

**PROHYLOBATES (PRIMATES) FROM THE EARLY MIOCENE OF LIBYA :
A NEW SPECIES AND ITS IMPLICATIONS FOR CERCOPITHECID ORIGINS**

by

Eric DELSON *

Abstract

Prohylobates simonsi n. sp. is described on the basis of a partial mandible with $M_2 - 3$ from the region of Gebel Zelten. It is nearly twice the size of the penecontemporaneous *P. tandyi* and has a relatively longer M_3 , but otherwise is nearly identical in morphology. *Prohylobates* is the most conservative known cercopithecoid, presenting incomplete bilophodonty, possible cingulum remnants, high relative width of M_2 and robust mandibular corpus. The variation in M_3 length is comparable to that within some later cercopithecoid species and between the species of *Propliopithecus*, the Oligocene catarrhine suggested to be nearest the ancestry of the *Cercopithecidae*. *Parapithecus* (including *Simonsius*) is not a cercopithecoid ancestor.

Résumé

Prohylobates simonsi nov. sp. est décrit à partir d'une mandibule incomplète avec $M_2 - 3$, provenant de la région de Gebel Zelten. Elle atteint presque deux fois la taille du *P. tandyi* pénecontemporain et présente une M_3 relativement plus longue, mais par ailleurs sa morphologie est presque identique. *Prohylobates* est le plus "conservateur" des cercopithécidés connus, par sa bilophodontie incomplète, ses restes possibles de cingulum, la grande largeur relative de la M_2 et son corps mandibulaire robuste. La variation en longueur relative de la M_3 est comparable à celle des espèces de cercopithécidés plus récentes et, parmi les espèces de *Propliopithecus*, le catarrhinien oligocène paraît être le plus proche des ancêtres des *Cercopithecidae*. *Parapithecus* (y compris *Simonsius*) n'est pas un des ancêtres des Cercopithécidés.

* Department of Anthropology ; Lehman College, C.U.N.Y. , Bronx, New York 10468 U.S.A. and Department of Vertebrate Paleontology, the American Museum of Natural History, U.S.A.

ERRATA

for E. Delson, "Prohylobates...cercopithecoid origins", Geobios, 1979.

Due to the short publication schedule, no proofs were available for corrections by the author. Some minor errors of omissions and commission have thus occurred in the text. Hyphens were inadvertently placed between initials of numerous authors who do not normally use them.

In the footnote to page 726, the locality "is likely to be low in the local sequence" (not "local in").

On page 728, tabl. 1, the two post-Miocene cercopithecoid taxa were included as they compare favorably in size with Prohylobates spp. Presbytis aygula is close to P. tandyi, while the Pliocene ?Parapapio ado has similar measurements (of M2 length and M3) to those of P. simonsi.

On page 729, last paragraph of text, line 3 should read: cercopithecoids. The spread of the four ratios in tabl. 1 between...

Introduction

The Old World monkeys, family *Cercopithecidae*, comprise a group of highly successful primates which is widely acknowledged to have undergone a relatively recent (Late Miocene to Pliocene) adaptive radiation [(1), (2) and (3)]. The earliest known fossil representatives of the family occur in Early Miocene deposits of eastern and northern Africa, while the first evidence of division into the two modern subfamilies (*Cercopithecinae* and *Colobinae*) derives from the early Middle Miocene of Maboko Island, Kenya (see below). To date, only two samples of Early Miocene cercopithecids have been described : an isolated upper molar with ancestral (“primitive”) morphology from Napak, Uganda (4) and three damaged mandibles of *Prohylobates tandyi* FOURTAU (5) from Wadi Moghara, Egypt, recently redescribed by E.-L. Simons (6). Another partial mandible with two teeth has now been identified as a new species whose closest affinities are with *P. tandyi*, but which differs in both size and morphology (7). Interpretation of this specimen sheds some light on the currently debated question of cercopithecoid origins.

The new fossil was recovered in 1967 by R.M. Eckert of the Mobil Oil Company from the region of Gebel Zelten, north-central Libya (approximately 15 km west of Zelten, 6 km east of Ora) *. This specimen was presented to the Department of Vertebrate Paleontology, American Museum of Natural History, where it was catalogued as A.M. N.H. 17768 and tentatively identified as a suid or dichobunid artiodactyl. Recently, Dr. Martin Pickford determined that the jaw was not that of an artiodactyl and, believing it to be a primate, drew it to my attention. No other primate specimen has been reported from Gebel Zelten, but this locality shares many taxa with Wadi Moghara [(8) and (9)]. Both localities are probably late Early Miocene in age, perhaps close to 18 million years old (10). This westward expansion of our knowledge of Early Miocene primates is mirrored by P. Andrews *et al.* 's recent report (11) of *Dryopithecus* (“*Proconsul*”) to the east in Saudi Arabia. A formal description of the new fossil as holotype of a distinct species is followed by an analysis of its meaning for the understanding of cercopithecoid evolution.

I. Systematics

Order Primates LINNAEUS, 1758
Suborder Haplorhini POCOCK, 1918
Infraorder Catarrhini GEOFFROY, 1812
Superfamily Cercopithecoidea GRAY, 1821
Family Cercopithecidae GRAY, 1821
Subfamily indeterminate
Prohylobates FOURTAU, 1918

Type Species : *Prohylobates tandyi* FOURTAU, 1918

Distribution : Early Miocene (Late Burdigalian Stage, Orleanian Land Mammal Age), North Africa.

Emended Diagnosis : *Prohylobates* species are small to medium sized “primitive” cercopithecids characterized by an incomplete development of bilophodonty on the lower cheek teeth (uppers unknown), moderate trigonid length, variable relative length of M_3 , wide M_2 , possibly a small median distal cuspule or hypoconulid on M_2 , and relatively deep and robust mandibular corpus. Tooth crowns are relatively high, but the occlusal surface relief is low : the cusps are only slightly raised above the foveae and the lingual notches are shallow. Lophids joining buccal and lingual cusps are poorly developed, but there probably was no true cristid obliqua as seen in ancestral catarrhines.

* Dr. R.J.G. Savage has indicated (personal communication) that the precise locality is likely to be local in the local sequence, probably within the Lower Marada Formation, in light of the regional structure and dip.

Discussion : The known species (represented only by four partial mandibles) present none of the derived diagnostic characters of the modern tribes or subfamilies (3). Instead, preserved morphology is comparable to that expected in a conservative early member of the family, prior to differentiation of sub-taxa. On known specimens [pl. 1, fig. 1 - 5 and in (6)], heavy wear obscures the original cusp and lophid delineation, but a low, nearly linear structure which appears to link the metaconid to the hypoconid is probably a portion of the worn median slope of the protoconid, rather than a cristid obliqua. The second (and probably first) lower molars are nearly square, and although worn, the trigonid basins (mesial foveas) were not especially short. They thus do not share the derived condition seen in colobines. The molars present deep median buccal clefts as part of their bilophodonty, but they also retain some basal cingular bulging (pl. 1, fig. 6, 8 and 9). This bulging is lost or develops into "flare" in later cercopithecids, while ancestral catarrhines possessed cingular shelves buccally [(2) and (3)]. The P₄ has a short trigonid and a bulging rather than flanged mesiobuccal corner, and its long axis is slightly oblique to those of the molars, all features shared (not necessarily homologously) with most colobines.

Prohylobates simonsi n. sp.

Holotype : A.M.N.H. 17768, fragment of left corpus with worn M₂₋₃ (pl. 1, fig. 1 - 3 and 7 - 10).

Hypodigm : holotype only.

Etymology : in honor of Dr. E.L. Simons, for his work on fossil primates in general and on *Prohylobates* especially.

Type locality : region of Gebel Zelten, north central Libya, probably Lower Marada Formation. Early Miocene (Orleanian).

Specific diagnosis : *Prohylobates simonsi* differs from the generitype in being approximately 65 % larger in M₂ dimensions and in having an M₃ considerably longer than M₂ (tabl. 1 and pl. 1, fig. 3 and 4).

Discussion : it is obviously hazardous to recognize a new species on the basis of a single fragmentary specimen, but no known taxon appears to be conceivably conspecific. The morphology is closely comparable to that seen in *Prohylobates tandyi*, but the size difference alone seems to rule out membership in an interbreeding population, as far as such details can be inferred from the fossil record. The holotype of *P. tandyi* is probably female, and an edentulous referred specimen is probably male but only slightly larger, thus negating the possibility that the *tandyi/simonsi* difference could be accounted for by sexual dimorphism within a single species. By comparison, P.-D. Gingerich (12), for example, has recognized new species for small samples only 10 - 20 % different in size and of identical morphology to closely related (and probably conspecific) populations. The difference in relative M₃ length between *Prohylobates* species may also be important and is discussed further below. The new species is allocated to *Prohylobates* pending recovery of more complete specimens permitting study of unworn morphology and of variation in dental proportions.

E.-L. Simons (6) described a small circular dentine exposure on the median distal margin of M₂ in the *P. tandyi* holotype which he interpreted as the remains of a true hypoconulid, as seen on M₁₋₃ of hominoids and early catarrhines (but only on M₃ of other cercopithecids). This region of M₂ in A.M.N.H. 17768 is worn, but no sign of a cuspule is observed. On the other hand, some specimens of *Theropithecus* (especially the large extinct *T. oswaldi*) present a similar cuspule on M₂. Although probably not a center of enamel growth (a cusp), such a surface feature may add to the complexity of crown morphology ; it may have little or no taxonomic significance.

The inferiorly broken corpus of A.M.N.H. 17768 prevents comparison of jaw depth with *P. tandyi*, but mandibular robusticity is similar, given the size differences. Moreover, the damage permits portions of the lower tooth roots to be observed in *P. simonsi* (fig. 7). The distal part of M₂ is supported by two fully independent roots, and the mesial roots, although broken, appear to have been separate ; the mesial root of M₃ is bifid at its base. Divided roots of mandibular molars are rare in primates, although common in suids among other mammals, but a larger sample of *Prohylobates* is necessary to confirm its consistent or usual presence.

Species Specimen	M ₂				M ₃				M ₂	M ₃
	MW ^a	DW ^b	Len ^c	MW/L	MW	DW	Len	MW/L	— MW M ₃	— Len M ₂
<i>Prohylobates tandyi</i> C.G.M. ^d 30936, type	5.8	5.5	6.0	96.7	5.0	—	(6.5)	76.9	116.0	108.3
<i>Prohylobates simonsi</i> A.M.N.H. 17768, type	11.0	10.4	10.4	105.8	9.1	8.2	12.9	70.5	120.8	124.1
<i>Victoriapithecus macinnesi</i> KNM ^e MB-1, type	6.0	5.7	7.0	95.7	5.5	5.0	7.7	71.4	109.1	110.0
KNM MB-37	6.0	5.9	6.7	89.6	5.6	4.6	7.0	80.0	107.1	104.5
KNM MB-36 (<i>V. cf. m.</i>)	7.8	7.4	8.1	96.3						
<i>Victoriapithecus</i> "leakeyi" KNM MB-34	6.2	5.8	7.7	80.5	5.7	5.0	9.8	58.2	108.8	127.7
<i>Presbytis aygula</i> (modern) mean, 1 male & 1 female	5.3	5.5	5.9	89.7	5.1	4.8	7.0	72.7	103.9	118.8
? <i>Parapapio ado</i> (Laetoli) mean, 3 specimens	8.5	8.7	10.7	79.0	8.5	8.1	12.9	65.9	97.2	120.9

Tabl. 1 — Measurements (in millimeters) and ratios (in percent) for M₂ - 3 of *Prohylobates* species and selected other cercopithecids.

^aMesial width, maximum across protolophid

^bDistal width, maximum across hypolophid

^cLength, maximum parallel to long axis of tooth

^dCairo Geological Museum ; measurements of this specimen from (6), checked on sharp cast

^eKenya National Museum, Nairobi

II Relationships and paleobiology of *Prohylobates*

Within *Cercopithecidae*, the phyletic relationships of *Prohylobates* are uncertain. It is the most conservative of known genera, less completely bilophodont than the slightly younger *Victoriapithecus* material from Maboko [(2), (3) and (13)]. Most of the latter remains are placed in *V. macinnesi*, about the size of *P. tandyi* (tabl. 1), a species which shares one or two derived characters with colobines. A few other fragments are classified as "*V.*" *leakeyi*, which appears more conservative, thus cercopithecine-like, although with well-marked lophids. These two species are the earliest potential evidence for the split between the modern subfamilies. *Prohylobates* and *Victoriapithecus* species may be classified as *Cercopithecidae incertae sedis* for the present (3), but more complete remains should permit allocation of the two Maboko taxa to different modern subfamilies (thus requiring the eventual definition of a new genus for "*V.*" *leakeyi*). *Prohylobates* may not only antedate the origin of the modern subfamilies, it might be phyletically far removed from the stock ancestral to them.

The dentitions of both *Prohylobates* species have low crown relief and thus appear adapted for frugivory, as is true for most other early catarrhines. However, the relatively deep and robust corpus (comparable to smaller colobines and deeper than in "*V.*" *macinnesi*) suggests heavier chewing, perhaps implying some folivory or ground-foraging on gritty food items. This might especially be true of *P. simonsi*, whose large size is unexpected in so early a cercopithecid. Forms of comparable dimensions do not appear again until the Pliocene, including a semiterrestrial cercopithecine and two colobines : an arboreal folivore and a semiterrestrial "grit-chewer". Postcranial elements would be important in resolving this question, as might other data on body size in *P. simonsi*, because R.-F. Kay (14) has recently shown that cercopithecid folivores have smaller molars compared to body size than is true for other primate families.

As the oldest known cercopithecoid genus, *Prohylobates* should be relevant to discussions of the origin of the family, especially as its apparently isolated phyletic position makes it a logical subject for comparison with the ancestral morphotype previously delineated (2). The combination of reduced cingulum with basal flaring in the molars (pl. 1, fig. 8) is as suggested for the morphotype, as are the moderate-length trigonids. Although the latter are badly worn, and thus seem short, they are about the size seen in cercopithecines of comparable wear and tooth size. If, instead, unworn trigonids of *Prohylobates* were found to be short (as in colobines, *V. macinnesi* and perhaps *Oreopithecus*, but no other catarrhines), this might be a derived feature of the genus, as the cercopithecoid morphotype is now interpreted.

Dental proportions in *Prohylobates* species are possibly of greater interest (tabl. 1). E.-L. Simons (6) utilized the short M_3 of *P. tandyi* as one of several features to link this taxon, and by inference all cercopithecids, to the Oligocene early catarrhine *Parapithecus**. To the contrary, analysis of dental morphology [(3) and (16)] suggests that a relatively long lower third molar is probably the ancestral condition for all catarrhines. Thus, given the long M_3 in *P. simonsi*, the subequal length of M_2 and M_3 in *P. tandyi* is probably a derived (autapomorphic) feature of this species, not characteristic of the genus or of the early members of the family. This finding reaffirms my previous arguments [(3) and (17)] that parapithecids are not specially related to the ancestry of cercopithecids, but rather are relatively conservative early catarrhines, while the *Cercopithecoidea* and *Hominoidea* (the eucatarrhines) shared a more recent common ancestry.

The observed difference in relative M_3 length between the two *Prohylobates* species is analogous to that found in several eucatarrhine genera. The Oligocene *Propliopithecus haeckeli* compares to *P. tandyi*, while *P. ("Aegyptopithecus") zeuxis* has a long and narrow M_3 like *Prohylobates simonsi*. This is especially relevant, as *Propliopithecus* is the most conservative known eucatarrhine, while *Prohylobates* is the least derived cercopithecoid. At the least, they shared an ancestor in the mid-Oligocene, but it is also possible that the stock represented by the several *Propliopithecus* species (e. g., *P. markgrafi*, which shows some phenetic resemblance to *Prohylobates*) could have already begun evolving toward cercopithecoid morphology. Although they are conservative in other morphological attributes, it appears that the smaller species of each early genus may be derived in having a short M_3 .

On the other hand, this fits the model of dental allometry presented by R.-S. Corruccini and A.-M. Henderson (18), who found M_3 area increased "faster" than M_2 or M_1 area as skull size increased among anthropoids, especially in cercopithecids. The difference between *Prohylobates tandyi* and *P. simonsi* is matched among cercopithecids by the observed ranges in three samples of Plio-Pleistocene European macaques ($N = 6 - 8$) and the sample of *Mesopithecus pentelici* from Pikermi ($N = 28$) (no specimens with greater wear than *Prohylobates* were included). Another metrical observation is that the mesial width of M_2 in *P. simonsi* (and *P. tandyi*) is high compared to both M_2 length and M_3 mesial width. No cercopithecoid taxon with second molars of comparable size matches the ratios found in *Prohylobates*. Further comparisons may reveal this pattern to be an ancestral feature, either of cercopithecids or of all catarrhines.

Acknowledgments

I thank Drs. A.L. Rosenberger, M. Pickford, R.J.G. Savage, G.G. Eck, R.H. Tedford, E.L. Simons, J.G. Fleagle and R.S. Corruccini for assistance in this study and Mr. C. Tarka for skilfully preparing plate 1. This research was supported in part by C.U.N.Y. PSC-BHE grants 11785 and 12188.

* There is no morphological evidence for P.-D. Gingerich's recent claim (15) that the unique holotype of *Parapithecus fraasi* is a specimen of *Apidium phiomense*. *P. fraasi* is clearly congeneric with *P. grangeri*, now represented by many specimens. Thus P.-D. Gingerich's new genus *Simonsius* (for *P. grangeri*) is merely a junior synonym of *Parapithecus*. *Apidium* and *Parapithecus* are sister-genera, placed in *Parapithecidae* because of numerous shared features, but readily distinguished by derived conditions in each (3).

References

- (1) SIMONS E.-L. — *Primate Evolution*, New-York (Macmillan), 1972.
- (2) DELSON E. — *Contrib. primatol*, Basel, 5, 1975, p. 167 - 217.
- (3) SZALAY F.S. & DELSON E. — *Evolutionary History of the Primates*, New-York (Academic), 1979.
- (4) PILBEAM D.-R. & WALKER A. — *Nature*, London, 220, 1968, p. 657 - 659.
- (5) FOURTAU R. — *Contribution à l'Etude des Vertébrés Miocènes de l'Égypte*, Cairo (Survey Department), 1918.
- (6) SIMONS E.-L. — *Nature*, London, 223, 1969, p. 687 - 689.
- (7) DELSON E. — *Amer. jour. phys. anthrop.*, Philadelphia, 47, 1977, p. 126.
- (8) SAVAGE R.-J.-G. & HAMILTON W.R. — *Bull. Br. Mus. Nat. Hist. (Geol)*, London, 22, 1973, p. 515 - 527.
- (9) HAMILTON W.-R. — *Bull. Br. Mus. Nat. Hist. (Geol.)*, London, 24, 1973, p. 351 - 395.
- (10) VAN COUVERING J.-A. & BERGGREN W.-A. — in *Concepts and Methods of Biostratigraphy* (KAUFFMAN E.-G. & HAZEL J.-E. *édit.*), Stroudsburg (Dowden, Hutchinson & Ross), 1977, p. 283 - 306.
- (11) ANDREWS P. *et alii.* — *Nature*, London, 274, 1978, p. 249 - 250.
- (12) GINGERICH P.-D. — *Univ. Michigan Pap. Paleont.*, Ann Arbor, 15, 1976, p. 1 - 140.
- (13) KOENIGSWALD G.-H.-R. von — *Foss. Verts. Africa*, London, 1, 1969, p. 39 - 51.
- (14) KAY R.-F. & SIMONS E.-L. — *Amer. jour. phys. anthrop.*, Philadelphia, 50, 1979, p. 453.
- (15) GINGERICH P.-D. — *Paläont. Zeits.*, 52, 1978, p. 82 - 92.
- (16) DELSON E. & ANDREWS P. — in *Phylogeny of the Primates* (LUCKETT W.P. & SZALAY F.S. *éd.*), New-York (Plenum), 1975, p. 405 - 446.
- (17) DELSON E. — *Coll. Inter. Cent. Nat. Rech. Sci.*, Paris, 218, 1975, p. 839 - 850.
- (18) CORRUCCINI R.-S. & HENDERSON A.-M. — *Amer. jour. phys. anthrop.*, Philadelphia, 48, 1978, p. 203 - 208.

PLATE 1

Prohylobates simonsi n. sp.

Holotype, A.M.N.H. 17768, Gebel Zelten, Lybia.

- Fig. 1 — Occlusal photograph of original.
- Fig. 2 — Occlusal photograph of cast, to avoid highlights.
- Fig. 3 — Occlusal view drawing.
- Fig. 7 — Oblique inferior view, note double distal root of M_2 and bifid tip of mesial M_3 root.
- Fig. 8 — Mesial view, note pattern of crown flare.
- Fig. 9 — Buccal view.
- Fig. 10 — Lingual view.

Prohylobates tandyi FOURTAU, 1918

Holotype, C.G.M. 30936, Wadi Moghara, Egypt.

- Fig. 4 — Occlusal photograph of cast (partial), brought to same M_2 length as fig. 1 - 3.
- Fig. 5 — Occlusal drawing (from 6), to scale.
- Fig. 6 — Lateral view (from 6), photographically reversed.

Prohylobates simonsi nov. sp.

Holotype, A.M.N.H. 17768, Gebel Zelten, Libye.

- Fig. 1 — Photographie en vue occlusale de l'original.
- Fig. 2 — Photographie en vue occlusale d'un moulage, pour éviter des points culminants.
- Fig. 3 — Dessin en vue occlusale.
- Fig. 7 — Vue inférieure oblique, notez la racine distale de la M_2 dédoublée et l'extrémité bifide de la racine mésiale de la M_3 .
- Fig. 8 — Vue mésiale, notez l'évasement de la couronne.
- Fig. 9 — Vue buccale.
- Fig. 10 — Vue linguale.

Prohylobates tandyi FOURTAU, 1918

Holotype, C.G.M. 30936, Wadi Moghara, Egypte.

- Fig. 4 — Photographie en vue occlusale d'un moulage (incomplet), même longueur de la M_2 sur les fig. 1 - 3.
- Fig. 5 — Dessin en vue occlusale [d'après (6)] à l'échelle des fig. 1 - 3.
- Fig. 6 — Vue latérale gauche [d'après (6)], renversée photographiquement.

