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A Revision of the European Eocene Primate Genus *Protoadapis* and Some Allied Forms

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ABSTRACT

The European Eocene primate genus *Protoadapis*, as generally conceived of, is long-lived and highly speciose, but nonetheless homogeneous. Reappraisal of the material involved shows, however, that among the 10 species allocated by Gingerich (1977) to *Protoadapis* and its closest relatives *Cercamoni* and *Pronycticebus*, three separate groups are discernible, together with three individual species that are clearly misattributed. Within the genus *Protoadapis* we recognize for the moment two species, *P. curviciuspidens* and *P. recticiuspidens*, both originally described (as species of *Plesiadapis*) by Lemoine in 1878. These two differ somewhat in trigonid morphology, but both are quite distinct from all other material subsequently referred to *Protoadapis*. As thus constituted, *Protoadapis* may be most closely comparable to *Agerinia*. A second genus, by priority

Pronycticebus, is represented by material formerly allocated to "*Protoadapis*" (or *Europolemur*) *klatti*, as well as by *Pronycticebus gaudryi* and by a new species we describe here. *Pronycticebus* may possibly bear affinities with certain *Pelycodus*. The third major morph in the assemblage is comprised of specimens allocated to "*Protoadapis*" *angustidens* (now *filholi*), "*Protoadapis*" (or *Cercamoni*) *brachyrhynchus*, and possibly "*Protoadapis*" *weigelti*; the earliest available name for the single species represented by this material is *Cercamoni* *brachyrhynchus*, and its affinities lie with the larger species of *Notharctus*. The species "*Protoadapis*" *ulmensis*, based on isolated teeth, appears to be related to *Adapis*, the genus in which it was originally described, and the affinities of the two species "*Protoadapis*" *russelli* and "*P.*" *loui* are unclear.

INTRODUCTION

Victor Lemoine, the French physician and paleontologist, described in 1878 a collection of teeth and fragmentary jaws, from various early Tertiary deposits near Reims, as belonging to four species of the primate genus *Plesiadapis*, which Paul Gervais had established the year before on specimens furnished

by Lemoine. Lemoine attributed the first group of material (from Cernay) to the type species of the genus, *Plesiadapis tricuspidens*; the rest, consisting of younger specimens from near Epernay (probably Ay), he divided among *Plesiadapis curviciuspidens*, *P. crassiciuspidens*, and *P. recticiuspidens*, listed in that

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order. Two years later Lemoine (1880) transferred these last three species to his new genus *Protoadapis*, listing them in similar order after his (apparently Paleocene) species *Protoadapis copei*, a form he neither described nor illustrated, and whose material basis is uncertain. A decade later, in a review of the entire assemblage of fossils he had recovered from the neighborhood of Reims, Lemoine (1891) reduced to two the number of species he recognized within *Protoadapis*: *P. curvicauspiciens* and *P. recticauspiciens*. He emphasized the resemblances of these to *Plesiadapis*, and regarded both genera as “formes plus lémuriennes” than other genera included in his fossil collection from the area of Reims.

Despite the rapid exit of the species *Protoadapis copei* and *P. crassicauspiciens*, and the fact that most recent authors have regarded *P. curvicauspiciens* and *P. recticauspiciens* as synonymous, the species content of *Protoadapis* has nonetheless expanded enormously since Lemoine's time. For example, Gingerich's (1977) recent summary list of European adapid species contains eight species of *Protoadapis*, almost a third of that author's total for the family.

Stehlin (1912) was the first paleontologist after Lemoine to contribute a new species to *Protoadapis*, in describing as *Protoadapis* (his *Protadapis*) *brachyrhynchus* a mandibular specimen from the French late Eocene Quercy locality of Prajoux. Teilhard de Chardin (1922) subsequently added Filhol's (1888) “*Adapis*” *angustidens*, represented by another dentary from the Quercy phosphorites, to the roster of *Protoadapis* species; and in 1932 Cooper described *Protoadapis eppsi* on the basis of a partial mandible and other material recovered at Abbey Wood, in the English earliest Eocene. Simons (1962) transferred *eppsi* to its own new genus, *Cantius* (whence some authorities would nowadays remove it to *Pelycodus*); but at the same time he synonymized Weigelt's (1933) *Europolemur klatti* (and its own synonym *Megatarsius abeli*) with *Protoadapis*, as *P. klatti*. Weigelt's material came from the middle Eocene brown coal deposits of the Geiseltal, near Halle, east Germany (DDR).

In 1971 Schmidt-Kittler described a new species of *Adapis*, *A. ulmensis*, from the late Eocene fissure fill deposits of Ehrenstein near

Ulm in southern Germany. In 1977 he transferred this species to *Protoadapis*, an action shortly endorsed by Gingerich (1977) and Szalay and Delson (1979). More recently yet, Gingerich (1975) removed *P. brachyrhynchus* from *Protoadapis* to its own genus, *Cercamonius*, but two years later created three new species of *Protoadapis*: *weigelti* from the Geiseltal, and *russelli* and *lousi* from the French earliest Eocene site of Avenay (Gingerich, 1977). He also proposed the new name *filholi* to replace Filhol's *angustidens*, on the grounds that *angustidens* had originally been described as a species of *Adapis*, and that the species name was therefore preoccupied by the trinomen *Adapis parisiensis angustidens* that had been created for other material by Filhol himself in 1883. Szalay and Delson (1979) recently returned *brachyrhynchus* to *Protoadapis*, while rejecting Gingerich's three new species (but not the new name, *filholi*); they further reinstated Weigelt's genus *Europolemur*.

From this brief taxonomic history it is quite evident that, while agreement among recent authorities is far from complete, *Protoadapis* would on the face of it appear to be not only the longest-lived (earliest Eocene to the latest Eocene) of the primates of the European Paleogene, but also by far the most prolific of species. Among other potential contenders *Adapis* has been the only other serious claimant for this distinction. Gingerich (1977), for instance, lists eight species of the genus. However, Gingerich's list of *Adapis* species contains a heterogeneous assortment of taxa of diverse affinities, and the assessment by Szalay and Delson (1979) of the genus as monotypic, containing only the species *A. parisiensis*, seems more reasonable. Similarly, our recent reappraisal of the material that has at one time or another been assigned to the genus *Protoadapis* has led us to the conclusion that over the years *Protoadapis*, like *Adapis*, has become a “catch-all” taxon that casts a distorting shadow of illusory uniformity over what is, in fact, another diverse assemblage of taxa. We present our conclusions in detail below; and, since sweeping systematic statements about the fossils at issue have been made regularly over the past century without much more than passing reference to the actual morphologies

involved, we preface them with descriptions of the material.

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ABBREVIATIONS

BNM, Naturhistorisches Museum, Basel
 CMNH, Carnegie Museum of Natural History, Pittsburgh
 FSL, Faculté des Sciences, Université de Lyon
 GPIH, Geiseltalmuseum (formerly Geologisches Paläontologisches Institut), Martin-Luther-Universität, Halle-Wittenberg, DDR
 MNHN, Institut de Paléontologie, Muséum National d'Histoire Naturelle, Paris
 PLV, Instituut voor Aardwetenschappen, Katholieke Universiteit te Leuven, Belgium

MORPHOLOGY

The type of *Protoadapis curviciuspidens* is MNHN AL-5179 (fig. 1), a right partial dentary with M_{2-3} , very greatly worn. The paraconid shelf on both lower molars preserved is quite broad; that on M_3 is situated more inferiorly than that on M_2 . On both lower molars the cristid obliqua terminates at the base of the protoconid; the buccal cingulid is complete on M_2 and partial on M_3 . The talonid seems to have been low, and the basin shallow, at least on M_2 ; and the talonid is only slightly broader than the trigonid. A small enamel swelling in the middle of the paraconid shelf may suggest a tiny paraconid, especially on M_2 ; there is a similar swelling at the buccal termination of the shelf. M_3 bears a moderately elongate heel, quite lin-

gually emplaced. In both preserved molars the metaconid and protoconid flow together at their bases, and in general the cusps seem to have been rather puffy.

Two referred dentaries also seem to belong to this species. AL-5180 (fig. 1) is a right partial mandible with three premolars and the first two molars, all very heavily worn. The most anterior premolar is small, single-rooted, and premolariform. That behind it is a rather tall premolariform tooth, with a strongly truncated talonid. The last premolar is more submolariform, with a small paraconid and a larger metaconid. Both cusps lie low on the lingual face of the tooth. The last two premolars as well as both molars possess strong, quite complete buccal cingulids. M_1 has a small but distinct paraconid that was closely approximated to the metaconid; in M_2 this small cusp is more medially placed. The entoconid on M_2 would have been small and apparently rather conical. A referred left dentary, FSL 1991, contains the last premolar and M_1 , and is a shade less worn than the other specimens. The preserved teeth are similar to their counterparts in AL-5180; in M_1 it appears that the cristid obliqua did not meet the metaconid, and that the paraconid was separated from the paracristid by a groove (as in some large species of *Notharctus* which, however, possess narrower talonids).

The holotype of *Protoadapis recticiuspidens* is MNHN AL-5182, a right dentary fragment containing M_{2-3} (fig. 1). This specimen is highly worn, and only M_3 preserves any significant morphology. The trigonid of this tooth is extremely compressed, and lacks a paraconid. The low paracristid arcs between the protoconid and metaconid; the cristid obliqua is very buccally situated and terminates at the buccal side of the base of the protoconid. The bases of the protoconid and metaconid are confluent and form a steep wall facing the talonid. The talonid cusps are relatively indistinct and peripheral, and the talonid heel is rather short and lingually emplaced. Two other dentaries, one with an excellent dentition, have been referred to this species, with which in fact they do not appear to belong (see below).

The type specimen of Filhol's "*Adapis*" *angustidens* (*Protoadapis filholi* of Gingerich, 1977) is a left dentary (fig. 2) that has been

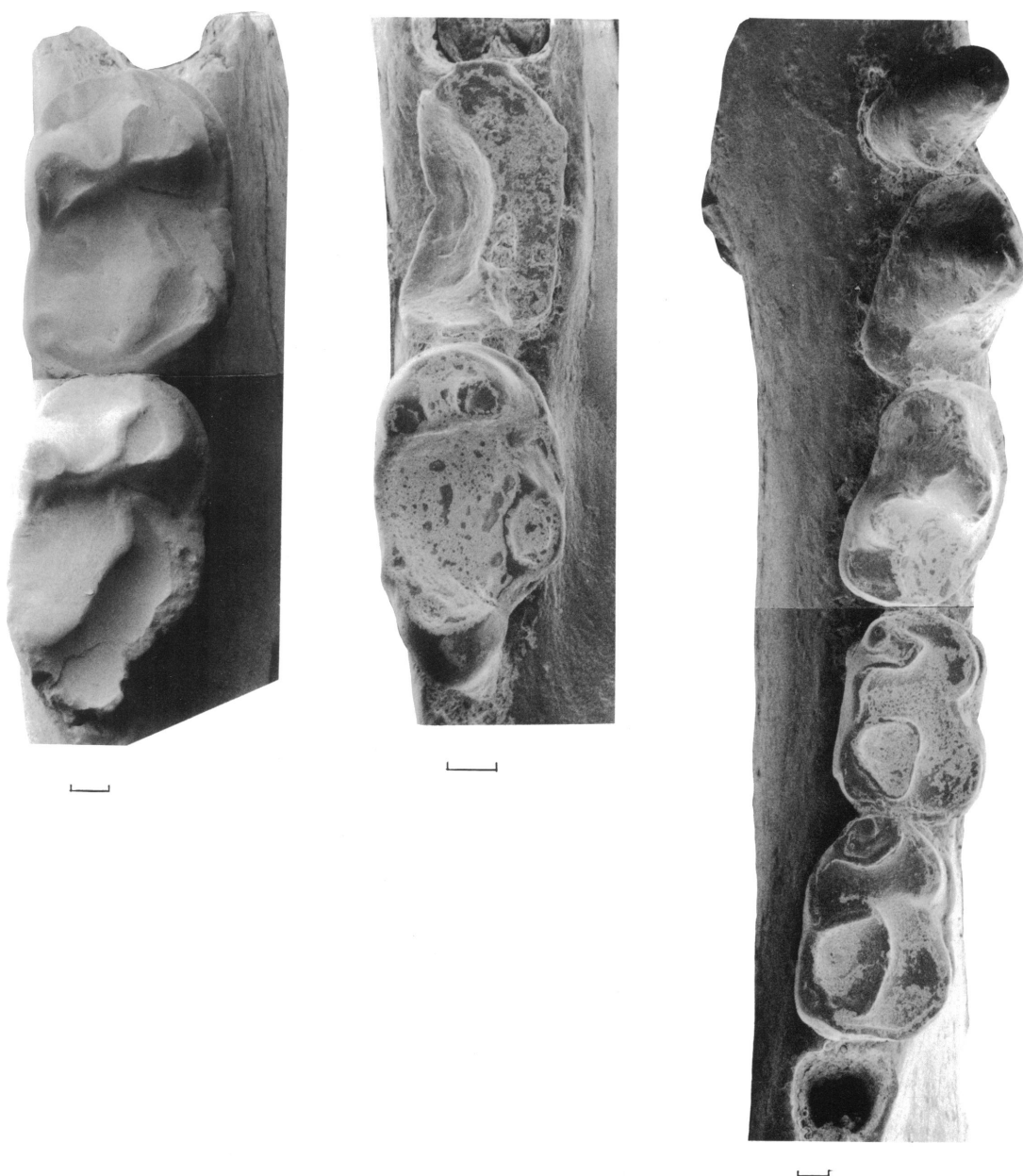


FIG. 1. Scanning electron micrographs of casts of: (left) MNHN AL-5179, type of *Protoadapis curvicuspidens*; (center) MNHN AL-5182, type of *Protoadapis recticuspidens*; (right) MNHN AL-5180, referred to *Protoadapis curvicuspidens*. All scales represent 1 mm.

lost since it was redescribed, illustrated, and assigned to *Protoadapis* by Teilhard de Chardin (1922). Another Quercy specimen properly referable to the species, a left dentary

containing M_{2-3} , exists, however, in the collections of the Katholieke Universiteit te Leuven, as PLV-35 (fig. 3). The "puffy" molars of this specimen have a small paraconid

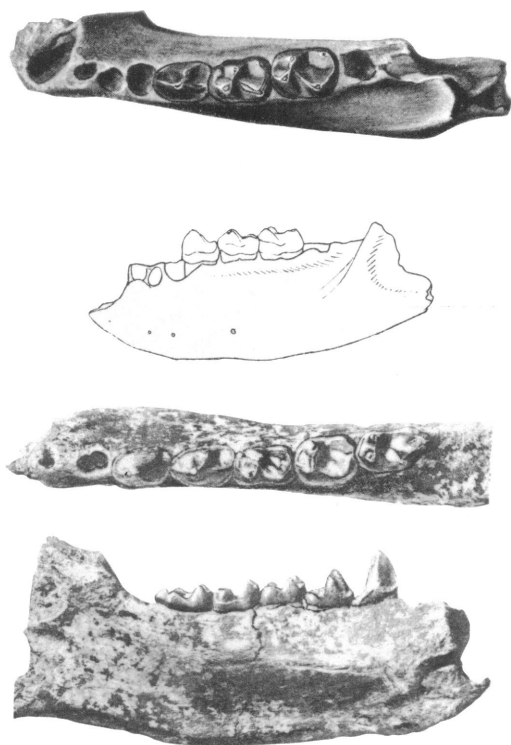


FIG. 2. Above: occlusal and lateral views, from Stehlin (1912), of BNM QV 619, type of "*Protoadapis*" *brachyrhynchus*. Below: occlusal and internal views, from Teilhard de Chardin (1922) of the type of "*Protoadapis angustidens*," now lost. Line drawing is approximately natural size; other illustrations are somewhat enlarged.

closely appressed in the midline to the bases of the metaconid and protoconid. This small cusp is the terminus of a small, arcuate paracristid. In both molars the cristid obliqua terminates medially, between the major trigonid cusps, creating a fairly deep hypoflexid notch. Both teeth show well-developed buccal cingulids. The paraconid on M_3 is lower on the face of the trigonid than is its counterpart on M_2 . In each tooth a small thickening of the enamel exists just lingual to the paraconid, separated from it by a narrow groove; this "pseudo-twinning" of the paraconid occurs further inferiorly on M_3 than on M_2 .

Stehlin's (1912) *Protoadapis brachyrhynchus*, transferred by Gingerich (1975) to its own genus *Cercamonius*, is based on BNM QV 619 (figs. 2, 4), a robust partial left lower



FIG. 3. Occlusal scanning electron micrograph of a cast of two teeth preserved in Leuven PLV-35, referred specimen of "*Protoadapis filholi*." Scale represents 1 mm.

jaw with the last premolar and M_{1-2} . In comparable parts the dentition of this specimen closely matches both Teilhard's illustration of the type of *Protoadapis angustidens*, and PLV-35; in preserved areas it also appears to display a similar alveolar count to the latter. Again, the cheek teeth are characterized by their "bulkiness." The last premolar is dominated by a low, broad protoconid that bears a stout metaconid closely approximated to it low down on its lingual face. The talonid is somewhat compressed, and the enclosed talonid basin is displaced lingually. The molar trigonids lack distinct basins, are somewhat



FIG. 4. Oclusal scanning electron micrograph of a cast of teeth remaining in BNM QV 619, type of "*Protoadapis brachyrhynchus*." Scale represents 1 mm.

compressed, and possess distinct paraconid shelves that end in small paraconid swellings, lower down on the trigonid in M_2 than in M_1 . The cristids obliquae of the two preserved

molars are rather straight and terminate at the juncture between the closely approximated paraconid/metaconid pairs. The talonid basins are quite shallow and lack distinct hypoconulids. All teeth preserved display strong buccal cingulids.

The primate usually known as *Europolemur* or *Protoadapis klatti* is represented by a series of Geiseltal specimens in the collections of the GPIH, and has also been reported from elsewhere. The holotype is a crushed cranium and mandible, GPIH 232/3656 (fig. 6), and notable referred specimens include an unnumbered mandible with the two posterior premolars and M_{1-3} (fig. 5), and the anterior part of a face, GPIH 4258 (fig. 6), with interlocked upper and lower teeth. Two further specimens are highly worn: GPIH 4234, an upper dentition, and GPIH 549, a lower dentition.

The lower canines of *klatti*, as represented by this tooth in GPIH 549, are classically caniniform: simple, conical, and trenchant, with no elaboration of the base. In the lower molars the paraconid is small but twinned, notably on M_1 , and lies at the terminus of an inferiorly trending paracristid. The paraconids lie a bit medial to the metaconid, and decrease in size from M_1 to M_3 . There is a complete rounded hypocristid between the hypoconid and the entoconid in M_{1-2} , uninterrupted by any notch or by the development of a hypoconulid. On M_{2-3} the cristid obliqua is arcuate but terminates midway between the metaconid and protoconid; on M_1 this crest probably contacted the metaconid, but wear makes this unverifiable. The last two premolars are laterally compressed; the posterior bears a small, medially placed "hypoconid," which is joined by a weak cristid obliqua that runs up the posterior face of the protoconid. The talonid basin is further delineated by a stronger crest emanating lingually from the protoconid and running inferiorly to join the hypoconid, creating an enclosed basin. The talonid is more weakly defined on the penultimate premolar. Both premolars possess a sharp, steeply sloping paracristid that turns lingually at the base of the tooth, forming a moderate depression lingually. Distinct cingulids are present on the posterior halves of the posterior premolars.

M₁ bears a virtually complete buccal cingulid; this structure is less complete posteriorly on M₂ and still less so on M₃. From the crushed type jaw the antepenultimate premolar appears rudimentary (it may be a retained deciduous tooth), but possesses two roots that seem disproportionately large compared to crown size. The canines are slightly flattened and at their apex curve lingually; they bear a deep anterior vertical groove. The lateral incisor is larger than the medial but both are similar in being spatulate and small crowned.

In the upper dentition, the crown of the central incisor is approximately half as large again as that of the lateral; both teeth are elongate and somewhat spatulate although lingually there is a marked margocrista. The upper canine seems to have been laterally compressed, bearing an anterior and a larger posterior vertical groove; the impression is of a pointed, daggerlike tooth. The antepenultimate upper premolar is small-crowned and of simple premolariform shape; the only elaboration is a tiny posterior swelling bearing slight medial and lateral cingula. The penultimate premolar of the type can be seen undamaged only laterally; in outline it appears as a roughly equilateral triangle. It bears cingular swellings in the para- and metastylar regions, which are joined by a weak cingulum. There appears to have been a lingual distension of the protocone region, which may have borne a small cusp. The last premolar is similar to the foregoing one in buccal outline, but is slightly smaller and bears more distinctly developed stylar regions and cingula. This tooth is quite transverse, and bears a relatively large protocone from which emanate a weak and truncated postprotocrista and a stronger preprotocrista and protocone fold. The postprotocrista becomes confluent with a small precingulum while the postcingulum reaches beyond the postprotocrista. The upper molars are characterized by very prominent trigon cusps and a very small talon. Of the crests of the talon the pre- and postprotocrista are the most emphasized, and are more V- than U-shaped in configuration. On M¹⁻² the preprotocrista bears a strong parastyle which is confluent with the precingulum, and also a paraconule. On all molars



FIG. 5. Occlusal scanning electron micrograph of a cast of "*Protoadapis klatti*," unnumbered specimen in GPIH. Scale represents 1 mm.



FIG. 6. Above: upper dentition of GPIH 232/3656, type specimen of "*Protoadapis klatti*." Below: lateral view of GPIH 4258, referred specimen of same. Each scale represents 3 mm.

the precingulum also extends down and around the face of the protocone and becomes confluent with an equally strong postcingulum. On M^{1-2} a distinct and pointed hy-

pocone occupies the posterolingual corner of the tooth, thereby giving these teeth a squarish appearance, although they are still highly transverse, dominated by the broad, short tri-

gon. Buccal cingula are complete and well developed on all upper molars, and M^1 additionally bears a small mesostyle. On the reduced M^3 the trigon enamel is somewhat wrinkled.

Protoadapis ulmensis is represented by the few isolated teeth described by Schmidt-Kittler (1971, 1977) from the late Eocene German site of Ehrenstein. As illustrated by Schmidt-Kittler, the upper molars of *ulmensis* are characterized in preserved parts by broad, arcuate protocristae; moderately compressed buccal cusps interconnected and bounded laterally by distinct crests; and well-defined pre- and postcingula that typically become confluent around the base of the large, somewhat compressed protocone. In all upper molars the posterior face of the tooth seems to be somewhat swollen, and a moderate ledge appears in the hypocone region. In all known upper molars the strong preprotocrista seems to arc past the paracone, from which it is separated by a narrow groove. Schmidt-Kittler's illustration of one of the referred upper molars of *ulmensis*, Ehrenstein 3, 1971, XXIV-4, shows an elaboration of the enamel fringing the lingual margin of the protocone to a degree that is also characteristic of *Lepilemur*. Another particular resemblance to the *Lepilemur* is found in a low, broad enamel ridge that diverges from the postprotocrista toward the postcingulum. Although these teeth as illustrated bear a remarkable resemblance to their counterparts in *Lepilemur*, they also differ in being slightly more transverse. But while the comparison with *Lepilemur* is reinforced on the one hand by the detailed similarity between the single known upper premolar of *ulmensis* and the middle upper premolar of the Malagasy form, on the other hand the isolated M_3 attributed to *ulmensis* is clearly dissimilar from that of *Lepilemur*. The fossil tooth is badly damaged, however, and its attribution can only be conjectural.

The Geiseltal specimen, GPIH 1209, on which Gingerich (1977) based his new species *Protoadapis weigelti*, is totally inadequate for such a purpose. A right dentary fragment with M_{1-2} , this fossil preserves virtually no surface detail of the teeth. From what little remains, the trigonid of M_2 seems to have been more compressed than that of M_1 . In both teeth

the cristid obliqua seems to have been straight, terminating medially and producing deep hypoflexid notches and rather narrow talonids.

In the same contribution, Gingerich created two additional new species of *Protoadapis*, *P. russelli* and *P. louisi*. Each new species was based on an isolated lower molar, and a largely unspecified variety of other specimens, also isolated teeth. The type of *Protoadapis russelli*, Louis coll. Av-183 from the earliest Eocene site of Avenay, a presumed right M_1 , has trigonid cusps that are very distinct and well-separated; the talonid is low, with a shallow basin. The metaconid and entoconid are separated by a steep slope, and the posterior face of the talonid is rather straight, bearing a small and medially positioned hypoconulid. The cristid obliqua is weak, and terminates medial to the base of the metaconid.

The type of *Protoadapis louisi*, Louis coll. Av-118, is also a presumed right M_1 from Avenay, but is larger than Av-183. The trigonid cusps of this specimen are tall, pointed, well-separated, and set in a large trigonid with a deep basin. The talonid cusps are lower but still pointed, with a small and medially placed hypoconulid. A distinct cristid obliqua terminates in the midline between the bases of the protoconid and metaconid, creating a narrow but deep hypoflexid notch. A deep groove separates the metaconid from the entoconid.

Two specimens that have generally been referred to *Protoadapis recticuspidens* (or *P. curvicuspidens*) have clearly been wrongly attributed. These are: MNHN-Louis-15-Ma (fig. 7), a left dentary with a large caniniform tooth followed by alveoli, the two posterior premolars, and M_{1-3} , from the French Cuisian site of Mancy; and MNHN AL-5181 (fig. 8), a left dentary from Epernay with the last premolar and M_2 , illustrated as *Protoadapis* but not ascribed to species, by Lemoine in 1891. Descriptions of these specimens follow.

Louis-15-Ma. The caniniform tooth in this jaw is genuinely caniniform: simple, pointed, tall, slightly recurved, and without basal elaboration. The two preserved premolars are relatively trenchant, especially the penultimate, which has a markedly truncated talonid. The

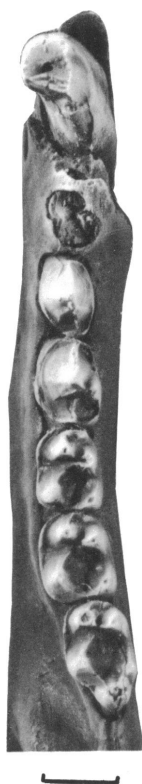


FIG. 7. Occlusal view of the dentition of MNHN-Louis-15-Ma, type of new species described in this paper. Scale represents 3 mm.

last premolar lacks a paraconid but possesses a distinct metaconid on the lingual face of the protoconid. It also has a distinct but somewhat truncated talonid whose basin is displaced lingually, and, like the molars, bears a relatively complete buccal cingulid. A sharp paracristid descends steeply down the face of the protoconid, at the base of which it arcs lingually and rises to become confluent with the metaconid. The cristid obliqua on M_1 meets the metaconid, but this crest terminates centrally on M_2 and M_3 . The talonid basins are shallow and somewhat narrow; they are rounded distally and lack hypoconulids on M_{1-2} . The trigonids become more compressed in the sequence M_{1-3} , and the small swelling at the terminus of the paracristid becomes smaller and shifts medially in the same sequence. Also in this sequence

the paracristid, bearing a small and diminishing paraconid, moves inferiorly. In M_3 the paracristid terminates at the base of the metaconid. Both M_2 and M_3 would have been larger than the corresponding teeth in the unworn type of *recticuspiciens*. The cristid obliqua of M_3 terminates low between the bases of the protoconid and metaconid, creating a relatively deep hypoflexid notch. The talonid heel of M_3 is rounded, not very elongate, and somewhat displaced lingually. There are two small alveoli in front of the caniniform tooth; behind this is an alveolus for a small, single-rooted tooth, and between this and the penultimate premolar, two roots for another tooth.

AL 5181. At the front of the jaw there is an enormous backwardly sloping alveolus with apparently no teeth in front of it (the symphyseal surface seems to be present in this specimen); possibly this alveolus is artificially enlarged and has "captured" smaller alveoli anterior to it. Behind the large alveolus is a small diastema followed by a small compressed alveolus followed in turn by two associated alveoli succeeded by a single alveolus of moderate size. The last premolar has a moderately sized metaconid low on the face of the protoconid; it also had a distinct and slightly buccal hypoconid and an enclosed, lingually displaced talonid basin. The last premolar also had a complete buccal cingulid, and a distinct paracristid descended the face of the protoconid to arc lingually and ascend to meet the metaconid. M_2 lacks a distinct paraconid; the paracristid slopes down the face of the protoconid and terminates at the base of the metaconid, enclosing a tiny fovea. The talonid cusps, especially the entoconid, are relatively small and relegated to the periphery of the tooth where they are more or less confluent with the cristids that enclose a relatively shallow talonid basin. The cristid obliqua terminates at the midline of the back of the trigonid, and there is a distinct although not robust buccal cingulid. The two preserved teeth in this jaw are very close in morphology to those of the L-15 Mancy jaw, which increases the probability that, originally, small teeth were indeed present at the front of the jaw.

Finally, it is with this group that Grandidier's (1904) species *Pronycticebus gaudryi* is

most appropriately described. This is uniquely known from the holotype, MNHN 1893-11 (fig. 9), an exquisitely preserved cranium and mandible from the French late Eocene (Headonian) site of Memerlein. Both the cranium and the mandible preserve the last two premolars and M_{1-3} , with alveoli anteriorly. The teeth of the mandible seem to be less worn than those of the upper jaw, which have lost a certain amount of detail. The penultimate upper premolar is dominated by a large buccal paracone, with a small protocone lingually. There is a distinct parastyle and a larger metastyle. In the last upper premolar these styler buildups are subequal in size and are connected buccally by a cingulum. The paracone is broader than in the penultimate premolar, and the protocone is distinctly larger. A well-developed preprotocrista connects the protocone and parastyle; a postcingulum runs from the metastylar region and terminates distally in a small swelling at the base of the protocone. The upper molars are characterized by their transverseness and are relatively short. M^1 is smaller than M^{2-3} , which are subequal in size. The anterior molar is convex on its anterior surface and concave posteriorly; this posterior waisting is emphasized by the distension of the hypocone and metacone regions. The metacone distension is caused in part by a distinct and prominent metastylar crest. The upper molar protocristae seem to have been neither broad nor parabolic in configuration. A crest that emanates from the paracone region and skirts the paracone to meet the precingulum appears not to be the preprotocrista, since the latter crest can be discerned, faintly, running to the apex of the paracone. M^2 is only slightly convex anteriorly, and posteriorly it is essentially straight sided. The paracone is much larger than the metacone, but as in M^1 the centrocristae are well emphasized. The hypocone is confluent with the postcingulum, and appears to have been more shelflike than cusplike. M^3 is roughly triangular, with a shelflike ridge posterior to the base of the protocone. As in M^2 , the buccal crests are emphasized and the paracone is dominant. All molars bear a distinct precingulum that reaches partway around the base of the protocone; in M^2 this structure terminates in a tiny style, and in M^3 in a distinct pericone.



FIG. 8. Occlusal scanning electron micrograph of a cast of teeth preserved in MNHN AL-5181, referred specimen of new species described in this paper. Scale represents 1 mm.

The penultimate lower premolar is dominated by the protoconid, which bears a small truncated talonid and lacks the posterior excavation characteristic of *Adapis* and its allies. The last premolar is also dominated by the protoconid; this bears anteriorly, at its base, a small paraconid shelf, and posteriorly, well down on its lingual surface, a small metaconid. The talonid is somewhat better expressed than is that of the penultimate lower premolar, and bears a minute, medially



FIG. 9. Occlusal scanning electron micrographs of casts of the upper (left) and lower preserved dentitions of MNHN 1893-11, type of *Pronycticebus gaudryi*. Scale represents 0.5 mm.

placed hypoconid from which emanates a cristid obliqua that runs down to the metaconid, and a hypocristid that encloses the talonid basin. In both preserved premolars the paracristid turns lingually to enclose a depression. Lingual to the hypoconid is a tiny, compressed cusp that may represent the entoconid. This weak buccal cingulid is more complete than on the penultimate premolar. Buccal cingulids on the molars occur primarily around the trigonids; such cingular

development increases in the sequence M_{1-3} . The trigonid cusps of the lower molars are somewhat compressed and the trigonids have sheer posterior walls. Except for the enlarged talonid heel of M_3 , the molars lack any sign of hypoconulids. The cristid obliqua on M_1 kinks round to the metaconid, but this crest terminates at the base of the protoconid on M_{2-3} . The trigonid of M_1 is somewhat compressed, that of M_2 more so, and that of M_3 more compressed yet. The molar trigonids

are all similar, however, in that a weak paracristid runs down from the protoconid and arcs lingually, where it becomes more expanded and supports twinned small cuspsules that may be identified as twinned paraconids. On M_{1-2} the talonid basin is enclosed by the rather arcuate cristid obliqua and hypocristid; from front to back in the molar sequence the cristid obliqua becomes less well defined, and the paracristid becomes lower. The talonid heel on M_3 is displaced lingually.

DISCUSSION

As we have already noted, *Protoadapis* as generally conceived is perhaps the most highly speciose and long-lived primate genus of the European Paleogene. However, within the material that has traditionally been allocated to this genus and its close allies, there are in fact three major groups discernible, in addition to three described species that are not only clearly not *Protoadapis*, but are also referable to none of these major groups. Insofar as can be told from the morphology preserved, the types of Lemoine's two species *curvicspidens* and *recticspidens* are not only somewhat dissimilar to each other, but both are distinctly different from all other specimens subsequently referred to *Protoadapis*. Because of the heavily worn condition of the specimens involved, it would be ill-advised to attempt to separate *curvicspidens* and *recticspidens* at other than the species level, at least at present. It may be noted, however, that *curvicspidens* differs strongly from *recticspidens* in having a much better developed trigonid, with a broad paracristid and the tips of the two main cusps divergent; the protoconids and metaconids are much more closely approximated in the somewhat smaller *recticspidens*, and the paracristid is both smaller and higher on the anterior molar face. In any event, at present it seems most prudent to regard these two species as congeneric, and as the only known representatives of *Protoadapis*. In this view, the distinctive characteristics of the restricted genus *Protoadapis* include the following: a broad paraconid shelf, a buccally emplaced cristid obliqua that terminates at the base of the protoconid, a low and shallow talonid basin, at least on M_2 , and a talonid that is not ap-

preciably broader than the trigonid. On the basis of such poor material it is perhaps unwise to speculate in unduly precise terms about the affinities of *Protoadapis*; nevertheless, one might note that the buccal emplacement of the cristid obliqua, the peripheralization of the cusps that leads to the complete enclosure of the talonid, at least of M_2 , and the truncated nature of the better-preserved M_3 of *recticspidens*, may invite comparison of *Protoadapis* with *Agerinia*, as was done by Szalay and Delson (1979).

The second major group represented in the assemblage consists of *Protoadapis klatti*, *Pronycticebus gaudryi*, and a previously unrecognized species represented by the MNHN specimens Louis-15-Ma and AL-5181. Although a substantial case could be made for recognizing three genera within this assemblage, it is clear that the forms comprising it are very closely related, and for the purposes of taxonomic simplicity we regard them here as belonging to a single genus, by priority *Pronycticebus*. We should note that Szalay and Delson (1979) have already emphasized the affinities between their concept of *Protoadapis* and *Pronycticebus*; this was presumably on the basis of the better Mancy specimen rather than on the type material. Before discussing further the enlarged genus *Pronycticebus*, we will formally name the new species, of which the morphology has been given at some length above.

ORDER PRIMATES

PRONYCTICEBUS GRANDIDIER, 1904

Pronycticebus mancyi, new species

Protoadapis curvicspidens (in part), Russell, Louis, and Savage, 1967.

TYPE: MNHN-Louis-15-Ma, left dentary preserving a large caniniform tooth, the last two premolars, and M_{1-3} (fig. 7).

TYPE LOCALITY: Mancy, France: early Eocene.

HYPODIGM: Type plus MNHN AL-5181, left dentary with last premolar and M_2 (fig. 8), from Epernay.

ETYMOLOGY: To reflect the provenance of the type specimen.

DIAGNOSIS: Larger than *Pronycticebus gaudryi* and comparable in size with *Pro-*

nycticebus klatti. Cheek teeth relatively much broader than in *gaudryi*; cusps more inflated. Differs from *klatti* in the greater height of its penultimate premolar, which has less distinct buccal cingulids but more lingual cingulid development, and which shows a well-defined internal depression. Bears one more (tiny) premolar than does *klatti*. The last premolar of *mancyi* is relatively larger and more inflated than that of *klatti*, with a more distinct metaconid and a broader talonid basin. All molars of *mancyi* bear stronger and more complete buccal cingulids than those of *klatti*, and show relatively larger (although still absolutely tiny) paraconids.

Pronycticebus gaudryi has traditionally been regarded as quite distinct among "adapid" primates (see, for example, Gingerich [1977]). Szalay and Delson (1979), however, have suggested that *Pronycticebus* may be descended from their concept of *Protoadapis* (which includes *filholi* and related forms, but excludes *klatti*). We concur with neither judgment; for if one allows for dental wear it is clear that morphologically *gaudryi* is very close to "*Protoadapis*" *klatti* as known from the Geiseltal. Distinguishing features in the lower dentition (the upper is known only in *gaudryi* and *klatti*) of a genus *Pronycticebus* that embraces the species *gaudryi*, *klatti*, and *mancyi* include the following: the presence in the lower molars of tiny twinned paraconids, most evident on M_1 but also discernible on the posterior molars; arcuate cristids obliquae on M_2 that are more internally directed than in *Protoadapis*; a cristid obliqua on M_3 that terminates on the lingual side of the base of the protoconid; and a more elaborate talonid heel than in *Protoadapis*.

The upper dentitions of *Pronycticebus gaudryi* and *Pronycticebus klatti* are known from decent specimens, the unique representative of the former (fig. 9) more heavily worn than the best specimens of the latter (e.g., fig. 6). In both species the upper molars are distinguished by being rather transverse, with distinct protocristae forming a V, and a somewhat ledgelike postcingulum that terminates lingually in a broad hypocone. The last two premolars are each dominated by a rather compressed and trenchant paracone

that bears some anterior and posterior styler development and buccal cingula. The penultimate premolar bears a small protocone swelling that is more discernible as a cusp on the last premolar, and a distinct protocone fold. To judge from the preserved roots in *gaudryi*, both species had a large, stout upper canine that may have been rather more compressed in *klatti*, at least at the alveolar margin. Distinctions between *gaudryi* and *klatti* also reside in the greater development of pre- and postcingula in *klatti*; these become confluent around the base of the upper molar protocones. *Pronycticebus gaudryi* also retains an additional (fourth) upper premolar that is absent in *klatti*; this disparity may also have been true of the lower dentition. In this regard *klatti* is also distinguished from *mancyi*, at least in the lower jaw.

At the present state of our knowledge it is difficult to postulate precise affinities for *Pronycticebus*. If, however, there is a genuine phylogenetic signal in characters such as the arcuateness of the cristid obliqua, the encirclement of the talonid basin by crests, the transverseness of the upper molars, the V-shaped configuration of the protocristae, and an apparent morphocline from front to back in the reduction of the paraconid and its transformation into a shelf in close proximity to the metaconid, then perhaps the most appropriate comparisons might lie among species of *Pelycodus* such as *P. ralstoni* and *P. trigonodus*.

The third group within the assemblage is the most distinctive and thereby the easiest to delineate. This is not least because it consists of a single species which contains the fossils that have been variously allocated to *Protoadapis filholi* (or *angustidens*), *Cercomonius* (or *Protoadapis*) *brachyrhynchus*, and possibly *Protoadapis weigelti*. Szalay and Delson (1979) have also recently suggested the synonymy of *weigelti* with *filholi*, and in the same contribution proposed that the latter might bear an ancestral relationship to *brachyrhynchus*. We should note that since the holotype of *Protoadapis weigelti* is totally inadequate to support analysis, we hazard that it belongs here largely on the basis of its size, almost the only character it retains.

The specimens referred to the species *fil-*

TABLE 1
Summary of Species Recognized or Discussed in This Paper, and Their Synonymies

This Paper	Synonyms	Reference
GROUP 1		
<i>Protoadapis curviciuspidens</i> (Lemoine, 1878)	<i>Plesiadapis curviciuspidens</i>	Lemoine, 1878
<i>Protoadapis recticiuspidens</i> (Lemoine, 1878)	<i>Plesiadapis recticiuspidens</i>	Lemoine, 1878
GROUP 2		
<i>Pronycticebus gaudryi</i> Grandidier, 1904		
<i>Pronycticebus klatti</i> (Weigelt, 1933)	<i>Europolemur klatti</i>	Weigelt, 1933
	<i>Megatarsius abeli</i>	Weigelt, 1933
	<i>Protoadapis klatti</i>	Simons, 1962
<i>Pronycticebus mancyi</i> , new species	<i>Protadapis</i> sp.	Lemoine, 1891
	<i>Protoadapis curviciuspidens</i>	Russell, Louis, and Savage, 1967
GROUP 3		
<i>Cercamoniuss brachyrhynchus</i> (Stehlin, 1912)	<i>Adapis angustidens</i>	Filhol, 1888
	<i>Protadapis brachyrhynchus</i>	Stehlin, 1912
	<i>Protoadapis angustidens</i>	Teilhard de Chardin, 1922
	<i>Protoadapis weigelti</i>	Gingerich, 1977
	<i>Protadapis filholi</i>	Gingerich, 1977
Other Taxa	Notes	
<i>Protoadapis eppi</i> Cooper, 1932	Transferred to new genus as <i>Cantius eppi</i> by Simons (1962); often regarded as <i>Pelycodus</i>	
<i>Protoadapis ulmensis</i> (Schmidt-Kittler, 1971)	Not <i>Protoadapis</i> ; appears to be an adapine <i>sensu stricto</i> .	
<i>Protoadapis russelli</i> Gingerich, 1977	Not <i>Protoadapis</i> ; primate <i>incertae sedis</i> .	
<i>Protoadapis louisii</i> Gingerich, 1977	Not <i>Protoadapis</i> ; primate <i>incertae sedis</i> .	

holi (or *angustidens*) and *brachyrhynchus* consist of lower jaws which differ strikingly from other material that has in the past been referred to *Protoadapis*. All have broad, "swollen" cheek teeth that show considerable lingual development and do not incorporate the cusps into shearing crest systems. The molar paraconids are appressed to the metaconids, further down the tooth in the sequence M_{1-3} . The "pseudo-twinning" of the paraconid is in fact no more than a wrinkling of the enamel, rather than a clear delineation of two cusps of the kind seen in *Pronycticebus*. The cristids obliquae are straight, and the talonid basins are very shallow. The entoconid is bounded internally by a narrow groove which appears posteriorly as a small notch.

Cercamoniuss brachyrhynchus is thus highly distinctive relative to other European primates, and has, indeed, regularly been com-

pared since Stehlin's time with North American Eocene primates such as *Pelycodus* and *Notharctus*. In our view, Teilhard's (1922) older, and Gingerich's more recent (1975) comparison with the larger species of *Notharctus* is highly appropriate. In the "puffiness" of the teeth, in the closed-up and lingually shifted trigonids, in the wrinkling and posterior lowering of the paraconid region, in the relative straightness of the cristids obliquae, and in the occurrence of a narrow and shallow entoconid notch, *Cercamoniuss brachyrhynchus* provides a remarkably close match for forms such as *Notharctus venticolus* (as represented by CMNH 37159). It differs from the largest *Notharctus*, *N. crassus*, in lacking robust cresting of the posterior premolar. Unquestionably, however, it is with this group of Eocene primates that *Cercamoniuss* is most closely allied.

This division of the total assemblage leaves the isolated teeth assigned by Schmidt-Kit-

tlar (1977) to *Protoadapis ulmensis*, and by Gingerich (1977) to *Protoadapis russelli* and *loui*. The *ulmensis* material seems referable to the clade of *Adapis sensu stricto*, as Schmidt-Kittler (1971) had originally concluded; it does not belong with any of the other material discussed here. The species *russelli* and *loui* are strikingly characterized by distinct and well-separated trigonid cusps, a feature which by itself distinguishes them from all of the other primates under consideration. Indeed, the remarkably large trigonids of these specimens demarcate them even from the most primitive species of *Pelycodus*. Both appear to belong to the same group, but their broader affinities are obscure to us. Certainly the suggestion by Szalay and Delson (1979) that they may belong with *filholi* seems inappropriate.

SUMMARY

Our review of the material that has been assigned at one time or another to the European Eocene primate genus *Protoadapis* shows that the genus has in fact become an umbrella for a heterogeneous assortment of taxa. We find that among this material three major groups are represented, together with three described species that belong to none of these. For convenience of reference we summarize our conclusions in table 1 by listing those species we recognize together with their synonyms.

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