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Editor's Introduction

An Anthropoid Enigma: Historical Introduction to the Study of *Oreopithecus bambolii*

Oreopithecus bambolii, a Late Miocene catarrhine from northern Italy, has been the focus of controversy over its systematic relationships since its first report in 1872. A team of researchers has recently undertaken the re-analysis of much of the famous partial skeleton recovered in 1958, and their results are presented in this issue and a forthcoming one. This introductory paper seeks to review the history of study of the enigmatic *Oreopithecus*, in order to provide the background for current research and obviate the repetition of these points by the other authors in the team. Following early development of the alternatives that *O. bambolii* was either a distinctive hominoid or cercopithecoid (to use modern terminology) or in some way intermediate between these two groups, opinions polarized along these lines. In the 1950s, J. Hürzeler proposed a special relationship to *Homo*, but most later authors found this to be based either upon misinterpretations of damaged morphology or upon shared primitive retentions. Most authors in the 1960–1980 interval accepted *Oreopithecus* as a distinctive hominoid, but F. Szalay, E. Delson and A. Rosenberger (separately and jointly) proposed that it was best seen as the sister-taxon of the Cercopithecidae, based on shared-derived dental features. T. Harrison and E. Sarmiento, among others, have attempted to refute this idea based on interpretations of postcranial morphology shared with living hominoids. F. Szalay and J. Langdon find the foot to share derived features with neither group. The controversy continues, but the papers in this series provide a detailed data base for further analysis.

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Introduction

Of all the anthropoid primates, none has been so well-known but subject to such widespread differences of phylogenetic interpretation as *Oreopithecus bambolii*. Eight years ago, in large part due to discussions with Alfred Rosenberger, I suggested (Delson, 1979; Szalay & Delson, 1979) that *Oreopithecus* was in fact best considered a close relative of cercopithecids, rather than a distinctive hominoid as most workers saw it. As a result, I was invited by my friend and colleague Prof. Augusto Azzaroli, of the Institute of Geology in Florence, to undertake a serious first-hand study of the material in his care, rather than just pontificate from a literature review. Other researchers had requested permission to conduct such a study, but none had carried it out. I had briefly observed the partially prepared 1958 skeleton in Florence in 1969–70, but had never examined it in any detail, nor had I seen any specimens in Basel later that year.

In 1982, I visited Florence again and surveyed the *Oreopithecus* sample, borrowing a few specimens for preliminary study. In order to understand the enigmatic nature of this species, Azzaroli and I agreed that a team of specialists should be formed to study the various aspects of the available remains. Frederick Szalay, who had previously studied both cranial and postcranial elements of *O. bambolii*, would collaborate with me on a re-analysis of the skull, which we hoped to separate and reconstruct, and with John Langdon on a study of the foot, while Rosenberger and I would work on the teeth. In

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addition, I invited several colleagues from SUNY at Stony Brook to undertake analyses of the skeleton: William Jungers, Jack Stern and Randall Susman, who determined which portions of the 1958 skeleton would be most important. After permission had been obtained from the Superintendent of Antiquities of the province of Tuscany, a green suitcase containing most of the Florence collection arrived in New York late in the spring of 1983. I also asked Dr Johannes Hürzeler, who had done so much to collect and interpret *Oreopithecus*, for permission to examine specimens in his care. Since this was not possible, I then asked him to prepare a paper on his current views on *O. bambolii* and its palaeoenvironment, but he declined.

The fossils remained in New York until September 1984, thanks to a generous extension of their loan. They were made available to participants in the "Ancestors" workshop and other colleagues (especially Terry Harrison and Esteban Sarmiento), many of whom offered advice on the laborious task of dissociation and reconstruction of the 1958 cranium. This work was undertaken by Otto Simonis as one of his last major projects before he retired from the staff of the Department of Vertebrate Palaeontology, at the American Museum of Natural History. During this period, Frederick Grine and then Lawrence Martin joined the Stony Brook faculty and joined the team with responsibility for dental ultrastructure. For the 1985 meeting of the American Association of Physical Anthropologists, I organized a symposium on *Oreopithecus* at which each of us was to report on results (to date). As Harrison had by then joined the NYU faculty, he was also invited, especially to discuss the African ancestry of this taxon. Susman could not attend the symposium, but Mike Rose and Sarmiento graciously filled in on short notice with their interpretations of the wrist and other aspects of the skeleton. As expected, there was little agreement among us on the phyletic position of *Oreopithecus*, and we differed on estimation of body size and other features of its palaeobiology as well. Abstracts of these papers included: Azzaroli & Delson (1985); Delson & Szalay (1985); Grine *et al.* (1985); Harrison (1985, published 1986); Rosenberger & Delson (1985); Stern & Jungers (1985); Susman (1985); and Szalay & Langdon (1985).

It was agreed that papers would be prepared for submission as a journal special issue, and when I became Co-Editor of *JHE*, this was chosen as the best outlet (with Peter Andrews supervising the review process). Most of the team has been slow to complete manuscripts, and because Harrison wished to publish his African oreopithecids immediately, he was asked to take on the broader task of evaluating the entire known morphology of *Oreopithecus*. In order not to delay any further those papers which had completed the review process by early 1987, it was decided to publish two issues devoted to *O. bambolii*, rather than waiting to include all papers in one. The papers in these two issues will make available to interested colleagues the detailed morphology of *Oreopithecus*, although the lack of agreement among team members may increase the diversity of published phylogenetic opinion. In this brief introduction, I will review the history of previous interpretations so that they need not be repeated in other papers. It is not intended to be exhaustive, as papers from the last decade, especially, are assessed in more detail by the authors in this series, as well as by Sarmiento (1987). Moreover, part of this survey is complementary to that given by Hürzeler (1958, pp. 1–2).

The Original Alternatives: Ape or Monkey?

The first report of *O. bambolii* was published by Paul Gervais (1872*a*) who had the

opportunity to observe the juvenile holotype mandible in Florence during an Italian trip. Gervais later described the new primate in more detail with illustrations (1872*b*). He compared it to a variety of living catarrhines, suggesting greatest similarity to the gorilla, which he thought showed some convergence toward cercopithecids in the molar dentition. Gervais also noted that the molar cusps in *Oreopithecus* were distinct and aligned transversely, as in macaques, but ranked his new genus among the anthropomorphs (hominoids). Other authors at first followed Gervais, but then began to offer alternative views. Rütimeyer (1876) indicated a relationship to gibbons. Forsyth Major (1880) noted some resemblance to humans in the bicuspid P_3. But it was Schlosser (1887), in his far-reaching monograph on European Tertiary mammals, who set the tone for the next several decades: he considered *Oreopithecus* to be a distinctive form of cercopithecid, in some ways similar to *Theropithecus* or *Papio*.

Additional remains of *Oreopithecus bambolii* were reported over the next two decades. In 1890, Ristori described nearly a dozen specimens, mainly from Casteani but also from Monte Bamboli and Montemassi (although that from the last site was not illustrated). His specimens comprise the bulk of the dental sample available in Florence, although several pieces have since been damaged. Among the most complete is a laterally crushed male lower face with almost all the cheek teeth, not previously well illustrated. Ristori repeated most of Schlosser's arguments and then listed seven characters linking *Oreopithecus* to cercopithecids (his "lower apes") and nine indicating similarity to hominoids (his Table 1). In conclusion, Ristori said (1890, pp. 102–103): "From direct comparison of these characters and consideration of their relative importance, it seems reasonable to me, following in part the opinion of Schlosser, that *Oreopithecus* could be among the lower apes, but just after the anthropomorphs or at the end of these, because if on the one hand, we cannot discern in this fossil ape characters of inferiority, especially in the mandibular dentition, it cannot be denied that in the upper teeth and some bones [. . .], there exist numerous and important characters relating *Oreopithecus* to the higher apes [Hominoidea]. Following on, it is in my opinion more accurate to consider *Oreopithecus* the ancestor of anthropomorphs rather than, as Schlosser argued, that of the [papionins], especially *Theropithecus*. In this case, to retain Schlosser's opinion would imply in *Oreopithecus* the presence of organic regression . . . inconsistent with present theories of evolution." Harrison (1987) has wrongly reported that Ristori agreed with Schlosser in grouping *Oreopithecus* with cercopithecids.

Ottolenghi (1898) described a partial left corpus with cheek teeth from Montemassi, but had no opinion about its systematic position. Merciai (1907) reported a number of fossils from Ribolla, including one complete and three partial maxillae and a partial mandible. He claimed to be in agreement with Ristori in thinking *Oreopithecus* potentially ancestral to anthropomorphs, while he followed Schlosser in classifying it formally within the "Cynopithecidae". The most intriguing report was that by Laskarev (1909), who claimed to have recovered the taxon in ?Late Miocene deposits near Tiraspol, Moldavian SSR. [These remains were never illustrated, and both Hürzeler (1958) and I have attempted to track down the material to no avail. Lungu (1974) also included *Oreopithecus* in his faunal list for Kalfa (late Middle Miocene of the same region), but never responded to my letters of further inquiry.]

Finally, Schwalbe (1915*a*,*b*) compared *O. bambolii* in detail to a variety of other primates, coming eventually to the conclusion that it was by no means a cercopithecid but not a

typical hominoid (anthropomorph) either. In modern terms, he recognized three families within Hominoidea (not including humans): "real anthropoids" (= Pongidae): living great apes, *Dryopithecus* and *Sivapithecus* (his *Palaeopithecus*]; Hylobatidae (including *Pliopithecus*); and Oreopithecidae (p. 219). Diagnostic characters of *Oreopithecus* for Schwalbe included: small canines, lack of diastema and "primitive condition" of the P_3.

The main alternative views early in this century were thus: (1) that *Oreopithecus* was a cercopithecoid relative, on the basis of its transversely aligned lower molar cusps; (2) that it was a distinctive ape (hominoid), perhaps belonging to its own family; or (3) somehow transitional from monkeys or primitive catarrhines toward hominoids (the latter two views were less clearly defined at the time). It was generally thought that while the lower molars were cercopithecid-like, the uppers were not, being more similar to hominoids (it must be recalled that hominoid teeth were then considered more "advanced" than those of Old World monkeys: cf. Straus, 1949; Delson, 1975). Little more of note was written about *Oreopithecus* for several decades. It was mentioned in numerous texts, but rarely detailed. Gregory (1920) placed it in Cercopithecidae on the basis of strong differences from the "anthropoids" (Hominoidea) in such features as the premetacone crest meeting the crista obliqua, combined with primitively cercopithecid-like paired cusps and elongate molars. He noted a possible resemblance to *Apidium* (later restated by Simons, 1960) in the lower molar elongation, greater length of M_3 than M_2 and presence of a centroconid. Simpson (1945, p. 187) included both taxa in Cercopithecidae (subfamily uncertain), writing: "*Oreopithecus* is certainly a cercopithecoid primate, but with certain peculiarities that make its position uncertain. It has been placed in a family by itself, which seems an undue distinction, and also in a separate subfamily of Cercopithecidae".

Hürzeler's Revision of the Argument

The revival of interest in this genus is clearly due to the interest and efforts of Johannes Hürzeler. In a series of papers, Hürzeler first (1949) described, illustrated and listed the known Florence (and a few Basel) specimens. He concluded that *Oreopithecus* could not be a cercopithecoid or a transitional form to anthropomorphs, in large part because it possessed a true (cingulum-derived) hypocone on the upper molars and this cusp's homology in cercopithecids was uncertain. In effect, he suggested an ancient common ancestry for the catarrhines, almost questioning their monophyly. In 1952, he reiterated the possibility that the hypocone of cercopithecids was quite possibly not homologous with that of apes, arguing that if this view were substantiated, it might be difficult to assume that their common ancestor was even a primate. The main purpose of the paper was to study the newly rediscovered (and since re-lost!) dP_4 of the holotype mandible, which had been removed by Gervais. Hürzeler compared it with numerous other modern and Late Cenozoic catarrhine dP_4s, concluding that it was most similar to those of anthropomorphs. As a final point, he noted that the P_3 of *O. bambolii* presented two well-defined cusps as in *Homo*, a feature not emphasized or well-illustrated in 1949.

Two years later, Hürzeler (1954) broadened his approach and reviewed the dental proportions of *Oreopithecus* and other taxa. This review led Hürzeler to place *Oreopithecus* within the "prehominines", alongside the australopithecines because of its combination of small female upper canine, bicuspid and relatively short P_3, P_4 slightly longer (rather than much shorter) than P_3, and to some degree the relative molar lengths. In 1955, he spoke

about *Oreopithecus* at a symposium on vertebrate evolution and concluded (Hürzeler, 1956) that *O. bambolii* was an early member of Hominidae because it shared what he effectively considered were derived characters with later hominids, and that the hominid–pongid split must have occurred at least by the early Miocene because of the presence then of a true pongid, *Proconsul*.

These reports led to great interest and some confusion among both paleontologists and the public. For example, Viret (1955, p. 320) wrote that the 1954 paper had "the effect of a bomb" on the scientific community, and agreed readily with the conclusions of his Swiss colleague. On the other hand, von Koenigswald (1955), working from studies of modern and fossil *Homo*, agreed with Hürzeler only as far as placing *Oreopithecus* in the Hominoidea. He noted that by the time of the Italian fossil, true cercopithecids (*Mesopithecus*) and pongids (*Dryopithecus*) were known in Europe, so that *Oreopithecus* could not have been a connecting link between these two groups. Nor was it a hominid ancestor, especially because it lacked such features as the *Dryopithecus* pattern of lower molars, large canines and P_3s and the diastema between them, all seen in Koenigswald's "Pithecanthropus". Thus, neither *Oreopithecus* nor the australopithecines were likely hominid ancestors. This view reminds one of Hrdlicka's (1935) study of the Siwalik primates, in which he argued that while *Ramapithecus* was surely not a hominid ancestor, it was closer to such an ancestor than were the australopithecines. Remane (1955) went even further afield, noting some similarities to platyrrhines, but concluding in essence that *Oreopithecus* was conservative in many features and not specially related to any living hominoid subgroup. Robinson (1956, footnote, p. 164) studied Hürzeler's material and noted a variety of similarities to cercopithecids. He concluded that "perhaps it can most easily be regarded as a late-surviving early cercopithecoid which had not acquired all the characters of this group".

Hürzeler's (1958) short monograph drew on and extended his previous work. He discussed several new specimens which he had gathered from a variety of museums or collected personally, especially from the Baccinello area. In addition to dental morphology and proportions, Hürzeler added analyses of the few postcranial fragments available to him. His conclusions were essentially expanded reiterations of his 1954 decision, that *Oreopithecus* was near the root stock of the Hominidae.

Butler & Mills (1959) described a juvenile maxilla of uncertain provenance and undertook a detailed analysis of its dental morphology and function. After comparison with a variety of catarrhines, they concluded that it was best left in its own family. It shared no important features with any of the modern families, although of them all, it was closest to the "primitive members" of Pongidae. They considered similarities to hominids in the anterior dentition to be the result of convergent facial shortening, while the cheek teeth resembled apes and did not support shared ancestry with hominids.

The 1958 Skeleton and Its Effect

Hürzeler submitted his 1958 paper in August 1957, and corrected proof in November. On 2 August 1958, workmen at the Baccinello lignite mine aided Hürzeler in recovering a slab and counter-slab containing a crushed skeleton of a subadult male *Oreopithecus bambolii*. This unique find led to a rash of new analyses, including our cooperative work. In one of the first descriptions of the new find, Hürzeler (1960) offered a preliminary reconstruction

of the skull, showing an orthognathous face, slightly projecting canines, a small gonial region and a large, rounded vault. The apparently elongate forelimbs suggested a "brachiate" adaptation which Hürzeler admitted as one of few non-hominid features, but which he suggested might be either a retention from a prehominid brachiating stage or the result of parallel development. He wrote a number of basically similar short papers through the early 1960s, culminating in his 1968 review, one of the last of his works to treat *Oreopithecus* directly. In that paper, Hürzeler discussed 18 characters linking *Oreopithecus* to hominids. Among these were the similarity of the rounded mandibular symphysis to that of the Mauer hominid as opposed to the more angled, sloping symphysis of, e.g., *Dryopithecus*; reduced canine sexual dimorphism compared to apes; short face; and aspects of the pelvis and vertebral canal. In conclusion, Hürzeler separated hominids from other anthropomorphs at the superfamily level, with his Hominoidea including Hominidae and a "family Heterohominidae" for *Oreopithecus*, *Australopithecus* and other taxa of uncertain placement.

Schultz (1960) examined the new find and provided a number of skeletal dimensions, estimating trunk length at *ca* 460 mm, based on similarity to male *Presbytis entellus* and *Pan troglodytes*, but suggested a body weight of *ca* 40 kg, much higher than either. Straus (1963) reported at length on aspects of the morphology of the 1958 skeleton, comparing it to cercopithecids and a variety of hominoids. He concluded that it was not a cercopithecid, sharing only conservative features with that group, nor was it a pongid. He preferred classifying it as a primitive member of Hominidae, but recognized the strong possibility that it should be placed in its own family among Hominoidea. Straus & Schön (1960) had also estimated the brain size from Hürzeler's reconstruction as between 276 and 529 cc. Simpson (1963) used *Oreopithecus* as a central example in his review of taxonomic principles and the terminology of classification for anthropologists. Based on Straus' work and his own study of *Oreopithecus* teeth, Simpson considered the fossil to represent a distinct family of Hominoidea, rather than either a cercopithecoid or a hominid. Knussmann (1967) studied several proximal ulnar fragments and again considered *Oreopithecus* to be a hominoid, probably representing a distinct family "between" Pongidae and Hominidae.

Research in the 1970s

After nearly a decade, the 1958 skeleton was returned to Italy, where it was prepared out of the lignite matrix and the separated bones displayed in Florence. Szalay & Berzi (1973) restudied the crushed cranium, recognizing that the large vault described by Hürzeler and Straus was in fact an artifact, resulting from the interpretation of cervical vertebrae and a sagittal crest as calvarial bone; they estimated brain size at about 200 cc. They also discussed the gonial region, showing that it was in fact enlarged, rather than small as claimed by Hürzeler, a point observed previously by Coon (1962). Szalay (1975) further described the astragalo-calcaneal joint in *Oreopithecus* as non-helical and thus similar to those of cercopithecine monkeys. Riesenfeld (1975) noted the high robusticity of the metatarsals, suggesting a terrestrial adaptation (or heritage). Then, especially as a result of suggestions by Rosenberger, Delson (1979; Szalay & Delson, 1979), reviewed casts and published analyses, arriving at the conclusion that *Oreopithecus* shared a number of derived dental (and some pedal) features with the cercopithecid morphotype. Thus, Oreopithecidae was included as a family of Cercopithecoidea, which led to the invitation to undertake original work, as discussed above.

Results of the Present Team Effort

In this issue are published three papers growing out of the new studies. Azzaroli *et al.* (1987) provide a summary of data on the fauna and age of the deposits yielding *O. bambolii* and a new model of Miocene Mediterranean paleogeography which is sure to engender further discussion. Based on a larger collaborative study by an Italian team, they suggest that a land connection was possible from North Africa to the Maremma region during the Tortonian (late Miocene, *ca* 11–9 Ma) as a result of tectonic folding and uplift, as well as one between the European continent and this isolated region. Mammals might have entered Maremma from the north and the south, but probably would not have passed through the region to the other side. Harrison (1987) has reviewed all aspects of the morphology of *Oreopithecus*, with emphasis on the postcranium. He argues that dental similarities between *Oreopithecus* and cercopithecids are probably the result of functional convergence, while the derived postcranial characters shared by *O. bambolii* and hominoids (living and extinct) are too numerous and detailed to be anything but homologies implying close relationship. Like numerous prior researchers, he places *Oreopithecus* in a distinct family of Hominoidea. The origins of this family can be traced to the East African middle Miocene taxa *Nyanzapithecus* and *Rangwapithecus*. Szalay & Langdon (1987) have concentrated on the pedal remains of *Oreopithecus*. They find the remains to be functionally quite similar to foot bones of chimpanzees, but consider this due to convergence, in light of distinctions in morphological detail. Phyletically, they interpret *Oreopithecus* to be neither specially close to cercopithecids (contra Szalay's previous work: 1975, Szalay & Delson, 1979) nor to living or most fossil hominoids. Although no precise classification is offered, they would derive *O. bambolii* from a form close to *Propliopithecus*, but do not see close links to any African Miocene taxa.

Four additional papers in progress will appear in a later issue of the *Journal of Human Evolution*. Delson & Szalay are describing the cranial remains of the 1958 skeleton and making a reconstruction. Rosenberger & Delson are presenting the details of their hypothesis that the dental similarities between *Oreopithecus* and the cercopithecid morphotype are in fact homologous synapomorphies, as well as providing illustrations of and metrical data on this insufficiently documented dentition. Grine, Martin & Kraus are describing the enamel thickness and prism patterns in *Oreopithecus* and their implications for its systematic position. Jungers is discussing body size estimates and limb proportions in *O. bambolii*.

This cooperative effort is by no means the last word on *Oreopithecus*. Sarmiento (1987) discusses a number of the same points raised by us, concluding that the Italian fossil was a close relative of the living large-bodied hominoids and in some ways a model for their common ancestor. Harrison is now beginning a study of Hürzeler's collection in Basel, which promises to provide still further insights into both the phyletic relationships and paleobiology of this still controversial taxon. Perhaps one of the strongest lessons that we can learn from *Oreopithecus bambolii* is not to jump too quickly to conclusions about the sequence of evolutionary transformations. While fossils may not allow us to read directly such sequences "from the rocks", they certainly demonstrate the diversity of the products of evolution and the variety of mosaic patterning of character states and complexes. The increasing dependence on molecular reconstructions of phylogeny must be tempered with the realization that no study of modern genetic material, no matter the precision or detail,

could ever reveal the existence of such distinctive catarrhines as *Parapithecus*, *Gigantopithecus* or *Oreopithecus bambolii*.

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