

ARBOREAL AND TERRESTRIAL TRAITS AS REVEALED BY THE PRIMATE ANKLE JOINT*

by

P. Y. SONDAAR** & A.A.E. VAN DER GEER***

I. INTRODUCTION

Among the recently discovered postcranial material of *Paradolichopithecus arvernensis* (VAN DER GEER & SONDAAR, this volume) a talus (PO 157) and a distal tibia (PO 228) belonging to the same individual are recognized, which makes comparisons regarding functional morphology possible. The talus has an intermediate position in transferring body weight, and together with the other ankle joint elements it informs us about the posture of foot and lower leg during locomotion and in rest position. The morphology of the ankle joint is crucial to judge whether it was capable of adjusting to and withstanding the stresses of various orientations as in arboreal species or was adapted to more nearly level orientations as in terrestrial species (SZALAY & DECKER, 1974). The ankle joint *sensu lato* consists of two parts, proximal the talocrural joint and distal the subtalar plus talo-calcaneonavicular joint. The first, or proximal talar joint, is a hinge joint, or ginglymus, with only plantar and dorsal flexion. The second or distal talar joint, though bipartite, functions as a single joint, and allows not only flexion but also rotational movements.

A general remark on methodology should be made. Observed differences may result in part from each having taken a different evolutionary pathway to a similar adaptation. For example, there appear to exist at least two different structural patterns behind the mode of "vertical clinging and leaping" (OXNARD, 1974).

One of the reasons behind a different solution is that the morphological expression of one particular set of adaptations may constrain the form of others (KAY & COVERT, 1984), resulting in alternative solutions for the same problem. Therefore, comparison with non-related species might obscure similarities in actual locomotion. Evidence from related species should weigh more, although it is often on the ground of observed similarities that taxonomic relations are based.

These considerations are important when we want to compare the morphology of the

* ενδρόβια και εδαφόβια χαρακτηριστικά όπως αποκαλύπτονται από τις ποδοκνημικές διαρθρώσεις των Πρωτευόντων.

** Zoologisch Museum Amsterdam, Faculteit Natuurwetenschappen, Universiteit van Amsterdam, Postbus 94766, 1090 GT Amsterdam, The Netherlands; Research Associate, Department of Mammology, American Museum of Natural History, Central Park West at 79th Street, New York, NY, USA.

*** Instituut Kern, Nonnensteeg 1-3, Universiteit Leiden, PO Box 9515, 2300 Ra Leiden, The Netherlands.

cercopithecoids with that of the hominoids, as the cercopithecoids evolved in tropical to sub-tropical savanna while the hominoids had their origins in tropical forest environments (ANDREWS & AIELLO, 1984). It may therefore be that in retaining the primitive habitat preference, the hominoids may have also retained primitive aspects of locomotion, where by the same criteria cercopithecoids may be derived (ANDREWS & AIELLO, 1984; ROSE, 1988; STRASSER, 1988). This difference in ancestral characteristics will certainly have influenced the adaptational possibilities and ranges of both groups. It sets the differences and the similarities in a broader context. We cannot expect to find exactly the same morphologies in the two groups even if the actual locomotion was identical or very similar.

In this contribution two related questions are discussed: Is it possible to discriminate between arboreal and terrestrial primates on the basis of the ankle joint? And if so, is it possible to specify the type of locomotion more precisely?

II. MATERIAL

The Vatera *Paradolichopithecus arvernensis* talus PO 157 and tibia PO 228 are compared with the following extant Papionini: *Papio hamadryas* (2 specimens from American Museum of Natural History, Department of Mammology, New York (hence AMNH), and 3 specimens from Nationaal Natuurhistorisch Museum Naturalis, Leiden, The Netherlands (hence: NNM), *Papio sphinx* (9 AMNH, 4 NNM), *P. leucophaeus* (4 AMNH), *P. tesseralus* (1 AMNH), *P. ursinus* (4 AMNH), *P. anubis* (2 AMNH), *P. cynocephalus* (1 AMNH), *Macaca* (8 NNM, 12 AMNH) and *Theropithecus gelada* (1 AMNH, 2 NNM). As addition, the following hominoids are taken into comparison: the Pliocene Hadar *Australopithecus afarensis* “Lucy” (A.L. 288-lar right distal tibia and A.L. 288-las right talus, both casts from AMNH and NNM), and the extant *Pan troglodytes* (chimpanzee; 4 NNM, 1 Natuurmuseum Rotterdam). The talus and tibia of A.L. 288-1 have been proven to belong to one individual (AIELLO *et al.*, 1988). Detailed anatomical descriptions of these species are presented elsewhere and are not repeated here. For *Paradolichopithecus arvernensis*, see VAN DER GEER & SONDAAR (this volume) and SZALAY & DELSON (1979), for *Australopithecus afarensis* A.L. 288-1, see JOHANSON *et al.* (1982) and LOVEJOY *et al.* (1982), for the extant anthropoids, see the relevant handbooks on primate anatomy. A final remark, as the curve of the talar head does not differ significantly between the compared species, the talo-calcaneonavicular joint is not paid attention to in this paper.

III. SUBTALAR JOINT

On the plantar side of the talus three different suspensory facets for articulation with the calcaneum can be discerned (fig. 1). The medial facet is flat in the compared species, except for *Pan* where it is clearly convex, and expanding over almost the total neck surface. In both *Australopithecus* and *Paradolichopithecus*, and to a lesser degree in the baboons, the medial facet ends with a clear ridge or border where it touches the talar head, whereas it merges gradually with the head in the mandrill. The large medial facet in *Pan* permits a considerable range of medial rotation of the calcaneum on the plantar surface of the talar neck, resulting in a high possible degree of lateral and medial flexion (or inversion and eversion of the foot in LE GROS CLARK & LEAKEY (1951). The functional implication of the aspects of the

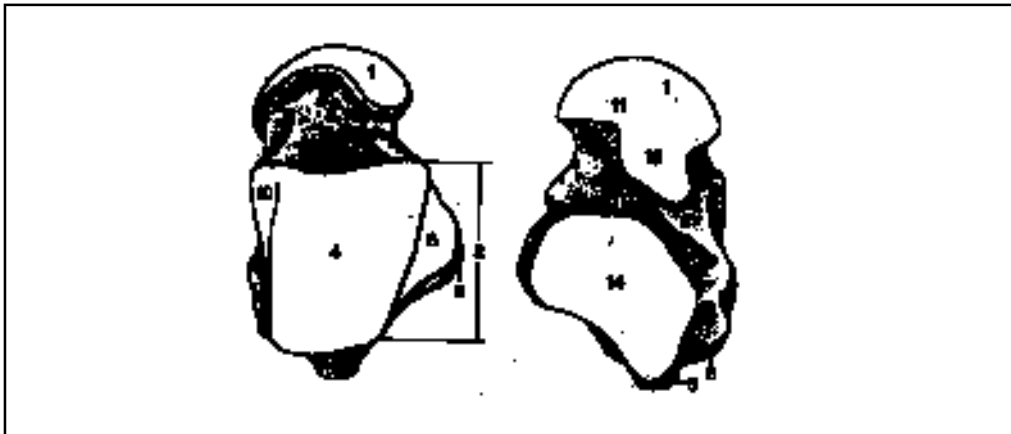


Fig. 1. General morphology of the primate talus. Right talus, left: dorsal view, right: plantar view. 1, caput; 2, corpus; 3, collum; 4, trochlea; 5, tuberculum laterale; 6, tuberculum mediale; 7, sulcus for long toe flexor; 8, facies malleolaris lateralis; 9, processus lateralis; 10, facies malleolaris medialis; 11, facies articularis calcanea anterior; 12, –media; 13, sulcus tali; 14, facies articularis calcanea posterior. Note that 11 is alternatively called distal facet, and 14 proximal facet. (After PLATZER, 1986).

contact area of the medial facet with the head might be that in the mandrill both the calcaneum and the navicular bone have a larger mobility range, as the facets unite. A possible spectrum might therefore consist of lateral and medial flexion, and dorsal and plantar flexion at the lower tarsal joint, typical for arboreal species. In the others, the facets are separated, thus confining movement of the navicular to lateral and medial. Thus, as terrestriality can be inferred from the aspect of the medial facet, it is possible to say that *Paradolichopithecus* was terrestrial.

Another feature is the shape and the degree of concavity of the posterior, or proximal, suspensory facet (fig. 2). This facet is equable parabolic in shape, shallow and compressed midway in African hominids, while it is more or less square and tightly curved in Papionini (see also STRASSER, 1988). Within the second group, the baboon and *Paradolichopithecus* have a more shallow shape; the latter even more than the first. This facet also extends further in proximo-distal direction in *Paradolichopithecus* and *Australopithecus* than in the baboon or the mandrill. Thus, it appears that within each taxon the terrestrial species have a more shallow posterior facet than the arboreal species. *Paradolichopithecus* is therefore certainly terrestrial.

IV. TALOCRURAL JOINT

A minor factor that contributes to the functionality of the ankle joint is the degree of movement in the proximal talar joint, or the angle formed by the tibia axis in maximal plantar flexion and maximal dorsiflexion (fig. 3). This movement is restricted in *Australopithecus* and *Paradolichopithecus*, compared to both *Pan* and *Papio*. Both the *Pan* and *Papio* ankle have a difference between maximal dorsiflexion and maximal plantar flexion of about 80 degrees, whereas the former reach only about respectively 55 and 65 degrees (*cf.* data of

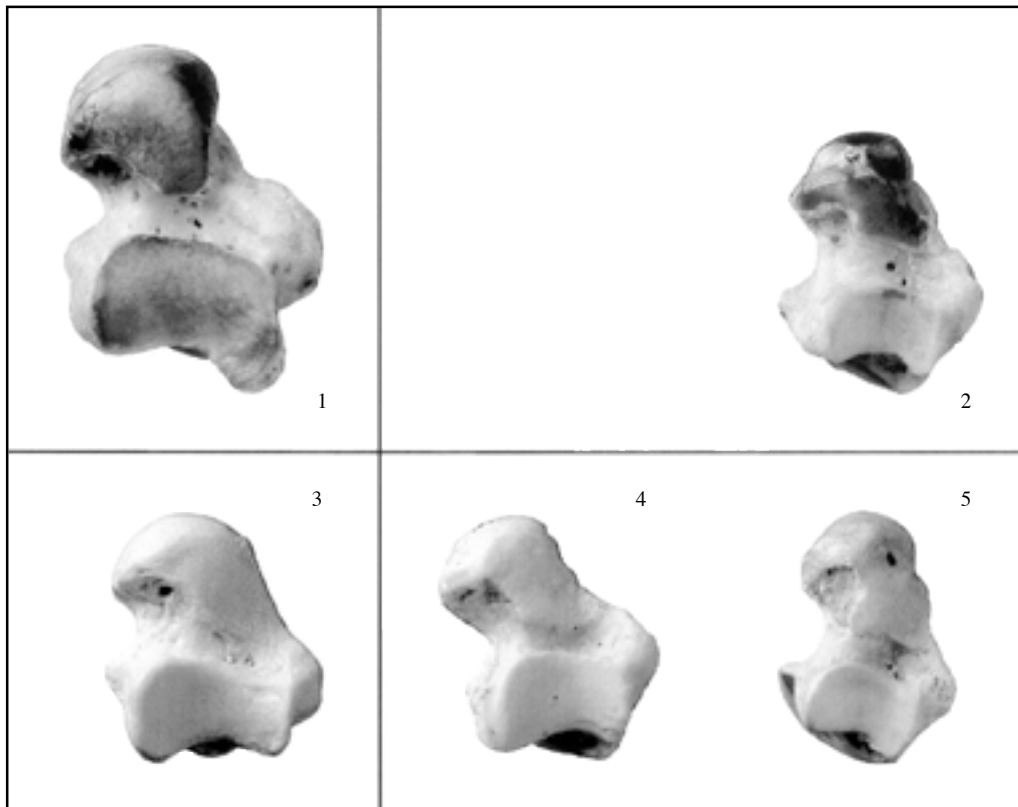


Fig. 2. Schematic representation of right tali, plantar view, distal bottom. 1, chimpanzee; 2, mandrill, 3, *Australopithecus*; 4, *Paradolichopithecus*. 5, baboon. Upper row: forest; Lower row: savanna. Note enlarged posterior facet in *Paradolichopithecus*, and pronounced curvature in the mandrill.

LATIMER *et al.*, 1987; they reach higher values for all species, most likely due to different interpretation of end of articulation area. Their data for *Pan* cannot be repeated in any way; in our opinion, *Pan* is much more mobile than *Homo* and *Gorilla*, what is confirmed in their text ($P < 0.01$).

Gorilla has a low angle, due to its high body weight; *Homo* due to its different locomotion. The restriction in flexion range is found mainly in the plantar flexion, the part of flexion that is needed in the take-off phase. The overall impression then is that the ankle of *Paradolichopithecus* is slightly stiffer than that of *Papio*, and the same is valid for *Australopithecus* if compared to *Pan*. This is, however, only a preliminary observation, as relative body size is a primary determinant of flexion range, and our specimens all have different sizes.

Judged from the combined movement of the tibia and talus, the foot is slightly turned inward in maximal plantar flexion in *Papio*, due to the ball-shaped form of the medial malleolus of the tibia that gives direction to the talar movement. ROSE (1994) notes that this stabilizing feature is present in cercopithecids and hylobatids. During dorsiflexion, the tibial

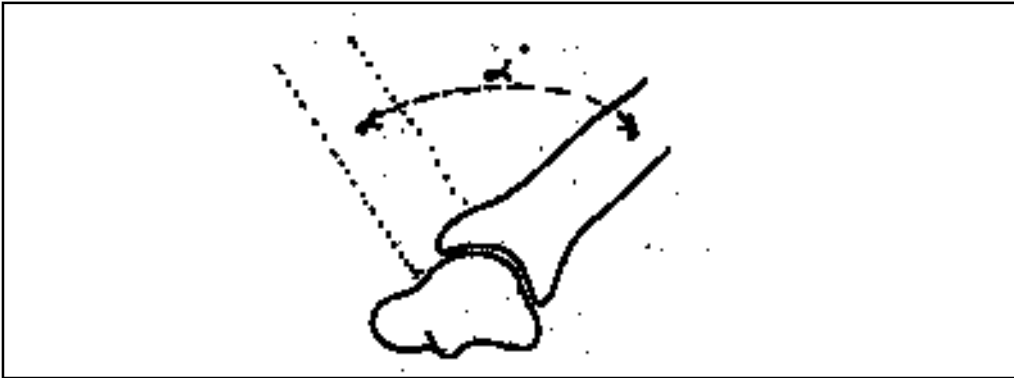


Fig. 3. Degree of movement (angle α) between maximal plantar flexion and maximal dorsal flexion in the tibiotalar joint.

malleolus articulates with the medial side of the talus, and turns the talus medially, or inward. This rotation, or mediolateral movement, is necessary for climbing, but incompatible with efficient cursorial bipedalism (SARMIENTO, 1985, 1998).

In *Paradolichopithecus* and *Australopithecus* on the contrary, no such rotation is observed, which was to be expected as the corresponding malleolus is flat. In addition, in species with a ball-shaped medial malleolus, we see that this malleolus remains within the cup-shaped talar depression. The mandrill and the chimpanzee are good examples, while the baboon shows a minimal malleolar movement compared with its maximal dorsiflexed position. In species with a flat medial malleolus on the other hand, we see that the malleolus leaves its fixed position and translates over a considerable distance on the medial side of the talus during plantar flexion. As a result, the axis of rotation is fixed in the chimpanzee, the mandrill and less so in the baboon, but transferring in *Paradolichopithecus* and *Australopithecus*. The malleolar movement leaves a trace in the form of a smooth and even articulation area on the talus, but unfortunately this is not always easy to judge in fossil specimens. In the species with an only rotating malleolus a ridge on the articulation area can be seen, indicating the end of the malleolar translation.

The form of the trochlea tali informs about the rest position (fig. 4). The wider the distal end is in relation to the proximal end, or the more wedged it is (fig. 5), the more bend the ankle joint is in rest position, as this is the situation with the highest load, thus necessitating the highest stability which is acquired by a maximal contact area (see for biomechanical explanation, MACCONAILL, 1950). In *Papio*, the rest position is the maximal dorsiflexed situation. In *Australopithecus* and *Paradolichopithecus*, weight transfer is likely to occur slightly more in the direction of the heel, towards the middle of the trochlea tali, as here the trochlea is not wedge-shaped but parallel (table 1). This progressive modification makes a more upright position for the tibia in *Paradolichopithecus* highly likely, similar to *Australopithecus*. The upright position for the tibia is linked to some form of bipedal gait in *Australopithecus*, and it is therefore tempting to assume a similar gait for *Paradolichopithecus*. Such a shape gives stability in all phases of flexion, whereas a wedge-shaped trochlea loses stability during maximal plantar flexion, enabling lateral movements (SHIPMAN *et al.*, 1985). Unsteadiness in plantiflexion is unlikely in both *Australopithecus*

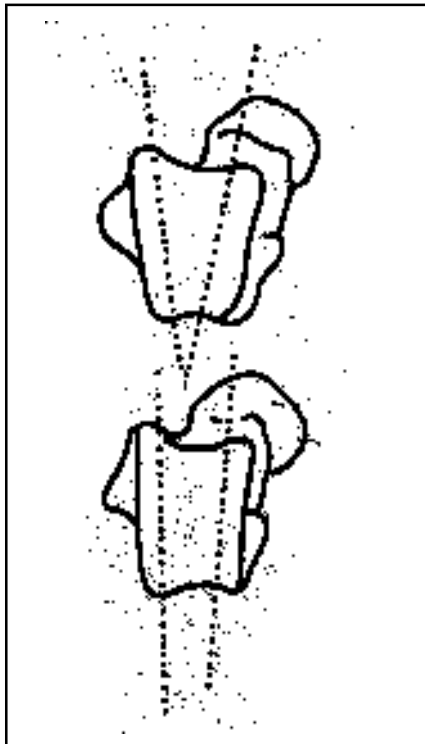


Fig. 4. Schematic representation of the trochlea tali, dorsal view.
Top: wedged trochlea.
Bottom: parallel trochlea.

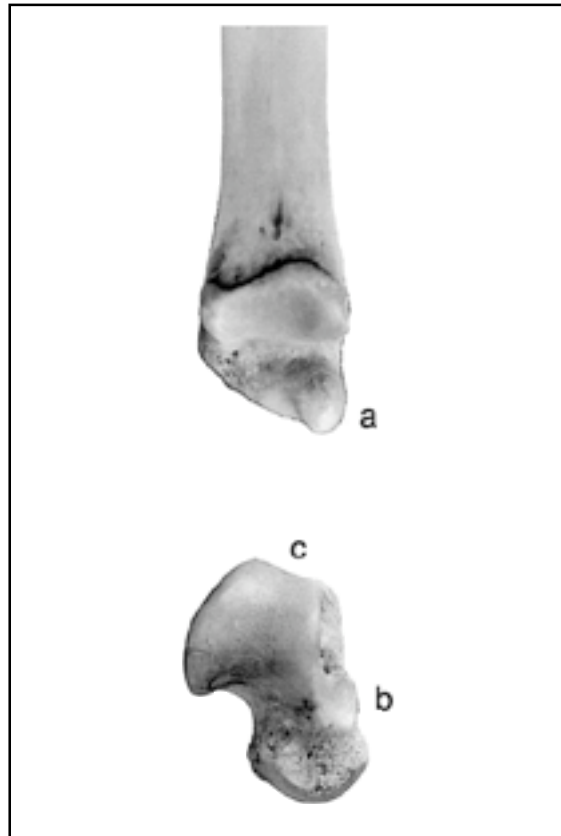


Fig. 5. Reference points to approximate degree of wedgedness; dorsal view. The higher the index (distal width divided by proximal width), the more wedged the trochlea is. Upper horizontal dashed line: DT prox (proximal width). Lower horizontal dashed line: DT dist (distal width). Vertical dashed line: tangent of straight running part of lateral ridge. Measurements are taken at cross-points.

and *Paradolichopithecus*, whereas it is in the other compared species. In contrast to *Australopithecus*, the trochlea of *Paradolichopithecus* is asymmetrical, with the lateral ridge higher than the medial, as expected in cercopithecoids (STRASSER, 1988), thus keeping its in essence cercopithecoid morphology.

CONCLUSION

The cercopithecoids and African hominoids differ in general architecture of the tarsal joint, but in function they can be compared. The main differences in the talus are as follows: Hominoids are characterized by almost symmetrical trochlear ridges and a profound groove

Table 1

specimen	number	DT prox	DT dist	index	mean
<i>Paradolichopithecus</i>	1	15.8	17.2	1.1	1.1
<i>Papio hamadryas</i>	2				1.5
NNM 24581		12.1	18.4	1.5	
AMNH 238099		13.0	18.8	1.5	
<i>Papio anubis</i>	2				1.3
AMNH 187369		12.2	15.3	1.3	
AMNH 51380		15.3	19.2	1.3	
<i>Papio ursinus</i>	5				1.3
AMNH 70372		13.2	18.3	1.4	
AMNH 216251		15.9	18.7	1.2	
AMNH 216250		11.9	14.2	1.2	
AMNH 216247		10.9	13.7	1.3	
AMNH 216249		15.7	18.3	1.2	
<i>Papio sphinx</i>	1				1.4
NNM n.n.		14.2	19.5	1.4	
<i>Papio</i> total					1.3
<i>Theropithecus</i>	2				1.2
NNM 11341		13.2	15.8	1.2	
NNM n.n.		12.2	13.2	1.1	
<i>Australopithecus</i>	1	16.4	19.2	1.2	1.2
<i>Pan troglodytes</i>	4	21.4	16.6		1.3
<i>Macaca</i>		5	4.3	5.7	

Table 1. Width of the trochlea tali in mm. DT prox (proximal width) is the width at the point where the lateral ridge bends inwards; DT dist (distal width) is maximal width at the distal end of the trochlea (see fig. 5). AMNH 216247 is an exceptional baboon, as the lateral flap is similar to that seen in *Paradolichopithecus*. However, the talar head projects clearly further, and stands at a more pronounced angle. *Australopithecus* is *A. afarensis* A. L. 288-1 (“Lucy”), and *Paradolichopithecus* is *P. arvernensis* from Vatera. *Macaca* species, all from NNM, are *M. fuscata*, *M. maura*, *M. nemestrina*, *M. schreata*, *M. nigra*. *Pan troglodytes* data (NNM) are lumped together.

for the tendon of the flexor hallucis longus (large toe flexor), whereas cercopithecoids are recognized by a pronounced lateral trochlear ridge and a but poorly developed tendon groove. Notwithstanding these obvious differences, parallels in function are obvious. The general systems are the same, and include a restriction to dorsal and plantar flexion in the proximal talar joint (tibia-fibula-talus), and dorsal, plantar, medial and lateral flexion plus rotation in the distal talar joint (talus-calcaneum-naviculare). Rotation and flexion in four directions is

therefore possible between calcaneum and talus, while only sagittal flexion is possible between the tibia-fibula and talus.

The maximal movement in the distal talar joint is more or less comparable in the species studied. Only the chimpanzee differs clearly, as here is a wide range of movements possibly in all directions. From this point of view *Pan* can be considered an extreme arboreal species, and though the overall shape of the talus of *Australopithecus* is similar to that of *Pan*, its plantar surface does not approach that of the chimpanzee at all, but is more comparable to that of the baboons. Extreme arboreality can be inferred from the shape of the plantar articular areas in combination with the shape of the talar head, but moderate arboreality cannot clearly be distinguished from terrestriality.

A crucial difference is seen in the shape and function of the medial malleolus of the distal tibia. In the arboreal and in the moderate terrestrial species it is ball-shaped, and remains in the corresponding cup-shaped depression of the medial side of the talus during the total range of flexion. The maximal plantar flexion involves a certain degree of medial rotation. In the extremely terrestrial species the tibial malleolus is flat, and moves over the articular surface on the medial side of the talus during flexion. The cup-shaped depression on the talus is hardly visible in these species, and does not function anymore as fixed basis of the talo-malleolar joint. The movement of this joint now has a rotator and a translator component, whereas it is strictly rotatory in the arboreal and moderate terrestrial species. Medial rotation of the talar head during plantar flexion cannot be discerned in the extremely terrestrial species. The tibial medial malleolus and its corresponding talar part provide a clear parallel between the papionin *Paradolichopithecus* and the hominid *Australopithecus*, when compared with their counterparts *Papio* and *Pan* respectively.

Another difference is seen in the talar trochlea. It is wedge-shaped, tapering to proximal in *Papio* and *Pan*, and parallel in *Paradolichopithecus* and in *Australopithecus*. This difference is slightly obscured by the fact that the trochlea is in general much more pronounced and asymmetrical in the cercopithecoids, especially due to the well-developed lateral ridge, than in hominoids, where both ridges are more or less equal. However, even with this general architectural difference in mind, it is clear that *Paradolichopithecus* provides a perfect parallel with *Australopithecus*.

The functional implications of these differences inform us about the possibilities and restrictions of locomotion and posture. Firstly, restriction of flexion in the proximal talar joint stiffens the joint in a way, indicating a decreased ability to move on extremely uneven substrates like trees and an increased ability to sustain stronger forces or higher body weight on the hindlimbs. At the same time it tells us that the rest position cannot differ that much from the maximal plantar and dorsiflexion as in species in which the flexion range is extended. This is indicative for a more vertical position of the tibia in rest as well as during locomotion. Secondly, the translatory component yields a more evenly distribution of vertical forces over the medial part of the talus, which makes it possible to increase force or body weight on the hindlimbs. Thirdly, a parallel trochlea tali distributes body weight more evenly, and yields more stability in plantiflexion, and thus facilitates keeping equilibrium in maximal plantiflexion, which is the upright position. The stability is further increased by the extended suspensory flap on the lateral side for the fibular malleolus. In the upright position, the talus is firmly hold in the malleolar fork.

In short, it is possible to discriminate between an arboreal and terrestrial way of life of primates on the basis of the ankle joint. There are differences in morphology between apes and monkeys, yet this does not hamper the conclusion. In both groups the underlying systems are the same: stability and only restricted flexion in the proximal talar joint, but flexion in four directions and rotation with less stability in the distal talar joint. If we take only the

functional interpretation, the *Paradolichopithecus* ankle resembles more that of *Australopithecus* than that of the mandrill or the baboon. In conclusion, the Eurasian cercopithecoid *Paradolichopithecus* had a terrestrial way of locomotion, and furthermore, it paralleled the way of locomotion of the African hominoid *Australopithecus*.

This leads us to the second question. Is it possible to analyze on the basis of the talus and distal tibia if *Paradolichopithecus* was bipedal or quadrupedal? We found that in every functionally significant feature examined, the *Paradolichopithecus* ankle joint is similar to that of the Hadar hominid A.L. 288-1 (“Lucy”). From these features it can be inferred that *Paradolichopithecus* walked like “Lucy”, or displayed at least a high percentage of australopithecine positional behavior in its daily locomotory repertoire. This then would on its turn mean that *Paradolichopithecus*, too, was more a specialist in endurance and covering long distances than its closest relative the baboon, who is more a sprinter. Such a specialization is promoted in an open environment, where distances between sources of food are large and seasonality is the norm. For parallels with hominid evolution, see DE VOS *et al.* (1998) and DE VOS (this volume). Seasonality indeed is indicated by the insectivore fauna of the Eastern Mediterranean (REUMER *et al.*, this volume), whereas the open environment is indicated by the presence of three antelopes, the stenorhinid horse, and a giraffid. If we take the ecology of the living baboon into consideration, we see that a population remains in a restricted area throughout the year (GRZIMEK, 1968), ranging from approximately 400 hectares for forest baboons (daily movements 1.5 km) to 4000 hectares (daily movements 5 km) for savanna baboons (KINGDOM, 1971), clearly determined by the availability of sufficient food at their disposition. The Pliocene Vatera environment, however, differed substantially from the biotope of the living baboon, compelling *Paradolichopithecus* to enlarge its territory in search for food, and possibly to migrate.

SUMMARY

The tarsal bone are important in the study of primate locomotion and posture, as it is here that the body weight is transferred to the ground in standing, walking and running, each with its particular demands.

Though there are systematic differences in general morphology between cercopithecoids and African hominoids, for example the shape of the talar trochlea and the groove for the large toe flexor, there are clear parallels in function. In the proximal talar joint, movement is restricted to dorsal and plantar flexion, whereas in the distal talar joint also rotation and medio-lateral movement are possible. It appears that especially the distal talar joint is useful to discriminate between arboreal and terrestrial ways of life, for example, rotation is typical for arboreal primates. The proximal talar joint is useful to specify the type of terrestrial locomotion. The degree of possible flexion differs between species, furthermore, in a number of species there is no medial rotation during maximal plantar flexion at all, whereas in most species at least a minimal degree occurs. In the species without medial rotation, such as *Paradolichopithecus*, the ridges of the trochlea tali tend to run more parallel than in other terrestrial species, like *Papio*, resulting in minimal trochlear wedging.

A functional analysis of the newly discovered ankle joint of the Late Pliocene Old World monkey *Paradolichopithecus arvernensis* leads to the conclusion that this monkey not only had a terrestrial way of life, but has also a gait similar to that of *Australopithecus afarensis*, revealing thus a parallel evolution between cercopithecoids and hominoids in this respect.

The evolution of the australopithecine-like locomotion in *Paradolichopithecus* leads to

the conclusion that the hominine pattern is not unique. The evolution of highly terrestrial locomotion in the Old World monkey *Paradolichopithecus* was, just as it was in *Australopithecus*, essential to enter an open plain to cover large distances in search for food. *Paradolichopithecus* shares its type of locomotion with *Australopithecus*, who is considered to have displayed a substantial degree of bipedalism in its locomotory repertoire.

ΠΕΡΙΛΗΨΗ

Τα ταρσικά οστά είναι σημαντικά για τη μελέτη του τρόπου βάδισης και στάσης των πρωτευόντων, καθώς μέσω αυτών το βάρος του σώματος μεταφέρεται στο έδαφος κατά την στάση, βάδιση και τρέξιμο. Παρόλο που υπάρχουν συστηματικές διαφορές στη γενική μορφολογία μεταξύ των Cercopithecoidea και των αφρικανικών Hominoidea, για παράδειγμα το σχήμα της τροχιλίας του αστραγάλου και η αύλακα για τον τένοντα του μακρού καμπήρα του μεγάλου δακτύλου, υπάρχουν σαφείς παραλληλίες στη λειτουργία. Στην εγγύς διάρθρωση του αστραγάλου, η κίνηση περιορίζεται στη ραχιαία και πελματιαία κάμψη, ενώ στην απώτερη διάρθρωση του αστραγάλου είναι επίσης δυνατή η περιστροφή και η ανάσπαση του έξω και έσω χείλους. Φαίνεται ότι ειδικά η απώτερη διάρθρωση είναι χρήσιμη για την διάκριση μεταξύ δενδρόβιας και εδαφόβιας διαβίωσης, για παράδειγμα, η περιστροφή είναι τυπική των δενδρόβιων πρωτευόντων. Ο βαθμός της δυνατής κάμψης διαφέρει μεταξύ των ειδών, επιπλέον, σε έναν αριθμό ειδών δεν υπάρχει προς τα έσω περιστροφή κατά την μέγιστη πελματιαία κάμψη, ενώ στα περισσότερα είδη παρατηρείται τουλάχιστον μια ελάχιστη τέτοια περιστροφή. Στα είδη χωρίς προς τα έσω περιστροφή, όπως στο *Paradolichopithecus*, τα χείλη της τροχιλίας του αστραγάλου τείνουν να είναι περισσότερο παράλληλα μεταξύ τους από ό,τι στα άλλα εδαφόβια είδη, όπως το *Papio*, έχοντας σαν αποτέλεσμα την ελάχιστη απόκλιση των χειλέων της τροχιλίας.

Η λειτουργική ανάλυση της πρόσφατα ευρεθείσας ποδοκνημικής διάρθρωσης του άνω πλειοκαινικού πιθήκου του Παλαιού Κόσμου *Paradolichopithecus* μας οδηγεί στο συμπέρασμα ότι αυτό το είδος δεν είχε απλώς εδαφόβιο τρόπο βάδισης, αλλά και στο ότι είχε βηματισμό παρόμοιο με εκείνον του *Australopithecus afarensis*, αποκαλύπτοντας έτσι μία παράλληλη εξέλιξη σε αυτό το χαρακτηριστικό μεταξύ των Cercopithecoidea και των Hominoidea.

Η εξέλιξη ενός τρόπου βάδισης παρόμοιου με του αυστραλοπίθηκου από τον *Paradolichopithecus* οδηγεί στο συμπέρασμα ότι πρότυπο των Hominiinae δεν είναι μοναδικό. Η εξέλιξη έντονα εδαφόβιου τρόπου βάδισης από το είδος του Παλαιού Κόσμου *Paradolichopithecus* ήταν, όπως και στην περίπτωση του *Australopithecus*, βασική για την είσοδο στις ανοιχτές πεδιάδες και την κάλυψη μεγάλων αποστάσεων για την αναζήτηση τροφής. Ο *Paradolichopithecus* μοιράζεται τον μηχανισμό βάδισης του *Australopithecus*, ο οποίος θεωρείται ότι είχε αναπτύξει έναν ουσιώδη βαθμό διποδισμού στον τρόπο κίνησής του.

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REFERENCES

- AIELLO, L., WOOD, B. KEY, C. & C. WOOD (1998). Laser Scanning and Paleoanthropology, an example from Olduvai Gorge, Tanzania. In: STRASSER, E., FLEAGLE, J., ROSENBERGER, A. & H. McHENRY. Primate Locomotion, Recent Advances. *New York: Plenum Press*, pp. 223-234.
- ANDREWS, P. & L. AIELLO (1984). An evolutionary model for feeding and positional behaviour. In: CHIVERS, D.J., WOOD, B.A. & A. BILSBOROUGH (eds.). Food acquisition and processing in primates, *New York: Plenum Press*, pp. 429-466.
- DE VOS, J., SONDAAR, P.Y. & J.W.F. REUMER (1998). The evolution of hominid bipedalism. *Anthropologie* 36 (1-2): 5 -16.
- DE VOS, J. (this volume). Locomotion, brainsize and adaptive radiation of Hominids.
- GRZIMEK, B., (1968). Enzyklopädie des Tierreiches. Band XII (Säugetiere), 4: 1-626. Zürich: *Kindler Verlag*.
- JOHANSON, D.C., LOVEJOY, C.O., KIMBEL, W.H., WHITE, T. D., WARD, S.C., BUSH, M.E., LATIMER, B.M. & Y. COPPENS (1982). Morphology of the Pliocene partial hominid skeleton (A. L. 288-1) from the Hadar Formation, Ethiopia. *American Journal Physical Anthropology*, 57: 403-452.
- KAY, R.F. & H.H. COVERT (1984). Anatomy and behaviour of extinct primates. In: CHIVERS, D.J., WOOD, B.A. & A. BILSBOROUGH (eds.). Food acquisition and processing in primates, *New York: Plenum Press*, pp. 467-508.
- KINGDON, J. (1971). East African Mammals, An Atlas of Evolution in Africa, vol. I. London, New York: *Academic Press*.
- LATIMER, B., OHMAN, J.C. & C.O. LOVEJOY (1987). Talocrural Joint in African Hominoids: Implications for *Australopithecus afarensis*. *American Journal of Physical Anthropology*, 74 :155-175.
- LE GROS CLARK, W.E. & L.S.B. LEAKEY (1951). The Miocene Hominoidea of East Africa. *Fossil Mammals of Africa* no. 1. London: British Museum (Natural History).
- LOVEJOY, C.O., D.C. JOHANSON & Y. COPPENS (1982). Hominid lower limb bones recovered from the Hadar Formation: 1974-1977 collections. *American Journal of Physical Anthropology*, 57 : 679-700.
- MACCONAILL, M.A. (1950). The movement of bones and joints. The synovial fluid and its assistance. *Journal of Bone and Joint Surgery* 32b: 244-252.
- OXNARD, C. E., (1974). Primate Locomotor Classifications for Evaluating Fossils. *Proceedings from the Symposia of the 5th Congress of the International Primatological Society*, S.

- KONDO, KAWAI, M., EHARA, A. & S. KAWAMURA (eds). Nagoya, Japan, August 1974: 269-286.
- PLATZER, W. (1986). Bewegingsapparaat. In: KAHLE, W., LEONHARDT, H. & W. PLATZER (eds). *Sesam Atlas van de Anatomie. Baarn: Bosch & Keuning.*
- REUMER, J. W.F., DOUKAS, C.S. & K. VASSILIADOU (this volume). Plio-Pleistocene Insectivore Diversity in the Eastern Mediterranean and the Asian Summer Monsoon, a preliminary note.
- ROSE, M. D. (1988). Another look at the anthropoid elbow. *Journal of Human Evolution*, 17: 193-224.
- ROSE, M.D. (1994). Quadrupedalism in some Miocene catarrhines. *Journal of Human Evolution*, 26: 387-411.
- SARMIENTO, E. – E. (1985). The evidence for terrestrial quadrupedalism in the hominid lineage. *American Journal of Physical Anthropology*, 66 (2): 224-225.
- SARMIENTO, E. – E. (1988). Generalized Quadrupeds, Committed Bipedes, and the Shift to Open Habitats: An Evolutionary Model of Hominid Divergence. *American Museum Novitates*, 3250, 78 pp. New York.
- SHIPMAN, P., WALKER, A. & D. BICHELL (1985). The human skeleton. Cambridge: *Harvard University Press*, 332 pp.
- STRASSER, E. (1988). Pedal evidence for the origin and diversification of cercopithecoid clades. *Journal of Human Evolution*, 17: 225-245.
- SZALAY, F.S. & R. LEE DECKER (1974). Origins, Evolution, and Function of the Tarsus in Late Cretaceous Eutheria and Paleocene Primates. In F.A. JENKINS (ed.). *Primate Locomotion*, pp. 223-259.
- SZALAY, F.S. & E. DELSON (1979). Evolutionary history of the Primates. San Diego: *Academic Press*, 580 pp.
- VAN DER GEER, A.A.E. & P.Y. SONDAAR (this volume). The postcranial elements of *Paradolichopithecus arvernensis* (Primates, Cercopithecidae, Papionini) from Lesvos (Greece).