Restoration of the Type and Palate of *Ankarapithecus meteai:* Taxonomic and Phylogenetic Implications

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ABSTRACT   A small number of large hominoid specimens are known from the late Miocene of Turkey. (This paper focuses on the two specimens known until 1996. New fossils described by Alpagut et al. ([1996] Nature *382:*349–351) are briefly discussed in this paper as well.) Among these, a fragmentary mandible is the type specimen of *Ankarapithecus meteai.* Another specimen, a partial face, is from the same taxon. Based on the morphology of this face, *Ankarapithecus meteai* was synonymized with *Sivapithecus* (Andrews and Tekkaya [1980], Paleontology 23:85–95). The facial specimen was recently restored by the authors, exposing much anatomy that had previously been obscured. The new anatomical details reveal many important differences from *Sivapithecus* and justify a revision of the nomen *Ankarapithecus. Ankarapithecus* was a large hominid (great apes and humans) in the clade that also includes *Sivapithecus* and *Pongo. Sivapithecus* and *Pongo* share derived characters not found in *Ankarapithecus,* which is thus the sister clade to the *Sivapithecus-Pongo* clade. While the results of this analysis support the sister relationship of *Sivapithecus* and *Pongo,* there is some uncertainty regarding paleobiogeographic and taxonomic relationships to the large hominids from the Siwaliks. An *Ankarapithecus*-like taxon may have been ancestral to *Sivapithecus,* or an early Siwalik (Chinji formation) taxon, which predates both *Sivapithecus* sensu stricto and *Ankarapithecus,* may be ancestral to both. Am J Phys Anthropol 105:279–314, 1998.   © 1998 Wiley-Liss, Inc.

Ankarapithecus meteai is the nomen given to a mandibular fragment and associated postcanine dentition from Central Anatolia (Ozansoy, 1965). It was recovered from the middle Sinap levels of what Ozansoy called the Sinap series, at a place called Sinap Tepe (Sinap Hill), near the town of Yassıören, 55 km northwest of Ankara (Ozansoy, 1957). A recent description of the fauna and magnetostratigraphy of Sinap Tepe places the Sinap formation, including the middle member from which the primates derive, in the early Vallesian mammal age, or MN 9 (Sen, 1991; Mein, 1986). More recent work on the Sinap sediments and magnetostratigraphy indicates an absolute date of 10.1 Ma for the levels from which the primates derive (Kappelman et al., 1996). Sen (1991) concludes that Sinap Tepe was probably a warm, humid savanna-woodland. The large number of herbivores are indicative of relatively open country, but an abundance of browsers and suids also implies more forested conditions. A great deal more recent work on this fauna will bring into much sharper focus the paleoecology of this site (Kappelman et al., 1996).

Ozansoy (1965, 1970) describes the hominoid mandibular specimen in detail, noting

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differences in dental size, morphology, and symphyseal morphology from other fossil apes (*Sivapithecus, Dryopithecus*), modern apes, and fossil humans. In particular, Ozansoy (1965, 1970) notes that *Ankarapithecus* differs from *Sivapithecus, Dryopithecus,* and living great apes in having relatively small lateral incisors, a narrow symphysis, a mental eminence, and broad molars. He also notes specific differences from *Sivapithecus* and *Dryopithecus* alone. According to Ozansoy, *Ankarapithecus* is distinguished from these other fossil great apes in having a smaller M_3/M_2 ratio, a broader M_3 with more rounded cusps, and more medially placed canines. He also notes specific resemblances to orangutans in symphyseal and canine morphology. He notes specific similarities to *Homo* as well (mental eminence, P_4 cusp morphology, and small M_3 [recognized by Ozansoy as a variable trait occasionally found in living great apes]. Ozansoy (1970) states that the dental eruption sequence in *Ankarapithecus* is most like that of *Homo erectus* and *Australopithecus,* though this conclusion must be considered speculative. In other details of molar proportions and occlusal anatomy, Ozansoy (1965, 1970) recognizes specific similarities to individual species of *Sivapithecus,* though none represent to him compelling evidence to include the Turkish specimen in the genus *Sivapithecus.*

Most other researchers have stressed morphological similarities to *Sivapithecus* from South Asia. Simons and Pilbeam (1965) synonymized *Ankarapithecus meteai* with *Dryopithecus indicus* (= *Sivapithecus indicus*). They note that the mandibular dental dimensions of the type of *Ankarapithecus meteai* are larger than in *Sivapithecus indicus,* but they attribute this to Cope's rule of increasing size in time successive populations. They also note that *Ankarapithecus* cannot be distinguished from *Sivapithecus indicus* on morphological grounds, though the morphology of the Turkish specimen is not described. At the time, *Dryopithecus indicus* and *D. sivalensis* (= *Sivapithecus* sp. today) included most of the hominoid material from the Siwaliks not included in *Ramapithecus* or *Gigantopithecus.* With the revision of *Ramapithecus* (Greenfield, 1979; Pilbeam,

1982) and the discovery of more specimens, this sample has generally been subdivided into several different species of the genus *Sivapithecus* (Kay, 1982; Kelley and Pilbeam, 1986).

Andrews and Tekkaya (1980) also indicate that the type of *Ankarapithecus* is morphologically very close to *Sivapithecus indicus.* Though they note that the teeth of *Ankarapithecus* are larger than in *Sivapithecus indicus,* they indicate that the molars of the Turkish specimen fall within the 95% confidence limits of the means for lengths and breadths in *Sivapithecus indicus* (Table 1 in Andrews and Tekkaya, 1980). More recently described specimens of *Sivapithecus,* attributed to *Sivapithecus parvada* (Dehm, 1983; Kelley, 1988), are considerably larger than both *Sivapithecus indicus* and *Ankarapithecus,* indicating that *Ankarapithecus* is dentally within the size range of *Sivapithecus.* *Ankarapithecus* as known only from the mandible does resemble *Sivapithecus* closely enough to be reasonably attributed to this taxon. Given the known amount of mandibular diversity in *Sivapithecus* (Brown, 1989), it would be reasonable to attribute this specimen to *Sivapithecus* despite the morphological and paleogeographic differences. The early Vallesian age of the middle Sinap level is also contemporaneous with some Siwalik *Sivapithecus* (Pilbeam et al., 1979; Kappelman et al., 1991), so the attribution of the mandible to *Sivapithecus* has not been controversial.

In 1980, a new specimen from the Sinap beds was described that seemed to mostly confirm the conclusions of Simons and Pilbeam (1965) based only on the mandible (Andrews and Tekkaya, 1980). This specimen, a palate, was found at a different location called Kayıncak, also near Yassıören, but about 1.7 km from Sinap Tepe (G. Sarac, personal communication). The palate came from a level within the middle Sinap slightly lower than the level from which the mandible was recovered (G. Sarac, personal communication; Alpagut et al., 1996). They are roughly contemporaneous in a geologic sense because the entire middle Sinap member is dated to MN 9 (Sen, 1991; G. Sarac, personal communication; Alpagut et al., 1996).

Nasoalveolar clivus length	36.7
Premaxillary alveolar process length (prosthion-nasospinale)	22.9
Premaxillary nasal sill length (nasospinale-anterior nasal spine)	10.4
Palatal length (estimated)	89
Tooth row length	84.7
Palatal breadth (between lingual root surfaces, except at I^2)	
At I^2 (between mesial root surfaces)	24.8
At I^2 (between distal root surfaces)	37.4
At canine	35.2
At P^3	32.4
At P^4	31.8
At M^1	30.8
At M^2	31.5
At M^3	31.1
Nasal aperture breadth at base (right side $\times$ 2)	23.0
Maximum nasal aperture breadth (right side $\times$ 2)	25.5
Nasal aperture height (estimated)	24.3
	Approximately
Nasal bone length (estimated)	50
Maximum nasal bone breadth (estimated)	7
Zygomatic root height	28.5
Zygomatic root breadth	8.4
Malar height (zygomatic tubercle to the orbit)	40.6
Infraorbital foramen-nasal aperture	15.6
Infraorbital foramen breadth	3.1
Incisive foramen maximum dimension	6.1
Rhinion-inferior orbital edge (estimated)	18.8
	(minimum)
Orbit-nasal aperture minimum	29.5
Maximary height (orbit to alveolar process at M^2)	69.8
Maximum palatine process thickness at midline	6.9
Temporalis foramen transverse diameter	41.0
Orbital breadth (estimated)	26.7

Maxillary dental dimensions (mesiodistal/buccolingual)

RI^1	11.3/—	LI^1	11.7/9.5
RI^2	5.8/7.0	LI^2	6.0/6.5
$R\underline{C}$	15.4/13.7	$L\underline{C}$	15.6/13.6
$R\overline{P^3}$	8.2/12.1	LP^3	8.6/11.7
RP^4	7.8/12.4	LP^4	7.7/12.1
RM^1	11.9/14.2	LM^1	11.9/13.8
RM^2	13.2/14.3	LM^2	13.3/14.4
RM^3	13.9/14.7	LM^3	14.0/14.4

Symphyseal thickness	20.8
Symphyseal length (estimated)	45
Symphyseal height (vertical)	42.2
Sublingual plane/alveolar plane angle	50°

Mandibular dental dimensions

$RI_{\underline{2}}$	6.2/9.1		
$R\overline{C}$	(worn)	$L\overline{C}$	14.0/10.2
RP_3	13.3/8.9		
RP_4	10.6/12.1		
RM_1	12.4/12.2		
RM_2	16.3/14.6		
RM_3	15.4/14.6		

Andrews and Tekkaya (1980) identify enough differences from *Sivapithecus indicus* to justify a species distinction, and they assign the specimens to *Sivapithecus meteai,* supporting the view that *Ankarapithecus* is synonymous with *Sivapithecus.* They also note similarities to specimens from older Turkish deposits at Paşalar and Candir (Andrews and Tekkaya, 1976, 1980; Andrews and Tobien, 1977), suggesting that *Sivapithecus* in Turkey had a temporal depth on the same scale as that for *Sivapithecus* in the Siwaliks but beginning earlier in time. Andrews and Tekkaya (1980) also found similarities between the Sinap material and the sample usually attributed to *Ouranopithecus macedoniensis* from Greece (de Bonis and Melentis, 1977). Based on these comparisons, they proposed that the Greek sample was synonymous with *Sivapithecus meteai,* which has publication priority over *Ouranopithecus.* These last two interpretations have been revised more recently, based on new discoveries and analysis of *Ouranopithecus* and new discoveries of hominoids at Paşalar. Today, most authors recognize *Sivapithecus* for the Sinap and Siwalik specimens, *Griphopithecus* for the Paşalar and Candir specimens, and *Ouranopithecus* (or *Graecopithecus*) for the Macedonian specimens (Martin and Andrews, 1984; Kelley and Pilbeam, 1986; de Bonis and Koufos, 1993; Begun, 1992, 1994, 1995; Andrews, 1992; Alpagut et al., 1990, 1996).

MATERIALS AND METHODS

In 1992 we examined the material attributed to *Sivapithecus meteai* in the collections of the Maden Tetkik ve Arama Enstitüsü (MTA) in Ankara, Turkey. We noticed that both the type mandible and the palate had been restored but that distortion in the palate and face remained (contra McHenry et al., 1980). Distortion was especially visible along the edges of the nasal aperture, in the positioning of the zygomatic bone on the maxilla (contra Martin, 1990), and in the palatal contour in palatal view (Fig. 1). We also noticed that the subnasal region was heavily reconstructed. The subnasal floor was covered midsagitally with a mixture of wax, glue, sediment matrix, and epoxy resin. It was not clear if this obscured underlying
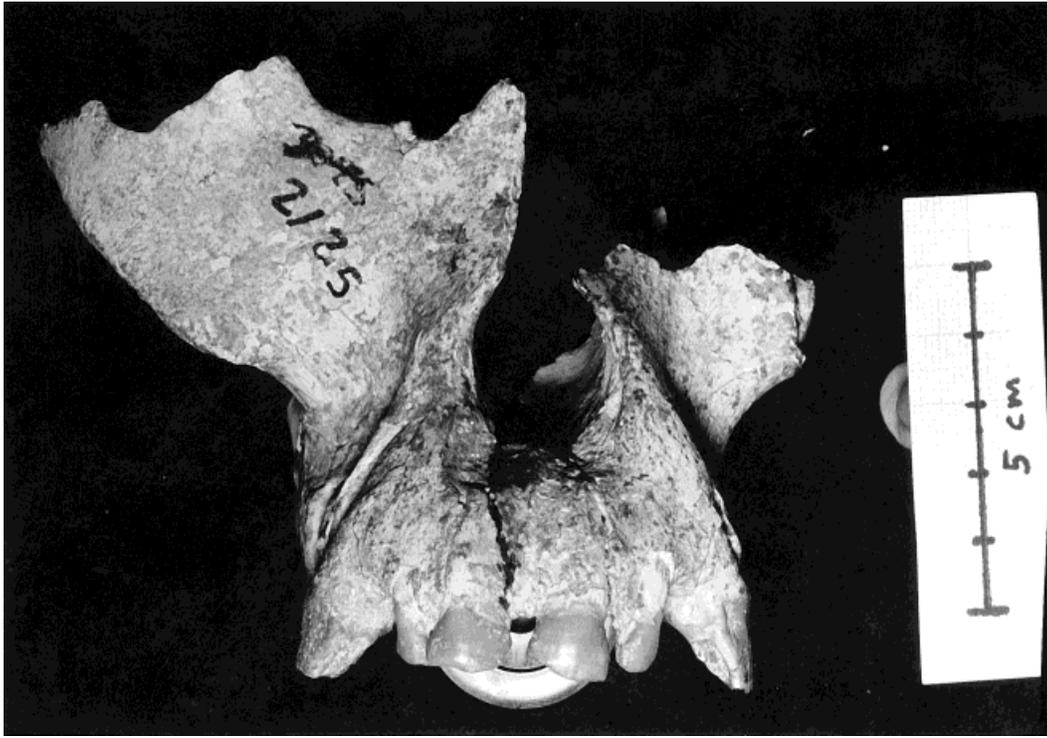
Fig. 1. Frontal view of the unrestored MTA 2125 palate.

bone or simply filled a damaged area. Some delicate probing revealed the presence of at least some bone, and it was decided that further preparation might reveal details of subnasal morphology previously unknown in this specimen. Since subnasal morphology is often considered informative of the phyletic relations among hominids and diagnostic of the *Sivapithecus-Pongo* clade in particular (Andrews and Cronin, 1982; Ward and Pilbeam, 1983; Ward and Kimbel, 1983; de Bonis and Melentis, 1987; McCollum et al., 1993), we sought permission to further prepare the specimens.

Plaster molded into the shape of a mandibular corpus and attached to the fractured left distal surface of the type mandible was removed. The type was cleaned and a new mold made. The specimen consists of a mandibular symphysis with the root of the left I_2, the left C-P_3, the right I_2-C, and the detached left P_4-M_3 (Fig. 2). The P_4 and molars belong to the same individual as the P_3 and anterior dentition, based on size, degree of

wear, and the perfectly matching interstitial facets between them. There is, however, no corpus preserved distal to the P_3.

Plaster, wax, glue, and epoxy resin were removed from the palate, along with a fair amount of matrix, which was saved for future analysis. Matrix was removed from the subnasal fossa, the maxillary sinuses, the palatal and facial surfaces, and the alveolar processes. The alveolar process on the right side was also found to consist mostly of matrix, which was removed, exposing the entire molar root system on the right side. The molars on the right side had been displaced laterally (Martin, 1990) and the gap between the lingual surfaces of the roots and the lingual edge of the maxillary alveolar process filled by plaster and wax. With the removal of the plaster, wax, and matrix, the molars were replaced in their correct anatomical position based on matching interstitial facets, which renders the palate symmetrical in palatal view (Fig. 3D). Much of the preserved face from the lateral border of

the nasal aperture to the right zygomatic bone was rotated out of anatomical position in all three standard planes. This piece was cleaned, removed, and repositioned in correct anatomical position, restoring the nasal aperture to near symmetry, exposing the entire anterior extent of the maxillary sinus, and reorienting of most of the maxillary and zygomatic surfaces.

Some restoration work remains. The palate has been glued together near the intermaxillary suture with epoxy resin, which proved resistant to our cleaning efforts. Enough resin was removed to expose the subnasal fossa completely, but enough remains between the broken surfaces of each maxillary bone to keep the two halves firmly bonded together, with the right half slightly superiorly rotated in frontal view relative to its normal anatomical position.

Once cleaning and restoration was completed, a new mold was made of the specimen without any new reconstruction. Following this, the right alveolar process, which consisted largely of surface bone clinging to the molar roots buccally and lingually, was reconstructed in white wax, which is easily removable if necessary.

Both specimens were photographed and measured before and after restoration. The postrestoration measurements appear in Table 1. These specimens were compared to samples of mandibles and palates of Miocene hominoids, extant hominoids, and casts of Plio-Pleistocene hominids. Analysis of quantitative data (univariate statistics, tests of significance, regressions) was carried out using Systat (Systat Inc., Evanston, IL) and Sigmastat (Jandel Scientific, San Rafael, CA) software. The frontal view of the palatal specimen was also more completely reconstructed digitally using Photoshop 3.0 (Adobe Systems Inc. Mountain View, CA) (Fig. 3F).

COMPARATIVE ANATOMICAL DESCRIPTIONS

Both the type mandible and the palate have been described elsewhere to some extent (Ozansoy, 1957, 1965; Andrews and Tekkaya, 1980). The descriptions that follow will emphasize new observations on the palate first, then the type. Particular attention will be directed to comparisons with

Siwalik *Sivapithecus.* Although metric comparisons include all available and appropriate Siwalik specimens, morphological comparisons are for the most part limited to the more complete specimens, including mandibles and palates with at least two teeth.

Both Sinap specimens are considered here to be males. In other publications on these specimens, sex attribution has not been made explicit, probably because the large overall size of the specimens and the relatively large size of the canines in particular made the sex of these specimens seem obvious. Unfortunately, the canine measurements Kelley (1995a,b) has found to be most discriminating between the sexes cannot be taken on these specimens. However, any doubts about the sex of these specimens are put to rest by the discovery of a new female specimen of the same species at the same site. AS95-500 is morphologically extremely similar to the male specimens from Sinap but is much smaller and has relatively lower crowned, smaller canines (Alpagut et al., 1996).

MTA 2125 (Figs. 3, 4)

Most of the maxillary sinus in the left alveolar process and the right maxillary sinus from the lateral wall of the nasal fossa to the zygomatic bone is exposed. The maxillary sinus extends into the zygomatic process of the maxilla but not into the zygomatic bone itself. The zygomaticoalveolar crest is relatively thin and unpneumatized, as in *Sivapithecus* (Ward and Brown, 1986; Brown and Ward, 1988), *Pongo,* and earlier Miocene hominoids, unlike the thicker, more pneumatized zygomaticoalveolar crests of *Dryopithecus, Ouranopithecus,* and living great apes. The minimum thickness of bone between the maxillary sinus and the surface bone of the zygomatic root is about 8.5 mm, making the zygomatic root a solid beam rather than a "hollowed-out shell," as in *Sivapithecus* (Ward and Brown, 1986:425), *Dryopithecus,* and African apes. However, in *Sivapithecus* and *Pongo* hollowing of the zygomatic process of the maxilla is displaced superiorly relative to the pneumatization seen in *Dryopithecus* and the African apes, so that, although the zygomatic process can be described as a hollowed-out shell, the zygomaticoalveolar crest (zygomatic root) is

Fig. 2.   Views of the type of *Ankarapithecus meteai.* **A:** Anterior. **B:** Lateral. **C:** Posterior. **D:** Inferior. **E:** Occlusal view of the anterior dentition and P_3. **F:** Occlusal view of the associated postcanine teeth. **G:** Buccal view of the associated postcanine teeth. **H:** Lingual view of the postcanine teeth. Scale in centimeters.

more robust in the Asian forms than in *Dryopithecus.* The anterior surface of the maxillary sinus is over P^4-M^1, as in most hominoids. At its closest, it is about 17 mm posterior to the tip of the canine root, placing the maxillary sinus more posterior relative to the canine than in living great apes, *Dryopithecus,* and *Sivapithecus* (Ward and Brown, 1986; Brown and Ward, 1988; Begun, 1994). This is related to the development of midfacial prognathism, which displaces the canine root anteriorly (see below).
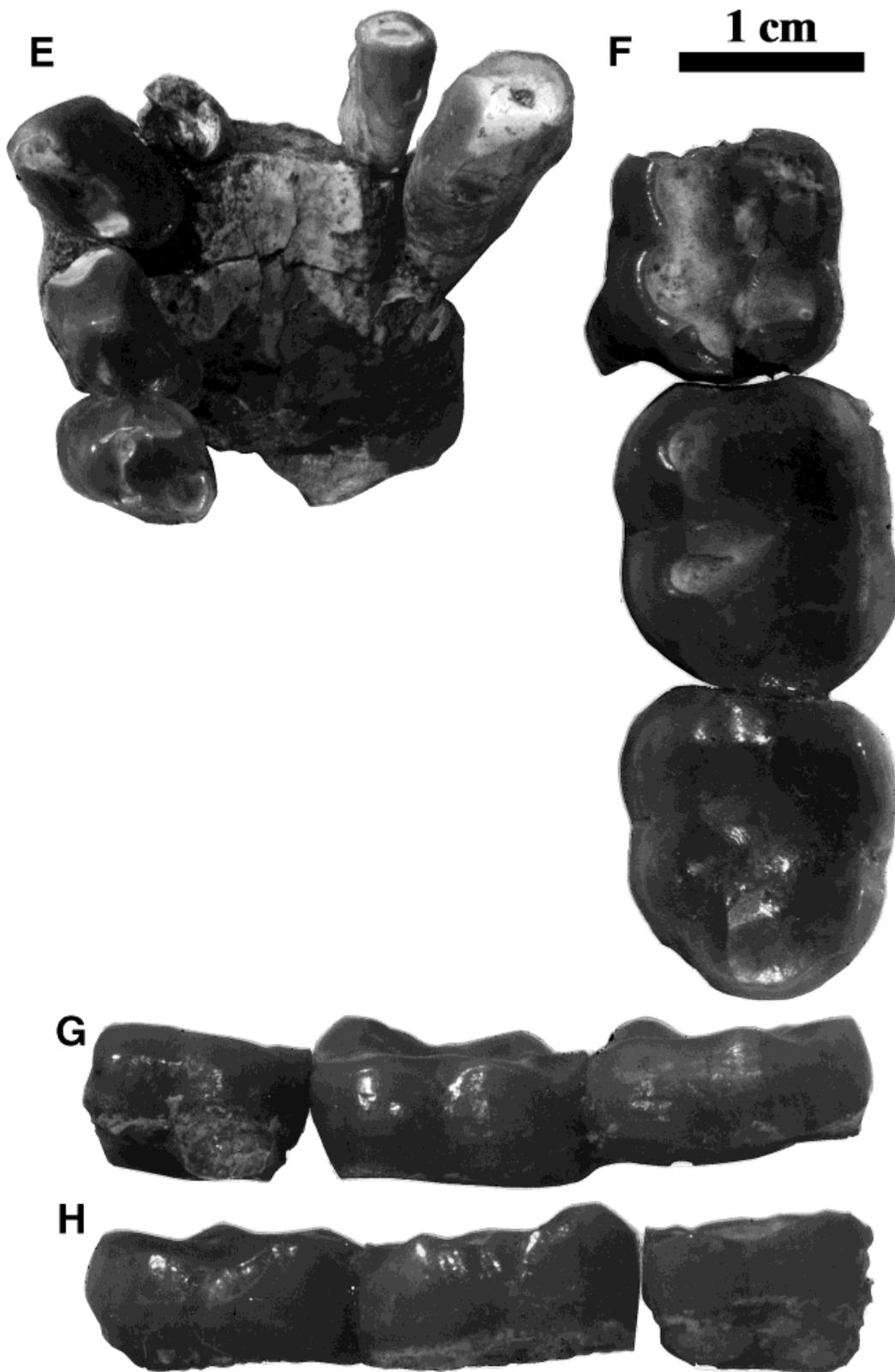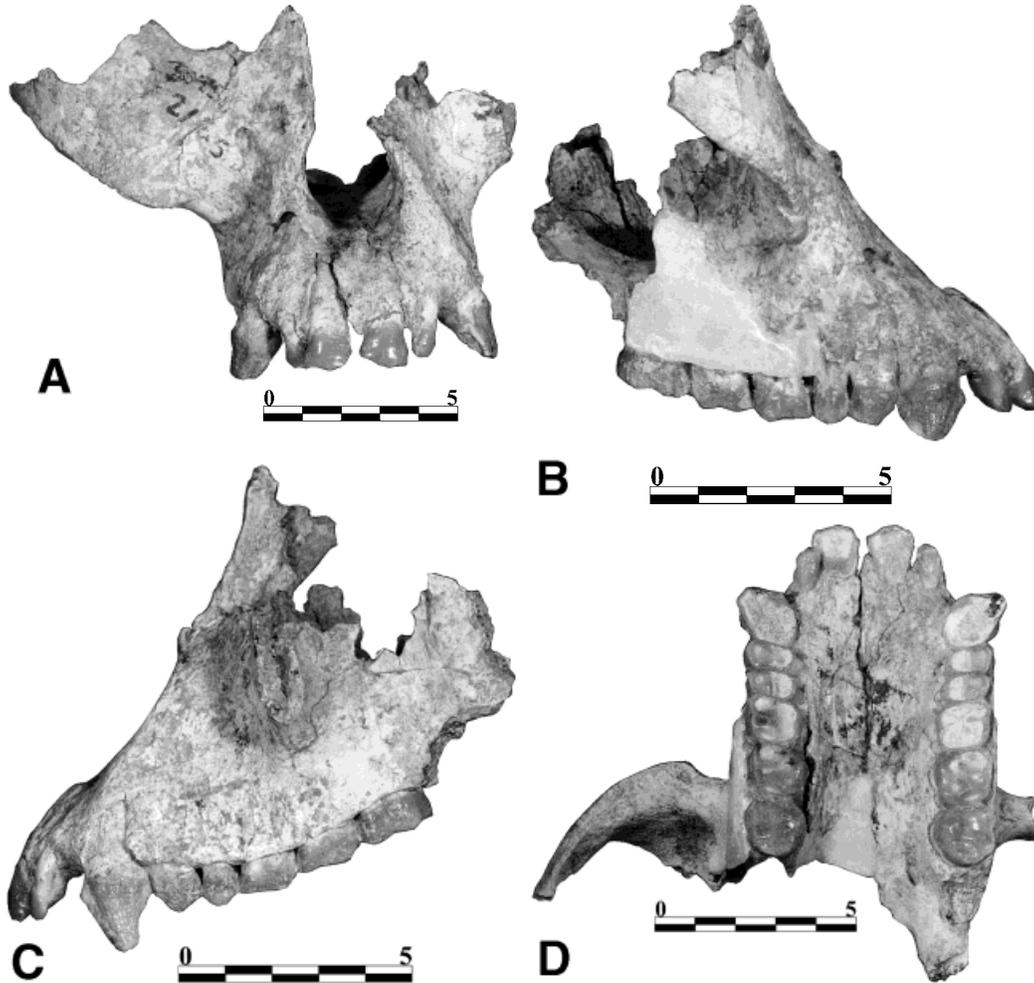
E

F

1 cm

G

H

Fig. 2.

Fig. 3.   Views of the restored MTA 2125. **A:** Anterior. **B:** Right side. **C:** Left side. **D:** Palatal. **E:** Superior. **F:** Photoreconstructed lower face. In F, the right zygomatic was mirror-imaged, moved, and blended to the left side, and the inferior orbital margins were retouched to obtain a more complete reconstruction. Scale in centimeters.

The position of the maxillary sinus relative to the canine in MTA 2125 is closer to that seen in *Proconsul* (KNM RU 16000, BMNH M-16647). If we judge by the position of the malar surfaces of specimens that do not expose the maxillary sinus, the same condition is probably also found in *Afropithecus* (KNM WK 16999) and another *Proconsul* specimen (KNM RU 7290).

The maxillary sinus is relatively constricted mediolaterally in the alveolar process. The floor of the sinus in the left alveo-lar process has poorly developed loculi and transverse septa and no penetration among the molar root tips. These are variable within hominid taxa. The maxillary sinus also fails to invaginate the frontal process of the maxilla, preserved on the right side. This process is therefore a robust, solid bony projection between the medial edge of the lacrimal fossa and the nasomaxillary suture, unlike the more delicate, pneumatized morphology of *Sivapithecus* and living great apes (Brown and Ward, 1988). Most of the canal for the
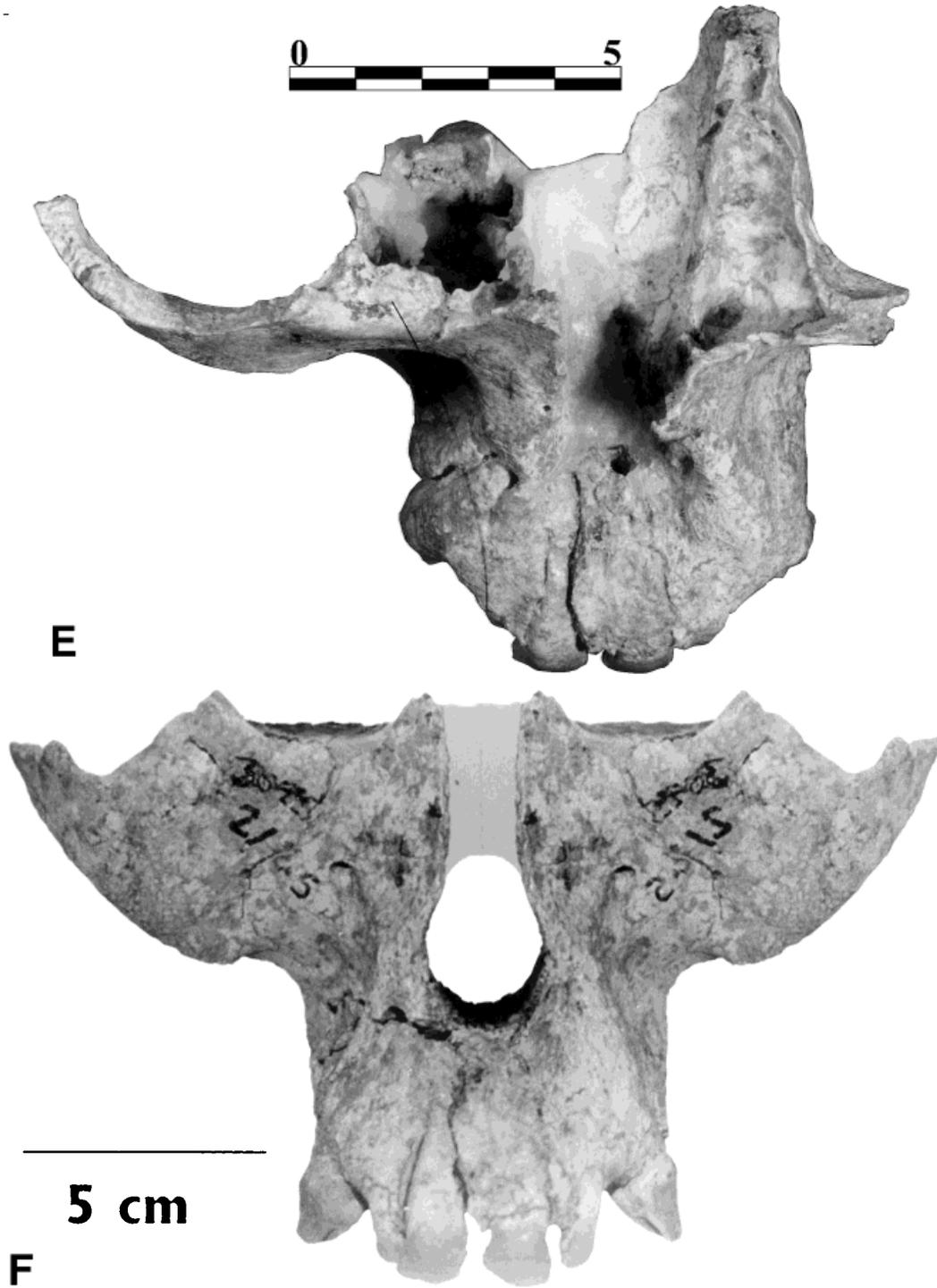
E

F

5 cm

Fig. 3.

Fig. 4. Views of the incisive canal complex. **Top:** Palatal view showing the large incisive foramen. **Bottom:** Subnasal view from behind showing the stepped clivus and incisive fossa. Scale in centimeters.

infraorbital neurovascular bundle is preserved in the anterior wall of the maxillary sinus. It is long and vertically oriented as a result of the substantial distance between the inferior orbital margin and the infraorbital foramen (Figs. 3 and 4).

Restoration of the facial fragment also reveals new characters in the anterior and lateral views (Fig. 3A–C). The nasal aperture is broader than before restoration. The relative size of the base of the nasal aperture is broad, as in AS95-500, *Gorilla,* and *Ouranopithecus* (Table 2). The nasal aperture margins are also more vertically oriented than previously reconstructed. The margin remains damaged on the right side and may be affected by pathology (see below). On the left side, the nasal margin is thick where it merges with the canine jugum. It becomes narrower and then sharp superiorly. On the right side, the nasal margin is thicker above the level of the canine jugum. Because both sides show evidence of some pathology, it is not clear if this asymmetry is pathological, differentially affecting each side, or simply normal variation independent of the bilateral pathology (see below).

The edges of the nasal aperture formed by the maxilla converge superiorly toward the midline. On the right side, the sutural surface for the right nasal bone is preserved, although the nasal bone itself is missing. This suture is more vertically oriented than the convergent edges of the maxilla, giving the aperture a more truly piriform morphology, as is the case generally in *Pongo* and also in AS95-500. Because of the absence of the nasal bone, it is not clear how close to the level of the orbit the apex of the nasal aperture was positioned, but it is clear that the maxillary edge of the nasal aperture is low on the face in relation to the inferior orbital margin. This is also true of AS95-500 and *Sivapithecus* (GSP 15000). The nasal process of the maxilla, between the nasal aperture and the orbit, is thus very broad and is also slightly concave (Table 2). In *Pan,* the most superior part of the maxillary edge of the nasal aperture (inferior to the nasomaxillary suture) is usually close to the level of the inferior orbital margins, while in *Pongo* it is often somewhat lower. In *Gorilla,* the nasal aperture it is often lower still, as is also the case for *Proconsul* (KNM RU 7290, BMNH M-16647) and *Morotopithecus* (UMP 62-11). *Afropithecus* (KNM WK 16999) has an exceptionally wide orbital-nasal distance (Table 2), though this includes a substantial horizontal component. In relation to the alveolar process, however, the nasal aperture is more superiorly positioned in MTA 2125 than in early Miocene forms (*Morotopithecus, Afropithecus, Proconsul*). It is superior relative to the roots of the incisors and canines, as in late Miocene hominids (AS95-500, *Dryopithecus, Sivapithecus, Ouranopithecus*) and modern great apes. The root tips of the canines of MTA 2125 barely rise above the base of the nasal aperture, as in hominids generally, whereas in early Miocene taxa and hylobatids the canine roots and their associated jugae in males define much of the borders of the nasal aperture.

TABLE 2. *Comparative facial ratios in large-bodied hominoids*[1]

Ratio	Ankara-pithecus	Pan (21)	Gorilla (29)	Pongo (30)	Siva-pithecus[2]	Dryo-pithecus[3]	Pro-consul[4]	Ourano-pithecus[5]	Moroto-pithecus[6]	Afro-pithecus[7]
Zygomatic height	131	54–84	81–129	70–102	128	—	108	—	—	164
		72 (8)	107 (14)	83 (10)	—	—	—	—	—	—
Zygomatic breadth	149	66–117	118–187	83–148	149	—	135	—	—	167
		103 (14)	149 (25)	116 (20)	—	—	—	—	—	—
Zygomatic arch height	57	28–46	40–65	27–43	43	—	43	—	—	65
		34 (5)	57 (6)	37 (6)						
Nasal aperture breadth	75	55–78	62–99	52–80	64	63–66	54–70	79	70	63
		63 (8)	79 (15)	60 (8)	—	—	63	—	—	—
Orbital-nasal breadth	96	33–44	50–101	24–48	94	—	83–90	—	—	—
		40 (4)	80 (16)	36 (8)	—	—	—	—	—	—
Nasoalveolar length	111	84–141	72–105	89–114	120	83–90	60–76	88	68	—
		99 (17)	92 (13)	104 (7)	—	—	—	—	—	—

[1] All ratios relative to palatal breadth at $P_4 \times 100$. Nasoalveolar length from prosthion to the anterior edge of the incisive fossa; zygomatic height from the inferior end of the zygomaticofacial suture to the closest point of the orbital margin; zygomatic breadth is a horizontal from the nasal margin to the inferior end of the zygomaticofacial suture; nasal aperture breadth is measured at the base of the aperture; orbital-nasal breadth is the minimum distance between the nasal aperture and the oribit; zygomatic arch height is the vertical dimension of the arch from the superior end of the zygomaticotemporal suture. Numbers in parentheses refer to sample sizes.
[2] GSP 15000.
[3] RUD 12 and 44.
[4] KNM-RU 7290 and 16000 and BMNH 16647 (not all specimens preserve all measurements).
[5] RPL 128.
[6] UMP 62-11.
[7] KNM-WK 16999.

The zygomatic bone is preserved on the right side, missing only its frontal process. It is broad mediolaterally, most like that of gorillas and other Miocene hominoids, and contributes to the strongly laterally flared zygoma of this specimen (Table 2). In keeping with the laterally flared temporal process, MTA 2125 has an extremely large temporalis foramen. The superoinferior height of the zygomatic maxillary process, from the orbital rim to the malar notch, is extreme. Its relative depth is above the ranges of the living great apes, as is also the case for *Afropithecus,* while *Sivapithecus* is just barely within the *Gorilla* range (Table 2). The malar notch is well marked and bounded laterally by a thick, mediolaterally extensive zygomatic tubercle that is deflected anteriorly. Posterolateral to the tubercle, the inferior edge of the root of the temporal process of the zygomatic is marked by a broad, roughened area for the masseter muscle. This continues along the inferior edge of the zygomatic arch as a strongly marked crest ending close to the zygomaticotemporal suture. The overall development of these features is similar to that seen in WK 16999 and very robust orangutans. Although the region is not well known in *Sivapithecus,* it appears similar to MTA 2125 in its development of the zygomatic tubercle and the scars for masseter. The zygomatic temporal process is also very deep superoinferiorly and flattened mediolaterally (Table 2). It is exceptionally deep in the area of the zygomaticotemporal suture on the arch, which is horizontally oriented. The notch between the temporal and frontal processes (jugale) is close to the level of the inferior orbital margin, typical of Miocene taxa but unlike living great apes, in which this notch is more inferiorly placed. The zygomatic arch is oriented superiorly, more than is typical in early Miocene forms but similar to *Afropithecus* and *Pongo.* In African apes, the zygomatic arch is more horizontal.

The zygomaticofacial foramen, preserved on the right side, is very large, ovoid, single, and roughly even with the inferior orbital margin. It is the same in relative size, shape, and position to that on AS95-500. The anterior half of the lacrimal canal is visible posterior to the inferior edge of the lacrimal crest. It is likely that the lacrimal fossa, which was superior to the preserved section of the canal, would have been visible in anterior view, as it clearly is in AS95-500. This is unlike the condition in *Pongo* and many other primates, in which the lacrimal fossa is hidden from anterior view by the lacrimal crest. In *Turkanapithecus, Afropi-*

thecus, African apes, *Dryopithecus,* and *Ouranopithecus,* the lacrimal fossa is also visible in anterior view.

Part of the inferior orbital margin is preserved. The transition from orbital plate to infraorbital surface is rounded, as in *Sivapithecus* and *Pongo,* unlike most other hominoids, in which it is marked by a ridge. The inferior orbital margin is not sufficiently preserved to estimate orbital breadth near the inferior orbital margin. However, a small surface of the orbital edge is preserved medially on the nasal process of the maxilla near the lacrimal canal. This is separated by a gap from the more laterally preserved inferior orbital margin. The distance from these portions of the orbital margin is greater in MTA 2125 than in GSP 15000, suggesting somewhat broader orbits. AS95-500, in which the orbits are well preserved, has broad orbits relative to height, and this is consistent with the morphology of MTA 2125.

The nasomaxillary suture is visible on the maxilla from close to its inferior end to just beyond the level of the inferior orbital margin. Reflecting the low position of the nasal aperture, this portion of the nasal suture is very long. Given that it is preserved only just superior to the level of the inferior orbital margin, the entire length of the nasal bones must have been exceptionally long, as was probably also the case in GSP 15000 (Ward and Brown, 1986). No part of the nasal bones is preserved. However, the nasomaxillary suture is very close to the midline in MTA 2125, even at its most inferior extent. This indicates that the nasal bones would have been narrow along their entire length. Furthermore, the distance between the medial orbital surface and the nasomaxillary sutural surface is small. Since both the nasal process and the inferred breadth of the nasal bones are narrow, the interorbital breadth was probably narrow as well, though it is not clear if it was as narrow as in *Sivapithecus* and *Pongo* (Andrews and Cronin, 1982). The interorbital thickness of AS95-500 is described as being similar to *Pongo* but also within the range of *Pan paniscus* (Alpagut et al., 1996).

There is well-developed nasal midfacial projection in MTA 2125, related in part to both the more vertical edges of the nasal aperture and its lower position. The margins of the nasal aperture are not in the same plane with the infraorbital and interorbital surfaces and the malar surface of the zygomatic bone, as in *Sivapithecus* (GSP 15000), *Pongo,* and to a lesser extent *Pan,* but are positioned well anterior to the malar surfaces, as in early Miocene forms. *Afropithecus* is distinct from other early Miocene forms (including *Morotopithecus*) in its extreme degree of midfacial prognathism (Leakey et al., 1988). *Gorilla* and *Ouranopithecus* are intermediate between *Proconsul* and *Morotopithecus* on the one hand and MTA 2125 on the other in the projection of the edges of their nasal apertures relative to the orbital margins, probably due to their more superiorly positioned aperture. Midfacial projection is also well developed on AS 95-500. The nasal midface in MTA 2125 projects anteriorly beyond the plane of the orbits even at the most superior portion of the maxillary contribution to the nasal aperture. In *Sivapithecus* and *Pongo,* this region lies in a plane with the orbits. The anterior position of the nasal aperture in MTA 2125 is obvious despite the probably more anterior position of the orbits relative to the alveolar process. The inferior orbital margin is probably above M^1 in MTA 2125, though it is somewhat difficult to assess without being able to orient the specimen along the Frankfurt plane. In *Sivapithecus* and *Pongo,* it is above M^2 (Ward and Brown, 1986). In coronal section at the level of the M^2, the orbits would probably be visible on MTA 2125, AS95-500, *Afropithecus, Proconsul, Morotopithecus, Dryopithecus, Ouranopithecus,* and African apes, whereas they are not in *Sivapithecus* and *Pongo* (Ward and Brown, 1986). Like GSP 15000 and most other primates but unlike most *Pongo,* a coronal section at M^2 passes posterior to the apex of the nasal aperture in MTA 2125 and AS95-500 (Ward and Brown, 1986).

The surface of the maxilla lateral to the nasal aperture and superior to the canine fossa faces more laterally as in *Gorilla, Ouranopithecus,* and early Miocene forms, which have more projecting midfaces in the nasal region, rather than more anteriorly, as in *Sivapithecus, Pongo, Pan,* and *Australopithecus* (Ward and Brown, 1986; Rak, 1983).

The canine fossae are also less strongly developed than in *Sivapithecus* and *Pongo,* though the fossa on the left side is more pronounced as a result of the nasal margin asymmetry noted above. The canine fossae are more strongly developed than in *Dryopithecus, Ouranopithecus,* and African apes. AS 95-500 is very similar to MTA 2125 in all of these characters. The difference in apparent depth between the canine fossae of *Sivapithecus/Pongo* and MTA 2125 is probably related to the greater anteroposterior length of the fossa in MTA 2125, which is in turn related to the increased midfacial prognathism in this specimen. MTA 2125 lacks the collapsed maxilla between the root of the canine and the malar surface known for *Sivapithecus, Pongo,* and to a lesser extent *Ouranopithecus,* having instead a shallow concavity (Ward and Brown, 1986). However, this portion of the maxilla is not smooth because it is inflated by the maxillary sinus, as in African apes (Ward and Brown, 1986). Rather, it is a solid column of bone, compressed mediolaterally and elongated anteroposteriorly between the canine root anteriorly and the maxillary sinus posteriorly, as is also the case in *Dryopithecus* (CL1 18000, RUD 44). It is continuous more superiorly with the robust frontal process of the maxilla noted above. Inferior to the canine fossa, the buccal surface of the alveolar process is also smooth, lacking the prominent canine jugae and the either fenestrated roots or visible root contours of the postcanine dentition of *Sivapithecus* and *Pongo* (Ward and Brown, 1986). In summary, the maxilla of MTA 2125 are robust, more closely resembling those of Miocene forms other than *Sivapithecus.* The surface bone is not collapsed around roots or into the maxillary sinuses, and the maxillary alveolar processes are buccolingually robust. The premaxillary alveolar process, which is generally more labiolingually gracile in early Miocene forms, is robust in MTA 2125, as in other hominids.

Reorientation of the molars on the right side restored the palatal shape and exposed the molar roots for description and analysis. The palate is large (Table 1), being closest in size to a large male chimpanzee or a female orangutan, with slightly buccally concave, posteriorly convergent postcanine tooth rows. MTA 2125 is similar to *Sivapithecus* (GSP 15000) in palatal length, with differences in alveolar proportions. The incisor region in GSP 15000 is slightly longer, reflecting the more horizontally oriented incisor roots, and the molar region is somewhat smaller, reflecting the smaller tooth size, but the end result is a palate of nearly equal length. MTA 2125, however, is considerably broader than GSP 15000. MTA 2125 is larger than AS95-500 but has the same length-breadth proportions, judging from the published measurements (Alpagut et al., 1996). In proportions, length, and breadth, MTA 2125 is closest to *Ouranopithecus* (ZIR-1, RPL-128, and especially NKT-89 [de Bonis and Koufos, 1993; Koufos, 1995]). The males (ZIR-1 and RPL-128) are slightly larger in overall dimensions, with more parallel tooth rows. The apparent female (NKT-89) is slightly smaller in overall dimensions and has a buccally convex alveolar contour (Koufos, 1995). The palatal size of MTA 2125 is also similar to *Morotopithecus,* though the proportions of the alveolar processes associated with each tooth type are different (Pilbeam, 1969). In MTA 2125, the premaxillary portion is similar in length to *Morotopithecus,* but the anterior palate is elongated overall due to the extreme size of the *Morotopithecus* canines. The premolar region is also longer in *Morotopithecus,* due to the very large size of the P^3, but the molar length is considerably smaller (Pilbeam, 1969). Two *Proconsul* males (KNM RU 16000, BMNH M-16647) have smaller palates of similar shape but with foreshortened premaxillae and slightly divergent tooth rows. *Afropithecus,* in contrast, has an elongated palate which, though damaged, appears to have been narrower than in MTA 2125 (Leakey et al., 1988). The tooth rows are longer than in MTA 2125, but this results from the very large size of the canines and the more horizontal orientation of the incisors in KNM WK 16999.

The posterior portion of the palate has been further prepared and reveals a few new anatomical features not previously described. The greater palatine foramen is large and oval but not slit-like as previously described (Andrews and Cronin, 1982). African apes

and humans tend to have slightly more rounded foramina than in orangutans, MTA 2125, and GSP 15000, but there is much variability in this character. The sharp distal border of the greater palatine foramen is placed roughly along the line connecting the distal edges of the M^3s. This is similar to other hominids for which the area is known (*Sivapithecus, Ouranopithecus, Dryopithecus,* living great apes, and humans). Early Miocene forms tend to have a more anterior placement of the greater palatine foramen. There is no trace of a lesser palatine foramen on MTA 2125, a similarity shared with orangutans and *Sivapithecus* (GSP 15000). Gorillas tend to have very small, supernumary foramina, while chimps and humans have one or a few larger foramina.

A portion of the horizontal plate of the palatine bone between the posterior border of the palate and the greater palatine foramen is preserved. This is relatively narrow compared to the condition in the few early Miocene forms in which it is preserved (UMP 62-11, BMNH M-16647) and more like GSP 15000 and other hominids, probably related to the more posterior placement of the greater palatine foramen in these forms. This surface is marked in MTA 2125 by a strong ridge, the palatine crest, continuous with the posterior edge of the greater palatine foramen. It continues lateral and posterior to the foramen to reach the posterior corner of the base of the maxillary tuberosity. The lateral portion of this ridge may represent the attachment of the tensor veli paltini muscle, while the more medial portion (medial to the greater palatine foramen) probably represents the attachment of the palatine aponeurosis. All of the palatine muscles and the palatopharyngeal sphincter portion of the superior constrictor muscle of the pharnyx have a connection to the palatine aponeurosis as they contribute to the formation of the soft palate. It is not clear why the palatine crest in this specimen is so strong, but similarly pronounced palatine crests can be seen on early Miocene hominoids (KNM WK 16999, KNM RU 16000, KNM RU 1850 [*Dendropithecus*], UMP 64-02 [*Micropithecus*], GSP 15000, orangutans, AL-200-1 [*Australopithecus*], and modern humans). Chimpanzees and gorillas have more

modestly developed palatine crests or no crest at all. Much of the maxillary tuberosity on MTA 2125 is lost, but the exposed section of the maxillary alveolar process posterior to the M^3 indicates that the tuberosity was quite large, buccolingually and mesiodistally, strongly projecting inferior to the palate, and unpneumatized. The maxillary tuberosities project less inferiorly in *Afropithecus* and *Morotopithecus,* probably related to the shallower posterior palates of these forms. Modern African apes have more strongly projecting maxillary tuberosities than orangutans but not as large as in MTA 2125 relative to overall size. Modern African ape maxillary tuberosities also tend to be inflated by the maxillary sinus (Ward and Brown, 1986).

Another feature that has not received much attention before is the position of the palatine pyramidal process between the maxillary tuberosity and the pterygoid plates of the sphenoid. In MTA 2125 and the Miocene hominoids in which it is at least partly preserved (GSP 15000, UMP 62-11, KNM WK 16999, and KNM WK 16950 [*Turkanapithecus*]), the pyramidal process is placed at roughly the same level as the greater palatine foramen when viewed from the midline. In modern hominids and *Australopithecus,* the pyramidal process projects inferiorly, contributing to the wall of the posterior palate distal to the maxillary tuberosity. The pyramidal process is very variable in hominids, but it tends to be shorter and more attenuated mediolaterally than in MTA 2125. Only in male gorillas, which are much larger in dental and other palatal dimensions, does the size of the pyramidal process approximate the size of MTA 2125. In *Morotopithecus,* the only other Miocene hominoid with a complete pyramidal process (both are preserved), the pyramidal process is superiorly placed, as in MTA 2125, but is small. In posterior view, the most inferior extent of the pterygoid fossa and the most anterior and inferior parts of the pterygoid plates are visible on MTA 2125. The fossa faces posteriorly and very slightly inferiorly as in modern hominids, in contrast to the more inferior orientation in *Morotopithecus.*

A thick rectangular column of bone, the pterygoid process (Ward and Brown, 1986),

rises superior to the palatine pyramidal process, anterior and superior to the pterygoid fossa, and immediately posterior to the maxillary sinus. The medial surface, consisting of part of the medial surface of the medial pterygoid plate posteriorly and part of the perpendicular process of the palatine bone anteriorly, forms the posterior wall of the nasal fossa, between the medial pterygoid plate and the greater palatine canal. Anteriorly, it forms the posterior wall of the maxillary sinus. In lateral view, the process has an undulating surface of fossae and crests, probably corresponding to the lateral side of the lateral pterygoid plate and the attachment sites for the lateral pterygoid muscle. Anterior to this surface is a groove probably corresponding to the pterygomaxillary fissure. Superiorly, the process is broken at a level inferior to the pterygomaxillary fossa. At this point, the greater palatine canal is quite large in caliber and less than 3 mm medial to the pterygoid fissure on the lateral surface. In GSP 15000, this portion of the sphenoid and palatine bones is not well preserved, but it is described by Ward and Brown (1986) as being compressed, as in African apes. In contrast, orangutans have a more robust pterygoid processes, like MTA 2125, *Proconsul, Afropithecus,* and *Morotopithecus.*

In *Morotopithecus,* the entire sphenopalatine complex is strongly inclined posteriorly, resulting in the aforementioned inferior orientation of the pterygoid fossae and in an inclined, much more posteriorly projecting extension of the maxillary sinus. In UMP 62-11, the most posterior edge of the maxillary sinus is more than 18 mm posterior to the distal edge of the M^3, whereas this distance is only about 5 mm in MTA 2125. This is due at least in part to the vertical orientation of the sphenopalatine complex and the posterior surface of the maxillary sinus in MTA 2125. In GSP 15000, the area is quite damaged, but a small portion of the posterior wall of the maxillary sinus appears to be present and is closer to the M^3 than in UMP 62-11, as in MTA 2125. In modern hominids, the maxillary sinuses do not extend posteriorly much beyond the contact between the maxilla and the pyramidal process of the palatine bone, and the

posterior surface of the sinus is vertical. In summary, the posterior portion of the maxilla and in particular the palatine bone in MTA 2125 are robust. The maxillary tuberosity and the palatine contribution to the pterygoid fossa (the inferior end of the fossa) afford attachment for the superficial fibers of the medial pterygoid muscle. The large size and robusticity of both the maxillary tuberosity and the lateral pterygoid plate suggest very powerful pterygoid muscles.

In buccal view, MTA 2125 has deep alveolar processes with superiorly placed maxillary sinus floors and a superiorly positioned, anteroposteriorly thick root of the maxillary zygomatic process (see above). All of these traits are typically found in hominids, including *Sivapithecus, Ouranopithecus* (the position of the zygomatic root is probably secondarily lower in *Ouranopithecus* [Begun, 1995]), and *Dryopithecus,* but not in early Miocene forms or apparently in *Oreopithecus* (personal observations). Lingually, the alveolar processes are sloped, giving the palate a domed appearance along most of its length. The dome is slightly flattened anteriorly near the incisors. Most other specimens close in size to MTA 2125 have flatter palatal roofs (GSP 15000, ZIR-1, RPL-128, NKT 89, KNM WK 16999, UMP 62-11, BMNH M-16647). All of these specimens share with MTA 2125 palates that deepen posteriorly, though the early Miocene specimens tend to have shallower palates than the later forms.

The buccal roots of the molars are buccolingually compressed and short. The mesial buccal roots of the M^{1-2} have bifid tips. The lingual roots of the molars are longer and more robust. They are flared lingually and have deep longitudinal grooves along their buccal surfaces. The roots of M^2 are much larger than those of M^1, while the M^3 roots are the largest.

Exposure of the surface bone in the subnasal fossa from the alveolar process of the premaxilla to the palatine processes of the maxillae has revealed a number of important anatomical details. Although the area is damaged, it is clear that there was a well-defined incisive fossa midsagitally (Fig. 4). This is a depressed area posterior to the posterior pole of the premaxilla formed by a more superior position of the premaxilla

relative to the palatine process of the maxilla in the midsagittal plane. The incisive fossa was less extensive than in African apes, in which this feature is largest, but more so than in *Sivapithecus* and *Pongo,* which have a smooth transition from premaxilla to maxillary palatine process midsagitally and therefore have a very restricted fossa or lack one altogether. Also midsagitally, there is a stepped subnasal floor—that is, a vertical drop between the posterior edge of the nasoalveolar clivus within the nasal fossa and the anterior edge of the subnasal floor (Fig. 4). Several early Miocene forms (*Morotopithecus, Afropithecus*) and some other primates, particularly New World monkeys, have an inferior margin of the nasal aperture that is superiorly positioned relative to the palatine process of the maxilla in the subnasal fossa. In these forms, however, there is no overlap between the premaxilla and the maxillary palatine processes, so the floor of the incisive fossa is bottomless, leading to a large aperture, or a fenestrated palate (Schwartz, 1983). Other primates with a fenestrated palate, which is the typical mammalian condition, also lack the raised nasal aperture (*Proconsul, Aegyptopithecus,* Old World monkeys, prosimians). The stepped subnasal floor of MTA 2125 is intermediate in development between *Gorilla, Pan,* and *Australopithecus,* which generally have stronger steps, and *Sivapithecus/Pongo,* which have a smooth transition between the clivus and the subnasal floor (Ward and Kimbel, 1983; McCollum and Ward, 1997).

The posterior edge of the nasoalveolar clivus is deep within the subnasal fossa and is marked midsagitally by a projecting and anteriorly postioned (relative to the nasal margins) anterior nasal spine. The spine is continuous with a well-developed anterior nasal spinous crest (as described in McCollum et al., 1993). Both the anterior nasal spine and crest are more prominent than in GSP 15000 and most *Pongo,* though a similar crest is visible on GSP 16075 (the spine is not preserved in this specimen). In African apes and *Australopithecus,* the nasal portion of the nasoalveolar clivus is smaller than in *Sivapithecus, Pongo,* and MTA 2125, with the incisive fossa in African taxa being

closer to the margins of the nasal aperture. Also like *Sivapithecus* and *Pongo,* the nasoalveolar clivus is more horizontally oriented in MTA 2125 than is typical of African apes and *Australopithecus.* However, unlike *Sivapithecus* and *Pongo,* the nasoalveolar process in MTA 2125 is smoothly convex transversely, lacking the prominent root contours for the incisors. In overall relative length, the clivus in *Sivapithecus* and MTA 2125 is long. Relative to palatal breadth, MTA 2125 is above the means for *Pan* and *Pongo,* while *Sivapithecus* (GSP 15000) is above the range for *Pongo* (Table 2). Both fossil taxa are above the ranges in other large hominoids. Interestingly, relative to molar size, the nasoalveolar clivuses of both GSP 15000 and MTA 2125 are at the low end of the range of variation in great apes, suggesting that the fossil taxa may have larger teeth relative to palatal dimensions (Begun, 1994).

Anterior to the maxillary palatine processes and deep to the incisive fossa is an incisive canal most similar in size to *Gorilla.* The canal is formed by the overlapping premaxilla and maxillary palatine processes and is not present in fenestrated palates. On the palatal surface, the canal leads to a relatively large incisive foramen. The incisive canal–foramen complex in MTA 2125 differs from the condition in *Dryopithecus* and *Ouranopithecus* in having a greater degree of premaxillary-maxillary overlap, associated with a smaller incisive fossa, a longer, smaller caliber incisive canal, and a smaller incisive foramen. In *Dryopithecus* and *Ouranopithecus,* the canals are quite short and broad because of minimal overlap between the premaxilla and maxilla (Begun, 1994). The incisive canal–foramen complex of MTA 2125 differs from *Pongo* and *Sivapithecus* in having a shorter, substantially larger caliber canal and a much larger incisive foramen. In fact, the canal and foramen in MTA 2125 are even larger in caliber than in *Pan* and *Australopithecus. Pongo* and *Sivapithecus* have such extensive overlapping of the premaxilla and maxilla that the incisive fossa has essentially been occluded by the encroachment of the premaxilla and the canals and foramina squeezed nearly closed (Ward and Pilbeam, 1983). MTA 2125

lacks this striking similarity between *Pongo* and *Sivapithecus.* In summary, there is a mixture of similarities and differences in the nasoalveolar and subnasal regions of MTA 2125 and other hominids. This suggests a complicated evolutionary history of the premaxilla in hominids, with some independence among characters in what is otherwise considered a single morphological complex (Ward and Kimbel, 1983).

Finally, cleaning exposed bilateral canine periapical abscesses, with a fenestration on the facial surface near the tip of the right canine and on the nasal surface near the left canine tip (Fig. 3A). The cause of this symmetrical pathology is unknown, and it may or may not be associated with the nasal margin asymmetry noted earlier. Wear to the canines does not appear to have exposed the pulp chambers, which could lead to periapical infection via the root canals (Hershkovitz, personal communication). The maxillary sinuses also appear to be clear of any obvious signs of infection that could have led to abscesses via the neurovascular bundle to the canine root. More intensive microscopic examination may reveal the underlying cause of this pathology.

Also exposed during the cleaning were bilateral accessory foramina piercing the superior corners of the maxilla, where they form the nasal margins medially and meet with the nasal bones superiorly (Fig. 3A,E). These may be associated with branches of the infraorbital nerve, and their unusual degree of development is consistent with the large size of both the infraorbital and zygomaticofacial foramina. All of these foramina transmit cutaneous branches of the maxillary division of the trigeminal nerve (the zygomatic and infraorbital nerves) to the skin of the face, but their large size and number in this specimen are probably not related to the development of cheek pads as seen in modern orangutan males. Orangutan males rarely have facial foramina the size of those on MTA 2125, and AS95-500, an apparent female, also has large zygomaticofacial and infraorbital foramina. If these foramina did transmit larger numbers of nerve fibers to the face, it is not clear why.

The mandible (Fig. 2)

The major restoration to the mandibular specimen was the removal of the plaster corpus attached to the left side of the specimen and some cleaning of the exposed root canals and alveoli of the anterior dentition. As noted above, this specimen was described in detail in Ozansoy (1965, 1970). There is some discrepancy among the accounts of several authors who have compared this specimen to other Miocene and recent hominoids (e.g., Simons and Pilbeam, 1965; Andrews and Tekkaya, 1980; Kelley and Pilbeam, 1986). Given these differing views and the discovery of new comparative material (e.g., Leakey et al., 1988; Alpagut et al., 1990) we will summarize our observations on the newly cleaned specimen here.

In anterior view, the narrow, deep symphysis is most similar to GSP 9564 and, to a lesser extent, to GSP 15000 and KNM SO 396 (in absolute dimensions and overall morphology). The GSP specimens are attributed to *Sivapithecus,* while KNM SO 396 is attributed to *Proconsul* (Brown, 1989). The symphysis is deeper than in other specimens attributed to *Sivapithecus* (e.g., GSP 4622, 13875) but not so deep as in *Afropithecus* (KNM WS 11599, KNM WK 16840) (Brown, 1989). It is narrower, as indicated by bicanine breadth, than the symphyses of *Ouranopithecus.* The symphysis of AS95-500 also appears to be narrow relative to postcanine dental dimensions (Alpagut et al., 1996). The symphysis is also deeper than in G 1313 from Paşalar, attributed to *Griphopithecus* (Alpagut et al., 1990). It shares with GSP 9564 a well-developed mental crest, also seen in WK 16840 and apparently in AS95-500 as well (Alpagut et al., 1996). Like GSP 9564, WK 16840, and WS 11599, the alveolar process of the type of *Ankarapithecus meteai* bulges lateral to the canines and tapers inferior to the canine alveoli. Although poorly preserved at the base of the symphysis, the type appears to widen again at the base, giving the symphysis a slightly waisted appearance. Waisting is strongly developed in the two *Afropithecus* specimens, probably more so than in *Ankarapithecus.* The incisors are nearly vertically oriented and barely project anteriorly beyond
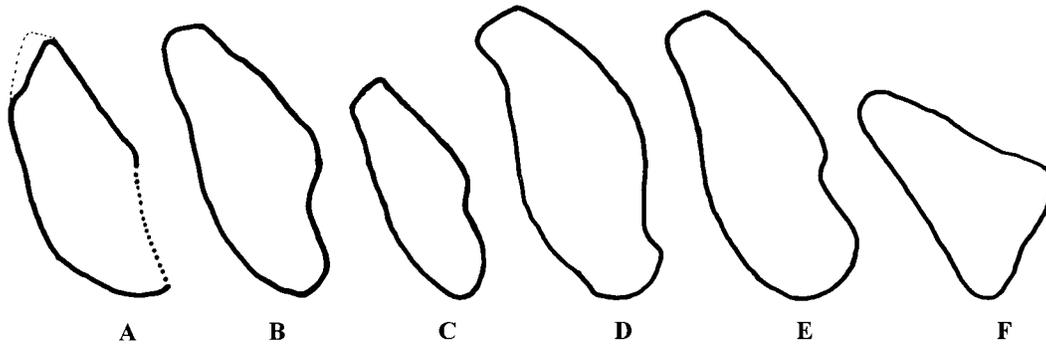
Fig. 5. Cross-section of the symphysis of the type of *Ankarapithecus meteai* compared to a series of symphyses of other hominoids. Comparative cross-sections taken from Brown (1989). **A:** *Ankarapithecus* type. **B:** GSP 9564 (*Sivapithecus*). **C:** AMNH 19411 (*Sivapithecus*). **D:** KNM WK 16840 (*Afropithecus*). **E:** KNM WS 11599 (*Afropithecus*). **F:** KNM SO 396 (*Proconsul*).

the mesiolabial corner of the canines, most similar to the condition seen in GSP 15000. *Afropithecus* has more procumbent lower incisors (Leakey et al., 1988; Leakey and Walker, 1997).

Part of the lingual surface of the symphysis is preserved. It is very narrow and strongly transversely concave or grooved between the anterior ends of the corpora. This surface is preserved to a level close to the tips of the canine roots and probably represents nearly all of the sublingual plane. It is smooth and vertically oriented. In mid-sagittal cross-section (Fig. 5), the symphysis thickens inferiorly as the sublingual plane diverges from the buccal surface of the symphysis. Though the genioglossal fossa is not preserved, the sublingual plane appears to be preserved to the superior transverse torus. The sublingual plane forms an angle with the alveolar plane of about 50° (Table 1). If the superior transverse torus is preserved in its entirely along the sublingual plane, then it extends to a level between the P_3/P_4. In these characteristics, the lingual surface of the symphysis is quite similar to AS95-500. The base of the symphysis is preserved just at the midline, giving an indication of the level of the inferior transverse torus. The base curves inwards toward the symphysis at the level between the P_4/M_1. This suggests that the inferior transverse torus was no more distally positioned than the level about mid M_1, judging from the overall pattern of similarity among *An-*

karapithecus, Afropithecus, and larger *Sivapithecus* (Brown, 1989) (Fig. 5). Ridges on the basal symphyseal surface correspond to a crescent-shaped anterior digastric impression (Brown, 1989). The lingual surface of this specimen appears to be quite distinct from G1313 (*Griphopithecus*), which is described as having a strongly sloped symphysis, demonstrated in part by the difference between symphyseal height and length. In G1313, these make a ratio of 0.73, whereas in *Ankarapithecus* the ratio is 0.94 (Table 1). This also illustrates the difference in symphyseal length between the two, which is consistent with the observation by Alpagut et al. (1990) that the inferior transverse torus of G1313 extends to the level of the M_2, a position probably more posterior than in *Ankarapithecus.* Overall, the lingual surface of the symphysis is very similar to that of *Afropithecus.* GSP 9564 also has a narrow labial symphyseal surface, but it has a more horizontal sublingual plane and a more prominent superior transverse torus.

The anterior half of the mental foramen is preserved inferior to P_3/P_4, fairly low down on the corpus. Although the position of this foramen is variable, it tends to be lower in early and middle Miocene forms and higher in late Miocene *Sivapithecus* and *Dryopithecus.* The roots of the canines are more externally rotated than in *Sivapithecus,* with their major axes oriented more buccolingually, as in most other Miocene hominoids, rather than more in line with the postcanine

TABLE 3. *Comparative dental ratios (samples, means, and ranges) among fossil and living hominoids, anterior dentition*[1]

	Ankarapithecus	AS95-500	Sivapithecus	Proconsul	Kenyapithecus	Dryopithecus	Ouranopithecus	Pongo	Pan	Gorilla	Australopithecus
Canine length/breadth											
Upper	1.12	—	1.25 (12) 1.13–1.39	1.28 (16) 1.11–1.46	1.37	1.33 (4) 1.27–1.43	0.98 (3) 0.92–1.05	1.27 (34) 1.10–1.47	1.31 (49) 1.11–1.53	1.37 (39) 1.12–1.56	0.98 (9) 0.87–1.14
Lower	1.37	—	1.30 (6) 1.23–1.44	1.26 (16) 1.09–1.38	1.36	1.44 (5) 1.28–1.70	1.52 (3) 1.48–1.58	1.23 (38) 1.09–1.42	1.17 (47) 1.03–1.32	1.26 (35) 1.11–1.40	0.94 (9) 0.71–1.20
I^1/I^2	1.95	1.6–1.64	2.12	1.43 (3) 1.39–1.51	1.65	1.68 (2) 1.66–1.69	1.66	1.55 (14)	1.29 (28)	1.38 (40)	1.63 (3) 1.54–1.79

[1] Canines from males only except in *Australopithecus*. *Proconsul* from Rusinga, Songhor, Chamtwara, Legetet, and Koru. *Kenyapithecus* from Fort Ternan (KNM-FT 28, 39). *Pongo* incisor values from *Pongo pygmaeus pygmaeus*. *P. pygmaeus abeli* has more incisor heteromorphy ($\bar{x}$ = 1.78). Numbers in parentheses refer to sample sizes. Data from Kelley et al. (1995) and personal observations.

tooth row, as in *Sivapithecus.* The mesial surface of the alveolus of the distal root of the P_3 is exposed. It is very long, descending almost as far inferiorly as the canine roots.

The dentition (Figs. 2, 3)

The dentition of the type of *Ankarapithecus meteai* and the MTA 2125 palate share a number of characteristics with *Sivapithecus* and *Ouranopithecus,* which was the primary reason for sinking these three genera in *Sivapithecus* (Andrews and Tekkaya, 1980). However, like the mandible and maxilla, important differences between the Sinap specimens and *Sivapithecus* and *Ouranopithecus* exist. Measurements of the teeth are given in Table 1.

The type specimen preserves the right I_2, both canines, and the left P_3 to M_3. The right I_2 root is long and robust and concave mesially, and it has a broad distal groove. The crown is tall, labiolingually thick, and slightly asymmetrical, as in great apes. In overall size and morphology, it is similar to that of GSP 15000, though less worn. The type I_2 is larger but morphologically similar to I_2 specimens of *Dryopithecus* (RUD 14, 17, and HGP 1 1902-12b). The lingual surface of the Turkish specimen has slightly more relief (low lingual, mesial, and distal pillars).

The canines of the type mandible are relatively low crowned. While the crown heights cannot be measured due to wear, the mesial and distal margins converge more strongly from the cervix than in most male canines of *Sivapithecus* and modern hominids. In length/breadth ratios, the ca-

nines of the type are most similar to the canines of *Sivapithecus* and *Kenyapithecus* (Table 3). The *Ankarapithecus* values are also in the range of variation of *Dryopithecus* but closer to those of geologically older *Dryopithecus* (*D. fontani*), which have broader canines relative to length than later *Dryopithecus* (*D. brancoi* and *D. laietanus*) (Begun, 1994). *Dryopithecus* and *Ouranopithecus* male lower canines are typically more slender buccolingually compared to their length and are high crowned relative to cervical dimensions. *Proconsul* male canines are more robust (buccolingual and mesiodistal diameters closer to the same value) on average than in *Ankarapithecus,* which is just at the extreme of the range of variation in *Proconsul* (Table 3). *Proconsul* male canines are generally higher crowned, unlike *Afropithecus,* in which the canines are even lower crowned relative to cervical dimensions than in the type of *Ankarapithecus.* Andrews and Tobien (1977) describe the male lower canines of *Griphopithecus* from Paşalar as robust, and they are morphologically very similar to those of *Ankarapithecus.* Male lower canines in living great apes are generally also more robust than in *Ankarapithecus,* which is at the high end of the ranges of *Pongo* and *Gorilla* but outside of the range of *Pan* and *Australopithecus. Australopithecus* males and females have small canines but with more reduction of the mesiodistal diameter compared to buccolingual diameter, leading to a lower ratio. *Ouranopithecus,* which is said to share canine reduction with *Australopithecus* (de Bonis and

Koufos, 1993), has a very high ratio of male lower canine length to breadth, suggesting that canine reduction in *Ouranopithecus* differs from that in *Australopithecus.* This is also suggested by the fact that in *Ouranopithecus* the male lower canines are quite high crowned, and only the uppers are low crowned, as in *Australopithecus.* In male canine robusticity and crown height, the pattern in *Ouranopithecus* is very different from that in *Ankarapithecus.*

The right canine is strongly worn, with large, elongated wear facets having removed the mesial beak mesially down to the cervix and most of the distal face of the crown. The tip is worn to the point where the pulp chamber is exposed. The left canine is substantially less worn, having somewhat less distal wear, a small wear facet on the mesial ridge toward the crown apex, and much less wear on the apex itself. The right canine seems to be implanted more vertically than the left, and this may account for the differential wear. The description below is therefore based on the left canine. The canine crown preserves a mesial beak at the junction of three ridges, a low, thick mesiolabial ridge running inferiorly toward the cervix, a sharper mesiolingual ridge running toward the crown apex and separating the mesiolingual and mesiolabial faces of the crown, and a mesiolingual cingulum running along the cervix lingually and continuous with a distal cingulum wrapping around the distal corner of the crown. Labial and distal to the mesiolabial ridge is a clear furrow, beginning as a moderately deep cleft toward the cervix and becoming broader and more shallow toward the apex. This furrow is not the mesial groove found in many Miocene hominoid male canines, and occasionally in living hominids as well (especially *Gorilla*), because the mesial groove is always lingual to the mesiolingual ridge. The faint traces of a mesial groove can be seen on the worn mesiolingual surface of the left canine of the type mandible. The mesiolabial ridge is prominent in this specimen because of the vertical displacement between the mesial beak and the flare of the cervix labially on the canine, which are linked by this ridge. The displacement of the mesial beak toward the apex is also clear in mesial view, where

the mesiolingual and mesiolabial ridges meet at an acute angle.

The configuration of ridges attached to the mesial beak in hominids is variable within species, but few specimens have such well-developed ridges as *Ankarapithecus.* In modern hominids, the mesial beak and associated ridges are usually poorly developed, and the mesial beak, when present, is closer to the lowest edge of the cervix than in *Ankarapithecus. Sivapithecus* is similar to *Ankarapithecus,* but the lingual cingulum is often less apparent, taking the form of a low, rounded ridge rather than a sharp, narrow ridge as in the *Ankarapithecus* type. Exceptions include the narrow, more sharply defined cingula on AMNH 19411 and AMNH 19412. The mesial furrow is quite similar in both forms and is nearly identical in the type and GSP 15000. *Griphopithecus* male canines have well-defined mesial grooves and ridges but poorly defined lingual cingula and mesiolabial ridges, perhaps related in part to the more cervical position of the mesial beak in this taxon. Most early Miocene taxa have low mesial beaks and thicker, more prominent lingual cingula. Though much more robust, the male canines of *Afropithecus* are similar in mesial ridge and beak configuration to *Ankarapithecus.*

Other late Miocene hominids (*Ouranopithecus* and *Dryopithecus*) are less like *Ankarapithecus* than is *Sivapithecus* in canine morphology. Both *Ouranopithecus* and *Dryopithecus* male lower canines tend to be more high crowned and buccolingually compressed, and both typically lack the arrangement of grooves and ridges described above. *Ouranopithecus,* for example, tends to have less well-developed cingula and more strongly developed mesial grooves. The geologically older species of *Dryopithecus* (*D. fontani*) has more strongly developed mesial beaks, some development of the mesial ridges, and somewhat more robust crowns but with more strongly developed mesial grooves and crowns that are nevertheless more compressed than in *Ankarapithecus.* Younger species (*D. laietanus* and *D. brancoi*) have even more compressed crowns and poorly developed ridges, grooves, and beaks.

As noted by Andrews and Tekkaya (1980), the P_3 of *Ankarapithecus* is very large, with

a large, fairly vertical, and relatively mesially facing upper canine wear facet, a strong mesial beak, and a very large, elongated talonid. It is flared at the cervix buccally, its lingual surface is nearly vertical, and the crown apex is roughly midway between the mesial and distal edges. Excluding *S. parvada,* P_3s of *Sivapithecus* are similar in relative size to those of *Ankarapithecus* (Kelley, 1988) but have more inclined canine facets associated with crown apices positioned more distally on the tooth. Siwalik specimens from stratigraphically later localities (GSP 15000, GSI 18039, GSP 6160, GSP 13445, D 197) tend to have relatively broader P_3s with inflated lingual surfaces, while those from older localities (AMNH 19411, 19412, YPM 13870) are narrower, or more elongated, and more similar to *Ankarapithecus.*[1] *Dryopithecus* and *Ouranopithecus* P_3s also tend to be broader, like the younger specimens of *Sivapithecus.* In fact, younger *Dryopithecus,* as well as *Ouranopithecus,* which is younger than most if not all *Dryopithecus* (Mein, 1986; de Bonis and Koufos, 1993), have very short, sometimes triangular P_3s with strongly flared lingual surfaces. *Ouranopithecus* P_3s in particular are quite distinctive, as noted previously by Andrews and Tekkaya (1980) and de Bonis and Koufos (1993).

The P_4 of the type is also large in absolute size but similar to *Sivapithecus* (excluding *S. parvada*), *Dryopithecus,* and *Ouranopithecus* in relative size. The tooth is broad compared to the somewhat more elongated P_4 in *Proconsul, Dryopithecus, Kenyapithecus,* and *Pongo* (Table 4). The P_4s of AS95-500 are even broader, falling outside of the range of variation of these taxa.[2] The P_4 of the type has a relatively tall trigonid, a prominent crest between the protoconid and metaconid (lateral protocristid), and a large, low, lingually displaced talonid. *Ankarapithecus* is again more similar to some of the older Siwalik specimens in P_4 relative breadth and trigonid and talonid morphology (especially AMNH 19411), though P_4 morphology is more variable than P_3. Most younger

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Siwalik P_4s are broader compared to length than *Ankarapithecus,* which is also true of *Ouranopithecus,* while *Dryopithecus* tends to have more elongated P_4s. The P_4 of *Ankarapithecus* also has prominent linear hypoplasias distobucally and lingually.

The M_1 of *Ankarapithecus* is very heavily worn and slightly damaged, preserving few anatomical details. It is broad relative to length compared to *Proconsul* and hominids, though this may be due to wear, which tends to decrease the mesiodistal diameter of molars more rapidly than buccolingual breadth (Table 4). Nevertheless, the tooth is quite broad even compared to the broadest and most worn M_1 specimens in other samples (Table 4). The M_1s of AS95-500 are slightly longer but still broad compared to most other samples (Table 4). Wear has flattened the lingual cusps and exposed large, coalesced pools of dentine buccally, as is seen most typically in hominoids with thick enamel (*Sivapithecus, Ouranopithecus, Australopithecus*). The M_2 is noticeably larger than the M_1, as is the case for *Proconsul* and *Kenyapithecus. Dryopithecus, Sivapithecus, Ouranopithecus, Australopithecus,* and the living great apes have first and second lower molars closer to the same size (Table 4). The M_1-M_2 ratio in the type of *Ankarapithecus* is outside of the range of variation of these genera. In AS95-500, the left M_1-M_2 ratio is within the range of variation of late Miocene to living hominids, while the right side ratio is below. Unlike the M_1, the M_2 is not distinctive in relative breadth (Table 4). AS95-500, however, does have broader M_2s, below the range of variation of M_2 length-breadth ratios for all Miocene taxa. The M_3 of *Ankarapithecus* is close in length and breadth dimensions to the M_2 but is tapered distally such that overall it is a smaller tooth. It is more flared buccally, especially buccal to the protoconid, and has a large, centrally positioned hypoconulid. Though morphologically diverse, the M_3s from the Siwaliks tend to be smaller than the M_2s, at least in breadth. Most of the exceptions to this observation are among the older specimens (D 198, GSP 16077, YPM 13814, AMNH 19412). Among the younger Siwalik specimens, a number of the smaller specimens have elongated, narrow M_3s unlike

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[1]This and subsequent references to the stratigraphy of Siwalik specimens are taken from Brown (1989).

[2]AS95-500 metric comparisons are taken from measurements in Alpagut et al., (1996).

TABLE 4. Comparative dental ratios (samples, means, and ranges) among fossil and living hominoids, Postcanine dentition[1]

	Ankarapithecus	AS95-500	Sivapithecus	Proconsul	Kenyapithecus	Dryopithecus	Ouranopithecus	Pongo	Pan	Gorilla	Australopithecus
M^1	0.84	0.87	0.90 (27) 0.75–1.00	0.85 (41) 0.77–0.95	0.92 (6) 0.87–1.00	0.88 (15) 0.82–0.92	0.89 (4) 0.86–0.92	0.92 (60) 0.80–1.02	0.92 (65) 0.81–1.02	0.96 (43) 0.85–1.10	0.92 (9) 0.85–1.00
M^2	0.92	0.89	0.89 (17) 0.80–0.99	0.84 (38) 0.77–0.91	0.84 (38) 0.77–0.91	0.96 (2) 0.91–1.02	0.91 (4) 0.86–0.94	0.88 (61) 0.78–0.98	0.89 (65) 0.75–1.03	0.98 (44) 0.87–1.20	0.88 (7) 0.84–0.91
M_1	1.03	1.06	1.12 (15) 1.06–1.28	1.16 (36) 1.04–1.23	1.16 (36) 1.04–1.23	1.14 (8) 1.07–1.23	1.14 (3) 1.11–1.16	1.10 (125) 1.03–1.23	1.11 (231) 1.00–1.28	1.15 (370) 1.00–1.23	1.04 (11) 0.97–1.13
M_2	1.10	1.02	1.16 (19) 1.03–1.19	1.16 (29) 1.03–1.25	1.16 (29) 1.03–1.25	1.10 (3) 1.07–1.16	1.12 (4) 1.08–1.19	1.07 (110) 0.94–1.33	1.06 (231) 0.92–1.27	1.14 (370) 0.98–1.27	1.04 (15) 0.93–1.18
M^1-M^2	0.86	0.80	0.86 (11) 0.72–0.97	0.78 (17) 0.65–0.94	0.78 (17) 0.65–0.94	0.72	0.81 (4) 0.78–0.86	0.97 (60) 0.80–1.09	0.96 (65) 0.76–1.09	0.87 (43) 0.70–1.04	0.84 (4) 0.8–0.92
M_1-M_2	0.67	0.76	74.6 (14) 58.7–86.7	68.8 (17) 58.9–84.7	68.8 (17) 58.9–84.7	62.5 (2) 61.0–64.0	81.8 (3) 78.0–86.9	84.8 (20) 76.0–100	98.2 (20) 84.0–115	80.0 (20) 73.0–87.0	83.6 (7) 79.2–94.6
P^3	0.78	0.60	0.74 (9) 0.60–0.82	0.67 (19) 0.58–0.82	0.67 (19) 0.58–0.82	0.68 (2) 0.68–0.68	0.70 (4) 0.65–0.77	0.77 (58) 0.61–1.03	0.78 (65) 0.56–1.08	0.77 (41) 0.60–0.95	0.72 (10) 0.66–0.77
P^4	0.63	0.64	0.66 (15) 0.56–0.77	0.61 (31) 0.48–0.69	0.61 (31) 0.48–0.69	0.64 (4) 0.58–0.67	0.62 (4) 0.58–0.67	0.73 (59) 0.64–0.81	0.71 (65) 0.62–0.81	0.72 (42) 0.64–0.81	0.75 (12) 0.63–0.98
P_4	0.89	0.78	0.86 (21) 0.74–1.00	0.95 (25) 0.83–1.16	0.95 (25) 0.83–1.16	0.94 (6) 0.84–1.15	0.84 (2) 0.80–0.88	0.94 (13) 0.83–1.00	0.89 (11) 0.80–0.96	0.89 (50) 0.71–1.06	0.87 (4) 0.78–0.93

[1] Data from Andrews (1978), Begun (1995) and additional observations. Numbers in parentheses refer to sample sizes.

those of *Ankarapithecus* (GSP 4622, GSP 13566, GSP 6153, YPM 13806), while other larger specimens are closer to *Ankarapithecus* in being broader and closer in size to M_2 (YPM 13828, GSI 18040). *Dryopithecus* M_3s are also variable but tend to be narrower than the M_2s and more tapered (Begun and Kordos, 1993). *Ouranopithecus* has large M_3s, usually larger than the M_2s in both length and breadth.

The MTA 2125 palate has a complete dentition. This has been described in some detail by Andrews and Tekkaya (1980). A few amendments to this description, taking into account the discovery of additional comparative material, are offered here. As noted by Andrews and Tekkaya (1980), upper incisor length heteromorphy is high in MTA 2125. Our measurements yield an upper incisor heteromorphy of 1.95 (from the left side) (Table 3). This is lower than the figure of 2.11 from Andrews and Tekkaya (1980). Kelley et al. (1995) suggest that upper incisor heteromorphy might be artificially elevated in this specimen and in GSP 15000 due to the differential effects of wear. They note, citing Greenfield (1992), that upper lateral incisors, which occlude distally with the lower canine in males, tend to lose more of their original length through wear than do central incisors. The upper lateral incisors of MTA 2125 are worn, but both retain some crown flare. The left one has a deeper canine wear facet but is actually slightly longer than the right, suggesting that most of the original length is preserved. Even at 1.95, the incisor heteromorphy of MTA 2125 is quite high in comparison to modern hominoids, falling within the range of variation only of the Sumatran subspecies of orang, *Pongo pygmaeus abelii,* (Kelley et al., 1995). Incisor hetermorphy is less marked in AS95-500, though still high compared to modern genera. Late Miocene hominids in general have higher levels of upper incisor heteromorphy than in modern hominoids, with values for most taxa falling well above the means and close to the maxima for modern taxa, including Bornean orangutans (Kelley et al., 1995). One specimen of *Sivapithecus parvada* exceeds the value recorded for MTA 2125 (Kelley et al., 1995), though it was suggested that other species of *Sivapithecus* probably had lower values, perhaps compa-

rable to MTA 2125. Although one *Ouranopithecus* specimen (RPL 128) is close to MTA 2125, with an I^1/I^2 ratio of 1.78 (Andrews and Tekkaya, 1980), we agree with Kelley et al. (1995) that this is probably exaggerated given damage and wear to the lateral incisor. A second, better preserved specimen (ZIR-1) has a lower value of 1.66 (Table 3). The incisor heteromorphy of ZIR-1 is the same as one specimen of *Dryopithecus* reported by Kelley et al. (1995) and very close to that of a new specimen of the same species (RUD 44/144, $I^1/I^2 = 1.69$) (Table 3). In sum, then, the incisor heteromorphy in MTA 2125 is probably large and closest to the means of *Sivapithecus* and modern Sumatran orangutans.

As noted by Andrews and Tekkaya (1980), the upper canines of MTA 2125 are broad relative to length (robust) compared to most taxa (Table 3). Two taxa, *Ouranopithecus* and *Australopithecus,* have more robust upper canines than *Ankarapithecus.* However, robusticity in these forms is related to a relative reduction in canine mesiodistal vs. buccolingual dimensions, as was suggested for the lower canines of *Australopithecus* (see above). Both canines are worn, especially the left one, where the mesial and distal wear facets have merged at the apex and substantially lowered the crown height compared to the right canine. Both specimens also have broad, flat mesial wear surfaces for the lower canine. Although these wear facets are strongly developed, very deep mesial grooves remain visible. As noted by Andrews and Tekkaya (1980), the crowns were probably relatively low. They also have an unusual degree of cervical flare both mesiodistally and buccolingually for male hominoid canines. In this regard, they are similar to the male canines of *Ouranopithecus* (RPL 128, 209, and ZIR-1) and to a lesser extent one specimen of *Sivapithecus* (GSP 9977). The canine crowns are strongly wrinkled on their labial surfaces and on the small, unworn lingual surfaces.

The premolars are similar to *Sivapithecus,* with a strongly triangular outline to the P^3 and a more rectangular P^4, as is also the case in other hominids (except *Ouranopithecus*). In MTA 2125, the P^3 tends to be short relative to breadth compared to living great apes and more like other Miocene taxa and *Australopithecus,* though there is a substantial overlap in ranges of variation (Table 4). In AS95-500, the P^3s are even shorter, at the low end of the range of variation for a number of taxa (Table 4). The P^4 in both MTA 2125 and AS95-500 is also broader than in living hominids and *Australopithecus* and more like that of the other Miocene taxa (Table 4). In all four premolars, the protocones are worn completely off. They have vertical sides, and the P^4s are broader lingually than buccally. Both these traits are typical of many hominoids except *Afropithecus* and *Morotopithecus,* which have strongly flared premolars, and chimpanzees and humans, which have flared P^4s lingually.

M^1 is close in length/breadth ratio to the sample of *Proconsul* and at the low end or below the range of variation of the other taxa (Table 4). M^1 length/breadth ratio in AS95-500 is closer to the means of the other Miocene taxa. The M^2 length/breadth ratio is above the range of variation only of *Proconsul* and *Australopithecus* (Table 4), although again the same ratio in AS95-500 falls within these ranges. M^1 is close in size to M^2 in hominids and unlike the condition in *Kenyapithecus* and *Proconsul.* Unlike the case in many hominids, M^3 is the largest tooth. This is also true of AS95-500 and *Ouranopithecus* (RPL-128, ZIR-1, NKT-89). Cingula are absent as in many hominids but unlike early and middle Miocene hominoids. Molar crowns are relatively high and flat-sided, like late Miocene and more recent hominids and unlike the lower crowned molars of most early Miocene hominoids, which also bulge bilaterally between the cervix and the occlusal surface. The enamel is worn completely off the lingual halves of the occlusal surfaces of M^1 on both sides, and the buccal cusps have been replaced by large dentine pools. These have coalesced on the left side with the large lingual dentine exposure, leaving just a trace of enamel on the occlusal surface. The M^2s have dentine pools on each cusp but with more wear buccally than lingually. The M^3 on each side is worn nearly flat, with only a tiny pit of dentine exposed on the protocone. There is no broken enamel surface to measure, but, based on the pattern of wear, the enamel was probably thick

and the enamel-dentine junction relatively flat.

Given the degree of completeness of MTA 2125, it should be possible to make some inferences of the behavior of this individual, and by extension the taxon as a whole, from its functional anatomy. While a more detailed functional analysis is in preparation, it can be noted here that MTA 2125 shares a suite of characters with other fossil hominoids that are very commonly associated with a powerful masticatory apparatus (Robinson, 1954; Kay, 1981; Kay and Covert, 1984; Rak, 1983; Kay and Grine, 1988). This includes large molars and premolars with thick enamel, flat occlusal planes, and low dentine penetrance, poorly developed shearing crests, anteriorly positioned and laterally flared zygoma, a large temporalis foramen, small lower incisors relative to molar size, and reduced canines. Molar megadontia is difficult to confirm without reliable evidence of body size independent of dental size. However, as noted above, for most of the cranial characters compared between MTA 2125 and other hominoids, ratios using molar size to standardize for body size were lower than those which used palatal breadth (Table 2), suggesting some degree of molar megadontia. MTA 2125 also shows a more idiosyncratic set of additional features suggestive of a very powerful masticatory apparatus. This includes a massive facial skeleton, an extremely deep zygomatic arch, a very robust posterior palate, and strongly developed muscle attachment sites for masseter and the pterygoid muscles.

DISCUSSION

Resurrecting *Ankarapithecus*

Because of the diversity of mandibular and dental morphology in *Sivapithecus,* it would not be possible to maintain a taxonomic distinction between *Sivapithecus* and *Ankarapithecus* given only the type of the latter. However, much of the newly revealed anatomy of MTA 2125 has a bearing on the issue of the taxonomic attribution of this specimen and its phylogenetic position. In order to investigate the phyletic affinities of the Sinap specimens more completely, we performed a character analysis based on the description of the specimens provided above.

Characters were polarized using *Proconsul* as the outgroup. Separate character states were assigned where discontinuous character states could be distinguished among taxa and where different states did not occur within a terminal taxon. Separate character states were assigned for continuous characters if there was evidence of a significant quantitative gap within a distribution. A large number of characters described here were judged of uncertain usefulness for the phylogenetic analysis due to excessive variability in the comparative samples. For the most part, these are quantitative characters of the dentition (see Table 5). Whenever possible, an attempt was made to minimize the complexity of characters by avoiding multistate characters. The majority of characters have only one derived state. A number have two, and one has four. The characters, character states, and their distribution are listed in Table 5. The data matrix generated from these characters was analyzed for patterns of shared derived character states using the phylogenetic program Hennig 86 (Farris, 1988). The analysis was run with the characters all equally weighted and unordered to exclude a priori expectations about the relative phylogenetic significance of characters or the directionality of multistate characters. However, even with ordered characters, the results are the same. The *ie* option in Hennig 86 was used to recover all maximally parsimonious cladograms. The results of this analysis are depicted in Figure 6.

Although only one most parsimonious cladogram was found, there is a large amount of homoplasy in this data set. Given this fact, a number of alternative branch topologies were examined using the XX function in Hennig 86 (Fig. 7). Several alternative branching patterns involving potential members of the clade that includes the Sinap material are considered below.

The nomen *Ankarapithecus* was used to label the terminal taxon represented by both the Sinap maxilla and the type mandible. *Ankarapithecus* is, strictly speaking, only the mandible; the palate has been referred to this taxon. Previous researchers (Andrews and Tekkaya, 1980; Kelley and Pilbeam, 1986) have found no reason to distinguish among these specimens taxonomically.

TABLE 5. *Character states for the taxa included in this analysis*[1]

	P	Af	M	G	K	An	S	D	O	Or	C	Go	Au
1. Zygomatic root pneumatization (0 = solid; 1 = hollow)	0	—	1	—	—	0	0	1	—	1	1	1	1
2. Infraorbital foramen-nasal aperture (0 = near apex; 1 = below apex)	0	0	—	—	—	0	0	1	1	1	1	0	1
3. Zygomatic depth (0 = shallow; 1 = deep)	0	1	—	—	—	1	1	—	—	0	0	0	0
4. Zygomatic orientation (0 = lateral; 1 = anterior)	0	0	—	—	—	1	1	0	0	1	0	0	1
5. Maxillary sinus/canine position (0 = posterior; 1 = anterior)	0	0	0	—	—	0	1	1	—	1	1	1	1
6. Maxillary nasal process (0 = robust; 1 = hollow)	0	—	—	—	—	0	1	0	—	1	1	1	1
7. Orbital/nasal distance (0 = large; 1 = small; 2 = very large)	0	2	—	—	—	0	0	—	—	1	1	0	1
8. Orbital/nasal surface (0 = concave; 1 = flat)	0	0	—	—	—	0	1	0	0	1	0	0	0
9. Interorbital distance (0 = broad; 1 = narrow)	0	0	0	—	—	1	1	0	0	1	0	0	0
10. Inferior orbital border (0 = crested; 1 = rounded)	0	0	—	—	—	1	1	0	0	1	0	0	1
11. Zygomatic arch/orbit (0 = same level; 1 = below)	0	0	—	—	—	0	0	—	—	1	1	1	0
12. Zygomatic temporal process (0 = shallow; 1 = deep)	0	—	—	—	—	1	0	0	0	0	0	0	0
13. Zygomatic arch angle (0 = inclined; 1 = more vertical; 2 = horizontal)	0	1	—	—	—	1	1	0	0	1	2	2	2
14. Nasal aperture breadth (0 = narrow; 1 = broad)	0	0	0	—	—	1	0	0	1	0	0	1	0
15. Nasal aperture/orbit position (0 = low; 1 = very low; 2 = high)	0	1	0	—	—	1	1	—	—	0	2	0	2
16. Nasal aperture/alveolar (0 = low; 1 = high)	0	0	0	—	—	1	1	—	1	1	1	1	1
17. Nasal aperture edges (0 = vertical; 1 = inclined; 2 = horizontal)	0	0	1	—	—	1	2	1	1	2	1	1	1
18. Nasal aperture shape (0 = oval; 1 = piriform)	0	1	—	—	—	1	1	—	0	1	0	0	0
19. Lacrimal fossa visible (0 = no; 1 = yes)	0	1	—	—	—	1	1	1	1	0	1	1	1
20. Nasal bone length (0 = short; 1 = long; 2 = very long)	0	1	—	—	—	2	2	—	1	1	0	1	0
21. Nasal aperture/malar surface (0 = anterior; 1 = intermediate; 2 = flat)	0	0	0	—	—	0	2	—	1	2	1	1	1
22. Inferior orbital margin/M^1 (0 = above; 1 = posterior)	0	0	0	—	—	0	1	—	0	1	0	0	0
23. Nasal apex/M^2 (0 = above; 1 = posterior)	0	0	0	—	—	0	0	—	—	1	0	0	0
24. Maxillary surface (0 = lateral; 1 = anterior)	0	0	0	—	—	0	1	0	0	1	1	0	1
25. Canine fossa (0 = shallow; 1 = deeper)	0	1	0	1	1	1	1	0	0	1	0	0	1
26. $\underline{C}$ root angulation (0 = vertical; 1 = medial)	0	0	0	—	—	1	1	0	1	1	0	0	0
27. $\underline{C}$ root rotation (0 = in line; 1 = externally rotated)	0	0	0	—	—	1	1	0	1	0	0	0	1
28. Maxillary alveolar process (0 = solid; 1 = collapsed; 2 = inflated)	0	0	0	1	1	0	1	0	1	1	2	2	2
29. Incisor orientation (0 = vertical; 1 = horizontal)	0	0	0	—	—	0	1	0	0	1	0	0	0
30. Greater palatine foramen (0 = round; 1 = more elongated)	0	—	—	—	—	1	1	—	—	1	0	0	0
31. Greater palatine position (0 = anterior; 1 = posterior)	0	0	0	—	—	1	1	—	—	1	1	1	1
32. Lesser palatine foramina (0 = absent; 1 = small; 2 = large)	0	0	0	—	—	0	—	—	—	0	2	1	2
33. Horizontal palatine (0 = broad; 1 = narrow)	0	0	0	—	—	1	1	—	—	1	1	1	1
34. Palatine crest (0 = strong; 1 = weak)	0	0	0	—	—	0	0	—	—	0	1	1	0
35. Posterior palate (0 = shallow; 1 = deep)	0	0	0	—	—	1	1	1	1	1	1	1	1
36. Pyramidal process position (0 = superior; 1 = inferior)	0	0	0	—	—	0	0	—	—	1	1	1	1
37. Pterygoid process (0 = robust; 1 = compressed)	0	0	0	—	—	0	1	—	—	0	1	1	1
38. Alveolar process depth (0 = shallow; 1 = deep)	0	0	0	0	1	1	1	1	1	1	1	1	1
39. Zygomaticoalveolar crest (0 = compressed; 1 = broad)	0	0	1	—	—	0	0	1	1	0	1	1	1
40. Zygomatic root height (0 = low; 1 = higher)	0	0	0	0	1	1	1	1	0	1	1	1	1
41. Incisive fossa (0 = absent; 1 = shallow; 2 = deep)	0	—	0	—	—	2	1	2	2	1	2	2	2
42. Subnasal floor (0 = fenestrated; 1 = stepped; 2 = smooth)	0	—	0	—	—	1	2	1	1	2	1	1	1
43. Nasal clivus (0 = short; 1 = long)	0	0	0	—	—	1	1	1	—	1	0	1	0
44. Nasoalveolar clivus length (0 = short; 1 = intermediate; 2 = long)	0	1	0	—	—	2	2	1	1	2	2	1	2
45. Nasoalveolar clivus orientation (0 = vertical; 1 = horizontal)	0	0	0	—	—	1	1	0	0	1	0	0	0
46. Incisive canal caliber (0 = absent; 1 = large; 2 = intermediate; 3 = small; 4 = very small)	0	—	0	—	—	2	4	1	1	4	3	2	3
47. Mandibular canine roots (0 = buccolingually oriented; 1 = internally rotated)	0	0	—	—	—	0	1	0	0	1	0	0	0
48. Lower central incisors (0 = large; 1 = small)	0	0	—	1	0	1	0	0	0	0	0	0	0
49. Lower incisors labiolingually (0 = small; 1 = large)	0	0	—	1	—	1	1	1	1	1	1	1	2
50. Lower canine crown height (0 = tall; 1 = short; 2 = very short)	0	1	—	1	0	1	0	0	2	0	0	0	1
51. Lower molar cingula (0 = strong; 1 = weak/absent)	0	0	—	0	—	1	1	1	1	1	1	1	1
52. Lower M_1/M_2 size ratio (0 = small; 1 = large)	0	0	—	0	—	0	0	1	1	1	1	1	0
53. Lower M_3/M_2 size ratio (0 = $M_3 \leq M_2$; 1 = $M_3 > M_2$)	0	0	—	0	—	0	0	0	1	0	0	0	1
54. I^1/I^2 size heteromorphy (0 = lower; 1 = high; 2 = very high)	0	0	0	1	1	2	2	1	1	1	0	0	1
55. I^2 morphology (0 = peg-shaped; 1 = spatulate)	0	0	0	0	0	0	0	0	0	0	1	0	1
56. Upper canine height (0 = tall; 1 = low; 2 = very low)	0	0	0	0	0	1	0	0	1	0	0	0	2
57. Upper canine cervical flare (0 = weak; 1 = strong)	0	0	0	0	0	1	0	0	1	0	0	0	0
58. P^4 shape (0 = broad; 1 = long)	0	0	0	0	0	0	0	0	0	1	1	1	1
59. P^3 shape (0 = triangular; 1 = rectangular)	0	0	0	0	0	0	0	0	1	0	0	0	1
60. Premolar buccal flare (0 = weak; 1 = stronger)	0	1	1	0	0	0	0	0	0	0	0	0	0
61. P^4 lingual flare (0 = weak; 1 = strong)	0	0	0	0	0	0	0	0	1	0	1	0	1
62. M^2 shape (0 = broad; 1 = long)	0	0	0	0	1	1	1	1	1	1	1	1	1
63. Upper molar cingula (0 = strong; 1 = weak/absent)	0	0	0	1	1	1	1	1	1	1	1	1	1
64. M^1/M^2 size ratio (0 = small; 1 = large)	0	0	0	0	1	1	1	1	1	1	1	1	1
65. Upper molar crowns (0 = low; 1 = high)	0	0	0	0	0	1	1	1	1	1	1	1	1
66. Upper molar sides (0 = bulging; 1 = vertical)	0	0	1	0	1	1	1	1	1	1	1	1	1

[1] Abbreviations of taxa: P, *Proconsul;* Af, *Afropithecus;* M, *Morotopithecus;* G, *Griphopithecus* (Děvíinská Nová Ves, Paşalar, Çandir, Maboko, Kaloma); K, *Kenyapithecus* (Fort Ternan); An, *Ankarapithecus;* S, *Sivapithecus;* D, *Dryopithecus;* O, *Ouranopithecus;* Or, *Pongo;* C, *Pan;* Go, *Gorilla;* Au, *Australopithecus afarensis* (character states taken from *A. africanus* if unknown in *A. afarensis*). In a number of cases, characters described in the text are not included because their states were considered either too variable within taxa or too numerous among the taxa to be very useful in a phylogenetic analysis. This is particularly true of a number of dental traits that seem to vary with time in genera with significant time depth (*Dryopithecus, Sivapithecus*).
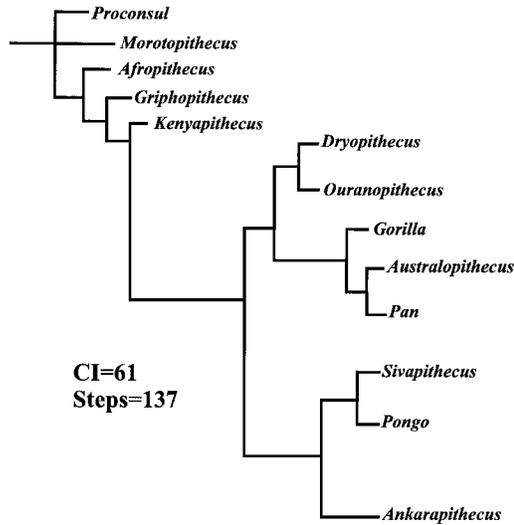
Fig. 6. Cladogram illustrating some of the relationships described in the text.

Our analysis supports this conclusion. We agree with Andrews and Tekkaya (1980) that the types and magnitudes of differences seen between the mandible and maxilla from Sinap, which are largely confined to the anterior portions of the jaws, could be duplicated in a large, single-sex sample of great apes and is in fact duplicated in the sample of maxillae and mandibles from the Siwaliks. The bicanine distance in the type is much less than that which would have been present in the mandible that was associated in life with MTA 2125. However, overall the morphology of both specimens is consistent with a single species interpretation.

Figure 6 includes a clade that consists of *Ankarapithecus, Sivapithecus,* and *Pongo. Ankarapithecus* is the sister clade to the clade that includes *Sivapithecus* and *Pongo.* As long as *Sivapithecus* and *Pongo* are retained as separate genera, which is advisable, *Ankarapithecus* cannot be synonymous with *Sivapithecus* because that would make the taxon *Sivapithecus* paraphyletic by excluding *Pongo.* Breaking up the *Sivapithecus-Ankarapithecus-Pongo* clade requires a large number of additional character state changes. The tree that places *Ankarapithecus* as the outgroup to all other hominids is the most parsimonioius tree without a *Siva-*

pithecus-Ankarapithecus-Pongo clade, but it requires 143 steps (Fig. 7A).

There is strong support in these data for a *Sivapithecus-Pongo* clade that excludes *Ankarapithecus.* The *Sivapithecus-Pongo* clade is supported by 11 synapomorphies, more than any other clade in Figure 6. Another seven support the placement of *Ankarapithecus* as the sister to this clade. The hypothesis that *Sivapithecus* and *Ankarapithecus* form a clade to the exclusion of *Pongo,* which would support the continued placement of the Sinap material in *Sivapithecus,* requires five additional steps (Fig. 7B). We feel these results strongly support the recognition of *Ankarapithecus* as a separate taxon, as originally suggested by Ozansoy (1957).[3]

Because the taxonomic revision we propose depends on the data from MTA 2125, we formally include it in the type series of *Ankarapithecus meteai,* which we redescribe as follows.

Ankarapithecus meteai Ozansoy, 1965

Holotype. Mandibular symphyseal fragment with both canines, RI_2, and LP_3 attached and the associated detached LP_4-M_3.

Paratype. MTA 2125, a palate with complete dentition and most of the maxillae, most of the right zygomatic bone, most of the left palatine bone, and small portions the left sphenoid bone.[4]

Descriptions. See above.

Species diagnosis (same for the genus). A large-bodied pongine hominoid sharing features with species of *Sivapithecus* and *Pongo,* including the following: large, flared zygoma; narrow interorbital distance; elongated greater palatine foramina; more horizontal nasoalveolar clivus; an inferior orbital border in the form of a crest; long nasoalveolar clivus; and medially inclined upper ca-

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[3]Several dates have been cited for the authorship of this taxon. Ozansoy (1957) does not include a description or diagnosis of the taxon. Ozansoy (1965) includes a formally designated type and description and so provides the proper date at which this nomen becomes available.

[4]The AS95-500 face and mandible are not included in the type series because we have not examined this specimen and cannot base the diagnosis on it. However, in all metric and qualitative characters described or listed in Alpagut et al. (1996) or visible in the photographs therein, AS95-500 is consistent with this diagnosis.
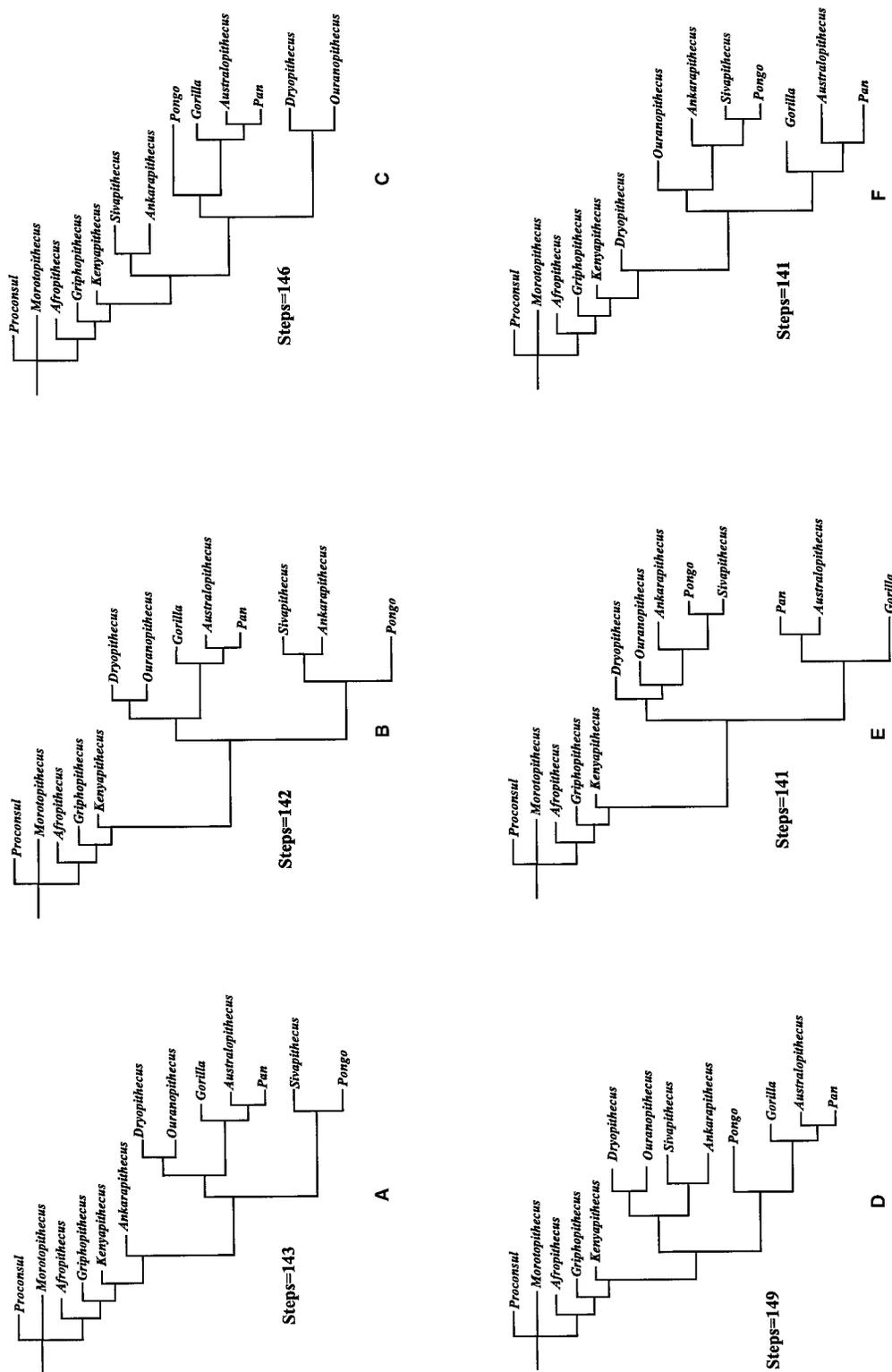
Fig. 7. Alternative cladograms less strongly supported by the evidence presented here. See text for discussion.

nine roots. *Ankarapithecus meteai* also shares with species of *Sivapithecus* very deep zygoma, an extremely elongated naso-maxillary suture, laterally rotated upper canine roots, broad orbital-nasal distance, high position of jugale relative to the orbital margin, low position of the nasal aperture, low infraorbital foramen in relation to the apex of the nasal aperture, nasal apex above M^2, inferiorly placed pyramidal process, M_1 small compared to M_2, broad P^4, less zygomatic root pneumatization, extreme upper incisor heteromorphy, and thick enamel. A number of these characters are also found in other Miocene hominoids and in Plio-Pleistocene hominids, but no taxa other than species of *Sivapithecus* share all of these features with *Ankarapithecus.* Compared to *Sivapithecus, Ankarapithecus meteai* is larger than all but *S. parvada* and is distinct from *Sivapithecus* and *Pongo* in having a less extensive maxillary sinus, a more laterally facing maxilla, a solid (smooth) maxillary alveolar process, a concave surface between the orbits and the nasal aperture, a nasal aperture anterior to the malar surface, an inferior orbital margin above M^1, a more vertical orientation of the margins of the nasal aperture, a broader nasal aperture, a more vertical orientation of the upper incisors, broader incisive fossae, a stepped subnasal floor, a large caliber incisive canal, low crowned male upper and lower canines, cervically flared upper canines, lower canine roots that are more buccolingually rotated, and a relatively broader M^1.

Orangutan phylogeny

This analysis provides new information on the evolutionary history of the lineage of the orangutan and also supports a number of previously held views. The data from this analysis strongly support the previous view that *Ankarapithecus* is a large-bodied great ape in the clade that includes other fossil great apes, living great apes, and humans (Ozansoy, 1965; Andrews and Tekkaya, 1980; McHenry et al., 1980; Alpagut et al., 1996) (Table 6). *Sivapithecus* and *Pongo* also form a clade to the exclusion of all other taxa considered here (Gregory et al., 1938; Andrews and Cronin, 1982; Pilbeam, 1982). Previous suggestions that the resemblances

TABLE 6. *Classification of taxa used in this analysis*

Hominoidea
Hylobatidae
Proconsulidae
Proconsul
Hominidae
Dryopithecinae
Dryopithecus
Ouranopithecus
Homininae
Pan
Gorilla
Ardipithecus
Australopithecus[1]
Homo
Ponginae
Ankarapithecus
Sivapithecus
Pongo
Hominoidea incertae sedis
Afropithecus
Turkanapithecus
Griphopithecus
Kenyapithecus
Hominidae incertae sedis
Oreopithecus
Lufengpithecus

[1] *Australopithecus* is probably a paraphyletic taxon including a number of forms more closely related to *Homo* than they are to *Australopithecus* sensu stricto (*Australopithecus africanus*). This problem is beyond the scope of this paper, so the paraphyletic taxon is used here to avoid confusion.

of the faces of *Pongo* and *Sivapithecus* may be homoplasies (Pilbeam et al., 1990; Pilbeam, 1996, 1997; Röhrer-Ertl, 1988) are contradicted by the results of this analysis.

Ankarapithecus shares seven synapomorphies with the clade that includes *Sivapithecus* and *Pongo* (Table 7). Other characters that have been suggested as synapomorphies of this clade cannot be confirmed or are refuted by the new evidence. Several subnasal characters (smooth subnasal plane, no subnasal step, small incisive foramina) listed as synapomorphies of *Sivapithecus* (including *S. meteai*) and *Pongo* (Andrews and Cronin, 1982) are now known to be lacking in *Ankarapithecus,* based on the new restoration described above. Zygomatic foramina size and position, also used in Andrews and Cronin (1982) in defining this clade, are judged here too variable to be reliable as phylogenetic indicators. Thick enamel, which Andrews and Cronin (1982) also used to define this clade, has since been found in many other taxa (*Kenyapithecus, Griphopithecus, Heliopithecus, Afropithecus, Ouranopithecus,* and *Australopithecus, Cebus*) (Kay, 1981; Martin, 1983; Kay and

TABLE 7. Synapomorphies of some fossil and living hominids clades[1]

Ankarapithecus/Sivapithecus/Pongo
    Anteriorly facing zygoma
    Narrow interorbital distance
    Inferior orbital border in the form of a crest
    Medially inclined upper canine roots
    More elongated greater palatine foramina
    Long nasoalveolar clivus
    More horizontal nasoalveolar clivus
Sivapithecus/Pongo
    Hollow maxillary nasal process
    Flat orbit/nasal surface
    More horizontal margins of the nasal aperture
    Nasal aperture in the same plane as the malar surface
    Inferior orbital margin posterior to M^1
    Anteriorly facing maxillary body
    More horizontal upper incisors
    Very shallow incisive fossae
    Smooth subnasal floor
    Very narrow incisive canal
    Internally rotated lower canine roots
Dryopithecus/Ouranopithecus and the African apes and humans
    Reduced nasal prognathism
    Shallow canine fossa[2]
    Broad zygomaticoalveolar crest
    M_1-M_2 close to the same size
African apes and humans
    Hollow maxillary nasal process[3]
    Inflated maxillary alveolar process
    Elongated P^4 [4]
Pan and *Australopithecus*
    Reduced orbital-nasal distance[4]
    Short nasal bones[5]
    Anteriorly oriented maxillary surface[3]
    Short nasal portion of the nasoalveolar clivus[6]
    Long nasoalveolar clivus[7]
    Small caliber incisive canal
    Spatulate I^2
    P^4 lingual flare

[1] Only characters included in this analysis are listed here. For a more complete list, see Begun et al. (1997).
[2] Shared convergently with *Proconsul* and *Morotopithecus*.
[3] Shared convergently with *Sivapithecus-Pongo*.
[4] Shared convergently with *Pongo*.
[5] Shared convergently with *Proconsul*.
[6] Shared convergently with early Miocene taxa.
[7] Shared convergently with *Ankarapithecus-Sivapithecus-Pongo*.

Grine, 1988; Andrews and Martin, 1991). Enamel thickness was also excluded from this analysis because of its excessive variability within and between taxa (Begun and Kordos, 1997). Finally, very pronounced upper incisor heteromorphy, said to define the *Sivapithecus-Pongo* clade including *Ankarapithecus,* is shared by *Ankarapithecus* and *Sivapithecus* but not *Pongo* (Kelley et al., 1995; see above). It could be a synapomorphy of the clade subsequently lost in *Pongo,* or it could equally parsimoniously have arisen independently in *Ankarapithecus* and *Sivapithecus.* Though the former history seems more likely, in view of the fact that some *Pongo* approach the upper incisor heteromorphy seen in the fossil forms, it would be speculative to conclude that this was a synapomorphy without more complete evidence on the history of incisor heteromorphy in *Pongo.*

The conclusion that a *Sivapithecus-Pongo* clade is the sister clade to *Ankarapithecus* is supported by 11 character states that link *Sivapithecus* and *Pongo* to the exclusion of *Ankarapithecus* (Table 7). Incisive fossae, incisive canal length and caliber, nasoalveolar length, and subnasal floor morphology are described as separate characters in this paper and in previous work on subnasal morphology (Ward and Pilbeam, 1983; Ward and Kimbel, 1983; Brown and Ward, 1988; McCollum et al., 1993). However, it is evident that they are at least in part correlated and may be more appropriately treated as one or more complex characters. There is no evidence of independence in the condition of two of these, the incisive fossa and the subnasal floor. All taxa that lack an incisive fossa have a fenestrated palate, all those with a deep fossa have a stepped subnasal floor, and all taxa with a shallow fossa have a smooth floor. These may in fact be a single trait. Changing them to one character has no impact on the most parsimonious tree topology. On the other hand, nasoalveolar length is partially decoupled from subnasal and incisive fossa morphology. Chimpanzees and *Australopithecus* share an elongated clivus with *Ankarapithecus, Sivapithecus,* and *Pongo,* though two different subnasal and incisive fossa morphologies are associated with these forms (Begun, 1994; McCollum and Ward, 1997). In addition, some evidence suggests that, at least in living forms, the premaxillary-maxillary fusion timing is different between *Pongo* and the African apes and humans, reinforcing the notion that clivus elongation is a homoplasy between the two groups (Krogman, 1930; Ashley-Montagu, 1935; McCollum and Ward, 1997). Similarly, incisive canal caliber is partly decoupled from incisive fossa and subnasal floor morphology. *Sivapithecus* and *Pongo* share very narrow canals, which is probably correlated to their combination of elongated clivuses, shallow incisive fossa,

and a smooth subnasal floor, but other taxa that share incisive fossa and subnasal floor morphology differ in their canal caliber. *Ankarapithecus* shares subnasal and incisive fossa morphology with *Dryopithecus, Ouranopithecus,* and the African apes and humans. However, this group of taxa have three different incisive canal calibers. *Dryopithecus* and *Ouranopithecus* have large caliber canals, *Ankarapithecus* and *Gorilla* have canals of intermediate caliber, and *Pan* and *Australopithecus* have small caliber canals (though larger than in *Pongo* and *Sivapithecus*). The intuitive functional and structural link between incisive caliber size and subnasal floor morphology does not hold in these taxa. This decoupling of characters that might otherwise be treated as a single character complex is only revealed by a new fossil showing a different configuration. It should serve as a warning against ad hoc character weighing or redefinition of characters sometimes advocated to account for what appear to be functionally correlated characters. A better strategy is to treat characters separately and then, in a post hoc analysis, consider options for reducing larger numbers of individual characters to smaller numbers of more complex characters.

Ankarapithecus and *Pongo* do not share character states not present in *Sivapithecus.* However, *Ankarapithecus* and *Sivapithecus* do share character states not present in *Pongo.* Extreme upper incisor heteromorphy and thick enamel have been noted above. *Ankarapithecus* and *Sivapithecus* also share very deep zygoma, little zygomatic root pneumatization, extremely elongated nasal bones, and medially rotated upper canine roots that are either homoplasious in these taxa or secondarily lost in *Pongo.* They also retain several primitive character states, including a broad orbital-nasal distance, a high position of jugale relative to the orbital margin, a low position of the nasal aperture, a lower position of the infraorbital foramen in relation to the apex of the nasal aperture, an inferiorly placed pyramidal process, a broad P^4, a nasal apex above M^2, and a M_1 small compared to M_2. *Pongo* shares the derived form of the first five of these characters with African apes and humans. However, these are more likely to be homoplasies

shared between *Pongo* and the African ape and human clade than synapomorphies of a clade consisting of the living great apes and humans. Placing *Pongo* alone (not including *Sivapithecus* and *Ankarapithecus*) as the sister to the African ape/human clade is much less parsimonious than the tree topology presented in Figure 6, requiring an additional nine steps (Fig. 7C). Although these characters do not link *Pongo* phyletically to living African ape and humans, it is interesting that five homoplasies of the face and dentition are shared exclusively between *Pongo* and the African apes and humans. Further analysis beyond the scope of this paper is needed on the morphology of the faces of fossil and living great apes to assess the extent to which these homoplasies result either from functional convergence or are emergent in the structural morphology of the great ape face.

Other phylogenetic hypotheses concerning *Ankarapithecus, Sivapithecus,* and *Pongo* can be examined in light of the results presented here. Alpagut et al. (1996) have suggested that *Ankarapithecus* is a stem hominid with no specific relationship to living great apes and humans. As noted above, the most parsimonious phylogeny with *Ankarapithecus* as a stem hominid requires 143 steps (Fig. 7A). Alpagut et al. (1996) further suggest that *Ankarapithecus* is linked with the European great apes *Dryopithecus* and *Ouranopithecus.* Placing all three of these taxa in one clade that would be the sister clade to the great apes and humans is much less parsimonious, requiring 12 additional steps (Fig. 7D). The mosaic of similarities between *Sivapithecus* and *Pongo* on the one hand and *Dryopithecus, Ouranopithecus,* African apes, and humans on the other lead Alpagut et al. (1996) to conclude that *Ankarapithecus* is a primitive hominid. They cite differences also noted here between *Ankarapithecus* and the *Sivapithecus-Pongo* clade (thick enamel and a more projecting midface). We interpret these to be primitive characters. Others differences, mainly in the frontal region, were not considered here but have a bearing on previous research (Begun, 1994, 1995; Begun and Kordos, 1997; Begun et al., 1997).

Alpagut et al. (1996) indicate that certain frontal and periorbital characters are shared between *Ankarapithecus* and *Dryopithecus, Ouranopithecus,* and the African apes and humans. Among them, square orbits are almost certainly primitive for hominids, being found in numerous Miocene and living catarrhines (Begun et al., 1997). The frontal sinus character is unclear, because the exact position of the frontal sinus in AS95-500 is not indicated by Alpagut et al. (1996). Frontal sinuses in the frontal squama are common in anthropoids (Begun, 1994), including *Afropithecus* and *Proconsul* (Leakey and Walker, 1997; Walker, 1997), but invasion of the interorbital space by an ethmoidal frontal sinus is only known in African apes and humans and possibly *Dryopithecus* (Cave and Haines, 1940; Begun, 1995). It remains to be seen how the frontal sinus in AS95-500 compares to other anthropoids. Although the supraorbital structures are described by Alpagut et al. (1996) as supraorbital tori, which are known in African apes and humans, they are much more reminiscent of the supraorbital rims of robust orangutans and large male *Cebus apella.* Given the robusticity of the face and dentition of *Ankarapithecus,* large supraorbital structures are perhaps not surprising in this taxon. Alpagut et al. (1996) note differences from African apes and humans in the morphology at glabella. The supraorbital superstructure is discontinuous here, separated by a glabellar depression, which is not the case in *Dryopithecus Ouranopithecus,* or African apes and humans. One *Dryopithecus* individual (CIl 18000) and *Ouranopithecus* have supraglabellar depressions, but these are superior to the supraorbital tori and do not bisect them. Our impression is that the supraorbital structures on AS95-500 are not supraorbital tori and do not link *Ankarapithecus* to African apes and humans. The morphology of AS95-500 reinforces the conclusion that *Ankarapithecus* is primitive for the *Sivapithecus-Pongo* clade but that it should be included as the sister taxon to that clade.

Another alternative phylogeny of the *Ankarapithecus-Sivapithecus-Pongo* clade was based on an analysis of *Dryopithecus* from Can Llobateres, Spain (Moyà-Solà and Köhler, 1993, 1995, 1996). These authors conclude that all European late Miocene hominoids are members of a clade that includes *Pongo* but not African apes or humans. As Alpagut et al. (1996) note, the data from *Ankarapithecus* contradict this interpretation. The most parsimonious cladogram consistent with this view requires 141 steps and links *Ouranopithecus* and *Dryopithecus* to the *Ankarapithecus-Sivapithecus-Pongo* clade (Fig. 7E). However, numerous synapomorphies of the neurocranium, and periorbital region not included in this analysis associate *Dryopithecus/Ouranopithecus* with the African apes and humans and not with *Pongo* and its fossil relatives (Begun, 1995; Begun and Kordos, 1997; Kordos and Begun, 1997).

Finally, it has been suggested that the *Sivapithecus-Pongo* clade is more closely related to African apes and humans than is *Dryopithecus* (Andrews and Martin, 1987; Andrews and Pilbeam, 1996). The most parsimonious alternative consistent with this hypothesis associates *Ouranopithecus* with the *Ankarapithecus-Sivapithecus-Pongo* clade (Fig. 7F). Once again, when other characters of the periorbital region are included, these tend to reinforce the conclusion that *Dryopithecus* and *Ouranopithecus* are more closely related to each other and to African apes and humans than they are to other hominids.

In most cases, alternatives to the most parsimonious hypothesis presented here have been proposed based on evidence not considered here, such as frontal morphology or postcranial evidence (Pilbeam et al., 1990; Pilbeam, 1996, 1997; Andrews and Pilbeam, 1996; Moyà-Solà and Köhler, 1996). A priori, any of these character sets could be used to reconstruct phylogenetic relations. However, when all of these data are combined, the resulting most parsimonious phylogeny is consistent with the one proposed in Figure 6 (Begun et al., 1997).

Taxonomy of Siwalik hominids

The comparisons presented above also suggest more similarity between older Siwalik specimens and *Ankarapithecus* than between *Anakarapithecus* and later Siwalik specimens. If these were confirmed by more detailed analysis of the Siwalik sample, it

may require the recognition of either *Ankarapithecus* or a new genus in the earlier Siwalik samples.[5] The most complete early *Sivapithecus* palatal specimen is GSP 16075 from the Chinji formation (Raza et al., 1983). These authors note that GSP 16075 has diagnostic *Sivapithecus* morphology, and they assign it to *Sivapithecus indicus.* The characters they cite, however, do not clearly differentiate this specimen from MTA 2125. GSP 16075 is said to have a nasoalveolar clivus that resembles GSP 15000, but the specimen is very damaged and does not preserve the incisive fossa. The premaxilla appears less projecting and less horizontal than in GSP 15000 and thus intermediate between it and MTA 2125. GSP 16075 also has a clear anterior nasal spinous crest, found in MTA 2125 but not GSP 15000, and a premaxillary palatal surface with a broad, sagittal groove leading to a depression in the midline at the level of the *C*-P^3. Though a similar groove is sometimes seen in modern orangutan palates, the morphology of this area in GSP 16075 is most like that in MTA 2125 and may mean a larger incisive foramen compared to GSP 15000. GSP 16075 also appears to be broader relative to length than GSP 15000, though damage makes this ambiguous. On the other hand, GSP 16075 shares with GSP 15000 an apparently collapsed maxillary alveolar process, and it differs from both in being considerably smaller and in having a transversely very gracile premaxilla. The polarity of these characters is mixed, and on the basis of such a small number of features it is not clear what the evolutionary implications of this pattern are or whether it is simply attributable to variation within *Sivapithecus.* If the Chinji hominoids are found to share synapomorphies with *Ankarapithecus,* then it may be necessary to recognize this taxon in the Siwalik sample. However, if they show a mixture of *Ankarapithecus* and *Sivapithecus* characters or if they lack derived charac-

ters of *Ankarapithecus* and *Sivapithecus,* it may be necessary to recognize a new genus for this sample.

Paleobiogeographic implications

This analysis provides evidence that *Ankarapithecus* represents a more primitive phase in the evolutionary history of the orangutan than does *Sivapithecus.* The common ancestor of the *Sivapithecus-Pongo* clade may have closely resembled *Ankarapithecus,* although there are several apparent autapomorphies that may exclude *Ankarapithecus meteai* from this position (depth of the temporal process of the zygomatic, maxillary alveolar process robusticity, broad nasal aperture, low crowned canines, and upper canine cervical flare). Two basic scenarios could explain the distribution in time and space of the various members of the orangutan lineage (Fig. 8). *Ankarapithecus* is more primitive than *Sivapithecus,* from the later Siwalik localities in particular, and is also earlier in time than a good percentage of *Sivapithecus* localities. Only the earliest hominids from the Chinji Formation of the Siwaliks are older than the middle Sinap (Sen, 1991; Kappelman et al., 1991). One possibility is that *Ankarapithecus* represents an Anatolian relict population of the proto–*Sivapithecus-Pongo* lineage that survived in Turkey after the initial appearance of *Sivapithecus* in the Siwaliks. Central Anatolia occurs along a potential migration route between Africa and South Asia, and it could be that *Ankarapithecus* represents an early stage in the evolution of Asian great apes from African ancestors (Fig. 8A). This could also explain possible morphological and phylogenetic affinities between *Ankarapithecus* and *Griphopithecus* (Alpagut et al., 1990; Andrews, 1983). *Griphopithecus* is much more primitive than *Ankarapithecus* and *Sivapithecus,* has much in common with African forms, particularly those from Maboko (Begun, 1992), and is much earlier in time (Bernor and Tobien, 1990). The link between *Griphopithecus* and *Ankarapithecus,* however, is not supported by the evidence presented here and has furthermore been criticized by others (Kappelman et al., 1991).

Another interpretation takes into account the diversity of *Sivapithecus* in the Siwaliks

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[5]Kelley and Pilbeam (1986) note that the type species of *Sivapithecus* is *Sivapithecus sivalensis,* the holotype of which is the GSI D-1 palate. The provenance of this specimen is unknown, but it is linked morphologically with the younger Potwar specimens including GSP 15000, the most complete specimen to which MTA 2125 was compared. If there is more than one genus within the material currently attributed to *Sivapithecus* from the Siwaliks, the nomen *Sivapithecus* would be retained for the younger material including GSP 15000.
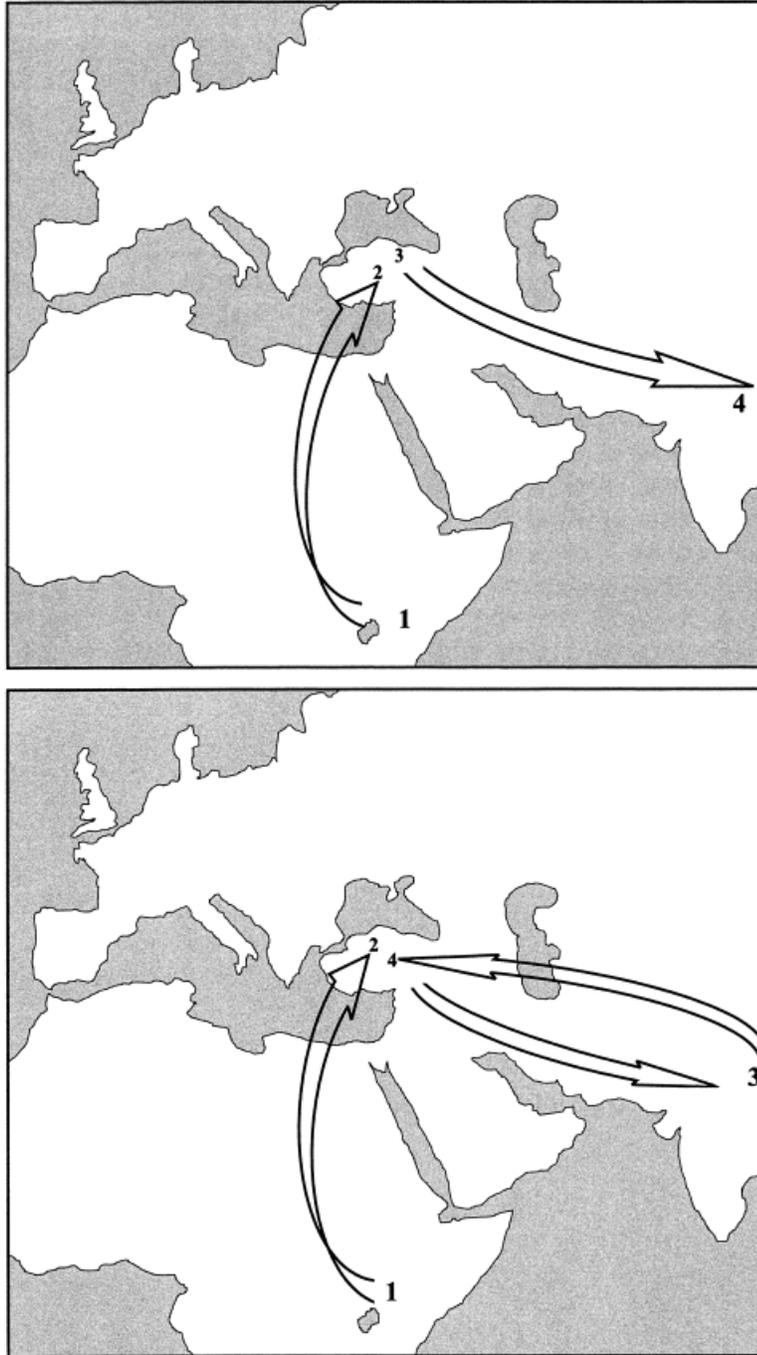
Fig. 8. Paleobiogeographic relations among the members of the *Pongo* lineage. **A:** A middle Miocene migration of a *Griphopithecus*-like taxon leads to the presence of *Griphopithecus* in Kenya and Turkey (1–2). In the late middle Miocene, this form evolves into an *Ankarapithecus*-like form (2–3) and migrates to South Asia (3–4). **B:** A middle Miocene *Griphopithecus*-like taxon spreads from East Africa to Asia (1–2), eventually reaching South Asia, where the *Ankarapithecus-Sivapithecus-Pongo* lineage first appears (2–3). An early branch of this lineage returns to western Asia to become *Ankarapithecus* (3–4). This scenario corresponds more closely to the geochronological evidence and is also supported by fossil evidence. See text for discussion.

and the evidence of faunal exchanges between African and Eurasia in the middle and late Miocene. Middle Miocene Paşalar has a faunal affinity with African localities of the same age (Bernor and Tobien, 1990), but the late Miocene sediments at Sinap and in the Siwaliks have a primarily Eurasian character (Sen, 1991; Pilbeam et al., 1979).

This is especially true of the more recent Siwalik faunas (Pilbeam et al., 1979), while the older Siwalik faunas, including Chinji, have closer affinities to East African faunas (Pilbeam et al., 1979; Raza et al., 1983; Kappelman, 1991). It may be that the lineage of the orangutan and its known members first appear in South Asia, with the earliest taxon represented by the chronologically oldest Chinji specimens (Fig. 8B). An adaptive radiation could have led to an early branch, *Ankarapithecus,* migrating southwest to Turkey, while *Sivapithecus* radiated in situ into a diversity of species of differing sizes, including at least *Sivapithecus sivalensis* and *Sivapithecus parvada* (Kelley and Pilbeam, 1986; Kelley, 1988) and possibly also *S. simonsi* or *S. brevirostris* (Kay, 1982; Greenfield, 1979; Kelley and Pilbeam, 1986). Another lineage, maybe aligned with a species of *Sivapithecus,* becomes hyperrobust (*Gigantopithecus*), while yet another, probably aligned with some species of *Sivapithecus,* becomes noticeably more gracile (*Pongo*).

Evidence of migrations routes among Africa, Western Asia, and South Asia based on widespread patterns of land mammal distributions, sedimentary facies, and other lines of paleontological evidence (Steininger et al., 1985; Bernor and Tobien, 1990) are consistent with either view. However, because of the morphological affinities between the Chinji and *Ankarapithecus* specimens and the greater geologic age of the Chinji specimens, we suspect that the second alternative may be the more likely. Whatever the scenario, it is clear that late Miocene South and Southwest Asian great apes represent a very successful radiation of early hominids. Like the human lineage, it radiated shortly after its appearance, became morphologically, chronologically, and geographically widespread, and then declined suddenly and dramatically, leaving just one, highly autapomorphic descendant taxon.

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