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The Phylogenetic Position of *Oreopithecus* and Its Significance in the Origin of the Hominoidea

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ABSTRACT

Since *Oreopithecus* was first described, its systematic position has been a subject of controversy. Despite the hominoid specializations in its postcrania, those classifications emphasizing the peculiarities in its dentition have arrived at numerous and varied interpretations. A review of the dental features of *Oreopithecus*, living catarrhines, and some known fossil catarrhines shows that those dental traits which may be used to classify *Oreopithecus* as either a hominoid, cercopithecoid, or early catarrhine exhibit a large degree of variability. Although only true hominoids exhibit the variability which encompasses all of the features of the *Oreopithecus* dentition, an early catarrhine or cercopithecoid could have possibly arrived at a similar dentition. The postcrania of *Oreopithecus*, however, shows conclusive evidence as to its hominoid affinities. As in hominoids, *Oreopithecus* exhibits the joint complex for forearm and shoulder

rotation, both parts of a forelimb specialization which allows hominoids to climb vertical supports of large diameters. The large number of anatomical elements incorporated into this specialization and the one-to-one correspondence of these elements in *Oreopithecus* and hominoids strongly argue for a uniquely shared evolutionary history. Furthermore, *Oreopithecus* shares a strikingly large number of traits with a hypothetical ancestor of the pongid-hominid lineage more than any other known fossil form. Nevertheless, the position of *Oreopithecus* within the hominoids is uncertain. Many of the traits it shares with hylobatids may be expected in an early forerunner of the pongid-hominid lineage. On the other hand, many of those traits it shares with pongids may be expected in a large hylobatid which, due to its size, emphasized slow climbing aspects of its locomotor behavior.

INTRODUCTION

Oreopithecus has been the focus of taxonomic discussion since the type specimen, a juvenile mandible, was first reported by Gervais (1872). Opinions as to its systematic position range from cercopithecoid (Schlosser, 1887; Gregory, 1922; Szalay and Delson, 1979; Rosenberger and Delson, 1985) to suid (Gregory, 1951). The beliefs of some contemporary paleontologists notwithstanding (Rosenberger and Delson, 1985; Szalay and Delson, 1979), Straus' (1963) and Schultz's (1960) analyses of the nearly complete skeleton have left no doubt that this form is a true hominoid.

However, controversy as to its hominoid status will always ensue due to its peculiar dentition. Although some paleontologists see the dentition as typically hominoid (Forsyth-Major, 1872, 1873; Hürzeler, 1949; Butler and Mills, 1959) others see it as indicative of cercopithecoid affinities (Gervais, 1872; Gregory, 1922; Szalay and Delson, 1979; Rosenberger and Delson, 1985). However, the cranial and postcranial remains are undoubtedly those of a hominoid (Delson and Andrews, 1975; Hürzeler, 1958; Schultz, 1960; Straus, 1963; Straus and Schön, 1960; Le Gros Clark, 1971; Sarmiento, 1983a, 1983b; Szalay and Langdon, 1985). Therefore, those paleontologists who emphasize the similarities in the dentition of *Oreopithecus* and cerco-

pithecoids as shared derived traits are faced with a dilemma. They must postulate that the traits shared by *Oreopithecus* and hominoids are parallelisms or the ancestral condition for catarrhines. Conversely, those paleontologists that interpret the similarities between *Oreopithecus* and hominoids as shared derived traits must explain similarities between the dentition of *Oreopithecus* and cercopithecoids as either parallelisms or remnants of the ancestral catarrhine condition. In light of the evolutionary principles of parsimony (Simpson, 1941, 1961), it is the object of this paper to examine which of the two alternative explanations, if either, is the most reasonable, and to arrive at a convincing systematic and taxonomic position for *Oreopithecus*.

MATERIALS AND METHODS

The complete collection of the original specimens of *Oreopithecus* housed in the Istituto di Geologia, University of Florence was studied. This collection includes the nearly complete 1958 skeleton of *Oreopithecus* uncovered by Hürzeler and the type specimen a juvenile mandible described by Gervais (1872). In addition, casts of specimens collected by Hürzeler and housed at the Museum of Natural History Basle were also

studied. Table 1 provides the catalog number and a brief description of the individual *Oreopithecus* specimens considered.

Estimates on the variability of specific traits in *Oreopithecus*, hominoids, and cercopithecoids are based on my observations of 604 catarrhine skeletal specimens and dissections on 71 individual cadavers (Sarmiento, 1985). To gain additional information on the variability and polarity of anthropoid dental traits, over 540 dentitions, including those of fossil forms presumed to be early anthropoids, hominoids, and cercopithecoids were also examined. Whenever possible the holotype or original fossil specimens were studied. Table 2 is a list of the dental traits considered and their presence in each primate genus. Figure 1 presents some possible systematic interpretations of *Oreopithecus* when only dental traits are considered. Although the author recognizes variation within species of a single primate genus and also the possibility that more than one species may be represented by the *Oreopithecus* material, this study focuses on generic differences. Overall, the genus is the taxonomic unit which best reflects the range of morphological characteristics common to a group (Simpson, 1941, 1961). Therefore, when constructing phylogenies it provides clear-cut, tangible evidence as to the similarities and differences, and hence the degree of relatedness of taxa.

Because classifications based on the adaptive specializations of the taxonomic group in question are both more accurate and biologically relevant than those which are based solely on the empirical description of morphological characters (see Simpson, 1961), this study emphasizes the adaptive specializations which distinguish hominoids from cercopithecoids. In this regard, a review of the central specializations of hominoids seemed appropriate and is included in this study.

ACKNOWLEDGMENTS

I would like to thank J. G. Fleagle and H. Covert for discussion and comments on the manuscript and E. Delson for discussion of *Oreopithecus* dental traits. I am especially indebted to M. D. Rose for engaging with me in long and detailed discussions of modern

TABLE 1
Oreopithecus Material Considered in This Study

Museum number	Brief description
<i>Instituto di Geologia Firenze</i>	
4330	Right i1-c1
4331	Right m3, left p3-i2, m3
4332	Palate complete
4333	Upper dentition, complete except for incisors
4334	Left p3-p4
4335 (holo-type)	Lower dentition complete
4350	Right p3-m3
4580	Right and left m3
4581	I1
10882	M3
10885	Palate, right P4-M3, left M3, P3-4
10886	Left C1-M2, right I1, P3
10890	Left p4-m1, right c1-2
11778	1958 skeleton, upper and lower dentition, nearly complete skeletal remains
4336	Right proximal ulnar fragment
4336	Proximal radius
<i>Museum of Natural History, Basel</i>	
32	Right second upper molar
51, 84	Right distal humeri
51	Right proximal radius
51	Right ulna
50, 35	Sacrum
49	Right proximal femur and innominate
66	Distal femur
37, 92	Calcaneus
37	Incomplete talus
?37	Talus
?37	Cuboid
?37	Navicular
?37	Entocuneiform
?37	Ectocuneiform
?37	Mesocuneiform
?37	1, 2, 4, 5 metatarsals
?37	First phalanx
34	Crushed hand skeleton, all rays present
<i>British Museum</i>	
11555	Left C1-M3, right C1-M3

hominoid adaptations, functional anatomy, and behavior. These discussions were crucial in forming a foundation for this manuscript. Foremost I would like to thank Johannes Hürzeler for his unflagging devotion in bringing *Oreopithecus* to the attention of

TABLE 2
Some Distinguishing Characters of Catarrhine Dentition and Their Distribution

	a	b	c	d	e	f	g	h	i	j	k	l	m	n	o
<i>Oligopithecus</i> (1c)		X	X		X									?	
<i>Apidium</i> (5)			X	X	?	X		X	X	U	var.			X	UL
<i>Parapithecus</i> (3c)			X	?	var.			X	var.	U	UL			X	UL
<i>Propithecus</i> (2c)	X		X	X				X		U	UL	X			U
<i>Aegyptopithecus</i> (3)	X		X	X				X	X	U	UL	X			U
<i>Limnopithecus</i> (2c)	X		X	X				X		U	L	X			L
<i>Dendropithecus</i> (1c)	X		X	X						U	UL	X		X	
<i>Proconsul</i> (5c)	X		X	X				X		U	L	X	var.		L
<i>Pliopithecus</i> (3)	X		X	X			m3?		X	U	L	X			L
<i>Victoriapithecus</i> (2c)	X?		m2?	X						var.		var.		X	
<i>Prohylobates</i> (2c)	?		m2?	X											
<i>Dryopithecus</i> (2c)	X		X	X							L				UL
<i>Oreopithecus</i> (14)	X		X	X	X	X	X	X	X	U	L	X	X		U
<i>Sivapithecus</i> (3)	X		X	X			X			X	X	X	var.		U
<i>Ramapithecus</i> (3)	X		X	X			X					X			UL
<i>Gigantopithecus</i> (2)	X		X	X		var.	X					X			X
<i>Australopithecus</i> (8)	X		X	X		var.	X					X			X
<i>Homo</i> (115)	X		100	78			X			var.	var.	X	var.		L
<i>Gorilla</i> (45)	X		X	X			X					X			X
<i>Pan</i> (60)	X		X	X			5					X			X
<i>Pongo</i> (35)	X		33	X			X					X	5		X
<i>Hylobates</i> (82)	X		76	68						X	X	X	12		X
<i>Colobus</i> (12)	X			X										X	U
<i>Pygathrix</i> (15)	var.			X										X	U
<i>Nasalis</i> (15)	X			X										X	U
<i>Presbytis</i> (22)	X			var.										X	U
<i>Cercopithecus</i> (15)	X			var.										X	U
<i>Theropithecus</i> (4)	X			X			m3?							X	U
<i>Papio</i> (28)	X			X			m3?							X	U
<i>Cercocebus</i> (15)	X			X										X	X
<i>Macaca</i> (25)	X			X										X	X

Key to symbols

- | | |
|--|--|
| a. 2123 dental formula | s. dendritic patterning or enamel wrinkling on molars |
| b. trigonid separate and/or projected above talonid | t. molar waisting |
| c. hypoconulid on m1-m2 | u. molars with lingual cusps displaced distally in respect to buccal cusps |
| d. hypoconulid on m3 | v. elongated m3 so that in mesiodistal length $m1 < m2 < m3$ |
| e. paraconid | w. mesiodistally compressed upper molars |
| f. centroconid (mesoconid) | x. incisor cingulum developed into internal cusps |
| g. development of sixth cusp on lower molars (tuberculum sextum) | y. mesiolingual groove on canine extending onto root |
| h. paraconule | z. crushing surface on p3 |
| i. metaconule | uu. single rooted p3 |
| j. lingual cingulum on molars | vv. single rooted p4 |
| k. buccal cingulum on molars | ww. bicuspid p3 |
| l. crista obliqua, crest from protocone to metaconule | xx. sectorial p3 with long axis mesiodistally directed |
| m. crest from hypocone to metaconule | yy. mesiodistally short c1 and p3 |
| n. transverse cresting or lophodonty | zz. absence of diastema |
| o. mesial (anterior) fovea on molars | yyy. nonsectorial p3 |
| p. distal fovea on molars | zzz. p3 with long axis oblique to dental row |
| q. bunodont molars | |
| r. high crowned molars | |

A cross (X) marks the presence of a specified trait. In cases of variability the number of individuals examined possessing the trait is provided. In cases where such variation seems to be related to species or subspecies differences the abbreviation var. appears for the specified trait. U and L denote a trait which is restricted to the upper or lower dentition, respectively. A question mark (?) appears for those traits which are uncertain due to their incomplete development or remains. Traits which are restricted to a single tooth are so specified by the conventional tooth symbol. Traits restricted to females of a specific genus are denoted by the symbol ♀. The numbers of individuals examined appear in parentheses next to their respective genus. The letter c next to this number denotes specimens studied from casts.

TABLE 2
Continued

p	q	r	s	t	u	v	w	x	y	z	uu	vv	ww	xx	yy	zz	yyy	zzz
				?										X				
U	X			X		X	X							X				
				X		var.	X							X				
L	X					X	X											X
L	X	X			U	X	X											
						X												
						X	X											X
L	X					X	X	X										X
L	X					X	X	X										X
		X		L	U	X	X		X									?
		X		L														?
	X				X	X												X
X	X	X?	?	L?	X	X	X	var.		X			X		X	var.	var.	X
X	X		X		X					X			X			var.		X
L	X		X		X					X			X			X	var.	X
X	X	X?	X		X	X				X	X	?	X		X	X	?	X
X	X		X		X					X	var.	var.	X		X	X	var.	X
	X		var.		X					X	X	X	X		X	X	X	X
X		X?	11	L?	X	30		5		7♀	3	1	4♀			5♀	8	X
L	X		38		X					X	32	22	X			10	12	X
X	X		X		X					X	1		15			3	5	X
L	X				X			var.		X				X				
		X		X		X			X					X	♀			
L	X			X		X			X					X	X			
L		X		X		X			X					X	♀			
L		X		X		X			X					X				
X		X		X		X			X					X				
X		X		X		X			X					X				
L	X	X		X		X			X					X				
X	var.	X		X		X			X					X				

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human collections in the Department of Anthropology at the AMNH. Finally, I would like to thank Guy Musser and the staff in the Department of Mammalogy at the AMNH for access to the collections and use of the facilities. This work was begun in 1979 and supported in part by a grant from F.R.O.M.

DENTAL EVIDENCE

CHARACTERS COMMON TO *OREOPITHECUS* AND EARLY CATARRHINES

The dentition of *Oreopithecus* has a number of characters which it shares with living hominoids and which distinguish it from

modern cercopithecoids. For example, as in hominoids, *Oreopithecus* has (1) cingula on the upper and lower molars, (2) lingual cusps on the upper and lower molars that are shifted distally in respect to the buccal cusps, (3) M1-3 with crista obliquas, and (4) hypoconulids (albeit reduced in size) on the m1 and m2. Moreover, *Oreopithecus* lacks the modern cercopithecoid bilophodonty and the full development of those traits associated with it.

However, as summarized in table 2, these characters and the absence of a fully developed cercopithecoid bilophodonty are not necessarily diagnostic of hominoid affinities. The earliest fossil catarrhines known, i.e., *Propliopithecus*, *Pliopithecus*, *Limnopithecus*, and *Aegyptopithecus* which cannot be classified realistically as either hominoids or cercopithecoids have these same hominoid dental characters (Szalay and Delson, 1979; Kay et al., 1981). A possible early hominoid *Proconsul africanus*² and the earliest recognizable cercopithecoids *Victoriapithecus* and *Prohylobates* also show many of these dental characters (von Koenigswald, 1969; Szalay and Delson, 1979; Andrews, 1978; Leakey, 1985). As is indicated by all these fossil forms and the comparative dental anatomy of living catarrhines, the bilophodont dentition characteristic of cercopithecoids was derived from a hominoidlike molar cusp pattern (Gregory, 1922; von Koenigswald, 1969; Delson, 1973; Szalay and Delson, 1979). Therefore, the presence of hominoidlike dental characters in *Oreopithecus* does not negate the possibility that this fossil is an early catarrhine with neither hominoid nor cercopithecoid affinities, or a cercopithecoid which

had not developed the bilophodonty characteristic of the living members of the group.

CHARACTERS COMMON TO *OREOPITHECUS* AND CERCOPITHECOIDS

Oreopithecus is reputed to show a number of dental features that arguably are modified in the direction of cercopithecoids (Szalay and Delson, 1979; Rosenberger and Delson, 1985; Simons, 1972). Chief among these are: (1) the reduction or the occasional near absence of hypoconulids on (lower) m1 and m2 associated with a large talonid basin, (2) waisted lower molars (the trigonid is pinched off from the talonid and the transversely opposing cusps are nearly aligned), and (3) incipient transverse cresting between distal cusps of the lower molars. As a whole these characters lend a bilophodont appearance to the lower molars. This "pseudobilophodonty," which is augmented by wear (Hürzeler, 1958), is unlike that of modern cercopithecoids. In contrast to the cercopithecoid bilophodont dentition, *Oreopithecus* lacks the true transverse cresting between opposing cusps of both lower and upper molars (Hürzeler, 1958). Moreover, the upper molars are not waisted and are typically hominoid in appearance (Hürzeler, 1958; Butler and Mills, 1959; Straus, 1963). Further distinguishing it from all recognized cercopithecoids, *Oreopithecus* lacks a continuous longitudinal groove on the mesiolingual border of the upper canine projecting onto the root and its p3 may variably possess a lingual cusp (Hürzeler, 1958; Delson and Andrews, 1975).

If *Oreopithecus* is to be considered a cercopithecoid on the basis of its dentition, this fossil must be interpreted as a very early member of this superfamily, a "eucercopithecoid." A form which diverged early from the common cercopithecoid stock would not show the full suite of cercopithecoidlike adaptations in the dentition. Notably, *Oreopithecus* shows a trend in the development of bilophodonty along a similar direction as that shown by the earliest recognized cercopithecoids (*Victoriapithecus* and *Prohylobates*). For example, *Victoriapithecus* shows reduction and/or variable loss of the hypoconulid on m1 and m2, waisted lower molars, the beginning of transverse cresting between op-

² The incomplete development of the characteristically hominoid features of the forelimb related with pronation and supination of the forearm and rotation of the shoulder in KNMR 2036, suggests that this fossil protohominoid has not yet reached that stage of development common to the living hominoids (see p. 17). Nevertheless, it is clear that in the development of those structures related to forearm and shoulder rotation, *Proconsul africanus* approximates the living hominoids. In this regard, this form provides a glimpse into an initial stage in the evolutionary development of the unique hominoid forelimb and hence the initial specializations of the hominoid lineage.

posing cusps on the lower molars, and hominoidlike upper molars variably possessing a crista obliqua (von Koenigswald, 1969; Leakey, 1985). The more fragmentary remains of *Prohylobates* seem to reflect a similar pattern (Simons, 1969; Szalay and Delson, 1979; Leakey, 1985). These facts may be construed to support the hypothesis that *Oreopithecus* represents an early member of the Cercopithecoidea.

But in showing a + molar cusp pattern, and the usual absence of the crista obliqua and molar cingulum (von Koenigswald, 1969; Leakey, 1985), *Victoriapithecus* approximates modern cercopithecoids more closely than *Oreopithecus*. In this regard, *Oreopithecus* would have to be interpreted as representing an even earlier offshoot of the Cercopithecoidea than either *Victoriapithecus* or *Prohylobates*. Additionally, as evidenced by the longitudinal mesiolingual groove on the upper canines, *Victoriapithecus*, unlike *Oreopithecus*, shows the development of the honing complex characteristic of modern cercopithecoids (von Koenigswald, 1969). Therefore, classifying *Oreopithecus* as a cercopithecoid also implies that (1) the very early stages of cercopithecoid bilophodonty must have preceded the appearance of a honing complex and (2) *Oreopithecus* diverged from the common cercopithecoid stock before the honing complex had evolved. Otherwise, the more unlikely supposition that *Oreopithecus* must have evolved the honing complex and then lost the complex in favor of the hominoid type bicuspid p3 must be posited. In this regard, even the females of the extremely short-faced species *Pygathrix* (*Rhinopithecus*) *roxellanae*, despite their small canine size, diminutive diastema, and relatively mesiodistally shortened premolars (fig. 2), have retained a single cuspid p3 and the mesiolingual groove on the upper canine,³ both central

characters of the cercopithecoid honing complex.

However, when the variability and distribution of those traits which can be used to place *Oreopithecus* in the Cercopithecoidea are examined their taxonomic validity enters into question, and such scenarios as hypothesized above are not necessary. First of all, it is debatable whether *Oreopithecus* has lost the hypoconulid on m1 and m2. More conservative paleontologists would rather state that it is reduced in size, but not altogether lost (Le Gros Clark, 1971; Schwalbe, 1915; Hürzeler, 1958; Delson and Andrews, 1975; Simons, 1960, 1972; this study). In this regard, diminutive hypoconulids are also features of the molars of orangutans, humans, and some of the late Miocene apes from the Siwaliks and Europe (Gregory, 1922; Gregory and Hellman, 1926; Gregory et al., 1938). The reduction of the hypoconulid in *Oreopithecus* is not a good indicator of cercopithecoid affinities. It is of note that one paleontologist (Simons, 1972) has interpreted the hypoconulid of *Oreopithecus* as indicative of hominoid affinities.

Even if *Oreopithecus* has undisputedly lost the hypoconulid, it would not give this character more weight when distinguishing cercopithecoids from hominoids. In most human populations, the hypoconulid is more often absent than present on the m2 and m3 (Gregory, 1922; Hellman, 1928; Cadien, 1972), and is also occasionally absent on m1 (Cadien, 1972, fig. 3). In hylobatids absence of the hypoconulid on m1-m3 occurs as a matter of variation (Frisch, 1965, 1973). Furthermore, within cercopithecoids themselves there is decided lability in the presence or absence of a hypoconulid. Although colobines generally possess the hypoconulid on m3, its absence is not rare in *Presbytis* and may actually be the rule in some species (i.e.,

³ The development of the mesiolingual groove on the root of the canine of cercopithecoids cannot be related directly or solely to canine honing. Specifically in the females of some species (i.e., *Pygathrix*, *Simia*), the groove is restricted to the root of the tooth. Moreover, in all cercopithecoids, the groove is associated with the shape of the nasal aperture and of the lateral wall of the nasal cavity. Therefore, the canine groove may also be related

with the varied functions of nasal cavity morphology. However, more than likely, in view of the wide mesiodistal diameter of the canine in cercopithecoids, this groove serves to further strengthen the canine against mesiodistal and buccolingual bending moments, and rotational forces. In turn, these bending moments can be associated with the cercopithecoid honing complex, but also must be related to other dental functions.

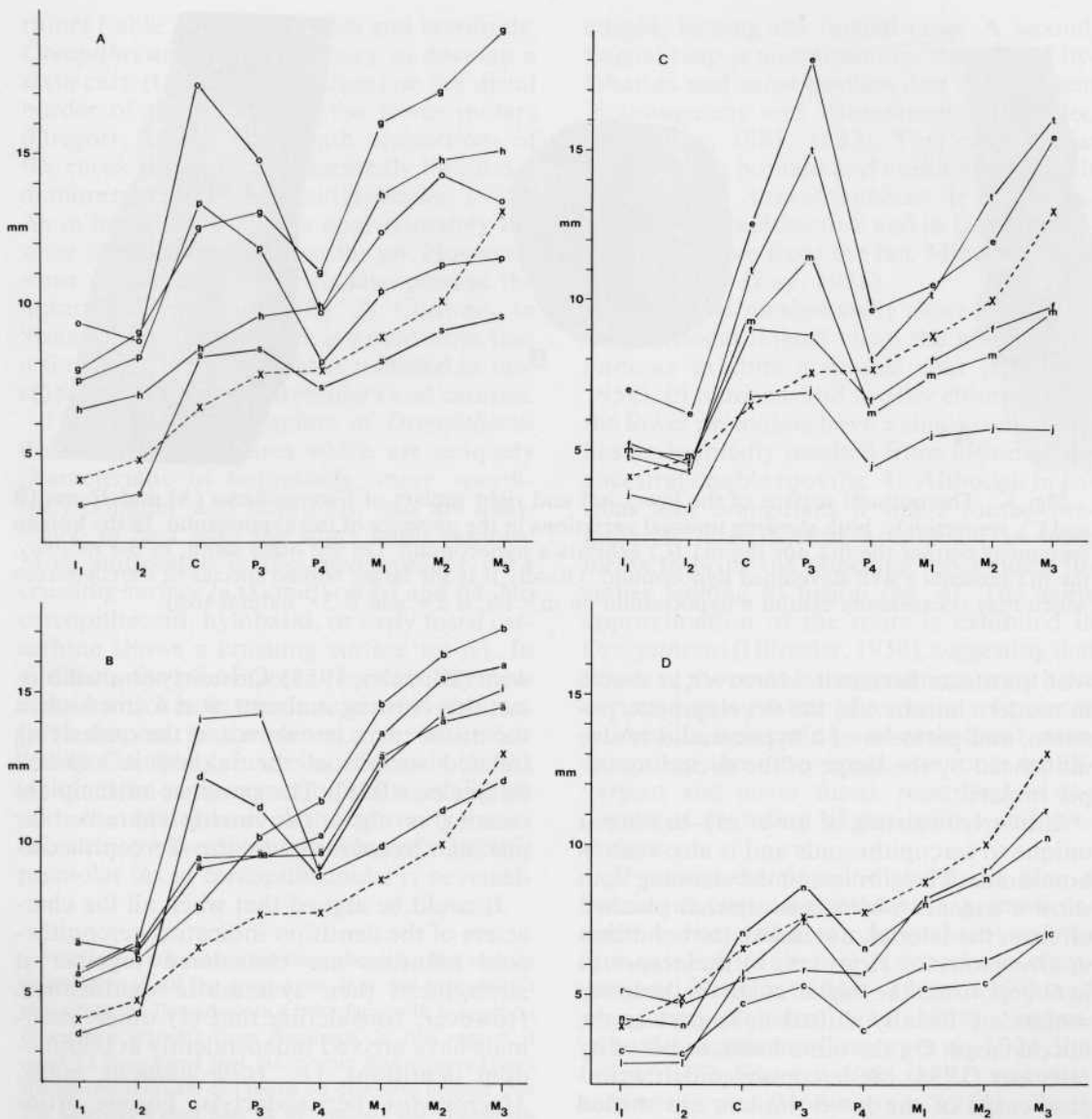


Fig. 2. Mesiodistal length of the lower dentition of *Oreopithecus* compared to (A) living hominoids, (B) fossil apes, (C) cercopithecines, and (D) colobines. Measurements for *Oreopithecus* and *Dryopithecus* are after Hürzeler (1968), *Sivapithecus* after Kay (1982), and australopithecines after White et al. (1981). Abbreviations: *Oreopithecus* (X), *Homo sapiens* (h), *Gorilla* (g), *Pan* (p), *Pongo* (o), *Symphalangus* (s), *Dryopithecus fontani* (d), *Australopithecus robustus* (b), *A. afarensis* (a), *A. africanus* (ä), *Sivapithecus indicus* (i), *Macaca* (m), *Cercocebus* (f), *Papio* (e), *Theropithecus* (t), *Cercopithecus* (j), *Presbytis* (l), *Pygathrix* (*Rhinopithecus*) *roxellanae* (r), *Nasalis* (n), *Colobus* (c).

P. potenziani). On the other hand, the absence of a hypoconulid on m3 is the rule for *Cercopithecus* (Jolly, 1964). However, this cusp is occasionally found among these forms,

notably among the larger body-size species (fig. 3). As noted by Gregory (1922), the loss of a hypoconulid is influenced greatly by the shape of the molar and its contact surface

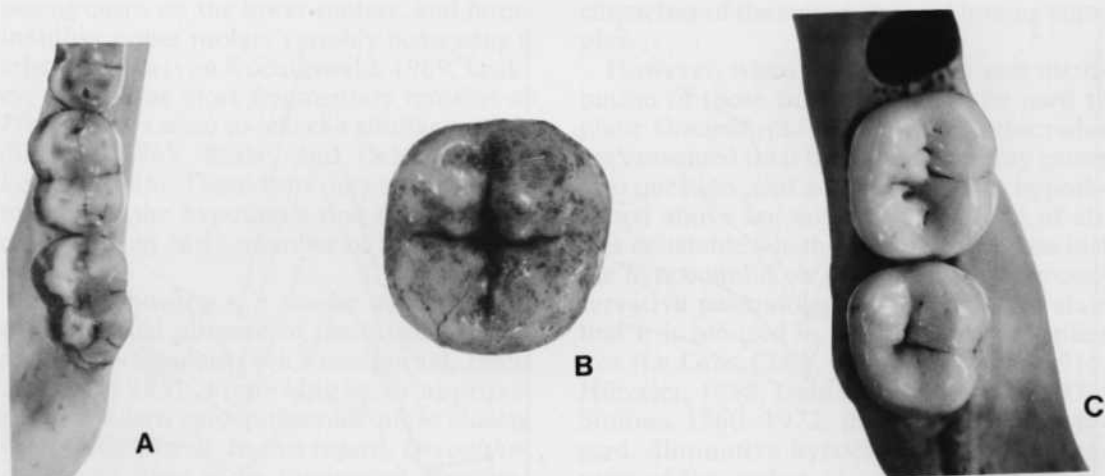


Fig. 3. The occlusal surface of the lower left and right molars of *Cercopithecus* (A) and *Homo* (B and C), respectively, both showing unusual variations in the presence of the hypoconulid. In the human specimens neither the m2 nor the m1 (C) exhibits a hypoconulid. On the other hand, in the monkey, the m3 presents a well-developed hypoconulid. Usually it is the larger bodied species of *Cercopithecus* which may occasionally exhibit a hypoconulid on m3. (A, C 2× and B 3× natural size).

with the molar distal to it. Moreover, as shown in modern hominoids, the development, position, and presence of a hypoconulid is also influenced by the shape of the occluding upper molars.

Similarly, waisting of lower m1-m3 is not unique to cercopithecoids and is also seen in hominoids. The gorilla and the siamang both show a trigonid which is somewhat pinched off from the talonid, not unlike the condition in *Oreopithecus*. However, in these apes as in *Oreopithecus* the lingual cusps on the lower molars are distally shifted in respect to the buccal cusps. On the other hand, as noted by Hürzeler (1958), in cercopithecoids the lingual cusps of the lower molars are shifted mesially in respect to the buccal cusps. Despite incipient molar waisting, *Oreopithecus* has kept the relative cusp position seen in hominoids. Nevertheless, lower molar waisting has been developed independently in platyrrhines (i.e., *Cebus*, *Lagothrix*, etc.) and early primates such as *Apidium*. Like the presence or absence of a hypoconulid, this character alone is too labile to use as an indicator of cercopithecoid affinities.

Finally, the transverse crestring which occurs across the distal cusps of *Oreopithecus* duplicating an important character of cercopithecoid bilophodonty is an artifact of

wear (Hürzeler, 1958). On newly erupted molars this crestring is absent. It is formed when the distal cusps are worn and the underlying inflated surface of the talonid is exposed (Hürzeler, 1958). The presence of incipient crestring is not a convincing character for placing *Oreopithecus* in the Cercopithecoidea.

It could be argued that when all the characters of the dentition indicating cercopithecoid affinities are considered together it strengthens their systematic significance. However, considering that (1) other mammals have arrived independently at bilophodont dentitions, i.e., *Hadropithecus*, suids, *Macropodus*, perissodactyls, Eocene artiodactyls, etc. (see Gregory, 1922, 1951; Hürzeler, 1958, 1968; von Koenigswald, 1969) and (2) the living hominoids may exhibit all those characters present in *Oreopithecus* which arguably reflect the early phylogenetic stages of bilophodonty, a classification based on these characters is at best tentative.

CHARACTERS IN *Oreopithecus* UNIQUE TO HOMINIDS

Oreopithecus also exhibits a number of dental traits which it shares with modern hominoids, not present in early fossil catar-

rhines (table 2). As in pongids and hominids, *Oreopithecus* has the tendency to develop a sixth cusp (tuberculum sextum) on the distal border of the talonid of the lower molars (Gregory, 1922). The length proportions of the cheek teeth are also decidedly hominoid or more specifically hominid (Hürzeler, 1958). As in hominids the p3 is approximately the same mesiodistal length as the p4. However, some cercopithecoid forms also possess the hominoid proportions (fig. 2). Contrary to Straus' (1963) conclusion, it would seem that a short face in some cases is reflected in mesiodistally shortened premolars and canines.

However, the premolars of *Oreopithecus* do show some features which are uniquely characteristic of hominoids, more specifically pongids⁴ and hominids, and are associated in part with the short blunt canines. Most noticeable is the development of a crushing surface (a talonid) on p3 and p4. No cercopithecoid, hylobatid, or early fossil catarrhine shows a crushing surface on p3. In addition, the p3 of *Oreopithecus* is often bicuspid with a base which is oriented obliquely in respect to the dental row (Hürzeler, 1958). Generally, in cercopithecoids the p3 is unicuspid with its mesiodistal axis aligned with the dental row. Although early catarrhines may have obliquely oriented p3's, this premolar (as in cercopithecoids) is never bi-

cuspid, lacking the lingual cusp. A second, lingual cusp is also absent on the p3's of hylobatids and most gorillas, but it is present in orangutans and chimpanzees (Hürzeler, 1968; Kay, 1981, 1982). This cusp is best developed in humans and hominidlike fossils of the genus *Australopithecus*. It is also exhibited in sivapithecines and in *Gigantopithecus*, both apes from the late Miocene of the Siwalik Hills (Kay, 1982).

Despite its mesiodistally short length and its additional lingual cusp, the p3 of *Oreopithecus* exhibits a double root (Hürzeler, 1958). In humans, and usually chimpanzees, the lower premolars have a single root which has undoubtedly resulted from fusion of the ancestral double root (fig. 4). Although in gorillas and orangutans a single rooted premolar is rare, there is a tendency in these forms to bring the opposing roots closer together leading to fusion (fig. 4). The same approximation of the roots is exhibited in *Oreopithecus* (Hürzeler, 1958), suggesting that fusion of the roots (as in great apes) may have occurred as a matter of variation. In cercopithecoids, hylobatids, and early fossil catarrhines, on the other hand, the roots are divergent and never fused, regardless of the degree of crowding of the canine and premolars.

A poorly developed diastema is also a hominoid trait associated with a small canine. A diastema as a rule is absent only in humans, but its absence is not rare in chimpanzees (Schultz, 1948, 1968, 1969) and orangutans (Schultz, 1941, 1948). Supposedly, *Ramapithecus* (Gregory et al., 1926; Pilbeam, 1972; Simons, 1964, 1972) and *Australopithecus* (Robinson, 1956), both decidedly hominoid forms, also lack pronounced diastemas. As in the modern pongids, *Oreopithecus* also shows the variable absence of the diastema, specifically among the smaller, possibly female specimens.

Finally, the molars of *Oreopithecus* as in most hominoids are decidedly bunodont (Hürzeler, 1958). The systematic import of this feature, however, is unclear, since bunodont molars have obviously been arrived at independently by some colobines and *Cercocebus*. Similarly, the high relief of the molar crowns in *Oreopithecus* is also a feature with ambiguous import for distinguishing cerco-

⁴ The term pongid is used throughout the text to refer collectively to all the great apes. It is not intended to mean that the Pongidae are a true clade with a common divergence separate from hominids. In this regard, it must be recognized that taxonomic distinctions above the species level are not based on objective criteria, but the classifier's own bias as to whether the differences exhibit a degree of distinction which merits separate groupings. Taxonomic classifications cannot always reflect the sequence of divergence and relatedness of taxa, but reflect more accurately the degree of differences existing between taxa. In some cases, the unique and markedly derived specializations of a particular taxon may merit the formation of a new grouping which separates it from its sister taxa and emphasizes these differences. As a result, sister taxa may be grouped with less closely related (considering the sequence of divergence) yet more similar forms. The use of the terms pongid and hominid is a reflection of the markedly derived nature of humans and not of the existence of a true Pongidae clade (encompassing African apes and orangutans), with a common origin separate from that of the Hominidae.

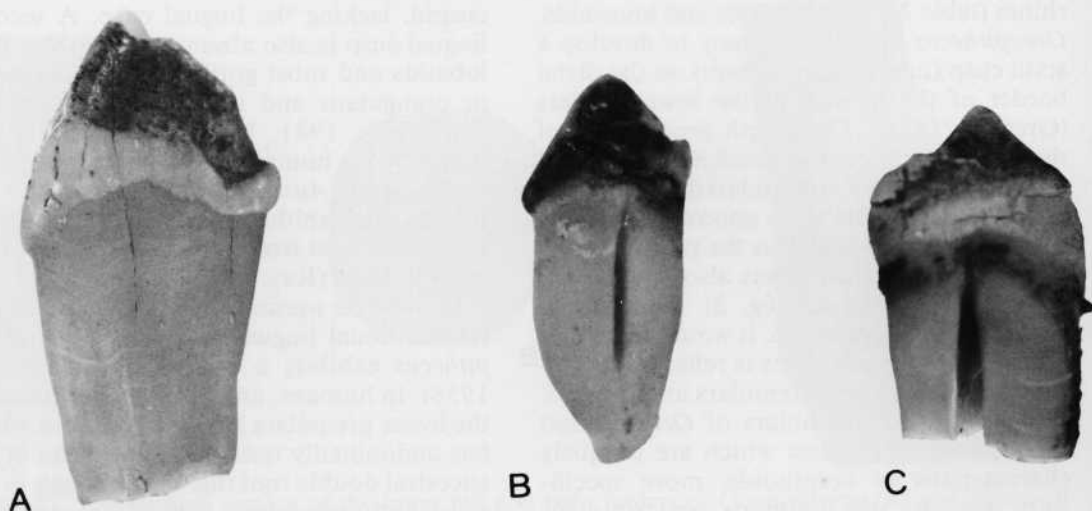


Fig. 4. Lingual view of the p3 of (A) *Gorilla* (right), (B) *Pan* (right), and (C) *Pongo* (left) showing a gradation in the fusion of the double root. Although fused roots are relatively rare in gorillas and orangutans, they occur in the majority of chimpanzees and are the rule in humans. In hylobatids and cercopithecoids the roots are never fused regardless of the crowding of the anterior dentition. (A-C 2× natural size).

pithecoids from hominoids, since high crowned molars are present in both gorillas and cercopithecoids. Nevertheless, the distribution of these traits among modern cercopithecoids and hominoids suggest that: (a) bunodont molars may have been the ancestral condition in hominoids and (b) high crowned molars may represent the ancestral condition of cercopithecoids.

DENTAL CHARACTERS UNIQUE TO *OREOPITHECUS*

Apart from cercopithecoidlike and hominoidlike characters in its dentition, *Oreopithecus* shows a number of other characters which are unique among living catarrhines. The upper incisors of *Oreopithecus* show well developed lingual cingula, forming an internal cusp, which is most pronounced on upper I1. As mentioned by Straus (1963) this cusp is homologous with the basal tubercles often exhibited in catarrhines. In gorillas and hylobatids the I1's cingula is very well formed, approximating the condition seen in *Oreopithecus* (fig. 5). Furthermore, gorillas and hylobatids resemble *Oreopithecus* in having nonoccluding upper lateral incisors. Instead, both sets of lower incisors occlude with both

the blade and cingula of the upper central incisors. Nevertheless, despite these similarities to modern hominoids, the internal cusp of the central incisors is extremely well developed in *Oreopithecus* and as such the tooth is unique (Hürzeler, 1958).

Despite the hominoidlike pattern of the upper molars, *Oreopithecus* has a unique crest connecting the hypocone with the metacone via the metaconule (Hürzeler, 1958; Butler and Mills, 1959). This crest is not seen in living hominoids or cercopithecoids. It may occur occasionally in some dryopithecines, hylobatids, and orangutans, but is always poorly developed (Hürzeler, 1958; Andrews, 1978; von Koenigswald, 1956). The strong development in *Oreopithecus* of the hypocone-metaconule crest which occludes with the talonid of the lower molars, is associated to the poorly developed hypoconulids and the large talonid basin. A similar association between crest development and hypoconulid is seen in the molars of those occasional hominoids which possess a crest.

Furthermore, unlike any living cercopithecoid or hominoid, *Oreopithecus* possesses a centroconid or mesoconid on the lower molars (Hürzeler, 1958). As seen in worn specimens this cusp does not appear to be formed

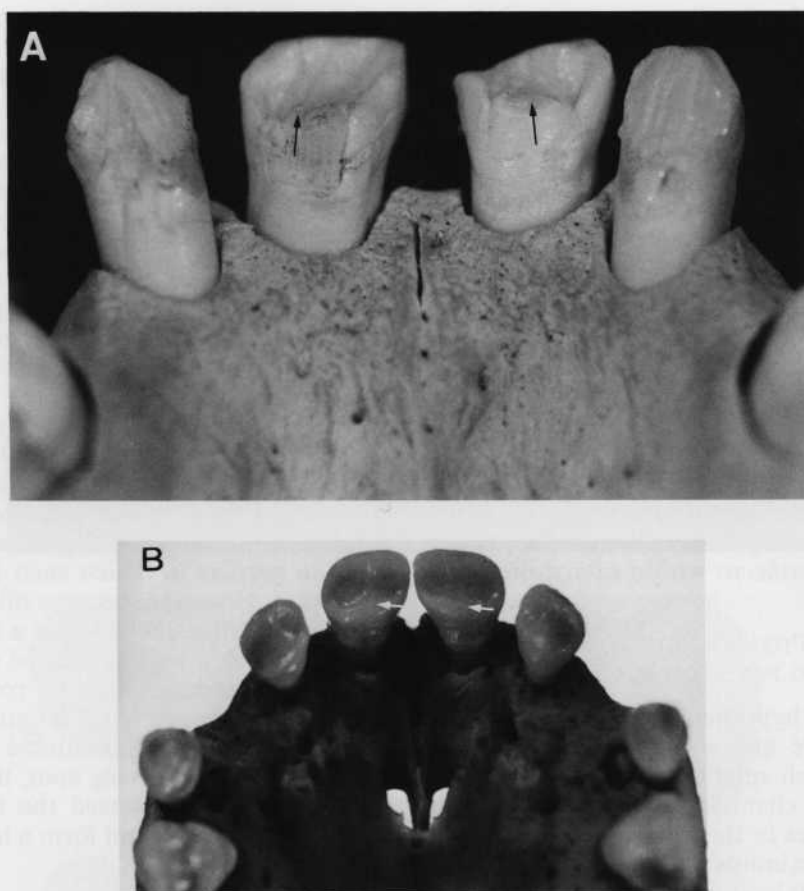


Fig. 5. The upper incisors of (A) male gorilla and (B) a male siamang. Note the polycuspidate cingula (arrow) of the gorilla's mesial incisors. In the gorilla this internal cingulum wears quickly with use and is best shown in captive specimens which are fed softer less abrasive diets or juveniles with newly erupted permanent incisors. Although they are not crenulated as in the gorilla, the siamang also exhibits well-formed lingual cingula (arrow). In both hylobatids and gorillas, the blades of the incisors are much higher than the cingulum. (A and B enlarged $1.75\times$ and $2\times$ natural size, respectively).

by underlying dentine and hence is not a real cusp. As noted by Gregory (1922), a centroconid is also seen in *Apidium*, an early primate (but see Hürzeler, 1958, 1968; Osborn, 1908) from the Oligocene of Egypt. This has led some paleontologists to posit an ancestor-descendant relationship for *Apidium* and *Oreopithecus*, respectively (Simons, 1960; Arambourg, 1963). However, *Apidium* exhibits three premolars which are all extremely primitive in morphology and a prosimianlike postcrania, rendering this hypothesis unlikely (also see Straus, 1963). It is more likely that the centroconid has evolved independently in these two forms.

My observations of fossil australopithecines and *Gigantopithecus* show that a centroconid or a cusp occupying that same position is occasionally exhibited on the lower molar of these forms. A centroconid is also seen in other mammalian forms, i.e., suids (Gregory, 1951; Hürzeler, 1968). Because development of a centroconid is common and has occurred in the hominoid lineage, the presence of a centroconid in *Oreopithecus* is not an unexpected feature or in itself of much systematic import.

On the other hand, the presence of a paraconid on the lower m1 and m2 of *Oreopithecus* seems to indicate a more primitive mo-

lar pattern. Such a cusp is seen in platyrrhines, i.e., *Alouatta* and in many Eocene primates, i.e., Notharctines, Omomyids, and some Adapids (Gregory, 1920, 1922; Szalay and Delson, 1979). It is not present in the permanent dentition of any living catarrhine. However, as noted by Hürzeler (1958, 1968), it is possible that this cusp is not homologous to the paraconid, but a product of budding off from the metaconid. If this is the case, the paraconid of *Oreopithecus* shows a derived condition. The centroconid on m1-m3, the lingual cusp on I1, the crest connecting the hypocone to the metaconule, and the possibly newly arrived at paraconid of *Oreopithecus* could as easily be derived from either the ancestral hominoid or ancestral catarrhine dentition. These unique traits offer no help when determining the phylogenetic placement of *Oreopithecus* within catarrhines.

POSSIBLE PHYLOGENETIC PATHWAYS ACCOUNTING FOR DENTAL CHARACTERS

Aside from hypotheses on cercopithecoid affinities, there are several other plausible scenarios which might account for *Oreopithecus*' dental characters. One possibility is that similarities in the dentitions of *Oreopithecus* and hominoids or of *Oreopithecus* and cercopithecoids have evolved independently. In this case, the dentition of *Oreopithecus* could have been derived from that of a form ancestral to both cercopithecoids and hominoids or from that of a form very similar to such an ancestor. Support for this interpretation may come from primitive characters in its molars which *Oreopithecus* shares with early Miocene catarrhines (Hürzeler, 1958; Butler and Mills, 1959). Furthermore, the derived nature of its dentition, as exemplified in its unique traits, may suggest a long evolutionary isolation from other groups of catarrhines and hence an early divergence. However, this scenario must hypothesize many more parallelisms which are not necessary when postulating cercopithecoid or hominoid affinities. In this case, both the set of characters *Oreopithecus* shares with hominoids and those it shares with cercopithecoids must be paralleled. If it is shown that these characters exist as a matter of variation in the early ancestral catarrhines, a very likely

expectation, this interpretation is as reasonable as any other.⁵

Another possibility is that all those dental characters *Oreopithecus* shares with hominoids indicate a common ancestry. Because many of the characters *Oreopithecus* has in common with hominoids are not seen in hylobatids, its divergence from the common hominoid stock after differentiation of the lesser apes may be postulated. Otherwise, it must be supposed that lesser apes initially possessed these traits in common with *Oreopithecus*. Neither of these two alternatives are at all unreasonable.

Regardless of the alternatives above, when positing a hominoid origin for *Oreopithecus*, the presence of a lingual cusp on p3 and the absence of a diastema must also be reconciled with the condition seen in great apes, specifically in gorillas in which such features are fairly rare. However, because all great apes, including gorillas, may exhibit a lingual cusp on p3 and lack a well developed diastema as a matter of variation (fig. 6), reconciliation of these characters within this framework does not present an unsurmountable obstacle. It could be that, as in living apes, the ancestral pongid-hominid possessed the tendency to reduce the diastema and form a lingual cusp,

⁵ It has been known for some time (Darwin, 1871; Gregory, 1920, 1922) that the independent development of similar traits is a characteristic tendency of closely related forms. According to Frisch (1965, 1973) there seems to be a considerable amount of parallelism in the development of secondary dental traits in hylobatids. Similar parallelisms have been exhibited in the dental traits of other groups of catarrhines. It follows that as long as traits occur as a matter of variability in an ancestral form, an independently arrived at fuller expression of such traits in two descendant groups is not a rare or unexpected phenomenon. However, the association of a number of traits into a specific structural complex already implies a relatively longer independent evolutionary period between two forms. A one-to-one parallelism of such a structural complex would be an extremely rare and unexpected occurrence. Unless it is shown that the dental traits which *Oreopithecus* shares with hominoids or those it shares with cercopithecoids are part of such a unique structural complex, and/or do not occur as variation within the common catarrhine ancestor, the parallel development of these traits in *Oreopithecus*, hominoids, and cercopithecoids is always a strong possibility.

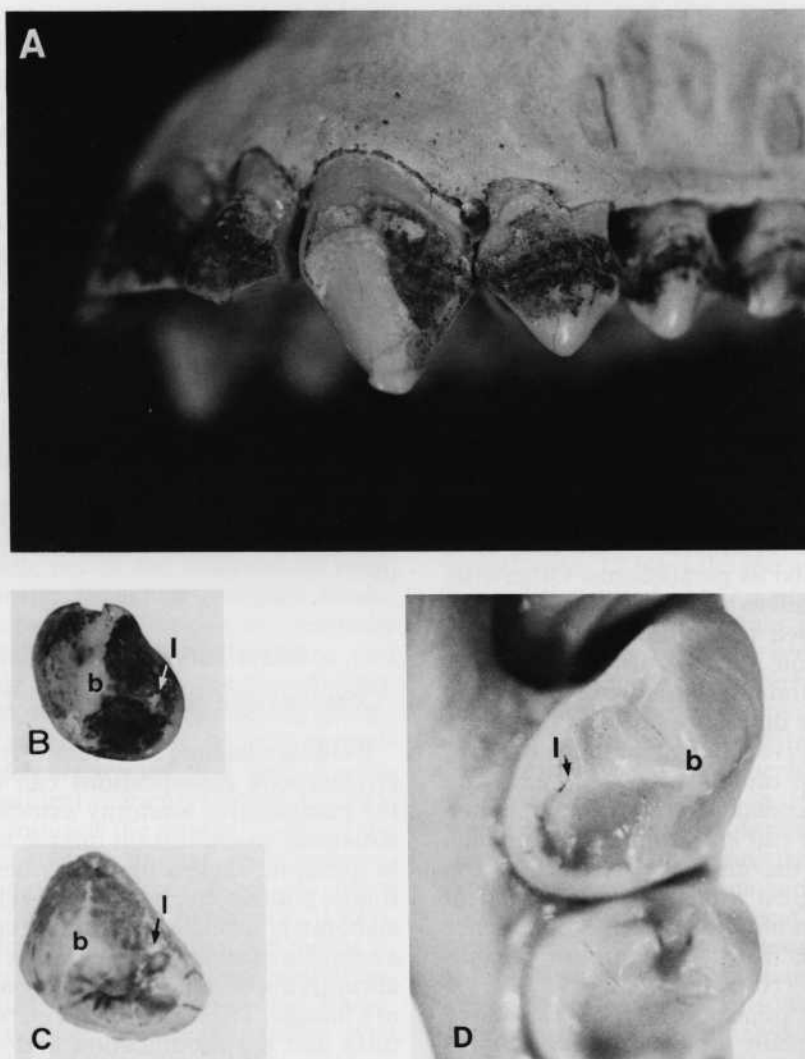


Fig. 6. The buccal aspect of the left upper anterior dentition of a female gorilla (A) and the occlusal surface of the p3 of (B) *Pan* (left), (C) *Pongo* (left), and (D) *Gorilla* (right). All the premolars show a buccal cusp (b) and a lingual cusp (l) which is well developed. In chimpanzees and orangutans a lingual cusp is relatively common. In gorillas, on the other hand, it is relatively rare and for the most part occurs only in females. Likewise the absence of a diastema as shown in (A) is also a rare trait in gorillas, exhibited only in the females. Nevertheless, all these traits do occur in gorillas as a matter of variation. (A–D 2× natural size).

but did not show the extreme development of these characters as seen in *Oreopithecus*. In this case, the condition in *Oreopithecus* is further derived from that of the ancestral pongid-hominid. The fact that *Oreopithecus* shows relatively quite a few unique dental characters, may be used to support this interpretation. Similarities in the dentition of

Oreopithecus and humans, owing to the extreme development of these characters, could be viewed as parallelisms.

On the other hand, the absence of a diastema, hominidlike dental proportions, small canines, vertically implanted incisors, and bicuspid p3 (all characters associated with a short face) may have evolved in common in

Oreopithecus and hominids, and represent the ancestral pongid-hominid condition. Support for this interpretation may come from fossil ramapithecines (or sivapithecines; see Kay, 1982) which show a similar stage in the development of these characters and have pongid cranial and postcranial adaptations (Smith and Pilbeam, 1980; Pilbeam et al., 1979; Ward and Kimbel, 1983; Rose, 1984). In this case, the large canine, lack of lingual cusps, and prognathism of living pongids must be derived from the ancestral condition.

It is also possible, as noted by Hürzeler (1958, 1968), that the similarities between hominids and *Oreopithecus* could indicate a common ancestry separate from that of pongids. The more progressive features in the molars of living pongids and hominids which are absent in *Oreopithecus* would then have to be interpreted as parallelisms. Otherwise, it must be postulated that the molars of *Oreopithecus* reverted to the more primitive ancestral condition. Whether it is possible that *Oreopithecus* and hominids share a common origin depends on the weight that the molar characters are given. Given that the primitive features in the molars of *Oreopithecus* are labile, the independent loss of these characters in pongids and hominids is not unlikely. Nevertheless, the unique characters of *Oreopithecus* suggest a considerable period of independent evolution after the divergence of this lineage from the common pongid-hominid stock (Hürzeler, 1968, 1977).

In summary, none of the hypotheses stated above that explain the dental characters of *Oreopithecus* are unreasonable. The hypothesis that *Oreopithecus* was derived from a catarrhine ancestral to both cercopithecoids and hominoids or one very similar to this ancestor is the most conservative. Given no additional evidence other than the dentition, this is the most prudent conclusion. Because of the labile and uncertain nature of those characters used to demonstrate a common ancestry between *Oreopithecus* and hominoids, or *Oreopithecus* and cercopithecoids, classification of this fossil as either a cercopithecoid or a hominoid on the basis of its dentition, is as likely to be correct as incorrect.

Nevertheless, the evidence from the premolar and canine slightly favor a classifica-

tion within the Hominoidea. Moreover, the fact that all the characters of the *Oreopithecus* dentition are exhibited as a matter of variation within the true hominoids, but not cercopithecoids, further suggests hominoid affinities. However, considering the apelike nature of the dentition of early catarrhines it is possible that the dental characters of *Oreopithecus* were also encompassed by the dental variation of these early forerunners. If such is the case, the number of unique traits in this fossil's dentition make a strong argument for the possibility of parallelism between hominoids and *Oreopithecus*.

However, taxonomic statements need not be based exclusively on dental characters. The skeleton of *Oreopithecus* offers conclusive evidence as to its systematic status. It is this conclusive evidence which we will now turn to.

NONDENTAL EVIDENCE

COMPARATIVE ANATOMY AND TAXONOMY

Evidence leading to accurate systematic or phylogenetic classifications can come from the comparative anatomy associated with a structural specialization unique to the group in question. Unless one subscribes to a creationist philosophy, it is inconceivable that an elaborately specialized structure composed of a complex of anatomical elements would have abruptly appeared in the phylogenetic history of a lineage. The formation of elaborate structures and the modification and/or incorporation of the anatomical elements which form it, occur gradually through a number of adaptive stages which characterize the evolutionary history of a lineage.

When the anatomical elements and those modifications associated with similar structural specializations in two organisms have a one-to-one correspondence, a shared evolutionary history is implied. For example, the atlantoaxial joint, which provides axial rotation of the head, is a unique specialization of terrestrial vertebrates. This specialization relies on the complex interaction of a number of anatomical elements which have all been modified to serve a specific function within the joint complex (Mookerjee, 1936; Evans, 1939; Williams, 1959). Presence or absence

of the anatomy corresponding to this joint can be used to distinguish higher vertebrates from amphibians and fishes. Similarly, the presence of three ear ossicles in the middle ear, which mechanically conduct sound from the tympanum to the oval window, are evidence of a common evolutionary history which distinguishes mammals from other vertebrates (Gaupp, 1913; Gregory, 1916; Guggenheim, 1948; Parsons, 1966). The different anatomical elements incorporated and the complexity of these specializations suggest that it is nearly impossible that any two forms will arrive at them independently.

Within mammals, the modification of anatomical elements and the complexity of their interaction, for any one unique specialization diagnostic of a family or superfamily grouping, may not be as great as those in the mammalian middle ear or the atlantoaxial joint. Given a shorter period of common evolutionary history, the generation time necessary to develop specializations as complex and hence unique as these may not be sufficient. Nevertheless, family and superfamily groupings within mammals often do have specializations which are related to a unique complex of anatomical elements (Simpson, 1941, 1961). In hominoids the rotatory joints of the forearm are such a unique specialization, which distinguishes them from all other mammals (Lewis, 1965; Sarmiento, 1985). This complex of joints allows the radius to rotate nearly 180° about the fixed ulna (Darcus and Salter, 1953; O'Connor and Rarey, 1979). As in those specializations for axial rotation and sound conduction, the rotatory joints of the forearm depend on the complex interaction of a number of anatomical elements (Lewis, 1965, 1971; Sarmiento, 1985). Therefore, although the dental traits of *Oreopithecus* are inconclusive for distinguishing between cercopithecoids and hominoids, the presence of the characteristic composite of anatomical elements associated with hominoid forearm rotation will provide conclusive taxonomic evidence.

ANATOMY ASSOCIATED WITH FOREARM ROTATION IN HOMINOIDS

Rotation of the radius around the ulna requires motion at the humeroradial, carpo-

antebrachial, and the proximal and distal radioulnar joints. When compared to cercopithecoids and other mammals, the hominoidtype joints have clearly been modified to provide and control for rotation. Despite inaccurate mechanical and behavioral interpretations, Lewis' work (1965, 1969, 1971, 1974) did much to reveal those modifications and anatomical elements in the distal radioulnar and carpoantebrachial joint which are related with forearm rotation and unique to hominoids.

The "semilunar meniscus" of Lewis (1969, 1974) is in reality functionally analogous to the annular ligament of the proximal radioulnar joint (Sarmiento, 1985). In those hominoids which have a distinct "semilunar meniscus," i.e., hylobatids and chimpanzees, the ligament wraps around the ulnar styloid process (Lewis, 1974). Like the annular ligament around the radial head, it prevents dislocation at the distal radioulnar joint, while allowing rotation around a central axis. The triangular articular disc, which has insertions on the ulnar fovea, the radius, and the carpus (Lewis, 1965), achieves a similar function, but through a different mechanical strategy (Möricke, 1964; Sarmiento, 1985). Since the fovea is the center of rotation for the distal part of the radius, the triangular articular disc, which anchors the radius and carpus to the ulna, will control for rotation impeding separation of the forearm bones and ulnocarpal joint (Möricke, 1964; Sarmiento, 1985). The triangular articular disc also serves an added function not directly related to forearm rotation. It impedes the proximodistal separation of the ulna from the radius and carpus when tensile forces are applied across the carpoantebrachial joint (Sarmiento, 1985; Huber, 1934).

As noted by Lewis (1965, 1969, 1971, 1974), the hominoid distal radioulnar joint is fully diarthrodial and totally separate from the carpoantebrachial joint. Although development of a rudimentary diarthrodial radioulnar joint is also seen in some cercopithecines (Lewis, 1965, 1974), in these forms this joint is never fully separate from the radiocarpal joint. A diarthrodial joint reduces the friction produced as a result of movement between the two bones (MacConaill, 1931, 1932). It is especially important when there

is compressive force across the joint, which increases the frictional force. In the radioulnar joint such forces may occur as a result of the actions of the rotatory muscles, or of the forces applied by the connective tissues controlling forearm rotation.

The diarthrodial radioulnar joint of hominoids is associated with a large, semilunar, and bifaceted ulnar head. The proximal, and usually largest, of the two semicircumferential articulations corresponds to the radius, the distal semicircumferential articulation to the triangular articular disc.

Although the ulnar fovea is the rotatory center for the distal radius, the ulna shifts medially and posteriorly during pronation and laterally and anteriorly during supination (Knese, 1950a; Huber, 1934; Sarmiento, 1985). Therefore, the axis of rotation of the radius and attached hand does not pass through the ulnar fovea. Rapid pronation and supination of the radius results in oscillations of the ulnar styloid process with respect to the hand. Loss of the ulnocarpal contact frees the ulnar styloid process from the carpus, allowing such oscillations to occur (Sarmiento, 1985). In the nonhominoid catarrhines the cuplike articulation for the ulnar styloid process formed by the triquetrum and pisiform or by the triquetrum alone (i.e., as in some *Ateles* and all *Brachyteles*), would not allow pronounced displacements of the ulnar styloid relative to the hand (Sarmiento, 1985).

The adaptive stages leading to the loss of the ulnocarpal contact in hominoids are not clearly known (Sarmiento, 1985). However, there is enough evidence from embryology (Lewis et al., 1970) and comparative anatomy (Lewis, 1974; Sarmiento, 1985) to conclude that loss of the ulnocarpal contact involves the separation of a secondary ossific center of the triquetrum, resulting in the formation of an os daubentonii (Sarmiento, 1985). Contrary to Lewis' (1969) belief that the os daubentonii serves the function of a lunula within the meniscus, the os daubentonii may be explained more realistically as a remnant portion of the triquetrum which in early catarrhines (i.e., *Pliopithecus*) and cercopithecoids participates in the stylopi-sotriquetral articulation (Sarmiento, 1985). Because the "semilunar meniscus" does not

function as a meniscus, the os daubentonii cannot be simply explained as a lunula (Sarmiento, 1985). It is possible that an increase in the rotatory movement of the joint led to greater oscillations of the ulna, forcing the disassociation of the cuplike triquetrum into two parts. Regardless of the exact evolutionary changes or whether loss of a stylotri-quetral articulation occurred initially as a response to forearm rotation, reduction in the mass of the triquetrum and loss of the cuplike stylotri-quetral articulation are correlates of forearm rotation in living hominoids (Sarmiento, 1985).

Because the hand attached to the radius rotates as a unit around the ulna, rotatory forces applied to the radius are also applied across the radiocarpal joint. The potential force which may be applied across the joint is greater with an increase in the degree of forearm rotation (Sarmiento, 1985). Therefore, in hominoids which have nearly 180° of forearm rotation, the ligaments attaching the antebrachium to the hand are strengthened. As noted by Lewis (1969), hominoids have a very well-developed palmar radiocarpal ligament and an ulnocarpal ligament which serves to connect the radius and ulna to the carpus. In skeletal preparations the development of the ulnocarpal ligament is evidenced in the deep fossa on the nonarticular face of the triquetrum, and of course in the deep ulnar fovea which is also the attachment site for the triangular articular disc. The deep indentation on the radial styloid process (Tuttle, 1967; Lewis, 1969), and the deep groove on the palmar border of the scaphoid's radial articulation which extends out onto the tubercle of the scaphoid, attest to the well-developed palmar radiocarpal ligament of hominoids.

The modifications of the hominoid brachioantebrachial joint and the proximal radioulnar joint are mostly restricted to the shape of the articular surfaces. The humeral trochlea of hominoids is spool shaped and markedly waisted midsagittally. The waisting of the trochlea corresponds closely with the midsagittal keel on the semilunar notch of the ulna. The close fit at the humeroulnar joint, which in transverse cross section resembles the relation between an open-end

wrench and the head of a bolt, serves to stabilize the joint against rotatory force around the long axis of the forelimb (Sarmiento, 1985). In this manner, the humerus and ulna, which have their axes of rotation close to each other, can act elastically as a single unit (Sarmiento, 1985). Obviously, rotatory forces across the humeroulnar joint are the result of the forces needed to rotate the radius and hand (Sarmiento, 1985). Conversely, during rotation of a forelimb suspended body beneath a fixed hand, rotatory forces across the humeroulnar joint may be applied as a result of the dissipation of the kinetic energy of the rotating body (Sarmiento, 1985).

The humeroradial articulation of hominoids is altered to allow and control for rotatory movement of the radius on the capitulum. The lateral aspect of the trochlear keel articulates with the proximal circumferential articulation around the proximal surface of the radial head. The capitulum articulates with the concavity on the radial head. At the end of radial runout the trochlear keel prevents displacements of the rotatory axis of the radius in respect to the humerus and fixed ulna (Sarmiento, 1985).

The proximal radioulnar articulation of hominoids is also constructed for controlling rotation. Hominoids have a strongly developed anular ligament which wraps around the radial head (Martin, 1958; Sarmiento, 1985). As noted, the radial head's anular ligament impedes displacement of the head away from its center of rotation. The circular outline of the radial head enables it to rotate freely within the anular ligament (Knese, 1950a; Martin, 1958). Like the distal radioulnar joint, the proximal radioulnar joint is a diarthrodial joint. The radial head is housed completely in this synovial cavity. The distal circumferential articulation on the ulnar half of the radial head articulates with the ulna's radial notch. There is also an articular surface on the radial side of the head where it articulates with the anular ligament.

Together with the unique modifications which allow motion between the radius and ulna, hominoids have strongly developed rotatory muscles, specifically the deep heads of pronator teres and supinator which only cross the radioulnar joints. These muscles are either

poorly developed or lacking in all other mammals (Sarmiento, 1985).

ADAPTIVE SIGNIFICANCE OF FOREARM ROTATION

Lewis (1969) claimed that the carpoantebrachial and radioulnar modifications of hominoids are associated with a brachiating lifestyle. However, atelines, which brachiate in the manner of hylobatids, lack the 180° of forearm rotation (Jenkins, 1981) or the structures associated with it (Lewis, 1971). In fact, 180° of forearm rotation is not a mechanical requisite of hylobatid or ateline brachiation. According to Jenkins (1981), what is crucial to the underarm brachiation practiced by hylobatids and atelines is rotation at the mid-carpal joint.

It could be argued that in brachiating forms the presence of a prehensile tail has a negative influence on the development of forearm rotation. During brachiation, hylobatids, which lack the extra point of support provided by the prehensile tail, might need the extra maneuverability and stability allowed by forearm rotation. However, forearm rotation is also exhibited in nonbrachiating hominoids. It is just as likely that this specialization could have arisen as a result of other behaviors practiced by hominoids (see Cartmill and Milton, 1977).

The role of forearm rotation in feeding behaviors presents alternative interpretations as to its adaptive significance. In forelimb-suspended terminal branch feeding and foraging, 180° of forearm rotation allows an organism to cover a larger spherical volume without changing handholds or supports (Grand, 1972). Moreover, after it has finished foraging in a particular area, forearm rotation allows the organism to about-face, facilitating its return toward the more supportive branches at the center of the trunk. Finally, when the organism feeds on large fruits, forearm rotation allows it to grasp and remove the fruit more easily with a single hand. The axial twisting motion of the hand associated with forearm rotation helps to separate the fruit from its stem. Moreover, the ability of the forearm to supinate, so that the hand is

able to wrap around the fruit, increases the effectiveness of the grip.

However, it is also likely that forearm rotation, being a unique, complex, and elaborate structural specialization also evolved in part as a response to climbing,⁶ a behavior which is central to all hominoids (Prost, 1965; Stern, 1971; Stern and Oxnard, 1973; Fleagle, 1976; Fleagle et al., 1981). When hominoids climb vertical supports, forearm rotation controls for the magnitude of normal force applied on the support by the forelimbs (Sarmiento, 1985). During climbing, normal forces are necessary for creating the frictional force which enables upward propulsion and maintains the organism on a vertical support (Cartmill, 1979, 1985; Sarmiento, 1985). Maximum forearm supination is seen when hominoids climb wide vertical supports in which forelimb adduction applies the majority of the needed normal force at the handhold (Sarmiento, 1985). Among other things, the medially rotated arm and supinated forearm are necessary to wrap the forelimbs around wide supports (fig. 7; Sarmiento, 1985). On the other hand, pronated postures of the forearm are exhibited by hominoids on relatively narrow supports in which the handgrip is able to effectively apply a normal force at the handhold (Sarmiento, 1985). Although maximum forearm pronation is never seen when hominoids climb vertical supports, it is commonly exhibited when they grasp overhead horizontal supports (Sarmiento, 1985). Therefore, the full range of nearly 180° of pronation and supination of the forearm can be interpreted as a specialization for climbing. More specifically, the large range of forearm supination is a requisite for climbing wide vertical supports.

⁶ The association of climbing and forearm rotation is exhibited to some degree in the vervet *Cercopithecus aethiops*. As noted by Rose (1979), vervets engage in a variety of climbing behaviors. Their semiterrestrial habitat emphasizes vertical ascensions up the base of supports of relatively large diameters. Notably, exclusive of hominoids *C. aethiops* is the primate with the highest degree of forearm rotation (O'Connor and Rarey, 1979; Sarmiento, 1985). Nonetheless, as would be expected considering its cercopithecoid origins, the vervet does not exhibit the hominoid anatomy associated with forearm and shoulder rotation.

The ability to wrap the forelimbs around wide supports, in an effort to apply an adductive force on the support, does not involve only forearm supination, but also medial rotation of the arm and considerable abduction of the shoulder joint (fig. 7; Sarmiento, 1985). In this sense, medial rotation of the arm and the associated anterolateral displacement of the shoulder blade (Knese, 1950b; Inman et al., 1944) improve the line of pull of the latissimus dorsi and pectoralis major for forelimb adduction (Sarmiento, 1985).

If forearm supination serves as a specialization for climbing supports of relatively wide diameters, then at one point in the evolutionary history of hominoids it must have evolved together with shoulder rotation and the ability to widely abduct and rotate the shoulder joint. Therefore, all those anatomical modifications associated with increasing shoulder mobility unique to hominoids—the dorsally positioned scapula, laterally directed glenoid, the anteroposteriorly flattened thorax, and the high humeral torsion—together with those anatomical modifications associated with forearm rotation can be considered as parts of an elaborate structural specialization for climbing. The large number of anatomical modifications associated with this specialization suggest that it reflects a relatively long common evolutionary period, characterized by a number of adaptive stages. Therefore, the odds that convergence would duplicate all the anatomical modifications in the forelimb joints associated with the hominoid specialization are infinitesimally small. Moreover, since no other living mammal has approximated the degree of modification in the forelimb joints seen in hominoids (Sarmiento, 1985), the odds of convergence or parallelism are further reduced.

FORELIMB ANATOMY OF *OREOPITHECUS*

The fortuitous discovery of a fragmentary proximal ulna (Hürzeler, 1958) prior to the discovery of the complete skeleton of *Oreopithecus* was the first unequivocal evidence of this fossil's hominoid status. The distinct morphology exhibited by the hominoid proximal ulna, which is matched point for point



Fig. 7. Photographs of a human in climbing behaviors. Photograph A shows typical pronated postures of the forearm when grasping overhead horizontal supports. Photographs B and C show the typically hominoid posture of the upper limb on relatively wide vertical supports. Note in B and C the strong supinated postures of the forearm and the medially rotated position of the arm (as evidenced in the laterally facing olecranon process). As can be seen when comparing B to C, both the degree of medial rotation of the arm and the degree of supination increase with an increase in support diameter. Both supination and medial rotation of the arm are necessary to wrap the upper limbs around large-diameter supports. Rotation of the arm also increases the magnitude of normal force that can be applied on the support through adduction of the upper limbs. On relatively wide supports, upper-limb adduction accounts for almost all the normal force applied at the handholds and is the only actively applied force needed to maintain the individual on the support (Sarmiento, 1985).

by that of *Oreopithecus*, led to Hürzeler's now famous statement "not even by the boldest mental acrobatics can this ulnar fragment be interpreted as anything but a hominoid" (Hürzeler, 1958, p. 35). However, some paleontologists at the time of its discovery failed to believe that this ulna could belong to an animal with the dentition of *Oreopithecus* (Hürzeler, 1958, 1968).

The subsequent discovery of the complete skeleton in 1958 (Hürzeler, 1959, 1960) convinced skeptics that the *Oreopithecus* dentition was associated with the hominoidlike ulna (Le Gros Clark, 1971). Moreover, it brought to light a number of other features of the forelimb joints of *Oreopithecus* which are uniquely hominoid. As noted by Schultz (1960), the costal angle in hominoids and *Oreopithecus* is acute, evidence of an antero-posteriorly flattened thorax and a dorsally positioned scapula. Among other things, in anthropoids and other mammals these traits are associated with high humeral torsion and a laterally directed glenoid cavity (Holl, 1891;

Fick, 1904; Grunewald, 1919; Braus, 1929; Sarmiento, 1985). As noted, these are parts of the complex of features which allow hominoids to climb relatively wide vertical supports. Therefore, in itself, an acute costal angle implies a considerable amount of shoulder mobility and the ability to widely abduct the forelimbs. However, the large humeral head (Schultz, 1960), the relative position of the greater and lesser tubercles demarcating a well-developed bicipital groove, and the seemingly high humeral torsion in *Oreopithecus* also suggest such shoulder mobility.

As in hominoids, shoulder mobility in *Oreopithecus* is associated with the ability to pronate and supinate the forearm. In accordance with the distinctly hominoid ulnar morphology (Hürzeler, 1958), the elbow joint of this fossil has the full suite of skeletal characters associated with forearm rotation in hominoids. The humeral trochlea is markedly waisted, corresponding to the pronounced midsagittal keel on the ulna's semi-

lunar notch (Straus, 1963). The trochlea also shows a well pronounced lateral keel, with a large articular surface for the proximal circumferential articulation of the radial head. As in hominoids, the radial head is almost perfectly circular in outline. The articulation around its circumference is divided into a distal and proximal surface. The distal of the two articular surfaces corresponds to the continuous articular surface on the radial notch of the ulna. As is typical in hominoids, the radial notch is not divided by the interosseus ligaments connecting the radius to the ulna. As a whole these traits, which correspond closely to those of hominoids, suggest the ability to pronate and supinate the forearm to the same degree as in hominoids.

Evidence that forearm rotation could be associated with axial rotation of the arm comes from the proximodistally short olecranon process. This short process suggests that the elbow joint was used in extended postures (Jolly, 1967; Sarmiento, 1985). It is only in extended elbow postures that axial rotation of the arm translates into forearm rotation.

Unfortunately, all the known skeletal remains of the distal radioulnar and proximal carpoantibrachial joint of *Oreopithecus* are badly crushed. Nevertheless, there are a number of traits which may be inferred from what does exist. The large bifaceted ulnar head in *Oreopithecus* is unique to hominoids and an integral part of the complex of forearm rotation. The distal facet on the ulnar head suggests the presence of an articular disc as in hominoids.

There is no direct evidence as to the nature of the ulnocarpal joint of *Oreopithecus*, since that diagnostic portion of the skeletal structure is either missing or crushed beyond recognition. However, the morphology of the hamate gives some clues as to the anatomical relations at the ulnocarpal joint. The almost exclusively ulnar orientation of the triquetrum's articular surface suggests that the ulnar styloid process did not unload weight through the triquetrum (Sarmiento, 1985; Sarmiento and Rose, 1985). Furthermore, the proximodistally elongated hamate and the distally directed hamulus suggest that the long axis of the pisiform was directed proximodistally and held close to the carpus, as in hylobatids (Jenkins and Fleagle, 1975; Jen-

kins, 1981). The above features of the hamate further suggest a distal migration of the pisiform articulation and a reduction in the contact between the triquetrum and the ulnar styloid process. Therefore, the ulnocarpal joint of *Oreopithecus* was probably not unlike that of hylobatids. The ulnar styloid process may very well have been elongated and had a small contact with the triquetrum. These features are in accordance with the morphology and rotatory capabilities of the brachioantibrachial and proximal radioulnar joint. Moreover, together with the mediolaterally narrow lunate, they suggest that *Oreopithecus* did not customarily use the hand in quadrupedal weight-bearing postures (Sarmiento and Rose, 1985).

The marked groove on the ulnopalmar border of the scaphoid, extending out onto its tubercle for the attachment of the palmar radiocarpal ligament, is also a feature unique to hominoids and *Oreopithecus*. As noted, the strong development of these ligaments reinforces the connection between the radius and hand. A strong connection helps to keep the carpus bound to the radius during forearm rotation (Sarmiento, 1985).

The skeletal evidence in *Oreopithecus* which implies the hominoid functional complex of forearm and shoulder rotation is overwhelming. Because there is one-to-one correspondence in those skeletal features associated with this unique complex in *Oreopithecus* and hominoids, the two must share a unique common evolutionary history. As noted, the large number of anatomical modifications which are associated with the functional complex of forearm and shoulder rotation negates the possibility of such a point-for-point convergence. Therefore, based on the anatomy of the forelimb joints, *Oreopithecus* cannot be classified as anything but a hominoid.

OTHER CLIMBING SPECIALIZATIONS

In addition, an assortment of hominoid-like climbing specializations in other localized areas of the skeletal anatomy of *Oreopithecus*, which can be associated to the complex of forearm and shoulder rotation, further attests to its hominoid status. The heel process (Straus, 1963; Sarmiento, 1983a); the re-

duced number of lumbar vertebrae (Schultz, 1961; Straus, 1963); the increased number of sacral vertebrae (Hürzeler, 1958; Schultz, 1960; Straus, 1963); the absence of a tail (Schultz, 1960; Ankel, 1965, 1966); the proportional indices of the limb bones, pelvis, and trunk (Schultz, 1960); the large femoral bicondylar angle (Schultz, 1960; Straus, 1963; Hürzeler, 1968); and the hooklike hands (restricted abduction and adduction at metacarpophalangeal joint, and increased abduction adduction at the midcarpal joint) (Sarmiento and Rose, 1985) are all hominoid specializations which in living mammals are associated with climbing (Straus and Wislocki, 1932; Yalden, 1972; Cartmill and Milton, 1977; Prost, 1980; Sarmiento, 1985).

Aside from its relation to shoulder mobility, the acute costal angle is also associated with another climbing specialization. The angle provides evidence that the vertebral column protrudes into the chest cavity. The position of the vertebral column together with the reduction in length of the lumbar column and trunk—hominoid features also exhibited in *Oreopithecus* (Schultz, 1960)—are requisites for erect postures (Keith, 1923; Sarmiento, 1985). As has been noted in hominoids (Prost, 1965, 1980; Kortlandt, 1968; Preuschoft, 1973a; Rose, 1974; Fleagle et al., 1981), erect postures are positional correlates of vertical climbing behaviors. A far-reaching number of soft tissue modifications (Washburn, 1950a, 1950b; Keith, 1903, 1923, 1934) are associated with carriage of an erect trunk and the anteriorly displaced vertebral column of hominoids. These modifications were also likely to have been present in *Oreopithecus*.

Most of the specializations in the skeleton of *Oreopithecus*, including the modification of the soft tissues associated with erect postures, can be interpreted as a part of a larger complex which is the requisite for a hominoidtype climbing. Such climbing relies solely on the normal force applied on the support by the frictional pads of the hands and feet, and emphasizes those structural modifications that increase the efficiency of vertical ascensions (Sarmiento, 1985, 1986). Because *Oreopithecus* and hominoids have arrived at the same morphological solutions to the mechanical problems imposed by climbing be-

haviors, convergence is a very unlikely supposition.

NONCLIMBING ADAPTATIONS

Oreopithecus shows other hominoid traits which cannot be directly related to climbing and the associated rotational specializations of the forelimb. Most importantly, as in hominoids, this fossil shows late eruption of the molars relative to fusion of the epiphyses, a characteristically hominoid trait (Schultz, 1968). As can be seen in the 1958 skeleton, epiphyseal fusion is almost complete (Straus, 1963), although the m2 and m3 are relatively unworn. Regardless of size and weight, monkeys as a rule show relatively early eruption of the molars in comparison to fusion of the epiphyses (Schultz, 1936, 1968). The molars of both Old and New World monkeys are well worn before complete epiphyseal fusion occurs.

The implications of late molar eruption are varied. They suggest that, as in pongids and hominids, *Oreopithecus* may have had a prolonged infancy dependency period, a longer adult life, and a K-selection strategy. The wear gradient exhibited in those associated molars and the large hominoid-size cranial volume (Straus and Schön, 1960) supports this hypothesis. With respect to the latter, there is some correlation in mammals between long life and a relatively large brain size (Sacher, 1959, 1975). However, Straus and Schön's estimate on brain volume has not had universal acceptance. The crushed calvaria has provided estimates of cranial volume below the range of variation of hominoids (Szalay and Berzi, 1973).

Furthermore, as in pongids, the 1958 skeleton of *Oreopithecus* shows complete obliteration of the cranial sutures (i.e., coronal, squamous, sagittal, frontozygomatic, maxillozygomatic, and sphenozygomatic sutures), despite the mentioned absence of full epiphyseal fusion. As a rule, in cercopithecoids and humans, the cranial sutures are not fully obliterated until after the dentition is well worn and epiphyseal fusion is complete (Singer, 1953; Schultz, 1956). In platyrrhines, cranial suture obliteration is further delayed and the sutures may persist throughout adult life (Schultz, 1956). Although the reasons be-

hind the differences in relative age at the onset of suture loss among anthropoids are unclear, early suture obliteration is characteristic of pongids (Schultz, 1956, 1968).

As shown by Grine and Krause (1985) in a preliminary report, *Oreopithecus* has a hominoid-type enamel structure, not present in the monkeys they examined. Considering a longer lifespan in *Oreopithecus*, a hominoid-type enamel structure, and relatively thicker enamel when compared to cercopithecoids may be expected. Whether this type of enamel can be easily converged upon or represents the ancestral structure present in all early catarrhines must await further studies which consider the enamel of other early fossil catarrhines and a larger number of Old and New World monkey genera. There is the possibility that the hominoid type enamel structure is primitive for catarrhines.

Finally, as noted by Schultz (1960), *Oreopithecus* lacks the well-developed congenital ischial callosities of cercopithecoids. Together with its hominoid climbing specializations, it implies *Oreopithecus* has hominoid-like postures (Rose, 1974). Interestingly the shape of the skeletal tuberosities of hylobatids seems to indicate that gibbons and siamangs also have much better-developed callosities than *Oreopithecus*.

OREOPITHECUS AND DOLLO'S LAW

With the exception of some peculiarities in the skeleton and dentition of *Oreopithecus*, it is remarkable how close this form's anatomy fits with the proposed theoretical models of hominoid differentiation (Keith, 1923; Gregory, 1934; Morton, 1924; Tuttle, 1967, 1969, 1970, 1974, 1975a, 1975b; Stern, 1971; table 3). Specifically, the remains of *Oreopithecus* correspond closely to a hypothetical stage prior to the divergence of pongids and hominids from the common hominoid stock. The close correspondence between the remains of *Oreopithecus* and an early hypothetical common ancestor is phylogenetically significant. With the lack of a complete fossil record of hominoid phylogeny, comparative studies of living forms provide theoretical models which

are used to embrace or dismiss fossils as possible ancestors.

Despite its close fit to the theoretical models, most paleontologists have dismissed *Oreopithecus* as a possible ancestor of any of the living hominoids (Gregory, 1951; Hürzeler, 1968; Le Gros Clark, 1971; Simons, 1972; Pilbeam, 1972; Szalay and Delson, 1979). Citing Dollo's principle (1893) of irreversibility or tacitly assuming it, these paleontologists believe that *Oreopithecus*—because of a number of peculiar traits—is too far derived to be such an ancestor (Gregory, 1951; Le Gros Clark, 1971; Simons, 1972; Pilbeam, 1972; Szalay and Delson, 1979). Alternatively, they prefer to bestow ancestor status to fragmentary remains of isolated jaw fragments which show only very few of the traits the theoretical model predicts for ancestral hominoids. Invariably, when more than fragmentary dental finds are uncovered, the hominoid status of these heralded ancestors becomes questionable (i.e., *Aegyptopithecus*, *Propliopithecus*, *Pliopithecus*) (Kay et al., 1981). The close fit of *Oreopithecus* to theoretical models, may challenge the claim of irreversibility bestowed by some on its peculiar features.

As noted by evolutionary theorists (Gregory, 1920; Mayr, 1963; Simpson, 1941) reversibility is a regular process of evolution. As long as certain features occur as a matter of variation, the possibility of reversals always exists (see p. 14 and Darwin, 1871). The principles of irreversibility more aptly applies to structures composed of a number of anatomical elements and not to disassociated features. While it is conceivable that the length of a digital ray could increase and decrease many times during the evolutionary history of a lineage, loss of a ray can never be regained without leaving a record that the new structure is not homologous to the original one. In *Oreopithecus* the traits which have been proposed as examples of Dollo's principle are not indisputedly irreversible features. These traits find an analog with fluctuations in the length of the ray rather than with its loss and reappearance.

For example, Szalay and Langdon (1985) believed that in *Oreopithecus* the distance from the center of the rotational axis of the talocalcaneal joint to the calcaneocuboid ar-

ticular surface is reduced beyond what may be expected in the ancestral hominoid. From an assemblage of a disparate number of fossil calcanea, some questionably primate (see MacPhee et al., 1983 and MacPhee and Cartmill, 1984), and the calcanea of some selected living primates, Szalay and Langdon attempted to show a trend in the reduction of this lever arm among primates. The lack of evolutionary continuity in the fossils chosen to demonstrate this trend notwithstanding, this trait is extremely labile. Not only does variation exist within species, but the trait seems to be affected during the individual's lifetime according to the forces applied (fig. 8).

The short outlever (load arm) and long inlever (power arm) of the *Oreopithecus* foot more aptly reflect the magnitude of force applied to plantarflex the foot (Schultz, 1963). The robust metatarsals (Riesenfeld, 1975), the proximodistally short distal tarsal row, and the pronounced medial deviation of the calcaneal neck, which are all associated with a reduction in outlever length, also reflect this force. However, a long inlever for plantar flexion is characteristic of the gorilla foot which, owing to body size, needs powerful plantarflexion (Schultz, 1963). In primates, as shown by Schultz (1963) (also see Ford, 1980), the proportional length of the inlever of plantarflexion increases with an increase in body size. When compared to that of apes of approximately the same body size (i.e., chimpanzees) the longer inlever for plantarflexion in *Oreopithecus* suggests that: (a) it was placing a greater percentage of its weight on its hindlimbs and/or (b) the outlever of plantarflexion may have been proportionately longer than in chimpanzees (fig. 9). In fact, the lack of well-developed weight-bearing tubercles on the calcaneus, navicular, and cuboid of *Oreopithecus* suggests that unlike the arrangement in chimpanzees (Weidenreich, 1922) the tarsal bones did not contact and unload weight directly onto the substrate. Therefore, the outlever of the *Oreopithecus* foot is actually the distance from the rotational axis of the tibiotalar joint to the metatarsophalangeal joint. The narrow dorsoplantar diameter of the cuboid, the shape of the cuboid metatarsal articular surface, and the hingelike naviculoentocuneiform joint, which

all indicate restricted dorsiflexion of the midtarsal and tarsometatarsal joints, further support this claim.

In *Oreopithecus* the relatively short proximodistal length of the metatarsus and of the tarsus distal to the tibiotalar joint axis (the outlever or load arm of plantar flexion) is necessary to achieve a working ratio between the inlever and outlever of plantarflexion. Because the distal tarsus of chimpanzees makes contact with the substrate (Weidenreich, 1922), the outlever of plantarflexion at some points of the stride is only the length of that part of the tarsus distal to the axis of the tibiotalar joint. Without the metatarsus contributing to the length of the outlever, the chimpanzee foot can achieve a working ratio with an inlever which is relatively shorter and a distal tarsus which is relatively longer than in *Oreopithecus*. A logarithmic linear equation of body weight versus the ratio of the power arm to the load arm (measured as the distance from the tibiotalar joint axis to the metatarsophalangeal joint, see Schultz, 1963) shows that *Oreopithecus* has the predicted hominoid ratio, while orangutans and chimpanzees have a lower than predicted ratio (fig. 9). At least for chimpanzees this reflects the fact that the long metatarsus does not consistently contribute to the outlever length—a seemingly derived condition for hominoids. In this regard, the ratios of the tarsus and metatarsus of *Oreopithecus* as well as those features which are associated with restricted movement at the midtarsal and tarsometatarsal joint are what may actually be expected in a generalized hominoid (see Appendix). However, it must be emphasized that these lever arms exhibit considerable variation and overlap between the different species of hominoids (Schultz, 1963). Therefore, reversals or parallelisms are a strong possibility, and the deciphering of the actual ancestral condition is at best a tentative undertaking.

Similarly, the supposedly nonhelical nature of the talocalcaneal joint is also a trait which may be easily reversed or paralleled (Delson and Andrews, 1975; Szalay and Delson, 1979), contrary to Szalay's (1975) earlier assumptions. The fact that both hominids and cercopithecoids exhibit this trait, but not pongids and platyrrhines, suggests that either parallelisms or reversals did occur. In fact,

TABLE 3

Comparison of Some Characters in *Oreopithecus* to Those of a Hypothetical Pongid-Hominid Ancestor and the Mechanical Functions and/or Behaviors Associated with Each Character in Hominoids^a

Hypothetical ancestor	Associated function	<i>Oreopithecus</i>
<i>Upper limb</i>		
1. Unfused os centrale	Midcarpal mobility in arboreal behaviors	Present
2. Reduction of contrahentes muscle in the hand ^b	Hooklike cheiridial grasp deemphasizing abduction-adduction of digits	Shape of metacarpophalangeal joints and mediolaterally narrow metacarpal shafts suggest reduced emphasis of abduction-adduction
3. Proximodistally elongated hamate with triquetral surface oriented ulnarly ^b	Hooklike hand grasp emphasizing mediolateral deviations at midcarpal joint	Present
4. Well-developed radiopalmar bifascicular ligament ^b	Pronation supination, suspensory behaviors	Well-formed attachment area for ligament
5. Emphasis on radial loading	Pronation supination, deemphasis on ulna for weight support functions	Narrow radial articular area of lunate relative to scaphoid's
6. Distally migrated pisiform ^b	Ulnar adduction Increased power to flex flexed wrist	Elongated hamate with superiorly directed hamulus
7. Nonarticulating ulnar styloid process ^c	Abduction-adduction of radiocarpal joint, forearm rotation	Present?
8. Semilunar meniscus and triangular articular disc ^d	Pronation supination	Suggested by distal articular surface on ulnar head
9. Neomorphic ulnar head with large bifaceted semilunar articular surface ^d	Pronation supination	Present
10. Distally shifted biceps tuberosity of radius ^b	Elbow joint flexion Pronation supination	Present
11. Spool-shaped trochlea ^d	Rotation of shoulder joint Pronation supination	Present
12. Reduced olecranon process	Increased degree of elbow extension Associated rotation of shoulder and forearm	Present
13. Deep humeral olecranon fossa	Increased degree of elbow extension	Present
14. Well-developed medially directed medial epicondyle	Mediolateral axis of hand held \perp to mediolateral axis of elbow Pronation supination	Present
15. Proximal epiphysis of ulna hafted medially on diaphysis ^d	Pronation supination	Present
16. Midsagittal keel on semilunar ulnar articulation ^d	Shoulder rotation Pronation supination	Present
17. Bifaceted circumferential articulation on radial head ^d	Shoulder rotation Pronation supination	Present
18. Continuous articular surface on radial notch	Pronation supination	Present
19. Well-developed short heads of pronators and/or supinators of forearm ^d	Pronation supination	Suggested by demarcation of origin on ulnar shaft
20. Trochlear keel on humerus ^d	Shoulder rotation Pronation supination	Present

TABLE 3
Continued

Hypothetical ancestor	Associated function	<i>Oreopithecus</i>
21. Mediolaterally wide humeral trochlea	Pronation supination Orientation of mediolateral axis of elbow joint along line of propulsion	Present
22. Well-delineated humeral bicipital groove ^d	Shoulder rotation	Present
23. Distally shifted deltoid tuberosity	Abduction of shoulder joint	Present
24. High humeral torsion <115° ^d	Dorsally positioned scapula Rotation and abduction of shoulder joint	Present
25. Relatively long and wide acromion process ^d	Mobility of shoulder joint Stability of humeral head	Present?
26. Well-developed coracoid process ^b	Abduction and rotation of shoulder joint Mobility of scapula	?
27. Dorsally positioned scapula ^d	Mobility of scapula Abduction of shoulder	Present
28. Laterally directed glenoid ^d	Abduction of shoulder	Present
29. Large humeral articular surface ^b	Shoulder mobility	Present
30. Well-developed lesser tubercle of humerus considerable separation from greater tubercle ^b	Rotation and stabilization of mobile shoulder joint	Present
31. Clavicle long relative to body length	Stabilization of shoulder mobility Dorsally positioned scapula Broad thorax	Present
32. Humerus and radius approximately equal length	Generalized arboreal forelimb	Present
33. Hand long in proportion to trunk length	Grasping ability Arboreality	Present
34. Relatively long vertebral border of scapula ^b	Mobility and stability of scapula	?
35. Upper limb long in proportion to trunk ^b	Forelimb suspensory behaviors Arboreality	Present
<i>Lower limb</i>		
36. Reduction of contrahentes in foot ^b	Emphasis on grasping ability of foot Arboreality	Mediolaterally narrow metatarsal shaft and metatarsophalangeal joint suggests reduced abduction-adduction
37. Interossei abduction axis through third digit	Generalized grasping foot	Present? Suggested by rotational joint between navicular and entocuneiform and attachment areas on metatarsals
38. Foot functional axis through 2nd digit	Emphasis on hallucal grasp	Present
39. Poorly developed plantar aponeurosis	Increased mobility of foot Specifically independent movement of midtarsal from tibiotalar and subtalar joints Arboreality	Present?
40. Plantar aponeurosis separate from plantaris tendon ^b	Plantar flexion of subtalar Independent of tibiotalar and knee joint position	Present

TABLE 3
Continued

Hypothetical ancestor	Associated function	<i>Oreopithecus</i>
	Cautious climbing Arboreality	
41. Well-developed flexor digitorum brevis contributing short flexor tendons to at least the 2nd and 3rd toes ^b	Flexion of pedal joints independent of position of tibiotalar joint Ability to wrap foot along diameter of support with heel process in opposition to toes Suspensory and climbing behaviors Arboreality	Well-developed plantar process of tuber calcanei
42. Well-developed intrinsic musculature for the 5th toe ^b	Grasping ability of the foot Mediolateral mobility of the 5th ray Plantar flexion of subtalar joint Arboreality	Strong development of peroneal trochlea and associated lateral ridge of calcaneus
43. Calcaneal neck only slightly dorsiflexed ^b	Restricted degree of dorsiflexion at cubo-calcaneal joint Arboreality	Present
44. Absence of weight-bearing tubercles on tarsal bones	Emphasis on arboreal grasping and locomotor behaviors	Tubercles absent
45. Large abductable hallux	Grasping of horizontal supports during bipedal and quadrupedal behaviors Grasping of medium size vertical supports Multipurpose grasping ability in arboreal behaviors	Present
46. Strong degree of dorsiflexion at tibiotalar joint	Climbing of vertical support keeping sole of foot in contact with support Arboreality	Present
47. Considerable mobility of subtalar and rotation of tibiotalar joint ^b	Fully plantigrade foot postures Grasping supports of different orientation Climbing on vertical supports keeping sole of foot in contact with support and placing longitudinal axis of foot along support diameter Arboreality	Present
48. Relative long in-lever (power arm) and short out-lever (load arm) of plantar flexion	Restricted dorsiflexion of midtarsal and tarsometatarsal joint Longitudinal plantar arch Grasping large diameter supports with foot's longitudinal axis around support diameter Arboreality and terrestrial bipedality	Present
49. Relatively short tarsal row ^b	Grasping large diameter supports with foot's longitudinal axis around support diameter Lack of strong toe off phase Arboreality	Present
50. Foot relatively wide mediolaterally	Large abductable hallux Mediolateral stability Arboreality	Present
51. Strong femoral bicondylar angle ^b	Control for distance of center of gravity from support in extended knee postures Emphasis on climbing vertical supports	Present

TABLE 3
Continued

Hypothetical ancestor	Associated function	<i>Oreopithecus</i>
52. Tibia 80% of femoral length	Emphasis on powerful abduction and flexion Vertical climbing	Present
53. Mediolateral diameter of patella wide relative to proximodistal diameter ^b	Knee joint used in extended or approximating extended postures Stability for rotation of leg and abduction-adduction of hindlimb	Present
54. Pit on femoral head for ligamentum teres	Stability of hip joint, de-emphasis on hindlimb suspensory behaviors	Present
55. Large spherical femoral head ^b	Mobile hip joint	Present
56. Mediolaterally wide and robust femoral shaft ^b	Emphasis on abduction-adduction of thigh Laterally rotated hip Climbing, arboreality	Present
57. Relatively large femoral neck angle > 100° ^c	Thigh mobility, specifically abduction Arboreality	Present
58. Relatively long femoral neck ^b	Hip stabilization Lateral and medial rotation Hip abduction Climbing and bipedalism	Present
59. Negative femoral torsion ^b	Ability to wrap limb around large-diameter vertical supports Strong adduction, enables lower limbs to cover greater volume of supports Climbing	Present?
60. Lower limb short relative to trunk length ^b	Powerful adduction of lower limb Climbing large-diameter vertical supports	Present
<i>Pelvis and trunk</i>		
61. Relatively wide ilia ^d	Hip stabilization Vertical climbing Bipedalism	Present
62. Relatively short ilia compared to African apes	Less stability of lumbar vertebral column relative to African apes	Present
63. Posteriorly facing iliac wings (alae)	Control for position of center of gravity relative to support diameter when climbing vertical supports Arboreality	Present
64. Coccygeal musculature refashioned into pelvic diaphragm	Erect postures Vertical climbing Bipedal behaviors (Related to absence of tail)	Present as suggested by ischial and sacral morphology
65. Absence of tail	Conservation of heat De-emphasis on leaping	Tail absent
66. Increased number of sacral vertebrae ^c	Reduction in lumbar vertebrae Loss of tail Cautious climbing Vertical climbing	Present
67. 3 or more sacral vertebrae participating in sacroiliac joint ^c	Reduced ischiosacral mobility Climbing vertical supports Erect postures	Present
68. Absence of ischial callosities ^b	Squatting postures	Callosities absent
69. Proximodistally narrow verte-	Short trunk	Present

TABLE 3
Continued

Hypothetical ancestor	Associated function	<i>Oreopithecus</i>
bral bodies relative to mediolateral X-section ^b	Restricted mobility of column Vertical climbing Erect postures	
70. 5 lumbar vertebrae ^b	Reduced lumbar length and mobility of lumbar column Climbing Erect postures	Present
71. 12 thoracic vertebrae ^b	Reduction in length of thoracic trunk Vertical climbing Erect postures	Present
72. Caudally directed spinous processes of thoracic and lumbar vertebrae	Erect postures Vertical climbing	Present
73. Less fasciculated and developed extensor back musculature ^b	Reduction in mobility of lumbar column Climbing Erect postures	Present (?)
74. Acute costal angle ^d	Dorsally positioned scapula Ventrally displaced vertebral column Climbing on large-diameter supports Erect postures	Present
75. Central pericardial ligament ^d	Short trunk length Climbing Erect postures	Presence suggested by trunk length
76. Reduced number of tracheal rings ^d	Short trunk length Climbing Erect postures	Presence suggested by trunk length
77. Fixture of duodenum retroperitoneal wall ^b	Erect postures	Present?
78. Sinistral deviation of cardiac apex ^b	Short trunk length Climbing Erect postures	Presence suggested by trunk length
79. Reduction of subpericardial sinus ^b	Reduction of trunk length Climbing Erect postures	Presence suggested by trunk length
80. Reduction of the retrodiaphragmatic portion of the pleural cavity Dome-shaped flattopped diaphragm ^b	Reduction of trunk length Climbing Erect postures	Presence suggested by trunk length and costal angle
81. Fusiform thoracic cage ^b	Greater increase of pleural cavity volume per unit length diaphragm descends relative to a cylindrical thorax (Associated with short trunk and abdominal cavity and posteriorly directed iliac blades)	Present
82. High intermembral index ^b	Emphasis on forelimb for locomotion Arboreality	Present
<i>Other</i>		
83. Prolonged maturation	—	Suggested by delayed fusion of epiphyses
84. Increased duration of infant dependency	—	Suggested by delayed fusion of epiphyses

nonhelical is a functional misnomer, since the movement at the human and cercopithecoid joint is of a helical nature (Manter, 1941; Lewis, 1980; Sarmiento, 1986). The only difference existing is the degree of movement allowed at the joint and not the anatomical elements associated with the movement (Lewis, 1980). The claim that *Oreopithecus* like *Homo* has restricted movement at this joint in no way excludes it from ancestry to any living lineage of hominoids. Nevertheless, *Oreopithecus* actually seems to have a range of movement at the subtalar joint comparable to that of chimpanzees and considerably more than humans.

Simons (1972) has emphasized the presence of a ventral midsagittal keel on the lum-

bar bodies of *Oreopithecus* as a derived trait suggestive of cercopithecoid affinities. However, as shown by the author's studies (Sarmiento, 1985), a ventral midsagittal keel is a trait which may be expected in a midsize hominoid which has not markedly reduced the number of lumbar vertebrae and joints. The strong anterior longitudinal ligament associated with this keel would provide the rigidity of the lumbar column needed for climbing (Sarmiento, 1985). For instance, in the midsize siamangs with four to five lumbar vertebrae (Schultz, 1944), the ventral midsagittal keel may occur as a matter of variation. Therefore, the presence of a keel in *Oreopithecus* is not a rare feature among some hominoid genera. Moreover, in theory it may

←

^a Question marks indicate the absence of relevant fossil material to ascertain presence of trait. Following "Present," a question mark indicates that the evidence suggesting the presence of a trait is not conclusive.

^b Traits unique to hominoids from among catarrhines.

^c Traits unique to hominoids from among anthropoids.

^d Traits unique to hominoids from among primates.

The following studies served as reference for the hypothetical traits of a common hominoid pongid ancestor:

1. Schultz, 1956, 1968; Tuttle, 1975b; Sarmiento, 1985; Corrucini, 1978.
2. Forster, 1916; Jouffroy and Lessertisseur, 1959; Markze, 1971.
3. Sarmiento, 1985.
4. Lewis, 1974; Sarmiento, 1985.
5. Lewis, 1969; Preuschoft, 1973a; Napier, 1963.
- 6 & 7. Mivart, 1867; Cartmill and Milton, 1977; Sarmiento, 1985.
- 8 & 9. Lewis, 1969; Sarmiento, 1985.
10. Le Gros Clark and Thomas, 1951; Napier and Davis, 1959; Sarmiento, 1985.
11. Washburn, 1950a; Hürzeler, 1958; Sarmiento, 1985.
12. Napier and Davis, 1959; Jolly, 1967; Sarmiento, 1985.
13. Napier and Davis, 1959.
14. Preuschoft, 1973a, 1973b; Sarmiento, 1985.
15. Oxnard, 1963; Sarmiento, 1985.
16. Mivart, 1867; Hürzeler, 1958; Sarmiento, 1985.
17. Sarmiento, 1985.
- 18 & 19. Hürzeler, 1958; Sarmiento, 1985.
20. Mivart, 1867; Preuschoft, 1973a, 1973b; Sarmiento, 1985.
21. Preuschoft, 1973a, 1973b; Sarmiento, 1985.
22. Gregory, 1934; Keith, 1934.
23. Le Gros Clark, 1971; Keith, 1934; Gregory, 1934.
24. Holl, 1891; Fick, 1904; Evans and Krah, 1944; Sarmiento, 1985.
25. Schultz, 1930, 1968; Ashton and Oxnard, 1964; Roberts, 1974.
26. Ashton and Oxnard, 1964; Oxnard, 1963, Oxnard, 1967.
- 27 & 28. Fick, 1904; Keith, 1934; Gregory, 1934; Schultz, 1956, 1968; Sarmiento, 1985.
29. Schultz, 1960.
30. Keith, 1934; Le Gros Clark, 1971.
31. Schultz, 1956, 1968.
32. Morton, 1924; Morton and Fuller, 1952; Gregory, 1934; Tuttle, 1975a.
33. Schultz, 1936, 1956, 1960, 1968.
34. Schultz, 1930; Erickson, 1963; Oxnard, 1963, 1967; Roberts, 1974.
35. Schultz, 1956, 1960, 1968.

36. Jouffroy and Lessertisseur, 1959; Straus, 1930.
37. Straus, 1930.
38. Morton, 1924; Morton and Fuller, 1952; Le Gros Clark, 1971.
39. Loth, 1908; Sarmiento, 1983a.
40. Loth, 1908; Sarmiento, 1983a.
41. Sawalashin, 1911; Sarmiento, 1983a.
42. Straus, 1930; Sarmiento, 1986.
43. Sarmiento, 1986.
44. Weidenreich, 1922; Morton, 1924; Midlo, 1934; Tuttle, 1975b.
45. Forster, 1922; Weidenreich, 1922; Sarmiento, 1986.
- 46 & 47. Sarmiento, 1986.
48. Schultz, 1963; figure 9.
49. Morton, 1924; Gregory, 1934; Sarmiento, 1986.
50. Schultz, 1956, 1960.
51. Prost, 1980; Sarmiento, 1985.
52. Schultz, 1930, 1936, 1968.
53. Schultz, 1960, 1968.
54. Mivart, 1866.
- 55 & 56. Schultz, 1960.
57. Schultz, 1960; Straus, 1963; Robinson, 1972; Sarmiento, 1986.
58. Schultz, 1960.
59. Sarmiento, 1985.
60. Schultz, 1956, 1968; Biegert and Mauer, 1972.
61. Schultz, 1930, 1936, 1968; Robinson, 1972; Sarmiento, 1986.
- 62 & 63. Schultz, 1930, 1936, 1961; Sarmiento, 1985.
64. Elftman, 1932.
65. Thorington, 1966; Schultz, 1968; Cartmill and Milton, 1977.
- 66 & 67. Schultz, 1961; Sarmiento, 1985.
68. Schultz, 1960, 1961; Rose, 1974.
69. Schultz, 1953, 1961; Sarmiento, 1985.
- 70 & 71. Schultz, 1961; Sarmiento, 1985.
72. Mivart, 1865; Ankel, 1966.
73. Keith, 1934; Tuttle, 1975a.
74. Schultz, 1960, 1961.
- 75-80. Keith, 1934; Washburn, 1950b.
81. Schultz, 1961; Schmid, 1983; Sarmiento, 1986.
- 82-84. Schultz, 1956, 1960, 1968.

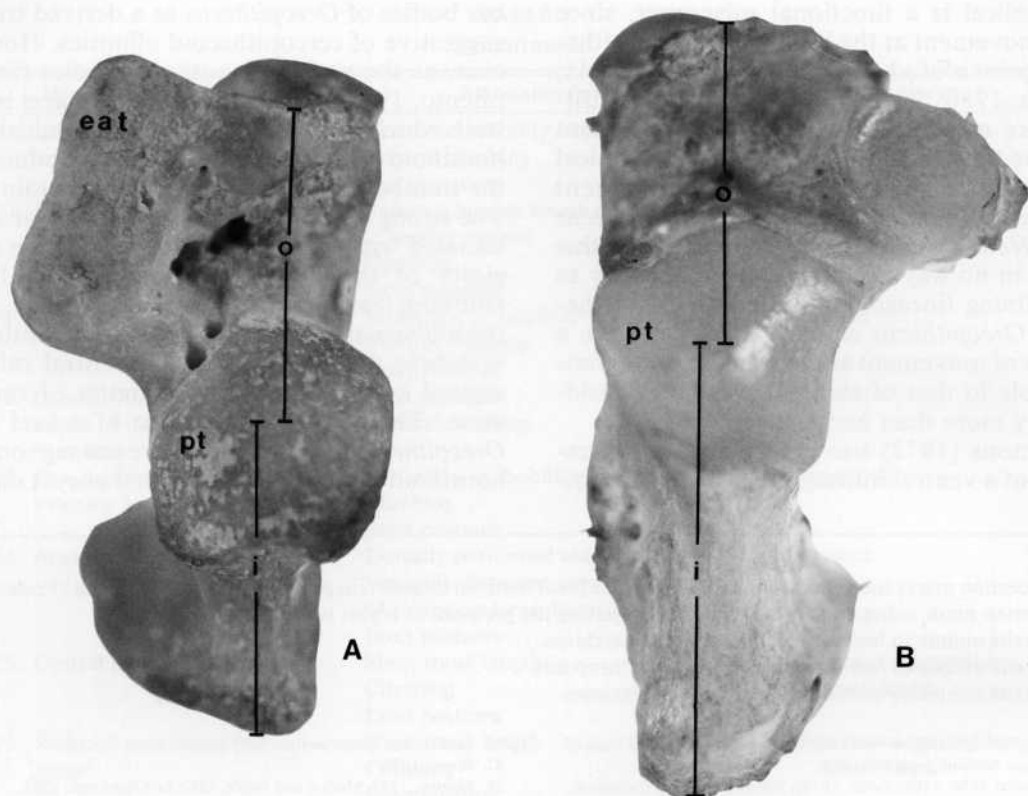
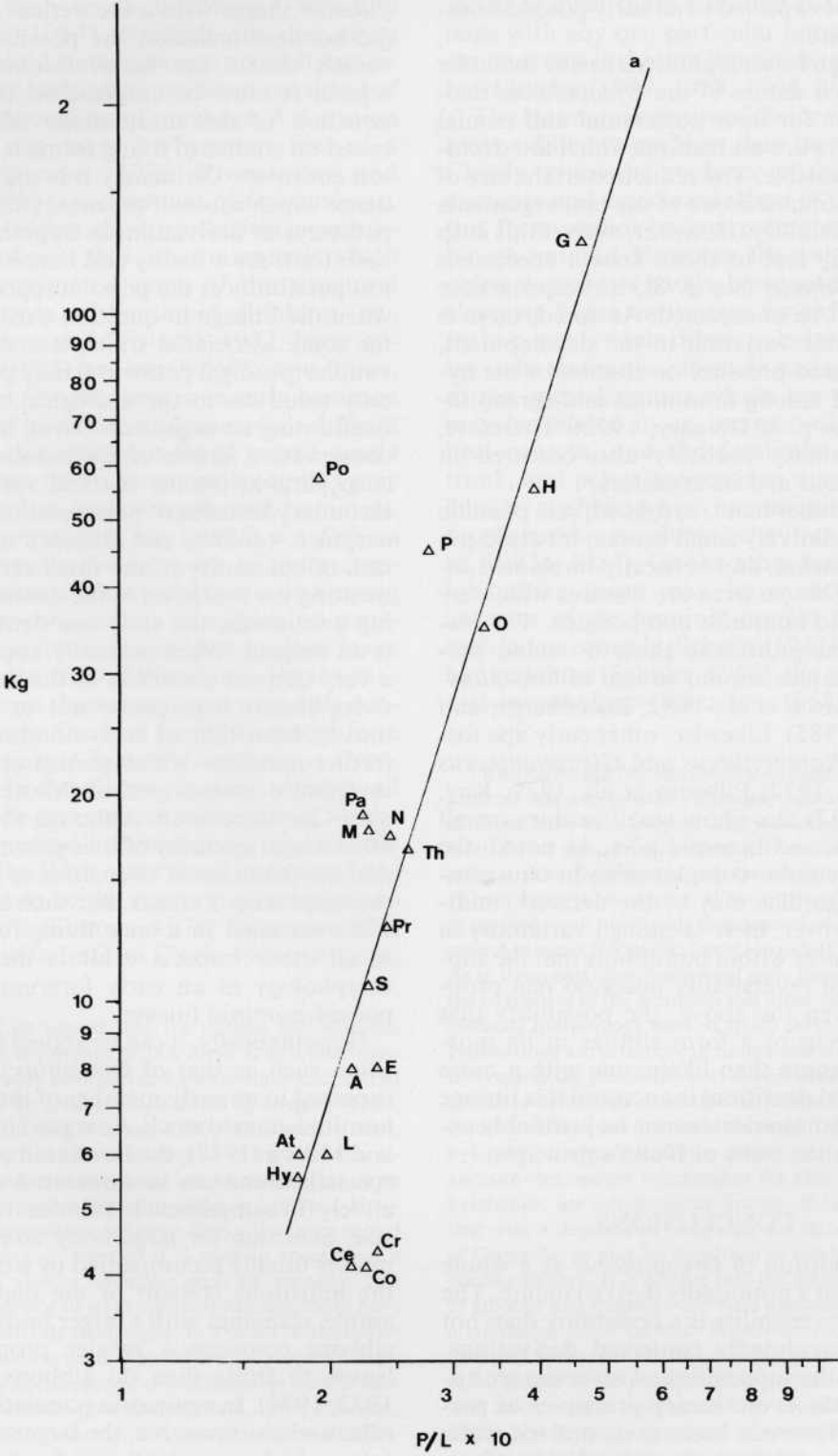


Fig. 8. Dorsal view of the right (A) and the left (B) calcanei of a wild caught and a captive female orangutan, respectively. Both animals have approximately equal upper-limb length. However, the captive animal weighed approximately twice as much as the wild caught individual. Note the absolutely much longer inlever (i) (or power arm) and shorter outlever (o) (or load arm) in the captive animal. Also note the differences in the subtalar articular surfaces. In the wild caught specimen the posterior talar facet (pt) is extended posteromedially and has a greater proximodistal concavity than in the captive individual. Moreover, the captive animal lacks the anterior extension of the anterior talar facet (eat). Wild caught male orangutans exhibit anterior talar facets similar to those of this captive female. (A and B $1.75 \times$ natural size).

Fig. 9. Logarithmic plot of the weight in kg (y-axis) versus the ratio of the power arm (P) to the load arm (L) times 100 (x-axis) in some anthropoid genera. Line a (slope 3.256, y-intcp. -0.38854 , correlation coefficient $r = 0.994898$) indicates the regression formed from the values plotted for humans, gorillas, *Oreopithecus*, and hylobatids. Chimpanzees with a relatively smaller lever arm ratio fall slightly below the 95% confidence limits of the above regression. Measurements of lever arm ratios are after Schultz (1963). Therefore, the distance from the axis of the tibiotalar joint to the metatarsophalangeal articulation is taken as the length of the load arm (outlever). The distance from the most posterior point on the tubercalcanei to the tibiotalar joint axis is taken as the length of the power arm. Weights presented for living genera are collected from field records of wild caught individuals (see Sarmiento, 1985). Relationship between vertebral body area and humeral and femoral circumference were used to estimate the 35 kg weight for *Oreopithecus* (Sarmiento, 1986). Abbreviations: H = *Homo*, G = *Gorilla*, P = *Pan*, Po = *Pongo*, O = *Oreopithecus*, S = *Symphalangus*, Hy = *Hylobates*, M = *Macaca*, Cr = *Cercocebus*, Pa = *Papio*, Th = *Theropithecus*, Ce = *Cercopithecus*, E = *Erythrocebus*, Pr = *Presbytis*, Co = *Colobus*, A = *Ateles*, AT = *Alouatta*, L = *Lagothrix*.



actually be expected in an early pongid-hominid ancestor.

Although better arguments can be made for the derived nature of the *Oreopithecus* dentition than for their postcranial and cranial traits, there are no features which are decidedly irreversible. The reduction in the size of the hypoconulid is one of the best arguments for irreversibility. However, even if this cusp was totally lost in those known specimens of *Oreopithecus* (see p. 8), its reappearance would not be unexpected. As noted, there is considerable variation in the development, position, and presence or absence of the hypoconulid among hominoids and cercopithecoids (see p. 8; Gregory, 1922). Therefore, this variability probably also occurred in *Oreopithecus* and its ancestors.

On the other hand, as argued, it is possible that the relatively small canine, bicuspid p3, small diastema, and vertically implanted incisors of *Oreopithecus* are features which are ancestral to hominids and pongids. The Hadar australopithecines show a canine premolar complex similar to that of *Oreopithecus* (Johanson et al., 1982; Rosenberger and Delson, 1985). Likewise, other early ape fossils, i.e., *Ramapithecus* and *Gigantopithecus* (Pilbeam, 1972; Pilbeam et al., 1979; Kay, 1981, 1982) also show small canines, small diastemas, and bicuspid p3's. As noted, the canine premolar complex seen in chimpanzees and gorillas may be the derived condition. However, there is enough variability in these features within hominoids that the supposition of reversibility poses no real problems. Given the above, the possibility that *Oreopithecus* or a form similar in its morphology (more than likely, one with a more generalized dentition) is ancestral to a lineage of living hominoids cannot be justifiably excluded on the basis of Dollo's principle.

CONCLUSIONS

The dentition of *Oreopithecus* as a whole does exhibit a profoundly derived nature. The fact that reversibility is a possibility does not justify convolutedly contrived derivations. As noted, the supposition of reversals are opposed to the evolutionary principles of parsimony. However, because its derived traits pale next to the large number of traits *Oreo-*

pithecus shares with a theoretical early pongid-hominid ancestor, the possibility of reversals should not be overlooked. In this regard, it must be emphasized that reconstruction of the morphology of ancestors based on studies of living forms is a theoretical endeavor. Ultimately it is the fossil evidence which shows if the most parsimonious pathways of derivation, as hypothesized for each trait, are a reality and hence an ecological possibility at the point in space and time when the lineage in question exists. At least for some associated traits, less direct derivations (prodigal pathways) may provide the only solutions to the ecological constraints confronting an organism. Given (a) the very conservative nature of the hominoid molar cusp pattern, (b) the marked variability of secondary features of hominoid molars (i.e., cusps, conules, and cingula), and (c) the lack of continuity in the fossil record documenting the evolution of the dentition of living hominoids, the early ape dental pattern is an enigma. What presently appears to be a very derived condition in the dentition of *Oreopithecus* may prove not to be so removed from that of early hominoids when further remains—which permit unequivocal taxonomic assessment of Miocene dental apes—are uncovered. Although the comparative dental anatomy of living forms suggests that the dentition of *Oreopithecus* is derived, the fossil record attests that such a dentition was associated to a once living form which in all other respects exhibits the expected morphology of an early forerunner of the pongid-hominid lineage.

Hypothetically, it can be argued that a dentition such as that of *Oreopithecus* may be expected in an early member of the common hominid-pongid stock. As argued by Cartmill and Milton (1977), the hominoid postcranial specializations can be associated with a relatively (in comparison to primates) large body size. Selection for large body size in mammals is usually accompanied by a decrease in the nutritious content of the diet. For example, siamangs with a larger body size than gibbons consume a greater proportion of leaves to fruits than do gibbons (Chivers, 1972, 1974). In sympatric populations of gorillas and chimpanzees, the larger size gorilla eats a higher percentage of greenery and

roughage than do chimpanzees (Tutin and Fernandez, 1984). Similarly the diet of an early hominid-pongoid ancestor which was increasing its body size may have consisted of a greater percentage of roughage. A dentition reflecting the more herbivorous diet of a browser (Simons, 1972; Rosenberger and Delson, 1985), as does that of *Oreopithecus*, would be within the hypothetical possibilities. It is of note that other mammals which have approximated some of the structural specializations of hominoid climbing, i.e., sloths (Straus and Wislocki, 1932; Sarmiento, 1983a, 1985), are largely folivorous forms.

Whether *Oreopithecus* is an early common ancestor of hominids and pongids is difficult to prove. A continuous fossil record would at best show that a form similar to this may be ancestral to both pongids and hominids. However, proof that this fossil is not such an ancestor awaits the recovery of more complete remains of other fossil forms. In keeping with the evolutionary principles of parsimony, these forms would have to show fewer derived traits than *Oreopithecus*. At the moment without these remains or with only dental fragments, the best plausible model for a common pongid-hominid ancestor is *Oreopithecus*.⁷ In a phylogenetic scheme this fossil may then be given status as the model for the common pongid-hominid ancestor, but only temporarily. With other fossil finds this form may prove to be the aberrant ape most have claimed it is (Simons, 1972; Pilbeam, 1972; Schultz, 1960; Le Gros Clark, 1971; Gregory,

1916) or even share a unique common heritage with any one particular hominoid genera or group including hominids, as claimed by Hürzeler (1949, 1958, 1968, 1977).

The taxonomic status of *Oreopithecus* presents a different problem than its phylogeny. Clearly, given the evidence of the forelimb anatomy and associated shape of the thorax, this form cannot be interpreted as anything but a hominoid. However, the systematic position it occupies within hominoids is not so clear cut. Some traits argue for a closer affinity to pongids while others to hylobatids, giving it the status of a "form de passage." Many of the specializations which are pongidlike may be related to an increase of size. The heel process, and the forelimb, hindlimb, trunk, and pelvis proportions may be paralleled by a gibbon which increases its size⁸ and must abandon acrobatic behaviors (Sarmiento, 1983a, 1985). On the other hand, the hylobatidlike traits may be expected in an ancestor of the hominid-pongoid stock. The unfused os centrale (Schultz, 1960), five lumbar vertebrae (Schultz, 1960), the overall cranial morphology (Hürzeler, 1968), and the

⁸ Rüttimeyer (1876) was the first to suggest that *Oreopithecus* was a hylobatid. Although claims to hylobatid affinities have been proposed for a number of different fossil forms (i.e., *Propithecus*, *Pliopithecus*, *Limnopithecus*, and *Dendropithecus*), the evolutionary history of hylobatids is an enigma. What exists of the skeleton of reputed fossil hylobatids shows conclusively that they cannot be correctly classified as hylobatids (Fleagle, 1984). As in those past classifications of early fossil catarrhines, the characters of the dentition and other features of craniofacial morphology used to group these fossils in the Hylobatidae are primitive in nature and size related. In this regard, the possibility that *Oreopithecus* may be ancestral to hylobatids cannot be fully discounted without evidence of a better hylobatid ancestor. Decidedly non-hylobatid irreversible traits, which exclude such an ancestor-descendant relationship for *Oreopithecus* and hylobatids, are not presently known. It is conceivable that with a decrease in body size, the elaborate molars of *Oreopithecus* may be simplified to reach a more gibbonlike pattern. It is of note that the smaller body size of gibbons and frugivory are both associated with such a simplified molar pattern. Moreover, considering the tendency in hylobatids to increase the relative mesiodistal length of the m3 and decrease that of c1 and p3 with an increase in body size (cf. fig. 2 to Hürzeler, 1958, 1968), the dental proportions of *Oreopithecus* are remarkably close to those of hylobatids.

⁷ It could be argued that the middle late Miocene stratigraphic occurrence of this fossil is at a later time period than may be expected for a common ancestor of humans and the great apes. As noted by Gregory (1922; also see Smith and Pilbeam, 1980; Ward and Kimbel, 1983), a separate lineage leading to orangutans can already be recognized by middle late Miocene times, at an absolute date earlier than *Oreopithecus bambolii*. However, that *Oreopithecus* is known from a later time period has no bearing on whether it is such an ancestor or a form which closely resembles such an ancestor. The common ancestor of great apes and humans could have persisted relatively unchanged, to a point in time after the differentiation of its descendants into separate taxa. The possible occurrence of *Oreopithecus* or a form similar to it at Maboko (von Koenigswald, 1969; Harrison, 1982), a middle Miocene site, would confirm the likelihood of such a vertical distribution.

exclusively arboreal characters of the hands and feet are all such examples.

However, further recovery of the midcarpal bones may prove that this form is closer to hylobatids. Although in *Oreopithecus* the hamate forms the majority of the articular surface with the proximal carpal row (Sarmiento and Rose, 1985), the morphology of the trapezocapitate embrasure is unknown. As shown by Jenkins (1981) the embrasure and the large articular surface of the hamate is a joint complex for midcarpal rotation which among hominoids is unique to gibbons and siamangs. Moreover, in the orientation of both radial circumferential articulations and in the expansive articular surface of the annular ligament around the radial head and neck, the brachioantibrachial joint of *Oreopithecus* also finds a close similarity with that of hylobatids. If *Oreopithecus* proves to be an early hylobatid, it will serve to support the hypothesis that during the evolutionary history of this family climbing preceded and was preadaptive to brachiation (Jungers and Stern, 1984; Cartmill, 1985).

Given what postcranial morphology exists and the seemingly derived dentition, it is probably best to place *Oreopithecus* in its own family the Oreopithecidae, as has been done before by a number of different authors (Schultz, 1960; Straus, 1963; Schwalbe, 1915; Thenius, 1958). However, contrary to the conclusions of these authors, this family may best be interpreted as one occupying an intermediate position between hylobatids and pongids.

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APPENDIX

In many features the foot of *Oreopithecus* resembles that of chimpanzees. The large abductable hallux, the associated morphology of the entocuneiform, and the degree of mobility at the tibiotalar and subtalar joints are all examples of such features. Because among the living hominoids the chimpanzee foot seems to be the least derived from the an-

cestral type (Weidenreich, 1922; Morton, 1924; Midlo, 1934; Rose, 1984), a similar pedal morphology may also be expected in a forerunner of the pongid-hominid lineage. However, despite its general similarity to the foot of chimpanzees, the foot of *Oreopithecus* differs significantly in one important functional respect: it lacks those chimpanzee specializations which are adaptations to partial terrestriality.

As noted, the absence of well-developed weight-bearing tubercles on the tarsals, i.e., the anterior plantar tubercle, navicular tuberosity, and the cuboid tuberosity, indicate that (unlike tarsal rows in the semiterrestrial chimpanzee and terrestrial cercopithecoids) the anterior tarsal row of *Oreopithecus* did not come into contact with and directly unload weight onto the substrate (Sarmiento, 1983a). The length proportions of the main parts of the foot, and the configuration of the metatarsocuboid and of the naviculoentocuneiform articulations, which reflect the restricted dorsiflexion at the midtarsal and tarsometatarsal joints, further support this claim. Finally, the seemingly dorsally restricted articular surfaces on the metatarsal heads of *Oreopithecus* suggest that, unlike the situation in terrestrial primates, the metatarsophalangeal joint did not have a high degree of dorsiflexion.

However, despite the absence of chimpanzee-like terrestrial adaptations, *Oreopithecus* lacks the markedly arboreal adaptations of the orangutan foot. The only similarity the two share is the ball-and-socket-like articulation between the navicular and entocuneiform. Mechanically this articulation provides for rotation in the transverse plane of the navicular around the entocuneiform and hence the ability to form a transverse tarsal arch. Otherwise *Oreopithecus* does not exhibit as much mobility in the tarsal joints and possesses relatively much shorter metatarsals than orangutans. Furthermore, unlike orangutans, it has a large abductable hallux. The orangutan foot specializations are associated with grasping supports of relatively small diameters in a hooklike fashion (Sarmiento, 1985; Rose, 1986). The preference for this type of grasp is also responsible for the relatively longer distal tarsal row of

orangutans when compared to *Oreopithecus*. The extra control afforded by lengthening the distal tarsal row and hence increasing the lever arm of the evertors and invertors of the foot (i.e., tibialis anterior and posterior, and peroneus longus and brevis) is important when the digital pads overlying the heel process and tarsus are not pressed against the support and do not provide a stabilizing frictional force.

On the other hand, a grasp, in which the foot is fully wrapped around the diameter of the support with its heel applied diametrically opposite to the toes, produces a frictional force which fixes the tarsus in respect to the support. In this case, increasing the lever arm of the invertors and evertors, as is accomplished by lengthening the distal tarsal row, is not necessary to stabilize for unwanted tarsal movements. Similarly, for such a foot grasp, a large laterally directed adductor tubercle on the fifth metatarsal is not needed to stabilize for eversion of the distal tarsus and abduction of the metatarsus, since such stability is provided for by the frictional force. In *Oreopithecus* the plantar orientation of the abductor tubercle of the fifth metatarsal and the associated posteroplantar ridgeline extension of the pongid trochlear process emphasize the role of the ossi metatarsi quinti as a flexor at the expense of its role as an abductor. Considering the configuration of the cuboid-metatarsal articulation, the action of the ossi metatarsi probably resulted in dorsiflexion at the subtalar joint and the associated plantar displacement of the tuber calcanei. In this manner, the foot which will present a plantar concavity along its longitudinal axis can be wrapped around the diameter of the support.

The proximodistally short distal tarsal row also suggests that *Oreopithecus* could not practice the toe-off movements of terrestrial bipeds. For example, in humans the long distal tarsal row provides a longer lever arm for the evertors and invertors of the foot, to control for the position of the center of gravity in respect to the support point during toe-off (Sarmiento, 1986). If *Oreopithecus* did prac-

tice bipedalism it practiced a less fluent stride similar to that seen in hylobatids, in which the foot is lifted all at once from the support surface (Ishida et al., 1978, 1984).

Therefore, the short distal tarsal row, the restricted dorsiflexion and plantarflexion of the midtarsal and metatarsal joints, and the attachment area of the ossi metatarsi quinti suggest that *Oreopithecus* had a preference for supports of relatively large diameters. When grasping large diameter supports, that section along the support's circumference corresponding to the proximodistally short cuboid (relative to foot length) subtends a small central angle θ ; where the angle (γ) formed between the metatarsals or calcaneus and the cuboid is equal to $180^\circ - \theta$. Hence for small values of θ only a small degree of flexion at the midtarsal and tarsometatarsal joints ($\gamma \rightarrow 180^\circ$) is necessary to wrap the respective parts of the foot around the support's circumference.

Considering a preference for large-diameter supports and its exclusively arboreal adaptations, the foot of *Oreopithecus* finds its best functional analog in hylobatids. The differences existing between the foot of hylobatids and *Oreopithecus* may be size-related features, i.e., the heel process (Sarmiento, 1983a), the proportions of the main parts of the foot, and the complete incorporation of the sesamoid of tibialis posterior into the navicular. Following the size-related trend in behavior set by the larger siamang when compared to the gibbon, it may be expected that the foot of *Oreopithecus* was used even less for leaping and more for grasping during slow climbing. Bipedalism along supports, in which the large abductable hallux was used in opposition to the toes as seen in hylobatids, may also have been a common behavior in this fossil. In this regard, the similarities between the chimpanzee and the *Oreopithecus* foot are not necessarily functional, but are likely to be in part size related. Nonetheless, these similarities almost certainly reflect the generalized hominoid pattern and shared hominoid ancestry of chimpanzees and *Oreopithecus*.