

# An upper dentition of *Aframoni* *dieides* (Primates) from the Fayum, Egyptian Eocene

(Adapidae/Prosimii/evolution)

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**ABSTRACT** The first known upper dentitions—an adult and subadult—of the cercamoniine adapiform primate *Aframoni* *dieides* are described. Comparisons show that *A. dieides* has an upper molar morphology resembling that of other cercamoniine adapids but the species lacks some of their typical specializations. The new dental material confirms that *Aframoni* stands closer to *Mahgarita* from west Texas and *Cercamoni* from Europe than it does to *Schizarodon* and *Omanodon* from Oman—all of which have been ranked as cercamoniines. Affinities of the latter two genera probably lie with the *Anchomomys* group. The presence of a cercamoniine adapid in the Eocene of Egypt supports the view that early African anthropoideans evolved not in isolation, but concomitantly with a contemporary Eocene prosimian radiation.

This paper describes the first discovered upper dentitions of the cercamoniine adapiform primate *Aframoni* *dieides* from quarry L-41, Jebel Qatrani Formation, Fayum Province, Egypt. The Jebel Qatrani is a sequence of variegated sand and mudstones approximately 340 m thick. L-41 is located about 45–47 m above the base of the Jebel Qatrani and has been provisionally dated to the late Eocene by paleomagnetic studies, faunal correlation, and marine transgression analyses (refs. 1–5, but see also ref. 6). Quarry L-41 contains a rich array of Paleogene animals, including multiple species each of primates, hyraxes, creodonts, rodents, and insectivores, as well as fish, lizards, frogs, snakes, turtles, crocodiles, and birds. The morphologic and taxonomic diversity of the L-41 primates is unrivaled at other African Paleogene localities. At present this quarry has yielded nine primate genera. Four of these are prosimians [*Wadilemur*, *Anchomomys* (7), *Plesiopithecus* (8, 9), *Aframoni* (10)]. The other five, *Serapia*, *Arsinoea* (8), *Catopithecus* (4, 5, 11), *Proteopithecus* (4), and *Qatrania* sp. nov., are archaic anthropoideans. *Serapia* and *Qatrania* are parapithecids, and *Catopithecus* is an oligopithecine. *Proteopithecus* and *Arsinoea* have uncertain anthropoidean affinities, and *Plesiopithecus* is an unusual large nocturnal prosimian. *Wadilemur* and *Anchomomys* are small cercamoniine adapids, and *Aframoni* is a large one. L-41 presents an unusual primate community structure in that two of the prosimians, *Plesiopithecus* and *Aframoni*, are larger than any of the four described anthropoideans (*Catopithecus*, *Arsinoea*, *Proteopithecus*, and *Serapia*), and two other prosimians (*Wadilemur* and *Anchomomys*) are much smaller than the smallest anthropoidean.

*A. dieides* was first described in 1995 on the basis of three mandibular specimens (10), and its recovery was the first documentation of a large cercamoniine in Africa. Two small adapids from Oman, *Omanodon* and *Shizarodon*, have been

attributed to the anchomomyiine tribe of this subfamily, but these specimens represent animals far smaller than *A. dieides*. In addition, *Omanodon* and *Shizarodon*, if separable from *Anchomomys*, are more closely related to the small anchomomyiines *Wadilemur* and *Anchomomys* from L-41 (12). A point of general significance concerning all of the L-41 primates is that, together with *Omanodon* and *Schizarodon* from Oman (12), *Djebelemur* from Tunisia (13), and *Algeripithecus* and *Tabellia* from Algeria (14), they show that Eocene members of Prosimii were widely distributed and morphologically diverse, and that early anthropoideans were, as stated by Rasmussen (15), “. . . older, smaller, structurally more primitive, and geographically more widespread” than previously suspected.

## TERMS

The common noun “anthropoids” is used by many to refer to early, middle, and late Cenozoic members of suborder Anthropoidea. However, especially in Europe, this term refers informally to the anthropoid apes. Other scientists, particularly in France, call members of this suborder simians. For more precise reference here, and in continuance of usage by one of us (E.L.S.), these animals are here called anthropoideans.

## SYSTEMATICS

**Order Primates Linnaeus, 1758; Suborder Prosimii, Illiger, 1811; Family Adapidae, Trouessart, 1879 (s.l.); Subfamily Cercamoniinae, Gingerich, 1975.**

### *Aframoni dieides*

*Holotype*. Cairo Geological Museum 42202, left dentary with well preserved P<sub>3</sub>–M<sub>3</sub> (see figure 1 of ref. 10).

*Hypodigm*. Duke University Primate Center (DPC) 15190 right maxillary fragment with alveolus of C<sup>1</sup> and P<sup>2</sup>–M<sup>3</sup>; DPC 9859 subadult left maxillary fragment with dP<sup>4</sup>, M<sup>1-2</sup>; DPC 11595, left dentary with alveoli for I<sub>1</sub>–P<sub>2</sub> and crowns of P<sub>3</sub>–M<sub>3</sub> (M<sub>1</sub> and M<sub>3</sub> broken); DPC 12437, left dentary with C<sub>1</sub>–M<sub>3</sub> and right dentary with a broken root of I<sub>2</sub>, base of C<sub>1</sub> crown, and P<sub>2</sub>–M<sub>3</sub> (see fig. 3 in ref. 10).

*Distribution*. Known only from the type locality: L-41, Fayum Province, Egypt.

*Diagnosis*. This is repeated in part from ref. 10. *A. dieides* is a cercamoniine with a relatively shallow dentary and symphyseal fusion in older individuals. The incisor roots are small and implanted vertically and the central incisor alveolus is smaller than that for the lateral one. The canines are dimorphic in size. There are three premolars; P<sub>2</sub>/2 is very reduced in size although it shows a honing facet for the upper canine. P<sub>3-4</sub> are both wedge-shaped and have a broad, complex talonid shelf. The lower molars are crested and have relatively long and narrow crowns. There is no paraconid, and the entoconid is positioned at the posterolingual corner of the talonid. The

Abbreviation: DPC, Duke University Primate Center.

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lower third molar has a narrow, but well developed, hypoconulid lobe on the talonid. *Aframomius* is most similar to *Protoadapis* and *Europolemur* in size and molar form but differs in having more complex premolars and more dimorphic canines, and in exhibiting fusion of the mandibular symphysis. The upper premolar size sequence is  $P^2 < P^3 < P^4$  with the crown of  $P^2$  less than 1/5th the size of  $P^3$ .  $P^2$  has no lingual cusp,  $P^3$  has no distinct lingual cusp but has a strong, sharp lingual cingulum, and  $P^4$  has a distinct inner cusp and strong surrounding basal cingula, as well as distinct styler flexures on each side of the buccal cusp. Upper molars are subequal with well developed basal cingula except on the buccal side of the hypocone, and slight parastylar flexures as well as pronounced, buccally flexed metastyles are present on all three upper molars. A hypocone, paraconule, and metaconule are present on  $M^{1-3}$  with the hypocone smallest on  $M^3$ . *A. dieides* differs from other cercamoniines in showing a pattern of fine wrinkling, somewhat as in *Aegyptopithecus*, on the lingual slopes of the protocone and posterior slope of the paraconule, as well as throughout the trigon basin, particularly on  $M^{2-3}$ . This wrinkling can be detected on unworn lower teeth as well.

### DESCRIPTION OF NEW MATERIAL

The upper right dentition of DPC 15190 (Fig. 1) is a comparatively unworn series so that tooth crown morphology can be readily studied. Both  $P^4$  and  $M^1$  are slightly damaged. The canine alveolus of DPC 15190 is incomplete as its outer edge is broken off, but judging from what can be seen the canine would have been relatively large. There are three upper premolars. The anterior premolar,  $P^2$ , is a small conical tooth with sharp mesial and distal crests. The middle premolar,  $P^3$ , is larger than  $P^2$  and triangular in occlusal outline.  $P^3$  has a single buccal cusp and a nearly complete basal cingulum.  $P^4$  is trapezoidal in occlusal outline, with the mesial portion being slightly longer than the distal. The buccal cusp is high and sharp, and the lingual cusp is about one-third the height of the buccal cusp and rises out of the mesiolingual cingulum.

Upper molars of DPC 15190 are transversely broad with buccal and lingual portions about equally developed. The trigon is clearly defined, and all three cusps are high and sharp. A paraconule is present and positioned far mesially. The preparacrista first descends mesially and then curves lingually to the paraconule. The preprotocrista descends directly mesially from the apex of the protocone to the paraconule. The enamel is wrinkled and particularly striated on the lingual aspect of the protocone and hypocone. No pericone is present. Mesial, buccal, and distal cingula are strong, and the hypocone is developed out of the lingual cingulum. A metaconule is either absent or weakly developed. There is no mesostyle, but there is slight buccal flexure of the ectoloph.

The upper first molar is broad with strong mesial, buccal, and distal cingula. The tips of the metacone and hypocone are broken in this specimen. The hypocone is a small distinct cusp formed out of the distolingual cingulum. A small paraconule is present. There is no metaconule, instead the postmetacrista and postprotocrista form a low continuous crest.

The second upper molar differs from  $M^1$  in having a larger and more distinct hypocone, and in having a metaconule that is present, although weak. The paraconule is small and inconspicuous. The postparacrista and premetacrista descend slightly buccally from the apices of the paracone and metacone, respectively, to form an ectoloph that is asymmetrically flexed with the distal portion (premetacrista) being longer and better defined than the mesial (postparacrista).

The third upper molar is almost as large as  $M^2$ .  $M^3$  has a large well developed protocone, and a hypocone is present as a small cusp arising from the lingual cingulum. The  $M^3$  hypocone is much reduced relative to the size of the  $M^2$  hypocone and is even smaller than the  $M^1$  hypocone. A small



FIG. 1. Scanning electron micrograph of DPC 15190. Upper right  $P^2$  to  $M^3$  of *A. dieides*. Note the large canine socket, the greatly reduced  $P^2$  as well as the similar-sized and highly crenulate molars. Scale  $\times 9$ .

paraconule is present. There is no distinct metaconule, but a low crest connects the bases of the metacone and protocone. Unlike  $M^2$ , the postparacrista and premetacrista are of approximately equal length. Unlike the lower molar series the upper molars do not increase in size from front to back.

The second maxillary fragment, DPC 9859, is a left subadult specimen with  $dP^4$  and  $M^{1-2}$  (Fig. 2). The  $dP^4$  is molariform and distinctly smaller and lighter colored than  $M^{1-2}$ , which are subequal in size and both a little smaller than in DPC 15190. DPC 9859 has a  $DP^4$  that lacks a hypocone and hence looks like a molar trigon; however, there is a flexure in the basal cingulum where the hypocone would be. Both paraconule and metaconule are present on the  $dP^4$ . A parastyle and metastyle are present, but as in the molars there is no mesostyle. The molar crown morphology of DPC 9859 confirms that seen in  $M^{1-2}$  of DPC 15190, including the presence of wrinkled enamel.

### COMPARISONS

The presence of broad molars with wide central basins, reduced  $P2/2$ , continuous or nearly continuous cingula, well developed hypocones isolated from the trigon, buccal flexure of the ectoloph, and occurrence of a paraconule along with weak or absent metaconules give *A. dieides* an upper molar morphology resembling that of other cercamoniine adapids such as *Periconodon* (16) and *Mahgarita* (17). At the same time, *A. dieides* is distinct in the simplicity of its upper molar structure as it lacks many specific features characteristic of its

closest relatives. For example, while the  $P^2$  of *A. dieides* is small, as in other cercamoniines, it is not peg-like as in *Mahgarita*. Also the  $M^3$  of *A. dieides* is a large tooth and not reduced as in *Mahgarita*. In addition, *A. dieides* lacks: (i) a pericone present in *Periconodon*, *Hoanghoni* (18), *Rencunius* (19), and *Djebelemur* (14); (ii) a mesostyle clearly developed in *Caenopithecus* (16, 20); (iii) the crescentic protoconule characteristic of *Hoanghoni*, and (iv) the expression of prominent metaconules and centrocrista seen in *Hoanghoni* and *Rencunius*.

*A. dieides* can be compared in absolute size to various cercamoniines, contemporary prosimians, and early anthropoideans. Size comparisons for those species that have upper premolars and molars intact are as follows:

*A. dieides*, length of  $P^2$ - $M^3$  is 19.7 mm.

*Mahgarita stevensi*, length of  $P^2$ - $M^3$  is 15.9 mm.

*Pronycticebus gaudryi*, length of  $P^2$ - $M^3$  is 15.5 mm.

*Caenopithecus lemuroides*, length of  $P^2$ - $M^3$  is 23.6 mm.

*Plesiopithecus teras*, length of  $P^2$ - $M^3$  is 14.0 mm.

*Catopithecus browni*, length of  $P^2$ - $M^3$  is 13.4 mm.

*Proteopithecus cocaenus*, length of  $P^2$ - $M^3$  is 11.5 mm.

### DISCUSSION

Simons *et al.* (10) discussed a number of mandibular features shared by cercamoniine adapids, including *A. dieides*, that possibly linked cercamoniines with early anthropoids. Among these were mandibular fusion, possession of canine dimorphism, and incipient development of a canine/premolar honing complex. Evidence of canine, and thus presumably sexual size dimorphism, was documented for most Fayum Oligocene anthropoideans many years ago by Fleagle *et al.* (21), and the same canine dimorphism has been recently reported for *Catopithecus* (22) and the mandibles of *Aframoni* (10). However, DPC 15190 is currently the only known adult maxilla of *A. dieides*, and recovery of a number of maxillae with the canine preserved will be necessary to document fully the degree of canine/sexual dimorphism and canine premolar honing function in this species. The large canine socket partially preserved in DPC 15190 may indicate that this individual is a male, and if so, the presence of a large upper canine would be in agreement with evidence from the lower dentition for their being considerable canine dimorphism in *Aframoni* (10).

In true catarrhines, as in the early anthropoideans *Oligopithecus* and *Catopithecus*,  $P2/2$  has been lost, and the upper canine hones against  $P_3$ . In DPC 12437, a lower jaw of *A. dieides*, the small size of  $P_2$ , and wear facets on  $P_2$  and  $P_3$  indicate that honing was in the process of being transferred distally. A similar transfer of honing function is also evident in *Caenopithecus* and perhaps also in *Djebelemur* and *Mahgarita*, although it cannot be confirmed in the later two genera. In the upper dentition of *A. dieides*, DPC 15190, the canine is not preserved but  $P^2$  is very small as would be expected if the second premolar was in the process of being lost and the canine premolar honing function shifted distally.

Information about the morphology and geographic distribution of cercamoniine adapids is important for interpreting the origin of anthropoid primates, as some researchers have argued for a close relationship between cercamoniines and early anthropoideans from Africa (15, 19, 23-25). For example, Rasmussen and Simons (26) discussed morphological similarities of the upper dentition shared between the cercamoniine *Protoadapis* (27), its allies (*Europolemur*, *Mahgarita*, *Periconodon*, and *Hoanghoni*), and the early anthropoidean *Oligopithecus*. Rasmussen (25) also noted affinities in molar structure between the cercamoniine *Mahgarita* and the early anthropoideans *Catopithecus*, *Oligopithecus*, and *Dolichocebus*. In terms of geographic distribution, the recovery of a cercamoniine adapid from North Africa, together with recent



FIG. 2. Scanning electron micrograph of DPC 9859. Upper left subadult  $dP^4$ ,  $M^{1-2}$  of *A. dieides*. Note the triangular, but molariform,  $dP^4$  and renulated molar enamel. Scale  $\times 11$ .

discoveries of Paleogene primates from Oman, Tunisia, and Algeria supports the position that early African anthropoids did not evolve in isolation but as part of a larger African Eocene primate radiation.

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