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Man's immediate forerunners

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[Plate 1]

Discoveries of the last five to ten years have greatly expanded the number of remains of earliest *Australopithecus*, reaching back to nearly 4 Ma ago in Africa. In Eurasia a broad range of recent finds has greatly extended knowledge of the diversity, the distribution and the facial anatomy of a series of small *Ramapithecus* and of several similar-sized larger apes (with the usual proliferation of names, namely *Budvapithecus*, *Ouranopithecus*, *Sivapithecus*, and *Ankarapithecus*). All these new Eurasian fossil hominoids seem to come from around 8–15 Ma ago. Improvements in dating and fossil documentation emphasize the so-called 'Pliocene gap' in knowledge of higher hominoid evolution. The period from 4 to 8 Ma in Africa, and apparently elsewhere, is devoid of a single dentition, skull, or limb bone of any hominoid, other than the Lothagam mandible at 5 or 6 Ma (holding but a single preserved tooth.)

In §1 recent discoveries at three sites in East Africa, five in Europe and Asia Minor and two in Asia are reviewed. These discoveries document an unexpected and widespread occurrence of hominoids with *Australopithecus*-like cheek teeth having thick enamel and set in robust jaws. Although both dental and facial resemblance between *Ramapithecus* and *Australopithecus* has been demonstrated by recent finds, the proliferation of new finds has somewhat confused discrimination of subsets among later Miocene hominoids; also some workers have stressed similarities between *Ramapithecus* and *Sivapithecus* or between the latter and *Pongo*.

In §2 new temporal, ecological and morphological evidence relevant to determining the time of origin and the definition of the taxonomic family of man, Hominidae, are summarized.

1. Nature of the evidence

Fossils indicating the nature of the radiation of the higher hominoids between about 4 and 13 Ma ago are of wide distribution in the Old World, except in Africa, where only a handful of fossils from this time-span have been recovered. If these few African fossils were to be the only basis for inferring anything about hominid origins this contribution could be brief. There is strong evidence against the extreme recency of the diversification of higher Hominoidea advocated by a few exponents of molecular clocks. Moreover, the three African fossil teeth aged 5.5, 7 and 10 Ma respectively all have thick enamel and low crowns, which implies relation to the similarly constituted hominoids of the Eurasian radiation. There is reason to believe that from time to time faunal exchange between Africa and Eurasia took place, especially at about 2, 7, 14, and 17 Ma B.P. All these factors combine to suggest that in African and Eurasian sites from 10 to 17 Ma in age we have and may find information relevant to the problem of the immediate forerunners of African Plio–Pleistocene *Australopithecus*. It is to be hoped that the absence of evidence of any quality in Africa from between 4 and 14 Ma B.P. will soon be remedied by the discovery of new hominoid fossils that are relatively complete and can be made the basis of settling the exact line of ancestry of humankind. I am yet to be convinced that the molecular clock is accurate enough to require a split between *Homo* ancestry and that of *Pan*/*Gorilla* in

Africa around 7 or 8 Ma. Rather it should be stressed that, even if *Ramapithecus*, the taxonomic position of which has recently been made so controversial, is set aside, there is extensive evidence that split-point times among primates and particularly higher Hominoidea do fall before 14 Ma B.P. These considerations sustain the relevance of considering all the evidence about hominoid evolution from middle Miocene to middle Pliocene times site by site as follows.

(*a*) *Sites in Kenya, East Africa*

In contrast to the present extensive documentation of *Australopithecus* and *Homo* in Africa, running back to about 3.5 Ma B.P., evidence of immediate forerunners of man in Africa before that time is scant. Each of the three known finds (all from Kenya) is, or contains, but a single tooth. These specimens are:

(i) *Lothagam*, a partial right mandibular fragment containing roots of M_2 and M_3 as well as the whole of M_1 (Patterson *et al.* 1970);

(ii) *Lukeino*, a left lower molar (Pikford 1975);

(iii) *Ngorora*, a left upper second molar, described by Bishop & Chapman (1970).

Lothagam is located in northern Kenya, near the west shore of Lake Turkana, just southwest of the mouth of the Kerio River. The latter two sites are in the Baringo Basin, Northern Kenya Rift Valley.

(i) *Lothagam*

As far as it can be analysed, this right horizontal ramus with M_1 resembles early *Australopithecus* from Laetoli, Tanzania, and Makapansgat, South Africa. The age seems to be well substantiated at 5.5–6 Ma. In consequence the Lothagam mandible may be regarded as constituting the earliest evidence so far recovered of *Australopithecus*. Recent reports (Smart 1976; Coppens 1978) put the age back to perhaps 6 Ma. Neither M_1 nor proportions or structure in this mandible and molar roots resemble *Pan* or *Gorilla*.

(ii) *Lukeino*

This left lower molar (KNM LU 335) was found at a horizon in the middle portion of member A of the Lukeino Formation at Chepboit. A series of K–Ar dates indicate a probable age of about 7 Ma. The tooth is low-crowned, has thick enamel and is broad, with faint traces of a lateral cingulum. Resemblance is to both robust and gracile *Australopithecus*, but the size is distinctly smaller, which might be significant in view of the tooth being about twice as old as the gracile *Australopithecus*. Like that of later hominids and unlike that of many earlier hominoids, the trigonid is long compared to the talonid basin. The swollen, rounded cusps suggest that enamel thickness is very great. Molar morphology is reminiscent of M_{1-3} in A.L. 288–1 at Hadar, in some of the material from Laetoli and to certain late *Ramapithecus* such as the Hasnot, Pakistan, mandible. Although absolute size and length–width proportions are close to those from some *Pan*, crown morphology and enamel development is not at all like that of either of the African apes. In all probability this molar is definable as hominid even in a narrow sense and it is tentatively placed in Hominidae by Andrews in Pikford (1975).

(iii) *Ngorora*

Found in 1968, this upper left second molar is from a level in the Ngorora Formation, Baringo Basin, Kenya, that has been dated to about 10 Ma B.P. This tooth resembles that from Lukeino in being low-crowned and broadened or flaring lingually. As with the previous two specimens there is evidence of enamel thickness and a general resemblance to Laetoli *Australopithecus*, *Ramapithecus* and *Sivapithecus*. The tooth does not resemble those of *Pan* or *Gorilla*. (For further discussion see Bishop & Chapman (1970), Bishop *et al.* (1971), Bishop & Pickford (1975) and Pickford (1975).)

(iv) *Fort Ternan and Maboko*

Before the above three finds the next youngest African site that has yielded hominoid fossils is Fort Ternan, Kenya, at an age of about 14 Ma. There also a species with thickly enamelled teeth, *Ramapithecus wickeri*, exists. As far as these Kenyan finds at Lothagam, Lukeino, Ngorora and Fort Ternan provide evidence about hominid origins, they all indicate an African radiation of species with thickly enamelled teeth. Taken altogether, the fossil record from African sites ranging from middle Miocene to Recent provides not a single thinly enamelled tooth that would document the lineage of either *Pan* or *Gorilla* at any period in the past whatsoever. The only African fossil apes bearing any resemblance to modern *Pan* or *Gorilla* are the smaller and the larger described species of *Dryopithecus* (*Proconsul*) from the early Miocene of Kenya and Uganda, which do exhibit thin enamel. The face of *D. major* from Moroto, does bear specific morphological resemblance to *Gorilla* at an age of about 16 Ma.

Lest the unwary student should be inclined to the idea that *Ramapithecus* and *Sivapithecus* represent an Eurasian radiation, it is necessary to stress that these genera have both been recorded as occurring in Africa for many years. Recent evidence (Andrews & Molleson 1979) strongly suggests that the type of *Sivapithecus africanus* (Clark & Leakey 1950) came from Maboko Island, Lake Victoria, Kenya, where faunas are thought to be about 15 Ma old. The current view is that the type specimen of *S. africanus*, together with a few other fragments from Maboko, is correctly assigned to genus *Sivapithecus*. This point has been emphasized by Madden (1980).

There is an extensive literature about *Ramapithecus* (= *Kenyapithecus*) *wickeri* (Leakey 1962) from Fort Ternan, Kenya. Its lack of generic distinctiveness was recognized by Simons (1963) and the genus *Kenyapithecus* coined for it was dropped by later authors, for instance Andrews (1971). Although this find at Fort Ternan is not the type species of *Ramapithecus*, it should be emphasized that the material of it from the Kenyan site has played an important role in developing the concept of *Ramapithecus*. For instance, it documents in the African Miocene a form with small incisors and canines, thick enamel, transverse P_3 with distinct metaconid cusp and contact facet for canine anteriorly (no diastema). Interestingly there are large canines at Fort Ternan (KNM FT 28, 37, 41), one of which (FT 37) shows pronounced apical wear and curved, barrel-shaped body reminiscent of *Sivapithecus*. The approximate estimated volume of the crowns and of these canines is about three to four times that of the small upper canine (KNM FT 46) associated with the upper left maxilla of *R. wickeri* by Leakey (1962). Conversely, from Maboko there is a small upper canine (KNM MB 70) resembling that of Fort Ternan *Ramapithecus*.

(*b*) *Sites in Greece*

(i) *Macedonia*

During recent years de Bonis has located at the 'Rain Ravine' site near Salonika, on the left bank of the Axios River in Macedonian Greece, 12 partial or complete mandibular dentitions in jaws and one palate (with all save one tooth) of Miocene hominoids. These creatures occur in a fauna of about 200 other mammalian specimens that is judged by de Bonis & Melentis

(1977*a*, 1978) to be of Vallesien provincial age, or about 10–11 Ma. Working on the assumption that the two size classes are of one species, they have named this species *Ouranopithecus macedoniensis*. As a whole these hominoids, of two distinct sizes, represent by far the most extensive series of hominoids from any single site in Eurasia, but not a single postcranial bone was found. At Rain Ravine fossils come from a sandstone channel deposit of limited extent. Apart from the hominoids the fauna consists mainly of jaws and limb bones of artiodactyls, including the genera *Mesembriacerus*, *Oioceros*, *Prostrepsiceros*, *Decennatherium*, *Paleotragus* of two species, and *Bohlinia*. The giraffids and bovids are considered by de Bonis to indicate a savannah mosaic environment where woodlands and grasslands were interspersed.

Perhaps the most important thing about these finds in Macedonia is the marked dimorphism indicated, if, in fact, the two morphotypes present at Rain Ravine do represent sexes and not a large and a small species. Arguing for the identity of the two morphotypes as one species is the similar morphology of postcanine teeth. However, differences in the canines and front premolars in the two morphotypes are at the extreme for highly dimorphic species now living. In the 'females' P_3 are more transverse and canines much smaller than in 'males'. Unlike *Ramapithecus*, P_3 metaconids are uniformly absent. If the Macedonian hominoids found so far may be taken as representative samples then the posterior teeth are more dimorphic than in any living species, including the gorilla and baboons. Also, apparently, absolute size increase posteriorly from P_3 through M_3 is greater in 'males' than in 'females'. Without personally revising this material it is difficult to have a certain opinion about the occurrence of one, or of two species at Rain Ravine. However, it is fair to say that, if Miocene hominoids had dimorphism that is both greater from and different to that seen in any living primate, then their taxonomic assessment is rendered most difficult.

As in African *Australopithecus* and in *Sivapithecus* from the Siwaliks of Pakistan and India, the upper central incisors in *Ouranopithecus* are large relative to upper lateral incisors. *Ouranopithecus* teeth all show very thick enamel with low, rounded cusps, and lower molars are, on average, broader relative to their length than is typical of most east Asian *Ramapithecus*, *Gigantopithecus* and *Sivapithecus*. Except for the third molars of the type specimen, a young 'female', most of the teeth in the other individuals are worn so that little crenulation can be seen. Symphyseal cross section and form of the horizontal mandibular ramus resemble more nearly *Gorilla* or *Gigantopithecus* than *Sivapithecus*. It would seem that the Macedonian hominoid represents at least one valid species. Were it not for the thick enamel one might consider that these have affinities with African apes. They come from a time and place where there is increasing evidence of African outmigrants (Azzaroli 1977). One such outmigrant, *Pliohyrax*, occurs nearby at Samos and apparently also at Pasalar, Turkey (Meyer 1978).

(ii) *Pyrgos*

At this site near Athens, which is also called 'Tour la Reine', was found a complete hominoid mandible with teeth that was later damaged by the World War II bombing of Berlin, where it had been sent for study. This specimen was described by von Koenigswald (1972) under the name *Graecopithecus freybergi*. Although according to von Freyberg (personal communication) this dentition was almost completely intact when discovered in 1945, now only right P_4–M_2 remain in the war-damaged find. On the basis of the limited associated fauna this site seems to be of Turolien provincial age, which would make this mandible the youngest of the European Miocene hominoids. Most students, having only seen uninformative casts, equivocate about this specimen. Nevertheless, it provides information. The posterior divergence of the tooth rows is about 20° and the front teeth are very small, while in contrast the molars are huge. Right M_2 appears to be broader buccolingually than is the jaw beneath it. My examination of the little-known type specimen of '*Graecopithecus*' *freybergi* at Erlangen, Germany, recently revealed the roots of the entire C–M_3 series on the left side, where all teeth have been broken away. The canine and similar-sized premolars are packed together and small. These and other features suggest assignment to *Ramapithecus*.

(*c*) *Sites in Turkey*

Finds of *Ramapithecus* and *Sivapithecus* at three different sites in Turkey have been made recently. These are (1) a mandible of *Ramapithecus* from Candir, about 60 km northeast of Ankara, (2) a palate with attached right lower face of *Sivapithecus* from the Sinap series, about 55 km northwest of Ankara, and (3) a considerable sample of isolated teeth of both *Sivapithecus* and *Ramapithecus*, recovered from deposits at Pasalar in eastern Turkey. The three sites appear to be of different ages, but since age estimates are made by faunal correlation some reservations must be retained. Pasalar seems to be the oldest (Vindobonian Provincial Age) at perhaps 15–16 Ma of age. The middle Sinap series fauna indicates an age of mid-Vallesian or perhaps 10–12 Ma. Candir has a fauna suggesting a Vindobonian age, or if *Hipparion* is actually present at the level of *Ramapithecus* a date as recent as 10–12 Ma B.P. is possible.

(i) *Candir*

Although Tekkaya (1974) originally assigned the well preserved type mandible from Candir to *Sivapithecus*, Andrews & Tekkaya (1976) as well as Simons (1976*b*) transferred this mandible to *Ramapithecus*. The main significance of this mandible is dual. It documents the presence of *Ramapithecus* in central Turkey and because of its completeness it provides or confirms interesting anatomical points about the genus seen less well in the east Asian materials recently reported on by Greenfield (1978, 1979) and Pilbeam *et al.* (1977). In size and morphology the Candir mandible is closely comparable to the best of the new finds from Pakistan, a mandible found near Gandekas and discussed below (see §1 (*e*)). The Gandekas mandible has been figured by Pilbeam *et al.* (1977) and by Simons (1979). Both mandibles show comparatively small and vertically emplaced incisor and canine sockets. There is a break across the right side of the symphysis so that the right ramus has been shifted slightly backwards and the right horizontal ramus bent towards the left ramus. This twisting has decreased somewhat the angle of posterior divergence indicated in the new find from Pakistan. In the Candir mandible the zygoma are situated further forward, arising at the front of M_2 rather than the front of M_3 in the Gandekas jaw. Left P_{3-4} in the Candir specimen are transversely broad and closed up against each other and the M_1. Although both the left and right canines have been lost there is a distinct contact facet for the canine on the anterolateral face of left P_3. Thus a closed C–M_3 tooth row is confirmed here as it is also for the Fort Ternan *Ramapithecus* mandible by a similar wear facet on P_3. There can hardly have been any gaps between lateral incisor and canine as the space that they occupied, judging from the position of canine and incisor roots, is small. The breadth across all four incisor roots between the canines is only 1.4 cm, while the estimated breadth across the outside of P_2 is 3.5 cm. Thus the Candir mandible provides strong evidence of a very reduced anterior lower dentition and a closed tooth row. Like Gandekas *Ramapithecus* this is a small creature with a small, flattened face and big molars. This mandible implies a face only about half the absolute size of that of *Sivapithecus* from Mount Sinap. P_{3-4} of the Candir mandible show considerable wear, so that there is no apex for a separate metaconid cusp; nevertheless, a distinct and extensive transverse wear facet is developed on the ridge running toward the inside of the tooth and the transverse long axis of left P_3 is almost parallel to P_4, as can easily be seen in fig. 3 of Andrews & Tekkaya. The general structure and orientation of P_3 is much as in *Ouranopithecus*, which on average shows no trace of a metaconid. Although P_3–M_1 are very well worn, M_3 wear is slight, and indication of the occurrence of differential wear. Mandibular morphology with double internal transverse tori strongly developed, an almost vertically orientated symphysis, closed-up tooth row with interstitial wear and large molars, thick enamel, differential wear, short face, and so forth, all show a clear model for origin of the *Australopithecus* dental mechanism. Even if jaws like those of Candir and Gandekas are regarded as only of female apes, it is difficult to see where resemblance to modern African apes, not seen also in *Australopithecus*, is to be found. Should males of *Ramapithecus* have had larger faces and bigger canines, later 'feminization' could have produced the condition seen in *Australopithecus*. It is less clear that dental/facial morphology of *Pan/Gorilla* could derive from such a species as occurs at Candir, Turkey.

(ii) *Pasalar*

This fossil-bearing site is located in western Turkey, about 125 km across the Hellespont, south-southwest of Istanbul. The probable age, as judged from the large associated mammalian fauna of over 45 species, would be 15–16 Ma. Primates are represented by 100 isolated teeth, which fall into two groups identified by Andrews & Tobien (1977). These are a smaller species, referred to *Ramapithecus wickeri*, and a set of larger species that they placed in the Vienna basin Vindobian species *Sivapithecus darwini*.

Morphologically each of these species appears to lie more or less between east African early Miocene *Proconsul* species and late Miocene *Ramapithecus* and *Sivapithecus* species from India and Pakistan. The larger species is about the same size as *Sivapithecus indicus* of the Siwaliks and the smaller stands close in size to *Ramapithecus* from Candir and Gandekas. Of the teeth, 14 are broken, which allows for measurement of enamel thickness. Both species have thick enamel and other advanced characters, such as partial reduction of upper lingual cingula. Consequently, Andrews & Tobien rightly referred them to the later Miocene genera and not to *Proconsul*. If the age correlation is correct, then this might be the oldest occurrence of *Ramapithecus* as well as of *Sivapithecus*.

(iii) *Mount Sinap*

This hominoid from the Sinap series northwest of Ankara was described under the name of *Ankarapithecus meteai* by Ozansoy (1957, 1965). It consisted of a symphysial fragment with crowns of left C–P_3 and right I_2–C; associated are broken-off left P_4–M_3. In 1967 a second specimen was found that was recently described by Andrews & Tekkaya (1980). This is an important find because of its completeness. MTA 2125 consists of a complete palate (with all teeth) and lower face that preserves most of the nasal region and parts of the right zygoma and orbit. The latter authors conclude from these two specimens that both belong to the species *Ankarapithecus meteai*, that this is the same species as *Ouranopithecus macedoniensis* from Greece, and that both genera belong in *Sivapithecus*. This face is clearly more advanced than any of the *Proconsul* group from the early Miocene of Kenya and Uganda. It combines a number of interesting features. The nasoalveolar clivus is long, so that the lower face is prognathic; the nasal opening is broad and the zygomatic process is very deep; central and lateral incisors are very different in size. Andrews & Tekkaya (1980) conclude from their study, not only that the Macedonian and Mount Sinap finds belong to the same species, but also that both of these species belong in genus

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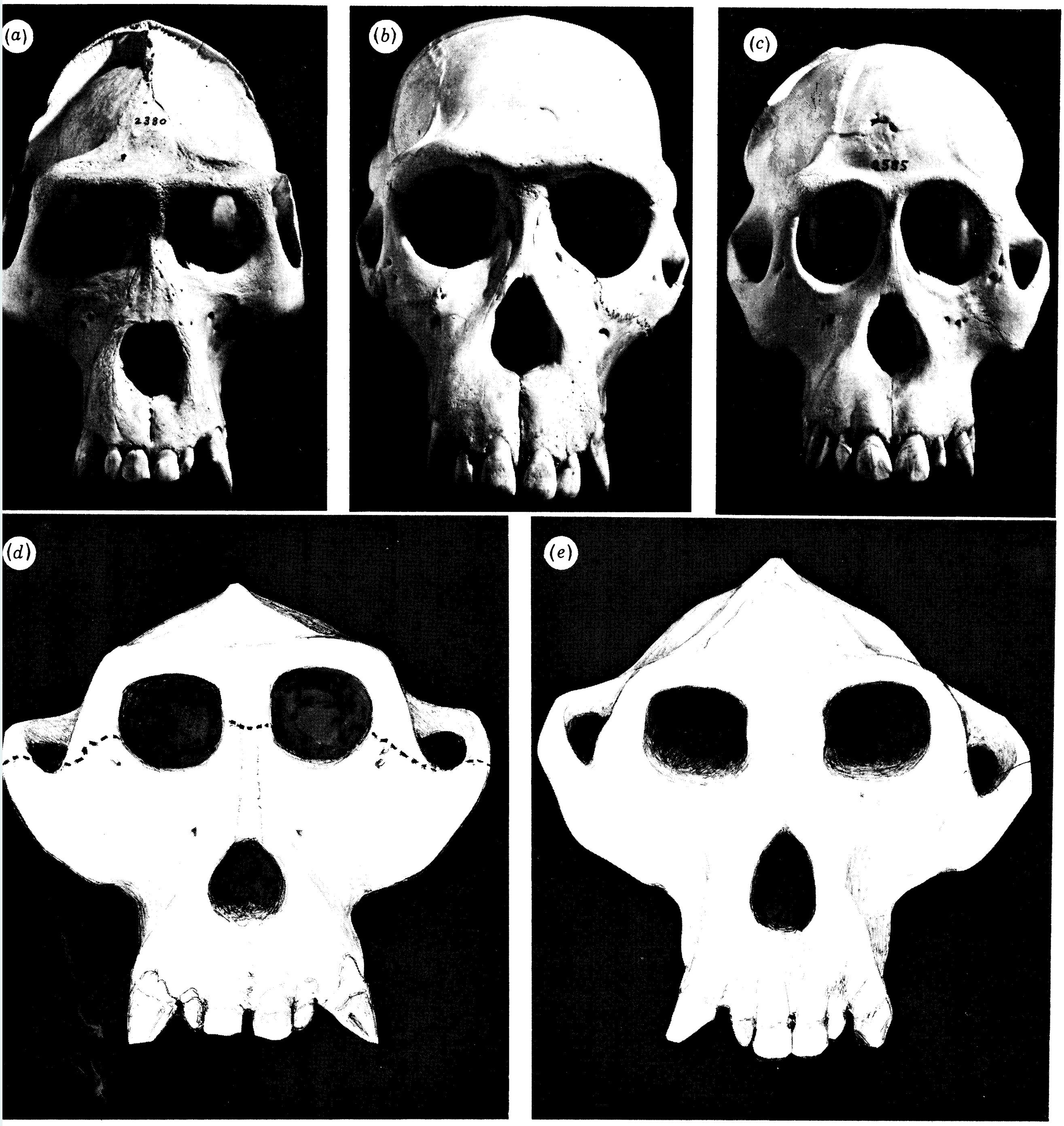

FIGURE 1. Comparison of the frontal aspect of the skull in the living great apes ((*a*) *Gorilla*, (*b*) *Pan*, (*c*) *Pongo*) with tentative restorations of two recently discovered skulls of *Sivapithecus* ((*c*) from Sinap, Turkey; (*d*) from Lufeng, China). All brought to the same approximate cranial height. ((*d*) Hypothetical above dashed line; (*e*) orbital and facial proportions partly hypothetical.) Cranial composition by F. A. Ankel-Simons, photographs by W. Sacco, drawings by E. L. Simons

(*Facing p.* 26)

Sivapithecus. They suggest further that the latter is very close to *Ramapithecus*. Nevertheless the face of *Ankarapithecus* shows considerable distinctiveness from that of *Ramapithecus*, for in the Turkish face the nasoalveolar clivus is long, not short, and prognathism is pronounced, rather than reduced. The zygoma of the Mount Sinap find arise much higher up and somewhat farther back than in *Ramapithecus* and the tooth rows in it diverge little posteriorly compared to those in the latter. In short, this face is as little like that indicated for *Ramapithecus* as are those of modern *Pan* and *Gorilla* like *Ramapithecus*. In the lower left corner of figure 1, plate 1, I have attempted a reconstruction by mirror-imaging the right side and correcting, as far as possible, for distortion.

The question of the relation of *Sivapithecus*, *Ankarapithecus* and *Ouranopithecus* is at present somewhat uncertain. My studies of the Macedonian ape and of Siwalik *Sivapithecus indicus* do not lead to the view that they are necessarily congeneric. *Ankarapithecus* shows little dental–gnathic difference from *Sivapithecus indicus*, but I believe that considerable facial differences may emerge with the description of the newly found face of *Sivapithecus indicus* from Pakistan. Tentatively, at present, the Mount Sinap species may be regarded as belonging to *Sivapithecus*.

One point should be developed about the face of *Sivapithecus meteai*. My study indicates that the upper face has been distorted by plastic flow and probably also by dislocation of the crack between the two halves of this face, which are glued together somewhat out of orientation. These distortions, which I detected on the original, can clearly be seen in Andrews & Tobien (1977, fig. 1 *a*, *c*). In both parts of this figure the tip of the maxilla running up between the ventromedial corner of the orbit and the nasal can be seen to go across a midline erected between central incisors onto the left side. Thus, any accurate calculation of width of nasals and interorbital septum in this specimen is impossible. As narrowness here would be an interesting similarity to *Pongo* the inadequacies of this specimen are regrettable. Walker & Andrews (1973) also contains a controversial interpretation of the orientation of parts of a crushed fossil, which I have analysed elsewhere (Simons & Pilbeam 1978). In an undescribed frontal fragment of Hungarian *Bodvapithecus* and both the newly discovered *Sivapithecus* face from Pakistan and the new *Sivapithecus* skull from Lufeng, China, the interorbital septum is broader, and none of these show the oval orbital outlines of *Pongo*.

In conclusion it is fair to say that some characteristics of *Sivapithecus*, *sensu lato*, may resemble those of *Pongo*, but the most probable meaning of this is that *Pongo* has retained certain resemblances to the middle Miocene radiation that evidently produced it. These features of similarity would be primitive retentions, not shared derived features. As long as the best specimens of most Miocene hominoid genera and species were known either from upper or lower dentition that were not directly associated with the respective opposing dentition (upper–lower), taxonomic judgments were hampered. This face from Mount Sinap, the undescribed jaws and face from Gandekas, Pakistan, and the new skull and jaws from Lufeng, China, all presently assigned to *Sivapithecus*, should make for better judgments as to whether all these finds represent one or more genera. Their full analysis will no doubt clarify the relationship of *Sivapithecus* and its relatives to the ancestry of man (see also Pilbeam 1979 *a*, *b*).

(*d*) *Site in Hungary*

Recent discoveries of Miocene hominoids at Rudabanya in northeastern Hungary have been summarized by Kretzoi (1975), who has proposed two new genera of hominoids: *Rudapithecus* and *Bodvapithecus*. Present also is a large species of *Pliopithecus*. The fauna and flora from this site are extensive and indicate a late Vallesian or early Turolian provincial age of approximately

9 or 10 Ma. *Bodvapithecus* is known from a not-quite-adult mandible Rud. 14, which preserves all lower teeth, save M_3, on one side or the other. The type, Rud. 7, is a maxillary fragment. These materials, although limited, are closely similar to *Sivapithecus indicus*. The other Hungarian form, *Rudapithecus*, is more *Ramapithecus*-like. Although much information is provided about *Rudapithecus* by the ten specimens reported so far, it is not quite clear whether placement of the species in *Ramapithecus* is warranted. Like *Ramapithecus* from India, Turkey and Kenya, *Rudapithecus* seems to show larger lateral incisors (above and below) than does *Sivapithecus*, as well as relatively small canines that are planed off by wear at an early dental age.

(*e*) *Sites in Pakistan*

From 1973 to 1980 joint research teams from Yale University and the Geological Survey of Pakistan have been carrying out a very broad programme intended to extend knowledge of the geology and paleontology of the Neogene deposits of the Potwar Plateau, Pakistan. In the course of this work the number of known fossil hominoids from the Indian subcontinent has been doubled. Extensive additions to scientific knowledge in the areas of dating, ecology and faunal assessment, summarized in Pilbeam *et al.* (1977), have been made through this project. These researches lead to many more new findings than can be dealt with in the few pages available here. I will therefore restrict consideration to the hominoid fossils. The major problem in interpreting the significance to human origins from the Siwaliks of north India and Pakistan before my expeditions in north India 1968 and 1969 and those of Pilbeam in Pakistan from 1973 onwards, was the problem of analysis of the very fragmentary hominoid fossils from scattered sites of different largely unknown ages. These finds had also been subjected to a proliferation of taxonomic names. Attempts to judge the meaning of various degrees of morphological intermediacy that were exhibited by the finds made before publication of the first revision of them by Simons & Pilbeam (1965) were largely futile. Since then Greenfield (1978, 1979), working largely with the same materials, has come up with further unsatisfactory conclusions that essentially derive from trying to rank fossils of unknown ages. Since they are synchronous samples of different species from the same sites the new finds from Pakistan can now be made the basis of more accurate deduction about the nature of *Sivapithecus* and *Ramapithecus*, both because they are more complete than earlier finds and because their ages, associations and relative stratigraphic positions are known. Nothing new has been added to knowledge of *Gigantopithecus* except for the possible reference to *G. bilaspurensis* of a large distal humeral fragment.

In understanding *Ramapithecus* from Pakistan the new finds there are informative. For *Ramapithecus* the best adult mandibles reported so far are GSP 4622/4857 (loc. 182) and GSP 9562/9902 (loc. 260). There is also an infant mandible from locality 260. Like the mandible from Candir, Turkey, the incisor root sockets are closely compressed between the canine root sockets. This condition indicates a small, closed, canine incisor row; premolar and molars are closely packed together against the canine without apparent diastema and mandibular corpora diverge posteriorly.

Andrews & Tekkaya (1980) discuss the front premolars of *Ramapithecus* as 'still primitively single-cusped', although this seems not to be so for the Siwalik type species, which Pilbeam *et al.* report as follows: 'P_3 has a small but distinct lingual cusp, and its long axis is orientated at some 45° to the mesiodistal line of the tooth row'. Shape and arrangement of P_3 in the jaw of the Siwalik species show an incipient bicusped structure that is not much more advanced in early

Australopithecus from Hadar or Laetoli, such as LH 4. Moreover, there is a distinct inner cusp on P_3 of Fort Ternan *Ramapithecus* (KNM-FT 45) and on Candir there is a transverse wear facet in this position. *Sivapithecus* species typically show anteroposteriorly orientated, not transverse, P_3 and, as is typically the case in *Gorilla* and *Pan*, the metaconid is rarely present. In *Ouranopithecus* P_3 is more transverse in the smaller morphotype, but in both 'sexes' there is no trace of a metaconid even though the tooth is extended inward. In many individuals of Siwalik *Ramapithecus*, when unworn, there is buccal flare in upper, and lingual flare in lower teeth. Tooth crowns become almost completely flattened out with advanced wear before dentine is exposed. This type of wear is associated with extreme enamel thickness, which is measured as between 2.5 and 3.0 mm on lower lateral cusps (Pilbeam *et al.* 1977). The mandible below the molars is typically robust (shallow, compared to thickness). The mandible diverges posteriorly at an angle of about 20°, while the symphysis is vertically attenuated, relatively vertically orientated, and has a shortened planum alveolare and well developed transverse tori. As I pointed out long ago (Simons 1964), these mandibular features of *Ramapithecus* (here newly confirmed) relate it morphologically to Plio-Pleistocene hominids. Finds from the new explorations in Pakistan have not confirmed that there is such a thing as a male *Ramapithecus*, with distinctly large canines, although, when taken together with other Indo-Pakistan finds, there is enough difference in size between individuals to allow for a moderate sexual size difference. It will be necessary, it seems, to find a male with large canines to attribute the progressive features of *Ramapithecus* to the expression of feminine and gracile qualities alone. My recent studies of *Pan paniscus* at Terveruren, Belgium, failed to indicate that there is a closer approximation between *Ramapithecus* specimens and female *P. paniscus* than there is between the former and female *P. troglodytes*.

Sivapithecus indicus finds made on the recent expedition (Pilbeam *et al.* 1977) are even more remarkable than those of *Ramapithecus*. These specimens include the only two individuals of this particular genus and species in which most of both the mandible and snout that come from the same individual are preserved. The first of these to be recovered, GSP 9977/01/05/9564, is figured by Pilbeam *et al.* (1977), but the second, yet to be described, includes much of the face, complete mandibles and all of the dentition. Although canines are large they are blunt compared to those of *Pan* or *Gorilla* and exhibit mesial, distal and apical wear. Central upper incisors are comparatively much larger than the laterals. There is moderate canine dimorphism; diastemata between C and P_3 is variably present; that between I 2/2 and C/C is typically present. Unlike in *Ramapithecus*, mandibular rami are deep, the planum alveolare and symphysis are long and at the top angled forward to hold procumbent teeth, and the inferior transverse torus is prominent relative to the superior buttress. Tooth rows are subparallel and concave buccally, incisor regions are broad and molar enamel is about as thick as in *Ramapithecus*, which, however, is a much smaller animal. Mandibular modelling is not reminiscent of the many mandibles of *Ouranopithecus macedoniensis*, in which jaw form is more like *Gorilla*. In *O. macedoniensis* the superior transverse torus is less developed, the jaws are less robust (narrower from side to side, although deep), and the tooth rows are straight with no buccal concavity, while molars are more rounded and have flatter crowns when little worn than in *S. indicus*. This suggests that the specific and generic distinction between *S. indicus* and *O. macedoniensis* should be sustained.

One of the most significant things that the new finds from the Postwar Plateau indicate is the confirmation of the important size and adaptive differences between *R. punjabicus* and *S. indicus* that occur at the same sites. I agree with Pilbeam *et al.* (1977), who state that a third species from the Siwaliks *Sivapithecus sivalensis* 'is the most enigmatic of the Siwalik hominoids and it is not absolutely clear that it exists as a separate species'.

One final set of discoveries from the Postwar is the series of 13 postcranial bones of hominoids recently reported (Pilbeam *et al.* 1977). Taken in sum these bones show some advanced morphological features similar to those of bones of living African hominids, at least they are advanced in comparison to what little is known from analysis of limb bones from the early Miocene of Africa. Particularly interesting is a large distal humerus, GSP 12271, which is said to have a size and morphology reminiscent of a female *Gorilla*. These bones have not been reported to resemble *Pongo* in any specific way. Unfortunately none of the bones was found in unequivocal association with cranial or dental material. In my judgement those materials recovered so far are inadequate to sustain the inference, by Pilbeam *et al.* (1977), that among these later Miocene apes postcranial bones are smaller relative to dental–facial size than in modern great apes. Moreover, these limb bone fragments are not adequate, it seems, to show whether or not *Sivapithecus* and/or *Ramapithecus* were knuckle walkers, incipient bipeds, or even arboreal climbers. This first discovery in Pakistan of many hominoid postcranials from known sites is to be applauded, but it seems that, in spite of these finds, almost everything is yet to be learned about the basic locomotor adaptation of middle and late Miocene hominoids. Without finding most of the fore- and hindlimb and pelvis one cannot say what was the locomotor adaptation of these Miocene hominoids, and I, for one, never have. Even if on recovery of better postcranial material no distinct, obvious bipedal adaptations could be discerned, we would still be in the clear for a full locomotor interpretation. Incipient specializations for arm swinging, knuckle walking or bipedalism might be difficult to detect. At present we have the whole period from about 16 to 6 Ma B.P. in which to look for the first traces of these modern adaptations.

(*f*) *Site at Lufeng, China*

Recent expeditions from 1975 through 1979 have been carried out from the Academia Sinica (I.V.P.P.) and the Yunnan Provincial Museum at a coal mine 9 km north of Lufeng, Yunnan Province, south-central China (Xu *et al.* 1978; Xu & Lu 1979). Fossils come from a stratum 6–7 m thick containing many alternating layers of brown coal and fine sand. The fauna is considerable, containing 30 species, which include varieties of *Hipparion*, *Stegodon*, rhinoceros, gibbon, *Sivapithecus*, *Ramapithecus*, sabre-toothed tiger, muntjac, takin and deer. The suggested faunal age correlation is 8 Ma.

Primate fossils have been described in 1978 and 1979 by Xu & Lu. These hominoid discoveries consist of two mandibles of different size, over a hundred isolated hominoid teeth, and an ape skull reported by Xu & Lu (1980). Because of their completeness these Miocene fossil hominoids are most important. The smaller mandible, number P.A. 580, has been assigned to a new species of *Ramapithecus*, *R. lufengensis*. This mandible preserves all teeth save the central incisor pair and it is at a young individual age. The lower jaw somewhat resembles the type of *Ouranopithecus macedoniensis*, but, unlike the latter, molars of the two morphotypes from Lufeng do not match each other. Therefore the two kinds of mandibles do not appear to be of different sexes.

Examination of a cast of the mandible of P.A. 580 indicates that relative to the molars, incisors, canines and premolars have nearly the same proportions as do these teeth in *Australopithecus afarensis*; that is, incisor size relative to cheek teeth is somewhat reduced compared to *Dryopithecus* or *Sivapithecus*. Paucity of evidence as to absolute and relative incisor size in *Rama-*

pithecus makes it unnecessary to speculate, as did McHenry & Coruccini (1980), that the supposed trend toward small incisor size would have to be reversed in any lineage relating *Ramapithecus* to *Australopithecus afarensis*. In fact, attached, intact incisor crowns are not known in any mandible of *Ramapithecus* described to date other than this one from Lufeng. We are hardly at a stage of knowledge to discuss reversal of trends in incisor proportions of *Ramapithecus* other than on the basis of this specimen, which is only a referred species. The Lufeng find of P.A. 580 is from a compressed coal seam and the canines and incisors have been splayed out and flattened away from P3. When restored by Xu & Wu the tooth series is closed and all anterior teeth contact without diastemata. The restored arcade that they figure is, in fact, arranged just as in *Australopithecus afarensis*. For instance, angles of posterior divergence of cheek tooth rows in the Lufeng jaw and that of the type of *A. afarensis* are very similar. Spacing between cheek tooth rows in the two is also nearly the same. P_4–M_3 length/inter-M_2 breadth is approximately the same in Lufeng number P.A. 580 as it is in the type of *A. afarensis*. In addition to showing interesting details of tooth crown anatomy (because of the early individual age at death) this specimen demonstrates that in this particular Miocene hominoid full canine eruption preceded that of M_3 (still not fully erupted in P.A. 580). This eruption sequence is that of *Australopithecus* and *Homo*, and not that of *Sivapithecus* or *Pongo*. In P.A. 580 lower canine roots are long, but canine crowns are small and do not project significantly above the level of the tooth row. Although somewhat pointed, these canines are about equal in crown volume to P_3 rather than have a distinctly larger bulk than P_3 as is typical in apes. As in some *Australopithecus* there is a small stylid cusp at the distal base of the canines (see, for instance, Sk 51 and Sts 50). An unusual feature is a posterior groove in the lower canine crown, running up and down the posterointernal face. The canine–premolar complex of this find appears to be structurally transitional between that of apes and *Australopithecus* as was explained for other specimens by Simons & Pilbeam (1978). There is some anterolateral extension of the P_3 in *Ramapithecus lufengensis*, implying a more pointed upper canine than usually occurs in *Homo*. Comparatively large upper canines are said to characterize *A. afarensis*. The long axis of P_3 in Lufeng P.A. 580 is situated more transversely and P_3 metaconid is larger (distinctly bicusped) than is typical of *Sivapithecus* or modern apes, while P_4 here is broader, compared to mesiodistal length, than in most Miocene apes. With a rather large heel, P_4 is somewhat molarized. The lower molars of P.A. 580 have rounder outlines, more rounded cusps and a much lower gradient of increase of anteroposterior size than in *Sivapithecus yunnanensis* from the same site. Molar metaconids do not appear to be significantly larger than in *Australopithecus africanus* or *A. afarensis*.

The mandible of *Sivapithecus* from Lufeng might be taken to represent a male of its contemporary at Lufeng, *Ramapithecus lufengensis*. Such a deduction would be based on the assumption that, as in *Ouranopithecus macedoniensis*, a very great sexual dimorphism obtained. Arguing against this are the clear-cut differences between *S. yunnanensis* and *R. lufengensis* in relative M_1-M_2 size and crown anatomy of molars, in contrast with *Ouranopithecus*, where both 'sexes' show almost identical molar crown anatomy and molar outlines. The very large sample of as yet undescribed isolated teeth from Lufeng should, when analysed, resolve the number of species present.

In spite of the resemblances cited above between a cast of P.A. 580 and the Laetoli materials of *Australopithecus*, *R. lufengensis* shows several differences from *Ramapithecus punjabicus*. In *R. punjabicus* lower molars are longer and have thicker enamel than in *R. lufengensis*. The pattern of crenulation on the molars of the Lufeng find appears also to be different from that typical of

R. punjabicus. Perhaps these two species should not be assigned to the same genus. Even so, both of these species show closer resemblances to early *Australopithecus* than can be found in females of such modern apes as *Pan paniscus*. Both '*Ramapithecus*' species show the general type of morphology suitable for origin of the *Australopithecus* dental mechanism. This would be true even if there were larger and more ape-like males found for each of these species. Should this be proved in future to have been so, then the *Australopithecus* dental mechanism could be considered to have arisen through the 'feminization' of a previously dimorphic species.

In addition to the nearly complete mandible referred to *Ramapithecus* at Lufeng, the much larger species, *Sivapithecus yunnanensis*, already cited, is represented by many teeth, a mandible preserving all teeth save M_3, and a skull found in December 1978. This cranium is the most complete skull of an ape ever found in Eurasia.

Cranium and dentition are characterized by deep canine fossae and prominent canine jugae with outward flaring upper canines, lateral incisors are small compared to upper centrals, and there is a pear-shaped nasal opening beneath a very broad interorbital septum. The naso-alveolar clivus is long and front teeth above and below appear to be procumbent. Although crushed, orbits show angled corners, heavy outer margins and eye sockets that are roughly quadrate in outline but appear to be somewhat broader than they are high; the reversed V-shaped temporal crests on the frontal, the marked postorbital constriction of the skull, the vertically short upper face and the quadrate and widely spaced eye sockets are all reminiscent of *Australopithecus*. The large central incisors and blunt canine tips resemble both *Australopithecus* and *Pongo*. However, since *Pongo* shares to some extent the thickness of tooth enamel of the Eurasian later Miocene Hominoidea and of *Australopithecus*, the various resemblances between *Sivapithecus* and *Pongo* in the teeth and lower face may be primitive retentions or symplesiomorphies and not shared derived characters or synapomorphies as has recently been argued by Andrews (1980) for a specimen of the lower face from Turkey that he considers may belong to *Sivapithecus*, but which others have referred to genus *Ankarapithecus*. Certainly the overall appearance of the skull of the Lufeng ape, which has been referred to *Sivapithecus*, is quite different from that of *Pongo* in many regards, particularly in its robust interorbital septum and in its possession of quadrate, laterally buttressed eyesockets.

As an illustrative exercise I have prepared figure 1, plate 1, which contains a tentative facial reconstruction (*d*) of the find from Sinap, Turkey, and an even more tentative reconstitution (*e*) of the new skull from Lufeng. The two skulls appear to indicate that these finds had both distinct similarities and distinct differences.

(2) Definition of the taxonomic family Hominidae

Three main considerations have figured in past attempts to diagnose the characteristics of our immediate forerunners exclusive of the apes, or, at least, each has had an influence on conceptualizations about hominid origins. These factors are (1) temporal, (2) ecological, and (3) morphological, both dental/facial and postcranial.

(*a*) *Temporal considerations*

It is not clear when or where the taxonomic subgroup of humans, the hominids arose. Recent discoveries by M. Leakey, at Laetoli, Tanzania, of trackways of presumed *Australopithecus* that are close to 4 Ma old, as well as the hindlimb structure of hominid fossils of similar age from the Hadar Formation of Ethiopia, show by then perfected bipedal walking in at least some hominids (Johanson & White 1979). I think that mammalian genera typically have a 6 to 8 Ma temporal survivorship. Therefore the generic characterization of *Australopithecus* at about 4 Ma B.P. need not then have been new, but could have been several million years old. Because of the general Pliocene gap in hominoid and other mammalian groups the first actual documentation of various genera of primates from around 4–5 Ma B.P. in all probability fails to record the time of initial emergence of any of them.

While finds in the Plio-Pleistocene of Africa have dated hominids back to about 4 Ma B.P. (Leakey *et al.* 1976), discoveries in Eurasia have extended the range of Miocene ramapithecines closer to the present. Many of the sites of occurrence of *Ramapithecus*, *Sivapithecus* and related form had been correlated with the appearance of *Hipparion* at 11 or 12 Ma B.P. While certain sites such as Pasalar, Turkey (13–15 Ma B.P.), and Fort Ternan, Kenya (probably 13.9 Ma B.P.), have yielded hominoid fossils with thick molar enamel that have been referred to *Ramapithecus*, other faunal correlations indicate ages of about 8 Ma at Pyrgos in Greece, Lufeng in China, and Gandekas in Pakistan. In the Haritalyanger region of India, ages are perhaps in the 9–12 Ma range. The youngest *Ramapithecus* fossils from the Potwar Plateau appear to be about 7 Ma old (perhaps even younger for one or two specimens).

There are at least two principal implications of the new evidence about time range for *Ramapithecus* and *Sivapithecus*. Earliest and latest occurrences are spread over such a long time period that certain species may prove to be outside the probable time spread for survivorship of a single genus. Consequently, a few species now assigned to either or both genera may prove to belong in other genera when more completely known. For instance, the type specimens of *Sivapithecus indicus* and *Ramapithecus punjabicus* seem to have come from the 9–11 Ma B.P. time range, while the type of *Sivapithecus sivalensis* from Jabi, Punjab, could well prove to be from 2 to 4 Ma younger than these. Depending on their specific ages, the former two could be 2–5 Ma younger than Pasalar and Fort Ternan. Likewise *R. wickeri*, at about 14 Ma of age, is much older than the referred find of *Ramapithecus*, *R. freyburgi* from Pyrgos, Greece, whose probable age is around 8 Ma.

The second important implication of the new radiometric dating is that the youngest 'ramapithecines' (at 7 or 8 Ma old) fall within the temporal limits imposed by advocates of the late split-point time for divergence of *Pan/Homo* ancestry. However, the attempt to create a controversy about the phyletic position of *Ramapithecus* in relation to *Pan/Homo* ancestry has, or should have been, a one-sided contention. This is because palaeontologists cannot deal in absolute phyletic judgements. The anatomy of the dentition and face of *Ramapithecus* bears sufficient similarity to that of *Australopithecus* to justify placement in the same family, but at all times the possibility has existed that the whole set of similarities could be due to convergence. Although I have considered the latter possibility from time to time it still seems to me unlikely. Nevertheless it will be the discovery of better anatomical evidence about *Ramapithecus* and its relatives that will shift them away from, or toward, particular associations with the African Plio-Pleistocene hominids.

One thing is clear. Strong advocates of the accuracy of 'molecular clocks' have shown a distressing lack of rigour in answering a sequence of problems posed by the series of seemingly late split-point times calculated generally throughout the family tree of primates. They need to come up with clearer answers to the numerous criticisms regarding confidence limits on dates, variance in rates of change and so forth. As I have stated recently (1977), the problem is not

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dependent upon whose ancestor is *Ramapithecus*, but is more general. There are at least half a dozen points in primate phylogeny where we have fossil evidence relating to branches of principal subgroups within the order. All of these are discordant with the dates determined by immunochemical distance by Wilson & Sarich (1969) or by Sarich & Cronin (1976). No adequate explanation of these discrepancies has yet been produced by proponents of 'molecular clocks'. Rather, extremists have begun to argue instead that split-point times determined by immunochemical distance have the same validity as radiometric determinations.

It is understandable that, as awareness of man's close biochemical similarity to the African apes has grown, later ancestral branch points between them should gain favour. The past twenty years has seen abandonment, by all authorities, of early divergence times of hominids from the apes. Living authorities have seriously advocated estimates that range all the way from a date before the end of the Cretaceous to the Oligocene. Now nearly all serious students of human origins agree that the ape–hominid divergence has to be much later. Estimates for this later split still spread between middle Miocene and middle Pliocene. It still seems to me that a split-point date in the Miocene around 12–15 Ma B.P. is more probable than a mid-Pliocene date of 4–5 Ma. Papers by Lovejoy *et al.* (1972), by myself (Simons 1976*a*), by Walker (1976), by Radinsky (1978) and by Romero-Herrera *et al.* (1979), as well as contributions not yet published (Baba *et al.* 1980; Korey 1980; Goodman 1980), all give reasons for inaccuracies or changes in rate of molecular evolution. These references and many others that could be cited forcibly call into question the validity of molecular clock dates. Interestingly, Goodman (1981) has demonstrated that, if one makes the assumption that molecular evolution proceeds in a clock-like manner, following the hypothesis originally proposed by Zuckerkandl & Pauling (1962), then a time of only 0.5 Ma was obtained for the *Homo–Pan* ancestral divergence. His method is based on counting the number of nucleotide replacements on four protein chains: α- and β-haemoglobin, myoglobin and cytochrome *c*. The new data summarized by Goodman indicate a clear-cut pattern of accelerations and decelerations in rates of molecular evolution throughout time.

It seems probable that higher primates, or most primates, show a slowed rate of molecular evolution. In Simons (1976*a*) I discussed the principal divergence times indicated from the fossil record. At least six of these present major difficulties for advocates of molecular clock dates for split points. These divergence dates are summarized in table 1.

Although various suggestions have been put forward as disallowing the relevance of the above indicated branching times, none of them have shown much rigour. The gelada baboon group traces back in Africa as far as does *Australopithecus*, yet it gives no immunochemical distance from common (*Papio*) baboons. The remarkable resemblance at 20 Ma B.P. of *Progalago* to modern genus *Galago* is so close as to hardly warrant their generic separation. Neither of these genera are lorisines, while *Mioeuoticus* is a lorisine related to *Perodicticus*. Small Miocene hominoids such as *Epipliopithecus* and *Micropithecus* show detailed specific resemblance to modern *Hylobates* and *Symphalangus*. The resemblance is particularly striking with *Epipliopithecus* from the European Vindobonian Miocene provincial age, where mandibles, face and skull can be compared (Zapfe 1960). The relationship between modern gibbons and *Epipliopithecus* has been explained away by the theories that all early apes would look like gibbons or that their primitive features, such as short forelimb and tail in *Epipliopithecus*, disqualify the relationship. Nevertheless, other early catarrhines whose face, jaws and skull are known, for example *Aegyptopithecus*, do not exhibit similarity to gibbons. New finds from the Fayum of parapithecid monkeys show them to have had many primitive features, but their advanced features resemble those of catarrine monkeys not those of the South American platyrrhines. These parapithecids are not very much like their ape contemporaries the Propliopithecidae from the Fayum, Egypt. For these two groups to have diverged as much as they have at 28 or 29 Ma B.P., the separation of Hominoidea must have been considerably earlier than the time of their existence and not, of

TABLE 1

divergence in ancestry of	fossil or geological evidence and date B.P./Ma		molecular clock date B.P./Ma
Papio–Theropithecus	age of oldest *Theropithecus* (= *Simopithecus*)	4	no immunochemical separation, therefore 0
galagines–lorisines	*Progalago* (galagine) and *Mioeuoticus* (lorisine) already separate at (see Walker 1978)	20	10
pongids–hylobatids	*Epipliopithecus* distinctly resembles gibbons facially and the same *Micropithecus*	16 20	10
hominoids–cercopithecoids	parapithecids and propliopithecids have evolved to level of distinct families at 29 Ma B.P. (allowing *ca.* 5 to 10 Ma for familial divergence)	34–39	22
catarrhines–platyrrhines	segregation of New and Old Worlds by North Atlantic rifting, and disallowing long distance South Atlantic rafting by ancestral platyrrhines	50+	36
Ramapithecus–Sivapithecus* from *Dryopithecus* regardless of whether each, or both are specially related to either *Homo* or *Pongo	geological time of appearance *Ramapithecus* and *Sivapithecus*	*ca.* 15	4–8

course, at 22 Ma B.P. Although one or two palaeontologists have suggested that the New World monkeys could have left Africa by rafting to populate South America with platyrrhine monkeys at about the time the Fayum lower fossil wood zone was being deposited, that is, about 35–38 Ma ago, this is highly improbable (Simons 1976*a*). The South Atlantic was then at least two-thirds as wide as it is now. At typical east-to-west ocean current rates a raft of vegetation crossing the South Atlantic at that time would have had a voyage lasting a minimum of six weeks. This is far too long to satisfy water and other physiological needs of monkeys. Moreover, although the parapithecids share many primitive features with ceboids they have not one synapomorphy that would link them with each other, that is, they do not show any shared derived or advanced feature. Finally, even if the ramapithecine–sivapithecine assemblage is related to the ancestry of *Pongo* and not *Homo* it is discordant with a separation of 7 Ma B.P., determined by immunochemical distance since *Sivapithecus* appears 16 Ma ago. On the basis of present evidence it seems more probable to me that the few broad similarities so far reported between *Sivapithecus* and *Pongo* are symplesiomorphies not synapomorphies.

Looked at overall, advocates of molecular date determinations as well as students of the form of fossils are both morphologists. The former are trying to quantify the degree of difference in the form of molecules, and palaeontologists are those who assess macromorphological differences and similarities. Each approach can be closely quantified and this in turn tends to lead to dogmatic statements about the meaning of molecular and of phenotypic similarities. Each system also has an Achilles heel. For advocates of molecular clock regularity this is the demonstrated change in evolutionary rates. For palaeontologists the weakness is that evolutionary processes can bring about convergence, which masks the degree of relatedness between particular forms. Whether the split between the ancestors of man and the African apes was before or after the time when *Ramapithecus* lived and what actually happened in the early stages of the development of the Hominidae will only be confirmed with the recovery of new fossils. The search for this evidence is a true challenge and stands as one of the most exciting intellectual frontiers yet available for exploration by anthropologists.

One final point may be worth mentioning in regard to the time of emergence of hominids. For those who take it to have been at 6 or 7 Ma B.P. in Africa it is probably then synonymous with origin of genus *Australopithecus*. In spite of the morphological distinctiveness that living hominids like to attribute to themselves, a group of so recent an origin can hardly be given family status. Except for families that have no fossil record at all, and thus no documented origin, even the youngest mammalian families, such as Bovidae, Muridae or Elephantidae, had 12–15 Ma B.P. origin times. The peak time for appearance of mammalian families in the fossil record is early Oligocene and after early Miocene familial group origins decline abruptly (Lilligraven 1972).

(*b*) *Ecological considerations*

The ecological context for hominid origins seen in middle and late Miocene hominoids has been much discussed, but these discussions have led to few clear conclusions. In the early Miocene of East Africa and in the western European middle Miocene, forest-adapted apes with thin tooth enamel appear to predominate (Andrews & Van Couvering 1975). Such species include the various dryopithecine species of genus or subgenus *Proconsul*, *Micropithecus clarki*, *Limnopithecus legetet* and *Dendropithecus macinnesi* in East Africa, and in Europe the various species of *Pliopithecus*, as well as *Dryopithecus fontani* and *Dryopithecus laietanus*.

For the middle and late Miocene sites, much enlarged faunal lists have recently been published for sites where *Ramapithecus*, *Sivapithecus*, and *Gigantopithecus* occur. Particularly extensive faunal associations with hominoid species are known at Lufeng in China, the Potwar Plateau sites in Pakistan, Pasalar in Turkey, Rain Ravine in Macedonia, Greece, Rudabanya in Hungary, and Fort Ternan in Kenya. It would appear that forest fruit, nuts and vegetation were probably available at or near all such sites, none of which appears to have been in either gallery forest or dry grassland savannah. In some Miocene hominoid sites, such as Rudabanya, forest conditions seem to predominate, but even there we have evidence for open woodlands nearby. The best reconstruction appears to be that at least some of the many new populations of middle and later Miocene hominoids occupied a mosaic environment of woodlands interspersed with grasslands.

Many of these sites, such as several Indo-Pakistan localities, Candir, Rain Ravine and Fort Ternan, show, in considerable numbers, bovids adapted to woodland savannah, as well as other open country elements. Hominoids, however, have high water requirements and may seldom have strayed far from water. Although the presence of thick tooth enamel typically in almost all known later Miocene and Pliocene hominoids suggests a diet different from that of both early Miocene and present-day African apes, neither meat-, nor grass-eating is indicated for these hominoids by tooth microwear (R. F. Kay & A. Walker, personal communication). In fact, Kay (1981) has suggested that the predominant element evoking thick cheek-tooth enamel may be cracking into thick fruit rinds and the husks and shells of nuts. Whatever evoked this thick enamel in Tertiary hominoids, it is not needed by *Pan* or *Gorilla* today and is not found in any African apes. *Pongo*, on the other hand, does retain fairly thick enamel and, if its diet, when further analysed, shows distinctive features the reason for this retention will become clear. The molar crown enamel is approximately twice as thick in *Pongo* as in *Australopithecus*, *Sivapithecus* and *Ramapithecus*. Therefore, the modern east Asian ape cannot be taken as an exact dietary analogue for the earlier forms.

(*c*) *Morphological considerations*

(i) *Dental/facial morphology*

The structure of the dental mechanism as well as of the face and skull of man's immediate forerunners may be inferred by three principal approaches. The first is the traditional comparison contrasting modern and Pleistocene fossil man to the living great apes. Such definitions of the difference between hominids and pongids are characterized by LeGros Clark (1955). These definitions were done when almost nothing informative had been published about middle or late Miocene apes and when, as is still the case, nothing about the immediate (Pliocene, late Miocene) ancestors of living African apes was known. Inferring the nature of man's ancestor along these lines led to the expectation that man's forbears would somehow be intermediate between Pleistocene humans and the living African apes. Here the characters indicated for hominid emergence revolve around their acquisition of transverse, bicusped P_3, development of small canines, a small snout and a broadening of tooth rows posteriorly. Thus, when one takes this general approach the modern African apes, not fossil forms, are seen as the common starting point from which hominids diverged. A recent variant of this approach has been developed by Zihlmann *et al.* (1978).

Another manner of approaching the question of ancestral hominid facial and/or gnathic morphology is to bring in the evidence of past fossil forms that are older than earliest *Australopithecus* in an attempt to judge which show the greatest relation to the latter. To do this one has to skip back from earliest well understood *Australopithecus*, at about 3.5 Ma of age to the middle and late Miocene fossils, whose age ranges from some 8 Ma to about 16 Ma. On taking up this line of approach a number of features of resemblance to *Australopithecus* that can not be observed in modern African apes are found in Miocene forms. Such features are generally related to development of enlarged molars with thick enamel and to reduction of the size of the face, incisors and canines relative to cheek teeth. The findings that can come from this type of approach are summarized in Simons (1968, 1976*b*).

A third approach to the question of the nature of the dental/facial anatomy of earliest Hominidae and their immediate forerunners is to extrapolate backwards a set of primitive features that may be inferred from earliest *Australopithecus*. This third approach only became possible recently, with the dating of several sets of *Australopithecus* at earlier than 2 Ma B.P. Preliminary assessments of this sort have been made by both Johanson (1980) and White (1980). Out of this type of assessment also grows what is probably a most important issue, the new evidence about what not to expect in hominids earlier than those now documented from the 3–4 Ma B.P. period. Brain to body size ratios are difficult to estimate from fragmentary remains and it is also most difficult to demonstrate same site, that is contemporaneous body size dimorphism. However, there does seem to be growing evidence that the level of body size and canine size dimorphism may be higher in earliest *Australopithecus* than in later hominids (Johanson & White 1979). It is also uncertain whether the brain in an immediate forerunner of *Australopithecus* in relation to body size would have been particularly larger than its ape contemporaries. My view is that it probably would have been, based on the present evidence from *Australopithecus*.

(ii) *Postcranial morphology* (locomotor mechanism)

The major outstanding question about man's immediate forerunners that could be clearly answered from the fossil record would be the time of emergence of the bipedal walking adaptation in these ancestors. Since the appearance of different aspects of the whole animal in structural evolution are not correlated, membership in the hominid family could be adumbrated first in dental/cranial features and later in a locomotor adaptation. An analogous case can be seen in

TABLE 2

name	locality	probable age/Ma	description
Dryopithecus fontani	St Gaudens, France	15	distal two-thirds left humerus
Proconsul africanus	Gumba, Rusinga Island, Kenya	18	distal four-fifths juvenile humerus
Epipliopithecus vindobonensis	Vienna Basin, Czechoslovakia	16	complete right humerus
?*Dryopithecus* (= *Austriacopithecus weinfurteri*)	Vienna Basin, Austria	16	central shaft of humerus
Dendropithecus mackinnesi	Hiwegi, Rusinga Island, Kenya	18	nearly complete humerus (lacks proximal two-thirds of head)
Proconsul nyanzae	Maboko Island, Lake Victoria, Kenya	15	central shaft of humerus

the gibbon group, where a strong facial and/or cranial similarity developed early in the middle Miocene; that is, *Micropithecus* from East Africa and *Epipliopithecus* from Europe have strong cranial resemblance of *Hylobates* and *Symphalangus*. We know that Miocene *Epipliopithecus* and the modern gibbons are closely similar in face and cranium and in the hindlimb as well. It is only in the forelimb that adaptations differ strikingly. From this, there is a strong inference that the taxonomic group of the gibbons segregated first (family Hylobatidae) and the forelimb elongation of this branch of the ape family tree came later. Incidentally this means that forelimb elongation and tail loss developed independently for similar, but by no means necessarily the same, reasons in the *Pan–Gorilla* and the *Hylobates–Symphalangus* lineages. By analogy the Miocene ancestors of *Australopithecus* could have been living and eating much as they did later, even before they were bipedal.

Another important point about Hominoidea before the Plio-Pleistocene is that the fossil record does not support the idea that all earlier Miocene apes had a primitive monkey-like postcranium, and that the barrel-chested, broad-shouldered condition of the modern hominoids developed in one particular branch of apes at a late date. Although the chest and shoulder region is not well preserved in the fossil record it would be necessary to show that all known Miocene Hominoidea are closely similar and uniformly primitive in the upper arm. Fortunately for establishment of this point it is the humerus that can be compared among a series of Miocene apes that are all 14 Ma or older, running back to about 20 Ma. The taxonomic assignments, localities, probable ages, and descriptions of these fossils are given in table 2.

These humeri fall into at least four general classes, indicated by differences in morphology and all in existence before 1 Ma B.P. Clearly, chests, fore- and hindlimbs and spines of early and middle Miocene hominoids were likely to have been diversified if such is the case for their humeri. The *Dryopithecus* humerus from Saint Gaudens, France, and that of *Proconsul* from Gumba, Rusinga, both subadult, are generalized, lightly built and straight shafted without being elongated. The Vienna Basin ?*Dryopithecus* humerus, like that from Maboko Island, Kenya, are both retroflexed as in terrestrial monkeys. Different from these is the well preserved humerus of *Epipliopithecus*, which is short and broad distally, possesses an entepicondylar foramen and indicates a generalized arboreal quadruped like *Aegyptopithecus*. In contrast, the humerus of *Dendropithecus* from Hiwegi, Rusinga, is longer, relative to its calibre, than any of the above, is straight (not retroflexed) and narrow distally, has no entepicondylar foramen and has an overall morphology suggesting incipient suspensory use of the forelimb (Simons 1972).

In conclusion, one has to say that we do not know how to choose from which of these upper-limb morphologies that of the hominids arose, but we do clearly know now that hominoids do not show early monkey-like postcranial uniformity. This is a point unrecognized, or glossed over by, many palaeoanthropologists who have focused their attention on the unknown last 10 Ma or so of ape evolution.

Recent confirmation of a perfected bipedal walking ability at Laetoli, Tanzania, and in the Hadar region of Ethiopia at about 3.5 Ma B.P. does not say anything about how much earlier the adaptation arose. Certainly we have not yet found any real evidence that would show whether or not any early Pliocene or late Miocene hominoids were possessed of bipedal adaptations. About this important issue, in spite of the numerous postcranial bones newly found in the Potwar region of Pakistan, we know essentially nothing.

In conclusion I should like to thank my wife, F. A. Ankel-Simons, and Dr R. F. Kay for valuable discussion and review of this paper. Thanks are also due to Dr I. Tekkaya, who allowed me to study the well preserved type mandible from Candir (see §1 (*c*) (i)).

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PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

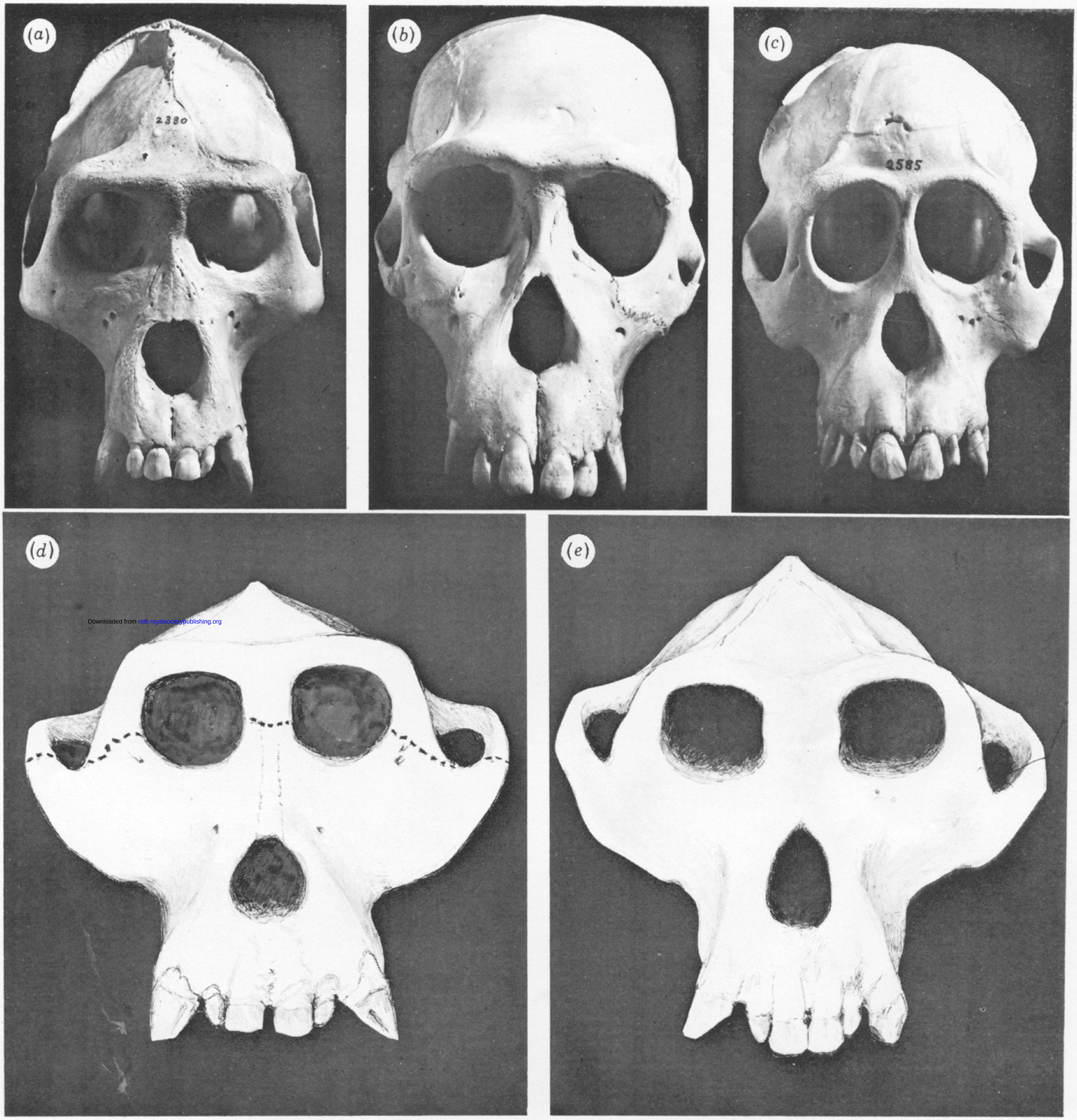

FIGURE 1. Comparison of the frontal aspect of the skull in the living great apes ((*a*) *Gorilla*, (*b*) *Pan*, (*c*) *Pongo*) with tentative restorations of two recently discovered skulls of *Sivapithecus* ((*c*) from Sinap, Turkey; (*d*) from Lufeng, China). All brought to the same approximate cranial height. ((*d*) Hypothetical above dashed line; (*e*) orbital and facial proportions partly hypothetical.) Cranial composition by F. A. Ankel-Simons, photographs by W. Sacco, drawings by E. L. Simons