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Received 2 February 1987 Revi-
sion received and accepted 14
July 1987.

Publication date November 1987

Keywords: Morphotypes,
Cercopithecidae,
Cercopithecinae, Colobinae,
Allenopithecina, foot morphol-
ogy, cladistic analysis.

Cladistic analysis of cercopithecoid relationships

The phyletic relationships of cercopithecoid higher taxa are fairly well understood. By reference to the outgroup Hominoidea, character state distributions for a variety of dental, cranial and postcranial features are reviewed and morphotypes are presented for supra-generic taxa. Cercopithecoids show 13 derived conditions relative to the eucatarrhine morphotype. Cercopithecines are further derived by eight features while the colobine morphotype shows an additional nine synapomorphies, including three newly identified pedal features. Within Cercopithecinae, the tribes Papionini and Cercopithecini are each characterized by several derived states. In turn, each tribe includes a relatively conservative and a more derived clade, recognized at the subtribal level: Macacina and Papionina (including the previously recognized Theropithecina) for Papionini; and the newly defined Allenopithecina and Cercopithecina among Cercopithecini. The distinctions within Colobinae appear comparable to those defining cercopithecine subtribes, and two taxa are accepted at that rank: the African Colobina, defined by three derived states; and the possibly paraphyletic Asian Presbytina. *Ptilocolobus* shares four synapomorphies with *Procolobus* and therefore is ranked as a subgenus of that taxon. The hypothesis that *Dolichopithecus* is the direct descendant of *Mesopithecus* is weakened on the basis of contrary pedal evidence.

Journal of Human Evolution (1987) **16**, 81–99

Introduction

The Old World monkeys, Cercopithecidae, are the most successful family of living primates in terms of species diversity and distribution. Their origin was probably in the late Oligocene to early Miocene, and while their diversity was apparently low during the early to middle Miocene, they experienced an explosive differentiation by the late Miocene to early Pleistocene (Szalay & Delson, 1979—*Note:* unreferenced details are discussed in this source). The family comprises 20 living genera and subgenera with up to 77 species and 263 subspecies (Napier, 1981, 1985; see Figure 1). As the result of studies by numerous investigators, the overall relationships of cercopithecoid higher taxa are rather well understood. In this paper, which is primarily designed as a review of current interpretations, a few alterations to existing classifications will be made while additional data are presented which support most previous cladistic analyses. Such a review is especially timely in light of the absence of any detailed discussion of cercopithecoids in the recent compendium edited by Swindler & Erwin (1986).

The types of data which have proven most useful for higher level cercopithecoid systematics are derived from studies of mainly hard tissues: the facial architecture, dentition and feet. The morphocline polarities and, indeed, distribution of many intriguing characters, such as biochemical and behavioral features or the anatomy of some soft tissues (e.g., genitalia), are not fully understood. Since these are most useful at lower taxonomic levels we will summarize here those features which permit the grouping of genera into supra-generic taxa, while commenting only briefly on the problems associated with the precise phyletic relationships of (sub)genera within such taxa.

The approach we have followed was to cull from the literature characters which have been suggested as diagnostic of cercopithecoid family-group taxa, complementing these

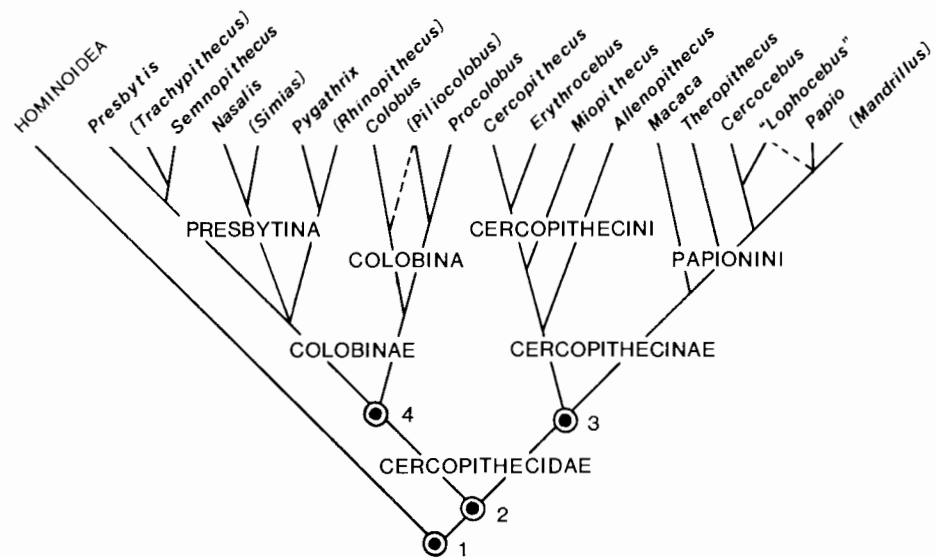


Figure 1. Cladogram of extant cercopithecoid genera and subgenera. Nodes, in numerical order, identify reconstructed morphotypes for: (1) family Cercopithecoidea; (2) subfamilies Colobinae and Cercopithecinae; (3) tribes Cercopithecini and Papionini; and (4) subtribes Presbytina and Colobina. Hominoidea is nearest extant sister taxon to Cercopithecoidea. Subgeneric names enclosed in parentheses. "*Lophocebus*" enclosed in quotation marks to indicate controversy as to its rank.

with features currently under study. Morphocline polarity was determined for the states of each character by reference to their distribution among extant and fossil cercopithecoids and in outgroups such as the Hominoidea, other catarrhines and, when necessary, platyrrhines (taxa as construed by Andrews, 1985), without reference to geochronology. Any divergence from this method will be specifically discussed. Only 37 characters were sufficiently understood to be included in this analysis, not counting those in which cercopithecoids retain a conservative state by comparison to an outgroup (e.g., presence of ischial callosities, tail or narrow thorax). Of the 37 characters studied, 13 distinguish Cercopithecoidea from its sister-taxon Hominoidea, and no more than nine are used to differentiate individual subtaxa (Figure 2). Since character concordancy was high, the resulting character trees were converted to the apparently most parsimonious taxon phylogeny by inspection, without utilizing numerical approaches. A separate analysis, now in progress, will evaluate alternative phylogenies using PAUP (Swofford, 1985) on the data matrix presented below.

In the following sections we review the characters at each of four major nodes which delineate Cercopithecoidea and its subclades, as well as selected generic distinctions. The states for each character are identified in Table 1 and their distribution among cercopithecoid (sub)genera is presented in Table 2. Each character is numbered, and in both tables and figures the postulated derived condition(s) is referenced by a primed number. The characters are not necessarily discussed individually or in numerical order, but by anatomical region, with interpretation of the transformations presented when possible.

Table 1 Character-state definition of features analyzed

Characters	Ancestral state (for eucatarrhines)	Derived state(s)	
inter-cusp cresting ¹	1 absent	1' bilophodont	
dP ₁ -M ₂ hypoconulid ¹	2 present	2' absent	
P ₃ flange ¹	3 short	3' long	
C ¹ mesial sulcus ¹	4 to cervix	4' on root	
nasal aperture ¹	5 high and oval	5' higher	5" wider
post. calcaneal facet ¹	6 helical	6' rotational	
anter. calcaneal facets ¹	7 single	7' double	
entocuneiform groove ¹	8 strong	8' reduced	
buccal pouches ¹	9 none	9' present	
stomach ¹	10 simple	10' 3-chambered	10" 4-chambered
external pollex ¹	11 long	11' short	11" absent
molar flare ¹	12 none	12' strong	12" reduced ³
trigonid length ¹	13 long ²	13' short	
molar relief ¹	14 low	14' moderate	14" high
I ₁₋₂ lingual enamel ¹	15 present	15' absent	
nasal bone length ¹	16 short	16' long	
lacrima fossa ¹	17 lacrima-maxilla	17' lacrima	
len. prox. ec-cu facet ¹	18 long	18' short	18" absent
astragalar groove ¹	19 absent	19' present	
pedal functional axis ¹	20 digit ray 3	20' digit rays 3-4	
M ₃ hypoconulid ¹	21 present	21' absent	
cheek tooth shape	22 subsquare	22' elongate	
interorbital distance	23 broad	23' narrow	
cranial vault height	24 high	24' low	
cerebral sulci	25 "colobine-like"	25' "cerc.-like"	25" "hominoid" ⁴
max. depth mandible	26 anterior	26' posterior	26" even ¹
insertion <i>m. flex. fib.</i>	27 digits 1,3,4	27' digits 3 & 4	
face length	28 short	28' long	
substrate preference	29 arboreal	29' semi-terr. ³	29" terrestrial ⁴
chromosome number	30 44?	30' [numbers]	
antorbital drop	31 shallow	31' steep	
facial fossae	32 absent	32' present	
F sexual skin cyclicity	33 present	33' absent	
male isch. callosities	34 continuous	34' discontinuous	
male perineal organ	35 absent	35' present	
median mental foramen	36 variable?	36' consistent	36" none ⁴
intermembral index	37 [numbers]		

¹ Indicates characters illustrated in Figure 3-5.

² See text, p. 89, for discussion of polarity alternatives.

³ State developed at least twice in parallel (see text).

⁴ State independently developed from ancestral condition, not secondarily derived.

The cercopithecoid morphotype

The node distinguishing cercopithecoids from hominoids can be defined by seven dental, one facial and three pedal characters. The most outstanding differences, and those that have been recognized the longest, involve the dentition, specifically the cheek teeth. The primitive condition for non-parapithecoid catarrhines (eucatarrhines) is that each lower molar bears five bulbous cusps arranged around the periphery of the tooth, a condition retained in hominoids. The ancestral cercopithecoid lost the hypoconulid on dP₄-M₂, elongated the cheek teeth, and realigned the cusps into a bilophodont condition (Figure 3,

chars 1–2; char. 22; *Note*: characters 22–37 not illustrated). A dentition of this sort is designed for folding and slicing food, which suggested to Andrews (1981) that early cercopithecids probably included a significant proportion of leaves in their diet. In addition, the catarrhine morphotype possessed cingula on the buccal face of lower cheek teeth and the lingual face of uppers. Delson (1975) suggested that most of the cingulum was lost in cercopithecoid ancestors through incorporation into the tooth sidewall, resulting in a “flared” condition wherein the tooth is widest at the cervix and narrows perceptibly toward the cusp apices (Figure 4, char. 12; see discussion below). Extant cercopithecids present cingula only as small remnants in the notches, while in the earliest fossils it is more extensive.

The ancestral eucatarrhine P_3 is reconstructed as being obliquely angled to the toothrow with its anterior surface carrying a slight flange for sharpening of the upper canine. This condition is retained or reduced in most hominoids (see Harrison, 1987), but in cercopithecids the flange is extended well below the alveolar surface of neighboring teeth providing, especially in males, an increased surface area for sharpening the dagger-like upper canines. The upper canine also has a sulcus or groove which in non-cercopithecoid eucatarrhines incises its mesial surface but stops short of the cervix. In cercopithecids, this groove extends beyond the cervix of the tooth and onto the root, where it locks onto a ridge of bone in the alveolus, probably providing resistance to twisting of the tooth during intensive activity (Figure 3, char. 3–4). In terms of facial morphology, Harrison (1982) and Andrews (1985) have recognized a high, oval nasal aperture as primitive for Old World anthropoids, with cercopithecids having a derived higher and more narrow configuration (Figure 3, char. 5). This may be in accommodation to elongated canine roots, again especially in males. Additionally, Vogel (1968) argued that a consistently present median mental foramen characterized this morphotype.

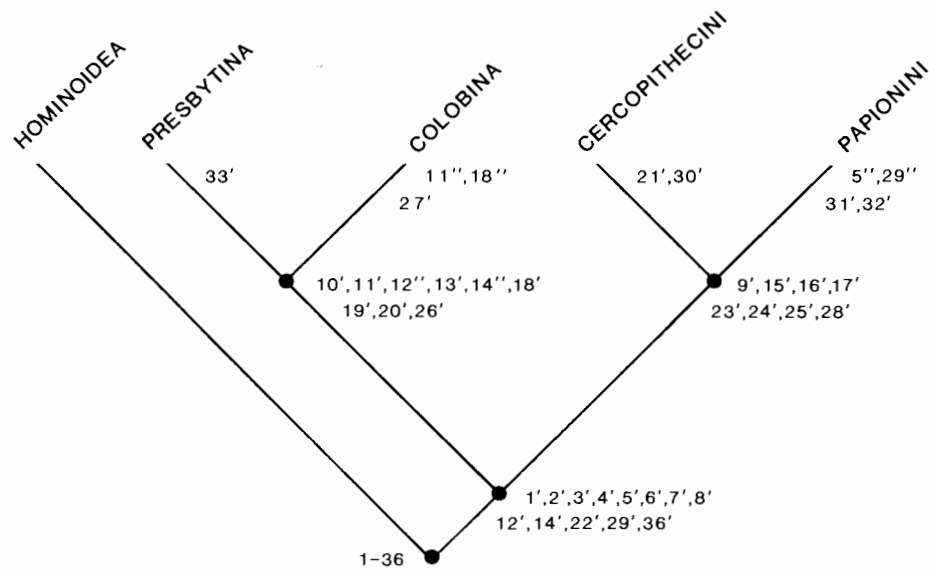


Figure 2. Character state distribution among the higher taxa of Figure 1. See Table 1 for character definitions and states, Table 2 for state definition by genus and Figures 3–5 for illustrations of selected states.

Table 2 Data matrix for distribution of character states under discussion¹

Ch #	Eu Mo	Ho Mo	+Cd Mo	+Ph Mo	+Vi Mo	Cn Mo	Al Mo	Mi Mo	Er Mo	Ce Mo	+Ma Mo	+Pr Mo	Th Mo	Cc Mo	Lo Mo	Pa Mo	Mn+Di Mo	+Pp Mo	+Go Mo	Co Mo	Pc Mo	Pt Mo	+Li Mo	+Ce Mo	+Pl Mo	+Rh Mo	Py Mo	Se Mo	Tr Mo	Pg Mo	Na Mo	+Me Mo	+Do Mo		
1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1		
2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	
3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	
4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	
5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	
6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	
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14	14	14	14	14	14	14	14	14	14	14	14	14	14	14	14	14	14	14	14	14	14	14	14	14	14	14	14	14	14	14	14	14	14	14	14
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16	16	16	16	16	16	16	16	16	16	16	16	16	16	16	16	16	16	16	16	16	16	16	16	16	16	16	16	16	16	16	16	16	16	16	16
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22	22	22	22	22	22	22	22	22	22	22	22	22	22	22	22	22	22	22	22	22	22	22	22	22	22	22	22	22	22	22	22	22	22	22	22
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30	44?	44?	44?	44?	44?	44?	44?	44?	44?	44?	44?	44?	44?	44?	44?	44?	44?	44?	44?	44?	44?	44?	44?	44?	44?	44?	44?	44?	44?	44?	44?	44?	44?	44?	44?
31	31	31	31	31	31	31	31	31	31	31	31	31	31	31	31	31	31	31	31	31	31	31	31	31	31	31	31	31	31	31	31	31	31	31	31
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36	36	36	36	36	36	36	36	36	36	36	36	36	36	36	36	36	36	36	36	36	36	36	36	36	36	36	36	36	36	36	36	36	36	36	36
37	(range of values)																																		

¹ Characters as listed in Table 1. Abbreviations as follows: (+ for extinct taxa) Eu Mo, eucatharine morphotype; Ho Mo, hominoid morphotype; Cd Mo, cercopithecid morphotype; Ph, *Prohylobates*; Vi, *Victoriapithecus*; Cn Mo, cercopithecidine morphotype; Al, *Allenopithecus*; Er, *Erythrocebus*; Ce, *Cercopithecus*; Ma, *Macaca*; Pr, *Proconocophagus*; Pd, *Paradolichopithecus*; Th, *Theropithecus*; Cc, *Cercocedus*; Lo, "*Lophocetus*"; Pa, *Papio*; Mn, *Mandrillus*; Di, *Dinopithecus*; Pp, *Parapapio*; Co, Mo colobine morphotype; Co, *Colobus*; Co, *Colobus*; Pc, *Procolobus*; Pt, *Ptilocolobus*; Li, *Lilypithecus*; Ce, *Cercopithecoides*; Pl, *Paracolobus*; Rh, *Rhinocolobus*; Py, *Presbytis*; Se, *Semnopithecus*; Tr, *Trachypithecus*; Pg, *Pygathrix*; Na, *Nasalis*; Me, *Mesopithecus*; Do, *Dolichopithecus*.

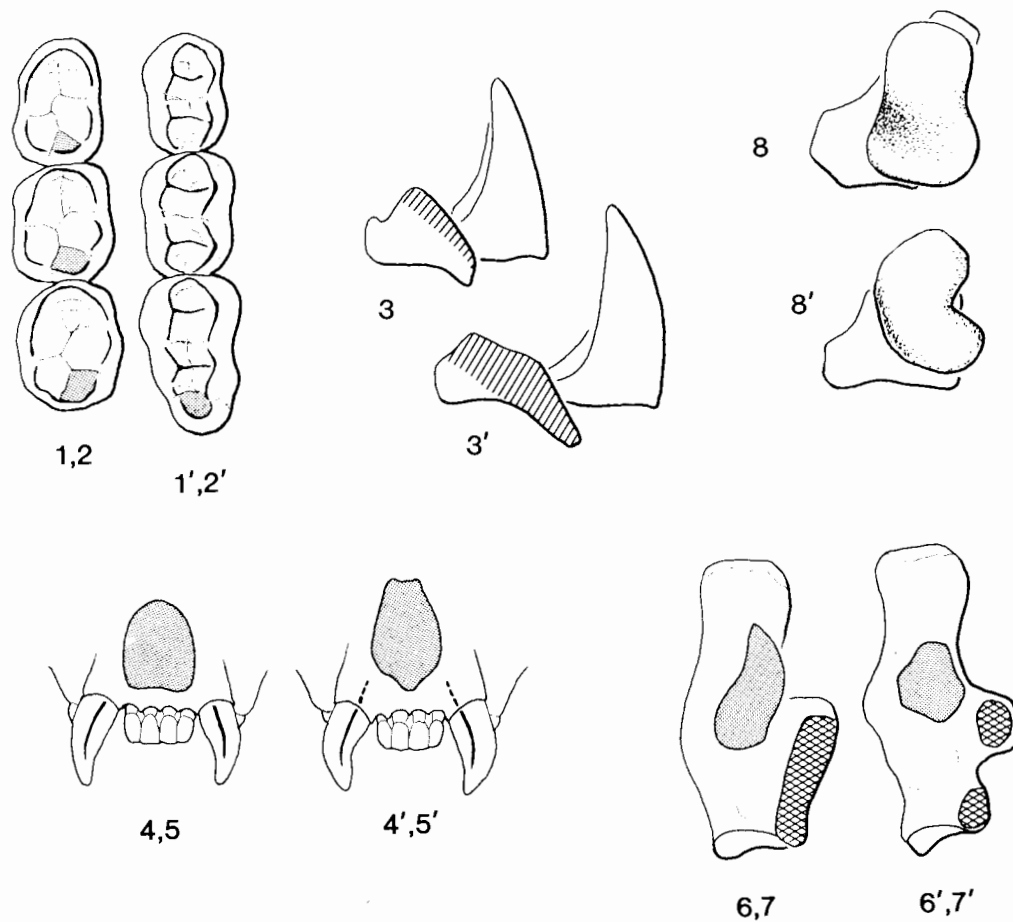


Figure 3. Selected characters at Node 1. Dorsal view RM_{1-3} , mesial to top, buccal to right: 1 peripheral bunodont cusps, 1' bilophodont cusps; 2 hypoconulid (stippled) on all cheek teeth, 2' hypoconulid on M_3 only. Buccal view RC_1-P_3 , mesial to right: 3 short P_3 flange, moderate wear facet (parallel lines), 3' flange extends below alveolar surface, well developed wear facet. Anterior view of lower face: 4 C^1 mesial sulcus restricted to crown, 4' C^1 mesial sulcus extends to root (dashed lines); 5 high, oval nasal aperture (stippled), 5' higher, narrower nasal aperture. Dorsal view right calcaneus, proximal to top, medial to right: 6 posterior astragalar facet (stippled) long and helical, 6' posterior astragalar facet short & rotational; 7 sustentacular and anterior astragalar facets (cross-hatch) united, 7' sustentacular (top) and anterior astragalar facets separate. Distal view left entocuneiform, plantar to bottom, proximal to left: 8 dorsal globular head, inferior helical groove, 8' kidney-shaped, groove peripheralized.

In the foot, the morphotypic condition for eucatarrhines, and indeed for all primates, is to have a calcaneus which bears posteriorly a long, helically-curving facet and anteromedially a single facet for the astragalus, which facilitates large degrees of inversion and eversion. As recognized by several authors (Szalay, 1975; Langdon, 1986; Gebo & Simons, 1987; Rose, 1987), most hominoids retain this morphology while cercopithecids have shortened the posterior facet and have divided the anteromedial facet into separate moieties for the astragalar head and neck (Figure 3, char. 6-7). This remodelling produces a lower ankle joint which emphasizes stability at the expense of limiting inversion.

In addition, the eucatarrhine morphotype is reconstructed to have had an entocuneiform joint surface for the hallux which presented a globular dorsal head surrounded inferiorly by a helical groove. This allows the hallux to rotate on its long axis while being adducted to the other digits (Lewis, 1972; Strasser, in prep. *a, b*). The cercopithecoid morphotype shows a remodelling of the entocuneiform surface into a kidney-shaped structure. The helical groove is essentially reduced and peripheralized, thereby restricting the amount of conjunct rotation that can accompany abduction-adduction (Figure 3, char. 8; Strasser, in prep. *a, b*).

This combination of characters suggests a scenario in which the ancestral cercopithecoid diverged from other eucatarrhines by exploiting resources in either a more open-country environment or on the forest floor. They may have occupied a niche exploited by few hominoids, due to their pedal adaptations which could have supported rapid travel along the ground and their dentition which facilitated the inclusion of more fiber in their diet.

Colobinae vs Cercopithecinae

The remaining 25 characters (plus char. 12 introduced above) serve to distinguish cercopithecoid subclades; in 21 cases, a primitive eucatarrhine character state has been retained from the cercopithecoid morphotype. A number of these characters are directly related to dietary specializations and, as recognized for a century, distinguish cercopithecin and colobine. Cercopithecin diverge from the morphotype by developing capacious buccal pouches for the temporary storage and preparation of food (Murray, 1975; Figure 4, char. 9), about which they are highly eclectic. Colobines lack cheek pouches, but correlated with their more specialized, mostly folivorous, they have a modified stomach. Extra chambers, added to the fundus, enhance fermentation by providing more space for a highly concentrated cellulose-digesting bacterial flora (Kuhn, 1964; Bauchop & Martucci, 1968; Figure 4, char. 10).

Cercopithecin show specializations of the incisors while retaining the primitive cercopithecoid molar crown configuration. The latter condition is one in which the crowns showed moderate relief, were broadly flared at the base but narrowed at the apex, and retained a relatively long trigonid (Delson, 1975; Figure 4, chars. 12-14). This group of features should not be dealt with as a "functional complex", as that would obscure the different presumptive histories of each character. The first character, crown relief, showed some increase relative to its development in most anthropoids, but not to the extreme degree seen independently developed in colobines and the *Theropithecus* clade, where deep notches incise the tooth walls.

The second character, molar flare, superficially presents a distribution among *extant* cercopithecoid tribes which is counter-intuitive to the inference that its strong development is primitive for the clade, since it is found consistently only in the papionins (Figure 2, char. 12). However, *Allenopithecus*, the most primitive member of Cercopithecin (see below) also shows strong flare. Additionally, the mid-Miocene African subfamily Victoriapithecin is not illustrated as one of the terminal taxa in Figure 2, but the species in this group also show a moderate to high degree of molar flare. Thus, strong molar flare is found in two of the three cercopithecoid subfamilies. Delson's (1975) hypothesis that flare is the result of cingulum incorporation could be tested by means of embryological studies, although this has not been done to date, and Benefit (1987) has argued against it. Nevertheless, the conclusion drawn from the distribution within the family is supported by reference to an

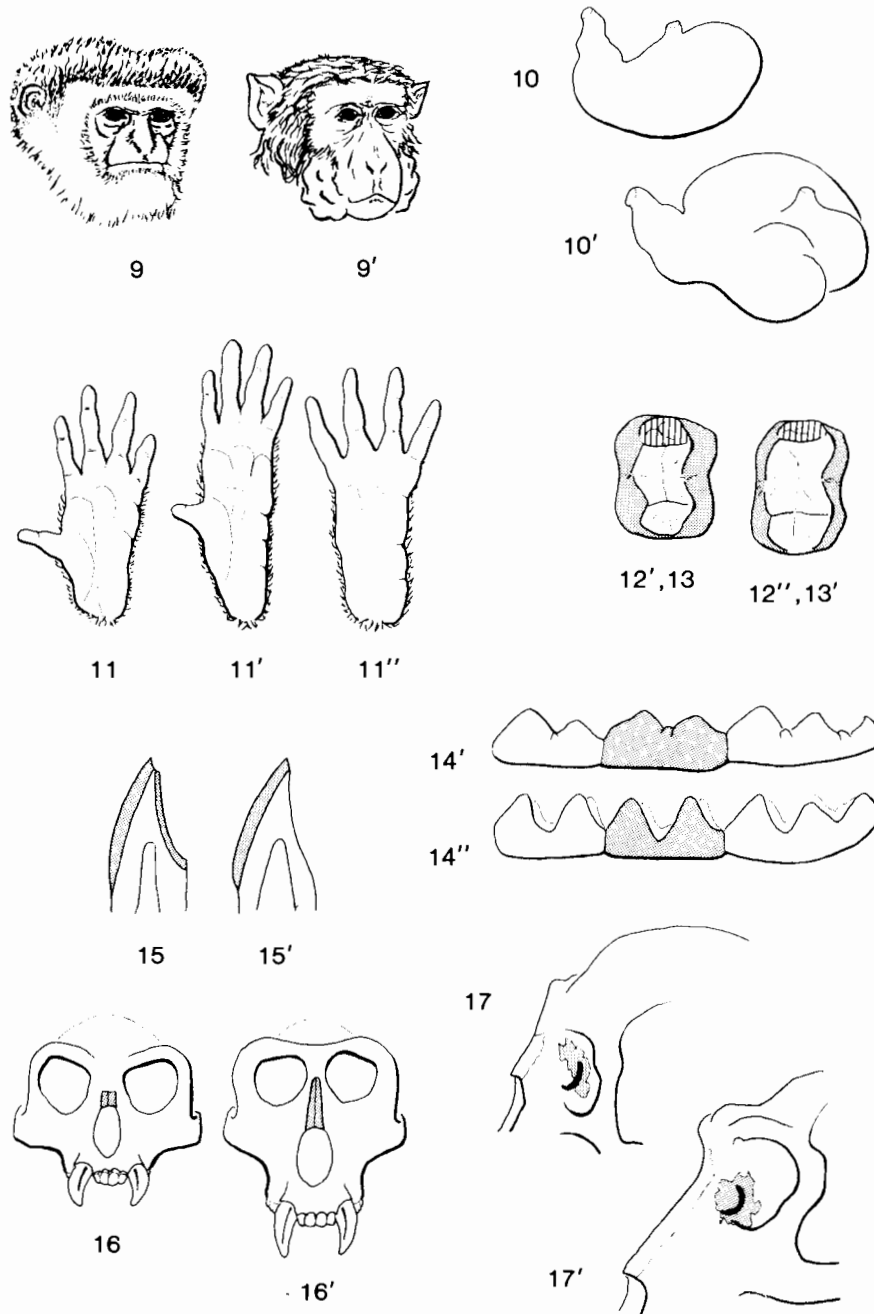


Figure 4. Selected characters at Node 2. Anterior view of face: 9 buccal pouches absent, 9' buccal pouches present. Anterior view stomach, pyloric region to left: 10 stomach simple, 10' stomach multi-chambered. Palmar view left hand: 11 pollex (thumb) well developed, 11' pollex reduced, 11'' pollex absent. Dorsal view RM_2 , mesial to top, buccal to right: 12 cingulum present (not illustrated), 12' molar flare well developed (stippled), 12'' molar flare secondarily reduced; 13 trigonid long (parallel lines), 13' trigonid short. Lingual view RM_{1-3} , mesial to left: 14 relief low, 14' relief high. Longitudinal cross-section I_1 , lingual to right: 15 enamel (stippled) present lingually, 15' lingual enamel absent. Anterior view skull: 16 nasal bones (stippled) short, 16' nasal bones long. Oblique left view skull, anterior to left: 17 lacrimal bone (stippled) within orbit & lacrimal fossa (bold line) straddles maxillary and lacrimal bones, 17' lacrimal bone at edge of orbit completely encloses lacrimal fossa.

outgroup. Both conditions in this postulated transformation series are found in *Propithecus*, where the molars of *P. markgrafi* do not show the cingulum present in those of its congeners, but instead are flared, although not as much as are cercopithecoid molars (Szalay & Delson, 1979).

The third feature in this complex, relative trigonid length, also is subject to alternative interpretation. Delson (1975) considered the colobines to have a relatively shorter trigonid basin than cercopithecines, and this observation has recently been supported by the quantitative work of Benefit (1987). Delson argued that parapithecids and propithecids have a rather long trigonid, implying that the cercopithecine condition was conservative and the colobine trigonid derived. Harrison (1982) and Benefit (1987) have countered that to them the trigonid appeared shorter in the eucatarrhine morphotype, implying that the colobine condition was less derived among cercopithecids. Resolution of this conflict requires quantitative and more detailed comparative analysis of this feature across anthropoids, which has not yet been undertaken.

The outcome may have a broader phylogenetic import, as Delson (1973) further argued that the presence in *Victoriapithecus macinnesi* of a short trigonid (as well as low relief) indicated that at least one derived colobine feature had already appeared in the middle Miocene. Moreover, he isolated at least one dental specimen (KNM MB 34) and a damaged distal humerus (KNM MB 19) as indicative of a potential second taxon in the Maboko Island assemblage and suggested that the cercopithecine–colobine divergence might be represented there, at 15 Ma (million years ago). Both Harrison (1982) and Benefit & Pickford (1986) have rejected this interpretation, arguing that only one cercopithecoid species is present, but Senut (1986) has also recognized two taxa on postcranial evidence. Benefit's analysis of the greatly increased sample of Maboko monkeys convincingly demonstrates that only one taxon is common; MB 34 could represent a rare second species but is probably best accepted as a slightly distinctive individual of *V. macinnesi*. The postcranial differences among far fewer specimens require further analysis, but we here abandon Delson's (1975) hypothesis of two cercopithecoid taxa at Maboko. If Benefit is correct about short trigonids being ancestral for cercopithecids, then *Victoriapithecus* shares few derived states with either modern subfamily, but we do not yet accept her interpretation. Butler (1986) further noted that in the character complex relating hypoconulid loss to molar wear orientations, *Victoriapithecus* presents a state intermediate between that of later cercopithecids (no cusp, phase II facets oriented transversely) and other eucatarrhines (cusp present, facets oblique). In *Victoriapithecus*, the hypoconulid has been lost (or is rarely present but small: Benefit, 1987), but the facets are oblique. The slightly older and much rarer *Prohylobates* is not yet known from unworn specimens in which the state is unambiguous, but there is a question as to whether it usually retains a hypoconulid (see Leakey, 1985).

To turn to the anterior dentition the distribution of enamel on the lower incisors in the cercopithecoid morphotype was primitively as in most other primates, with a thick layer on the labial side of the teeth and a somewhat thinner deposit on the lingual. It was first noted by Noble (1969) and later confirmed by Delson (1975) that papionins, like rodents and New World marmosets (Rosenberger, 1978), have eliminated the lingual layer of enamel, effectively producing a self-sharpening, chisel-like edge on these teeth. Shellis & Hiiemae (1986) recently tested this observation using histological techniques and documented that this is a characteristic shared by all cercopithecines (Figure 4, char. 15). They furthermore argued that the blunt-edged colobine incisors are better designed for gripping and tearing

leaves while the cercopithecine condition enhances the cutting and scraping that is often necessary for preparing fruits for consumption.

As regards facial architecture, Vogel (1968) postulated that the ancestral eucatarrhine had a broad interorbital distance with short nasal bones and a lacrimal fossa which straddled the border of the lacrimal and maxillary bones, as seen in colobines and most hominoids (Figure 4, char. 16–17; char. 23). Cercopithecines show a derived condition for these characters, all of which are probably associated with lengthening of the face. Thus, they have a narrower interorbital distance, longer nasal bones and a lacrimal fossa which lies entirely within a lacrimal bone that has expanded to such an extent that it extends outside the orbit. Additionally, cercopithecines have a longer and lower-vaulted cranium, a derived sulciferous pattern, and a mandibular corpus which increases in depth mesially while the colobine morphotype retains the primitive high-vaulted cranium and cerebral sulci as well as a mandibular corpus which is expanded in the gonial region and shallows mesially (chars 24–26).

In the postcranium there are a number of derived features which characterize the colobine morphotype. These are not as readily correlated with their dietary specialization, but may be interpretable *vis-à-vis* their locomotor behavior. Colobines are agile leapers and runners in the forest canopy and generally are more slender in build than cercopithecines of the same body size, as is reflected in their longer limbs and iridia. It is especially in the latter that they have diverged from the cercopithecine morphotype. The most obvious synapomorphy is the reduction of the external pollex and, in some cases, its entire loss (Figure 4, char. 11). Furthermore, as Gabis (1960) noted, colobines have a relatively shorter tarsus for any given foot length than do cercopithecines and the inferred cercopithecine morphotype. Such shortening effectively reduces the lever arm for the extrinsic muscles working on the distal foot and is clearly reflected in the contacts of the cuboid with the ectocuneiform (Figure 5, char. 18). The primitive condition among anthropoids, and retained in cercopithecines, is to have a long proximal and short distal contact between these two bones. In colobines these proportions are reversed, and in some taxa the proximal contact is lost altogether.

In addition, colobines have modified the functional axis of the foot, that is, the line of weight bearing through the digit rays. It is inferred from the distribution of relative metatarsal length, robusticity and attachment of muscles that the axis primitively passes through the middle of the foot travelling along the third digit ray. In cercopithecines this primitive axis is retained and the external flexors of the digits, which pass into the foot behind the astragalus, are arranged so that digits 1, 3 and 4 are operated by *m. flexor fibularis* (*m. flexor hallucis longus*) and the medially disposed *m. flexor tibialis* (*m. flexor digitorum longus*) manages digits 1, 2 and 5. Colobines are inferred to have shifted the axis laterally, between digits 3 and 4, since the fourth digit is invariably equal in length and robusticity to the third (Figure 5, char. 20). Furthermore, in colobines and some presbytines, *m. flexor fibularis* completely loses its attachment to the hallux while in most presbytines its contribution appears to be reduced (char. 27; Polak, 1908; Lewis, 1962). Thus, at least in many colobines, *m. flexor fibularis* is solely responsible for managing the elongated digits which flank the functional axis. This leaves *m. flexor tibialis* as the exclusive hallucal operator, albeit with assistance from *m. flexor accessorius* (*m. quadratus plantae*). This probably explains the presence of a groove on the proximal astragalus in colobines which supports a well developed retinaculum that in turn resists the displacement of *m. flexor tibialis* during its activity (Figure 5, char. 19).

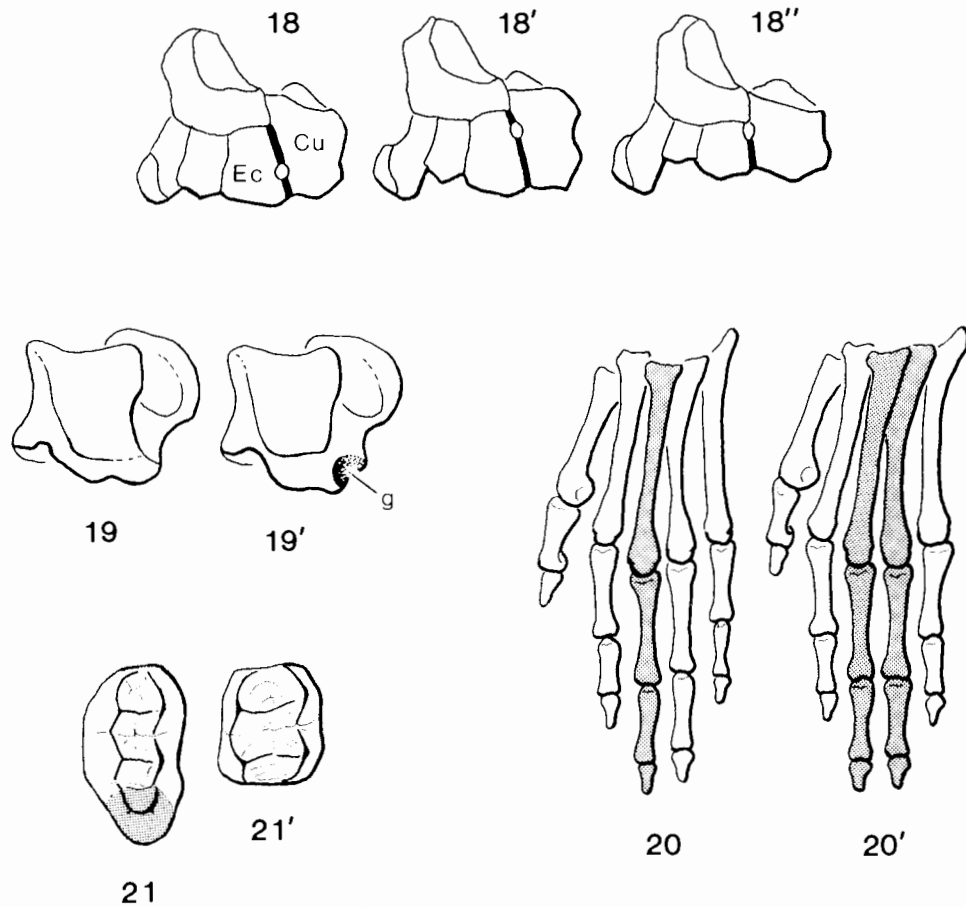


Figure 5. Selected characters at Nodes 2–4. Dorsal view left distal tarsals, proximal to top, lateral to right, Ec ectocuneiform, Cu cuboid, bold lines indicate articulations: 18 proximal facet long & distal facet short, 18' proximal facet short & distal facet long, 18'' proximal articulation missing. Proximal view left astragalus, lateral to left: 19 m. flexor tibialis groove (g) absent, 19' groove well developed. Dorsal view left pedal digit rays, medial to left: 20 functional axis through third digit ray (stippled), 20' functional axis between digit rays 3–4. Dorsal view RM_3 , mesial to top, buccal to right: 21 hypoconulid (stippled) present, 21' hypoconulid absent.

Major subdivisions within the extant subfamilies

The Cercopithecinac are today commonly divided into two tribes (following Kuhn, 1967): Papionini, the macaques, baboons, drills, mangabeys and gelada; and Cercopithecini, the forest guenons and relatives. The papionins have secondarily increased the maximum width of their nasal aperture (Figure 3, char. 5) and generally have both relatively longer faces and stronger adaptations to terrestrial life than does the cercopithecin morphotype (chars 28–29). Cercopithecins, on the other hand, show three synapomorphies compared to the ancestral condition. They have lost the hypoconulid on the third molar, and in parallel with colobines, all cercopithecins except *Allenopithecus* have secondarily reduced the amount of molar flare (Figure 4, char. 12; Figure 5, char. 21). Finally, cercopithecins

show a great deal of fragmentation of their chromosomes, having diploid numbers between 48 and 72, while papionins all have 42 and colobines mainly 44 (char. 30).

The subfamily Colobinae was tentatively divided by Szalay & Delson (1979) into two groups which appear to be less distinct than the cercopithecine tribes and which were therefore ranked as subtribes: the Asian Presbytina and the African Colobina. As noted above, characters 11 and 18 presented a complex morphocline, and it is the presbytine morphotype which retains the more primitive colobine condition for both characters. This comprises a reduced external pollex and a small proximal contact between the lateral tarsals, while the ancestor of African colobines was more derived in eliminating both of these features.

Notes on generic relationships within higher taxa

The majority of the foregoing analysis is well-accepted, with only the potential reversal in character 13 (trigonid length) leading to hesitation. The greatest uncertainty relates to generic relationships within each of the four cercopithecoid taxa reviewed above. Within Papionini, Szalay & Delson (1979) recognized three subtribes as did Jolly (1966) and Kuhn (1967). On mainly biogeographic grounds Delson (1973, 1975) postulated that the origin of these subtribes was related to their separation by the enlargement of the Sahara desert, interpreted as a vicariant event in the late Miocene (*ca* 9–6 Ma). Neither the North African and Eurasian Macacina nor the sub-Saharan Papionina are characterized by consistent derived features, while the monotypic Theropithecina is simply autapomorphic. Living and fossil *Macaca* can be separated from African papionins as a genus which persistently retains primitive states, especially in terms of facial profile, lack of facial fossae and locomotor morphology (chars 29, 31–32). Two extinct large-bodied Eurasian genera appear to be “derived macaques”, differing mainly in their greater adaptations to terrestriality. Until *Procynocephalus* (late Pliocene of India and China) is better-known cranially, and it is possible to determine if it shared the apparently reduced cranial sexual dimorphism seen in *Paradolichopithecus* (Pliocene of Eurasia), it is perhaps best to retain these similar forms as distinct genera. Compared to the Macacina, most papionins including *Theropithecus*, share greater facial elongation with a steep anteorbital drop, development of facial fossae and increased adaptations to terrestriality. Within this group, *Theropithecus* is clearly the most derived dentally, facially and postcranially (see Jolly, 1972). It is first documented in the fossil record at least 4 Ma, and on the assumption that a considerable period of time was required to develop its numerous autapomorphies, Szalay & Delson (1979) recognized a subtribe Theropithecina. What remains uncertain is whether *Theropithecus* is the sister-taxon to all (other) papionins or a member of that taxon, with its closest relative one specific genus (such as *Papio*). Despite its early presence in the fossil record, *Theropithecus* could well have been a rapidly evolved offshoot from a *Papio*-like stock, as Cronin & Meikle (1979) suggested partly on the basis of molecular studies. At present, it would seem best to include *Theropithecus* within Papionina, whose other relationships also require further analysis. For example, the monophyly of the mangabeys needs detailed investigation (Groves, 1978; Klüberdanz, in prep.), as does the placement of *Mandrillus* as either a subgenus of *Papio* or a quite distinct genus. It may be thought inconsistent to retain *Paradolichopithecus* while eliminating Theropithecina, but the combination of the two Eurasian genera (if required by future analysis) is less confusing than the erection of an infrasubtribal category and taxon for *Theropithecus* which now

appears to belong within the Papionina. Of the Plio-Pleistocene fossil papionins, *Gorgopithecus* (late Pliocene of S. Africa) is clearly derived in its reduced dental sexual dimorphism and mid-facial/zygomatic morphology, but the contemporaneous *Dinopithecus* (also known from the Pliocene of Ethiopia and Angola) is best considered as a subgenus of *Papio* (see Delson, 1984). The long-lived *Parapapio* (late Miocene to late Pliocene of Africa) is conservative, in many ways similar to *Macaca*, although its facial profile is straighter and less concave, possibly implying a transformation series whose polarity is yet unclear. Until the relationships of the living genera are better clarified, it is nearly impossible to interpret these still fragmentary fossil finds.

The Cercopithecini is a less diverse group at the generic level, but the relationships of the very successful *Cercopithecus* species continue to frustrate attempts at resolution (cf. Maranto, 1986 and Muleris *et al.*, 1986). Ignoring that problem leaves four species, often placed in three distinct genera: *Allenopithecus*, *Erythrocebus* and *Miopithecus*. Of these, the first would seem to be readily interpreted as a species with many retained ancestral cercopithecine features such as molar flare, continuous male ischial callosities and cyclic changes in female sexual skin; it also has only 48 chromosomes, the lowest diploid number in the tribe (chars 12, 30, 33–34). The difference between *Allenopithecus* and the remaining cercopithecins appears roughly as distinct as that between the subtribes of Papionini and Colobinae. On this basis we suggest formal recognition of a subtribe Allenopithecina, defined by the three cited retentions and based on *A. nigroviridis*.

It may be argued that one should not define a taxon based solely on conservative retention of characters which define the higher taxon to which it belongs. However, there are three points to consider in this regard. First, it is quite probable that further study may permit the delineation of autapomorphies for *Allenopithecus*. Moreover, this species does present the derived characters of the Cercopithecini, although it is conservative by comparison to other species in that tribe. Most importantly, if one insists that any taxon must be defined by autapomorphies, and at the same time argues that the presence of an autapomorphy prevents one species from being ancestral to its sister taxon, the possibility of ever identifying ancestors is excluded. Ancestral species obviously did exist, and if a “real” ancestor cannot be recognized because of a definitional stumbling block, systematic progress is surely not being furthered. A similar problem can be recognized with regard to *Homo erectus*, a species probably ancestral to the broadly defined *Homo sapiens*, but showing autapomorphies only in Asian populations (see Rightmire, 1987). This is not to say that *Allenopithecus* is being suggested as the potential ancestor of the Cercopithecina—what we are addressing here is the broader methodological argument that non-autapomorphic taxa may have a place in systematics without running the risk of being dismissed as paraphyletic (in the definition, for example, of Patterson, 1982).

The nominate cercopithecine subtribe, Cercopithecina Gray, 1825, would be defined by the derived loss of molar flare and connected male ischial callosities, as well as an increased diploid number. Among cercopithecins, only *Miopithecus* presents sexual skin cyclicality, and on this basis Groves (1978) has questioned its placement even among the Cercopithecini. This appears unlikely in light of the presence in *Miopithecus* of all cercopithecine and three of the four cercopithecine characters. Moreover, Verheyen's (1962) analysis of cranial form, among others, convinces us that *Miopithecus* is a neotenuous, phylogenetically dwarfed *Cercopithecus*, but the presence of female cycling leads us to rank it as a full genus, perhaps the most distinct one in the subtribe. *Erythrocebus*, on the other hand, is more distinct cranially and posterocranially, but has lost cyclicality. Both of these taxa have low

diploid numbers of 54, suggesting fairly early differentiation from the main *Cercopithecus* lineage, but they have not yet been unambiguously linked to any species groups thereof.

The phyletic geometry of the Colobinae is even more confused, with the two subtribes being neither widely accepted nor definitely holophyletic. Among the Colobina, three extant taxa are commonly recognized, often as the single genus *Colobus*, with three subgenera. However, some recent classifications, such as those by Thorington & Groves (1970) and Napier (1985) following Groves (1970), link *Piliocolobus* with *Colobus*; others, especially Kuhn (1967), include *Piliocolobus* in *Procolobus*. Napier (1985) has clearly tabulated a series of characters which vary among these three species groups, consistently grouping *Piliocolobus* and *Procolobus*. The polarity of some of these characters is uncertain, but it appears to us that the lack of female sexual swellings (also found in presbytinans), and the probably inter-related large larynx and sub-hyoid sac are derived features of *Colobus*, while the discontinuous male ischial callosities (also seen in *Pygathrix*), male perineal organ and four-chambered stomach are synapomorphies of *Procolobus* and *Piliocolobus* (chars 10, 34–35; Kuhn, 1972). Brandon-Jones (1985) has grouped these two taxa in *Procolobus*, adding the common presence of a sagittal crest in males; we tentatively consider this feature also a true synapomorphy, possibly implying relatively smaller brain size. Pending further work in progress, we recognize *Procolobus* to include subgenera for the olive and red colobus, with *Colobus* restricted to the black and white group. *P. (Procolobus)* is further distinguished by the (presumably conservative) lack of pattern in its pelage and by the presence of a median mental foramen, otherwise common in cercopithecines, rare in hominoids (10–20% occurrence) and very rare to absent in other extant colobines (char. 36; Vogel, 1968). Yet, the Plio-Pleistocene African fossil colobines *Cercopithecooides* and *Rhinocolobus* also present this foramen, and its phyletic implication is thus uncertain (Leakey, 1982). These and other African fossils are tentatively included in the Colobina, although most are too fragmentary to permit determination of the diagnostic features of the subtribe: extreme pollicial reduction, the loss of the proximal contact between cuboid and ectocuneiform (the latter state is observable in the Pliocene *Paracolobus*), and loss of insertion by *m. flexor fibularis* onto the hallux.

There is perhaps even less agreement about the relationships among Asian colobines. We have presented presbytinans as an unresolved trichotomy in Figure 1 because there is no one character uniting any two of the three lesser groups. At the generic level, we follow Groves (1970) in including *Simias* within *Nasalis* and *Rhinopithecus* as a subgenus of *Pygathrix*, Delson (1975) in allowing a subgenus for *N. (Simias)* and tentatively Brandon-Jones (1985) in distinguishing *Semnopithecus* and *S. (Trachypithecus)* from *Presbytis*. Groves (1970) has made the most detailed analysis of this group, but could find no clearly derived features which linked any pair of genera. Even the long-accepted grouping of *Presbytis* with *Semnopithecus* (s.l.) is based on no more than a mainly intermediate condition in facial structure (e.g., face shorter than *Nasalis* but longer than *Pygathrix*), relatively shorter arm compared to leg length (char. 37; like most colobines, but not the apparently conservative *Nasalis* and *Pygathrix*), and other features which are probably of low phyletic value. Kuhn (1967) went so far as to suggest that *Nasalis* might be the sister-taxon to all other colobines, a view which cannot be fully refuted as yet.

The relationship between Asian and African colobines is thus problematical. Other than geographic separation, a few features clearly distinguish members of the two subtribes. Extant colobines certainly form a clade whose ancestor was characterized by derived thumb reduction and tarsal shortening. However, both of these features are parts of trends

seen in *Presbytina* which, as mentioned above, may be a paraphyletic taxon. Further study is required to discern the more precise relationships of individual Asian colobines to the African forms. Consideration of the extinct Mio-Pliocene European colobines *Mesopithecus* and *Dolichopithecus* leads to further confusion. The younger genus, *Dolichopithecus*, was thought to be more derived on a number of morphoclines than its purported ancestor, representing one of the few acceptable cases of a generic ancestor-descendant relationship in the catarrhine fossil record (Delson, 1975). More recent studies (Strasser, in prep. *a*) reveal that while *Mesopithecus* presents the derived loss of the proximal cuboid-ectocuneiform facet, *Dolichopithecus* retains that contact, albeit reduced, much as in *Pygathrix* and *Nasalis*. Such loss in *Mesopithecus* and retention in *Dolichopithecus* weakens the hypothesis of direct descent in the European clade but does not imply any phyletic relationship for these forms to extant colobines. Indeed, until the phylogeny of Asian colobines is better resolved the taxonomic allocation of these European forms must remain *Colobinae incertae sedis*.

The resulting classification of Cercopithecidae to the level of subgenus is presented in Table 3. We have discussed in the text most modifications to existing classifications. However, a brief comment on the phyletic and taxonomic position of *Victoriapithecus* (and *Prohylobates*) may be worthwhile. These mid-Miocene species are especially interesting because they are the oldest representatives of the Old World monkeys. Benefit (1987) has argued that they should be grouped in a monophyletic taxon (named as *Victoriapithecinae* by Koenigswald, 1969) on the basis of a shared derived mandibular symphysis morphology and the supposedly oblique orientation of the long axis of P_4 (see also Leakey, 1985, who implied a possible synonymy of the two genera). Although many characters are unknown in these fossils, and the polarity of others (such as the trigonid length) is uncertain, they may not share any derived conditions with either later subfamily. On this basis, Benefit (1987) has proposed that the mid-Miocene taxa be placed in a distinct family of Cercopithecoidea, but we prefer to retain them as a subfamily until these arguments are further elaborated and the character polarities assessed, demonstrating our uncertainty with a trichotomy.

Summary

In this paper we present the derived features which characterize the hypothetical ancestors of Cercopithecidae and its subclades. While some typical features have been recognized since the time of Linnaeus, continued research reveals additional characteristics that allow the refinement of hypotheses of phylogenetic relationship. The cercopithecoid ancestor is distinguished by 13 derived features which we suggest allowed it to successfully exploit a "niche" unavailable to early hominoids. These include: the alignment of cusps into a bilophodont condition; the incorporation of cingulum into the molar sidewall resulting in a flared tooth; the elongation and increased relief of molars; the loss of the hypoconulid on dP_4-M_2 ; the elongation of the P_3 flange for increased honing of C^1 ; the extension of C^1 mesial sulcus onto the root; the development of a high and narrow nasal aperture; the modification of the posterior and anterior compartments of the lower ankle joint to stabilize it and limit the extent of pedal inversion; and the reduction of hallucial axial rotation during ab-adduction. The mid-Miocene *Victoriapithecus* and *Prohylobates* appear to be linked by one possibly derived feature, but this clade is ranked as a subfamily rather than a

Table 3

Outline classification of Cercopithecidae

Order Primates
Semioorder Euprimates
Suborder Haplorhini
Hyporder Anthropoidea
Infraorder Catarrhini
Parvorder Eucatarrhini
Superfamily Cercopithecoidea
Family Cercopithecidae
Subfamily Cercopithecinae
Tribe Cercopithecini
Subtribe Allenopithecina
<i>Allenopithecus</i>
Subtribe Cercopithecina
<i>Cercopithecus</i>
<i>Miopithecus</i>
<i>Erythrocebus</i>
Tribe Papionini
Subtribe Papionina
<i>Papio</i>
<i>P. (Mandrillus)</i>
† <i>P. (Dinopithecus)</i>
<i>Cercocebus</i>
“ <i>Lophocebus</i> ”
† <i>Gorgopithecus</i>
<i>Theopithecus</i>
† <i>Parapapio</i>
Subtribe Macacina
<i>Macaca</i>
† <i>Procy노cephalus</i>
† <i>Paradolichopithecus</i>
Subfamily Colobinae
Subtribe Colobina
<i>Colobus</i>
<i>Procolobus</i>
<i>P. (Piliocolobus)</i>
† <i>Libypithecus</i>
† <i>Cercopithecoides</i>
† <i>Paracolobus</i>
† <i>Rhinocolobus</i>
Subtribe Presbytina
<i>Presbytis</i>
<i>Semnopithecus</i>
<i>S. (Trachypithecus)</i>
<i>Pygathrix</i>
<i>P. (Rhinopithecus)</i>
<i>Nasalis</i>
<i>N. (Simias)</i>
Subfamily Colobinae, incertae sedis
† <i>Mesopithecus</i>
† <i>Dolichopithecus</i>
Subfamily Victoriapithecinae
† <i>Victoriapithecus</i>
† <i>Prohylobates</i>

† Extinct genus or subgenus.

separate family to emphasize our uncertainty about its phyletic relationship to the later subfamilies.

The cercopithecine morphotype is characterized by the acquisition of buccal pouches; loss of lingual enamel on the lower incisors; facial elongation with the concomitant decrease in interorbital distance, lengthening of nasal bones and complete enclosure of the lacrimal fossa within the lacrimal bone; elongation of a low-vaulted cranium; development of a derived cerebral sulcal pattern and a mandibular corpus which increases in depth mesially. Within Cercopithecinae there are two tribes, each one of which contains one persistently conservative and one holophyletic and probably derived subtribe. The morphotype for the tribe Papionini shows a secondary increase in the maximum width of their nasal aperture; facial elongation; and stronger adaptations to terrestrial life. Macacins retain the morphotypic conditions while papioninans show a trend in developing: a steep anteorbital drop; facial fossae; and further postcranial adaptations to terrestrial life. *Theropithecus* is included within the latter subtribe until further study clarifies the relations of fossil and recent baboons and mangabeys. The morphotype for the tribe Cercopithecini is distinctive in the loss of the hypoconulid on M_3 and the tendency towards chromosomal fragmentation. Within this tribe, the morphotype for Cercopithecina (containing *Cercopithecus*, *Miopithecus* and *Erythrocebus*) is further derived by secondarily reducing the amount of molar flare and separating male ischial callosities. Guenons and patas, but not talapoinns, have also lost cyclic changes in female sexual skin, which leads us to rank *Miopithecus* as a genus, rather than the subgenus suggested elsewhere. The newly recognized subtribe Allenopithecina retains the more conservative condition for these features. It is reasonable to recognize such "persistently primitive" taxa both because they do present derived features of their clade as a whole and in order to avoid rendering the identification of putative ancestral species definitionally impossible.

The colobine morphotype presents: a complex, sacculated stomach; molar teeth in which flare is secondarily reduced and the trigonid shortened; a mandible with an expanded gonial region; a reduction of the pollex; a shifting of the functional axis of the foot with the development of a proximal astragalar groove for *m. flexor tibialis*; and a shortened tarsus reflected in the contacts of the cuboid and ectocuneiform. Two subtribes are recognized within Colobinae: Presbytina for the Asian colobines and Colobina for the African. The presbytinan morphotype is the more primitive of the two, retaining a small external thumb and a reduced proximal facet between the cuboid and ectocuneiform. The colobinan morphotype is characterized by three losses: of the external pollex; the proximal facet between the cuboid and ectocuneiform; and the insertion of *m. flexor fibularis* onto the hallux. Within Colobina we recognize *Colobus* for the black-and-white colobus and *Procolobus* for the red and olive forms. The former is characterized by apparently derived enlargement of the larynx and presence of a sub-hyoid sac. *Procolobus* and *P. (Piliocolobus)* share four synapomorphies: a four-chambered stomach, male perineal organ, discontinuous ischial callosities and a sagittal crest. Among the presbytinans, generic distinction is less clear, but at present we recognize *Nasalis*, *N. (Simias)*, *P. (Pygathrix)*, *P. (Rhinopithecus)*, *Presbytis*, *S. (Semnopithecus)* and *S. (Trachypithecus)*. While the phyletic relationships among fossil and living colobines are not yet resolved, pedal characters are beginning to clarify the situation; e.g., *Mesopithecus* presents a derived feature not seen in its putative descendant *Dolichopithecus*, casting doubt upon this hypothesis of descent.

Acknowledgements

We thank Fred Grine, John Fleagle and Lawrence Martin for inviting us to participate in the Hennig VI Symposium, for which this paper was prepared; Chester Tarka, Lorraine Meeker and Suzanne Walker for advice on the preparation of illustrations by E. S.; Guy Musser, David Dean and three reviewers for comments on drafts of the manuscript; and the curators and staffs of the following institutions for access to collections in their care: American Museum of Natural History, Museum of Comparative Zoology, National Museum of Natural History, Field Museum of Natural History, The University of Wisconsin-Milwaukee Tappen collection, British Museum (Natural History), Powell-Cotton Museum, Musée Royal de l'Afrique Centrale, Rijksmuseum van Natuurlijke Historie, Zoologisk Museum (Copenhagen), Zentrum Anatomie (Georg-August-Universität, Göttingen), Natur-Museum Senckenberg, Zentrum der Morphologie der Klinikum der Johann Wolfgang Goethe-Universität, Naturhistorisches Museum Wien, Naturhistorisches Museum Basel, Museo di Geologia e Paleontologia (Firenze), Anthropologisches Institut und Museum der Universität Zürich-Irchel, Muséum National d'Histoire Naturelle (Paris), the National Museums of Kenya, the Transvaal Museum, the Paleontological Museum of the Academy of Sciences (Moscow) and the Institute of Vertebrate Paleontology and Paleoanthropology (Beijing).

Research upon which this work is based was supported, in part, by PSC-CUNY grants 13610 & 667370 and NSF grant BNS-8419939 to E.D., NSF BNS-8407911 to E.D. and E.S., and a C.U.N.Y. Mina Rees Award, Smithsonian Predoctoral Fellowship and Wenner-Gren grant to E.S.

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