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Evolution

Dentition of *Proteopithecus sylviae*, an archaic anthropoid from the Fayum, Egypt

(Anthropoidea/primate evolution/dental morphology)

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ABSTRACT ***Proteopithecus sylviae*** **is an archaic anthropoid from the late Eocene quarry L-41, Fayum Province, Egypt. The dentition of *Proteopithecus* is very primitive and does not closely resemble that of other, better known, primates from the Fayum (e.g., parapithecids and propliopithecids). The dental morphology, much of which is described herein, shows a platyrrhine-like level of organization, suggesting that *P. sylviae* may occupy a position near the base of the modern anthropoid radiation.**

The type specimen of *Proteopithecus sylviae*, a maxillary fragment with M^1–M^3 and associated P^3, was recovered about a decade ago from the late Eocene quarry L-41, Fayum Province, Egypt (1). On the basis of this single specimen, *P. sylviae* was originally thought to resemble the oligopithecine anthropoids *Catopithecus* (L-41) and *Oligopithecus* (quarry E, early Oligocene) (1). However, subsequent recovery of additional specimens revealed morphological features—including the presence of three premolars—demonstrating that *P. sylviae* retains a more primitive dental structure than any oligopithecine (2). The presence of three premolars is a feature shared between *P. sylviae* and parapithecids (*Qatrania wingi, Qatrania fleaglei, Apidium phiomense, Apidium moustafai, Apidium bowni, Parapithecus fraasi,* and *Parapithecus grangeri*) another kind of archaic anthropoid from the Fayum. However, the dental morphology of *P. sylviae* does not resemble that of parapithecids nor does it share many features in common with the Fayum propliopithecids.

SYSTEMATICS

Order Primates Linnaeus, 1758; Suborder Anthropoidea Mivart, 1864; Superfamily Hominoidea Gray, 1825; Family incertae sedis.

Proteopithecus sylviae. *Holotype.* Cairo Geological Museum (CGM) 41886, left maxillary fragment with M^{1-3} and associated P^3, lingual third of M^1 is broken (as shown in a figure in ref. 1).

Revised hypodigm. Duke University Primate Center (DPC) 10370 right mandible has crowns of P_3–M_2, a partial ascending ramus, and alveoli for P_2 and M_3. M_1 is slightly damaged lingually. DPC 10371 has worn right mandible with M_2, alveolus for M_3, and a substantial portion of the ascending ramus. DPC 12131 has buccal portion of a right mandible with buccal half of the canine, P_2 and P_3, roots of P_4–M_2. DPC 13101 has worn left mandible with P_2–M_3 and a partial ascending ramus, and P_2 is displaced from its alveolus. DPC 13613 has partial right maxilla with C–M^2 and lingual portions of P^4 and M^2 damaged. DPC 13614 has partial right maxilla with P^{2-3} and lingual halves of P^4–M^2. DPC 13615 has left mandible with alveoli for P_{2-3}, area around P_4 damaged, and crowns of M_{1-3}. DPC 14095 has partial skull with left and right C–M^3 and right I^1. DPC 14234 has right mandible with P_3–M_3; crowns are moderately worn. DPC 14518 has partial left maxilla with P^4–M^2. DPC 15305 has right mandible with crowns of P_4–M_3 very slightly worn. DPC 15416 has right mandible with canine displaced, P_2 missing, and P_3–M_3 in good condition. DPC 15518 has left maxilla with C–M^3. P^2 is broken, P^3 is damaged down its midline, and P^4–M^3 are in good condition. DPC 16873 has left tibia. DPC 17031 has left femur. CGM 40928 has left mandible with alveoli for P_{2-3}, broken base of P_4, and worn crowns of M1–3. CGM 40936 has right mandible with alveolus for P_3, damaged crowns of P_4–M_3, and a partial ascending ramus. CGM 41851 has moderately worn right mandible with fragmentary P_{3-4}, crowns of M_{1-2}, the buccal portion of M_3, and part of the ascending ramus. CGM 41917 has right mandibular fragment with M_{1-2}. CGM 41944 has damaged right maxilla with broken M^1–M^3. CGM 42200 has right maxilla with M^1–M^3. CGM 42209 has left mandible with P_{2-4}, M_{1-2} with coronoid, and articular and angular processes preserved. CGM 42214 has partial skull with large right canine alveolus, right P^3–M^3, and lingual halves of left P^3–M^3. CGM 42217 has right tibia. CGM 42833 has left maxilla with P^3–M^3.

DESCRIPTION OF NEW MATERIAL

The maxillary dental morphology of *P. sylviae* has been briefly described previously (1) and new material confirms the presence of (*i*) three premolars, (*ii*) upper molars that are broad buccolingually and narrow mesiodistally, (*iii*) upper molars with clearly delineated trigons bounded by a paracone—with pre- and postparacrista, a metacone as nearly as tall as the paracone and a much smaller protocone, (*iv*) M^1 and M^2 with moderately large hypocones, (*v*) M^1 with a metaconule; and (*vi*) a proportionally small M^3 (Fig. 1). P^2 morphology is obscured by damage to the specimen figured but the P^2 morphology is shown clearly in (1).

P. sylviae has spatulate upper central incisors and, judging from the size of the alveoli, upper lateral incisors somewhat smaller than the central ones. The upper canine is relatively large and is broad buccolingually and long anteroposteriorly at the base, although the crown height is comparatively short. The anterior face of the canine has a distinct vertical groove that ends at the base of the enamel.

The three upper premolars increase in size posteriorly and that P^4 is broader than M^1. All three upper premolars have distinct inner and outer cusps, but unlike the case with the lower P_2 the upper P^2 is distinctly smaller than P^3. All three premolars show an accessory shelf or cuspule on the posterior base of the inner cusp. M^1 is slightly larger than M^2 and both

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Abbreviations: CGM, Cairo Geological Museum; DPC, Duke University Primate Center.

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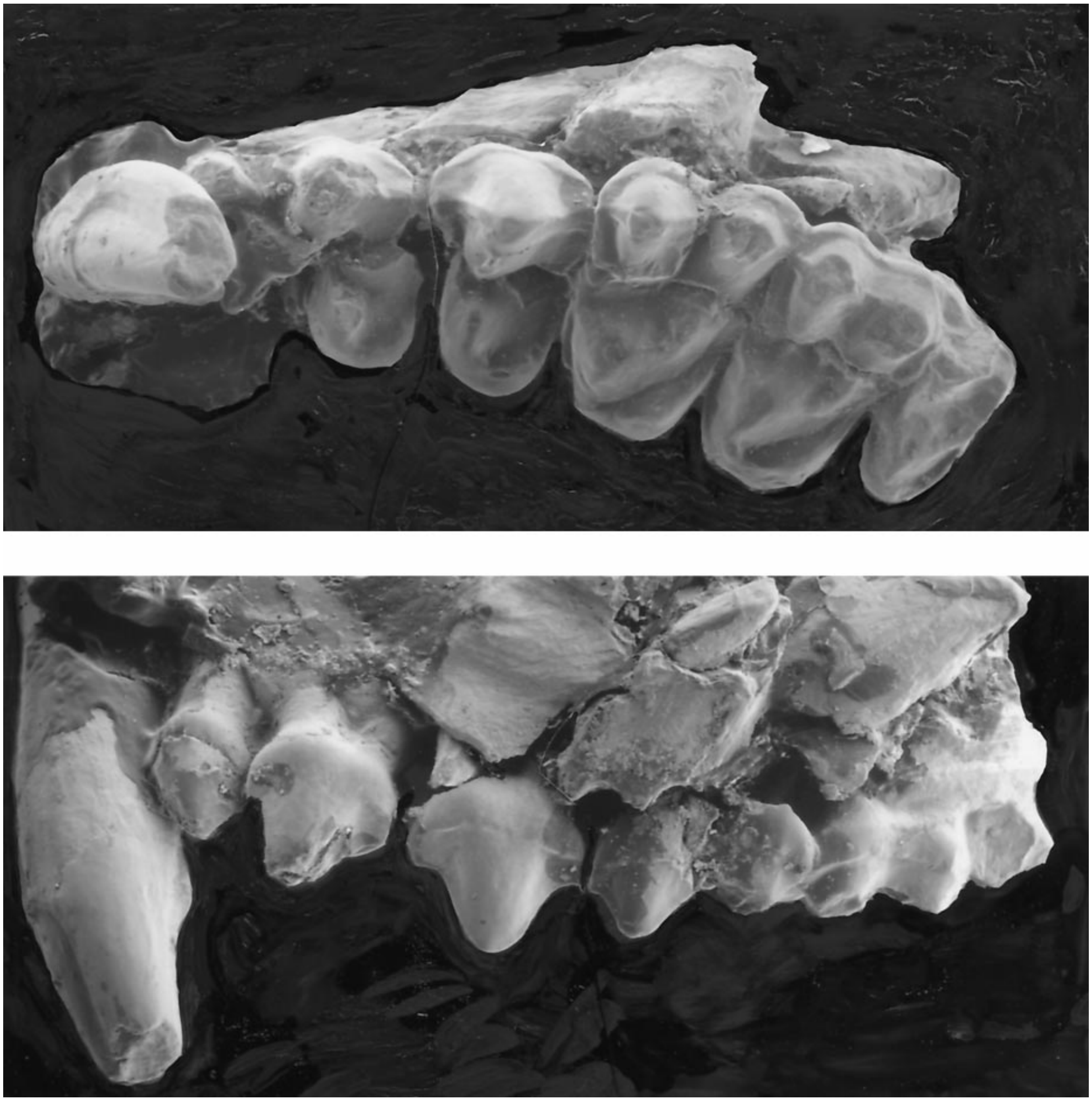

FIG. 1. Maxillary dentition of *P. sylviae* DPC 15518. Scanning electron micrograph crown view (*Upper*) and lateral view (*Lower*). Magnification, ×11. Note anterior groove on canine, large P^4, subequal M^{1-2} with distinct hypocones, and small M^3.

teeth have distinct hypocones. M^3 is relatively very small, being only about half the surface area of M^2, and has only a buccal and a lingual cusp.

The mandibular corpus is shallow and even, deeping only slightly posteriorly. Premolar and molar cusps are rounded and dental enamel is smooth. Both premolars and molars are buccally inflated, so that buccal cusps appear to be situated closer toward the midline of the tooth, and lingual cusps—particularly of the talonid—occupy the lingual margin. Very worn specimens show that both premolars and molars wear down flat. Details of the symphyseal region and lower incisor morphology are unknown. In DPC 12131, the canine is large relative to other teeth and projects well above the postcanine tooth row. However, the canine is more stout and heavily constructed than it is high and sharp. A comparison between the canine associated with DPC 15416 and that of DPC 12131 shows that *P. sylviae* canines exhibit two morphs, likely indicating that, as among other Fayum anthropoids, *P. sylviae* had sexually dimorphic canines.

P. sylviae has three lower premolars (Fig. 2). A typesetting error in a previous publication (3) mistakenly suggested the existence of a P_1 in *P. sylviae* but this is not the case. P_2 occludes with the upper canine and is larger and more projecting than P_3. The first two premolars are simple conical teeth, although both P_3 and P_4 are double-rooted and P_4 has a bicuspid trigonid. The P_4 protoconid is slightly taller than the metaconid and is situated more mesially. There is a prominent preprotocristid—stronger than that on M_1—that arcs mesially and then lingually to form the mesial margin of the tooth. There is no premetacristid. The combination of a mesially shifted protoconid, a prominent preprotocristid that extends to the mesial margin in front of the metaconid, and lack of a premetacristid gives the impression of a trigonid that is situated slightly lingually off center and has a mesiolingual slope. The P_4 trigonid is high and the talonid is a short shelf, formed out of a broad but ill-defined distal cingulum that is slightly longer mesiodistally behind the metaconid than the protoconid. In one specimen (DPC 14300), the P_4 distal cingulum extends around the buccal side of the tooth.

Lower first and second molars have a generally square occlusal outline that is especially apparent on worn specimens. On M_1, the protoconid and metaconid are of approximately

FIG. 2. Mandibular dentition of *P. sylviae*. Stereopair scanning electron micrograph of left lower partial dentition of CGM 42209. Magnification, ×11. Canine and M_3 are reversed from a micrograph of DPC 15416, a right lower partial dentition. Note large P_2, size disparity between P_3 and P_4, the twinned hypoconid-entoconid on M_1 and M_2, and the small size of M_3.

equal height and a rounded preprotocristid arcs mesiolingually to a small paraconid perched on the mesial margin of the tooth. There is no premetacristid. The trigonid is not greatly elevated but is high relative to the broad basin-like talonid (Fig. 3). Specimens with only slight wear (e.g., DPC 10370 and DPC 15305) show that the trigonid basin is small and in some cases is little more than a central sulcus separating the two major cusps. The trigonid is typically "pinched" and triangular in occlusal outline, and the talonid is more squared. The second lower molar differs from M_1 in being slightly shorter mesiodistally and lacking a paraconid, so that the trigonid has a less constricted appearance. Both the cristid obliqua and preentocristid are rounded. Most specimens have a hypoconulid on M_1 and M_2, and when present, the hypoconulid is small and twinned with the entoconid.

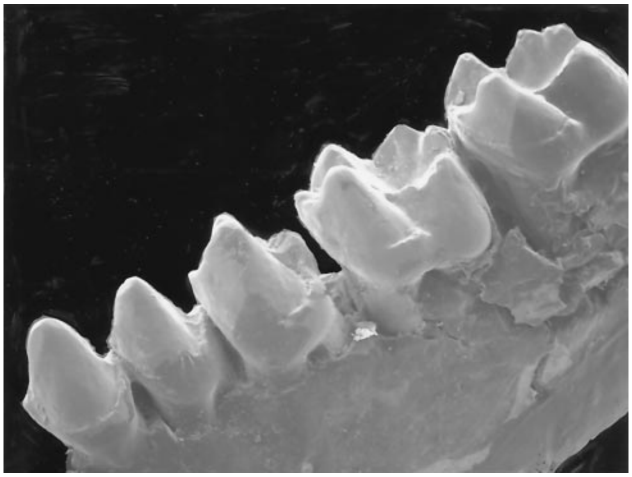

FIG. 3. Scanning electron micrograph of *P. sylviae*. Magnification, ×8.1. Three quaters lateral view of tooth crowns in CGM 42209. Note the height difference between the molar trigonids and talonids, the retention of a paraconid on M_1, and its loss on M_2.

The third lower molar is the smallest and most morphologically variable tooth in the lower molar series. M_3 trigonids are similar to M_2 trigonids but M_3 talonid morphology is much more diverse. DPC 15305 has a large hypoconid but no entoconid or hypoconulid, giving the lingual portion of the talonid a smooth flat appearance. DPC 13101 is slightly worn but clearly shows a relatively large hypoconid along with a twinned entoconid–hypoconulid, separated only by an entoconid sulcus. In DPC 14234, the talonid basin is slightly more elongate than in other specimens and the hypoconulid is positioned centrally.

COMPARISONS

Proteopithecus sylviae shares with parapithecids (e.g., Apidium and Parapithecus) a few features that are likely to be primitive for the suborder such as having (*i*) three premolars and (*ii*) extremely broad cheek teeth with P^2 smaller than the other premolars and M^3 smaller than the other molars. However, the occlusal morphology of *P. sylviae* is not like that of parapithecids. *P. sylviae* has much better defined trigon/ids and talon/ids, molar cusps that are much less bulbous and little occlusal elaboration in the form of extra conules/ids and styles/ids other than the occurrence of a prominent metaconule on M^1. *P. sylviae* has also been shown to be unlike parapithecids postcranially. Parapithecids have an appressed tibia–fibula, whereas *P. sylviae* lacks elongate tibio-fibular syndesmosis and has instead a hindlimb morphology similar to that of New World anthropoids (4, 5).

P. sylviae and *Catopithecus browni*—both archaic anthropoids from quarry L-41 (1)—resemble each other in some of the same ways that many archaic anthropoids do, for example, in having broad upper cheek teeth, and in the occurrence of a twinned entoconid–hypoconulid. However, *P. sylviae* differs from *C. browni* in (*i*) being 15% smaller in linear dimensions (1), (*ii*) retaining a P2, (*iii*) having a P_4 with a shorter talonid and without a large buccal cingulum, (*iv*) having a substantially higher more-restricted molar trigonid relative to the talonid, (*v*) possessing sharper molar cusps, (*vi*) sharper preentocristid and cristid obliqua that form a more closed talonid basin, (*vii*) upper molars that are more compressed mesiodistally, (*viii*) a bicuspid P^3, (*ix*) substantially higher molar hypocones, and (*x*) a higher more-restricted trigon.

Seven features have been listed (6) as linking *Eosimias sinensis* and *Eosimias centennicus*, proposed anthropoids from the Eocene of China, with archaic African anthropoids. These are (*i*) an anteroposteriorly shortened but dorsoventrally deep mandibular symphysis, (*ii*) vertically implanted incisors, (*iii*) large projecting canines, (*iv*) slight exodaenodonty and oblique orientation of P_3 and P_4, (*v*) M_3 with wider trigonid than talonid, (*vi*) a reduced hypoconulid lobe on M_3, and (*vii*) a rounded nonprojecting angular region (5). From what can be seen, *P. sylviae* and *E. centennicus* have fairly similar rounded gonial angles. The symphyseal portion of the jaw and lower incisor morphology of *P. sylviae* are unknown so no comparison with *Eosimias* is possible. In the one specimen of *P. sylviae* where the lower canine is preserved *in situ* (DPC 12131), this tooth is high and sharp, but it is not nearly as high relative to the cheek tooth row as it is in *Eosimias*. Also, the apex of the canine in *Eosimias* is recurved posteriorly, a feature not seen in *P. sylviae*. In the lower premolars, the presence of slight exodaenodonty and an oblique orientation for P_3 and P_4 are features shared between eosimiids and parapithecids but they are not characteristic of *Proteopithecus, Catopithecus*, or modern anthropoids. The M_3 of *Proteopithecus* and particularly the morphology of the hypoconulid lobe is the most variable feature of the lower molar row, but *P. sylviae* is not like *Eosimias* in that the M_3 trigonid is not strikingly wider than its talonid. In addition, (*i*) although *Eosimias* is described as having a molariform P_4, the tooth is not as molariform as it is in *Proteopithecus*; (*ii*) the P_2 of *Eosimias* is diminutive in size relative to P_3 and P_4, whereas in *P. sylviae* and platyrrhines P_2 is slightly to much larger than the other premolars; and (*iii*) *Eosimias* is unlike African anthropoids and all Paleogene primates in possessing prominent and anteriorly projecting paraconids on M_1–M_3.

In some very general ways, *P. sylviae* resembles many living platyrrhines, particularly in having a relatively large P_2 and a P^2 that is smaller than the other premolars and also because the upper molars of platyrrhines tend to be broad. Among platyrrhines, *P. sylviae* shares more features in common with *Saimiri, Saguinus*, and *Callimico* than other New World monkeys, especially in having a well-demarcated trigon and a well-defined hypocone. However, the following differences between *P. sylviae* and modern platyrrhines are readily apparent: (*i*) although the upper P^2 in platyrrhines is smaller than P^3 and P^4, it is not as reduced as in *P. sylviae*; (*ii*) the long axis of the lower canine in *P. sylviae* is oriented to the cheek tooth row rather than being set obliquely as in extant platyrrhines; and (*iii*) no platyrrhine has premolars and molars as transversely expanded as *P. sylviae.*

Comparisons with early fossil platyrrhines, some of whose taxonomic affiliations are uncertain such as *Branisella*, *Dolicocebus*, *Soriacebus*, and *Carlocebus* shed little light on the affinities of *P. sylviae*, primarily because these early platyrrhines already appear to be derived in the direction of their younger South American counterparts. *P. sylviae* shares one notable feature in common with *Soriacebus* and *Carlocebus* in that the M_1 trigonid is aligned more obliquely to the cheek tooth row than the M_2 trigonid. However, *P. sylviae* differs from *Branisella boliviana* in having broader upper molars and in lacking an inflated protocone. *P. sylviae* differs from *Doliocebus gaimanensis* (e.g., MACN-CH 354) in lacking a shelf-like distal cingulum on P_4, a tall protocone, paraconules, metastyles and/or ectostyles, in retaining an M_1 paraconid, and in lacking expanded trigonids. *Soriacebus* differs from *P. sylviae* in having anterior teeth that are large relative to the size of the posterior teeth, in having large molar trigonids relative to the size of their talonids, and in having talonid basins completely encompassed by crests, a distal border to M_1 that is oriented oblique to the cheek tooth row, and rounded talonid cusps with a bulbous hypoconid that abuts the base of the protoconid so that the cristid obliqua is short. *Carlocebus carmenensis* differs from *P. sylviae* in having more-squared bulbous and inflated teeth, with rounded crests connecting the major cusps, in lacking a distinct hypoconulid, in having molar trigonids nearly as wide as talonids, and in exhibiting a much more closed and restricted trigonid.

Comparisons of *P. sylviae* with a number of omomyid and adapid groups were equivocal as neither the upper nor lower dentition of *P. sylviae* is particularly like that of these early primates. Upper M^1 and M^2 of *P. sylviae* are transversely broad with simple triangular trigons and a hypocone rising out of the distolingual cingulum. In some respects, the upper molars of *P. sylviae* are perhaps more like those of cercamoniine adapids (e.g., *Periconodon* and *Pronycticebus*) than other Eocene prosimians, in that the molars are buccolingually broad because the lingual portion of the tooth has been expanded rather than because the trigon has been enlarged. Interestingly, the cercamoniines are a group that some authors have proposed as more closely related to anthropoids than are other adapids or omomyids (7, 8). On the other hand, *Teilhardina* and *P. sylviae* both have a buccal indentation on M^1 and M^2, between the paracone and metacone, a feature only suggested in *Periconodon*. The lower dentition of *P. sylviae* is neither strongly omomyid nor adapid-like, and any dental resemblances between *P. sylviae* and these families could well represent only primitive retentions.

DISCUSSION

Many of the occlusal structures seen in *P. sylviae* (e.g., broad upper molars, retention of a paraconid on M_1, presence of a twinned entoconid-hypoconulid, and development of the lingual structures of the tooth) have been identified as primitive for Anthropoidea, as they are found among a number of archaic prosimians and other early anthropoids. These features, along with the presence of well-demarcated trigons, moderately large hypocones, triangular trigonids paired with larger more basin-like talonids, and—aside from the presence of a metaconule—lack of structures such as crista/ids or style/ids combine to give *P. sylviae* a very simple and generalized archaic anthropoid dental pattern. As for the origin of this anthropoid pattern from a nonanthropoid one, comparative studies provided no strong support for the derivation of *P. sylviae* from either an omomyid or adapid ancestry. Similarly, the nature of the relationship between the morphological pattern evident in *P. sylviae* and that of extant anthropoids remains unresolved. Although *P. sylviae* shares some features in common with fossil platyrrhines, all of these characteristics appear to be symplesiomorphic for anthropoids.

The question of whether an early fossil primate such as *P. sylviae* might have given rise to the platyrrhines is of great interest because it bears on the long-debated question of a possible African origin for the New World monkeys (e.g., refs. 9–11). However, phylogenetic hypotheses concerning the origin of platyrrhines are extremely difficult to test because platyrrhines seem not to exhibit any universal shared-derived dental features. This makes the best approach for interpreting the origin of platyrrhines one that evaluates the dental morphology evident in *P. sylviae* in light of what can be learned about its cranium and postcranium. At present, however, all that is known about *P. sylviae* allows only a conservative assessment of its taxonomic place, and that is that *P. sylviae* resembles platyrrhines in some respects because platyrrhines retain a number of features probably found among archaic anthropoids.

Thus, results from comparative analyses of the dental morphology of *P. sylviae* have confirmed four points. (*i*) Dentally, cranially, and postcranially, parapithecids are too specialized away from a primitive anthropoid pattern to be considered anything other than collateral early anthropoids unrelated to the evolution of modern catarrhines and platyrrhines (11). (*ii*) In regard to the phylogenetic relationship of *Proteopithecus* with respect to *Eosimias*, all that can be said is that *Eosimias* does not appear to have any of the anthropoid features present in *Proteopithecus*. (*iii*) At present, no other fossil primate known provides as good a model of a generalized anthropoid as *P. sylviae. Serapia eocaena* is specialized in the direction of parapithecids, *Catopithecus browni* has lost P2/2, and *Arsinoea kallimos* is too poorly known at present to assess its phylogenetic affinities (3). (*iv*) Current evidence supports the idea that *P. sylviae* occupies a place closer to the base of the modern anthropoid radiation than any other primate known.

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