

# Skeletal and dental morphology supports diphyletic origin of baboons and mandrills

(primate phylogeny/Papionini/molecular systematics/feeding ecology)

JOHN G. FLEAGLE\*<sup>†</sup> AND W. SCOTT MCGRAW<sup>‡</sup>

\*Department of Anatomical Sciences, School of Medicine, Health Sciences Center, State University of New York, Stony Brook, NY 11794-8081; and <sup>‡</sup>Department of Anatomy, New York College of Osteopathic Medicine, New York Institute of Technology, Old Westbury, NY 11568

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**ABSTRACT** Numerous biomolecular studies from the past 20 years have indicated that the large African monkeys *Papio*, *Theropithecus*, and *Mandrillus* have a diphyletic relationship with different species groups of mangabeys. According to the results of these studies, mandrills and drills (*Mandrillus*) are most closely related to the *torquatus-galeritus* group of mangabeys placed in the genus *Cercocebus*, whereas baboons (*Papio*) and geladas (*Theropithecus*) are most closely related to the *albigena-aterrimus* mangabeys, now commonly placed in the genus *Lophocebus*. However, there has been very little morphological evidence linking mandrills on the one hand and baboons and geladas on the other with different groups of mangabeys. In a study of mangabey locomotion and skeletal anatomy, we have identified features of the postcranial skeleton and the dentition that support the molecular phylogeny and clearly link mandrills with *Cercocebus* and *Papio* with *Lophocebus*. Moreover, the features linking *Cercocebus* and *Mandrillus* accord with ecological studies of these species indicating that these two genera are a cryptic clade characterized by unique adaptations for gleaning insects, hard nuts, and seeds from the forest floor.

Mangabeys are a group of large African monkeys characterized by moderately projecting snouts, large incisors, hollow cheek bones, long limbs, and long tails (1–3). They are found throughout much of sub-Saharan Africa from Senegal on the west to Kenya and Tanzania on the east (4). Traditionally placed in a single genus *Cercocebus* (5–6), these monkeys are commonly divided into two species groups—the terrestrial species *galeritus*, *torquatus*, *atys*, and *agilis* in one group, and the arboreal species *albigena* and *aterrimus* in another group. The three largest African monkeys, mandrills, baboons, and geladas have long been considered a single radiation of closely related species, commonly placed in three separate genera *Mandrillus*, *Papio*, and *Theropithecus*. In 1976, immunological studies by Cronin and Sarich (7) and Hewett-Emmett *et al.* (8) demonstrated that the two species groups of mangabeys were polyphyletic with respect to other papionins. The *albigena* group was more closely related to baboons and geladas, whereas the *torquatus-galeritus* group was more closely related to mandrills and macaques. Groves (2) reported numerous cranial differences between the two species groups and urged separation of the *albigena* group into a separate genus, *Lophocebus*. Most recently Nakatsukasa (9–11) has documented skeletal differences between the two genera of mangabeys that distinguish the more terrestrial (12–15) *Cercocebus* from the more arboreal (16–19) *Lophocebus*. Subsequent molecular studies, especially by Disotell (20, 21) and colleagues (22, 23) have confirmed the polyphyly of the mangabeys and clarified

that the central African mandrills and drills (*Mandrillus*) are the sister taxon of *Cercocebus* whereas *Lophocebus*, *Papio*, and *Theropithecus* form a separate, unresolved clade.

Despite considerable molecular evidence that mandrills are phylogenetically distinct from baboons and geladas and morphological studies documenting differences between *Cercocebus* and *Lophocebus*, there is limited morphological evidence supporting the *Cercocebus-Mandrillus* clade (3, 20). In the course of a study designed to identify skeletal features associated with the different locomotor habits of the two mangabey groups (24), we found many osteological features that distinguish the more arboreal *Lophocebus* on the one hand from the terrestrial *Cercocebus* as well as all the larger papionins, (*Mandrillus*, *Papio*, and *Theropithecus*). However, in addition to the features that commonly distinguish arboreal and terrestrial primates, we found features of the postcranial skeleton that link *Cercocebus* uniquely with *Mandrillus* and also link the arboreal *Lophocebus* with the terrestrial *Papio* and *Theropithecus* (Table 1; Fig. 1).

Compared with *Lophocebus* and *Papio*, *Cercocebus* and *Mandrillus* are characterized by a scapula that is relatively deep, with an expanded supraspinous fossa and prominent inferior angle. The shaft of the humerus of *Cercocebus* and *Mandrillus* is characterized by a very broad deltoid plane, a proximally extended supinator crest, and a broad brachialis flange (Fig. 2). The distal articulation of the humerus of *Cercocebus* and *Mandrillus* is characterized by a narrow olecranon fossa with a deep lateral ridge. The ulna articulation is characterized by a narrow coronoid process and a relatively large radial notch. Compared with *Lophocebus* and *Papio*, the ulna and radius of *Cercocebus* and *Mandrillus* are distinguished by prominent interosseous lines. Overall, the upper extremity of *Cercocebus* and *Mandrillus* is marked by skeletal features indicative of powerful limb adduction and flexion of the elbow and digits. The latter accords with earlier observations that mandrills have a much greater forelimb flexor mass than *Papio* (25).

The lower extremity of *Cercocebus* and *Mandrillus* is distinguished by a relatively robust ilium, a femur with a reduced gluteal tuberosity, subequal and sharp borders on the patellar margins, and a tibia with a more rounded midshaft dimension. The most striking dental feature that unites *Cercocebus* and *Mandrillus* is their common possession of relatively large, rounded posterior premolars in both the lower and upper dentition (Table 1, Fig. 3). Both the large size and the extreme wear of these teeth indicate that they are used in powerful crushing.

Because of their rapid terrestrial locomotion and shyness resulting from their susceptibility to human hunting, *Cercocebus* and *Mandrillus* are among the most poorly known of all nonhuman primates. Nevertheless, there are several unusual shared features of their foraging behavior that suggest a similar overall ecological adaptation associated with their unique

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<sup>†</sup>To whom reprint requests should be addressed.

Table 1. Morphological and dental features distinguishing *Cercocebus* and *Mandrillus* from *Lophocebus* and *Papio*

Index	<i>Cercocebus</i>	<i>Mandrillus</i>	<i>Lophocebus</i>	<i>Papio</i>	P value
(Supinator crest height/humerus length) × 100	35.2 (1.6), 6	33.2 (0.85), 6	31 (3.34), 6	30.2 (2.68), 5	0.002
(Deltoid plane width/humeral head width) × 100	88.3 (6.7), 6	84 (10.7), 6	73.1 (8.13), 6	70.1 (9.8), 5	<0.001
(Coronoid width/articular notch width) × 100	54.9 (6.14), 6	55.6 (8.36), 6	71.9 (9.77), 4	70.7 (7.13), 5	<0.001
(Tibia mid AP diameter/mid ML diameter) × 100	132.3 (1.29), 6	123.5 (.964), 6	152.5 (0.77), 4	144.2 (4.32), 5	<0.001
(Scapula maximum height/maximum length) × 100	90.9 (8.22), 6	91.2 (3.67), 6	80.9 (3.49), 7	72.9 (4.32), 5	0.002
(Ilium minimum width/maximum acetabular diameter) × 100	111.8 (8.85), 5	117 (9.8), 5	86.2 (6.56), 4	100.6 (1.17), 6	<0.001
(P <sup>4</sup> m-d × b-l/M <sup>1</sup> m-d × b-l) × 100	90.3 (10.9), 10	95.3 (13.66), 12	57 (7.13), 13	61.1 (9.2), 6	<0.001
(P <sub>4</sub> m-d × b-l/M <sub>1</sub> m-d × b-l) × 100	85.6 (6.4), 10	86 (14.4), 12	57.6 (5.3), 13	55.5 (4.2), 6	<0.001

The means of *Cercocebus* and *Mandrillus* and those of *Lophocebus* and *Papio* were compared using the Games and Howell method and were not significantly different. Subsequently the combined means of *Cercocebus*-*Mandrillus* and *Lophocebus*-*Papio* were compared using Student's *t* test. All measurements are of males. Values given as mean (SD), *n*. m-d = mesiodistal length, b-l = buccolingual breadth.

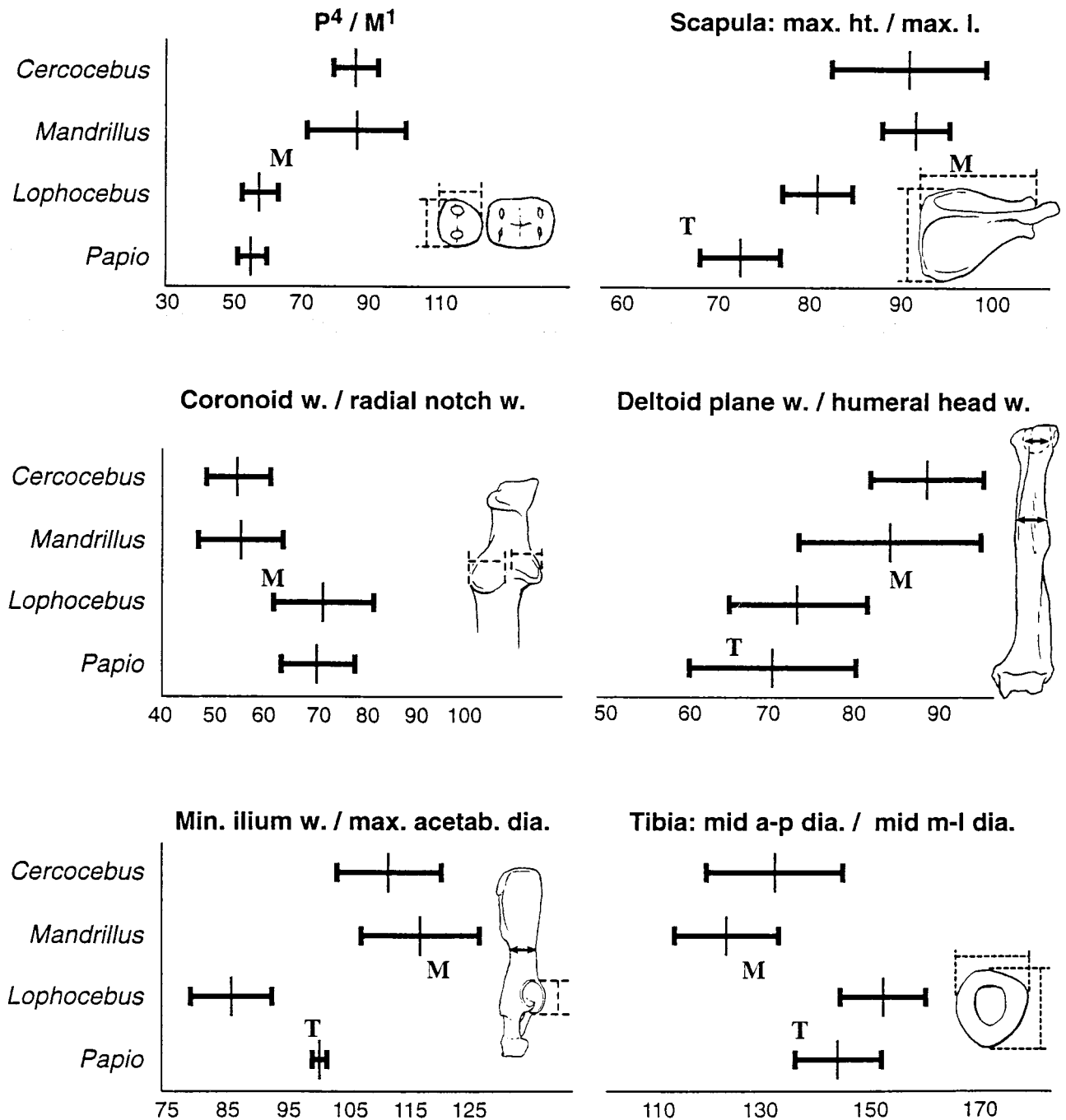


FIG. 1. Morphological and dental features distinguishing *Cercocebus*, *Mandrillus*, and *Macaca nemistrina* (M) from *Lophocebus*, *Papio*, and *Theropithecus* (T).

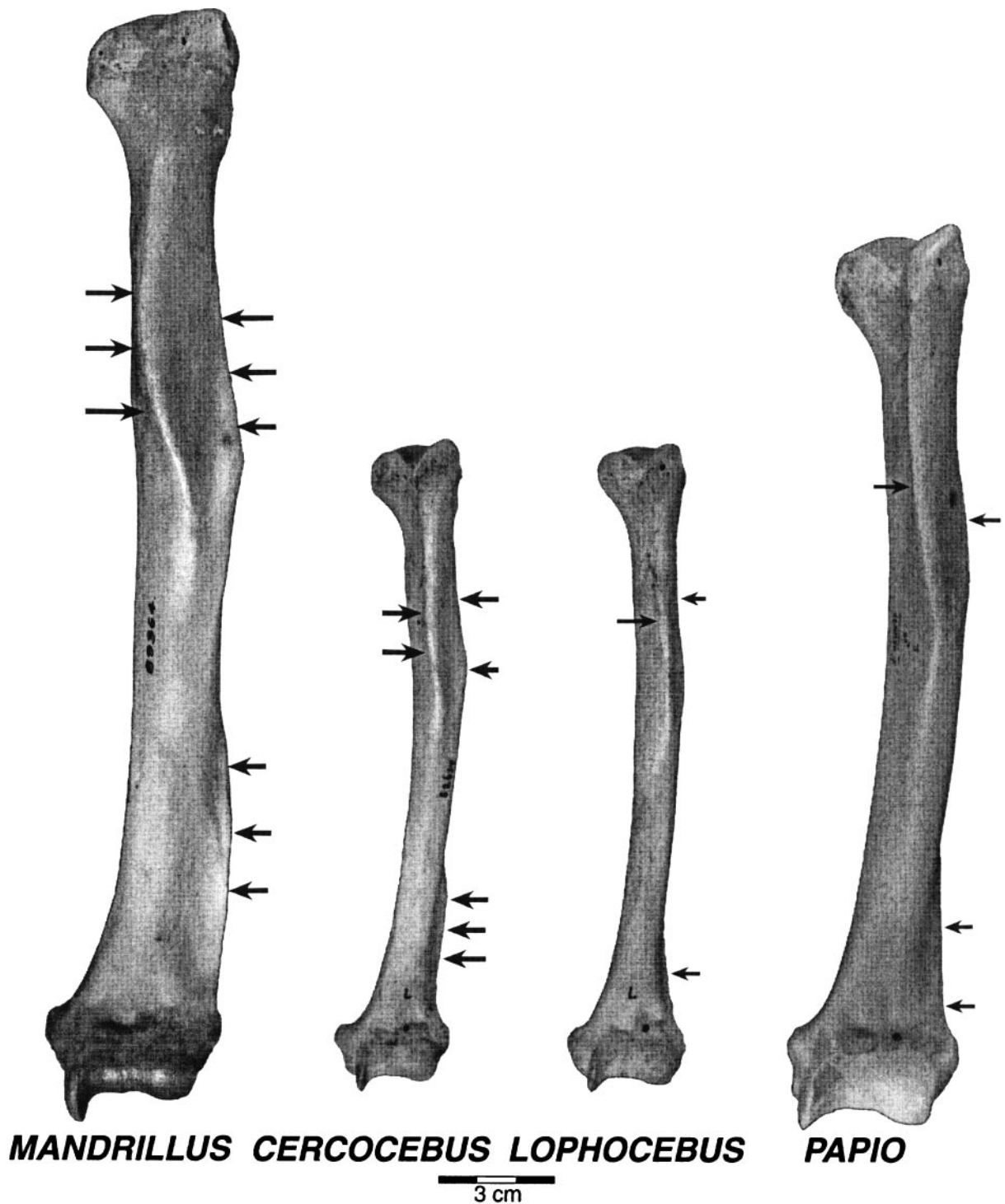


FIG. 2. Anterior view of the left humerus of *Mandrillus*, *Cercocebus*, *Lophocebus*, and *Papio* showing the prominent deltoid plane and proximally extending supinator crest in *Mandrillus* and *Cercocebus*.

anatomical adaptations. Both *Cercocebus* and *Mandrillus* are terrestrial monkeys that forage predominantly on the forest floor, where they manually search through the decomposing wood of fallen trees and the leaf litter for arthropods and fallen fruit seeds and nuts (26–29) but also climb trees for arboreal foods. Mandrills have been reported to regularly rip apart rotten wood and termite mounds in search of food. This powerful manual foraging as well as their habit of climbing vertical tree trunks is probably responsible for their prominent development of forelimb flexor muscles. Both mandrills and *Cercocebus* regularly consume extremely hard nuts and seeds

that they find on the forest floor (18, 26–29). Hard nuts and seeds that can lie on the forest floor for months without decomposing are the major food of mandrills in Cameroon during the dry season when fruits are scarce; in Ivory Coast, *Cercocebus* are most easily located by the loud sound of cracking nuts with their teeth. The suite of dental and postcranial features that enable *Mandrillus* and *Cercocebus* to uncover and break open hard nuts and seeds that they harvest from the leaf litter of the forest floor enables this group of African monkeys to utilize a unique adaptive niche in the African rainforests.

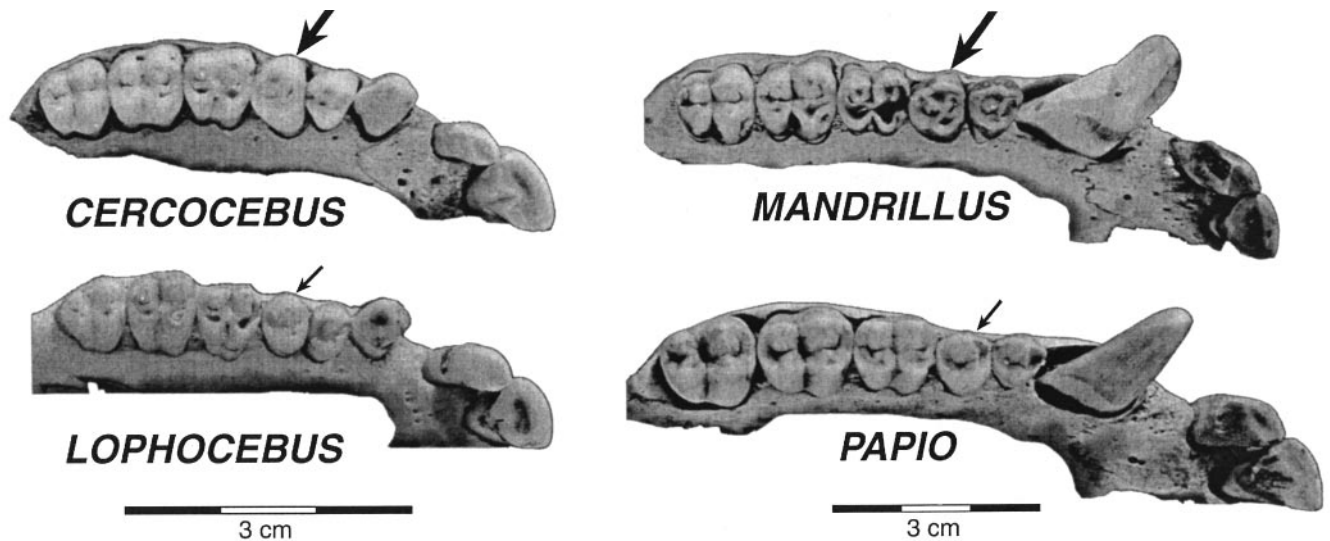


FIG. 3. Right upper dentitions of *Cercocebus*, *Lophocebus*, *Mandrillus*, and *Papio* showing the enlarged posterior premolars of *Cercocebus* and *Mandrillus*.

Identifying which of these features distinguishing the *Cercocebus*–*Mandrillus* clade from *Lophocebus* and *Papio* are derived and which represent the primitive condition can only be evaluated after a broader phylogenetic study of cercopithecin morphology. However, a simple comparison with a single individual of *Macaca nemestrina*, a member of the immediate outgroup to mangabeys and baboons, indicates that the skeletal features characterizing *Cercocebus* and *Mandrillus* are probably primitive for papionins (Fig. 1). Indeed, the foraging strategies and locomotor adaptations of *Macaca nemestrina* have been noted to be similar to those of mandrills and terrestrial mangabeys (ref. 30 and N. Shah, personal communication). In contrast, premolar enlargement in *Cercocebus* and *Mandrillus* seems to be a derived feature of that clade.

Any attempt to identify morphological homologies and synapomorphies within a closely related group of animals ultimately depends on the phylogenetic relationships among the taxa (31). Although such a phylogenetic criterion is potentially circular, it is nevertheless inevitable. For this group, the molecular evidence supporting a *Cercocebus*–*Mandrillus* clade is extremely strong in contrast with the largely impressionistic traditional morphological evidence that has been advanced so far in support of alternative phylogenies (22). A more comprehensive phylogenetic analysis of this group, including the many fossil papionins, is long overdue. Clearly there are some morphological features that distinguish the large-bodied African papionins from mangabeys (5) and many that distinguish the arboreal *Lophocebus* from the terrestrial taxa (24) as well as those that seem to accord with the molecular phylogeny. How these morphological features are best characterized and analyzed in conjunction with the molecular data are difficult issues with no easy answers.

In recent decades, molecular systematics has identified many cryptic species and clarified a variety of debated issues in primate phylogeny. The discovery of a diphyletic origin of mandrills and baboons among the mangabeys is one of the most striking departures from traditional views of primate phylogeny and has not been widely accepted. However, careful examination of the postcranial skeleton and dentition of these monkeys reveals a suite of morphological features that support the molecular phylogeny and identify *Cercocebus* and *Mandrillus* as a cryptic clade of African monkeys with unique adaptations to terrestrial foraging. In the absence of a good molecular phylogeny for this group of primates, it is quite likely

that the skeletal and dental adaptations of this clade of poorly known and difficult-to-study primates would have gone unrecognized.

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