A REVISION OF THE TURKISH MIOCENE HOMINOID *SIVAPITHECUS METEAI*

by PETER ANDREWS *and* I. TEKKAYA

ABSTRACT. A new specimen of fossil ape is described from the late Miocene of Turkey. It consists of a complete palate and lower face, with much of the nasal and zygomatic regions preserved and part of the right orbit. It is considered to belong to the same species as the previously described *Ankarapithecus meteai* from the same deposits, and it is confirmed that the affinities of this taxon are with the genus *Sivapithecus*. Detailed comparisons with the other species of *Sivapithecus*, however, demonstrate that it is different from them, and its synonymy with *S. indicus* proposed by Simons and Pilbeam (1965) is therefore rejected. It now appears that the genus *Sivapithecus* contains three and possibly four species which have only minor differences from *Ramapithecus* species. The generic distinction is nevertheless retained on the basis of morphological differences in I^1, premolars, and mandibular and maxillary robustness. The possibility of relationship between *S. meteai* and the orang-utan, based on similarities in the maxilla and lower face, is discussed.

PALAEONTOLOGICAL work in Turkey is providing evidence for the existence of several fossil ape species living there in the Miocene. This note describes one of these, *Ankarapithecus meteai* Ozansoy, 1957, based on the type mandibular fragment described by Ozansoy (1957, 1965) and a new specimen found in 1967 but described here for the first time. Both specimens were discovered in the Middle Sinap series in Turkey, the mandible from the lower level of the Middle Sinap and the new specimen, which consists of a complete palate and lower face, from the upper level.

The Sinap series was named by Ozansoy (1955) for a sedimentary sequence nearly 100 m in thickness to the north of the village of Yassörien (4 km north-west of Kazan, 55 km north-west of Ankara, Central Anatolia). The lowest deposits in the sequence appear to lack *Hipparion* (Ozansoy 1965), but they are only sparsely fossiliferous. The middle Sinap beds have produced an abundant fauna which indicates a middle Vallesian age for the deposits.

The type mandible of *A. meteai* consists of a left tooth row, P_4–M_3, associated with a symphysis with the crowns of left C–P_3 and right I_2–C. The rest of the body of the mandible was originally present but was broken in the course of excavation, so that there is no doubt that the teeth belong to one individual. The incisor and canines are low-crowned teeth, similar in size to the largest specimens of *Sivapithecus indicus* from the Siwaliks (Simons and Pilbeam 1965) and with the upper part of the range of variation of *Dryopithecus macedoniensis* from Greece (de Bonis *et al.* 1974, 1975). The P_4 is larger than known *S. indicus* specimens, as are M_1 and M_3, but they are only just beyond the range of variation for the Asian species, and M_2 is exceeded in size by at least two specimens. All the molars are within the 95% confidence limits of the *S. indicus* sample: see Table 1. Molar morphology is practically identical to that of *S. indicus*, and on these grounds Simons and Pilbeam (1965) discounted the slight size difference and synonymized *A. meteai* and *S. indicus*.

There has been no reason to question the synonymy of Simons and Pilbeam (1965) until recently, when new evidence for the presence of a large dryopithecine from Greece has been provided by French workers (de Bonis *et al.* 1974, 1975; de Bonis and Melentis 1977a). This dryopithecine was first named *D. macedoniensis* but, on the recovery of a nearly complete palate, it was reassigned to a new genus, *Ouranopithecus*. *O. macedoniensis* is a thick-enamelled form, very similar to *S. indicus* in molar morphology but bigger and with a distinctive morphology of the P_3. The incisors are relatively broad mesiodistally, low crowned, and more robust than those of *S. indicus* (Tattersall and Simons 1969). The I^1 is very much bigger than I^2 and the canines are very robust. The palate is relatively very broad, more so than in *S. indicus*, and the diverging mandibular tooth rows are similarly wider

TABLE 1. Comparison of lower molar sizes between *Ankarapithecus meteai*, '*Ouranopithecus macedoniensis*', and *Sivapithecus indicus* (data for *S. indicus* is taken from Simons and Pilbeam, 1965).

		A. meteai	*S. indicus*		'*O. macedoniensis*'	
			Mean	95% confidence limits	Mean	95% confidence limits
M₁	md*	12·9	11·6	10·0–13·3	14·5	10·4–18·6
	bl*	12·0	10·6	9·7–11·5	13·7	9·1–18·3
M₂	md	15·9	14·2	12·2–16·2	16·0	12·8–19·2
	bl	14·2	12·8	11·2–14·4	15·0	11·7–18·3
M₃	md	15·8	14·8	13·0–16·7	18·3	13·5–23·1
	bl	14·3	12·6	10·6–14·6	15·5	11·5–19·5

* md signifies mesiodistal length and bl buccolingual breadth. All measurements are in millimetres.

apart than in *S. indicus*. The mandibular symphysis and body are deeper and more gracile in *O. macedoniensis* than in *S. indicus*.

The similarity of the *A. meteai* mandible to the new Greek specimens led one of us (Andrews 1976) to group them in one species. As *meteai* has priority over *macedoniensis*, and as it was considered that the new species was simply a larger version of *S. indicus*, the resulting name used was *S. meteai* (Ozansoy 1957). The subsequent description of a nearly complete palate from Greece (RPL 128, de Bonis and Melentis 1977*b*), and its comparison with the new and even more complete palate and lower face from similar-aged deposits in Turkey, raises a number of interesting questions, for example:

1. Is the new palate attributable to *A. meteai* which is from the same series of deposits in Turkey?
2. Is the Turkish hominoid the same as *S. indicus* or *O. macedoniensis* and are these two taxa themselves justified?
3. Does this and other more complete material throw any light on the relationships of the fossil species with any of the living species of ape or with man?

The new palate is registered MTA 2125 and is housed at the Maden Tetkik ve Arama Enstitüsü in Ankara, Turkey.

DESCRIPTION OF NEW SPECIMEN

MTA 2125 consists of a palate with much of the lower face including part of the right orbit at the right zygomatic process of the maxilla. The palate contains the complete dentition, and the alveolar processes are complete on both sides except for a small portion missing posteriorly on the right side. The left palatal process of the maxilla is complete but the right side is broken medio-posteriorly. The right nasal, orbital, and zygomatic processes of the maxilla are complete while, on the left side, the superior and posterior portions are broken away. The nasal bones are missing but, apart from that, the nasal aperture is completely outlined, and the inferior and medial walls of the right orbit are present in two regions. The base of the right zygomatic is preserved, so that the whole of the right lower face is present. There are fresh breaks along the limits of the parts preserved on the right side, so possibly more of this specimen may yet be found. The specimen is shown in text-figs. 1 and 2.

Maxilla

The most striking feature of the maxilla, MTA 2125, is the great development of the zygomatic region. This is preserved intact on the right side (text-fig. 1). The root of the zygomatic process is situated relatively posteriorly, above M², and it is sharply angled, passing directly laterally and slightly anteriorly before passing posteriorly into the zygomatic arches. This is best seen in top view (text-fig. 1c). Between the zygomatic process of the maxilla and the alveolar and nasal processes there is a very deep canine fossa, a product of the sharp
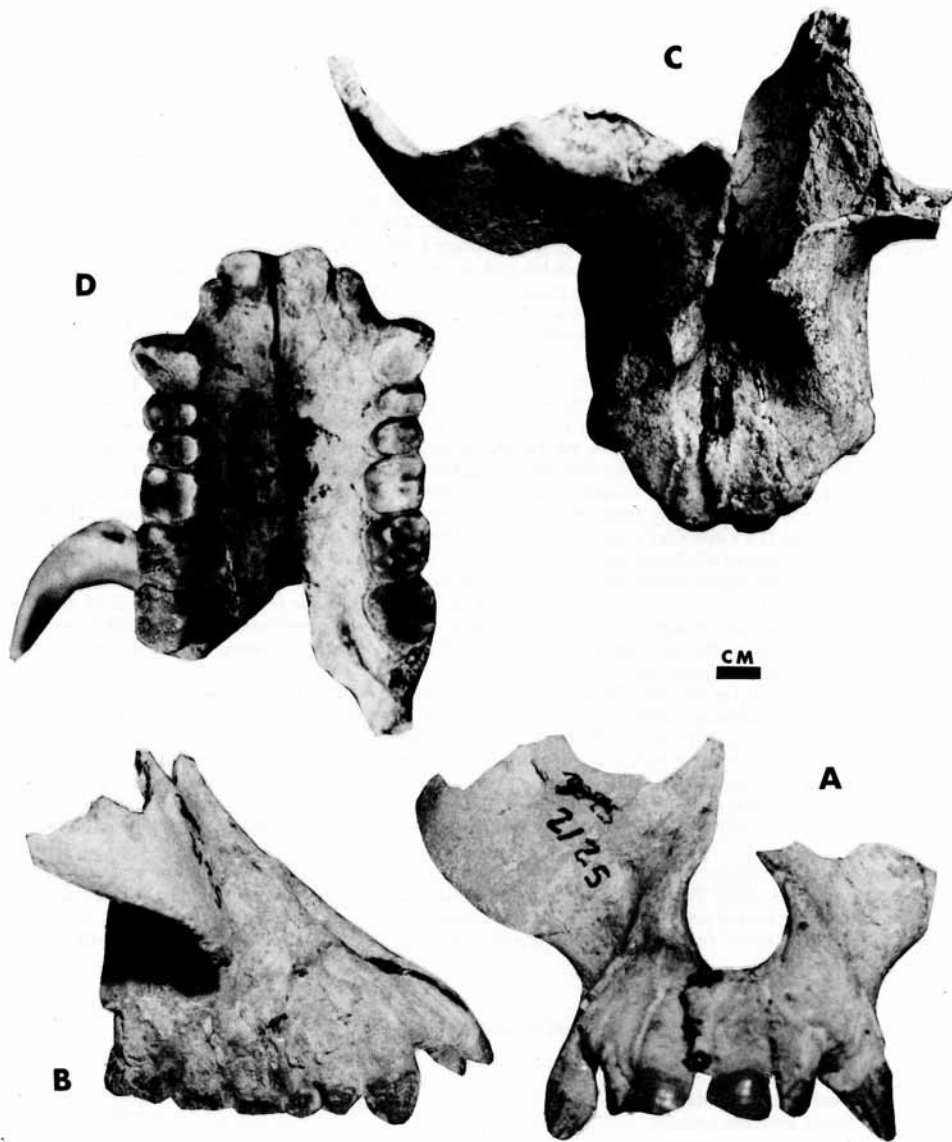
TEXT-FIG. 1. Specimen MTA 2125. A, frontal view; B, view from the right side; C, superior view showing the inferior surface of the right orbit and the matrix filled left maxillary sinus; D, palatal view.

angulation of the zygomatic rather than, as is more usual, of the compression of the anterior part of the face. This specimen therefore has the unusual combination of a flat upper face, resulting from the flattened zygomatic processes, and a projecting snout. The latter is partly the result of the posterior position of the zygomatic processes, but is also emphasized by the high degree of premaxillary prognathism. This is indicated by two measurements in Table 2, the projection in a horizontal plane of the premaxilla and maxilla in front of the lower edge of the zygomatic processes, and the length of the premaxilla from alveolare to nasospinale.

The bizygomatic width of the face could be estimated by measuring from the right side of the process to the midline and doubling (text-fig. 1A) and the resulting value of 155·2 is very high for a primate of this size. It is within the range for male gorillas and is intermediate between male and female orang-utans. Similarly the depth of the zygomatic process, which was estimated by measuring the distance between the lowest point on the lower border of the orbit and the base of the zygomatic process, giving a value of 39·5 mm, is only matched by male gorillas and orang-utans. The flattened zygomatic region of the face is therefore both very wide and very deep, and this is coupled with a long lower face due to the projecting snout. It does not, however, appear to be coupled with a long upper face, for the nasal bones are short, and the nasal height, estimated from the distance from nasospinale to the superior break of the orbital process of the maxilla, which was undoubtedly only a few millimetres short of nasion, has a minimum value of 66·5 mm. This is below the range of variation of the gorilla, above that of chimpanzees, and intermediate between male and female orang-utans.

The right nasal bone, which is missing but which has been broken off along the nasomaxillary suture, was a short and narrow bone (text-fig. 1A). The maximum width of the bone, from the nasomaxillary suture to the midline, is 5·5 mm, so that the basal width across the nasal bones can be estimated as 11·0 mm. The nasal bones tapered sharply towards nasion (text-fig. 1A) and although the nasal process is broken just short of the maxillofrontal suture it would appear that they narrowed almost to a point. This resembles the condition found in all of the living great apes and is closest to the orang-utan, in which the nasal bones are narrower at the base as well, but it differs sharply from the condition seen in the African early Miocene apes. All three species of *Proconsul* (Le Gros Clark and Leakey 1951; Pilbeam 1969) have long, fairly broad, and almost parallel-sided nasal bones (Whybrow and Andrews 1978). The length of the nasal bones in MTA 2125, from the base of the nasomaxillary suture to the break just short of the nasofrontal suture, is 31 mm, and this compares with similarly measured minimum lengths of 46 mm for *P. major* (Pilbeam 1969) and 34 mm for *P. nyanzae* (Whybrow and Andrews 1978). In the same way the estimated nasal height of 66·5 mm for MTA 2125 is well below that of both *P. nyanzae* and *P. major*, so that its nasal region is considerably shorter than in comparable-sized species of *Proconsul*.

Consistent with this is the relatively broad nasal aperture in MTA 2125. Is is almost as broad as it is long (Table 2) and is unlike the long narrow apertures of the African early Miocene apes (Andrews 1978). It is, however, very similar to the nasal aperture of the recently described *O. macedoniensis* palate from Greece (RPL 128, de Bonis and Melentis 1977) which has slightly larger nasal aperture dimensions of approximately 25·8 mm broad and at least 27·0 mm high. Among the living great apes this combination of narrow tapered nasal bones and broad nose appears most commonly in chimpanzees; orang-utans tend to have very narrow nasal bones but they also have relatively high narrower noses, while gorillas often have very broad nasal bones and rather broader noses.

The position of the right orbit relative to the midline permits some approximate measurements to be made of the orbits on MTA 2125. The right orbit has an estimated minimum breadth of 32·5 mm, but its height is unknown. The most medial point of the right orbital border is 6 mm from the midline, so that the estimated minimum breadth between the orbits is approximately twice this (Table 2). The distance of the most medial

TABLE 2. Facial measurements of MTA 2125.

Bizygomatic width	155·2
Alveolare to nasospinale	19·5
Nasal height (minimum)	66·5
Nasal aperture breadth	23·0
height	24·5
Horizontal projection of alveolare from the plane of the zygomatic processes	53·0
Orbit breadth	32·5
Minimum biorbital breadth	12·0
Biorbital breadth across lacrymal crests	15·2
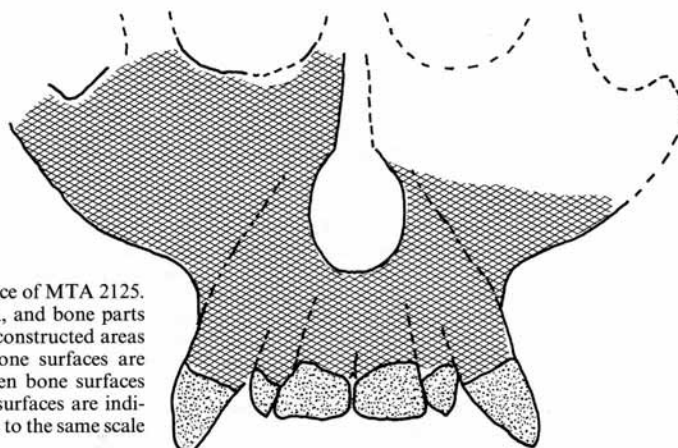
TEXT-FIG. 2. Reconstruction of the face of MTA 2125. The drawing is based on text-fig. 1A, and bone parts present are shown stippled, while reconstructed areas are left blank. Intact or sutural bone surfaces are shown by a heavy black line, broken bone surfaces left blank, and reconstructed bone surfaces are indicated by a dotted line. The drawing is to the same scale as text-fig. 1.

and superior point of the lacrymal fossa from the midline is 7·6 mm, so that the distance between the orbits across these two points is 15·2 mm (Table 2). This compares with values ranging from 14·6 to 24·8 mm for the three species of *Proconsul* (Whybrow and Andrews 1978) using the same points and is less than the values for male chimpanzees and gorillas, although it just comes within the range given for female chimpanzees (Pilbeam 1969). It is well within the range for orang-utans, and there is no doubt that, like the orang-utans, the orbits of MTA 2125 were set very close together. This is illustrated in text-fig. 2, which shows a reconstruction of some of the missing parts on the left side drawn in to match the equivalent parts on the right.

The alveolar processes of the maxilla are straight and almost parallel. The external borders of the palate diverge posteriorly so that the breadth across the M^2 exceeds that across the canines (see Table 3). The Greek palate RPL 128 (de Bonis and Melentis 1977b) resembles the Turkish one in this respect except that over all the palate of MTA 2125 is 6–8 mm narrower than RPL 128. Both specimens contrast with *P. major*, in which the tooth rows converge posteriorly as in male great apes, although the degree of sexual variation in this feature is so great as to render the difference insignificant (Pilbeam 1969). Internally also the breadths between endomolaria in MTA 2125 and RPL 128 are almost identical to the bicanine width, but the palate of MTA 2125 again appears narrower over all than the Greek palate RPL 128 (see Table 3).

It was not possible to measure the length of the palate because posteriorly the central part of the palate is missing. However, the length of the alveolar process could be measured on the left side, and this gives an approximation to palate length. It has very similar dimensions to the alveolar process of *P. major* and as a result the internal palate shape, as indicated by the endomolare breadth divided by the length of the alveolar process, is similar in the two specimens (Table 3). The palate from Greece, RPL 128, appears much broader (see Table 3), but a new palate of *S. indicus* from Pakistan (Pilbeam *et al.* 1977) has similar proportions to MTA 2125. The palate of MTA 2125 is rather shallow, as in most fossil apes, approximately 11·5 mm at the level of M^1. The greater palatine foramina are set well forward alongside the crowns of M^3.

TABLE 3. Palatal measurements of MTA 2125 compared with the roughly contemporary palate from Greece (RPL 128, de Bonis and Melentis 1977b) and the palate of *Proconsul major* from early Miocene deposits in Uganda (UMP 62-11, Pilbeam 1969).

	MTA 2125	RPL 128	UMP 62-11
External breadth across the canines	59·0	64·0	66·5
External breadth across the M^2	61·9	70·8	62·5
B at M^2/B at C $\times 100$	105·0%	110·6%	94·0%
Endomolare breadth (M^2)	34·4	40·0	33·4
Length of alveolar process	93·5	(89)	95·8
Endomolare B/L alveolar process $\times 100$	36·8%	45%	34·9%

The alveolar processes of MTA 2125 appear to be fairly robust, but it has not been possible to assess their degree of inflation because the matrix has not yet been removed from the maxillary sinuses. The extent of the floor of the left maxillary sinus is shown, in text-fig. 1c, to be limited in extent, not passing into either the zygomatic processes or the posterior tuberosities of the alveolar processes, even though both these elements are relatively large. The floor of the maxillary sinus extends anteriorly only as far as the distal half of M¹ rather than to P⁴ as is normally the case. Even the relatively restricted maxillary sinus of *P. major* (Pilbeam 1969) extends anteriorly to the P⁴ and passes also into the zygomatic processes and the alveolar tuberosities.

Dentition

The upper central incisor on MTA 2125 is a large spatulate tooth (text-fig. 1D). It is similar in size to the I¹ of *S. indicus* but is slightly stouter and is much lower crowned. The degree of wear on the incisors, however, is so great that the height measurements, given in Table 4, must be considerably lower than on unworn teeth. The I¹ of *S. darwini* from Pasalar in Turkey is smaller and even more high crowned than *S. indicus* (Andrews and Tobien 1977). The I¹ on MTA 2125 is most similar to that of the Greek palate, RPL 128 (de Bonis and Melentis 1977), and comparative measurements for this specimen and for *S. indicus* are given in Table 4. Both the Greek and the Turkish specimens have low-crowned incisors, and in both the I¹ is very much larger than the I². This is particularly true of MTA 2125, in which I¹ is more than twice the length of I², but the relation of I¹ to I² on RPL 128 approaches this, with an index value (I¹/I² × 100) of 179%. The incisors of the African apes and most dryopithecines are closer to each other in size, with I¹/I² index values ranging between 120% and 150% (Andrews 1978), and only in the orang-utan among living apes is the I¹ nearly twice the size of I².

The canine of MTA 2125 is also very low crowned (text-fig. 1D). In crown area it is slightly bigger than in *S. indicus*, but in crown height it is smaller than in most fossil ape species. It is also considerably more robust than in *S. indicus* and *S. darwini*. Indeed, it is more robust and low crowned (with one exception) than in any other fossil or living ape known at present, the index values for breadth against length and length against height being 89% and 95% respectively (Table 4). The exception again is the Greek palate (RPL 128), in which the canine index values are 87% and 99% respectively (Table 4). In both specimens the canine is considerably worn, so that the height measurement may be underestimated, but the other dimensions are not affected. Little morphological detail can be seen because of the wear, but both specimens have an unusually deep mesial groove. In many apes the mesial groove is obliterated by wear at a fairly early stage in dental wear, but on these two specimens, even though they are both heavily worn, the mesial groove is still prominent.

Although the incisors and canines in the Turkish and Greek palates (MTA 2125 and RPL 128) are practically identical in size and morphology, they have rather different proportions to their respective postcanine teeth. The molars and premolars of MTA 2125 are considerably smaller than in RPL 128, so that the ratios between the anterior and posterior teeth are much higher. This can be illustrated by comparing the cross-sectional areas of the canine and the first molar. In MTA 2125 the C is larger than M¹, the index (C/M¹ × 100) being 122%, and in RPL 128 it is smaller, the index being 95%. At first sight such a difference is reminiscent of sexual variation. The C/M1 ratio is one often used to measure sexual dimorphism, as it relates the size change of the dimorphic canine to the more stable M1, but in this case the canines are identical in size and it is the

TABLE 4. Measurements of detition of MTA 2125 compared with RPL 128 from Greece (de Bonis and Melentis 1977*b*) and mean values for *Sirapithecus indicus* (sample sizes are given in brackets).

	Length*			Breadth*			Buccal height		
	MTA 2125	RPL 128	*S. indicus* mean	MTA 2125	RPL 128	*S. indicus* mean	MTA 2125	RPL 128	*S. indicus* mean
I¹	11·6	11·6	11·6 (1)	9·4	9·5	8·9 (1)	9·4	8·0	13·1 (1)
I²	5·5	6·5	—	6·6	6·0	—	7·1	4·8	—
C	14·9	14·9	15·5 (4)	13·2	13·0	10·9 (4)	15·7	13·1	20·5 (2)
P³	8·9	9·7	9·0 (3)	12·0	13·7	11·9 (3)			
P⁴	7·8	9·2	7·6 (4)	12·4	14·4	11·9 (4)			
M¹	11·8	13·7	11·4 (7)	13·7	14·8	12·4 (7)			
M²	13·5	15·0	12·5 (7)	14·3	16·3	14·2 (7)			
M³	14·5	14·6	12·2 (4)	14·7	15·7	13·4 (4)			

* Lengths are mesiodistal and breadths are buccolingual, except in the case of the canine, in which the length is the maximum length of the crown and the breadth is measured perpendicular to the maximum length.

molars that are different. As such it appears that the Turkish palate must represent a smaller individual with relatively larger canines than in the Greek palate.

The upper premolars on MTA 2125 are almost equal in size, the P^3 being slightly smaller than the P^4. The P^3 is buccally elongated so that it has a bluntly triangular outline: the midline length of P^3 is 7·8 and the lingual length is 6·9, comparing with the buccal length (Table 4) of 8·9. In these dimensions the P^3 is very similar to the P^3 of *S. indicus* and *S. darwini*, except that on the former the mesiobuccal angle of the crown projects mesially into a beak-like process which is absent on the Turkish specimens. They all differ from the Greek palate (RPL 128) on which the P^3 is considerably larger, the mesial and distal borders of the crown are almost parallel, and the P^3 is exactly the same size as the P^4. The P^4 on MTA 2125 is almost identical to that of *S. indicus* and *S. darwini* and again differs from the P^4 of RPL 128 in being considerably smaller (Table 4).

The upper molars of MTA 2125 are flattened by wear (text-fig. 1D). Almost all the enamel has been worn away from M^1 and dentine exposed; M^2 has dentine exposed mesiolingually and P^4 lingually; and the enamel on M^3 is worn flat but with no exposure of dentine. The molars have squared outlines, with large areas of contact with each other, and they increase in size from M^1 to M^3. Little crown detail can be seen on M^1 because of the wear, but M^2 has a well-defined crista obliqua and no traces of lingual cingulum. The protocone becomes progessively bigger on M^1 to M^3, and the distal cusps are progressively reduced, but this has not resulted in any reduction in size of the M^3, which is both the longest and the broadest tooth in the tooth row (text-fig. 1D).

In both size and morphology the molars of MTA 2125 correspond most closely to those of *S. indicus* and *S. darwini*. There are, however, a few differences, particularly in the molar proportions and the squared outline of the molars. The M^1 of MTA 2125 is at the top of the size range of *S. indicus* and *S. darwini* but is smaller than the M^1 of the Greek palate RPL 128; but the M^3 approaches the latter in size and is very much bigger than the M^3 of *S. indicus* and *S. darwini*, on both of which the M^3 is smaller than M^2 (Table 4). An enlarged M^3 is an unusual feature in dryopithecines, and only occurs in one other group, *Rangwapithecus* species from the early Miocene of East Africa (Andrews 1978), but with only one specimen it is difficult to assess the significance of this character in the Turkish specimen. The squared appearance of the molars also differs from the condition in both *S. indicus* and *S. darwini*, as well as the Greek palate RPL 128, all of which have molars with more rounded crown outlines and with some degree of distal abbreviation of the crowns on M^2 and M^3. Again, the significance of this difference is uncertain because of the small number of specimens, although the pattern is well established for *S. indicus* and *S. darwini*.

Association of MTA 2125 with the type specimen of Ankarapithecus meteai

A number of palatal and mandibular dimensions have been compared with each other to assess the degree of similarity between MTA 2125 and the mandible of *A. meteai*. These include intercanine, interincisor (I2), and intermolar widths plotted against tooth row length for samples of chimpanzees, gorillas, and orang-utans. Comparing the Turkish mandible and palate with the samples of living apes, the over-all shape and relative breadths of mandible and palate are consistent with each other even to the extent of belonging to the same sex (probably male). In other words, the over-all similarity in shape between the fossil mandible and maxilla is greater than would occur within one species of living ape if different sexes were compared. The degree of difference displayed by the five mandibles and one palate from Greece (de Bonis *et al.* 1974, 1975; de Bonis and Melentis 1977a) confirms that they also belong to a single species, and it also suggests that the palate RPL 128 could be a female, for it is closer to the small mandible (RPL 54) than to the three larger ones (RPL 55, 56, and 75). This is contrary to the conclusions of de Bonis and Melentis (1977b), but a female sex for RPL 128 is also indicated by the relatively broad palate, the posterior divergence of the tooth rows, and the small canine size relative to M1.

Much of the morphological detail in the palate MTA 2125 is also consistent with its association in one species with the mandible of *A. meteai*. The deep symphysis of the mandible is consistent with the very long premaxilla (Table 2) and the degree of alveolar prognathism. The laterally compressed incisor tooth row on the mandible is consistent with the maxillary incisor compression, and the upper and lower I2s are similarly more robust than the I2s of the Greek specimens. The more robust I_2 could also be related to the relatively larger I^1 of MTA 2125, as both I_1 and I_2 occlude against I^1, and only to a lesser extent against I^2, in most ape species. The bilaterally compressed canine in the mandible of *A. meteai* seems to contrast with the exceptionally robust upper canine in MTA 2125, but

the same pattern is present in the Greek sample: breadth/length × 100 indices range from 62% to 68% for the lower canines on the four Greek mandibles compared with 87% for the upper canine in RPL 128. The corresponding values for the two Turkish specimens are 71% and 89%. Finally, the upper molars of MTA 2125 are consistent both in size (e.g. M_1–M_3 lengths) and morphology with the lower molars of the *A. meteai* mandible.

RELATIONSHIPS OF THE TURKISH HOMINOIDS

As it appears that the new palate from Turkey is consistent morphologically with the type mandible of *A. meteai*, it remains now to decide on the taxonomic affinities of these specimens. In the course of the description of the palate, comparisons have been made with species of *Sivapithecus* and *Ouranopithecus* as these are clearly the most similar to the Turkish specimens. and these comparisons will now be briefly reviewed.

The upper dentition of MTA 2125 shows many similarities with *S. darwini*, which is known from earlier deposits in Turkey. The incisors and canines, however, are larger and lower crowned and, in the case of the C, are also more robust. In these features *S. darwini* retains the primitive dryopithecine condition and MTA 2125 has the derived character state (Andrews and Tobien 1977), a state that it shares with *O. macedoniensis*. Similarly in the lower dentition, *S. darwini* retains a number of primitive characters, such as molar cingula, compressed trigonid basins, and elongated M_3 talonids that are changed or absent in the mandible of *A. meteai*. There is therefore little doubt that these specimens represent something different from *S. darwini*.

The Turkish specimens also have many similarities with *S. indicus*. They can, however, be distinguished from *S. indicus* by the following characters: the I^1 is more robust and lower crowned; I^2 is extremely small relative to I^1; C is more robust and $\overline{C}$ is less robust; the mesial edge of P^3 is straight, not beaked as in *S. indicus*; P_4 is larger and more molariform; the upper molars increase in size from M^1 to M^3, so that M^3 is large and is not reduced as in *S. indicus*; upper molars are more elongated; and M_3 also is relatively larger than M_1 and M_2 than in *S. indicus*. In all of these characters, except possibly the degree of bilateral compression of the lower canine, *S. indicus* retains what may be interpreted as the ancestral dryopithecine condition, and the new Turkish specimens have the derived condition which is often shared with *O. macedoniensis*. In the case of the lower canines, a bilaterally compressed crown would appear to be the ancestral dryopithecine character state, but it is then associated with a similarly compressed upper canine. It may be that the combination of a compressed lower canine and a very robust upper canine may itself be a derived character state, and it has been shown that there is good evidence for accepting this combination in both the Greek *O. macedoniensis* and in the Turkish specimens. When these differences in proportion and morphology between the Turkish specimens and *S. indicus* are combined with the slight size difference between them, we consider that they are sufficiently distinct to make their allocation to separate species necessary.

This leaves one further species to be considered, *O. macedoniensis*. The palate of *O. macedoniensis* is wider than in MTA 2125, the tooth rows are more diverging, and the postcanine teeth have different proportions to the incisors and canines. The first two of these differences may be exaggerated by the distortion of the palate in RPL 128, the only maxillary specimen of *O. macedoniensis*, and in any case they are often the product of sexual variation: in modern ape species females have relatively wider and more diverging palates than the males and, as ranges of variation of 10–15% are quite common (Pilbeam 1969), the difference between the Turkish and Greek specimens (9%) could be the result of sexual variation. In this case MTA 2125 with its narrow palate would be at the male end of the range of variation, and RPL 128 towards the female end. However, the third difference appears inconsistent with this, for it has been shown that RPL 128 is larger than MTA 2125 in its postcanine dentition (Table 4) while their canines and incisors are of approximately equal size. In the four most complete mandibles of *O. macedoniensis*, which shows an enormous degree of sexual dimorphism (de Bonis and Melentis 1977b), the canine/first molar crown area index has a range of 48–77%, and the equivalent index for the maxilla RPL 128 is 91%. The

index for the mandible of *A. meteai* is 95%, well above the highest value for the Greek mandibles, and for the maxilla MTA 2125 the value is 122%, also higher than in the single Greek maxilla. This degree of difference, however, is less than that within single species of living great apes, but the larger first molar of RPL 128 suggests that it came from a larger individual than did MTA 2125 which nevertheless had a relatively larger canine.

There are two minor characters in the dentition that distinguish the Turkish material from *O. macedoniensis*. One of these concerns the distinctive morphology of the P_3 on all of the *O. macedoniensis* mandibles. The P_3 has a triangular outline because of the greatly expanded mesiobuccal part of the crown, and the axis of the crown has rotated transversely so that the distolingual ridge, which is very prominent, runs almost directly lingually and delimits a very prominent distal basin or fovea. This appears to be a unique specialization of the P_3 of *O. macedoniensis*, and distinguishes it from the P_3 on the *A. meteai* mandible, which has retained the primitive condition in common with *S. indicus*. The other feature of the dentition is the enlarged M^3 of MTA 2125, which differs from the primitively reduced M^3 of *O. macedoniensis* and most other fossil apes.

It is concluded that the new Turkish material confirms the distinction at the species level between *A. meteai* and *S. indicus*, contrary to the synonymy proposed by Simons and Pilbeam (1965), but there appears to be no good reason for separating them generically. Similarly *O. macedoniensis* appears conspecific with *A. meteai* and, since *meteai* Ozansoy, 1957 has priority over *macedoniensis* de Bonis *et al.*, 1974, and *Sivapithecus* Pilgrim, 1910 has priority over *Ankarapitheicus* Ozansoy, 1957, and *Ouranopithecus* de Bonis and Melentis 1977*b*, the name for the Greek and Turkish material is *S. meteai* (Andrews, 1976). This shares with other species of *Sivapithecus* the suite of derived characters mainly related to the thick enamel on the molars (Andrews 1976) and superimposed on this are the species-specific characters mentioned earlier. Thus *S. darwini* is within this group but still retains many primitive dryopithecine characters. *S. indicus* and *S. meteai* share a minor suite of derived characters which distinguish them from *S. darwini*, for example the enlarge molar trigonid, reduced M_3, and loss of molar cingula. Finally, *S. meteai* has a further suite of derived characters distinguishing it from *S. indicus*, which retains the primitive condition with respect to these characters, for example low crowned I^1 and C, enlarged I^1 relative to I^2, robust C̲ and enlarged P_4. The Greek material of *S. meteai*, with its unique P_3 morphology and relatively small canine, and the Turkish material, with its enlarged M^3 relative to M^2, both have derived conditions relative to each other (and to *indicus*), but it is considered that these characters are of insufficient importance to separate them specifically.

DISCUSSION

The three species of *Sivapithecus* discussed here have a time span of at least five million years. They first appear in the beginning of the middle Miocene, at which time the closely related genus *Ramapithecus* is also first known (Andrews and Tobien 1977), and both genera survive well into the late Miocene. *Ramapithecus* and *Sivapithecus* are also extremely similar in morphology, and it must be questioned whether their recent division into separate subfamilies (Pilbeam *et al.* 1977) is justified by the evidence. Pilbeam gives, as his only reason for distinguishing the Ramapithecinae and the Sivapithecinae, the small and less dimorphic canines in *Ramapithecus*, but even with all the new material that has been described in recent years there is still only one known association of a canine with posterior teeth, on the type specimen of *R. wickeri* (Leakey 1962). Pilbeam's evidence, therefore, must be based on the small number of isolated teeth known for this genus (Andrews and Walker 1976; Pilbeam *et al.* 1977), but isolated teeth must be used with extreme caution because their identification is often doubtful. This is particularly true of the Siwalik specimens, for it is possible that the larger canines that are assigned to *Sivapithecus* may include some *Ramapithecus* specimens, in which case the sample is biased for the very character on which the distinction is being made between the two subfamilies.

The presence of a bias is suggested by the present confusion over the affinities of another supposed species of *Sivapithecus*, *S. sivalensis* (Simons and Pilbeam 1965). This species is very similar in

both size and morphology to *Ramapithecus*, and it differs, in fact, only in having very slightly larger canines. For example, the length and breadth dimensions of KNM-FT 46, the only known associated canine of *Ramapithecus*, are 10·0 and 8·5 mm, while the ranges for three specimens of *S. sivalensis* (GSI D 1, GSI D 299–300, and K23/212) are 10·8 to 13·5 and 7·4 to 11·2, lengths and breadths respectively in millimetres. It seems very likely that these specimens could represent the upper end of the range of variation of *R. punjabicus* together with the isolated teeth of similar size, and in this case Pilbeam's (1977) distinction drawn between *Sivapithecus* and *Ramapithecus* disappears.

Ramapithecus and *Sivapithecus* are in fact so similar that it may be questioned whether they should even be retained in separate genera. They share the character complex related to thick enamel on the cheek teeth, which was mentioned earlier as being diagnostic of the *Sivapithecus* Group, and on this evidence alone they may be considered as sharing a common ancestry, and their systematic distinction must depend on the presence in one or both of derived characters not shared by the other. One such difference may be seen in the morphology of I^1, which in *Sivapithecus* species has a massive lingual cingular swelling (Tattersall and Simons 1969) that is interpreted as a derived condition compared with the primitive lingual tubercle present in *Ramapithecus* (Andrews and Tobien 1977). Other differences, on the premolars, are the large size of the lower premolars relative to the molars and the strongly oblique angle of the P_3 with respect to the molar tooth row in *Ramapithecus*: although still primitively single-cusped, as in *Sivapithecus*, the large size and angulation of the P_3 and the large size of P_4 in *Ramapithecus* are interpreted as derived conditions probably related to initial molarization of the premolars, and *Sivapithecus* retains the primitive condition in these characters. Finally, a possible third difference is in the greater robustness of the mandibular and maxillary bodies of *Ramapithecus* (Simons and Pilbeam 1965; Andrews and Walker 1976), but this formerly clearcut difference is becoming less distinct as more material is added to the collections. As the species of *Ramapithecus* share these three characters and none of the *Sivapithecus* species do so, it may be tentatively concluded that the generic distinction between them can be retained.

In the description of the maxilla and dentition of *S. meteai*, the closest comparisons in most cases were with the orang-utan, and this could indicate some degree of relationship between it and the orang-utan. The significance of the orang-like morphology in *S. meteai* is, however, by no means clear. It has a deep and widely flaring zygomatic process, marked alveolar prognathism that is combined with a short upper face, and a narrow interorbital distance, all of which are characters of the maxilla that are shared only with the orang-utan among hominoid species. The dentition lacks the characteristic secondary wrinkling seen in orang-utan teeth today, but the large I^1 relative to I^2 and the large squared molars are characters shared exclusively with the orang-utan. In contrast to this, the characters shared with the African apes are less impressive: the shape of the nose is more similar to that of the chimpanzee, and the length of the molar teeth, with the large M^3, is closest to the condition seen in gorillas. Some of these characters are also present in the maxillae of *S. indicus* and *Ramapithecus*, but whether all of them are therefore related to the orang-utan or whether the similarity is due to a functional convergence resulting, perhaps, from similar dietary adaptations in similar habitats, is not known at present. *Sivapithecus* species have been considered by many authors in the past (see Simons and Pilbeam 1965 for discussion and references) to represent ancestral orangutans mainly because the fossils are known in the right place (Asia) and the right time (middle to late Miocene). Such arguments carry no weight in the absence of morphological similarity, but with the evidence of similarity presented here between *S. meteai* and the orang-utan the likelihood must be increased that they are related.

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PETER ANDREWS

Department of Palaeontology
British Museum (Natural History)
Cromwell Road
London SW7 5BD

I. TEKKAYA

Paläontoloji Servisi
Maden Tetkik re Arama Enstitüsü
Ankara, Turkey