THE PARAMYID RODENT *AILURAVUS* FROM THE MIDDLE AND LATE EOCENE OF EUROPE, AND ITS RELATIONSHIPS

by

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The complex taxonomic history of the paramyid rodent genus *Ailuravus* is reviewed. It has been described as *Hyracotherium*, as a creodont carnivore and as a lemuroid primate — errors at the ordinal level that are most unusual for a rodent. The genus is a member of the poorly known subfamily Ailuravinae, probably derived from some European Early Eocene species of *Paramys*. *Ailuravus* was a large arboreal paramyid with highly rugose cheek teeth, very well developed hypocone, and a remarkably weak lower incisor. It was tropical to subtropical. Three named species are recognized, *A. macrurus* from the Lutetian of Messel; the genotype, *A. picteti*, from Egerkingen, Buchsweiler and the Geiseltal, slightly later in the Lutetian; and *A. stehlinschaubi*, new name, from the Bartonian of Mormont-Eclépens and Robiac. One or more unnamed species are present in the Ypresian of Cuis. The species are close to a phyletic sequence. No later representatives of the genus are known. The late Eocene to earliest Oligocene North American paramyid *Mytonomys*, whose relationships have been obscure, is tentatively referred to the Ailuravinae.

On passe en revue l'histoire taxonomique complexe du genre *Ailuravus*, un rongeur paramyidé. On l'a considéré comme un représentant du genre *Hyracotherium*, comme un carnassier créodonte, et comme un primate lémuroïde — erreurs au niveau ordinal qui sont bien remarquables pour un rongeur. Le genre fait partie de la sous-famille Ailuravinae, encore mal connue. La sous-famille trouve probablement son origine dans une des espèces de *Paramys* de l'Eocène inférieur Européen. *Ailuravus* était un grand paramyidé arboricole avec des dents jugales très plissées, à hypocone bien développé, et une incisive inférieure très faible. Il était tropical ou sub-tropical. Trois espèces sont connues : *A. macrurus* du Lutétien de Messel; le type générique, *A. picteti*, d'Egerkingen, de Bouxwiller et du Geiseltal, un peu plus récent dans le Lutétien; et *A. stehlinschaubi*, nouveau nom, du Bartonien de Mormont-Eclépens et de Robiac. Des espèces non nommées se trouvent dans l'Yprésien de Cuis. Les espèces s'approchent d'une série phylétique. On ne connait pas de représentants plus récents du genre. Le genre paramyidé *Mytonomys*, provenant de l'Eocène supérieur et de l'Oligocène inférieur de l'Amérique du Nord, dont les affinités sont incertaines, est placé à titre d'hypothèse parmi les Ailuravinae.

Die komplexe Geschichte der Taxonomie des paramyiden Nagers *Ailuravus* wird untersucht. Man hatte ihn ehemals als *Hyracotherium*, als einen Creodontiden und als lemuroïden Primaten identifiziert — Irrtümer in der zuweisung zu Ordungen die für Nagetiere selten sind. Die Gattung gehört zu der Unterfamilie Ailuravinae, die nicht sehr bekannt ist Diese Unterfamilie leitet sich wahrscheinlich von einer Art der Gattung *Paramys* ab, welche in frühen Eozän Europas lebte. *Ailuravus* war ein grossen baumlebender Paramyide. Die Backenzähnen sind gerunzelt und mit einem grossen Hypoconus versehen; die untere Incisiven sind sehr kurz. Die Gattung war tropisch oder subtropisch. Drei Arten sind bekannt : *A. macrurus* aus dem Lutetien von Messel (der Genotypus), *A. picteti* aus dem späten Lutetien von Egerkingen Buchsweiler und dem Geiseltal, sowie *A. stehlinschaubi* (neu name) aus dem Bartonien von Mormont-Eclépens und Robiac. Einige nicht benannte Arten finden sich im Ypresien von Cuis. Die Arten bilden beinahe eine phyletische Reihe. Spätere Vorkommen der Gattung sind nicht bekannt. Die Nordamerikanische späteozäne bis frühoHgozäne Paramyidengattung *Mytonomys*, derem Verwandschaftsbeziehungen bisher unsicher waren, wird versuchsweise zu den Ailuravinae gerechnet.

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HISTORICAL REVIEW

Determination that a fossil does or does not belong to the Rodentia is normally very easy. As pointed out by Viret (1955, p. 1934, footnote 1), « Les cas d'erreur sont extrêmement rares. On cite celui du genre *Ailuravus* RÜT. qui n'est pas un Créodonte comme le pensait Rütimeyer, mais un Rongeur ». It is interesting that two other cases of ordinal error also occurred in material here referred to *Ailuravus*. The upper teeth later described as *Maurimontia picteti* were originally figured by Pictet and Humbert (1869, pl. 25, fig. 5) as *Hyracotherium*. The *Ailuravus* from the Geiseltal was first described as a primate, *Megachiromyoides schlüteri* (Weigelt, 1933 b, p. 109).

Rütimeyer (1891), in his description of Eocene mammals from Egerkingen, Canton Solothurn, Switzerland, described a new genus and species of supposed carnivore, *Ailuravus picteti* (p. 94-98), based on two third lower molars (pl. 7, fig. 18-19). In the same paper (1891, p. 89) he described, but did not illustrate, *Plesiarctomys schlosseri*, on the basis of an unspecified number of lower jaws with a cheek tooth length of 24 mm and a depth of jaw below P_4 of 16 mm. These values fit specimens of *Ailuravus picteti* in the Basel collections from Egerkingen, as noted by Stehlin and Schaub (1951, p. 21). Rütimeyer also tentatively referred three isolated teeth, one LP_4 and the others RM^3, to *Plesiarctomys*, illustrated on pl. 8, fig. 20. These are unquestionably *A. picteti* (Stehlin and Schaub, 1951, p. 354).

Haupt (1912, p. 17) listed *Plesiarctomys* sp. ... from the lignite of Messel, northeast of Darmstadt. Ten years later, he introduced a throroughly confusing taxonomic item (1922, p. 177) when he referred this form to a new genus and species to which he gave the name *Palaeomarmota sciuroides,* n.g., n.sp., and which he stated " ist nahe verwandt mit *Plesiarctomis Schlosseri* Rüt., der aber kein *Plesiarctomis* ist, sondern zu unserer neuen Gattung gehört " (Wood, 1970, p. 238). Haupt also stated (1922, p. 177, footnote 6): "Nach der Untersuchungen von Herrn STEHLIN-Basel hat *Plesiarctomys schlosseri* RÜT. mit der Gattung *Plesiarctomys* nichts zu tun, wie der Vortragende sich selbst überzeugt hat. Da ferner nach STEHLIN *Ailuravus picteti* RÜT., identisch ist mit *Plesiarct. schlosseri* RÜT. und die Messeler Art hiermit nahe verwandt ist, so müsste nach dem Prioritätsgesetze der Name *Ailuravus* gewählt werden. Da der Name *Ailuravus* aber völlig irreführend ist, da er einem Ahnen der Waschbären bedeutet, so hat sich der Vortragende entschlossen, in diesem Falle das Prioritätsgesetz zu durchbrechen und einem neuen Name eingeführt." *Palaeomarmota* is, of course, an exact synonym of *Ailuravus*. Haupt's new species, *Palaeomarmota sciuroides,* was a *nomen* *nudum* since there was neither any description nor the designation of a type, as pointed out by Weitzel (1949, p. 6).

Heller (1930) reported the occurrence of fossil mammals in the middle Eocene of the Geiseltal. He mentioned (p. 16-17) and figured (pl. 1, fig. 7-10) isolated rodent-like lower incisors. One of them was flattened on the median and markedly arched on the lateral side, which suggests the shape of an *Ailuravus* incisor. Furthermore, the enamel extended "auf der Aussenseite bis über die Mitte der ganzen Breite..." (*op. cit.*, p. 17). He stated that this was one of the larger incisors, which does not agree with measurements made from his illustrations (pl. 1, figs. 7-10. This tooth is fig. 9). At a guess, this tooth may belong to *Ailuravus*.

Weigelt (1933 b) reported on excellent material of primates from the Geiseltal, near Halle-a.-d.-S., including a new genus and species, *Megachiromyoides schlüteri*, clearly establishing its distinctness from all other primates. This taxon was based on the lower jaws, much of the skeleton and a badly disintegrated skull of a single individual. Weigelt later recognized that this was a rodent, which he considered to be a relative of *Marmota*, "aber viel primitiver bezahnte" (1942, p. 31).

Weitzel (1949) described the interesting material from the Braunkohl of Messel-bei-Darmstadt. There were a number of specimens of a large rodent, including two almost complete skeletons with skulls and another associated skull and jaws. These were described in detail (1949, p. 7, 11-14). He compared tooth patterns with those of *Ailuravus picteti*, in process of being redescribed in Stehlin's monograph on rodent teeth, then being completed by Schaub, and thought the two closely related. He also compared it with *Megachiromyoides schlüteri*, which he thought (1949, p. 11) was also very close to *A. picteti*. Weitzel described the Messel material as a new species, *Ailuravus macrurus*, which he regarded as a relative of *Paramys*, but which he placed (1949, p. 6) in the "U. Familie : Sciurinae".

In their monograph, Stehlin and Schaub refigured the teeth from Egerkingen (1951, fig. 19, 307, 309), together with specimens from the Geiseltal (fig. 20, 620). They combined, in the one species *A. picteti*, the various specimens that Rütimeyer had identified (1891) as *A. picteti*, *Plesiarctomys schlosseri* and *Plesiarctomys* ?, as well as the materials from Buchsweiler, the Geiseltal and Messel (1951, p. 354). They showed that *Ailuravus* was ultimately related to *Paramys*. They did not like Rütimeyer's transliteration that gave the name *Ailuravus*, and emended the spelling to *Aeluravus*, a change not justified under the rules of nomenclature. Schaub (Stehlin and Schaub, 1951, p. 354-355) discussed the relationships of *Ailuravus* and concluded that it was close to *Prosciurus* and *Plesiarctomys*. A rodent from Mormont-Eclépens, related to *Ailuravus*, was described as *Maurimontia picteti*, n.g., n.sp. (1951, p. 355; also p. 20-21, 206-207; fig. 18, 310).

Tobien (1954, p. 13-18; pl. 1, fig. 1; pl. 2, fig. 1) redescribed the material of *A. macrurus* from Messel, providing excellent illustrations of the cheek teeth, and recognizing it as a species more primitive than *A. picteti* (p. 16). He considered the material of *Ailuravus* from the Geiseltal to be more like the genotype, and presumably within the range of variation of that species (p. 17). He reverted to Rütimeyer's original spelling, *Ailuravus.*

Viret (1955, p. 1527 and fig. 1504) also used Rütimeyer's spelling. He stated that *Ailuravus* was "connu des sables yprésiens du Bassin de Paris, ainsi que du Lutétien d'Egerkingen et de Messel."

Later, Schaub (1958, p. 750) also used the original spelling of the generic name, and placed *Ailuravus* in the Prosciurinae, within the Family Ischyromyidae, of which the Paramyinae were another subfamily.

In his review of the Paramyidae, Wood (1962, p. 236-238) was unable to fit *Ailuravus* and *Maurimontia* into any of his subfamilies, and left them *incertae sedis* within the family. He did not accept Schaub's reference of them to the Prosciurinae, stating that "These two rodents cannot, it is believed, represent the ancestral stages of the prosciurines, but are more likely an independent line of Eocene paramyids, developing in Europe and paralleling the trends established slightly later in the Prosciurinae" (Wood, 1962, p. 238). Wood followed Tobien in recognizing two species of *Ailuravus,* and Stehlin and Schaub in accepting *Maurimontia* as a distinct genus closely related to *Ailuravus.* The descriptions of these forms (1962, p. 236-240) were based on the literature, and the illustrations (1962, fig. 88) were redrawn from those of Stehlin and Schaub (1951) and Tobien (1954).

During my visits to Basel and Darmstadt in 1966-67, I became convinced that *Ailuravus* was an isolated paramyid; that *A. picteti* and *A. macrurus* were validly distinct species, the latter being the more primitive; and that *Maurimontia* was not generically distinct from *Ailuravus, M. picteti* being a third valid species of *Ailuravus;* but I was still uncertain of the higher taxonomic placement of these rodents.

Michaux (1968, p. 155-162) solved the problem of what to do with *Ailuravus* and *Maurimontia* by erecting the new subfamily Ailuraviinae (*sic*) within the Paramyidae for these genera and a new, early Eocene genus, *Meldimys.* He identified two undescribed species of *Ailuravus* from the late Ypresian (Cuis).

Sudre (1969, p. 107, 114) cited "Ailuravinae gen. indét.", from Robiac-Nord, on the basis of identifications by Hartenberger.

Wood (1970, p. 237) stated that Rütimeyer "described, but did not illustrate, *Plesiarctomys schlosseri* from Egerkingen, on the basis of an unspecified number of lower jaws with a cheek tooth length of 24 mm and a depth of jaw below P_4 of 16 mm. These values fit specimens of *Ailuravus picteti* in the Basel collections. He also tentatively referred three isolated teeth to *Plesiarctomys,* illustrated on Pl. 8, fig. 20. These are unquestionably *A. picteti.*"

Hartenberger (1973, table 1) has reached the same conclusions that I did, that *Maurimontia* is not generically distinct from *Ailuravus.* He did not take any action with regard to renaming the species described by Stehlin and Schaub, citing it as "*Ailuravus* n.sp. (*Maurimontia picteti*)".

TAXONOMY AND DESCRIPTION

Family **PARAMYIDAE** MILLER and GIDLEY, 1918

For reasons explained in detail elsewhere (Wood, 1976), I desagree with the conclusions reached by Black (1968) that the Paramyidae should be reduced to a subfamily of the Ischyromyidae, and continue to recognize the Family Paramyidae. Wahlert has recently concluded that the cranial foramina of paramyids and ischyromyids show "that the two groups are distinct at the familial level" (1974, p. 407), and that the ischyromyids have a closer relationship to the cylindrodonts than to the paramyids and sciuravids.

Subfamily ***Ailuravinae*** MICHAUX, 1968 (emended spelling)

Subfamily Ailuraviinae, Michaux, 1968.

EMENDED DIAGNOSIS : Large paramyids; hypocone progressively enlarged but small in primitive forms such as *Meldimys*; protostyle large, sometimes approaching hypocone in size; M^3 unusually like M^{1-2}; P^3 usually present, with well-developed pattern; conules progressively elongate anteroposteriorly; entoconid generally isolated from large, rounded hypoconulid; large mesoconid in a strong ectolophid, sometimes isolated from buccal margin of crown; incisors proportionately small, both in cross section and in length, with thin enamel; cross section of lower incisors ovate, narrow end forward; lower incisors progressively end beneath M_2 ; arboreal, at least some forms with a long, hairy, prehensile tail; fore-limbs proportionately long; scaphoid and lunar not fused.

DISTRIBUTION : Eocene of Europe, probably late Eocene to perhaps earliest Oligocene of North America.

GENERA : *Meldimys* and *Ailuravus*; probably *Mytonomys*.

The Ailuravinae have been a very poorly understood group. As indicated above, they have been misclassified in an unusually large variety of ways. The best material so far reported is that from the Braunkohl of Messel, which includes some of the best preserved fossil rodents in the world, including skulls, skeletons and even hair. Perhaps because of their preservation in lignite, they have not received the attention they deserve in studies of rodent evolution. There is also good material from the Geiseltal, and a maxilla and several jaws from Switzerland.

The typical members of the subfamily were rather large rodents (Michaux, 1968, p. 162), that do not seem to have developed any great diversity. *Ailuravus* was about the size of a marmot (Tobien, 1955, p. 98, fig. 11). The tail was long, with about 40 caudal vertebrae (Tobien, 1969, p. 170, fig. 10), and was thickly covered with bushy hair (Tobien, 1969, p. 170). The total length was over 60 cm (Weitzel, 1949, p. 13). The curvature of the tail as preserved strongly suggests that it was prehensile (Tobien, 1969, fig. 10). The fore limbs were proportionately long (Weitzel, 1949, p. 11). "Bau und Proportionen der Extremitäten lassen den Schluss zu, dass *Ailuravus* ein Baumkletterer gewesen ist, dessen Fertigkeiten allerdings noch nicht zu der Vollkommenheit entwickelt waren wie bei unseren heutigen Eichhörnchen" (Tobien, 1955, p. 98). The lake at Messel in which the fossils were preserved "war von einer üppigen, subtropisch-tropischen Vegetation umgeben, die Urwald-artigen Charakter hatte" (Tobien, 1969, p. 175). The relative scarcity of ailuravine fossils, except at Messel and Egerkingen, was probably due to their restriction to thickly wooded areas. The environment of the Geiseltal area would seem to have been similar to that of Messel (Weigelt, 1933a, p. 15).

Ailuravus RÜTIMEYER, 1891

Ailuravus, Rütimeyer, 1891, p. 94.

Plesiarctomys, Rütimeyer, 1891, p. 89.

Plesiarctomys?, Rütimeyer, 1891, caption of pl. 8.

Palaeomarmota, Haupt, 1921, p. 177.

Plesiarctomis Rütimeyer, Haupt, 1921, p. 177.

Megachiromyoides, Weigelt, 1933, p. 109.

Aeluravus Rütimeyer, Stehlin and Schaub, 1951, p. 353.

TYPE : *A. picteti* RÜTIMEYER, 1891.

DISTRIBUTION : Lutetian, early Bartonian and possibly latest Ypresian of France, West Germany, East Germany and Switzerland.

DIAGNOSIS : Large paramyid, about the size of a marmot; cheek teeth with fundamental paramyid pattern, but progressively develop numerous accessory ridges with over-deepening of many valleys into deep, narrow trenches; P^3 primitively present and complex; P^4 progressively large and massive; hypocone and protostyle of subequal size, both progressively enlarging and both derived from cingulum; hypocone progressively set off from protocone by a lingual valley; M^3 unusually molariform, but hypocone often small; ectolophid of lower cheek teeth strong; mesoconid and hypoconulid progressively large and distinct; entoconid large, conical, and usually isolated from posterior cingulum; M_3 the largest lower tooth, P_4 usually the next largest; upper cheek teeth with three roots, lowers with two; lower incisor with thin enamel, rounded anterior face, and egg-shaped cross section, narrow end forward; lower incisor very short, ending in the genotype below the posterior part of M_2; *main mental foramen in front of* P_4, *often with one or more* accessory foramina; symphysis highly convolute, permitting no motion between rami; tail long, with about 40 caudal vertebrae, apparently prehensile; humerus, ulna and tibia subequal in length and only slightly shorter than femur; scaphoid and lunar separate bones; claws long.

DESCRIPTION.

One of the most striking features of the teeth of this genus is the progressive development of wrinkling and deepened valleys on the crowns of the cheek teeth. Superficially, this resembles the situation in the North American paramyid *Thisbemys,* but in *Ailuravus* the complexity seems to have developed by deepening pre-existing valleys, the general appearance being that of a maturely dissected landscape that has been uplifted, resulting in entrenched valleys. In *Thisbemys,* on the contrary, the complexity results from the formation of accessory ridges, which then become elevated. As a result, in *Thisbemys* wear will break through the enamel on the tops of the ridges, whereas in *Ailuravus* wear is concentrated on the major cusps and connecting crests, and accessory worn areas do not extend through the dentine. The Late Eocene (Uintan) *Mytonomys* (Wood, 1956; 1962, p. 227-231, fig. 84; Black, 1968 b) closely approximates *Ailuravus* in many features of the dental pattern.

P^3. — This tooth was probably lost during the evolution of the genus. There is no suggestion that it was present, and some evidence that it was not, in *A. stehlinschaubi* from Mormont-Eclepens (fig. 6 A); it was very large with a well developed pattern in *A. macrurus* from Messel (fig. 5 A); it is unknown in material of *A. picteti* from either Egerkingen or Buchsweiler. There was a fairly large and complex anterior premolar in *A. picteti* from the Geiseltal (Stehlin and Schaub, 1951, fig. 620), but it seems probably to have been dP^3, since it is associated with dP^4. However, the type of *Megachiromyoides schlüteri,* which was fully adult, includes an unworn third premolar, therefore presumably P^3 (Weigelt, 1933 b, pl. 3, fig. 4).

P^4. — This tooth is never fully molariform. The hypocone is small and the anterior cingulum cusp (protostyle) is also weak (fig. 5 A, 6 A). The mesostyle is prominent and protrudes laterally. The generic peculiarities are less well developed than on the molars.

M^{1-2}. — There is a very prominent protostyle, primitively as large as the hypocone (*A. macrurus,* fig. 5 A-B). Progressively, it is less distinct, although still strongly separated from the protocone (fig. 6 A). The protocone in *A. macrurus* is continued as a swelling into the median valley, as in many of the larger paramyids (Wood, 1962, fig. 9 E, K; 14 C; 33 A; 38; 58 C; 78 F), but progressively this swelling becomes a ridge that connects with the posterior side of the protoconule (fig. 6 A, M^1) and sometimes also reaches the anterior side of the metaconule (fig. 4 A; 6 A, M^2; 6 C). Both anterior and posterior cingula are well developed, and progressively acquire numerous small cuspular enlargements. The overdeepening of the valleys is particularly noteworthy in *A. stehlinschaubi*.

M^3. — As in typical paramyids, M^3 has a smaller hypocone than do M$^{1-2}$. It can be identified in about half the specimens as a posterolingual expansion of the marginal crest (fig. 1 A, B; 5 C). In one specimen of *A. picteti*, however (fig. 1 C), it is a very prominent cusp, separated by a deep notch from the protocone. On the other hand, in the type of *A. stehlinschaubi* (fig. 6 A) there is no suggestion of a hypocone. The connections of the buccal slope of the protocone with the protoconule and metaconule are as in the anterior molars. Mesostyles are likewise large, although in *A. macrurus* (fig. 5 C) it looks as though the cusp may be a metastyle rather than a mesostyle.

Lower Teeth. These are progressive for a paramyid in having a large mesoconid, generally connected with both the protoconid and the hypoconid to form an ectolophid (fig. 1 H-F, 2 C, 5 G, 6 E). The entoconid is almost always isolated from the hypoconulid (fig. 1 D-H, 2, 4 B, 5 E-F, 6 E). The protoconid is continued forward by an anterior arm that generally connects with the anterior end of the metaconid. There is usually a connection from the middle or posterior part of the protoconid to the rear of the metaconid, closing off a distinct trigonid basin (fig. 1 D, E, G; 2; 4 B; 5 E, F; 6 E), although occasionnally the connection is weak (fig. 5 F, M_3 ; 6 E, M_1). The lingual outlet of the talonid basin is usually dammed by what seems to be a metastylid rather than a mesostylid, although sometimes there seems to be no barrier here at all. The mesoconid frequently develops buccal connections with the hypoconid, but occasionally there are connections between the protoconid and hypoconid, separating the mesoconid from the margin of the tooth.

dP^4. — This tooth is known from *A. picteti* from the Geiseltal (Stehlin and Schaub, 1951, fig. 620) and in the type of *A. stehlinschaubi* (fig. 6 B; Stehlin and Schaub, 1951, fig. 18). It is much more advanced in its pattern than the molars, with a very prominent hypocone and nearly complete cingula except on the lingual side. The tooth is almost completely bilophate. The parastylar region is very prominent, and the tooth is much smaller than was P^4 or any of the molars (table 2).

Incisors. — *Ailuravus* is very unusual for a rodent in the rarity of known incisors, which are known only in *A. macrurus* and in the type of *Megachiromyoides* from the Geiseltal (Weigelt, 1933 b, pl. 1), unless one of Heller's isolated incisors from the Geiseltal belongs here (1930, pl. 1, fig. 9). There is an extensive coat of very thin enamel, reaching well past the middle of the lateral side of the tooth (fig. 5 D, G). The lower incisor is most like that of *Leptotomus* (Wood, 1962, fig. 22 H, I; 23 J; 25 C; 30 B-E), but the upper resembles those known from that genus only in the thinness and distribution of the enamel; of all the paramyids figured by Wood (1962), the cross section of the upper incisor resembles only those of *Franimys amherstensis* and *Rapamys* sp. (fig. 48 F, 52 J), both members of the Reithroparamyinae. The most striking feature of the lower incisor is its shortness. I

TABLE 1.
Measurements (in mm) of lower teeth of *Ailuravus*

	Ailuravus picteti Basel Nos.										*Ailuravus macrurus* Darmstadt Nos. Me							*Ailuravus stehlinschaubi* Lausanne 39561
	Em 3b Lecto-type	Em 3	Em 3a	Em 3c	Eg 588	Eg 589	Eg 590	Ek 192	BCHS 501	BCHS 566	67 Type	2		4	51	53	154	
	L	L	R	L	R	R	L	R	R	R	R	L	R	L	R	L	L	R
$P_4 - M_3$		23.5						24.0			17.6*			20.6*			10.6*	19.0
P_4 anteroposterior		5.69	5.76		5.56	6.10	5.88	5.57				5.75		4.78				5.10
width metalophid		4.00	3.80		4.10	4.97	4.47	4.27				ca.3.9		3.32				ca.3.8
width hypolophid		5.65	5.18		4.96	5.92	6.12	4.96				4.90		4.30				ca.4.4
M_1 anteroposterior		5.62	5.02					ca.5.7						4.70	4.79	4.80		4.35
width metalophid		3.96	3.90					4.31						3.70	3.69	3.68		3.69
width hypolophid		4.67	4.96					5.12						4.43	4.43	4.02		ca.4.0
M_2 anteroposterior		5.50	5.47					5.50				4.60		5.19	4.93			4.55
width metalophid		4.10	3.88					4.77						4.10	4.16			3.93
width hypolophid		4.85	5.10					5.29						4.63	4.65			4.28
M_3 anteroposterior	7.40	6.53		7.00				7.60	6.80	6.80			6.12	5.71	5.50			5.17
width metalophid	4.87	ca.4.5		4.90					4.68	4.34			4.83	4.27				4.35
width hypolophid	4.84	4.50		4.82					4.65	4.76			4.62	4.53	4.68			3.90
I_1 anteroposterior		alv. 4.18										4.23						
transverse		alv. 3.19										3.23						
ratio												.76						

* After Weitzel, 1949.

TABLE 2
Measurements (in mm) of upper teeth of *Ailuravus*

	Ailuravus picteti Basel Nos.				*Ailuravus macrurus*			Darmstadt Nos.Me			*Ailuravus stehlinschaubi*	
	Em 7	Em 8	Em 9	BCHS 6359	67 Type	2		3	50	52	Lausanne 39559, Type	Basel Mt 1767
	R	R	R	R	R	R	L	L	L	L	R	L
Length upper cheek teeth					21.5*						20.2	
dP^4 anteroposterior							3.15 #				5.14	
width protoloph							3.58 #				5.7+	
width metaloph											5.81	
P^4 anteroposterior						5.37	5.11	4.58			5.34	
width protoloph							6.25	5.57			5.30+	
width metaloph							6.68	5.77			5.95+	
M^1 anteroposterior							5.02			4.80	5.00	5.14
width protoloph							6.13			5.40	5.49	5.7+
width metaloph							5.55			4.95	5.42	5.81
M^2 anteroposterior				5.34		5.42					5.01	
width protoloph				5.80		5.86					5.37	
width metaloph				5.26		5.26					5.13	
M^3 anteroposterior	5.63	5.40	5.73				5.35		5.10		5.05	
width protoloph	5.74	5.81	6.13				5.40				5.21	
width metaloph	5.68	5.40	5.69				5.46		5.06		5.20	
I^1 anteroposterior							5.29					
transverse							4.22					
ratio							.80					

* After Weitzel, 1949
# P^3

know of no other rodent in which this tooth is so short, which certainly must indicate secondary reduction. The closest approach that I have seen in this respect is in the late Eocene *Mytonomys* of North America (Ferrusquia and Wood, 1969, fig. 1 B). The curvature of the mandible shows that the posterior end of the incisor of *A. macrurus* must have been beneath M_2 or M_3 (fig. 5 H). In *A. picteti,* the incisor is nearly horizontal and its alveolus is completely closed beneath the posterior end of M_2 (fig. 3 F). The incisor itself is small in cross section (fig. 3 D and E and table 1), and apparently was not firmly held in the alveolus, as it fell out before fossilization in the three specimens from Egerkingen. Both incisors are preserved in the skeleton from the Geiseltal (Weigelt, 1933 b, pl. 1). In *A. stehlinschaubi,* it again was very small (fig. 6 F), fell out before fossilization, and, from the curvature of the jaw, may have ended beneath M_1 (fig. 6 D).

Skull and Skeleton. — These are well preserved in the material from Messel. Their description need not be repeated from Weitzel (1949, p. 6-7, 11-13). I would, however, doubt that there was a massive postorbital process (1949, p. 7). The infraorbital foramen is of the protrogomorphous type, if anything rather small even for a paramyid. The lower jaw of *A. macrurus* is slender, with a flat ventral side (fig. 5H); that of the other two species is similar, so far as can be determined (fig. 3 A, B, D; 6 E). The masseteric fossa is poorly demarcated, especially the ventral ridge for the insertion of the *masseter lateralis.* There is presumably a direct relationship between the weakness of the incisor and that of the masseter, indicating poor gnawing ability. This, together with the arboreal aspects of the skeleton, suggests a frugivorous diet, which would fit with the generally rounded cusps of the cheek teeth, in contrast to the normal paramyid pattern and diets. The angle, where known, is fully sciurognathous (fig. 5 H). In *A. macrurus,* there were two mental foramina, a large one in front of P_4 and a smaller one below that tooth. In *A. picteti,* the foramina become complex (fig. 3 C), and none is present on the part of the jaw preserved in *A. stehlinschaubi,* indicating that the foramen was considerably farther forward in that species than in either of the others.

The limb measurements (Weitzel, 1949, p. 11) indicate that the fore and hind limbs were of nearly equal length, with an intermembral index of about 87 and a revised intermembral index (Wood, 1935, p. 103, table V) of about 60. Weitzel thought the body form most like that of *Ratufa.* The tail, with about 40 caudal vertebrae, is much longer than in any other paramyid where it is known (*Paramys, Reithroparamys* and *Ischyrotomus*), and its apparent prehensible nature is unique. The complete separation of the scaphoid and lunar (Weitzel, 1949, p. 12) is a primitive feature, and one that separates *Ailuravus* from *Paramys, Leptotomus* and *Reithroparamys,* in the known specimens of which the bones are fused (Wood, 1962, p. 24, 70, 126; but see p. 70 for a discussion of the situation in Matthew's material of *L. leptodus*). *Pseudotomus robustus* and *Ischyrotomus petersoni,* otherwise very different from *Ailuravus,* agree with it in the lack of fusion of these bones (Wood, 1962, fig. 62, 67).

DISCUSSION.

The lower jaw shows the great weakness of the *masseter lateralis* in all three species, since there is never any masseteric crest for the insertion of this muscle and at most only a slight roughness (fig. 3 D, 6 E). The rugosity for the tendon of the anterior part of the *masseter medialis* is present in the early species, *A. macrurus* (fig. 5 H), but absent in the other two (fig. 3 A, D; 6 E). This weakness of the masseter is presumably related to the small incisors with thin enamel, that progressively become more and more reduced. The wear of the cheek teeth, though sometimes fairly extensive, only rarely results in the elimination of much of the enamel cover of the crown, suggesting that the food could not have been very abrasive.

The pattern of the lower incisor closely resembles that of *Leptotomus;* the strength of the ectolophid, the isolation of the entoconid, the development of crown complexities, and the shortening of the lower incisor can all be found in *Mytonomys* from the late Eocene of Utah (Wood, 1956, fig. 1; Black, 1968 b, fig. 1) and the latest Eocene or earliest Oligocene of Chihuahua (Ferrusquia and Wood, 1969, fig. 1). It seems probable that this is a real relationship.

In view of what is known of the environment in which these rodents lived, both at Messel and in the Geiseltal, and of the apparent arboreal adaptations of the skeleton, it would seem most probable that *Ailuravus* was primarily frugivorous.

Ailuravus picteti RÜTIMEYER 1891

Fig. 1-4

Ailuravus picteti, Rütimeyer, 1891, p. 97.

Plesiarctomys schlosseri, Rütimeyer, 1891, p. 89.

Plesiarctomys ?, Rütimeyer, 1891, caption of pl. 8.

Palaeomarmota sciuroides, Haupt, 1921, p. 177.

Plesiarctomis schlosseri Rütimeyer, Haupt, 1921, p. 177.

Megachiromyoides schlüteri, Weigelt, 1933 b, p. 109.

Aeluravus picteti Rütimeyer, Stehlin and Schaub, 1951, p. 354.

TYPE : Basel Em 3 b, isolated LM$_3$, selected by Wood (1962, p. 238) as the lectotype.

HYPODIGM : Type; Basel Em 3, Em 3 a, Ek 152 and Ek 192, lower jaws; Basel Eg 588, Eg 589 and Eg 590, isolated lower premolars; Basel Em 3c, isolated M$_3$; Basel Em 7, Em 8 and Em 9, isolated M^3 ; Basel BCHS 501 and BCHS 566, isolated M$_3$; Basel BCHS 6359, isolated RM$^{1 \text{ or } 2}$, probably M^2; a damaged skull with associated jaws and skeleton and No. 3483, dP$^{3\text{-}4}$ M$^{1\text{-}2}$, figured by Stehlin and Schaub (1951, fig. 620), both in the Geologisches Institut, Halle-an-der-Saale (not seen).

DIAGNOSIS : Surfaces of cheek teeth wear into broad, smoothly curved areas; cheek teeth with deeply intrenched valleys; M_3 considerably elongate with respect to the other teeth; mesoconids generally triangular and near center of teeth, often connected, after wear, with buccal slope of hypoconid, but occasionally cut off from buccal margin of tooth by crests from protoconid and hypoconid; ectolophid complete from protoconid to hypoconid after very little wear; anterior ends of hypoconulid and entoconid united; numerous minor crenulations in little worn teeth; hypocones of upper teeth well developed; conules beginning to lengthen anteroposteriorly; usually single protoconules, but sometimes a subsidiary one develops from the protocone; mesostyles large; protostyle very variable in size; lower incisor short, usually lost before fossilization, and ending below M_2, its cross-sectional area small in comparison with the cheek teeth; masseteric fossa of lower jaw weak, the masseteric crest being especially poorly developed; mental foramina complex; strong chin process; highly corrugated symphysis; well developed tongue groove; tooth measurements as given in tables 1-2.

DISTRIBUTION : Basel BCHS specimens from Buchsweiler, Alsace, France; Basel Em, Eg and Ek specimens from Egerkingen, Canton Solothurn, Switzerland; other specimens from the Geiseltal, south of Halle-an-der-Saale, East Germany. Lutetian, Middle Eocene.

DESCRIPTION.

P_4 . — The metaconid is high, but of only about the same areal extent as the protoconid (fig. 1 D-F; 2). The valley between the two cusps is narrow, open anteriorly but sometimes closed posteriorly, as in the molars of *A. macrurus* (Tobien, 1954, p. 15-16). The mesoconid is a triangle, with its base along the ectolophid and the apex directed laterally. In unworn teeth (fig. 1 D) it may be separated from the protoconid. The round, conical hypoconid is usually (fig. 1 D, E; 2) continued forward by a crest that runs along the buccal side of the tooth, and that may unite with the lateral tip of the mesoconid (fig. 1 E). The hypoconulid is round, widely separated from both the hypoconid and entoconid; it remains isolated even after extensive wear (fig. 1 F). Between the hypoconulid and the entoconid is a deep, narrow and very persistent valley. Many of the minor valleys show clear overdeepening. There is a valley that starts from the middle of the lingual side of the tooth and is nearly continuous to the posterior margin of the crown, between the hypoconid and hypoconulid.

M_{1-2} . — In general, the pattern of these teeth is very similar to that of the premolar. The mesoconid may have weaker connections with the hypoconid via the ectolophid, and stronger ones along the buccal margin of the tooth (fig. 2) than in the premolar. The long valley from the midlingual area may be interrupted by an elevation connecting the hypoconulid and mesoconid (fig. 2 C). M_1 can be very highly worn, with the enamel reduced merely to isolated patches on the crown, at a time when P_4 is barely worn (fig. 2 B). A less worn example is Basel Em 3 a (fig. 2 C).

nudum since there was neither any description nor the designation of a type, as pointed out by Weitzel (1949, p. 6).

Heller (1930) reported the occurrence of fossil mammals in the middle Eocene of the Geiseltal. He mentioned (p. 16-17) and figured (pl. 1, fig. 7-10) isolated rodent-like lower incisors. One of them was flattened on the median and markedly arched on the lateral side, which suggests the shape of an *Ailuravus* incisor. Furthermore, the enamel extended "auf der Aussenseite bis über die Mitte der ganzen Breite..." (*op. cit.*, p. 17). He stated that this was one of the larger incisors, which does not agree with measurements made from his illustrations (pl. 1, figs. 7-10. This tooth is fig. 9). At a guess, this tooth may belong to *Ailuravus.*

Weigelt (1933 b) reported on excellent material of primates from the Geiseltal, near Halle-a.-d.-S., including a new genus and species, *Megachiromyoides schlüteri,* clearly establishing its distinctness from all other primates. This taxon was based on the lower jaws, much of the skeleton and a badly disintegrated skull of a single individual. Weigelt later recognized that this was a rodent, which he considered to be a relative of *Marmota,* "aber viel primitiver bezahnte" (1942, p. 31).

Weitzel (1949) described the interesting material from the Braunkohl of Messel-bei-Darmstadt. There were a number of specimens of a large rodent, including two almost complete skeletons with skulls and another associated skull and jaws. These were described in detail (1949, p. 7, 11-14). He compared tooth patterns with those of *Ailuravus picteti,* in process of being redescribed in Stehlin's monograph on rodent teeth, then being completed by Schaub, and thought the two closely related. He also compared it with *Megachiromyoides schlüteri,* which he thought (1949, p. 11) was also very close to *A. picteti.* Weitzel described the Messel material as a new species, *Ailuravus macrurus,* which he regarded as a relative of *Paramys,* but which he placed (1949, p. 6) in the "U. Familie : Sciurinae".

In their monograph, Stehlin and Schaub refigured the teeth from Egerkingen (1951, fig. 19, 307, 309), together with specimens from the Geiseltal (fig. 20, 620). They combined, in the one species *A. picteti,* the various specimens that Rütimeyer had identified (1891) as *A. picteti, Plesiarctomys schlosseri* and *Plesiarctomys* ?, as well as the materials from Buchsweiler, the Geiseltal and Messel (1951, p. 354). They showed that *Ailuravus* was ultimately related to *Paramys.* They did not like Rütimeyer's transliteration that gave the name *Ailuravus,* and emended the spelling to *Aeluravus,* a change not justified under the rules of nomenclature. Schaub (Stehlin and Schaub, 1951, p. 354-355) discussed the relationships of *Ailuravus* and concluded that it was close to *Prosciurus* and *Plesiarctomys.* A rodent from Mormont-Eclépens, related to *Ailuravus,* was described as *Maurimontia picteti,* n.g., n.sp. (1951, p. 355; also p. 20-21, 206-207; fig. 18, 310).

Tobien (1954, p. 13-18; pl. 1, fig. 1; pl. 2, fig. 1) redescribed the material of *A. macrurus* from Messel, providing excellent illustrations of the cheek teeth, and recognizing it as a species more primitive than *A. picteti* (p. 16). He considered the material of *Ailuravus* from the Geiseltal to be more like the genotype, and presumably within the range of variation of that species (p. 17). He reverted to Rütimeyer's original spelling, *Ailuravus.*

Viret (1955, p. 1527 and fig. 1504) also used Rütimeyer's spelling. He stated that *Ailuravus* was "connu des sables yprésiens du Bassin de Paris, ainsi que du Lutétien d'Egerkingen et de Messel."

Later, Schaub (1958, p. 750) also used the original spelling of the generic name, and placed *Ailuravus* in the Prosciurinae, within the Family Ischyromyidae, of which the Paramyinae were another subfamily.

In his review of the Paramyidae, Wood (1962, p. 236-238) was unable to fit *Ailuravus* and *Maurimontia* into any of his subfamilies, and left them *incertae sedis* within the family. He did not accept Schaub's reference of them to the Prosciurinae, stating that "These two rodents cannot, it is believed, represent the ancestral stages of the prosciurines, but are more likely an independent line of Eocene paramyids, developing in Europe and paralleling the trends established slightly later in the Prosciurinae" (Wood, 1962, p. 238). Wood followed Tobien in recognizing two species of *Ailuravus,* and Stehlin and Schaub in accepting *Maurimontia* as a distinct genus closely related to *Ailuravus.* The descriptions of these forms (1962, p. 236-240) were based on the literature, and the illustrations (1962, fig. 88) were redrawn from those of Stehlin and Schaub (1951) and Tobien (1954).

During my visits to Basel and Darmstadt in 1966-67, I became convinced that *Ailuravus* was an isolated paramyid; that *A. picteti* and *A. macrurus* were validly distinct species, the latter being the more primitive; and that *Maurimontia* was not generically distinct from *Ailuravus, M. picteti* being a third valid species of *Ailuravus;* but I was still uncertain of the higher taxonomic placement of these rodents.

Michaux (1968, p. 155-162) solved the problem of what to do with *Ailuravus* and *Maurimontia* by erecting the new subfamily Ailuraviinae (*sic*) within the Paramyidae for these genera and a new, early Eocene genus, *Meldimys.* He identified two undescribed species of *Ailuravus* from the late Ypresian (Cuis).

Sudre (1969, p. 107, 114) cited "Ailuravinae gen. indét.", from Robiac-Nord, on the basis of identifications by Hartenberger.

Wood (1970, p. 237) stated that Rütimeyer "described, but did not illustrate, *Plesiarctomys schlosseri* from Egerkingen, on the basis of an unspecified number of lower jaws with a cheek tooth length of 24 mm and a depth of jaw below P_4 of 16 mm. These values fit specimens of *Ailuravus picteti* in the Basel collections. He also tentatively referred three isolated teeth to *Plesiarctomys,* illustrated on Pl. 8, fig. 20. These are unquestionably *A. picteti.*"

Hartenberger (1973, table 1) has reached the same conclusions that I did, that *Maurimontia* is not generically distinct from *Ailuravus.* He did not take any action with regard to renaming the species described by Stehlin and Schaub, citing it as "*Ailuravus* n.sp. (*Maurimontia picteti*)".

TAXONOMY AND DESCRIPTION

Family **PARAMYIDAE** MILLER and GIDLEY, 1918

For reasons explained in detail elsewhere (Wood, 1976), I desagree with the conclusions reached by Black (1968) that the Paramyidae should be reduced to a subfamily of the Ischyromyidae, and continue to recognize the Family Paramyidae. Wahlert has recently concluded that the cranial foramina of paramyids and ischyromyids show "that the two groups are distinct at the familial level" (1974, p. 407), and that the ischyromyids have a closer relationship to the cylindrodonts than to the paramyids and sciuravids.

Subfamily ***Ailuravinae*** MICHAUX, 1968 (emended spelling)

Subfamily Ailuraviinae, Michaux, 1968.

EMENDED DIAGNOSIS : Large paramyids; hypocone progressively enlarged but small in primitive forms such as *Meldimys*; protostyle large, sometimes approaching hypocone in size; M^3 unusually like M^{1-2}; P^3 usually present, with well-developed pattern; conules progressively elongate anteroposteriorly; entoconid generally isolated from large, rounded hypoconulid; large mesoconid in a strong ectolophid, sometimes isolated from buccal margin of crown; incisors proportionately small, both in cross section and in length, with thin enamel; cross section of lower incisors ovate, narrow end forward; lower incisors progressively end beneath M_2 ; arboreal, at least some forms with a long, hairy, prehensile tail; fore-limbs proportionately long; scaphoid and lunar not fused.

DISTRIBUTION : Eocene of Europe, probably late Eocene to perhaps earliest Oligocene of North America.

GENERA : *Meldimys* and *Ailuravus*; probably *Mytonomys*.

The Ailuravinae have been a very poorly understood group. As indicated above, they have been misclassified in an unusually large variety of ways. The best material so far reported is that from the Braunkohl of Messel, which includes some of the best preserved fossil rodents in the world, including skulls, skeletons and even hair. Perhaps because of their preservation in lignite, they have not received the attention they deserve in studies of rodent evolution. There is also good material from the Geiseltal, and a maxilla and several jaws from Switzerland.

The typical members of the subfamily were rather large rodents (Michaux, 1968, p. 162), that do not seem to have developed any great diversity. *Ailuravus* was about the size of a marmot (Tobien, 1955, p. 98, fig. 11). The tail was long, with about 40 caudal vertebrae (Tobien, 1969, p. 170, fig. 10), and was thickly covered with bushy hair (Tobien, 1969, p. 170). The total length was over 60 cm (Weitzel, 1949, p. 13). The curvature of the tail as preserved strongly suggests that it was prehensile (Tobien, 1969, fig. 10). The fore limbs were proportionately long (Weitzel, 1949, p. 11). "Bau und Proportionen der Extremitäten lassen den Schluss zu, dass *Ailuravus* ein Baumkletterer gewesen ist, dessen Fertigkeiten allerdings noch nicht zu der Vollkommenheit entwickelt waren wie bei unseren heutigen Eichhörnchen" (Tobien, 1955, p. 98). The lake at Messel in which the fossils were preserved "war von einer üppigen, subtropisch-tropischen Vegetation umgeben, die Urwald-artigen Charakter hatte" (Tobien, 1969, p. 175). The relative scarcity of ailuravine fossils, except at Messel and Egerkingen, was probably due to their restriction to thickly wooded areas. The environment of the Geiseltal area would seem to have been similar to that of Messel (Weigelt, 1933a, p. 15).

Ailuravus RÜTIMEYER, 1891

Ailuravus, Rütimeyer, 1891, p. 94.

Plesiarctomys, Rütimeyer, 1891, p. 89.

Plesiarctomys?, Rütimeyer, 1891, caption of pl. 8.

Palaeomarmota, Haupt, 1921, p. 177.

Plesiarctomis Rütimeyer, Haupt, 1921, p. 177.

Megachiromyoides, Weigelt, 1933, p. 109.

Aeluravus Rütimeyer, Stehlin and Schaub, 1951, p. 353.

TYPE : *A. picteti* RÜTIMEYER, 1891.

DISTRIBUTION : Lutetian, early Bartonian and possibly latest Ypresian of France, West Germany, East Germany and Switzerland.

DIAGNOSIS : Large paramyid, about the size of a marmot; cheek teeth with fundamental paramyid pattern, but progressively develop numerous accessory ridges with over-deepening of many valleys into deep, narrow trenches; P^3 primitively present and complex; P^4 progressively large and massive; hypocone and protostyle of subequal size, both progressively enlarging and both derived from cingulum; hypocone progressively set off from protocone by a lingual valley; M^3 unusually molariform, but hypocone often small; ectolophid of lower cheek teeth strong; mesoconid and hypoconulid progressively large and distinct; entoconid large, conical, and usually isolated from posterior cingulum; M_3 the largest lower tooth, P_4 usually the next largest; upper cheek teeth with three roots, lowers with two; lower incisor with thin enamel, rounded anterior face, and egg-shaped cross section, narrow end forward; lower incisor very short, ending in the genotype below the posterior part of M_2; main mental foramen in front of P_4, often with one or more accessory foramina; symphysis highly convolute, permitting no motion between rami; tail long, with about 40 caudal vertebrae, apparently prehensile; humerus, ulna and tibia subequal in length and only slightly shorter than femur; scaphoid and lunar separate bones; claws long.

DESCRIPTION.

One of the most striking features of the teeth of this genus is the progressive development of wrinkling and deepened valleys on the crowns of the cheek teeth. Superficially, this resembles the situation in the North American paramyid *Thisbemys,* but in *Ailuravus* the complexity seems to have developed by deepening pre-existing valleys, the general appearance being that of a maturely dissected landscape that has been uplifted, resulting in entrenched valleys. In *Thisbemys,* on the contrary, the complexity results from the formation of accessory ridges, which then become elevated. As a result, in *Thisbemys* wear will break through the enamel on the tops of the ridges, whereas in *Ailuravus* wear is concentrated on the major cusps and connecting crests, and accessory worn areas do not extend through the dentine. The Late Eocene (Uintan) *Mytonomys* (Wood, 1956; 1962, p. 227-231, fig. 84; Black, 1968 b) closely approximates *Ailuravus* in many features of the dental pattern.

P^3. — This tooth was probably lost during the evolution of the genus. There is no suggestion that it was present, and some evidence that it was not, in *A. stehlinschaubi* from Mormont-Eclepens (fig. 6 A); it was very large with a well developed pattern in *A. macrurus* from Messel (fig. 5 A); it is unknown in material of *A. picteti* from either Egerkingen or Buchsweiler. There was a fairly large and complex anterior premolar in *A. picteti* from the Geiseltal (Stehlin and Schaub, 1951, fig. 620), but it seems probably to have been dP^3, since it is associated with dP^4. However, the type of *Megachiromyoides schlüteri,* which was fully adult, includes an unworn third premolar, therefore presumably P^3 (Weigelt, 1933 b, pl. 3, fig. 4).

P^4. — This tooth is never fully molariform. The hypocone is small and the anterior cingulum cusp (protostyle) is also weak (fig. 5 A, 6 A). The mesostyle is prominent and protrudes laterally. The generic peculiarities are less well developed than on the molars.

M^{1-2}. — There is a very prominent protostyle, primitively as large as the hypocone (*A. macrurus,* fig. 5 A-B). Progressively, it is less distinct, although still strongly separated from the protocone (fig. 6 A). The protocone in *A. macrurus* is continued as a swelling into the median valley, as in many of the larger paramyids (Wood, 1962, fig. 9 E, K; 14 C; 33 A; 38; 58 C; 78 F), but progressively this swelling becomes a ridge that connects with the posterior side of the protoconule (fig. 6 A, M^1) and sometimes also reaches the anterior side of the metaconule (fig. 4 A; 6 A, M^2; 6 C). Both anterior and posterior cingula are well developed, and progressively acquire numerous small cuspular enlargements. The overdeepening of the valleys is particularly noteworthy in *A. stehlinschaubi*.

M^3. — As in typical paramyids, M^3 has a smaller hypocone than do M^{1-2}. It can be identified in about half the specimens as a posterolingual expansion of the marginal crest (fig. 1 A, B; 5 C). In one specimen of *A. picteti*, however (fig. 1 C), it is a very prominent cusp, separated by a deep notch from the protocone. On the other hand, in the type of *A. stehlinschaubi* (fig. 6 A) there is no suggestion of a hypocone. The connections of the buccal slope of the protocone with the protoconule and metaconule are as in the anterior molars. Mesostyles are likewise large, although in *A. macrurus* (fig. 5 C) it looks as though the cusp may be a metastyle rather than a mesostyle.

Lower Teeth. These are progressive for a paramyid in having a large mesoconid, generally connected with both the protoconid and the hypoconid to form an ectolophid (fig. 1 H-F, 2 C, 5 G, 6 E). The entoconid is almost always isolated from the hypoconulid (fig. 1 D-H, 2, 4 B, 5 E-F, 6 E). The protoconid is continued forward by an anterior arm that generally connects with the anterior end of the metaconid. There is usually a connection from the middle or posterior part of the protoconid to the rear of the metaconid, closing off a distinct trigonid basin (fig. 1 D, E, G; 2; 4 B; 5 E, F; 6 E), although occasionnally the connection is weak (fig. 5 F, M_3 ; 6 E, M_1). The lingual outlet of the talonid basin is usually dammed by what seems to be a metastylid rather than a mesostylid, although sometimes there seems to be no barrier here at all. The mesoconid frequently develops buccal connections with the hypoconid, but occasionally there are connections between the protoconid and hypoconid, separating the mesoconid from the margin of the tooth.

dP^4. — This tooth is known from *A. picteti* from the Geiseltal (Stehlin and Schaub, 1951, fig. 620) and in the type of *A. stehlinschaubi* (fig. 6 B; Stehlin and Schaub, 1951, fig. 18). It is much more advanced in its pattern than the molars, with a very prominent hypocone and nearly complete cingula except on the lingual side. The tooth is almost completely bilophate. The parastylar region is very prominent, and the tooth is much smaller than was P^4 or any of the molars (table 2).

Incisors. — *Ailuravus* is very unusual for a rodent in the rarity of known incisors, which are known only in *A. macrurus* and in the type of *Megachiromyoides* from the Geiseltal (Weigelt, 1933 b, pl. 1), unless one of Heller's isolated incisors from the Geiseltal belongs here (1930, pl. 1, fig. 9). There is an extensive coat of very thin enamel, reaching well past the middle of the lateral side of the tooth (fig. 5 D, G). The lower incisor is most like that of *Leptotomus* (Wood, 1962, fig. 22 H, I; 23 J; 25 C; 30 B-E), but the upper resembles those known from that genus only in the thinness and distribution of the enamel; of all the paramyids figured by Wood (1962), the cross section of the upper incisor resembles only those of *Franimys amherstensis* and *Rapamys* sp. (fig. 48 F, 52 J), both members of the Reithroparamyinae. The most striking feature of the lower incisor is its shortness. I

TABLE 1.

Measurements (in mm) of lower teeth of *Ailuravus*

	Ailuravus picteti Basel Nos.										*Ailuravus macrurus* Darmstadt Nos. Me							*Ailuravus stehlinschaubi* Lausanne 39561
	Em 3b Lecto-type	Em 3	Em 3a	Em 3c	Eg 588	Eg 589	Eg 590	Ek 192	BCHS 501	BCHS 566	67 Type	2		4	51	53	154	
	L	L	R	L	R	R	L	R	R	R	R	L	R	L	R	L	L	R
$P_4 - M_3$		23.5						24.0			17.6*			20.6*			10.6*	19.0
P_4 anteroposterior		5.69	5.76		5.56	6.10	5.88	5.57				5.75		4.78				5.10
width metalophid		4.00	3.80		4.10	4.97	4.47	4.27				ca.3.9		3.32				ca.3.8
width hypolophid		5.65	5.18		4.96	5.92	6.12	4.96				4.90		4.30				ca.4.4
M_1 anteroposterior		5.62	5.02					ca.5.7						4.70	4.79	4.80		4.35
width metalophid		3.96	3.90					4.31						3.70	3.69	3.68		3.69
width hypolophid		4.67	4.96					5.12						4.43	4.43	4.02		ca.4.0
M_2 anteroposterior		5.50	5.47					5.50				4.60		5.19	4.93			4.55
width metalophid		4.10	3.88					4.77						4.10	4.16			3.93
width hypolophid		4.85	5.10					5.29						4.63	4.65			4.28
M_3 anteroposterior	7.40	6.53		7.00				7.60	6.80	6.80			6.12	5.71	5.50			5.17
width metalophid	4.87	ca.4.5		4.90					4.68	4.34			4.83	4.27				4.35
width hypolophid	4.84	4.50		4.82					4.65	4.76			4.62	4.53	4.68			3.90
I_1 anteroposterior		alv. 4.18										4.23						
transverse		alv. 3.19										3.23						
ratio												.76						

* After Weitzel, 1949.

TABLE 2
Measurements (in mm) of upper teeth of *Ailuravus*

	Ailuravus picteti Basel Nos.				*Ailuravus macrurus*			Darmstadt Nos.Me			*Ailuravus stehlinschaubi*	
	Em 7	Em 8	Em 9	BCHS 6359	67 Type	2		3	50	52	Lausanne 39559, Type	Basel Mt 1767
	R	R	R	R	R	R	L	L	L	L	R	L
Length upper cheek teeth					21.5*						20.2	
dP^4 anteroposterior							3.15 #				5.14	
width protoloph							3.58 #				5.7+	
width metaloph											5.81	
P^4 anteroposterior						5.37	5.11	4.58			5.34	
width protoloph							6.25	5.57			5.30+	
width metaloph							6.68	5.77			5.95+	
M^1 anteroposterior							5.02			4.80	5.00	5.14
width protoloph							6.13			5.40	5.49	5.7+
width metaloph							5.55			4.95	5.42	5.81
M^2 anteroposterior				5.34		5.42					5.01	
width protoloph				5.80		5.86					5.37	
width metaloph				5.26		5.26					5.13	
M^3 anteroposterior	5.63	5.40	5.73				5.35		5.10		5.05	
width protoloph	5.74	5.81	6.13				5.40				5.21	
width metaloph	5.68	5.40	5.69				5.46		5.06		5.20	
I^1 anteroposterior							5.29					
transverse							4.22					
ratio							.80					

* After Weitzel, 1949
\# P^3

know of no other rodent in which this tooth is so short, which certainly must indicate secondary reduction. The closest approach that I have seen in this respect is in the late Eocene *Mytonomys* of North America (Ferrusquia and Wood, 1969, fig. 1 B). The curvature of the mandible shows that the posterior end of the incisor of *A. macrurus* must have been beneath M_2 or M_3 (fig. 5 H). In *A. picteti,* the incisor is nearly horizontal and its alveolus is completely closed beneath the posterior end of M_2 (fig. 3 F). The incisor itself is small in cross section (fig. 3 D and E and table 1), and apparently was not firmly held in the alveolus, as it fell out before fossilization in the three specimens from Egerkingen. Both incisors are preserved in the skeleton from the Geiseltal (Weigelt, 1933 b, pl. 1). In *A. stehlinschaubi,* it again was very small (fig. 6 F), fell out before fossilization, and, from the curvature of the jaw, may have ended beneath M_1 (fig. 6 D).

Skull and Skeleton. — These are well preserved in the material from Messel. Their description need not be repeated from Weitzel (1949, p. 6-7, 11-13). I would, however, doubt that there was a massive postorbital process (1949, p. 7). The infraorbital foramen is of the protrogomorphous type, if anything rather small even for a paramyid. The lower jaw of *A. macrurus* is slender, with a flat ventral side (fig. 5H); that of the other two species is similar, so far as can be determined (fig. 3 A, B, D; 6 E). The masseteric fossa is poorly demarcated, especially the ventral ridge for the insertion of the *masseter lateralis.* There is presumably a direct relationship between the weakness of the incisor and that of the masseter, indicating poor gnawing ability. This, together with the arboreal aspects of the skeleton, suggests a frugivorous diet, which would fit with the generally rounded cusps of the cheek teeth, in contrast to the normal paramyid pattern and diets. The angle, where known, is fully sciurognathous (fig. 5 H). In *A. macrurus,* there were two mental foramina, a large one in front of P_4 and a smaller one below that tooth. In *A. picteti,* the foramina become complex (fig. 3 C), and none is present on the part of the jaw preserved in *A. stehlinschaubi,* indicating that the foramen was considerably farther forward in that species than in either of the others.

The limb measurements (Weitzel, 1949, p. 11) indicate that the fore and hind limbs were of nearly equal length, with an intermembral index of about 87 and a revised intermembral index (Wood, 1935, p. 103, table V) of about 60. Weitzel thought the body form most like that of *Ratufa.* The tail, with about 40 caudal vertebrae, is much longer than in any other paramyid where it is known (*Paramys, Reithroparamys* and *Ischyrotomus*), and its apparent prehensible nature is unique. The complete separation of the scaphoid and lunar (Weitzel, 1949, p. 12) is a primitive feature, and one that separates *Ailuravus* from *Paramys, Leptotomus* and *Reithroparamys,* in the known specimens of which the bones are fused (Wood, 1962, p. 24, 70, 126; but see p. 70 for a discussion of the situation in Matthew's material of *L. leptodus*). *Pseudotomus robustus* and *Ischyrotomus petersoni,* otherwise very different from *Ailuravus,* agree with it in the lack of fusion of these bones (Wood, 1962, fig. 62, 67).

DISCUSSION.

The lower jaw shows the great weakness of the *masseter lateralis* in all three species, since there is never any masseteric crest for the insertion of this muscle and at most only a slight roughness (fig. 3 D, 6 E). The rugosity for the tendon of the anterior part of the *masseter medialis* is present in the early species, *A. macrurus* (fig. 5 H), but absent in the other two (fig. 3 A, D; 6 E). This weakness of the masseter is presumably related to the small incisors with thin enamel, that progressively become more and more reduced. The wear of the cheek teeth, though sometimes fairly extensive, only rarely results in the elimination of much of the enamel cover of the crown, suggesting that the food could not have been very abrasive.

The pattern of the lower incisor closely resembles that of *Leptotomus;* the strength of the ectolophid, the isolation of the entoconid, the development of crown complexities, and the shortening of the lower incisor can all be found in *Mytonomys* from the late Eocene of Utah (Wood, 1956, fig. 1; Black, 1968 b, fig. 1) and the latest Eocene or earliest Oligocene of Chihuahua (Ferrusquia and Wood, 1969, fig. 1). It seems probable that this is a real relationship.

In view of what is known of the environment in which these rodents lived, both at Messel and in the Geiseltal, and of the apparent arboreal adaptations of the skeleton, it would seem most probable that *Ailuravus* was primarily frugivorous.

Ailuravus picteti RÜTIMEYER 1891

Fig. 1-4

Ailuravus picteti, Rütimeyer, 1891, p. 97.

Plesiarctomys schlosseri, Rütimeyer, 1891, p. 89.

Plesiarctomys ?, Rütimeyer, 1891, caption of pl. 8.

Palaeomarmota sciuroides, Haupt, 1921, p. 177.

Plesiarctomis schlosseri Rütimeyer, Haupt, 1921, p. 177.

Megachiromyoides schlüteri, Weigelt, 1933 b, p. 109.

Aeluravus picteti Rütimeyer, Stehlin and Schaub, 1951, p. 354.

TYPE : Basel Em 3 b, isolated LM_3, selected by Wood (1962, p. 238) as the lectotype.

HYPODIGM : Type; Basel Em 3, Em 3 a, Ek 152 and Ek 192, lower jaws; Basel Eg 588, Eg 589 and Eg 590, isolated lower premolars; Basel Em 3c, isolated M_3 ; Basel Em 7, Em 8 and Em 9, isolated M^3 ; Basel BCHS 501 and BCHS 566, isolated M_3; Basel BCHS 6359, isolated R$M^{1 \text{ or } 2}$, probably M^2; a damaged skull with associated jaws and skeleton and No. 3483, dP^{3-4} M^{1-2}, figured by Stehlin and Schaub (1951, fig. 620), both in the Geologisches Institut, Halle-an-der-Saale (not seen).

DIAGNOSIS : Surfaces of cheek teeth wear into broad, smoothly curved areas; cheek teeth with deeply intrenched valleys; M_3 considerably elongate with respect to the other teeth; mesoconids generally triangular and near center of teeth, often connected, after wear, with buccal slope of hypoconid, but occasionally cut off from buccal margin of tooth by crests from protoconid and hypoconid; ectolophid complete from protoconid to hypoconid after very little wear; anterior ends of hypoconulid and entoconid united; numerous minor crenulations in little worn teeth; hypocones of upper teeth well developed; conules beginning to lengthen anteroposteriorly; usually single protoconules, but sometimes a subsidiary one develops from the protocone; mesostyles large; protostyle very variable in size; lower incisor short, usually lost before fossilization, and ending below M_2, its cross-sectional area small in comparison with the cheek teeth; masseteric fossa of lower jaw weak, the masseteric crest being especially poorly developed; mental foramina complex; strong chin process; highly corrugated symphysis; well developed tongue groove; tooth measurements as given in tables 1-2.

DISTRIBUTION : Basel BCHS specimens from Buchsweiler, Alsace, France; Basel Em, Eg and Ek specimens from Egerkingen, Canton Solothurn, Switzerland; other specimens from the Geiseltal, south of Halle-an-der-Saale, East Germany. Lutetian, Middle Eocene.

DESCRIPTION.

P_4 . — The metaconid is high, but of only about the same areal extent as the protoconid (fig. 1 D-F; 2). The valley between the two cusps is narrow, open anteriorly but sometimes closed posteriorly, as in the molars of *A. macrurus* (Tobien, 1954, p. 15-16). The mesoconid is a triangle, with its base along the ectolophid and the apex directed laterally. In unworn teeth (fig. 1 D) it may be separated from the protoconid. The round, conical hypoconid is usually (fig. 1 D, E; 2) continued forward by a crest that runs along the buccal side of the tooth, and that may unite with the lateral tip of the mesoconid (fig. 1 E). The hypoconulid is round, widely separated from both the hypoconid and entoconid; it remains isolated even after extensive wear (fig. 1 F). Between the hypoconulid and the entoconid is a deep, narrow and very persistent valley. Many of the minor valleys show clear overdeepening. There is a valley that starts from the middle of the lingual side of the tooth and is nearly continuous to the posterior margin of the crown, between the hypoconid and hypoconulid.

M_{1-2} . — In general, the pattern of these teeth is very similar to that of the premolar. The mesoconid may have weaker connections with the hypoconid via the ectolophid, and stronger ones along the buccal margin of the tooth (fig. 2) than in the premolar. The long valley from the midlingual area may be interrupted by an elevation connecting the hypoconulid and mesoconid (fig. 2 C). M_1 can be very highly worn, with the enamel reduced merely to isolated patches on the crown, at a time when P_4 is barely worn (fig. 2 B). A less worn example is Basel Em 3 a (fig. 2 C).

M_3. — The third molar is considerably longer than the other teeth (table 1), due particularly to a backward displacement of the hypoconid (fig. 1 G, H; 2 A, B). The posterior arm of the protoconid, on the anterior teeth merely a weak crest across the rear of the trigonid basin, is a prominent ridge, giving rise to a number of minor cusplets (fig. 1 G) and uniting with a crest extending backward from the metaconid. As in the anterior molars, the mesoconid is usually connected through the ectolophid with the protoconid and hypoconid, and also through its buccal tip with the lingual crest of the hypoconid (fig. 1 H). The entoconid is well forward of the posterior side

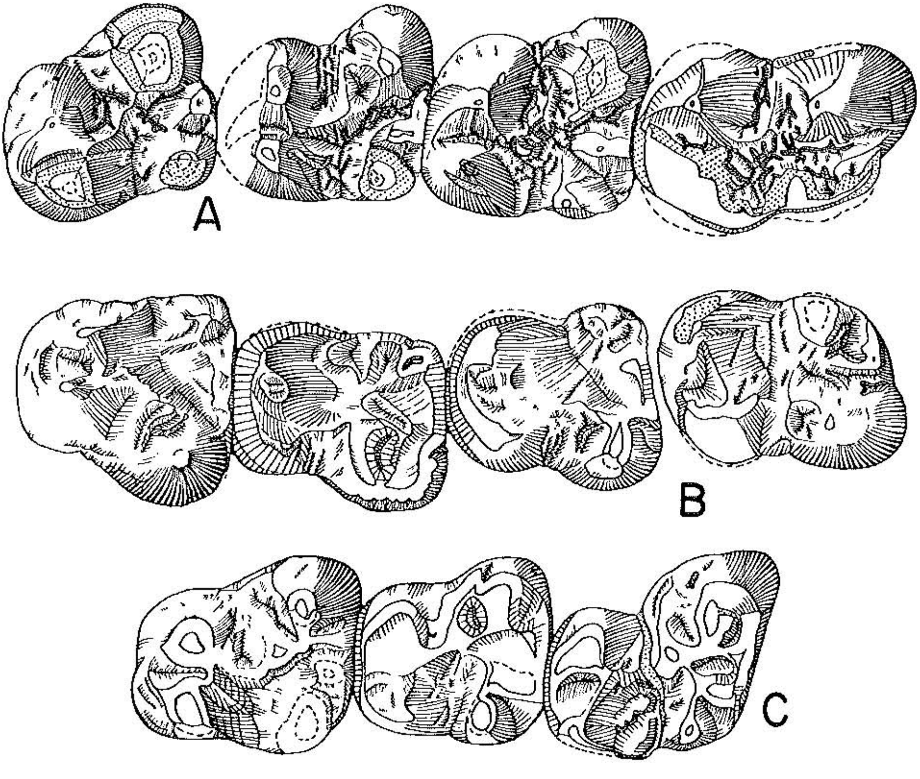

FIGURE 1. — Lower dentitions of *Ailuravus picteti* from Egerkingen, × 5. Dotted or diagonally ruled areas are broken enamel.

A. RP_4-M_3, Basel Ek 192.

B. LP_4-M_3, Basel Em 3 (Stehlin and Schaub, 1951, fig. 309).

C. RP_4-M_3, Basel Em 3 a (Stehlin and Schaub, 1951, fig. 308).

of the tooth, having been displaced to the lingual side by the backward growth of the hypoconid (fig. 1 G, H). This is true, to a lesser extent, of M_{1-2} (fig. 2). The two isolated RM_3 from the slightly earlier locality of Buchsweiler (Basel BCHS 501 and 566) are like the corresponding tooth of the still earlier *A. macrurus* in many respects. The connection between protoconid and metaconid is primarily via the anterior cingulum, although the trigonid basin is also closed posteriorly, as in *A. macrurus* (fig. 4 B). A ridge, from the entoconid to the ectolophid in BCHS 566, is less well developed in BCHS 501 (fig. 4 B).

Upper teeth. — I know the upper teeth largely from the literature. Stehlin and Schaub (1951, fig. 620) illustrate an upper dentition (dP^{3-4}, M^{1-2}) of Halle 3483, and an upper molar (fig. 20; after Weigelt, 1933 b, pl. 3, fig. 3), both from the Geiseltal. Weigelt illustrated (1933 b, pl. 3) isolated teeth, apparently from the damaged skull of his holotype. He identified these as " M_3 sup " (actually $M^{1 \text{ or } 2}$); " M_2 sup " (also $M^{1 \text{ or } 2}$); and " Praemolar (P_4 ? sup) " (actually P^3). I have seen one upper molar (cf. M^2, fig. 4 A) from Buchsweiler and three third molars from Egerkingen (fig. 1 A-C). The pattern of P^3, in so far as can be told from Weigelt's figure (1933 b, pl. 3, fig. 4), was probably like that described below for *A. macrurus.*

M^{1-2}. — The hypocone is widely separated from the protocone (fig. 4 A; Stehlin and Schaub, fig. 20 and 620). There is apt to be a large protostyle, but it is not so distinct, especially after wear (fig. 4 A), as in *A. stehlinschaubi.* The anteroposterior alignment of the conules (fig. 4 A) is especially clear in the unworn teeth (Stehlin and Schaub, 1951, fig. 620). There is clearly an accessory ridge from the protocone, which is the ancestor of the lingual protoconule of *A. stehlinschaubi.* The metacone-metaconule crest is directed toward the protocone, and is separated from the hypocone by a deep valley (fig. 4 A; Stehlin and Schaub, 1951, fig. 20, 620). The anterior and posterior cingula are complete ridges along the respective borders of the teeth. The mesostyles are large. Basel BCHS 6359 (fig. 4 A) is very poorly preserved, and the enamel has disintegrated over most of the crown. This tooth shows the pinching of the anterior face, between the protocone and protostyle (fig. 4 A), that occurs in *A. stehlinschaubi* (fig. 6 A).

M^3. — The hypocone is quite variable in size among the three specimens of this tooth from Egerkingen. In one specimen (fig. 1 A), it is even difficult to be sure where the hypocone is, but it is probably the lingual end of the posterior cingulum. In the other two specimens, it is a well developed cusp, separated from the protocone by a valley (fig. 1 B) that may be very deep (fig. 1 C). In this latter specimen, the metaloph is well developed, with a much stronger connection with the hypocone than with the protocone. The tooth generally has a more advanced pattern, in its resemblance to the anterior molars, than is true of most paramyids. The mesostyles are prominent. A protostyle is recognizable only on one specimen (fig. 1 C).

dP^3. — The upper premolars figured by Stehlin and Schaub (1951, fig. 620) are clearly deciduous, dP^4 being more worn than M^1 and dP^3

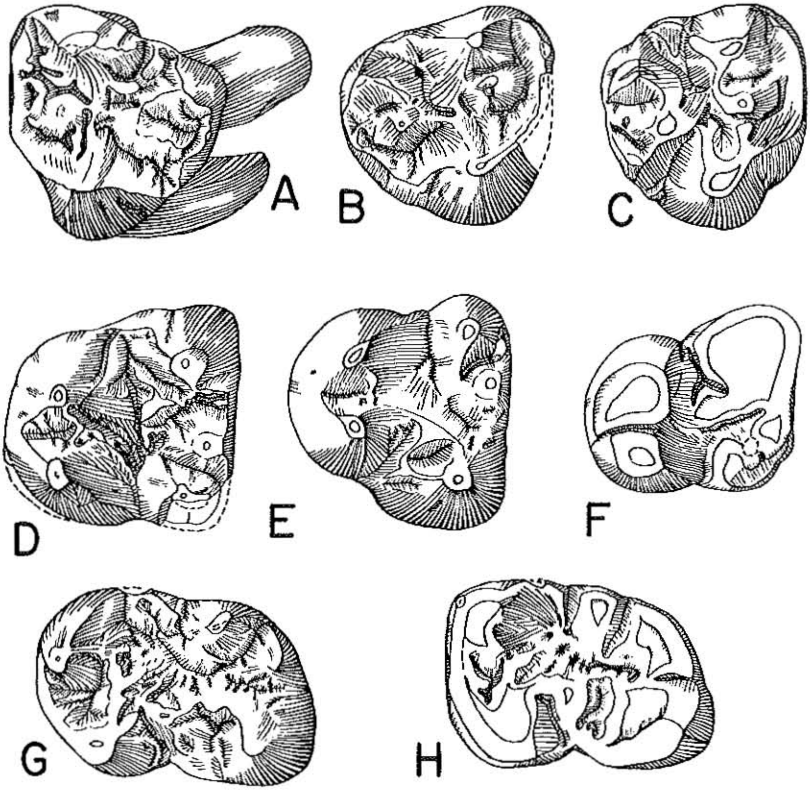

FIGURE 2. — Isolated cheek teeth of *Ailuravus picteti* from Egerkingen, ×5.

A. LM^3, Basel Em 9 (Rütimeyer, 1891, pl. 8, fig. 20 A, right specimen, identified as *Plesiarctomys spectabilis;* Stehlin and Schaub, 1951, fig. 19 C).
B. RM^3, Basel Em 7, anterior end to the right (Stehlin and Schaub, 1951, fig. 19 A).
C. RM^3, Basel Em 8, anterior end to the right (Rütimeyer, 1891, pl. 8, fig. 20 A, left specimen, identified as *Plesiarctomys spectabilis;* Stehlin and Schaub, 1951, fig. 19 B).
D. RP$_4$, Basel Eg 589, restored to eliminate thrust-faults and gaps (part of type material of *Plesiarctomys schlosseri* Rütimeyer 1891).
E. LP$_4$, Basel Eg 590 (part of type material of *Plesiarctomys schlosseri* Rütimeyer 1891).
F. RP$_4$, Basel Eg 588 (Rütimeyer, 1891, pl. 8, fig. 20 B, part of type material of *Plesiarctomys schlosseri*).
G. LM$_3$, Basel Em 3 b, lectotype (Rütimeyer, 1891, pl. 7, fig. 18; Stehlin and Schaub, 1951, fig. 307 A).
H. LM$_3$, Basel Em 3 c (Rütimeyer, 1891, pl. 7, fig. 19; Stehlin and Schaub, 1951, fig. 307 B).

more worn than dP^4. dP^3 apparently consisted of a main conical cusp, with a lower heel along the posterior margin of the tooth, which wore against the metaconid of dP$_4$. This shelf was connected at both ends to the main cusp, and was continued along the posterobuccal margin of the tooth by a cingulum. This tooth is identical to the P^3 of *A. macrurus* described below, and is apparently more complicated than P^3 of Weigelt's type (Weigelt, 1933 b, pl. 3, fig. 4). Since no P_4 of *A. picteti* shows the wear on the anterior end that exists in *A. macrurus*, resulting from contact with P^3, perhaps this latter teeth was often reduced or absent in *A. picteti*.

dP^4. — This tooth is much smaller than the molars (table 2). The hypocone and protostyle are strong, and the anteroloph swings forward, with a prominent parastylar area. The conules are large, and are beginning to elongate anteroposteriorly. They have incipient connections with the anterior and posterior cingula. The mesostyle is weak (Stehlin and Schaub, 1951, fig. 620).

Incisors. — The incisors are present in the two jaws of the type of *Megachiromyoides schlüteri* from the Geiseltal, but are missing from all the jaws from Egerkingen, having fallen out before fossilization. This is presumably related to the shortness of the incisors. The incisor has a small cross section in comparison to the area of the cheek teeth (table 1; fig. 3 E), and the shape is clearly that characteristic of *Leptotomus*, narrow at the front and enlarging toward the posterior surface. The radius of curvature of the incisor was about 6.5 mm, centered 1.5 mm above the talonid of P_4. Specimens broken at or behind the rear of M_2 show no trace of the alveolus of the incisor. Careful excavation in the jaw of Basel Em 3 a showed that what had at first appeared to be the alveolus of the incisor, beneath the rear of M_2, was actually a series of passages for the alveolar blood vessels, and that the alveolus ends in the rounded mass medial and ventral to the vascular passages (fig. 3 F; I).

Mandible. — The jaw is slender, with a strong chin process beneath P_4 (fig. 3 A, B, D), bearing at most a few nutritive foramina. The process is preserved completely only on Basel Ek 192 (fig. 3 A, B). The lateral crest (Woods, 1972, fig. 1 A), which served as the dorsal limit of the insertion of the *masseter medialis*, is reasonably well developed. It passed the alveolar level shortly behind M_3 (fig. 3 A, D), and runs as far forward as beneath the middle or front of M_2. The masseteric crest, which usually extends from the anterior end of the lateral crest to the angular process, and which serves for the insertion of the *masseter lateralis*, is completely absent, suggesting that this muscle was very weak. One specimen (Basel Em 3, fig. 3 D), is roughened in the area where the masseteric crest normally is found. The tuberosity, where the two crests meet, for the attachment of the anterior tendon of the *masseter medialis*, is also absent (fig. 3 A, D), suggesting that there was no tendonous attachment of this muscle. The mental foramina are complex but variable. In Basel Ek 192, there are two main mental foramina facing forward, one just in front of P_4 and one below its anterior root (fig. 3 A). There are minute nutritive foramina inside the openings of each of these mental foramina (fig. 3 C), and a tiny foramen between and above the two. A channel leads forward from the anterior foramen, and turns upward to a depression from which two passages enter the bone, each about a third the size of the anterior mental foramen. In Basel Em 3, the anterior mental foramen is similar to that described above, but the forwardly directed channel does not re-enter the bone (fig. 3 D). The posterior mental foramen, however, opens backward, and is continued as a groove in the bone, turning upward toward the posterior root of M_1. Perhaps this groove is homologous to a foramen, in Basel Ek 192, that likewise faces backward (fig. 3 A). Basel Em 3a is intermediate between the other specimens. The symphysis (preserved only in Basel Ek 192, fig. 3 B) is highly rugose, indicating that there was no motion between the mandibles and that the *transversus mandibulae* muscle was absent. The fossa for the *genioglossus* is weakly developed. There is a promi-

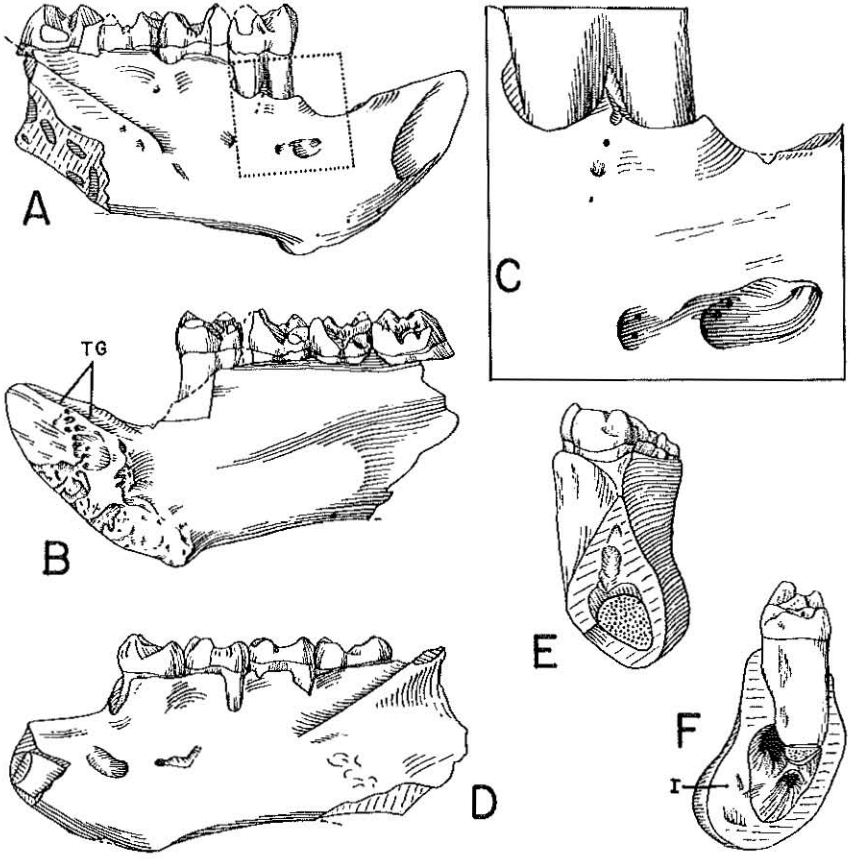

FIGURE 3. — Lower jaws of *Ailuravus picteti* from Egerkingen, C × 5, others × 1,5.

A-C. Basel Ek 192.

A. Lateral view. Shaded areas on the broken rear portion are matrix-filled; none is the alveolus of I_1. Area outlined by dotted lines is enlarged as fig. 3 C.

B. Medial view, showing corrugated symphysis and tongue groove (TG).

C. Detail of area of mental foramina, showing complex of foramina.

D. Basel Em 3, lateral view.

E-F. Cross sections ol lower jaw, Basel Em 3 a.

E. Section of jaw varying from 2.7 to 0.0 mm in front of P_4, showing incisive alveolus.

F. Section of jaw at rear of M_2. I = closed bony cover of rear of incisive alveolus.

nent tonguegroove on Basel Ek 192, extending most of the length of the diastema (fig. 3 B). The groove was either much smaller or absent on the other specimens. A rounded elevation on the body of the mandible, below M_2, marks the closed rear of the alveolus of the incisor in Basel Em 3, Ek 152 and Ek 192 (fig. 3 B).

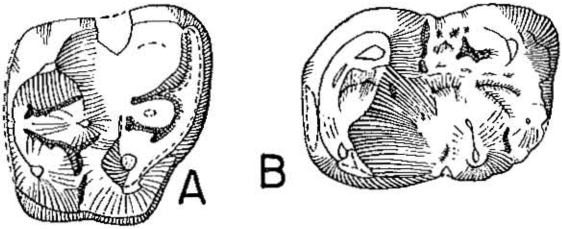

FIGURE 4. — *Ailuravus picteti* from Buchsweiler, × 5.
A. $RM^{1 \text{ or } 2}$, probably M^2, anterior end to the right, Basel BCHS 6359.
B. RM_3, Basel BCHS 501.

DISCUSSION.

Some of the Egerkingen specimens (Basel Em 3, 3a, 3b, 3c, Ek 152 and 192 (fig. 1 A, G, H; 2 B, C) are intermediate, in complexity of pattern and deepness of the valleys, between the Buchsweiler specimens (fig. 4) and the remaining Egerkingen specimens (fig. 1 B, C, D, E, F; 2 A). If the first group is from the lower levels at Egerkingen and the latter from the upper ones, it would suggest that evolution was proceeding fairly rapidly in this genus at that time.

No measurements of the Geiseltal specimens are given in tables 1-2. Weitzel (1949, p. 8) gives the length of LP_4-M_3 of *Megachiromyoides schlüteri* as 28.0 mm. Measurements made from Weigelt's plates vary (depending on precisely what he meant by "ca. 3 fach") from 22 to 28.6 mm. Measurements of the individual teeth from these plates gave highly uncertain results. Stehlin and Schaub illustrate one specimen that they were able to study (1951, fig. 620); measurements taken from their figure would be accurate. They also redrew an upper molar after Weigelt, but do not give any magnification.

Ailuravus macrurus WEITZEL 1949

Fig. 5

TYPE : Hessisches Landesmuseum Darmstadt Me 67, an essentially complete skeleton with skull and lower jaws, missing about 14 caudal vertebrae, but with impressions preserved (Weitzel, 1949, pl. 1, fig. 1-3).

HYPODIGM : Type and Darmstadt Me 49, another skeleton with a damaged skull (Weitzel, 1949, pl. 2, fig. 4); Me 1029, a larger skeleton lacking the skull but including a lower jaw; Me 156, a hind leg, sacrum and most of the tail, including tail hairs; Me 2, a skull and lower jaw (Weitzel, 1949, pl. 2, fig. 5-7; Tobien, 1954, pl. 1, fig. 1); Me 4, LP_4-M_3 (Weitzel, 1949, pl. 2, fig. 8-10; Tobien, 1954, pl. 2, fig. 1), isolated but associated teeth; Me 51, RM_{1-3} (Weitzel, 1949, pl. 2, fig. 11); Me 3, LP^4 (Weitzel, 1949, pl. 3, fig. 14a); Me 50, LM^3; Me 52, LM^1 or LM^2 (Weitzel, 1949, pl. 3, fig. 14b). Me 154 is a much smaller specimen, about 2/3 the size of Me 67 and Me 49, including most of the vertebral column, part of the fore limb and the hind limb.

DIAGNOSIS : Skull about 90 mm long; upper cheek teeth with well developed protostyle and hypocone and large mesostyle; incipient anteroposterior elongation of conules; lateral swelling from protocone into central valley as in *Paramys*; two protoconules; metaloph of M_3 unusually molariform; P^3 large with a main conical cusp and a broad posterior heel; lower teeth increase in size from P_4 to M_3 ; mesoconid and hypoconulid triangular; hypoconulid connected with entoconid through posterior cingulum; metastylid continuous with posterior crest of metaconid; tooth measurements as given in tables 1-2.

DISTRIBUTION : Middle Eocene (Lutetian) oil shales of Messel-bei-Darmstadt.

DESCRIPTION.

This species has been well described by Weitzel (1949, p. 5-14), and the dentition was discussed carefully by Tobien (1954, p. 13-18). Therefore I include only points where I disagree with, or can add something to their descriptions. Illustrations are included (fig. 5) because they show some slightly different features and for comparison with the other two species.

The infraorbital foramen of Me 2 is clearly of the protrogomorphous type, and is, if anything, small for a paramyid. Weitzel (1949, p. 7) states that the frontals are fused, but it is not clear that this is for their entire length; partial fusion is normal in paramyids. He points out that the heavy occipital crest and the long spines of the cervical vertebrae indicate heavy neck muscles (1949, p. 7), likewise a rather general feature of paramyids.

Weitzel (1949, p. 7) indicates that, in the type, "sind die Unterkieferäste leicht gegeneinander verschoben; sie waren im Symphysenteil nicht fest verwachsen und konnten... gegeneinander bewegt werden." He then indicates that there was probably a *transversus mandibulae* muscle. This would seem to be rather different from the situation in *A. picteti* (fig. 3 B). The symphysis reaches to beneath the rear of P_4 (Weitzel, 1949, p. 7), somewhat farther than in *A. picteti* (fig. 3 B). There does not seem to be good evidence of a chin process — certainly in Me 2 (fig. 5 H) there is breakage in this area. As Weitzel pointed out, the diastema bends downward, in contrast to the situation in *Paramys delicatus*. However, the situation is very variable among paramyids, and *Reithroparamys*, several species of *Leptotomus*, *Mytonomys* and many manitshines resemble *Ailuravus* in this respect. There is also variation in *A. picteti* (fig. 3 A). As Weitzel stated (1949, p. 7), the strong coronoid process indicates that there was a well developed *temporalis*.

Upper Teeth. — In the upper teeth, the hypocone is large and widely separated from the protocone (fig. 5 A-C). Whether this indicates that this cusp is a true hypocone in contrast to a pseudohypocone derived from the protocone in many other paramyids, as Stehlin and Schaub thought (1951, p. 20), or whether the hypocone arose from the junction of the posterior cingulum and protocone in all paramyids, but occasionally later shifted backward from the protocone, as believed by Wood (1962, p. 8), cannot be determined without more fossils. The latter suggestion seems the more probable to me, especially as the hypocone of *Meldimys* was "encore peu développé et non séparé nettement du protocône" (Michaux, 1968, p. 155). The protostyle of the molars is as large and almost as distinct as the hypocone. The valleys leading forward from the protoloph or backward from the metaloph, between the main cusps and the conules, are deep — almost canyons. The lingual of the two protoconules may be merely an enlargement of the anterior arm of the protocone (fig. 5 A). The metaloph is very clearly directed toward the protocone, and is widely separated from the hypocone. This is much more primitive than the condition in *A. stehlinschaubi*, where the metaloph is in the midst of shifting its attachment to the hypocone (fig. 6 A, M^{1-2}).

P^3. — This single-rooted tooth is about half the dimensions of the other teeth (table 2). There is a large anterior cone, which forms most of the tooth (fig. 5 A), considered by Tobien (1954, p. 13) to be homologous to the paracone of the molars. A broad ridge, highly worn on Me 2, extends along most of the posterior part of the tooth. This area wore against the metaconid of P_4. The buccal and lingual ends of the worn area are continued by cingula, and a ridge bearing two minute cuspules, identified by Tobien (1954, p. 13) as metacone and metaconule, runs from the buccal end of the worn surface half way to the peak of the conical cusp. Not enough is known about the evolution of P^3 in paramyids to permit one to draw definite conclusions, but the tooth is most similar to that of *Paramys copei* (Wood, 1962, fig. 22 C; but not like that of fig. 22 B), among paramyids where this tooth is known. Stehlin (Stehlin and Schaub, 1951, p. 205) believed Teilhard's "*Paramys* forme *major*" to be *Ailuravus;* in this he was followed by Viret (1955, p. 1527) and by Schaub (1958, p. 751). Wood, however (1962, p. 51), discussed "*Paramys* forme *major*" as "*Paramys* sp. near *P. copei*". It is possible that both of these suggested relationships for "*Paramys* forme *major*" are correct. The tooth in Me 2 is more worn than P^4, but probably no more worn than is M^1, suggesting that it is P^3 and not a retained dP^3. Tobien (1954, p. 14) stated that "Die 3 Haupthugel und das Hintercingulum der folgenden Zähne, sind am P^3 mithin identifizierbar". I do not feel quite so certain of this as he did.

P^4. — There is an anteriorly extended parastyle on this tooth, somewhat damaged since Tobien's figure (1954, pl. 1, fig. 1) was drawn. The protostyle is weak, and poorly separated from the protocone. The whole anterior face of the protoloph is smoothed by wear from the protoconid and metaçonid of P_4. Similar wear surfaces are present on the molars (fig. 5 C). As Tobien indicated (1954, p. 14), some specimens lack the hypocone. The protoconule is double as in the molars (fig. 5 A), in contrast to its single nature in the other species. The metaconule is single and large. The mesostyle is prominent (Tobien, 1954, p. 14).

M^{1-2}. — As shown by Tobien (1954, p. 14) these teeth are more quadrilateral than P^4 because of the marked posterior expansion of the hypocone (fig. 5 A, B). A further feature that is involved is the forward expansion of the protostyle, to become more or less a mirror image of the hypocone. The protoconule is double on both teeth, the lingual protoconule probably being derived from an arm of the protocone (fig. 5 A). The metaconule is no larger than the lateral protoconule. As Tobien observed (1954, p. 14), the hypocone of M^2 (fig. 5 B) is not as well developed as that of M^1. In spite of the size of the hypocone, there is only a single lingual root on all the upper teeth.

M^3. — This tooth is more typical of paramyids than is that of *A. picteti*. The hypocone is hardly recognizable as an enlargement of the posterior cingulum (fig. 5 C). I consider this primitive rather than reduced (Tobien, 1954, p. 14, "der Hypocon stark abgeschwächt"). The metacone, even though small, is rather large for a paramyid M^3. The metaloph runs from the metacone at the middle of the rear of the tooth, through the large metaconule, and is weakly connected with the protocone (fig. 5 C). By comparison with other paramyids, this is presumably an enlarging rather than a reduced metacone, in contrast to Tobien's characterization of it as " der Metacon nahezu völlig geschwunden" (Tobien, 1954, p. 14). The mesostyle is weaker than on M^{1-2}.

Lower Teeth. — The lower teeth increase in size from P_4 to M_3 , although P_4 and M_1 are of almost equal size (table 1 and fig. 5 F). The metaconid is a high crest-like cusp on all teeth (fig. 5 E, F), with a pronounced wear surface on its posterior face, formed by wear against the anterior side of the protoloph of the upper cheek teeth. The trigonid basin is deep and narrow (Weitzel, 1949, p. 6). The blade of the metaconid continues backward into the elongate metastyle that blocks the lingual exit of the central valley. The mesoconid, rounded rather than triangular as in *A. picteti*, unites quickly with the protoconid and hypoconid, to form a continuous ectolophid along the buccal half of the teeth. The entoconid is an isolated cone on the molars; its condition on P_4 is unknown, due to breakage, and it has been restored in fig. 5 F on the basis of the molars. The valley behind the entoconid is deep, and separates it widely from the hypoconulid (fig. 5 E, F). The hypoconulid was present on P_4 (fig. 5 F), although most of it is broken off, leading Weitzel to believe it to have been absent (1949, p. 6). The hypoconulid usually, although not always, joins the hypoconid wear surface (fig. 5 E). A few overdeepened valleys may remain on the crowns (fig. 5 E, M_3 ; Weitzel, 1949, p. 6), as foreshadowings of the condition in *A. picteti* (Rütimeyer, 1891, p. 94). The initial stages in the mesoconid-hypoconid union along the lateral margins of the teeth, characteristic of *A. picteti* (Tobien, 1954, p. 16), can also sometimes be seen (fig. 5 E, F — P_4). The trigonid widths of P_4-M_1 are much less, and of M_2 somewhat less, than the talonid widths (table 1). The talonid width of M_3 is slightly less than that of the trigonid.

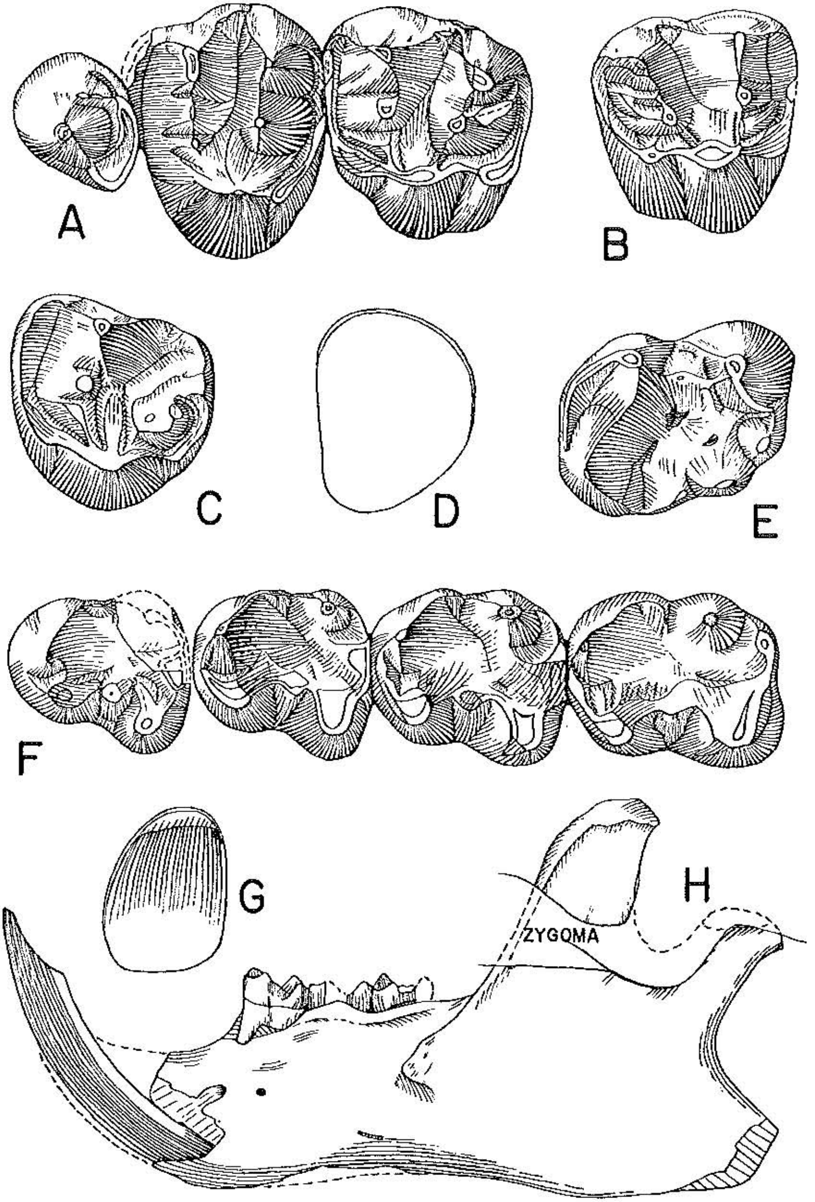

FIGURE 5. — *Ailuravus macrurus* from Messel, H × 1.5; others × 5.

A. LP^3-M^1, Darmstadt Me 2 (Tobien, 1954, pl. 1, fig. 1).

B. RM^2, Darmstadt Me 2, anterior end to the right (Tobien, 1954, pl. 1, fig. 1).

C. LM^3, Darmstadt Me 2 (Tobien, 1954, pl. 1, fig. 1).

D. Cross section of LI^1, Darmstadt Me 2, partly restored; lateral limit of enamel uncertain.

E. RM$_3$, Darmstadt Me 2.

F. LP$_4$-M$_3$, Darmstadt Me 4, isolated teeth that have been rotated so that all crowns are in the same plane (Weitzel, 1949, pl. 2, fig. 8-10; Tobien, 1954, pl. 2, fig. 1).

G. Wear surface of LI$_1$, Darmstadt Me 2.

H. Lateral view of left lower jaw, Darmstadt Me 2; part of jaw concealed behind zygoma.

As pointed out by Tobien (1954, p. 16), the isolated LM_2 (Me 53) possesses both the primitive entoconid-hypoconulid connection through the posterior cingulum, and the typical *Ailuravus* connection from the entoconid to the anterior corner of the hypoconulid.

Incisors. — The upper incisors of Me 2 are present but are crushed. They are small in cross section, but seem to have originated about as far back in the snout as is normal among paramyids. The thin enamel extends for an uncertain distance around into the lateral side, and the anterior face is rounded (fig. 4 D).

The lower incisor of Me 2 was still present beneath M_1, where the jaw is broken. At this point, the pulp cavity is not especially large, suggesting that there may have been an appreciable part of the tooth behind this point. However, from the shape of the jaw in this species (fig. 5 H), it is difficult to visualize its having extended much beyond a point below the rear of M_2, as in the genotype. Weitzel (1949, p. 8) thought that the chisel edge of the lower incisor extended "weit über die anderen Unterkieferzähne...". This extension did not seem so prominent to me (fig. 5 H).

DISCUSSION.

There is very considerable size variation among the specimens referred to *A. macrurus,* which might indicate the presence of a large and a small (Darmstadt Me 154) form. But, at present, this cannot be demonstrated. The cheek teeth have received rather heavy wear, perhaps having been used more extensively than in other paramyids because of the slender incisors and the relatively weak *masseter lateralis.*

None of the cheek teeth shows the overdeepened valleys as clearly as do those of *A. picteti,* but the deepening was beginning, as shown by M_3 of Darmstadt Me 2 (fig. 5 E).

Weigelt (1949, p. 6) stated "Die generische Identität der neuen Messeler und der Egerkinger Form steht fest; Detailunterschiede lassen folgern, das der Schweizer Vertreter eher ein nahe Seitenverwandter als ein Deszendent des Messeler Nagers ist". I believe that he was correct that there is ample basis to separate this species from *A. picteti;* I am not convinced that *A. macrurus* could not have been directly ancestral to *A. picteti.*

Ailuravus stehlinschaubi, new name

Fig. 6

Hyracotherium, Pictet and Humbert, 1869, pl. 25, fig. 5.

Maurimontia picteti Stehlin and Schaub, 1951, p. 355.

Ailuravus n.sp., Hartenberger, 1973, table 1.

TYPE : Left maxilla with dP^4, P^4 within the alveolus, and M^{1-3}, Mus. Géol. Lausanne 39559 (formerly ML 2906, as cited by Wood, 1962, p. 240, footnote 11, and by Stehlin and Schaub, 1951, in the caption of fig. 18 on

p. 20. The number LM 2910, given by Stehlin and Schaub on p. 355 was an error).

HYPODIGM : The type; Mus. Géol. Lausanne 39551, right lower jaw with P_4-M_3 (formerly LM 2910); and Basel Mt 1767, an isolated LM^1. There are also specimens from Robiac that I have not seen.

DIAGNOSIS : Cusps (especially conules) of upper cheek teeth tend to be elongate anteroposteriorly; valleys between cusps deeper than in *A. picteti;* single protoconule; metaconule developing an anteroposterior doubling; mesostyles very prominent and buccally extended, especially on P^4; M^3 primitive as in *A. macrurus* in absence of hypocone; mesoconid of lower teeth very large, triangular, and cut off from buccal margin of teeth; posterolophid of molars almost non-existent except for the hypertrophied hypoconulid; incisor smaller proportionately than in genotype, its posterior end probably farther forward; mental foramen farther forward than in other species; tongue-groove not so large as in some specimens of *A. picteti;* tooth measurements as given in tables 1-2.

DISTRIBUTION : Mormont-Eclépens, Canton Vaud, Switzeland, and Robiac-Nord, Department of Gard, France; Bartonian or earliest Ludian (Stehlin and Schaub, 1951, p. 355) or mid-Bartonian (Hartenberger, 1973, table 1).

DESCRIPTION.

During 1967, while I was studying at the Naturhistorisches Museum, Basel, it became apparent to me that there was no valid basis for the recognition of *Maurimontia* as a genus distinct from *Ailuravus*, although *M. picteti* was clearly specifically separable from *A. picteti*. This therefore results in the necessity for a new specific name for the animal from Mormont. Since the two great Swiss paleontologists were both involved in the study of this animal, as well as in their review of rodent dentition, I have tried to recognize this in the new specific name.

Hartenberger (1973, table 1) likewise recognized *Maurimontia picteti* as an unnamed species of *Ailuravus*, identified in the collections from Robiac (Sudre, 1969, p. 114) as well as from Mormont.

The Mormont species is smaller than that from Egerkingen, but was about the same size as *A. macrurus* (tables 1-2). In any event, the size differences do not seem to have been very significant. The cheek tooth pattern of *A. stehlinschaubi* seems to be a modification of that of *A. picteti*, with an increase in the anteroposterior development of the individual cusps of the upper teeth, especially the conules, which was sufficiently marked so that in some teeth the metaconule is double (fig. 6 A, M^3; B, C). Large mesostyles are present on all the upper molars (fig. 6 A, C), an advanced character. The parastylar region swings around the anterior and buccal slopes of the paracone. A similar cingular area lies lateral to the metacone on M^{1-2} of the type (fig. 6 A), as in *Rapamys* (Wood, 1962, fig. 52 C), although the rest of the tooth is quite different. The protoloph is continuous from the protocone to the rear of the protoconule, although it may be interrupted before wear (fig. 6 A-C).

P^4. — The upper deciduous tooth was removed from over P^4 between the time that the drawing was made for Stehlin and Schaub (1951, fig. 18) and when I studied the material in Basel in 1966. The permanent tooth, partly buried within the alveolus, has no visible suggestion of a hypocone, as in *Mytonomys* (Black, 1968 b, fig. 2), and the cusps have much less anteroposterior elongation than in the molars. The mesostyle is very prominent, as in *A. macrurus*.

M$^{1\cdot2}$. — The hypocones are large, making the teeth quadrate, but the protostyle is very small (fig. 6 A, C) in contrast to the earlier species. The hypocone has established connections with the metaconule as strong as those of the protocone. The conules and the metacone are elongate anteroposteriorly. The mesostyle is large and, together with the protostyle, takes part in a nearly complete buccal cingulum, which is continuous with the anterior cingulum.

M^3. — This tooth does not differ greatly from that of *A. picteti*. There is no hypocone (fig. 6 A), but a small protostyle. The buccal cingulum of the other molars is absent. The conules are elongate. The metacone is a large posterior cusp.

dP^4. — This ultramolariform tooth has a large hypocone. The anterior and posterior cingula almost meet at the middle of the buccal side of the tooth. The lingual valley between the protocone and hypocone extends into the middle of the tooth, arising from a col between the protoconule and metaconule. There is a large hypoconule on the posterior cingulum. The tooth is considerably smaller than the molars (table 2).

Lower Teeth. — The most striking feature of the lower teeth is the large, triangular mesoconid, located almost in the center of the tooth (fig. 6 F). With wear, the posterior arm of the protoconid would unite with the anterior slope of the hypoconid, separating the mesoconid from the buccal wall of the tooth. The entoconid is large and conical, isolated from the hypoconulid by a deep valley, the shallowest part of which is between the anterior ends of the cusps (fig. 6 F). The entoconid and hypoconid are widely separated. The hypoconulid is a distinct, rounded cusp, isolated on the molars, until after considerable wear, from both the hypoconid and the entoconid. Its relationships on P$_4$ are uncertain, due to breakage.

Incisor. — The lower incisor is not preserved. However, from the size and shape of the alveolus (fig. 6 D), it clearly had the same cross-sectional shape as in *A. picteti* and *A. macrurus*, but was proportionately even smaller. The curvature of the mandible (fig. 6 E) suggests that the tooth may have ended beneath M$_1$.

Skull. — The type preserves small portions of the maxillary and palatine (fig. 6 A). There is no evidence for the presence of P^3 or dP^3, but portions of the bone in front of the protocone and protoconule of P^4 are broken and such a tooth might have been present but minute. It probably

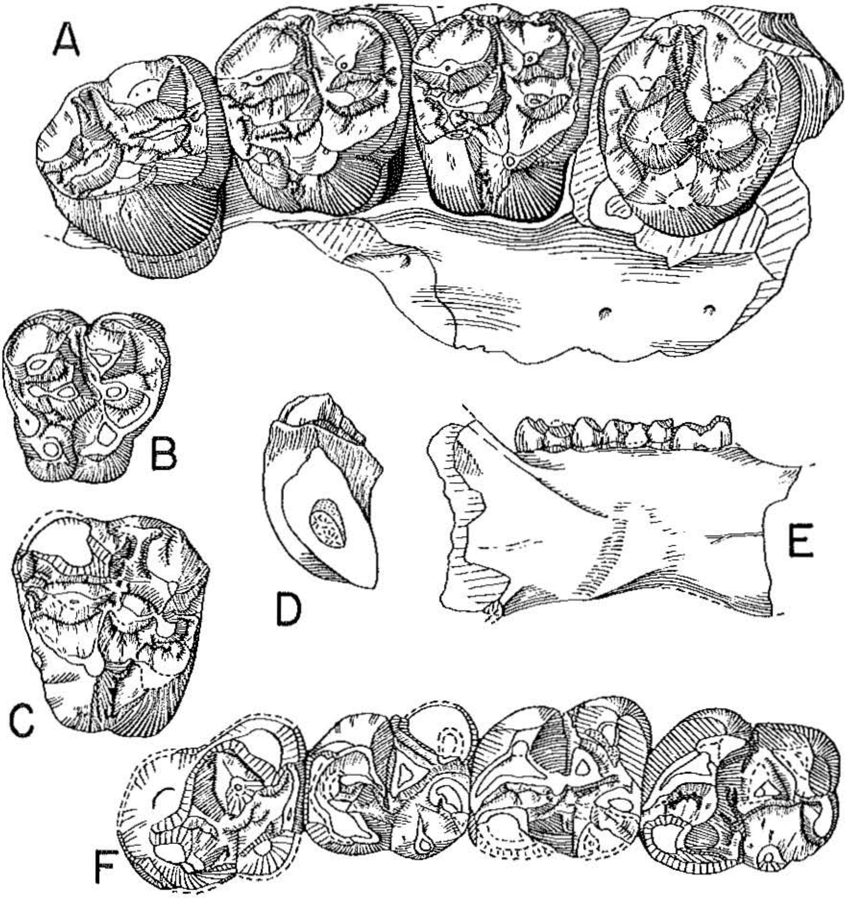

FIGURE 6. — *Ailuravus stehlinschaubi* from Mormont. Teeth × 5, jaw × 1.5.

A. Type, Lausanne 39559, RP^4-M^3, anterior end to the right (Stehlin and Schaub, 1951, fig. 18).

B. Type, Lausanne 39559, RdP^4, anterior end to the right (Stehlin and Schaub, 1951, fig. 18).

C. Basel Mt 1567, LM^1.

D. Lausanne 39561, anterior view of lower jaw broken in front of P$_4$. Dots are matrix; dashes are calcite crystals.

E. Lausanne 39561, lateral view of lower jaw.

F. Lausanne 39561, RP$_4$-M$_3$ (Stehlin and Schaub, 1951, fig. 310).

was absent, however, in view of the extensive area of bone, with no trace of alveoli, that apparently extended over this area before dP^4 was removed (Stehlin and Schaub, 1951, fig. 18). The maxillary-palatine suture crosses the palate by the rear of M^1, and almost reaches the alveolus of M^2, behind which point the suture turns backward close to the alveoli. Two posterior

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palatine foramina are in the palatine opposite the front of M^2 (fig. 6 A). One leads forward and one backward into the bone. I know of no other paramyid that resembles this condition.

Lower Jaw. — The lower jaw is somewhat more slender than in the other species. There seems to have been a prominent chin process (fig. 6 E), and the jaw attained a minimum depth beneath M_1, probably marking the end of the incisor. There is no trace of a mental foramen on Lausanne 39551, so that the foramen was farther forward than in the other two species. The coronoid process, as in *A. picteti,* passes the alveolar level behind M_3. The anterior end of the rather strong lateral crest, for the origin of the *masseter medialis,* ends as in *A. picteti,* with no rugosity for an anterior tendon of this muscle. There is no masseteric crest but only a somewhat rugose area across the ventral half of the mandible beneath M_2, perhaps for the insertion of the *masseter lateralis.* However, the angular process arises from the body of the mandible just back of the level of M_3 (fig. 6 E). If this indicates the insertion of the posterior part of the *masseter lateralis,* as it should, the anterior part may have been well behind the rugose area. An area ventral to the angular process may mark the insertion of the *masseter superficialis.* There is no tongue-groove on the part of the mandible preserved, suggesting that this structure was weaker than in *A. picteti,* if indeed it was present at all.

DISCUSSION

Ailuravus stehlinschaubi seems to have continued from *A. picteti* the trends that separated the latter from *A. macrurus.* A few features seem out of line here (size; position of the mental foramen; size of the tongue groove), but we know nothing of individual variation of these features in *Ailuravus.* Therefore, whether or not the line *A. macrurus — A. picteti — A. stehlinschaubi* is a true phyletic sequence, the three are certainly closely related.

Ailuravus sp.

Michaux (1968, p. 159-162) has reported two unnamed species of *Ailuravus* from Cuis, based on isolated teeth. From his description and illustrations (1968, pl. 6, fig. 5-8; pl. 7, fig. 1-6) there seems no reason to question that these are referable to *Ailuravus.* However, what little is known (tables 1-2) of the size range within populations of the genus suggests that these may represent a single species with considerable size variation, although there are morphological differences between the large and small individuals, as pointed out by Michaux (1968, p. 161-162).

The tooth that Michaux identified as *? Ailuravus* (1968, p. 161; pl. 7, fig. 6) is rather progressive for P^3 or dP^3 of this genus, on the basis of the few specimens that are known.

These teeth, as pointed out by Michaux (1968, p. 162), are more primitive than those of middle Eocene *Ailuravus,* but the Cuisian *Ailuravus* and *A. macrurus* « semblent ... assez proches l'un de l'autre » (Michaux, 1968, p. 162).

Hartenberger (1973, Table 1) lists *Ailuravus* from the early Lutetian of Mas de Gimel, near Montpellier, France.

Relationships of *Ailuravus*

Meldimys and *Ailuravus* are a line of European paramyids, evolving while that continent was isolated. *Ailuravus* and *Plesiarctomys* were the largest European paramyids, and among the largest, if not the largest European Eocene rodents, reaching about the size of a modern marmot. They were significantly smaller than the North American paramyids of the subfamily Manitshinae. As stated by Tobien (1954, p. 17), " Die Aszendenten des *Ailuravus* werden wohl unter den *Paramys*-Formen mit echtem Hypocon zu suchen sein, derartige Tiere sind offensichtlich im Sparnacien und Yprésien Belgiens und Frankreichs vertreten ".

Although the sequence *A. macrurus* — *A. picteti* — *A. stehlinschaubi* is one of generally increasing complexities in cheek tooth pattern and progressive reduction of the lower incisors, the evidence is not fully convincing that it represents an actual phyletic line, although the species are not far from such a line. I am aware of no evidence that the line persisted in Europe after the middle Late Eocene of Mormont.

The Ailuravinae are not among the abundant European Eocene rodents, and presumably owe their relative rarity to their having occupied a forested habitat, an environment always poorly represented in fossil collections.

There are clear analogies between *Ailuravus* and the North American *Leptotomus*, including incisor pattern, shape and general slenderness of the jaws, and the generally rounded cusps. These seem to represent similar adaptations for corresponding diets and not close relationship. Both genera were most probably frugivorous and arboreal. The resemblances to *Mytonomys* seem more significant of genetic relationship, and it seems possible that the best interpretation of the situation would be to refer *Mytonomys* to the Ailuravinae, as was tentatively done above. Resemblances to the Prosciuridae (as Prosciurinae) have been pointed out both for *Ailuravus* (Schaub, 1958, p. 749-751) and for *Mytonomys* (Wood, 1962, p. 227-228), although it now seems clear that neither genus was related to prosciurids. Almost every feature listed above in the subfamilial diagnosis (p. 122) characterizes *Mytonomys* as well as *Ailuravus*.

Schaub (Stehlin and Schaub, 1951, p. 205) reports that Stehlin's notes indicated that he had come to an agreement with Teilhard that the latter's " *Paramys* forme *major* " from the Ypresian was referable to *Ailuravus* and represents the earliest stage of that genus. Wood (1962, p. 51-52) referred " *Paramys* forme *major* " to *Paramys* sp. near *P. copei*, and disagreed (p. 52) as to its similarity to *Ailuravus*. As indicated above, there is similarity in the pattern of P^3 between the North American *P. copei* and *Ailuravus*, which may indicate that a species of *Paramys* near *P. copei* was the ancestor of the Ailuravinae. However, I still do not think that Teilhard's material can be referred to the Ailuravinae, especially in view of the definite representation of *Ailuravus* in the Ypresian (Michaux, 1968, p. 159-162).

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Specimens identified in the text as " Basel "are in the collections of the Naturhistorisches Museum, Basel; those labelled " Darmstadt " are in the Hessisches Landesmuseum, Darmstadt; " Halle " refers to the Geologisches Institut, Halle-an-der-Saale; and " Lausanne " to the Musée Géologique de Lausanne.

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