

## Catarrhine Evolution

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The first scientific session included six presentations on a variety of topics dealing with the "prehuman" phases of paleoanthropology. Elwyn Simons began the program with a discussion of the Fayum primates of the Egyptian Oligocene, especially the *Aegyptopithecus-Propliopithecus* group, which he placed in the Hominoidea. One question asked of him was whether those taxa might also be potentially related or ancestral to the Old World monkeys and went on to ask what features made them hominoids, as opposed to members of yet a third major group of catarrhines. Simons replied that both the limb bones and teeth of cercopithecoids have a rather stereotyped morphology quite different from that of living hominoids or of *Aegyptopithecus*. Although the dentition of Old World monkeys could have been derived from something like *Aegyptopithecus*, as perhaps could have been the postcranium, the oldest known monkey postcrania suggest to Simons a rather different predecessor. In fact, he argued, features of the teeth in *Parapithecus* resemble those of cercopithecids in ways not seen in the Fayum hominoids, while the hind limb of the parapithecoid *Apidium*, although "strangely adapted for leaping," similarly resembles monkeys. The best way to answer the question, however, would be to find fossils that are transitional between later cercopithecoids and one or another early catarrhine.

Asked how *Aegyptopithecus* is linked to the Early Miocene African hominoids such as *Proconsul*, Simons cited the close similarity of their talus, calcaneum, and tibia, which differ greatly from those of early Old World monkeys. He suggested that if "monkey-like creatures [were found] contempo-

rary with *Proconsul*, it would be possible to suppose that an earlier form had given rise to both" lines. Simons noted that those who wish to use the features of Miocene to modern hominoids as a basis for a definition of Hominoidea would find *Aegyptopithecus* "an uncomfortable little creature," because it is a mosaic of hominoid molars, fused frontal and hind limb, and other features that are more primitive.

David Pilbeam reviewed his recent finds in the Miocene of Pakistan and their implications for human origins. In response to the same questions asked of Simons, he indicated that he would include *Proconsul* in Hominoidea without question, one reason being its hominoid-like vertebral column: that of *Proconsul africanus* is gibbon-like, while the vertebrae from the Middle Miocene site of Moroto (Uganda) are rather like those of chimpanzees. However, he added that it is possible that these are convergences, because they are not too different from vertebrae of spider monkeys. The oldest fossil that Pilbeam would accept as a cercopithecoid is a single, clearly bilophodont molar from Napak, close to 20 million years (m.y.) old. He said that he is "enough of a cladist to feel most comfortable with a definition of Hominoidea which links everything on the basis of shared-derived features," but that few *Proconsul* features outside the vertebrae are synapomorphic with Middle Miocene to living hominoids.

Herbert Thomas discussed the land connections and faunal migration patterns among Africa, Arabia, and Eurasia in the earlier Miocene, with special reference to the hominoids. He was asked about the relationship between woodlands and aridity

after Africa connected to Eurasia. He replied that the bovids of the "Chinji" horizon in the Siwaliks revealed a fairly closed environment, while apparently contemporaneous environments in Arabia (Hofuf Formation) were very open, based on rodents such as the sciurids and ctenodactylids.

Alan Walker (Johns Hopkins University) spoke on functional morphology and Miocene hominoids. Although he was unable to prepare a manuscript, I will briefly summarize his major findings. He first reviewed recent finds of additional portions of the skeleton of *Proconsul africanus* and *P. nyanzae*, both in the field and in wrongly identified museum collections, much of which information has been published by Walker and Pickford (1983). In sum, the brachial index of *P. africanus* is gorilla-like, while the crural and intermembral indexes are more like those of macaques. "In robusticity, it's quite a chunky little animal, not a slim, gracile leaper of the sort that perhaps we've been led to believe from the forelimb analysis." Moreover, while the hand, forelimb and thigh are rather monkey-like, the foot, lower leg (with strong fibula), scapula, upper arm, and even elbow are more apelike. He then noted even more recent discoveries at the late Early Miocene (older than 17.5 m.y.) site of Buluk in northern Kenya. The primates include one or two species of monkey, like *Prohylobates*, being described by Meave Leakey; two bits of a small hominoid like *Micropithecus clarki*; and some jaw fragments and isolated teeth of larger hominoid, which, he said, is definitely not a *Proconsul*. The maxilla has a long, curved canine root and deep canine fossa, with the premaxillary suture curving into the nasal aperture. An  $M^2$  in place has thick enamel and no cingulum. The reconstructed mandible showed close-set parallel toothrows, double mandibular torus, rotated stubby canines with a hollow behind the root, inflated corpus, and steep ramus. All of these features differed greatly from *Proconsul* specimens to which he compared them, but were similar to those of the younger Pakistan *Sivapithecus*. Walker suggested that the Buluk fossils might represent the morphology of the common ancestor of the great apes and humans, but not a special link to the Asian orangutans.

Neither John Fleagle nor Richard Kay was able to be present at the symposium, although their paper is included in this sec-

tion. Instead, Jeffrey Schwartz (University of Pittsburgh), who had participated in the pre-symposium study session, was willing to fill in for them on short notice by presenting a summary of his paper that had just appeared in *Nature* and drawn much attention (Schwartz, 1984). Schwartz's analysis of the cladistic relationships of the living larger hominoids resulted in the surprising finding that the orangutan (*Pongo*) shares the greatest number of derived features with *Homo* and thus is the closest relative of humans. He considered that most of the features shared by humans and African apes are either primitive retentions or of low phyletic weight, while the synapomorphies joining *Homo* and *Pongo* are stronger. Reinterpretation of the previously widely accepted molecular biological analyses suggested to Schwartz that most of the protein and DNA similarities between humans and African apes were symplesiomorphies or that it was impossible to determine the polarity of transformation in these characters, thus rendering them useless for phylogeny reconstruction. The fossil *Sivapithecus* was found to share a number of the *Homo-Pongo* synapomorphies and thus was placed (along with *Gigantopithecus*) in a derived clade separate from the African great apes or gibbons. When asked about chromosomal and other features that seem to link humans and chimpanzees, specifically, Schwartz suggested that most were probably symplesiomorphies—that is, shared primitive retentions. He noted that a recent paper by Marks (1983) reviewed the hominoid cytological literature, concluding that many of the published conclusions were insufficiently supported by the underlying data.

Schwartz was also asked to comment on how his study of the palatine fenestrae and related morphology led to a diametrically opposing result from that reached by Ward (Ward and Pilbeam, 1983; Ward and Kimbel, 1983) on similar material. He replied that Ward and colleagues, as he read them, compared the floor of the nasal cavity in *Pan* and *Australopithecus afarensis* and found them similar in having large foramina on either side of the midline; from this, they generalized to all African apes and humans sharing this complex and thus distinct from the *Sivapithecus-Pongo* group with small foramina. In fact, Schwartz argued, both orangs and modern humans have small foramina; this did not suggest that they were

specially related, but that the large foramina might be the primitive condition. On the other (oral cavity) side of the palate, as Schwartz had shown previously, humans and orangs share a single foramen as opposed to the double, primitive condition seen in other catarrhines. The confusion between these two aspects of the problem might have resulted in some uncertainty as to their interpretations.

Peter Andrews finished the program with a broad survey of the relationships among all major groups of catarrhines. He differed from most of the preceding speakers in his interpretation of the phyletic positions of *Aegyptopithecus*, *Proconsul*, and *Pongo*, supporting each decision with an analysis of the polarity of transformation at one of several major branching points on his catarrhine cladograms. One specific point on which he was questioned was the placement of the Early Miocene East African *Dendropithecus* outside of both the hominoid and cercopithecoid lineages, as defined by derived characters shared among their respective living members. He replied that the lack of an auditory region made it difficult to interpret this taxon: the parapihithecoids and propliopithecoids of the Fayum have a ring-like meatus, living hominoids and cercopithecoids a tube, and Miocene pliopithecoids an intermediate condition. *Dendropithecus* shares all the features found in common among hominoids and cercopithecoids (for which fossils are known), but none of the derived characters distinguishing the two modern superfamilies. Therefore, it was placed *incertae sedis* within Andrews's "true" Catarrhini.

A question about the relationships of *Proconsul*, whether it is phyletically closer than the gibbons to the living large hominoids or more distant, was taken up by both Andrews and Walker. Walker indicated that gibbons were quite distinctive morphologically, with features he could not see in *Proconsul*; he thus did not consider them to have been derived from that taxon. *Proconsul*, Walker said, presents a number of quite ape-like characters that are not just primitive. Andrews replied that "you don't have to be able to see gibbon characters in *Proconsul* in order to say whether its position is 'above' or 'below' that of gibbons." Instead, Andrews argued, he finds that *Proconsul* is more derived than *Dendropithecus* in sharing features found otherwise only in both gibbons and great apes (including humans), but not

in either of those two groups alone. Andrews asked Walker which characters of *Proconsul* might be shared with great apes but not by gibbons, thus linking the former two groups most closely. Walker, evading the question, responded that he understood this method of analysis but did not agree with it. Rather, he preferred to "pull it together and have a feel for the organism. As an old-fashioned biologist-paleontologist," Walker would "like to think of things as animals, not as traits."

The discussion during this symposium session revealed an apparent dichotomy among primate systematists that is common to most such disciplines: "cladists" on the one hand and "evolutionary systematists" on the other. In fact, however, I see it more as a morphocline or graded series than as a strict dichotomy. Walker and Simons argued for relationships based on the overall pattern of resemblance among the animals involved, looking for ways to incorporate the paleobiology of the fossils and their "total morphological pattern" into the analysis (see also Tobias, 1985). Pilbeam, like a number of current workers, has accepted part of the cladists' mode of approach, but not all; while Andrews and Schwartz (and I) emphasize that relationship depends on recency of common ancestry as reflected by the sharing of derived (or "advanced") characters distinct from those ancestral features of wider distribution. For Walker to say that he speaks of animals rather than traits (or collections of traits, as some phrase it) sidesteps the issue.

For most extinct mammals, we have only a collection of fragmentary fossils from which we can try to deduce two different aspects of the animal's natural history: its phyletic position and its paleobiology. The only way to approach the former with reasonable reliability is to search out the derived characters that link it to its closest genealogical relatives. Neither shared conservative retentions from an earlier ancestry nor convergent or analogous similarities tell anything about its phylogeny—that can be deduced only from a study of homologous traits shared with a small group of closest relatives. On that basis, the position of *Proconsul* is still unclear: if Andrews is correct, it is near the base of the hominoid radiation, but Walker appeared to interpret it as closer to great apes in certain features. If he were willing to elucidate those features, I would be most interested, not least because I argued (Szalay and Delson, 1979) that *Procon-*

*sul* did share certain postcranial features with the great ape and human clade not seen in gibbons. Both Andrews and I now agree that this clade can be termed Hominidae, as separate from the Hylobatidae, and the question thus resolves to: Is *Proconsul* a hominid?

The second aspect of paleontological reconstruction, paleobiology, is well treated in the paper by Fleagle and Kay. Although teeth surely give evidence about dietary adaptations, the limbs are usually dominant in these considerations. Thus, Walker's careful poring over the old collections and backdirt on Rusinga was important for both paleobiology and phylogeny. He ended his symposium discussion of *Proconsul* hoping someday to see the pelvis, sacrum, and tail of this animal. Incredibly, several months later, he and Kenyan colleagues recovered most of the skeletons of five individuals on Rusinga—the power of positive thinking!

Three other questions brought up in this session lead me to add some comments. Simons noted that the distal hindlimb of *Apidium* and the molars of *Parapithecus* are rather similar to those of Old World monkeys, supporting his long-held views of a special relationship between parapithecids and cercopithecids. But several recent papers by Simons and his co-workers have actually weighed heavily against these views. Fleagle and Simons (1979) indicated that parapithecoid pelvises show no trace of the ischial callosities expected not only in early cercopithecoids but in the common ancestor of all living catarrhines: the parapithecids must thus have predated such an ancestor and cannot be related to cercopithecoids specifically. Fleagle and Simons (1983) reported that the tibia and fibula of *Apidium phiomense* were partly fused or at least more strongly appressed distally than in any other known anthropoid. Although Simons argued in the discussion that this might have been the ancestral condition for Old World monkeys, there is no evidence for that supposition, and it seems more likely that *Apidium* (and perhaps other parapithecids) were uniquely derived in this region. Finally, Kay and Simons (1983) showed that the permanent lower incisors of *Parapithecus grangeri* were entirely lost, leaving the lower canines to meet in the symphyseal midline. This is also a unique derived condition (not seen in *Apidium*), which suggests that this animal was not likely ancestral to any later group. It also may be the only valid reason for re-

suscitating Gingerich's (1978) genus *Simonsius* for *P. grangeri*.

In sum, the two well-known genera of Parapithecidae show a number of highly derived features distinct from those of all later catarrhines. I continue to argue that parapithecids—or paracatarrhines, as I called them (Delson, 1977), based on the "para" in *Parapithecus*—represent the sister-taxon of all the remaining Old World higher primates, which I have termed eucatarrhines. Andrews argues here that the shared retentions used by Szalay and Delson (1979) to unite *Propithecus* (including *Aegyptopithecus*) and *Pliopithecus* in the Pliopithecidae are insufficient; he thus recognized two essentially monotypic superfamilies for these genera. Fleagle and Kay (1983) used similar arguments to suggest two subfamilies for these taxa, as had Delson and Andrews (1975) earlier. I agree that proliferation of new categories and new higher taxa is the bane of a purely cladistic classification, and this would result from Andrews' scheme. The alternative is to accept the paraphyletic combination of the two families in the Pliopithecoidae, which I tentatively favor.

Turning to later hominoids, *Proconsul* has taken center stage once again. Andrews has argued persuasively that it has no hominid or hylobatid features and thus has placed it in a separate hominoid family, Proconsulidae. I would accept this taxonomy if Andrews' interpretation of the branching sequence were further supported, but I would place *Proconsul* within Hominidae (perhaps as a third subfamily or within Dryopithecinae) if Walker's *gestalt* interpretation is confirmed by new data. Andrews and I agree (at present) on the inclusion of most larger African Early Miocene hominoids within *Proconsul*.

On the other hand, two groups of African earlier Miocene fossils clearly do not belong in that genus: *Kenyapithecus* and specimens from Buluk (and perhaps Moroto). Walker argued that the Buluk fossils would represent *Silvapithecus*, distinct from *Proconsul* in a number of gnathic features. Instead, having seen casts through Walker's courtesy, I would suggest that these specimens are best placed in *Dryopithecus*, known from Europe and less widely from Asia ("*Silvapithecus*" *simonsi* and a new jaw from Wudu, Gansu province, China). The Buluk mandible fragment shows double symphyseal tori as do other jaws I place in *Dryopithecus*, and

the maxilla does not present the diagnostic *Sivapithecus* morphology described by Ward and Pilbeam (1983). Enamel thickness and microstructure may yield further information. For example, Martin (1983) has said that "*S.* *simonsi* is less derived dentally (as far as can be told from a long-lost holotype) than *Kenyapithecus* and suggested that the Moroto fossils are not *Proconsul*, but that the new Saudi Arabian hominoid is *Dryopithecus*. If *Dryopithecus* is thus redefined, it falls between *Proconsul* and *Sivapithecus* along a hominoid morphocline. It is still unclear where *Dryopithecus* falls with respect to the hominine-pongine divergence, but neither Andrews nor I think it shares derived features with members of either extant lineage. We further agree that Schwartz's arguments, while provocative, are not yet sufficient to rebut the bulk of the molecular evidence for a *Homo-Pan* clade.

I disagree with Andrews, however, on the relative placement of *Dryopithecus* and *Kenyapithecus*. He argues that the latter taxon shares more derived conditions with the modern hominid clades than does the former. In fact, his article lists four synapomorphies linking these fossils and younger hominids and five features with respect to which the two fossils differ. Of these five, *Dryopithecus* shares three with hominids: an enlarged maxillary sinus, spatulate I<sup>2</sup>, and keeled humeral trochlea; *Kenyapithecus* presents the primitive hominoid condition for all of these. On the other hand, *Kenyapithecus* shares thick enamel with the pongines and *Australopithecus*, but more data on its formation rate is needed to understand its phyletic position; Martin (1983) has shown that thickness alone can be convergent and confusing. In addition, *Kenyapithecus* has mesiodistally elongated upper premolars, found in living hominids but no Miocene fossils. I tend to see both these characters as having low phyletic weight, because convergence is likely, and thus I consider Andrews' interpretation the weaker of the two alternatives, on available data. Analysis of the new specimens attributed to *Kenyapithecus* from Baragoi (Pickford, 1983) will be important in assessing the affinities of this group.

The original charge to the participants in this session was to concentrate on the content and relationships of the higher taxa of catarrhines (families and superfamilies). Further analysis of *Dendropithecus*, the Late Miocene Italian *Oreopithecus*, and other,

lesser-known taxa should lead to a reevaluation of the basal characters of the Cercopithecoidea and Hominoidea and, one hopes, greater understanding of their original divergence.

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# *Ancestors: The Hard Evidence*

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