

A REAPPRAISAL OF THE EUROPEAN EOCENE PRIMATE *PERICONODON*

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ABSTRACT. The Eocene primate *Periconodon* has recently been widely regarded as belonging to the family Adapidae, and several authors have synonymized it with *Anchomomys*, another adapid. Re-examination of the type material of *Periconodon* has revealed that the genus is distinct, and that its affinities lie not with Adapidae but with the otherwise exclusively North American family Omomyidae. *Periconodon* contains only the type species, *P. helveticus*; recently named new species of *Periconodon* are wrongly assigned.

THE primate genus *Periconodon* was created in 1916 by Stehlin, to accommodate two maxillary fragments from the Swiss middle Eocene (Auversian) locality of Egerkingen (Huppersand). These specimens had originally been described some years earlier by Rüttimeyer, who had allocated one of them to ?*Pelycodus* (Rüttimeyer 1888), and who with more confidence had based on the other (text-fig. 1) a new species of *Pelycodus*, *P. helveticus* (Rüttimeyer 1891). Stehlin compared *Periconodon* quite widely with other Eocene primates, European and North American, and concluded that the closest comparison was with certain North American forms generally regarded today as omomyids. He was more strongly struck, however, by the close resemblances he perceived between the upper molars of *Periconodon* and the squirrel monkey *Saimiri* (his '*Chrysothrix*') *sciureus*, although he felt that the gap in time precluded any close relationship. In 1945 Simpson affirmed his acceptance of the tarsiid affinities of *Periconodon*, but placed the form *incertae sedis* in his family Anaptomorphidae (which included the subfamily Omomyinae, more or less as defined by Wortman in 1904, and limited to North American genera). Subsequently Simons (1962) assigned *Periconodon helveticus* to the tarsiid family Omomyidae, to which Omomyinae had been raised by Gazin in 1958.

An alternative suggestion as to the affinities of *Periconodon*, and one that rapidly gathered general acceptance, was put forward by Russell, Louis and Savage (1967), who concluded that *Periconodon* might better be classified in the family Adapidae. In particular, they suggested a relatively close affinity between *Periconodon* and the adapid *Anchomomys* (although they did not specify a species of *Anchomomys*, a genus that seems to us as currently classified to represent a non-homogeneous assemblage). In 1974 Szalay followed Russell, Louis and Savage in stressing the resemblances between *Anchomomys* and *Periconodon*, and three years later Gingerich (1977) took the step of synonymizing *Periconodon helveticus* with *Anchomomys pygmaeus*, an action that resulted in the new combination *Periconodon pygmaeus*. Szalay subsequently concurred with this synonymy (Szalay and Delson 1979), and reaffirmed his belief in the adapid affinities of *Periconodon*.

Gingerich (1977) proposed two new species of *Periconodon*. One of these, *P. lemoinei*, he based on an assortment of isolated teeth from the French lower Eocene site of Grauves, plus a fragmentary lower jaw from Castigaleu, Spain, that had been assigned by Crusafont (1967) to his new genus *Agerina* (now *Agerinia*); the other, *P. huerzeleri*, he based on a right dentary from the middle Eocene (Lutetian) site of Buchweiler (Bouxwiller) in Alsace, and on unspecified other material from Buchweiler and elsewhere. Gingerich suggested that his *P. lemoinei* was descended from a form he named *Protoadapis lousi*, and that *P. huerzeleri* and *P. pygmaeus* represented later, successive, stages in a linear sequence leading to *Anchomomys*; between *lemoinei* and *huerzeleri* he interposed '*Periconodon*' *roselli*, as a result of having synonymized Crusafont's species *Agerinia roselli* with *Periconodon*. Szalay (Szalay and Delson 1979) objected to this set of conclusions, pointing to the lack of morphological justification provided by Gingerich; provisionally, he assigned the *P. lemoinei*

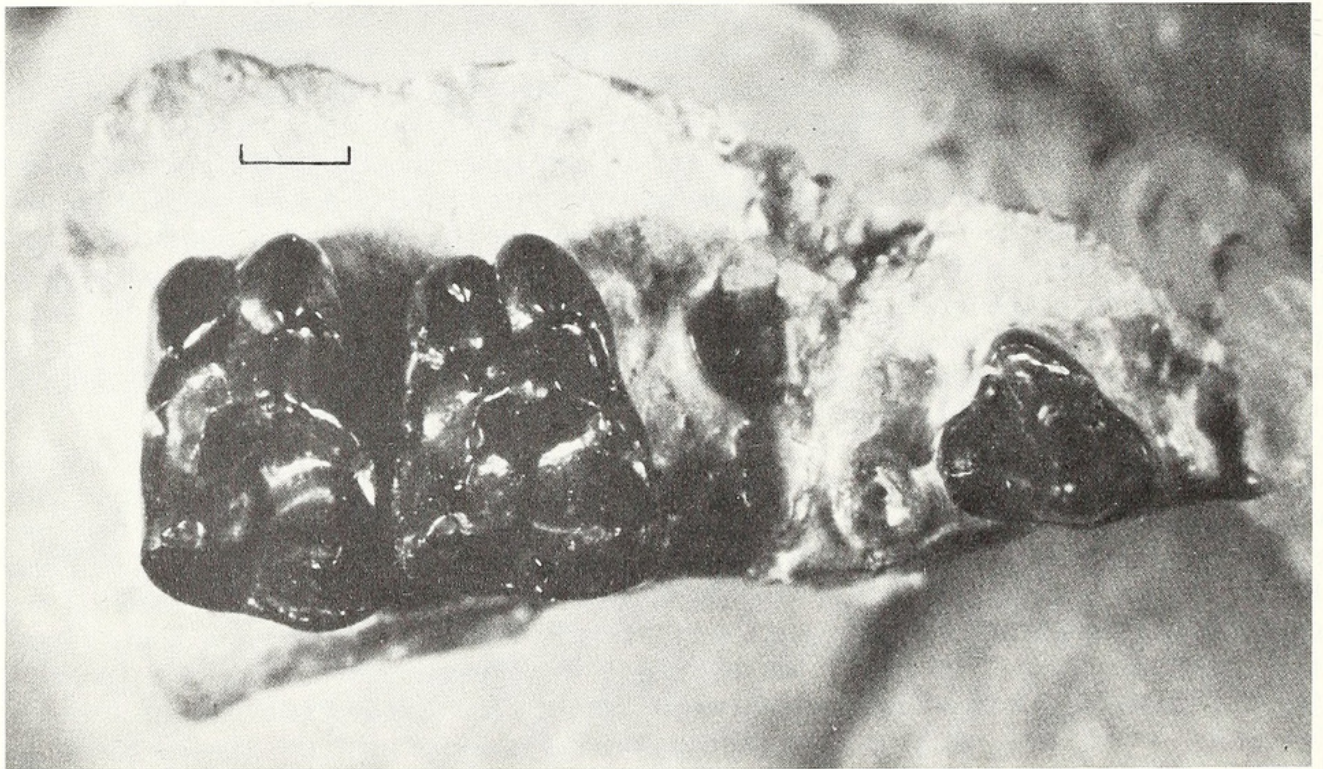
specimens to *A. roselli*, and claimed that *P. huerzeleri* merely represented the lower dentition of *P. pygmaeus*.

DESCRIPTION AND DISCUSSION

Whatever their disagreements, recent authors have thus unequivocally assigned *P. helveticus* to the family Adapidae, and have noted particular resemblances to *Anchomomys*. Recently, however, we have had the opportunity to examine the type specimen and other material of *P. helveticus* in the collections of the Naturhistorisches Museum, Basel (BNM), and it is clear to us that recent assessments of the form's affinities are inaccurate. Since statements about the relationships of *Periconodon* have been made liberally since the time of Stehlin without more than passing reference to the morphologies involved, we describe the pertinent material below.

The holotype of *P. helveticus*, BNM Ef 366 from the Huppersand locality of Egerkingen (text-fig. 1), consists of a partial left maxilla containing the penultimate premolar, M^{1-2} , three roots for the last premolar, two alveoli for M^3 , and a partial alveolus anterior to the preserved premolar. The remaining premolar appears to be three-rooted; it is a simple tooth, essentially single-cusped, and is premolariform although high-crowned. M^{1-2} are markedly transverse; there is a very long lingual slope to the protocone, resulting in a very broad but truncated trigon. The buccal cusps are moderately compressed, and the pre- and postprotocristae are sharp. The preprotocrista in M^{1-2} swings anteriorly around the paracone and terminates in a small parastyle; in M^1 this crest bears a small paraconule that is barely represented on M^2 . Both molars show distinct buccal cingulae. M^1 is slightly smaller than M^2 , from which it also differs in having a small style on the lingual face of the hypocone. M^3 may, on the evidence of the alveoli, have been subequal in size to M^2 .

In sum, the upper molar morphology of *P. helveticus* is totally un-adapid. In those characters of the upper dentition in which *P. helveticus* departs most markedly from the adapids, however, it closely approaches the omomyids with which it was associated by Simons (1962) and, by implication, earlier authors. The strong transverseness of the upper molars, the broadly parabolic protocristae, the development of the hypocone, and particularly the long lingual slope of the strong protocone, all



TEXT-FIG. 1. BNM Ef 366, type of *Periconodon helveticus*: occlusal view. Scale represents 1 mm.

point to the omomyid affinities of *Periconodon*, which most closely resembles *Washakius* among North American primates.

Just as its identification as an adapid is inappropriate, the synonymy of *P. helveticus* with *Anchomomys pygmaeus* favoured by Gingerich (1977) and Szalay (Szalay and Delson 1979) is unwarranted. The type specimen of *A. pygmaeus* is BNM Ef 367, an upper first molar from Egerkingen. The species was first described by Rüttimeyer (1890) as *Caenopithecus pygmaeus*, and was transferred to *Anchomomys* by Stehlin (1916), who also allocated to it BNM Ef 372, another upper molar from Egerkingen. Other material subsequently referred to *A. pygmaeus* by Szalay (1974) does not belong in the species, as Gingerich (1977) also recognized; we will discuss it elsewhere. The type M¹ lacks a buccal cingulum but shows traces of buccal enamel pillars on the rather buccolingually compressed paracone and metacone. A large paraconule is present, and a diminutive metaconule; there is a small but distinct parastyle but barely a hint of a metastyle. A precingulum extends from the parastyle and terminates at the base of the protocone in a small style. The hypocone is more like a shelf than a cusp, and is confluent with a postcingulum. The protocristae are broad and the trigon basin is truncated but deep. The referred M² Ef 372 is very similar to the tooth just described. Together, these two teeth are totally distinctive, and the relationships of the species they represent are unclear to us. Certainly no special affinity of *A. pygmaeus* to *Periconodon* is indicated.

The type specimen of Gingerich's new species *P. huerzeleri* is a right dentary from Bouxwiller, BNM Bchs 495, that preserves the last premolar and the three molars. Direct comparison of this specimen with the type of *P. helveticus* is impossible, since the latter is represented by the upper dentition. However, it is clear that while the latter aligns with Omomyidae, '*P.*' *huerzeleri* does not. None of the molars of Bchs 495 bears a well-defined paraconid, while this cusp is characteristically distinct on the lower molars of omomyids, especially M₁. The last premolar of Bchs 495 is highly compressed laterally, and is relatively long; it bears a very pronounced, centrally positioned hypoconid, and a smaller paraconid anteriorly. A strong buccal cingulid connects these two cusps, which are dwarfed by the protoconid. In omomyids, on the other hand, the last lower premolar, although dominated by the protoconid, bears a broad, tear-shaped talonid that terminates posteriorly in a wide, transverse 'heel'. Paraconid development is variable. Since Bchs 495 thus fails to show any convincing evidence of omomyid affinities, there is no obvious reason for allocating it to a new species of *Periconodon*. In fact, among known primates Bchs 495 is most reminiscent of certain cheirogaleids, most notably *Mirza* and *Phaner*, particularly, in the morphology of the last premolar, the latter.

The holotype of Gingerich's other new species of *Periconodon*, *P. lemoinei*, is an isolated lower right molar (Louis coll. Gr-106) from the French early Eocene site of Grauves. This specimen is heavily worn. The trigonid is not greatly compressed, and bears a broad paracristid that terminates at the base of the metaconid, from which it is separated by a distinct groove. The cristid obliqua seems to have arched across to meet the metaconid, thus forming a deep hypoflexid notch. A rather arcuate hypocristid encloses the talonid basin, and a well-developed buccal cingulid is present, especially around the trigonid and posterior to the hypoconulid. Like BNM Bchs 495, Gr-106 is totally non-omomyid in aspect and thus provides no grounds for its allocation to *Periconodon*. In its trigonid construction, and particularly in its downwardly sweeping, shelf-like paracristid that fails to become confluent with the base of the metaconid, this tooth is quite characteristic of *Protoadapis*, the genus to which we prefer to assign it.

Conclusion

We conclude that the affinities of *Periconodon* lie not with the lemuriform primate family Adapidae, but with the tarsiiform family Omomyidae. This latter family is otherwise known only from North America; and this confirmation of the existence of a European representative enhances the growing realization that the Eocene primate faunas of Europe and North America show a greater unity than is generally believed. *Periconodon* is, moreover, a clearly distinct genus, showing no affinities with any species that has ever been referred to the genus *Anchomomys*. As currently known this genus is

monotypic, containing only the type species *P. helveticus*; two new species recently erected within *Periconodon* have been misattributed.

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