

A NEW EOCENE PRIMATE GENUS, *CANTIUS*,
AND A REVISION OF SOME ALLIED
EUROPEAN LEMUROIDS



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Pp. 1-36 ; *Pls.* 1-3 ; 4 *Text-figures*

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY

Vol. 7 No. 1

LONDON : 1962

THE BULLETIN OF THE BRITISH MUSEUM
(NATURAL HISTORY), *instituted in 1949, is
issued in five series corresponding to the Departments
of the Museum, and an Historical series.*

*Parts will appear at irregular intervals as they become
ready. Volumes will contain about three or four
hundred pages, and will not necessarily be completed
within one calendar year.*

*This paper is Vol. 7, No. 1 of the Geological
(Palaeontological) series.*

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PRINTED BY ORDER OF THE TRUSTEES OF
THE BRITISH MUSEUM

Issued May, 1962

Price Fifteen Shillings

A NEW EOCENE PRIMATE GENUS, *CANTIUS*, AND A REVISION OF SOME ALLIED EUROPEAN LEMUROIDS

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CONTENTS

	Page
I. A NEW EUROPEAN OMOMYID <i>Cantius</i>	3
Taxonomic Revision	5
II. REVISION OF THE SPECIES OF <i>Protoadapis</i> Lemoine	8
III. NOTES ON <i>Pronycticebus gaudryi</i> GRANDIDIER	14
IV. THE TAXONOMIC POSITION OF <i>Anchomomys</i> STEHLIN	21
V. RELATIONSHIPS OF EARLY TERTIARY LEMUR-LIKE PRIMATES	23
VI. CLASSIFICATION OF EUROPEAN EOCENE PRIMATES	27
VII. CONCLUSIONS	34
VIII. ACKNOWLEDGEMENTS	34
IX. REFERENCES	34

SYNOPSIS

Cantius, a new European early Eocene lemur-like Primate genus, is described and additions to knowledge of anatomy and affinities for three Eocene lemuroid genera, *Protoadapis*, *Pronycticebus* and *Anchomomys* are made. The significance of the terms "tarsioid" and "lemuroid" is discussed as these concepts bear on a consideration of the relationships of early Cenozoic European and American lemur-like Primates to each other and to contemporary tarsier-like prosimians. The classification of European Eocene Primates is revised from Simpson (1945) and the conclusions drawn that some European Eocene lemuroids may relate closely to subsequent stocks as well as to American prosimian families contemporary with them.

ABBREVIATIONS

- A.M.N.H.—American Museum of Natural History, New York.
 B.M.N.H.—British Museum (Natural History).
 G.P.I.H.—Geological and Paleontological Institute, University of Halle/Wittenburg.
 M.C.Z.—Museum of Comparative Zoology, Harvard.
 P.U.—Princeton University.
 S.M.G.C.—Sedgwick Museum of Geology, Cambridge.

I. A NEW EUROPEAN OMOMYID *CANTIUS*

A RECENT examination of fossil mammals from the London Clay at the British Museum (Natural History) resulted in the discovery of an undescribed upper and two partial lower dentitions of *Protoadapis eppsi* Cooper (1932). The specimens belong to a new genus which can be assigned to the prosimian family Omomyidae.

Gazin (1958 : 47) proposed family status for the Omomyinae, which have previously been ranked as a subfamily of Anaptomorphidae. The latter taxon is now understood to be a separate stock primarily characterized by reduced dental formula and much

enlarged third and fourth premolars. There are at least two European primate species, *Cantius eppsi* (described below) and *Teilhardina belgica*, which can best be assigned to the Omomyidae, although each presents some features of difference from typical omomyids. One might establish a new family or subfamily for these European species, but until they are better known such a procedure has little to recommend it.¹ Higher categories among early Cenozoic Primates have already been too much multiplied. This may be due principally to the difficulties of grouping species which are usually known only from dentitions, on rare occasions associated with fragmentary skeletal materials, and to the emotional element involved in the study of human relatives and ancestors, deservedly criticized by Simpson (1945 : 181) and elsewhere, and which, apparently, has even pervaded some discussions of fossil prosimians. Both *Cantius* and *Teilhardina* come from deposits containing Sparnacian (early Eocene) faunas and consequently represent some of the oldest Old World Primates. They are the earliest, in fact, that could possibly be near the basal stock or ancestry of any of the surviving European, Asian, or African members of the order.

Evidence as to whether or not Eocene omomyids were more lemur-like or more tarsier-like is scanty, for skull parts, other than maxillae, are practically unknown in this group. Hürzeler (1948) appears to be correct in stressing dental similarities between the early Eocene primate *Teilhardina*, from Belgium, and the much better known necrolemurines. This view is shared by the writer and is also implied by Gazin (1958 : 92). The Necrolemurinae are quite definitely tarsier-like, and close correspondence between premolar and molar cusp patterns in unspecialized necrolemurines and omomyids reinforces the idea that *Omomys* and its allies are nearer to true tarsioids than to such distinctly lemuriform Primates as *Adapis* or *Pronycticebus*. There is a reasonable probability that necrolemurines, North American omomyids, and even Old World Anthropoidea were derived from a form like the generalized prototarsoid *Teilhardina*, which has a lower dental formula of 2.1.4.3., and which lacks specializations in known parts that could rule out this possibility. Of course, *Teilhardina* itself, of Sparnacian Eocene provincial age, occurs too late in time to have such a position.

A skull fragment of an omomyid, *Hemiacodon*, discussed and illustrated by Gazin (1958 : 55, pl. 4, fig. 4) indicates some expansion of the dorso-frontal area in at least one member of this family—together with reasonably large orbits. Between the orbital apertures the rostrum, however, is relatively broader than in the probably omomyid derived genus *Necrolemur*, being about as in *Microchoerus* (S.M.G.C. 9669). In degree of forward rotation the orbits of *Hemiacodon* appear to be intermediate between these latter two necrolemurines.

Simpson (1940 : 190–197) discussed a pelvis, some vertebrae, and some elements of the hind limb which probably belong to *Hemiacodon* (A.M.N.H. 12613) and concluded that the “ skeleton of *Hemiacodon*, as far as known, is at least as lemuroid as tarsoid, probably more ”. Such judgements ultimately depend on how these two

¹ It also seems possible that *Periconodon*, *Lushius* and *Hoanghoni* represent three other Old World omomyids. Together with broad similarities in known parts, both of these Primates possess an unusual cusp on the antero-internal base of the protocone which has been called a pericone. This structure often occurs in *Omomys* but is known in very few other members of the order. For discussion of *Lushius*, see Chow (1961).

concepts are defined. It seems unlikely that the features of the postcranial skeleton in any Eocene primate would be closely similar to those in a highly specialized modern form like *Tarsius*. The earliest tarsioid *postcranial* distinctions remain elusive. Segregating out osteological characters of value in determining earlier radiations of higher categories, or in indicating phyletic relationships, is always difficult and uncertain. Nevertheless, an attempt to do so can be made for *Tarsius*. In the class of late and unusual specializations (of uncertain value in determining tarsioid phylogeny) may be the following characters: (1) Much enlarged orbits with flaring bony rims. (Occurring also, in a somewhat less exaggerated form, among other primarily nocturnal animals, such as *Nycticebus*, *Aotes*, owls, etc.) (2) Greatly elongated calcaneum and astragalus. (This specialization is seen elsewhere in galagos and in an analogous way in anurans.) (3) Fused tibia and fibula. (Such fusion occurs in a variety of hopping tetrapods including many rodents, lagomorphs, in some marsupials and insectivorans, as well as among Aves. See Barnett & Napier (1953: 12) for further discussion of the adaptive significance of this feature.) Should these characters be relatively recent acquisitions among tarsiines, even the direct Eocene ancestor of *Tarsius*, in lacking them, would be difficult to distinguish from lemuroids postcranially. In view of this possibility, evidence provided by the postcranial bones of *Hemiacodon* appears to be equivocal in relating the animal either to Tarsiiformes or Lemuriformes. What would help to indicate the affinities of such omomyids would be knowledge of such features as the size and shape of component parts of the brain (their size relative to each other), extent of facial shortening, proportions of palate and skull vault, amount of forward shifting of the foramen magnum, and various other characters of the basicranium, particularly degree of inflation of the auditory bullae and mastoid region, and situation or relationships of entocarotid circulation, of the ectotympanic pterygoid alae, and of cranial foramina. Although for omomyids these cranial features are not known they can be observed in *Necrolemur*, which in most of these areas closely resembles *Tarsius*, and which dentally (at least) shows affinity with Omomyidae.

As knowledge of the earliest Primates grows with new finds, taxonomic separation, at all grades of classification, can be expected to become more arbitrary. In this respect, some European Primates, particularly *Cantius*, evidence a closer relationship between Notharctidae and Omomyidae than has previously been documented; although this possibility was briefly considered by Gazin (1958: 47). Perhaps both of these families, assuming the two groups deserve separate family status, are not far removed from a common late Paleocene ancestry.

TAXONOMIC REVISION

Genus *CANTIUS*¹ nov.

(Pl. 1)

TYPE SPECIES. *Protoadapis eppsi* Cooper, 1932.

GENERIC CHARACTERS. As for the species.

¹ From the Latin for County Kent, England (*Cantium*, *Cantia*) in which all specimens of this primate have been discovered and in analogy with such related forms as *Washakius*, from the North American Eocene.

DISCUSSION. Size: *Cantius* is a large omomyid, intermediate in size between *Hemiacodon* and *Ourayia*, but distinctly smaller than any of the species of *Protoadapis*, and may have been about the size of the living African Giant Galago, *Galago crassicaudatus*.

The discovery of a right maxilla with P^3-M^3 of this species (Pl. 1a) from the early Eocene deposits at Abbey Wood, Kent (since Cooper's original description) confirms that the species belongs to a genus distinct from *Protoadapis*, a conclusion which can also be demonstrated by features of the lower dentition of *Cantius epsi* (B.M.N.H., M-13773) originally reported on by Cooper (1932), and by two other partial lower dentitions found subsequently (Pl. 1b). Indeed, Cooper himself suggested the possibility that the British species belonged to a distinct genus. Re-examination of all available specimens of *Protoadapis* indicates that this is so.

Some differences between *Cantius* and *Protoadapis* (in the lower dentition) are that the former is somewhat smaller, has paraconids on P_4, M_1, M_2 , a much longer and more complex M_3 talonid, and a considerably smaller and lower P_3 . A characteristic feature of *Protoadapis*, sometimes seen in species of the North American genus *Pelycodus* as well, is that the P_3 stands noticeably higher than P_4 . In *Protoadapis* the paraconid decreases in expression posteriorly in the molar series but not in the same way as in *Cantius* where the paraconid and metaconid are increasingly drawn together in the series M_{1-3} , compare Pls. 1b and 3f. Throughout the lower molar series of *Protoadapis* the paraconid remains widely separated from the metaconid and in M_3 is represented only by a slight crest—still considerably removed from the metaconid. In *Cantius* paraconids are clearly delimited in all three molars and are nearly as high as metaconids.¹

In this progressive alteration of trigonid elements posteriorly *Protoadapis* resembles closely *Notharctus*, while *Cantius* is much more like some specimens of *Omomys* in which, although a distinct paraconid is retained throughout the lower molars, the paraconid is closer to the metaconid in M_{2-3} than in M_2 . *Cantius*, in its enlarged and complex M_3 talonid, also agrees well with the elaboration of this element in omomyids. Yet another distinction in the lower dentition between *Cantius* and *Protoadapis* is that in *Cantius* a clearly defined paraconid cusp is present in the P_4 , a structure which never occurs in *Protoadapis* (see Pl. 3f, and Stehlin, 1912: 1282).

Recognition of the Abbey Wood species as generically distinct from *Protoadapis* was delayed, in part, because of the scarcity of comparative material in European museums. The total number of good specimens belonging to all species of both of these genera is probably less than ten. Nevertheless, the significance of the facts that *Cantius*, an omomyid, and *Protoadapis*, a notharctid-like adapid, occur in the European Eocene should be stressed. Knowledge of such ranges gives added import to the more extensively known North American Primates of the omomyid-notharctid type because it indicates that forms closely affined to them were present in the early Tertiary of the Old World. The possibility is thus strengthened that some North

¹ Paraconid and metaconid of the M_3 in the holotype of *C. epsi* cannot be distinguished, either because of wear or because they are coalesced. In B.M.N.H., M-15147a, b, however, these M_3 cusps are separate but closely approximated.

American species may approximate morphological, or even linear stages in the ancestry of Old World Primates.

The upper dentition from the Abbey Wood locality (Pl. 1a; B.M.N.H., M-15145)—quite apart from its occluding well with the type lower dentition of *Cantius eppsi* (both are of the right side)—shows definite omomyid affinities to about the same degree as do the lower teeth. Hence there is little reason to doubt that it can be assigned to *Cantius eppsi*. Taken as a whole, this upper dentition is close to that of *Omomys* and of *Teilhardina* but is one-half larger than that of either of these small Primates. P³ and P⁴ are rather simple teeth with a constriction between the inner and outer cusps and are similar in conformation to those of *Omomys*, *Teilhardina* and *Hemiacodon*. P³ has but a single outer and inner cusp and is smaller relative to P⁴ than in some specimens of *Omomys*. Both P³ and P⁴ are less crenulate than in *Hemiacodon*, but exhibit slight enamel wrinkling, particularly on the median slope of P⁴ protocone. P⁴ carries a small cuspule on the anterior slope of the outer cusp which occurs also in *Hemiacodon* and *Washakius*, but apparently not in typical *Omomys*. The anterior, median and posterior protocone crests of the P⁴ of *Cantius* are situated about as in *Washakius* (see Gazin 1958, pl. 9, No. 1).

An interesting similarity of *Cantius* to necrolemurines (and to *Tetonius* as well) is that the posterior protocone crest of M¹ and M² turns down toward the posterolingual part of the basal protocone cingulum, thus breaking the ridge running toward the metaconule. This forms a so-called "nannopithec-fold". There is, however, practically no indication of an incipient hypocone element, other than a slight thickening of the posterolingual part of the basal protocone cingulum. As in other omomyids the para- and metaconules are distinct on all three upper molars. These elements are usually less well defined in notharctids. Also unlike notharctids *Cantius* lacks any suggestion of an upper molar mesostyle. Molar para- and metacones are connected by straight crests on their facing slopes, much as in *Omomys* and *Washakius*. Nearly continuous lingual and labial basal molar cingula in *Cantius* are also quite like those of *Omomys*. Another resemblance to *Omomys*, to *Teilhardina*, to some of the more generalized late Paleocene Primates particularly *Navajovius*, and also to *Tetonius* is the small size of the M³ compared to M¹⁻². Para- and metastyle elements are present, as in most omomyids, except on M³ metacone.

The recent identification of an upper dentition of *Protoadapis* in the collections of the Geological Institute of the University of Halle/Wittenburg makes possible further comparative remarks about it and *Cantius*. *Protoadapis*, unlike *Cantius*, shows no indication in the upper molars of a nannopithec-fold, and the internal cingulum is typically pronounced and continuous around the lingual base of the protocone, the hypocone is large, and there is no indication of a metaconule on any of the upper molars, see Pl. 3. In these differences from *Cantius*, *Protoadapis* more closely resembles the notharctid *Pelycodus*.

In conclusion, *Cantius* has not been found to exhibit any features of resemblance to notharctids or adapids not occurring in the North American Omomyidae, and in view of numerous similarities to *Omomys* and *Hemiacodon* it is assigned to the latter family. The dental formula of *Cantius* is apparently more reduced than in *Teilhardina*, but evidence regarding the exact number of antemolar teeth remains inadequate.

Cantius eppi (Cooper)

(Pl. 1)

1932. *Protoadapis eppi* Cooper, p. 461, pl. 11, figs. 2, 3.

HOLOTYPE. Right ramus of mandible with P_3 - M_3 and partial alveolar borders of I_3 - P_2 , B.M.N.H., M-13773.

MATERIAL. B.M.N.H., M-13773 (Holotype), B.M.N.H., M-15145, maxilla with P^3 - M^3 ; B.M.N.H., M-15147a, mandibular fragment with M_1 - M_3 ; and B.M.N.H., M-15147b, mandibular fragment with M_{2-3} .

HORIZON AND LOCALITY. Blackheath Beds (Sparnacian); Abbey Wood, one and three-quarter miles east of Woolwich, Kent.¹

DESCRIPTION. *Lower dentition*: Dental formula: 2(?) . 1 . 3(?) . 3. One small incisor alveolus, followed by a much larger canine alveolus, narrow anteroposteriorly and broad buccolingually. If only one premolar was present anterior to P_3 it may have been two-rooted. Two-rooted P_3 with crown lower than P_4 and lacking distinct para- and metaconids. Para- and metaconids well developed on P_4 , connected to protoconid by crests; well-defined central crest on talonid, running posteriorly along mid-line of tooth from protoconid and with small posterior cuspule; P_4 not molarized. Trigonid of M_1 large, with three well-separated cusps; paraconid and metaconid joined to protoconid by low ridges; talonid much larger than trigonid with distinct ento- and hypoconid, small hypoconulid present on slope of posterior crest of hypoconid. Outline of M_2 (crown view) more nearly circular than that of M_1 , as in *Ourayia*, *Hoanghoni*, etc. M_2 trigonid broad transversely, narrower anteroposteriorly, with more closely approximated paraconid and metaconid than M_1 . Paraconid and metaconid of M_3 trigonid either coalesced as a single cusp (M-13773) or closely approximated (M-15147a and b).

Upper dentition: B.M.N.H., M-15145: P^{3-4} with slight constriction between protocone and outer cusp. P^4 with small anterior cuspule, as in *Hemiacodon*. M^2 , M^1 , M^3 ; no mesostyle or distinct hypocone on upper molars; antero-internal base of molar protocone projecting most mesiad; nannopithec-fold present on posterior slope of M^1 and M^2 ; paraconule and metaconule present on M^{1-3} .

II. REVISION OF THE SPECIES OF *PROTOADAPIS* LEMOINE*History of Study*

Preparation of the foregoing section on the British early Eocene primate *Cantius* necessitated investigation of all the available material of *Protoadapis*. It soon became clear that species of this genus were much in need of revision.

Unfortunately Stehlin's discussion of members of *Protoadapis* (1912: 1284-1286) intruded some taxonomic confusion, as well as a misspelling of the generic name; this was largely corrected by Teilhard (1921: 66, 67, 88-91) but Stehlin's views, and additional misconceptions of dating quoted by Osborn (1890: 55) have continued to

¹ Dr. G. G. Simpson of Harvard University has suggested in a personal communication that the species of *Hyracotherium* from Abbey Wood indicate an earliest Eocene age for this fauna. This is also indicated by an M_3 of *Coryphodon* from the same locality figured by Cooper (1932: 459).

Measurements (in mm.) of Cantius eppi (Cooper)

(All specimens in the British Museum of Natural History)

<i>Mandible :</i>		M-13773	M-15147a	M-15147b
Depth of jaw beneath M ₂	.	6.7	—	—
Anteroposterior length of P ₃ -M ₃	.	17.2	—	—
Anteroposterior length of M ₁₋₃	.	11.4	11.5	—
Anteroposterior length of M ²⁻³	.	8.1	8.0	8.2
Anteroposterior diameter of P ₃	.	2.8	—	—
	P ₄	3.3	—	—
	M ₁	3.6	3.6	—
	M ₂	3.6	3.7	3.8
	M ₃	4.5	4.3	4.4
Transverse diameter				
(trigonid)	P ₃	1.8	—	—
	P ₄	2.3	—	—
	M ₁	2.5	2.3	—
	M ₂	3.3	3.0	3.1
	M ₃	3.0	2.9	3.1
(talonid)	M ₁	2.8	2.8	—
	M ₂	3.1	3.0	3.2
	M ₃	2.4	2.4	2.8
<i>Maxilla : M-15145</i>				
Anteroposterior diameter of P ³	.	15.0	(Transverse diameter)	
Anteroposterior diameter of P ³	.	3.0	3.2	
	P ⁴	3.0	3.8	
	M ¹	3.6	4.7	
	M ²	3.7	5.4	
	M ³	3.0	4.3	

affect the literature on this primate. These errors were largely reproduced by Hill (1953 : 482-487).

Further complications derive from the observation, made during a recent visit to the Halle/Wittenburg Geological and Paleontological Institute, that the holotypes of two Eocene Primates, "*Europolemur*" *klatti* and "*Megatarsius abeli*" described by Weigelt (1933) can be assigned with confidence to *Protoadapis*. As it was not possible for Weigelt (1933) to make direct comparisons with previously described fossil Primates some specific and generic assignments which might have been recognized for the Geiseltal species were not noted by him. In fact, at that time Weigelt probably could not have determined his two new genera as upper dentitions and skulls of *Protoadapis*, since the associated upper and lower dentition, G.P.I.H. 4310, discussed below, had not then been discovered.

The assumption that species of this genus occur in the French Paleocene of Cernay and Rilly dates from an erroneous citation in Lemoine & Aumonier (1880 : 611) as stated by Teilhard (1921).¹ However, this misapprehension was repeated in Hill

¹ Lemoine & Aumonier list a species of this genus, *P. copei*, as occurring in the Cernay Paleocene. It was not figured or described and is now lost, probably because Lemoine later referred the specimen to a different genus and species, not *Protoadapis*.

(1953:483). Lemoine later stated (1891:28) that this genus is restricted to the Eocene. D. E. Russell who is currently revising the French Paleocene faunas, informs me that it does not occur at Cernay. The recognition of several specimens of *Protoadapis* from the Middle Eocene Brown Coals of the Geiseltal, Germany, now in the collections at Halle, serves to date the earlier members of this genus better than the rather scanty and poorly associated Cuisian fauna with which the French specimens of *Protoadapis curvicspidens* and "*Protoadapis recticspidens*" were recovered.

A further error in the literature on this genus is its recorded occurrence in the Belgian Eocene deposits (Hill, 1953:483). There is no real evidence for such a record, but a specimen of *Protoadapis* from the Quercy phosphorites of south-central France was, at the time of Teilhard's writing, in a private collection at Louvain and his reference to it may have led to this confusion of range.

All the materials of this genus discussed by Lemoine, Stehlin, and Teilhard, as well as the specimens at Halle, belong (after the removal of "*Protoadapis*" *eppsi*) to no more than three species. *Protoadapis recticspidens* Lemoine, 1878, is based (in spite of published remarks to the contrary) on a single specimen in which the teeth are so worn that only a few characters of M_3 can be determined. This tooth, and the mandible, now in the Paris Museum, are distinctly smaller than are those of *Protoadapis curvicspidens* (here designated as the type species of the genus) and it may not belong to *Protoadapis*. I would prefer to regard *Protoadapis recticspidens* as a *nomen vanum*.

As Teilhard stressed, the specimen called *Protiadapis recticspidens* by Stehlin (1912, fig. 278) is actually *P. curvicspidens*, the holotype of which is now in the Muséum National d'Histoire Naturelle in Paris. It is on the basis of this specimen that the genus *Protoadapis* was first defined.

TAXONOMIC REVISION

Genus **PROTOADAPIS** Lemoine

(Text-fig. 1)

TYPE SPECIES. *Protoadapis curvicspidens* Lemoine (1878). (Unnumbered holotype and two other specimens in National Museum of Natural History, Paris.)

AMENDED DIAGNOSIS. Size: somewhat larger than *Adapis parisiensis*; lower dental formula: 1?.1.3.3. incisors missing in type but one or more alveoli appear to be present in other specimens; canine large (alveolus); P_1 absent, replaced by diastema; P_2 short with single pointed cusp, and with two obliquely situated roots, the anterior located more buccally. P_3 distinctly larger, much higher and more pointed than P_2 with nearly vertical anterior margin, no distinct paraconid or metaconid; P_4 lower than P_3 (unlike *Cantius*) lacking paraconid, but with well-defined metaconid and talonid possessing central ridge; molar paraconids reduced, but extending much more lingually than in *Adapis*, less so than in *Cantius*. M_1 and M_2 with small hypoconulid on posterior hypoconid crest; M_3 hypoconulid making up a distinct lobe; length from P_4 to M_3 —22 mm., depth of horizontal ramus beneath M_2 from 10 to 12 mm.

DISCUSSION. Two French species of this genus are accepted here as valid, *Protoadapis curvicauspiciens* collected in Paris Basin deposits, perhaps of Cuisian age, and *Protoadapis angustidens* (Filhol, 1888) from the Quercy phosphorites (see Text-fig. 1). *Protoadapis brachyrhynchus* Stehlin (1912) is clearly a synonym of the latter species, as Teilhard (1921: 97) concluded. A third species, *Protoadapis raabi*, from the Middle Eocene Brown Coals of the Geiseltal, Germany, is slightly smaller than

COMPARISONS OF MANDIBLES OF Protoadapis species
(ALL X 2 APPROX., INTERNAL ASPECT)

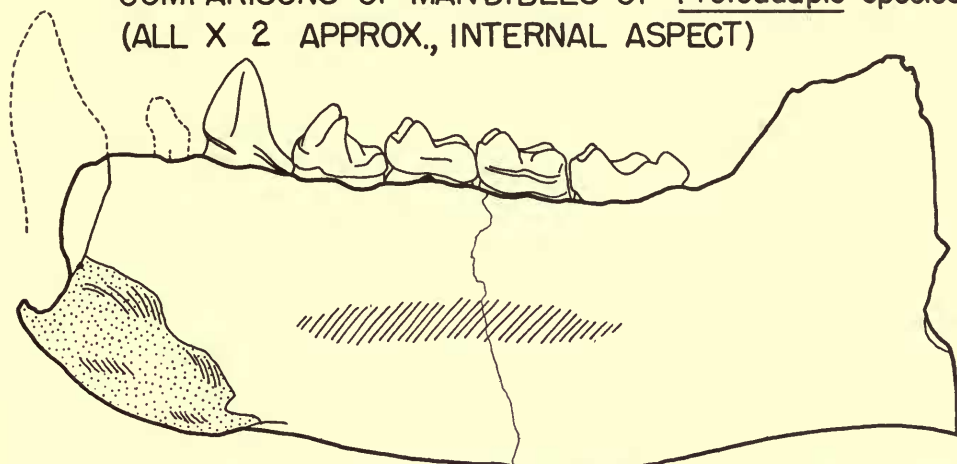
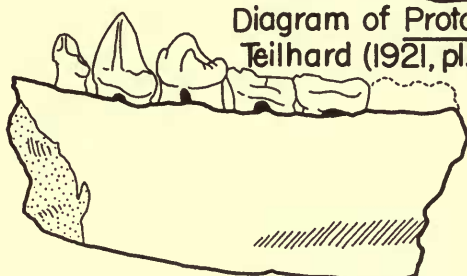
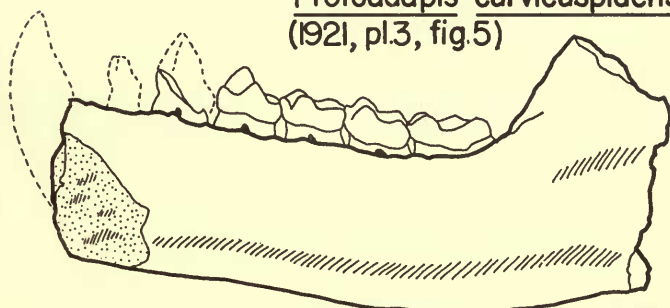


Diagram of Protoadapis angustidens from
Teilhard (1921, pl.4, fig.12 reversed)



Protoadapis curvicauspiciens from Teilhard
(1921, pl.3, fig.5)



Protoadapis curvicauspiciens from Stehlin
(1912, fig.288)

FIG. 1. Species of *Protoadapis* Lemoine from French deposits.

P. curvicspidens but does not differ greatly from it otherwise, in so far as these two species can be compared. Better materials may prove that the latter two "species" intergrade but pending such an eventuality, it is advisable to retain a separate species for the Geiseltal finds.

SPECIFIC DIAGNOSES. Teilhard (1921) has published full descriptions of the two species of this genus from the French Eocene and consequently they will not be separately diagnosed here.¹

***Protoadapis klatti* (Weigelt)**

(Pls. 2, 3)

1933. *Europolemur klatti* Weigelt, p. 123, pl. 4, fig. 5 ; pl. 6, fig. 4.

1933. *Megatarsius abeli* Weigelt, p. 141, pl. 4, fig. 4 ; pl. 6, figs. 1-3.

MATERIAL. In addition to the holotypes of "*Europolemur*" *klatti* and "*Megatarsius abeli*" (No. 4234) ; numbers 4238, 4258, 4280, 4292 and 4310 of the collections of the Geological and Paleontological Institute of the University of Halle/Wittenburg are referable to this species. Some of these specimens were regarded by Heller (1930) as belonging to *Adapis*, but this genus does not occur in the Geiseltal fauna.

DIAGNOSIS. A medium-sized primate—apparently about the size of *Pronycticebus* or the Recent Potto, *Perodicticus*. Dental formula : $\frac{2.1.3.3}{?1.1.3.3}$; anterior lower incisor not known (if present), I_3 procumbent and spatulate ; \bar{C} long and pointed with slightly developed posterior shelf—appearance about as in *Notharctus*, \bar{C} followed by diastema ; P_2 two-rooted with simple pointed crown and posterior heel, lacking metaconid and protoconid ; P_3 much higher than P_2 and P_4 and lacking protoconid ; P_4 - M_3 as in *Protoadapis curvicspidens* but smaller, M_1 and M_2 with distinct hypoconulid on posterior slope of hypocone, M_3 hypoconulid and entoconid large.

I^2 larger than I^3 , spatulate with crown anteromedially directed and somewhat procumbent ; I^3 small and simple, may be separated from \bar{C} by a diastema ; \bar{C} much larger and longer than in *Adapis*, furrowed along its external face by anterior and posterior vertical grooves and followed by a diastema ; P^2 less than half as large as P^3 , and with small protocone (two rooted) ; P^3 and P^4 with single ectoloph and large protocone ; M^1 lacking mesostyle and metaconule, but with distinct paraconule and prominent internal and external cingula, internal cingulum with large hypocone, basal cingulum sometimes incomplete across internal face of protocone ; M^2 slightly larger than M^1 with more continuous lingual cingulum and larger hypocone ; M^3 smaller than M^1 - M^2 , lacking a distinct hypocone, but with pronounced internal cingulum.

DISCUSSION. "Two" undescribed specimens in the Halle collection form a valuable basis for the clarification of the dental structure of *Protoadapis*. One of these G.P.I.H. 4310, from the Leonhardt Coal Mine (the locality of "*Europolemur*") includes the left P_4 through M_3 , the right M_3 an associated right lower canine and M^{1-3} (M^{1-2} somewhat damaged) see Pl. 3e, f. The second specimen, G.P.I.H. 4258 (Pl. 2), crushed facial region with attached lower jaw fragment of the left side with I^2 through P^3

¹ *Protoadapis angustidens* is larger and occurs later in time than *P. curvicspidens*.

and I_3 through P_3 was also collected from Leonhardt Mine. The specimen card of No. 4310 states that these teeth probably belong to the same individual as No. 4258, and this association is reinforced by similarity of colour, wear, matrix, and the fact that the two specimens do not share any overlapping parts, which would rule out such a possibility. In any event, both are referable to *Protoadapis* and together they preserve almost the entire dentition intact. Dental comparisons indicate that the skull of "*Europolemur*" *klatti* belongs to the same species as the foregoing specimens and is therefore a synonym of *Protoadapis*. The holotype of "*E.*" *klatti* (apparently lost during the last war) has upper molars of the same size and conformation as those of G.P.I.H. 4310 (judging from Weigelt's published information) and in so far as these two finds can be compared, there is no basis for a specific distinction. Teilhard (1921, pl. 3, fig. 6) illustrated an upper left molar which he suggested might be of *P. curvicauspiciens*; this is confirmed by the Halle specimens. Because of crushing, measurements on Brown Coal fossil Primates, other than on teeth, are not very reliable and thus have reduced value when drawing taxonomic distinctions. However, the length of P^4 - M^3 series of *Protoadapis klatti* is about 15 mm. in the type and the length of P_4 - M_3 in G.P.I.H. 4310 is about 17.2 mm. Similar measurements for *Cantius eppsi* are 14.2 and 15.1 mm. respectively.

Regarding the teeth of "*Megatarsius abeli*" from the Cecilia Coal Mine (locality Leichenfeld II), as Weigelt noted (1933: 142):

" die Beschaffenheit der Kronen ist
eigenartig stumpf, als wenn die oberste
Schmelzschicht fehlte . . . "

There is no doubt that this condition is due to post-mortem chemical absorption of the enamel and some of the dentine of the canine and P^4 through M^3 of the right side (all of the dentition that remains in "*Megatarsius*"). This sort of erosion of fossil teeth is quite common in early Cenozoic mammals. Neither Heller (1930)¹ nor Weigelt (1933) appear to have taken into account the fact that many of the Geiseltal Primates have lost almost all significant dental characters in this way. Such erosion also explains the extraordinary appearance of the canine of "*Megatarsius*" figured by Weigelt (1933, pl. 6, fig. 1). In this tooth, the enamel and much of the dentine of the crown has been removed and there has also been erosion around the base of the tooth. The odd basal cingulum and the whole appearance of the tooth is unreal misleading. In "*Megatarsius*", G.P.I.H. 4234, the upper dental formula is the same as in G.P.I.H. 4258-5310, *Protoadapis*. Furthermore, the eroded crowns of M^1 and M^2 show metaconule and mesostyle absent, but paraconule present, and allowing for the reduction in size caused by enamel erosion, M^{1-3} of "*Megatarsius*" are of appropriate size for *Protoadapis klatti*. For the writer, no doubt remains that "*Megatarsius*" is referable to *P. klatti*. In any case, G.P.I.H. 4234 is not adequate as a type specimen, and if not *Protoadapis* would be a *nomen vanum*.

Weigelt's discussion of the skulls of "*Europolemur*" and "*Megatarsius*" describes adequately these much damaged specimens. In overall morphology the skull of *Protoadapis* is more like that of *Pronycticebus* than of *Adapis*. With *Pronycticebus*,

¹ Heller's holotype of *Adapis minimus* is an indeterminate specimen for the same reason, all of the enamel having been removed by chemical solution.

it shares a comparatively shorter rostrum, larger orbits, more slender zygoma, P⁴ with a single outer cusp and two-rooted P², but differs in having lost P 1/1. "*Megatarsius*" has a broad interorbital septum about 1 cm. wide and resembles that of *Pronycticebus* in the disposition of the medial end of the supraorbital margin. On the antero-dorsal face of this skull between the temporal crests is a broad and slightly depressed area. The temporal ridges converge to the mid-line about 2.25 cm. behind the posterior end of the nasals. Conformation and extent of the nasals can be determined in G.P.I.H. 4234. These bones are slightly expanded posteriorly as in *Pronycticebus*. The orbital region is much crushed and, consequently, the lacrymal foramen cannot be located, but fragments suggest that the post-orbital bar was more slender than in *Adapis*.

Relationships of Protoadapis

Now that both the upper and lower dentitions and something of the skull are known in *Protoadapis*, it takes a more significant position in early Primate history. Placement of this genus as a typical lemuroid primate seems beyond doubt, and in fact it is the only Old World early Cenozoic form which has the same dental formula as any of the living lemuroids, although it lacks the specialized tooth comb below which is typical of the latter taxon. Being older, and yet having a more reduced dental formula, it cannot be near the lines which gave rise to such Eocene lemuroids as *Adapis*, *Pronycticebus* and *Notharctus*. Perhaps its greatest similarities are with *Pelycodus* and *Pronycticebus* which, however, retain P 1/1. In *Pelycodus* the manner of hypocone formation may also be different. Some specimens of *Pelycodus*, for instance A.M.N.H. 15022 (see Gregory, 1920, pl. 35), appear to have an incipient hypocone on the basal cingulum and at the same time another "pseudohypocone" developing from the nannopithec-fold on the posterior slope of the protocone. In the line leading to *Notharctus* the hypocone derived from the basal cingulum is suppressed, while in *Protoadapis* the nannopithec-fold is absent. The nearest known upper molar morphology that could give rise to both these patterns is that of *Cantius* but this form is too late to be ancestral to *Pelycodus* and its dentition too generalized for classification with the adapids. As suggested by Teilhard (1921), Simpson (1940), and others, *Protoadapis* shares with the North American notharctids many of the features which distinguish the latter group from the Adapidae. The upper dentitions and the anterior teeth preserved at Halle add somewhat to this conclusion, but in several respects this primate tends to link adapids and notharctids as *Cantius* links the omomyids with the latter families. In view of dental similarities with *Caenopithecus* and *Pronycticebus*, together with its European provenance, *Protoadapis* is here referred to the Adapidae.

III. NOTES ON *PRONYCTICEBUS GAUDRYI* GRANDIDIER

(Text-fig. 2)

The unique skull and mandibular fragment of *Pronycticebus* was discovered in 1893 and reported, in the original studies of Grandidier (1904, 1905), to be of Bartonian, late Eocene age, from Memerlein-le-Quercy in south-central France. The Abbé René Lavocat has suggested in a personal communication to the writer that

judging from his studies of mammals of Oligocene provenance, there is a similarity in the colour of bone and matrix of this specimen to those of the European Oligocene. This interesting observation implies, at least, that *Pronycticebus* may be from the latest levels of the Quercy caves. If so, it could be of Stampian Oligocene provincial age.

Pronycticebus has long been a difficult form to assess taxonomically, due in part to the lack of specialization of the teeth and the presumed absence of a post-orbital bar. Grandidier originally suggested affinities with the living loriform Primate *Nycticebus*, hence its generic name. This view has some merit. Subsequently Gregory (1920) and others held that the species has tarsiod affinities. This conclusion appears to have been based largely on the brachycephaly of the skull (considerably more pronounced than in *Adapis* or *Notharctus*) and which, at the time of Gregory's writing, was rivalled in degree, among Eocene Primates, only by *Necrolemur* skulls (also from Quercy) and by a fragmentary skull, lacking dentition, from the Middle Eocene of North America described by Granger & Gregory (1917) as "*Aphanolemur gibbosus*".

Gazin, in a revision of the Middle and Upper Eocene Primates of North America (1958), has shown that *Aphanolemur* is a synonym of *Smilodectes*. Several specimens figured by him indicate that expansion of the brain case in the latter primate (apparently closely related to *Notharctus*) has reached about the same level as in *Pronycticebus*. Skulls of *Smilodectes*, and to a lesser extent of *Notharctus*, demonstrate, therefore, that the degree of brain expansion which occurred in *Pronycticebus* was not unique among Eocene lemuroids. *Protoadapis*, judging from the crushed skulls at Halle, also had a rather large brain.

On other grounds, Le Gros Clark's careful study (1934) of the cranial anatomy of *Pronycticebus* has already demonstrated that this genus is not a tarsiod, a position recently re-affirmed by Piveteau (1957 : 55, 56).

Re-examination of the Evidence

Orbital Region

It is, perhaps, an amusing commentary on the nature of appraisal of fossil specimens that the zygomatic arch of the one known skull of *Pronycticebus* can be said to have been "evolving" almost continuously since Grandidier's original studies on this primate in 1904 and 1905. Apparently some time before the original description, the zygomatic arch was buried in a thick layer of plaster of Paris, which closely resembles the colour of the original bone. In 1934 Le Gros Clark remarked that the zygoma was not quite as broad as is indicated in Grandidier's illustrations and figured a narrower arch. Piveteau's plate (1957 : 61) shows a still more slender arch. In the same year, the writer was able to remove most of the remaining plaster which exposed a yet more gracile arch and the very distinct base of a post-orbital process (Text-fig. 2). Furthermore, the region of the frontal attachment of the post-orbital bar shows distinct fractures on both sides of the skull, where the bar has been broken off. The cross-sectional extent of this area is shown by hatching in Text-fig. 2. One can clearly distinguish the broken surface, and although this area of attachment is not very extensive in the vertical dimension, this correlates well the slender zygoma,

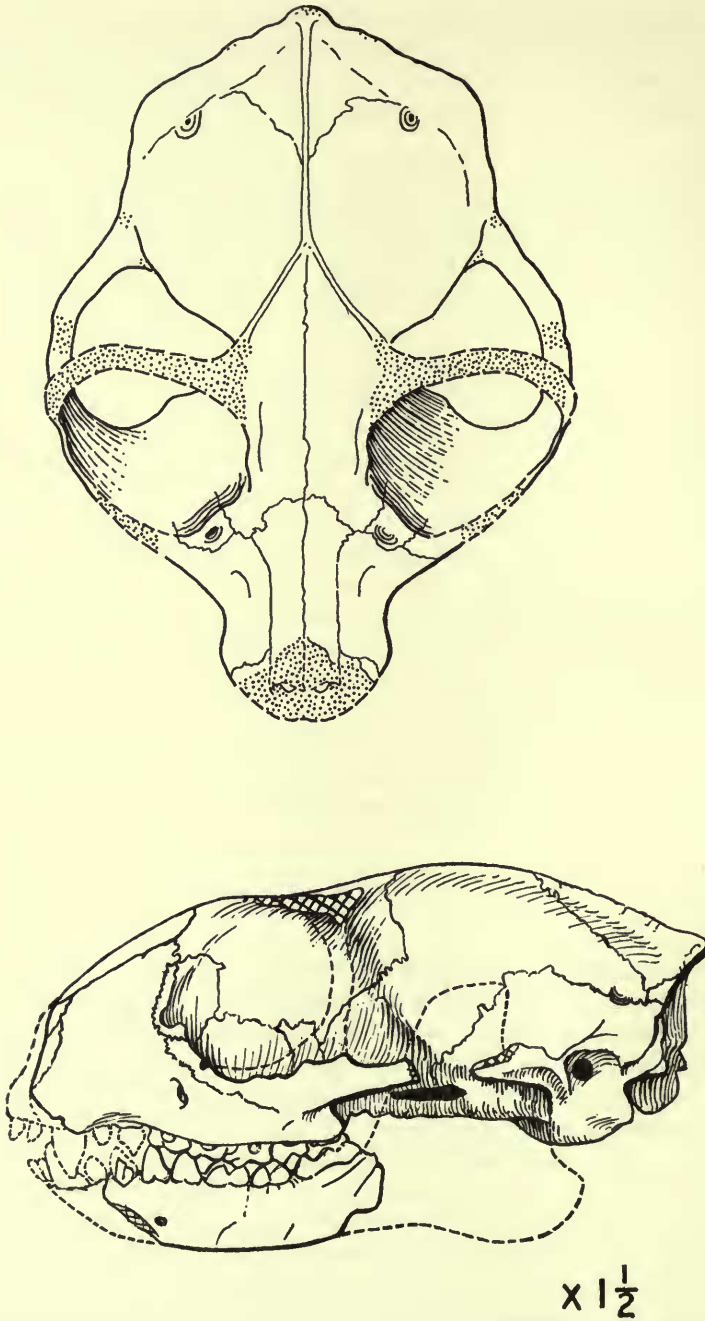


FIG. 2. Dorsal and lateral views of the skull of *Pronycticebus gaudryi* (Holotype). Hatching indicates broken surfaces, stipple missing parts. In dorsal view, right side restored from left.

found under the plaster, and with the much enlarged orbit indicated by the remaining median part of the orbital margin.¹ Living and fossil Primates with comparatively large orbits often have a slender post-orbital bar and a thin and flaring zygoma, as in *Galago* and *Necrolemur*. In fact, in some *Galago* species, the temporal base of the post-orbital bar in cross-sectional area is less extensive (when compared to total skull size) than is this area in *Pronycticebus*.

In view of the observed presence in *Pronycticebus* of both a frontal and a zygomatic base for the post-orbital bar, the large brain compared to *Adapis*, the complete absence of any evidence that other primates of the grade of advance seen in *Pronycticebus* lack the post-orbital bar, and the suggestion that enlarged orbits do sometimes correlate with relatively small frontal areas of attachment for the bar, no basis now remains for thinking that the bar was not continuous. Text-fig. 2 presents a conjectural restoration of its position.

Le Gros Clark (1934 : 20-27) noted most of the observable characters in the skull of *Pronycticebus* and discussed occurrences of many of these features in other Primates. The numerous new fossil primate specimens, which have been discovered or restudied since that time justify further comparison of some of these structures. Contrary to the current assumption *Pronycticebus gaudryi* is not a conservative form. With existence of a post-orbital bar in this species established, little remains to be seen in it that is particularly primitive for an Eocene primate. In fact, the expansion of the brain case, the large, forward-directed eyes and the short rostrum are all features that have been considered "advanced".

Location of the lachrymal foramen, together with part of the lachrymal bone, outside the orbit in *Pronycticebus* was suggested as a difference from *Adapis* by Le Gros Clark (1934). However, a specimen of *Adapis magnus*, P U. 11481, indicates that in this species the position of the foramen and forward extension of the lachrymal may sometimes be about as in *Pronycticebus*. In Malagasy lemurs the lachrymal foramen typically lies further outside the orbit than in the foregoing, while in living lorises, and the potto in particular, the position of foramen and lachrymal is about as in *Pronycticebus*, except for the smaller size of the lachrymal itself. *Necrolemur* (M.C.Z. 1179) and *Tarsius* have also a facial location of this foramen, but in *Smilodectes*, *Notharctus* and most platyrrhines this foramen clearly lies within the anterior orbital margin, as in pongids and man. In this character it would seem that *Adapis* and *Pronycticebus* approach more closely the living lemuroids than they do members of the Notharctidae and Anthropeidea. Forsyth Major (1901 : 151) concluded that the primitive condition for Primates is to lack a great facial expansion of the lachrymal. Shape and position of the foramen and lachrymal in *Pronycticebus* appear to be equivocal in relating it either to living lemuroids or lorises.

Rostrum

The comparatively foreshortened face of this primate is evident from the parts preserved. A vertical position of the premaxillo-maxillary suture (as well as the anterior recurving of the alveolar border around the canines) indicates that the missing

¹Relative to skull size *Pronycticebus* has larger orbits than most, if not all, other early Tertiary Primates. This may indicate nocturnal habits.

anterior tip of the skull can hardly have been much longer than the conjectural reconstruction shown in Text-fig. 2. The sharp constriction in transverse diameter of the rostrum immediately posterior to the canines in *Pronycticebus* is not as distinct in living lemurs and is absent in *Adapis*. However, this feature can be seen in *Loris* and *Nycticebus*, and is one of the reasons why this skull is reminiscent of that of *Nycticebus coucang*.

Dorsal Aspect of Skull

Cleaning of the skull has revealed sutures on the top of the brain case more clearly, and allows further comparison of this aspect of the skull in *Pronycticebus* with that of *Adapis*. Unlike *Adapis*, in *Pronycticebus* the posterior margins of the frontals extend on to the anterior part of the brain case. A sinus canal, near the posterior extremity of the parietal, is single in *Pronycticebus*, but in *Adapis parisiensis* it is multiple, as noted by Le Gros Clark (1934 : 22) and indicated by Stehlin's figures (1912). A large size for this canal has been said to be a primitive feature. After cleaning, sutures can be determined in *Pronycticebus* delimiting paired interparietals and (posterior to the sinus canal) small accessory ossicles (see Text-fig. 2). These bones have not been reported as occurring in *Adapis*. Taken as a whole the dorsal aspect of the brain case of *Adapis* does not closely resemble that of *Pronycticebus*. Such distinctions suggest that by the Middle or Late Eocene (the exact time range for both forms is uncertain) these two lemuroids had already diverged considerably. Such an assumption is reinforced by distinctions in other skull components, discussed above, such as the different shape of the muzzle, divergent character of the dentition, and difference in position and size of the orbits in these two Primates of the Quercy phosphorites. At present, it is probably better to retain them in the same family, as has been done by Hill (1953) and Piveteau (1957). Nevertheless, *Pronycticebus* and *Adapis* are as distinct morphologically as forms from the North American Eocene currently placed in different families, for example the notharctid, *Pelycodus*, and omomyid, *Ourayia* see Simons (1961a : 5).

Apart from the construction of the inside of the auditory bulla the basicranium of *Pronycticebus* was fully described by Le Gros Clark (1934). It will not be reconsidered in detail here. A possible alternative for an identification made by him (1934 : fig. 3) is that the foramen indicated as the hypoglossal canal may be the inferior petrous sinus.

On obtaining permission to examine the interior of the auditory bulla it was determined that the ectotympanic is not tubular, thus completely confirming, in this regard, Le Gros Clark's thesis that this primate is not a tarsioid. It is noteworthy that the annulus lies very near the external auditory meatus and, unless it has been displaced, appears to be fused with the bulla wall in its posterior third, just internal to the posterior rim of the external meatus. From this point the annulus arches inward and downward, so that its ascending anterior limb lies some distance from the antero-lateral wall of the bulla. Near the ventral extremity of the ring (and external to it) is a shelf on the lateral bulla wall for the support of the annulus membrane. Compared to that of *Adapis* this shelf is quite small. Hill (1953 : 113) figures a dissection of the auditory bulla of *Loris tardigradus* which indicates only

slightly greater reduction of the annulus. The position of the tympanic ring in *Pronycticebus*, close to the external meatus, is an additional indication that Grandidier may have been nearer the truth than has sometimes been thought, when he suggested an affinity between this species and the modern lorises.

Dentition

It was principally because of the somewhat enlarged brain and generalized characters of the dentition (resembling teeth of *Anchomomys* a supposed tarsioid), that such students as Stehlin (1916 : 1422), Gregory (1922) and Abel (1931 : 186) referred this primate to the tarsioids. Founding his conclusions principally on characters of the skull Le Gros Clark demonstrated that this primate cannot be considered a tarsioid. However, it may not have been sufficiently stressed that the dentition also, although unspecialized, is not *Tarsius*-like. Some principal reasons why this dentition does not indicate tarsioid relationships are as follows :

The cross-sectional area of the upper canine base is considerably greater relative to adjacent teeth than it is in *Tarsius* while in necrolemurines the upper canine is even smaller proportionately than in *Tarsius*. Tarsiids, with the possible exception of *Nannopithex*, lack the P¹ present in *Pronycticebus*. The latter primate, like *Adapis*, *Protoadapis*, *Anchomomys* and *Progalago*, has two-rooted second premolars above and below, while in tarsiines, these teeth are always single-rooted. In configuration of the remaining teeth *Pronycticebus* closely resembles *Protoadapis*, but differs from it dentally in having a less well-developed lingual cingulum on the upper molar protocone, and a more reduced M₂₋₃ paraconid. However, these are rather slight distinctions, known to be variable in other primate species.¹ Otherwise, these two forms agree in such features as the absence of mesostyles, and of a distinct hypocone on M³ (although it is well developed on M¹ and M²). Also, they are closely similar in proportion and size. It is just possible that better specimens might even show that species of these two types of Primates are not separable generically. Unlike tarsioids, *Pronycticebus* has, as Simpson (1940 : 202) remarks (with reference to *Caenopithecus*) "open trigonids and the peculiar mode of paraconid reduction so characteristic of *Adapis* and its close allies and unknown among any forms of really probable tarsioid affinities".

Cranial Proportions

A logarithm of ratio diagram (Text-fig. 3) indicates graphically the close similarity in linear proportions between *Pronycticebus* and *Nycticebus* and in contrast to those of an early Cenozoic lemuroid species *Adapis magnus*? and a Recent Malagasy lemur.²

¹ Even in *Protoadapis*, as is indicated by isolated upper molars from the Geiseltal coals at Halle, the lingual protocone cingulum of the upper molars is sometimes incomplete, as it also is in *Pronycticebus*.

² Measurements indicated in Text-fig. 4 are as follows : (1) Transverse diameter from mid-line of skull to greatest flare of zygomatic arch. (2) Length of skull, from posterior margin of canine to anterior margin of foramen magnum. (3) Length of skull from posterior margin of canine to posterior extremity of skull. (4) Length of dentition from anterior face of canine to posterior edge of M³. (5) Greatest transverse width of dentition. (6) Greatest transverse diameter of the cranium. (7) Least post-orbital diameter of skull. (8) Length from posterior margin of the canine to end of hard palate. (9) Length from anterior margin of canine to point of least post-orbital diameter. (10) Length from point of least post-orbital diameter to posterior tip of skull. (11) Greatest diameter of orbit from base of post-orbital bar to opposite rostral orbital margin. (12) Greatest transverse diameter across auditory bullae. (13) Greatest transverse diameter across canines. (14) Least transverse diameter of muzzle across upper second premolars.

The major differences between *Nycticebus* and *Pronycticebus* are in plots 4, 7, and 8. Measurement number 4, the length of the upper teeth might be expected to be less in *Nycticebus* as its dental formula is more reduced, and the same would apply to measurement number 8, the approximate length of the hard palate. Measurement

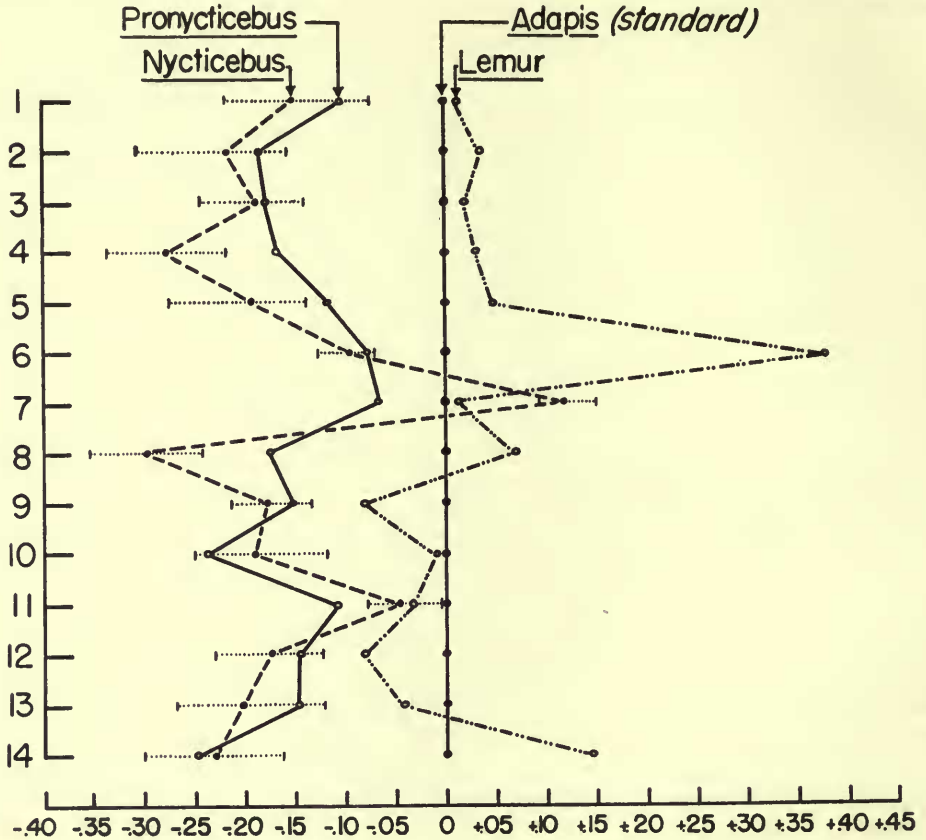


FIG. 3. Logarithm of ratio diagram comparing cranial proportions in four prosimians; *Adapis* (standard). Mean, and extremes of range are indicated for a sample of ten *Nycticebus coucang*.

number 7, the least post-orbital diameter of the skull (much smaller in *Pronycticebus*) is a primitive feature, correlated with a comparatively unexpanded brain, and is common to all Eocene lemuroids. In the remaining measurements *Pronycticebus* falls within (or very close to) the range of size variation of a small sample of the living lorid *Nycticebus coucang* (10 individuals).

CONCLUSIONS

Perhaps all the above-mentioned similarities are due to parallelism produced by similar adaptations in *Pronycticebus* and lorises, but such a view appears to be rather

strained. A more likely conclusion is that *Pronycticebus* does have some relationship to the radiation which produced extant Lorisiformes. Nevertheless, because of many primitive structures also shared with the contemporary *Adapis* and *Protoadapis* it seems best not to remove this genus from the Adapidae, at present.

IV. THE TAXONOMIC POSITION OF *ANCHOMOMYS* STEHLIN (1916)

(Text-fig. 4)

This rather small primate, originally described by Stehlin (1916) occurs in deposits ranging from early Lutetian to early Ludian age in Europe. Four species have been proposed, differing little in known parts except for size. Taxonomic placement of this genus has varied considerably. Abel (1931 : 175) and others considered it a tarsiod, but Simpson (1940 : 202) quite correctly pointed out that such an assignment was most improbable. Of European Eocene lemuriforms the closest dental resemblances to *Anchomomys* are to be seen in *Pronycticebus* and *Caenopithecus*, but because of a common simplicity in cusp pattern their similarities can, perhaps, be over-emphasized. In some respects these three genera also resemble *Adapis*, particularly in type of paraconid reduction, but all three differ from *Adapis* in having M_3 hypoconulid much more distinctly set off as a separate lobe from the hypoconid. They also lack the bicusped ectoloph of P^4 and continuous lingual upper molar cingula seen in *Adapis*.

For *Anchomomys* the closest dental resemblances appear to be with a Miocene lorisiform of Kenya, *Progalago*. In fact, in spite of the differences in time and place of occurrence of the species belonging to these two genera, some of the European Eocene forms, particularly *Anchomomys quercyi*, can hardly be distinguished generically, on the basis of parts preserved, from *Progalago doraе*. Species of these genera also overlap as far as size is concerned and similarities in the lower molars are particularly striking. Both exhibit reduced paraconids, well-developed entoconids, a large M_3 hypoconulid, with remaining molar cusps of closely corresponding shape and situation relative to one another. Both these prosimians also display in the major molar cusps a fairly distinctive angular or pyramidal form.

The upper molars of *Anchomomys* are quite like those of *Progalago* although in some, but not all, species of *Anchomomys* the paraconule and metaconule are more distinctly developed. In *Progalago doraе* and *Anchomomys quercyi* the latter two cusps are absent, see Text-fig. 4. These two species are alike in having a subquadrate M^1 with large hypocone, more triangular M^2 with smaller hypocone and lack a distinct M^3 hypocone, see Text-fig. 4 ; Le Gros Clark (1956, pl. 1) and Stehlin (1916, figs. 327, 328, 332). Moreover, at least one specimen of *Progalago doraе* (Le Gros Clark & Thomas, 1952, pl. 3, fig. 9) shows that in this species the P^2 was a much elongated and two-rooted tooth. If the same applies to the maxilla of *Anchomomys quercyi* figured by Stehlin, and shape of the anterior alveoli strongly indicates this possibility, then the upper dental formulae of both species are identical, at least from the canine posteriorly.

Perhaps the best preserved skull of *Anchomomys* is that of the unnumbered holotype of *Anchomomys latidens* (now in Paris) described by Teilhard (1921 : 13)

from the Quercy phosphorites and identified as "Rossignol Collection 1893: 11". The specimen is much broken and distorted, but careful preparation could probably expose more of the cranial anatomy. As in *Pronycticebus* and *Progalago* there is a single large infra-orbital foramen above P^4 . The anterior root of the zygoma appears to arise about M^2 , and through this anterior root opens to the rear a relatively large posterior infra-orbital canal. On the antero-dorsal surface posteriorly converging

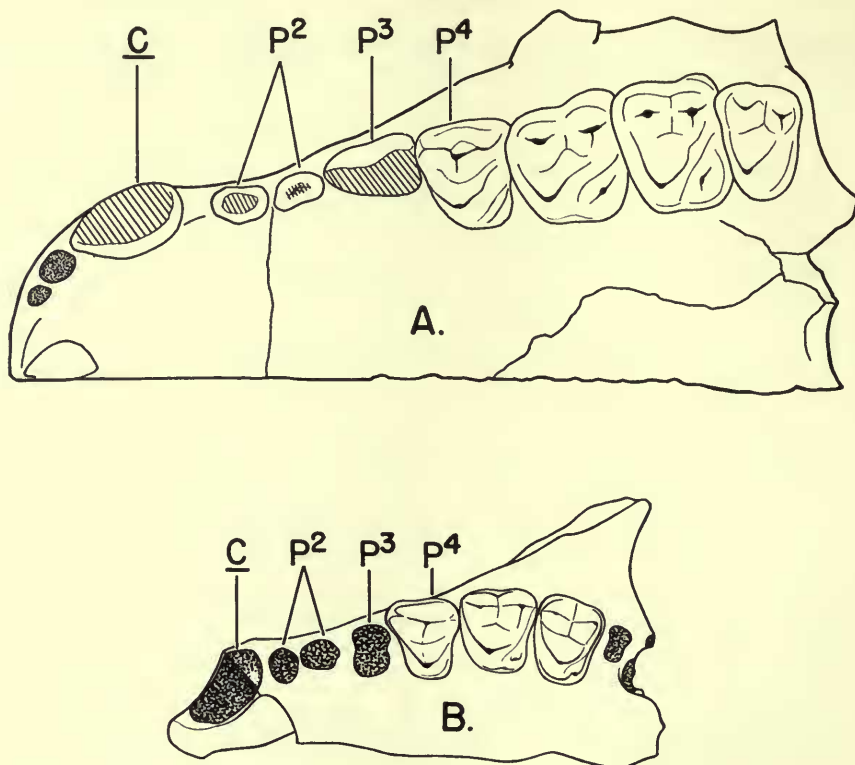


FIG. 4.—Comparison of upper dentition in *Anchomomys* and *Progalago*. A. *Progalago* sp.. [Diagram after Le Gros Clark, 1956, pl. 4, fig. 1.] Right maxilla, reversed, $\times 7.5$ approx. B. *Anchomomys quercyi*. [After Stehlin, 1916, fig. 332.] $\times 7.5$ approx.

temporal ridges are evident, but the dorsal insertion of the post-orbital bar cannot be distinguished. Between these temporal ridges, there is a broad depression, appearing rather as does this area in *Pronycticebus*. An apparently distinctive feature of *Anchomomys latidens* is the character of the surface of the temporal bone which is covered by numerous minute foramina, a condition certainly not to be seen (to this extent, if at all) in *Adapis* or *Necrolemur*. At the back of this skull are well-developed nuchal crests. These are typical of Eocene Primates and their presence is consistent with the retention of similar strong ridges in this position in *Progalago*.

Taxonomic Position

Stehlin (1912 : 1426) tended to favour the idea that *Pronycticebus* and *Anchomomys* have about the same relationship to the Galagidae ["Nycticebiden"] as *Adaplis* has to the lemuriform lemurs, but remarked that until the position of the carotid foramen and situation of the extotympanic was revealed for one of these Primates their taxonomic position would remain uncertain. Now that the annulus of *Pronycticebus* is known to show a possible foreshadowing of the condition seen in loriform Primates, Stehlin's analysis is strengthened. The subsequent placement of these two genera among the tarsioids, proposed for *Anchomomys* by Teilhard (1921), and for both *Pronycticebus* and *Anchomomys* by Gregory (1922) and Abel (1931) can now be seen to have marked a step backward in determination of their relationship to other prosimians.

Teilhard, although stressing tarsioid relationships for *Anchomomys latidens*, did however remark (1921 : 16) : "Tout au plus pourrait-on le rapprocher des *Galago* pour le développement de l'hypocône et la tendance à la molarisation de P 4 ...". This observation is important taxonomically because the fourth upper premolar in species of the genera *Anchomomys*, *Progalago* and *Galago* has an interesting similarity in basic plan, in addition to the other features of resemblance between these genera mentioned above. The view that these forms were tarsioids was rejected by Simpson (1940) after Le Gros Clark's study of the cranial anatomy of *Pronycticebus*, but since then their position among the non-tarsioid Prosimii has remained uncertain.

The very close dental relationship between *Anchomomys* and *Progalago*, and the similarities which the latter in turn has with living loriforms reinforce the idea that this phylum can now be traced back with a fair degree of accuracy as far as the European Middle Eocene.

V. RELATIONSHIPS OF EARLY TERTIARY LEMUROID PRIMATES

The Concept of "Lemuroid" Primates

One objective of the research reported here and in Simons (1961) has been to determine whether tarsier-like and lemur-like Primates can be distinguished in the early Cenozoic. For at least one subfamily of this period, Necrolemurinae, a definite relationship with *Tarsius* is indicated. Most remaining Paleocene and Eocene Primates have (or should have) been termed "lemuroid" in the past. A great many fossil genera have consistently been classified as tarsioid when there is no basis, in known parts, for so doing. If one examines the better known lemuroid Primates they seem to be of four general kinds, as follows :

- (1) Species on the border-line between Primates and Insectivora as these orders are currently understood, of the families :

Amphilemuridae
 Microsyopidae
 Apatemyidae

- (2) Specialized Primates of early extinction. Forms too specialized dentally to be near ancestral lines of later stocks :

Families :

Plesiadapidae

Carpolestidae

Anaptomorphidae [in part]

Paromomyidae [=Phenacolemuridae, in part]

- (3) Relatively generalized groups that could be near the ancestry of some living families, but which show no convincing evidence of having reached a tarsiod, or higher, grade of advance.

Families :

Adapidae

Notharctidae

- (4) Generalized Primates, possibly close to the stocks which gave rise to living groups, but which are not well enough known to indicate their grade of advance.

Omomyidae

perhaps some [paromomyids and anaptomorphids]

Past usage has roughly equated the term lemuroid with at least some members of each of the four groups of extinct families listed above. Such usage implies, however, that all these types can be assigned to the Lemuridae, which is not the case. On the other hand, it is surely valid to assume that the ancestral stocks of all the groups which have advanced beyond the lemur-like state (represented today by tupaiids and lemurids) went through such a level of advancement, and consequently their ancestors of the early Cenozoic can correctly be called lemuroid or lemur-like. Obviously then, among fossil forms that are distinctly lemuroid may be found ancestors of the more advanced Primates : tarsiods, and anthropoids. Some members of the above families do foreshadow tarsiods. For instance, *Navajovius* of the Tiffanian Paleocene of Colorado and *Teilhardina* of the Sparnacian Eocene of Belgium, both exhibit interesting dental resemblances to the European Middle Eocene tarsiid, *Nannopithec*, while the only skull with advanced (or tarsiod) features ever discovered in North America (*Tetonius* ; A.M.N.H. 4194) also possesses upper molars that, together with a general similarity of detail, share with those of *Nannopithec* an unusual feature, the nannopithec-fold. At present these four genera are assigned to three different families, viz.

<i>Navajovius</i> and <i>Teilhardina</i>	.	Omomyidae (Simpson, 1940 : 208)
<i>Nannopithec</i>	Tarsiidae (Simons, 1961 : 61)
<i>Tetonius</i>	Anaptomorphidae (Gazin, 1958 : 73)

Dental variation among these primates is not as great as their assignment to different families implies, being in most ways far less than seen in the Malagasy family Lemuridae. Yet, until better cranial remains are known for some omomyids, paromomyids and anaptomorphids it will remain difficult to judge whether or not these

groups show the same definite indications of tarsioid relationships in their osteology than they do in their dental anatomy. All these most interesting Primates fall within the fourth group listed on p. 24. In regard to the first three groups primatologists are on safer ground, for they are either so primitive dentally that tarsioid relationships cannot be considered or they are known from skulls that show no convincing tarsioid features. In the broadest sense it appears reasonable to call these forms lemuroid, and it is with them that the following paragraphs will be concerned.

Border-line Primates

Amphilemuridae

This family, proposed by Heller (1935) for the reception of *Amphilemur eocaenicus* from the Middle Eocene deposits of the Geiseltal, has recently been assigned to the Erinaceoidea (Insectivora) by McKenna (1960 : 58). To this subfamily McKenna also assigns, among others, the following North American Paleocene and Eocene genera : *Entomolestes*, *Macrocranium* and *Sespedectes*. As far as Primate classification is concerned, this procedure is not likely to improve the taxonomy of the genera involved, for the type of *Amphilemur* cannot be located at Halle, and if lost makes an unsatisfactory choice as the type genus of a subfamily known otherwise only in the New World, and to which it may not belong. Both Simpson (1945) and Hill (1953) refer *Amphilemur* to the Adapidae, *incertae sedis*. In its poorly-known state, now entirely dependent on Heller's text and figures, there is little basis for placing it elsewhere. In *Adapis parisiensis* the lower canine is often very small and otherwise the antemolar teeth exhibit gradual and nearly unbroken size-decreases from back to front, which is not unlike the size sequence of these lower teeth in *Amphilemur* and which shows that the same general kind of tooth proportions seen in *Amphilemur* can occur in a primate.

Microsyopidae

McKenna (1960 : 76) has re-defined this family so as to include the following genera : *Microsyops*, *Craeseops* and *Cynodontomys*. His view, that this family belongs among the Primates appears to have sound justification. He is of the opinion that the nearest affinities of the Microsyopidae, as re-defined by him, are with the more primitive plesiadapids of North America. Moreover, he remarks (1960 : 78, 79) while discussing Microsyopidae :

“Recently Hürzeler (1948a, pp. 343-356) has described a new genus and species, *Alsaticopithecus leemanni*, from the Lutetian of Alsace, based on excellent dental material. The animal was placed in the Primates *incertae sedis*. *Alsaticopithecus* appears to me to be a microsyopid . . . As Hürzeler notes, the genus is indeed primateline. Thus *Alsaticopithecus* has a bearing on the problem of microsyopid origins. The genus is an interesting extension of the known stratigraphic and geographic range of microsyopids.”

In view of this assignment of *Alsaticopithecus*, taken together with what is now known of microsyopid anatomy, including cranial material, soon to be reported on

by McKenna, Hürzeler's conjecture that this form has significant dental resemblances to Anthropoidea is no longer tenable.

Apatemyidae

The series of genera now assigned to this family were first clearly distinguished from plesiadapids by Jepsen (1934). Although they are retained provisionally in the order Primates by Gazin (1958), research on the basicranium reported by Hürzeler (1949: 485) indicates that this group is almost certainly not to be referred to the Primates, as the order is now defined. Notwithstanding this, the apatemyids may have had their origin in the same eutherian stock from which the Primates arose—a conclusion which is indicated principally by molar-pattern resemblances. They certainly have no close connection with Paleocene-Recent Primates and will not be considered further here.

Specialized Lines of Early Extinction

A number of divisions of the order of family and subfamily status, which became extinct before the end of the Eocene, exhibit such pronounced dental specializations that it is clear they could not be near the ancestry of any living Primate species. Of these, the carpolestids are the least well understood, but conformation of the fourth lower premolar alone (elongate and saw-like) removes them from consideration as ancestral to surviving lines. The same applies to plesiadapids, and to *Phenacolemur*¹ because of the marked reduction of their anterior dentition. Even so, *Plesiadapis* is of interest because of its geographical distribution. Species of this genus are known from the late Paleocene of both Europe and North America. This occurrence demonstrates that climatic conditions as well as the requisite land-bridges, allowing not only other mammals but prosimians to communicate between these two continents then existed, and helps to explain the presence of omomyids, microsyopids and possibly other primate families, in both continents in the early Eocene.²

Among the plesiadapids, carpolestids, and paromomyids the cranial and post-cranial anatomy is poorly known except in two species of *Plesiadapis*. The limb bones of *Plesiadapis* studied by Simpson (and greatly amplified by undescribed specimens recently collected by Russell in the Cernay Paleocene deposits near Rheims in central France) are primitive, but can be spoken of as lemur-like. Russell (1960) briefly reported on a remarkably well-preserved skull of *Plesiadapis* from the Cernay region. This is the oldest primate skull yet to be described. The skull of *Plesiadapis* is very broad, flat, with a small brain-case, while the premaxillaries are enormously expanded and make up most of the muzzle. Elsewhere, among Primates such expanded premaxillaries occur only in the Madagascan lemur *Daubentonia*. However, a relationship with the latter is excluded by the presence in *Plesiadapis*, but not in *Daubentonia*, of a tubular ectotympanic element. Finally, it is clear that in *Plesiadapis* there is no post-orbital bar, nor any indication of post-orbital processes.

¹ Here regarded as a paromomyid, following McKenna (1960: 70).

² Basically all living prosimians are tropical forest dwellers. Uniformitarian reasoning would suggest that their early Cenozoic forerunners were also warm-climate animals.

From this feature of the Cernay *Plesiadapis* skull it must be concluded that the basal stock of the order lacked the post-orbital bar, although it occurs in all other undoubted Primates (for which this part of the skull is known) with the single exception of *Anagale* from the Oligocene of Mongolia.

The families Anaptomorphidae and Paromomyidae are known only from North America. In terms of present knowledge, they include the most likely candidates for a relationship with the rise of tarsioids and of surviving higher Primates, possibly by way of containing forms ancestral to the omomyids. Regrettably members of these families, with the exception of *Tetonius*, are known only from dentitions, and consequently, little can be said as to whether they are lemur-like or tarsier-like. The same is true for omomyids. Nevertheless, dental analogies suggest that some of the species referred to these families were at least transitional to the tarsioid grade and such an assumption is further indicated by the large, forward-directed orbits and expanded brain of *Tetonius*.

VI. REVISED CLASSIFICATION OF EUROPEAN EOCENE PRIMATES

Revisions included here, in Simons (1961), and in a number of other works published since Simpson (1945) now make it possible to assign taxonomically certain European early Cenozoic Primates formerly listed by Simpson as *incertae sedis*, as well as to transfer others for which a better placement can be supported. The most recent extensive treatment of these forms is by Hill (1953, 1955), but Hill's taxonomy is clearly synoptic and no revision of fossil prosimians is included in these works. The following section, therefore, attempts to bring the classification of the fossil Primates of Europe up to date.

Genera to be considered here are listed in Simpson (1945) as follows :

Plesiadapidae :

Megachiromyoides Weigelt, 1933. M. Eoc.; Germany.

Adapidae *incertae sedis* :

Caenopithecus Rüttimeyer, 1862. M. Eoc.; Switzerland.

(?) PROSIMII of uncertain infraorder or family :

Ceciliolemur Weigelt, 1933. M. Eoc.; Germany.

Europolemur Weigelt, 1933. M. Eoc.; Germany.

Megatarsius Weigelt, 1933. M. Eoc.; Germany.

Microtarsioides Weigelt, 1933. M. Eoc.; Germany.

Two additional Eocene Primates from Europe described by Hürzeler (1946, 1947) are also discussed in the following pages.

Gesneropithecus peyeri Hürzeler, 1946. M. Eoc.; Switzerland.

Alsaticopithecus leemanni Hürzeler, 1947. M. Eoc.; Alsace.

Inasmuch as the European plesiadapids, and a specimen from the Walbeck Paleocene of Germany, referred to *Phenacolemur* by Weigelt (1947) but of uncertain generic and familial assignment are currently under study by others they are not discussed here in detail. These groups are, however, indicated in Text-chart 1, in

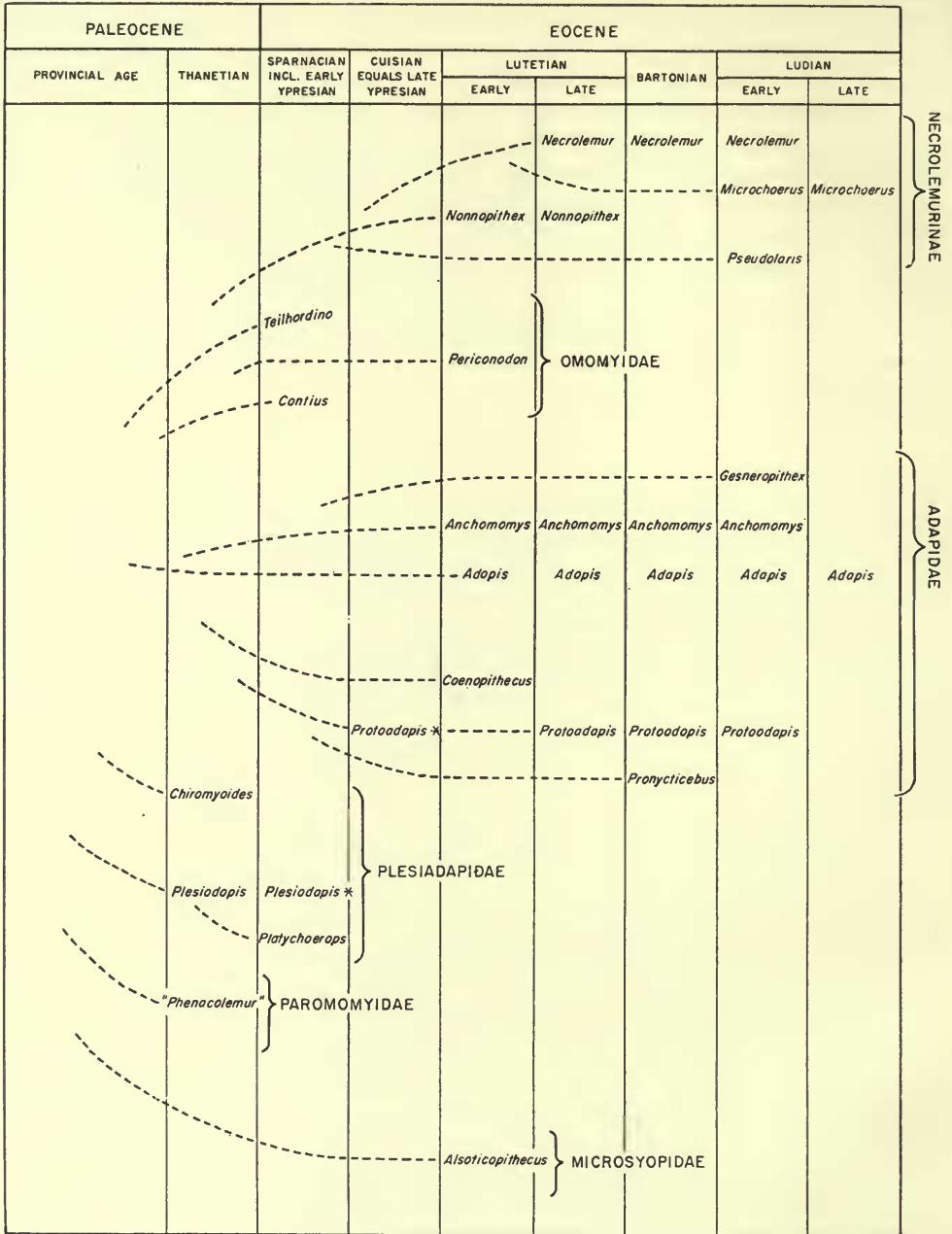


CHART I
 Temporal occurrence of early Cenozoic European primate genera indicating approximate interrelationships. (* Occurrence in this horizon dubious.)

CHART I.

which temporal occurrences and approximate interrelationships of all European early Tertiary Primates are shown.

Megachiromyoides

Since *Megachiromyoides* is frequently referred to in the literature as a primate, it should be emphasized that Stehlin & Schaub (1951: 21) stated that it is a rodent, assignable to the genus *Aeluravus*. A recent examination, by the writer, of the holotype of "*Megachiromyoides*" from the Geiseltal Brown Coals (described by Weigelt, 1933) has confirmed the view that this form cannot possibly be a plesiadapid.

Caenopithecus

This interesting primate from Middle Eocene (Lutetian) deposits near Egerkingen, Switzerland was originally described by Rüttimeyer (1862). Stehlin (1916) discussed the species further and figured a mandible which shows only one incisor alveolus on either side. He stated that his material indicated the same lower dental formula as in *Tarsius*, and noted other advanced features including the loss of the first upper and lower premolars, and a short rostrum.

Corroboration of Simpson's placement (1940) of this primate among adapids can be drawn from its similarities with the Lutetian species *Protoadapis klatti*. Principally *Caenopithecus* differs from *Protoadapis* in showing more reduced molar paraconids, in the possession of distinct mesostyles and in having less well-developed upper molar lingual cingulum. *Protoadapis* also exhibits a more distinct P³ protocone. In spite of these generic differences, however, *Caenopithecus* and *Protoadapis* are, in upper and lower dental conformation, in dental formula and in what is known of the skull, much closer to each other than either is to *Adapis*, but (in different ways) both exhibit some features of resemblance to a species of the latter genus.

Stehlin (1916: 1319) remarked that knowledge then available of *Caenopithecus lemuroides* indicated affinities with *Protoadapis* and *Pelycodus* and this view has been strengthened by the better material of *Protoadapis klatti* now known. *Protoadapis* and *Caenopithecus* agree in possessing the following features, some of which are unknown among other European Eocene Primates: Long and large canines (above and below)—not very procumbent; P₁/I absent and replaced by diastema; P₃ higher than P₄; metaconule of upper molars lacking but distinct paraconule present; well-developed hypocones on M¹⁻² only; upper molar cingula (labial and lingual) well defined and in some individuals continuous across lingual base of protocones; similar proportions in lower molars.

Common possession of pronounced upper molar cingula, absence of a distinct P³ protocone and near identity in overall proportions of the lower molars between *Caenopithecus* and *Adapis parisiensis*, tend to link species of these two genera as well. Weigelt noted a slight mesostyle on the M² of *Protoadapis klatti* (also in agreement with *Caenopithecus*) and expressed the view that his Brown Coal species was closer to *Caenopithecus* than to *Adapis*. Moreover, his illustration of the skull of *P. klatti* (1933, pl. 6, fig. 4) indicates a vertically deepened anterior base for the zygomatic arch, as in *Caenopithecus lemuroides*. One further similarity between

these two types of Primates is the possible loss (reported for species of both genera) of all but one pair of lower incisors. Because of the low angle at which the anterior alveolar border of the mandible of *Caenopithecus* (Basel Eh. 733) from which this was deduced, is broken off, the possibility remains that there were more incisors below. In some specimens of *Adapis parisiensis* in the Paris Museum, where this margin is broken off in a similar way, the incisor alvoli are entirely missing. If these were the only known specimens of *A. parisiensis* its lower incisor formula would be equally uncertain. The exact number of lower incisor pairs in given Eocene primate species can seldom be stated categorically. Both *Caenopithecus* and *Protoadapis* could have had two pairs of these teeth, but present evidence is not adequate to prove that they did.

A further note of some interest regarding *Caenopithecus*, and the nature of true hypocones and pseudohypocones, is provided by a specimen of this primate at Basel (Eh. 727) which shows both kinds of hypocone formation in one individual. The retention of both of these patterns in this dentition suggests that a latency for producing pseudohypocones, as in the line leading to *Notharctus* as well as for true hypocone production in *Adapis*, probably existed in the ancestral adapid-notharctid stock.

Periconodon

The genus *Periconodon* was established by Stehlin (1916) for a species "*helveticus*" which had been assigned by Rüttimeyer (1891: 115) to the North American genus *Pelycodus*. Like most *Caenopithecus* materials the type of *Periconodon helveticus* came from Middle Eocene deposits near Egerkingen, Switzerland. Apparently no additional specimens referable to this genus have been discovered since Stehlin's discussion.¹ The individual illustrated by Stehlin (1916, pl. 22 fig. 3), which preserves P³ and M¹⁻² shows a distinctive pericone on the antero-internal base of M¹⁻² protocones. Since a pericone sometimes occurs here in *Omonyx* (see Gazin, 1958, pl. 6, figs. 3-4) but not elsewhere among early Tertiary Primates, and because omomyids are known to have been present in the European Eocene fauna, the provisional reference of *Periconodon* to this family seems advisable. Furthermore, the small size of the species and general conformation of the teeth does not suggest adapid or notharctid affinities.

Ceciliolemur and *Microtarsioides*

Ceciliolemur is now considered by Matthes (1957), and by others, to be an insectivore, primarily because it seems to have had dental spines. Recent examination of the holotypes of *Ceciliolemur*, G.P.I.H. 4237, and of *Microtarsioides*, G.P.I.H. 4235, both from the Geiseltal Brown Coals of Cecilia mine, locality Leichenfeld II, indicates strongly that they belong to the same species. Cheek teeth do not survive in either specimen, so dental formula and affinities cannot be determined. Moreover, the

¹ Heller (1930) and Weigelt (1933) both mention the presence of isolated upper molars of this Primate in the Geiseltal Brown Coals. These teeth do not belong to *Periconodon*, but are those of a larger Primate from which the enamel has been resorbed. What remains of the cusp bases suggests their reference to *Protoadapis klatti*.

condition of bones and of eruption of lower teeth indicate that both are very young individuals, perhaps pre-natal. No basis remains for referring either of these specimens to the Primates. It is a remarkable accident of fossilization that either of these very delicate specimens were preserved, considering that the body excluding the tail, in both cases, is only about 4 cm. long. Locality data indicates recovery from the same place, and possibly they are from the same "litter".

Europolemur and *Megatarsius*

As discussed above (pp. 13, 14) these primate genera are junior synonyms of *Protoadapis*.

Alsaticopithecus

The species *Alsaticopithecus leemanni* Hürzeler (1947) can be assigned to the family Microsyopidae, as re-defined by McKenna (1960 : 76), see p. 25.

Gesneropithex

Gesneropithex peyeri Hürzeler (1946) is based on a lower jaw containing P_4 - M_2 and one second upper molar collected in Ludian deposits near Bösgen, Switzerland. The lower teeth differ from *Alsaticopithecus* and resemble such adapids as *Anchomomys*, in that M_{1-2} lack distinct hypoconulids. Moreover, conformation of the upper second molar is within the general range of variability of species now assigned to the Adapidae. M^2 is most similar in size and cusp pattern to those of *Anchomomys latidens*, but wear obscures some of its features. *Anchomomys* and *Gesneropithex* also agree in one rather unusual feature of M^2 ; both have a strong anterior crest running from the metaconule to the metacone. Presence of an upper molar mesostyle in *Gesneropithex* is in agreement with *Caenopithecus*. It seems reasonable to assume that *Gesneropithex peyeri* can be referred to the Adapidae (s.s.).

REVISED CLASSIFICATION¹

Order PRIMATES

Suborder PROSIMII

Family TARSIIDAE Gray, 1870

Subfamily NECROLEMURINAE Simpson, 1933

MICROCHOERUS Wood, 1844

Synonyms—*Microchaerus* Forbes, 1894

Necrolemur : Filhol, 1880 (in part)

Microchoerus erinaceus Wood, 1844

Microchoerus edwardsi (Filhol, 1880)

Synonym—*Necrolemur edwardsi* Filhol, 1880

Microchoerus ornatus Stehlin, 1916

¹ Since a revision of the European plesiadapids is currently being undertaken by Russell at the Paris Museum they have been omitted from this classification.

NECROLEMUR Filhol, 1873*Necrolemur antiquus* Filhol, 1873*Necrolemur zitteli* Schlosser, 1887*NANNOPTHETHX* Stehlin, 1916Synonyms—*Necrolemur* Chantre & Gaillard, 1897*Pseudoloris* : Weigelt, 1933*Nannopithex filholi* (Chantre & Gaillard, 1897)Synonyms—*Necrolemur filholi* Chantre & Gaillard, 1897*Nannopithex pollicaris* Stehlin, 1916*Nannopithex raabi* (Heller, 1930)Synonyms—*Pseudoloris abderhaldini* Weigelt, 1933*Necrolemur raabi* Heller, 1930*PSEUDOLORIS* Stehlin, 1916Synonym—*Necrolemur* : Filhol, 1889*Pseudoloris parvulus* (Filhol, 1889)Synonym—*Necrolemur parvulus* Filhol, 1889

Family OMOMYIDAE Gazin, 1958

TEILHARDINA Simpson, 1940Synonym—*Omomys* Teilhard, 1927*Teilhardina belgica* (Teilhard, 1927)Synonym—*Omomys belgicus* Teilhard, 1927*CANTIUS* nov. gen.Synonym—*Protoadapis* : Cooper, 1932*Cantius eppsi* (Cooper, 1932)Synonym—*Protoadapis eppsi* Cooper, 1932*PERICONODON* Stehlin, 1916Synonym—*Pelycodus* Rüttimeyer, 1891*Periconodon helveticus* (Rüttimeyer, 1891)Synonym—*Pelycodus helveticus* Rüttimeyer, 1891

Family ADAPIDAE Trouessart, 1879

ADAPIS Cuvier, 1822Synonyms—*Aphelotherium* Gervais, 1848*Leptadapis* Gervais, 1852*Palaeolemur* Delfortrie, 1873

Adapis parisiensis Blainville, 1841¹

Adapis magnus Filhol, 1874

Adapis rutimeyeri Stehlin, 1912

Adapis priscus Stehlin, 1916

Adapis sciureus Stehlin, 1916

PROTOADAPIS Lemoine, 1891

Synonyms—*Plesiadapis* : Lemoine, 1878 (in part)

Protadapis : Stehlin, 1912

Megatarsius Weigelt, 1933

Europolemur Weigelt, 1933

*Protoadapis curvicuspiciens*² Lemoine, 1878

Synonym—*Protadapis recticuspiciens* : Stehlin 1912 (in part)

Protoadapis angustidens (Filhol, 1888)

Synonyms—*Adapis angustidens* Filhol, 1888

Protadapis brachyrhynchus Stehlin, 1912

Protoadapis klatti (Weigelt, 1933)

Synonyms—*Europolemur klatti* Weigelt, 1933

Megatarsius abeli Weigelt, 1933

CAENOPITHECUS Rüttimeyer, 1862

Caenopithecus lemuroides Rüttimeyer, 1862

PRONYCTICEBUS Grandidier, 1904

Pronycticebus gaudryi Grandidier, 1904

ANCHOMOMYS Stehlin, 1916

Synonym—*Caenopithecus* : Rüttimeyer, 1891

Anchomomys pygmaeus (Rüttimeyer, 1891)

Anchomomys gaillardi Stehlin, 1916

Anchomomys quercyi Stehlin, 1916

Anchomomys latidens Teilhard, 1916

GESNEROPITHEX Hürzeler, 1946

Gesneropithecus peyeri Hürzeler, 1946

Family MICROSYOPIDAE new sense, McKenna (1960)

ALSATICOPITHECUS Hürzeler, 1947

Alsaticopithecus leemanni Hürzeler, 1947

?Primates *incertae sedis*

AMPHILEMUR Heller, 1935

Amphilemur eocaenicus Heller, 1935

¹ For numerous synonyms of the various species of *Adapis*, see Stehlin (1912, 1916).

² Here designated as the type species of *Protoadapis*.

VII. CONCLUSIONS

The occurrence of a new omomyid prosimian genus, *Cantius*, from the English Sparnacian is reported on and its distinctions from the Middle Eocene genus *Protoadapis* outlined. Assignment of this form to the Omomyidae reinforces the extension of the range of this family into the Old World suggested by a few previously described forms. Although additional resemblances to North American notharctids are noted for *Protoadapis*, it is referred to the Adapidae on the basis of its greater similarities with *Caenopithecus* and *Pronycticebus*. Preliminary evidence suggests that Notharctidae and Adapidae, as defined by Gazin (1958) may not actually be distinguishable, but solution of this problem requires additional comparative study.

Certain loris-like features of the genus *Pronycticebus* are pointed out. Just possibly, these can be interpreted as indicating the differentiation of the lorisiform prosimians from the general stock of the Adapidae (*s.l.*). A high degree of dental similarity between an undoubted lorisoid prosimian, *Progalago*, of the early Miocene of Kenya, and the late Eocene European primate *Anchomomys* is stressed. These findings are in contrast to the widespread opinion that no close relationship of early Cenozoic with Recent prosimian families can be demonstrated, but is in line with the vertical taxonomic association of necrolemurines and tarsiines proposed by Simons (1961). However, zoogeographical and morphological considerations alone are sufficient to indicate that it would be unwise to regard any such relationships direct ancestor-descendant lineages.

A number of species previously regarded as *incertae sedis* are here re-assigned or removed from the order and the taxonomy of European Eocene Primates revised.

VIII. ACKNOWLEDGEMENTS

I should like to thank Dr. K. P. Oakley of the British Museum (Natural History), Dr. J.-P. Lehman of the National Museum of Natural History, Paris, and Drs. H.-W. Matthes and G. Krumbiegel of the Geological and Paleontological Institute of the Martin Luther University of Halle/Wittenburg for the opportunity to study and report on Eocene Primates in their respective collections. Thanks are also due to Dr. G. L. Jepsen of Princeton University, Sir Wilfrid Le Gros Clark, and to many others with whom this subject has been discussed. Figures were prepared by Miss Christine Court of Oxford University and Mrs. Margaret E. Freeman of New Haven, and early completion of the work facilitated by a grant from the Wenner-Gren Foundation for Anthropological Research.

IX. REFERENCES

- ABEL, O. 1931. *Die Stellung des Menschen im Rahmen der Wirbeltiere*. 398 pp. Jena.
 BARNETT, C. H. & NAPIER, J. R. 1953. The rotatory mobility of the fibula in eutherian mammals. *J. Anat. Lond.*, **87**: 11-21.
 CHOW, MIN-CHEN. 1961. A New Tarsioid Primate from the Lushi Eocene, Honan. *Vertebrata Palasiatica*, Peking, **5**: 1-5, 3 figs.
 CLARK, W. E. LE GROS. 1934. On the skull structure of *Pronycticebus gaudryi*. *Proc. Zool. Soc. Lond.*, **1934**: 19-27, 3 figs.
 ——— 1956. A Miocene lemuroid skull from East Africa. *Fossil Mammals of Africa*, **9**, 6 pp. 1 pl. British Museum (Nat. Hist.), London.

- CLARK, W. E. LE GROS & THOMAS, D. P. 1952. The Miocene Lemuroids of East Africa. *Fossil Mammals of Africa*, 5, 20 pp., 3 pls. British Museum (Nat. Hist.), London.
- COOPER, C. FORSTER. 1932. On some mammalian remains from the Lower Eocene of the London Clay. *Ann. Mag. Nat. Hist.*, London (10) 9 : 458-467, pls. 11-12.
- FILHOL, H. 1888. Description d'une nouvelle espèce d'*Adapis*. *Bull. Soc. philom. Paris*, 7, 12 : 10-12.
- FORSYTH MAJOR, C. I. 1901. On some characters of the skull in the lemurs and monkeys. *Proc. Zool. Soc. Lond.*, 1901 : 129-153, pls. 11-13.
- GAZIN, C. L. 1958. A review of the Middle and Upper Eocene Primates of North America. *Smithson Misc. Coll.*, Washington, 126 : 1-112, pls. 1-14.
- GRANDIDIER, G. 1904. Un nouveau Lemurien fossile de France, le *Pronycticebus Gaudryi*. *Bull. Mus. Hist. nat. Paris*, 10 : 9-13, 3 figs.
- 1905. Les lemuriens disparus. *Nowv. Arch. Mus. Hist. nat. Paris* (4) 7 : 1-42.
- GREGORY, W. K. 1920. On the structure and relations of *Notharctus*, an American Eocene primate. *Mem. Amer. Mus. Nat. Hist.*, New York (n.s.) 3 : 49-243, pls. 23-59.
- 1922. *The origin and evolution of the human dentition*. xviii + 548 pp., 14 pls. Baltimore.
- GRANGER, W. & GREGORY, W. K. 1917. A revision of the Eocene Primates of the genus *Notharctus*. *Bull. Amer. Mus. Nat. Hist.*, New York, 37 : 841-859, pls. 103-107.
- HELLER, F. 1930. Die Säugetier fauna der mitteleozänen Braunkohle des Geiseltales bei Halle. *Jb. halesch. Verb. Erf. mitteldtsch. Bodensch.*, Halle (n.f.) 9 : 13-41, pls. 1-5.
- 1935. *Amphilemur eoecenicus* n. g. et n. sp., ein primitiver Primate aus dem Mitteleozän des Geiseltales bei Halle a. S. *Nova Acta Leop. Carol.*, Halle a. S. (n.s.) 2 : 293-300.
- HILL, W. C. O. 1953. *Primates. Comparative Anatomy and Taxonomy. I. Strepsirhini*. xxiv + 798 pp., 34 pls. Edinburgh.
- 1955. *Primates. Comparative Anatomy and Taxonomy. II. Haplorhini : Tarsioidea*. 347 pp., 14 pls. Edinburgh.
- HÜRZELER, J. 1946. *Gesneropithecus Peyeri* nov. gen. nov. spec. von Gosgen (Solothurn). *Ecl. geol. Helv.*, Lausanne, 39, 2 : 354-361, 4 figs.
- 1947. *Alsaticopithecus Leemanni* nov. gen. nov. spec., ein neuer Primate aus dem unteren Lutetien von Buchweiler im Unterelsass. *Ecl. geol. Helv.*, Lausanne, 40 : 343-356, 12 figs.
- 1948. Zur Stammesgeschichte der Necrolemuriden. *Abh. schweiz. paläont. Ges.*, Zurich, 66 : 1-46, 41 figs.
- 1950. Über die europäischen Apatemyiden. *Ecl. geol. Helv.*, Lausanne, 42, 2 : 485.
- JEPSEN, G. L. 1934. A revision of the American Apatemyidae and the description of a new genus, *Sinclairella*, from the White River Oligocene of South Dakota. *Proc. Amer. Phil. Soc.*, Philadelphia, 74 : 287-305, pls. 1-3.
- LEMOINE, V. 1878. Communication sur les ossements fossiles des terrains tertiaires inférieurs des environs de Reims. *Bull. Soc. Hist. nat. Reims*, 1878 : 90-113, pls. 1-5.
- 1891. Étude d'ensemble sur les dents des mammifères fossiles des environs de Reims. *Bull. Soc. géol. Fr.*, Paris (3) 19 : 263-290, pls. 10, 11.
- LEMOINE, V. & AUMONIER, M. 1880. Terrains tertiaires des environs de Reims. *Ass. Franc. Avanc. Sci.*, Paris, 9 : 605-619, pl. 5.
- MATTHES, H. W. 1957. Die mitteleozäne Saugerfauna des Geiseltales and ihre verwandtschaftlichen Beziehungen. *Wiss. Z. Univ. Halle, Math. Nat.*, 7 : 37-62, 22 figs.
- MCKENNA, M. C. 1960. Fossil mammalia from the early Wasatchian Four Mile fauna, Eocene of northwest Colorado. *Bull. Dep. Geol. Univ. Calif.*, Berkeley, 37 : 1-130, 64 figs.
- OSBORN, H. F. 1891. A review of the Cernaysian Mammalia. *Proc. Acad. Nat. Sci. Philad.*, 1890 : 51-62, 6 figs.
- PIVETEAU, J. 1957. Primates, paléontologie humain. *Traité de Paléont.*, Paris, 7 : 1-675.
- RUSSELL, D. E. 1960. Le crane de *Plesiadapis*. *Bull. Soc. géol. Fr.*, Paris, 7 : 312-314, pl. 18.

- RÜTIMEYER, L. 1862. Eocäne Säugethiere aus dem Gebiete des schweizerischen Jura. *Denkschr. schweiz. Ges. Naturw.*, Zurich, **19** : 1-248, pls. 1-6.
- 1891. Die Eocäne Säugethier-welt von Egerkingen. *Abh. schweiz. paläont. Ges.*, Zurich, **18** : 1-153, pls. 1-8.
- SIMONS, E. L. 1961. Notes on Eocene Tarsioids and a revision of some Necrolemurinae. *Bull. Brit. Mus. (Nat. Hist.) Geol.*, London, **5** : 43-69, pls. 12-14.
- 1961a. The dentition of *Ourayia* :—its bearing on relationships of omomyid prosimians. Postilla, Yale Peabody Mus., New Haven, Conn., **54** : 1-20, 3 figs.
- SIMONS, E. L. & RUSSELL, D. E. 1960. Notes on the cranial anatomy of *Necrolemur*. *Breviora Mus. Comp. Zool. Harv.*, Cambridge, Mass., **127** : 1-14, 3 figs.
- SIMPSON, G. G. 1940. Studies on the earliest primates. *Bull. Amer. Mus. Nat. Hist.*, New York, **77** : 185-212, 8 figs.
- 1945. The principles of classification and a classification of mammals. *Bull. Amer. Mus. Nat. Hist.*, New York, **85** : 1-350.
- 1955. The Phenacolemuridae, new family of early primates. *Bull. Amer. Mus. Nat. Hist.*, New York, **105** : 415-441, pls. 30-35.
- STEHLIN, H. G. 1912. Die Säugetiere des schweizerischen Eocaens. *Abh. schweiz. paläont. Ges.*, Zurich, **38** : 1165-1298, figs. 244-288.
- 1916. Die Säugetiere des schweizerischen Eocaens. *Abh. schweiz. paläont. Ges.*, Zurich, **41** : 1299-1552, pls. 21-22.
- STEHLIN, H. G. & SCHAUB, S. 1951. Die trigonodontie der simplicidentaten nager. *Abh. schweiz. paläont. Ges.*, Zurich, **67** : 1-385, 620 figs.
- TEILHARD DE CHARDIN, P. 1921. Les mammifères de l'Eocene inférieur Français et leurs gisements. *Ann. Paléont.*, Paris, **10** : 171-176 ; **11** : 9-116, 42 figs.
- WEIGELT, J. 1933. Neue Primaten aus der mitteleozänen (oberluteitischen) Braunkohle des Geiseltals. *Nova Acta Leop. Carol.*, Halle (n.f.) **1** : 97-156, pls. 1-11.

PLATE 1

Cantius eppsi (Cooper)

A. Right maxilla, B.M.N.H., M 15145, with P³-M². B. Right mandible, B.M.N.H., M 13773 (Type), with P₃-M₃. × 6.0 approx.

