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The joints of the evolving foot. Part III. The fossil evidence

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INTRODUCTION

In the previous two papers (Lewis, 1980*a*, *b*) an analysis of form and function in the joints of the primate foot revealed that the human foot presents certain unique features. Yet affinity with other Primates, and particularly the great apes, is abundantly manifest and the unique human attributes are progressive modifications of functional complexes which were initially evolved for arboreal life; in this sense the arboreal foot was pre-adaptive to the specialized structure required by terrestrial bipedal man.

In the present paper an attempt will be made to formulate an hypothesis which can explain the morphological changes which could have remodelled an ape-like foot in such a way as to adapt it to essentially human functions. Ideally, this hypothesis should highlight the key features of changed morphology. Modern methods of constructing phylogenies (Delson, 1977; Tattersall & Eldredge, 1977) largely focus attention on such derived, specialized or apomorphic characters. Using these apomorphic features some of the fossil evidence will be examined with a view to establishing a phylogenetic tree and eventually a reasonable scenario for the evolution of man.

Fortuitously, fossil tali and calcanei which carry the imprints of many of the apomorphic characters are relatively abundant. Even more valuable is the almost complete tarsus and metatarsus from Bed I, Olduvai Gorge (Olduvai Hominid 8) dated at 1·7 million years before the present. Because of difficulties of access to relevant fossil material a fully comprehensive analysis of the evidence is not at this stage possible. However, although the material itself may not be available, the relevant literature may sometimes be used to establish the presence or absence of certain morphological features, even though these may receive little more than passing mention in the formal descriptions. Furthermore, in the present study museum casts have often been used and this is open to obvious criticism. In defence it should be stated that good casts, used judiciously, and with an adequately detailed background of morphological knowledge derived from extant species, can provide much information even if it is not entirely definitive.

A preliminary report of some of the findings has been presented by Lewis (1980*c*).

The remodelling of ape into human foot – an hypothesis

The human foot is manifestly different from that of other primates but apart from simple overt differences, such as the lack of divergence of the hallux, its distinctions are subtle and have proved difficult to pinpoint. Any reasoned analysis of the fossil record, however, requires such insights.

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The usual view about the evolutionary conversion of an essentially arboreally adapted foot to the human condition involves modifications like the following: the hallux has been adducted and rotated so that its plantar surface faces the ground and the whole foot has been everted so as to face downwards rather than inwards (Gregory, 1916). Such a model, however, means that in such an attitude the key first tarsometatarsal joint would be in an unstable, loosely packed position. This joint, in fact, is most stable and attains its position of maximum congruence when the hallux is in arboreal grasping posture – abducted, somewhat flexed, and pronated (Lewis, 1972). With the basal joint of the hallux screwed into this position, the first ray of the foot is effectively flexed and thus would be created a stable foot which moreover possessed a well developed medial longitudinal arch. It seems that such a close packed position of the hallucial tarsometatarsal joint was a central requirement in the elaboration of the arched human foot. This accords with the fact that the human subtalar axis, although no longer very obliquely disposed towards the long axis of the foot, is nevertheless still more or less in line with the hallux, just as in subhuman primates; it is, however, markedly more vertical. Consideration of this apparently changed disposition of the subtalar axis might be expected to yield useful information about the evolutionary changes which have occurred. It seems, in fact, that the forefoot has been realigned towards the stable hallux (and so the subtalar axis) rather than *vice versa*.

There is no doubt that some physical realignment of the human hallux itself towards the other digits has occurred. The change in direction, however, has been brought about essentially by a changed disposition of the joint surface of the medial cuneiform (Schultz, 1930). Much of the masking of the divergence of the hallux, however, results from a remodelling of the anterior foot skeleton (Fig. 1A, B, C). The remodelling of the lateral part of the foot has apparently been achieved by refashioning of the cuboid, and its calcaneal articulation. In the feet of *Pan* and *Gorilla* the cuboid is distorted in such a way that its distal portion is deflected dorsally and laterally. In man the distortion is quite contrary so that the distal aspect of the bone is bent plantarwards and medially, carrying the lateral two metatarsals towards the already reorientated hallux. This means that these two bones form an arched complex bowed in the medial and plantar direction; in *Pan* and *Gorilla* the complex is arched in the opposite direction. Elftman & Manter (1935) perceived something of this when they suggested that the human transverse tarsal joint has become relatively fixed in a position of plantar flexion.

The lateral cuneiform has been remodelled in a comparable way. Its distal portion is deflected medially and somewhat plantarwards. These changes could be expected to be reflected in a changed pattern of articulations between the intermediate and lateral cuneiforms and the cuboid. In *Homo sapiens* the distal articulations between these three bones are lost and their territory is usurped by the enlarged interosseous ligaments binding them together (Lewis, 1980*b*). These distal articulations are retained in *Gorilla* and *Pan*; the distal articulation between the intermediate and lateral cuneiform may, however, sometimes be lacking in *Pan*. The second and third metatarsals are further approximated to the first by an obvious angulation of their bases. Significantly, this angulation develops during embryonic life (Čihák, 1972) when it is even exaggerated in degree.

In the posterior part of the foot the heel has apparently been deviated laterally, again to be aligned more closely towards the subtalar axis. Effectively this shifts the posterior talar surface medially away from the side of the calcaneus, where in

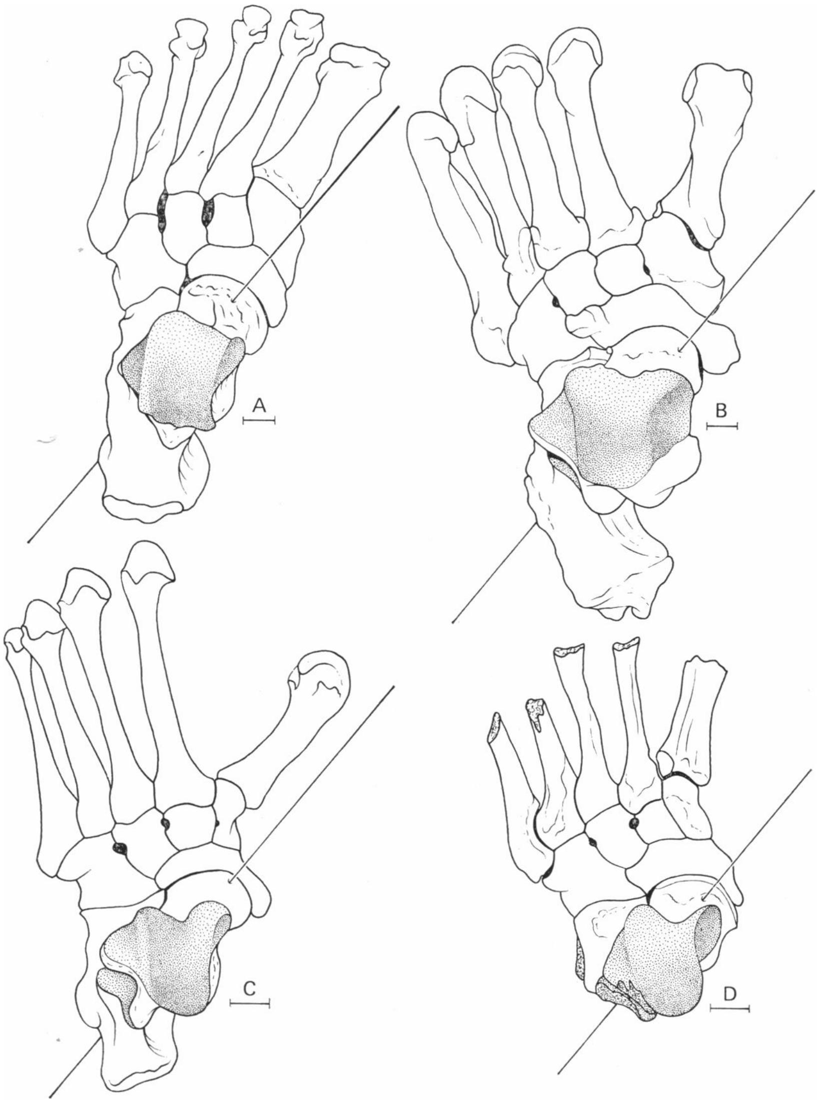

Fig. 1. Dioptograph tracings of the articulated tarsus and metatarsus of *Homo sapiens* (A); *Gorilla gorilla*, B.M. 1978–1226 (B); *Pan troglodytes*, B.M. 76–437 (C); and the casts of OH8 (D). In each case the subtalar axis is shown and the specimens are so orientated that these axes are parallel. The specimens are not all drawn to the same scale and in each case the bar represents 1·0 cm.

primates other than the hominoids the posterior talocalcaneal joint communicates with the ankle joint. The remodelling of the functional axis of the foot to come more into line with the subtalar axis is completed by what is effectively a medial rotation of the trochlea of the talus in respect to the remainder of the bone, thus diminishing the talar neck angle; this characteristic of the human talus was previously noted by Elftman & Manter (1935).

The relatively transverse orientation of the subtalar axis in *Pan* and *Gorilla* is reflected in the way in which the tendons of flexor fibularis and flexor tibialis enter the foot. In these apes the directions of the grooves are rather similar, and contrast with the arrangement in *Homo sapiens*. The flexor fibularis enters from far laterally and the posterior tubercle of the talus is thus located laterally in relation to the trochlea of the talus. The massive flexor fibularis tendon then runs in a deep groove below the sustentaculum tali flanked medially by the groove for the flexor tibialis. In man, of course, the groove for the flexor fibularis tendon (the flexor hallucis longus of human anatomy) is not only redirected but it is relatively small because a large portion of the substance of flexor fibularis has descended to the foot to form the characteristically human medial head of flexor accessorius (Lewis, 1962). The anterior elevation of the human subtalar axis, as has been noted in the previous paper (Lewis, 1980*b*), is really a reflection of the remodelling of the subtalar joint surfaces into counter-rotating screws.

In order for the plantar surfaces of the metatarsal heads to contact the substrate, torsion has occurred in their shafts as noted by Elftman & Manter (1935). In *Pan troglodytes* (Fig. 2) there is some torsion of the first metatarsal in the sense that the head is rotated, relatively to the base, so as to face towards the ground; in *Gorilla* this is even more apparent. Such a rotation is present also in *Homo sapiens* but is even further accentuated. Since the direction of torsion in apes and man is similar this is not a particular feature of contrast in the human foot. In the other metatarsals, however, it is. In *Pan* and *Gorilla* the second metatarsal has its head rotated to face the hallux whilst in *Homo sapiens* the comparable bone has its head rotated in the opposite direction. For the third metatarsal in *Pan* and *Gorilla* the torsion is similar to that of the second but of less marked degree – the plantar surface of the head is somewhat rotated towards the hallux. In *Homo sapiens*, as for the second metatarsal, the converse is true; the head of the bone is twisted in the opposite direction so that its plantar surface is apposed to the ground. The fourth and fifth metatarsals of *Pan* and *Gorilla* show little torsion but the arched form of the transverse tarsal arch means that nevertheless their plantar surfaces are directed somewhat towards the hallux. In the fourth and fifth metatarsals of *Homo sapiens* the direction of torsion is similar to that of the second and third metatarsals but is even more accentuated than in those bones. This external rotation of the heads of the human bones means that, despite the transverse tarsal arch, the weight-bearing plantar surfaces of the bones are firmly applied to the ground.

When the talus is removed, the disposition of the navicular is quite similar in *Pan* and *Gorilla* and the form of the bone is also quite similar with a characteristically projecting tubercle. In *Homo sapiens* the bone has a more squat form but its articular surface for the talus is not orientated in a markedly different fashion from the other two species. This would lead one to suspect that the position of the head of the talus – its torsion relative to the neck – would not differ very significantly in the three species. How then can this be reconciled with the findings in the literature, indicating a considerably increased torsion in man when compared with the great apes? The fallacy, of course, resides in the method by which the neck torsion angle has traditionally been measured – by taking the angle between the trochlear head plane and the median axis of the head. This traditional measurement is satisfactory for the anthropological purposes for which it was devised but is quite inappropriate for between-species comparisons. The trochlear head plane, entering into the ankle joint, varies with little direct relationship to changes in function of the intrinsic joints of the foot. Thus, in the great apes, particularly *Gorilla*, the medial margin of the trochlea is quite depressed whereas in man this

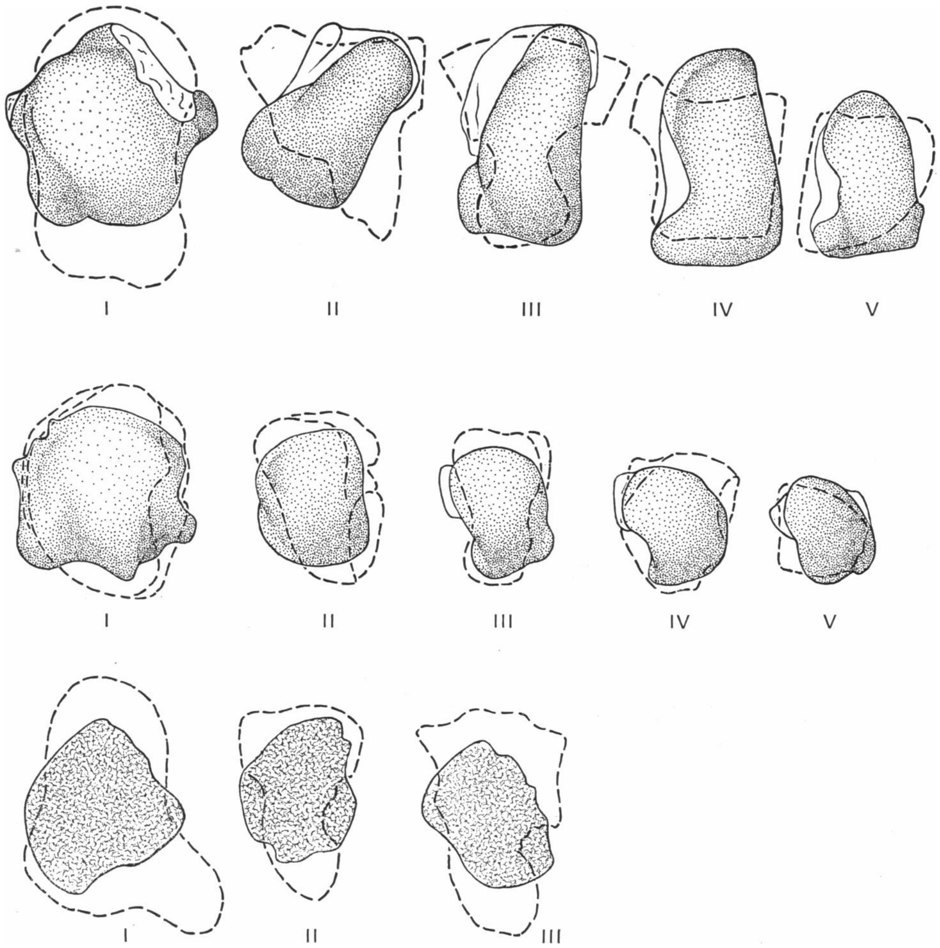

Fig. 2. Diagrams illustrating the direction and degree of torsion of the metatarsals of the left foot of *Pan troglodytes*, B.M. 76–437 (upper); *Homo sapiens* (middle); Olduvai Hominid 8 (lower); the numbers of the metatarsals are indicated by Roman numerals. For *Pan troglodytes* and *Homo sapiens* the heads of the metatarsals have been accurately superimposed by a photographic method on the outlines of the articular surfaces of the bases of the same bones (indicated by broken lines). For OH8 the broken surfaces of the shafts at the junction with the missing heads of the bones are similarly superimposed upon the bases, giving a reasonable indication of the torsion; this is only possible for metatarsals I, II and III.

region of the bone is elevated. A much more valid method of estimating the degree of talar neck torsion in the reality of its setting in the foot would be to relate it to the plane of the inferior surface of the talus, where the bone enters into the subtalar articulations. When the tali are thus orientated on their basal surfaces (Fig. 3) it can be seen that the neck torsion angles vary little between *Pan* and *Gorilla* and differ relatively slightly from *Homo sapiens*. It is preferable to orientate the bones thus rather than by comparing them one to the other by positioning them with the subtalar axes parallel. This latter method, employed by Elftman & Manter (1935), is an improvement on the usual technique, and is more functionally meaningful, but carries with it a new source of error: the axis really is only an abstraction and does not merely represent the true position of the bone in the foot but also

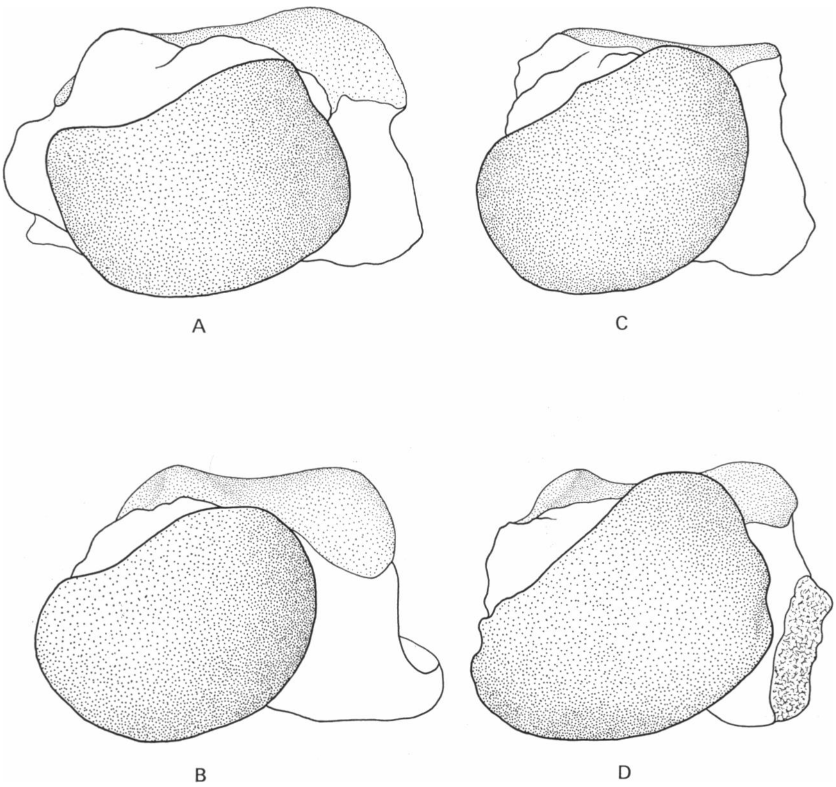

Fig. 3. Distal views of the tali of *Gorilla gorilla*, B.M. 1978–1226 (A); *Pan troglodytes* (B); *Homo sapiens* (C); OH8 cast (D). In each case the bones are resting on the standard basal talar plane.

reflects the form and function of the subtalar articular surfaces, particularly in man with his more vertical axis.

MATERIAL

Good casts of the fossil tarsals and metatarsals (EM 1344-EM 1355) of Olduvai Hominid 8 were available from the British Museum (Natural History); these casts are of excellent quality and considerably better than certain others which have recently become available. The original fossils have also been examined in Nairobi and some, but not all, of the features mentioned were verified there. Also available from the British Museum (Natural History) were casts of four specimens previously described by Clark & Leakey (1951): an articulating calcaneus KNM-SO-390 (CMH 146), and talus, KNM-SO-389 (CMH 145), from Songhor; two tali from Rusinga, KNM-RU-1743 (CMH 147) and KNM-RU-1745 (B2).

Dr Peter Andrews of the British Museum (Natural History) kindly lent a number of casts from his own collection (in each case the designation SO refers to Songhor and RU to Rusinga): nine tali – KNM-SO-392, KNM-SO-478, KNM-SO-966, KNM-SO-967, KNM-SO-968, KNM-SO-1402, KNM-RU-1744, KNM-RU-1745, KNM-RU-1748; six calcanei – KNM-SO-427, KNM-SO-969, KNM-RU-1659, KNM-RU-1660, KNM-RU-1755, KNM-RU-1757.

Comparative osteological observations, amplifying the findings in the previous papers (Lewis, 1980*a*, *b*) were carried out on material available in the British Museum (Natural History) and when specimens are particularized they are identified by their catalogue numbers.

OBSERVATIONS AND DISCUSSION

The first Primates – Cretaceous and Palaeocene

The first supposed Primate, *Purgatorius ceratops* appears in the late Cretaceous of Montana and is said to be a paromomyid (a member of the Paromomyiformes) with resemblances to condylarths and lepticid and erinaceoid insectivores (Van Valen & Sloan, 1965). The lepticids appear to be central to insectivore evolution (Van Valen, 1967) and many believe that tupaiids and primates were independently derived from them (McKenna, 1966; Van Valen, 1965; Bown & Gingerich, 1973).

This would accord with the view previously stated in this series of papers. The marsupial–placental dichotomy leading from the advanced therians of the early Cretaceous was envisaged as probably the consequence of habitat selection: the marsupials were committed to arboreal life and the placentals to the more terrestrial niches of the forest floor. The latter then would presumably include the lepticids. It seems likely that they already had the following as part of the morphology inherited from the advanced therians: an oblique subtalar joint axis; a rotatory calcaneocuboid joint; a grasping hallux. Retention and accentuation of these features with re-invasion or restriction to the arboreal niche was probably the factor characterizing the evolution of the Primates.

Recently, however, in a study of the tarsus of Cretaceous Eutheria and Palaeocene Primates, Szalay & Decker (1974) seem to have overstressed the likely terrestrial specialization in the tarsus of the precursors of the Primates. The model they propose is the condylarth tarsus (the ungulate orders of course originated from the condylarths). There are a number of major fallacies in their argument, however, not least of them misapprehensions about the true nature of the apparently primitive calcaneofibular contact, which has been discussed in Parts I and II of this series of papers. In fact, a critical assessment of their work leaves little doubt that the tarsus of the palaeoryctoid insectivore *Procerberus* described by them is closer to that which would have been predicted from the present work as ancestral to that of the Primates. The condylarth tarsus similarly is quite plausibly a derived form, originating from some similar stock, rather than being primitive; in fact, as regards the calcaneofibular contact and the disposition of the subtalar axis, the condylarths appear to parallel the derived trends seen in *Macropus* among the marsupials.

These primitive presumptive Primates (The Paromomyiformes) formed a radiation of four families in the Palaeocene–Paromomyidae, Plesiadapidae, Carpolestidae and Picrondontidae (Savage, 1975). The suborder was probably arboreal, the central family being the Paromomyidae whilst the better known Plesiadapidae were cranially aberrant. It is, however, arguable whether the Paromomyiformes were arboreal or should even be considered as Primates (Kay & Cartmill, 1977).

The insistence by Szalay, Tattersall & Decker (1975), Szalay & Decker (1974) and Szalay (1975) on the primate status of *Plesiadapis* rests in the final analysis on certain key tarsal characters, said to represent emergent primate synapomorphies. These are a screw-like or helical subtalar joint, a calcaneocuboid joint of pivotal nature and a posteriorly retracted trochlear process (peroneal tubercle). The first of these is, however, an ancient therian character, which has been secondarily refined and elaborated in the Primates. The second is similarly an ancient therian character, (Szalay & Decker, 1974, themselves note it in fossil Metatheria); Szalay (1977) appears to consider that a pivot joint requires the elaboration of a plantar prominence on the cuboid – this is not so, for many monkeys (and *Hylobates*) have no more of a protuberance than such diverse forms as *Sarcophilus*, *Phascolarctos* and *Tenrec*. The last character is certainly a feature of Primates but is also seen in *Tupaia* and occurs in some rodents and in *Didelphis* (Stains, 1959); its value in cladistic analysis is diminished, therefore, as it has occurred convergently on a number of occasions.

The form of the trochlea in *Plesiadapis* is merely primitive – an early terrestrial modification – and is paralleled by, for example, *Sarcophilus* and *Antechinus* among marsupials. Simpson (1935) early argued for the inclusion of *Plesiadapis* among the Primates on the grounds of various resemblances to *Tupaia* and *Lemur*. However, it is now more usual to consider the Tupaiidae as lepticid-like insectivores with some special similarities to Malagasy lemurs and thus as the closest living non-primate relatives to the Primates (McKenna, 1966). The Paromomyiformes may be fossils in a similar related category. However, from some such stock undoubted Primates arose, in North America and/or Asia (Szalay, 1973). With little doubt these were the fossil lemuriforms, the Adapidae.

The adapid tarsus is quite well known (Decker & Szalay, 1974) and appears to show the the transition from a form like that of *Plesiadapis* to that of undoubted lemurid type. A trend can be shown from adapines to notharctines for lengthening of the anterior part of the calcaneus, with the attainment of a quite considerable articulation of the calcaneus with the navicular – in effect the primitive type of alternating tarsus (talus articulating with cuboid) has been reversed to produce a new type of alternating tarsus. The importance of this to the function of the arboreal primate foot has been shown in the previous paper (Lewis, 1980*b*). Associated with this is an accentuation of the helical nature of the posterior talocalcaneal joint. The slightly concave and convex conarticular surfaces of the calcaneocuboid joint also achieve the typical primate form with elaboration of a small plantar tongue on the cuboid. The absence of lengthening of the calcaneus to achieve contact with the navicular in adapines, reflected in a high calcaneal index, means that this group lack a characteristic primate attribute. As with *Plesiadapis* their primate status is therefore arguable, as already noted by Martin (1979).

It has been shown in the previous paper (Lewis, 1980*b*) that the lemuriform tarsus is the likely precursor of that of the higher Primates. Indeed, one of the divergent views on the origin of the higher Primates holds (Gingerich, 1973, 1975; Gingerich & Schoeniger, 1977) that the Adapidae were ancestral, not only to the living lemuriforms but also to the higher Primates. There is no conflict here with the above view.

The alternative view, which has been particularly sponsored by Szalay (1975, 1977), and which accords best with all morphological evidence, is that the Strepsirhini (including the living lemuriforms) and the Haplorhini (higher Primates plus the tarsiiforms) were derived from some early adapid stock. This means that the tarsal modifications typical of Primates, as realized in the notharctines, must already have been present in that stock.

Oligocene fossils of the Fayum of Egypt

The earliest known Anthropoidea (higher Primates – monkeys and apes) are from Oligocene deposits in the Fayum and comprise six genera. The three largest and most ape-like are *Aeolopithecus, Propliopithecus* and *Aegyptopithecus*, the last often considered as the ancestral ape. *Parapithecus* and *Apidium* are much smaller (about the size of a marmoset) and have been said to be the ancestors of the Cercopithecidae. The oldest, but very poorly known genus, is *Oligopithecus*.

The overriding impression is of their generally primitive morphology and there is thus a strong case for considering them as merely ancestral Anthropoidea, rather than as having special affinity with either apes or monkeys (Delson & Andrews, 1975; Delson, 1975, 1977). However, there is little doubt that from this or related stock arose the undoubted apes of the African early Miocene, and also the Cercopithecidae.

The Fayum Primates show a number of resemblances to platyrrhine monkeys (Conroy, 1976). This has prompted the highly attractive, but unsubstantiated, hypothesis that the platyrrhines in the late Eocene reached South America from Africa perhaps by rafting (Hofstetter, 1974); at this time South America was little further from Africa than from North America, the other postulated source of the platyrrhines (Orlosky & Swindler, 1975). At least it seems acceptable that an essentially platyrrhine grade of structure was ancestral for the catarrhines (Szalay, 1975, 1977). This is in accord with the view taken in the present series of papers that the platyrrhine foot of *Saimiri, Cebus* or *Pithecia* provides a good ancestral model for the higher Primates.

Five primate tali and five calcanei are known from the Fayum and these have been described by Conroy (1976). Access to this material has not been possible and the published illustrations are of unsatisfactory quality. However, some tentative comments can be made on the published data. The tali are what one would expect of an arboreal Primate having a well angulated neck (indicative of an oblique subtalar axis) and well-marked cup for the medial malleolus (indicative of the ankle joint mechanism of arboreal Primates). The calcaneus also accords with structure expected as ancestral to apes and monkeys. The posterior talocalcaneal joint appears to have had a marked screw-like action (Szalay, 1975). Associated with this one would expect a reasonable articulation of calcaneus with navicular; no data are available on this but the published illustrations make it appear likely. According to Conroy (1976) "the articular surface for the cuboid is a crescentic-shaped, gently concave facet"; it seems thus to have had the likely ancestral anthropoid form as preserved today in extant monkeys, and not to have elaborated the marked plantar excavation which apparently characterized emergent ape evolution.

Early Miocene fossils of East Africa

Fossils of undoubted apes are found first in the early Miocene interrift localities of East Africa. The six species known are all members of the Dryopithecinae (Andrews, 1974; Delson & Andrews, 1975) and it is now probably preferable to allocate them to three genera (Andrews, 1977; Pilbeam *et al.* 1977) – *Proconsul major, Proconsul nyanzae, Proconsul africanus, Rangwapithecus vancouveringi, Rangwapithecus gordoni* and *Limnopithecus legetet*. Also found here is *Limnopithecus macinnesi*, now assigned to the genus *Dendropithecus* (Andrews & Simons, 1977);

this species has with considerable reservations (Delson & Andrews, 1975) been allocated to the Hylobatidae but it may be better to consider it as a conservative leftover from the Oligocene catarrhines which in a few ways has converged on the gibbons. All the early Miocene sites were in forested areas (Andrews & Van Couvering, 1975). There is little doubt that the gibbons were derived from the ape stock earlier than the fossils represented in these sites; the orangutan, in contrast, was probably derived from this stock or later. It has been suggested that *Proconsul major* was ancestral to *Gorilla* and *Proconsul africanus* to *Pan* but this seems unlikely and resemblances are more probably the results of ecological and size related convergence (Delson & Andrews, 1975).

Fossil tarsal bones are known from two two early Miocene sites – Songhor and Rusinga Island. There are no satisfactorily documented accounts of monkey fossils from either site and the foot bones belong, at least presumptively, to apes. Cranial and dental remains suggest that the common species present at Songhor were *Proconsul major*, *Rangwapithecus gordoni* and *Limnopithecus legetet*. At Rusinga the common species are *Proconsul africanus*, *Proconsul nyanzae* and *Dendropithecus macinnesi* (Andrews & Van Couvering, 1975). Casts were available of three tali and one calcaneus previously described and illustrated by Clark & Leakey (1951). These specimens are: a large articulating talus and calcaneus (KNM-SO-389 and KNM-SO-390) reasonably assigned to *Proconsul major*; a somewhat smaller talus (KNM-RU-1743) reasonably assigned to *Proconsul nyanzae*; a small talus (KNM-RU-1745) which may be *Proconsul africanus*. In addition casts were available of nine tali and six calcanei (detailed in Material) from the collection of Dr Peter Andrews. On considerations of size, none of these is attributable to *Proconsul major* or *Proconsul nyanzae* but their precise attribution to any particular one of the smaller apes would be hazardous.

It has been noted in the first paper of this series (Lewis, 1980*a*) that a basic arboreal feature of the primate ankle joint is the deeply articular cup at the anterior end of the tibial malleolar surface on the talus. This feature is well accentuated in all the fossil specimens and, indeed, is more obvious than in the extant great apes, with the possible exception of *Pongo*.

Taken together, the tali and calcanei allow a clear assessment of the functional anatomy of the subtalar joint complex. It has been shown in the previous paper (Lewis, 1980*b*) that in the basic arboreal primate condition the anterior articulating surfaces on the talus for the calcaneus form an L-shaped area on the surface of a cylinder formed by the head and neck of the talus and that the axis of this cylinder is the axis of the subtalar joint complex; the ligamentum cervicis tali attaches in the angle of the L-shaped area. The posterior articulating surfaces are so aligned that they impart a helical action to the joint movement. This can be clearly appreciated even by visual inspection of the under-surface of the talus where it can be seen that the axis of the anterior cylinder formed by the head and neck intersects the posterior joint surface at an angle. The subtalar axis is set very obliquely to the functional anteroposterior axis of the foot and lies in a quite flat plane. The essentials of these features are conserved in *Hylobates* and *Pongo*. *Pan* and *Gorilla*, however, share certain derived features which give every impression of having been superimposed on this basic arboreal morphology. In both these largely terrestrial great apes the talus is much more squat in form, with a shortened neck and broadened head and with the component limbs of its L-shaped articular surface for the calcaneus partially blended to form what is almost a single continuous semilunar area.

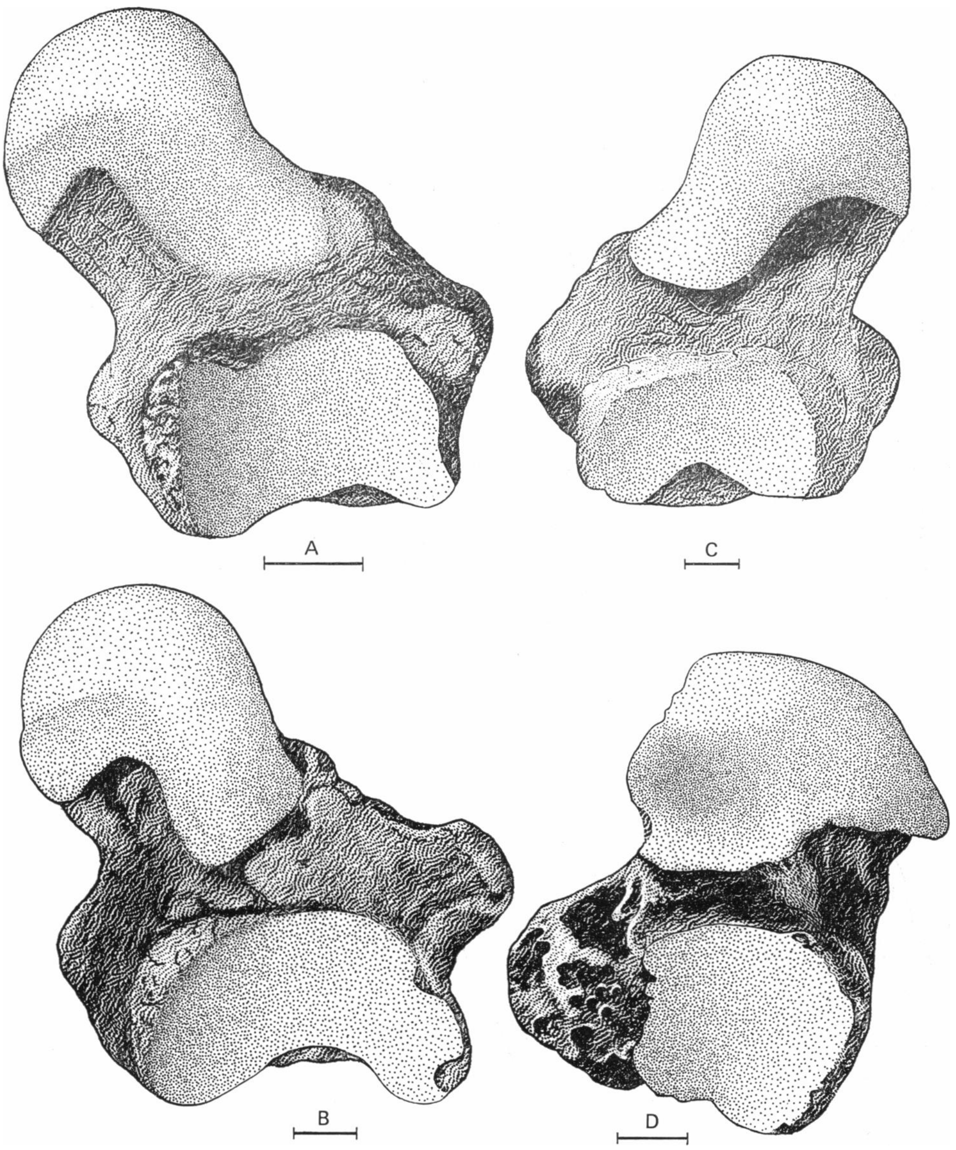

Fig. 4. The under-surfaces of casts of a right talus attributed to *Proconsul africanus*, KNM-RU-1745 (A); a right talus attributed to *Proconsul major*, KNM-SO-389 (B); a left talus attributed to *Proconsul nyanzae*, KNM-RU-1743 (C); and OH8 (D). In each case the bar represents 0·5 cm.

In all the fossils the basic primate arrangement, devoid of the specializations characterizing *Pan* and *Gorilla*, is conserved (Fig. 4). It is particularly clearly evident in the matching talus and calcaneus attributed to *Proconsul major* (KNM-SO-389 and KNM-SO-390). The under-surface of the talus of *Proconsul nyanzae* (KNM-RU-1743) and the small talus (KNM-RU-1745) also unequivocally show these features.

No fossil cuboids are known from these sites but all the calcanei quite clearly show the form of the articular surface for that bone. As has been shown in the

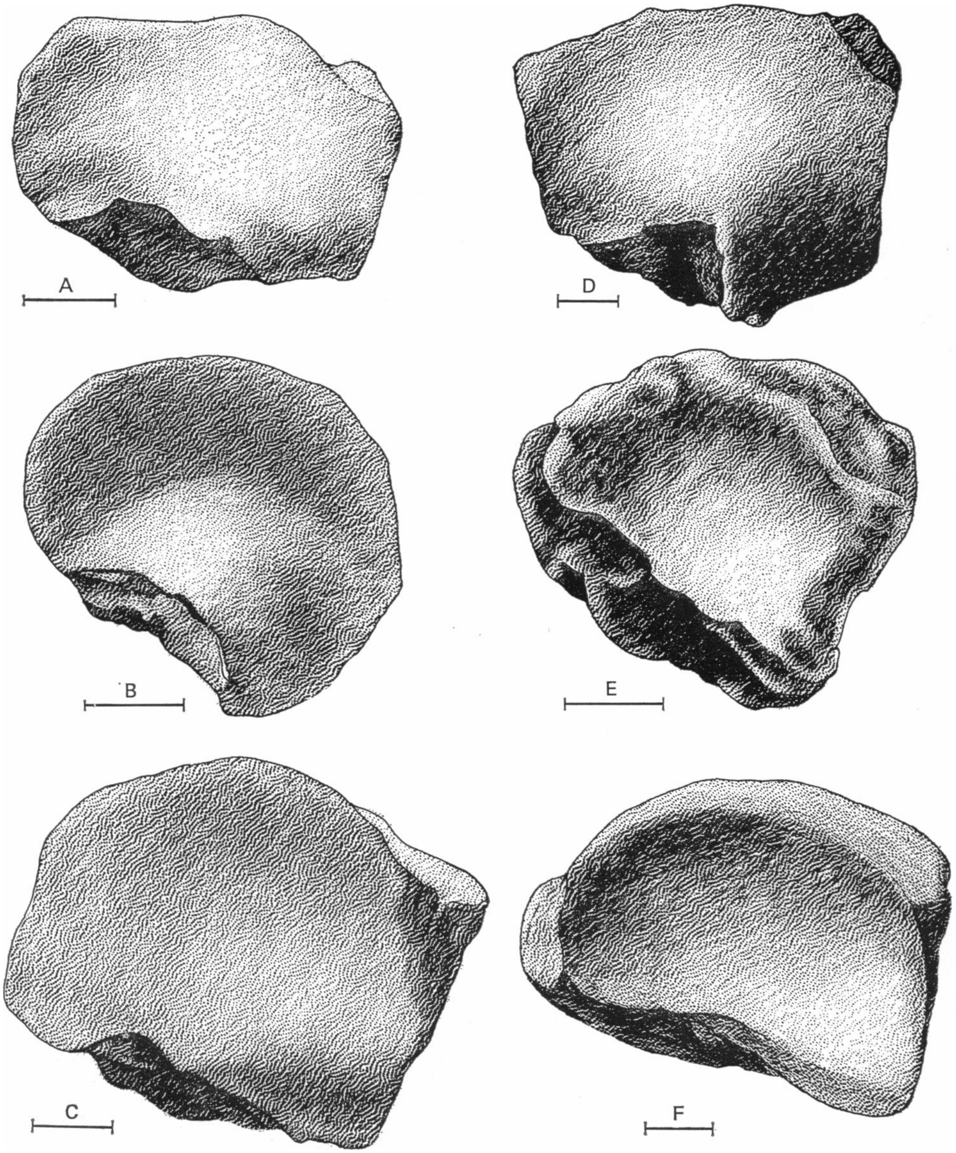

Fig. 5. Proximal views of the left cuboids of *Pan troglodytes*, B.M. 76–437 (A); *Pongo pygmaeus*, B.M. 1948-11-23-1 (B); *Gorilla gorilla*, B.M. 1948-2-27-1 (C); *Gorilla gorilla*, B.M. 1978–1226 (D); OH8 cast (E); *Homo sapiens* (F). In each case the bar represents 0·5 cm.

previous paper, evolutionary change in the calcaneocuboid joint seems to have played a highly significant role in Primate evolution.

It has been noted in the previous paper (Lewis, 1980*b*) that in monkeys and prosimians the articular surface on the cuboid is kidney-shaped with a varying tendency towards elaboration of a protuberant ventral convexity; the calcaneus is reciprocally shaped and movement is largely rotatory. A similar morphology is retained in gibbons. In the pongids, however, the morphology is modified, with chimpanzees apparently occupying a central and relatively conservative status in

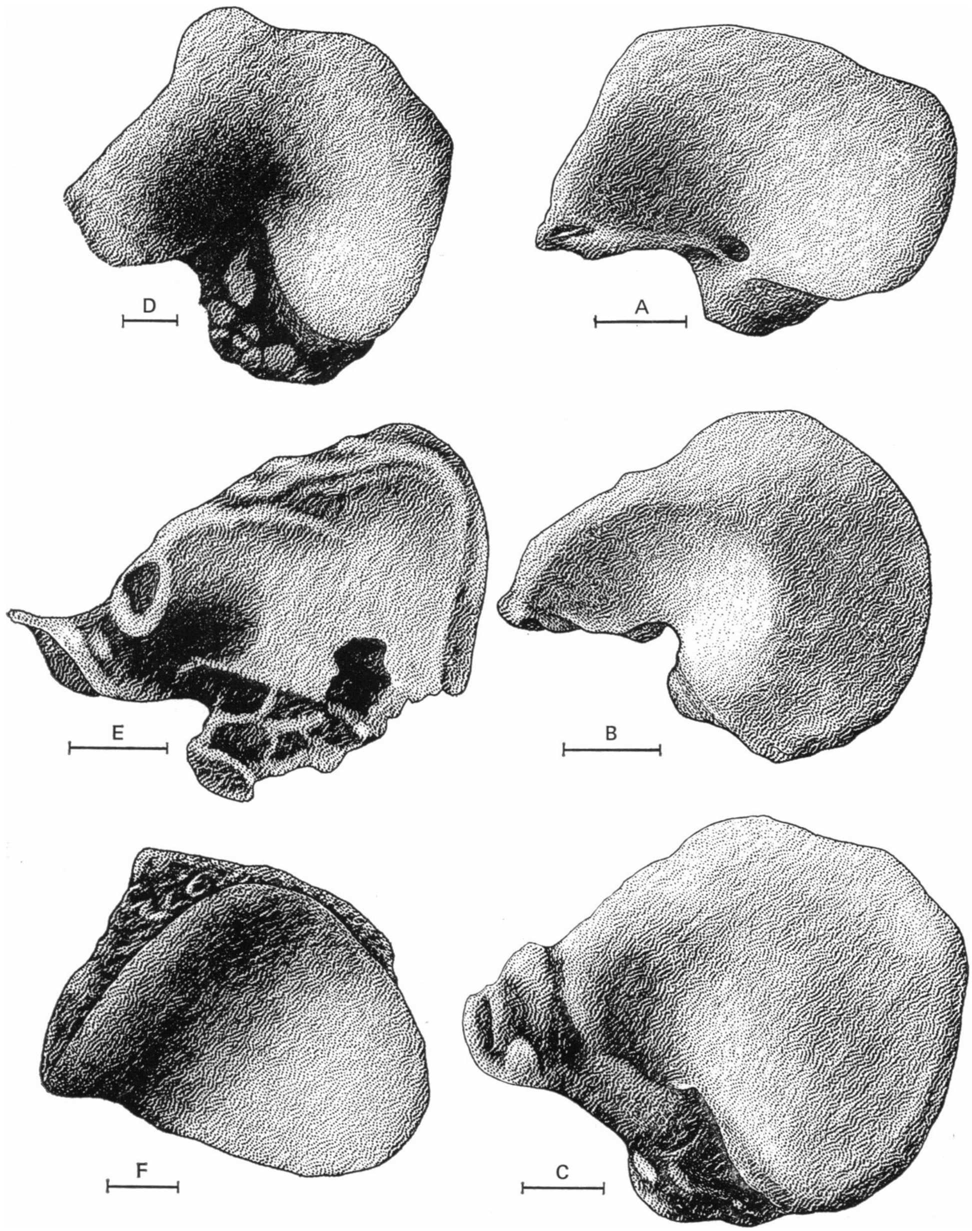

Fig. 6. Distal views of the left calcanei of the same specimens as shown in Fig. 5: *Pan troglodytes*, B.M. 76–437 (A); *Pongo pygmaeus*, B.M. 1948-11-23-1 (B); *Gorilla gorilla*, B.M. 1948-2-27-1 (C); *Gorilla gorilla*, B.M. 1978–1226 (D); OH8 cast (E); *Homo sapiens* (F). In each case the bar represents 0·5 cm.

this evolutionary change. In *Pan* the ventral beak on the cuboid (and the corresponding calcaneal concavity) is greatly enlarged and shows a tendency towards a medial shift. The beak may be fairly central (e.g. B.M. 1968-6-27-1 and illustration in previous paper) or it may be quite medially displaced (Figs. 5A, 6A) giving the surface an asymmetrical form (B.M. 1976–437).

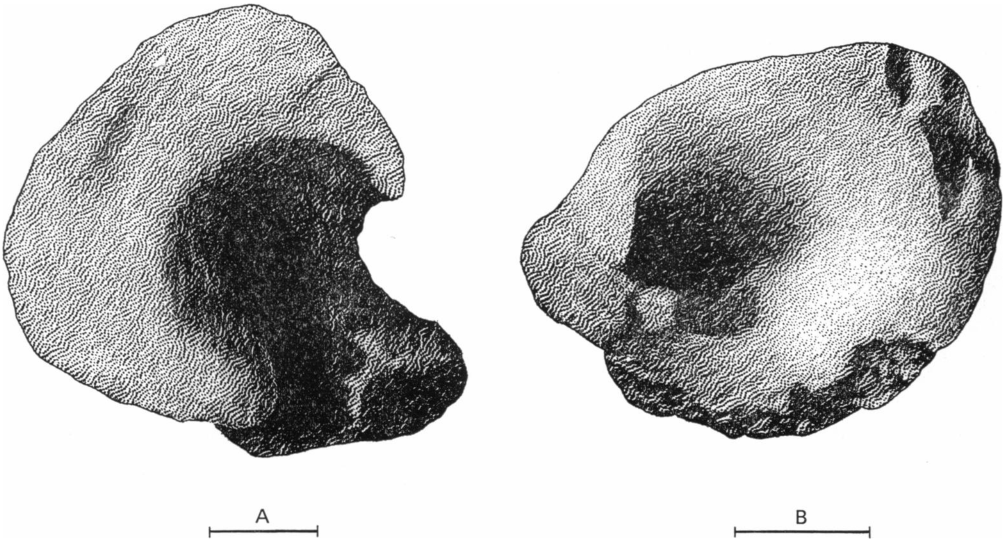

Fig. 7. The distal aspect of the cast of the right calcaneus of *Proconsul major*, KNM-SO-390 (A) and of a left calcaneus from Songhor, KNM-SO-427 (B). In each case the bar represents 0·5 cm.

The situation in *Gorilla gorilla* shows trends which, one may speculate, are derivative from a morphology similar to that found in *Pan*. The tendency is towards suppression of the plantar convexity on the cuboid with elaboration of the surrounding flat surface. This gives rise to virtually flat conarticular surfaces (Figs. 5C, 6C) with only a residual hint of protuberance on the cuboid and depression on the calcaneus. This is easily the most common finding in gorillas (e.g. B.M. 1948-2-27-1 and nine other specimens). Occasionally, the elevation and receptive depression are more obvious, recalling the condition in *Pan* (B.M. 1948–436; B.M. 1976–440). In occasional specimens, however, the calcaneus is excavated (perhaps even to a greater extent than is usual in chimpanzees) and this deep depression is surrounded by a relatively flattened articular rim; it so happens that the single wet specimen ('Guy', B.M. 1978–1226) available for study and described in the previous paper (Lewis, 1980*b*) has this morphology (Figs. 5D, 6D) and it is also shown in B.M. 1948-12-20-2. As will be seen this pattern somewhat resembles that which is characteristic of the orangutan.

Pongo pygmaeus shows another interestingly derivative morphology, recalling features of both the above. The beak on the cuboid has been further elaborated into a prominent eccentrically located hemispherical eminence, received into a correspondingly deep cup in the calcaneus. This protuberance is partially bounded dorsally and laterally by a broad plane surface. All thirteen specimens examined (e.g. B.M. 1948-11-23-1) revealed this highly individual morphology (Figs. 5B, 6B).

The calcaneal fossils from both Rusinga and Songhor, with one notable exception, show a morphology close to that of *Pan* in the form of the articular surface for the cuboid. In one (KNM-RU-1757) the excavation on the calcaneus for the cuboid is fairly centrally located (as in *Pan* B.M. 1968-6-27-1), but in all the others the joint is asymmetrical (as in *Pan* B.M. 76–437). Indeed the excavation may be rather more accentuated than that usually seen in *Pan*. This morphology (Fig. 7B) is perfectly adequate as a precursor to that seen in *Pan* and seems also to represent a plausible ancestral morphology for those unusual variants among *Gorilla* calcanei (e.g. B.M. 1948–1226) in which there is a deep excavation for the cuboid. Progressive flattening of this surface then appears to have been the evolutionary trend which is characteristic of the *Gorilla*.

The notable exception is the large specimen (KNM-SO-390) which has reasonably been attributed to *Proconsul major*. This calcaneus (Fig. 7A) articulated with the cuboid in a manner strikingly resembling that found in *Pongo*. Could it, therefore, be that here is represented the ape stock for the Asiatic orangutan whose transit out of Africa could then have been effected, since a land bridge to Eurasia is known to have formed at the beginning of the middle Miocene (Andrews & Van Couvering, 1975). Some support for this notion comes from the description of a palate, also from Songhor, which is said to show suggestive orangutan affinities (Andrews, 1970). Separate derivation of *Pongo* from this early ape stock, leaving certain members of the remainder to evolve progressively along the line leading to *Pan* and *Gorilla*, and even man, would appear to provide a best fit to the overall morphological pattern.

An alternative view, although less satisfactory on balance, must be considered. The form of the cuboid surface on the calcaneus of *Proconsul major*, although very like *Pongo*, is also not markedly dissimilar to that found in the variant form of *Gorilla* (B.M. 1948–1226); could, therefore, both of these extant pongids be derived from *Proconsul major*?

Clark & Leakey (1951) previously described certain of these specimens – a left talus (KNM-RU-1743) and a right talus (KNM-RU-1745) from Rusinga and the articulating right talus and calcaneus (KNM-SO-389 and KNM-SO-390) from Songhor. Surprisingly, they came to the conclusion that these tarsal bones indicated an habitually everted posture of the foot associated with largely terrestrial quadrupedal locomotion, and that the nearest modern counterparts were to be found among the cercopithecoid monkeys. These conclusions seem to have been prompted by the inadequate background morphological data then available and are clearly not reconcilable with the additional functional data described in the present series of papers. Among the features cited to support their conclusion was the cup-shaped hollow at the anterior end of the medial malleolar facet and the form of the articular surface on the under aspect of the head and neck of the talus; in reality the pattern of these features is clearly correlated with arboreal activities and, among the apes, reach their most clear-cut expression in *Hylobates* and *Pongo*. Similarly they interpreted the considerable lateral extent of the articular surface on the talar head as reflecting provision for a greater degree of eversion at the forefoot; in reality the functional studies reported in the previous paper (Lewis, 1980*b*) show that this is concerned with just the opposite, namely providing for movement of the navicular during supination of the forefoot in an arboreal setting. The dorsal tubercle of the talar neck was seen as a further cercopithecoid feature, supposedly associated with locking of the dorsiflexed ankle joint; as has been noted it is a universal primate feature – the site of attachment of the strong dorsal talonavicular ligament. They noted the remarkable form of the calcaneocuboid joint surface of *Proconsul major* (KNM-SO-390) and although recognizing its resemblance to that of the orangutan, then interpreted it as a specialization for stability in quadrupedal terrestrial activities; in fact, it clearly serves the opposite function – rotatory mobility in an arboreal setting. They noted the posteromedial extension of the posterior talocalcaneal articulation and interpreted this as a provision for occasional assumption of an erect posture; in fact, it merely indicates a well developed helical action at the joint, to be expected in an arboreal foot. Clark (1952) subsequently reported on a further left talus from Rusinga (R234'50) again stressing the cercopithecoid resemblances.

Three of these tali – KNM-SO-389, KNM-RU-1743 and 234'50 – have been subjected to multivariate statistical treatment by Day & Wood (1969) who reached the conclusion that their morphological affinities were with modern African pongids, KNM-SO-389 being rather closer to *Gorilla* and the other two to *Pan*. Pilbeam (1969) utilized these findings, suggesting that KNM-SO-389 belonged to *Proconsul major* (and was probably ancestral to *Gorilla*) and that the other two belonged to *Proconsul nyanzae*. The study by Day & Wood (1969) has been trenchantly criticized on methodological grounds by Oxnard (1972) who re-interpreted the data as showing that the *Proconsul* tali were unique and well separated from either the African apes or modern man. Wood (1973), in a revised study, reached the conclusion that the two Rusinga tali (KNM-RU-1743 and 234'50) showed the same morphological features as cercopithecoid quadrupeds, essentially the position earlier taken by Clark (1952). In the most sophisticated multivariate study (Lisowski, Albrecht & Oxnard, 1974) the conclusion was reached that the *Proconsul* tali all lie within the envelope of arboreal species and specifically rather close to, although significantly different from, the orangutan.

As shown in a later study this seemed to be particularly true of the larger specimens (KNM-RU-1743) and (KNM-SO-389) ascribed to *Proconsul nyanzae* and *Proconsul major* respectively; the smaller specimens (e.g. KNM-RU-1745), ascribed to *Proconsul africanus*, were said to be even closer to *Hylobates* (Lisowski, Albrecht & Oxnard, 1976). There is no denying the ingenuity and sophistication of the mathematical techniques involved in studies such as this. Doubts, however, arise about the full credibility of the conclusions when one considers the relative simplicity of the underlying morphological data used. Most of the dimensions utilized are standard measures reflecting overall shape, although sometimes they may be chosen because of some intuitive notion that they may contain information of biomechanical importance. However, it is recognized by at least the more responsible workers that important information that is accessible to trained observation may not easily be incorporated in these multivariate studies. This appears to be precisely the situation in the present case. The eight measurements used take no account of the various apomorphic features stressed in the present series of papers, yet it is these functionally related specializations which are the raw material for evolution, and are the basis of cladistic analysis. Perhaps rather fortuitously then, multivariate analysis seems to have arrived at a similar conclusion: that the early Miocene *Proconsul* tali are those of apes preserving arboreal specializations and in this they are primitive even when compared to those of the extant knuckle-walking and largely terrestrial *Pan* and *Gorilla*.

The Olduvai Hominid 8 *foot*

These foot bones, consisting of the tarsals and metatarsals, were recovered from an occupation floor (site FKL NN) in Bed I of Olduvai Gorge, dated at about 1·7 Myr before the present. They were associated with hand bones (OH7) and the juvenile skull bones and mandible which form the Type of the controversial taxon *Homo habilis* (Leakey, 1971), but clearly were from a different individual. The attribution of these remains to the taxon *Homo* has been a source of controversy; meaningful morphological assessment of this foot should contribute key information about the locomotor capabilities and more precise phylogenetic and taxonomic status of this population of fossil Primates.

As has been noted, certain articulations – the subtalar complex and the calcaneocuboid – present highly significant apomorphic changes in *Homo sapiens*. A preliminary assessment of OH8 can therefore be profitably directed to these articulations. In man the subtalar joint axis has been re-aligned towards the long axis of the foot or, to express the mechanism more realistically, the foot has been remodelled about this axis. Further, the talocalcaneal conarticular surfaces underlying the talar head and neck have been remodelled to form a counter-rotating screw which, combining its action with that of the helical posterior talocalcaneal joint, imparts a rotatory motion to the talus as a whole. This effectively is reflected in an anterior elevation of the compromise axis. The importance of this in the human gait is the way in which it facilitates the transfer of weight first towards and then away from the supporting foot during the stance phase. In OH8 the joint surfaces retain the apelike form and the axis is very obliquely disposed (Fig. 1D) as in *Pan*. The talus itself shows the squat foreshortened appearance seen in the extant African apes and the calcaneal articular surfaces on its head and neck are similarly merged and no longer conserve the primitive L-shaped pattern (Fig. 4D).

It follows logically, from the obliquity of the axis, that the fossil heel should not be realigned towards the axis by being laterally deviated as it is in *Homo sapiens*; the heel, in fact, is missing but its broken attachment clearly indicates a disposition similar to that of *Gorilla* and *Pan*. Similarly, the trochlea of the talus has not been medially rotated towards the subtalar axis; the talar neck is thus angulated on the body rather as in *Pan*. Although the posterior tubercle of the talus is missing in OH8 its disposition can readily be inferred from the situation of the broken surface. It is clear from this that the mode of entry of the tendons of flexor fibularis and flexor tibialis into the sole was similar to the arrangement in *Pan* and *Gorilla* and quite unlike the derived condition characteristic of *Homo sapiens*. It may reasonably be assumed from this, also, that OH8 lacked the uniquely human medial head of flexor accessorius (Lewis, 1962) with its significant functional role in the human gait. The posterior part of the foot is thus strikingly conservative in OH8 and in functional morphology is therefore quite similar to that of the great apes.

It has been noted that the calcaneocuboid joint of man has had striking modifications apparently grafted onto the type of morphology generally characteristic of apes. New dimensions have been introduced into the movement in man which provide for the untwisting of the lamina pedis, bringing it into the close-packed position (CPP), during the support phase of the gait. In OH8 rotatory movement is greatly limited and is far less than that found in *Pan*, *Gorilla* and *Pongo*; *Pan*, *Gorilla* and *Pongo*, despite prominently projecting articular beaks on the cuboid, have quite free rotatory movement. Movement in OH8 is also much less, and quite different in character, from that found in *Homo sapiens* despite a superficial resemblance between the form of the articular surfaces. Thus the lateral expansion of the cuboid is less than that in man and the rotatory motion of calcaneus upon cuboid quickly brings the joint into the close-packed position, arresting movement before the heel is laterally deviated as in *Homo sapiens*. In CPP the whole joint is very stable, with the projecting tongue of the cuboid impacting itself under the sustentaculum tali, and with the expanded flat lateral areas in contact. The joint, then, has acquired a new stability which is in striking contrast to the situation in *Pan*. The joint in *Pan* and *Pongo* does not lock in such a way, whilst in man it is modified to facilitate lateral deviation of the heel. This stable locking joint could be envisaged as a reasonable transitional arrangement between that of arboreal apes and bipedal man. Its structure could not have been predicted from the study of extant primates alone. Elftman & Manter (1935) postulated that during the evolution of man the transverse tarsal joint had become relatively fixed in a position of plantar flexion. This was a quite inspired prediction; thus in one form, at least, close to the lineage of man (OH8) the joint has become stabilized but not in an attitude of the plantar flexion – this appearance in man is, in fact, largely the result of further remodelling of the cuboid.

The joint surfaces of the calcaneocuboid joint of OH8 could readily have evolved from a morphology like that shown by *Pan troglodytes* and this would be in accord with a considerable body of evidence linking the derivation of the hominid line to that of the evolving African apes. In fact, the distal aspect of the OH8 calcaneus with its deep excavation, is even more like that of the early Miocene apes, for example KNM-SO-427 (Fig. 7B). This does not necessarily argue for an early Miocene derivation of an independent hominid line, for the derived features in *Pan troglodytes* are likely to be of relatively recent acquisition. Moreover, a single specimen of the foot of the pygmy chimpanzee (*Pan paniscus*) which was briefly available to the author showed a calcaneal articulation for the cuboid strikingly similar to that shown in Figure 7B. Further material then, when available, may lend support to the interesting contention of Zihlman, Cronin, Cramer & Sarich (1978) that the pygmy chimpanzee may offer us the best prototype of the prehominid ancestor.

The forefoot, in contrast to the hinder part, presents a rather more human appearance, at least in its medial part. This results largely from the comparative lack of divergence of the hallux, which in turn has been realized by remodelling of the medial cuneiform, and presumably correlated with this there is a single confluent articulation between the medial and intermediate cuneiform as in man, rather than dual ones as in apes (Fig. 8). There has, however, been a prevailing tendency to over-emphasize the degree of this adduction of the hallux which has, in part, been dictated by indications of an articulation between the bases of the first and second metatarsals.

Great play has been made of the presence of this apparent joint between the first and second metatarsals in the OH8 foot. It has been cited as a feature demonstrating 'unequivocally' or 'indisputably' the lack of divergence of the hallux (Day & Napier, 1964; Day, 1978). Articulations between these two bones certainly are quite frequently encountered in human feet, and indeed one was present in the foot shown in Figure 1A. They vary considerably in refinement of structure, often being more of the nature of a pseudarthrosis, with a synovial cavity of bursal type and quite thick fibrous or fibrocartilaginous pads, fashioned from ligamentous attachments, forming the emergent articular surfaces on the apposed bones.

Synovial joints are known to be formed at a number of anomalous anatomical sites, for example, between coracoid process and clavicle (Lewis, 1959); in such cases the articular surfaces are remodelled from the ligamentous attachments to the bones and the cavity is derived from a bursa. In the case of the foot the articular surface on the second metatarsal is a progressive modification of the raised pro-

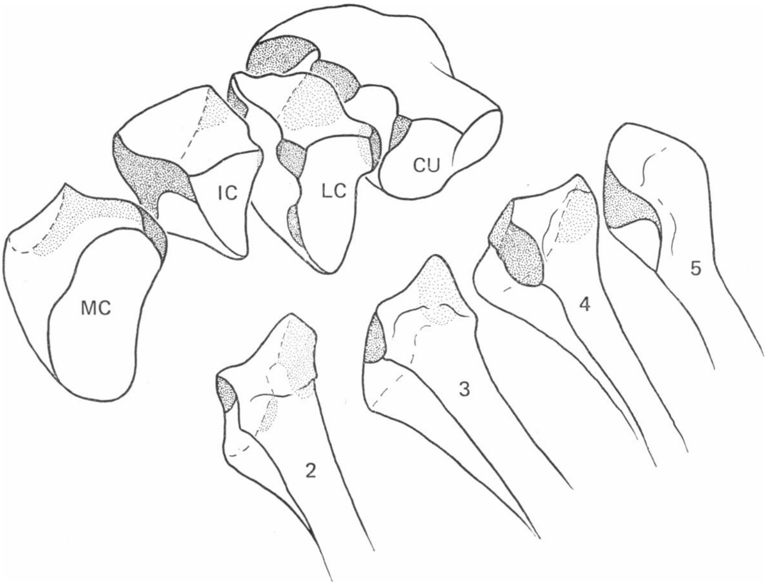

Fig. 8. An 'exploded' diagram of the distal tarsal and metatarsal bases of OH8 showing the intervening articulations. MC, medial cuneiform; IC, intermediate cuneiform; LC, lateral cuneiform; CU, cuboid; 2–5, bases of metatarsals 2–5.

tuberance which is the site of attachment of the ligament of Lisfranc; that on the first metatarsal is remodelled from the adjacent elevation giving attachment to converging oblique ligaments on the medial site of the hallucial tarsometatarsal joint. These ligamentous markings are, of course, present in the absence of a synovial joint, but when a joint cavity is present they show a varying degree of elaboration, sometimes achieving the appearance of smooth, elevated articular facets. Similar closely opposed ligamentous tuberosities are present in *Gorilla gorilla* (Fig. 1B). In fact, no synovial articulation was present in this particular example, which was dissected as a wet specimen, but such a finding would not have been surprising on general principles. It is quite apparent that the impressions on the adjacent first and second metatarsals of the OH8 foot similarly are basically ligamentous ones. By analogy with comparable human examples there is little doubt that a rather rudimentary synovial joint was present. When, however, the foot is reconstructed with due allowance being made for the probably quite thick fibrous investments of the bones, it is clear that the hallux would be somewhat divergent. Moreover, when the first tarsometatarsal joint is brought into CPP some divergence of the hallux is quite obvious, and the form of the conarticular surfaces (Lewis, 1972) is quite in accord with some residual grasping function.

The remainder of the anterior tarsus and of its articulations with the metatarsal bases (Fig. 8) is essentially conservative and resembles particularly *Pan troglodytes*. The form of the cuboid lacks the human apomorphic features and is arched dorsally as in *Pan* and *Gorilla* – no lateral longitudinal arch is therefore present. The lateral cuneiform similarly is like that of the African apes and lacks the human apomorphic features. The distal articulations between the intermediate and lateral cuneiforms and cuboid also are present as in apes and not relinquished as in man to encroaching interosseous ligaments. The bases of the medial four metatarsals of OH8 also show little of the angulation characteristic of man and the articulations between them are like the chimpanzee. The fifth metatarsal, however, is received into a dorsoventrally concave surface on the cuboid, unlike the situation in man where the cuboid surface is convex or sellar. This prompted speculation that the structure in OH8 was pathological, the result of arthritic changes (Day & Napier, 1964). Although in the African apes the cuboid usually articulates with the fifth metatarsal by a convex surface, examples are found where the cuboid bears a dorsoventral concavity strikingly like that of OH8 (e.g. *Pan troglodytes schweinfurthii* B.M. 1922-12-19-2 and *Gorilla gorilla* B.M. 1948-3-31-1). Taken overall, the forefoot, just like the hindfoot, lacks the remodelling towards the subtalar axis which is characteristic of *Homo sapiens*.

Not surprisingly, torsion of the fossil metatarsals (Fig. 2) is intermediate between that of apes and man. In OH8 the first metatarsal seems to show a direction and degree of torsion comparable to that of *Pan* and possibly even less than that of *Gorilla*; this is logically correlated with its incompletely adducted position and presumed retention of some residual grasping capability. Thus the direction of torsion is the same in *Homo sapiens*, *Pan*, *Gorilla* and OH8; in *Homo sapiens*, however, it is more accentuated than in the other three. The remaining metatarsals, or at least the second and third, appear to have a direction and degree of torsion comparable to that of man, in contrast to the ape condition. The extent of damage to the fourth and fifth metatarsals makes it impossible to estimate their degree of torsion, and this is just where it would have been most informative.

Estimates of the talar neck torsion angle, measured of course according to the traditional method, have suggested that it is within the range of subhuman Primates (Lisowski, 1967) or even similar to that of man (Day & Wood, 1968). When the lamina pedis is viewed, however, it is apparent that the orientation of the navicular (which must determine the true orientation of the talar head in the foot) differs little between OH8, apes and man. When the OH8 talus is orientated on its basal surface (the standard basal talar plane) after reconstruction of the broken posterior talocalcaneal surface, it is apparent that the talar neck angle then differs little from apes or man (Fig. 3).

The first description of the OH8 foot was by Day & Napier (1964). They concluded that the principal affinities of the foot were with *Homo sapiens* noting that "this is particularly apparent in the anatomy of the metatarsal bones". They were considerably influenced by the apparent absence of hallucial divergence and by the robusticity formula of the metatarsal bones which, with one exception, shows a similarity to modern man rather than to the African apes; this difference, they suggested, might be an individual variation or an indication that the human pattern of weight distribution had not been fully evolved. Archibald, Lovejoy & Heiple (1972) did, in fact, show that variants, including that found in the OH8 foot, occur in human populations. Putting undue emphasis on the preponderant robusticity of metatarsals four and five as an indicator of advanced bipedal capability, however, requires caution, for the specimen of *Gorilla gorilla* (B.M. 1978–1226) illustrated in Figure 1B shows just that same feature with a particularly strong and buttressed fifth metatarsal. The overall conclusion reached by Day & Napier (1964), however, was that the foot was adapted to the upright stance and a fully bipedal gait. It is noteworthy that conservative arboreal features of the tarsus stressed in this paper escaped comment.

In contrast with these findings emphasizing the apparent human aspect of the foot, Lisowski (1967) noted that the talar neck angle of the OH8 foot fell within the range of subhuman primates, including the African apes and *Proconsul*, and was markedly greater than in *Homo sapiens.*

Day & Wood (1968) also studied a number of angles and indices of the OH8 talus which were believed to be significantly related to its functional morphology. They again noted the ape-like talar neck angle. They found this feature rather perplexing since in the fossil foot (of their reconstruction) the hallux was fully adducted, yet a high neck angle has been commonly considered to be correlated with a divergent hallux. They sought a solution to this problem by suggesting that compensation was achieved in the fossil by an altered orientation of head upon neck of the talus. As has been noted above, there is really no conflict; the talar neck angle is an expression of the orientation of the subtalar axis and is not causally associated with the degree of divergence of the hallux. These authors also found that the talar neck torsion angle was of similar extent to that found in man (cf. Lisowski, 1967). These authors then used these and other talar parameters in a multivariate statistical study which purported to reveal that the fossil talus was intermediate in form between that of bipedal man and the African apes. This study has been subject to the same methodological criticisms by Oxnard (1972) as that by the same authors on the *Proconsul* tali. Oxnard (1972) re-interpreted the same data as showing that the OH8 talus was uniquely different from both the African apes on the one hand and modern man on the other, but was close to the *Proconsul* tali; yet again Lisowski *et al.* (1974) claimed to show that the OH8 talus (with the *Proconsul* tali) was closest in form to the orangutan. The strictures applying to uncritical acceptance of this view are mentioned above in the discussion on multivariate studies on the *Proconsul* tali. Wood (1974) in a reappraisal of the OH8 talus cautiously inclined to the view that it should be attributed to the genus *Australopithecus*, thus further down-grading the assumption that it had specifically hominine affinities. The culmination of this reaction has been reviewed by Oxnard (1975) with the suggestion that the australopithecines (including OH8) were at least partially arboreal primates retaining efficient climbing capabilities associated with a bipedal capacity probably of a type no longer seen. This is reflected in some morphological resemblances (the result of functional parallels) to the orangutan. This view has recently been attacked (Howell, Washburn & Ciochon, 1978) because of the implication that some genetic affinity with *Pongo* was involved; nothing of the kind was suggested and the ample evidence of molecular biology for genetic affinity of man with African apes remains unchallenged.

Thus multivariate statistical studies have generated a mounting wave of scepticism against the view that the Olduvai foot was essentially human. Yet it is inherent in the technique that it is virtually impossible to unravel the causal morphological factors.

The present study has, it is hoped, gone some way towards showing in readily understandable terms of functional anatomy, that the OH8 foot retained to a considerable extent the essential morphology seen in extant apes, and its closest affinities are clearly with the African apes. Its main distinction is seen in the remodelling of the medial cuneiform with a consequent diminution in divergence of the hallux. There can be little doubt that this is a specialization associated with bipedal locomotion, but clearly the gait must have lacked those finely tuned functional qualities found in modern man, as hinted at the outset by Day & Napier (1964).

It is clear that the OH8 foot lacked the re-orientation of the subtalar axis which is characteristic of man and which apparently plays a key role in human locomotion by deviating the centre of gravity first to the support side and then the back towards the mid-line. In fact, the axis is aligned essentially as in *Pan*. Important data derived by cineradiographic analysis (Jenkins, 1972) is available for chimpanzee bipedalism and this may give some insight into the workings of the OH8 hindlimb. In the chimpanzee weight is transferred to the support side by a considerable pelvic sway and tilt – the pelvis on the side of the swing phase is elevated, whereas in humans it is depressed. It seems reasonable to assume that some similar device operated in OH8.

It is clear that the OH8 foot cannot be considered to belong to the genus *Homo*; it is reasonable, however, to attribute it to the genus *Australopithecus*. In that case, it would not be surprising if the remainder of the hindlimb was australopithecine in type. The wide flaring of the ilium and long femoral neck might then be associated with exaggerated pelvic tilt necessitated by the lack of the pedal modifications characteristic of *Homo sapiens*. The high femoral bicondylar angle might similarly represent a solution to the problem of tilting body weight to the supported side. Taken overall, the OH8 foot might represent a transitional stage, still perhaps with some arboreal capability, in the evolution of an ape foot towards one perfected for terrestrial bipedal locomotion. Alternatively it might represent an abortive evolutionary experiment, perhaps one of a number, in the attainment of this goal.

SUMMARY

The fossil record supports the conclusions derived from the study of extant species that the Primates evolved a unique suite of characters in the articulations of the foot.

The tarsal bones of African Miocene apes show specializations characteristic of hominoid evolution and provide reasonable precursors for the morphology of *Pan*, *Gorilla* and even *Pongo*.

The OH8 foot is essentially ape-like in its major features, with many close resemblances to *Pan*. Although fairly clearly from a bipedal primate, it lacked important functional specializations found in the human foot.

I would like to express my thanks to the staff of the British Museum (Natural History), and particularly to Dr Peter Andrews, for allowing access to the material in their care, and also to Mr Richard Leakey, Director of the National Museum of Kenya, for permitting examination of the original fossil foot bones of Olduvai Hominid 8.

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