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Systematics of early and middle Miocene Old World monkeys

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ABSTRACT

New information about the early cercopithecoids *Prohylobates tandyi* (Wadi Moghra, Egypt) and *Prohylobates* sp. indet. (Buluk and Nabwal, Kenya) is presented. Comparisons are made among all major collections of Early and Middle Miocene catarrhine monkeys, and a systematic revision of the early Old World monkeys is provided. Previous work involving the systematics of early Old World monkeys (Victoriapithecidae; Cercopithecoidea) has been hampered by a number of factors, including the poor preservation of *Prohylobates* material from North Africa and lack of comparable anatomical parts across collections. However, it is now shown that basal cercopithecoid species from both northern and eastern Africa can be distinguished from one another on the basis of degree of lower molar bilophodonty, relative lower molar size, occlusal details, symphyseal construction, and mandibular shape. Results of particular interest include: 1) the first identification of features that unambiguously define *Prohylobates* relative to *Victoriapithecus*; 2) confirmation that *P. tandyi* is incompletely bilophodont; and 3) recognition of additional victoriapithecid species.

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Introduction

Recent research on fossil cercopithecoid material from Wadi Moghra (=Moghara), early Miocene, Egypt, combined with reanalysis of other penecontemporaneous cercopithecoid collections, provides new insight into the systematic relationships and degree of adaptive diversity present among the earliest known Old World monkeys. The earliest known Old World monkeys belong to the Victoriapithecidae, an extinct family of cercopithecoids commonly considered to represent the sister-group to extant Old World monkeys (e.g., Benefit and McCrossin, 2002; but see Leakey et al. [2003] and Cooke [2006] for an alternative view). Members of Victoriapithecidae span a time range of ca. 20–12.5 Ma, and a geographic range across northern and eastern Africa of ca. 4500 km between the most distant localities (Fig. 1). Currently, the family comprises four or five species in two genera. These taxa, along with their sample size and locality, are listed in Table 1.

Some victoriapithecid species are represented by relatively large sample sizes (e.g., *Victoriapithecus macinnesi*, $n =$ ca. 2500; *Prohylobates kipsaramanensis*, $n = 89$), and material of *V. macinnesi* has been particularly well-studied (e.g., Benefit, 1987, 1993, 1994; Harrison, 1989; Benefit and McCrossin, 1991, 1997). However, interpreting the systematic relationships among members of the Victoriapithecidae has always been problematic. One major reason is that *Prohylobates tandyi* from Wadi Moghra, Egypt – the first named genus and species (Fourtau, 1918) – is represented by only a few specimens with abraded teeth, so there has never been a clear understanding about which features actually diagnose *Prohylobates*. This problem is compounded by the fact that a second genus, *Victoriapithecus*, from eastern Africa, was erected without comparing the material to that of *Prohylobates* (von Koenigswald, 1969). In fact, as M. Leakey discussed more than twenty years ago, "there are no clearly defined characters separating the two genera *Prohylobates* and *Victoriapithecus*, and it is possible that the genera are synonymous" (Leakey, 1985: 9). Because *Prohylobates* is the name with priority, Leakey (1985) assigned fossil cercopithecoid

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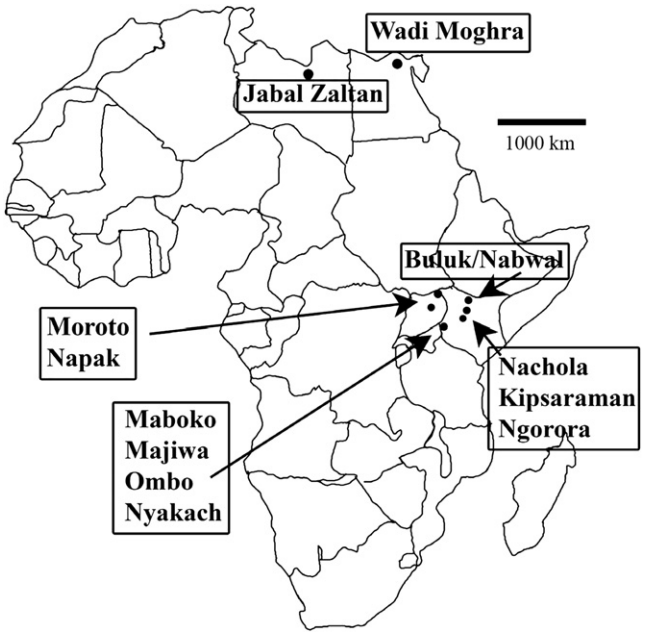

Figure 1. Map of early and middle Miocene cercopithecoid localities.

material from Buluk, Kenya, to an indeterminate species of *Prohylobates* rather than to *Victoriapithecus*, although she acknowledged that this might become untenable with future discoveries.

Placement of the Buluk material in *Prohylobates* sp. indet. (Leakey, 1985), coupled with only a vague diagnosis of the type material of *Prohylobates*, has contributed to a situation whereby early cercopithecoid specimens with obviously comparable dental morphology sometime reside not only in different species but in different genera. For example, material from Moroto, Uganda, has been allocated to *Prohylobates macinnesi* (Pickford and Kunimatsu, 2005) rather than *Victoriapithecus macinnesi*, and material from Kipsaraman, Kenya, was named *Prohylobates kipsaramanensis*, despite both collections being described as morphologically similar to *Victoriapithecus macinnesi* (Pickford et al., 2003; Pickford and Kunimatsu, 2005). In other cases the converse of this problem holds true. For example, recent work indicates that two morphologically distinct cercopithecoid taxa from Moghra are conflated under the name *Prohylobates tandyi* (see below). In addition, reassessment of the mandibular fragment originally named *Prohylobates simonsi* from Jabal Zaltan, Libya, indicates that the specimen is distinct from other victoriapithecids and warrants placement in a new genus, *Zaltanpithecus* (Benefit, 2008).

In this contribution, analysis of new, as well as previously described Early and Middle Miocene fossil cercopithecoid material from northern and eastern Africa, is used to systematically revise species currently assigned to the Victoriapithecidae. This revision is based on the identification of: 1) features that clearly distinguish *P. tandyi* from other early and middle Miocene taxa; 2) characteristics that differentiate *Prohylobates* from *Victoriapithecus*; and 3) identification of new taxa from both eastern and northern Africa.

Abbreviations

An upper case letter denotes a tooth in the maxillary series and a lower case letter a tooth in the mandibular series. For example, M2 is an upper second molar, m1 a first lower molar, and dp4 a deciduous lower fourth premolar. Institutional abbreviations are as follows: AMNH, Department of Vertebrate Paleontology, American Museum of Natural History, New York; CMK-BAR, Community Museum of Kenya; CGM, Cairo Geological Museum; DPC, Duke University Primate Center Division of Fossil Primates, Durham; KNM-MB, Kenya National Museums, Maboko Island; KNM-NL, Kenya National Museums, Nabwal; KNM-WS, Kenya National Museums, West Stephanie (Buluk); UMP-MOR, Uganda Museum of Paleontology, Moroto; CUWM, Cairo University, Wadi Moghra (WM numbers are field numbers, the material does not have accession numbers); YPM, Yale Peabody Museum, New Haven.

Systematics

Order Primates Linnaeus, 1758
Suborder Anthropoidea Mivart, 1864
Infraorder Catarrhini Geoffroy, 1812
Superfamily Cercopithecoidea Gray, 1821
Family Victoriapithecidae von Koenigswald, 1969
Included *genera Prohylobates* Fourtau, 1918; *Victoriapithecus* von Koenigswald, 1969; *Noropithecus* gen. nov.

Diagnosis An extinct family of Old World monkey distinguished from Cercopithecidae (Colobinae and Cercopithecinae) by having incomplete development of bilophodonty in either the upper or lower molar series, variable retention of crista obliqua and m1/m2 hypoconulids, p4 oriented strongly oblique to the cheek tooth row, and a high degree of molar flare due to the close approximation of cusp tips relative to crown width.

Remarks

Many of the features listed above as diagnostic of Victoriapithecidae (e.g., presence of a crista obliqua, presence of hypoconulids, incomplete bilophodonty) are also characteristic of basal non-cercopithecoid catarrhines, which means that the Victoriapithecidae is largely diagnosed on the basis of primitive features. Such a reliance on primitive traits may be considered suboptimal, but the situation may have a parallel in the Platyrrhini, a group whose members form a coherent clade, although no shared derived morphological features uniting all platyrrhines have ever been identified. Instead, the group is diagnosed by the retention of many primitive anthropoid features.

Table 1
Victoriapithecid sample sizes and localities.

Taxon	*P. tandyi*[a]	*P.* sp. indet.[b]	*P. simonsi*[c]	*P. kipsaramanensis*[d]	*V. macinnesi*[e]
N	5	17	1	89	2500
Localities	Egypt (Wadi Moghra)	Kenya (Buluk, Nabwal)	Libya (Jabal Zaltan)	Kenya (Kipsaraman)	Kenya (Maboko Island, Ombo, Loperot, Majiwa, Nyakach, Nachola, Ngorora); Uganda (Napak, Moroto)

[a] Miller, 1996, 1999.
[b] Harris and Watkins, 1974; McDougall and Watkins, 1985.
[c] Delson, 1979.
[d] Pickford and Kunimatsu, 2005.
[e] Benefit, 1987.

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