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Journal

Proceedings of the National Academy of Sciences of the United States of America, 116(13)

ISSN

0027-8424

Authors

Rasmussen, D Tab
Friscia, Anthony R
Gutierrez, Mercedes
et al.

Publication Date

2019-03-26

DOI

10.1073/pnas.1815423116

Peer reviewed

Primitive Old World monkey from the earliest Miocene of Kenya and the evolution of cercopithecoid bilophodonty

D. Tab Rasmussen[a,1], Anthony R. Friscia[b], Mercedes Gutierrez[c], John Kappelman[d,e,2], Ellen R. Miller[f], Samuel Muteti[g], Dawn Reynoso[h], James B. Rossie[i], Terry L. Spell[h], Neil J. Tabor[j], Elizabeth Gierlowski-Kordesch[k,3], Bonnie F. Jacobs[j], Benson Kyongo[g], Mathew Macharwas[g], and Francis Muchemi[g]

[a]Department of Anthropology, Washington University, St. Louis, MO 63130-4899; [b]Department of Integrative Biology and Physiology, University of California, Los Angeles, CA 90095-7246; [c]Department of Integrative Biology and Physiology, University of Minnesota, Minneapolis, MN 55455; [d]Department of Anthropology, The University of Texas, Austin, TX 78712; [e]Department of Geological Sciences, The University of Texas, Austin, TX 78712; [f]Department of Anthropology, Wake Forest University, Winston Salem, NC 27109-7807; [g]Palaeontology Section, National Museums of Kenya, 00100 Nairobi, Kenya; [h]Department of Geoscience, University of Nevada, Las Vegas, NV 89154-4010; [i]Department of Anthropology, Stony Brook University, Stony Brook, NY 11794; [j]Roy M. Huffington Department of Earth Sciences, Southern Methodist University, Dallas, TX 75275-0395; and [k]Department of Geological Sciences, Ohio State University, Athens, OH 45701-2979

Old World monkeys (Cercopithecoidea) are a highly successful primate radiation, with more than 130 living species and the broadest geographic range of any extant group except humans. Although cercopithecoids are highly variable in habitat use, social behavior, and diet, a signature dental feature unites all of its extant members: bilophodonty (bi: two, loph: crest, dont: tooth), or the presence of two cross-lophs on the molars. This feature offers an adaptable Bauplan that, with small changes to its individual components, permits its members to process vastly different kinds of food. Old World monkeys diverged from apes perhaps 30 million years ago (Ma) according to molecular estimates, and the molar lophs are sometimes incompletely developed in fossil species, suggesting a mosaic origin for this key adaptation. However, critical aspects of the group's earliest evolution remain unknown because the cercopithecoid fossil record before ~18 Ma consists of only two isolated teeth, one from Uganda and one from Tanzania. Here we describe a primitive Old World monkey from Nakwai, Kenya, dated at ~22 Ma, that offers direct evidence for the initial key steps in the evolution of the cercopithecoid dentition. The simple dentition and absence of bilophodonty in the Nakwai monkey indicate that the initial radiation of Old World monkeys was first characterized by a reorganization of basic molar morphology, and a reliance on cusps rather than lophs suggests frugivorous diets and perhaps hard object feeding. Bilophodonty evolved later, likely in response to the inclusion of leaves in the diet.

Old World monkeys | Cercopithecoidea | Africa | Miocene | bilophodonty

O ld World monkeys (Cercopithecoidea) are the most successful living superfamily of nonhuman primates with a geographic distribution that is surpassed only by humans. The group occupies a wide spectrum of terrestrial to arboreal habitats and exploits a diverse range of diets that includes variable amounts of fruits, leaves, insects, seeds, rhizomes, and, more rarely, vertebrates (1). Their success in processing such a wide range of food types is clearly facilitated by the signature dental feature that unites all living cercopithecoids, bilophodonty (bi: two, loph: crest, dont: tooth), or the presence of two transverse lophs that connect the buccal and lingual cusps on the molars (2). Rather than offering a rigidly fixed morphology, bilophodonty instead offers a flexible molar Bauplan that can readily evolve in response to the specific demands required to process foods with different mechanical properties. For example, the two major cercopithecoid subfamilies emphasize different aspects of bilophodonty, with taller cusps, longer shearing crests, and thinner enamel found in the generally more folivorous species of the Colobinae, and the opposite configurations seen in the more frugivorous species of

the Cercopithecinae, with some members of each subfamily possessing intermediate morphologies and diets (3).

Given the ubiquity of bilophodonty in Old World monkeys, it has long been thought that this trait was likely to have been key to the success of Old World monkeys since the group's divergence from apes, perhaps as long as 30 million years ago (Ma) as based on molecular estimates (4–7). The fossil record for Old World monkeys is fairly abundant from the late Early Miocene onward and has long appeared to offer broad support for the antiquity of bilophodonty even though the lophs are sometimes incompletely developed in fossil species, suggesting a mosaic origin for this key adaptation (8, 9). However, the group's earliest evolution remains largely unknown because there are only two isolated teeth older than ~18 Ma, an isolated M^1 or M^2 from Uganda dating to 19 ± 2 Ma and therefore close in age to the younger fossils (10), and a M_3 from Tanzania dating to 25.2 Ma (11).

Significance

Almost nothing is known about the origin and evolution of Old World monkeys (cercopithecoids) because the first ~12 million years of their fossil record is documented by only two isolated teeth. We describe a new primitive monkey from Kenya that dates from ~22 million years ago and reveals a previously unknown stage of evolution. Comparisons between this monkey and other cercopithecoids offer detailed insights into the development of the novelties associated with the evolution of the cercopithecoid dentition, and particularly bilophodonty. Results suggest that this fossil monkey exhibited dental adaptations for frugivory and perhaps hard object feeding. Bilophodonty, the dental trait that unites all living cercopithecoids, evolved later, likely in response to the inclusion of leaves in the diet.

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Here we describe a primitive Old World monkey from Nakwai, Kenya, and its date of ~22 Ma places it in the middle of this 6-million-year gap. This new species offers direct evidence for the initial key steps in the evolution of cercopithecoid bilophodonty.

The new primate from Nakwai is a member of a diverse but primitive African mammalian fossil fauna (12, 13). Our results demonstrate that this monkey, known from three fossil localities at Nakwai, dates to the earliest portion of the Early Miocene, ~21.9 to ~22.2 Ma (*SI Appendix, Supplementary Information Notes 1 and 2,* Figs. S1–S9, and Tables S1–S3) (14, 15).

Systematic Paleontology

Order Primates Linnaeus, 1758; Suborder Anthropoidea Mivart, 1864; Infraorder Catarrhini Geoffroy, 1812; Superfamily Cercopithecoidea Gray, 1821; Family indet.; Genus *Alophia* gen. nov.

Etymology. *Alophia* from the Greek *loph* (crest), with prefix *a-* for "without," in reference to having a molar occlusal structure without cross lophs.

Generic Diagnosis. Differs from all noncercopithecoid catarrhines in having lower molars with columnar buccal cusps and a deep U-shaped median buccal cleft. Differs from all crown cercopithecoids in lacking full development of bilophodonty. Differs from members of Victoriapithecidae in having an incipient partial protolophid present on M_1 and M_2 and in lacking any other development of lophids on lower molars; M_1 and M_2 with only moderate basal flare, cusps bunodont and located on the periphery of the crown. Further differs from *Victoriapithecus* and *Noropithecus* in having an M_3 with a buccolingually narrow talonid, differs from *Zaltanpithecus* and *Nsungwepithecus* in being much smaller in size.

Type Species. *Alophia metios* sp. nov.

Etymology. The species name, *metios*, is from *Metis*, the Greek goddess of crafty thought and wisdom. *Metis* was feared for the prophecy that she would give rise to descendants more powerful than their sire.

Holotype. KNM-NW (National Museums of Kenya, Nakwai) 49735, partial right mandible preserving P_4-M_3 (Fig. 1*A*) from locality TOP-01 dated at ~21.9 Ma (*SI Appendix,* Fig. S2).

Referred Specimens. KNM-NW 49731, partial left mandible with P_3-M_1 (Fig. 1*B*) from locality TOP-69 dated at ~22.0 Ma (*SI Appendix,* Fig. S2). KNM-NW 49732, partial left mandible with M_2–M_3 (Fig. 1*C*) from locality TOP-73 dated at ~22.2 Ma (*SI Appendix,* Fig. S2). Specimens are housed in the National Museums of Kenya, Nairobi, Kenya.

Locality and Horizon. Earliest Early Miocene, Lokichar Basin, localities TOP-01, TOP-69, TOP-73, Nakwai, West Turkana, Kenya (*SI Appendix,* Figs. S1 and S2).

Specific Diagnosis. As for genus. For additional description and metrics, see *SI Appendix, Supplementary Information Notes 3 and 4,* Figs. S10 and S11, and Tables S4–S6.

Discussion

Alophia resembles members of the Victoriapithecidae, an extinct family of primitive Old World monkeys distinguished from Cercopithecinae and Colobinae by lacking full development of bilophodonty in either the upper or lower molar series, variable retention of a crista obliqua, variable presence of M_1 and M_2 hypoconulids, and P_3 and P_4 oriented in a strongly oblique direction to the cheek tooth row (8) (Fig. 1 and *SI Appendix,* Fig. S10). Victoriapithecids (Fig. 2)
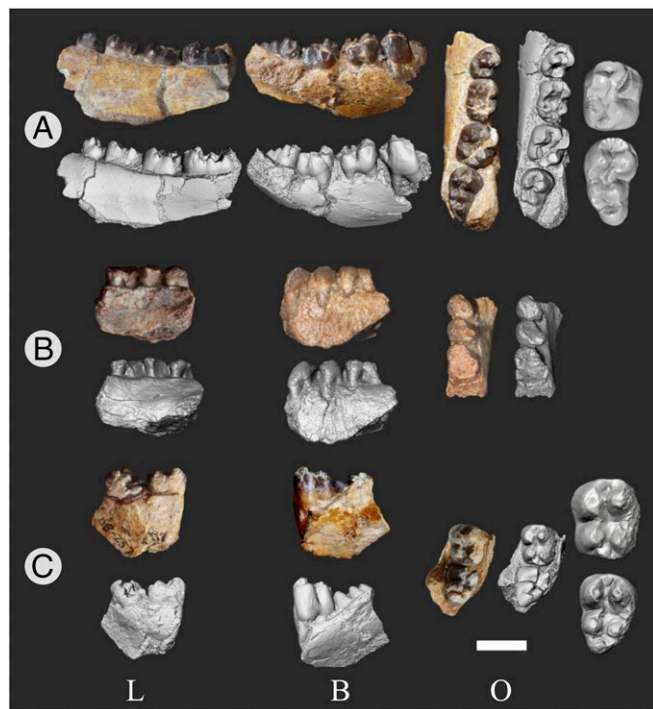

Fig. 1. Specimens of *A. metios* gen. et sp. nov. from Nakwai. Photographs (color) and CT scans (gray) illustrate lingual (L), buccal (B), and occlusal (O) views. (*A*) KNM-NW 49735 holotype, partial right mandible preserving P_4-M_3 from locality TOP-1. All teeth and the partial mandible display some degree of postmortem cracking and displacement. CT scans of the M_2 and M_3 were segmented and cracks closed, with the virtual reconstructions of the M_2 (*Top*) and M_3 (*Bottom*) shown enlarged ~2× at far *Top Right*. The cusp tip of the M_2 protoconid is missing. (*B*) KNM-NW 49731 partial left mandible with heavily worn P_3-M_1 from locality TOP-69. (*C*) KNM-NW 49732 partial left mandible with M_2-M_3 from locality TOP-73. There is postmortem pitting on its lingual surface. The M_3 of this young individual is not fully erupted. CT scans of the M_3 were segmented and used to virtually extract the tooth from its crypt to reveal its features, and the renderings of the M_2 (*Top*) and M_3 (*Bottom*) are shown enlarged ~2× at far *Bottom Right*. (Scale bar: 1 cm.) See *Methods* and *SI Appendix, Supplementary Information Notes 3 and 4,* Figs. S10 and S11, and Table S4 for discussion.

also typically show a high degree of basal molar flare due to the close approximation of cusp tips relative to crown width, but this is less developed in *A. metios*, which has only moderate flare because the conical molar cusps are positioned closer to the margin of the crown, and the cusp tips are oriented more superiorly, except perhaps for the M_1 metaconid, which appears to be shifted very slightly buccally (Figs. 1 and 2). Like *Noropithecus* and *Victoriapithecus*, *Alophia* also possesses a cristid obliqua that terminates slightly lingual to the protoconid (Fig. 2 and *SI Appendix,* Fig. S11).

Alophia is exceptional in having incipient-to-no development of lower molar cross-lophids (Fig. 2), the major defining feature that unites Old World monkeys. Distal lophids are invariably absent, although the M_1 and M_2 of KNM-NW 49735 exhibit what may be an incipient development of the mesial lophid (Fig. 2*B*). The buccal side of the M_2 metaconid in KNM-NW 49735 consists of a mesial and a distal facet, which meet to form a raised ridge that extends from the cusp apex in a buccal direction. The two facets and the ridge that surmounts them descend buccally to terminate at the base of the protoconid (Fig. 2*B*), forming an incipient lingual protolophid, or half of the mesial lophid that is present in all other cercopithecoids (Fig. 2 *C* and *D* and *SI Appendix, Supplementary Information Note 3* for detailed descriptions). The development of this feature on the M_2 of KNM-NW 49732 (Fig. 2*A*) is not clear because much of the metaconid is abraded by postmortem etching.
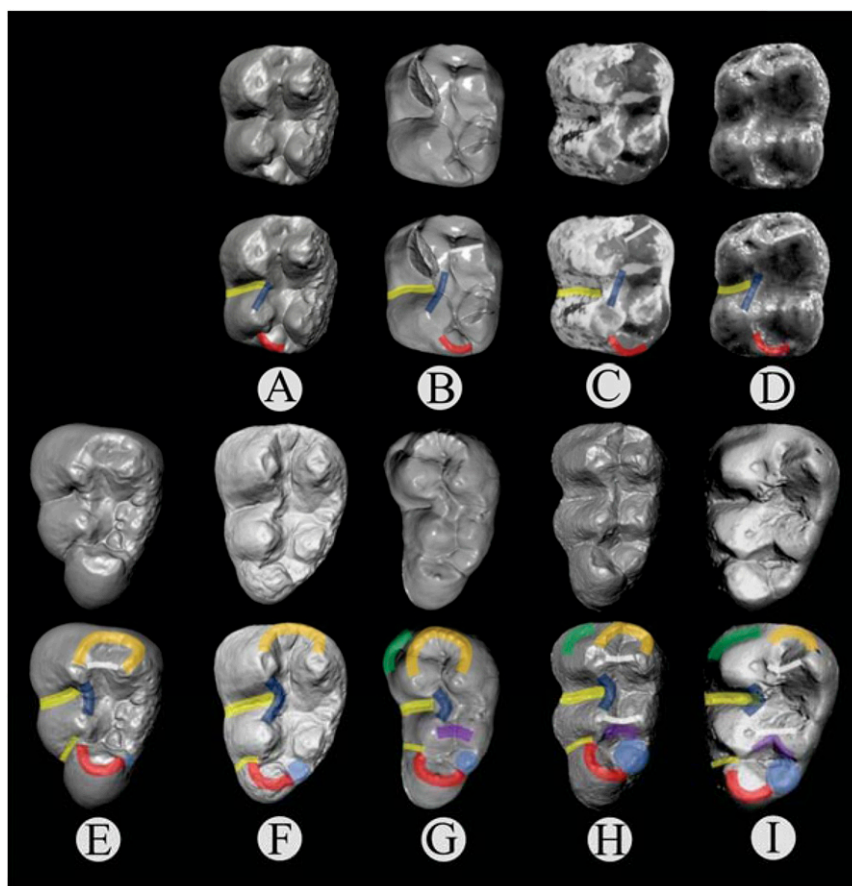
Fig. 2. Diagnostic features of early cercopithecoid dental evolution through time. Species are arranged from left to right by geologically oldest to youngest and scaled to the same mesiodistal length for ease of comparison. Paired *Top* row illustrates important features of the M_2 as colored overlays of (*A*) *Alophia*, KNM-NW 49732 (~22.2 Ma), Kenya, left M_2; (*B*) *Alophia*, KNM-NW 49735 (~21.9 Ma), Kenya, right M_2 (reversed for comparison); (*C*) *Noropithecus*, KNM-WS 12638 (16 Ma), Kenya, right M_2 (reversed for comparison); and (*D*) *Victoriapithecus*, KNM-MB 34 (~15.5 Ma), Kenya, left M_2. *Alophia* shares with *Noropithecus* and *Victoriapithecus* an incipient lingual protolophid (*B* only), buccal cleft, hypoconulid, and an obliquely oriented cristid obliqua. Paired *Bottom* row illustrates important features of the M_3 as colored overlays of (*E*) *Nsungewepithecus*, RRBP 11178 (~25.2 Ma), Tanzania, left M_3; (*F*) *Alophia*, KNM-NW 49732 (~22.2 Ma), Kenya, left M_3; (*G*) *Alophia*, KNM-NW 49735 (~21.9 Ma), Kenya, right M_3 (reversed for comparison); (*H*) *Noropithecus*, KNM-WS 12642 (16 Ma), Kenya, right M_3 (reversed for comparison); and (*I*) *Victoriapithecus*, KNM-MB 18993 (~15.5 Ma), Kenya, right M_3 (reversed for comparison). All M_3 teeth share a pair of buccal clefts (yellow lines). A tiny cuspulid identified as C6 cusp (tuberculum sextum) (blue circle) is present in (*E*) *Nsungewepithecus* (11) but is more fully developed in the younger species. A mesial lophid (white line) is present in (*E*) *Nsungewepithecus* while both mesial and distal lophids are present in (*H*) *Noropithecus* and (*I*) *Victoriapithecus*; both lophids are absent in *Alophia* (*F* and *G*). See *SI Appendix, Supplementary Information Note 3* and *Fig. S11* for discussion. M_2 legend: yellow, buccal cleft; red, hypoconulid; white, lingual protolophid; dark blue, cristid obliqua. M_3 legend: orange, C-shaped paracristid; green, slight buccal cingulum; yellow, deep median (thick) and distal (thin) buccal clefts; red, cristid flanking hypoconulid (postcristid and prehypoconulid cristid); white, lophid; dark blue, cristid obliqua; purple, mesial wall of posterior fovea composed of steep distal facets of hypoconid and entoconid; light blue filled circle, C6 cusp (tuberculum sextum). (*A*, *B*, and *E*–*I*) CT scan 3D renderings; (*C* and *D*) photographs.

A case could be made that *Alophia* represents the sister group to all other victoriapithecids because its dentition is more morphologically primitive than any previously known cercopithecoid. We include the Nakwai monkey in the Cercopithecoidea but refrain from assigning *Alophia* to the Victoriapithecidae because researchers have recognized for some time that the Victoriapithecidae likely "...encompasses a number of different stem cercopithecoids occupying varying degrees of relationship to one another and perhaps to crown cercopithecoids" (8, p. 210). Attempting to resolve this issue by erecting a nested series of monotypic sister taxa has been considered undesirable because it leads to instability. This situation is reflected in the phylogenetic analysis (Fig. 3), which indicates that *Alophia* is the most primitive cercopithecoid known and that Victoriapithecidae may be paraphyletic.

It should be noted that the late Oligocene *Nsungwepithecus*, known from a single lower M_3, has indistinctly developed and low-relief distal cusps set amid a large number of small accessory lingual cuspulids (11), thus complicating a comparison with the better represented *Alophia*. Until *Nsungwepithecus* is known by more informative material, its precise phylogenetic position (Fig. 3) should be regarded as tentative. Given the limited morphology observable for *Nsungwepithecus*, it seems clear that the presence of a mesial lophid (Fig. 2*E*) is responsible for its more derived placement in the phylogeny, but in most other respects it appears even more primitive than *Alophia*.

Models seeking to identify an adaptive impetus for the divergence of apes and monkeys based primarily on neontological information (16, 17) sometimes run afoul of the fossil record because early members of both groups often lack some of the important traits used to define crown clades [e.g., suspensory adaptations of apes (18–22), and bilophodonty in Old World monkeys (9, 23)]. Proposing better-informed theories requires direct empirical evidence about the basal members of a clade, which can come only from fossils.

The most abundant source of information regarding the morphology of stem cercopithecoids is found in the wealth of fossils
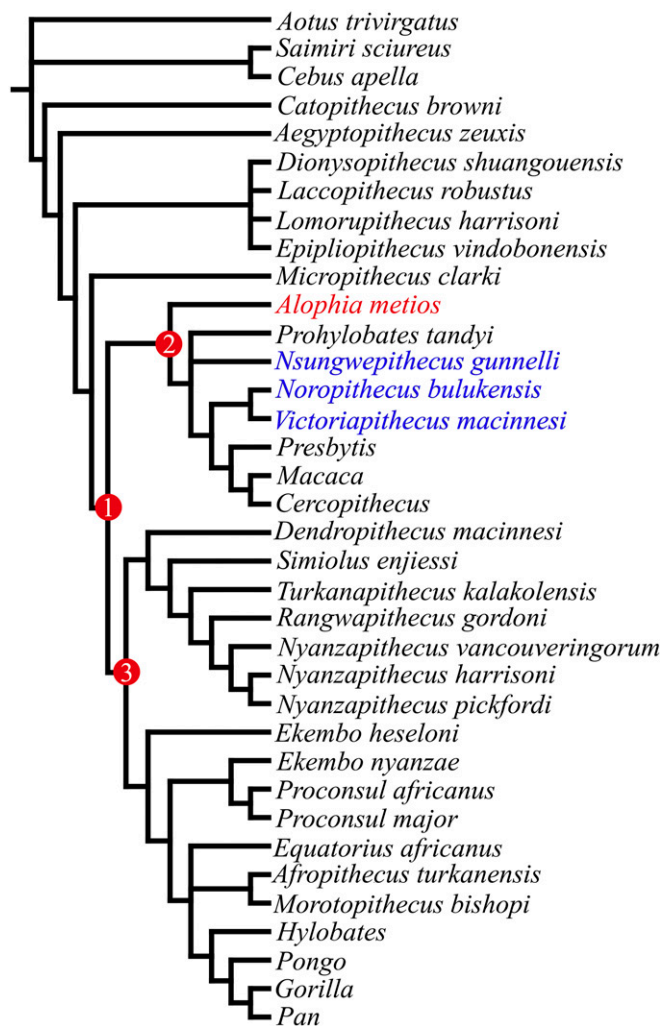
ANTHROPOLOGY

Fig. 3. Phylogenetic placement of *A. metios*. Strict consensus of 24 equally most parsimonious trees derived from parsimony analysis of 194 craniodental and postcranial characters indicates that *Alophia* is the most primitive cercopithecoid known. Taxa illustrated in Fig. 2 are labeled in color. *Nsungwepithecus* is known from a single M_3 only; the addition of such a fragmentary taxon can be problematic, but it is included here because it was not included in the phylogenetic analysis that accompanied its description (11). Tree length: 833; consistency index: 0.339; homoplasy index: 0.663; retention index: 0.622. Labeled nodes: 1—crown Catarrhini; 2—Cercopithecoidea; 3—Hominoidea. See *Methods* and *SI Appendix, Supplementary Information Note 4* for discussion.

from Maboko Island, Kenya (9) belonging to the genus *Victoriapithecus*. Maboko is dated to the early Middle Miocene, or ~15.5 Ma (24), only ~3 million years older than the earliest known fossil colobines (25), and likely postdates the origin of cercopithecoids by perhaps as much as 10–15 Ma (4–7, 9, 26). Nonetheless, the morphology of *Victoriapithecus* exhibits several primitive features that provide insight into the mosaic nature of the cercopithecoid dentition (e.g., variable retention of crista obliqua and hypoconulids) (9) and the evolution of bilophodonty.

Primitive as *Victoriapithecus* is, it is clearly a cercopithecoid because of its bilophodont lower molars (9, 27). It is inevitable that the identification of increasingly basal members of the cercopithecoid clade will be complicated unless the condition of "bilophodonty" can be identified in a recognizable form near the base of the clade. The variably complete lophs seen in *Victoriapithecus* strongly suggest that we should not expect this outcome, and *Alophia* confirms this point. Although *Alophia* lacks complete

lophids, much of the overall structure of the lower molar crowns is cercopithecoid-like: The crowns are occupied by four principal cusps symmetrically arranged in a rectangular shape, the buccal cusps are columnar and distinct, the buccal clefts are deep, the median buccal cleft is particularly cercopithecoid-like with its greater width and extension toward the central portion of the tooth, and the M_3 hypoconulid is rotated distobuccally by the expansion of the C6 cusp (tuberculum sextum).

Until now, because bilophodonty offered an easy way to identify fossil cercopithecoids, it was unnecessary to enumerate other traits that might diagnose membership in this clade. However, in cases such as the early evaluation of *Prohylobates tandyi*, a species in which the molars are too heavily worn to provide unequivocal evidence of lophids, Szalay and Delson (28) noted that its co-lumnar buccal cusps and distinctive median buccal cleft were features unique to cercopithecoids, and in doing so implicitly identified the morphology of the median buccal cleft as diagnostic of cercopithecoids in the absence of demonstrable bilophodonty. *Alophia* now confirms that both the columnar buccal cusp form and presence of a median buccal cleft were present at an early stage in cercopithecoid evolution, when the protolophid was incipient and the hypolophid had not yet evolved. Since the median buccal cleft is not observed among stem catarrhines, this feature now appears to serve as a diagnostic trait of primitive stem cercopithecoids even in the absence of bilophodonty.

This view of early cercopithecoid molar morphology makes it possible to hypothesize about early stages in the acquisition of cercopithecoid bilophodonty. Dental features observed in *Alophia* suggest that the phenotypic starting point for the cercopithecoid dentition was a generalized basal catarrhine pattern, such as that observed among the Fayum propliopithecines (27). The initial steps toward bilophodonty included alignment of the four main molar cusps into a mesial and a distal pair and the development of pronounced buccal clefts separating the mesial and distal moieties. Development of the median buccal cleft appears to have been accommodated initially by a more lingual deflection of the cristid obliqua as seen in *Alophia* (Fig. 2 *A*, *B*, *F*, and *G* and *SI Appendix, Fig. S11*). This step was followed or accompanied by reduction of M_1 and M_2 hypoconulids (Fig. 2 *A* and *B*), features unknown for *Nsungwepithecus* because it is represented by a single M_3. Subsequently, cusp tips became more closely approximated as cusp bases became inflated, perhaps through incorporation of the cingulum. The development of the transverse shearing crests that adorn the lophs and lophids appear, on present evidence, to have been asynchronous. The first cristid seems to have been the medial protocristid on the lingual side of the mesial lophid. How long it took for the completion of the mesial cristids, or the development of the cristids on the distal lophid is still unclear. However, *Victoriapithecus* adds support to the inference that the mesial cristids evolved in advance of the distal cristids by virtue of the frequent retention of the crista obliqua in *Victoriapithecus*, a feature that occupies the area into which the distal lophids should occlude. In fact, given the structure of the primitive catarrhine upper molar, one might have predicted that the mesial lophid and cristids would evolve first since their occlusal pathway across the trough formed by the mesial and distal fovea of the upper molars is not interrupted by cristae. In addition to retaining occasional cristae obliqua, *Victoriapithecus* also variably possesses hypoconulids and retains a degree of bunodonty. Younger crown cercopithecoids further refine bilophodonty by evolving upper and lower molars that are increasingly similar, with complete loss of M_1 and M_2 hypoconulids, loss of the crista obliqua, and heightened crest development.

Although comparisons among a small number of time-successive cercopithecoid teeth cannot definitively establish an evolutionary trend, M_3 specimens of *Nsungwepithecus*, *Alophia*, *Noropithecus*, and *Victoriapithecus* (Fig. 2 *E–I*) suggest a starting point for the cercopithecoid lower third molar wherein the median and distal buccal clefts provide embrasures for the buccal cusps of the upper

molars. The distal cusps next become increasingly distinct, the lingual and buccal cusps move closer together, the cristid obliqua becomes more acutely angled in the lingual direction, mesiolingual accessory cuspulids begin to coalesce into what later becomes the postmetacristid and preentocristid, the more centrally positioned cuspulids disappear, and the distolingual cuspulid expands in size to become the C6 cusp (tuberculum sextum), the increasing size of which causes the hypoconulid to rotate distobuccally (*SI Appendix, Supplementary Information Note 3* and Fig. S11). However, the variation seen within the younger large *Victoriapithecus macinnesi* sample cautions against overinterpretation of these observations.

Functional explanations of bilophodont molars usually emphasize the kinematics of interlocking transversely aligned blades (29–31), which excel at both shearing and crushing functions. However, because *Alophia* shows only incipient development of the mesiolingual portion of the anterior lophid, its shearing capacity would have been less than in extant cercopithecoids. This observation raises the questions of what adaptive advantage might be gained and what dietary niche might be occupied by a monkey with only incipient development of transverse lophs. Previous work on the utility of bilophodonty (3, 32) has demonstrated that the lophs and lophids of upper and lower molars, respectively, occlude in a dynamic manner during mastication and are guided by complementary embrasures as they move into occlusion (phase I of a chewing cycle). In the lower molars, these embrasures are largely composed of the aforementioned buccal clefts that are so distinctive of cercopithecoids. The median buccal cleft is the largest of these clefts, and it accommodates the mesial loph of the upper molar (principally the lingual surface of the paracone). The distal lophs are guided by embrasures formed between the molars as a result of their curved corners and presence of mesial and distal buccal clefts. All of these embrasures are present in *Alophia*. In combination with the transverse alignment of the cusps, this geometry would have permitted the same pattern of chewing and occlusion seen in modern cercopithecoids, but with less development of shearing structures. Interestingly, although the buccal halves of the molar lophids are not involved in shearing, the lingual halves of the lophids are (3, p. 333). The incipient M_2 lingual protolophid, present in KNM-NW 49735, bears the wear facets 7n and 5, which develop partly as a result of shearing across the premetacristid and postmetacristid by the posthypocrista and preprotocrista (3, 32). In other words, *Alophia* appears to have begun to evolve the half of the protolophid involved in shearing.

Accordingly, the primary advantage of the occlusal morphology seen in *Alophia* was presumably the guidance of the cusps through phase I of the chewing cycle, terminating with the impact of the lingually oriented crushing surfaces of the lower molar (10n) against the buccally oriented surfaces of the upper molars (9, 10n). If so, this early stage of cercopithecoid dental evolution witnessed in *Alophia* may have been driven by its advantages in crushing food items rather than in shearing them, thus suggesting the importance of harder foods in the diet, like fruits and seeds (33, 34) rather than leaves. The incipient mesial lophid possessed by *Alophia* in KNM-NW 49735 hints that it may exhibit the initiation of selective pressure for shearing, a feature more fully expanded in the later evolution of full bilophodonty. However, the apparent persistence of a reliance on cusps rather than lophs suggests that a simpler dentition lacking true bilophodonty was a stable adaptation for the first several million years of cercopithecoid evolution.

Pollen recovered from an exploration well in the Lokichar Basin dating from the Late Oligocene to Early Miocene demonstrates that this region had rainfall between 1,200 and 1,600 mm/y, a well-defined dry season, and a mosaic of semideciduous forest and humid woodland similar to that along the southern border of the Guineo-Congolian rainforest (35). This habitat reconstruction, combined with evidence from *Alophia*'s occlusal morphology, strongly suggests that *Alophia* was a forest-dwelling primate with a primary diet of fruits and seeds rather than leaves. These data add no support to the notion that the initial divergence of Old World monkeys and apes was linked with environmental change toward more open habitats, as has been hypothesized based on later members of Victoriapithecidae (24, 36).

The recovery of *Alophia*, a basal member of the cercopithecoid radiation from the earliest portion of the Early Miocene, offers support for molecular estimates of a late Paleogene date for cercopithecoid-hominoid divergence (4–7, 26) and contributes morphological information about the origin and evolution of the Old World monkeys from a critical but rarely sampled time interval in Sub-Saharan Africa.

Methods

Phylogenetic Analysis. A previously published character/taxon matrix (37) was updated for the phylogenetic analysis of *Alophia* (Fig. 3 and *SI Appendix, Supplementary Information Note 4*) by adding several new characters to capture more subtle aspects of dental evolution in cercopithecoids. In addition to *Alophia*, the matrix was also expanded by adding *Nsungwepithecus gunnelli*, *Prohylobates tandyi*, and *Noropithecus bulukensis*. Four taxa included in the previous analysis (*Pliopithecus antiquus*, *Kalepithecus songhorensis*, *Limnopithecus evansi*, and *Limnopithecus legetet*) had behaved as "wild card" taxa (38), taking up numerous equally parsimonious positions and concatenating the number of equally most parsimonious trees. These taxa were also among the most poorly known fossils, being represented by no postcranial or cranial characters. As is common practice (e.g., refs. 39–42), we excluded these taxa to allow the better-supported signal among other taxa to emerge. *Nsungwepithecus* is known from a single M_3 only; the addition of such a fragmentary taxon may be inadvisable, but it is included here because it was not included in the phylogenetic analysis that accompanied its description (11).

As in the original analysis (37), the matrix includes both quantitative and qualitative characters. Quantitative characters were coded using weighted gap coding (43). Some of the characters were treated as ordered to reflect hypothesized character transformations (44, 45) while most (142 in total) were treated as unordered. The matrix was analyzed using the heuristic search function in PAUP 4.0 (46) with 10,000 replicates. Three platyrrhines were employed as outgroup taxa, and all other taxa were unconstrained. See *SI Appendix, Supplementary Information Note 4*, for discussion.

Maximum likelihood (ML) and Bayesian analyses have been employed with increasing frequency in phylogenetic studies, including some recent work focusing on catarrhine primates (refs. 11 and 47 but not refs. 40, 42, 48, and 49). Our choice to forgo such an approach is due only in small part to our philosophical preference for parsimony over probabilistic methods, and we fully acknowledge the suitability of model-based methods for nucleotide data. However, we deem it inappropriate to apply Bayesian or ML methods, which assume and apply a common mechanism of evolutionary change, to our cladistic character matrix of morphological traits compiled with no effort to document autapomorphies and composed of a wide range of character types including binary, qualitative, meristic, and discretized characters binned from continuous metric data (50–53). Had this been a total evidence analysis (e.g., ref. 47), a large portion of the data would have been amenable to ML or Bayesian methods, and a partitioned approach might have been taken.

Computed Tomographic Scanning. All scans were performed at the Evolutionary Studies Institute, University of the Witwatersrand, Johannesburg, South Africa, in the Microfocus Computed Tomographic (CT) Laboratory, using a Nikon XTH 225/320 LC system with a Perkin-Elmer 1621 flat panel detector. Samples were held in place by custom foam mounts within Plexiglas containers, and three reference calibration images were collected by averaging 256 images for each one. X-rays were generated using the parameters 75 kV and 100 μm for KNM-NW 49731 and KNM-NW 49732. The parameters 80 kV and 130 μm were used for KNM-NW 49735 with a 3.1-mm aluminum filter. For each specimen scanned, 3,142 projections were acquired and two frames were averaged for each projection. The raw data were reconstructed to generate volume files using CT Pro-3D (Nikon), and 16-bit TIFF images were obtained using VGStudio Max (Volume Graphics). See scanning parameters (*SI Appendix, Table S4*) for acquisition parameters, data voxel dimensions, and scaling and artifact-processing parameters.

3D Reconstruction. Data volumes were loaded into Avizo (FEI) to produce the 3D element and segment the individual tooth, or tooth fragments along fracture planes, with each object saved as an .stl file. These files were imported into Maya (Autodesk) and repositioned, reoriented, and aligned

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along fracture planes to reconstruct the element in 3D. Measurements and stereo pairs were made with Avizo.

Digital Photography. Digital photographs of the original fossils and replica casts were taken against a black felt or neutral background, while 3D CT renderings were saved within Maya. Image files were imported into Adobe Photoshop C5.1 Extended at full resolution. The element was isolated with the lasso tool and cut and pasted onto a solid color background with stereo views composed of elements in different layers. Overlays of dental features were made in Powerpoint (Microsoft).

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