The unique Postcranial of the Old World Monkey
Paradolichopithecus: more similar to *Australopithecus* than to Baboons*

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ABSTRACT: This article deals with the unique postcranial of an Old World Plio-Pleistocene monkey (*Paradolichopithecus*) and its possible way of locomotion as far as this can be inferred from the present material. The postcranial material is described and compared with that of its living close relatives *Papio*, *Macaca*, and *Theropithecus*. As some unique features were found in *Paradolichopithecus*, the comparison was extended with *Australopithecus anamensis, A. afarensis* (AL 288-1) and *Pan troglodytes*. The studied postcranials of *Paradolichopithecus* comprise the recently found associated ankle joint and arm of Vatera (Greece) and the elbow joint of Valea (Roumania). It appeared that features with which *Australopithecus* differs from African apes, make also *Paradolichopithecus* differ from baboons. A parallel was found, which was unexpected in the light of the general morphological differences between monkeys and apes.

The morphological features that are unique for *Paradolichopithecus* amongst the monkeys are described for the talus, distal tibia and the humerus, and are as follows: The talus is discriminated by its almost parallel trochlea, the large flap-like, protruding fibular suspensory facet, and a slightly deeper facet for the spring ligament on the talar head. These features are suggestive for a baboon-like ankle joint with the body weight more evenly distributed over the talar trochlea, a greater proportion of the weight transfer through the lateral (fibular) side, and with approximate the same stability in maximal dorsiflexion as in maximal plantar flexion. In these aspects *Paradolichopithecus* resembles *Australopithecus*.

The distal tibia is discriminated by a more massive, square and blunt malleolus that lacks the typically pronounced ball-shaped area, a wider groove (*sulcus malleolaris*) for the tendon of the *M. tibialis posterior*, a more square cross-section, clear scars for the fibula, and a double tendon groove on the dorsal surface (either for a bifurcated tendon for the *M. flexorum tibialis posterior* or a pronounced groove for the long toe flexor), which follows the parasagittal plane. None of these features is unique, and they make *Paradolichopithecus* resemble *Australopithecus*, a trained Japanese macaque and to a lesser extent some other macaques. The combination indicates a maintainance of the close-packed situation from dorsiflexion to plantar flexion, an increased importance of the fibula in weight transfer, a stronger plantar flexion, and possibly a slightly abducted foot. The flat tibial malleolus in *Paradolichopithecus* and *Australopithecus*, compared to *Papio* and *Pan* respectively, in combination with the corresponding facet on the talus acts as a blocking mechanism, preventing further dorsiflexion rotation during maximal dorsiflexion. This makes this ankle unsuitable for climbing.

The humerus is discriminated by an increased articulation area on the head compared to *Papio*, a wide and deep groove for the biceps tendon, a gradually descending capitulum, and an oblique axis for flexion-extension through the elbow joint. During flexion, the ulna deviates from the parasagittal plane, and ends in a position medially to the humerus instead of parallel above it, due to the trochlear shape and axis. This unique feature yields a significant increased mobility. Considering the unique features of the ankle and elbow of *Paradolichopithecus*, it may be expected that its locomotion differed from that of baboons. Main differences are the increased fibular component, the increased stability in plantar flexion, a more evenly distribution of stability during locomotion, and an equal medio-lateral stability in maximal plantiflexion and in maximal dorsiflexion. In our view, such a type of locomotion finds a parallel in *Australopithecus* and in trained Japanese macaques. The latter appear to develop significant modifications during training, especially in the hind limb, to satisfy the functional requirements for increased habitual bipedalism. Amongst others, the malleolus of the tibia has been remodeled under the influence of the greater stress and became less cusp-shaped, and the talar malleolar facet correspondingly more planar. The varus knee in the trained macaque further requires an increased fibular compound. This may have its parallel in *Paradolichopithecus* and *Australopithecus*, in whom we also find an increased fibular component. It should be stressed, however, that the kind of bipedalism of the trained macaque differs essentially from the striding gait bipedalism with erect trunk and straight knees of the genus *Homo*. The macaque bipedalism is characterised by high energy cost and bent knees. Considering the similar biomechanical features in *Paradolichopithecus*, *Australopithecus* and the trained macaque, it is tempting to conclude that also the two former genera had an all-round, energetically expensive bipedal mode with bent knees. This development then was not restricted to the hominoid clade, but appeared also in the papionins, as evidenced by the difference between *Australopithecus* and *Pan* on one hand and *Paradolichopithecus* and *Papio* on the other hand. The pattern shared indicates similar mechanical stresses, and reflects a shared increased frequency of bipedalism in the daily locomotor behavior, possibly but not necessarily, accompanied by an increased mobility of the arm.

Key-words: *Paradolichopithecus, morphological features, biomechanical features, Australopithecus.*

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* Μοναδικά μετακρανιακά του πιθήκου του Παλαιού Κόσμου *Paradolichopithecus:* Μεγαλύτερη ομοιότητα με τον *Australopithecus* από ό,τι με τους βαβουίνους.

ΠΕΡΙΛΗΨΗ: Η μελέτη αυτή αναφέρεται στα μοναδικά μετακρανιακά ενός πιθήκου του Παλαιού Κόσμου του Πλειο-Πλειστοκαίνου (*Paradolichopithecus*) και στον πιθανό τρόπο βάδισης όπως αυτός συμπεραίνεται από το υπάρχον υλικό. Το μετακρανιακό υλικό περιγράφεται και συγκρίνεται με αυτό των σημερινών πλησιέστερων συγγενών του, *Papio, Macaca* και *Theropithecus*. Καθώς βρέθηκαν κάποια μοναδικά στοιχεία στο *Paradolichopithecus*, γίνεται σύγκριση και με το *Australopithecus anamensis, A. afarensis* 11513 (AE 288-1) και το *Pan troglodytes*. Τα μετακρανιακά σκελετικά στοιχεία που μελετήθηκαν, περιλαμβάνουν την ποδοκνημιαία διάρθρωση και το βραχίονα που βρέθηκε πρόσφατα στα Βατερά (Ελλάδα) και τη διάρθρωση του αγκώνα που βρέθηκε στο Valea (Ρουμανία). Από ότι φάνηκε, τα μέρη τα οποία κάνουν τον Αυστραλοπίθηκο να διαφέρει από τους αφρικανικούς πιθήκους, είναι τα ίδια που κάνουν και τον *Paradolichopithecus* να διαφέρει από τους βαβουίνους. Η παραλληλία αυτή ήταν απροσδόκητη στο φως των γενικών μορφολογικών διαφορών μεταξύ μαϊμούδων και πιθήκων. Τα μορφολογικά στοιχεία που είναι μοναδικά για τον *Paradolichopithecus* ανάμεσα στις μαϊμούδες διακρίνονται στον αστράγαλο, το απώτερο τμήμα της κνήμης και το βραχιόνιο και είναι ως εξής: Ο αστράγαλος διακρίνεται από τη σχεδόν παράλληλη τροχαλία, μία μεγάλη και πλευρικά εκτεινόμενη αρθρική επιφάνεια για την περόνη και μια ελαφρώς βαθύτερη αρθρική επιφάνεια για τον τένοντα της κεφαλής του αστραγάλου. Τα χαρακτηριστικά αυτά είναι ενδεικτικά μιας ποδοκνημιαίας διάρθρωσης ενός βαβουίνου που το σωματικό του βάρος κατανέμεται ισομερώς γύρω από την τροχιλία καθώς μια σημαντική αναλογία του βάρους μεταφέρεται διαμέσου της πλευρικής (προς την περόνη) μεριάς και με περίπου την ίδια σταθερότητα τόσο στην μέγιστή ραχιαία κάμψη όσο και στην μέγιστη πελματιαία κάμψη. Σύμφωνα με αυτά τα στοιχεία ο *Paradolichopithecus* μοιάζει με τον *Australopithecus*. Το κάτω άκρο της κνήμης διακρίνεται από ένα πιο συμπαγές, τετράγωνο και αμβλύ σφυρικό το οποίο στερείται της τυπικά εμφανούς σφαιρικής περιοχής, μια πιο ευρεία αυλάκωση (*sulcus malleolaris*) για τον τένοντα του *M. tibialis posterior*, μια πιο τετράγωνη διατομή, εμφανή σημάδια για την περόνη, και μια διπλή αυλάκωση τένοντα στη ραχιαία επιφάνεια (είτε για έναν διχαλωτό τένοντα του *M. flexorum tibialis posterior*, είτε για μια βαθιά αυλάκωση για τον καμπτήρα του μεγάλου δακτύλου), η οποία ακολουθεί το παραοβελιαίο επίπεδο. Κανένα από αυτά τα χαρακτηριστικά δεν είναι μοναδικά και κάνουν τον *Paradolichopithecus* να μοιάζει με τον *Australopithecus*, ένα εκπαιδευμένο Ιαπωνικό μακάκο και σε μικρότερο βαθμό άλλα είδη μακάκων. Ο συνδυασμός υποδεικνύει ένα περιορισμό της κίνησης από τη ραχιαία στη πελματιαία κάμψη, μια αυξανόμενη σημασία της περόνης στην μεταφορά του βάρους, μια πιο ισχυρή πελματιαία κάμψη και πιθανότατα μικρότερη ανάσπαση του ποδός. Το επίπεδο κνημικό σφυρικό του *Paradolichopithecus* και του *Australopithecus* συγκρίνεται με το *Papio* και *Pan* αντιστοίχως, σε συνδυασμό με την ανάλογη αρθρική επιφάνεια του αστραγάλου λειτουργεί ως μηχανισμός εμπλοκής, αποτρέποντας την περαιτέρω ραχιαία περιστροφή κατά τη διάρκεια της μέγιστής ραχιαίας κάμψης. Αυτό καθιστά τον αστράγαλό του ακατάλληλο για σκαρφάλωμα. Το βραχιόνιο διακρίνεται από μια μεγάλη περιοχή άρθρωσης στην κεφαλή, συγκριτικά με το *Papio*, μια πλατιά και βαθιά αυλάκωση για το δικέφαλο τένοντα, μια σταδιακά βυθιζόμενη κεφαλή και ένα λοξό άξονα κάμψης διαμέσου της ένωσης του αγκώνα. Κατά τη διάρκεια της κάμψης, η ωλένη παρεκκλίνει από το παραοβελιαίο επίπεδο και καταλήγει σε μια θέση ενδιάμεσα στο βραχιόνιο αντί για παράλληλα επάνω από αυτό, εξαιτίας του άξονα και του σχήματος της τροχιλίας. Αυτό το μοναδικό χαρακτηριστικό αποφέρει σημαντική αύξηση της κινητικότητας. Λαμβάνοντας υπ' όψιν τα μοναδικά χαρακτηριστικά του αστραγάλου και του αγκώνα του *Paradolichopithecus* θα μπορούσε να περιμένει κανείς ότι η μετακίνησή του διέφερε από αυτή των βαβουίνων. Οι κυριότερες διαφορές είναι η συμετοχή της περόνης, η αυξανόμενη σταθερότητα στη πελματιαία κάμψη, μια περισσότερο ισομερής διανομή της σταθερότητας κατά τη διάρκεια της κίνησης και μια ίση μέσο-πλευρική σταθερότητα στην μέγιστη πελματιαία κάμψη και στην μέγιστη ραχιαία κάμψη. Κατά την άποψή μας, το είδος αυτό της κίνησης βρίσκει παράλληλο στον *Australopithecus* και στους εκπαιδευμένους μακάκους της Ιαπωνίας. Οι τελευταίοι άρχισαν να αναπτύσσουν συγκεκριμένες αλλαγές κατά την εκπαίδευση, κυρίως στο οπίσθιο άκρο, προκειμένου να ικανοποιήσουν τις λειτουργικές ανάγκες που προκύπτουν από τον αυξανόμενο διποδισμό. Ανάμεσα σε άλλα, το σφυρόν της κνήμης έχει αναδιαμορφωθεί εξαιτίας της επίδρασης μεγάλης πίεσης και έχει γίνει λιγότερο μυτερό και η αρθρική επιφάνεια του σφυρικού οστού του αστραφάλου έγινε αντίστοιχα περισσότερο επίπεδη. Η εξάρθρωση του γονάτου στον εκπαιδευμένο μακάκο απαιτεί επιπλέον μια αυξανόμενη περονική συμετοχή. Αυτό μπορεί να έχει μια παραλληλία στον *Paradolichopithecus* και *Australopithecus*, στον οποίο επίσης παρατηρούμε μια αυξανόμενη συμετοχή της περόνης. Ωστόσο, θα πρέπει να τονιστεί, ότι το είδος του διποδισμού του εκπαιδευμένου μακάκου διαφέρει σημαντικά από τον δίποδο δρασκελισμό με όρθιο κορμό και με ίσα γόνατα του γένους *Homo*. Ο διποδισμός του μακάκου χαρακτηρίζεται από υψηλή κατανάλωση ενέργειας και λυγισμένα γόνατα. Λαμβάνοντας υπ' όψιν τα παρεμφερή βιο-μηχανικά χαρακτηριστικά του *Paradolichopithecus*, του *Australopithecus* και του εκπαιδευμένου μακάκου, είναι δελεαστικό να καταλήξει κανείς στο ότι και τα δυο προηγούμενα γένη είχαν μια γενική, ενεργειακά δαπανηρή διποδική κίνηση με λυγισμένα γόνατα. Οπότε η εξέλιξη αυτή δεν περιοριζόταν μόνο στον κλάδο των Hominidae, αλλά εμφανίστηκε και στους βαβουίνους, όπως αποδεικνύεται από τη διαφορά μεταξύ του *Australopithecus* και του *Pan* από τη μια μεριά και του *Paradolichopithecus* και του *Papio* από την άλλη. Το πρότυπο υποδηλώνει παρόμοιες μηχανικές πιέσεις και αντανακλά μια μοιρασμένα αυξανόμενη συχνότητα του διποδισμού στην καθημερινή κίνηση, πιθανά αλλά όχι απαραίτητα, συνοδευόμενη από μια αυξανόμενη ευκινησία του βραχίονα.

Λέξεις-κλειδιά: *Paradolichopithecus*, μορφολογικά χαρακτηριστικά, βιο-μηχανικά χαρακτηριστικά, *Australopithecus*.

INTRODUCTION

In 1997, a Late Pliocene mainland vertebrate fauna was discovered near Vatera on the island of Lesvos, Greece; a year later excavations started there (Fig. 1). The fauna of Vatera can be placed in the MN 17 zone (St Vallier Faunal Unit, or 2.4 to 1.8 Ma ago) on the ground of the faunal elements (DE

Vos *et al.*, 2002). During the Pliocene, the island was part of the mainland Anatolia. Amongst the vertebrate material recovered, there are two mandibles and several postcranial elements, including an articulated ankle joint, that are clearly primate in morphology (DERMITZAKIS *et al.*, 1999). These materials are assigned to the Old World papionin monkey *Paradolichopithecus arvernensis* (DÉPÉRET, 1929),
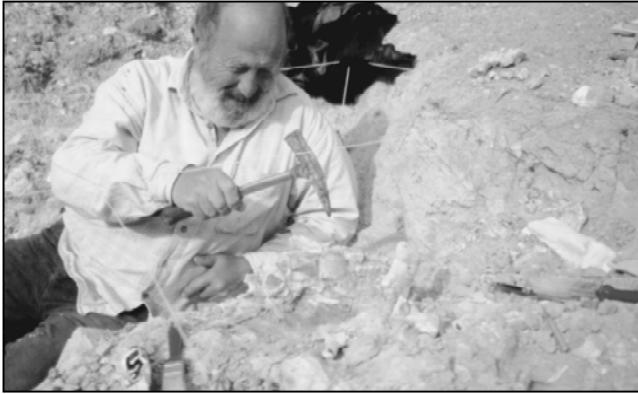
Fig. 1. Dr Paul Sondaar excavating at the site Vatera on Lesvos, Greece (autumn 1998). This is how we all know Paul, and this was how he was on his best: in direct contact with the fossils.

as the cranial and dental material does not differ significantly from that of Sénèze (France; type skull for the species) and Valea Graunceanu (Romania) of the same period (pers. comm. Eric Delson). The ankle joint has the shared cercopithecid pattern, but presents a unique and derived morphology clearly distinguishing it from all other known cercopithecids (VAN DER GEER, 2002). As the ankle joint reflects foot use in loading and propulsion, its unique features are useful for the determination of the type of locomotion practiced by this Old World monkey. The morphology of the tarsus informs us 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). Locomotion, however, as such can not be studied in extinct species, but can be inferred from morphological particularities and comparison with extant species, because direct correlations between structure and adaptation can be made only for living animals. For this reason, the comparison material we used consists of ankle joints (tibia and talus) of recent baboons, geladas and macaques, including a macaque trained for a traditional Japanese bipedal performance (NAKATSUKASA *et al.*, 1995). As none of the ankles showed complete similarity with the *Paradolichopithecus* ankle, we also studied (casts of) *Australopithecus afarensis* (AL 288-1, 'Lucy') and of *A. anamensis*, which we compared on turn with recent chimpanzees, as this ape shows the most similarities with the australopithecines.

MATERIAL

The postcranial material of *Paradolichopithecus arvernensis* (Table 1) used in this study belongs to the University of Athens, Department of Geology, Section Historical Geology and Palaeontology and are stored at the Vrissa Natural History Collection, Vrissa, Polychnitos, Lesvos (Greece); casts of the Roumanian *P. arvernensis* material from Valea Graunceanu were provided to us by E.

The postcranial elements of *Paradolichopithecus arvernensis* from Vatera, Lesvos (Greece). The fossils of *Paradolichopithecus arver - nensis* all originate from the F-site of the so-called Vatera Formation, Polychnitos, Lesvos, Greece. The age of the site is Plio-Pleistocene, or MN 17. The numbers are the inventory numbers of the Vrissa Natural History Collection, Polychnitos, where the material is stored and exhibited. Apart from the postcranial elements, also jaws with full dentition and separate teeth have been found at the same site. In this study, the tibia, talus and humerus are the main subject.

Number	Element	remarks
PO 059F	ulna, sin.	olecranon
PO 157F	talus, dex.	complete
PO 200F	humerus, sin.	lower half
PO 225F	humerus, dex.	complete
PO 228F	tibia, dex.	distal part
PO 229F	ulna, dex.	distal part missing
PO 431F	radius, dex.	distal part missing
PO 498F	radius, sin.	shaft fragment
PO 501F	radius, dex.	shaft part
PO 502F	radius, sin.	shaft fragment
PO 630F	radius, sin.	shaft fragment

Delson (American Museum of National History, New York), and consisted of a right distal humerus, a right almost complete ulna, and a right radius lacking articulation areas, all with number VGr 350 and belonging to one individual. The postcranial material of living cercopithecoids (Table 2) were studied in Naturalis, Nationaal Natuurhistorisch Museum, Leiden (The Netherlands) and in the American Museum of National History (Department of Mammology); casts of tali and distal tibias of *Macaca fuscata* 'Jiro' and of distal tibias of *Erythrocebus pat a s* were provided to us by M. NAKATSUKASA (Tokyo University) and E. SARMIENTO (AMNH) respectively. Casts of *Australopithecus anamensis* and of *A. afarensis AL 288-1* were studied at the AMNH, Department of Anthropology and at Naturalis, Leiden, respectively. The postcranial material of fossil cercopithecoids were studied at the Frick Collection (AMNH, New York), and comprises limbs of *Mesopithecus penteli*, *Dolichopithecus ruscinensis*, and *Paracolobus che - meroni*.

MORPHOLOGY OF THE POSTCRANIAL MATERIAL

The talus

The general architecture of the *Paradolichopithecus* talus is typically cercopithecoid with asymmetrical trochlear ridges, a wedge- shaped trochlea and a weakly developed sulcus for the tendon of the flexor fibularis. It is also typically cercopithecine and not colobine, as the medial malleolar cup approaches the plantar border of the talus (*sensu* STRASSER,

TABLE 2

Material used for comparison. Complete skeletons of a number of living baboons, geladas and macaques have been compared with the fossils of the monkey *Paradolichopithecus* from Vatera (Greece) in order to reconstruct its locomotory behaviour. Most skeletons originated from wild animals, a few from zoo specimens, and one from a bipedally trained Japanese macaque, named Jiro (Kyoto, Japan); essential differences between wild and zoo animals could not be found. Two fossil species were also taken into consideration: *Australo - pithecus afarensis* (the famous Lucy) and *A. anamensis*. It appeared that the morphology of *Paradolichopithecus* is more close to *Australopithecus* and Jiro than to its more close relatives *Papio* and *Macaca*. Institutional abbrevations:

AMNH = Department of Mammology, American Museum for Natural History,

New York, USA; NNM = Naturalis, National Natural History Museum, Leiden, The Netherlands.

Species	*Storage number*	*Additional data*
Macaca leonina	AMNH 011091	adult female
Macaca tonkeana	AMNH 153400	young adult female
	AMNH 153401	young adult male
	AMNH 153402	young adult male
Macaca fascicularis	AMNH 103654	adult female
	AMNH 103649	young adult male
	AMNH 103661	juvenile female
Macaca mulatta	AMNH 201050	young adult female
Macaca brunnescens	AMNH 30613	adult male
Macaca arctoides	AMNH 112727	adult male
Macaca fuscata	'Jiro'	adult male
	AMNH 201287	adult male
Macaca nemestrina	AMNH 35075	adult (zoo), no skull
Macaca sylvanus	AMNH 202786	adult (zoo)
Papio sphinx	AMNH 089357	adult female
	AMNH 089358	adult female
	AMNH 089365	adult female
	AMNH 089367	young adult female
	AMNH 170364	adult male
	AMNH 39387	adult
	AMNH 170366	young adult male
	AMNH 70303	adult male (zoo)
	AMNH 202584	adult male
	NNM n.n.	
Papio leucophaeus	AMNH 120388	
	AMNH 35693	
	AMNH 202416	adult male (zoo)
	AMNH 70245	adult male
Papio tesselatus	AMNH 051380	young adult male
Papio ursinus	AMNH 216251	young adult male
	AMNH 216247	adult female
	AMNH 216250	adult female
	AMNH 80771	adult male
Papio hamadryas	AMNH 216249	young adult female
	AMNH 238099	adult male (zoo)
	NNM 24581	
Papio anubis	AMNH 187369	juvenile male
	AMNH 51380	young adult male
Papio cynocephalus	AMNH 35042	adult male (zoo)
Theropithecus gelada	AMNH 201008	young adult male
	NNM 11341	
	NNM n.n.	
Australopithecus afarensis	AL 288-1ar and al	adult; casts in AMNH and NNM
Australopithecus anamensis	KNMP 89280 B	adult; casts in AMNH and NNM

Fig. 2. The talus (astragalus) of the fossil baboon *Paradolichopithecus arvernensis* from Vatera, Greece, in plantar view (left), dorsal view (centre) and distal view (right). a = talar head (caput), b = talar neck (collum), c = articulation area with fibula, d = proximal end of trochlea, e = suspensory facet for malleolus of the fibula. Photograph VAN DER LAAN.

1988), the head is not strongly rotated (low talar head torsion), and the proximal talo-calcaneal facet is mildly curved (Fig 2). A feature that distinguishes it from *Papio* is the more planar facet for the malleolus of the tibia (VAN DER GEER, 2002), while it is clearly bowl-shaped in *Papio*. This is paralleled only in some macaques (*M. mulatta, M. fuscata*, including the bipedally trained macaque 'Jiro'), and in *Australopithecus*. In all other cercopithecoids, and also in *Pan*, the facet for the tibial malleolus is clearly bowl-shaped.

Two features distinguish *Paradolichopithecus* from other cercopithecoids (Fig 3), and are considered unique for this taxon (VAN DER GEER, 2002). Firstly, the trochlea is only slightly wedge-shaped, in other words, its mediolateral diameter is only slightly larger anteriorly than posteriorly (Table 3). Secondly, the dorsal aspect or horizontal part of the fibular articulation is large and protrudes laterally (Fig. 3) to the extent seen in some hominoids. This flap-like horizontal part is perpendicular to the lateral side like in *Australopithecus*, whereas it slopes gradually in baboons and the chimpanzee. These features in the *Paradolichopithecus* talus are closer in morphology to those of *Australopithecus* than to those of cercopithecoids, recent (*Papio*, *Macaca*) and extinct (*Mesopithecus penteli, Dolichopithecus rusci - nensis, Paracolobus chemeroni*). The facet for the spring ligament (lig. talocalcaneum interosseum) on the talar head seems slightly deeper than in the largest baboons (*P. ursinus*, *P. sphinx*), although these have the same body size as *Paradolichopithecus*. T h e re is some postmortem damage to this area, so the size of this facet cannot be measured with certainty. When the talar features are considered together it suggests a baboon-like ankle joint with the body weight more evenly distributed over the talar trochlea, a greater proportion of the weight transfer through the lateral (fibular) side, and with approximate the same stability in maximal dorsiflexion ('close-packed' position) as in maximal plantar flexion. In the latter aspect *Paradolichopithecus* resembles the bipedally trained Japanese macaque, and to a lesser degree *M. mulatta* and non-trained *M. fuscata*, whereas in all three aspects it resembles *Australopithecus*.

TABLE 3

Width of the talar trochlea in mm. The width of the trochlea of the talus, as seen from proximal was measured at two points in order to determine the degree of parallelism. The first point, or DT prox (proximal width) is the point at which the lateral ridge bends inwards. The second point, or DT dist (distal width) is the distalmost point at the end of the trochlea. 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 the available adult males of *M. fuscata*, *M. maura*, *M. nemestrina*, *M. schreata*, *M. nigra*. *Pan troglodytes* data (NNM) are lumped together, as no significant difference was observed. It appeared that a more or less parallel trochlea was found in *Paradolichopithecus* as well as in *Australopithecus*.

Species	Inventory number	number	DT prox	DT dist	index	mean
Paradolichopithecus		1				1.1
	PO 157 F		15.8	17.2	1.1	
Papio hamadryas		2				1.5
	NNM 24581		12.1	18.4	1.5	
	AMNH 238099		13.0	18.8	1.5	
Papio anubis		2				1.3
	AMNH 187369		12.2	15.3	1.3	
	AMNH 51380		15.3	19.2	1.3	
Papio ursinus		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	
Papio sphinx		1				1.4
	NNM n.n.		14.2	19.5	1.4	
Papio, total		10				1.3
Theropithecus		2				1.2
	NNM 11341		13.2	15.8	1.2	
	NNM n.n.		12.2	13.2	1.1	
Australopithecus	AL 288-1	1	16.4	19.2	1.2	1.2
Pan troglodytes		4	21.4	16.6		1.3
Macaca		5	4.3	5.7		1.3

The distal tibia

The distal tibia also differs from that of the baboons in having a more massive, square and blunt malleolus (Fig. 4); for detailed comparison see VAN DER GEER (2002). The malleolus has a regular and flat articular surface without the typically pronounced ball-shaped area (Figs 5 & 6), and a wider groove (sulcus malleolaris) for the tendon of the *M. tibialis posterior* (function: plantar flexion with supination). These differences provide a strong similarity with the distal tibia of *Australopithecus*, but also, though to a lesser extent, with that of macaques who are characterized by a poorly developed ball-shaped area (*M. mulatta*, *M. arctoides*, *M. fuscata*). The trained macaque has even a less developed ball-shaped convexity, and approaches the *Paradolichopithecus* situation. Other macaques are like baboons in this respect (*M. fascicularis*, *M. brunnescens*, *M. nemestrina*, *M. sylvanus*, *M. tonkeana*). In addition, the tendon for the flexor tibialis posterior in *Paradolichopithecus* is either bifurcated, or accompagnied by that for the flexor digitorum longus, with each tendon or tendon part running through a separate channel (Fig. 6). The direction of the channel differs also, and follows the parasagittal plane like in *Australopithecus*, whereas it deviates disto-medially in other primates. A similar situation, but less pronounced, is seen in one specimen of *Erythrocebus patas* and in some *Theropithecus gelada*.

The decreased mediolateral width of the tibia in relation to its antero-posterior width can be explained as a typical terrestrial trait. The same applies to the stronger fixation of the distal fibula to the tibia as inferred from the bony crests around the fibular depression. The combination of all these features again indicates a maintainance of the close-packed situation from dorsiflexion to plantar flexion, and an increased importance of the fibula in weight transfer. Theoretically, the development of the tendon can be explained in two ways: in dorsiflexion the foot was supinated, or during locomotion plantar flexion played an important role. A supinated position is unlikely, as weight transfer was shifted to the lateral side. A stronger plantar flexion thus seems to be characteristic for the locomotion of *Paradolichopithecus*. The direction of the groove for the tendon of the *M. tibialis posterior* has a direct link to foot posture. The foot can be expected to be slightly abducted, as the *M. tibialis posterior* tendon has a groove orientated in a direction that suggests this.
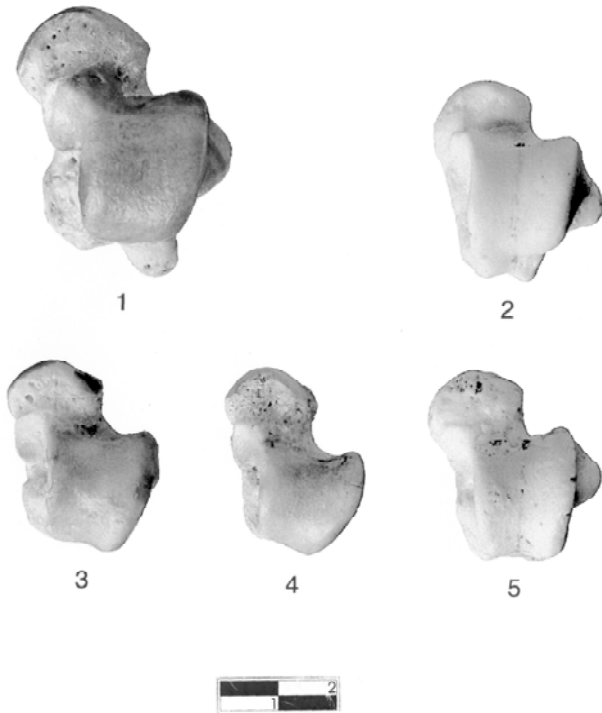
Fig. 3. Five tali of living and fossil primates, seen from above, or dorsal. The upper row represents the African apes, the lower row the baboons. The left column represents the forest dwellers, the middle column the clearing edge dweller, and the right column the plain dwellers. It appears that the trochleas of the plain dwellers are less wedge-shaped or more parallel than those of the forest dwellers, and they have a much more pronounced suspensory facet for the fibula (to the right). The depression for the tibial malleolus (to the left) is much flatter and less deep. Legend: 1 = chimpanzee *(Pan troglodytes)*, 2 = cast of 'Lucy' (*Australopithecus afarensis* AL 288-1), 3 = mandrill *(Papio sphinx)*, 4 = baboon *(Papio hamadryas)*, 5 = fossil b a b o o n *Paradolichopithecus arvernensis* from Vatera, Greece (cast). Scalebar 1:1. Photograph VAN DER LAAN.
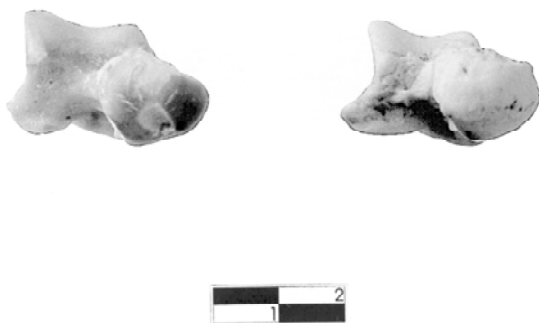

Fig. 4. The talus of the fossil baboon *Paradolichopithecus arvernensis* from Vatera, Greece (right) and of the living mandrill *Papio sphinx* (left) compared. The suspensory flap to sustain the downward pressure of the distal fibula or lateral malleolus at the lateral side (at the left) is much larger in *Paradolichopithecus* and its direction seems slightly more towards the horizontal. These features indicate a higher fibular compound in the ankle joint, and point to a more equally distributed weight and a varus knee. Scalebar 1:1. Photograph VAN DER LAAN.

Fig. 5. Five distal tibias of living and fossil primates, upside down, seen from lateral. The upper row represents the African apes, the lower row the baboons. The malleoli of the right column (the plain dwellers) are more square, blunt and massive than those of the middle column (the forest-edge dweller) and the left column (the forest dwellers). The amount of bone material increases logarithmically with the stress applied on it, and as a consequence, the shape of the tibial malleolus informs us about the total stress applied on the medial side of the lower leg. In addition, the malleolus is characteristically ball-shaped in the forest and forest-edge dwellers (1, 3, 4), but more or less flattened in the plain dwellers (2, 5). As a result, the type and degree of movement in the upper ankle joint differs essentially, as the shape of the malleolus gives direction to the movement, and determines its range, too, by acting as a stop-facet. Legend: 1 = chimpanzee *(Pan troglodytes)*, 2 = cast of 'Lucy' (*Australopithecus afarensis* AL 288-1), 3 = mandrill *(Papio sphinx)*, 4 = baboon *(Papio hamadryas)*, 5 = fossil baboon *Paradolichopithecus arvernensis* from Vatera (Greece). Scalebar 1 : 1. Photograph VAN DER LAAN.

Fig. 6. The distal tibia of Paradolichopithecus seen from lateral (left), medial (centre) and distal (right). a = the ball-shaped malleolus, which is much less developed, and hardly elevated; b = either a bifurcated channel for the flexor muscle of the tibia or an accessory channel.

The humerus

The proximal humerus of *Paradolichopithecus* differs from that of other baboons by its larger articulation area on the head, and by a wide and deep groove for the biceps tendon. The distal humerus (Fig. 7) is characterized by a gradually descending capitulum, and an oblique axis for flexion-extension through the elbow joint, compared to the straight axis of the mandrill. These features of the distal humerus seem also to have been present in the Late Pliocene *Procyno-cephalus wimani*, as judged from the drawings (TEILHARD DE CHARDIN, 1938) of the now lost material.

MECHANICS OF THE JOINTS

The ankle joint

The movement of the talus in the tibia in the recent cercopithecoids consists of two movements: a dorso-plantar flexion varying between 70 and 100 degrees, and a rotation of about 30 degrees.

In maximal dorsiflexion there is still some rotation possible. In general, this rotation is mainly given direction by the spherical medial malleolus of the tibia which fits perfectly in a

Fig. 7. The distal right humerus of the fossil baboon compared to that of the living mandril. To the left the mandrill *(Papio sphinx)*, to the right *Paradolichopithecus arvernensis* (cast of VGr 350 from Valea Graunceanu, Roumania), both in planar view. The axis through the lateral trochlea border and that through the capitulum, the articulation area for the radius, meet each other at a much more distal point in *Paradolichopithecus* than in the mandrill. The result is a deviating ulna in the former, so that in maximal flexion of the arm the hand will end more medially, somewhere on the clavicle, instead of on the shoulder as in the mandrill and other monkeys. Scalebar 1 : 1. Photograph VAN DER LAAN.

cup-shaped facet on the medial side of the talus during maximal dorsal flexion. This stabilizing feature is especially pronounced in cercopithecids and hylobatids (ROSE, 1994). During dorsiflexion, the tibial malleolus articulates with the medial side of the talus, and turns the talus medially, or inward.

If we compare the tibio-talar joint of *Paradolichopithecus* and *Australopithecus* with that of *Papio* and *Pan*, we see that the tibial malleolus is flat instead instead of spherical. Now this same articulatory facet acts in combination with the corresponding facet on the talus as a kind of stop facet, or blocking mechanism, preventing further dorsiflexion, and preventing rotation during maximal dorsiflexion. This rotation, or mediolateral movement, is necessary for climbing, but incompatible with efficient cursorial bipedalism (SARMIENTO, 1985, 1998). The climbing abilities in *Pan* are further facilitated by the large medial facet, which permits a considerable range of medial rotation of the calcaneum on the plantar surface of the astragalar neck, resulting in a high possible degree of inversion of the foot (LE GROS CLARK & LEAKEY, 1951). This is completely lacking in *Paradolichopithecus*. In the latter, the talus is firmly kept into its position by the malleolar fork.

The elbow joint

In a situation with an increased hindlimb component, as can be inferred from the morphology of the ankle joint, the mobility in the arm might secondarily be substantially increased (MOYY-SOLY *et al.*, 1999). In *Paradolichopithecus* this is evidenced by a non-baboonlike flexion in the elbow, during which the ulna deviates from the parasagittal plane, ending in a position medially to the humerus instead of parallel above it, due to the shape and axis through the trochlea of the humerus. Together with the increased articulation area on the humeral head, this yields a significant increased range of possible movements.

THE ECOLOGY RECONSTRUCTED

The fossils of Vatera are found in a lens-shaped deposit along a former river, thus obviously washed ashore. The faunal assemblage is characterized by a diversity in bovids (amongst others, *Gazella borbonica*), a giraffid, two or three deer, *Equus stenonis*, *Nyctereutes megamastoides*, *Geochelone*, *Anancus arvernensis*, *Mammuthus meridionalis* and of course *Paradolichopithecus arvernensis*. If we take all faunal elements into consideration (DE VOS *et al.*, 2002), the picture of a forest clearing and forest egde environment (*sensu* ROSE, 1984) arises. Furthermore, seasonality of the area is indicated by the insectivore fauna (REUMER *et al.*, 2002). 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
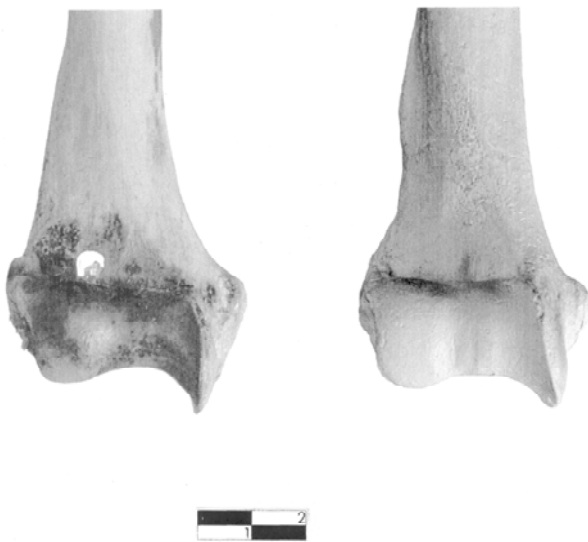
movements 1,5 km) to 4000 hectares (daily movements 5 km) for savanna baboons (KINGDON, 1971), clearly determined by the availability of sufficient food at their disposition. The Pliocene Vatera environment, however, differed substantially from the biotoop of the living baboon, compelling *Paradolichopithecus* to enlarge its territory in search for food. The body mass of the Vatera specimen can be estimated between 31,6 and 63,1 kilo, based upon midshaft antero-posterior width of the humerus, using data for male specimens (DELSON *et al.*, 2000), as the dimensions of our humerus fall outside the range for *Paradolicho-pithecus* females. This body mass fits very well with that of Graunceanu males, estimated from humeral shafts: 34 kilo (DELSON *et al.*, 2000). *Paradolichopithecus* was significantly larger than European and North African Cercopithecinae in a time range from 5.5 Ma to present-day, but similar to the largest African Papionini (other than the gelada *Theropithecus*) *Papio* (*Dinopithecus*) in a time range from 4.2 Ma to 1.77 Ma. By that time, *Dinopithecus* got extinct, like the similar sized *Paradolichopithecus* in Eurasia, and its position got occupied by the slightly heavier gelada (*Theropithecus*, from 2.0 Ma to 0.4 Ma). It might be possible to infer a number of biological data from what we know of *Dinopithecus*, as there seems to be some similarity.

DISCUSSION

Considering the fact that the *Paradolichopithecus* ankle joint can clearly be distinguished from other cercopithecoids, as it shows some unique features, it may be expected that its locomotion also differed. The increased importance of the fibular component clearly shows an increased lateral contribution. The increased stability in plantar flexion can be explained in two ways. First, it might inform us about a more plantar flexed rest position, or weight-bearing attitude. Second, it might also be explained by the necessity for a more evenly distribution of stability during locomotion. A poorly wedged, almost parallel trochlea can only be explained by the need of a medio-lateral stability that is equal in maximal plantar flexion and in maximal dorsi-flexion. A type of locomotion that requires an increased fibular compound, combined with a lateral stability that is equal in all positions finds a perfect parallel in *Australo-pithecus* and also, but less so, in trained Japanese macaques. A strong plantar flexion with a more lateral shifted position of the tendon groove is seen only in *Australopithecus*, whereas a strong plantar flexion alone is also present in the mandrill, the chimpanzee and the macaque.

The locomotion of *Australopithecus* can only be inferred from skeletal remains, but that of trained Japanese macaques (*M. fuscata*) (IWAMOTO, 1985; NAKATSUKASA *et al.*, 1995) can be studied after death as well as during life. It appears that these trained monkeys develop significant modifications to satisfy functional requirements (AMT-MANN, 1979; HAYAMA, 1986; HAYAMA *et al.*, 1992; NA-

KATSUKASA *et al.*, 1995; NAKATSUKASA & HAYAMA, 1999; PAUWELS, 1960, 1965; PREUSCHOFT *et al.*, 1988). Though bipedal posture and locomotion are part of the daily behavioral repertoire of all non-human primates (FLEAGLE, 1976, 1984; IWAMOTO, 1985; MITTERMEIER, 1978; ROSE, 1976; WRANGHAM, 1980), the degree in which it is adopted or displayed is increased substantially by the training. ISHIDA *et al.* (1974:288) trained six primates to walk bipedal, and it took them two years for *Hylobates agilis* (dark-handed gibbon), four years for two *Macaca fuscata* individuals (Japanese monkey), five years for another *Ma-caca fuscata*, for *Papio hamadryas* (Hamadryas baboon) and *Ateles geoffroyi* (black-handed spider monkey), and six years for *Pan troglodytes* (chimpanzee).

As bone remodels in response to applied stresses (KUM-MER, 1970, 1972; PAUWELS, 1960; WOLFF, 1892), a change in positional behavior from quadrupedality to bipedality is likely to result in bone remodeling especially in the hindlimb. Thus, crucial changes are to be expected in the ankle (tibiotalar) joint. Indeed the articular surface of the distal tibia is increased in the two bipedally trained Japanese macaques, compared to untrained adult Japanese macaques (NAKATSUKASA *et al.*, 1995). Furthermore, the medial malleolus of the tibia is slightly less cusp-shaped than in normal *M. fuscata*, a situation that is only seen in the much smaller *M. mulatta*. The corresponding facet on the medial side of the talus is thus more planar. Body weight is more evenly distributed over the malleolar surface, and stability during flexion is increased with a loss of medio-l a t e r a l movement or rotation. Under the influence of greater stress, the shape of the medial malleolus is remodeled. The b i p e d a l posture results in a higher compressive force on the articular surface of the distal tibia, and this force is even more increased on the fibula due to the fact that the bipedal monkey stands and walks with the knee in a varus position, which yields a higher stress on the lateral side than on the medial side of the limb. The mode of bipedalism shown by the Japanese macaques is characterized by less extended hip and knee joints, a varus knee and a forward sloping trunk. This is quite different from the modern human type of bipedalism, which is characterized by a very low level of muscle activity (OKADA, 1972), straight knees while standing and in the stance phase of walking, an erect trunk, and the ability to run bipedally (MCNEILL ALEXANDER, 1991:255). The modern human type is referred to as striding gait, whereas the other type can be considered an all-round gait (DE VOS *et al.*, 1998). In our view, the gait of *Australopithe-cus afarensis*, *Paradolichopithecus arvernensis* and the trained *Macaca fuscata* might very well have been more or less identical, which means all-round, and not striding.

The transition from exclusive quadrupedalism towards substantial bipedalism was thus not restricted to the hominoid clade, but was also developed in the papionins. It seems reasonable to assume that this transition demands similar adaptations in the tibio-talar joint in cercopithecoids and in hominoids. For the ankle joint of apes and monkeys

is basically similar in function and general architecture. Crucial differences between the ankle joint of the living baboons and of *Paradolichopithecus* might therefore be helpful to explain similar differences that are observed between the African apes and *Australopithecus*. The pattern shared by *Paradolichopithecus* and *Australopithecus* indicates similar mechanical stresses, and is also partly repeated in Japanese macaques, especially in those individuals that are trained to walk bipedal. In all these forms, it may reflect a shared increased frequency of bi-pedalism in their daily locomotor behavior, possibly at the same time accompagnied by an increased mobility of the arm, but not necessarily so.

ACKNOWLEDGMENTS

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