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BY
PHILIP D. GINGERICH

MUSEUM OF PALEONTOLOGY
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A NEW GENUS OF ADAPIDAE (MAMMALIA, PRIMATES) FROM THE LATE EOCENE OF SOUTHERN FRANCE, AND ITS SIGNIFICANCE FOR THE ORIGIN OF HIGHER PRIMATES

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Abstract.– A primate mandible from the late Eocene *Phosphorites du Quercy* of southern France, originally described by Stehlin (1912) as *Protoadapis brachyrhynchus*, is here placed in the new genus *Cercamonius*. Comparison with other Eocene primates indicates that the genus represents a new subfamily, Cercamoninae, of the lemuriform family Adapidae. The Cercamoninae resemble the North American Notharctinae in molar structure, but differ from that group in having a more anthropoid anterior dentition. The lower canine alveolus in *Cercamonius* indicates that the canine was very large, and the alveoli for P_2 and P_3 indicate that those teeth were analogous to the anterior lower premolars of *Leptadapis*, where a very reduced anterior premolar and an enlarged, obliquely oriented following premolar together form a dental hone for a large upper canine. The large interlocking canines and P_3 dental hone indicated by the preserved alveoli form a character complex suggesting that *Cercamonius* may have been closely related to the origin of Old World anthropoid primates. The morphology of the lower teeth of primitive higher primates such as *Aegyptopithecus* could easily be derived from that of *Cercamonius*, but *Cercamonius* lacks the crowded premolars and broad molars characteristic of anthropoids, and it is thus retained in the Adapidae.

INTRODUCTION

Living primates can be divided into three major groups, each of which is placed in a separate infraorder. These infraorders are, respectively, the Tarsiiformes (of which *Tarsius* is the only living representative), the Lemuriformes (represented today by a diverse group of lemuroids and lorisoids), and the "Anthropoidea" or Simiiformes, to use Hoffstetter's (1974) term (including all the living Old World apes and monkeys, and the New World monkeys). It has long been recognized that the anthropoid Simiiformes represent an evolutionary grade advanced over the prosimian Tarsiiformes and Lemuriformes and this is the basis of a long-standing division of primates into the suborders Anthropoidea and Prosimii.

Certain characters of soft anatomy (especially the structure of the rhinarium and placenta) suggested to Pocock (1918), Hill (1953), and others that *Tarsius* is phylogenetically closer to anthropoids than the lemurs and lorises are, and hence many authorities have united *Tarsius* with the anthropoids in the suborder Strepsirhini. For many years the apparently tarsier-like anterior dentition of the Oligocene anthropoid *Parapithecus* added strong paleontological weight to a postulated origin of higher primates from a tarsier-like ancestor (Schlosser, 1911; Smith, 1919, p. 474).

Fossils discovered and described in the past fifteen years have contributed greatly to our knowledge of many early primates. Of particular importance are those from the Oligocene of Egypt collected by E.L. Simons. *Parapithecus* is now known from more complete specimens which show the tarsier-like anterior dentition of the mandible described by Schlosser (1911) to be an artifact of breakage (Simons, 1972, p. 190). Simons' expeditions have also discovered a nearly complete skull of *Aegyptopithecus* and cranial fragments of *Apidium*, both of which are early anthropoids from the Oligocene of Africa. These fossils are of particular importance as they provide the first documented record of the primitive anthropoid condition in two important functional complexes of the skull: 1) the anterior dentition of *Aegyptopithecus, Parapithecus,* and *Apidium* included nearly vertical, sectorial incisors with projecting upper and lower canine teeth. Significantly, the lower central incisors were smaller than the lateral ones (Simons, 1972); and 2) the auditory region of *Aegyptopithecus* is essentially that of a modern platyrrhine monkey (Simons, 1969), while the auditory region of *Apidium* combines features characteristic of platyrrhines with those of Eocene adapoids (Gingerich, 1973). Thus, in the morphology of both the anterior dentition and the middle ear, primitive Oligocene anthropoids are now known to resemble Eocene lemuriform primates rather than Eocene Tarsiiformes.

In addition to recent discoveries in the African Oligocene, restudy of a number of Eocene primates has shed further light on the transition from a prosimian ancestor to the anthropoid Simiiformes. Recent discussion of the systematic position of *Amphipithecus, Pondaungia,* and *Oligopithecus* (see Szalay, 1970, 1972; Simons, 1971a, 1972, p. 209) has centered on the question of whether these genera represent anthropoid or "lemuroid" primates – this discussion in and of itself indicates the close relationship of Eocene adapoids and Oligocene anthropoids. Recent study of Eocene Tarsiiformes has linked them phylogenetically to archaic primates of the infraorder Plesiadapiformes (Gingerich, 1975a) – thus it is not surprising that taxa such as *Navajovius* and *Berruvius* have repeatedly been transferred back and forth between the Plesiadapiformes and Tarsiiformes. Significantly, however, there is no fossil genus (for which at least the anterior dentition and/or the basicranium is known) that cannot be placed with confidence in the Plesiadapiformes-Tarsiiformes group on one hand, or in the Simiiformes-Lemuriformes group on the other hand. When the evidence of the fossil record is considered, it seems clear that the major phylogenetic division within the Primates separates the Plesiadapiformes and Tarsiiformes from the Simiiformes and Lemuriformes, and thus each of these four groups has been included as an infraorder within one of two suborders: Plesitarsiiformes (Plesiadapiformes + Tarsiiformes) or Simiolemuriformes (Simiiformes + Lemuriformes) (see Gingerich, 1975b).

The purpose of the present paper is to describe an additional specimen, from the late Eocene of France, which is intermediate between adapid Lemuriformes and primitive Simiiformes. The specimen was previously described as a species of *Protoadapis* by Stehlin (1912), but it clearly represents a new genus.

SYSTEMATIC PALEONTOLOGY

Order PRIMATES

Suborder SIMIOLEMURIFORMES

Infraorder LEMURIFORMES

Family **Adapidae**

Subfamily **Cercamoninae** n. subfam.

Cercamonius n. gen.

Protadapis (in part), Stehlin, 1912, p. 1286. Stehlin, 1916, p. 1545. [Stehlin's spelling of Lemoine's *Protoadapis* is clearly a *lapsus calami.*]

Protoadapis (in part), Gregory, 1920, p. 189. Teilhard, 1922, p. 96. Simons, 1962, p. 11. Russell, et al., 1967, p. 38.

Genotype.– *Protoadapis brachyrhynchus* Stehlin, 1912.

Included species.– The type species only.

Etymology.– The genus is named for Cercamon, a provencal troubadour of Aquitaine, whose *vida* reads as follows: "*Cercamons si fo uns joglars de Gascoingna, e trobet vers e pastoretas a la usanza antiga. E cerquet tot lo mon lai on el pos anar, e per so fez se dire Cercamons.*"[1] (Boutiereet Schutz,

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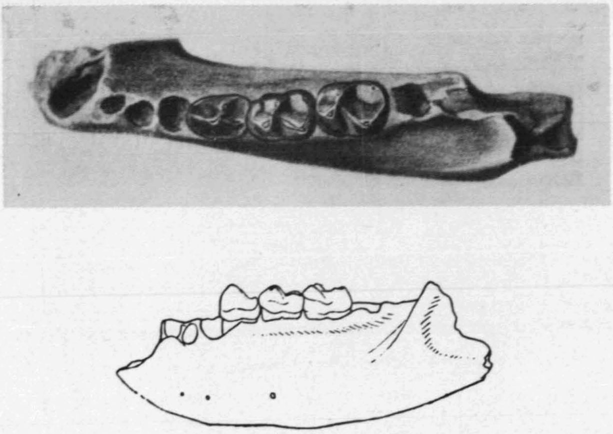
[1] Cercamon was a minstrel from Gascony, and he composed poems and pastorals in the old manner. He wandered all over the world wherever he could go, which is why he was called Cercamon. (M.E.)



TEXT-FIG. 1– Type specimen of *Cercamonius brachyrhynchus* (Stehlin) in occlusal view (top, enlarged to approximately x1½), and lateral view (bottom, natural size). Reproduced from Stehlin (1912, fig. 289).

1964, Biographies des Troubadours) The presence of a genus with *Notharctus*-like cheek teeth in France suggests that in the late Eocene this group, like Cercamon, "*cerquet tot lo mon.*"

Diagnosis.– *Cercamonius* resembles most closely *Protoadapis* and *Notharctus* in molar structure, but differs from those genera in having a shorter, relatively deeper mandible; in having a relatively larger, more vertically implanted lower canine; and in lacking P_1, having P_2 reduced to a small single-rooted tooth, and having P_3 significantly larger than P_4. The anterior premolar conformation most nearly resembles that in *Caenopithecus*, but the molars of *Cercamonius* are relatively broader, less crested, and lack the metastylid cusp on the lower molars which is characteristic of *Caenopithecus*, *Adapis*, and *Leptadapis.*

Cercamonius resembles some early higher primates in having a relatively short and deep mandible, with a large lower canine alveolus and, judging from alveoli, in having an enlarged, obliquely set P_3 which (together with P_2) probably functioned as a hone for a large upper canine. In these characteristics and in size *Cercamonius* resembles most closely *Aegyptopithecus* from the Oligocene of North Africa (as described by Simons, 1961, 1965, 1971b, and 1972). *Cercamonius* clearly differs from *Aegyptopithecus* in retaining P_2, and from *Aegyptopithecus* and all other anthropoids in having relatively narrow premolars and molars.

Cercamonius brachyrhynchus (Stehlin, 1912)

Text-figs. 1, 2-B

Protadapis brachyrhynchus Stehlin, 1912, p. 1286, fig. 289.

Protadapis brevirostris Stehlin, 1916, p. 1545 (this name is clearly a junior objective synonym of *P. brachyrhynchus*, representing again a *lapsus calami*).

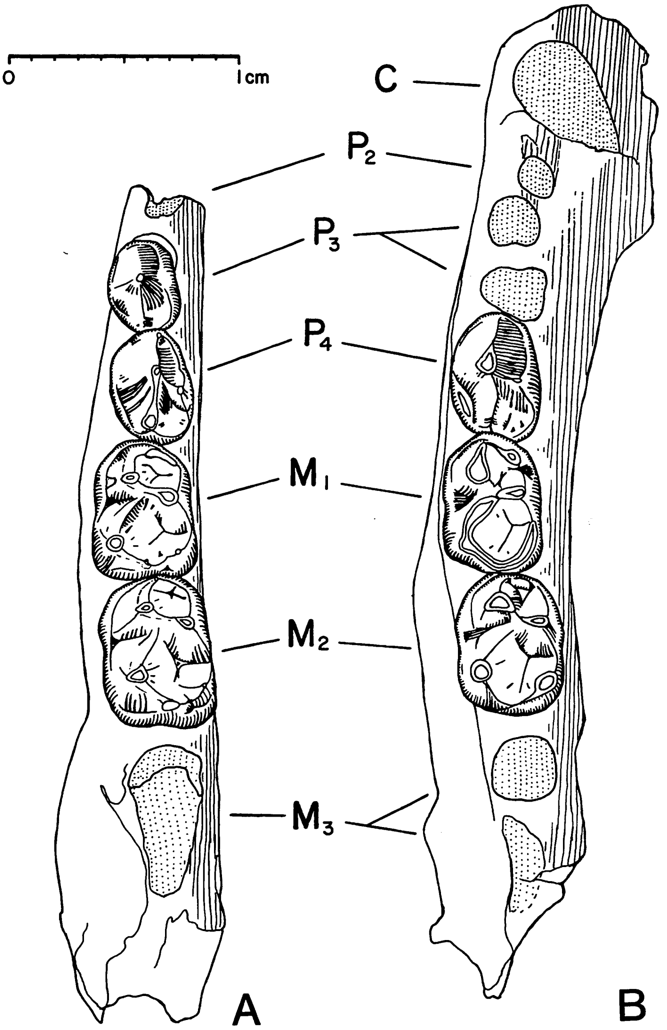
Protoadapis brachyrhynchus, Gregory, 1920, p. 189, fig. 70.

Protoadapis angustidens var. *brachyrhyncha*, Teilhard, 1922, p. 97.

Protoadapis angustidens (in part), Simons, 1962, p. 11. Russell, et al., 1967, p. 38.

Type.– Specimen number Q.V. 619 in the Naturhistorisches Museum, Basel; a left mandible preserving the alveoli for the lower canine, P_2, P_3, and M_3, and preserving the crowns of P_4, M_1, and M_2 intact.

Type locality.– Quercy phosphorite deposits near Prajous (Lot) in southern France. On the basis of the presumed relationship of the specimen here placed in *Cercamonius* to early Eocene specimens of *Protoadapis*, and considering the morphology of several specimens of a perissodactyl from the same fissure (referred by Stehlin to *Pachynolophus cayluxi*, an identification not followed or discussed by subsequent authors), Stehlin (1912) assigned the deposit yielding *"Protoadapis" brachyrhynchus* to the Bartonian (*s.s.*) or early late Eocene. In the absence of any stronger evidence, reference to the Bartoni-



TEXT-FIG. 2– (A) *Notharctus robustior* Leidy, British Museum of Natural History, London, specimen no. M-21924. (B) *Cercamonius brachyrhynchus* (Stehlin), type specimen, Naturhistorisches Museum, Basel, specimen no. Q.V. 619, shown for comparison. As noted by Stehlin (1912), the anterior portion of the mandible of *Cercamonius* resembles apes and monkeys. *Cercamonius* is very similar to *Notharctus* in molar structure, but differs from that genus in having a very small P_2 and enlarged P_3. By analogy with the comparable region of the mandible of *Leptadapis* (see text-fig. 3), both P_2 and P_3 probably participated in formation of the lower premolar-upper canine hone. This, together with the large alveolus for the lower canine, suggests that *Cercamonius* had a P_3 hone and large interlocking canine teeth similar to those of *Aegyptopithecus* and living Old World apes and monkeys.

an (*s.s.*) seems overly precise and *Cercamonius* is here regarded as being simply late Eocene in age, with the possibility of an early Oligocene age not completely ruled out.

Diagnosis.– *C. brachyrhynchus* is the only species of *Cercamonius* yet known. It differs from the species of *Protadapis, Notharctus, Aegyptopithecus* and other genera as outlined in the generic diagnosis.

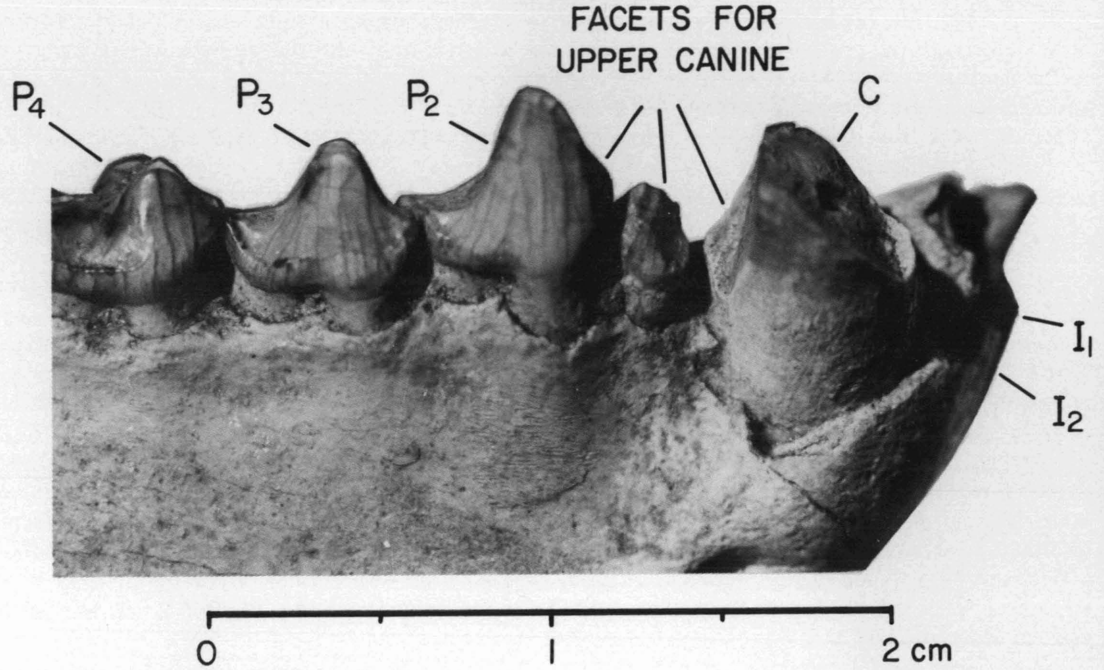
Description.– The length of P_4-M_2 in the type specimen of *Cercamonius* is 17.5 mm. Compared to the early Eocene *Protoadapis* from Epernay, the difference in height between the trigonid and talonid of M_1 and M_2 is somewhat less, and the entoconid is somewhat stronger than its homologue in *Protoadapis*. Otherwise the molar structure of *Cercamonius* agrees closely with that of *Protoadapis*, especially in the conformation of the paracristid. The alveolus behind M_2 indicates that M_3 was also rather small and narrow. I can note no important differences in the P_4 of *Protoadapis* and *Cercamonius*. In front of P_4 there are three deep adjoining alveoli, of which the posterior two are evidently for P_3, and the appreciably smaller anterior one represents P_2. P_2 in *Cercamonius* was single-rooted and significantly smaller than the P_2 of *Protoadapis recticuspidens*. P_3 was somewhat longer than P_4 and its anterior end, judging from the arrangement of alveoli, overlapped the posterior end of P_2 slightly. Because of damage to the alveolar margins, it is not possible to determine whether there was a small diastema in front of P_2 or if P_2 rested directly against the canine. The incompletely preserved alveolus of the canine in *Cercamonius* indicates a strong and flattened root similar to that of the canine in *Protoadapis recticuspidens*, but the long diameter of its cross section is somewhat more obliquely oriented in *Cercamonius* (the posterior margin being more medially and the anterior margin more laterally placed compared to *Protoadapis*). No information is available regarding the incisors of *Cercamonius*. Anteriorly the mandible is somewhat flattened, as in apes and monkeys. The horizontal ramus of the mandible is thicker and deeper than in the species of *Protoadapis*, and it has a somewhat more strongly curved lower margin. The symphysis ends under the posterior root of P_3, which, due to the shortened premolar row, is somewhat farther back than is seen in *Protoadapis*. There are three small mental foramina preserved, one under the anterior root of M_1, one under the anterior end of P_3, and the third in between the first and second. The masseter and diagastric insertions are marked in an analogous way to those in *Protoadapis*, but nothing is preserved of the mylohyoid groove. [Edited translation of the original description by Stehlin, 1912, p. 1285-1286.]

DISCUSSION

In addition to Stehlin's comparison of *C. brachyrhynchus* to species here retained in *Protoadapis*, the mandible deserves close comparison with the North American adapid genus *Notharctus*. When first studying the fourth premolar and the first and second molars in the type specimen of *Cercamonius brachyrhynchus*, their morphology immediately suggested a close relationship to *Notharctus*, the similarity to that genus being even more marked than to typical early and middle Eocene *Protoadapis*.

Comparing the mandible of *Cercamonius* to that of *Notharctus*, in particular to a little-worn mandible of *N. robustior* from Twin Buttes, Wyoming, now in the British Museum of Natural History (M-21924), the morphology of P_4-M_2 in *Cercamonius* is seen to match very closely the morphology of these teeth in *Notharctus* (see text-fig. 2). The molars of the British Museum specimen of *Notharctus* are of almost identical size and proportion to those of *Cercamonius*. Both specimens have the paracristid identically developed, and the development of external cingula is identical in the two. The teeth of *Cercamonius* are slightly more worn that those of the *Notharctus* specimen, but the talonid basin and the configuration of cusps on the heel of M_1 and M_2 in the two specimens are nearly identical as well. A small but distinct hypoconulid is present on the molars of *Notharctus* forming part of a strong postcristid, and this hypoconulid is connected to the entoconid by a weak enamel crest. While M_1 in the specimen of *Cercamonius* is slightly too worn to show the presence of a hypoconulid, the relationship of hypoconid, postcristid, hypoconulid, and entoconid on M_2 in *Cercamonius* are clearly very similar to the arrangement seen in *Notharctus*.

The principal difference between the dentition of *Cercamonius* and that of *Notharctus* is in the premolar region. The lower fourth premolar of *Cercamonius* is significantly larger than P_4 in *Notharctus* (although the basic morphology is very similar) and, judging from alveoli, P_3 was considerably larger in *Cercamonius*. On the other hand the single-rooted P_2 of *Cercamonius* was much smaller than that tooth in *Notharctus* (where P_2 is generally double-rooted). Judging from the conformation of the alveoli and the relative sizes they indicate for the teeth, it is likely that the premolar hone for the upper canine in *Cercamonius* was developed very much as in the adapid genus *Leptadapis* (see text-fig. 3), where the upper canine was honed by a small single-rooted premolar *and* the front of the following enlarged premolar (though the honing teeth clearly were not homologous in the two genera).



TEXT-FIG. 3– Canine and premolars of a mandible of the late Eocene adapid *Leptadapis magnus* in the collections of the Muséum National d'Histoire Naturelle, Paris. Incisors are represented by alveoli only, and much of the crown of the lower canine is broken off. In *Leptadapis*, the large upper canine occluded against the back of the lower canine (C), the crown of P_1, and the front of P_2 – both of the latter two teeth together forming the premolar hone. Note the enlargement of the honing P_2 relative to P_3 in *Leptadapis*. *Cercamonius* apparently had enlarged canines and a premolar hone analogous to that illustrated here in *Leptadapis*, except that the hone was formed by P_2 and P_3, and in *Cercamonius* P_3 was enlarged relative to P_4 in connection with its participation in the premolar hone. This particular specimen of *Leptadapis* is important also in showing how the number of premolar teeth has been reduced in the course of primate evolution while the premolar hone was retained functionally undisturbed. In *Pelycodus* and *Notharctus* the upper canine was honed by P_1 alone, whereas in Oligocene and later Catarrhini the hone is on P_3, having moved progressively back as P_1 and P_2 were lost.

Considering the primitive anthropoids known from the Oligocene, *Cercamonius* compares most closely in size and morphology with *Aegyptopithecus* from the Fayum of Egypt. Simons has described specimens of *Aegyptopithecus* in many papers (of most relevance here are Simons, 1961, 1965, and 1971b). Compared to *Aegyptopithecus*, the mandibular ramus of *Cercamonius* is longer and perhaps slightly more shallow in depth, but the cheek teeth approximate closely those of *Aegyptopithecus* in length. The canine in both genera was very large and implanted almost vertically, and in both the P_3 was significantly larger than P_4 and obliquely placed in the jaw – features which can be explained in *Cercamonius* only by development of a P_3 hone for the upper canine like that of *Aegyptopithecus* and Old World anthropoids in general. *Cercamonius* lacks the anteroposteriorly crowded, relatively broad cheek teeth of *Aegyptopithecus*, late Eocene *Amphipithecus*, and other anthropoids, and for this reason *Cercamonius* and the Cercamoninae are best retained, at least provisionally, in the Adapidae.

The close resemblance of late Eocene "*Protoadapis*" to *Notharctus*, it should be noted, led Teilhard (1922) to recognize *Protoadapis* as a European member of the otherwise North American subfamily Notharctinae. However, early and middle Eocene species of *Protoadapis* seem clearly related to the origin of *Adapis* from a *Pelycodus*-like ancestral stock, and the genus *Protoadapis* is thus properly classified in the subfamily Adapinae. The close resemblance in the cheek tooth morphology of *Cercamonius* to *Notharctus* suggests that *Cercamonius* might be placed in the Notharctinae, but important adaptive differences in the anterior dentition are unlike those in any known notharctine and for this reason *Cer-*

camonius is placed in a new subfamily, Cercamoninae, of the primate family Adapidae. In a strictly cladistic classification, the Cercamoninae might be included as a tribe within the Notharctinae to show that these two groups appear to be more closely related than either is to the Adapinae. Further study of the late Eocene *"Protoadapis" angustidens* is in progress to determine whether that species properly belongs in the genus *Protoadapis* and, if not, whether the genus represented should be included in the Adapinae, Notharctinae, or Cercamoninae.

CONCLUSIONS

Apart from recognition of *Cercamonius* as a new genus of the Adapidae, several more general conclusions emerge from study of its dental and mandibular anatomy. *Cercamonius* from the late Eocene of southern France is intermediate in morphology, geographical position, and geological age between the known faunas of primitive Lemuriformes and the Oligocene faunas of the Egyptian Fayum which first adequately document the anatomy of primitive Old World higher primates. As with *Amphipithecus* from the late Eocene of Burma, differences of opinion could reasonably be entertained concerning retention of *Cercamonius* as an advanced member of the Lemuriformes or its inclusion with the primitive anthropoids. While *Amphipithecus* appears to show an anthropoid balance of characters, *Cercamonius* appears more similar to Eocene lemuriform primates and for this reason it is retained in the Adapidae. *Cercamonius*, however, is in many respects more suitable than *Amphipithecus* as an ancestor for the Old World higher primates, particularly the Hominoidea and Cercopithecoidea, and it is clearly a more suitable ancestor than any plesiadapiform or tarsiiform primate yet discovered. This, together with evidence presented elsewhere (Gingerich, 1975a), lends additional support to division of the order Primates into two suborders: Plesitarsiiformes and Simiolemuriformes (Gingerich, 1975b).

The apparent close relationship of European *Cercamonius* (and possibly *"Protoadapis" angustidens* as well) to the North American Notharctinae lends considerable paleogeographic support to an adapid rather than omomyid common ancestor of Old and New World higher primates – adapids are common members of the Eocene mammalian faunas of Europe and North America, whereas the Omomyidae are virtually confined to North America, being replaced in Europe by the Microchoeridae.

Finally, it should be noted that an impression emerging from increasingly detailed stratigraphic and paleogeographic studies of Eocene prosimians suggests that the origin of higher primates involved a broad adaptive shift, with similar structural modifications in several independent lineages of Eocene primates. This parallel change in different lineages may have been a response to some world-wide change such as a general climatic deterioration in the late Eocene or it may simply be the result of independent evolutionary progression. Regarding the climatic deterioration hypothesis, it should be noted that primates of modern aspect and many of the modern orders of mammals first appeared following a similar deterioration in the late Paleocene.

While the living primates placed in the Simiiformes or "Anthropoidea" are in a cladistic sense undoubtedly a monophyletic group, the Eocene ancestors of the Old and New World higher primates (including their last common ancestor) might well have been prosimians adaptively. *Cercamonius*, *Amphipithecus*, and the still hypothetical late Eocene ancestor of the New World monkeys appear to represent three independent acquisitions of anthropoid adaptive morphology (in the dentition at least), and other late Eocene transitional forms will undoubtedly be discovered. Thus, if some particular anatomical feature (such as the acquisition of broad cheek teeth, or postorbital closure) is chosen to define an arbitrary boundary between advanced adapids and primitive anthropoids, the resultant grouping of higher primates is likely to be polyphyletic. Parallelism, or the independent derivation of shared morphological characters in related groups of mammals, appears to be a more important aspect of adaptation than is recognized in current evolutionary theory.

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National d'Histoire Naturelle in Paris, and he generously provided a cast of the type specimen of *Cercamonius*. I thank Dr. Theya Molleson for access to fossil primates in the collections of the British Museum (Natural History), including the specimen of *Notharctus* figured here. I am indebted to Professor E.L. Simons of Yale University for unrestricted access to the Oligocene primate fossils from the Fayum, and for numerous discussions on the origin of higher primates. I also thank Dr. M.C. McKenna for access to the type specimen of *Amphipithecus* and other fossil primates in the American Museum of Natural History, New York. Margaret Egan kindly permitted me to quote her translation of Cercamon's *vida* from the original Provençal. Figure 2 was drawn by Mrs. Krystyna Butterfield, and I thank Mr. Karoly Kutasi and Mrs. Gladys Newton for assistance with photography and typing, respectively. This research was supported initially by a Shadle Fellowship of the American Society of Mammalogists, and more recently by a Faculty Research Grant from the Rackham School of Graduate Studies, University of Michigan.

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