direction is apparent in *Pan* and *Gorilla*.

The transverse tarsal joint complex – morphology and function

This again is not an anatomical entity but includes part of the talocalcaneonavicular joint (the talonavicular part) and the calcaneocuboid joint. Further, in subhuman primates there is an articulation of variable extent between the calcaneus and navicular. The effective part of this composite articulation, determining the type and range of movement, is the calcaneocuboid joint; the talonavicular articulation is a passive appendage, the navicular being carried across the head of the talus by its strong attachment to the cuboid.

Precise definition of the movements involved is essential for any reasoned discussion on function. Hicks (1953) focussed attention on twisting of the forefoot. Thus, flexion of the first ray of the foot, with progressively diminishing flexion laterally of the other rays, was said to impart a pronation twist to the forefoot. If such a foot, however, is to remain flat on the ground a compensatory movement in the opposite direction must occur at the subtalar joint complex. MacConaill & Basmajian (1969) likewise recognized twisting of the whole of the subtalar skeleton of the foot which they called the ‘lamina pedis’. By analogy with the forelimb they called twisting pronation, and untwisting supination. They reserved the terms inversion and eversion for movements at the subtalar joint complex, a similar convention to that adopted in the present paper.

MacConaill & Basmajian (1969) correctly focussed attention on the calcaneocuboid joint as the main centre of torsion (pronation) or untwisting (supination) of the lamina pedis. Their terminology will also be adopted here only for those movements of the forefoot upon the hindfoot at the calcaneocuboid joint. Thus, movement increasing twist of the lamina pedis (and thus effectively depressing the first

ray and elevating the lateral border of the foot) is called pronation; supination is the converse, untwisting of the lamina pedis by forefoot movement. Difficulties arise, however, when movement of the calcaneus upon a stationary cuboid is considered. Movement increasing torsion of the lamina pedis must involve inward rotation of the heel and hinder part of the sole and it would be illogical and confusing to term this also pronation; it will here be called endorotation of the calcaneus. The converse movement effecting untwisting of the lamina pedis will be called exorotation. The form of the lamina pedis will be described as 'twisted' and 'untwisted' (rather than as pronated and supinated respectively): the former is achieved by pronation of the forefoot or by endorotation of the calcaneus; the latter is achieved by supination of the forefoot or by exorotation of the calcaneus.

The primate joint

It is advantageous first to consider morphology and function in an arboreal monkey, and then to consider variations found in other primates.

Colobus polykomos (Fig. 11 B). The calcaneus, as has been noted, articulates distally not only with the cuboid, but also with the lateral margin of the navicular. The surface on the cuboid is kidney-shaped showing a slightly protuberant ventral convexity adjacent to the 'hilum' whilst the periphery of the surface is flattened or even concave. Navicular and cuboid are bound together dorsally by a tough transverse ligament and a longitudinal ligamentous band from calcaneus to cuboid again overlies this dorsally; this latter band presumably corresponds to the calcaneocuboid part of the human bifurcated ligament (there is no calcaneonavicular band). Ventrally the joint is strengthened by a very tough plantar calcaneocuboid ligament radiating symmetrically forwards from the anterior plantar tubercle on the calcaneus to the ventral concave margin of the cuboid. This ligament is clearly homologous with the short plantar ligament of human anatomy, but its more superficial fibres are prolonged forward across the groove for the peroneus longus tendon, towards the cuboid ridge and the metatarsal bases – this is the distal attachment of the long plantar ligament of human anatomy. This more superficial lamina has, however, not extended its attachment posteriorly, as in *H. sapiens*, to the area of the calcaneus between the anterior tubercle and the calcaneal tuberosity. At the joint the movement consists essentially of rotation about an axis approximately in the long axis of the foot. The habitual movements in the arboreal setting then are supination and pronation of the forefoot upon the hindfoot; as will be seen these complement the movements occurring at the subtalar joint complex in a highly effective way.

It is instructive, for later comparisons, to analyse the mechanics of the movement a little more by considering movement of the calcaneus upon the stationary cuboid in a ligamentous preparation (Fig. 11 B).

Movements consist essentially of rotation (spin) of calcaneus upon cuboid, with a slight element of sideways displacement (swing) on the calcaneus. As the calcaneus is exorotated (position 'b' in Fig. 11 B) its distal surface engages firmly on to the more medial part of the cuboid facet and fits snugly in against the articular margin of the navicular. As the calcaneus is endorotated (position 'a' in Fig. 11 B) it rotates onto the more lateral part of the cuboid facet. The fulcrum of the movements is the tough plantar calcaneocuboid ligament and alternately the medial or lateral parts of this radiating band are tightened. As the calcaneus moves into endorotation its posterior aspect is translated laterally.

Structure and function are essentially similar in other monkeys, including both

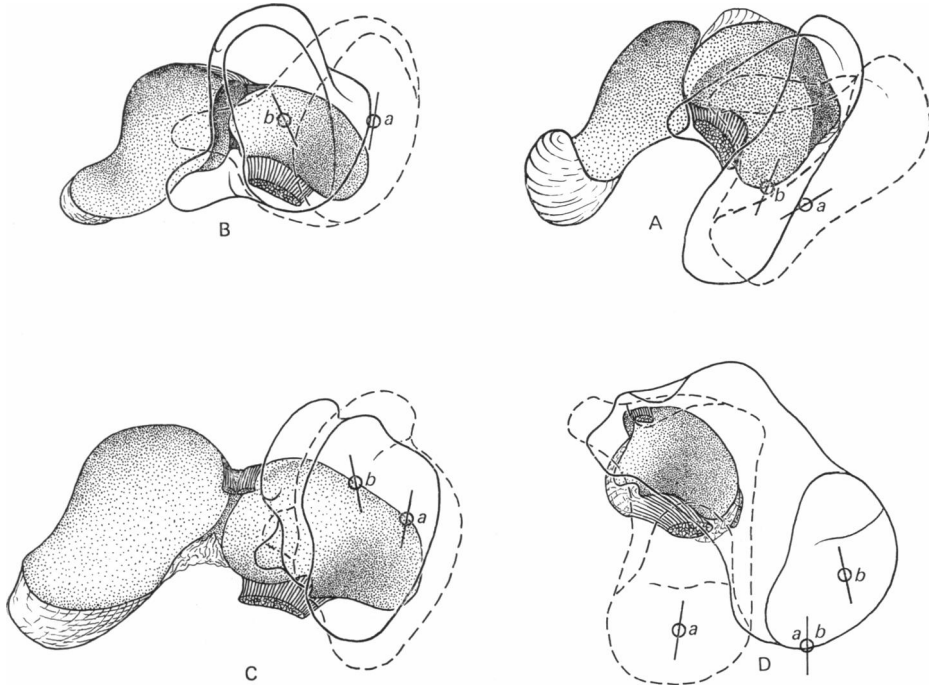


Fig. 11. Diagrams illustrating the movements at the calcaneocuboid joint, drawn from superimposed radiographs of right-sided ligamentous preparations of *Trichosurus vulpecula* (A), *Colobus polykomos* (B), *Pan troglodytes* (C), *Homo sapiens* (D). In each case the form of the distal articular surface – navicular and cuboid in A, B and C, and cuboid alone in D – is shown together with the associated ligaments; the outline of the calcaneus is superimposed in endorotation (broken line) and exorotation (solid line). A marker inserted in the tuberosity of the calcaneus allows estimation of rotation of the bone in its long axis between the positions of full endorotation (*a*) and full exorotation (*b*); *ab* is a position intermediate between these two attitudes.

New World and Old World species. This has been verified in wet specimens of *Procolobus verus*, *Cercopithecus nictitans*, *Pithecia monachus* and *Cebus nigrivittatus*. There are, of course, as already noted, variations in the extent of contact between the calcaneus and navicular and also slight variations in the amount of protuberance of the ventral convexity on the cuboid surface.

Lemur catta. The form of the articular surfaces, the ligamentous apparatus and the function show no noteworthy differences from monkeys. The plantar protuberance on the cuboid articular surface is no more accentuated than that found in some monkeys (e.g. *Cebus nigrivittatus*).

Galago senegalensis moholi. Here the calcaneocuboid joint has been translated distally by enormously disproportionate lengthening of the anterior portion of the calcaneus and the attachments of the plantar calcaneocuboid ligament are similarly translated distally. The basic structure and ligamentous apparatus of the joint are, however, recognizably primate. The joint surfaces are somewhat modified: the plantar convexity on the cuboid is greatly accentuated, forming a peg-like projection which is eccentrically disposed, lying towards the medial aspect of the joint. This form is closely attuned to the pivoting function of the joint and is dramatically convergent to that which will be described in certain hominoids. The functions of the joint, allied with a proximal articulation between navicular and calcaneus, provide

for movements of supination and pronation of the forefoot and are strikingly analogous to the movements of pronation–supination in the human forelimb. The small movements of inversion–eversion of the calcaneus below the talus at the subtalar joint complex supplement the pivotal movements and are strikingly analogous to the secondary movements of the ulna which occur in pronation–supination of the forearm (Kapandji, 1966).

Hylobates lar leuciscus. In structure and function there are no significant differences from the monkeys referred to above. The articular surface on the cuboid shows no more of a ventral convex protuberance adjacent to the plantar calcaneocuboid ligament than may be found in monkeys.

Pan troglodytes (Fig. 11C). The cuboid articular surface is modified by a considerable accentuation of the ventral convexity as seen in monkeys, into a prominent articular beak. This is somewhat eccentrically placed, being rather more towards the medial than the lateral side. The surface on the calcaneus is reciprocally shaped with a deep excavation lodging the cuboid projection, and the calcaneus contacts the navicular along a small linear strip. Ventrally a massive plantar calcaneocuboid ligament radiates forward from the anterior calcaneal tubercle; there is still no separately differentiated long plantar ligament extending this attachment backwards. Dorsally, there is a calcaneocuboid ligament but now associated with it is a calcaneo-navicular band (apparently a dissociated part of the dorsal talonavicular ligament secondarily attached to the calcaneus); thus is constituted the homologue of the human bifurcated ligament. Despite this altered form, function appears to be essentially similar to that in monkeys with the joint providing for the rotary motion involved in supination of the forefoot, which again includes a component of angular displacement – slight adduction of the forefoot.

It is to be noted that in the juvenile specimen of *Pan* which was dissected the calcaneus was excluded from contact with the navicular by intrusion of the cuboid into the talocalcaneonavicular joint creating an alternating tarsus. This might merely represent a phase of growth. Alternatively it may be a variant pattern, but it is certainly not the usual condition in adult chimpanzees.

Gorilla gorilla. In the gorilla dissected ('Guy') the morphology was very similar to that described above for *Pan* with the cuboid possessing a prominent beak, lodged within a deep excavation in the calcaneus. The calcaneus contacted the navicular along a linear strip. The ligamentous apparatus was similar to that of the chimpanzee with a very strong plantar ligament and with a bifurcated ligament dorsally.

It is to be noted that the particular morphology exhibited by this specimen is unusual for gorillas, but it does demonstrate a structural affinity with chimpanzees. The more usual joint architecture as seen in a range of osteological preparations will be considered in the next paper, since it is particularly relevant in the consideration of the fossil record.

Pongo pygmaeus. The orang-utan presents a particular morphology of its own but familial resemblances with the preceding two pongid species are readily apparent. The cuboid protuberance is remodelled into a large and clearly demarcated hemispherical elevation which is bounded laterally by a quite broad and flat articular rim. It thus has the classical form of a pivot joint. Plantar calcaneocuboid and bifurcated ligaments are present. Again, the morphology of this joint will be considered in more detail, in the phylogenetic context, in the next paper.

Homo sapiens (Fig. 11D). Here modifications in joint architecture have quite dramatically changed the type and range of movement.

The cuboid articular surface could readily be imagined as derived from one such as seen in *Pan*. The essential changes needed to realize this would involve distortion so that the plantar convex beak is displaced medially to form a columnar inner margin to the surface. The flattened or concave lateral part of the surface is greatly enlarged into a flaring, concave area. The resulting form is markedly asymmetrical when compared to that of *Pan*. The medially displaced convex component carries with it the plantar calcaneocuboid ligament to form the canonical short plantar ligament of human anatomy which is now very obliquely disposed, in contrast to the disposition in apes, and forms the plantar wall of the joint. Dorsally lies the calcaneocuboid part of the bifurcated ligament; the calcaneonavicular part walls the talonavicular joint, from which the calcaneus is now excluded. In fact, the joint has been remodelled into one of strikingly sellar or saddle-shaped form, and has a functional analogue in the trapeziometacarpal joint of the human thumb.

Rotatory movement still occurs, as in subhuman primates, but now as a concomitant (conjunct rotation) of a greatly amplified angular or swing movement. Further, the lateral swing is now correlated with exorotation of the calcaneus – the reverse of that occurring in lower primates. The whole complex of movements has a quite close analogy with those occurring at the carpometacarpal joint of the thumb during the first part of opposition, as described by Pieron (quoted by Landsmeer, 1976).

Plausible comparison can be made between the right calcaneocuboid joint (Fig. 11D) and the left trapeziometacarpal joint. In the position shown at 'a' (endorotation of the calcaneus) the joint is close-packed only dorsally; at 'b' (exorotation of the calcaneus) it is congruent also in the region of the plantar convexity on the cuboid. In this latter position, of course, as the calcaneus moves laterally with a rotatory motion, bringing the joint into the position of maximum congruence, so then is the lamina pedis untwisted. It is noteworthy then that this uniquely human movement has tensed the now obliquely disposed short plantar ligament, and also the bifurcated ligament and the plantar calcaneonavicular (spring) ligament. The important role served by this mechanism during the stance phase of the human gait will be considered later.

MacConaill (1945) and MacConaill & Basmajian (1969) realized that untwisting of the lamina pedis, such as occurs when standing with the feet wide apart, involved movement of the calcaneus of the type referred to here as exorotation and that it included lateral displacement of the heel. They further appreciated that the movement must occur at the calcaneocuboid joints but they did not go on to analyse the form and function of this joint.

Manter (1941) described the movement at the calcaneocuboid joint as occurring about dual axes. In fact, there is no real conflict here with the description given above. Manter (1941) was, in effect, artificially resolving the habitual movement into two components – a rotation (spin) about an axis longitudinally disposed in the foot and an angulation (swing) about a transverse axis running upwards and medially through the joint. Manter (1941) also described a screw-like character for the movement about the longitudinal axis – left-handed in the right foot; again, this is an implicit feature of the whole movement described above.

Elftman (1960) also described the joint as a saddle-shaped one with two axes and deduced from this the sort of direction that a resultant transverse tarsal axis must take up. Visualization of the type of movement which would occur about such a resultant is in accord with the experimental findings shown in Figure 11D.

Precursors of the primate joint

The basic structure described above, subject to varying emphases in different species, seems to be a fundamental primate heritage character. However, it seems likely that the eutherian stock from which the primates were derived, and the advanced therians before them, already possessed a morphology and function in this joint which foreshadowed the fully elaborated primate condition. In a marsupial such as *Trichosurus vulpecula* (Fig. 11A) the cuboid has a virtually flat proximal articular surface which is rimmed by an articular cuff enveloped by the overlapping calcaneus. In function the joint is not unlike that in primates although movement is less free. In *Sarcophilus harrisi* and *Phascolarctos cinereus* the joint even more closely resembles that of primates for the cuboid bears a protuberance not unlike that of monkeys and the calcaneus no longer overlaps the periphery of the articular surface. In *Tenrec ecaudatus* the cuboid is again slightly convex and movement is pivotal; the calcaneus, although not overlapping the cuboid, presents a prominent bony shelf, the trochlear process (or peroneal tubercle) at its distal extremity. In *Tupaia* this process is retracted posteriorly as in primates, but it should be noted, however, that such a posterior displacement of the process has occurred convergently in a number of groups including certain rodents and marsupials (Stains, 1959). In *Tupaia*, however, the calcaneocuboid joint is not a pivot one, for the cuboid surface presents a prominent dorsoventral convexity prolonged quite far forwards at its plantar extremity; in this species the joint provides for dorsoventral hinging between fore-foot and hindfoot. The source of the primate morphology can be envisaged as a compromise between the structure of these two extant insectivores – one in which the trochlear process is retracted as in *Tupaia*, but with a cuboid retaining a slightly convex pivotal conformation as in *Tenrec* (or better, as in the marsupials *Phascolarctos* and *Sarcophilus*).

The tarsometatarsal joints, and the distal intertarsal joints

There is little doubt that in its primitive therian form the tarsometatarsal joint of the hallux possessed concavoconvex joint surfaces. Such an arrangement is found for instance in the marsupial *Trichosurus vulpecula*, and certainly such a joint is characteristic of prosimian primates such as *Lemur catta* and *Perodicticus potto*.

In the higher primates, however, the joint has been the site of a complex series of morphological changes which have been described in detail by Lewis (1972). The study suggested that one of the morphological novelties possessed by the earliest Anthropoidea was the participation of a bony prehallux in the joint at the base of the opposable hallux. Such a joint persists in extant Ceboidea and Hylobatidae but has apparently been lost in parallel in the later hominoids and in cercopithecoids. Some confirmation for this view comes from the recent description by Conroy (1976) of the apparently prehallux-containing type of joint in the Oligocene anthropoid *Aegyptopithecus zeuxis*.

The broad basic plan of the tarsometatarsal joints conforms strikingly to the primitive pattern of the carpometacarpal joints of the hand, described by Lewis (1977). This basic pattern is found in prosimians (*Lemur catta*, *Perodicticus potto*, *Galago moholi*), New World monkeys (*Saimiri sciureus*, *Pithecia monachus*, *Cebus nigrivittatus*) and some Old World monkeys (*Procolobus verus*, *Cercopithecus nictitans*). The essence of the arrangement is as follows (Figs. 12B, 13A):

The base of the third metatarsal articulates with the large lateral cuneiform and

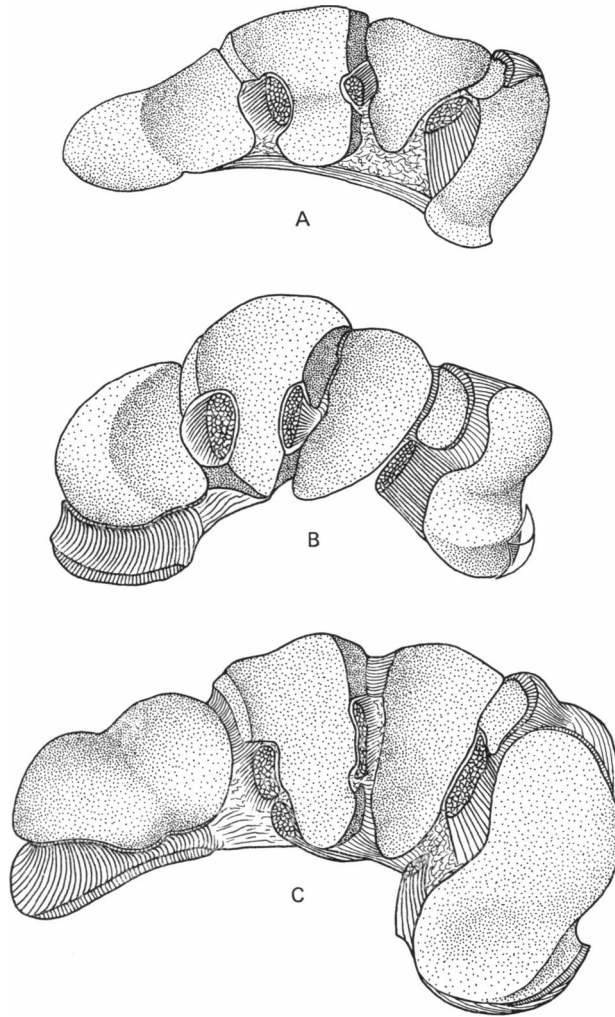


Fig. 12. The distal aspects of the right tarsus of wet specimens of *Pan troglodytes* (A), *Saimiri sciureus* (B), and *Homo sapiens* (C). In each case the metatarsals have been disarticulated to reveal the articular surfaces and ligaments of the tarsometatarsal joints. The position of the prehallux is shown in line, articulating with the medial cuneiform of *Saimiri sciureus* (B).

is braced either side by interosseous tarsometatarsal ligaments joining these bones. Anterior and posterior to these ligaments the bases of the second and fourth metatarsals articulate with the third, the adjoining sides of these metatarsal bases thereby possessing dual facets. The second metatarsal is stabilized by deep indentation into the tarsus articulating laterally with the adjacent lateral cuneiform by proximal extensions of the dual intermetatarsal articulations. The second metatarsal also bears a facet on the dorsomedial aspect of its base for the medial cuneiform. A massive ligament radiates from the medial cuneiform to the second metatarsal on the plantar aspect of this articulation; this is the so-called ligament of Lisfranc so well described and illustrated by Jones (1944). Another ligament walls the joint dorsally. Laterally the lateral cuneiform protrudes forward beyond the cuboid so that the dual facets on the fourth metatarsal (just as on the second) articulate not



Fig. 13. 'Exploded' diagrams of the distal tarsals and metatarsal bases of right feet of *Cebus nigrivittatus* (A) and *Pan troglodytes* (B) showing the intervening articulations. *MC*, medial cuneiform; *IC*, intermediate cuneiform; *LC*, lateral cuneiform; *CU*, cuboid; 2-5, bases of metatarsals 2-5.



Fig. 14. An 'exploded' diagram of the distal tarsals and metatarsal bases of a right foot of *Homo sapiens* showing the intervening articulations. Labels as in Fig. 13.

only with the third metatarsal but also with the sides of the lateral cuneiform. Interestingly, this arrangement contrasts with the primitive condition in the carpus where the hamate, serial homologue of the cuboid, protrudes beyond the capitate.

The fourth and fifth metatarsals articulate with the cuboid, the former typically being received into a concave depression on that bone. The surface on the cuboid for the fifth metatarsal is slightly convex from side to side but, as a variant, may be found to be dorsoventrally concave in some monkeys and apes. Between the fourth and fifth metatarsals there is typically a single intermetatarsal articulation.

The most significant source of variation from this basic pattern involves that ventral articulation between the medial side of the base of the fourth metatarsal on the one aspect and the base of the third metatarsal and lateral cuneiform on the other. This joint appears to be rather unstable in its expression and may be lacking in monkeys (*Colobus polykomos*). Its absence, however, is a characteristic feature of hominoids: in *Hylobates lar* it is rudimentary; in *Pan troglodytes* (Figs. 12A, 13B) and *Gorilla gorilla* it is absent. In *Homo sapiens* (Fig. 14) it is similarly absent and a strong slip of the tibialis posterior tendon has become insinuated between the metatarsal bones, here reinforcing the interosseous tarsometatarsal ligament. In *Homo sapiens* the residual dorsal articulation in this situation is commonly purely intermetatarsal and the lateral cuneiform then fails to contact the fourth metatarsal (Jones, 1944).

On the other side of the third metatarsal the ventral articulation is less commonly deficient. The intermetatarsal part, even including the ventral articulation between

the lateral cuneiform and the second metatarsal, may be lacking in *Pan troglodytes*. The whole articulation here is absent in *Gorilla gorilla*.

Pongo pygmaeus shows a striking departure from the basic primate architecture for in this species the lateral cuneiform fails to project beyond the intermediate one. Thus, the second metatarsal is not deeply indented into the tarsus and fails to articulate with the lateral cuneiform, although it has the usual dorsal and ventral articulations with the third metatarsal. Despite this derived condition, the primitive pattern of dorsal and ventral articulations between the third and fourth metatarsals is retained, although only the dorsal one includes participation by the lateral cuneiform.

The intertarsal articulations between the cuneiforms and cuboid can profitably be considered in conjunction with the tarsometatarsal ones.

Typically (Fig. 13) between adjacent cuneiforms, and the lateral cuneiform and cuboid, there are dual articulations. The proximal one is usually a dorsoplantar articular strip; the distal one is dorsally located and here communicates with the articulations of the protruding medial and lateral cuneiforms with the bases of the second and fourth metatarsals. Between proximal and distal articulations are strong interosseous ligaments. This pattern is apparently a stable primate heritage and only occasional variations are observed in prosimians, monkeys and apes.

Man, however, is a notable exception (Fig. 14). Here typically the distal articulations between the intermediate and lateral cuneiforms, and between the lateral cuneiform and the cuboid are lacking. This may be correlated with considerable elaboration of the interosseous ligaments uniting the bones. Another characteristic human derived condition is that the proximal and distal facets between the medial and intermediate cuneiforms are dorsally confluent, encircling the interosseous ligament between the bones, and also continuous distally with the articulation between the medial cuneiform and the second metatarsal. However, as noted by Jones (1944) there may be interruption of the articulation into proximal and distal facets – a reversion to the primitive morphology; conversely, in *Pan troglodytes* the two facets may be very nearly confluent, closely approaching the human condition.

DISCUSSION

Function of the foot in arboreal primates

In the New World monkeys certain basic features of the subtalar and midtarsal joint mechanisms, clearly attuned to the prehensile functions of the arboreal foot, are most strikingly displayed. As seen in, for example, *Pithecia monachus* (Fig. 15) the joint surfaces of the posterior talocalcaneal joint are markedly helical and a screw-like action accompanies movement about the compromise axis.

In terrestrial activities the foot is everted (Fig. 15A), and the helical motion retracts the calcaneus beneath the talus; conversely, one might consider that the talar head is firmly impacted into the acetabulum pedis, and so against the navicular. The retraction of the calcaneus thus tenses the plantar calcaneonavicular (spring) ligament so satisfying the weight-bearing requirements.

During arboreal activities the foot is characteristically dorsiflexed at the ankle, particularly when grasping near vertical supports. Because of the characteristic movement at the ankle joint (Lewis, 1980a) the foot is abducted but the sole is also turned inwards. A congruent movement of inversion occurs at the subtalar joint complex.

The screw-like action at the posterior talocalcaneal joint advances the calcaneus

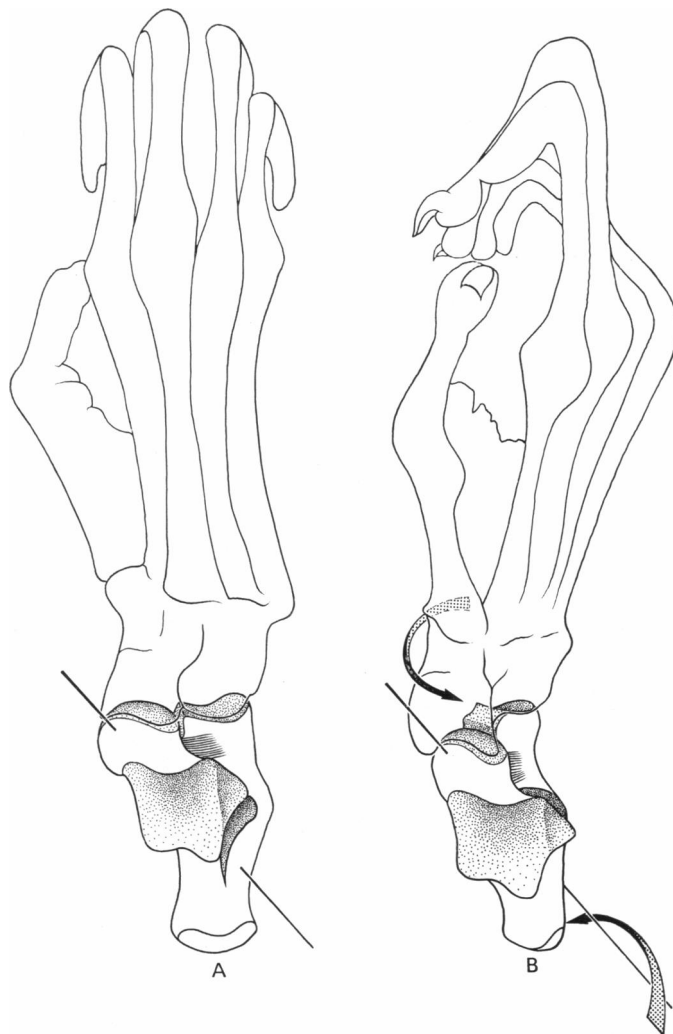


Fig. 15. Dorsal views of the right foot of *Pithecia monachus* in the everted position (A) and in the inverted grasping attitude (B), with the subtalar axis indicated in each case. The lower arrow in B indicates the screwing motion of the lamina pedis about the subtalar axis during inversion; the upper arrow indicates the accompanying movement of the forefoot during supination at the calcaneocuboid joint.

and the head of the talus rises up laterally from the acetabulum pedis, exposing quite a considerable part of its distal articular surface (Fig. 15B). A congruent movement of supination occurs at the midtarsal joint complex and, as noted above, this movement involves medial folding, or adduction of the forefoot. This is rendered possible only because the helical movement at the subtalar complex has provided scope for it. As supination of the forefoot occurs the navicular rides up on to the exposed part of the talar head and the calcaneus is impacted against its articulation with the navicular. The joints are then in stable close-packed condition.

Szalay & Decker (1974) and Szalay, Tattersall & Decker (1975) similarly had some insight into the correlation of helical action at the subtalar joint with posterior movement of the navicular during supination at the transverse tarsal joint complex.

Szalay (1975), however, maintained that such helical movement was a derived apomorphic character unique to the primates; as noted above, there are persuasive indications that the primate precursors possessed at least a rudimentary facility of this sort which was then refined and elaborated by the primates. There appears to be no foundation for the view also expressed by Szalay (1975) that this type of movement was independently lost in most cercopithecoids and in hominids. Certainly it is considerably reduced in the more terrestrial cercopithecines, but is quite well marked (and not of different nature) in colobines. The contention that it is lost in hominids is particularly mystifying since it was first and most elegantly demonstrated in man by Manter (1941).

Function of the foot in Homo sapiens

The behaviour of the joints of the foot in man during weight support could be expected to reveal any particular adaptive features specifically associated with the erect posture. Detailed direct analysis of these joint movements during gait has not so far proved possible. However, a plausible reconstruction can be achieved based on knowledge of the mechanics of the relevant joints; this can then be checked against the circumstantial evidence derived by many different techniques. The following account draws heavily upon the important work of MacConaill (1945) and MacConaill & Basmajian (1969), supplemented by some new insights into aspects of human anatomy which have been highlighted by the comparative observations recorded above.

It has been established (Carlsöö, 1972) that during the support or stance phase of gait, the centre of gravity first moves laterally towards the support side and then deviates back towards the midline. First the heel's posterolateral part is loaded, then also its medial part, then the outer side of the sole and then one by one the lateral metatarsals and finally the great toe (Barnett, 1956; Carlsöö, 1972). The sequence of joint responses seems to be as follows (Fig. 16). During the swing phase, the foot is carried in slight inversion (Bowden, 1967) and the lateral part of the heel first strikes the ground. During the early part of the support phase (Fig. 16A) as the centre of gravity veers laterally on the support side, changes occur both within the lamina pedis and at the subtalar joint complex. The lamina pedis becomes increasingly twisted by movement occurring at the calcaneocuboid joint; this is the movement defined in this paper as endorotation of the calcaneus. Also the leg (with talus) is effectively folded upon the foot about the oblique hinge formed by the subtalar axis into the position of inversion, made most apparent, however, by lateral rotation of leg upon foot.

As the leg moves into the latter part of the support phase (Fig. 16B) the centre of gravity returns towards the midline and the ankle dorsiflexes; as noted previously (Lewis, 1980a) this is accompanied by some medial rotation of the leg at the ankle joint. Congruent motion is communicated to the subtalar joint and the talus is effectively screwed home into the acetabulum pedis, about the comparatively upright subtalar axis, and the leg bones reflect this movement by showing medial rotation. As the full weight is thus applied to the foot the lamina pedis becomes flattened or untwisted and this plays its part in causing the centre of gravity to veer back towards the other side. The major part of this untwisting movement occurs at the calcaneocuboid joint – effectively the calcaneus is exorotated. The lamina pedis is now in a close-packed position with the plantar calcaneocuboid (short plantar) ligament, plantar calcaneonavicular (spring) ligament and bifurcated ligament all tensed.

The significance of the remodelling of the joint surfaces in the human subtalar

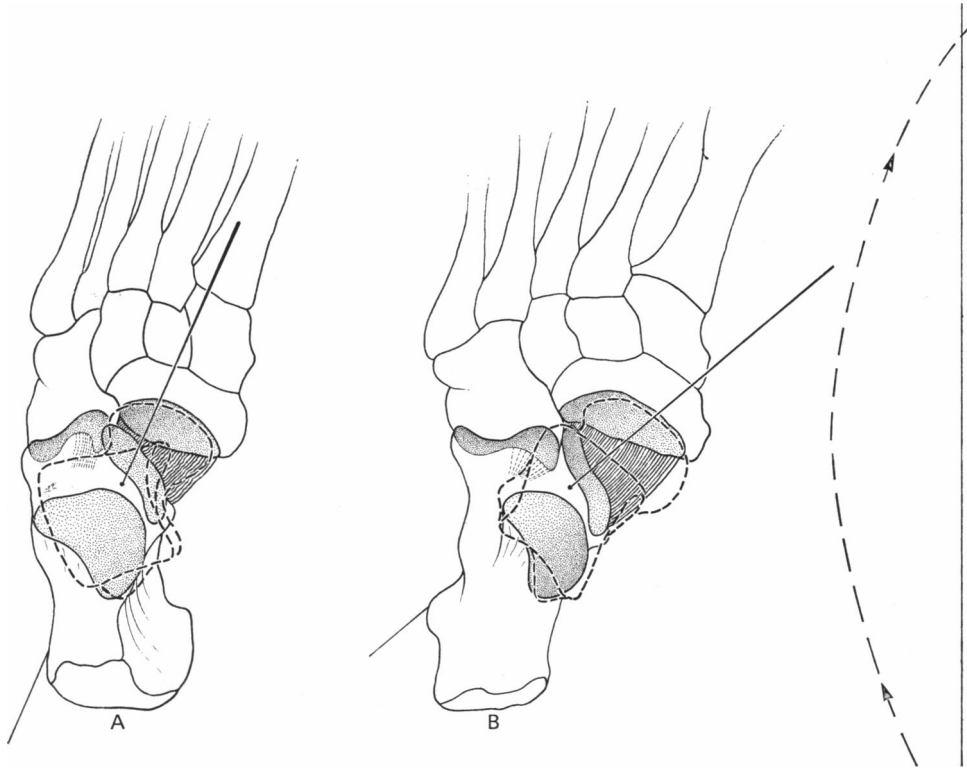


Fig. 16. Diagrams illustrating the joint movements in the human foot during the stance phase of gait. The broken line with arrows indicates the traverse of the centre of gravity in relationship to the line of progress (vertical line) and foot B indicates the position of the supporting foot in relation to this. The foot offset at A shows the attitude of the joints during the early part of the stance phase; foot B indicates the changed structure at the latter part of the stance phase. In each case the subtalar axis is shown and the talus is indicated in broken line, superimposed on the lamina pedis. The plantar calcaneonavicular (spring) ligament is shown and the plantar calcaneocuboid (short plantar) ligament is indicated in broken line as though visualized through the foot; both ligaments are under tension in B. For further description see the text.

joint complex to produce a screwing action of the talus about a comparatively upright axis is now apparent. The rotary movement of the talus, carrying with it the supported body, is clearly a major factor in the transfer of weight to the support side. The remodelling of the calcaneocuboid joint provides a mechanism for tensing important ligaments, so bringing the lamina pedis into a close-packed position, and providing a stable platform for the pivotal movements of the talus.

SUMMARY

A description is given of the functional morphology of the intrinsic joints of the foot, with particular reference to the primates, and an attempt is made to define the key human derived features.

In the human subtalar joint the compromise axis has become reoriented into a very elevated position and more nearly in line with the functional foot axis than it is in subhuman primates. This provides for torque of the talus, and so the supported body weight, about the axis, during the stance phase of gait. In the subhuman

primates the very oblique subtalar axis is important in inverting the foot into a grasping attitude.

In subhuman primates the transverse tarsal joint complex plays an important role in supination of the forefoot, which complements inversion at the subtalar joint complex in achieving the ideal grasping position. This movement is only rendered possible by a helical action at the subtalar joint complex. In man the calcaneocuboid joint has been remodelled so as to bring the lamina pedis into a close-packed position during the latter part of the stance phase of gait.

The joints between the cuneiforms and the cuboids, and the associated tarso-metatarsal joints show significant modifications in man.

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