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Evolution and Interrelationships of the Catarrhine Primates

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I. Introduction

The object of this chapter is to present our assessment of phyletic relationships among Old World higher primates in the light of the "cladistic" methodology when possible, and to suggest possible phylogenetic and classification scheme(s) for this group consistent with this interpretation. In the first section of the paper, morphological data (mostly dental, cranial and postcranial skeletal) in a number of catarrhine groups will be presented. The typical morphologies which can be inferred within each group are taken to correspond to the hypothetical (ancestral) morphotype, that which would be expected in the latest common ancestor of the animals on which data have been provided. Fossils will be included with the groups to which they belong where such relationships are clear. Other extinct forms will be treated separately in this phase.

The second section attempts to provide a reconstruction of the morphology to be expected in the ancestral catarrhine based on a combination of the several subordinate morphotypes. This correctly implies that we do consider all animals treated here to have

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had a single common ancestor, of as yet uncertain age and distribution. With this catarrhine morphotype as a basis, each of the major taxa will be reanalyzed in terms of the relationships of its constituent genera, modern and extinct. The result of these analyses will be a series of possible cladogram/phylogenies, with the taxonomic problems discussed for each group synthesized in a final proposed classification.

The essence of cladistic interpretation of relationships as seen here is that only those linkages based on shared derived ("advanced," apomorphic) characters reflect true phyletic relationships. Those based on shared ancestral ("primitive," conservative, plesiomorphic) features merely reflect common ancestry at some previous point in time and are thus not useful in forming subgroups of a larger taxon. For a further discussion

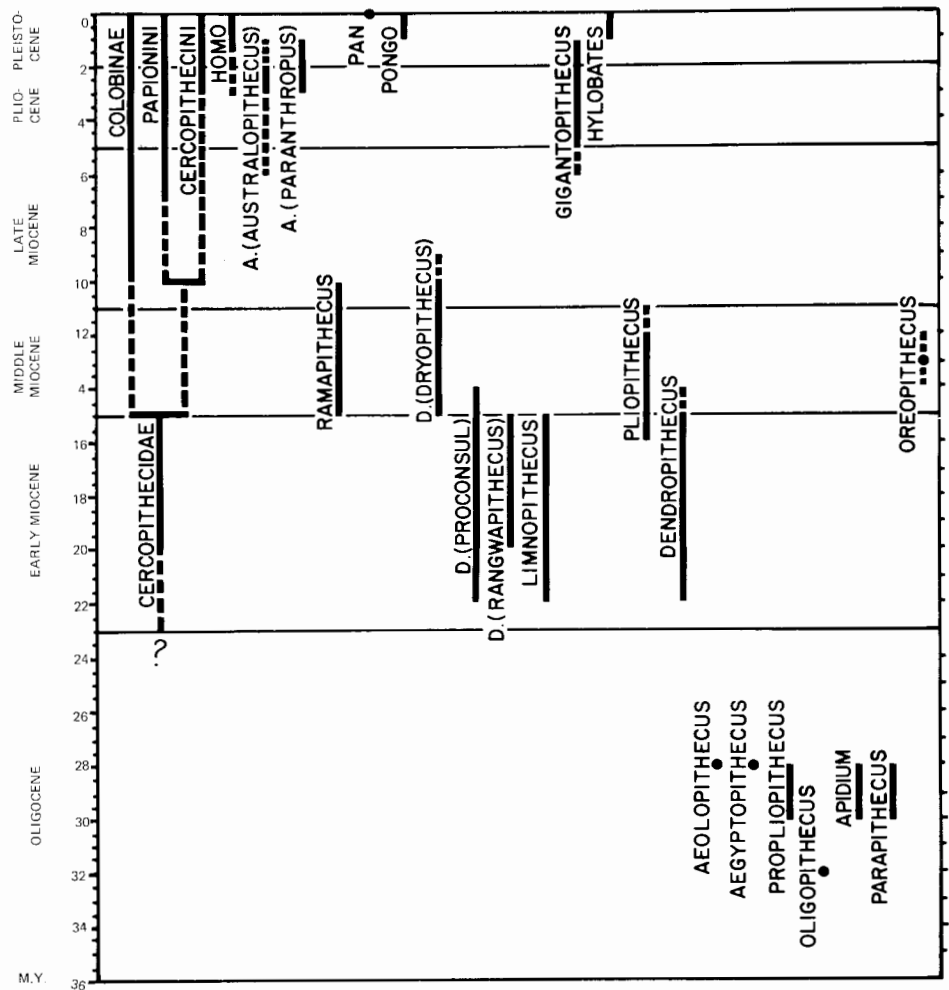


Fig. 1. Temporal ranges of cercopithecoid higher taxa and all other genera (and some subgenera) of catarrhines. Dashed lines indicate uncertain ranges, large dots single occurrences.

of this subject reference may be made to other papers in this volume and also to Schaeffer *et al.* (1972), Eldredge and Tattersall (1975), and Delson (1976).

Fossils may be incorporated in the deduction of ancestral morphotypes in order to increase the range of character variation available for study, but their age is not considered. Theories of relationship may be tested by comparing reconstructed morphotypes to known early fossils in order to see if any do agree with the prediction (Delson, 1975c). There may be cases where polarity along the morphocline is unclear, and we take the view that early fossils are more likely to be conservative in most features, having changed less from the actual ancestral condition. Thus, the morphology present in one or more early fossil members of the group under consideration, if it is one of the two alternative choices, is tentatively accepted as the less-derived one. This may introduce some circularity, but it appears to us better than merely ignoring that line of evidence until (if ever) more data become available. Additional theoretical aspects of the application of cladistics to paleontology, and especially to classification, will be considered at relevant points in the general discussion.

II. Distribution of Morphological Characters in the Catarrhini

In this section the six main groups we can distinguish are treated together with their potential fossil relatives. Because temporal occurrence is not emphasized at this point, we include for reference a stratigraphic range chart (Fig. 1). Other than for the Old World monkeys, whose single-family status seems clear, taxonomic ranking of the groups is studiously avoided in order to preclude biasing the conclusions. This may make the discussion more verbose, but it should permit clearer analysis eventually.

The majority of our interpretations and conclusions are based on skeletal elements that can be studied in fossils as well as in modern species. Owing to the frequency with which dental remains of extinct forms are preserved, teeth have been subjected to intensive study. The major results are discussed by group and summarized in Table 1, which also includes a list of dental features of the catarrhine morphotype. Additional information drawn from cranial and postcranial morphology, soft tissues, and karyology is summarized in Table 2.

Many researchers have utilized data on the relative lengths of skeletal segments as indicators of taxonomic and/or locomotor affinity among the primates. Recently, however, Biegert and Maurer (1972) have shown that many such features may reflect allometric modifications, and their results have been confirmed by the work of Andrews and Groves (1975). Comparing relative lengths of individual long bones and especially of the arm or leg to an axial vertebral length, Biegert and Maurer found that almost all catarrhines fall on a single regression line for each measure. Arm length increases more rapidly than leg length as body size increases, and thus the rise in intermembral index (radius + humerus/femur + tibia) from small monkeys to gorillas is size dependent, not phyletically (nor fully locomotorily) significant. Thus the most interesting cases are those of nonalignment with this general trend. Several basic long-bone indexes are presented for reference in Table 2, along with indications of placement with respect to

TABLE I
DENTAL CHARACTERS OF THE CATARRHINE ANCESTRAL MORPHOTYPE AND THEIR DISTRIBUTION IN THE INFRAORDER^a

Catarrhine ancestral morphotype ^b	Colobinae	Cercopithecini	Papionini	Hylobates	Pliopithecus and Dendropithecus	Homo (and Australopithecus)	Pongo and Pan	Gigantopithecus	Dryopithecus	Propithecus and Aegyptopithecus	Parapithecus and Apidium	Oreopithecus	Oligopithecus
I ¹ spatulate, long mesiodistally	A	A	D?	A	A	A	A	O	A	A?	O	A	O
I ² narrow conical crown	A	A	AD	D	A	D	AD	O	A	A?	O	A	O
C ₁ ¹ tall and bilaterally compressed	A	A	A	A	A	D	A	D	A	A	A	A	A?
sexually dimorphic	A	A	A	D	A	D	A	A?	A	A	A	A	O
C ¹ with prominent mesial groove not extending onto root	D	D	D	A	A	D	A	O	A	A	A	A	O
P ₂ ⁻ only 2 (AA = P ₂ retained—see text)	A	A	A	A	A	A	A	A	A	A	AA	A	A
P ₃ single-cusped	A	A	A	A	A	D	A	D	A	A	*	D	A
"sectorial" (C ¹ -honing) and bilaterally compressed	A	A	A	A	A	D	D	D	D	A	**	D	A
P ₄ two subequal cusps	AD	A	A	A	A	A	A	A	A	A	AD	A	A
P ⁻ two cusps, buccal more projecting	AD	A	A	A	A	D	A	A?	A	A	A	A	O
buccolingually broad	D	D	D	D	A	D	D	A	A	A	A	A	O
M ₁ ⁻ six cusps—													
paraconid retained	D	D	D	D	D	D	D	D	AD	D	A	D(A?)	A
hypoconulid developed	D	D	D	A	A	A	A	A	A	A	A	A	A
buccal cingulum developed	D	D	D	AD	A	D	AD	D	A	A	D	A	A
talonid broad, lower than trigonid	D	D	D	A	A	A	A	A	A	A	A	A	A
M ₃ larger than M ₂ larger than M ₁	A	A	A	D	A	D	AD	A	A	AD	AD	A	O(A?)
M ₃ narrow with larger hypoconulid	A	D	A	A	A	D	D	A	A	A	A	A	O
M ⁻ four cusps, hypocone small	D	D	D	A	A	D	D	D	A	A	A	D	O
lingual cingulum developed	D	D	D	AD	A	D	AD	D	A	A	A	A	O
M ¹ (at least) with protoconule	D	D	D	D	A	D	AD	D?	A	A	A	A	O
crowns buccolingually wide	D	D	D	D	A	D	D	A	A	A	A	D	O
M ² larger than M ³ larger than M ¹	AD	D	AD	A	A	D	D	O	A	A	A	A	O

^a A = Retention of ancestral condition, D = Development of a derived condition, O = Character state unknown (not preserved), ? Indicates uncertainty, * P₃ of *Parapithecus* and *Apidium* bicuspid, but probably part of different morphocline, ** Retained P₂ of *Parapithecus* (and *Apidium*?) apparently adapted to honing C¹

^b A dash indicates all teeth of the particular series (e.g., M⁻ refers to all upper molars in the series).

arm and leg allometries. Thoracic breadth is under similar allometric control among catarrhines (Andrews and Groves, 1975), but it is not yet certain how strongly such additional characters as vertebral number and lengths of hand, foot, clavicle, and tail are also dependent upon size (compare data in Table 2).

A. Old World Monkeys (Cercopithecidae)

The most characteristic feature of the cercopithecids is their dentition. As in most catarrhines, the dental formula is 2-1-2-3. Relative incisor size varies within the group. The canines are large stabbing weapons that show high sexual dimorphism; uppers, especially of males, present a deep, compressed cleft or sulcus on the mesial face that continues through the cervix onto the root. The P_3 is a unicuspid tooth with a sloping mesiobuccal flange for honing the C^1 and a distal fossa homoplastic, but probably not homologous, to the molariform-tooth talonid; in females the flange does not project far beyond the alveolar plane (if at all), but in males it sinks deeply below this level. All other cheek (postcanine) teeth are lophodont, with a single loph on premolars and two on molariform teeth (M and dP).

The molariform teeth of Cercopithecidae are all based on a single ground plan, consisting of a high ("hyposodont" of authors) crown with 4 marginal cusps linked by transverse ridges or loph(id)s, and 3 foveas separated by the 2 ridges. Upper teeth are, in general, mirror images of their mandibular isomer, with buccal and lingual feature reversed. The teeth widen or "flare" outward laterally from the cusp apexes to the cervix, especially on the buccal face of lowers and the lingual face of uppers, but there is no cingulum. Exceptions to this plan are found in M_3 and dP_3 ; in M_3 a hypoconulid is developed on the distal shelf in most forms; a paraconid is present on dP_3 mesial to the trigonid basin and is often joined to the protoconid by a paralophid. The P^4 consists of a small trigonid, subequal metaconid and protoconid linked by a molariform metalophid and a large talonid basin. The upper premolars are somewhat D-shaped, with straight buccal faces. On both P^4 and, especially, P^3 there is a prolongation of enamel onto the mesiobuccal root; this is apparently not functional and may represent an "overflow" effect from the canine-premolar honing field that induces the flange on P^3 . Cercopithecid dental function involves shearing along upper buccal and lower lingual notches combined with crushing (and guidance control) by loph(id)s (R. Kay, personal communication).

Despite the arguments of Schultz (1970) that the Old World monkeys are remarkably uniform in their morphology, a more detailed examination of at least some character complexes denies this homogeneity, in fact, to the point where further characterization of the family as a whole becomes difficult. The cranium of monkeys is quite variable in both size and form, with two main types noted below. In general the brain is relatively smaller compared to body size than in modern apes. According to Radinsky (1973, 1974), cercopithecid brains are characterized by a V- or C-shaped arcuate sulcus anteriorly. The external auditory meatus is tubular.

Other characters common to all cercopithecids may depend on their generally small size among catarrhines. There is little variation in precausal vertebra number, with generally 18 or 19 thoracic + lumbar and 2-4 sacral, but caudal number ranges between

TABLE 2
SUMMARY OF THE DISTRIBUTION OF SELECTED NONDENTAL CHARACTERS IN MAJOR CATARRHINE GROUPS^a

	Colobinae	Cercopithecini	Papionini	Hyllobates	Ptilopithecus	Dendropithecus	Homo (Australopithecus)	Pongo	Pan	Gigantopithecus	Dryopithecus (and Limnopithecus)	Propliopithecus and Aegyptopithecus	Parapithecus and Apidium	Oreopithecus	Oligopithecus
Relative depth of mandible S, shallow; M, moderate; D, deep	D/M	D/M	M	S	S/M	S/M	M	M	M	D	M/D	M	M	M/D	M/S
Mandibular shape C, constant; D, deepens; S, shallows mesially	C/S	D	D	D	D	D	C?	C	C	S	C/D?	C?	S?	C	C
Choanal shape W, wide and low; N, narrow and high; V, variable	V	N	N	W	O	O	N	N	N	O	O	N	O	O	O
External auditory meatus R, ring; T, tube	T	T	T	T	R	O	T	T	T	O	T	R	R	T	O
Inter-orbital distance W, wide; I, intermediate; N, narrow	W	N	N	W	W	O	W	N	W	O	I/W	I/W	O	W	O
Length of ulnar olecranon L, long; I, intermediate; S, short	L	L	L	S	L	L	S	S	S	O	L/I	L	O	S	O
Ulnar-carpal articulation S, styloid; L, lunula; D, derived (several types)	S	S	S	L	S	O	D1	D2	D3	O	D4(??)	O	O	O?	O
Astragalo-calcaneal joint H, helical; R, rotational	R	H	H	H	H?	H?	R	H	H	O	H?	H?	O	R	O
Tail P, present; A, absent	P	P	P	A	P?	O	A	A	A	O	O(P?)	P?	P?	O(A?)	O
Number of lumbar vertebrae	6-7	6-7	6-7	5	6-7	0	5	4	3-4	0	0	0	0	0	0
Number of sacral vertebrae	2-4	2-4	2-4	4-5	3	0	5-6	5-6	5-6	0	0	0	0	0	0
Intermembral index (range) (R + H/F + T) × 100	73-98 (105)*	74-90	81-100	120-155	94	96	64-79	135-150	100-125	0	?	0	0	119	0
Humero-femoral index (range) (H/F) × 100	71-90 (103)*	71-86	72-97 (103)*	115-125	85	90	68-74	128-147	98-122	0	?	0	0	117	0
Radio-humeral index (range) (R/H) × 100	90-110 (85-120)*	90-110	90-110+	105-135	105	104	65-85	92-109	73-100	0	86	0	0	95	0
Relation to allometric trend, arm: trunk T, near trend; L, limb long; VL, very long	T	T	T	VL	T	O	T	L	T	O	O	O	O	VL	O
Relation to allometric trend, leg: trunk: T, near trend; L, limb long; VL, very long	T	T	T	VL	T	O	VL	T	T	O	O	O	O	L	O
Appearance of ischial callosities PO, postnatal; PR, prenatal	Early PR	Early PR	Early PR	Early PO	O	O	Never	Later PO	Later PO	O	O	O	O	O	O
Diploid chromosome number 2n=	44-48	48-72	42	44-52	O	O	46	48	48	O	O	O	O	O	O

^a O, condition unknown; ?, condition uncertain; asterisks (*) indicate range increase by fossil.

3 and 30 (Schultz, 1970). Hand length is always less than foot length, and the upper limb longer than the lower. On the basis of data from several sources (sometimes measured by different methods), the intermembral index ranges from 73 to 100 (possibly to 105 in some fossils), the brachial (R/H) index from 90 (or 85?) to at least 116, and the humerus/femur index from 71 to 97 (100 or even 104 in some fossils). The trunk is relatively long and narrow, the clavicle short, and the scapula dorsolateral. The ulna possesses large olecranon and styloid processes with no carpal meniscus. The astragalo-calcaneal joint is typically not helical, as in most primates, but of a simple rotational form considered to be more derived (secondarily—see Szalay, 1975). Chromosome number is highly variable between groups as is the digestive system, but ischial callosities which appear early in prenatal development, are constant, although of varying separation across the midline.

The morphological diversity within the family permits the distinction of at least three main groups of genera. Most important are the subfamilies Colobinae and Cercopithecinae, but the latter may be further subdivided into tribes. The Colobinae, or leaf-eating cercopithecids, are characterized by facial and dental form and by their possession of sacculated, ruminant-like stomachs for processing of cellulose from the leaves that form the major part of their diet. The increased relief of their cheek teeth is similarly related to food processing (Walker and Murray, 1975). The molariform teeth are squarish, with low lateral flare, and the lowers present short trigonids and deep lingual (intercusp) notches. The protocone of P^3 is often reduced, especially in African colobines; on P_4 the metaconid may be subequal in size to the protoconid or may be strongly reduced or lacking. The incisors are relatively small, with I^2 typically conical and I_2 with a distolateral projection. Cranially the colobines are generally round skulled and especially short faced. The interorbital distance is high, as is total facial width. The nasals are short and wide, although they may lengthen in longer-faced forms such as *Nasalis*. The ethmoid bone contributes to the medial orbit wall; the lacrimal bone is also within the orbit, and the lacrimal fossa is formed partly by the maxilla. Choanal shape varies from wide and low to high and narrow, with no clear relationship to facial form. The mandibular body is either of relatively constant depth beneath the cheek teeth or is shallow mesially; the ramus is vertical. All colobines show some combination of expanded gonial region, "bulging" under the rear molars and possibly relatively deep corpus. Colobine long bones are usually gracile and the foot elongate, related to their principally arboreal locomotor pattern. The majority of colobines have 44 chromosomes; *Nasalis* has 48. Females do not have cyclic sexual swellings.

The Cercopithecinae have simple stomachs like those of other catarrhines (and most primates) and have cheek pouches for temporary storage of undigested food. For the most part their teeth are lower crowned (more "bunodont"), with little relief between cusp apexes and basin floors, long trigonids, and moderate to high lateral flare. The P^4 cusps either are subequal or the metaconid is wider and/or taller than the protoconid. The incisors are generally larger, with the uppers typically expanded and I^2 often tilted and not conical. Other features must be described for dentally distinct subgroups. Cranially the cercopithecinines are long faced, with long and narrow nasals, low interorbital and facial width, and great facial height, especially in the zygoma. The ethmoid

apparently grows forward in the midline and is covered by the frontal, the vomer expands to form part of the medial orbit wall, and the lacrimal expands mesially beyond the inferior orbit margin and envelops the lacrimal fossa; all of these features are clearly part of a single complex of facial lengthening (see Jones, 1972; Vogel, 1966; Verheyen, 1962—the latter two are especially important on catarrhine facial form). The choanae of cercopithecines are typically high and narrow, which may also reflect facial shape. The mandibular ramus is typically tilted back, but it may approach the vertical in shorter-faced forms (*Theropithecus*, *Cercopithecus*); a median mental foramen is present (it occurs rarely in other catarrhines; see Vogel, 1968); the body increases in depth mesially. The brain differs from that of colobines in several sulcal features reflecting rostral expansion of the occipital lobe and in positional changes of the sulcus rectus and the arcuate sulcus (Radinsky, 1974). The long bones of the often semiterrestrial cercopithecines are relatively robust. Chromosome numbers vary widely, but some patterns exist at lower taxonomic levels.

The Cercopithecini are mostly small arboreal forms, but the larger *Erythrocebus* is highly terrestrial, although gracile. They share strongly reduced third molars, with no hypoconulid on M_3 and a compressed distal loph on M^3 . The teeth are generally elongate with low flare, but in *Allenopithecus* flare is as great as in *Cercocebus*. The ischial callosities are separated by an area of haired skin. Female sexual swelling occurs only in *C. (Miopithecus) talapoin*; otherwise this species is a craniodentally typical cercopithecine. Chromosome number is strongly variable within this group, even within species of *Cercopithecus*, ranging from 60 to 72, with most at 60, 66, or 72. This pattern of spacing by units of 6 is continued by *Erythrocebus* and *C. talapoin* at 54, and apparently by *Allenopithecus* at 48 (see, *inter alia*, Boer, 1971).

The Papionini include small or medium-sized semiarboreal species of *Mocaca* and *Cercocebus*, along with larger and more terrestrial members of these genera, *Papio*, *sensu lato*, and *Theropithecus*. The chromosome number is 42 in all species, and female sexual swelling is pronounced. Dentally the group is most distinguished by the lack, or strong reduction, of enamel lingually on lower incisors, as well as relatively high lateral flare and often accessory cuspules on molars. *Theropithecus* departs from other papionins in converging on the high relief of colobines, while retaining large trigonids and flare; cranially this genus is also distinctive in its vertical ramus, anteriorly placed temporalis muscle, somewhat shortened face, and small incisors compared with large molars. These features are all part of a feeding complex described by Jolly (1970).

Determination of an ancestral morphotype for cercopithecids depends in part on characters present in other catarrhine taxa, but the ancestral state of some of the cercopithecoid dental specializations can be discussed here. Such obviously derived conditions as the loss of M_3 hypoconulids in Cercopithecini and of lingual incisor enamel in Papionini can be discounted immediately, but other polarities are more difficult to assess. The mesial groove of the upper canine passing continuously onto the root, as well as the bilophodont molar pattern and the absence of dP_4-M_2 hypoconulids, are further shared derived features of all Cercopithecidae that are probably part of the ancestral cercopithecoid morphotype, but are not to be expected in earlier ancestral catarrhines. For the lower premolars, it seems likely that the P_4 cusps were of subequal development in

early cercopithecids (or perhaps the protoconid was slightly higher; see below), and we expect such forms to have possessed rather strong development of C^1/P_3 honing, with a P_3 flange extending below the alveolar plane. It would appear that a relatively large (macaque-like?) trigonid was present in the lower molars of ancestral cercopithecids, based on comparisons within the group and with other catarrhines, but it is more certain that the high relief and deep lingual notches on the lower molars of colobines and *Theropithecus* are derived within the Cercopithecidae. Finally, lateral flare may have been moderately present in the early Old World monkeys, a point to be discussed at greater length below, in connection with the reconstruction of a precercopithecoid ancestor. In terms of other bodily systems, both types of digestive specialization within the Cercopithecidae (sacculated stomachs and cheek pouches) are just that, and are not to be expected in a common ancestor of the two subfamilies; Radinsky (1974) has suggested that the cercopithecine cerebral differences from colobines are derived, while the presence of an arcuate sulcus probably is a derived feature of monkeys among catarrhines; finally, Pocock (1925) considered that ischial callosities separated by haired skin (as in the Cercopithecini) were ancestral for the family, but he further thought that callosities were independently acquired in gibbons and monkeys, a point we contest.

B. Gibbons and Possible Extinct Relatives—Lesser Apes

An understanding of the relationships of the gibbons* to the other groups of catarrhine primates is fundamental to understanding the phylogeny of the Old World higher primates. The gibbons are usually linked with the Hominoidea (Simpson, 1945), but it has been suggested recently by Chiarelli (1968*b*) that gibbons belong to the Cercopithecoidea on the basis of their karyologic resemblances with the Colobinae. There is little support for this in other lines of evidence, especially when it is considered that within the gibbons themselves there is considerable variation, the concolor and siamang gibbons being phenetically closer to the great ape condition. Evidence from biochemistry (Goodman, this volume; Romero-Herrera *et al.*, 1973), comparative anatomy (Remane, 1960; Le Gros Clark, 1971; Groves, 1972; Schultz, 1973; Tuttle, 1972, this volume) and paleontology (Le Gros Clark and Leakey, 1951; Zapfe, 1960; Andrews, 1973) is all consistent with the gibbons being a group of the "Hominoidea," or "anthropomorph" catarrhines (to use a term with less taxonomic implication).

Another line of evidence that might be taken to show the hominoid status of the gibbons is the structure of the teeth. Indeed gibbon teeth are remarkably similar to those of the great apes. They share elongate lower molars with 5 main cusps placed marginally, and squarish uppers with 4 cusps. On the lowers the hypoconulid is usually buccal to, or on, the midline, resulting in the appearance of 3 buccal and 2 lingual cusps. True crests crossing the lower molars are rare, but a mesial fovea (trigonid basin) is separated from the main talonid basin by a low ridge, and a distal fovea is similarly separated by a hypoconulid-entoconid crest. Other crests link neighboring cusps along the tooth

* Following Groves (1972), only one genus, *Hylobates*, is recognized to receive all gibbons, siamangs, "concolors," etc. The terms gibbon and lesser apes will here be used interchangeably with *Hylobates*, unless specifically noted otherwise.

margin. The cusps are separated internally by grooves defining a "y" or "+" pattern. On upper molars the mesial fovea is delimited by a crest from the paracone to the margin mesial to the protocone; a protoconule there is very rare in modern apes. The large talon area is separated from the trigon by the crista obliqua, linking protocone and metacone, sometimes via a metaconule. The hypocone is generally large and well separated, on the margin of the crown. Cingula may be present lingually on uppers and buccally on lowers, but not very strongly in modern forms. In gibbons it is quite rare on lower molars, and it varies among species on uppers from massive to merely a slight bulge (Frisch, 1965, 1973). The premolars of gibbons (and other "hominoids") are bicuspid (except for P_3), with the buccal cusp larger than the lingual; a cingulum may be present lingually on the uppers.

The dentition of gibbons is distinguished from that of other hominoids by such features as small hypocones, the small size of M_3^3 , large canine with low sexual dimorphism and strong premolar honing, and incisor morphology. The third molars of modern gibbons are always shorter than the M_2^2 , often shorter than M_1^1 (especially M^1), and there is often concomitant reduction of distal cusps. The teeth of males are on the average larger than those of females of the same taxon, but there is overlap even in canine height, with the female range often greater (Frisch, 1973); a similar instance among cercopithecids occurs in *Colobus guereza* (Delson, 1973). The canines of both sexes are high and sharp, and they participate in C^1/P_3 honing of the type seen in cercopithecids. The lower incisors of gibbons are moderately narrow, while the I^1 is rather broad; I^2 is conical in shape, as in colobines (Vogel, 1966).

The skull of gibbons is also strongly colobine-like: the face is even shorter; bone relationships in the orbit are as described above for colobines (Vogel, 1966); and the choanae are low and wide. The orbits are large and surrounded by a projecting marginal ring. The mandibular body is gracile, long and shallow, deeper anteriorly than posteriorly; the ascending ramus is vertical. The brain is relatively larger than it is in monkeys, but Radinsky (1974) implies it may be the most conservative in terms of sulcal geometry.

Gibbons present ischial callosities invariably, but they appear much later in ontogeny than they do in cercopithecids; Pocock (1925) reported that the area between the callosities was relatively hairy, as it is in *Cercopithecus*. No female sexual swellings occur. Most gibbons have 44 chromosomes, but siamangs have 50 and "concolors" 52. We follow Groves (1972) in recognizing these forms as the subgenera *H. (Symphalangus)* and *H. (Nomascus)*, respectively. In all but the latter form, specializations of the male sexual organs occur, with the testes para- or prepenial and the scrotum suppressed. It is finally worth noting that all gibbons so far observed live in parental family groups, do not build nests, are strongly territorial, and have displays in which the female plays a major part (Chivers, 1972). Groves (1972) has attempted to determine the polarity of evolutionary trends within the gibbons, and he has also discussed potential ancestral traits of hominoids, which will be considered below.

The major morphological features distinguishing modern gibbons from other higher primates are those related to their ricochet, brachiating locomotion. It must be noted that we employ the term "brachiation" to imply habitual support of the body

below extended arms during locomotion. Thus, the modern "great apes" are not brachiators, although many of the following morphological features that apparently relate to this type of locomotion are found also in modern larger apes (including man).

In all modern anthropomorphs the trunk is transversely broad and somewhat shortened, the scapula dorsal, the clavicle robust and long relative to trunk length (especially in gibbons and orangutans), and the humeral head large, dorsally facing, and medially directed. The tail has been lost, the lower back vertebrae reduced in number (mostly 17 or 18 in gibbons), and the sacrum lengthened (to 4 or 5 vertebrae in gibbons), which in turn leads to greater mobility of the shoulder and lessened flexibility of the trunk. The internal organs have been rearranged and supported craniocaudally, rather than dorsoventrally. The flexibility of the elbow joint has been increased by the reduction of the olecranon process, while the ulnar styloid has retreated somewhat from the wrist articulation; in gibbons there is a bony lunula within the small meniscus separating the ulna from the carpus (Lewis, 1972a). The lower ankle joint is helical.

Gibbons have carried locomotor specializations farther than most other catarrhines (save *Homo*, at least), with dominance of the upper limb, and especially its distal components. Thus the upper limb is much larger than the lower (intermembral index is 120 to 155), the humerus longer than the femur (index 114 to 136), the radius longer than the humerus (index 105 to 124), the hand very long compared to trunk size, and the thumb, although long, is short compared to the long palm and thus is out of the way of the hooklike grasping fingers (see Van Horn, 1972). The long bones generally are gracile with a minimum of muscle markings. Biegert and Maurer (1972) have clearly illustrated the appendicular lengthening compared to trunk height seen in gibbons. Among all catarrhines, *Hylobates* spp. fell farthest from the allometric trend lines of both arm and leg length on trunk length. The relative arm and leg lengths seen in gibbons are greater than in any other known form and would be expected only in a catarrhine whose body size greatly exceeded that of a gorilla. This specialization might be predicted for the forelimb, as seen also in *Pongo*, but not for the hindlimb as well. We are tempted to suggest that the ancestor of modern gibbons was much larger than any *Hylobates* species (also suggested by Dr. Colin Groves, personal communication).

Two rather well-known fossils have been long considered as potential ancestors or relatives of the gibbons, but their status in this regard is now increasingly in doubt.* *Pliopithecus* is known as a number of supposed species from the middle Miocene of Europe. Its dentition has been considered in detail by Hürzeler (1954), and excellent cranial and postcranial remains of one variety have been described by Zapfe (1960). Andrews (1973) has shown that *Limnopithecus legetet* is closely related to *Dryopithecus* and not pertinent to gibbon evolution, but that the species known as *L. macinnesi* may well be gibbon-like. It was therefore necessary to transfer this species to the new monotypic genus *Dendropithecus* (Andrews, Pilbeam and Simons, 1976).† This species is known in two subspecific variants from the early (and probably middle) Miocene of East Africa (Andrews, 1973). *Dendropithecus* and *Pliopithecus* dentitions are well known and basically gibbon-like

* Simons (1972) has recently reported a gibbon-like tooth from Miocene deposits in the Siwaliks.

† Owing to the lengthy delays beyond our control, this article has not yet appeared in print. The name *Dendropithecus* is therefore used as a *nomen nudum* in the present paper.

with narrow incisors (by comparison to contemporary *Dryopithecus*); canines sexually dimorphic, but large in both sexes and honing on a specialized high-crowned P_3 ; and a moderate degree of intercuspal cresting. The elongate M_3^3 , however, is unlike that of gibbons. No skull is known of *Dendropithecus*, but that of *Pliopithecus* is gibbon-like, with a short and broad face and nasals, gracile and mesially deepening mandibular body, and projecting orbital margins; the lack of an ossified tubular auditory meatus is distinctly unlike gibbons or other modern catarrhines. The skeleton of *Pliopithecus* is most gibbon-like in its gracility, but the limb proportions are more as in monkeys, although suggestive of a trend toward gibbons; the intermembral index is 94, the radiohumeral, 105, and the humerofemoral, 85. The ulna has large olecranon and styloid processes and lacks marking distally that would indicate the presence of a meniscus, as in gibbons, while the humerus retains an entepicondylar foramen. There are 6 or 7 lumbar vertebrae and 3 sacra. Ankel (1965) suggested the presence of a long tail, but this is questionable and remains undocumented by direct fossil evidence. The data of Biegert and Maurer (1972) also show that *Pliopithecus* was typically catarrhine in relative limb proportions for its trunk size. *Dendropithecus* postcranial elements are more fragmentary, but ulnar morphology is similar between the two genera, as is that of the astragalus. The humerus and femur of the African form are morphologically similar to *Pliopithecus*, but more elongate and thus more gibbon-like; the distal humerus of *Dendropithecus* is also close in form to that of *Hylobates*, and there is no entepicondylar foramen; femora of the two fossils are of similar length, but the humerus of *Dendropithecus* is longer. Its estimated limb indexes are: intermembral, 96; radiohumeral, 104; humerofemoral, 90; all are close to *Pliopithecus*, as is overall size.

In the past opinions as to the relationship of these fossils and gibbons has varied widely. Ferembach (1958) suggested that *L. legetet* was a small "pongid," while "*L. macinnesi*" was morphologically conservative, much like early catarrhines; Groves (1972, 1974) has also denied these forms gibbon relationship, because of their lack of similarity to modern *Hylobates*. On the other hand, Tuttle (1972), Simons and Fleagle (1973), and others find these fossils to have morphology that is reasonable to expect in a gibbon ancestor, as the specializations of the modern gibbons must have developed mosaically. We consider *Dendropithecus* phenetically closer to gibbons than *Pliopithecus*, but evaluation of cladistic relationship depends on the comparison of these fossils to the ancestral catarrhine features to be determined below.

C. Larger "Anthropomorphs"

In this group especially, there is a problem with nomenclature, both formal and informal. Large apes will imply Miocene to modern nongibbon "hominoids" except *Oreopithecus* and *Homo*, unless otherwise qualified (e.g., modern, fossil, African, etc.). Of the modern forms, three genera are recognized: *Pongo*, *Homo*, and *Pan*. The latter is tentatively divided into the subgenera *P. (Pan)* with two species and *P. (Gorilla)*. *Homo* and *Australopithecus*, or their ancestral morphotype as discussed by Eldredge and Tattersall (1975) and Delson (1976), are here considered men. For many characters the large apes are similar to gibbons, and these will not be further discussed. Otherwise, differences among the modern forms will be considered by organ system, rather than by taxon.

1. *Modern Great Apes and Men.* The dentition and trunk are most similar among larger apes and men. The shoulder girdle is generally as in gibbons, with clavicle longest in orangutans (as in gibbons), intermediate in *Homo*, and shortest in *Pan* (although still longer than in monkeys). The lower back is further shortened, with thoracic + lumbar vertebrae numbering 15 (or 16) in *Pongo*, 17 (of 16) in *Pan*, and 17 in *Homo*; sacral vertebrae number 5 or 6. Lewis (1972a, b) has shown that the wrist of larger apes is more derived than that of gibbons in the removal of the ulna from carpal articulation, through the increase in size of the meniscus and lack of the bony lunula therein. There appear to be three major types of wrist here, characterizing *Pongo*, *Pan*, and *Homo*, but questions remain as to the polarity of change and the functional value of the different morphologies. Orangutans seem most clearly adapted for suspensory locomotion, while *Pan* knuckle-walks habitually in the adult stage. *Homo* may have developed from a suspensory ancestral condition, but probably never had knuckle-walking or truly brachiating ancestors (see Tuttle, 1974, this volume). Further specializations of men include adaptations to bipedal striding, such as the short and broad ilium, inflexible foot, and related muscular changes. All large anthropomorphs present long upper limbs relative to trunk length, and in men the lower limb is further elongated. This is reflected also in Biegert and Maurer's (1972) analysis, in which the relative arm length of *Homo* is typical for catarrhines of its trunk length, while its leg is longer even than in *Hylobates*. The situation is reversed in *Pongo*, although its upper limb is not so extremely elongated as is the lower one in men. *Pan* species are "typical" catarrhines in limb length with the long forelimbs a result of the large size they share with orangutans and men. Unfortunately, there are no large catarrhines that are standard quadrupeds to serve as "controls" in order to separate the effects of allometry from those of locomotor pattern.

In dental morphology, the larger apes and men are close to the gibbons. Cingula may be more prominent on molars, and the third molars are not as reduced, although usually smaller than the second (Mahler, 1973). In *Pan* and *Pongo* sexual dimorphism is high, especially in the canines, with a marked decrease in canine-premolar honing. These teeth in men are even less dimorphic, metrically and morphologically, with the P_3 becoming bicuspid as an adaptation to increased grinding, while the canine takes on the functions of an incisor. In *P.* (*Pan*) and *Pongo* the central upper incisors are quite large, and the lowers are also often large compared to molar size; in gorillas the lowers are smaller, while I^2 is a more conical tooth than in other large apes (see Vogel, 1966). Incisor proportions vary greatly among taxa of men, but the ancestral condition was probably narrow and high, with a moderately large I^1 . The mandibular body is of relatively constant depth in modern larger apes, neither very shallow nor very deep anywhere; the ascending ramus may be slightly back-tilted, and a chin is present in *H. s. sapiens*.

Cranial differences are more important, as has been shown especially by Vogel (1966). In *Pan* and *Pongo* the face is moderately long and high, with great depth in the maxilla and zygoma; the orbital construction and lacrimal fossa are as in colobines and gibbons; however, Schultz (1950) has noted that a frontomaxillary suture in the orbit wall is common only in *Pan*. The interorbital region is broad in *Pan*, narrower in *Pongo*, while the nasal bones of both are moderately elongated. In *Homo*, and less so in *Australo-*

pithecus, the face is shorter, the orbits widely spaced, and the nasals short and broad. The choanae are high and narrow in all large apes, including short-faced *Homo*. The brain is largest in these forms among primates, especially so in later men, but morphologically not different from gibbons in sulcal patterns at least (see Radinsky, 1974; Holloway, 1972). The chromosomes of larger apes are strongly similar, but *Homo* has 46, while *Pan* and *Pongo* have 48; Chiarelli (1968a) has suggested a simple behavioral model for the reduction. Ischial callosities are found in many individuals of *Pan* and *Pongo*, but they develop very late in ontogeny; none are present in *Homo* (Schultz, 1968; Rose, 1974).

2. *Extinct Large Apes*. A number of fossil forms have been considered as relatives of the modern larger apes. Three to be considered here are of Miocene–Pleistocene age: *Dryopithecus* (and *Limmopithecus*), *Ramapithecus*, and *Gigantopithecus*; three others are of Oligocene age, namely *Propliopithecus*, *Aegyptopithecus*, and *Aeolopithecus*. *Dryopithecus* is the best known of these, represented through the Miocene (and possibly latest Oligocene) in Africa, Europe, and Asia. Andrews (1973, 1974) recognized the seven species accepted by Pilbeam and Simons, adding the new subgenus *D. (Rangwapithecus)* to receive two new African species; the lack of clear distinction (other than zoogeographic) between *D. (Dryopithecus)* and *D. (Sivapithecus)* resulted in their synonymy. Other new species named since 1965 are considered synonyms of previous taxa, and material formerly placed as *Sivapithecus* (or *Kenyapithecus*) *africanus* is now assigned to species of *D. (Proconsul)*. *Dryopithecus* remains are mostly dental, with some cranial and postcranial portions represented. The dentition is basically similar to that in other apes, differing in smaller and more gracile incisors and canines; canines participating in honing with P₃ more than in modern larger apes; broader upper premolars; cingulum more common on cheek teeth, but variable among species; and lowers often elongate. The mandibular corpus is of moderate to great depth, either constant or deeper mesially; the simian shelf present on some *Pan* and *Pongo* is lacking. Parts of two skulls of *D. (P.) africanus* (Davis and Napier, 1963) indicate a relatively wide interorbital region and face of moderate length (perhaps slightly more than gibbons), no brow ridges (found in most other apes), and a brain of essentially modern ape form and size compared to body weight (Radinsky, 1974; Andrews, 1974). A frontal sinus is present in at least *D. (P.) major* and *D. (P.) africanus* and is found in modern larger apes only in *Pan* and *Homo*, not *Pongo*. Postcranial remains are known basically from *D. (P.) africanus* and *D. (D.) fontani* (= "*Austriacopithecus*" and "*Paidopithecus*"). The ulnar olecranon of the former species is long and monkey-like (Preuschoft, 1973), while shorter and more apelike in the latter, younger taxon (Zapfe, 1960). The ulnar styloid of *D. africanus* has withdrawn from carpal articulation more than that of gibbons (Lewis, 1972b). Humeri and femora from Africa and Europe are morphologically similar to those of *P. (Pan)* species, but more gracile, while the finger bones are like those of *Pan* and some monkeys. The radiohumeral index of *D. africanus* is 86. Functional locomotor interpretations of *Dryopithecus* have varied among an agile, quadrupedal "probrachiator" similar to some modern colobines (Napier and Davis, 1959), a brachiator (Lewis, 1971, 1972b), a knuckle-walker (Pilbeam and Simons, 1971, Conroy and Fleagle, 1972), and an *Ateles*-like arboreal quadruped that may have suspended itself from its forelimbs, but that could not knuckle-walk (Schön and Ziemer, 1973; Preuschoft, 1973). In part, these differences are the re-

sult of concentration on the limited data from specific body systems, not always the total morphology available. On the one hand, Conroy and Fleagle (also Tuttle, 1974) argued that Lewis is incorrect in referring to the wrist of larger apes as that of a brachiator, as they in fact are primarily knuckle-walkers (or mixed, in the case of *Pongo*). On the other hand, Schön and Ziemer's investigation of the wrist bones suggests habitual dorsiflexion of the hand, as in *Ateles* and *Alouatta* when moving quadrupedally, but they do not deny the possibility of some arm-suspension as well. Further study and integration of data is obviously needed, but the similarity of *Ateles* to *Pliopithecus* and *Dendropithecus* in the forelimb also is most interesting.

Both *Gigantopithecus* and *Ramapithecus* have been suggested as possible human ancestors, although they differ greatly in their known gnathic morphology. The former genus is known from one mandible of probably late Miocene age in India and three mandibles and some thousand teeth of later Early to Middle Pleistocene age in South China; *Ramapithecus* is represented by a dozen or so teeth and fragmentary jaws of middle to late Miocene age (ca. 15–10 million years) in East Africa, India, China, and western Eurasia (see Simons, 1972, 1976). *Gigantopithecus* species were very large animals with heavy, robust mandibles; the body is deep, shallowing mesially, the symphysis heavily buttressed, ascending ramus possibly upright, and the face probably short (Pilbeam, 1970). The incisors are rather small and vertical; the canines are low crowned, robust, not honed on P_3 , and probably function with like premolars than incisors; the P_3 is nearly bicuspid, but with a large trigonid and a small mesial flange. Other cheek teeth are strongly molarized, with thick enamel, low cusp relief, and high interproximal attrition; molar crowns may have increased in height from the Miocene to Pleistocene. *Ramapithecus* species were much smaller animals, in size like *D. africanus* or *D. nyanzae*, with dental arcades apparently diverging slightly posteriorly, much as in *Gigantopithecus*. The alveolar process of the maxilla is deep, the mandibular body shallow and robust, and the ramus may have been upright, leading again to suggestions of a broad- and short-faced primate adapted to heavy chewing. The incisors are quite small and slightly procumbent; the cheek teeth show low relief and thick enamel, much interproximal wear, and a steep wear gradient; the canine is low crowned; and the incipiently bicuspid P_3 has only a small honing flange. An interrelated assemblage of features indicates increased lateral chewing, without incorporation of the canine into the grinding apparatus (see Simons, 1964, 1972, 1975; Andrews, 1971; Walker and Andrews, 1973).

The mid-Oligocene Fayum beds of Egypt have yielded a number of fossil primate taxa that are here divided into three groups. Three are treated in this section, two others (*Apidium* and *Parapithecus*) considered next, and the last, *Oligopithecus*, is known so little that we hold it until last. These species have been discussed by Schlosser (1911), Kálin (1961), Simons (1965, 1972), Simons and Fleagle (1973), Szalay (1970, 1972) and Delson (1975c), among others. Of the three largest Fayum primates (all are smaller than modern apes and *Dryopithecus* spp.), *Aeolopithecus* is known from a single weathered mandible; *Propliopithecus* (including *Moeripithecus*) is represented by a number of mandible fragments; and *Aegyptopithecus* is the best known, with several mandibles and loose teeth, a nearly complete skull, and a number of undescribed postcranial elements.

The teeth of *Aeolopithecus* are too eroded to preserve crown details, but it is clear that the M_3 is short, the canines robust and tall, and the P_3 elongated and narrow, indicating well-developed honing. The type of *Propliopithecus* has no incisors (nor are any known *in situ*), but the canine is low and the single-cusped P_3 little adapted to honing; it is probably a female, however, and another specimen attributed to this genus has a well-developed honing facet on P_3 . In *Aegyptopithecus* there are no known lower canines, but a C^1 is long and laterally compressed, while P_3 seems clearly a honing tooth. The P_4 of both genera has subequal trigonid cusps. The molar morphology of *Propliopithecus* and *Aegyptopithecus* is similar to that in *Dryopithecus*, and thus to other apes as well: there are 5 rounded cusps, the buccal 2 slightly larger and lower than the lingual; the hypoconulid is centrally placed on M_1 and more buccal on M_{2-3} ; low ridges demarcate a raised trigonid, while the talonid is narrow and crowded by the 3 distal cusps; the hypoconulid is linked to the entoconid, rather than to the hypoconid, as in *Dryopithecus* species; buccal cingulum development is variable, from great to almost none; the third molar is slightly longer to much longer than the second, and always narrower. The upper premolars of *Aegyptopithecus* are much broader than long, while those of most modern forms (and even *Dryopithecus*) are more nearly square; lingual cingulum is present as a swelling, rather than as a shelf [as in *Dendropithecus* and *D. (Proconsul)*]. The upper molars have a cingulum that varies between a shelf and a swelling, the occlusal ridges vary in degree of development, and there is always a small distinct protoconule and a smallish hypocone, placed lingually. The mandible is of moderate and constant depth in most specimens.

The cranium of *Aegyptopithecus* has not been fully described, but a few important points may be noted. The interorbital pillar is rather wide, and although the face and nasal bones are long, a comparison of interorbital width/nasion-prosthion length results in an index almost identical with that in *D. africanus*, which is intermediate in value between *Hylobates* and *Pan*. There is marked postorbital constriction and moderate nuchal and sagittal crests, reflecting the large size of the face relative to the brain case. The chonanae are high and quite narrow. There is no ossified external auditory tube, merely a platyrrhine-like ring, as in *Pliopithecus*. Radinsky (1973) reported the brain to be essentially modern, with catarrhine-like large size and a central sulcus, increased visual cortex, smaller olfactory bulbs than in prosimians, but still a smaller frontal lobe than in modern anthropoids. A nearly complete *Alouatta*-like ulna, with long olecranon and robust, nearly straight shaft suggests an arboreal quadrupedal locomotor pattern for this genus (Fleagle, Simons, and Conroy, 1975; Conroy, 1976). The relationships of these early fossils will be considered later, but it may be noted here that although 4 species have previously been recognized, a reduction to as few as 2 is conceivable. The only major differences are in size, relative size of lower molars, and relative cingulum development.

D. Parapithecus and *Apidium*

These two genera, each apparently represented by a species in each of the upper two Fayum horizons, are, respectively, the second and first most abundant primate

species. Both are small, about the size of marmosets or the smallest cercopithecids; are known mostly from teeth and jaws, with some fragmentary cranial and limb elements; and share a number of features that lead to their being discussed here together. One feature that sets these animals clearly apart from other catarrhines is their possession (retention) of 3 premolars, of which the most anterior (P_2) is strikingly caniniform. Delson (1973, 1975c) has suggested that this tooth might well be involved in honing of the C^1 in some *Parapithecus*, and the same may be true of *Apidium*. The lack of cingulum, especially on the lower molars, and some aspects of crown morphology also indicate a close link between these two taxa. Incisors are poorly known, but the lowers are quite small, narrow, vertical teeth, the laterals especially small. The canines are robust, but not very tall, and thus if honing was indeed present, it may not have been strongly developed, nor ancient. The P_2 is caniniform, with a single crown cusp and very little talonid development, if any (at least in the *P. fraasi* type); P_{3-4} are similar teeth, lower crowned, but more robust than P_2 , with large protoconid, small metaconid and short talonid; P_4 is larger, with a higher metaconid. The lower molars, as in the three Fayum primates noted above, are moderately high crowned, but with low relief, having 4 main cusps and a small but distinct midline hypoconulid. The trigonid basin is moderately large, bounded by a rather distinct ridge linking metaconid and protoconid, with no paraconid clearly present. The upper teeth have not been formally described, but it can be noted that they are broad, with well-marked conules placed on the lines connecting the mesial and distal cusp pairs, not mesial to these lines, as in apes and *Oreopithecus*. *Apidium* is distinguished by its much smaller premolars compared to molar size; its tendency to polycuspidation, resulting in the well-known centroconid (mesoconid) on lower molars; an elongate M_3 but reduced M^3 ; and generally more bulbous cusps. *Parapithecus*, by contrast, is more crest oriented (but *P. fraasi* is bulbous), the molars wearing quite flat; M_3 is smallest of the molars, its talonid especially reduced; a paraconid may be present on dP_4 ; the lower molars are somewhat constricted by the in-turning median buccal notch.

The mandibular body is variable in both genera, usually of constant depth, but sometimes shallowing slightly mesial; depth is less in *P. fraasi* than in other species, but may vary intraspecifically; reconstructed rami are rather vertical. Cranial fragments referable to *Apidium* have been described: the frontal demonstrates postorbital closure and a fully fused metopic suture (Simons, 1959); the brain (Radinsky, 1974) may have had relatively larger olfactory bulbs than in *Aegyptopithecus*; there was again no ossified external auditory meatus, as in *Pliopithecus* and *Aegyptopithecus* (Gingerich, 1973). Humeri, ulnae, astragali, and calcanei described by Conroy (1976) indicate a generalized arboreal quadruped similar to *Saimiri* or *Cebus*.

E. *Oreopithecus*

This most enigmatic primate is known only from five lignite localities in Tuscany, which may be of late middle Miocene age (11–13 million years). Despite published reports (Leakey, 1968; Koenigswald, 1969) no close relatives are known from Africa. Numerous remains, including a crushed partial skeleton, have been incompletely

described (Hürzeler, 1958; Straus, 1963; Szalay and Berzi, 1973). After Hürzeler, the dentition has been discussed in greatest detail by Butler and Mills (1959), who considered it quite distinct from that of other catarrhines. The incisors are vertically implanted, with conical I^2 and large I^1 presenting a strong projecting lingual cusp. The canines are sexually dimorphic and robust, but not tall, although they do interlock; the upper canines show tip wear and did not hone strongly on P_3 , nor do they have the cercopithecoid continuation of the mesial sulcus onto the root; lower canines honed on the uppers, but not on the small I^2 . The lower premolars are both bicuspid, with subequal protoconid and metaconid (sometimes smaller on P_3) and moderate talonid, especially on P_4 ; upper premolars have large paracone, lower protocone, and sometimes a small metacone. The lower molars are elongate, with the standard 4 catarrhine cusps marginally, a centroconid much as in *Apidium*, and a midline hypoconulid, small on M_{1-2} , larger on the M_3 talonid; the cusps are partly linked by crests, relief is high and lingual notches rather deep; a paraconid is variably present on M_1 ; there is little cingulum. The upper molars are elongate, as in modern catarrhines, not squarish, as in earlier Miocene forms; the 4 main cusps are joined by distinct protoconule and large metaconule, which are important in the formation of the ridge delimiting the small fovea anterior and the crista obliqua; the 4 main cusps are acute, the trigon deep but small in area. The crest delimiting the long, deep, and narrow fovea anterior ends at the protoconule, which restricts the fovea to the buccal part of the tooth. The strong crista obliqua passes via a well-defined metaconule and is further connected to the distolingual hypocone; this results in a large and open fovea posterior. With wear, the metaconule may merge into the crista obliqua. There is lingual cingulum on upper cheek teeth, but it is not continuous around the protocone.

The skull of *Oreopithecus* has previously been considered to closely approach hominids in morphology (Hürzeler, 1958), but Szalay and Berzi (1973) have recently shown that this was a misinterpretation of the crushed specimen. The face is somewhat gibbon-like, with broad interorbital region and sloping snout; there are large supra-orbital tori and clear sagittal and nuchal crests, the latter high on the vault; the mandible has a smoothly rounded symphysis, expanded gonial region, and vertical ramus; the body is of constant and rather great depth. The postcranial skeleton reveals some contrasting specializations by comparison with modern catarrhines. Straus (1963) has reported an intermembral index of 119, a radiohumeral index of 95, and a humero-femoral index of 117; all of these indexes are within the range of *Pan* spp. but perhaps not found together in a single species or individual of that genus. Straus considered that these indexes reflected short legs and not very long arms. Biegert and Maurer (1972), however, found that the relative elongation of the arm in *Oreopithecus* was greater than that in *Pongo*, although much less than in *Hylobates*. They apparently did not accept Straus' estimate of tibial length, but that value seems reasonable, and its inclusion yields a relative leg elongation greater than that of any catarrhine except *Homo* and *Hylobates*. Thus, both limbs are moderately elongated for body length, contrary to Straus' interpretation. There are 5 lumbar vertebrae, as is common in men and gibbons (fewer in other apes), and 6 in the narrow sacrum; the vertebrae also reveal a strong ventral keel, which otherwise occurs only in cercopithecids for attachment of a longitudinal ligament. The

ulnar olecranon is reduced, as in modern apes, but this may in part reflect large size as well as suspensory postures. Straus considered the astragalus mobile and cercopithecoid-like, while the calcaneus more closely resembled larger apes. Szalay (1975) has noted that the astragalocalcaneal joint is nonhelical, as found otherwise only in cercopithecines and *Homo*. *Oreopithecus* has often been considered a brachiator, especially as its remains are found in coal swamps where it would have been unlikely to walk terrestrially, but Zapfe (1958) has remarked that some Austrian *Pliopithecus* and *Dryopithecus* specimens also derive from lignite deposits, and he has suggested that they did in fact walk on the bog. Various cercopithecids also are known from such deposits, which may merely reflect forest habitats and/or taphonomic effects, not necessarily locomotor modes.

F. *Oligopithecus*

Oligopithecus savagei is represented by a single mandibular fragment with C_1 - M_2 , from the lowest Fayum horizon; it is thus the oldest known catarrhine (see Szalay, 1970, 1972; Simons, 1971, 1972). The canine is moderately tall, but broken below the tip. There are two premolars, of which the anterior (P_3) is unicuspid and adapted to hone the C^1 , while P_4 is bicuspid as in other catarrhines. The fact that the honing flange on P_3 has been worn down through enamel to dentine, a condition not seen in any other catarrhines that hone, suggested to Delson (1975c) that such honing was a relatively recent acquisition in the ancestry of this animal. The P_4 metaconid is only slightly lower than the protoconid, a small paraconid may be discerned and the talonid is large but low. On the two preserved molars, cingulum is almost nonexistent; the 4 main cusps surround a large and wide talonid basin, while a short and somewhat higher trigonid may be bounded mesially by a small paraconid (M_1); a hypoconulid is present lingual to the midline, but its pattern of wear suggests incipient confluence with the entoconid; intercuspid ridges are poorly developed. This specimen shows that *Oligopithecus* was clearly catarrhine in its possession of cuspidate hypoconulid and broadened talonid, as well as the C^1 - P_3 honing and deep mandibular body (compared to earlier primates).

III. Morphotype Deduction and Phylogeny Reconstruction

A. Postulated Ancestral Morphotype for Catarrhini

Based on the data presented above, a reconstruction has been attempted of the hypothetical ancestral morphotype of the catarrhines, essentially equivalent to the common ancestor of all these animals. Some comparisons have also been made with relevant conditions in other primate groups, especially the Paleogene forms thought to reflect conditions potentially ancestral for Anthropoidea/Haplorhini. A number of questions have arisen that will be discussed after descriptions of these features on which there is more certainty.

In the dentition the incisors of ancestral catarrhines would have been small relative to molar size, relatively narrow and high crowned; I^2 was probably conical or caniniform,

involved in honing the lower canines; I^1 was the widest (longest) tooth mesiodistally. The canines would have been tall and bilaterally compressed, showing sexual dimorphism in size and probably in form, with C^1 involved in honing on C_1 and P_3 , and C_1 on I^2 as noted. A major problem involves the number of premolars; certainly 3 were present at one time, but for now it will be assumed that P_2^2 was already lost and the time and manner of that loss will be discussed below. In that case, the anterior lower premolar, P_3 , would have been bilaterally compressed, sexually dimorphic, and involved in C^1 honing, but without extreme extension of enamel onto the mesial root; the crown was of moderate height, not very high as in fossil "lesser apes," and only 1 main cusp was present. The P_4 would have had the two main cusps subequal in size, or the protoconid slightly higher than the metaconid; a small trigonid basin, possibly with a small marginal paraconid, was somewhat higher than a broad talonid basin. The upper premolars were homomorphic, bicuspid, with a broad oval shape, not elongate or trefoil-shaped as in some Paleogene forms; the paracone was higher than the protocone, especially on P^3 . There may have been some lingual cingulum related to the broadening of these teeth, and it seems doubtful that a protoconule was present. The lower molars would have had 6 cusps, the 4 main ones as well as small paraconid and hypoconulid, the latter placed on the midline. The talonid was as broad as the trigonid, but slightly lower and longer mesiodistally. There may have been some buccal cingulum, and cusps probably did not rise far above the surrounding area—relief was low, although the crowns were moderately high. In length M_1 was smallest, with M_2 equal or slightly shorter than M_3 ; the latter was probably narrow, whatever its length, and may have had a larger hypoconulid. The upper molars would have had 4 cusps, the hypocone small, low, and cingulum-linked. As in other primates (e.g., adapids), with the increase in size and height of the hypocone, the paraconid would have been reduced in size even further, and the hypoconulid perhaps increased as well. Upper molars would have been rather wide, subsquare in shape, with lingual cingulum (probably related to the increase in width) present, but perhaps not continuous around the large protocone. A small protoconule would probably have been present on the tooth margin, mesial (and slightly buccal) to the protocone, not between paracone and protocone; a crest linking it to the paracone would have demarcated a distinct mesial fovea. No metaconule would have been present, but a strong crista obliqua set off the trigon from the fovea posterior. The size progression $M^2 > M^3 > M^1$ probably held; both large and small M^3 are considered derived characters. These features are summarized in Table 1.

In the skull, ancestral catarrhines are reconstructed as rather short-faced, with short, broad nasals, lacrimal fossa overlapping onto the maxilla, ethmoid participating in the orbit wall, a brain the relative size of that of *Aegyptopithecus* and with similar form, much like that of gibbons. The circumorbital bar would have been closed, with much filling in of the rear orbital wall; the symphysis and metopic suture fused early in life; the bulla was probably inflated and the whole region pneumatized, but there was no ossified external auditory tube, only a ring. Mandible depth was probably constant along the jaw and (absolutely) greater than that in Eocene primates, although these characters may have been variable; the ramus was likely upright. Choanal shape, among other features, is uncertain, but possibly low and wide. Basically, the face was most similar to

gibbons and colobines among recent forms, as Vogel (1966) and Delson (1973), among others, have suggested.

Postcranial reconstructions are even chancier than the above, but for the sake of completeness, it is suggested that trunk form was much as in cercopithecids, perhaps more gracile; the tail was long. Small body size would have resulted in lower limbs only slightly longer than upper, radius slightly shorter than humerus, and chest narrow. Estimates of limb bone indexes (ranges) might be: radiohumeral, 90–100; humero-femoral, 80–90; intermembral, 90–95. The early catarrhine ulna would have had monkey-like olecranon and styloid processes, the humerus an entepicondylar foramen (present in prosimians), the lower ankle a helical joint (unlike the derived states in cercopithecids and *Oreopithecus*). It may finally be hypothesized that the ancestral catarrhine diploid chromosome number was 44 (as found in most gibbons and colobines) and that ischial callosities were present and separated by an area of haired, not specialized, skin.

B. Apes and Men

A substantial number of characters indicate that the current practice of linking the greater and lesser apes closely is justified, which in turn permits the reconstruction of the ancestral morphotype of the (modern) apes. The dental apparatus of the early apes appears to have been highly conservative. The only significant change in the dentition would have involved loss of honing (sharpening) effect of the P_3 on the upper C, with the correlated reduction of bilateral compression of these two teeth and the lower C. Cranial form was similarly conservative, except for a possible slight increase in relative brain size. Postcranial differences between early apes and the ancestral ape morphotype would have been mainly those related to the enormous size increases that are known to have taken place by the early Miocene (Le Gros Clark and Leakey, 1951; Pilbeam, 1969; Andrews, 1973). These include the broadening of the thorax, with all the changes associated with that: longer clavicle, dorsal position of scapula, elongation of the scapula, and medial rotation of the humeral head; and the lengthening of the forelimb relative to the hindlimb. Reduction of the lumbar and caudal regions and lengthening of the sacral articulation with the ilia may have been partly independent of the size increase, and so also might have been the changes in the elbow joint and the carpal articulation. According to this reconstructive hypothesis, all of these changes need not have occurred at one time, but all must at least have been well advanced before the major split among the apes occurred, between gibbons and others. Inferences based on this cladistic model result in specific interpretations of certain fossil apes, while a model permitting widespread parallelism in acquisition of these features is more flexible (and less precise), as will be seen especially with the lesser apes.

1. *Evolution of the Larger Apes and Men.* The shared derived features of the common ancestor of at least the modern forms would have included: reduction of canine honing; increase in size of incisors relative to molars (variable in modern *Pan*, however); development of facial lengthening, with associated elongation of nasal bones and probably of choanae; increase in relative brain size and complexity; continued decrease in number

of lower back vertebrae and increase in sacrals; loss of carpal lunula if present at first and increase in meniscus size; increase in overall body size and muscularity, leading to a longer forelimb and greater muscle markings on limb bones; reduction of ischial callosities; and probably increase in chromosome number to 48 (or 46).

Modern apes and men are all somewhat more derived than the *Dryopithecus* group in such features as very large I¹, small cingulum and slightly reduced M₃, more reduced canine honing, possibly more "advanced" carpal and especially elbow joint morphology (see below) and, according to some researchers, a more restricted locomotor pattern (size-related?). It thus appears that *Dryopithecus* (and the little-known *Limmopithecus legetet*) represents a form close to the ancestry of modern larger apes and men before the split between Asian and African lineages, possibly including that ancestor. Preuschoft (1973) has shown that the olecranon was long in some *D. (Proconsul)*, while it was quite short in *D. (Dryopithecus)*, suggesting greater diversity than expected. Moreover, Pilbeam (1969) has shown that at least *D. (P.) major* had a frontal sinus, not found in *Pongo* or "lower" catarrhines; if this feature were present in all species, it would imply a separation of *Pongo* before that of *Dryopithecus* and *Pan*/men. It has previously been suggested that *D. major* is ancestral to gorillas (and *D. africanus* to chimps), but this seems to carry ancestor-hunting too far; the similarities are more probably seen as ecological or size-related convergences. Pilbeam (1970) has suggested an origin for *Gigantopithecus* within *Dryopithecus*, and he (also Andrews, 1973) has gone so far as to posit the lineage *D. major*→(unpublished Turkish material)→*D. indicus*→"*D. giganteus*"→*Gigantopithecus* spp. Again, if one wishes to find "ancestors," this is most elegant, but in fact it is based on a morphocline involving too few characters and is not yet testable. Here, *Gigantopithecus* is considered the sister group of *Dryopithecus*/*Limmopithecus*; its supposed links to men seem unsubstantiated.

Recent cladistic studies of Plio-Pleistocene human relatives (Eldredge and Tattersall, 1975; Delson, 1976) have suggested that the more "gracile" type of *Australopithecus* represents a close approach to the morphotype expected in a late Miocene (5-7 million years) human ancestor. The paper by Pilbeam and Gould (1974), although problematical, does suggest an allometry within *Australopithecus* spp. supporting their placement in a single genus as well as a distinctive trend in cerebral increase within *Homo*, which potentially began with *A. africanus*. Delson (1976) has accepted two subgenera of *Australopithecus*, with perhaps a third for the actual common ancestor, while realizing that this is in itself a stretching of cladistic methods; Robinson's view of *Homo* vs. *Paranthropus* is more cladistic superficially, but neglects both the strong shared features of *Australopithecus* species and the derived nature of *A. (P.) robustus*. Looking farther back in time, it appears that the status of *Ramapithecus* as a human ancestor is not as clear as some have thought, but known parts do agree well with the postulated morphotype, differing only in the more honing type of P₃ and U-shaped dental arcades (both conservative). The wide face and very narrow incisor region demonstrated by Walker and Andrews (1973) do not clash with this reconstruction, but require further study. *Ramapithecus* is clearly distinct from contemporary *Dryopithecus* species and must be considered a sister group either of *Dryopithecus* or of *Australopithecus* plus *Homo* (Fig. 2).

Little more can be said here about the three most apelike of the Fayum primates,

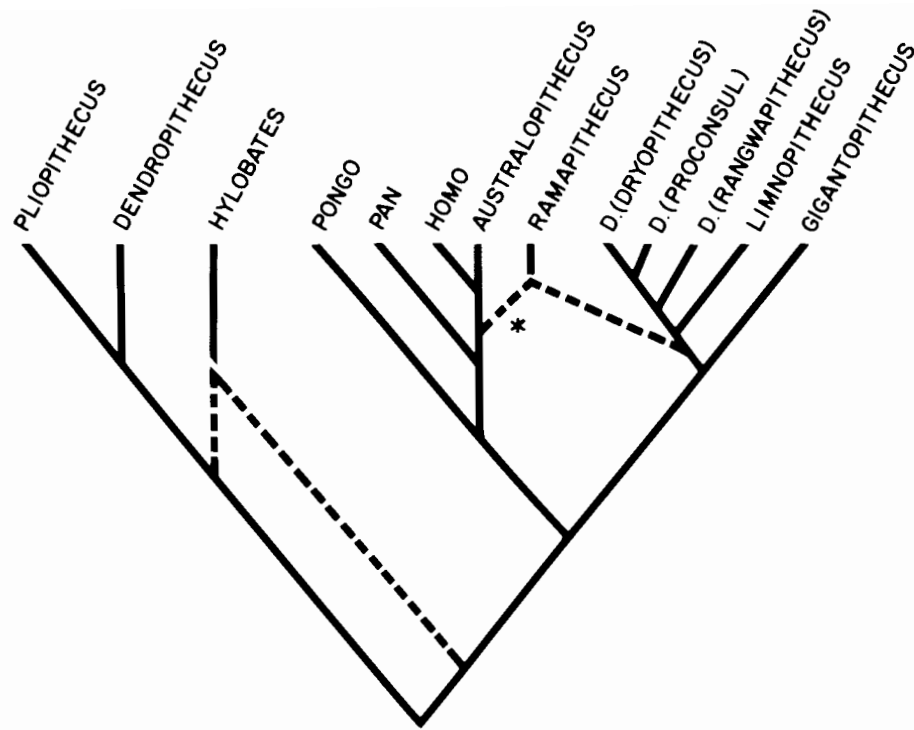


FIG. 2. Relationships of the Miocene to modern apes and men. In Figs. 2-5, there is no true time axis, but lineage branchings closer to the top of the cladogram are later than those below, along any given clade/lineage. Dashed lines indicate possible alternatives; the preferred choice among these, if any, is marked with an asterisk.

other than emphasizing that they are strongly conservative. This is to be expected of early forms, and is not (altogether) circular reasoning, as their age was not considered when the ancestral morphotype was inferred. Until these animals are fully studied, it seems best to group them closely and to consider them either the potential sister group of all later apes or as part of the *Dryopithecus* (or *Pliopithecus*) group (see Fig. 3 and pp. 429-430). We argue below for one of the two latter views, but the first has merit in that *Aegyptopithecus* essentially conforms to an ape ancestral morphotype. If gibbons diverged before this time, the retention by *Aegyptopithecus* of a long olecranon and an auditory tube would imply convergence in these complexes between greater and lesser apes. Szalay (1975 and this volume, chapter 5) has tentatively proposed that an auditory tube may have developed independently in monkeys and apes, but his reasoning is incomplete, and he further has denied the chance of convergence in this region among other primates (to the degree of similarity seen in catarrhines). Even more confusingly, the teeth of *Aegyptopithecus* show close similarities both to those of *Dendropithecus* (in the uppers) and to *Limnopithecus*/*Dryopithecus* (in lowers, see also Andrews, 1970), while retaining "primitively" large cingula. In part resolution of this potential dilemma depends on the interpretation of the lesser apes.

2. *Phylogeny of Gibbons and Relatives.* In many respects *Hylobates* is the most conservative of all modern catarrhines. Vogel (1966) expressed this view in detail as regards the facial skeleton and incisors, arguing that the group of features shared by colobines, gibbons, and men (and *Oreopithecus*) in the facial region were to be regarded as ancestral. The difficulty with this view is that those characters in *Homo* are not conservative retentions, but surely secondarily derived character states. Koenigswald (1968, 1969) has also remarked upon similarities between gibbons and monkeys, indeed implying a special phyletic relationship between them; in fact, such similarities as do exist are all ancestral retentions, the rare presence of semibilophodont molars in gibbons not having much phyletic weight other than as an indication of how early catarrhine teeth might have been altered in the ancestry of cercopithecoids (see below). Compared to the ancestral ape, *Hylobates* has continued to retain basic catarrhine dental and cranial form, as well (possibly) as chromosome number, ischial callosities,* and intermediate development of sacral dominance and rigidity. Thus, the derived characters of modern gibbons are limited to: the shallow mandible, deeper posteriorly; reduced sexual dimorphism; projecting orbits; bony lunula in the carpal meniscus (if not ancestral); extreme elongation of hind- and forelimb (especially the radius) and the ricochetal brachiating form of locomotion; and the paired-family social organization. It is therefore most difficult to reconstruct earlier stages in the evolutionary history of *Hylobates*. Tuttle's (1972) scenario is most intriguing but suffers because the stages are not as far along as he suggested. Instead of early and late prehylobatines, his earlier phases (depending on the models discussed below) would correspond more closely to our concept of early catarrhines and ancestral apes, and even his later stages may require some reordering of the mosaic sequence of evolutionary events.

These problems become all too apparent when the focus shifts to the fossil forms *Pliopithecus* and *Dendropithecus*. These two are extremely similar, with the lesser-known *Dendropithecus* slightly more derived toward gibbons in its loss of the entepicondylar foramen, generally less musclemarked limb bones and longer humerus with respect to the femur (although still within the estimated ancestral catarrhine range). Recalling the characters presented above, *Pliopithecus* is linked specially to *Hylobates* only by its projecting (if somewhat lateral) orbits, somewhat shallow mandible (not as extreme), molars with low cusps and simple crowns, gracile and long humerus, and especially quite long radius (see also Simons, 1972). On the other hand, as Groves (1972) has argued, *Pliopithecus* is in most other characters among the most conservative of all known catarrhines: its basic cranial and dental patterns are ancestral, as are those of gibbons; it lacks an ossified external auditory meatus and any indication of a carpal meniscus; and it retains typical catarrhine body proportions, the ancestral number of lumbar and sacral vertebrae, humeral entepicondylar foramen, a long ulnar olecranon, and perhaps a femoral third

* Groves (1972, p. 81) has attempted to reconstruct the course of morphological evolution within *Hylobates*, including the suggestion that the ischial callosities (and perhaps 44 chromosomes) of the otherwise derived *H. (H.) lar* group might be secondary features. No strong supporting evidence for this theory is presented, and it would seem that Groves was overly impressed with *H. lar* as a derived lineage. In fact, no one group would be expected (empirically or theoretically) to have only derived characters, and the concept of mosaic evolution suggests that unrelated derived character states would be well dispersed within a group.

trochanter and a tail (possibly in the process of reduction) (see also Simons and Fleagle, 1973). Moreover, although the radius of these forms is long relative to the humerus, the data of Biegert and Maurer (1972) reveal that neither bone is especially long compared to trunk length, certainly not comparable to *Hylobates*.

There are two possible interpretations of the phyletic position of these smaller Miocene apes. First, *Pliopithecus* (and *Dendropithecus*?) may have been part of an ape side branch which converged on gibbons in the above-listed features (probably before the ancestors of modern gibbons became so specialized), while still retaining a number of conservative character states; this view has been put forward by Groves (1972, 1974), less strongly by Simons and Fleagle (1973) and essentially also by Ferembach (1958), on fewer data. The presence of a long olecranon in *D. (Proconsul)* spp. (Preuschoft, 1973) implies that this genus also retained ancestral features, and thus the split between gibbons and other apes might have been earlier than generally thought. The demonstration in *Pliopithecus* (and/or *Dendropithecus*) of derived characters not shared with *Hylobates* would be a strong argument for this model, indicating that relationship between these "lesser apes" was only phenetic, not phyletic.

In the second hypothesis, *Pliopithecus* (and especially *Dendropithecus*) might represent forms close to the actual ancestry of *Hylobates*, in which case the carpal, elbow joint, and auditory region modifications considered above as shared derived features of all apes were in fact developed independently in gibbons and larger apes; most authors, including Andrews (1973, 1974) and Simons (1972), have accepted this view, while ignoring the convergence question. There is no problem in explaining the disparity between relative age and "primitiveness" between the two fossil genera. *Pliopithecus* (of the middle Miocene) may represent a more conservative lineage that exited Africa still retaining features already lost in the ancestry of forms we know as early Miocene *Dendropithecus*. This explanation would be especially meaningful if the African form proves to have auditory and carpal modifications similar to those of *Dryopithecus* spp. A phyletic relationship between *Hylobates* and these fossil genera might be supported directly if it were shown that the two groups shared additional derived features apart from other apes not likely to be convergent, such as might be found by a detailed study of the morphocline polarity of the cheek teeth, joint surfaces or ear region. Further and more intensive analyses of these functional complexes would certainly permit more explicit assessments of convergence (see also Szalay, chapter 5, this volume; and Tuttle, this volume).

At present, it is not possible to decide unequivocally whether greater weight should be given to those characters linking gibbons to other apes or to *Pliopithecus* (with *Dendropithecus* potentially intermediate). In the latter case, larger and lesser apes would be the major sister groups, probably best ranked at family level; *Propliopithecus*, *Aegyptopithecus*, and *Aeolopithecus* might then best be considered as the sister group of some or all *Dryopithecus*-like taxa, perhaps as a tribe of Dryopithecinae (this view is currently held by Andrews). On the other hand (as tentatively preferred by Delson), it may be better to consider that *Pliopithecus* and *Dendropithecus* were persistently conservative holdovers that had in some few ways converged upon the gibbons. In this case, following Groves (1972, 1974), and less precisely, Zapfe (1960), a family Pliopithecidae could be recognized

with one subfamily for *Pliopithecus* and *Dendropithecus*, another for the three Oligocene taxa; gibbons would then be granted subfamily status within a single family including all apes. More specific taxonomic rankings are presented in the final classification, but in any case, it does not seem meaningful to keep men and other large apes apart at the family level any longer. Simpson (1963) has presented the most persuasive arguments for such separation, based on the different adaptive zone occupied by what are here called "men," yet he used almost the same set of intergeneric relationships as we have. The fact that gibbons and other apes are phyletically sister groups must certainly be indicated in a classification now, with the level dependent on the model followed for gibbons. The question then devolves to the placement of *Pan* among modern genera—with *Homo* (plus *Australopithecus*, etc.) on grounds of clade, or with *Pongo* by Simpson's grade argument, which is tentatively followed here; the *Dryopithecus* group would appear to be the sister group of all three modern large apes, as shown in both versions of Fig. 3.

C. Evolutionary History of Monkeys

Current knowledge of the interrelationships of the cercopithecids may be greater than that for the apes. As noted above (p. 413), the mesially grooved C^1 , molar bilophodonty, and absence of hypoconulids on dP_4-M_2 are considered to be features of the

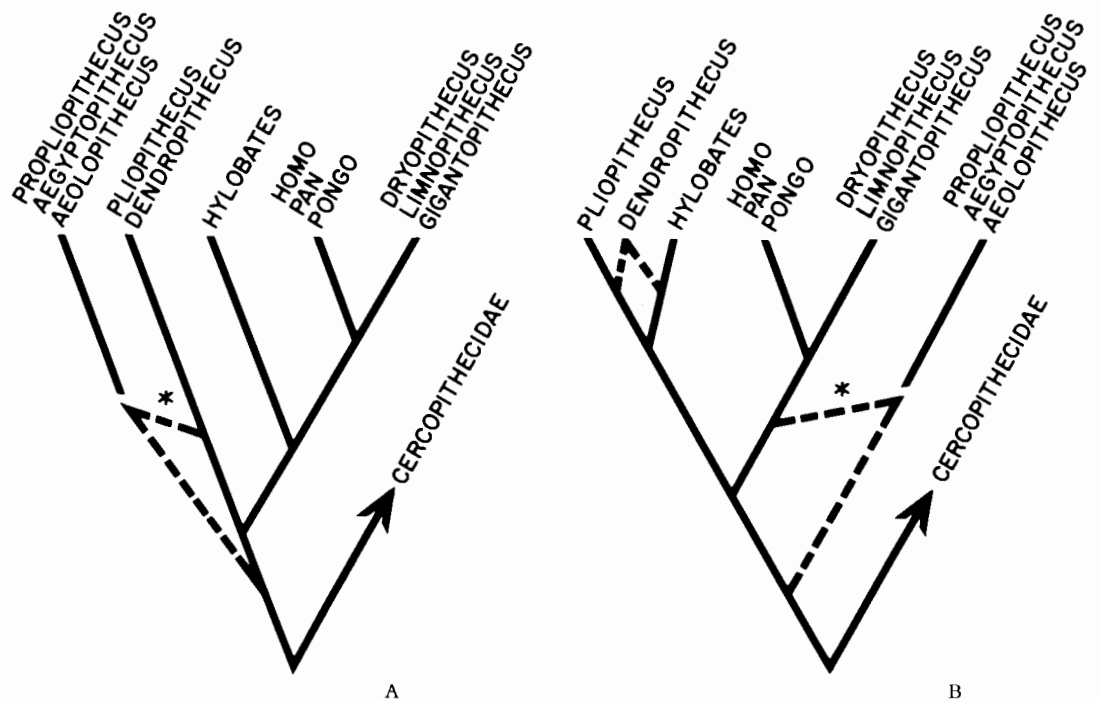


FIG. 3. Alternatives in the higher-level phylogeny of apes and men; notes as in Fig. 2. A: *Hylobates* closer to other modern apes, *Pliopithecus* persistently conservative. B: *Hylobates* and *Pliopithecus* closely related, forming the sister group of other apes.

earliest cercopithecoid—in a sense, the presence of these characters defines their holder as the first “true” cercopithecoid. It was also suggested that such an animal would have P⁴ cusps and canine honing similar to that postulated for the ancestral catarrhine morphotype, except perhaps with a stronger P₃ honing flange. By comparison with the ancestral catarrhine morphotype and variability among known cercopithecoids, it may be expected that early members of the family had incisors of moderate to small size relative to molars, conical I², variably a crista obliqua (see Koenigswald, 1969; Delson, 1975c, and below), and long M₃; it is not certain how chewing would have progressed in an animal with loph(id)s and also a crista obliqua, but one such (*Victoriapithecus*) is now under study by Delson. The cranial and truncal patterns of the ancestral catarrhine were probably retained by ancestral cercopithecoids, which appear conservative in all but dental features. Such forms would thus have had the skull, chromosomes, and incisors of a colobine, ischial callosities and perhaps body form of a *Cercopithecus*, and cheek teeth (with low, rounded cusps, large and shallow trigonid, moderate flare, low relief, and large M₃) of a macaque. As discussed by Napier (1970) and Delson (1973, 1975b), these animals may have been early Miocene arboreal or semiarboreal inhabitants of seasonal deciduous forests. In this environment, fruit might not have been abundant throughout the year, and a dental adaptation that allowed early monkeys to supplement their diet with leaves would have been of great value.

The earliest known fossil cercopithecoids are of early Miocene age, from Napak (Uganda) and Wadi Moghara (Egypt). *Prohylobates* from Moghara (see Simons, 1969) is apparently less than fully bilophodont, but incomplete material makes further analysis difficult. The Napak molar (Pilbeam and Walker, 1968) is clearly cercopithecine-like (ancestral), while the frontal fragment may be colobine-like (also ancestral); Radinsky (1974) has suggested that its endocranial cast is possibly gibbon-like, but a conservative early monkey would also have that morphology. The first evidence for the separation of the two modern subfamilies is from the middle Miocene of Maboko Island (Kenya), whence come specimens assigned to two species or morphs of *Victoriapithecus* (see Koenigswald, 1969). One type has long molars with large trigonids and low relief and may be associated with larger and more terrestrially-adapted limb bones. A second and more common set of molars are squarer, with the same low relief (shallow lingual notches), but short, colobine-like trigonids; they may be associated with a few more arboreal-seeming limb fragments. Delson (1973, 1975a) has argued that these fossils suggest an early phase in a split between colobines, that began to concentrate on folivory (with concomitant changes in teeth and later stomach) in an arboreal environment, and cercopithecines, that retained or enlarged an eclectic diet but experimented with semiterrestrial locomotion, leading in turn to allometric facial lengthening (and related reorganization of facial bones) and to cheek pouches. It is possible that a reduction to 42 chromosomes also occurred in the ancestral cercopithecine at this (mid-Miocene) time.

By the late Miocene (11 million years?), colobines may have divided into more arboreal and more semiterrestrially adapted forms. The former seem to have remained in Africa, splitting into at least three units: modern *Colobus* subgenera; latest Miocene *Libypithecus* (Egypt); and Plio-Pleistocene species of the large *Paracolobus* and *Cerco-*

pithecoïdes in eastern and southern Africa. On the other hand, some early colobines left Africa by way of a semiopen corridor to Eurasia, whence *Mesopithecus* and its possible descendant *Dolichopithecus* became increasingly terrestrial in Europe. Colobines first appear in Asia by the latest Miocene, but relationships of the modern genera (*Presbytis*, *Pygathrix*, and *Nasalis*) to the extinct European lineage are uncertain.

A major split among cercopithecines also may have occurred around 10–12 million years ago, leading to the differentiation of cercopithecins and papionins. The former group may have reinvaded the high forest to compete with colobines, converging on their dental patterns by decreasing flare while also reducing M_3^3 distally. Diversification of chromosome numbers may have aided in rapid adaptive radiation into new niches—the pattern of difference between species in multiples of 6 is interesting, as is the fact that the most distinctive forms have the lower numbers (42 in papionins, 48 in *Allenopithecus*, 54 in *Erythrocebus* and *C. talapoin*, 60–72 in others). The Papionini share the derived dental feature of reduced lower incisor lingual enamel (and often increased flare), which must be of late Miocene age at least, as climatic changes allowed the tribe to divide into its three major components by the early Pliocene: Eurasian conservative macaques and their larger and more terrestrial descendants, *Paradolichopithecus* and *Procynocephalus*; African conservative *Parapapio* and *Cercocebus* and more derived *Papio* and *Dinopithecus* species; and dentally derived *Theropithecus*, represented today by a relict species, but far more widespread and of large size during the Plio–Pleistocene. This pattern of evolutionary relationship is reflected in Fig. 4.

The large amount of data now available on the evolution of cercopithecids has been summarized quite briefly here because of its recent analysis elsewhere (Delson, 1973, 1975a), including more complete treatment of fossil taxon ranges, generic relationships, and classification. More relevant to this paper is the attempt to work backward from the reconstructed morphotype of the ancestral monkey to its predecessor, a form that would not be called a monkey, on dental evidence at least. As discussed by Delson (1975c), such an animal would not (yet) have possessed the bilophodont dental pattern of later cercopithecids; that is, the rearrangement of cusps and development of loph(id)s in response to functional adaptive pressures (for increased shearing?) had not begun. The results of that analysis have been included in the deduction of the ancestral catarrhine morphotype, and as presented above, such an early catarrhine would (by definition) be potentially ancestral to both apes and monkeys.

The upper molars of precercopithecids might be expected to have 4 cusps and a crista obliqua, and the lowers to have 5 cusps (no paraconid, moderate hypoconulid) without clear talonid crests. The metaconid ridge is simple to envisage. Other features of known cercopithecids that were probably lacking in their early ancestors would include very high crowns, high relief, and lateral flare on molars. Because crown height and especially relief are greater in cercopithecids than in most other primate families, they would have been less developed in the early catarrhine ancestor of monkeys. The distribution of molar flare, most pronounced lingually on uppers and buccally on lowers, agrees with the distribution of cingulum in other catarrhines and most other primates as well. It may be suggested that whereas cingulum itself was increased in the ancestors of catarrhines in order to widen cheek teeth, it was then lost in the later history of this

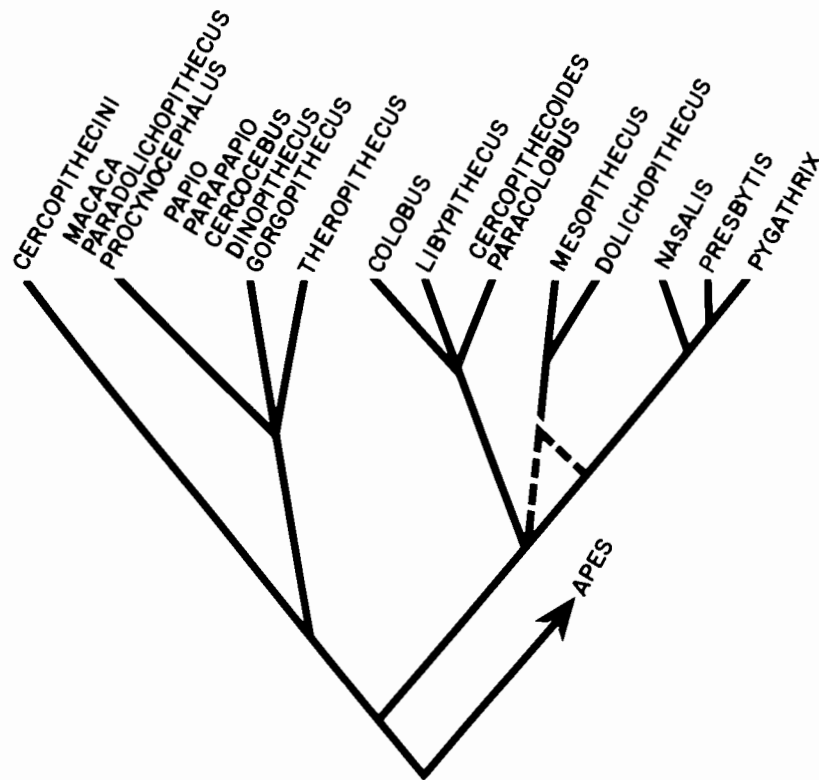


FIG. 4. Relationships of the Cercopithecidae; notes as in Fig. 2.

group. While apes seem to have lost it by simple reduction of cingular shelves as the tooth crown lengthened [except in *D. (Proconsul)* and *D. (Rangwapithecus)*], in monkeys the cingulum was incorporated directly into the external tooth wall, producing a smooth surface slightly bulged out near the cervix-flare. It is therefore expected that some cingulum would have been present in precercopithecids, much as in generalized early catarrhines. One of the major benefits of cladistics as applied to paleontology is that no early fossils have been included in this assessment of the precercopithecid ancestor, and such fossils can now be tested against the reconstruction without fear of circularity.

D. *Parapithecus* and *Apidium*

Simons (1972, and earlier articles summarized in Delson, 1975c) has argued strongly that new specimens of *Parapithecus* show strong morphological similarities to certain monkeys and thus represent the ancestor of Cercopithecidae. Taxonomically, he has suggested that *Parapithecus* (and its close ally *Apidium*) should be considered as a subfamily of monkeys, rather than as the family Parapithecidae, as is more common. Morphologically, Simons' view rests upon high molar crowns, a general shape (and

size) similarity between *Parapithecus* and *Cercopithecus* (*Miopithecus*) *talapoin* and the cranial evidence of symphyseal and frontal fusion and postorbital closure in *Apidium* at least. It will be recalled that relatively high crowns (by comparison to those of earlier primates) are common to all Fayum catarrhines and also that *C. talapoin* is a rather distinctive member of a highly derived tribe of cercopithecids. Therefore, it has little to recommend it for comparison to potential cercopithecid relatives (much less ancestors) except size; comparison with either dentally conservative macaques, or preferably with the postulated precercopithecid morphotype, is of greater interest. Such comparison (Delson, 1975c) reveals that *Parapithecus* has a very low P_4 metaconid, short M_3 , and lack of cingulum, none of which conform to expectation. The presence of a dP_4 paraconid and especially of 3 premolars are probably ancestral retentions, but the development of C^1 honing on P_2 would be a major derived feature. It seems quite unlikely that such a specialization would be lost and then redeveloped on P_3 if P_2 were dropped; Simons has admitted that if *Parapithecus* were ancestral to cercopithecids, they would have developed C_1 - P_3 honing convergently with apes, but there seems little to support this hypothesis. Nor do the alternatives of losing either P_3 or P_4 seem likely: such occurrences have purportedly been documented among other potential lineages of early primates (J. Schwartz, personal communication), but the morphologies involved were quite distinct from those here considered. Another possible character of importance is the strong development of conules on the upper molars of both *Parapithecus* and *Apidium*, which might be incorporated into functional lophs to increase shear; the metaconule of *Cebus* spp. may be involved in a phenetically similar situation (A. Rosenberger and W. Kinzey, personal communications). Contrary to their reasoning, however, it seems that such conules would not be expected in an intermediate stage of loph building in early cercopithecids, because the highest point on a "conule-loph" between the main cusps would be at the conule apex; in known cercopithecids, on the other hand, the midpoint of a loph is a deep notch.

Overall, it appears that *Parapithecus* and *Apidium* are not easily regarded as phyletically linked to Old World monkeys. They both are rather conservative forms in many ways (cusp pattern, retention of 3 premolars, and an auditory ring), but they also share a number of derived features not found in contemporary or later catarrhines (P_2 honing, little cingulum, extra cusps). Simons' argument that they have reached anthropoid or "monkey" grade is well taken, but there is a marked difference between grade (or phenetic) similarity and phyletic relationship. The phenetic similarity does suggest that the Parapithecidae (as we here rank them) may have been the ecological vicars of Old World monkeys in the Fayum region at least, but such morphological resemblances as do exist are seen as convergent and are not the result of a common ancestry with monkeys.

The actual place of parapithecids in primate phylogeny is then open to question, with three other potential answers. First, they could be specially related to the apes, but this seems as little supported by shared derived features as does linkage with monkeys. Second, they could be equally related to monkeys and apes, forming a "triple point" of the type strict cladists abhor but working systematists must always consider. This view is interesting, but still assumes that P_2 was lost independently in apes and monkeys after the time when the three groups separated from a common ancestor; evidence for

such independent loss would support this view. The last hypothesis is the most extreme, but at present seems the only acceptable one: parapithecids are essentially the sister group of all other catarrhines so far discussed. From a common ancestor with 3 premolars (none honing) and perhaps some cingulum, the parapithecids diverged to lose cingulum and develop P_2 honing, strong conules, and other characters, while another catarrhine branch lost P_2 , developed P_3 honing, and emerged as the ancestor described above (p. 423). Delson (1975c) arrived at this view with less substantiating evidence and then offered the suggestion that in some ways parapithecids were well suited geographically, temporally, and morphologically to be the long sought sister group of the platyrrhines. Hoffstetter (1974) has also considered this point in a commentary on the study by Gingerich (1973), but more detailed analysis of known morphology is urgently needed. One other possible relationship of the parapithecids has previously been suggested: *Oreopithecus*.

E. *Oreopithecus*

The summary of the known morphology of *Oreopithecus bambolii* presented above intentionally did not consider any of the many theories regarding its phylogenetic position. As reviewed by Hürzeler (1958) and Straus (1963), these have ranged among the same alternatives noted for parapithecids. Some early authors viewed *Oreopithecus* as monkey-like, and Szalay (1975) has recently returned to a suggestion of this affinity, based on shared derived features of the lower ankle joint. As the rotational, rather than the helical, type of astragalocalcaneal surface is found in *Homo* as well as cercopithecines, it seems likely to be a convergent pattern related to locomotion, rather than a shared feature of common ancestry in all animals that present it. The potential implication of at least some terrestriality in *Oreopithecus* is unexpected, to say the least (but see also Riesenfeld, 1975). Most modern authors have accepted *Oreopithecus* as an ape of some type, based on such (shared derived) characters as the reduced ulnar olecranon, 5 lumbar vertebrae, high intermembral and brachial indexes, and general shape of the trunk and axial skeleton. Once again, it is likely that most, or even all, of these features are under allometric control and thus the corollary of the nondiagnostic criterion of size. Nonetheless, *Oreopithecus* does appear to have significantly long arms and (to a lesser degree) legs for its trunk length, thus suggesting some potential links with apes. Hürzeler (1958) has argued that *Oreopithecus*, among apes, is specially related to men, because of its short face, bicuspid P_3 , small canines, and some other characters, and Straus (1963) more or less accepted this view. Szalay and Berzi's (1973) study of the crushed skull has shown that some of these features are not as Hürzeler had implied, while others are seen to be merely conservative among catarrhines, and the short legs are definitely not manlike; but the small canine and bicuspid P_3 still remain. A fourth alternative has been to consider *Oreopithecus* as a distinctive type of ape or "hominoid," separated at a high taxonomic level from the others. It combines conservative facial features with small canines, bicuspid P_3 , large internal cusp on I^1 , deep jaw with large gonion, and especially the large conules and centroconid, all derived features isolating *Oreopithecus* from other modern types of catarrhines.

It is just those features, however, which combine to link it to *Apidium*, as suggested by Gregory and later by Simons (1960). Since then, Simons has refrained from pressing his point, but his 1972 review of both genera adds other features in common. The two forms are among the few catarrhines that present clear protoconule and metaconule, the latter perhaps as part of a distal upper molar loph. They are nearly unique among primates in possession of a centroconid, whose relationships to other cusps are quite similar in the two genera, although *Oreopithecus* is much more cristodont than is *Apidium*. Furthermore, it is most suggestive to note that if indeed an *Apidium*-like form were to have lost a honing P_2 , the two remaining premolars would be bicuspid and nonhoning, and the canine probably small, as seen in *Oreopithecus*—of course the actual reduction would be under selectional control and not so simplistic. This relationship is more worthy of consideration now than ever before, but it in turn brings up the difficulties mentioned above and more: the shared derived features of apes and *Oreopithecus* would be convergences if *Apidium* is far from the modern catarrhines; and parapithecids must be closer to the last if *Oreopithecus* is. Even a relationship among parapithecids, cercopithecids, and *Oreopithecus* would be conceivable, but much less so than others have thought. Further detailed study is needed of both *Oreopithecus* and all Fayum primates—either clear examples of nonconvergent shared derived features or morphologically intermediate fossils to show the morphocline are needed to permit choice among the alternatives. Figure 5 summarizes the major options available in terms of the phylogeny of *Oreopithecus*, parapithecids and other main catarrhine groups.

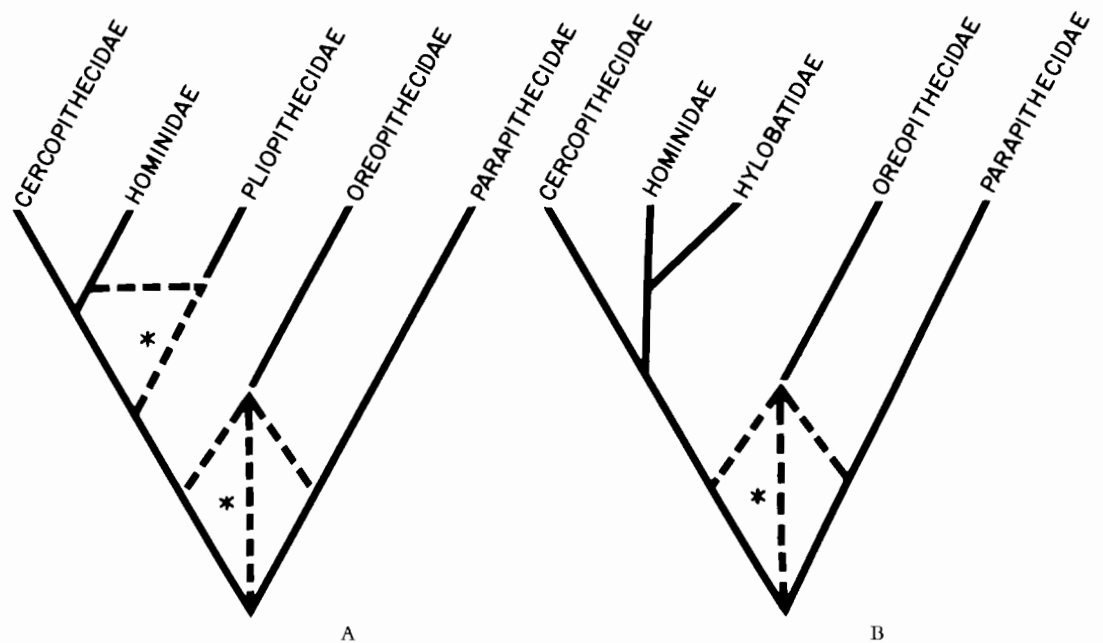


FIG. 5. Alternatives in the higher-level phylogeny of catarrhines; notes as in Fig. 2. A: as in Fig. 3A, modern families roughly equally distant from one another. B: as in Fig. 3B, hylobatids and hominids phyletically linked, classified as Hominoidea.

F. *Oligopithecus*

None of the above has yet answered the question of Old World monkey ancestry asked previously. In his original description of *Oligopithecus*, Simons considered a relationship to monkeys possible, but he has since withdrawn from that view. Delson (1973, 1975c) was unable to find any known fossil primate that matched the ancestral precercopithecoid morphotype in all respects, but he did suggest that a series of such features were found variably in species of *Oligopithecus* and *Propithecus*: 2 premolars, the anterior with well-developed C¹ honing, the posterior with subequal metaconid and protoconid and 2 large foveas; lower molars that have lost the paraconid and moderately enlarged the trigonid, linking protoconid and metaconid by a ridge (only in *Propithecus*); high tooth crowns with low relief; moderate-sized hypoconulid with evidence of appression to the entoconid (this is clearest in *Oligopithecus*, but also indicated in some *Propithecus*); a cingulum, especially buccally, around the lower molars (in *P. haeckeli*, very little in *O. savagei*, and none(?) in *P. markgrafi*, which instead shows lateral sloping of the lower crown, almost as in monkey flare). *Propithecus* is clearly similar to *Aegyptopithecus* and *Aeolopithecus*, while *Oligopithecus* is quite distinctive in its lack of cingulum combined with conservative molar form and "new" honing, but the known variation in these Fayum catarrhines suggests that in some unknown animal, probably in another environment, this mosaic of features was combined in a single species that began the lineage leading eventually to cercopithecids. *Oligopithecus* itself may be considered as a basically conservative remnant of the ancestral (modern-type) catarrhines. As such, it may be classed either as the sister group of all nonparapithecids, or of all catarrhines, or be placed with the relatively conservative *Aegyptopithecus* group. Because of the lack of knowledge about its anterior and upper dentition, much less the skull and postcranium, we here take the easy way out and consider it as Catarrhini, *incertae sedis*.

IV. Conclusions—Phylogeny and Classification

A. The Relationship between Classification and Phylogeny

Two of the most important aspects of evolutionary studies are the determination of phylogeny and the erection of a classification of the group under study; the relative importance accorded to these two types of result differs widely among evolutionists. In the preceding section, we have attempted to present sufficient argument validating the phylogenies that we have determined—at this point, it becomes possible to formalize some of these relationships in the Linnean hierarchy. The relationships between phylogeny and classification have been specifically discussed in recent years, with the resulting delineation of two major opposing views.

The cladists (e.g., Hennig, 1966; Nelson, 1972, 1973) strongly assert that a classification should precisely reflect the phylogeny on which it is based, the only open questions being which branch points (nodes) on the cladogram need be formally named. Some authors have suggested that taxonomic rank should be determined by the age of origin

of a group or taxon, but this is considered superfluous by most practitioners—thus, at least one rank must be determined *a priori*, as is true as “evolutionary” systematics. Only one cladistic classification could thus be erected from a phylogeny in which all nodes are understood, and in this classification all taxa would be maximally monophyletic (holophyletic), that is, all descendants of an ancestral taxon would be grouped together at all ranks. Nelson (1974) has recently cited some of Darwin’s (1871) writings on the classification of catarrhines to show that Darwin accepted the above tenets, at least in theory.

The second major school of taxonomic philosophy has been termed “evolutionary” by its practitioners (e.g., Simpson, 1961, 1963, 1971, this volume; Mayr, 1969, 1974; Bock, 1973), but a more neutral term would be preferable. Supporters of their views consider that a classification should be more than just a verbalized phylogeny, namely, an “information-retrieval system.” Thus, in selected cases, one member of a sister-group pair would have to be raised in taxonomic rank by comparison to the other in order to reflect great divergence from the ancestral condition and/or numerical diversity. The basic logic of cladistic analysis and the cladists’ desire to classify or group related taxa together are now fully accepted by the “evolutionary” school (see Mayr, 1974), but they wish to add further information to their classifications than can be found in a phylogeny or cladogram. In retort, the cladists have argued that classification cannot serve this function without introducing the element of “art” acknowledged by Mayr and others, thus decreasing reproducibility given the same data; further, it has been asked whether the information put into such a classification can in fact be “retrieved” without additional textual material (e.g., Cracraft, 1973). Mayr (1974) and others have in turn attempted to show that Darwin was in fact an “evolutionary” taxonomist, who aimed to produce “cladistic” classifications in theory, but who was pragmatic enough to bend his rules in certain cases.

As will be obvious from the body of this study, we are fully aware of the power and importance of cladistic analysis in the determination of phylogenetic relationships. We further accept that a classification must be based on a specific phylogeny, with which it should agree and not contradict. But we argue that there may in fact be cases in which one of two sister groups has diverged so strongly from the ancestral condition that to accord it equal taxonomic rank with its sister would be a distortion of the Linnaean system. This situation might occur especially when dealing with fossil organisms, given an ancient split from which a single low-rank taxon persisted conservatively for a short time and a large, diverse, and increasingly derived group of taxa proliferated over a much longer time (even if all are today extinct), it seems wasteful to rank both “sisters” at elevated levels in the hierarchy. Mayr (1974, p. 121) has commented on this point with examples from Darwin’s *Origin* (1895, pp. 420–421) and from Darwin’s classification of the barnacles. It may be useful here to cite a passage from the *Descent of Man* (1871, pp. 187–188) that follows immediately after one of the lines cited by Nelson (1974, p. 456), considering the classification of man. Darwin has suggested that man is clearly an anthropoid primate and thus might be ranked as

merely a Family, or possibly even only a Sub-family. If we imagine three lines of descent proceeding from a common stock, it is quite conceivable that two of them might after the

lapse of ages be so slightly changed as still to remain as species of the same genus, whilst the third line might become so greatly modified as to deserve rank as a distinct Sub-family, or even Order. But in this case, it is almost certain that the third line would still retain through inheritance numerous small points of resemblance with the other two. Here, then, would occur the difficulty, *at present insoluble*, how much weight we ought to assign in our classifications to strongly marked differences in some few points,—that is, to the amount of modification undergone; and how much to close resemblance in numerous unimportant points, as indicating the lines of descent or genealogy. To attach much weight to the few but strong differences is the most obvious and perhaps the safest course, though it appears more correct to pay great attention to the many small resemblances, as giving a truly natural classification [emphasis ours].

The remainder of that section is devoted to proving that man is a catarrhine, indeed a “hominoid,” and that our ancestors would have also been so, but Darwin makes no further decision concerning the relative ranking of *Homo* (the only “hominid” known to Darwin). As usual, Darwin’s views are penetrating, not only for his time but for ours: his reference to three forms from a common stock fits precisely with our interpretation of man, chimpanzee, and gorilla, and his inability to choose between the cladistic and “evolutionary” philosophy is exactly our dilemma. In fact, although this is almost by chance, we opt for the subfamilial rank he mentions, as a potential compromise between tradition and strict cladism.

B. Application to the Catarrhines

To return to the question of catarrhine classification, and to begin at the beginning, it is necessary in either the cladistic or the “evolutionary” system to assign at least one supraspecific rank *a priori*. Considering the results of this symposium and the general consensus among primatologists (and also Simpson’s 1945 analysis of all mammalian families), it appears reasonable to assign the rank of family to the Old World monkeys and that of infraorder to the catarrhines as a whole. From this base, Simpson (1963) has argued that the diversity among apes and men requires two families, of which he allocated one for men alone. On an “evolutionary” basis, this may be too high a ranking if monkeys are allocated a single family; on a cladistic basis, the important question is the geometry of the phylogeny involved. Our two alternative interpretations of the latter are given in Fig. 3, from which we infer somewhat different classifications, in each case accepting the lowest major node as a split between two families.

Following Fig. 3A, it appears that the apes can be divided into a “modern” versus a conservative, archaic group. Pending evidence to the contrary, the three Fayum genera are allied most probably with the conservative Miocene forms in a single family, while the latter genera (*Pliopithecus* and *Dendropithecus*) may be set off as a derived subfamily. No name has been seriously proposed for a family-group taxon encompassing or based on the three Fayum genera, but Straus (1961), in a paper that lacked some understanding of the Rules of Nomenclature, did propose a family Propliopithecidae; this nomen may be employed here. A second family, Hominidae, would then encompass the modern apes and the *Dryopithecus* group, which seems phyletically closer to the great apes. Gibbons could be accorded a subfamily of their own, while the modern apes and all men would rank as one tribe, the dryopithecids as another, in a second subfamily. Within

the Dryopithecini, *Gigantopithecus* might be given subtribal rank, but this may be pushing our fragmentary knowledge to the limits; similarly, *Pongo* might be set off from *Pan* and men on a cladistic argument as a subtribe. At this rate, in order to distinguish *Pan* from *Homo* and *Australopithecus* (and perhaps *Ramapithecus*), a new rank lower than subtribe would have to be employed. It is at this point that we would fall back on Darwin's reasoning and raise the rank of the taxon for men, leaving Hominidae with Hylobatinae, Ponginae (Pongini and Dryopithecini) and Hominae. For those wishing to employ a fully cladistic classification, the subtribe Hominina would be available for *Pan*, *Homo*, and the fossils noted.

If, on the other hand, the arrangement illustrated in Fig. 3B were substantiated, the major split between anthropomorph families would separate gibbons from great apes. Here, a family Hylobatidae might be subdivided into Hylobatinae and Pliopithecinae if necessary. The placement of *Dendropithecus* would depend on clear indication of its relationship, now in doubt. A second family, Hominidae, might be cladistically divided into Hominae vs. either Dryopithecinae or Propiopithecinae, depending upon whether the Fayum forms were considered the sister group of Neogene large apes or of the dryopithecids—they might even be considered a sister group of all hominids, but this seems least likely to us at present. Once again, if the rank of *Homo* and its closest relatives were raised to subfamily level, the Hominidae would include Hominae, Ponginae (Pongini, Dryopithecini), and Propiopithecinae; or alternatively, Hominae, Ponginae, and Dryopithecinae (Dryopithecini, Propiopithecini). The last of these, favored here, is in many ways closest to the presently most accepted classification, save for the high-level separation of the gibbons.

Four other fossil genera are less well known. *Apidium* and *Parapithecus* appear to share a number of traits, although many of these may be ancestral for the catarrhines in the widest sense, as may be seen from Table 1. They do seem to share the derived conditions of P₂ honing and loss of cingulum on lowers, however, and it is our opinion that they are best grouped as the family Parapithecidae. *Oreopithecus* is highly distinctive, being conservative in many characters and strongly derived in a number of others (Tables 1 and 2). It may also be given family rank, although one could also argue that it be ranked as Catarrhini *incertae sedis*. We take the latter action with regard to *Oligopithecus*, although it most probably is closer to modern forms than to the parapithecids, because our knowledge of it is so meager.

Grouping at the suprafamilial level depends again on which of the models of catarrhine phylogeny (Fig. 5) is followed. It appears rather clear to us that in either case, the Parapithecidae are to be regarded as the sister group of at least the modern families, if not of all other catarrhines. Thus, one may question whether there is a need to separate modern apes and monkeys any longer at the superfamily level. One potential (cladistic) division of the infraorder might then be Parapithecoidae vs. Cercopithecoidae (a name antedating Hominoidea by 4 years). Oreopithecidae would be *incertae sedis*, unless it were shown clearly to fit into one of the two superfamilies. This would certainly work well if the phylogeny of Fig. 5A were accepted, but under that of Fig. 5B, the hylobatids and hominids are surely closer to one another phylogenetically than either is to the cercopithecids. Thus, here, it might be useful to retain the common Hominoidea vs. Cerco-

TABLE 3. CLASSIFICATIONS OF THE INFRAORDER CATARRHINI

"Evolutionary" classifications—reflecting divergence of "men"		Strict cladistic classification
I	II	III
After Figs. 3A and 5A (preferred by Delson)	After Figs. 3B and 5B (preferred by Andrews)	
(Cercopithecoidea)	(Cercopithecoidea)	Cercopithecoidae
Cercopithecidae	Cercopithecidae	Cercopithecidae
Cercopithecinae	Cercopithecinae	Cercopithecinae
Cercopithecini	Cercopithecini	Cercopithecini
Papionini	Papionini	Papionini
Colobinae	Colobinae	Colobinae
Cercopithecidae <i>incertae sedis</i>	Cercopithecidae <i>incertae sedis</i>	Cercopithecidae <i>incertae sedis</i>
† <i>Victoriapithecus</i>	† <i>Victoriapithecus</i>	† <i>Victoriapithecus</i>
† <i>Prohylobates</i>	† <i>Prohylobates</i>	† <i>Prohylobates</i>
Hominidae	(Hominoidea)	Hominidae
Homininae	Hominidae	Homininae
<i>Homo</i>	Homininae	Hominini
† <i>Australopithecus</i>	<i>Homo</i>	Hominina
†(<i>Ramapithecus</i>)	† <i>Australopithecus</i>	(infratribe unnamed)
Ponginae	†(<i>Ramapithecus</i>)	<i>Homo</i>
Pongini	Ponginae	† <i>Australopithecus</i>
<i>Pongo</i>	<i>Pongo</i>	†(<i>Ramapithecus</i>)
<i>Pan</i>	<i>Pan</i>	(infratribe unnamed)
†Dryopithecini	†Dryopithecinae	<i>Pan</i>
†(Dryopithecina)	†Dryopithecini	Pongina
† <i>Dryopithecus</i>	†(Dryopithecina)	<i>Pongo</i>
† <i>Limnopithecus</i>	† <i>Dryopithecus</i>	†Dryopithecini
†(Gigantopithecina)	† <i>Limnopithecus</i>	†Dryopithecina
† <i>Gigantopithecus</i>	†(Gigantopithecina)	† <i>Dryopithecus</i>
(Ponginae <i>incertae sedis</i>)	† <i>Gigantopithecus</i>	† <i>Limnopithecus</i>
†(<i>Ramapithecus</i>)	(Dryopithecini <i>incertae sedis</i>)	†Gigantopithecina
Hylobatinae	†(Ramapithecus)	† <i>Gigantopithecus</i>
<i>Hylobates</i>	†Propithecini	(Dryopithecini <i>incertae sedis</i>)
†Pliopithecidae	† <i>Propithecus</i>	†(<i>Ramapithecus</i>)
†Pliopithecinae	† <i>Aegyptopithecus</i>	Hylobatinae
† <i>Pliopithecus</i>	† <i>Aeolopithecus</i>	<i>Hylobates</i>
† <i>Dendropithecus</i>	Hylobatidae	Hominidae <i>incertae sedis</i>
†Propithecinae	(Hylobatinae)	† <i>Pliopithecus</i>
† <i>Propithecus</i>	<i>Hylobates</i>	† <i>Propithecus</i>
† <i>Aegyptopithecus</i>	†(Pliopithecinae)	† <i>Aegyptopithecus</i>
† <i>Aeolopithecus</i>	† <i>Pliopithecus</i>	† <i>Acolopithecus</i>
†(Parapithecoidea)	Hylobatidae <i>incertae sedis</i>	† <i>Dendropithecus</i>
†Parapithecidae	† <i>Dendropithecus</i>	†Parapithecoidea
† <i>Parapithecus</i>	†(Parapithecoidea)	†Parapithecidae
† <i>Apidium</i>	†Parapithecidae	† <i>Parapithecus</i>
(Catarrhini <i>incertae sedis</i>)	† <i>Parapithecus</i>	† <i>Apidium</i>
†Oreopithecidae	† <i>Apidium</i>	Catarrhini <i>incertae sedis</i>
† <i>Oreopithecus</i>	(Catarrhini <i>incertae sedis</i>)	†Oreopithecidae
Family <i>incertae sedis</i>	†Oreopithecidae	† <i>Oreopithecus</i>
† <i>Oligopithecus</i>	† <i>Oreopithecus</i>	Family <i>incertae sedis</i>
	Family <i>incertae sedis</i>	† <i>Oligopithecus</i>
	† <i>Oligopithecus</i>	

† Indicates wholly extinct taxon.

pithecoidea division, with Parapithecidae also given superfamily rank or potentially a new, higher rank (between infraorder and superfamily). The most conservative arrangement, which we here tentatively, is to accept 5 families within the Catarrhini, with no further subdivision.

In order to demonstrate both our uncertainty and the major variants conformable with our phyletic inferences, we have provided three parallel catarrhine classifications (Table 3). The first reflects the phylogeny of Fig. 3A and 5A, the second 3B and 5B. In both, "men" have been differentially raised to subfamilial rank. Family-group taxa listed parenthetically are optionally named or alternatives, while genera in parentheses have more than one possible placement. A third classification is strictly cladistic, accurately reflecting the sequence of cladogram branching points and nothing else, as well as indicating the uncertainties involved in the relationships of *Pliopithecus*, *Aegyptopithecus*, etc. Nelson (1972) has argued that fossils should be ranked *incertae sedis* if there is doubt as to their placement, but denies this procedure in most cases for recent organisms. We disagree, holding that all taxa must be treated in the same manner, with those least understood (empirically most often fossils) being relegated when necessary to the *incertae sedis* category. The order of generic taxa within family-group higher taxa is determined by neither of the criteria discussed by Nelson (1973), but instead merely by date of authorship, save that nominate genera are listed first.

V. Summary

The distribution of morphological characters is presented for the major groups of catarrhine primates. Concentration is on dental characters (summarized in Table 1), with the addition of cranial, postcranial, and some other features (Table 2). Utilizing the methods of cladistic analysis, and without considering the geological age of any taxa (see Fig. 1), ancestral morphotypes are reconstructed for each higher taxon. The phyletic relationships of *Hylobates* are seen as central to understanding the phylogeny of the catarrhines—it may be closest to the modern apes and men or it may be linked to *Pliopithecus*, which retains many ancestral features and may have converged partially on gibbons postcranially. It appears that the living apes and man (including *Australopithecus*) form a natural group apart from the more conservative dryopiths; the position of the three Fayum "apes" is equivocal. Phylogeny cladograms reflecting the major alternatives are presented in Figs. 2 and 3. *Apidium* and *Parapithecus* on the one hand, and *Oreopithecus* on the other, are conservative in many respects but have derived characters setting them off from other catarrhines.

A hypothetical morphotype of the ancestral catarrhine is reconstructed from those of the lower taxa. None of the oldest fossils fit this morphotype completely, but it does appear that *Parapithecus* and *Apidium* separated from other catarrhines (unless *Oreopithecus* is indeed related to them) at a stage before the loss of P_2 , which may have already developed into a canine honing tooth in these forms. The phylogeny of apes, Old World monkeys (Fig. 4), and catarrhines in general (Fig. 5) are reviewed and interpreted. Classifications must be based on such phylogenies, but need not reflect them perfectly. In the

catarrhine classification(s) presented, Hominidae is expanded to include men and apes (excluding either *Hylobates* and *Pliopithecus* or *Pliopithecus* and the three Fayum "apes"), but the human lineage is raised in rank to a subfamily. Neither Parapithecidae nor Oreopithecidae appear to be phylogenetically close to Cercopithecidae, and *Oligopithecus* must for now be ranked as Catarrhini, *incertae sedis*.

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