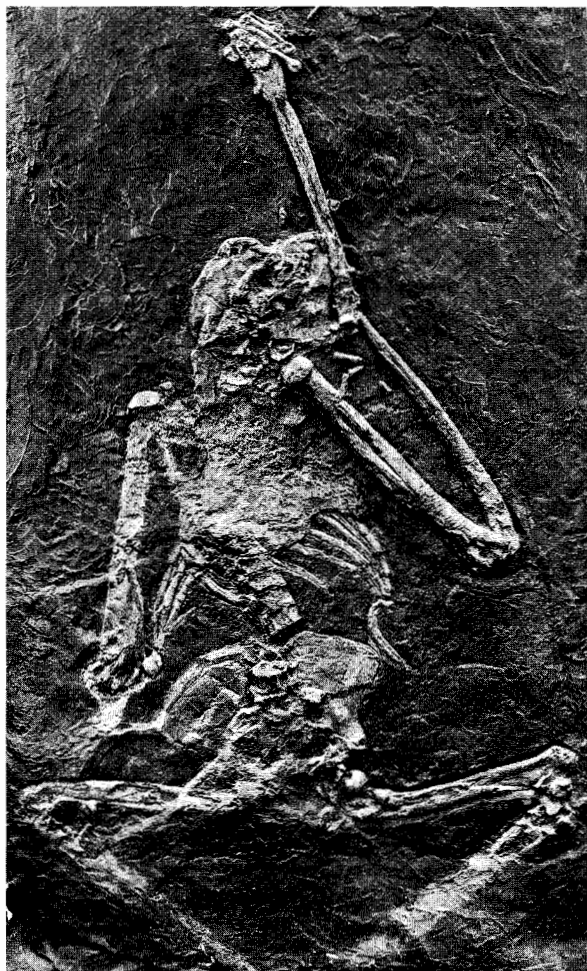


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## WITH THE COMPLIMENTS OF:

Eric Delson  
Department of Vertebrate Paleontology  
American Museum of Natural History  
New York, NY 10024



*Oreopithecus bambolii* skeleton (cast) as originally recovered in 1958.

### **Oreopithecus**

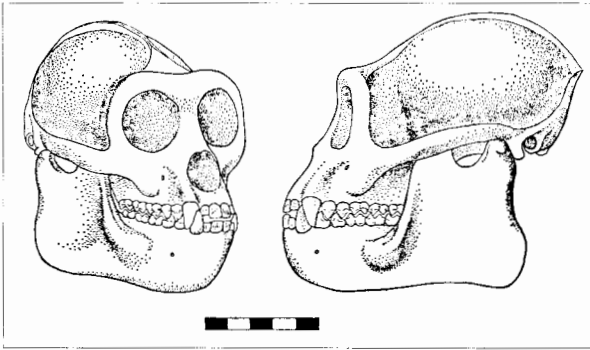
European Miocene catarrhines, now classified in the subfamily Oreopithecinae, family Hominidae. There has been some controversy as to whether *Oreopithecus* is more closely related to the living hominoids or to the Old World monkeys. The latter, minority opinion is no longer followed here.

*Oreopithecus bambolii* was first reported in 1872 on the basis of a juvenile mandible. The original describer, P. Gervais, considered that it was most similar dentally to the gorilla but that it also had features in common with cercopithecids. Over the next 70 years, a variety of authors offered their opinions, mostly based on incomplete studies of poor replicas (casts). Some argued that *O. bambolii* was a hominoid,

others that it was a cercopithecoid, still others that it was somehow intermediate between these major groups.

In 1915, G. Schwalbe placed *Oreopithecus* in its own family, which most authors continued to include in the Hominoidea. An additional dozen jaws and a few postcranial fragments were described from a cluster of five localities in the Tuscan region of North-Central Italy. The age of these fossils was also uncertain but generally estimated at ca. 12 Ma. In the 1990s more specimens have been recovered from a locality in Sardinia and from additional horizons in Tuscany; all are now dated close to 8–7 Ma.

In the late 1940s and through the 1950s, Swiss paleontologist<sup>†</sup> J. Hürzeler reawakened scientific and popular interest in *Oreopithecus* through his restudy of known specimens and collection of new fossils. He argued that *Oreopithecus* was a close human relative, if not an ancestor (at that time, *Australopithecus* was poorly known and thought by many European scholars to be a distinctive ape). Hürzeler thought that *Oreopithecus* had a small canine and tooth proportions most similar to those of *Homo erectus*. He recognized that in some ways (e.g., a large central cusp on lower molars) *O. bambolii* was unique, but for him the majority of observed features were shared with human ancestors as he interpreted them. In 1958, with the aid of local Tuscan miners, Hürzeler recovered a partial skeleton of a young adult male. It was



Reconstruction of the cranium of *Oreopithecus bambolii* in oblique and lateral views. After Szalay and Berzi, 1973.

badly flattened like most of the *Oreopithecus* fossils (which are found in a lignite, or soft brown coal, deposit laid down in a swampy forest). Hürzeler made a partial reconstruction of the skull, which indicated a large brain, supporting his view that *Oreopithecus* was a human forebear.

More recently, several researchers have studied parts of this skeleton, coming to quite different conclusions. The supposedly large brain has been shown to be based on the misinterpretation of large sagittal and nuchal crests as being the top of the skull and of crushed vertebrae as the rear; in fact, the brain is only about the size of that of monkeys of similar body weight. Male canines are quite large, and sexual dimorphism is high, as in most Miocene catarrhines. The gonial region of the mandible (where the corpus meets the ramus) is expanded, as in colobines and other leaf-eating mammals, and the molar teeth emphasize crests, for slicing leafy food items. The face is short and rather wide, admittedly as in humans, but also as in gibbons, colobines, and conservative catarrhines generally. Thus, almost all modern-day students think that *Oreopithecus* resembles humans only convergently, in a few characters, while they see closer phyletic links to either hominoids or cercopithecids.

A. Rosenberger and E. Delson have suggested that, in a number of dental features, *Oreopithecus* is intermediate in a homologous way between ancestral cercopithecids (e.g., victoriapithecines or the inferred common ancestor of all cercopithecids) and early catarrhines. For example, *O. bambolii* has elongate upper molars (while those of most hominoids are square or wide); reduced hypoconulids on  $dP_4-M_2$ ; reduced cingulum on upper and lower molars, with remnants in the same places as seen (further reduced) in cercopithecids; molar cusps placed in transverse pairs (protoconid opposite metaconid, paracone opposite protocone, etc.), rather than offset as in hominoids, and with some development of transverse creasting; increased relief of molar teeth (tall cusps and deep clefts); and a partial approach to the mirror-image pattern of occluding uppers and lowers seen in Old World monkeys. It is clear that *Oreopithecus* is not bilophodont, as are modern cercopithecids, but neither was the earliest ancestor of monkeys. What Rosenberger and Delson were suggesting was that a common ancestor of cercopithecids and oreopithecids had already experienced selection for a number of shared trends before the two groups diverged in different directions.



Occlusal views of *Oreopithecus bambolii* from Baccinello, Italy: left  $P_2-MP$  of subadult female (left), left  $P_3-M_3$  of male individual in other figures. Photographs of casts (for clarity of detail).

T. Harrison has suggested that two or three African Miocene species are related to *Oreopithecus*. *Nyanzapithecus* species are poorly known, but their teeth look quite similar to those of *O. bambolii* in form and elongation. *Rangwapithecus* also presents some dental features similar to *Oreopithecus*, especially molar elongation and slight creasting. If these forms were truly close to the ancestry of *Oreopithecus*, it would imply a long independent history for the genus back to the Early Miocene and possibly support a link to cercopithecids. Other workers, such as F.S. Szalay, have considered that the foot of *Oreopithecus* is uniquely evolved, sharing no derived features with either hominoids or cercopithecids.

But the majority of researchers today interpret *Oreopithecus* as a derived hominid, sharing most postcranial (and some cranial and dental) morphology with modern apes. Harrison has extended his research to review all known material of this genus, and, based mainly on his results, it appears that *Oreopithecus* shares 11 major, nearly independent complexes of the postcranium with the ancestral hominid morphotype. For example, the forelimb and hindlimb are adapted to different biological roles as evidenced by proportions; posture is relatively orthograde (upright); the joint complexes at shoulder, elbow, wrist, hip, and knee are similar

in detail to those of hominids; and the hand and foot are adapted to powerful grasping. Moreover, there are a large number of synapomorphies shared with living hominids but not seen in Kenyapithecinae. Among these are detailed similarities of the vertebrae, ulna, pelvis, and various foot bones. In the dentition, the mesiobuccal surface of  $P_3$  is short as in later hominids, rather than very long as in cercopithecids or intermediate as in early hominoids and eocatarrhines; the upper premolars are relatively large by comparison to the molars, intermediate between living hominids and other hominoids; and the upper molars are elongate as in cercopithecids and some modern hominids. In the skull, *Oreopithecus* lacks a subarcuate fossa on the temporal bone (a condition seen only in hominids, including *Dryopithecus*) and has nasopalatine and supraorbital torus constructions similar to those of gorillas (inferred as conservative for modern hominids).

Harrison thus joins such previous workers as W.L. Straus, Jr., and E. Sarmiento in considering that the above-noted dental features were evolved convergently by oreopithecids and cercopithecids, due to similar dietary adaptations. They argue that the detailed similarities in the shapes of the thorax (chest), and shoulder, elbow, and knee joints, must reflect a long period of shared ancestry between *Oreopithecus* and hominids (in our sense, not that of Hürzeler). It is difficult to argue that the shared postcranial features are all convergences due to similar locomotor adaptation, but, even if some of them are, it is more likely that the dental similarities to cercopithecids are also convergent.

Therefore, *Oreopithecus* is here included in the Hominoidea. But should it still be placed in its own family, or can it be ranked within the Hominidae, and, if so, where? The fossil hominid most similar to *Oreopithecus*, according to Harrison, is *Dryopithecus*, a slightly older and more widespread European form. The two taxa share a number of craniodental and postcranial features that link them to the modern hominids but place them as somewhat more conservative, perhaps near the common ancestry of Homininae and Ponginae. It is, in fact, possible that a species of *Dryopithecus* that became isolated in the Tusco-Sardinian geographical area might have been ancestral to *Oreopithecus*. One alternative might thus be to include the two genera in the same subfamily, which for reasons of priority would have to be termed Oreopithecinae. But, given the many unique features of *Oreopithecus*, it seems wiser at present to retain Oreopithecinae as a separate subfamily including only its type genus.

There is less argument about the paleobiology of *Oreopithecus*. The same features of the skeleton that indicate relationship to the hominids demonstrate that this animal had a longer forelimb than hindlimb; well-developed adaptations for raising the forelimb above the head, for a variety of movements at the elbow joint, and for flexibility of the wrist and mobility of the hindlimb; relatively erect posture during feeding and locomotion; and a flexible ankle with powerful grasping foot. Taken together, these functional interpretations allow reconstruction of *O. bambolii* as a powerful climber of vertical tree trunks and a suspensory arm swinger and arm hanger. There are similarities in this interpretation to both modern orangutans and chimpanzees, although not precisely to either ape.

The body weight of *Oreopithecus* was probably ca. 32 kg for a male, as estimated both by statistical analysis of weight-bearing joint surfaces (by W.L. Jungers) and by general comparisons of long-bone lengths (Szalay). This is nearly twice the weight estimated by several authors from anthropoid tooth size/body size ratios, implying that the dentition of *O. bambolii* was quite small for its probable body size. The dentition itself was apparently adapted to a folivorous diet, which fits well with the swampy forest habitat in which the species probably lived. Given seasonal variation in the availability of potential foods, perhaps aquatic plants or evergreen leaves were its staple diet.

See also Catarrhini; Cercopithecidae; Dryopithecinae; Dryopithecus; Europe; Hominidae; Hominoidea; Locomotion; Miocene; Skeleton; Teeth. [E.D.]

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