

# THE POSTCRANIAL ELEMENTS OF *PARADOLICHOPITHECUS ARVERNENSIS* (PRIMATES, CERCOPITHECIDAE, PAPIONINI) FROM LESVOS, GREECE\*

by

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## I. INTRODUCTION

Recently, a rich Late Pliocene locality with land vertebrates was discovered along a dust road in an olive orchard near the village Vatera on Lesvos Island, Greece. The faunal assemblage of this site is characterized by, among others, a diversity in bovids, a giraffid, deer, *Equus stenonis*, *Nyctereutes megamastoides* and *Gazella borbonica*. In the same Vatera Formation *Anancus arvernensis* and *Mammuthus meridionalis* were found. The fauna is indicative for an open savanna mainland fauna of Middle Villafranchian age (MN 17). Besides the classical elements of the Middle Villafranchian, St. Vallier Faunal Unit, fossil remains were found of a giant tortoise and *Paradolichopithecus arvernensis* (DEPÉRET, 1929). This monkey is known from a few Late Pliocene localities, but only fossil material from Valea Grâunceanului (Romania) gives some information on postcranial morphology of this large extinct Old World monkey.

Besides a number of postcranial elements (see Table 1), two mandibles are present among the material so far excavated at the Vatera F site. The larger mandible (PO 114) contains I<sub>1-2</sub>, DC, DP<sub>3-4</sub>, M<sub>1-2</sub>, the smaller one (PO 170) I<sub>1-2</sub>, C, P<sub>3-4</sub>, M<sub>1-3</sub>.

Until now, *Paradolichopithecus* was considered to have a way of life similar to that of the recent baboons and geladas with a terrestrial, quadrupedal locomotion adapted to an increased speed in the savanna. In size, *Paradolichopithecus* was a little larger than the largest extant baboon, *Papio (C.) hamadryas*, and comparable to the mandrill, *Papio (P.) sphinx*. The general architecture resembles that of the baboons, which observation is in agreement with SZALAY & DELSON (1979) who state that the *Paradolichopithecus* resembles macaques cranially and baboons postcranially. Within the Papionini, however, *Paradolichopithecus* can clearly be distinguished. In the present study, the material is compared with extant baboon and mandrill, and with the ankle bones of *Australopithecus*.

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\* Τα Πετακρανιακά σκελετικά στοιχεία του *Paradolichopithecus arvernensis* από τη Λέσβο.

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## II. MATERIAL

The postcranial material (Table 1) from Vatera that can be attributed to *Paradolichopithecus arvernensis* (DEPÉRET, 1929) consists of a slightly damaged but complete right humerus (PO 225), a left humerus without proximal part (PO 200), a right ulna (PO 229) and a right radius (PO 431), both missing the distal part, a separate left olecranon (PO 059), an upper third right radius missing the proximal articulation (PO 501), two upper shaft fragments of two left radii (PO 498 and PO 502), an upper sixth part of a left radius (PO 630), a distal right tibia (PO 228), and a right talus (PO 157). The right humerus (PO 225), ulna (PO 229) and radius (PO 431) belong to the same individual. Though the distal tibia (PO 228) and talus (PO 157) are of one individual, they cannot be assigned with certainty to the former individual. All specimens are comparable in size, and more or less also in shape, to the extant mandrill, *Papio (P.) sphinx* (LINNAEUS, 1758).

Comparison material consists of five complete skeletons of the large baboon *Papio (C.) hamadryas*, thirteen of the mandrill *Papio (P.) sphinx*, three of the gelada *Theropithecus gelada*, casts of the Romanian postcranials (right distal humerus, right almost complete ulna, and right radius without articulation areas, all with number VGr 350 and belonging to one individual) and casts of the distal tibia and talus of the Hadar hominoid *Australopithecus afarensis* A.L. 288-1 («Lucy»). The materials are stored at Naturalis, National Natural History Museum, Leiden, The Netherlands, and at the American Museum of Natural History, New York. The *Paradolichopithecus* specimens are stored at the Vrissa Natural History Collection, Lesvos. For general measurements of the *Paradolichopithecus arvernensis* postcranial material, see Table 2; for a photograph of the Romanian material (humerus, radius, ulna), see SZALAY & DELSON (1979).

**Table 1**

number	element	symmetry	remarks
PO 059	ulna	left	olecranon
PO 157	talus	right	complete
PO 200	humerus	left	lower half
PO 225	humerus	right	complete
PO 228	tibia	right	distal part
PO 229	ulna	right	distal part missing
PO 431	radius	right	distal part missing
PO 498	radius	left	shaft fragment
PO 501	radius	right	shaft part
PO 502	radius	left	shaft fragment
PO 630	radius	left	shaft fragment

**Table 1.** Postcranial elements of *Paradolichopithecus arvernensis* found at the F-site, Vatera Formation, Polychnitos, Lesvos, Greece. Plio-Pleistocene, MN 17.

**Table 2**

element	number	length	DAP prox	DT prox	DAP dist	DT dist
talus	PO 157	33.3	—	11.2	14.5	22.2
talar head	PO 157	14.3	14.8	13.2	13.4	17.9
radius	PO 431	?252	20.0	22.2	—	—
humerus	PO 225	225.0	32.0	43.9	27.5	49.9
humerus	PO 200	—	—	—	29.4	44.9
humerus (Romania)	VGr 350	—	—	—	27.7	43.8
ulna	PO 229	—	21.0	23.1	—	—
ulna	PO 059	—	21.4	22.2	—	—

**Table 2.** Measurements of postcranial material of *Paradolichopithecus arvernensis* (Late Pliocene) in mm.

***Humerus (PO 225)***

The incomplete humerus PO 200 (figs 2 and 3) has exactly the same morphology as PO 225 (figs 1, 2 and 3), so the description will focus on PO 225 (fig. 4).

The humeral shaft is relatively robust, to the extent seen in the mandrill. The proximal shaft is slightly retroflexed, and inclines medially in anterior view, as in to *P. hamadryas* and *P. sphinx*. Unfortunately the humeral head is damaged in the Lesvos



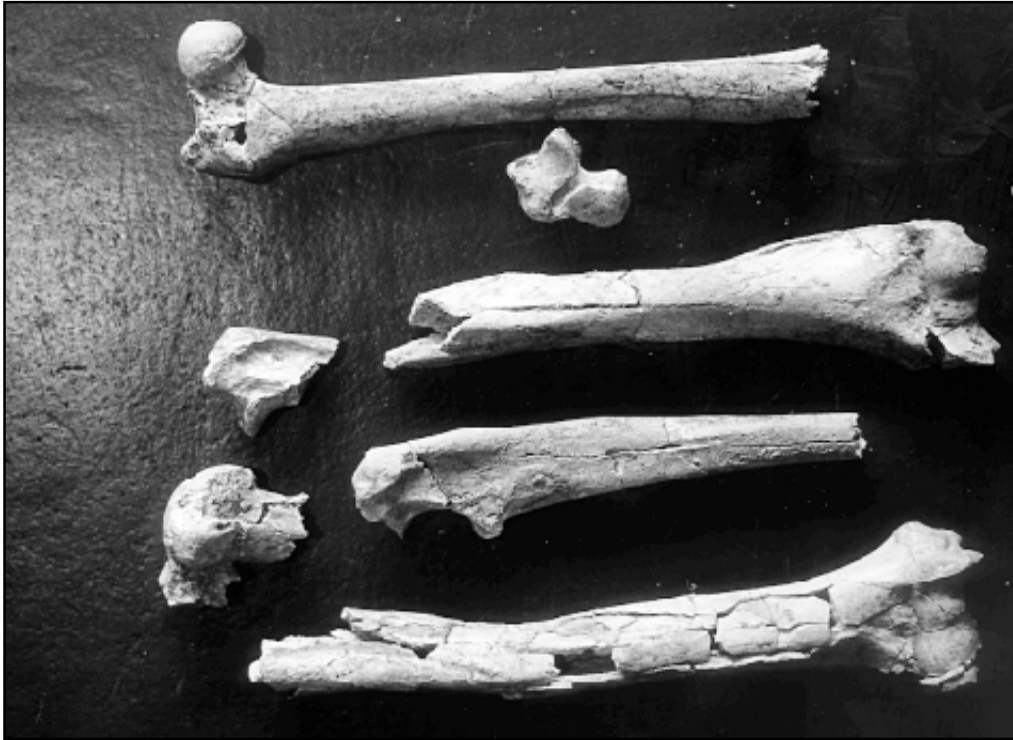
**Fig. 1.** Humerus PO 225 of *Paradolichopithecus* from Vatera, Lesvos, Greece. Posterior view, after repair.



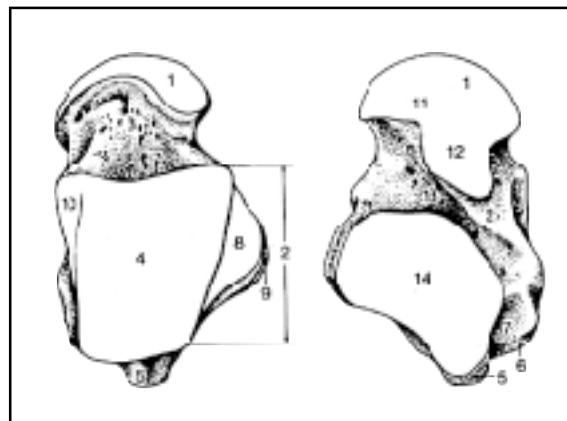
**Fig. 2.** Humerus PO 200 with detached head (posterior view, before repair), ulna PO 229 (lateral view), olecranon PO 059 (lateral view), talus PO 157 (anterior view) of *Paradolichopithecus* from Vatera, Lesvos, Greece.

fossil, though a number of details can still be studied. The shape of the humeral head in side-view differs from the situation as seen in *Papio*, as the total articulation area is larger in *Paradolichopithecus*. This larger area is due to the different slope of the humeral head: in *Paradolichopithecus* the head descends more gradually, without a steep part, and over a larger track.

The greater tubercle is well developed in the baboon, the mandrill and *Paradolichopithecus*, maybe the most in the latter. The groove for the tendon of the biceps is almost similar wide in *Papio* and *Paradolichopithecus*, although slightly deeper in the last. The medial epicondyl, though eroded in both specimens, is large and caudally orientated, or bent posteriorly, in *Paradolichopithecus* as well as in the other baboons. The *capitulum humeri*, or the articulation with the radius, descends gradually to the depression in the middle of the trochlea, whereas it is much rounder in *P. hamadryas* and *P. sphinx* where it ends at a sharper angle. The axis of flexion-extension in the elbow by definition coincides with the axis through the *condylus humeri* (trochlea plus capitulum). In *Paradolichopithecus*, this axis is clearly oblique, running from antero-medially to postero-laterally, whereas it is more or less straight in *Papio*. This results in a non-parasagittal flexion in *Paradolichopithecus*, in contrast to the expected flexion in a parasagittal plane as in *Papio*.



**Fig. 3.** Same elements, reverse side: humerus PO 200 with detached head (anterior view, before repair), ulna PO 229 (medial view), olecranon PO 059 (medial view) talus PO 157 (posterior view).



**Fig. 4.** 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).

Thus, *Paradolichopithecus* is unique in having a larger articulation area on the humeral head, a wide and deep groove for the biceps tendon, a gradually descending capitulum, and an oblique axis for flexion-extension through the elbow joint (Table 4). The last two features, however, might be present also in *Procynocephalus*.

### ***Ulna (PO 229)***

The olecranon PO 059 does not differ from that of PO 229 (figs 2 and 3), so is not included in the description below. The olecranon is equally robust in *Papio sphinx*, *P. hamadryas* and in *Paradolichopithecus*. However, when seen from posterior there is a significant difference. In both *Papio* species, the axis through the posterior border of the olecranon deviates slightly in medial direction when compared to the axis through the corpus of the ulna. In other words, the olecranon is slightly inclined medially. In the mandrill this is more marked, while in *Paradolichopithecus* it is extreme. The most proximal end of the olecranon has the same direction as the above mentioned axis in *Paradolichopithecus* and the hamadryas baboon, but bends back laterally in the mandrill, yielding an almost upright position of the olecranon.

If we look at the top of the olecranon, where the attachment area for the tendon of the *M. triceps brachii* is, we see that in both *Papio* this area is very smooth, with hardly any roughness at all, whereas in *Paradolichopithecus* it is rougher, as in the mandrill. The *incisura trochlearis*, or trochlear notch, where the ulna articulates with the humerus is more circular in the mandrill than in the baboon, and continues medially even further sloping down a bit in the mandrill, whereas it stops more abruptly in the hamadryas baboon, so that it is more platform-like in the latter. In *Paradolichopithecus*, this notch is more like *Papio*, but less circular and more shallow at the distal end of the articular facet. The *incisura radii*, or radial notch, is a clearly concave, hollow and bowl-like articular facet in *P. sphinx*, whereas it is more like a shallow plain in *P. hamadryas*. In this respect, *Paradolichopithecus* resembles more *P. hamadryas*, although the border might be eroded in the fossils. The concavity at medial side of the ulna for the ulnar heads of the *M. flexor carpi ulnaris* and to a lesser degree for the *M. flexor digitorum profundus*, is strongly developed in *Paradolichopithecus* and in *P. hamadryas*, much stronger than in *P. sphinx*.

**Table 3**

species	length	width	index
<i>Papio hamadryas</i>	17.7	6.8	2.6
<i>Papio sphinx</i>	14.9	7.3	2.0
<i>Paradolichopithecus</i>	15.7	9.4	1.7
A.L. 288-1 ar	14.2	8.1	1.8

**Table 3.** Measurements of the tibial medial malleolus of the tibia in mm. Length is defined as the maximal antero-posterior dimension (DAP) and width as the maximal medio-lateral dimension (DT). *Paradolichopithecus* has the most massive malleolus of the baboons.

**Table 4**

<b>anatomical unit</b>	<b>feature</b>	<b>baboon</b>	<b>mandrill</b>	<b><i>Paradolichopithecus</i></b>
Humeral head	baboon-like	+	+	—
	extended surface	—	—	+
Greater tubercle	large	+	+	+
Biceps tendon groove	wide, shallow	+	+	—
	wide, deep	—	—	+
Medial epicondyl	large, retroflexed	+	+	+
Capitulum humeri	descends gradually	—	—	+
	descends abruptly	+	+	—
Axis through condyl	straight	+	+	—
	oblique	—	—	+
Olecranon	medially inclined	+	+	+
	strongly inclined	—	—	+
Trochlear notch	platform-like end	+	—	+
Radius head	elliptical	+	+	—
	subcircular	—	—	+
Radius	slightly longer			
	than humerus	—	+	—
Medial malleolus	longer than humerus	+	—	+
	elliptical	+	+	—
same, articulation area	oblong	—	—	+
	ball-shaped, small	—	—	+
Sulcus malleolaris	flat, large	+	+	—
	unipartite	—	—	+
Trochlea tali	bipartite	—	—	+
	wedged	+	+	—
Malleolar articulation	parallel	—	—	+
	cup-shaped	+	+	—
Fibular articulation	flat	—	—	+
	small, descending	+	+	—
	large, extending	—	—	+

**Table 4.** Summary of the most striking features of the humerus, ulna, radius, tibia and talus of *Papio hamadryas* (large baboon), *Papio sphinx* (mandrill) and *Paradolichopithecus arvernensis* of Vatera.

To sum up, *Paradolichopithecus* differs from the baboons in having a highly inclined olecranon, and a more shallow distal end of the trochlear notch (Table 4).

### ***Radius (PO 431)***

The radius is very similar to that of the mandrill, but broader and more round in transversal section. Its proximal articulation is almost circular, whereas this is more elliptical in the mandrill and the hamadryas baboon.

The radius is much longer than the humerus in *P. sphinx*, and in *P. hamadryas* only slightly longer. Although the distal part is missing, we have the impression that the total length of the *Paradolichopithecus* radius PO 431 is about 25.2 cm. The right humerus PO 225, belonging to the same individual, measures about 22.5 cm. This means that the *Paradolichopithecus* radius of the Vatera Formation is a bit longer than the humerus, similar to *Papio sphinx*. The radius fragments PO 498, PO 501, PO 502 and PO 630 do not differ from the corresponding parts of PO 431.

The only, yet obvious and unique, difference between *Paradolichopithecus* and the other papionins is seen in the subcircular shape of the proximal articulation area (Table 4).

### ***Tibia (PO 228)***

The tibia of *Paradolichopithecus* is represented by a distal, right tibia. In distal view, the architecture of the articular surface is very similar to that seen in the mandrill, both in shape as in size. A striking difference, however, is found in the medial malleolus, which sets *Paradolichopithecus* clearly apart. The articular surface of the malleolus is clearly bowl-shaped and large in the mandrill, whereas it is almost flat and much smaller in *Paradolichopithecus*. The non-articular area of the malleolus is very robust in *Paradolichopithecus*, oblong and tapering dorsally at the articular area bearing part. In both *P. hamadryas* and *P. sphinx* the non-articular area is elliptical, thus tapering at both ends. The articular area bearing part is larger and more massive than the plantar part, in contrast to *Paradolichopithecus* where both parts are massive and the plantar part even more so. On the whole, the *Paradolichopithecus* malleolus is more massive (Table 3), and almost oblong.

In medial view, the malleolus also differs between *Paradolichopithecus* on one side and *Papio* at the other side. In the latter, the slope of the distal border makes an angle of about 45 degrees in *P. sphinx*, about 35 degrees in *P. hamadryas*, but 25 degrees in *Paradolichopithecus*. As a result, the dorsal part extends further distally, yielding a quite pointed apex, in the extant baboons than in *Paradolichopithecus*, where the malleolus is more equally massive with a blunt distal end. In *Australopithecus* the malleolus is oblong in both distal and medial view, which makes it even more massive and more equal in all directions than in *Paradolichopithecus*.

Another difference with the extant baboons is the division of the *sulcus malleolaris* on the plantar side of the malleolus in two separate parts. This bipartite sulcus occupies the complete medial half of the plantar side. In the extant baboons, the unipartite sulcus occupies just one-sixth of the plantar side. Furthermore, the direction of the sulcus is clearly distal in *Paradolichopithecus*, but medio-distal in *Papio*, with an angle of about 10-15 degrees.

In short, the uniqueness of the tibia of *Paradolichopithecus* is found in the



massiveness and flatness of the medial malleolus, and the bipartite groove (Table 4).

### *Talus (PO 157)*

The talus PO 157 (figs 2 and 3) is well-preserved and fits perfectly to the distal tibia PO 228.

The talus, or astragalus, is characterized by a number of articular facets, due to its intermediate position (fig. 4). The head carries the facet for the navicular bone, the plantar side of the body the three facets for the calcaneum and the dorsal side of the body forms the trochlea for the tibia. On the medial and the lateral side are the malleolar facets for the malleolus fork formed by the tibia and the fibula. The main differences between the cercopithecoid talus and the hominoid talus are found in the pronounced lateral ridge of the trochlea in cercopithecoids, whereas the ridges are (almost) equal in the hominoids, and in the pronounced groove for the tendon of the large toe flexor in hominoids, whereas this groove is hardly visible in the cercopithecoids. The talus of *Paradolichopithecus* follows therefore clearly the cercopithecoid pattern, contrary to the clearly hominoid pattern of *Australopithecus*.

The talar trochlea of *Paradolichopithecus* is not typically cercopithecoid in wedgedness, as it is more or less parallel, whereas it diverges from proximal to distal in the other baboons (see also SONDAAR & VAN DER GEER, this volume). The proximal width of the trochlea is in *Paradolichopithecus* 15.8, the distal width is 17.2, resulting in an index of 1.1. In *P. hamadryas* these measurements are 12.1, 18.4, index = 1.5, and in *P. sphinx* 14.2, 19.5, index = 1.4. In a way *Paradolichopithecus* is comparable with *Australopithecus*: 16.4, 19.2, index = 1.2.

In *P. hamadryas*, seen from lateral, two distinct phases are seen in the curvature of the proximal face. The proximal half is round, but the distal half is more gradually descending. The transition point is situated exactly halfway. In the mandrill and *Paradolichopithecus*, however, there is only one phase that is gradually curved.

At the lateral side a large suspensory flap for articulation with the fibula is present in *Paradolichopithecus*, whereas it is only small in both *Papio* species. Seen from proximal, it extends 1.3 mm in *P. hamadryas*, 2.3 mm in *P. sphinx* and 3.7 mm in *Paradolichopithecus*, who is similar to *Australopithecus* (3.8 mm) in this respect. The shape of the suspensory facet for the fibular malleolus is more or less round in *P. sphinx* and *Australopithecus*, but pyramidal in *P. hamadryas* and *Paradolichopithecus*. The apex is tapering in *Papio*, and blunt in *Paradolichopithecus*. In the papionins the facet is symmetrical, in contrast to *Australopithecus* where the distal part has a larger surface than the proximal part.

The curve of the articular head does not differ much between the species studied. In *P. sphinx*, *Paradolichopithecus* and *Australopithecus* it is elliptical. The mandrill is characterized by a distinct fossa at the plantar side of the talar head. *P. hamadryas* shows a slightly more round curvature than both mandrill and *Paradolichopithecus*.

The medial suspensory facet is (almost) flat in the studied tali. In both *Australopithecus* and *Paradolichopithecus*, and to a lesser degree in the hamadryas baboon, the medial facet ends with a clear ridge or border where it touches the *caput tali*, whereas it merges gradually in the mandrill.

Another striking feature is the degree of hollowness of the posterior facet. This facet is parabolic in shape in *Australopithecus* and *Paradolichopithecus*, but very circular or round in *Papio*. This facet also extends further in proximo-distal direction in

*Paradolichopithecus* and *Australopithecus* (1.5 cm against total plantar length of 3.5 cm), than in *P. hamadryas* (1 cm against 3 cm) or *P. sphinx* (1 cm against 3.5 cm).

The groove for the tendon of the large toe flexor (*flexor hallucis longus*) is as a rule but poorly developed in the cercopithecoids, in contrast to the hominoids. *Papio* and *Paradolichopithecus* are no exception in this case, though the groove is slightly deeper in *P. hamadryas* and *Paradolichopithecus* than in *P. sphinx*.

In short, the talus of *Paradolichopithecus* differs to a great extent from the baboons, though it is still cercopithecoid in architecture. Unique features are the parallel trochlea, the highly extending suspensory flap for the fibula, the absence of a cup-shaped depression for the tibial malleolus (Table 4), a more shallow and larger posterior suspensory facet for the calcaneum, and a clear separation between the medial suspensory facet and the talar head. These features are shared by *Australopithecus*, and probably also by *Procynocephalus* as inferred from the drawings (TEILHARD DE CHARDIN, 1938).

### III. DISCUSSION

#### Fore-limb

The slight retroflexion and medial inclination of the humerus shaft is a consistent feature of extant cercopithecines (PILBEAM *et al.*, 1990) which can also occur in Asian apes (BEGUN, 1992). Its functional significance is not clear, and it might be a characteristic of quadrupedality (ROSE, 1994), although it also might be merely the ancestral condition.

The more gradually curved, enlarged articulation area of the humeral head makes the degree of arm movement in *Paradolichopithecus* more than in *Papio*. This indicates a freer use of the arms.

In the baboons the greater tubercle has a clear lever function. Two muscles insert on its upper part: the *M. supraspinatus* on the upper facet, and the *M. infraspinatus* on the middle facet. Action of the first muscle is stabilization of humerus in the joint, tensor of the joint capsule, and abduction of the forelimb. Action of the second muscle is strengthening of the shoulder capsule, but its main function is exorotation of the forelimb. Both muscles add to the stability of the joint, and move the limb outward and away from the body. It is easy to imagine that the strong infra- and supraspinatus muscles in *Papio* are very suitable for quick turns during swift quadrupedal runs, as it demands considerable muscle action to give the whole body mass another direction, especially at high speed when the impulse is high. In *Paradolichopithecus* another explanation might be valid. Here the enlarged articulation area on the head of the humerus needs additional stability, which is solved by the joint stabilizing action of both muscles.

A deeper groove for the biceps tendon may, too, reflect an increased need for stability, which is the case in a loaded situation or in a situation with increased mobility. The action of the biceps is quite complicated due to its two heads and the fact that it acts on two joints. Its main action is anteversion of the shoulder (in humans: lifting the arm in the sagittal plane) and flexor and powerful supinator of the elbow. *Paradolichopithecus* seems to have used its biceps in approximately the same order as the extant baboons, but with more force or more freedom of movement. A tentative explanation for the strong biceps might be its increased use for carrying things, which is very suitable in open plains with its scattered food sources. For

parallels with hominids, see amongst others HEWES (1961), KORTLANDT (1967), LEAKEY & LEWIN (1979). In our opinion, however, even if *Paradolichopithecus* had arms that were suitable for carrying things, it is only an additional advantage, and not a reason on itself. Locomotion is primarily an adaptation to environment in order to be more effective in a certain habitat, as DE VOS (this volume) and DE VOS *et al.* (1998) demonstrate for *Hipparion* and *Australopithecus*.

The form of the capitulum informs us about the elbow joint. The articulation of the humerus with the radius is less stable in *Paradolichopithecus* than in the baboons, but at the same time more mobile, which makes this joint less suitable for a loaded, quadrupedal walk. A better explanation is free movement of the lower arm. This is not only confirmed by the more prominent supination and pronation factor indicated by the subcircular section through the proximal radius, but also by the flexion in a non-parasagittal plane of the lower arm. In other cercopithecoids the ulna runs parallel with the humerus during maximal flexion, whereas the ulna deviates medially in *Paradolichopithecus*.

The lack of a prominent olecranon process excludes the lever function for the *M. triceps brachii*, the elbow extensor. This lever can be missed only without impact if the posture of the ulnar joint is the extended one, or if there is no balance needed against a flexing load (PREUSCHOFT, 1974). PREUSCHOFT observed that the modern pongids extend their elbows in quadrupedal positions, so that no flexing load is present. This makes knuckle-walking as well as fist-walking possible, as now full body weight can be transferred through the forelimbs. In the monkeys this is not possible for two reasons. Firstly, the maximal extension is less than in apes, due to the architecture of the olecranon and the trochlear notch in particular. Secondly, the articular surface is too small to sustain a large force without overstressing the cartilage, although KIMURA *et al.* (1979) showed that primates as a rule carry the majority of their body weight on their hindlimbs. However, due to the limited extension, the forelimbs of none of the baboons are apted for knuckle or fist-walking. This implicates that a higher degree of terrestriality cannot be expressed in this typically ape form of quadrupedal locomotion.

The form of the trochlear notch might be explained with a greater mobility in the mandrill, a lesser mobility in the baboon, and an even lesser mobility in *Paradolichopithecus*.

The difference in radial notch between the baboon and *Paradolichopithecus* on the one side, and the mandrill on the other side is best explained by a more restricted ulnar-radial mobility in the first, yielding a restricted but more powerful supination.

The aspect of the humeral medial epicondyl shows that *Paradolichopithecus*, and *Papio* to a lesser degree, have a strong flexion ability with abduction. On this epicondyl, the humeral heads of two flexors arise: the *M. flexor carpi ulnaris* (flexion of the hand with abduction) and the *M. flexor digitorum profundus* (flexion of the hand and the digits). The strong development in the baboons fits perfectly well with their terrestrial behavior in which the flexors are used during the acceleration phase. *Paradolichopithecus* and *Papio* have the strongest development, which may be a logic consequence for their inward directed hands. Of these two, *Paradolichopithecus* is the strongest, because the medial epicondyl of the humerus is more pronounced than in *Papio*.

The brachial index of *Paradolichopithecus* and *Papio* is somewhere between that of a power-orientated movement and that of a speed-orientated adaptation. A high brachial index reflects a longer radius in relation to the humerus, and this is

associated with rapidity of movement at the elbow joint whereas a short radius is associated with a power-orientated movement (ANDREWS & AIELLO, 1984). This indicates that *Paradolichopithecus* and *P. hamadryas* are stronger than *P. sphinx* in this respect, and less fast in their arm movements.

### Hind-limb

The absence of the cup-shaped depression for the tibial malleolus on the medial side of the talus provides a kind of locking mechanism to restrict all movements other than strictly dorsal and plantar flexion. A similar construction is seen in *Australopithecus*. *Papio* has a clear depression, to enable rotation of the tibial malleolus, and forms, together with the suspensory flap for the fibula at the lateral talar, the axis of flexion-extension through the ankle. During flexion-extension, the tibial malleolus remains in the cup-shaped talar depression in *Papio*, whereas it slightly departs from it in *Paradolichopithecus* and *Australopithecus*. The shape of the contact area on the medial malleolus of the tibia corresponds perfectly well with the shape of the depression on the medial side of the talus. This articulation determines the direction of movement in the tibio-talar joint. In the baboons, there is a degree of inversion during maximal dorsiflexion, in contrast to *Paradolichopithecus* and *Australopithecus* where the movement remains strictly in the sagittal plane. The permanent contact of tibial malleolus with the talar depression yields a very stable construction, with one rotation axis only. The slight departure in *Paradolichopithecus* and *Australopithecus* results in a compound movement with a rotational and a translational component.

The massive aspect of the tibial malleolus in *Paradolichopithecus*, as in *Australopithecus*, indicates an ability to transfer a greater force. Such an increased force may have been due to a higher body mass or to frequent jumping. A higher body mass need not necessarily be absolute, but may also be relative, which occurs when a larger part of the total body mass is carried on the hindlimbs, or the percentage of bipedal behavior increases as is suggested for *Australopithecus*.

The asymmetrical talar trochlea, due to a higher lateral ridge, yields a more stable tibio-talar joint in the cercopithecines, whereas it fails to do so in *Australopithecus*, who might be thus considered quite unstable in this respect. The advantage, however, of the quite flat trochlea is a more even distribution of body weight over the upper ankle joint. In the baboons the body weight is transferred for the greater part through the lateral side of the talus, the clearest in *Paradolichopithecus* and *Papio*. This means that *Paradolichopithecus* walked mainly on the lateral side of the foot, with the toes curved inwards.

The one-staged, gradual curvature of the lateral trochlear ridge implicates a more evenly body weight distribution in all postures, and does not indicate a preference for a certain posture in the mandrill and *Paradolichopithecus*. The unique two-staged curvature in *P. hamadryas* indicates a very stable rest position.

The three articulation facets for the calcaneum are essential in transferring body weight from the tibia to the calcaneum, and subsequently to the ground. The functional implication of the aspects of the contact area of the medial facet with the talar head might be that in the mandrill the calcaneum and navicular bone have a larger mobility range, as the facets unite. A possible spectrum might therefore consist of eversion, inversion, and flexion at the lower ankle joint, typical for arboreal species. In the others, the facets are separated, thus confining movement of the navicular to eversion and inversion. In general, the very flat medial facet in

*Paradolichopithecus* is very similar to that of *Australopithecus*. Such a flat facet is very suitable in transferring body weight evenly over the lower ankle joint. Differences between the species taken into account are, however, only minimal, thus quite probably they all have a more or less equal calcano-talar joint.

The transfer of body weight on the heel in *Paradolichopithecus* and *Australopithecus* is, as regards the shape of the posterior facet, very comparable, and both are definitely plantigrade walkers. Both have a larger posterior articular area, that transfers the body weight not only more evenly, but is also apted to transfer a larger body weight, absolutely or relatively (see above).

Finally, *Paradolichopithecus* had a toe-flexion comparable to the baboon and mandrill, which is typically cercopithecine. This is one of the major differences with the hominoids, who have an abductable large toe. *Australopithecus* for example was able to use the large toe in grasping things. Development of this flexor is more related to postural behavioral aspects, like holding food particles and picking up things, than to positional aspects, or locomotion.

### **Relation to *Procynocephalus***

The postcranial elements of *Paradolichopithecus* from Vatera might shed some light on the still unclear taxonomic position of *Procynocephalus wimani* SCHLOSSER, 1924 (Late Pliocene, China and India). This large-sized cercopithecine is considered macaque-like with adaptations to cursorial habits in the postcranial, and a dentition adapted similar to that of living savanna baboons. As already suggested by JOLLY (1967) and SIMONS (1970), the genus might be synonymous with *Paradolichopithecus* as they share those features which are used to distinguish *Procynocephalus*. However, till now the relationship between the two genera is unsolved, mainly due to the fact that, despite the large number of references, the latter genus is known from very few specimens, of which the best were never published and are now lost. From the depictions (TEILHARD DE CHARDIN, 1938), however, it is very clear that the unique features of the talus and distal humerus that distinguish *Paradolichopithecus* from the baboons are also shared by *Procynocephalus*. Drawings of this type are usually not conclusive, but the discriminating features are so obvious and unequivocal that a misinterpretation can be excluded. The lateral suspensory facet for the fibular malleolus in proximal view projects only in *Paradolichopithecus* and *Procynocephalus* in such a remarkable degree. The parallel trochlea tali is also a feature that cannot be drawn easily in a wrong way. The gradually descending capitulum of the distal humerus is again a feature that cannot be mistaken.

### **CONCLUSION**

Taking all elements into account, the picture emerges of a highly terrestrial monkey. This is not surprising as many fossil cercopithecines are found in open country habitats and show terrestrial adaptations, such as *Dinopithecus* (Late Pliocene, Africa), *Procynocephalus* (Late Pliocene, China and India), *Paradolichopithecus* (Pliocene, Spain and Asia), *Theropithecus* (Middle Pleistocene – Holocene, Africa) and, among the colobines, *Paracolobus* (Pliocene, East Africa) and *Dolichopithecus* (Pliocene, Europa) (SZALAY & DELSON, 1979). In addition, the larger

species tend to be terrestrial (FLEAGLE, 1998), possibly as a response to predator pressure (KAY & COVERT, 1984). This, too, makes a terrestrial adaptation of our large *Paradolichopithecus* very probable.

Body weight was carried more posterior, as the architecture of the olecranon and the trochlear notch are less apted for sustaining heavy load than is the case in the extant baboons. The morphology of the arm indicates an increased mobility in the elbow joint, with a departure from the sagittal plane during flexion. *Paradolichopithecus* could very well have used his strong arms for carrying food while walking or standing. Another option is the use of the arms in fights and defense.

The massive medial malleolus of the tibia also shows that a larger (part of the) body weight was carried on the hindlimbs. The suspensory facet for the fibular malleolus indicates an increased importance of the lateral malleolus in transferring body weight, and an increased fixation of the talus in the malleolar fork, formed by both the malleoli together.

As to the ankle joint, a remarkable parallel is seen with *Australopithecus*. Unique features that distinguish *Paradolichopithecus*, and probably also *Procynocephalus*, from the other papionins are seen also in *Australopithecus*, though the overall architecture of the *Paradolichopithecus* talus is typically cercopithecoid (pronounced lateral trochlear ridge, hardly developed groove for large toe flexor), whereas it is typically hominoid for *Australopithecus* (symmetrical trochlea, pronounced large toe flexor).

The terrestrial traits in the postcranial elements show that this large monkey was clearly adapted to the habitat: an open savanna/bushland environment with seasonal availability of food, and large distances between the food sources.

## SUMMARY

The faunal record of the Vatera site (Lesvos, Greece; Late Pliocene, MN 17) contains elements that are typical for a savanna environment. Savannas are open habitats, in which a higher degree of terrestriality is advantageous in seasonal foraging. Such a higher degree is also indicated by the morphology of the postcranial material attributed to the monkey *Paradolichopithecus arvernensis* (DEPÉRET, 1929). Though this material has a size and general architecture similar to the mandrill (*Papio (P.) sphinx*) and the baboon (*Papio (C.) hamadryas*), it shows some unique features that clearly distinguish *Paradolichopithecus* from the other cercopithecoids. As regards the talus and tibia, the only taxa that appear to share these unique features are the papionin *Procynocephalus wimani* SCHLOSSER, 1924 (Asia; Late Pliocene) and the hominoid *Australopithecus afarensis* (Africa; Plio-Pleistocene), indicating a kind of parallel evolution between cercopithecoids and hominoids in this respect. The described post-cranial material comprises the humerus, ulna, radius, tibia and talus.

## ΠΕΡΙΛΗΨΗ

Η πανίδα της θέσεως Βατερά (Λέσβος, Ανώτερο Πλειόκαινο, MN 17) περιέχει τυπικά στοιχεία περιβάλλοντος σαβάννας. Οι σαβάννες είναι ανοιχτά ενδιαιτήματα, στα οποία η

αυξημένη ικανότητα κίνησης επί του εδάφους προσφέρει σημαντικό πλεονέκτημα για ένα είδος. Τέτοια ικανότητα δηλώνει η ορφολογία του κρανιακού σκελετικού υλικού που αποδίδεται στον *Paradolichopithecus arvernensis* (DEPERET, 1929). Αν και το υλικό αυτό ομοιάζει ως προς το μέγεθος και τη γενική ορφολογία του με τα αρτίγονα είδη *Papio sphinx* και *Papio hamadryas*, εμφανίζει ορισμένα ιδιαίτερα χαρακτηριστικά, τα οποία διαχωρίζουν σαφώς τον *Paradolichopithecus* από τους άλλους κερκοπιθήκους. Όσον αφορά τον αστράγαλο και την κνήμη, τα δύο είδη που εμφανίζουν όμοιους χαρακτήρες είναι τα *Procynocephalus wimani* SCHLOSSER, 1924 (Ασία, Ανώτερο Πλειόκαινο) και *Australopithecus afarensis* (Αφρική, Πλειο-Πλειστόκαινο), δείχνοντας παράλληλη εξέλιξη σε αυτόν τον τομέα μεταξύ των κερκοπιθήκων και των ανθρωποειδών. Το κρανιακό υλικό που περιγράφεται στην παρούσα μελέτη περιλαμβάνει τα οστά βραχιόνιο, ωλένη, κερκίδα, κνήμη και αστράγαλο.

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