

A REVIEW OF THE EUROPEAN  
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AND SOME ALLIED FORMS

JEFFREY H. SCHWARTZ AND IAN TATTERSALL

VOLUME 57 : PART 5  
ANTHROPOLOGICAL PAPERS OF  
THE AMERICAN MUSEUM OF NATURAL HISTORY  
NEW YORK : 1983





# A REVIEW OF THE EUROPEAN PRIMATE GENUS *ANCHOMOMYS* AND SOME ALLIED FORMS

JEFFREY H. SCHWARTZ

*Research Associate, Department of Anthropology  
American Museum of Natural History  
Associate Professor, Department of Anthropology  
University of Pittsburgh*

IAN TATTERSALL

*Curator, Department of Anthropology  
American Museum of Natural History*

This Part completes Volume 57.

ANTHROPOLOGICAL PAPERS OF  
THE AMERICAN MUSEUM OF NATURAL HISTORY

Volume 57, part 5, pages 344–352, figures 1–4

Issued January 28, 1983

Price: \$1.60 a copy

## ABSTRACT

We review the history of study of the European Eocene primate fossils that at one time or another have been assigned to the genus *Anchomomys*. Critical re-evaluation of this material reveals that only the type species, *A. gaillardi*, is properly regarded as belonging to *Anchomomys*. "*Anchomomys*" *pygmaeus*, to which much material has recently been referred, is in fact represented only by two teeth, for which we erect a new genus. Szalay's (1974) transfer of "*Anchomomys*" *quercyi* to the new genus *Huerzeleris* is confirmed, and

Gingerich's (1977) "*Anchomomys*" *stehlini* is allocated to a new genus. We also confirm Szalay's (1974) conclusion that Teilhard's (1916–1921) "*Anchomomys*" *latidens* should be excluded from Primates. The affinities of *gaillardi* appear to lie with Cheirogaleidae, as do those of *quercyi*; the relationships of *pygmaeus*, whose suggested synonymy with *Periconodon* is rejected, may lie with the galagids. Finally, *stehlini* is morphologically reminiscent of some North American Eocene primates.

## INTRODUCTION

The primate genus *Anchomomys* was established in 1916 by Stehlin, who based his new species *Anchomomys gaillardi* upon associated left maxillary and mandibular fragments from the French middle Eocene (Auversian = early Bartonian) site of Lissieu. These specimens (fig. 1) are now both catalogued as L 46 bis in the collections of the Faculté des Sciences, Université de Lyon (UL). In the same publication Stehlin also described and illustrated a left dentary, Basel Naturhistorisches Museum (BNM) Eh 748 (fig. 4), and an isolated left M<sub>3</sub>, BNM Eh 794, from the slightly earlier Swiss site of Egerkingen, both of which he referred to *Anchomomys* cf. *gaillardi*. He further transferred to *Anchomomys*, as the species *A. pygmaeus*, Rüttimeyer's (1890) *Caenopithecus pygmaeus*, an Egerkingen species represented by BNM Ef 367 (fig. 3), a right M<sup>1</sup>, and added to it BNM Ef 372, a right M<sup>2</sup>. To complete the roster of species assigned by him to *Anchomomys*, Stehlin (1916) based the species *A. quercyi* on BNM QH 470 (fig. 2), a left maxilla with three teeth that had been recovered from one of the upper Eocene phosphorite deposits of Quercy, France. As the generic name he bestowed upon these specimens suggests, Stehlin was impressed by the resemblances he perceived between them and the North American omomyid *Omomys*. Among European primates he most closely compared them with *Pronycticebus*, a form that he believed showed tarsiod affinities; he excluded both *Pronycticebus* and *Anchomomys* from the direct tarsier lineage, but

believed that they could have been related to the Eocene ancestor of *Tarsius*.

Stehlin's analysis set the tone for discussion of *Anchomomys* over the next two decades. In 1921 Teilhard de Chardin (1916–1921) described another species of *Anchomomys*, *A. latidens*, represented by a badly crushed cranium with upper cheek dentition from the Quercy phosphorites. Although at that time Teilhard remarked that *Anchomomys* resembled *Galago* in certain details of the upper dentition, he rejected any strepsirrhine affinity for the form, essentially because its premolar morphology differed from that of *Lemur* and its allies. Instead, Teilhard opted to regard *Anchomomys* as a tarsiod offshoot, an arrangement also adopted by Gregory in 1922 and Abel in 1931. It was thus not until Clark (1934) restudied the skull of *Pronycticebus* and concluded that the genus should properly be classified as belonging to Adapinae, that the way was opened for reinterpretation of *Anchomomys* as an adapine also, a step formally taken in 1940 by Simpson. Subsequent authors (notably Simons, 1962; Szalay, 1974; Russell, Louis and Savage, 1967; Gingerich, 1977; Szalay and Delson, 1979) have uniformly followed Simpson's allocation of *Anchomomys* to the subfamily Adapinae, or at least to the family Adapidae.

The dentition of *Anchomomys* and its bearing on the affinities of the genus were discussed at some length by Simons (1962), who emphasized the resemblances between *Anchomomys* and the Kenyan Miocene lo-

risoid *Progalago*. He was particularly struck by the similarities he noted between *Progalago doriae* and *Anchomomys quercyi*, and clearly implied his belief in *Anchomomys* as a lorisoïd ancestor.

The first major taxonomic revision of the species of *Anchomomys* was carried out by Szalay (1974). In this contribution Szalay firmly allocated all Egerkingen material that had previously been referred to any species of *Anchomomys* to *A. pygmaeus*. He also referred to this species several other Egerkingen specimens, including BNM En 1, a partial right dentary with the last premolar and all molars preserved. At the same time Szalay separated Stehlin's *Anchomomys quercyi* from the other species of *Anchomomys*, placing it in its own new genus *Huerzeleris*. Finally, he excluded Teilhard's *A. latidens* from Primates altogether, regarding it as an erinaceid insectivoran. Shortly thereafter, Gingerich (1977) also radically revised *Anchomomys*. He removed the Egerkingen dentary BNM En 1 from *Anchomomys pygmaeus* and made it the type (and only specimen) of a new species, *Anchomomys stehlini*. Gingerich also synonymized *Anchomomys pygmaeus* with Stehlin's *Periconodon helveticus*, a species based on a maxillary fragment originally attributed by Rütimeyer (1891) to *Pelycodus*. He concluded that *Anchomomys* was

descended from *Periconodon*, and rejected Szalay's genus *Huerzeleris*. Most recently, Szalay (Szalay and Delson, 1979) concurred in Gingerich's transfer of the original material of *pygmaeus* to *Periconodon*; however, he now transferred to *gaillardi* the specimens he had in 1974 added to the hypodigm of *pygmaeus*. He also maintained the generic distinction of his own *Huerzeleris*, while rejecting Gingerich's *stehlini* as a species of *Anchomomys* distinct from *gaillardi*. At the same time, Szalay created Anchomomyini, a new subtribe within the subfamily Adapinae, to contain *Anchomomys*, *Huerzeleris*, and *Periconodon*.

#### ACKNOWLEDGMENTS

We thank Drs. Burkart Engesser and Johannes Hürzeler of the Basel Naturhistorisches Museum for their help and for permitting us to study material in their care; also M. Marc Godinot of the Faculté des Sciences de Montpellier for allowing us access to Université de Lyon specimens currently on loan to him. Travel to European museums was made possible by the generosity of the Richard Lounsbery Foundation. This is Contribution No. 2 of the Lounsbery Laboratory, Department of Anthropology, American Museum of Natural History.

#### DISCUSSION

As the tortuous history summarized above amply suggests, the systematics of *Anchomomys* and its allies are by now in a state of profound confusion. This confusion results partly from legitimate differences in interpretation, but to some extent it is because recent discussions of these forms have tended to neglect substantive reference either to the actual morphologies involved, or to the histories of study of the specimens at issue, so that the "starting point" taxonomies of the authors are at times unclear. Evidently, clarification and a fresh appraisal are badly needed, and it is this that we attempt to provide here. In doing so, we have found it necessary to erect two new genera. We recognize that the creation of new genera on the basis

of old specimens goes somewhat against the spirit of the times; nevertheless, we have chosen to erect new genera where compelling morphological reasons exist, since to leave disparate material classified together on what amounts to no better justification than tradition can lead to serious distortions, as Szalay (1974) explicitly emphasized.

The type material of *Anchomomys gaillardi* consists of a left maxilla with  $M^{1-3}$ , and an associated left partial mandible with  $M_{1-3}$ , both UL L 46 bis (fig. 1). In the maxilla it is possible to distinguish the posterior margin of the zygoma, which originates above the posterior edge of  $M^3$ ; it is rather gracile, and curves upward at a relatively sharp angle, without much flare. On all upper molars the

trigon is the dominant portion of the tooth.  $M^2$  is the most transverse tooth, and is broader than  $M^1$ . On all upper molars the preprotocristae bear a low but distinct paraconule, and become confluent with the parastylar region anterior to the paracone. Conules are lacking on the weaker postprotocristae. A postcingulum is present on all upper molars; it is least prominent on  $M^3$ , where it fades out well before reaching the lingual face. On  $M^{1-2}$  this crest is more shelflike, and terminates in a small hypocone. The postcingulum is most shelflike and the hypocone most distinct on  $M^1$ . All upper molars bear a weak precingulum that fades out just superior to the apex of the protocone.  $M^{1-2}$  possess distinct postmetacristae that arc buccally and into the metastylar region. The buccal cusps are minimally compressed, but are accentuated by distinct centrocristae.

The lower molars of *Anchomomys gaillardi* UL L 46 bis are characterized by an emphasis on mesiodistal length.  $M_3$  is narrower and less filled-out than the other lower molars, and is reminiscent of lorisoid strepsirrhines, especially cheirogaleids. All molars have a fairly deep hypoflexid notch that becomes less shallow in the sequence  $M_1$ – $M_3$  as a result of the buccal migration of the anterior terminus of the cristid obliqua, which meets the metaconid only on  $M_1$ . The trigonids are dominated by the protoconid and metaconid, which are more oblique on  $M_{1-2}$  than on  $M_3$ ; these cusps are confluent at their bases, and form a sheer wall facing on the talonid. All lower molars lack a paraconid and are characterized by a sharp paracristid that proceeds anteriorly down the face of the protoconid, then turns back to terminate at the base of the metaconid. There is no trace of a hypoconulid on  $M_{1-2}$ , but the talonid heel of  $M_3$  is well developed, with a large, centrally placed hypoconulid. The hypocristid of  $M_{1-2}$  is weak but discernible. All lower molars bear buccal cingulids that are most prominent in the region of the trigonid. The mandible is robust.

Referred material from Lissieu is generally similar to the type maxilla and dentary. UL L 46, a left dentary with  $M_{1-2}$ , differs from the type mandible in being a little less deep and robust and in displaying a more medially-swinging cristid obliqua on  $M_2$ . A referred

$M_2$  (also numbered L 46 bis) is similar to its homologue in the type except in having a slightly flattened area near the base of the hypoconid that hints at a hypoconulid; and an  $M_1$  of the same number differs from that in the type only in having a somewhat more compressed talonid.

Comparison of the morphology of Lissieu *Anchomomys gaillardi* with that of other strepsirrhines, living and extinct, reveals that its similarities lie broadly with the lorisoids, and particularly with *Microcebus*. Like *Anchomomys*, lorisoids are characterized by having the protoconid and metaconid obliquely set, confluent at their bases, and forming a sheer posterior trigonid wall, especially on  $M_{1-2}$ . These primates also lack a paraconid, but develop a distinct paracristid that runs down the face of the protoconid to turn at a sharp angle toward the metaconid. In cheirogaleids especially, the heel of  $M_3$  (secondarily lacking in *Phaner*) is more lingually placed than in *A. gaillardi*, but both the fossil and living taxa show a distinctive broad, shallow notch between the hypoconid and hypoconulid. In the upper dentition cheirogaleids are primitive among lorisoids in their molar morphology, and this applies to *Anchomomys* also. Particular resemblances to *Microcebus* include the compression and angulation of the metacone, and the accentuation of the centrocristae. The distinct paraconules of *A. gaillardi* are absent in *Microcebus*, but the two do resemble each other in the weakness of the preprotocristae on all upper molars, in the general disposition of the cusps, in the excavation of the trigon basin, and in the sheeriness of the posterior face of the trigon. Generally, both *Microcebus* and *A. gaillardi* show a conformation of the upper molars that is primitive for the lorisoid clade, with a triangular structure lacking much talon elaboration. The comparison between the lower molars of *Microcebus* and those of *A. gaillardi* is less close, largely because of the notable elongation of these teeth in the latter, and because the cristid obliqua of *Microcebus* does not meet the metaconid on  $M_1$ . The elongated lower molars and in-swinging cristid obliqua of *A. gaillardi* are probably derived characteristics, in which *Microcebus* reflects a more primitive condition.



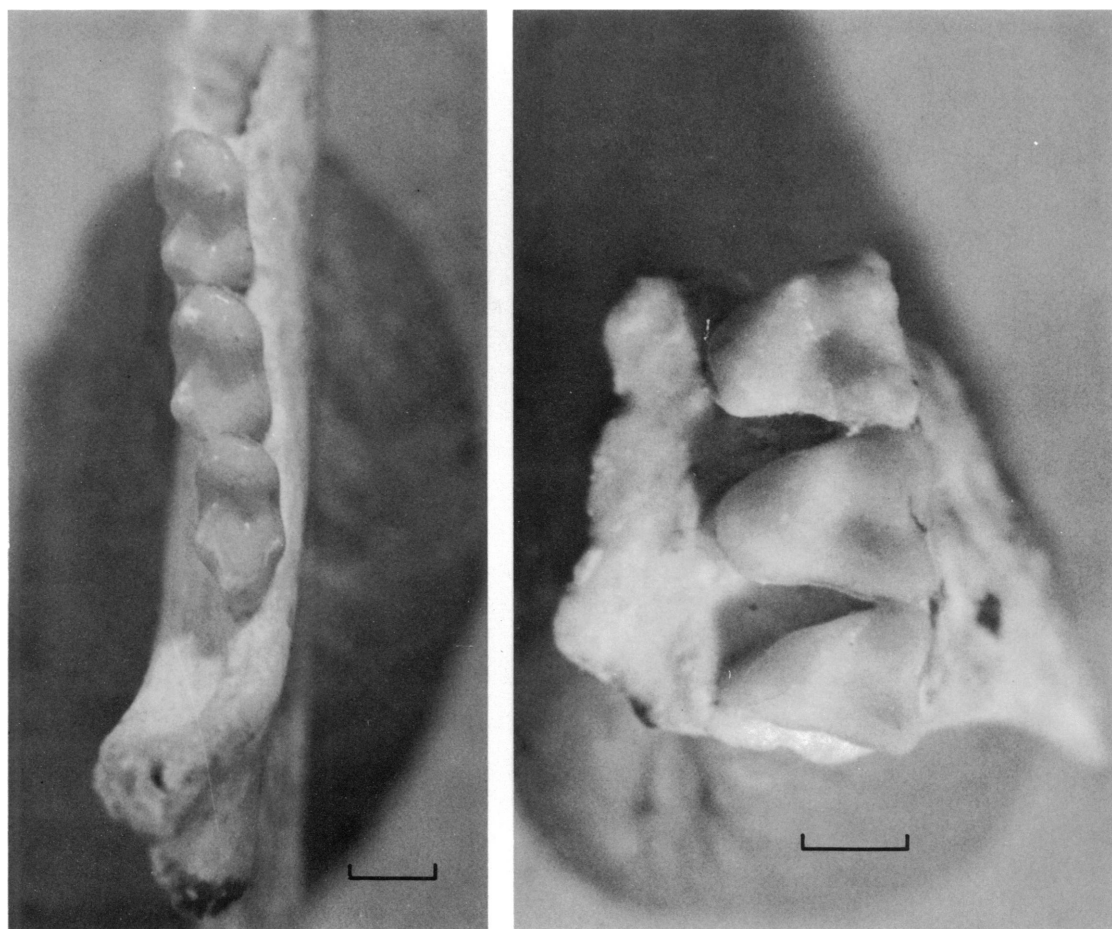


FIG. 1. Type material of *Anchomomys gaillardi* from Lissieu, UL L 46 bis. Each scale represents 1 mm.

The type material of *Anchomomys pygmaeus* is much less satisfactory than that of the generitype, consisting as it does of a single right M<sup>1</sup>, BNM Ef 367 (fig. 3). Stehlin additionally, and correctly, referred to *pygmaeus* another Egerkingen upper molar, BNM Ef 372, which closely resembles the type. Together these teeth are quite distinctive, and they differ in many features from their homologues in the generitype. These features argue strongly for generic distinction of *pygmaeus* from *gaillardi*, and we describe and discuss the new genus that these specimens represent below.

None of the other material that has at one time or another been allocated to *pygmaeus*

can be viewed as belonging to the same species or even to the same genus. The left dentary BNM En 1 (fig. 4) allocated by Szalay to *pygmaeus* in 1974, and to *gaillardi* in 1979, is considerably smaller than either and was justifiably assigned to the new species *stehlini* by Gingerich in 1977. Also referable to this new species is BNM Eh 748 (fig. 4), the Egerkingen dentary originally placed in *Anchomomys* cf. *gaillardi* by Stehlin. Together these specimens provide evidence of yet another distinct primate genus, which we name below.

Stehlin's *Anchomomys quercyi* was transferred by Szalay (1974) to the new genus *Huerzeleris*. There can be no question that such generic separation is justified. The max-

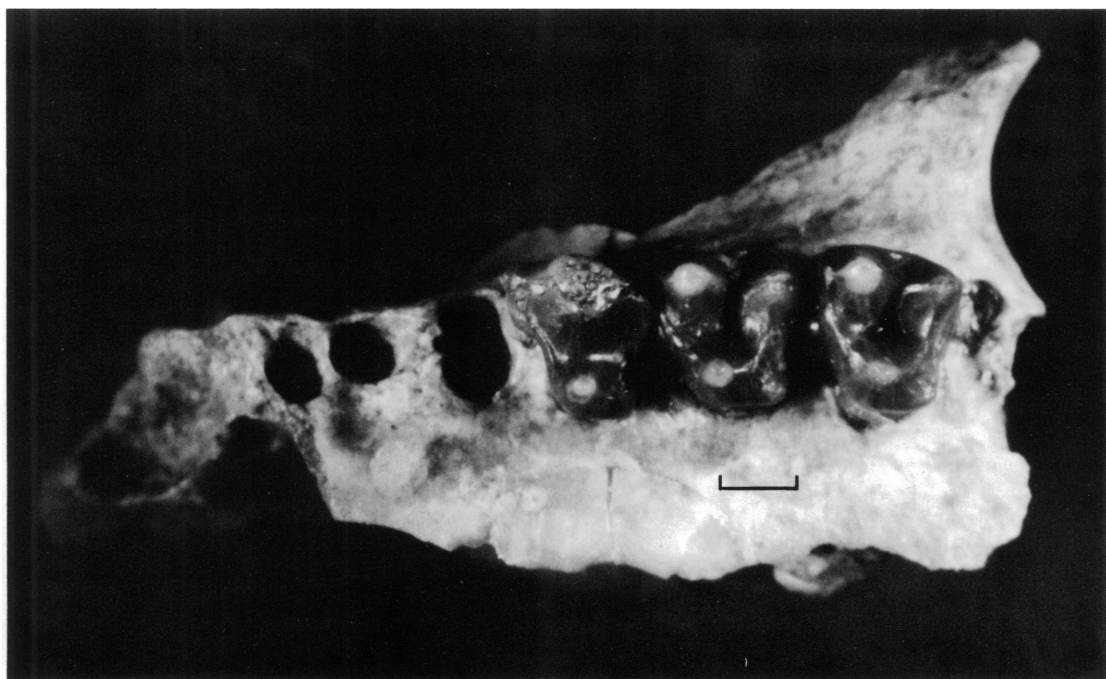


FIG. 2. Holotype of *Huerzeleris quercyi*, BNM QH 470. Scale represents 1 mm.

illa of the type (and only) specimen (fig. 2) bears a large infraorbital foramen that opens just anterior to the last premolar. The zygomatic arch originated at about the midpoint of  $M^3$  (as judged from vacant alveolae). The anterior masseteric tubercle is strong, prominent and rounded, and confined to the region above  $M^2$ . No premaxillary component appears to be preserved in this specimen. The two upper molars present are similar in lacking conule development; at best there are slight enamel swellings on the rather weak pre- and postprotocristae. The preprotocrista skirts the large paracone and terminates in a minute parastyle. Each molar possesses a small hypocone at the terminus of a narrow postcingulum; the paracone is slightly bigger on  $M^1$  than on  $M^2$ . Both teeth are distinguished by their lack of transverseness and by their broad trigons. The last premolar is a three-rooted tooth dominated by the paracone, which bears small anterior and posterior styles. This tooth is slightly greater in width than either molar and has a protocone of moderate size. Anterior to the last premolar is an hourglass-shaped alveolus that

presumably housed a pair of fused roots, and in front of this is a single posteriorly inclined alveolus that presumably accommodated another root of the same tooth. Mesial to this is a small alveolus that lies behind a large excavated area. It seems likely that the small alveolus housed a single-rooted tooth, and the large one in front of it, a big tooth. The preserved root and two broken alveoli that represent  $M^3$  suggest that this molar was very little smaller than  $M^2$ .

*Huerzeleris quercyi* is remarkable for the resemblances it shows to those cheirogaleids that retain a relatively primitive condition of the upper cheek teeth. *Phaner*, *Mirza*, and *Microcebus* show somewhat more lingual elaboration of the upper molars than is seen in *Huerzeleris* (although much less than in the more derived lorisoids); but the underlying structure of the molars is closely similar, and *Huerzeleris* is plausibly interpreted as evincing an upper molar morphology close to the condition primitive for Cheirogaleidae. The modest expansion of the hypocone region in the last upper premolar of *Huerzeleris* does, however, appear somewhat



derived relative to the simpler condition seen particularly in *Mirza* and *Phaner*; but, again, the basic morphology of the tooth is the same throughout the group. Among the cheirolaids *Phaner* provides the closest match with *Huerzeleris*; both genera have subsquare upper molars that emphasize the mesiodistal length of the dominant trigon.

Examination of the type and only specimen of Teilhard's (1916–1921) *Anchomomys latidens* confirms Szalay's (1974) contention that the form is not primate; it is possible that the form is an erinaceid insectivoran, as Szalay suggested, if a somewhat atypical one. In any event, its affinities do not lie with any known primate taxon.

## SYSTEMATICS

### ORDER PRIMATES

#### SUBORDER STREPSIRHINI

#### *FENDANTIA*, NEW GENUS

*Caenopithecus* Rüttimeyer, 1890.

*Anchomomys* Stehlin, 1916.

*Anchomomys*: Szalay, 1974.

*Periconodon*: Gingerich, 1977.

*Periconodon*: Szalay and Delson, 1979.

TYPE SPECIES: *Fendantia pygmaea* (Rüttimeyer, 1890).

INCLUDED SPECIES: Type species only.

DISTRIBUTION: Lutetian or Bartonian of Switzerland.

DIAGNOSIS: As for type species.

DISCUSSION: See under type species.

ETYMOLOGY: To honor another notable product of Switzerland.

#### *Fendantia pygmaea* (Rüttimeyer, 1890)

*Caenopithecus pygmaeus* Rüttimeyer, 1890.

*Anchomomys pygmaeus*: Stehlin, 1916.

*Anchomomys pygmaeus*: Szalay, 1974.

*Periconodon pygmaeus*: Gingerich, 1977.

*Periconodon pygmaeus*: Szalay and Delson, 1979.

HOLOTYPE: BNM Ef 367, right M<sup>1</sup> (fig. 3).

TYPE LOCALITY: Egerkingen (Huppersand), Solothurn, Switzerland. Middle Eocene: Bartonian.

HYPODGM: Type plus BNM Ef 372, right upper molar.

DESCRIPTION AND EMENDED DIAGNOSIS: The type upper cheek tooth is cracked, but is otherwise in good condition, and preserves a distinctive morphology. The referred tooth, Ef 372, is in poorer condition but closely resembles the type in preserved morphology. The type lacks a buccal cingulum but shows traces of buccal enamel pillars on the rather

compressed paracone and metacone. There is a fairly large paraconule and a diminutive metaconule, a small but distinct parastyle, and the trace of a metastyle. A precingulum runs from the parastyle and terminates at the base of the protocone in a small swelling. The hypocone is more shelflike than cusplike, and is confluent with a rather broad postcingulum. The protocristae are broad, and the trigon basin is truncated but deep. The preprotocrista arcs around the paracone to meet the parastylar region. Perhaps the most distinctive feature of the tooth is a stout prehypocone crista that extends from the hypocone to join the protocone. *Fendantia pygmaea* is distinguished from *Anchomomys* (and indeed, from all the fossils to which it has been compared, except *Periconodon*) by the presence of a prehypocone crista. However, this structure in *pygmaea* is much stouter and shorter than that of *Periconodon*, reflecting the lack of the long protocone slope characteristic of *Periconodon*, which is in fact an omomyid (Tattersall and Schwartz, in press). The buccolingual cuspal compression and the accentuation of crests, especially the protocristae, seen in *pygmaea*, are somewhat reminiscent of *Adapis* and its closest allies, in which, however, this tendency is much more greatly marked.

DISCUSSION: Both Gingerich (1977) and Szalay (Szalay and Delson, 1979) have recently referred *pygmaea* to the genus *Periconodon*. Presumably, this transfer was made on the basis of the development of the lingual aspect of the protocone region. However, such development in *pygmaea* is of considerably lesser degree than in *Periconodon*, from which it differs strongly in other respects. The closest similarities to *pygmaea* are to be found

among the extant lorisooids: as a clade the galagids and lorisooids are also distinguished by the possession of a prehypocone crista, at least on  $M^1$ . Other features that point toward broad lorisoiform affinities for *Fendantia pygmaea* include the linking of the preprotocrista with the parastylar region; within this larger group galagid affinities are further suggested by the relatively broad but deep trigon basin bounded by a weak postprotocrista that bears a diminished metaconule.

LAURASIA, NEW GENUS

*Anchomomys* Stehlin, 1916.  
*Anchomomys*: Szalay, 1974.  
*Anchomomys*: Gingerich, 1977.

TYPE SPECIES: *Laurasia stehlinae* (Gingerich, 1977).

INCLUDED SPECIES: Type species only.

DISTRIBUTION: Lutetian or Bartonian of Switzerland.

DIAGNOSIS: As for type species.

DISCUSSION: See under type species.

ETYMOLOGY: To express the widespread distribution of the group to which the genus belongs.

*Laurasia stehlinae* (Gingerich, 1977)

*Anchomomys* cf. *gaillardi* Stehlin, 1916.  
*Anchomomys pygmaeus*: Szalay, 1974.  
*Anchomomys stehlini*: Gingerich, 1977.  
*Anchomomys gaillardi*: Szalay and Delson, 1979.

HOLOTYPE: BNM En 1, right partial dentary with  $M_{1-3}$  and last premolar (fig. 4).

TYPE LOCALITY: Egerkingen locality gamma, Solothurn, Switzerland. Middle Eocene: early Bartonian or possibly late Lutetian.

HYPODIGM: Type plus BNM Eh 748, left mandibular ramus with  $M_{1-2}$  and numerous alveoli (fig. 4).

DESCRIPTION AND EMENDED DIAGNOSIS: In both known specimens  $M_1$  bears an arcuate cristid obliqua that contacts the metaconid, and an arcuate hypocristid that encloses the talon basin. The trigonid is open lingually, and is bounded anteriorly by a strong and inferiorly-sloping paraconid shelf. This tooth is especially characterized by its narrow breadth.  $M_2$  is similar to  $M_1$ , but differs in having a less robust paraconid shelf (although

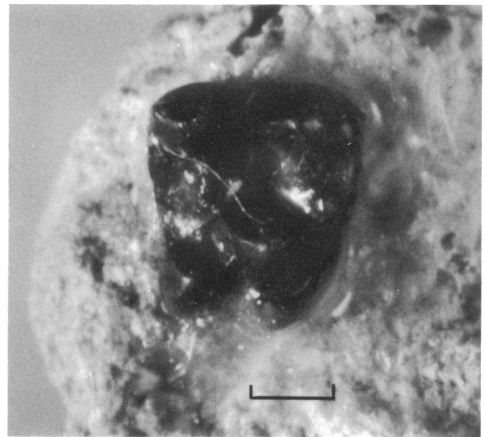


FIG. 3. Holotype of *Fendantia pygmaea*, BNM Ef 367. Scale represents 1 mm.

this may possibly be an artifact of breakage; the shelf is larger and less sloping in Eh 748 than in En 1). The cristid obliqua of  $M_2$  is somewhat arcuate, but it terminates medially, near the metaconid. The talonid basin of this tooth is completely enclosed, despite the presence of a talonid heel. All three molars bear buccal cingulids, especially well developed around the trigonid; on  $M_{1-2}$  the cingulid at the base of the protoconid is thickened to suggest a protostylid.

DISCUSSION: The arcuateness of the cristid obliqua, and its contact on  $M_{1-2}$  with the metaconid, together with the high, compressed trigonid, are reminiscent of *Smilodectes*. In contrast with the latter genus, however, *Laurasia stehlini* lacks a broad, medially-terminating paraconid shelf joined to the protoconid by a paracristid. It also lacks the entoconid-hypocristid groove characteristic of *Smilodectes*. In the rounding of the talonid and the enclosure of its basin, however, *L. stehlini* is more reminiscent of certain *Pelycodus*, e.g., *P. ralstoni*: forms that also display an arcuate cristid obliqua that meets the metaconid on  $M_1$ . In many features of its lower dentition, then, *Laurasia* is closer to North American than to European primates, and, indeed to certain of the more derived North American forms, such as *Smilodectes*, "*Notharctus*" *limosus*, and some *Copelemur*. This is particularly seen in the de-emphasis of the paraconids and the

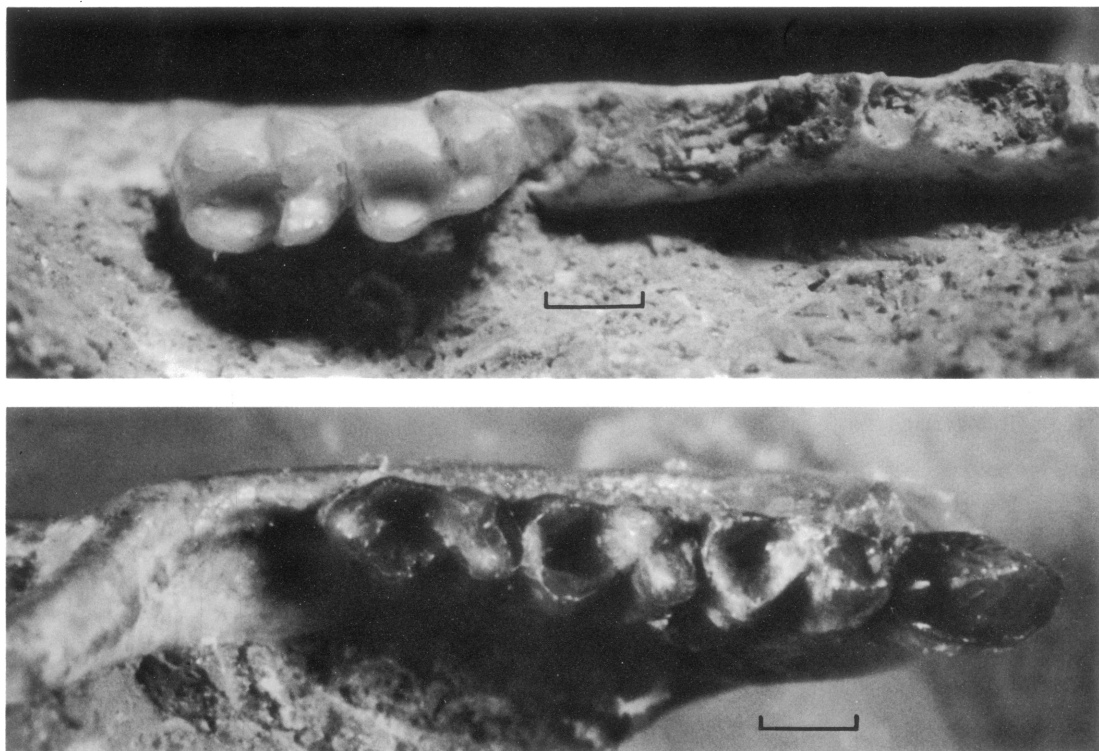


FIG. 4. Holotype of *Laurusia stehlinae*, BNM En 1. Scale represents 1 mm.

arcuateness of the medially directed cristid obliqua on all lower molars, especially  $M_{1-2}$ .

Clearly, the affinities of *Laurusia* lie with this major group.

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# ANTHROPOLOGICAL PAPERS OF THE AMERICAN MUSEUM OF NATURAL HISTORY



Volume 57  
1981–1983

PUBLISHED BY ORDER OF THE TRUSTEES  
NEW YORK : 1983

Edited by  
**FLORENCE BRAUNER**

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