NEW PALEOCENE INSECTIVORES AND INSECTIVORE CLASSIFICATION

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INTRODUCTION

THE PRESENT STUDY began as a simple description of a few new genera to which reference elsewhere was desirable. It proved difficult to fit some of them into the received classification, and the relatively wide comparisons necessary made it feasible to construct an interim classification of the insectivores and deltatheridians based on recent work.

The dental nomenclature used in the present paper is that of Van Valen (1966). Approximately 90 per cent confidence intervals (not standard errors) are given for those measurements that need them.

The following abbreviations are used:

A.M.N.H., the American Museum of Natural History, Department of Vertebrate Paleontology

A.M.N.H.(M.), the American Museum of Natural History, Department of Mammalogy

C.M., Carnegie Museum, Pittsburgh

H.L., Hessische Landesmuseum, Darmstadt

N.M.K., National Museum of Kenya

Y.P.M., Peabody Museum, Yale University

ORDER INSECTIVORA

FAMILY PANTOLESTIDAE

Palaeosinopa simpsoni,[1] new species

Plate 6, figures 1 and 2

Palaeosinopa senior SIMPSON, 1937b, referred specimens only.

TYPE: A.M.N.H. No. 33991, right M^1.

REFERRED SPECIMEN: A.M.N.H. No. 33828, right M^2 (lingual face of protocone slightly broken).

AGE AND LOCALITY: Late Paleocene, Tiffanian, Scarritt Quarry, Melville Formation, Crazy Mountain Field, Montana.

DIAGNOSIS: *Palaeosinopa simpsoni* is about the size of *P. didelphoides*, or somewhat smaller than *P. veterrima;* the hypocone is basal and somewhat more lingual than in these species; the conules are more basal; the lingual face of the protocone is somewhat less steep; central conule wings are present on M^1 as well as M^2; and the protocone apex is less acute. The paracone and metacone are about as connate as those of *P. didelphoides*. *Palaeosinopa simpsoni* is considerably larger than *P. lutreola* and *P. osborni*, both known from mandibles only.

DISCUSSION: The three teeth placed by Simpson (1937b) in *Palaeosinopa senior* now seem to be referable to two species of different families. The lower tooth presents more differences from the Eocene species of *Palaeosinopa* than do the upper teeth, and the lower tooth was unfortunately taken as the type. This choice leaves the referred upper teeth, which were the basis for the generic reference, nameless.

The lower tooth is discussed below as a new genus (*Paleotomus*) of the Deltatheridia. I regard it as distinct from the upper teeth mainly because it is much more similar to that of deltatheridians than to that of *Palaeosinopa*, whereas the reverse is true for the upper teeth. In addition, however, there is a transverse wear facet on the paracingulum of the M^2, caused by the tip of the protoconid of M_2 in more or less transverse movement. The protoconid of the lower tooth

[1] For George Gaylord Simpson.

is much too tall to produce such a facet. Even though the lower tooth is an M_3, the large difference between the trigonid heights of M_2 and M_3 necessary to produce this wear facet would not be similar to the condition in *Palaeosinopa*.

Palaeosinopa simpsoni is closest to *P. didelphoides* and may be directly ancestral to it. The somewhat smaller species (species E in the discussion of *Pantinomia*, below) from the Four Mile and Bitter Creek is also a possible ancestor of *P. didelphoides*, but because of its size may not have been derived from *P. simpsoni*. It is also possible that species E is a later subspecies of *P. simpsoni;* if so, the size reduction may represent a trend later (and presumably also earlier) reversed. The upper dentition of *P. didelphoides* is figured in plate 6, figure 3.

A.M.N.H. No. 22175, a right M^1, and A.M.N.H. No. 22221, the labial half of an upper molar, both from Bear Creek, are referable to *Palaeosinopa* and may well belong to *P. didelphoides*. These teeth are more advanced than those of *P. simpsoni* in that the crown relief is somewhat lower, the hypocone is more labial, and the lingual part of the tooth is longer anteroposteriorly relative to the labial part of the tooth. These conditions are probably all also true for Eocene *P. didelphoides*. Central conule wings are present; their condition is unknown in Eocene *P. didelphoides*.

CF. FAMILY PANTOLESTIDAE

Pantinomia ambigua,[2] new genus and species

Text figure 1; tables 1 and 2

TYPE AND ONLY KNOWN SPECIMEN: A.M.N.H. No. 16591; nearly complete left mandibular ramus with C, P_4, and M_2, right

[2] *Pantinomia*, from *Pantolestes* and Greek *antinomia*, antinomy. An antinomy is the conjunction of two mutually contradictory propositions, each of which is provable within the system used (Kant's usage is somewhat different). Antinomies have been important in the development of mathematical logic, and their resolution produces a deeper understanding of the relations in which they are involved. *Pantinomia* approaches the condition of a phylogenetic antinomy.

The name *ambigua* is given with reference to the uncertain taxonomic position of this species.
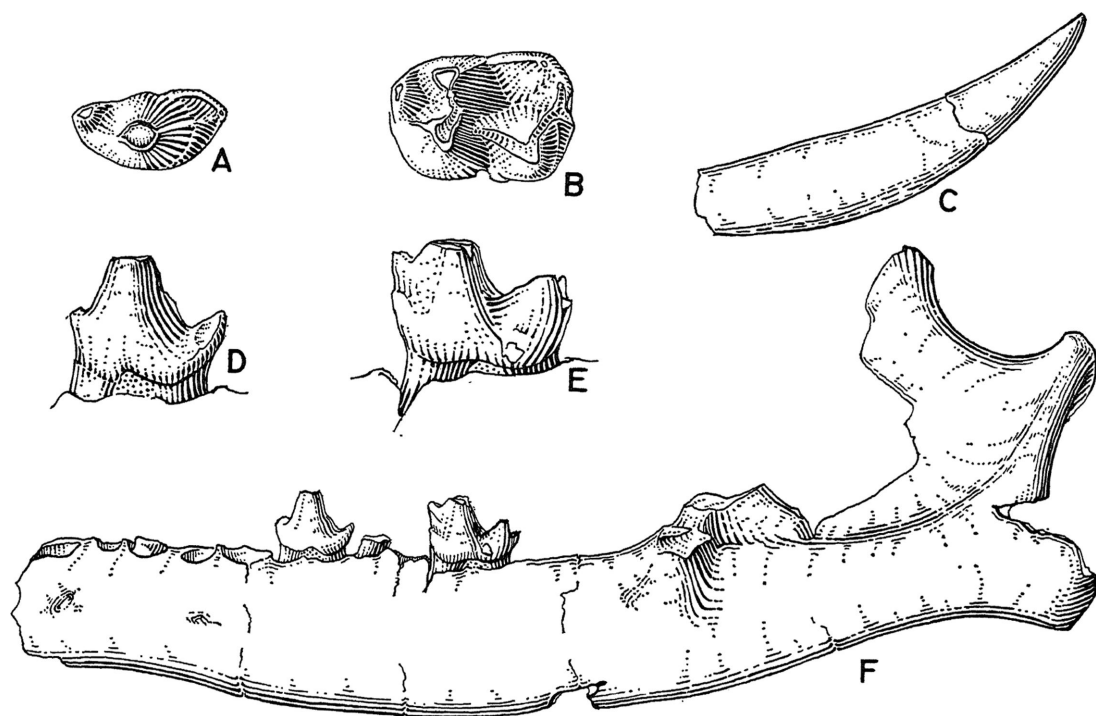
FIG. 1. *Pantinomia ambigua*, type specimen. A. Left P₄, occlusal view. B. Left M₂, occlusal view. C. Left lower canine, lingual view. D. Left P₄, labial view. E. Left M₂, labial view. F. Mandible, labial view. A–E, ×5; F, ×2.5.

humerus, one partial lumbar vertebra, and three halves of caudal centra.

AGE AND LOCALITY: Middle Paleocene, Torrejon Fauna, East Fork of Torrejon Arroyo, San Juan Basin, New Mexico.

DIAGNOSIS: Posterior mental foramen below anterior root of P_3; hypoconulid moderately lingual of midline on M_2, entocristid relatively strong, posterior and labial cingula present on M_2 although weak, trigonid of moderate height, metacristid completely absent, no trace of a secondary protolophid across the middle of prefossid, paralophid extending anterolingually from apex of protoconid; talonid of P_4 narrow, labial cingulum absent from P_4. These are the major distinctions of *Pantinomia* from *Palaeosinopa* and *Oxyclaenus*.

COMPARISONS: *Pantinomia* is most similar to *Palaeosinopa veterrima* and *Oxyclaenus simplex*, and is compared in detail with these species and with *Propalaeosinopa albertensis diluculi* (for this nomenclature, see below).

From *Palaeosinopa veterrima*, *Pantinomia*

differs in the following respects. The teeth are somewhat smaller relative to the jaw size; the mental foramen is below P_3, not below M_1 or even M_2 as in *Palaeosinopa;* the anterior end of the scar for the insertion of the temporal muscle is somewhat more posterior; and the concavity in the ventral margin of the ascending ramus is somewhat shallower. M_2 is lower-crowned than in at least most specimens of *P. veterrima* (a similarity to *P. didelphoides*); it is somewhat more transverse than in even most specimens of *P. veterrima;* the postvallid is considerably less vertical; the labial slopes of the protoconid are somewhat less vertical; the paralophid lacks a carnassial notch (it is very weak in *P. didelphoides*); the prefossid is shallower (as in *P. didelphoides*); the paraconid is smaller and less anterior (as in *P. didelphoides*); the hypoconulid is moderately lingual of the midline and slightly less posterior; the entoconid is relatively strong (as in *P. lutreola*); the entocristid is stronger; there is a posterior cingulum extending basolabially from the

	M₂	P₄
Length	4.5	3.9
Trigonid width	3.3	2.0
Talonid width	3.4	—

hypoconulid; there is a weak labial cingulum
in the hypoflexid; and the anterior cingulum
is weaker. The anterior border of the pro-
toconid of P_4 is straight in lateral view, not
strongly convex as in *Palaeosinopa;* the
talonid is narrower; the entocristid is some-
what stronger; and there is a posterolingual
vertical crest on the protoconid, as in *P.
didelphoides*, but weaker. In addition,
Pantinomia is smaller than *P. veterrima*,
being about the size of *P. didelphoides* speci-
mens from the Lost Cabin.

Pantinomia is somewhat smaller than
Oxyclaenus simplex and differs structurally as
follows. The paraconid of M_2 is larger and
somewhat more projecting anteriorly relative
to the base of the tooth (usually true also in
O. cuspidatus); the paralophid extends an-
terolingually, not anteriorly, from the apex of
the protoconid; there is no trace of a secon-
dary protolophid across the middle of the pre-
fossid; the metacristid is completely absent;
the talonid cusps are lower relative to those of
the trigonid; the labial surface of the hypo-
conid and the lingual surface of the meta-
conid are flat in the apicobasal direction, not
convex; the entocristid is as anterior as the
hypoconid (occasionally true also in *O.
cuspidatus*); the labial and posterior cingula
are smaller; and the tooth is slightly higher-
crowned. The P_4's of *O. simplex*, *O. cuspida-
tus*, and *O. antiquus* (=*Chriacus antiquus*
Simpson) are rather different from one an-
other, but the P_4 of *Pantinomia* differs from
them all in a number of respects. The para-
lophid is weaker; the posterolingual crest on
the protoconid meets the posteromedian crest
on the protoconid only near the apex of the
protoconid, not midway down the posterior
slope (the posterolingual crest is in some
cases absent from *O. cuspidatus* and *O.
antiquus*); the lingual and labial sides of the

protoconid are distinctly convex in the
apicobasal direction, not nearly flat; the
posterior slope of the protoconid is less verti-
cal; the entocristid is somewhat stronger; the
interradicular notch is markedly anterior to
the midpoint of the tooth, not nearly at the
midpoint; and a labial cingulum is absent.

From *Propalaeosinopa albertensis*, in addi-
tion to larger size, *Pantinomia* differs in the
following respects. The teeth are considerably
smaller relative to the jaw; the posterior
mental foramen is under the anterior root of
P_3 rather than under M_1 or M_2; the ascending
ramus is longer anteroposteriorly relative to
the horizontal ramus; there are small diaste-
mata at each end of P_2; the canine is probably
relatively larger; and P_4 is shorter than M_2,
not longer. The cusps of M_2 are considerably
less acute; the trigonid is considerably lower;
the postvallid is less steep; the widest part of
the trigonid is near the base, not above the
level of the talonid or even near the trigonid
apex, as in *Propalaeosinopa*, and the trigonid
cusps are therefore less marginal; the para-
conid is slightly less lingual and is nearly as
high as the metaconid; the narrowing be-
tween the trigonid and talonid is nearly or
quite absent; the entocristid is stronger; the
crista obliqua is less transverse; the hypo-
conulid is somewhat more lingual and less
posterior; and labial and posterior cingula

C–M₃, alveolar length	29.3±0.4
Mandible depth below M₂ protoconid	7.8±0.2
Distance from M₃ alveolus to subcondy- lar fossa	26.2±0.4
Distance from M₃ alveolus to middle of posterior edge of condyle	23.1±0.3
Distance from M₃ alveolus to dental foramen	14.8±0.2
Width of condyle	7.4
Anteroposterior length of C₁ at base of enamel	3.4
Maximum anteroposterior length of root of C₁	4.2
Transverse width of C₁ at base of enamel	2.4
Posterior height of C₁ from base of enamel	8.4

are present although weak. P_4 is less transverse; the paraconid is somewhat larger; the talonid cusp is lingual, not labial, to the apex of the protoconid; and the talonid is slightly smaller.

In the above comparisons, all the specimens of the respective taxa in the American Museum have been utilized, and also a few specimens from other institutions.

The small-toothed specimen from the Torrejonian of Rock Bench figured by Jepsen (1930) and referred by him to *Palaeosinopa*, may belong to *Pantinomia*. As I have not been permitted to examine this specimen, no detailed comparison is now possible. An infraorbital foramen is figured for this specimen under the anterior border of M_1, but it is small, about the size of that of *Pantinomia ambigua*, and not enlarged as in *Palaeosinopa* and later pantolestids. The Rock Bench specimen seems more similar to *Palaeosinopa didelphoides* than to *P. veterrima* or (probably) the poorly known species *P. lutreola*. *Palaeosinopa osborni*, from the late Ypresian of Epernay, France, is a small species (the size of *P. lutreola*) that combines characters of *P. veterrima* and *P. didelphoides*. The presence of four species of *Palaeosinopa* in Gray Bull time (if *P. lutreola* is correctly referred to this genus) is suggested by the relatively small specimens (here called species E) reported by Gazin (1962) and McKenna (1960a), which are probably conspecific with A.M.N.H. No. 16239, a mandible fragment from Laguna Colorado, Arroyo Blanco, New Mexico. A.M.N.H. No. 16943, maxillae from the Gray Bull of South Elk Creek, in the Bighorn Basin, Wyoming, is specifically different from *P. veterrima* and presumably represents *P. didelphoides*. It occludes adequately with the type mandible of the latter species, and is too large to represent species E. A.M.N.H. No. 16943 differs from *P. veterrima* especially in having the paracone and metacone more connate.

DISCUSSION: *Pantinomia* is intermediate between *Oxyclaenus* and *Palaeosinopa*, as can be seen from the fact that almost no differences from one are differences from the other also. It is intermediate in time as well as in known morphology. However, there also exists another middle Paleocene genus that is similar to *Palaeosinopa*, namely, *Propalaeo-*

sinopa (=*Bessoecetor*). *Propalaeosinopa* does not approach *Oxyclaenus*, but rather approaches the Leptictidae, the Erinaceoidea, and the Palaeoryctidae (e.g., *Cimolestes magnus* Clemens and Russell, 1965). I believe that these two or more possible ancestries are mutually exclusive. The Arctocyonidae come from a species like the late Cretaceous *Protungulatum donnae* Sloan and Van Valen, 1965, and *Cimolestes* is the same age as *Protungulatum* and differently specialized. The Leptictidae are probably intermediate between these genera phyletically as well as structurally.

I see no adequate basis at present for choosing among the following possibilities: (1) *Propalaeosinopa* is at least approximately ancestral to *Palaeosinopa*, and *Pantinomia* is an arctocyonid convergent toward *Palaeosinopa*. (2) *Pantinomia* is at least approximately ancestral to *Palaeosinopa*, and *Propalaeosinopa* is a leptictid, erinaceoid, or palaeoryctid convergent toward *Palaeosinopa*. (3) *Propalaeosinopa* gave rise to *Palaeosinopa didelphoides*, and the unrelated *Pantinomia* gave rise to *Palaeosinopa veterrima*, these being the species of *Palaeosinopa* to which these genera are closest. (4) *Propalaeosinopa* and *Pantinomia* are related to each other, one or even both giving rise to *Palaeosinopa* and the differences between the Paleocene genera being due to rapid divergence. The first possibility may be tentatively preferred to the second,[1] because *Propalaeosinopa* is better known than *Pantinomia* and none of this greater knowledge contradicts a relationship with *Palaeosinopa* (but, on the other hand, there are two lineages known in or near *Pantinomia* and only one in *Propalaeosinopa*), and the third possibility seems the least likely because of the similarity to one another of at least the three better-known species of *Palaeosinopa*, but any of the four possibilities may be true with evidence now available. If *Palaeosinopa* should prove to be an arctocyonid derivative, the major classification of Paleocene placentals would need reconsideration.

[1] As a result of comparisons with an undescribed species of *Protungulatum* from Purgatory Hill, I now (January, 1967) believe that *Pantinomia* is an arctocyonid and is probably only convergent to the Pantolestidae.

In the above discussion no mention is made of several taxa that might be thought to have a bearing on the relationships of *Palaeosinopa*, namely, the oldest named species of *Palaeosinopa* (*P. senior*), from the late Paleocene of Montana; *Amaramnis gregoryi* Gazin, 1962, from the early Eocene of Wyoming; the two pantolestids described by Donald E. Russell (1964) from the late Paleocene of France; and the Paleocene group Pentacodontinae, which since its establishment has been regarded as a subfamily of the Pantolestidae. Furthermore, the skull and skeleton of *Pantolestes* were ignored.

As shown by Matthew (1909), the skeleton of *Pantolestes* is more or less adapted to an aquatic existence. Most of the characters he cited as indicating insectivore affinities can be used at least equally well to indicate arctocyonid affinities. For example, the astragalus of *Pantolestes* is at least as similar to that of *Loxolophus* as to that of *Prodiacodon*, but is rather different from both. No diagnostic postcranial skeletal material is known for *Palaeosinopa*. Furthermore, there are no Paleocene families or higher taxa of small or moderate body size that are now distinguishable on the basis of non-dental features of their crania, with the exception of the possible bat described by Edinger (1961, 1964) and perhaps primates. With a considerable increase in the number of genera for which crania are known, it may eventually be possible to control lower-level variation, which is now demonstrable, and find cranial characters diagnostic of some families. But at present this control cannot be made. Most skulls of Paleocene placentals and their close relatives are divergent to only a slight degree from one another and presumably from a common ancestral form. Cranial features of middle Eocene pantolestids, or most other groups, are therefore of dubious value now in establishing their relationships with Paleocene families.

The posterior mental foramen in at least most specimens of *Pantolestes* is, as noted by McDowell (1958), double, with an anterior and a posterior foramen opening into a fossa on the mandible. I have not been able to demonstrate this feature in any earlier pantolestid, however, and from some speci-

mens it is definitely absent. The foramen is relatively large, and occasionally there is a blind pouch extending anteriorly from the fossa, but I have found no foramen there in *Palaeosinopa* or *Propalaeosinopa*.

The humerus of *Pantinomia* was figured by Matthew (1937, pl. 8, fig. 3). The photograph was taken at an oblique angle to the distal end, which is wider than would appear from the figure. The humerus is of the standard primitive placental type. The entepicondylar foramen is slightly more distal than usual, as in *Plesiadapis*, and the deltoid crest is broad and relatively robust as in most of the Arctocyonidae, the Periptychidae, *Prodiacodon*, the Miacinae, and *Onychodectes*, rather than narrow as in *Didymictis*, *Loxolophus*, *Plesiadapis*, *Metacheiromys*, and *Pantolestes*.

Matthew (1937, p. 67) referred the type specimen of *Pantinomia ambigua* to *Chriacus* as an undetermined species.

I cannot distinguish *Propalaeosinopa albertensis*, described by Simpson (1927) from the approximately late Paleocene Paskapoo Formation of Alberta, from *Bessoecetor diluculi*. On the other hand, I cannot disdistinguish it generically from *Palaeosinopa*. The only tooth known of *P. albertensis* is a P_4 that is too worn to be adequately diagnostic. Provisionally, *Bessoecetor* may be synonymized with *Propalaeosinopa*, and *B. diluculi* may well be referable to *P. albertensis*. As noted, however, the material now available is too poor for a firm judgment to be made. Nevertheless, by the principle "*Species non sunt multiplicanda praeter necessitatem*,"[1] and because of the geographic and stratigraphic proximity of their localities, I use the name "*Propalaeosinopa albertensis*" for "*Bessoecetor diluculi*" (see also the next paragraph). The name "*P. albertensis*" is not a *nomen vanum*, because further collecting should produce additional specimens which would be readily identifiable by the type. Both "*Bessoecetor*" and "*Propalaeosinopa*" are in current use, and, as I cannot distinguish their species, I synonymize them, even though such a course means that the resulting species has a name

[1] "Species should not be multiplied beyond necessity." This maxim (with the substitution of "*species*" for "*entia*") is a probably post-Ockham version (*fide* Sarton, 1947) of Ockham's razor.

with a poor type. If additional collecting should show the species or genera to be distinct, one of the later names could be revived.

"*Bessoecetor thomsoni*," from the late Paleocene Scarritt Quarry, Montana, also cannot be distinguished specifically from "*B. diluculi*," which is from the middle Paleocene of Gidley Quarry, Montana. (Simpson, 1937b, reported "*B. diluculi*" also from the middle Paleocene Silberling Quarry; the only specimen in the American Museum so labeled is apparently referable to *Palaeictops*, but I have not examined the material in the United States National Museum.) There is broad overlap between the available samples of these populations in all the characters used as diagnostic by Simpson (1937b) except the less compressed (transversely) paracone on P^4 of "*B. thomsoni*" and the smaller lingual cingula of P^4, the latter not mentioned by Simpson. The populations are distinct, but I do not believe it is a useful or a valid procedure to regard as separate species all populations that can be shown to be distinct, although such practice is common in paleontology. If taxonomic separation is desired, "*B. diluculi*" can be regarded as a temporal subspecies, *Propalaeosinopa albertensis diluculi*. The probably Tiffanian age of the Alberta sample suggests that synonymy on the subspecific level should be between *P. albertensis* and *B. thomsoni*.

Pagonomus dionysi Donald E. Russell, 1964, from the late Paleocene of Cernay, France, is a puzzling species. The M$^{?1}$, P$_4$, and M$_{?1}$ resemble those of the pentacodontines *Aphronorus* and (except the P$_4$) *Coriphagus*, and the M$^{?2}$ resembles the M^1 of the pantolestine *Palaeosinopa*. All the teeth are isolated. There are sufficient differences between the teeth regarded as M^1 and M^2 that I suspect they belong to different species; I cannot, however, prove it. If my conjecture is correct, *Pagonomus* would become a synonym of *Palaeosinopa* because an M$^{?2}$ was the type, and the other species would be nameless. In any event, as noted by Russell, at least most of the teeth are referable to the Pentacodontinae and are therefore irrelevant to the ancestry of *Palaeosinopa*. The upper molars from Cernay referred by Russell to "Pantolestidé n. gen. et n. sp." do not seem to me

generically distinguishable from those of *Propalaeosinopa*. The M^3 figured in his plate 6, figure 8e, could possibly belong to the pentacodontine.

Amaramnis gregoryi, an early Eocene species from Wyoming, appears to be the last survivor of the Pentacodontinae and not a close relative of *Palaeosinopa*. "*Palaeosinopa senior*" and the Pentacodontinae are discussed elsewhere in this paper.

Opsiclaenodon and *Dyspterna*, from the late Eocene and early Oligocene of England, have been regarded as arctocyonids (Hopwood, 1927; Butler, 1947; Russell and McKenna, 1961). I have shown (Van Valen, 1966) that the upper dentition from Italy referred by Dal Piaz (1930) to *Dyspterna woodi* is in fact an apheliscine. An examination of the specimens at the British Museum (Natural History) has shown that *Opsiclaenodon* and *Dyspterna* are related, as Butler believed, that *Opsiclaenodon* could be directly ancestral to *Dyspterna*, and that *Opsiclaenodon* is unquestionably a pantolestid closely related to *Palaeosinopa* and *Pantolestes*. The P$_4$ of *Opsiclaenodon* is very similar to that of these pantolestids, and the mandible and the lower molars and canine are also comparable. The P$_2$ of *Opsiclaenodon* is rather similar to that of the genus *Galethylax* from the French Phosphorites (cf. Van Valen, 1966) and may possibly indicate the affinities of *Galethylax*. *Kochictis*, described by Kretzoi (1943) from the middle Oligocene of Hungary, may possibly belong to the Pantolestidae rather than to the Paroxyclaenidae, where I have provisionally placed it (Van Valen, 1965a), but a photograph given by Kretzoi differs considerably from a drawing on the same plate, and the morphology of this genus is best regarded as unknown in detail.

Cryptopithecus sideroolithicus Schlosser, 1890, is a pantolestid, as noted elsewhere (Van Valen, 1966). I have compared a good cast of the type (the cast is A.M.N.H. No. 55957) with Butler's figures (1947) of, and my notes on, *Opsiclaenodon major*, and it does not seem possible to separate these species generically. I therefore synonymize *Opsiclaenodon* with *Cryptopithecus*. *Cryptopithecus sideroolithicus* has a perhaps slightly smaller paraconid than *C. major*, and its hypoconulid seems less posterior.

Kelba, described as an oxyclaenine arcto-cyonid by R. J. G. Savage (1965) from the Miocene of East Africa, is known from three isolated upper molars. They are at least as similar to those of *Pantolestes* as to those of any oxyclaenine. Because pantolestids occur in the Oligocene in both Europe and North America and no oxyclaenine is known either after the earliest Eocene or outside North America, I believe that *Kelba* is better placed in or near the Pantolestidae. I have elsewhere (Van Valen, 1966) suggested that *Ptolemaia* and another, as yet unnamed, genus from the Oligocene of Egypt were derived from the Pantolestidae. The upper teeth of these Egyptian genera are unknown. I therefore propose that *Kelba* represents the upper dentition of a genus of the Ptolemaiidae. Such an allocation is occlusally possible but not mandatory, in view of the relatively un-specialized nature of the teeth involved. Whether *Kelba* is congeneric with either Egyptian genus or not cannot now be de-termined. The possibility is worth passing consideration that the ptolemaiids, or pre-ptolemaiid pantolestids, gave rise to the Macroscelididae.

Pantomimus leari,[1] new genus and species

Text figure 2; table 3

TYPE AND ONLY KNOWN SPECIMEN: A.M.N.H. No. 35300, left maxilla fragment with M^1, most of M^2, and the roots of P^4 and M^3.

AGE AND LOCALITY: Middle Paleocene, Lebo Formation, Locality 25 of Simpson (1937a), Crazy Mountain Field, Montana. This locality is at a lower level than the Gidley and Silberling Quarries and has a dis-tinctly different fauna.

DIAGNOSIS: This is a moderately small in-sectivore with rather low-cusped teeth. The parastyle of M^2 is distinctly the most external part of the upper tooth row; the stylar shelf is moderately wide on the upper molars; the labial part of the molar is much longer ante-

[1] *Pantomimus*, from Greek *pan(tos)*, all, and Latin *mimus* (Greek *mimos*), imitator. Reference is to *Pantolestes* and to the resemblance of *Pantomimus* to several groups.

Leari is for Lear, King of Wessex, with allusion to the Crazy Mountain Field and the difficulty of allocating this species.

roposteriorly than the lingual part; the para-cone and metacone are moderately close but by no means connate; the protocone apex is on the lingual third of the tooth; the conules are weak and without central wings; the preprotocrista is much taller than the post-protocrista; a hypocone is absent; the lingual cingula are relatively weak but continuous lingually; and the lingual cingula are low on the crown, and extend labially only a short distance. Vertical shear is weak; the largest wear facet extends posterolabially and strongly basally from the protocone apex. The labial border of M^1 is 3.2 mm. long.

COMPARISONS: *Pantomimus* has similari-ties especially to the Pantolestidae, primitive Erinaceoidea, Arctocyonidae, and Paroxy-claenidae. I compare it in detail with *Palaeo-sinopa veterrima*, *Propalaeosinopa albertensis*, *Leptacodon tener*, *Protungulatum donnae* Sloan and Van Valen, 1965, the paroxyclaenid *Pugiodens simplicidens* (Van Valen, 1965a), the primitive leptictid *Procerberus formi-carum* Sloan and Van Valen, 1965, and *Gyp-sonictops* spp.

Pantomimus differs from the rather vari-able species *Palaeosinopa veterrima* as follows, in addition to being considerably smaller. The metastylar region of M^1 and the parastylar region of M^2 extend considerably farther labially, and the parastylar region of M^1 pro-jects more anteriorly. The cusps are some-what lower. The metastylar region of M^2 is moderately reduced, and the lingual region of the molars is shorter anteroposte-riorly relative to the labial region. The metacingulum does not extend so far labially as the apex of the metacone. The protocone is somewhat more lingual, and the postproto-crista is lower relative to the preprotocrista. A hypocone is absent, and the lingual cingula extend much less far labially. The infraorbital foramen opens above P^3, not above M^1, and the concavity between the zygomatic arch and the dentiferous portion of the maxilla extends anteriorly to the middle of M^2, not M^3.

From *Propalaeosinopa albertensis*, *Panto-mimus* differs in the following respects. The cusps and crests are considerably lower. The metastylar region of M^2 extends much less labially, and the parastylar region of M^2 is more labial. The metacingulum does not ex-

FIG. 2. *Pantomimus leari*, type specimen, left M^{1-2}. ×7.5.

tend so far labially as the apex of the meta-cone. Central conule wings are absent, and the postprotocrista is probably lower relative to the preprotocrista. A hypocone is absent, and the lingual cingula extend less far labi-ally. The differences in the maxilla are the same as with *Palaeosinopa*.

Pantomimus differs from the primitive erinaceoid *Leptacodon tener* as follows, in ad-dition to being much larger. The upper molars are considerably more transverse, are shorter lingually, and have lower cusps. The sharp central conule wings of *Leptacodon* are absent, as is the hypocone. The metastylar region of M^1 and the parastylar region of M^2 are more labial. The parastylar region of M^1 projects more anteriorly. The metacingulum does not extend so far labially as the apex of the meta-cone. The postprotocrista is lower relative to the preprotocrista. The lingual cingula extend less far labially and are continuous lingually. The lingual root of P^4 is probably more posterior and perhaps more labial. Most of

these differences, and others, are also differ-ences from the maxilla of *Scenopagus* de-scribed by McKenna and Simpson (1959).

Pantomimus is larger than *Gypsonictops* spp., and differs structurally as follows. The stylar shelf is somewhat wider, and the metastylar region of M^1 and the parastylar region of M^2 project more labially. The cusps are lower; the paracone and metacone are more transverse and somewhat more sepa-rate; and the centrocrista is lower. Central conule wings are absent. The metacingulum does not extend so far labially as the apex of the metacone. The lingual cingula are weaker, do not extend so far labially, and are con-nected lingually, and the postcingulum has no trace of a hypocone. The maxilla of *Gypsonic-tops* has not been described.

Pantomimus has considerably lower cusps than the Cretaceous leptictid *Procerberus formicarum*. The parastylar region of M^2 pro-jects labially considerably more than the metastylar region and is wider transversely on both M^1 and M^2. The metastylar region of M^1 is somewhat larger and extends farther labially. The conules are somewhat larger, and the protocone is somewhat more lingual. The lingual cingula are larger and are con-tinuous lingually; the postcingulum is larger than the precingulum. The concavity be-tween the zygomatic arch and the dentiferous part of the maxilla extends anteriorly to the middle of M^2, not M^3.

The stylar region and maxilla of *Pantomi-*

TABLE 3

MEASUREMENTS (IN MILLIMETERS) OF THE
TEETH OF THE TYPE OF *Pantomimus leari*

	M^1	M^2
Labial length	3.2	2.9 ± 0.1
Length at conules	1.9	1.9
Length at hypocone	2.1	1.9
Mid width	4.0	4.2 ± 0.1

mus differ from those of *Protungulatum don-nae* in the same ways as from those of *Procerberus*. The molars are considerably shorter lingually. M² is about the same size as M¹, not larger. The conules are somewhat smaller; the metaconule is more labial; and the preprotocrista is more pronounced. The protocone is lower, and its apex is more lingual, and the protofossa is larger. The lingual cingula are continuously lingually and do not extend so far labially. The metacingulum also extends less far labially and is weaker.

Among paroxyclaenids (Van Valen, 1965a), *Pugiodens* is more similar to *Pantomimus* than is any other genus except perhaps the poorly known *Kochictis*. *Pantomimus* differs from *Pugiodens* in the following respects. M² is no smaller than M¹. The parastylar region of M² projects labially considerably more than the metastylar region, but the reverse is true for M¹. The parastyle of M¹ forms a distinct anterior projection. The centrocrista is lower, and the paracingulum extends to the parastyle. The paracone and metacone are somewhat smaller. The preprotocrista is distinctly higher than the postprotocrista, and these two crests meet at a somewhat more acute angle. Lingual cingula are present. M³ extends farther lingually than M².

DISCUSSION: The relationships of *Pantomimus* are not obvious. It is probably not a leptictid or an ancestral paroxyclaenid, but beyond such a statement it is difficult to go. The central position of the lingual root of P₄ proves that *Pantomimus* is not a miacid, unless it is an ancestral miacine that had not yet developed a carnassial P⁴. The molars are somewhat similar to those of the primitive miacine *Oodectes*. The upper molars probably referable to *Prothryptacodon* (A.M.N.H. Nos. 35358 and 35852) show that arctocyonids can produce more or less similar teeth, although the genera are clearly distinct and probably not closely related.

The inferences that can be made from the wear surfaces about the lower dentition of *Pantomimus* are not particularly helpful. The well-developed transverse facet on the parastylar lobe was caused by transverse movement of the protoconid after a more vertical stroke. Because of the moderately low paracone and metacone, the protoconid was probably also not particularly tall. The presence of moderate prevallum and postvallum shear indicates that the prevallid and postvallid were more or less vertical. The large wear facet on the posterolabial face of the protocone can be produced in different ways, so is not useful for prediction. The trigonid was probably relatively short anteroposteriorly, as indicated by the short interdental embrasure.

The roots of M³ indicate that this tooth was moderately or very transverse and was shifted lingually in position although not greatly if at all reduced in width. Enough of the labial and posterolabial enamel of M² is preserved (examined under ultraviolet as well as ordinary light) to indicate that the posterolabial region probably did not extend much farther labially than the part that is preserved.

Pantomimus leari is too small to be from the same population as *Pantinomia ambigua*. In addition, the trigonid of the M₂ of *Pantinomia* may be too long anteroposteriorly for *Pantomimus*. Generic separation seems necessary at present.

FAMILY **PENTACODONTIDAE**
(SIMPSON, 1937), NEW RANK

As noted elsewhere (Van Valen and McKenna, MS), *Aphronorus*, *Bisonalveus*, *Coriphagus*, *Pentacodon*, and an undescribed genus form a more or less distinct group of insectivores that has (except for *Coriphagus*) traditionally been referred to the Pantolestidae as the subfamily Pentacodontinae. The more recently described genus *Amaramnis* Gazin (1962) and the Cernay species discussed above are probably also referable to the Pentacodontidae.

The relationships of the Pentacodontidae are obscure. They, the primitive erinaceoids, and the hyopsodonts form a complex within which broad phyletic relationships are for the most part not clearly visible. Furthermore, some erinaceoids are very similar to leptictids and appear to have originated from that family, and some hyopsodonts are very similar to arctocyonids and appear to have originated from the latter group. These paths of descent are mutually exclusive, and either one is incorrect or, more probably, there has been later convergence. If there are in fact at least two phyletically rather separate taxa

involved, as seems probable, it is uncertain to which group several genera should be referred. The late Eocene genus *Proterixoides*, regarded by Stock (1935) and McKenna (1960b) as an erinaceoid, has been compared favorably by McKenna (1960b) and Donald E. Russell (1964) with *Litolestes*, which Russell (as did Simpson, 1937b) regarded as a hyopsodont. Donald E. Russell (1964), unlike previous writers, placed *Paschatherium* (= "*Adapisorex*" *dolloi*) in the Hyopsodontidae rather than the Erinaceidae. Other doubtful cases also exist.

Protentomodon ursirivalis was described by Simpson (1928) from the late Paleocene (cf. Van Valen and Sloan, 1966) of Bear Creek, Montana, and referred by him to the family Nyctitheriidae, which he established in that paper. McKenna (1960a) abandoned this family, noted a similarity of *Protentomodon* to apatemyids, *Viverravus*, and *Micropternodus*, and referred *Protentomodon* to the Insectivora or Menotyphla, *incertae sedis*. A.M.N.H. No 22184 shows two features of the mandible that are not visible on the type: the symphysis extends to about the boundary of P_3 and P_4, and the posterior mental foramen is below the posterior part of M_1. The molars are more similar to those of *Aphronorus* and *Coriphagus* than to those of any other genus with which I have compared them, and the talonid of P_4 (preserved in A.M.N.H. No. 22184) is similar to that of *Coriphagus*. I therefore tentatively refer *Protentomodon* to the Pentacodontidae, while recognizing that it may eventually fall in the Adapisoricidae of my classification or even elsewhere.

The pentacodontids are in some respects more similar to the hyopsodonts and the erinaceoids than to the pantolestids. Because of this uncertainty I raise them to family level, while recognizing that such action will probably not be justified when the lineages are adequately known. It is possible that they may revert to the Pantolestidae, the Adapisoricidae of my classification, or the Hyopsodontidae, but which relationship is correct it is not now possible to determine. McKenna (1960a) has mentioned the possibility that the pentacodontids may belong in the Hyopsodontidae, although the suggestion was made together with favorable mention of

their convergent (as I see them) similarities to the Apheliscinae. It is relevant to the similarity in the posterior position of the mental foramen in some pentacodontids and pantolestids that the same situation occurs in an undoubted leptictid, *Leptictidium*. In H.L. No. Me4420, the posterior mental foramen is below the posterior part of M_1 or the border of M_1 and M_2, but in H.L. No. Me6224 it is below the border of P_4 and M_1.

The Apheliscinae, placed by Saban (1954, 1958) in the Pantolestoidea and by Gazin (1959) in the Pantolestidae because of similarities to the Pentacodontidae, must also be considered. I follow McKenna's placement of the Apheliscinae as a subfamily of the Hyopsodontidae, for reasons to be discussed below. I do not believe that this allocation has any necessary bearing on the relationships of the Pentacodontidae, to which *Apheliscus* is demonstrably convergent in some respects but to which it may possibly be related through a common ancestor probably in the Hyopsodontidae.

FAMILY LEPTICTIDAE

I give below a provisional classification of the Leptictidae. It is not meant as a substitute for an adequate review of this family, which is badly needed. The genera and subfamilies are briefly discussed following the classification; the listing of one species as distinct from another does not imply any judgment as to their separate identity. An asterisk denotes the type species of each genus recognized here.

Subfamily Procerberinae Sloan and Van Valen, 1965
  Procerberus Sloan and Van Valen, 1965
    *P. formicarum Sloan and Van Valen, 1965; latest Cretaceous, North America
    (Unnamed species) Van Valen and Sloan, 1965; early Paleocene, North America
    (Unnamed genus and species) L. S. Russell, 1962; late Cretaceous, North America
  Leptonysson, new genus
    *L. basiliscus, new species; middle Paleocene, North America
  Diaphyodectes D. E. Russell, 1964
    *D. prolatus D. E. Russell, 1964; late Paleocene, Europe
  Leptictidium Tobien, 1962
    *L. auderiense Tobien, 1962; middle Eocene, Europe

Subfamily Leptictinae Gill, 1872

Palaeictops Matthew, 1899 (including *Parictops* Granger, 1910)

(Undescribed species from Purgatory Hill); early Paleocene, North America

(Two or three undescribed species from Gidley and Silberling Quarries); middle Paleocene, North America

P. septentrionalis (L. S. Russell, 1929); late Paleocene, North America

P. tauricinerei (Jepsen, 1930); early Eocene, North America

(Unnamed species from Four Mile) McKenna, 1960; early Eocene, North America

P. pineyensis (Gazin, 1952); early Eocene, North America

**P. bicuspis* (Cope, 1880); early Eocene, North America

P. multicuspis (Granger, 1910); early Eocene, North America

P. bridgeri (Simpson, 1959); middle Eocene, North America

Prodiacodon Matthew, 1929 (=*Palaeolestes* Matthew, 1918, preoccupied)

**P. puercensis* (Matthew, 1918); middle Paleocene, North America

Myrmecoboides Gidley, 1915

**M. montanensis* Gidley, 1915; middle Paleocene, North America

Diacodon Cope, 1875

D. concordiarcensis (Simpson, 1935); middle Paleocene, North America

D. pearcei (not *D. piercei*) Gazin, 1956; late Paleocene, North America

D. packi (Jepsen, 1930); late Paleocene, North America

**D. alticuspis* Cope, 1875; early Eocene, North America

Hypictops Gazin, 1949

**H. syntaphus* Gazin, 1949; middle Eocene, North America

Leptictis Leidy, 1868 (=*Ictops* Leidy, 1868; *Mesodectes* Cope, 1875; *Isacis* Cope, 1873, preoccupied; *Nanohyus* Leidy, 1869; *Ictidops* Weber, 1904)

(Unnamed species from Sespe) Stock, 1935; late Eocene, North America

L. thomsoni (Matthew, 1903); early Oligocene, North America

L. tenuis (Douglass, 1905); early Oligocene; North America

L. acutidens (Douglass, 1901); early Oligocene, North America

L. montanus (Douglass, 1905); early Oligocene, North America

L. intermedius (Douglass, 1905); early Oligocene, North America

L. major (Douglass, 1905); early Oligocene, North America

**L. haydeni* Leidy, 1868 (=*Ictops dakotensis* Leidy, 1868; =*Nanohyus porcinus* Leidy, 1869); middle Oligocene, North America

L. bullatus (Matthew, 1899); middle Oligocene, North America

L. caniculus (Cope, 1873); middle Oligocene, North America

Subfamily Gypsonictopinae, new

Gypsonictops Simpson, 1927 (including *Euangelistes* Simpson, 1929)

**G. hypoconus* Simpson, 1927; latest Cretaceous, North America

G. petersoni (Simpson, 1929); latest Cretaceous, North America

A provisional phylogeny is given in text figure 3.

The Procerberinae have for the most part a more piercing dentition than do the Leptictinae. The postcingulum of procerberine upper molars is invariably smaller than that of the Leptictinae, and a hypocone is not well developed, unlike that in the Leptictinae. The molar paraconids are large and lingual in the Procerberinae, whereas they are reduced and usually central in the Leptictinae. The lingual face of the molar protoconid is concave or occasionally flat in the Procerberinae, convex or flat in the Leptictinae. The cusps are usually more acute in the Procerberinae.

PLATE 6

1, 2. Unretouched stereophotographs of upper molars of *Palaeosinopa simpsoni*, occlusal view. 1. Right M^1, A.M.N.H. No. 33991. $\times 6.6$. 2. Right M^2, A.M.N.H. No. 33828. $\times 4.6$.

3. Unretouched stereophotographs of *Palaeosinopa didelphoides*, right P^4-M^3, A.M.N.H. No. 16943. $\times 3$.

4, 5. Unretouched photographs of *Paleotomus senior*, right M_3, A.M.N.H. No. 33990. 4. Stereophotographs of occlusal view. $\times 4.5$. 5. Labial view. $\times 4.7$.
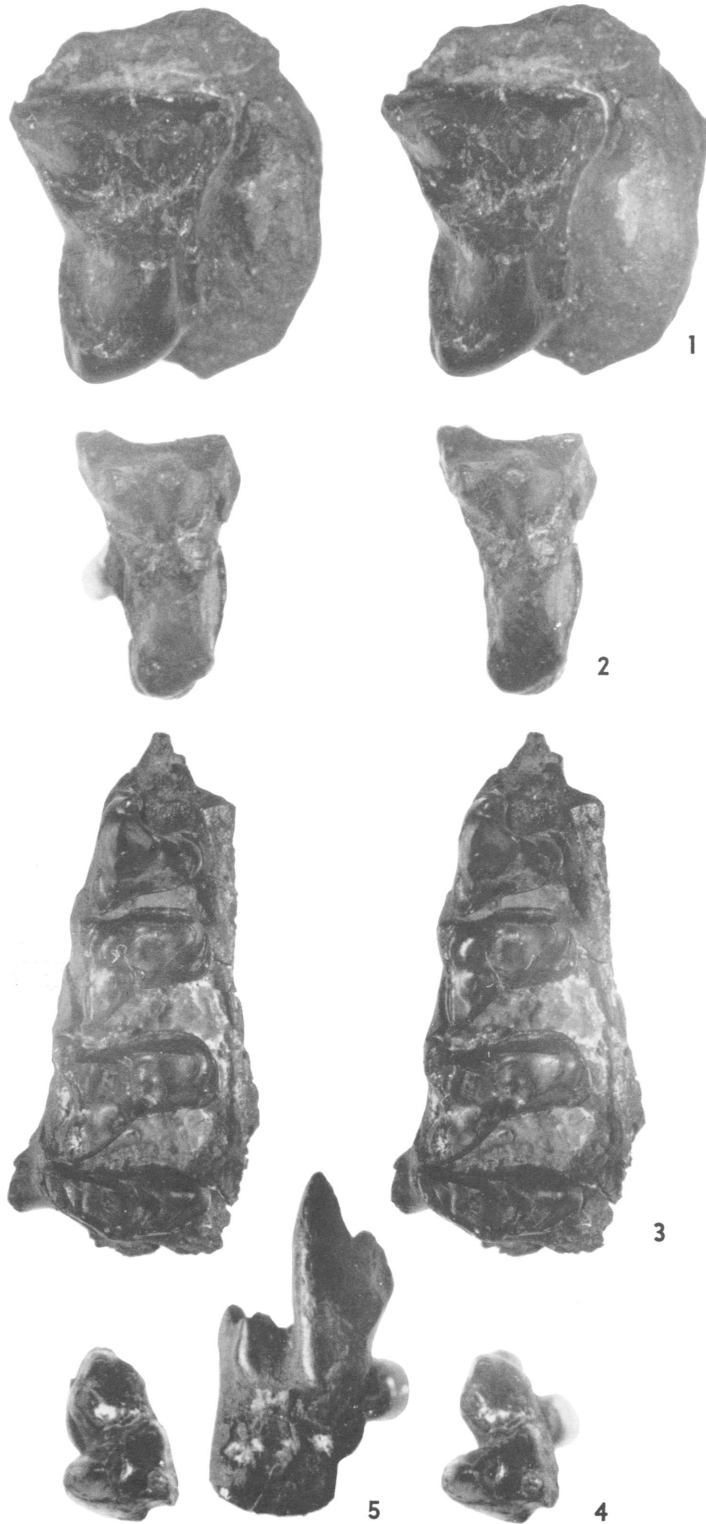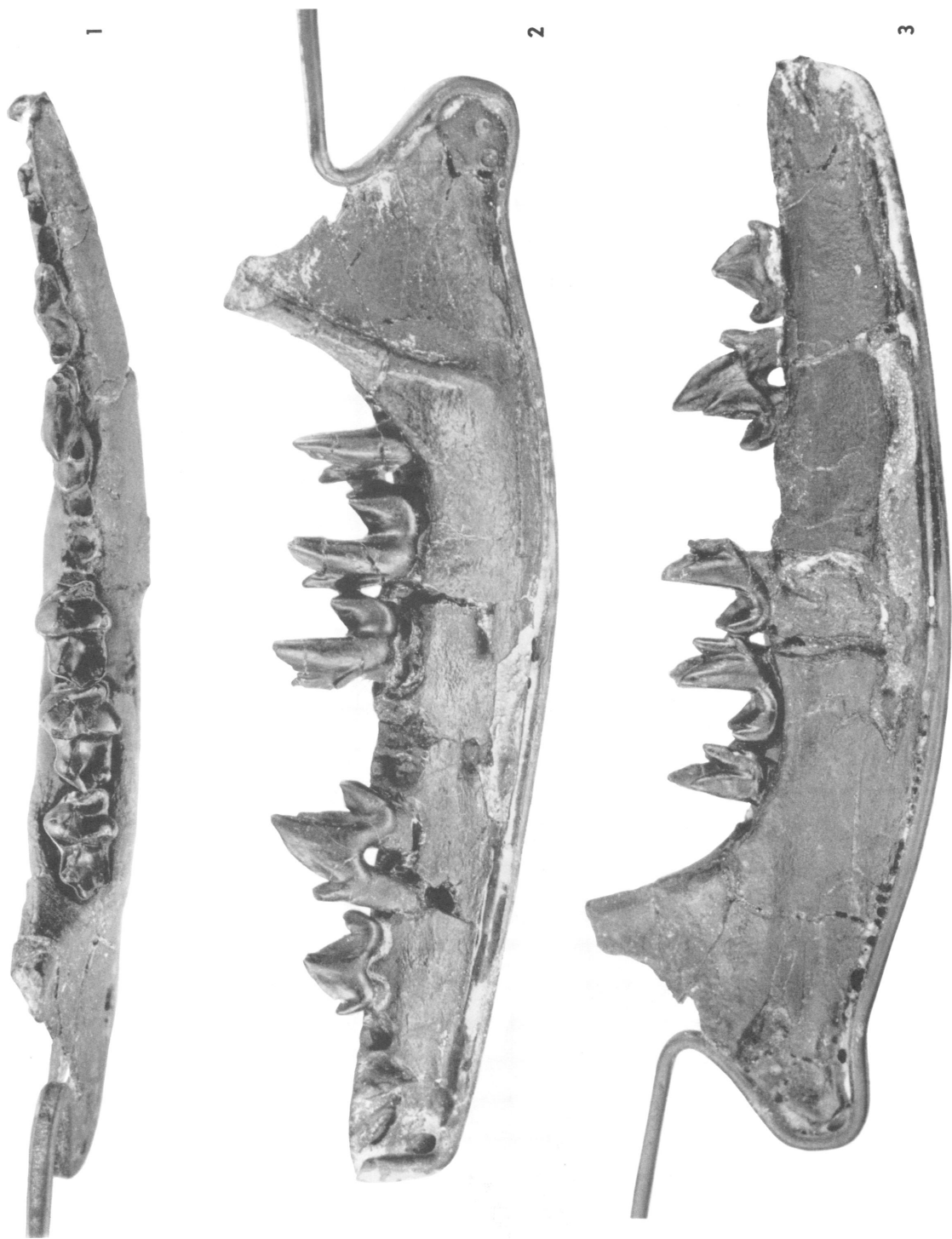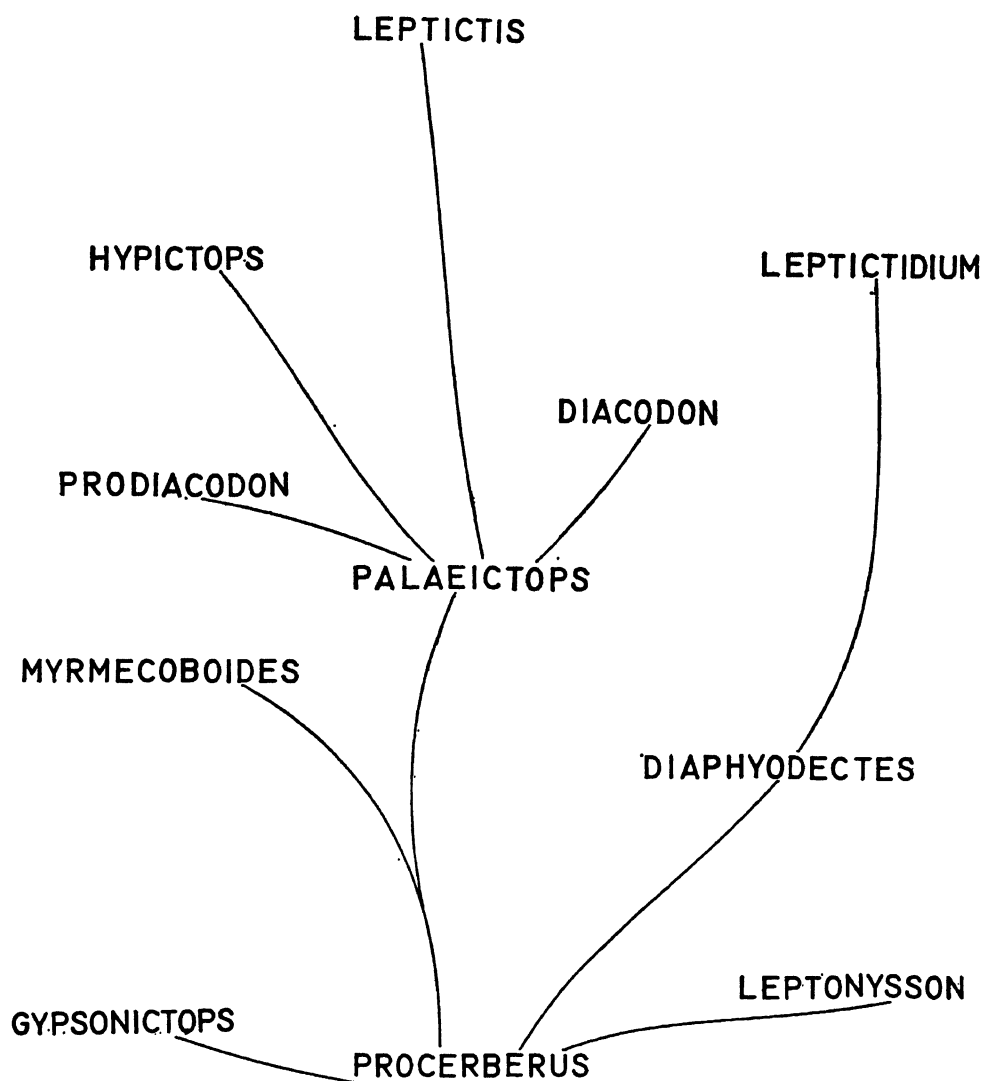
FIG. 3. Possible phylogeny of leptictid genera.

Adunator is quite differently specialized from all other leptictids, and, if it is in fact a leptictid, it would probably merit a separate subfamily. There is, however, a greater possibility that it is an erinaceoid related to *Leptacodon* and *Adapisorex*, although a close leptictid ancestry is very possible and compatible with such a relationship.

Zalambdalestes could well be referred to the Leptictidae as a separate subfamily, but it is rather highly specialized, and I do not take this step.

PLATE 7

1–3. *Leptonysson basiliscus*, A.M.N.H. No. 35295, left mandible with DP_{2-3} and M_{1-3}. 1. Occlusal view, retouched. 2. Labial view, unretouched. 3. Lingual view, unretouched. All $\times 5.1$.

A single P_4 (just possibly DP_4 but not a molar as described) from the Campanian of Scabby Butte, Alberta, represents the oldest known probable leptictid (Loris Shane Russell, 1962). It is probably generically distinct from *Procerberus*.

The occurrence of the Leptictinae outside North America is not yet well established. A P_4 from the early Eocene of Abbey Wood, England, figured by Forster Cooper (1932) as a creodont molar, is probably referable to *Palaeictops* but may be related to *Adunator*. A crushed skeleton from the early Cenozoic of Menat, France, was described by Guth (1962); it appears to be a leptictid, as Guth concluded, and is probably closest to *Palaeictops* or *Diaphyodectes*. Lavocat and Lapperent (1947) briefly described, without a figure, a tooth from the middle Eocene of France and referred it to the Leptictidae. Their description is inadequate even to verify this placement.

Ictopidium Zdansky (1930) was transferred to the Erinaceidae by Butler (1956b). *Gypsonictops* may belong to the Leptictidae or to a separate family, possibly in the Erinaceoidea (cf. Simpson, 1951). *Gypsonictops* was in any event clearly derived from the Procerberinae. *Leptacodon* has been revised by McKenna (1960a) and transferred to the Erinaceoidea. The figure of "*Leptacodon*" *munusculum* given by Simpson (1937b) is inaccurate. The specimen is at least now fractured and partly covered with resin, but it is possible to determine from direct comparison of the types that *L. tener*, "*L.*" *ladae*, and "*L.*" *munusculum* are about equally distinct from each other. F. S. Szalay (personal communication) has recently shown that, despite the dissimilarities of the published figures, *Mckennatherium libitum* is a synonym of "*Leptacodon*" *ladae*. An examination of the type of "*L.*" *ladae* indicates, however, that this species is generically distinct from *L. tener* and *L. jepseni*, and that therefore *Mckennatherium* is a valid genus although not a primate. *Leptacodon*, but not *Mckennatherium*, is in some respects similar, and very possibly ancestral, to *Entomacodon* and the Soricidae. The shrewlike appearance of *Leptacodon* was first noted by M. C. McKenna (personal communication). After seeing the type of *Mckennatherium ladae*, I am now somewhat more favorable

than not to the hypothesis that the primates originated from primitive adapisoricids rather than leptictids or even arctocyonids. *Androsorex* Quinet (1964) is at present a *nomen nudum*. *Acmeodon* and *Emperodon* (a synonym of *Gelastops*), listed by Simpson (1945) in the Leptictidae, had previously been transferred by him (Simpson, 1937b) to the Deltatheridiidae (now Palaeoryctidae), an allocation that I follow. *Adapisorex* is now regarded as a probable erinaceoid (Donald E. Russell, 1964), as is *Praolestes* (cf. Van Valen, 1966). Butler (1948) and Van Valen (1966) have placed *Xenacodon* in the Erinaceoidea. *Pseudictops* may be related to the lagomorphs and probably belongs to the Anagalidae (Van Valen, 1964).

I do not see any means of distinguishing *Protictops* from the erinaceoid *Geolabis*, which has priority, and therefore synonymize these genera. Peter Robinson and M. C. McKenna (personal communications) have also done so. The type of *P. alticuspidens* (C.M. No. 11917), from the Duchesne River of Utah, is apparently conspecific with A.M.N.H. No. 32648, from the Chadronian of Pipestone Springs, Montana. These two specimens may or may not belong to *Geolabis marginalis*, in which M_3 is reduced, which is not the case in the two specimens mentioned. The two isolated teeth from Saskatchewan named "*Protictops? borealis*" by Loris Shane Russell (1965) are not *Geolabis*. These teeth may belong to the Leptictidae, in which case they represent a new genus, or to the Adopisoricidae of my classification. The type upper tooth may possibly be a DP^4.

Sespedectes has rather bulbous cusps, and the talonid and paraconid of P_4 are reduced. These characters suggest reference to the Erinaceoidea, as Stock (1935) originally proposed, or possibly to the Hyopsodontidae, rather than to the Leptictidae. McKenna (1960a) placed *Sespedectes* in the erinaceoid family Amphilemuridae.

McKenna (*in* McKenna, Robinson, and Taylor, 1962) has proposed that Y.P.M. No. 11888, the type of *Viverravus nitidus* Marsh, 1872, may represent the P_4 of *Hypictops syntaphus*. The tooth has a double paraconid and is relatively low-crowned, and the roots, although covered with glue, seem moderately divergent. These are all characteristics of

DP₄'s of leptictids and related families. I therefore believe that this specimen is a DP₄. It is almost as long as the P₄ of the type of *Palaeictops bridgeri* and therefore probably represents the DP₄ of *P. bridgeri*, but there is insufficient evidence for synonymy.

Palaeictops, as used here, is a broad genus that lacks clearly defined subgroups. Its detailed phylogeny is obscure. Whether subdivision is desirable, and, if so, how this should be accomplished, are uncertain. *Parictops* is, nevertheless, probably a strict synonym of *Palaeictops*. It is conceivable that the species here referred to the morphologically definable genus *Diacodon* arose from *Palaeictops* at more than one time. *Diacodon packi* is morphologically the most marginal species here referred to *Diacodon*.

It now seems reasonably certain that the names *Leptictis haydeni* and *Ictops dakotensis*, both proposed by Leidy (1868), refer to the same species. Scott and Jepsen (1936) suggested such a possibility but believed the differences were too great to warrant it. They noted that the only differences are the absence of a protocone and metacone on the P³ of *L. haydeni*, and the fact that the labial border of P³ (and thus the paracone) is shifted lingually in that species. These differences are common intraspecific variants (see, e.g., Bateson, 1894), and, moreover, intermediates exist in Brulé leptictids between both "typical" situations. The only known "typical" *L. haydeni* is the type skull. This skull has a metacone, although a small one, on P³, whereas A.M.N.H. No. 38916, in which the labial border of P³ is as in *I. dakotensis*, completely lacks a metacone on at least the right P³. The protocone of the right P³ of this latter specimen is also absent as a distinct cusp, although the protocone lobe is larger than in the type of *L. haydeni* and the left P³ has a moderately large protocone. In A.M.N.H. No. 1412 a largely erupted P³ is in almost the same position as that of the type of *L. haydeni*, and has a large protocone. I therefore synonymize *Ictops dakotensis* with *Leptictis haydeni*. Although *Ictops* is the better-known name, *Leptictis* is also widely known. If the name *Ictops* rather than *Leptictis* were preserved, there would be no genus *Leptictis* in the Leptictidae. I therefore make *Ictops* a synonym of *Leptictis* rather than the reverse.

It is quite possible that *Leptictis* as now constituted is a diphyletic genus, but the dichotomy is not that of *Leptictis* and "*Ictops*." The Pipestone Springs species *L. thomsoni* and *L. tenuis* have slicing teeth that are dissimilar to those of the other members of *Leptictis* and suggest the possibility of an origin from *Diacodon alticuspis*. In such a case a new genus would be required. The angle of the mandible of *L. tenuis* is smaller but more discrete than that of *L. haydeni*. The main group of *Leptictis* species is very similar to *Palaeictops bridgeri* and *P. bicuspis*, and the generic placement of the latter two species (and of the Sespe *Leptictis*) is arbitrary. The differences between *P. bridgeri* and *Leptictis* that were given by Simpson (1959) are all matched in the variation of *Leptictis*. The only important difference is the single rather than double sagittal crest in at least *P. bicuspis*, and the figures of Douglass (1905) suggest that the double sagittal crest was a late and possibly not universal development in *Leptictis*. I am not sure that the reconstructed differences in the shape of the skull of *P. bicuspis* (in Matthew, 1918) are accurate, although they may be.

The genera of leptictids are compared in tables 4 and 5. All species showing a character were considered. Any genus not represented in one of these tables now lacks all the teeth compared there.

Leptonysson basiliscus,[1] new genus and species

Plate 7; text figure 4; table 6

TYPE AND ONLY KNOWN SPECIMEN: A.M.N.H. No. 35295, horizontal ramus of left mandible with DP₂₋₃ and M₁₋₃.

AGE AND LOCALITY: Middle Paleocene, Torrejonian, Gidley Quarry, Lebo Formation, Crazy Mountain Field, Montana.

DIAGNOSIS: The canine is small, perhaps incisiform (at least such is true for the deciduous canine); the molar trigonids are quite tall, with carnassial notches in the paralophid and protolophid; the paraconid is relatively central on M₁ and M₂; the lingual face of the protoconid is strongly concave; the ento-

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[1] *Leptonysson* (masculine) from Greek *leptos*, slender or small (and with allusion to *Leptictis*), and *nysso*, puncture.

The specific name is a Latin word meaning "petty king."

TABLE 4

COMPARISON OF UPPER TEETH OF LEPTICTID GENERA

(The numbers under each heading refer to the same characters for each genus.)

	P³	P⁴	Lingual Cingula	Upper Molars
Procerberus	1 Somewhat longer antero-posteriorly than wide 2 Protocone central 3 Metacone of moderate size 4 Protocone considerably lower than metacone	1 Paracone considerably higher than metacone 2 Paracone and metacone moderately connate 3 Tooth about as wide as long 4 Conules nearly or quite absent 5 Protofossa considerably longer than wide	1 Absent from P⁴ 2 Very small on molars 3 Precingulum larger than postcingulum 4 Postcingulum not extending to lingual margin of protocone 5 Hypocone absent 6 (Inapplicable) 7 Precingulum and postcingulum extending about equally lingually	1 Stylar shelf relatively broad 2 Ectoflexus moderately deep 3 Conules small 4 Conules lingual 5 Paracone and metacone slightly connate 6 Metacingulum not reaching to ectocingulum 7 Protocone tall 8 Tooth moderately transverse 9 Parastyle of M² about as labial as metastyle
Prodiacodon	1 About as long 2 Central 3 Relatively large 4 Protocone almost as tall	1 Paracone slightly higher 2 Moderately connate 3 Considerably wider than long 4 Conules similar to those of molars 5 Considerably wider than long	1 Present on P⁴ 2 Relatively large 3 Postcingulum larger 4 Extending to lingual margin of protocone 5 Present 6 Postcingulum of P⁴ considerably lower than that of M¹ 7 Lingual end of precingulum almost as far lingual as base of lingual end of postcingulum	1 Moderately broad 2 Moderately deep 3 Moderately large but low 4 Somewhat labial 5 Slightly connate 6 Nearly or quite reaching ectocingulum 7 Relatively low

TABLE 4—(Continued)

	P³	P⁴	Lingual Cingula	Upper Molars
				8 Quite transverse 9 About as labial
Myrmecoboides	(P³ unknown)	1 (Unknown) 2 Separate 3 Considerably wider than long 4 Conules similar to those of molars 5 Considerably wider than long	1 Present on P⁴ 2 Relatively large 3 Postcingulum larger 4 Extending lingual of lingual margin of protocone 5 Present 6 (Unknown) 7 Considerably labial to base of lingual end of postcingulum	1 Relatively broad 2 Moderately deep 3 Moderately large 4 Relatively labial 5 Slightly connate 6 Not reaching ectocingulum 7 (Unknown) 8 Quite transverse 9 Parastyle much more labial
Palaeictops	1 Considerably longer than wide to about as long as wide 2 Somewhat posterior of center 3 Relatively small 4 Protocone considerably lower	1 (Unknown) 2 Moderately connate to separate 3 Somewhat wider than long 4 Conules similar to those of molars 5 Somewhat wider than long	1 Present on P⁴ 2 Relatively large 3 Postcingulum larger 4 Extending to lingual margin of protocone 5 Present 6 Postcingulum of P⁴ about as high as that of M₁ 7 Considerably labial to base of lingual end of postcingulum	1 Moderately broad to narrow 2 Moderate 3 Moderately large 4 Somewhat to considerably labial 5 Separate 6 Probably reaching ectocingulum 7 Relatively low 8 Moderately transverse 9 Parastyle somewhat more to about as labial
Diacodon[a]	(P³ unknown)	1 (Unknown) 2 (Unknown) 3 (Unknown) 4 (Unknown)	1 Present on P⁴ 2 Relatively large 3 Postcingulum larger 4 Extending to lingual margin of protocone	1 Narrow 2 Nearly absent 3 Moderately large 4 Somewhat labial

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TABLE 4—(Continued)

	P³	P⁴	Lingual Cingula	Upper Molars
		5 Wider than long	5 Present 6 Postcingulum of P⁴ about as high as that of M¹ 7 Considerably labial to base of lingual end of postcingulum	5 Slightly connate 6 Almost reaching ectocingulum 7 (Unknown) 8 Quite transverse 9 About as labial
Hypictops	1 Slightly longer than wide 2 Posterior of center 3 Relatively large 4 Protocone considerably lower	1 Probably higher 2 (Unknown) 3 Considerably wider than long 4 Probably present 5 Wider than long	1 Present on P⁴ 2 Relatively large 3 Postcingulum larger 4 Extending to lingual margin of protocone on M¹ only 5 Probably absent except perhaps on M¹ 6 Postcingulum of P⁴ about as high as that of M², which is lower than that of M¹ 7 Slightly labial to base of lingual end of protocone	1 Narrow 2 Nearly absent 3 Probably moderate or large 4 Somewhat labial 5 (Unknown) 6 Not reaching ectocingulum 7 (Unknown) 8 Quite transverse 9 About as labial
Lephichis[b]	1 Considerably longer than wide 2 Posterior of center 3 Relatively small to absent 4 Protocone considerably lower	1 About as high 2 Separate 3 Slightly wider than long 4 Conules similar to those of molars 5 Somewhat wider than long	1 Present on P⁴ 2 Relatively large 3 Postcingulum larger 4 Extending to lingual margin of protocone 5 Present 6 Postcingulum of P⁴ about as high as that of M¹	1 Narrow 2 Shallow to nearly absent 3 Large but low 4 Somewhat labial 5 Separate 6 Continuous with ectocingulum

TABLE 4—(Continued)

	P³	P⁴	Lingual Cingula	Upper Molars
			7 Considerably labial to base of lingual end of postcingulum	7 Relatively low 8 Moderately transverse 9 About as labial
Leptictis thomsoni and *L. tenuis*	1 Considerably longer than wide 2 Posterior of center 3 Relatively small 4 (Unknown)	1 About as high 2 Separate 3 Slightly wider than long; trigon transverse 4 Conules apparently absent from P⁴ 5 Somewhat wider than long	1 Present on P⁴ 2 Relatively small to moderate 3 Postcingulum larger 4 Extending to lingual margin of protocone 5 Present 6 Postcingulum of P⁴ somewhat lower than that of M¹ 7 Precingulum absent	1 Narrow 2 Shallow to nearly absent 3 Conules large but nearly obliterated, merging with protocristae 4 Somewhat labial 5 Separate 6 Not reaching ectocingulum 7 Of moderate height 8 Quite transverse 9 About as labial
Adunator	1 Somewhat longer than wide 2 Central 3 Apparently relatively large 4 (Unknown)	1 Paracone considerably higher 2 Moderately connate 3 Somewhat wider than long 4 Conules similar to those of molars 5 About as wide as long	1 Present on P⁴ 2 Relatively large 3 Postcingulum larger 4 Extending more lingually than lingual margin of protocone on M¹, to lingual margin of protocone on M² 5 Present 6 Postcingulum of P⁴ probably lower than that of M¹	1 Narrow 2 Shallow to nearly absent 3 Large 4 Relatively labial 5 Separate 6 Continuous with ectocingulum

TABLE 4—(Continued)

	P³	P⁴	Lingual Cingula	Upper Molars
			7 Considerably labial to base of lingual end of postcingulum	7 (Unknown) 8 Subquadrate 9 About as labial
Diaphyodectes	(P³ unknown)	(P⁴ unknown)	1 (Unknown) 2 Of moderate size 3 Postcingulum larger 4 Extending to lingual margin of protocone 5 Present but small 6 (Unknown) 7 (Unknown)	1 Relatively broad 2 Shallow 3 Paraconule relatively large, metaconule small 4 Lingual 5 Separate 6 Nearly or quite reaching ectocingulum 7 (Unknown) 8 Moderately to quite transverse 9 Parastyle almost as labial
Leptictidium	1 Considerably longer than wide 2 Protocone absent 3 Metacone absent 4 (Inapplicable)	1 (Unknown) 2 (Unknown) 3 (Unknown) 4 (Unknown) 5 (Unknown)	1 (Unknown) 2 Relatively small 3 Postcingulum slightly larger 4 Not extending so lingually as lingual margin of protocone 5 Very small 6 (Unknown) 7 Slightly labial to base of lingual end of postcingulum	1 (Unknown) 2 (Unknown) 3 Small 4 Lingual 5 (Unknown) 6 (Unknown) 7 Relatively tall 8 (Unknown) 9 (Unknown)

a Based in part on A.M.N.H. No. 16795, cf. *Diacodon alticuspis*, from the upper Gray Bull or the Lysite equivalent of the Bighorn Basin.
b Excluding *Leptictis thomsoni* and *L. tenuis*.

COMPARISON OF LOWER TEETH OF LEPTICTID GENERA

(The numbers under each heading refer to the same characters for each genus.)

	C_i and P_3	P_4	Molar Trigonids	Molar Talonids
Procerberus	1 C of moderate size 2 Posterior accessory cusp absent on P_3	1 Tooth elongate 2 Trigonid short anteroposteriorly 3 Trigonid tall 4 Paraconid close to protoconid 5 Metaconid distinctly posterior to protoconid 6 Metaconid somewhat lower than protoconid 7 Paraconid tall 8 Length of talonid, posteriorly from deepest point of crista obliqua, one-third of length of tooth 9 Hypoconid much taller than entoconid 10 Hypoconulid twinned with hypoconid 11 Entocristid absent 12 Entoconulid absent	1 Moderately tall 2 Carnassial notches absent or weak 3 Lingual face of protoconid flat to slightly concave 4 Metaconid about as tall as protoconid 5 Paraconid lingual 6 Paraconid moderately anterior 7 Paraconid unreduced 8 M_3 (whole tooth) unreduced, considerably longer than M_2 9 Cusps acute on whole tooth	1 Narrower than trigonid 2 Moderate decrease in width from M_1 to M_3 3 Entocristid incomplete 4 Mesoconid present 5 Entoconid about as tall as hypoconid 6 Elongate on M_1 and M_2 7 Entoconulid usually absent 8 Hypoconulid central
Prodiacodon	1 Moderate 2 Present but weak	1 Moderately wide 2 Short 3 Tall 4 Paraconid close 5 Almost as anterior as protoconid 6 Almost as tall as protoconid 7 Moderately tall	1 Moderately tall 2 Absent 3 Flat to slightly convex 4 About as tall as protoconid 5 Central 6 Moderately anterior 7 Moderately small	1 As wide as trigonid on M_1 2 Strong decrease in width 3 Complete 4 Absent 5 Lower than hypoconid 6 Moderately transverse on M_1 and M_2 7 Present

TABLE 5—(Continued)

	C_i and P_3	P_4	Molar Trigonids	Molar Talonids
		8 Two-fifths of tooth length 9 Moderately taller than entoconid 10 Distinct 11 Weak 12 Present	8 Unreduced, considerably longer than M_2 9 Moderately acute	8 Central
Myrmecoboides	1 Moderate 2 Absent	1 Elongate 2 Long 3 Low 4 Paraconid far anterior 5 As anterior as protoconid 6 Nearly as tall as protoconid 7 Low 8 Two-fifths of tooth length 9 About as tall as entoconid 10 Hypoconulid nearly absent 11 Moderately strong 12 Present	1 Moderately low 2 Absent 3 (Unknown) 4 Taller than protoconid 5 Lingual 6 Nearly fused with metaconid 7 Moderately small 8 Unreduced, slightly longer than M_2 9 (Unknown)	1 Narrower than trigonid 2 Same width 3 Complete 4 Probably absent 5 Probably of similar height 6 Elongate on M_1 and M_2 7 Present 8 Central
Palaeictops	1 Small 2 Primitively absent, later present	1 Primitively elongate, later moderately wide 2 Long or moderately long 3 Primitively tall, later low 4 Paraconid moderately close or far 5 Primitively distinctly posterior of protoconid, later almost as far anterior 6 Somewhat lower than, or almost as tall as, protoconid	1 Moderately tall to moderately low 2 Absent 3 Flat to slightly convex 4 Taller than, or about as tall as, protoconid 5 Central to lingual 6 Moderately anterior	1 Usually as wide as trigonid on M_1, rarely so on M_2 2 Slight decrease in width; talonid of M_2 occasionally even wider than that of M_1 3 Complete or incomplete 4 Absent 5 Lower than or as tall as hypoconid 6 Moderately transverse to elongate on M_1 and M_2

TABLE 5—(*Continued*)

C_i and P_3	P_4	Molar Trigonids	Molar Talonids
	7 Moderately low to moderately tall 8 One-third to two-fifths of tooth length 9 Moderately to considerably taller than entoconid 10 Usually distinct, rarely almost twinned with hypoconid 11 Weak 12 Usually absent, occasionally present	7 Small to moderately small 8 Unreduced, or rarely very slightly reduced; slightly longer than or as long as M_2 9 Moderately acute	7 Present or absent 8 Central
Diacodon 1 Small 2 Absent	1 Elongate or moderately wide 2 Short or moderately short 3 Tall 4 Paraconid close or moderately close 5 Almost as anterior as protoconid 6 Almost as tall as protoconid 7 Moderately tall 8 One-third to two-fifths of tooth length 9 Moderately to considerably taller than entoconid 10 Distinct 11 Moderate to weak 12 Absent	1 Moderately tall 2 Absent 3 Flat to slightly convex 4 About as tall as protoconid 5 Central to moderately lingual 6 Moderately to unusually anterior 7 Moderately small 8 Unreduced, slightly longer than, or as long as, M_2 9 Acute or moderately acute	1 Usually narrower than trigonid, occasionally as wide on M_1 and M_2 2 Moderate or slight decrease in width 3 Complete 4 Present or absent 5 Lower than hypoconid 6 Moderately to quite transverse on M_1 and M_2 7 Present or absent 8 Central
Leptictis[a] 1 Small	1 Moderately wide	1 Moderately low to moderately tall	1 Wider than trigonid on M_1, narrower on M_3, about as wide as trigonid on M_2

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TABLE 5—(*Continued*)

C$_i$ and P$_3$	P$_4$	Molar Trigonids	Molar Talonids
2 Present	2 Moderately short	2 Absent	2 Moderate or slight decrease in width
	3 Moderately low	3 Flat to slightly convex	3 Complete
	4 Paraconid moderately close	4 About as tall as protoconid	4 Absent, or present only as a trace
	5 As far anterior as protoconid	5 Central	5 As tall as hypoconid
	6 As tall as protoconid	6 Moderately anterior to moderately retracted	6 Moderately elongate to moderately transverse on M$_1$ and M$_2$
	7 Moderately tall	7 Small to moderately small	7 Absent or vestigial
	8 Two-fifths of tooth length	8 Unreduced in length, slightly reduced in width; as long as M$_2$	8 Central
	9 Considerably taller than entoconid	9 Moderately acute to somewhat bulbous	
	10 Distinct		
	11 Moderate		
	12 Absent		
Adunator			
1 Probably small	1 Moderately wide	1 Moderately low	1 Wider than trigonid on M$_1$, narrower on M$_3$, about as wide as trigonid on M$_2$
2 Absent	2 Moderately long	2 Absent	2 Moderate to no decrease in width from M$_1$ to M$_2$, considerable decrease to M$_3$
	3 Moderately low	3 Strongly convex	3 Complete
	4 Paraconid moderately close	4 Somewhat lower than protoconid	4 Present
	5 Almost as anterior as protoconid	5 Central	5 Taller than hypoconid
	6 Somewhat lower than protoconid	6 Moderately anterior	6 Moderately transverse on M$_1$ and M$_2$
	7 Moderately low	7 Small to moderately small	7 Present
	8 Two-fifths of tooth length	8 Reduced, shorter than M$_2$	8 Central
	9 Moderately taller than entoconid	9 Moderately acute	

TABLE 5—(Continued)

	C_i and P_3	P_4	Molar Trigonids	Molar Talonids
		10 Distinct 11 Moderate 12 (Unknown)		
Leptonysson	1 Small, perhaps incisiform 2 (P_3 unknown; cusp present on DP_3)	(P_4 unknown)	1 Quite tall 2 Present and well developed in paralophid and protolophid 3 Strongly concave 4 About as tall as protoconid 5 Moderately lingual 6 Moderately anterior 7 Unreduced 8 Unreduced, as long as M_2 9 Acute	1 Narrower than trigonid 2 Moderate decrease in width 3 Complete 4 Absent 5 Taller than hypoconid 6 Elongate on M_1 and M_2 7 Absent 8 Central
Diaphyodectes	1 (Unknown) 2 (P_3 unknown)	1 Elongate 2 Moderately long 3 Tall 4 Paraconid moderately far 5 Distinctly posterior to protoconid 6 Somewhat lower than protoconid 7 Tall 8 Less than one-third of tooth length 9 Moderately taller than entoconid 10 Absent 11 Weak 12 (Unknown)	1 Moderately tall 2 Present in paralophid and protolophid 3 Strongly concave 4 Taller than protoconid 5 Lingual 6 Unusually anterior 7 Unreduced 8 Unreduced, about as long as M_2 9 Acute	1 As wide as trigonid on M_1 and M_2 2 About the same width on M_1 and M_2, slightly less than these on M_3 3 Complete 4 Present 5 Lower than hypoconid 6 Elongate on M_1 and M_2 7 Present 8 Central

TABLE 5—(*Continued*)

	C_i and P_3	P_4	Molar Trigonids	Molar Talonids
Lepticidium	1 Moderate	1 Elongate	1 Moderately tall	1 Wider than trigonid on at least M_1
	2 Absent	2 Short	2 (Unknown)	2 (Unknown)
		3 Moderately tall	3 (Unknown)	3 Complete
		4 Paraconid in front of meta-conid and moderately close to it	4 Somewhat lower than pro-toconid	4 Absent
		5 As far anterior as proto-conid	5 Lingual	5 Lower than hypoconid
		6 As tall as protoconid	6 More than usually anterior	6 Moderately elongate on M
		7 Moderately tall	7 Moderately large	7 Absent
		8 Half of tooth length	8 Somewhat reduced, shorter than M_2	8 Near entoconid
		9 Moderately taller than en-toconid	9 Moderately acute	
		10 Hypoconulid indistinct, twinned with entoconid		
		11 Strong		
		12 Absent		

[a] Lower teeth of *L. thomsoni* and *L. tenuis* are poorly known and are not included.

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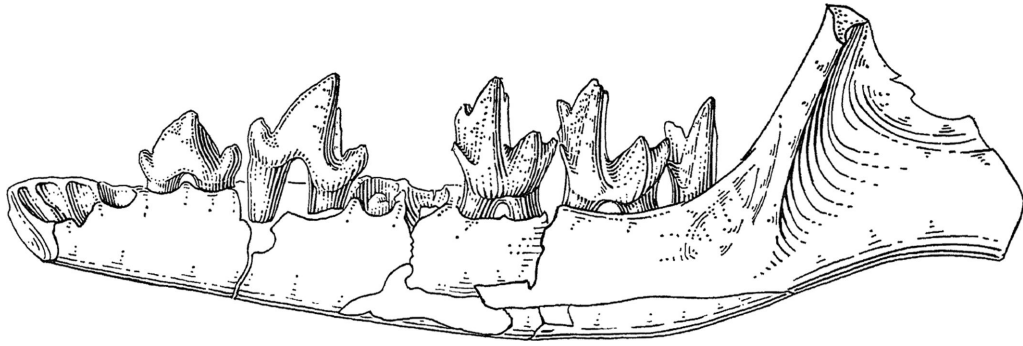
Fig. 4. *Leptonysson basiliscus*, type specimen, labial view of left DP_{2-3}, M_{1-3}. ×4.

cristid is complete; a mesoconid is absent; the entoconid is taller than the hypoconid; the hypoconulid is at least as large as the entoconid on M_1 and M_2; M_3 is about as long as M_2; the metaconid of M_3 is somewhat lower than the protoconid. Most other known characters are similar to those of *Procerberus*, but *Leptonysson* differs from *Procerberus*, in addition to the characters listed above, as follows: the paraconid is less anterior on M_1; the paralophid is stronger; there is more differentiation among the molars from M_1 to M_3; the crista obliqua is less oblique; and the talonid cusps are more distinct from each other.

DISCUSSION: *Leptonysson* is obviously derived from *Procerberus*, and may be regarded as a *Procerberus* that has become more specialized for slicing, despite the reduction of the deciduous canine. Although DP_3 is in place, a hole in the mandible gives no indication of a calcified P_3 below it. M_3 is largely erupted, and it therefore appears that the delayed eruption of the permanent premolars characteristic of later leptictids was present even in the middle Paleocene. Indeed, because *Leptonysson* is related to these later leptictids only through *Procerberus*, this delay of eruption was probably true for *Procerberus* as well and was therefore probably present in the latest Cretaceous.

There are five or, probably, six closely spaced alveoli in front of DP_2. The two most posterior of these alveoli probably held DP_1; the three or four other alveoli are small and project forward, so it is probable that the deciduous canine was incisiform. It cannot, however, be excluded that DP_1 was single-rooted and that the small, nearly vertical alveolus in front of it held DC_i. The only mental foramen visible is below the posterior root of P_4.

ORDER CONDYLARTHRA

SUBORDER ARCTOCYONOIDEA

FAMILY HYOPSODONTIDAE

SUBFAMILY APHELISCINAE

PARAPHELISCUS,[1] NEW GENUS

TYPE SPECIES: *Parapheliscus wapitiensis*, new species.,

REFERRED SPECIES: *Parapheliscus bjorni*, new species.

KNOWN DISTRIBUTION: Latest Paleocene to early Eocene, northwest Wyoming and adjacent Montana.

DIAGNOSIS: The protocone of P^4 is not expanded basally; the lingual cingula of M^1 are smaller than those of *Apheliscus*, and M^1 is somewhat less transverse than in that genus; P_4 is relatively broader and the talonid is much smaller than in *Apheliscus;* the large groove on P_4 for the paracone of P^4 is mainly on the protoconid; the base of the enamel on

[1] *Para-* and *Apheliscus.*

TABLE 6

MEASUREMENTS (IN MILLIMETERS) OF THE TEETH
OF THE TYPE OF *Leptonysson basiliscus*

	Length	Trigonid width	Talonid width
DP_2	3.2	1.1	—
DP_3	3.8	1.5	—
M_1	3.3	2.2	2.0
M_2	3.4	2.5	1.7
M_3	3.5	2.2	—
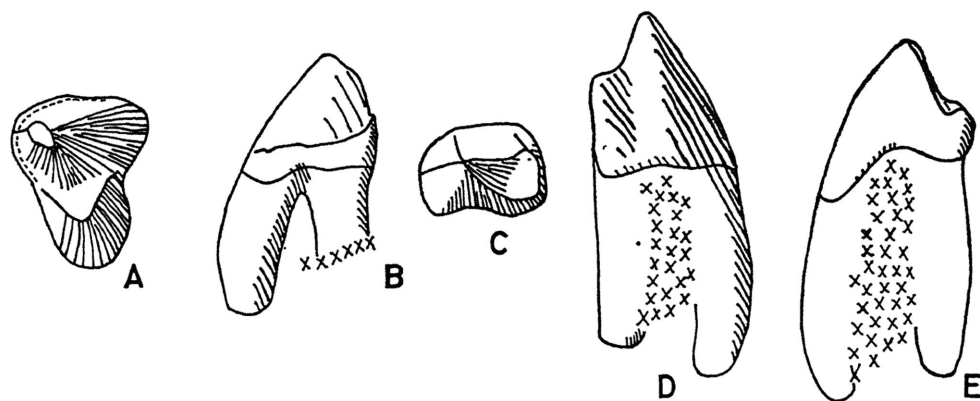
FIG. 5. *Parapheliscus bjorni*. A–B. A.M.N.H. No. 22245, right P⁴. A. Occlusal view. The relationship of the protocone lobe to the paracone is hypothetical. B. Labial view. C–E. A.M.N.H. No. 22244, right P₄. C. Occlusal view. D. Labial view. E. Lingual view. Dots represent occlusal surfaces, crosses represent matrix, and broken lines represent concavities. ✕6.8.

the anterior and labial sides of P₄ is much lower than in the posterolingual region; and there is a sharp crest from the apex of the protoconid to each side of the talonid.

Parapheliscus bjorni,[1] new species

Text figure 5; table 7

TYPE SPECIMEN: A.M.N.H. No. 22244, right P₄.

REFERRED SPECIMEN: A.M.N.H. No. 22245, right P⁴ (protocone broken off but preserved in the same piece of matrix).

AGE AND LOCALITY: Approximately latest Paleocene (cf. Van Valen and Sloan, 1966),

[1] For Björn Kurtén. "Björn" and "bjørn" are the words, in various Scandinavian languages, for bear; Kurtén is the leading student of fossil bears; and the only known specimens of *P. bjorni* are from Bear Creek.

TABLE 7

MEASUREMENTS (IN MILLIMETERS) OF *Parapheliscus bjorni* AND *Parapheliscus wapitiensis*

	Length	Width
P. bjorni		
A.M.N.H. No. 22244, P₄	2.8[a]	2.0[a]
A.M.N.H. No. 22245, P⁴	2.7	—
P. wapitiensis, A.M.N.H. No. 16935		
P³	1.5	0.9
P⁴	2.0	2.1
M¹	1.8	2.0

[a] Perpendicular to the roots.

Vein 3, Eagle Coal Mine, Bear Creek, Montana.

DIAGNOSIS: *Parapheliscus bjorni* is considerably larger than *P. wapitiensis*, a precingulum is absent from P⁴, the postcingulum is slightly weaker, and the paracone of P⁴ is more transverse relative to both its anteroposterior length and to the transverse width of the protocone.

Parapheliscus wapitiensis,[2] new species

Text figure 6; table 7

TYPE AND ONLY KNOWN SPECIMEN: A.M.N.H. No. 16935, right P³–M¹.

[2] From "wapiti," a synonym of (American) "elk," after South Elk Creek.
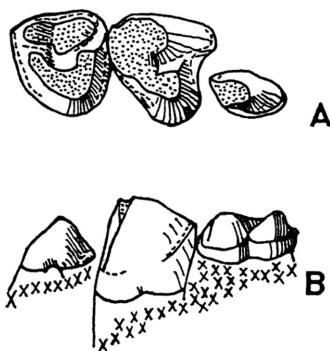
FIG. 6. *Parapheliscus wapitiensis*, type specimen, left P³–M¹, A. Occlusal view. B. Labial view. Dots represent occlusal surfaces, crosses represent matrix, and broken lines represent concavities. ✕6.8.

AGE AND LOCALITY: Early Eocene, probably lower Gray Bull; Willwood Formation, South Elk Creek, Big Horn Basin, Wyoming.

DIAGNOSIS: See *P. bjorni*.

DISCUSSION OF *Parapheliscus*

Parapheliscus is separated from *Apheliscus* because the P⁴ of *Apheliscus insidiosus* is more highly specialized than that of *Parapheliscus*, whereas the reverse is true of the P₄, although neither P₄ could easily be derived morphologically from the other. This unusual situation demands some consideration.

The two known specimens of *P. bjorni* are isolated teeth found separately and are therefore associated by inference only. If they are incorrectly associated, both species of *Parapheliscus* would be referable to *Apheliscus*, but I believe that the probability of such a mistake is negligible. The P⁴ of *P. bjorni* is sufficiently similar to that of *P. wapitiensis* and that of *A. nitidus* that there is no question about its belonging to an apheliscine. In addition to *P. bjorni*, the P₄ is known among apheliscines for *A. insidiosus*, *A. nitidus*, and *Phenacodaptes sabulosus*. There is no close similarity of the P₄ of *P. bjorni* with that of *A. insidiosus* or that of *A. nitidus*, but with *Phenacodaptes* the situation is different. The P₄ of *P. bjorni* differs from that of *Phenacodaptes* only in having lower anterolabial enamel, a smaller talonid, a lingual crest bounding the talonid and extending to the protoconid apex, and a large labial groove for the paracone of P⁴. All these differences are occlusally related to the differences in the P⁴. Furthermore, the P⁴ and P₄ of *P. bjorni* are about the same size, and occlusion is good when allowance is made for the diagenetic shift of the protocone. Furthermore, there is no other known mammal from Bear Creek that could have such a lower premolar, and there is no known mammal anywhere with a closely similar P₄.

P⁴ is the tooth that is most similar between *P. bjorni* and *A. nitidus*. Despite this moderate similarity, the single specimen of *P. bjorni* differs from *A. nitidus* in several respects. A postprotocrista is present in *P. bjorni* but not in *A. nitidus;* the postcingulum

is weaker in *P. bjorni;* a paracingulum is absent from *P. bjorni* but present in *A. nitidus;* the protocone is less acute in *P. bjorni*, but its apex is more lingual; the angle in anterior view between the preprotocrista and the lingual face of the protocone is about 90 degrees in *P. bjorni* but distinctly acute in *A. nitidus;* there is a ridge down the lingual face of the paracone in *A. nitidus* but not in *P. bjorni;* and the outline (in occlusal view) of the posterolabial corner of the tooth is less rounded in *P. bjorni*. In all of these features that can be determined in the two Gray Bull species of apheliscines, *P. bjorni* is similar to *P. wapitiensis* and *A. nitidus* is similar to *A. insidiosus*. The P₄ of *A. nitidus*, known from the Four Mile, is similar to that of *A. insidiosus*. There is a remote possibility that *P. bjorni* is conspecific with *A. nitidus*, but in view of the pattern of similarities to the divergent later species it seems better to draw the generic boundary between them.

The M¹ of *P. wapitiensis* has a more rounded outline than that of *A. nitidus;* the styles are slightly smaller; the small hypocone and ectoflexus of *A. nitidus* are absent; the lingual part of the tooth is relatively longer anteroposteriorly; and the precingulum is about as strong as the postcingulum.

It is possible that A.M.N.H. No 22181, an incompletely prepared mandible from Bear Creek with M₁₋₃, belongs to *P. bjorni* rather than to another *Haplaletes*-like hyopsodont. However, the probable presence of such a *Haplaletes*-like form at Bear Creek is shown by A.M.N.H. No. 22172, an isolated P₄, which is more similar to that of *Haplaletes disceptatrix* than is A.M.N.H. No. 22244 and does not occlude adequately with the P⁴ of *P. bjorni*. The upper cheek tooth of *Paramys atavus* is too small to be conspecific with *P. bjorni*.

In *Apheliscus insidiosus* the paracone of P⁴ shears against the protoconid and paralophid of M₁ and the long crista obliqua of P₄. In *Parapheliscus bjorni*, on the other hand, the talonid of P₄ is reduced, and the large groove on P₄, into which the paracone of P⁴ slides in occlusion, is more anterior, being mainly on the labial side of the trigonid and producing an unusual occlusion. From *Epapheliscus*, a genus from the early Oligocene of Italy (Van

Valen, 1966), the protocone of P^4 is probably absent. *Epapheliscus* was therefore probably not derived from *Apheliscus insidiosus*, in which the protocone is expanded on P^4, but could have come from any other known apheliscine.

There seems to be a good evolutionary sequence from Silver Coulee *Phenacodaptes sabulosus* through Clark Fork *Apheliscus nitidus* and then Four Mile *A. nitidus* to the Gray Bull and San José *A. insidiosus*. The specimens of *A. nitidus* from the Four Mile are intermediate between *A. insidiosus* and Clark Fork *A. nitidus*.

RELATIONSHIPS OF THE APHELISCINAE

I agree with Gazin's conclusion (1959) that *Phenacodaptes* is at least morphologically ancestral to *Apheliscus*. It stands in this relation to *Parapheliscus* as well. It follows from these relationships that *Apheliscus* and *Parapheliscus* need be considered in determining apheliscine relationships only insofar as they may provide characters unknown in *Phenacodaptes*.

The first suggestion as to the origin of *Phenacodaptes* was made by Simpson (1936, 1937a, 1945), who regarded this genus as a probable hyopsodont. McKenna (1955, 1960a) came to the same conclusion for *Apheliscus* itself. Gazin (1959), however, proposed that *Phenacodaptes* was especially related to the pentacodontids *Aphronorus* and *Pentacodon*. The similarities he mentioned were the premolars and the structure of the molar talonids. The upper premolars, however, are not at all similar except for the convergent P^4 evolved by *Apheliscus insidiosus*. As all the figured characters of *Phenacodaptes sabulosus* can be found in one or more of the middle Paleocene hyopsodonts *Promioclaenus acolytus*, *P. aquilonius*, and especially *Haplaletes disceptatrix*, except for the reduction of P^3 and the relatively smaller protocone of P^4, it does not seem useful to make lengthy comparisons with the considerably more specialized pentacodontids. It is nevertheless possible that the pentacodontids were also derived from hyopsodonts and are therefore somewhat related to the apheliscines, as McKenna (1960a) suggested.

ORDER **DELTATHERIDIA**
FAMILY **PALAEORYCTIDAE**
SUBFAMILY **DIDELPHODONTINAE**
PALEOTOMUS,[1] NEW GENUS
Plate 6, figures 4, 5

TYPE SPECIES: *Palaeosinopa senior* Simpson (1937b, type specimen only).

AGE AND LOCALITY: Late Paleocene, Tiffanian, Scarritt Quarry, Melville Formation, Crazy Mountain Field, Montana.

DIAGNOSIS: The paraconid is moderately high and sectorial but is not shifted forward; the trigonid is high; the labial border of the protoconid is a circular arc; the protoconid is considerably higher than the metaconid; the paralophid and the protolophid each have a deep carnassial notch; the talonid is considerably narrower than the trigonid; and an entoconid is distinct and is higher than the hypoconid. Both prevallid and postvallid shear are well developed.

DISCUSSION: As mentioned under the description of *Palaeosinopa simpsoni* above, the type specimen of *Palaeosinopa senior* appears to be a palaeoryctid. A new generic name is required. The M_3 of *Paleotomus senior*, the only tooth known of this species, differs from that of *Prototomus* only in not having the paraconid shifted forward and in having a differentiated entoconid. Both these characters are found in the Didelphodontinae (e.g., in *Didelphodus* and *Avunculus*), but the trigonid is unusually tall and the tooth is unusually large for a didelphodontine. Until we have further knowledge, *Paleotomus* may be regarded as a didelphodontine that was to some extent parallel to the early hyaenodontids, although a direct ancestral relationship to hyaenodontids is not really excluded.

The occurrence of a perfectly good species of *Oxyaena* as early as the Tiffany (Van Valen, 1966), and the much more primitive condition of all known Graybullian hyaenodontids, lend support to the possibility that, despite the similarity of *Dipsalidictides* to *Prototomus*, the Oxyaenidae may have originated from the Palaeoryctidae at a separate point from the Hyaenodontidae. The evidence on this matter is still ambiguous.

[1] *Paleo-* and Greek *tomos*, slice, with analogy to *Prototomus*, Paleocene, and Palaeoryctidae.

CHANGES IN DELTATHERIDIAN CLASSIFICATION

Recent work by Savage (1965) and myself (Van Valen, 1965b) necessitates some modifications in the classification of the Deltatheridia given elsewhere (Van Valen, 1966). This last paper was written considerably earlier than that of 1965 (Van Valen, 1965b). I discuss the work of Savage here and give a reclassification of the Hyaenodontinae as part of the larger classification that is given below.

Savage's paper concerned the Miocene faunas of east Africa. One remarkable new genus, *Teratodon*, was made the type of a new family of the Oxyaenoidea, a superfamily that I am now restricting to the Oxyaenidae because of probably independent origin from the Hyaenodontidae. *Quercitherium* was also included by Savage in the Teratodontidae, which is specialized by the presence of large, crushing premolars. Such an adaptation is surely no more different from *Prototomus* than is the extreme carnassiality of *Hyaenodon*. I therefore would reduce Savage's family to the rank of a tribe in the Hyaenodontinae, if I retained tribes in this subfamily, but I prefer to abandon tribes here for the present because of the very possible polyphyly of the Hyaenodontini. Neither *Teratodon* nor *Quercitherium* is derivable from the other, at least with the species now known; it is even possible that *Teratodon* originated from *Proviverra minor* (Filhol), a contemporary of *Quercitherium*. Savage's grouping is nevertheless possible and is at least as likely to be correct as is the usual grouping of the Hyaenodontini.

A new genus *Anasinopa* from east Africa is distinguished by Savage from *Paracynohyaenodon*, from the French Phosphorites, by the statement that in the latter genus "the paraconid is very low, smaller than the metaconid." Savage apparently relied on the drawings of Martin (1906), which show the paraconid about as low as, but larger than, the metaconid. My drawings (Van Valen, 1965b) showed that the paraconid is large. Although the paraconid of "*Anasinopa*" *leakeyi* is somewhat taller than that of *Paracynohyaenodon schlosseri*, generic difference has not been shown by this character or

others, and I therefore transfer "*A.*" *leakeyi* to *Paracynohyaenodon*, at least until the latter genus (or the ancestry of *P. leakeyi*) is better known.

"*Metasinopa*" *napaki* is not referable to *Metasinopa* because of the moderate size of the metaconid on M_3, the only lower tooth preserved in the Miocene species. This cusp is already nearly absent from the early Oligocene species *M. fraasi*. "*Metasinopa*" *napaki* is not clearly distinct from *Paracynohyaenodon* or *Prodissopsalis* on the basis of M_3, and may tentatively be referred to *Paracynohyaenodon* because of geographical and stratigraphical proximity. *Paracynohyaenodon napaki* is probably, but not certainly, distinct at the specific level from *P. leakeyi;* the populations are very probably distinct. I do not regard the presence or absence of a small parastyle on P^4 as a character that is in itself adequate to define a genus, or to exclude a new species from an established genus.

Savage proposed a new hyaenodontine genus, *Leakitherium*, from the African Miocene (not from the early Oligocene, as stated in his table 3), characterized by the absence of M^3, and the presence of a protocone on M^1 and also, but much reduced, on M^2. The paratype (N.M.K. No. CMF.4025) is stated to consist of a maxilla fragment with P^4 and M^1. The more anterior of these teeth is generally similar to the DP^4 of *Pterodon dasyuroides* figured by Schlosser (1887) and Martin (1906), and also to the DP^4 of *Apterodon altidens* (A.M.N.H. No. 13268, a specimen in which P^4 is exposed above DP^4). I therefore identify this more anterior tooth as DP^4. M^2 on the type specimen of *Leakitherium hiwegi* is unworn, and the evidence for the absence of M^3 is not presented. I do not regard the absence of M^3, by itself, as adequate to separate *Leakitherium hiwegi* from *Metapterodon;* M^3 is reduced in the latter genus. (*Hyaenodon* differs from *Pterodon* in, among other characters, lacking M^3, but at least many species referred to *Hyaenodon* differ from those of *Pterodon* in a whole group of characters.) However, *Leakitherium* appears to be a valid genus, in part because of the incompletely connate paracone and meta-

cone, and it is probable that the species described by Savage as *Hyaenodon* (*Isohyaenodon*) *andrewsi* represents its lower dentition. *Hyaenodon andrewsi* is slightly smaller than *L. hiwegi*, if the relation between upper and lower teeth in American species of *Hyaenodon* is applicable, but the difference if present is slight. In any event the upper and lower dentitions do not appear to be generically distinct. *Leakitherium hiwegi* has a moderate protocone on M^1 and a small protocone on M^2. Concomitantly, *H. andrewsi* has a moderate talonid on M_1 and a small talonid on M_2, features that are not characteristic of *Hyaenodon*. The shear is nearly anteroposterior in both dentitions. I therefore synonymize Savage's subgenus *Isohyaenodon* with *Leakitherium*. Whether the three other species referred by Savage to *Isohyaenodon* are also referable to *Leakitherium* is a question that only a revision of *Hyaenodon* can determine.

Savage referred several specimens from Kenya to the Southwest African species *Metapterodon kaiseri* Stromer, 1923. (Several of Stromer's taxa were referred to as new in several papers, of which this is the earliest that I have seen.) If we rely on the figures of Stromer (1926) and Savage (1965) (and Savage gave no indication of having seen Stromer's specimen), then it is apparent that the two east African species distinguished by Savage are much more similar to each other than are the east African and Southwest African forms of "*M. kaiseri*." The Southwest African species is distinguished especially by a much larger protocone on the molars, especially M^2, a smaller metacrista, a less transverse P^3, and a parastylar lobe on P^4. I do not know whether the differences between Savage's new species *M. zadoki* and the east African specimens he refers to *M. kaiseri* are of more significance than individual variation, although specific distinction is possible. These differences seem of about the same magnitude, although involving different characters, as those between his upper dentitions of *Leakitherium hiwegi*. *Metapterodon zadoki* and *M.* cf. *M. zadoki* are more advanced than *M. kaiseri*, being of about the grade of an advanced species of *Pterodon*, but both (or all) species of *Metapterodon* do seem related to each other and may be retained in the same genus. Both (or all) species have a completely

connate paracone and metacone. However, the name of the genus to which these species should be referred is not *Metapterodon*. I agree with Savage that the type figure of *Pterodon biincisivus*, which is from the Quercy Phosphorites, does not suggest generic separation from the African species of *Metapterodon*. However, this figure also does not suggest even specific separation from *Pterodon dasyuroides*, the type species of *Pterodon*, as can be seen by comparison with the figures of the latter in Filhol (1882), Martin (1906), and Matthew (1909). The synonymy of *P. biincisivus* with *P. dasyuroides* was made by Martin (1906). I therefore synonymize *Metapterodon* with *Pterodon*. Although the latter genus may be heterogeneous, I see no reason why the type species of the two named genera should not be placed together now. I, too, have been confused by the *Pterodon-Metapterodon* labyrinth and have erroneously said that the two genera could not have the same origin (Van Valen, 1965b).

The problem of the possibly polyphyletic origin of *Pterodon* is somewhat accentuated by A.M.N.H. No. 13262, a mandible that may or may not be conspecific with the type of *Metasinopa fraasi*. The latter is from the upper Fluvio-Marine Beds of the Fayum, Egypt, and the former is from the lower Fluvio-Marine Beds. A.M.N.H. No. 13262 differs from the type of *M. fraasi* in lacking a metaconid on at least M_2 and M_3 (this cusp is nearly absent from the type), having a slightly smaller talonid on at least M_2, and having a somewhat more anterior paraconid on at least M_2 and M_3. These differences are all similarities to *Pterodon*, but the two specimens are strikingly similar in most characters.

"*Pterodon*" *hyaenoides*, described by Matthew and Granger (1925) from the late Eocene Shara Murun Formation of Mongolia, bears on the possibly polyphyletic origin of *Hyaenodon*. Despite the statement of Matthew and Granger, it can be definitely seen that the protocone is absent from M^1 and M^2, particularly if comparison is made with specimens (such as *Pterodon zadoki*, *Hyaenodon exiguus*, and A.M.N.H. No. 14452, the supposed upper dentition of *Metasinopa fraasi*) that have a very small protocone present. It is therefore more advanced in this character than some species referred to *Hyaenodon* al-

though it still has M^3, and may be related to the ancestry of the contemporaneous short-faced group of *Hyaenodon*.

According to Savage, the species of *Pterodon* "are strikingly similar and vary mainly in size." In *Pterodon* he included Cope's species *Hemipsalodon grandis* from Saskatchewan, but he did not mention Schlaikjer's species *H. cooki* from Wyoming. The skull of *Hemipsalodon grandis*, described by Loris Shane Russell (1938), is strikingly different from that of *Pterodon* as figured by Schlosser (1911) and Filhol (1882), if all are accurately portrayed, and is sufficient to show distinction at the generic level. Of the lower teeth of *H. grandis*, only a broken M_3 and the roots of the other cheek teeth are known, but some differences from *Pterodon* are visible even from this material. The teeth are smaller relative to the jaw; there is much less difference in tooth size from M_1 to M_3; the talonid of at least M_3 is somewhat larger; and the paraconid of M_3 is perhaps less anterior and is certainly more expanded basolabially. *Hemipsalodon cooki* is probably correctly referred to *Hemipsalodon* and shows, as Schlaikjer (1935) noted, that M_1 also has a relatively large talonid and that the talonid basin of P_4 is better developed than in *Pterodon*. A metaconid is probably absent from both M_1 and M_3, but the only known lower molars of *Hemipsalodon* are moderately worn. On the basis of the specimens mentioned above, it would probably be undesirable to separate *Hemipsalodon* and *Dissopsalis* at the generic level. However, Loris Shane Russell (1934) described a set of upper molars from the type area of *H. grandis* and referred them to this species. These molars are of the *Pterodon-Hyaenodon* grade and are generally similar to those of *Pterodon*, although the protocone is larger and M^3 is less reduced. *Hemipsalodon* may therefore be retained as a valid genus unless these upper molars are incorrectly referred.

A.M.N.H. No. 13252, a P^4 of *Pterodon* the size of, and presumably referable to, *P. africanus* (A.M.N.H. No. 13251, a maxilla tentatively referred by Osborn in 1909 to *P. africanus*, belongs to *P. phiomensis* on the basis of size), has a taller metacrista, a smaller parastyle, and a larger protocone lobe than the Miocene specimen figured by Savage. I

do not know whether these differences are of specific rank. The posterior upper dentitions referred to *P. africanus*, at least as figured by Andrews (1906) and Schlosser (1911), are too imperfect for adequate comparisons. However, in the figure of Schlosser P^4 is considerably larger than M^1, but in Savage's figure P^4 is smaller than M^1. I provisionally refer Savage's specimen to *Hyainailouros* (below). These specimens, and one Oligocene M_3 from Egypt referred by Savage to his Miocene species *Hyaenodon andrewsi*, constitute the remaining evidence for conspecificity of some east African Miocene carnivores with any species elsewhere. This evidence may be valid but cannot be evaluated without reference to the specimens.

Megalopterodon, described by Dashzeveg (1964) from the Mongolian Oligocene, is probably not generically separable from *Pterodon*, and I provisionally synonymize the genera, even though Dashzeveg's species is one of the more distinctive in the genus. It may even be a large species of *Hyaenodon*. The following points are comments on Dashzeveg's distinctions between *Megalopterodon* and *Pterodon*. P_1 is usually present in *Pterodon*. The mandible is quite long in *Pterodon leptognathus*. The symphysis extends to the anterior part of P_4 in *Pterodon africanus* and even more posteriorly in *P. dasyuroides* (A.M.N.H. No. 11048). The number of mental foramina is variable intraspecifically; there are only two, e.g., in A.M.N.H. No. 13258, a specimen referable to *P. africanus*. The number of incisors is unknown in most species of *Pterodon*. The metaconid is absent from all species of *Pterodon* and is the major defining character of the *Pterodon-Hyaenodon* grade. The greater talonid reduction on M_2 of *Megalopterodon mongoliensis* is probably a valid distinction, but the reduction is not much more than that in *P. dasyuroides* and by itself is insufficient for generic separation. The last point is a similarity to *Hyaenodon*, from which the only known distinction is the presence of one lower incisor instead of three. The symphysis extends nearly as far posteriorly in *Hyaenodon horridus* as in *?P. mongoliensis;* the paraconids of M_1 and M_2 in several species of *Hyaenodon* are as long and robust as the protoconid; and the canine in several species of *Hyaenodon* is of similar

development to that of ?$P.$ mongoliensis. The distinction between Pterodon and Hyaenodon is not known to be a phyletic one, and some species placed in Hyaenodon probably descended from some that would now be referable to Pterodon. A genus Megalopterodon may be valid, and some of the above comments may indicate merely that not all species now placed in Pterodon are correctly referred, but until a revision of the advanced Hyaenodontinae is made, such conclusions cannot be demonstrated.

The enormous carnivore Hyainailouros has been considered in the last 50 years to be related to the Felidae and perhaps to the Hyaenidae, except by Viret (1951), who regarded it as an oxyaenine, and Kretzoi (1945), who placed it in his heterogeneous order Creophaga (Hyaenodontidae, Oxyaenidae, Palaeoryctidae, Mesonychidae, Ptolemaiidae, and Triisodontinae). Having overlooked Viret's paper, I recently (Van Valen, 1966) followed the consensus originated by the paper of Helbing (1925) and placed Hyainailouros in the Carnivora. However, Viret had pointed out that Helbing and others had misidentified the homologies of the teeth, and Viret believed that Hyainailouros was related to Patriofelis. I believe that Viret also misidentified the teeth and return to the homologies and relationships given by Pilgrim (1912), who later (Pilgrim, 1932) followed Helbing's conclusion. In the mandible of H. sulzeri figured by Helbing (1925), there is a space between the second and third teeth from the posterior end. This space probably contained a small M_1, unless this tooth had been completely lost by the Vindobonian. The dentition has no particular similarity to that of Patriofelis or other oxyaenids that is not present to a greater degree in the advanced Hyaenodontinae. Derivation from Pterodon phiomensis or a similar species seems plausible. Hyainailouros is the latest survivor of the Hyaenodontidae if the fauna of Heudorf is later than that of Chinji. The maxilla from Napak referred by Savage (1965) to Pterodon africanus compares well with that of Hyainailouros and is probably referable to that genus. As Savage noted, it is generically separable from my concept of the type species of Pterodon (a synonym of which he regarded as referable to Metapterodon),

and my disagreement with him is therefore less striking than the nomenclatural changes seem. Savage's species Pterodon nyanzae may also be referable to Hyainailouros. Hyainailouros has previously been reported in the African Miocene by von Koenigswald (1947).

Hyainailouros contains the largest known carnivorous land mammal (H. maximus). This distinction has previously been given to the mesonychid Andrewsarchus, but Szalay and Gould (1966) have pointed out striking similarities between Andrewsarchus and the entelodont artiodactyls that suggest a similar, omnivorous adaptation for both. Such is decidedly not the case for Hyainailouros, which has strongly carnassial adaptations and deep shear facets that indicate that shear was used. Although known from a number of sites, in keeping with its enormous size and inferred predatory habits Hyainailouros is a rare animal and is as yet known only from fragments. It is too poorly known for one to have an adequate opinion on its maximum size relative to Andrewsarchus, although Hyainailouros was more probably the smaller than the larger. The European species Hyainailourous sulzeri, to which is apparently referable the Indian species H. bugtiensis, had an M_3 length of about 55 mm. and an M_2 length of about 43 mm. (measurements from the type of H. bugtiensis, cast, A.M.N.H. No. 9892) in the early and middle Miocene; M_1 is unknown. The length of M_3 in Hemipsalodon grandis is 35 mm., and in Pterodon africanus it is 32 mm. The length of M_2 in ?Pterodon mongoliensis is 21 mm. (Dashzeveg, 1964), whereas the length of the lower dentition of Dinocyon thenardi posterior to the anterior border of P_3 is only 81 mm. (Zapfe, 1951). In Sarkastodon mongoliensis, an oxyaenid that was probably the second largest terrestrial mammalian carnivore, M_2 is about 49 mm. long and M_1 is about 33 mm. long, including a small amount of plausible reconstruction. According to Szalay and Gould (1966), the lengths of the upper molars of Andrewsarchus are 34, 44, and 47 mm. for M^1, M^2, and M^3, respectively, but Hyainailouros is characterized by a short face. A possibly slightly incomplete M^1 of H. sulzeri is about 38 mm. long (measurement taken from pl. 6 of Helbing, 1925). Hyainailouros maximus (probably not more than a temporal subspecies of

H. sulzeri, but the name *maximus* has priority) of the Pontian was ostensibly even larger, the type M^1 measuring 42.5 mm. in length (Helbing, 1925).

Clinopternodus is occlusally and structurally aberrant for a palaeoryctid, as noted elsewhere (Van Valen, 1966), and I now place it in the Nyctitheriinae for lack of a better refuge. *Paleotomus*, described in the present paper, should be added to the Didelphodontinae of my previous classification (Van Valen, 1966).

The differences given by Patterson (1962) in his diagnosis of the solenodontid *Antillogale* do not appear to me adequate to distinguish it generically from *Solenodon*. The apparently central position of the paraconids of *Antillogale* in his figure 1 is in part caused by inclusion of a component of the height of the taller metaconid by means of a slightly labial view. The three known species of solenodontids (*S. poeyanus* Barbour, 1944, is presumably a subspecies of *S. cubanus*) appear to me about equally distinct, and, in agreement with M. C. McKenna (personal communication), I synonymize *Antillogale* with *Solenodon*.

An interesting genus, *Butselia*, has recently been described by Quinet and Misonne (1965) from the Oligocene of Hoogbutsel, Belgium. It is generally similar to *Aboletylestes* and *Didelphodus* and may be provisionally placed in the Didelphodontinae until we have better knowledge of the lineages in this subfamily. *Butselia* also shows some similarities to the Potamogalinae, as noted by Quinet and Misonne, and to the Geolabidinae. Its upper molars have a hypocone but also have a large stylocone and are in this and other respects remarkably primitive for an Oligocene genus.

Although not a deltatheridian, *Miacis? macintyri* Van Valen, 1965, is probably referable to the supposed viverravine *Quercygale* Kretzoi, 1945 (=*Humbertia* Beaumont, 1965), as suggested by Beaumont's figures. However, the validity of *Quercygale* as more than a subgenus is questionable. Beaumont (1965) noted that it is very similar to the North American miacine genus *Tapocyon* except for the absence of M_3, but regarded the latter character as sufficient to place them in different subfamilies. I do not consider this difference in the presence of M_3, or any other difference that I can determine from the figures and descriptions of Stock (1934) and Beaumont (1965), to be adequate for even a generic distinction. M_3 is much reduced in *Tapocyon occidentalis;* its loss in the European forms was probably not of great importance to the living animal. If the preceding argument is correct, however, the Miacinae can no longer be unambiguously distinguished from the Viverravinae on the basis of the presence of three molars rather than two. The loss of M_3 must have occurred in the middle or even early Eocene because of its absence from the Lutetian species "*Quercygale*" *helvetica*. If there was no migration between Europe and North America during this period (*Proviverra* may have evolved independently on the two continents from *Prototomus;* Van Valen, 1965b), the two lines could have been separate since the early Eocene or, more probably, an Asian species that retained M_3 could have migrated to North America in the late Eocene in the company of *Pterodon*, *Hyaenodon*, and other mammals. Kretzoi's family Quercygalidae is a synonym of Miacinae.

THE CLASSIFICATION

IT WILL BE APPARENT from the preceding discussion that there is no satisfactory way at present to classify the insectivores and their relatives. Text figure 7 shows diagrammatically the relationships for which there is evidence at the present time. There is no time axis. Many of these possible relationships are mutually contradictory, and which of these and other alternatives are correct cannot now be determined. I nevertheless present an interim classification of the Insectivora and Deltatheridia, and I am therefore forced to make choices. My comments are not meant as a defense of these choices, and other alternatives may well prove to be correct.

There are many questionable points at all levels from generic ranges to orders, but some arrangement is necessary. Many of the genera have been placed, and their ranges given, on the authority of the most recent, more or less reliable literature, rather than on the basis of original study. I have not revised the Insectivora; in fact one purpose of this classification is to direct orderly attention to areas needing intensive study. The suprageneric groupings, and many of the genera and ranges, are nevertheless based on evidence that I have personally evaluated. The few genera placed *incertae sedis* were either so placed by their latest reviser or have no published evidence for closer allocation. The use of these names is for historical purposes and does not imply even provisional recognition of their validity. In some cases there is little evidence for the placement given a taxon but even less, or at least no more, for other possibilities. So much of this classification is speculative that I have not singled out the most doubtful cases with question marks. Question marks with stratigraphic and geographical names indicate only doubtful reference of a specimen to a genus. Most insectivores are to some degree *incertae sedis*.

In the present classification and in others (including the Mammalia: Van Valen, 1960) I have made wide use of horizontal ancestral taxa at various levels. These are not wastebasket taxa but are necessary when no later taxon of similar rank is clearly more primitive than others. These horizontal taxa are designed to accommodate not groups of unknown relationships, but rather groups with a common origin which have not diverged (adaptively and in complexity of radiation) sufficiently from this common origin to warrant the erection of a separate taxon at the rank considered. The concept is, of course, old, but it is applicable in many more cases than those in which it is familiar. Part of the Insectivora itself is such a taxon with respect to the Eutheria.

A number of unpublished genera and range extensions known to me have been omitted until they are documented. No generic synonymies are new except those justified elsewhere in the present paper. Authority for the synonymies after about 1942 and for changes in placement of genera after about 1942 (except Simpson, 1945) can usually be found in the references given with an appropriate higher taxon, either in the classification itself or in a comment on that taxon, or elsewhere in the present paper or in Van Valen (1966). Range extensions have usually not been documented here; references for these and for the establishment of individual genera can be obtained through the appropriate bibliographies. "South Asia" applies to genera restricted to the Indian faunal region, and "southeast Asia" refers to the Indo-Malayan faunal region. "North Africa" refers to part of the Palearctic faunal region for Pleistocene and Recent genera only. Previous to the Pleistocene, and probably for much of the Pleistocene, Africa was presumably more unified faunally than it is today. Subdivisions of continents are otherwise ignored. North America includes Central America. The Ural River, rather than the western boundary of Kazakhstan, is here regarded as part of the boundary between Europe and Asia. Genera restricted to islands are so noted, but genera occurring on the mainland may also occur on continental or even semi-oceanic islands in the same region. Recent genera may be assumed to occur also in the Pleistocene of the same region, even when I have not seen a specific discovery of them. I have not always
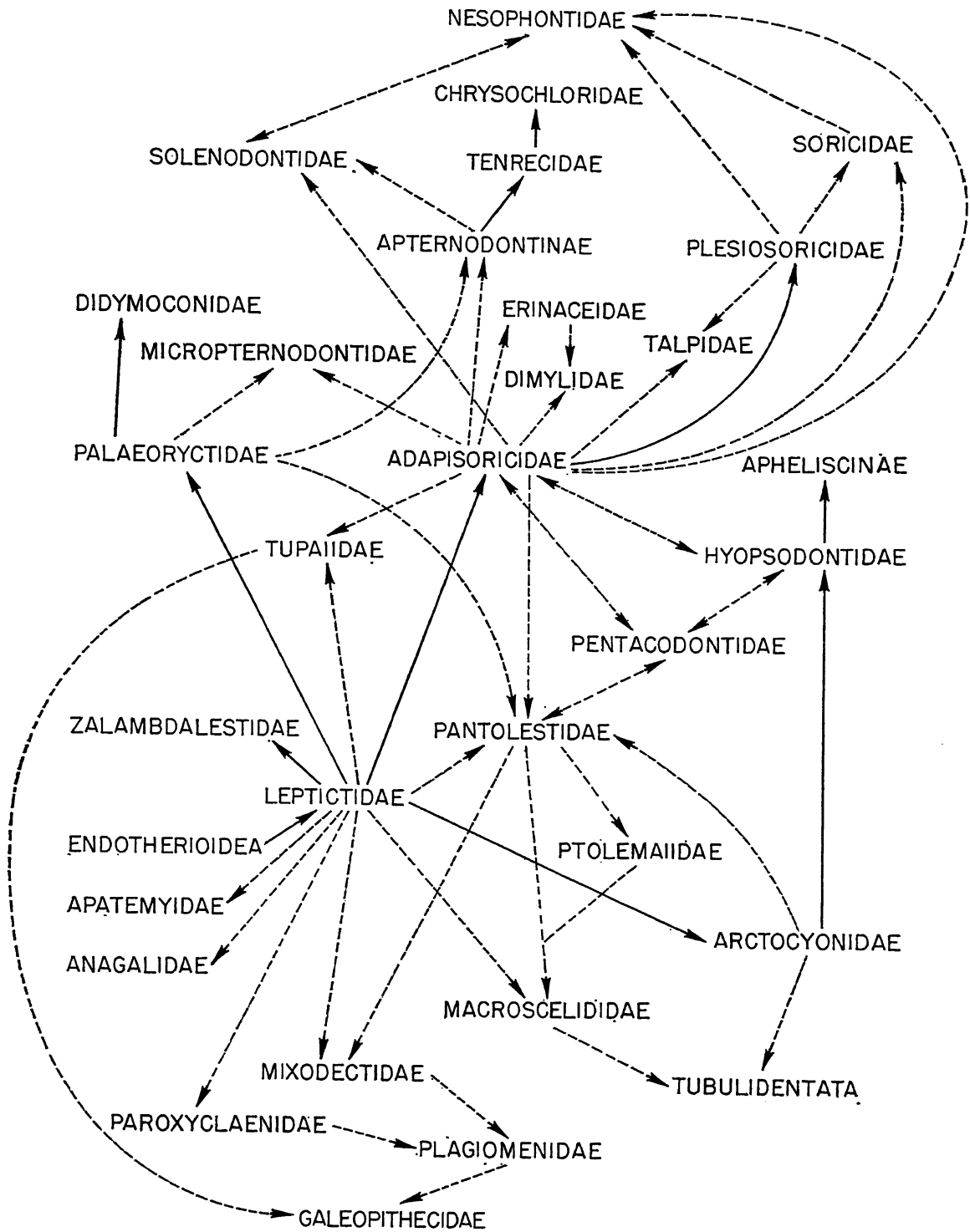
FIG. 7. Possible relationships among insectivores and a few other groups. There is no time axis. The arrows indicate direction of possible phylogeny. Relationships indicated by solid lines are reasonably well established, as is the relationship between the Adapisoricidae and the Erinaceidae.

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rechecked stratigraphically early records of well-known recent genera, and some are probably incorrect. Stratigraphic correlations follow Thenius (1959) for the most part, but in a few cases I differ from him. I have not rechecked many of the older stratigraphic records, and undoubtedly some of these differ by a third of an epoch from Thenius' usage.

Lefeld (1965) has given evidence that the mammal skulls recently collected from Bain Dzak (Shabarakh Usu), Mongolia, by the Polish-Mongolian expedition are from strata of Cretaceous age in which *Protoceratops* occurred. Until one or more of these mammal specimens is shown to belong to a species present in the American Museum material from this locality (the American Museum material has several instances of conspecific specimens), the possibility remains that the American Museum specimens came from a higher horizon than the Polish-Mongolian ones. The time of extinction of dinosaurs in Mongolia has an uncertainty of about an epoch. The incompletely known structure of *Endotherium* and the geological evidence discussed by Patterson (1956) make it improbable that *Endotherium* is appreciably older

than the Albian, middle Cretaceous in a tripartite division of the Cretaceous. The Belgian locality Dormaal (Orsmael) is provisionally regarded as late Paleocene and the Mongolian locality Gashato (Hashiato) is provisionally regarded as early Eocene by Van Valen and Sloan (1966).

Comments on certain taxa, and diagnoses of those that are new, follow the classification in the same order in which the taxa are arranged. These comments are supplementary to those made elsewhere in the present paper and in Van Valen (1966). Important references since Simpson's review (1945), other than Van Valen (1966) and the present paper, are given after taxa in the classification when discussion is unnecessary. The genera of the Hyaenodonta have been arranged elsewhere (Van Valen, 1966) but are repeated at the suggestion of M. C. McKenna. The author of more or less the present concept of a taxon, insofar as the included taxa were then known, appears without parentheses if he used any name at any level for the taxon; the author by Article 36 of the Code appears in parentheses if different.

Order Insectivora (G. Cuvier, 1817) Illiger, 1811 (=Subterranea Illiger, 1811). Middle Cretaceous-Recent; North America, Asia. Middle Paleocene-Recent; Europe. Early Oligocene-Recent; Africa. Recent; South America
  Suborder Proteutheria (Romer, 1966) McKenna, 1960. Middle Cretaceous-middle Oligocene; North America. Middle Cretaceous-Recent; Asia. Middle Paleocene-middle Oligocene; Europe. Early Oligocene; Africa
    Superfamily Endotherioidea (Shikama, 1947), new. Middle Cretaceous; Asia, North America
      Family Endotheriidae Shikama, 1947. Middle Cretaceous; Asia
        Endotherium Shikama, 1947. Middle Cretaceous; Asia
      Family Pappotheriidae Slaughter, 1965. Middle Cretaceous; North America
        Pappotherium Slaughter, 1965. Middle Cretaceous; North America
    Superfamily Tupaioidea (Gray, 1825), new. Late Cretaceous-early Oligocene; North America. Late Cretaceous or Paleocene-Recent; Asia. Middle Paleocene-middle Oligocene; Europe. Early Oligocene; Africa
      Family Leptictidae Gill, 1872 (=Isacidae Cope, 1874; Ictopsidae Schlosser, 1887). Late Cretaceous-middle Oligocene; North America. Late Paleocene-middle Eocene; Europe
        Subfamily Procerberinae Sloan and Van Valen, 1965. Late Cretaceous-middle Paleocene; North America. Late Paleocene-middle Eocene; Europe
          Procerberus Sloan and Van Valen, 1965. Late Cretaceous-early Paleocene; North America
          (Unnamed genus) L. S. Russell, 1962. Late Cretaceous; North America
          Leptonysson, new. Middle Paleocene; North America
          Diaphyodectes D. E. Russell, 1964. Late Paleocene; Europe
          Leptictidium Tobein, 1962. Middle Eocene; Europe
        Subfamily Leptictinae Gill, 1872 (including Diacodontinae Trouessart, 1879). Early Paleocene-middle Oligocene; North America. ?Early Eocene; ?Europe
          Palaeictops Matthew, 1899 (including *Parictops* Granger, 1910). Early Paleocene-middle Eocene; North America. ?Early Eocene; ?Europe

Prodiacodon Matthew, 1929 (=*Palaeolestes* Matthew, 1918). Middle Paleocene; North America

Myrmecoboides Gidley, 1915. Middle Paleocene; North America.

Diacodon Cope, 1875. Middle Paleocene-early Eocene; North America

Hypictops Gazin, 1949. Middle Eocene; North America

Leptictis Leidy, 1868 (=or including *Ictops* Leidy, 1868; *Mesodectes* Cope, 1875; *Isacis* [or *Isacus*] Cope, 1873; *Nanohyus* Leidy, 1869; *Ictidops* Weber, 1904). Late Eocene-middle Oligocene; North America

Subfamily Gypsonictopinae, new. Late Cretaceous; North America

Gypsonictops Simpson, 1927 (including *Euangelistes* Simpson, 1929). Late Cretaceous; North America

Family Zalambdalestidae Gregory and Simpson, 1926. Late Cretaceous or Paleocene; Asia. ?Middle Paleocene; ?North America

Zalambdalestes Gregory and Simpson, 1926. Late Cretaceous or Paleocene; Asia

(Unnamed genus) Van Valen, 1964. Middle Paleocene; North America

Family Anagalidae Simpson, 1931. Early Eocene-Oligocene; Asia. [See McKenna, 1963a; Van Valen, 1964]

Pseudictops Matthew, Granger, and Simpson, 1929. Early Eocene; Asia

Anagale Simpson, 1931. Early Oligocene; Asia

Anagalopsis Bohlin, 1951. ?Oligocene; Asia

Family Paroxyclaenidae Weitzel, 1933 (including Kochictidae Kretzoi, 1943). Middle Eocene-middle Oligocene; Europe. Middle Eocene; Asia. [See Van Valen, 1965a]

Kopidodon Weitzel, 1933. Middle Eocene; Europe

Pugiodens Matthes, 1952 (=or including *Vulpavoides* Matthes, 1952; *Russellites* Van Valen, 1965). Middle Eocene; Europe

Dulcidon Van Valen, 1965. Middle Eocene; Asia

Paroxyclaenus Teilhard de Chardin, 1922. Late Eocene; Europe

Kochictis Kretzoi, 1943. Middle Oligocene; Europe

Family Tupaiidae Gray, 1825. Middle-late Paleocene; Europe. Recent; Asia

Subfamily Adapisoriculinae, new. Middle-late Paleocene; Europe

Adapisoriculus Lemoine, 1885. Middle-late Paleocene; Europe

Subfamily Ptilocercinae Lyon, 1913. Recent; southeast Asia

Ptilocercus Gray, 1848. Recent; southeast Asia

Subfamily Tupaiinae Gray, 1825 (=Cladobatina Bonaparte, 1838; Glisoricina Pomel, 1848). Recent; Asia. [See Davis, 1938]

Dendrogale Gray, 1848. Recent; Southeast Asia

Tupaia Raffles, 1822 (=or including *Sorexglis* G. Cuvier and É. Geoffroy Saint-Hilaire, 1821; *Glisorex* Desmarest, 1822; *Cladobates* F. Cuvier, 1824; *Hylogale* Temminck, 1827; *Hylogalea* Müller and Schlegel, 1843; *Glisosorex* Giebel, 1855; *Glirisorex* Scudder, 1882; *Glipora* Jentink, 1888; *Tana* Lyon, 1913; *Lyonogale* Conisbee, 1913). Recent; southeast Asia

Urogale Mearns, 1905. Recent; Philippines

Anathana Lyon, 1913. Recent; south Asia

Family Pantolestidae Cope, 1884 (including Dyspternidae Kretzoi, 1943). Middle Paleocene-early Oligocene; North America, Europe

Propalaeosinopa Simpson, 1927 (including *Bessoecetor* Simpson, 1936). Middle-late Paleocene; North America. ?Late Paleocene; ?Europe

Palaeosinopa Matthew, 1901. Late Paleocene-early Eocene; North America. Early Eocene; Europe

Pantomimus, new. Middle Paleocene; North America

Pagonomus D. E. Russell, 1964. Middle-late Paleocene; Europe

Pantinomia, new. Middle Paleocene; North America

Pantolestes Cope, 1872 (=or including *Passalacodon* Marsh, 1872; *Anisacodon* Marsh, 1872). Middle Eocene; North America

Androconus Quinet, 1965. Early Oligocene; Europe

Chadronia Cook, 1954. Early Oligocene: North America

Cryptopithecus Schlosser, 1890 (including *Opsiclaenodon* Butler, 1946). Late Eocene; Europe

Dyspterna Hopwood, 1927. Early Oligocene; Europe

Galethylax Gervais, 1848–1852. Late Eocene; Europe

Family Ptolemaiidae Osborn, 1908. Early Oligocene-Miocene; Africa

　　Ptolemaia Osborn, 1908. Early Oligocene; Africa

　　(Unnamed genus referred to *Ptolemaia*) Schlosser, 1911. Early Oligocene; Africa

　　Kelba R. J. G. Savage, 1965. Miocene; Africa

Family Pentacodontidae Simpson, 1937. Middle Paleocene-early Eocene; North America. Late Paleocene; Europe

　　Aphronorus Simpson, 1935. Middle Paleocene; North America

　　Coriphagus Douglass, 1908. Middle Paleocene; North America

　　Pentacodon Scott, 1892. Middle Paleocene; North America

　　Bisonalveus Gazin, 1956. Late Paleocene; North America

　　Protentomodon Simpson, 1928. Late Paleocene; North America

　　Amaramnis Gazin, 1962. Early Eocene; North America

　　(Most referred specimens of *Pagonomus*) D. E. Russell, 1964. Late Paleocene; Europe

Superfamily Apatemyoidea (Matthew, 1909) Scott and Jepsen, 1936. Middle Paleocene-middle Oligocene; North America. Late Paleocene-late Eocene; Europe

Family Apatemyidae Matthew, 1909. Middle Paleocene-middle Oligocene; North America. Late Paleocene-late Eocene; Europe. [See McKenna, 1960b, 1963b]

　　Subfamily Apatemyinae Matthew, 1909 (including Hétérohyins Gervais, 1859). Middle Paleocene-middle Oligocene; North America. Late Paleocene-late Eocene; Europe

　　　Jepsenella Simpson, 1940. Middle Paleocene; North America

　　　Labidolemur Matthew and Granger, 1921. Late Paleocene; North America

　　　Apatemys Marsh, 1872 (including *Teilhardella* Jepsen, 1930). Late Paleocene-late Eocene; North America

　　　Eochiromys Teilhard de Chardin, 1927. Late Paleocene; Europe

　　　Heterohyus Gervais, 1848–1852 (=or including *Necrosorex* Filhol, 1890; *Heterochiromys* Stehlin, 1916; *Amphichiromys* Stehlin, 1916). Middle-late Eocene; Europe

　　　Stehlinella Matthew, 1929 (= *Stehlinius* Matthew, 1921). Late Eocene; North America

　　　Sinclairella Jepsen, 1934. Early-middle Oligocene; North America

　　Subfamily Unuchiniinae Van Valen and McKenna, new. Late Paleocene; North America

　　　Unuchinia Simpson, 1937. Late Paleocene; North America

Suborder Macroscelidea Butler, 1956 (= Dipogales Murray, 1866). Early Oligocene-Recent; Africa

Family Macroscelididae Bonaparte, 1838. Early Oligocene-Recent; Africa. [See Patterson, 1965; Butler and Hopwood, 1957; Roux, 1947.]

　　Subfamily Macroscelidinae Bonaparte, 1838. Early Oligocene-Recent; Africa

　　Tribe Macroscelidini Bonaparte, 1838. Early Oligocene-Recent; Africa

　　　Metolbodotes Schlosser, 1910 (spelling corrected 1911; = *Metoldobotes* Schlosser,ʳ1910). Early Oligocene; Africa

　　　Palaeothentoides Stromer, 1932. Pleistocene; Africa

　　　Elephantulus Thomas and Schwann, 1906 (including *Elephantomys* Broom, 1938). Pleistocene-Recent; Africa

　　　Nasilio Thomas and Schwann, 1906. Pleistocene-Recent; Africa

　　　Macroscelides A. Smith, 1829 (= *Eumerus* I. Geoffroy Saint-Hilaire, 1829; *Macroscelis* J. B. Fischer, 1830; *Rhinomys* Lichtenstein, 1831; *Diposorex* Blainville, 1838). Recent; Africa

　　　Petrodromus Peters, 1846. (including *Cercoctenus* Hollister, 1916; *Mesoctenus* Thomas, 1918). Recent; Africa

　　Tribe Rhynchocyonini Gill, 1872. Miocene-Recent; Africa

　　　Rhynchocyon Peters, 1847 (including *Rhinonax* Thomas, 1918). Miocene-Recent; Africa

　　Subfamily Mylomygalinae Camp, Welles, and Green, 1953. Pleistocene; Africa

　　　Mylomygale Broom, 1948. Pleistocene; Africa

　　Subfamily Myohyracinae Andrews, 1914. Miocene; Africa. [See Whitworth, 1954]

　　　Myohyrax Andrews, 1914. Miocene; Africa

　　　Protypotheroides Stromer, 1922. Miocene; Africa

Suborder Dermoptera Illiger, 1811 (= Pterophorae Gray, 1822; Ptenopleura van der Hoeven, 1858; Galeopithecia Cabrera, 1925). Middle Paleocene-late Eocene; North America. Late Paleocene; Europe. Recent; Asia

Superfamily Mixodectoidea Cope, 1883. Middle-late Paleocene; North America. Late Paleocene; Europe

Family Mixodectidae Cope, 1883 (= Oldobotidae Schlosser, 1907). Middle-late Paleocene; North America. Late Paleocene; Europe

Dracontolestes Gazin, 1941. Middle Paleocene; North America

Mixodectes Cope, 1883 (= or including *Indrodon* Cope, 1884; *Olbodotes* [not *Oldobotes*] Osborn, 1902). Middle Paleocene; North America

Remiculus D. E. Russell, 1964. Late Paleocene; Europe

Elpidophorus Simpson, 1927. Middle-late Paleocene; North America

Eudaemonema Simpson, 1935. Middle Paleocene; North America

Superfamily Galeopithecoidea Gray, 1821. Late Paleocene-late Eocene; North America. Recent; Asia

Family Plagiomenidae Matthew, 1918. Late Paleocene-late Eocene; North America

Subfamily Plagiomeninae Matthew, 1918. Late Paleocene-early Eocene; North America

Planetetherium Simpson, 1928. Late Paleocene; North America

Plagiomene Matthew, 1918. Early Eocene; North America

Subfamily Thylacaelurinae, new. Late Eocene; North America

Thylacaelurus L. S. Russell, 1954. Late Eocene; North America

Family Galeopithecidae Gray, 1821 (= or including Pleuropteridae Burnett, 1829; Pterocebineae Lesson, 1840; Colugidae Miller, 1906; Galeopteridae Thomas, 1908; Cynocephalidae Simpson, 1945). Recent; Asia

Galeopithecus Pallas, 1780 (= or including *Cynocephalus* Boddaërt, 1768, suppression pending; *Galeopus* Rafinesque, 1815; *Pleuropterus* Burnett, 1829; *Dermopterus* Burnett, 1829; *Colugo* Gray, 1870). Recent; Philippines

Galeopterus Thomas, 1908. Recent; southeast Asia

Suborder Erinaceota, new. Middle Paleocene-Recent; North America, Europe. Early Eocene-Recent; Asia. Miocene-Recent; Africa. Recent; South America

Superfamily Erinaceoidea (Fischer von Waldheim, 1817) McDowell, 1958. Middle Paleocene-Recent; North America, Europe. Early Eocene-Recent; Asia. Miocene-Recent; Africa

Family Adapisoricidae (Schlosser, 1887), new. Middle Paleocene-late Oligocene; North America. Middle Paleocene-middle Eocene; Europe. Early Eocene-late Oligocene; Asia

Subfamily Geolabidinae McKenna, 1960 (= or including Centetodontinae Trouessart, 1879, *nomen oblitum;* Metacodontidae Butler, 1948). Middle Paleocene-late Oligocene; North America. Early Eocene; Asia. [See McKenna, 1960b; McKenna, Robinson, and Taylor, 1962]

Stilpnodon Simpson, 1935. Middle Paleocene; North America

Praolestes Matthew, Granger, and Simpson, 1929. Early Eocene; Asia

Opisthopsalis Matthew, Granger, and Simpson, 1929. Early Eocene; Asia

Hyracolestes Matthew and Granger, 1925. Early Eocene; Asia

Centetodon Marsh, 1872 (= *Hypacodon* McKenna, 1960). ?Early Eocene, middle Eocene; North America

Myolestes Matthew, 1909. Middle Eocene; North America

Embassis Cope, 1873. Middle Oligocene; North America

Geolabis Cope, 1884 (= or including *Protictops* Peterson, 1934; *Metacodon* J. Clark, 1936). Middle Eocene-late Oligocene; North America

Subfamily Adapisoricinae Schlosser, 1887. Middle Paleocene-early Eocene; North America. Middle Paleocene-middle Eocene; Europe. [See Tobien, 1962; D. E. Russell, 1964]

Mckennatherium Van Valen, 1965. Middle Paleocene; North America

Leptacodon Matthew and Granger, 1921. Middle Paleocene-early Eocene; North America

Adunator D. E. Russell, 1964. Middle-late Paleocene; Europe

Adapisorex Lemoine, 1883. Middle-late Paleocene; Europe

Paschatherium D. E. Russell, 1964. Late Paleocene; Europe

Messelina Tobien, 1962. Middle Eocene; Europe

Subfamily Creotarsinae (Hay, 1930) new (including Amphilemuridae Heller, 1935; Dormaalidae Quinet, 1964). Late Paleocene-late Eocene; North America, Europe. Early-late Oligocene; Asia. [See McKenna, 1960a; Tobien, 1962; D. E. Russell, 1964]

Litolestes Jepsen, 1930. Late Paleocene; North America

Xenacodon Matthew and Granger, 1921. Late Paleocene; North America

Talpavus Marsh, 1872. Early-late Eocene; North America

Creotarsus Mathew, 1918. Early Eocene; North America

Dormaalius Quinet, 1964. Late Paleocene; Europe

(Genus called "*Nyctitherium*" by McKenna, 1960a, and "*Talpavus*" by McKenna, Robinson, and Taylor, 1962). Early-middle Eocene; North America

Entomolestes Matthew, 1909 (including *Leipsanolestes* Simpson, 1928). Late Paleocene-middle Eocene, ?late Eocene; North America

Scenopagus McKenna and Simpson, 1959. Middle Eocene, ?late Eocene; North America

Macrocranion Weitzel, 1949 (=*Aculeodens* Weitzel, 1949). Middle Eocene; Europe

Amphilemur Heller, 1935. Middle Eocene; Europe

Sespedectes Stock, 1935. Late Eocene; North America

Proterixoides Stock, 1935. Late Eocene; North America

Amphidozotherium Filhol, 1876. Late Eocene; Europe

Ictopidium Zdánsky, 1930. Early Oligocene; Asia

Tupaiodon Matthew and Granger, 1924. Late Oligocene; Asia

Subfamily Nyctitheriinae Simpson, 1928. Middle Eocene-early Oligocene; North America. [See McKenna, 1960a]

Nyctitherium Marsh, 1872. Middle-late Eocene; North America

Clinopternodus J. Clark, 1937 (=*Clinodon* J. Clark, 1936). Early Oligocene; North America

Family Erinaceidae Fischer von Waldheim, 1817 (=Acanthionidae Schulze, 1900). Late Eocene-Recent; Europe. Middle Oligocene-early Pliocene; North America. Late Oligocene-Recent; Asia. Miocene-Recent; Africa. [See Butler, 1948, 1956b]

Subfamily Galericinae Pomel, 1848 (=Anachantes Murray, 1866). Late Eocene-late Miocene; Europe. Middle Miocene-early Pliocene; North America. Miocene; Africa. Recent; Asia

Tribe Galericini Pomel, 1848 (=Parasoricidae Schlosser, 1887). Early Oligocene-late Miocene; Europe. Miocene; Africa

Tetracus Aymard, 1850. Early Oligocene; Europe

Galerix Pomel, 1848 (=*Parasorex* Meyer, 1865). Late Miocene; Europe. Miocene; Africa

Pseudogalerix Gallard, 1929. Late Miocene; Europe

Tribe Neurogymnurini Butler, 1948 (=Cayluxotheriini Winge, 1917). Late Eocene-middle Oligocene; Europe

Neurogymnurus (not *Necrogymnurus*) Filhol, 1877 (=*Cayluxotherium* Filhol, 1880). Late Eocene-middle Oligocene; Europe

Tribe Echinosoricini (Cabrera, 1925) Gill, 1872 (=Gymnurinae Gill, 1872; Hylomidae J. Anderson, 1879). Middle-late Miocene; Europe. Middle Miocene-early Pliocene; North America. Recent; Asia

Lanthanotherium (not *Lantanotherium*) Filhol, 1888. Middle-late Miocene; Europe. Late Miocene-early Pliocene; North America

Ocajila MacDonald, 1963. Early Miocene; North America

Podogymnura Mearns, 1905. Recent; Philippines

Echinosorex Blainville, 1838 (=*Gymnura* Lesson, 1827). Recent; Asia.

Hylomys Miller, 1829 (including *Neotetracus* Trouessart, 1909; *Neohylomys* Shaw and Wong, 1959). Pleistocene-Recent; Asia

Subfamily Erinaceinae Fischer von Waldheim, 1817. Early Oligocene-Recent; Europe. Middle Oligocene-early Pliocene; North America. Late Oligocene-Recent; Asia. Miocene-Recent; Africa

Tribe Protericini Butler, 1948 (including Brachyericini Butler, 1948). Early Oligocene-late Miocene; Europe. Middle Oligocene-early Pliocene; North America. Late Oligocene-early Miocene; Asia. Miocene; Africa

Proterix Matthew, 1903. Middle Oligocene; North America

Brachyerix Matthew, 1933. Late Miocene; North America

Amphechinus Aymard, 1850 (including *Palaeoerinaceus* [not *Paleoerinaceus*, *Palaerinaceus*, or *Palerinaceus*] Filhol, 1879; *Palaeoscaptor* Matthew and Granger, 1924; *Parvericius* Koerner, 1940). Early Oligocene-late Miocene; Europe. Late Oligocene-early Miocene; Asia. Miocene; Africa. Middle-late Miocene; North America

Dimylechinus Hürzeler, 1944. Early Miocene; Europe

Metechinus Matthew, 1929. Late Miocene-early Pliocene; North America

Tribe Erinaceini Fischer von Waldheim, 1817. Early Miocene-Recent; Europe. Miocene-Recent; Africa. Pleistocene-Recent; Asia

Gymnurechinus Butler, 1965. Miocene; Africa

Postpalerinaceus Crusafont-Pairó and Villalta-Comella, 1948. Early Pliocene; Europe

Protechinus Lavocat, 1961. Late Miocene; Africa

Mioechinus Butler, 1948. Early-late Miocene; Europe

Erinaceus Linnaeus, 1758. (=or including *Setiger* É. Geoffroy Saint Hilaire, 1803; *Atelerix* Pomel, 1848; *Peroechinus* Fitzinger, 1866; *Herinaceus* Mina-Palumbo, 1868; *Aethechinus* Thomas, 1918; *Mesechinus* Ognev, 1951). Late Miocene-Recent; Europe. Pleistocene-Recent; Asia, Africa

Hemiechinus Fitzinger, 1866 (including *Ericius* Sundevall, 1842; *Erinaceolus* Ognev, 1928). Recent; Asia, North Africa

Paraechinus Trouessart, 1879 (including *Macroechinus* Satunin, 1907). Recent; Asia, North Africa

Family Dimylidae Schlosser, 1887. Middle Oligocene-early Pliocene; Europe. [See Hürzeler, 1944]

  Subfamily Dimylinae Schlosser, 1887. Middle Oligocene-middle Miocene; Europe

    Exodaenodus Hürzeler, 1944. Middle Oligocene; Europe

    Dimyloides Hürzeler, 1944. Late Oligocene; Europe

    Dimylus von Meyer, 1846. Early Miocene; Europe

    Cordylodon von Meyer, 1859. Early-middle Miocene; Europe

    Pseudocordylodon Hürzeler, 1944. Early Miocene; Europe

    Metacordylodon Schlosser, 1911. Late Miocene; Europe

  Subfamily Plesiodimylinae Hürzeler, 1944. Middle Miocene-early Pliocene; Europe

    Pleisodimylus Gaillard, 1897. Middle Miocene-early Pliocene; Europe

Family Talpidae (Fischer von Waldheim, 1817) Vicq d'Azyr, 1792 (=Myaladae Gray, 1822; Orycteri Blainville, 1834). Late Eocene-Recent; Europe. Early Oligocene-Recent; North America. Middle Pliocene-Recent; Asia. [See McDowell, 1958; Stroganov, 1948]

  Subfamily Proscalopinae K. M. Reed, 1961 (=Arctoryctinae C. A. Reed and Turnbull, 1965). Early Oligocene-middle Miocene; North America. [See K. M. Reed, 1961; C. A. Reed and Turnbull, 1965]

    Cryptoryctes C. A. Reed, 1954. Early Oligocene; North America

    Oligoscalops K. M. Reed, 1961. Middle Oligocene; North America

    Proscalops Matthew, 1901 (including *Arctoryctes* Matthew, 1907). Middle Oligocene-middle Miocene; North America.

    Mesoscalops K. M. Reed, 1960. Middle Miocene; North America

  Subfamily Uropsilinae Dobson, 1883. Recent; Asia. [See Ellerman and Morrison-Scott, 1951]

    Uropsilus A. Milne Edwards, 1872 (=*Nasillus* Thomas, 1911; *Rhynchonax* Thomas, 1912). Recent; Asia

  Subfamily Desmaninae (Thomas, 1912) Mivart, 1871 (=Myogalina Mivart, 1871). Middle Oligocene-Recent; Europe. Middle Pliocene; North America

    Paratalpa Lavocat, 1951. Middle Oligocene; Europe

    Mygalea Schreuder, 1940. Late Miocene; Europe

    Mygalinea Schreuder, 1940. Early Pliocene-Pleistocene; Europe

    Desmana Güldenstaedt, 1777 (=or including *Desman* Lacépède, 1799; *Mygale* G. Cuvier, 1800; *Desmanus* Rafinesque, 1815; *Myogalea* J. B. Fischer, 1829; *Caprios* Wagler, 1830; *Myogale* Brandt, 1836; *Palaeospalax* Owen, 1846). Early Pliocene-Recent; Europe

    Galemys Kaup, 1829 (=*Mygalina* I. Geoffroy Saint Hilaire, 1835; *Galomys* Agassiz, 1846). Pliocene-Recent; Europe

    Gaillardia Matthew, 1932 (=or including *Hydroscapheus* Shotwell, 1956). Middle Pliocene; North America

    Geomana Brunner, 1957. Pleistocene; Europe

    Desmagale Kretzoi, 1954. Pleistocene; Europe

  Subfamily Talpinae Fischer von Waldheim, 1817. Late Eocene-Recent; Europe. Early Miocene-Recent; North America. Middle Pliocene-Recent; Asia

    Tribe Scaptonychini, new. Late Eocene-late Miocene; Europe. Recent; Asia

    Myxomygale Filhol, 1890. Late Eocene; Europe

    Geotrypus Pomel, 1848 (including *Protalpa* Filhol, 1877). Late Eocene-middle Oligocene; Europe

    Mygatalpa Schreuder, 1940. Middle-late Oligocene; Europe

    Scaptonyx A. Milne Edwards, 1872. ?Middle-late Miocene; ?Europe. Recent; Asia

Tribe Urotrichini Dobson, 1883. Early Miocene-Recent; North America. Miocene; Europe. Middle Pliocene-Recent; Asia
 Domninoides Green, 1956. Early Miocene-early Pliocene; North America
 Parascalops True, 1894. Pleistocene-Recent; North America
 Mydecodon Wilson, 1960. Middle Miocene; North America
 Scalopoides Wilson, 1960. Middle Miocene; North America
 Proscapanus Gaillard, 1899 (=*Proscapaneus* Winge, 1917). Miocene; Europe
 Neurotrichus Günther, 1880. Recent; North America
 Urotrichus Temminck, 1841 (including *Dymecodon* True, 1886). Recent; Japan
 Scapanulus Thomas, 1912. Middle Pliocene-Recent; Asia
Tribe Talpini Fischer von Waldheim, 1817. Late Miocene-Recent; Europe. Pleistocene-Recent; Asia. [See Schwarz, 1948; Imaizumi, 1955; Stein, 1960]
 Talpa Linnaeus, 1758 (= or including *Mogera* Pomel, 1848; *Heterotalpa* Peters, 1863; *Talpops* Gervais, 1868; *Parascaptor* Gill, 1875; *Euroscaptor* Miller, 1940; *Eoscalops* Stroganov, 1941; *Asioscalops* [not *Asioscaptor*] Stroganov, 1941). Late Miocene-Recent; Europe. Pleistocene-Recent; Asia
 Scaptochirus A. Milne Edwards, 1867 (= *Chiroscaptor* Heude, 1898). Recent; Asia
Tribe Condylurini Trouessart, 1879. ?Late Miocene, Pleistocene-Recent; North America
 Condylura Illiger, 1811 (=*Talpasorex* Schinz, 1821; *Astromycter* Harris, 1825; *Rhinaster* Wagler, 1830). ?Late Miocene, Pleistocene-Recent; North America
Tribe Scalopini Trouessart, 1879 (including Scapanei Winge, 1917). Early Pliocene-Recent; North America
 Scapanus Pomel, 1848 (=*Scapaneus* Winge, 1917). Early Pliocene-Recent; North America
 Scalopus É. Geoffroy Saint Hilaire, 1803 (= or including *Scalops* Illiger, 1811; *Talpasorex* Lesson, 1827; *Hesperoscalops* Hibbard, 1941). Early Pliocene-Recent; North America
(Subfamily unknown)
 Galeospalax Pomel, 1848. Late Oligocene; Europe
 Hyporyssus Pomel, 1848. Late Miocene; Europe
 Scaptogale Trouessart, 1879 (=*Echinogale* Pomel, 1848). Early Miocene; Europe
 Mystipterus Hall, 1930. Early Pliocene; North America
Superfamily Soricoidea Fischer von Waldheim, 1817. Middle Eocene-Recent; North America. Late Eocene-Recent; Europe. Early Miocene-Recent; Asia. Miocene-Recent; Africa. Pleistocene-Recent; Asia. Miocene-Recent; Africa. Pleistocene-Recent; South America
Family Plesiosoricidae (Winge, 1917), new. Middle Eocene-early Pliocene; North America. Late Eocene-late Miocene; Europe. ?Early Miocene; ?Asia
 Entomacodon Matthew, 1909. Middle Eocene; North America
 Saturninia Stehlin, 1940. Late Eocene; Europe
 Plesiosorex Pomel, 1848. Middle Oligocene-late Miocene; Europe. Middle Miocene; North America. ?Early Miocene; ?Asia
 Meterix Hall, 1929. Early Pliocene; North America
 Ankylodon Patterson and McGrew, 1937. Late Eocene-middle Oligocene; North America
Family Nesophontidae H. E. Anthony, 1916. Sub-Recent; Greater Antilles. [See McDowell, 1958]
 Nesophontes H. E. Anthony, 1916. Sub-Recent; Greater Antilles
Family Soricidae (Fischer von Waldheim, 1817) Vicq d'Azyr, 1792. ?Late Eocene, Early Oligocene-Recent; North America. Middle Oligocene-Recent; Europe. Early Miocene-Recent; Asia. Miocene-Recent; Africa. Recent; South America. [See Repenning, in press]
Subfamily Heterosoricinae Viret and Zapfe, 1951. ?Late Eocene, early Oligocene-late Miocene; North America. Middle Oligocene-early Pliocene; Europe
 Domnina Cope, 1873 (= *Miothen* Cope, 1873; *Protosorex* Scott, 1895). ?Late Eocene, early Oligocene-early Miocene; North America
 Paradomnina Hutchison, 1966. Late Miocene; North America
 Ingentisorex Hutchison, 1966. Late Miocene; North America
 Trimylus Roger, 1885 (=*Heterosorex* Gaillard, 1915). Middle Oligocene-late Miocene; North America. Middle Oligocene-early Pliocene; Europe
Subfamily Crocidurinae A. Milne Edwards, 1872. Early Miocene-Recent; Europe. Miocene-Recent; Africa. Pleistocene-Recent; Asia
Tribe Crocidurini A. Milne Edwards, 1872. Early Miocene-Recent; Europe. Miocene-Recent; Africa. Pleistocene-Recent; Asia

Miosorex Kretzoi, 1959. Late Miocene; Europe

Crocidura Wagler, 1832 (= or including *Rhinomus* Murray, 1861; *Leucodon* Fatio, 1869; *Paurodus* Schulze, 1897; *Heliosorex* Heller, 1910). ?Miocene, Pleistocene-Recent; Africa. Pleistocene-Recent; Asia, Europe

Diplomesodon Brandt, 1853. Pleistocene; Africa. Recent; Asia

Feroculus Kelaart, 1852. Recent; Ceylon

Myosorex Gray, 1838 (including *Congosorex* Heim de Balsac and Lamotte, 1956). Pleistocene-Recent; Africa

Paracrocidura Heim de Balsac, 1956. Recent; Africa

Praesorex Thomas, 1913. Recent; Africa

Solisorex Thomas, 1924. Recent; Ceylon

Soricella Doben-Florin, 1964. Early Miocene; Europe

Suncus Ehrenberg, 1833 (= or including *Pachyura* Sélys Longchamps, 1839; *Sunkus* Sundevall, 1843; *Paradoxodon* Wagler, 1855; *Plerodus* Schulze, 1897). Early Pliocene-Recent; Europe. Pleistocene-Recent; Africa. Recent; Asia

Surdisorex Thomas, 1906. Recent; Africa

Sylvisorex Thomas, 1904. Recent; Africa

Tribe Scutisoricini J. A. Allen, 1917. Recent; Africa

    Scutisorex Thomas, 1913. Recent Africa

Subfamily Limnoecinae Repenning, 1967. Middle Miocene-middle Pliocene; North America

    Angustidens Repenning, 1967. Middle Miocene; North America

    Limnoecus Stirton, 1930. Late Miocene-middle Pliocene; North America

Subfamily Soricinae (Fischer von Waldheim, 1817) Vicq d'Azyr, 1792. Middle Oligocene-Recent; Europe. Middle Miocene-Recent; North America. Middle Pliocene-Recent; Asia. Recent; South America

Tribe Soricini (Fischer von Waldheim, 1817) Vicq d'Azyr, 1792. Middle Oligocene-Recent; Europe. Middle Miocene-Recent; North America. Middle Pliocene-Recent; Asia

    Crocidosorex Lavocat, 1951 (including *Oligosorex* Kretzoi, 1959). Middle Oligocene-early Miocene; Europe

    Antesorex Repenning, 1967. Middle Miocene; North America

    Sorex Linnaeus, 1758 (=or including *Musaraneus* Brisson, 1762; *Oxyrhin* Kaup, 1829; *Amphisorex* Duvernoy, 1835; *Corsira* Gray, 1838; *Otisorex* De Kay, 1842; *Hydrogale* Pomel, 1848; *Neosorex* Baird, 1858; *Atophyrax* C. H. Merriam, 1884; *Homalurus* Schulze, 1890; *Soricidus* Altobello, 1927). Late Pliocene-Recent; Europe, North America. Pleistocene-Recent; Asia

    Drepanosorex Kretzoi, 1941. Pleistocene; Europe

    Microsorex Baird, 1877. Pleistocene-Recent; North America

    Alluvisorex Hutchison, 1966. Late Miocene-early Pliocene; North America

    Blarinella Thomas, 1911. Middle Pliocene-Recent; Asia

    Petenyia Kormos, 1934. Pliocene-Pleistocene; Europe

    Zelceina Sulimski, 1962. Pliocene; Europe

Tribe Blarinini (Stirton, 1930) Repenning, 1966. Late Miocene-Recent; North America. Pliocene-Pleistocene; Europe. Pleistocene; Asia. Recent; South America

    Adeloblarina Repenning, 1967. Late Miocene; North America

    Cryptotis Pomel, 1848 (=*Brachysorex* Duvernoy, 1842; *Soriciscus* Coues, 1877). Middle Pliocene-Recent; North America. Recent; South America

    Paracryptotis Hibbard, 1950. Middle-late Pliocene; North America

    Shikamainosorex Hasegawa, 1957. Pleistocene; Japan

    "*Sorex*" *dehneli* Kowalski, 1956. Pleistocene; Europe

    Blarina Gray, 1838 (=*Talposorex* Pomel, 1848; *Anotus* Wagner, 1855; *Mamblarinaus* Herrera, 1899). Late Pliocene-Recent; North America

    Blarinoides Sulimski, 1959. Pliocene; Europe

    Peisorex Kowalski and Li, 1963. Pleistocene; Asia

Tribe Neomyini Repenning, 1966 (=or including Hydrosoridae [anonymous], 1838; Crossopinae A. Milne Edwards, 1872; Nectogalinae J. Anderson, 1879; Anourosoricinae J. Anderson, 1879; Soriculi Winge, 1917; Amblycoptinae Kormos, 1926). Early Pliocene-Recent; Europe. Middle Pliocene-Recent; Asia, North America

    Neomys Kaup, 1829 (=*Leucorrhynchus* Kaup, 1829; *Hydrogale* Kaup, 1829; *Crossopus*

Wagler, 1832; *Hydrosorex* Duvernoy, 1835; *Amphisorex* Duvernoy, 1835; *Pinalia* Gray, 1838; *Myosictis* Pomel, 1854). Pliocene-Recent; Europe. Recent; Asia

Petenyiella Kretzoi, 1956 (= or including *Allopachyura* Kormos, 1934). Pliocene-Pleistocene; Europe

Episoriculus Ellerman and Morrison-Scott, 1951 (including *Asoriculus* Kretzoi, 1959). Late Pliocene-Pleistocene; Europe. Recent; Asia

Chodsigoa Kashchenko (usually given in the German transliteration, Kastschenko), 1907. Pleistocene-Recent; Asia

Beremendia Kormos, 1934. Pliocene-Pleistocene; Europe. Pleistocene; Asia

Nesiotites Bate, 1945. Pleistocene; Mediterranean islands

Nectogale A. Milne-Edwards, 1870. Recent; Asia

Soriculus Blyth, 1854. Recent; Asia

Chimarrogale J. Anderson, 1877 (including *Crossogale* Thomas, 1921). Recent; Asia

Anourosorex A. Milne-Edwards, 1870 (= *Pygmura* J. Anderson, 1875; *Anurosorex* J. Anderson, 1875). Middle Pliocene-Recent; Asia

Amblycoptus Kormos, 1926. Early Pliocene; Europe

Hesperosorex Hibbard, 1957. Middle Pliocene; North America

Notiosorex Baird, 1877. Late Pliocene-Recent; North America

Deinsdorfia Heller, 1963. Late Pliocene-Pleistocene; Europe

Megasorex Hibbard, 1950. Recent; North America.

Tribe Allosoricini Fejfar, 1966. Middle Miocene-late Pliocene; Europe

"*Sorex*" *gracilidens* Viret and Zapfe, 1951. Middle Miocene; Europe

Allosorex Fejfar, 1966. Late Pliocene; Europe

(Subfamily uncertain)

(Isolated molar) Bohlin, 1942. Early Miocene; Asia

Podihik Deraniyagala, 1958. Recent; Ceylon

Cf. Insectivora, *incertae sedis*

Anomodon LeConte, 1848. Pleistocene; North America

Mysarachne Pomel, 1848. Late Oligocene; Europe

Centracodon Marsh, 1872. Middle Eocene; North America

Nyctilestes Marsh, 1872. Middle Eocene; North America

Camphotherium (or *Comphotherium*, or *Gomphotherium*) Filhol, 1884. Late Eocene; Europe

Telacodon[1] Marsh, 1872. Late Cretaceous; North America

Ceciliolemur Weigelt, 1933 (= *Microtarsioides* Weigelt, 1933). Middle Eocene; Europe

Order Deltatheridia Van Valen, 1965. Late Cretaceous-Recent; North America. Late Cretaceous or Paleocene-late Miocene; Asia. Middle Paleocene-early Pliocene; Europe. Early Oligocene-Recent; Africa

Suborder Hyaenodonta, new. Late Cretaceous-early Miocene; North America. Late Cretaceous or Paleocene-late Miocene; Asia. Middle Paleocene-early Pliocene; Europe. Late Eocene-Miocene; Africa

Superfamily Palaeoryctoidea (Winge, 1917) Van Valen, 1966 (including Deltatheridioidea, first used as superfamily by Simpson, 1931). Late Cretaceous-early Miocene; North America. Late Cretaceous or Paleocene-late Oligocene; Asia. Middle Paleocene-early Oligocene; Europe

Family Palaeoryctidae (Winge, 1917) McDowell, 1958. Late Cretaceous-early Miocene; North America. Late Cretaceous or Paleocene; Asia. Middle Paleocene-early Oligocene; Europe

Subfamily Didelphodontinae Matthew, 1918 (including Cimolestidae Marsh, 1889; Butselidae Quinet and Misonne, 1965). Late Cretaceous-middle Eocene; North America. Late Cretaceous or Paleocene; Asia. Middle Paleocene-early Oligocene; Europe

Cimolestes Marsh, 1889 (= or including *Nyssodon* Simpson, 1927; *Puercolestes* Reynolds, 1936). Late Cretaceous-early Paleocene; North America

(Genus B) Van Valen, 1966. Early Paleocene; North America

Paleotomus, new. Late Paleocene; North America

Deltatheroides Gregory and Simpson, 1926. Late Cretaceous or Paleocene; Asia

Acmeodon Matthew and Granger, 1921. Middle Paleocene; North America

Aboletylestes D. E. Russell, 1964. Middle-late Paleocene; Europe

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[1] The possibility should not be entirely ignored that *Telacodon*, a valid genus, is an ancestral apatemyoid. It may, however, be a senior synonym of *Gypsonictops*.

Butselia Quinet and Misonne, 1965. Early Oligocene; Europe

Gelastops Simpson, 1935 (= *Emperodon* Simpson, 1935). Middle-late Paleocene; North America

Avunculus Van Valen, 1966. Middle Paleocene; North America

Didelphodus Cope, 1882 (= or including *Didelphyodus* Winge, 1923; *Phenacops* Matthew, 1909). Early-middle Eocene; North America

Subfamily Deltatheridiinae Gregory and Simpson, 1926. Late Cretaceous or Paleocene; Asia. Late Cretaceous; North America

Deltatheridium Gregory and Simpson, 1926. Late Cretaceous or Paleocene; Asia

Hyotheridium Gregory and Simpson, 1926. Late Cretaceous or Paleocene; Asia

Batodon Marsh, 1892. Late Cretaceous; North America

Subfamily Palaeoryctinae Winge, 1917. Middle-late Paleocene; North America

Palaeoryctes Matthew, 1913. Middle-late Paleocene; North America

Pararyctes Van Valen, 1966. Late Paleocene; North America

Family Micropternodontidae Stirton and Rensberger, 1964. Early Eocene; Asia. Early Oligocene-early Miocene; North America

Sarcodon Matthew and Granger, 1925. Early Eocene; Asia

Micropternodus Matthew, 1903 (= *Kentrogomphios* T. E. White, 1954). Early Oligocene-early Miocene; North America

Family Didymoconidae Kretzoi, 1943 (including Tshelkariidae Gromova, 1960). Late Eocene-late Oligocene; Asia

Mongoloryctes Van Valen, 1966. Late Eocene; Asia

Ardynictis Matthew and Granger, 1925. Early Oligocene; Asia

Didymoconus Matthew and Granger, 1924. Late Oligocene; Asia

Tshelkaria Gromova, 1960. Late Oligocene; Asia

Superfamily Hyaenodontoidea Leidy, 1869. Early Eocene-middle Oligocene; North America. Early Eocene-early Pliocene; Europe. Late Eocene-Miocene; Africa. Late Eocene-late Miocene; Asia

Family Hyaenodontidae Leidy, 1869. Early Eocene-middle Oligocene; North America. Early Eocene-early Pliocene; Europe. Late Eocene-Miocene; Africa. Late Eocene-late Miocene; Asia

Subfamily Hyaenodontinae Leidy, 1869 (including Proviverridae Schlosser, 1886; Hyaenaelurinae Pilgrim, 1932; Hyainailourinae Simpson, 1945; Teratodontidae R. J. G. Savage, 1965). Early Eocene-middle Oligocene; North America. Early Eocene-early Pliocene; Europe. Late Eocene-Miocene; Africa. Late Eocene-late Miocene; Asia

Prototomus Cope, 1874 (including *Protoproviverra* [not *Protoviverra*] Lemoine, 1891). Early Eocene; North America. Early-middle Eocene; Europe

Proviverra Rütimeyer, 1862 (= *Prorhyzaena* [not *Prorhizaena*] Rütimeyer, 1891. Including *Sinopa* Leidy, 1871; *Stypolophus* Cope, 1872; *Leonhardtina* Matthes, 1952; *Geiselotherium* Matthes, 1952). Middle Eocene; North America. Middle-late Eocene; Europe

Arfia Van Valen, 1965. Early Eocene; North America

Tritemnodon Matthew, 1906. Early-middle Eocene; North America

Prodissopsalis Matthes, 1952 (= *Imperatoria* Matthes, 1952). ?Early Eocene, middle Eocene; Europe

Cynohyaenodon Filhol, 1873 (including *Pseudosinopa* Depéret, 1917). Middle-late Eocene, ?early Oligocene; Europe

Paracynohyaenodon Martin, 1906 (including *Anasinopa* R. J. G. Savage, 1965). Late Eocene; Europe. Miocene; Africa

Metasinopa Osborn, 1909. Late Eocene-early Oligocene; Africa.

Propterodon Martin, 1906. Late Eocene; Asia. ?Early Oligocene, ?North America

Dissopsalis Pilgrim, 1910. Miocene; Africa. Late Miocene; Asia

Pterodon Blainville, 1839 (including *Metapterodon* Stromer, 1926; *Megalopterodon* Dashzeveg, 1964). ?Middle Eocene, late Eocene-early Oligocene; Europe. Late Eocene; North America. Late Eocene-early Oligocene; Asia. Early Oligocene-Miocene; Africa

Hyainailouros Biedermann, 1863 (= or including *Harpalodon* Meyer, 1837, *nomen oblitum; Hyaenailurus* Rütimeyer, 1867; *Hyaenaelurus* Stehlin, 1907). Miocene; Africa. Early-middle Miocene; Asia. ?Early Miocene, middle Miocene-early Pliocene; Europe

Hemipsalodon Cope, 1885. Early Oligocene; North America

Ischnognathus Stovall, 1948. Early Oligocene; North America

Leakitherium R. J. G. Savage, 1965 (including *Isohyaenodon* R. J. G. Savage, 1965). Miocene; Africa

Hyaenodon Laizer and Parieu, 1838 (including *Pseudopterodon* Schlosser, 1887; *Taxotherium* Blainville, 1841; *Neohyaenodon* Thorpe, 1922; *Protohyaenodon* Stock, 1933). ?Middle Eocene, late Eocene-middle Oligocene; Europe. Late Eocene-middle Oligocene; Asia, North America. Early Oligocene, ?Miocene; Africa

Apterodon Fischer von Waldheim, 1881 (including *Dasyurodon* Andreae, 1887). Early-middle Oligocene; Europe. Early Oligocene; Africa

Quercitherium [not *Quercytherium*] Filhol, 1880. Late Eocene; Europe

Teratodon R. J. G. Savage, 1965. Miocene; Africa

Subfamily Limnocyoninae Wortman, 1902. Early-late Eocene; North America. ?Early Eocene, late Eocene; Europe

Tribe Limnocyonini Wortman, 1902. Early-late Eocene; North America. ?Early Eocene, late Eocene; Europe

Prolimnocyon Matthew, 1915. Early Eocene; North America, ?Europe

Thinocyon Marsh, 1872 (including *Entomodon* Marsh, 1872). Middle Eocene; North America

Limnocyon Marsh, 1872 (=*Telmatocyon* Marsh, 1899). Middle-late Eocene; North America

Oxyaenodon Wortman, 1899. Late Eocene; North America

Thereutherium Filhol, 1877. Late Eocene; Europe

Tribe Machaeroidini Matthew, 1909. Middle-late Eocene; North America

Machaeroides Matthew, 1909. Middle Eocene; North America

Apataelurus Scott, 1937. Late Eocene; North America

Superfamily Oxyaenoidea Cope, 1877. Late Paleocene-middle Eocene; North America. Early-late Eocene; Europe. Late Eocene; Asia

Family Oxyaenidae Cope, 1877. Late Paleocene-middle Eocene; North America. Early-late Eocene; Europe. Late Eocene; Asia

Subfamily Oxyaeninae Cope, 1877. Late Paleocene-middle Eocene; North America. Early Eocene; Europe. Late Eocene; Asia

Dipsalidictides Denison, 1938. Early Eocene; North America

Oxyaena Cope, 1874 (including *Dipsalidictis* Matthew, 1915; *Argillotherium* Davies, 1884). Late Paleocene-early Eocene; North America. Early Eocene; Europe.

Protopsalis Cope, 1880. Early Eocene; North America

Patriofelis Leidy, 1870 (=or including *Limnofelis* Marsh, 1872; *Oreocyon* Marsh, 1872; *Aelurotherium* Adams, 1896). Middle Eocene; North America

Sarkastodon Granger, 1938. Late Eocene; Asia

Subfamily Palaeonictinae Osborn, 1892 (including Ambloctonidae Cope, 1880). Late Paleocene-early Eocene; North America. Early-late Paleocene; Europe

Dipsalodon Jepsen, 1930. Late Paleocene; North America

Palaeonictis Blainville, 1842. Early Eocene; North America, Europe

Ambloctonus Cope, 1875 (=*Amblyctonus* Cope, 1880). Early Eocene; North America

Paroxyaena Martin, 1906. Late Eocene; Europe

Suborder Zalambdodonta Gill, 1884. Middle Eocene-Recent; North America. Miocene-Recent; Africa

Superfamily Tenrecoidea Gray, 1821. Middle Eocene-Recent; North America. Miocene-Recent; Africa

Family Tenrecidae Gray, 1821 (=Centetina Bonaparte, 1838). Middle Eocene-middle Oligocene; North America. Miocene-Recent; Africa

Subfamily Apternodontinae Matthew, 1910. Middle Eocene-middle Oligocene; North America

(Undescribed genus) McKenna, Robinson, and Taylor, 1962. Middle Eocene; North America

Oligoryctes Hough, 1956. ?Late Eocene, early Oligocene; North America

Apternodus Matthew, 1903. ?Late Eocene, early-middle Oligocene; North America

Subfamily Potamogalinae Allman, 1865 (=Mystomyidae Cope, 1883). Miocene-Recent; Africa. [See Guth, Heim de Balsac, and Lamotte, 1959–1960]

Protenrec Butler and Hopwood, 1957. Miocene; Africa

Erythrozootes Butler and Hopwood, 1957. Miocene; Africa

Potamogale Du Chaillu, 1860 (=*Mystomys* Gray, 1861; *Mythomys* Gray, 1861; *Bayonia* Bocage, 1865). Recent; Africa

Micropotamogale Heim de Balsac, 1954 (including *Mesopotamogale* Heim de Balsac, 1956= *Kivugale* Kretzoi, 1961). Recent; Africa

Subfamily Oryzorictinae Trouessart, 1879 (including Geogalinae Trouessart, 1879). Miocene-Recent; Africa

Geogale H. Milne-Edwards and A. Grandidier, 1872 (including *Cryptogale* G. Grandidier, 1928). ?Miocene; Africa. Recent; Madagascar

Oryzorictes A. Grandidier, 1870 (including *Nesoryctes* Thomas, 1918). Recent; Madagascar

Microgale Thomas, 1882 (including *Nesogale* Thomas, 1918; *Leptogale* Thomas, 1918; *Paramicrogale* G. Grandidier and Petit, 1931). Recent; Madagascar

Limnogale Forsyth Major, 1896. Recent; Madagascar

Subfamily Tenrecinae Gray, 1821 (= or including Centetina Bonaparte, 1838; Echinogalinae Murray, 1866). Recent; Madagascar

Tenrec Lacépède, 1799 (=*Setifer* Tiedemann, 1808; *Centetes* Illiger, 1811; *Tanrecus* Blainville, 1838). Recent; Madagascar

Setifer Froriep, 1806 (=*Ericulus* I. Geoffroy Saint Hilaire, 1837; *Tendrac* Blainville, 1838; *Hericulus* Gloger, 1841). Recent; Madagascar.

Hemicentetes Mivart, 1871 (=*Setiger* G. Cuvier, 1800; *Eteocles* Gray, 1821; *Ericius* Giebel, 1871; *Echinodes* Trouessart, 1879). Recent; Madagascar

Dasogale G. Grandidier, 1928. Recent; Madagascar

Echinops Martin, 1838 (=*Echinogale* Wagner, 1841). Recent; Madagascar

Family Solenodontidae Gill, 1872. Pleistocene-Recent; Greater Antilles. [See McDowell, 1958]

Solenodon Brandt, 1833 (including *Atopogale* Cabrera, 1926; *Antillogale* Patterson, 1962). Pleistocene-Recent; Greater Antilles

Superfamily Chrysochloroidea (Gray, 1825) Gill, 1872. Miocene-Recent; Africa

Family Chrysochloridae Gray, 1825 (including Eremitalpinae Simonetta, 1957; Amblysominae Simonetta, 1957). Miocene-Recent; Africa. [See Ellerman, Morrison-Scott, and Hayman, 1953; Simonetta, 1957]

Prochrysochloris Butler and Hopwood, 1957. Miocene; Africa

Proamblysomus Broom, 1941. Pleistocene; Africa

Amblysomus Pomel, 1848 (including *Calcochloris* Mivart, 1867; *Chrysotrica* Broom, 1907; *Neamblysomus* Roberts, 1924; *Chlorotalpa* Roberts, 1924; *Huetia* Forcart, 1942; *Carpitalpa* Lundholm, 1955). Pleistocene-Recent; Africa

Cryptochloris Shortridge and Carter, 1938. Recent; Africa

Chrysochloris Lacépède, 1799 (=or including *Chrysoris* Rafinesque, 1815; *Aspalax* Wagler, 1830; *Ducantalpa* Boitard, 1842; *Engyscopus* Gistel, 1848; *Kilimatalpa* Lundholm, 1955). Pleistocene-Recent; Africa

Chrysospalax Gill, 1883 (including *Bematiscus* Cope, 1892). Recent; Africa

Eremitalpa Roberts, 1924. Recent; Africa

COMMENTS ON TAXA

ORDER INSECTIVORA

Cuvier (1817) used the name and concept "Insectivora" before Bowdich, who, in an unoriginal manual (1821), was perhaps the first to use the Latinized form and is now usually credited with authorship. Cuvier (1817, p. 131) used "insectivores" as a "famille" of his "carnassiers," at the same rank as his "cheiroptères" and "carnivores." Authors writing in French frequently still use semi-vernacular forms for suprageneric taxa, including new proposals, and it would be both

ungenerous and historically inaccurate not to recognize these names when (as with Cuvier's) they are clearly meant to be names of taxa.

However, Illiger (1811, p. 123) had previously recognized exactly the group that Cuvier called "insectivores" as the "Familia Subterranea," placed under the "Ordo Faculata." This is the earliest classification known to me that groups together all insectivores then known (except the peripheral Dermoptera) and excludes all carnivores and others. I

do not propose a revival of the name "Sub-terranea." The first use that I have seen of "Insectivora" or the equivalent is that of Blainville (1816, p. 250), who presented a classification from which the following extract is taken:

MAMMIFÈRES

Sous-classe 1. *Monodelphes*

. . .

IIᵉ degré d'organisation, ou Ordre. *Les Carnassiers?*
Normaux
Plantigrades, Omnivores
Digitigrades, Carnivores
Insectivores

Blainville did not indicate the contents of his "Insectivores," but the Talpidae are excluded because they were placed elsewhere. I believe that the headings used by Blainville are to be regarded not as names of taxa in the modern sense, but rather as descriptive groupings. "Normaux" could scarcely have been meant other than as a descriptive subdivision of "Les Carnassiers?." This criticism does not apply to Cuvier's taxa.

The name "Insectivora" may therefore be dated from Cuvier (1817), whereas the concept is derived from Illiger (1811). I have elsewhere (Van Valen, 1966) given reasons why I believe that "Insectivora" is not a senior synonym of "Lipotyphla," which remains the name appropriate for a grouping of the Erinaceota and Zalambdodonta of the present classification, if such a grouping should prove desirable. The Insectivora consist of the stem placentals and those groups that have not diverged sufficiently from the stem placentals to be separated at the ordinal level.

The following definitely or possibly supra-familial names, and undoubtedly others, have been used for groupings not recognized in the present classification:

Lipotyphla Haeckel, 1866: Erinaceota and Zalambdodonta
Menotyphla Haeckel, 1866 (= Glisoricina Pomel, 1848; Macroscelidoidea Gill, 1872; Tupaioidea Gill, 1874): Tupaiidae and Macroscelididae
Mixodectomorpha Saban, 1954: Apatemyidae and Mixodectidae
Proglires Osborn, 1902: Mixodectidae and Microsyopidae
Soricomorpha Gregory, 1910: Soricidae and Talpidae
Soricomorpha Saban, 1954: Palaeoryctidae, Zalambdodonta, Nesophontidae, Soricidae, Talpidae, and some of the Adapisoricidae
Erinaceomorpha Gregory, 1910: Leptictidae, Erinaceidae, and Dimylidae
Erinaceomorpha Saban, 1954: Erinaceidae, Dimylidae, Apheliscinae, Plesiosoricidae, and most of the Tupaioidea and Adapisoricidae
Scandentia Wagner, 1855 (= Tupaioidea Straus, 1949; Tupaiiformes Schultz, 1953; Tupaii Broers, 1963): Tupaiidae
Echinoidea Pomel, 1848 (= Aculeata Wagner, 1855): Tenrecidae and Erinaceidae
Galerices Pomel, 1848 (= Galechinidae Murray, 1866): Tenrecidae, Erinaceidae, Tupaiidae, and Macroscelididae
Spalacogalae Pomel, 1848: Talpidae, Soricidae, Chrysochloridae, and Solenodontidae

SUPERFAMILY ENDOTHERIOIDEA

I place *Endotherium* in a distinct superfamily not because of peculiarities of its own structure, which is poorly known, but because its probably middle Cretaceous age suggests that it is related to *Pappotherium* and any other placentals from the Trinity (Patterson, 1956; Slaughter, 1965). The superfamily Endotherioidea is used here for an as yet largely hypothetical group, the basal placentals and those other placentals not sufficiently divergent from them (or not belonging to sufficiently divergent groups) to warrant distinction at the level of superfamily. It is probable but far from certain that *Endotherium* belongs to this group (cf. Chow, 1953). If it does not, a new name will, of course, be necessary. Families here referred to the Tupaioidea may have originated from the Endotherioidea at different times; when and if such origin is demonstrated, a reclassification will be necessary.

GYPSONICTOPINAE, NEW SUBFAMILY

This subfamily is established for the named and unnamed late Cretaceous species now grouped as *Gypsonictops* (for which, see Simpson, 1951). *Euangelistes* is a synonym of *Gypsonictops*, as shown by recent collections (cf. faunal list in Sloan and Van Valen, 1965). Other genera, such as *Ankylodon*, may also prove to belong to the Gypsonictopinae. It is even conceivable, although I think it unlikely, that *Xenacodon* and its possible de-

scendant *Creotarsus* were derived from *Gypsonictops* (cf. Van Valen, 1966), in which case Hay's name Creotarsidae would have priority. The Gypsonictopinae are characterized by a P₄ with a much reduced paraconid, a metaconid comparable to the protoconid, and a large talonid; high molar trigonids and a large and central hypoconulid; and somewhat connate paracone and metacone of the upper molars.

ADAPISORICULINAE, NEW SUBFAMILY

As shown elsewhere (Van Valen, 1965c), *Adapisoriculus* is probably a tupaiid. It combines primitive characters of both recent subfamilies, and I therefore propose for it a new subfamily. The diagnosis of this subfamily consists of the differences of *Adapisoriculus* from recent tupaiids given by Van Valen (1965c). The genus *Nycticonodon* Quinet (1964), from the late Paleocene or early Eocene of Dormaal, Belgium, is at present a *nomen nudum*.

UNUCHINIINAE VAN VALEN AND McKENNA, NEW SUBFAMILY

Unuchinia was tentatively placed in the Apatemyidae by McKenna (1963b). Whether or not such allocation is correct (and I suspect that it is), *Unuchinia* is evidently distinct at the subfamily level from any other named suprageneric taxon, so it belongs in a subfamily of its own. The molars are very primitive for an apatemyid, but the P₄ is relatively advanced. The P₄ is tall, simple, and single-rooted. The lower molars are relatively long anteroposteriorly, with the trigonid tall, the paraconid bladelike, and the paralophid nearly straight in occlusal view, and the talonid cusps are well differentiated from the talonid rim. The mental foramen is just anterior to P₄.

SUBORDERS MACROSCELIDEA AND DERMOPTERA

Butler (1956a) placed the Macroscelididae in an order of their own, by analogy with the Dermoptera. I follow his arrangement but reduce both these orders to suborders because they seem insufficiently distinct adaptively from the Proteutheria to warrant ordinal separation (cf. Van Valen, 1963, 1966). The Dermoptera as here constituted

form one of the more tenuous taxa of the present classification. Although this segment of the classification more or less follows custom (if not a previously formalized custom), I suspect that the Plagiomenidae are unrelated to the Galeopithecidae and that the latter originated from the Adapisoriculinae.

Patterson (1965) has recently added several genera to the Macroscelidea and given a review and reclassification which I follow except for the reduction of the Rhynchocyoninae to a tribe. The hypsodont macroscelidid *Mylomygale* was mentioned by Broom (1946), who thought it represented a new but unnamed family of menotyphlans. His 1948 paper validated the genus but did not name a family. Camp, Welles, and Green (1953) first used the name "Mylomygalidae," crediting Broom (1946), but they placed it in the Soricoidea. The only possible reason for this allocation would seem to be the similarity of the name to *Mygale*, a synonym of *Desmana*, at a time when the moles were usually or always classified as soricoids.

If diversity is to be used as a criterion for ranking the Macroscelidea as a separate order, and this is Patterson's major criterion in his favorable discussion of Butler's order, then this diversity should certainly be expressed (or classified) at the family or superfamily level. However, Patterson included all the Macroscelidea in one family, and in this action I follow him. One may almost as well make separate orders for moles, shrews, or tupaiids (and this has actually been done for tupaiids) as for macroscelidids.

THYLACAELURINAE, NEW SUBFAMILY

This subfamily is established for *Thylacaelurus montanus*, described by Loris Shane Russell (1954) from about the latest Eocene of British Columbia. As noted by McKenna (*in* Van Valen, 1965a), *Thylacaelurus* is not a marsupial. Although it may belong to the Plagiomenidae, its structure and affinities are obscure, and it is badly in need of restudy. It nevertheless appears to represent a new subfamily. From the published figures it differs from the Plagiomeninae in that P⁴ is enlarged, with a very transverse protocone lobe; the upper molars have an enlarged protofossa that extends between the paracone and the metacone; and M² is smaller than M¹.

FAMILY GALEOPITHECIDAE

I am returning to this unambiguous name despite the well-known ruling of the International Commission on Zoological Nomenclature in 1925 (Opinion 90) that caused the name *Cynocephalus*, the name of a genus of baboons for more than a century, to be transferred to *Galeopithecus*. Forty-one years after that decision, one still cannot use the name *Cynocephalus* without a strong risk that the subject will be misunderstood as a baboon. A proposal for reversal of their ruling has been submitted to the Commission, so the present course is legal until and unless the reversal is denied. For persons who prefer to use the name *Cynocephalus*, the correct family name is Galeopteridae, if two genera are admitted. As noted in the discussion of the Echinosoricini, the difference between *Galeopithecus* and *Galeopterus* is greater than that between some previously unquestioned insectivore genera.

ERINACEOTA, NEW SUBORDER

The taxon Erinaceota is equivalent to the Lipotyphla without the zalambdodonts (cf. Butler, 1956a; and McDowell, 1958), although *Solenodon* may belong to the Erinaceota. The exclusion of most or all zalambdodonts is only speculative, but if they are excluded a new name seems desirable. The Erinaceomorpha of Saban (1954) were contrasted with the Soricomorpha, and only two of the six families in his Erinaceomorpha are among the seven in the Erinaceota. The name Erinaceomorpha of Gregory (1910) and Osborn (1910; probably Gregory's contribution) was proposed for the Erinaceidae, Leptictidae, and Dimylidae and was also contrasted with the Soricomorpha. Other authors have used similar classifications. To my knowledge no other subordinal name is available and even remotely suitable. The suborder Zalambdodonta should perhaps not be renamed in the very possible event that *Solenodon* is removed to the Erinaceota. *Solenodon* would not represent the only acquisition of zalambdodonty independent of the Zalambdodonta: this is present also in *Notoryctes*, some of the advanced Hyaenodontinae (in a different way), and the upper dentitions now known of dryolestoids, and is

incipient in *Geolabis* (although the latter may be related to *Solenodon*).

FAMILY ADAPISORICIDAE

The genera included in this basal family of the Erinaceota are sufficiently different from the Erinaceidae that familial distinction seems useful. It is very possible that some of the groups here placed in the Adapisoricidae were derived independently from the Leptictidae. If such a possibility is shown to be correct, one or more groups should probably be removed to the Tupaioidea. The subfamilies here recognized are not sharply distinct from one another. Probably not all are valid, but it is now unclear which ones should be combined. The similarity of *Adapisorex* to *Aphronorus* suggests the possibility of a close relationship between these genera. The pertinence of *Adapisorex* to the Erinaceoidea, and therefore the family name Adapisoricidae, are thus to some degree questionable. However, a more likely alternative would be the inclusion of the Pentacodontidae in the Adapisoricidae, although similarity with some members of the Hyopsodontidae complicates the picture further. The family Adapisoricidae is the insectivore family for which the greatest amount of supraspecific revision seems necessary.

SUBFAMILY CREOTARSINAE

This subfamily lacks the unity of the Amphilemuridae as recognized by McKenna (1960a), but it is not now evident how it should be subdivided. When the ancestry and relationships of the erinaceid subfamilies are established, probably some genera now in the Creotarsinae must be removed to the Erinaceidae.

TRIBE ECHINOSORICINI

Neotetracus is very similar to *Hylomys*, and I regard them as only subgenerically distinct. The only differences I have noted are the following: the tail is substantially longer in *Neotetracus*; the canines are usually more reduced in *Neotetracus*, but the first incisors are usually larger; the angle of the mandible is lower in *Neotetracus*; and *Neotetracus* has usually lost one of the reduced promolars usually present in *Hylomys*. On the last point, of 22 specimens of *Neotetracus sinensis* from

Yunnan in the American Museum, 20 are symmetrical with three upper premolars, one has four on the right and three on the left, and one has three on the right and two on the left. All 22 specimens of this species from north Burma have three upper premolars. Of three specimens of *Hylomys s. suillus* from Java in the Archbold Collections, one has four upper premolars on the right and three on the left, one has three on each side, and one has four on each side. All four specimens from Sumatra (representing a different subspecies) are symmetrical with four upper premolars. The more southeastern subspecies of *H. suillus*, as represented by A.M.N.H.(M.) No. 87313 and specimens in the Archbold Collections, have a moderately large I_1 and I^1, although I_1 is still smaller than that of *Neotetracus*. *Neotetracus* and *Hylomys* are substantially less distinct from each other than are *Galeopterus* and *Galeopithecus*, which are here regarded as generically distinct. *Neohylomys* Shaw and Wong, 1959, is intermediate between *Hylomys* and *Neotetracus* and is therefore of necessity included in *Hylomys* in the present sense.

TRIBE PROTERICINI

The North American genera *Brachyerix*, *Metechinus*, and *Parvericius* were placed by Butler (1948) in a tribe Brachyericini, and provisionally related to *Neurogymnurus*. At the suggestion of M. C. McKenna, I have re-examined this question and find little evidence for relationship to *Neurogymnurus*. The Barstovian species *Brachyerix montanus* Matthew (*in* Matthew and Mook, 1933) appears to have been derived from *Proterix* and is rather similar to that genus, as noted by Meade (1941). The Clarendonian *Metechinus nevadensis* Matthew, 1929, and its Barstovian relative *M. fergusoni* Henshaw, 1942, are at least morphologically derivable from the vicinity of the Barstovian species *Parvericius montanus* Koerner, 1940. A mandible from the Hemingfordian Marsland or Runningwater Formation (on which see McKenna, 1965b) was described by Meade (1941) as *Metechinus marslandensis*. It is more primitive than the later species of *Metechinus* and for this reason may be provisionally transferred to *Parvericius*, of which the lower dentition is otherwise unknown. *Parvericius* is also

similar to *Proterix* and was probably derived from that genus, although separately from *Brachyerix*. Both *Metechinus* and *Brachyerix* are short-skulled, but the hypocone is reduced in *Brachyerix* from its condition in *Proterix* and expanded in *Parvericius* and *Metechinus*. *Metechinus* may deserve distinction at the tribal level from *Proterix*, but I do not take this step pending better knowledge of American erinaceids. The Arikareean mandible described as *Ocajila makpiyahe* by Macdonald (1963) is rather similar to that of *Proterix* (judged by the figures in both cases) if Macdonald (1961) correctly identified the lower dentition of the latter genus. *Ocajila* may represent the otherwise unknown lower dentition of *Brachyerix* but is more probably a synonym of the echinosoricine *Lanthanotherium*.

Parvericius is very similar to the Old World genus *Amphechinus* and seems to be an immigration of *Amphechinus*. The incisors are unknown in *Parvericius*, but a lower incisor is enlarged in at least *Metechinus fergusoni* as it is in *Amphechinus*. The skull is relatively short in *Amphechinus* as in at least *Metechinus*, and the teeth of *Parvericius* and *Amphechinus* are quite similar. I therefore synonymize *Parvericius* with *Amphechinus*. *Dimylechinus* is a European derivative of this stock in the Aquitanian and is rather similar to the later North American genus *Metechinus*, which had a similar origin. P^4 is specialized in different directions in *Dimylechinus* and *Metechinus* from the *Amphechinus* condition, however, and there are other differences. The placement of *Dimylechinus* with *Amphechinus*, and the exclusion of other Old World genera, are done on the authority of Butler (1956b). Further tribal subdivision, and revision of the early species of *Amphechinus*, are left for future workers.

SUBFAMILY PROSCALOPINAE

It is now reasonably well established (Charles A. Reed and Turnbull, 1965) that the humerus known as *Arctoryctes* belongs with the skull known as *Proscalops* (and with related genera). However, Reed and Turnbull also agreed with the suggestion of Dale A. Russell (1960) that the *Cryptoryctes* type of humerus belongs with the skull of *Micropternodus*. If *Cryptoryctes* is directly or approxi-

mately ancestral to *Arctoryctes*, as Reed and Turnbull believed, a serious problem arises. It would be very difficult to derive the upper molars of *Proscalops* from those of *Micropternodus*. In *Micropternodus* there is a very large postcingulum with a sizable hypocone rather far from the trigon; the paracone and metacone are more or less connate (especially on M^1); and the paracone is larger than the metacone. In the Proscalopinae, when a hypocone is developed it appears to be an expansion of the metaconule; there is no hypocone in the Oligocene genera. The metacone is larger than the paracone on M^1 and is widely separated from it. If *Cryptoryctes* is a synonym of *Micropternodus*, then *Cryptoryctes* has nothing to do phyletically with *Arctoryctes*, an improbable situation. I have elsewhere (Van Valen, 1966) suggested that *Micropternodus* may have been derived from the Palaeoryctidae, and the humerus of *Palaeoryctes* also suggests some fossorial adaptation. Whether or not this origin is correct, however, I believe that *Micropternodus* is unrelated to *Proscalops*.

SCAPTONYCHINI, NEW TRIBE

I erect this tribe to have a place for those primitive genera that do not have the specializations characteristic of the other tribes of the Talpinae. They are the ancestral burrowing moles and their relatively unmodified descendants. *Scaptonyx* itself is probably related to the Urotrichini, and I originally placed it there, but it is sufficiently unspecialized in its anterior dentition that it can be made the type of the basal tribe. The Scaptonychini differ from the Talpini especially in having a less-specialized humerus and an unexpanded tympanic, from the Urotrichini especially in having I^1 not or only incipiently enlarged and the upper canine little reduced,[1] from the Scalopini in all the ways that the Urotrichini do, and from the Condylurini especially in having the upper canine enlarged instead of I^1 and especially I^3, and in lacking

[1] The Scaptonychini differ also from all known Urotrichini in that four upper and lower premolars and the upper canine are all present and two-rooted. However, because all premolars are present in *Parascalops* as well as in *Scapanus*, and three double-rooted premolariform teeth are present in each jaw in *Neurotrichus* and *Urotrichus*, the ancestral urotrichine was probably similar to *Scaptonyx* in this character.

the elongated snout and nasal fringes. The Scaptonychini differ from the Uropsilinae especially in being more specialized in the forelimbs for digging. The zygomatic arch is weaker in the Scaptonychini; the infraorbital foramen is above M^3 or the M^{2-3} border rather than above M^1; the infraorbital canal is very short and really a foramen; the premolars are relatively thin, not bulbous; the upper canine is little reduced, and the upper molars lack the relatively expanded hypocone (morphologically the metaconule and metacingulum). The last two features, at least, are surely specialized in *Uropsilus* and are not to be taken as characteristic of its subfamily. The Uropsilinae and Proscalopinae probably diverged in the Eocene. The Uropsilinae soon gave rise to the Desmaninae and the Scaptonychini. From the latter originated, independently, the Talpini and the Urotrichini; the Scalopini are surely derivatives of the Urotrichini. The Condylurini probably originated from a primitive member of the Urotrichini but could have come from the Scaptonychini directly.

Ellerman and Morrison-Scott (1951), following Schwarz (1948), included *Scaptochirus* as a subspecies of one of the species of *Talpa* entirely on the basis of geographic distribution. Such a conclusion, as well as the procedure, is startling if one looks at the skulls of these forms. No intermediate populations have been reported. *Scaptochirus* differs from *Talpa* (including *Mogera* and *Parascaptor*) as follows: it is more hypsodont, the paralophid of M_1 is directed less strongly anteriorly; there is a larger parastyle on M^1; the upper molars are less transverse; the rostrum is less elongate; the protocone lobe of P^4 is larger; the metaconule region of the upper molars is more expanded; and (*fide* Campbell, 1939) the humerus is somewhat less specialized. I therefore regard *Scaptochirus* as a valid genus.

The desman *Gaillardia* is a presumptive senior synonym of *Hydroscapheus*, which is the only other known American desman and is of comparable age and size. *Gaillardia* is known from a mandible and *Hydroscapheus* from humeri.

TRIBE UROTRICHINI

The recent genera put into the Scalopinae

in the received classification, except for *Scaptonyx*, *Scalopus*, and *Scapanus*, differ from the last two genera about as much as they do from the other three tribes of the Talpinae as here recognized. In most or all respects the Urotrichini are more primitive than the Scalopini, but one difference (the enlargement of the metaconule region) may be a divergent specialization. The Urotrichini are Talpinae (burrowing moles) with the following characters: tympanic bone ring-shaped, not expanded into a bulla as it is in the Talpini and Scalopini; protocone lobe of P⁴ present and of moderate size, as in the Talpini, Scaptonychini, and Condylurini; metaconule region of the upper molars more or less expanded posterolingually, as in the Condylurini and to some degree the Scaptonychini; upper canine reduced, as in the Scalopini and Condylurini; I¹ distinctly enlarged, as in the Scalopini and to some degree the Condylurini. Most of the extinct genera put into the Urotrichini are so placed because of their relatively brachyodont teeth, a condition not found in recent Scalopini but also not true of some recent Urotrichini. The presently more consistent differences between these tribes are usually unknown in the extinct genera. The recent Scalopini are perhaps unique among mammals in that the metacone is expanded posterolingually, especially on M¹, and often approaches the position and function of a hypocone. The humerus of the Urotrichini is fossorially specialized, but is not so advanced as that of the Scalopini, even though the humerus of the parallel (and probably also related) genus *Parascalops* makes a rather close approach. The Scalopini are a grade but probably a monophyletic one, and tribal distinction from the Urotrichini seems useful to express this relatively large average difference.

FAMILY PLESIOSORICIDAE

Plesiosorex is a troublesome genus. It combines characters suggestive of the Erinaceidae (McKenna, 1960b; Viret, 1940), adapisoricids (Butler, 1948, and personal observations), and soricids (Wilson, 1960) with other features of its own. I agree with Wilson (1960) that its ancestry may be found in the vicinity of *Saturninia*. The latter genus is generally regarded as soricoid, and the skull of *Plesioso-*

rex described by Wilson is also compatible with this placement. It is out of the question, however, to place *Plesiosorex* and *Meterix* in the Soricidae; fortunately Winge's name is available for this group. *Entomacodon* is poorly known and is placed here from hope rather than conviction. *Ankylodon* is provisionally placed here at the suggestion of J. H. Hutchison, but it may be an adapisoricid.

The Talpidae may have arisen from a stock that would be included in the Plesiosoricidae, as the Soricidae seem to have done. Such a possibility is not supported by evidence from the poorly known Plesiosoricidae themselves, but rather from resemblances between the Soricidae and Talpidae. McDowell (1958) has shown that the Talpidae could not easily have originated from the Soricidae as the latter family is now understood, but this finding does not entail the impossibility of an earlier common ancestry after the Adapisoricidae.

HYAENODONTA, NEW SUBORDER

The zalambdodonts must go somewhere. I have elsewhere (Van Valen, 1966) discussed the problems of their possible affinities with the Erinaceota and with *Palaeoryctes*. If the zalambdodonts belong in the Deltatheridia, as seems somewhat more plausible than not, then a new suborder must be erected for the other deltatheridians. The Hyaenodonta are the deltatheridians with a metacone (except a few advanced Hyaenodontinae and Oxyaeninae, on the one hand, and the Potamogalinae, on the other).

SUBFAMILY HYAENODONTINAE

Szalay (1967), in part on the basis of material from Mongolia that he has recently described, disputes my argument (Van Valen, 1966) that *Apterodon* is probably a mesonychid. I believe his conclusion is correct and therefore return *Apterodon* to the Hyaenodontidae. *Apterodon* has become quite differently specialized, however, from all other hyaenodontids except perhaps the morphologically very different teratodontines, having abandoned the otherwise ubiquitous trend of increasing carnassiality. With its crushing, rather mesonychid-like molars, *Apterodon* could not, despite frequent claims

to the contrary, have readily been the precursor of any genus of the Hyaenodontini. It has lost the metaconid on its lower molars and is in this respect, as well as in its divergent adaptation, as advanced as the probably polyphyletic tribe Hyaenodontini. I would therefore, as does Szalay (1967), place *Apterodon* in a tribe of its own, briefly definable as narrow-skulled Hyaenodontinae that lack a metaconid on the lower molars and have a reduced molar paraconid, a reduced metacrista, and relatively bulbous molar cusps, except that subdivision of the Hyaenodontinae does not seem desirable pending resolution of the phylogeny of the advanced carnassial genera. Despite the diversity of the subfamily, I therefore prefer to abandon the use of formal tribes in the Hyaenodontinae until the subfamily is better known. The named groupings are grades and can be discussed informally by such means as "primitive Hyaenodontinae," "*Pterodon-Hyaenodon* grade," or "crushing hyaenodonts." A more satisfactory tribal grouping may prove to be that of *Prodissopsalis* and its descendants, on the one hand, and the remaining Hyaenodontinae, on the other. *Prodissopsalis* may well have given rise to *Dissopsalis*, *Apterodon*, and the *Pterodon-Hyaenodon* grade. Unfortunately it is not yet established that *Prodissopsalis* was ancestral to any later genus, let alone to all the advanced genera. Because of the removal of the Hyaenodontidae from the Oxyaenoidea, if this removal is sustained, consideration should be given to Gazin's ranking of the Limnocyoninae as a family.

FAMILY SOLENODONTIDAE

If one still wishes to maintain a special relationship between *Solenodon* and *Nesophontes* (and in my opinion this view is about as defensible as its contradiction), as well as between *Nesophontes* and the Soricoidea, then a reinterpretation of the homologies of the cusps of the cheek teeth of *Solenodon* seems necessary (cf. also Van Valen, 1966). With these relationships true, the zalambdocone of *Solenodon* would probably be homologous to the metacone of *Nesophontes*, not to the protocone, as maintained by McDowell (1958), or to the paracone, as usually believed. The occlusal relationships are then normal, the homology of the paracone is that of McDowell, and the enlarged metacone of *Nesophontes* would simply be further enlarged in *Solenodon*. Evolution in the reverse direction is also possible if *Solenodon* is related to apternodonts or geolabidines and *Nesophontes* is only convergent toward shrews.

TAXA EXCLUDED FROM THE INSECTIVORA

The Picrodontidae (for which, see McGrew and Patterson, 1962), are here regarded as primates (cf. Van Valen, 1965d; McGrew and Patterson had suggested such a possibility). This course will be justified elsewhere, but the evidence is not conclusive. If insectivores, they would perhaps best be considered members of the Tupaioidea of the present classification. The Microsyopidae were included in the Primates by McKenna (1960a) and were returned to the Insectivora by him in 1965 (1965a). Frederick S. Szalay (personal communication) has new evidence that they are primates, and, on the basis of this evidence, I return the Microsyopidae to the Primates. The Apheliscidae are placed in the condylarth family Hyopsodontidae above in the present paper, in agreement with McKenna (1960a). Patterson (1958) has shown conclusively that the Necrolestidae are marsupials, as Leche (1907) and especially Winge (1923) had previously believed on more or less adequate evidence. *Herpetotherium* is unquestionably a didelphid, on the basis of the type specimen. I do not know the affinities of *Pseudorhynchocyon* Filhol, 1892, which was based on a peculiar, edentulous fragment of mandible from the French Phosphorites. Patterson (1965) also commented on this genus and also reached no positive conclusion. The possibility should be considered that *Pseudorhynchocyon* was based on an individual of some better-known species in which most of the temporalis musculature on the left side had become functionless some time before its death, thus permitting atrophy of part of the ascending ramus.

The following classification of the Microsyopidae (family established by Osborn, 1892) is given, because this family is being omitted from a complementary classification of the Prosimii being prepared by McKenna.

Alsaticopithecus Hürzeler, 1948. Middle Eocene; Europe

Cynodontomys Cope, 1882. Early Eocene; North America

Microsyops Leidy, 1872 (= or including *Palaeaco-* *don* Leidy, 1872; *Bathrodon* Marsh, 1872; *Mesacodon* Marsh, 1872). Middle-late Eocene; North America

Craseops Stock, 1934. Late Eocene; North America

SYNOPTIC CLASSIFICATION

Order Insectivora
  Suborder Proteutheria
    Superfamily Endotherioidea
      Family Endotheriidae
      Family Pappotheriidae
    Superfamily Tupaioidea
      Family Leptictidae
        Subfamily Procerberinae
        Subfamily Leptictinae
        Subfamily Gypsonictopinae
      Family Zalambdalestidae
      Family Anagalidae
      Family Paroxyclaenidae
      Family Tupaiidae
        Subfamily Adapisoriculinae
        Subfamily Ptilocercinae
        Subfamily Tupaiinae
      Family Pantolestidae
      Family Ptolemaiidae
      Family Pentacodontidae
    Superfamily Apatemyoidea
      Family Apatemyidae
        Subfamily Apatemyinae
        Subfamily Unuchiniinae
  Suborder Macroscelidea
    Family Macroscelididae
      Subfamily Macroscelidinae
      Subfamily Mylomygalinae
      Subfamily Myohyracinae
  Suborder Dermoptera
    Superfamily Mixodectoidea
      Family Mixodectidae
    Superfamily Galeopithecoidea
      Family Plagiomenidae
        Subfamily Plagiomeninae
        Subfamily Thylacaelurinae
      Family Galeopithecidae
  Suborder Erinaceota
    Superfamily Erinaceoidea
      Family Adapisoricidae
        Subfamily Geolabidinae
        Subfamily Adapisoricinae
        Subfamily Creotarsinae
        Subfamily Nyctitheriinae
      Family Erinaceidae

        Subfamily Galericinae
        Subfamily Erinaceinae
      Family Dimylidae
        Subfamily Dimylinae
        Subfamily Plesiodimylinae
      Family Talpidae
        Subfamily Proscalopinae
        Subfamily Uropsilinae
        Subfamily Desmaninae
        Subfamily Talpinae
    Superfamily Soricoidea
      Family Plesiosoricidae
      Family Nesophontidae
      Family Soricidae
        Subfamily Heterosoricinae
        Subfamily Crocidurinae
        Subfamily Limnoecinae
        Subfamily Soricinae
Order Deltatheridia
  Suborder Hyaenodonta
    Superfamily Palaeoryctoidea
      Family Palaeoryctidae
        Subfamily Didelphodontinae
        Subfamily Deltatheridiinae
        Subfamily Palaeoryctinae
      Family Micropternodontidae
      Family Didymoconidae
    Superfamily Hyaenodontoidea
      Family Hyaenodontidae
        Subfamily Hyaenodontinae
        Subfamily Limnocyoninae
    Superfamily Oxyaenoidea
      Family Oxyaenidae
        Subfamily Oxyaeninae
        Subfamily Palaeonictinae
  Suborder Zalambdodonta
    Superfamily Tenrecoidea
      Family Tenrecidae
        Subfamily Apternodontinae
        Subfamily Potamogalinae
        Subfamily Oryzorictinae
        Subfamily Tenrecinae
      Family Solenodontidae
    Superfamily Chrysochloroidea
      Family Chrysochloridae

SUMMARY

New genera and species are *Pantinomia ambigua* and *Pantomimus leari*, both possible pantolestids from the middle Paleocene; *Leptonysson basiliscus*, a middle Paleocene leptictid; and the apheliscines *Parapheliscus bjorni* and *P. wapitiensis*, the former from the late Paleocene and the latter from the early Eocene. *Palaeosinopa senior* is made the type of a new genus, *Paleotomus*, of the Palaeoryctidae, and the formerly referred specimens of this species are made a new species, *Palaeosinopa simpsoni*, of the Pantolestidae.

These new taxa and other evidence indicate that the interrelationships of early Cenozoic insectivores are even more poorly understood than is commonly believed. The Pentacodontinae are removed from the Pantolestidae, provisionally as a separate family, and a number of generic synonymies and transfers of genera are made. These changes, together with a generic revision of the Leptictidae and other suggestions, do not greatly clarify which similarities among the families are convergent and which are indicative of relationship.

A classification of the insectivores and deltatheridians is given that differs in a number of respects from the others available. New suprageneric taxa are the following: Erinaceota and Hyaenodonta, new suborders; Adapisoriculinae, Unuchiniinae Van Valen and McKenna, Thylacaelurinae, and Gypsonictopinae, new subfamilies; and Scaptonychini, new tribe. Primitive erinaceoids are more or less arbitrarily grouped into four subfamilies of the Adapisoricidae. The interrelations of moles are discussed. A family Plesiosoricidae is included in the Soricoidea. All zalambdodonts are tentatively removed from the Insectivora to the Deltatheridia, and recent work on the Hyaenodonta is critically reviewed. The Dermoptera and Macroscelidea are treated as suborders of the Insectivora.

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