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Origins of the Apatemyidae (Mammalia, Insectivora)

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INTRODUCTION

Since the publication of McKenna's (1963) detailed study of Paleocene apatemyids, several unique upper molars of *Jepsenella praepropera* have been recovered from the Swain Quarry of Torrejonian age in south-central Wyoming. These previously unknown upper molars of *Jepsenella* allowed speculations concerning the origin of the Apatemyoidea.

A comparison of the new specimens with recently published Mammalia of the Paleocene of France strongly suggests that apatemyids were present in Europe during the Cernaysian.

All presently available evidence also suggests that, in respect to their specialized construction of the incisors and their less peculiar, but distinctive, molar morphology the apatemyids evolved from palaeoryctids during the late Cretaceous. Leptictid origins for either the Apatemyoidea or Erinaceoidea appear unlikely.

Throughout this paper I use the term "erinaceoid" in the sense of Van Valen (1967). Although the taxonomic status of the groups classified as the Erinaceoidea will surely be modified in the future, the stem erinaceoids (i.e., the bulk of the genera referred to the Adapisoricidae by Van Valen, 1967) appear to be a natural group. They probably share a common descent from an unknown stock of palaeoryctids.

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I prefer to classify the Palaeoryctidae in the Insectivora, rather than in the Deltatheridia as did Van Valen (1966, 1967), in consideration of the usefulness and total balance of classification of primitive placental mammals. Because palaeoryctids gave rise, probably at different times, at least to the miacid carnivorans, the two families of carnivorous deltatheridians, zalambdalestids, didymoconids, the zalambdodonts, erinaceoids, apatemyoids, leptictids, and probably mixodectids, the retention of palaeoryctids in the Insectivora is necessary. To remove the Palaeoryctidae from the Insectivora renders that order polyphyletic on the level of several of its early Tertiary families, merely causes confusion as to what an insectivoran is, and does not result in a clearer, more useful classification. To place the palaeoryctids in the Deltatheridia does not clarify, but confuses, phyletic relationships of several groups of placentals on the ordinal level. Because the term "creodont," or the formal category Creodonta, is confusing, as discussed by Van Valen (1966, pp. 94-97), the Deltatheridia, including the hyaenodontids and oxyaenids only, will remain a highly useful category at the subordinal or ordinal level.

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Figure 4 was prepared by Miss Biruta Akerbergs.

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The abbreviations used are:

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

AW, anterior width

L, length

PW, posterior width

W, width

UPPER MOLARS OF *JEPSENELLA*

Three unique specimens from the Torrejonian Swain Quarry probably represent upper molars of the apatemyid *Jepsenella praepropera*. This species was previously known only from the type mandible, with three molars, from Gidley Quarry, upper Lebo Formation, Montana (see Simpson, 1940, McKenna, 1963, and references in the latter). A brief description of the three upper molars, supplemented by stereophotographs

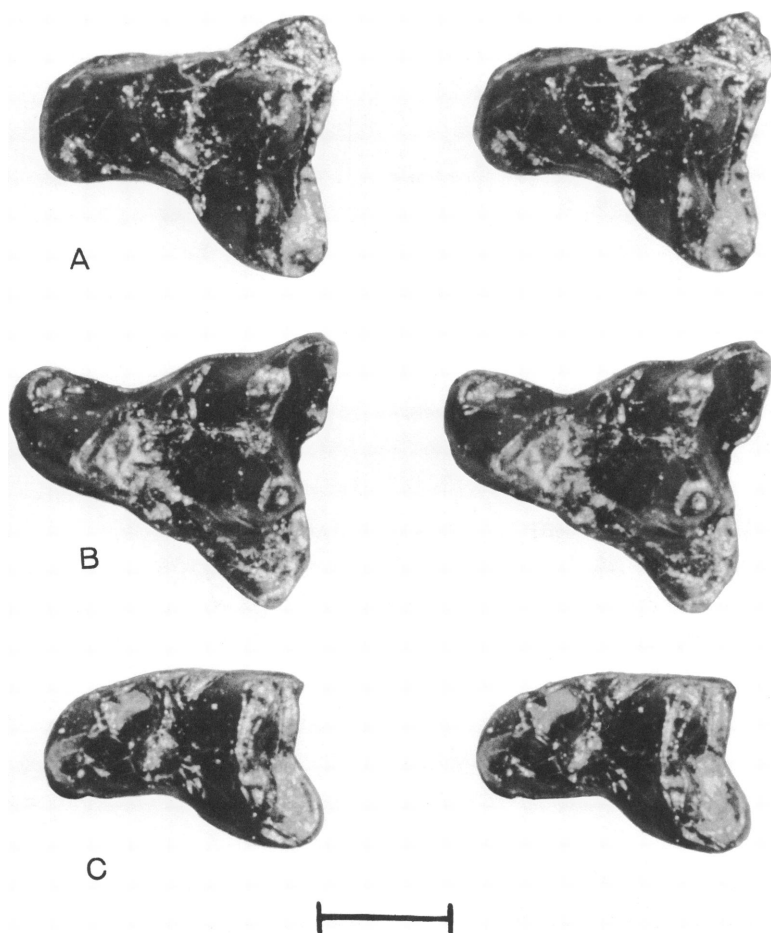


FIG. 1. *Jepsenella praepropera*, Swain Quarry, Torrejonian. A. A.M.N.H. No. 89513, left M^1 . B. A.M.N.H. No. 89512, right M^2 . C. A.M.N.H. No. 89514, left M^3 . The bar represents 1 mm.

and a reconstruction of the molar dentition, follows. A single lower molar from Swain Quarry, probably M_1 , is also illustrated, but not described. The lower dentition was thoroughly described by McKenna (1963, pp. 14–18), and the lower molar from Swain Quarry adds nothing significant to the morphology of the species. Although the upper molars are somewhat worn, etched, and slightly chipped, their morphology can be seen on the stereophotographs.

A.M.N.H. No. 89513 (figs. 1, 4) is probably a left M^1 , A.M.N.H.

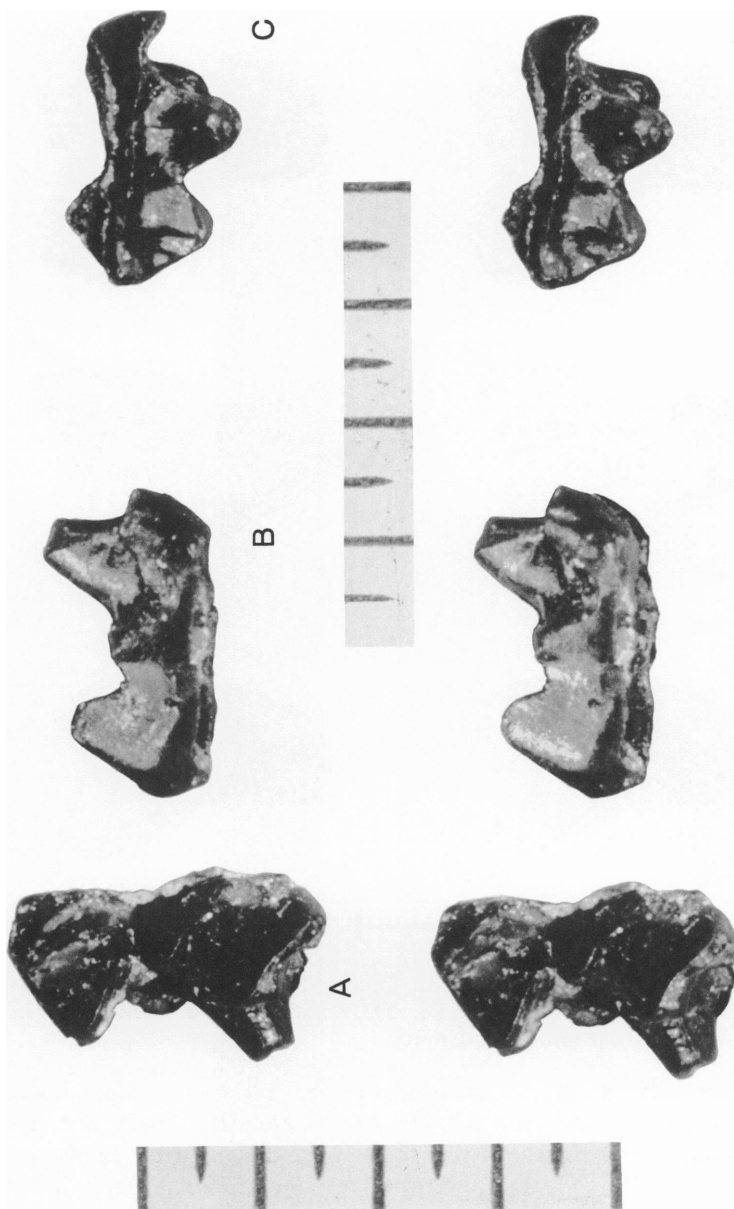


FIG. 2. *Jepsenella praetropena*, Swain Quarry, Torrejonian. A.M.N.H. No. 89512, right M¹. A. Buccal view. B. Anterior view. C. Posterior view. Scale subdivisions represent 0.5 mm.

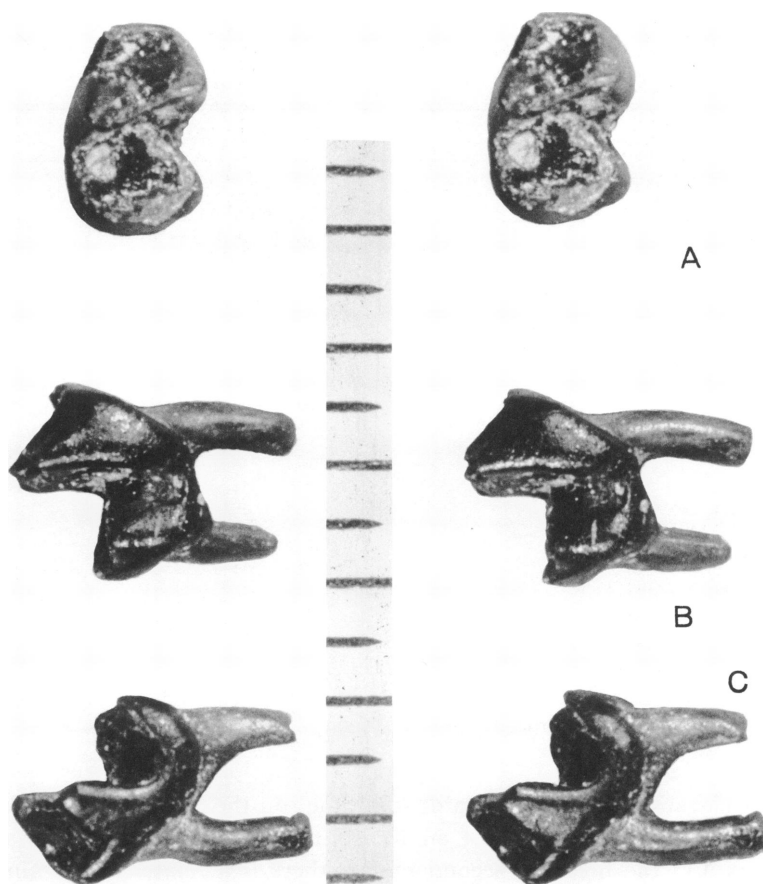


FIG. 3. *Jepsenella praepropera*, Swain Quarry, Torrejonian. A.M.N.H. No.89515. A. Occlusal view. B. Buccal view. C. Lingual view. Scale subdivisions represent 0.5 mm.

No. 89512 (figs. 1, 2, and 4) probably a right M^2 , and A.M.N.H. No. 89514 a left M^3 (figs. 1, 4). The buccal halves (i.e., the area buccal to the lingual border of the paracone and metacone) of both M^1 and M^2 are considerably wider than the lingual halves of all three molars. The paracones are primitively larger than the metacones, and the stylar shelf is somewhat reduced. The ectoflexus is barely an indentation on the buccal border of M^1 , it is slightly stronger on M^3 , whereas it is quite pronounced on M^2 .

The preparamacrista is reduced, but a discernible remnant leads to a

TABLE 1
MEASUREMENTS^a (IN MILLIMETERS) OF UPPER AND LOWER MOLARS OF
Jeppenella praepropera

	M ₁	M ₂	M ₃	M ¹	M ²	M ³
A.M.N.H. No. 3592, type						
L	1.72	1.65	1.50	—	—	—
PW	1.20	1.23	0.84	—	—	—
AW	1.25	1.30	1.13	—	—	—
Depth of mandible below	4.1	4.0	4.0	—	—	—
A.M.N.H. No. 89515, from Swain Quarry						
L	1.62	—	—	—	—	—
PW	1.12	—	—	—	—	—
AW	1.16	—	—	—	—	—
A.M.N.H. No. 89513						
L	—	—	—	2.14	—	—
W	—	—	—	2.06	—	—
A.M.N.H. No. 89512						
L	—	—	—	—	2.20	—
W	—	—	—	—	2.26	—
A.M.N.H. No. 89514						
L	—	—	—	—	—	1.38
W	—	—	—	—	—	1.87

^a Width measurements of the upper molars were taken from the most lingual limit of ectoflexus to the lingual border of the tooth.

slight elevation (probably a faint stylocone) on the buccal border of the tooth, which is most evident on M², but very faint on the other two molars. On the first and second molars there is a relatively prominent area anterior to the paracone, the preparamacrista, and the stylocone. This whole surface is probably best referred to as the parastyle-lobe. On M³ the parastyle-lobe is completely reduced. The postmetacrista is not reduced on any of the known molars of this species, and it was of obvious functional importance judged from the long shearing edge on the crest of M².

The conules are worn and were probably also faint in the unworn condition on M¹ and M³. They are, however, well developed on M². On the latter tooth the paraconule and metaconule were probably of equal size prior to the breakage of the metaconule. What remained of the metaconule is a pit in place of the apical part of the structure. The cusplule is reconstructed on the composite upper molars of the species (fig. 4). The preparamacrista, although worn, is more clearly defined than the postparamacrista.

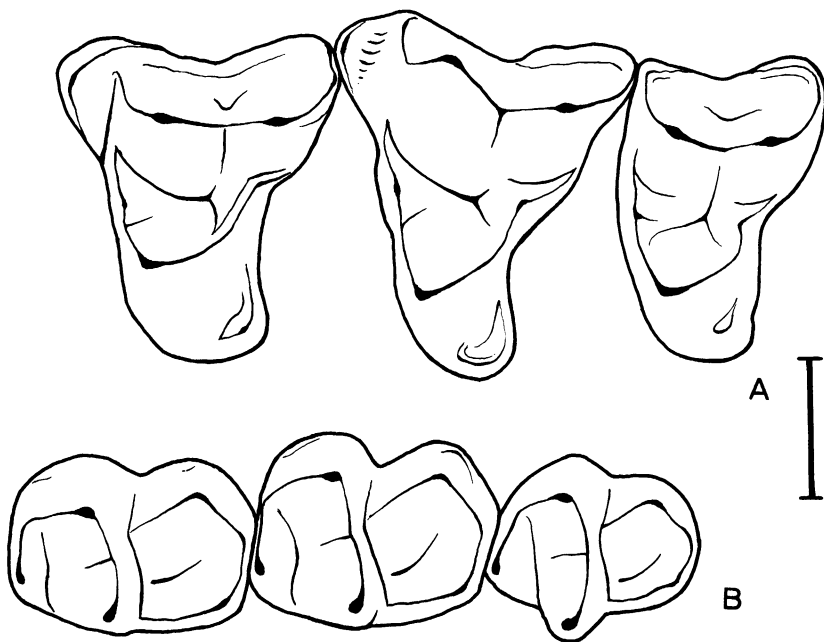


FIG. 4. *Jepsenella praepropera*, middle Paleocene, North America. Composite upper and lower molar dentition. A. Upper molars. Left to right: A.M.N.H. No. 89513, 89512 (reversed), and 89514. B. Lower molars. A.M.N.H. No. 35292 (type); the paraconid on M_1 is reconstructed from A.M.N.H. No. 89515. The relationship of the three lower molars on the type is the result of postmortem distortion. This restoration shows the occlusal surfaces of the lower molars in the presumed correct orientation one to another. The bar represents 1 mm.

The lingual halves of the upper molars are relatively small and are anteroposteriorly constricted in comparison with the buccal halves. The protocone is anteriorly skewed, extending directly lingual to the paracone. The hypocone is a small but distinct ledge formed by a slight broadening of the postcingulum at the very base of the posterolingual border of the protocone. On M^1 and M^2 , but not on M^3 , the hypocone makes the molars transversely wider than they would be without the hypocone.

The question arises: On what basis can the upper molars be allocated to (a) an apatemyid, and (b) specifically to *Jepsenella*? A brief comparison with U.S.N.M. No. 17765, *Apatemys* sp. (figured by McKenna, 1963) fig. 5), from Bridger C beds of the Bridger Basin, and with the upper molar referred to *Eochiromys* (I believe correctly) by Teilhard (1927,

pp. 14–15, text fig. 10, and pl. 3, fig. 11) from the Dormaal¹ (Orsmael) fauna of western Europe (Belgium) clearly shows that the upper molars belonged to an apatemyid. *Eochiromys* is more primitive, judged from its morphology, and is older than *Apatemys* from the Bridger Formation. As does *Eochiromys*, *Jepsenella* has the buccal half of the first and second molars much wider than do most other primitive placentals. Although the stylar shelf is somewhat wider in *Jepsenella*, as expected in an older representative of the family, the arrangement of the cusps and cuspules, and the extent and position of the parastyle-lobe, are very similar. In both genera the hypocone is formed the same way, although in the slightly more advanced *Eochiromys* the protocone is more prominent than in *Jepsenella*, and it is anteroposteriorly thickened as in the Bridger *Apatemys*.

I am well acquainted with the taxa of Swain Quarry, and my belief is, based on the size and occlusal relationship with the only lower tooth of *Jepsenella* (A.M.N.H. No. 89515, fig. 3) from that quarry, that the upper teeth are correctly allocated to the genus. It is unlikely that the upper molars represent a new apatemyid.

CERNAYSIAN ?APATEMYID FROM EUROPE

Russell, Louis, and Poirier (1967, pp. 851–852, pl. 21, fig. 2) recently reported an isolated right upper molar from a Paleocene locality near Berru (Mouras Quarry at Berru). The authors, after comparing the tooth to various Paleocene and Eocene placentals, allocated the molar to *Aboletylestes*(?) sp.

In my opinion, the Cernaysian tooth does not belong to the genus *Aboletylestes*. The presence of a well-defined, characteristic hypocone and the relatively long buccal half of the tooth clearly separate it from the palaeoryctid *Aboletylestes*. The presence of the hypocone, as opposed to its absence from the type species of *Aboletylestes*, is mentioned by the authors. Unlike these authors, I find no meaningful similarities between *Bessoecetor* (?) *leveii*, described in the same report, and the upper molar referred to *Aboletylestes*(?) sp. This tooth (L-121-BR) appears to me generically distinct from all Paleocene mammals illustrated by Russell (1964) and by Russell, Louis, and Poirier (1967), and it is probably

¹ The age of the Dormaal local fauna is somewhat disputed. Although it is generally thought to be Sparnacian (early Eocene), Van Valen and Sloan (1966) considered it latest Paleocene because of the conspicuous absence of artiodactyls and perissodactyls. I tentatively consider the Dormaal mammals Sparnacian, probably synchronous with earliest Wasatchian assemblages.

also distinct from all other described Paleocene mammals on the generic level.

Several unique characters are found in the upper molars of *Jepsenella* (the first and second molars in particular) and in the upper molar from the Paleocene of Berru. These character combinations are: the relatively long buccal part of the upper molars, a reduced preparacrista, a large parastyle-lobe, a relatively small protocone, and a small hypocone at the basal part of the protocone. Although many of these features are shared by other taxa (see discussion under origins), I believe the combination to be restricted only to *Jepsenella* and the European genus.

Until the presence or the absence of enlarged incisors in the European genus can be ascertained, allocation to the Apatemyidae cannot be affirmed or denied.

ORIGINS OF THE FAMILY

I have compared *Jepsenella* and the upper molar L-121-BR from the Cernaysian of Europe with the following groups and taxa (in addition to the genera listed, comparisons were made with many other genera of the families): *Pappotherium*, a very primitive Albian therian; the early Paleocene primitive palaeoryctids, such as *Puercolestes simpsoni*; the early Eocene *Didelphodus*, and its Cretaceous structural ancestor, *Cimolestes*; *Leptacodon tener*, one of the earliest true erinaceoids, and other early Tertiary representatives of the Erinaceoidea; *Gypsonictops*, the earliest true leptictid; *Propalaeosinopa*, an early pantolestid; *Protungulatum*, the earliest and most primitive presently known condylarth; *Purgatorius* and *Teilhardina*, the most primitive primates in their molar morphology.

In all the foregoing genera and groups, except primitive therians such as *Pappotherium* and the palaeoryctids, the size of the protocone is relatively larger in relation to the buccal half of the tooth than in *Jepsenella*. The relatively large protocone in leptictids, pantolestids, miacids, several Paleocene erinaceoids (e.g., *Leptacodon* and *Litolestes*), mixodectids, primates, and condylarths is clearly an advanced condition.

Possibly the relatively small protocone of *Jepsenella* and the Cernaysian upper molar represents a slight secondary reduction of the cusp. It may be argued that the disproportionate emphasis on the buccal half of the upper molars may have occurred at the expense of the protocone. Nevertheless, it appears to me that a protocone relatively smaller in *Jepsenella* than in leptictids, pantolestids, early primates, and primitive erinaceoids reflects the condition of the primitive apatemyid ancestry.

Furthermore, the leptictid wear, as well as the reduced parastyle-lobe of *Gypsonictops*, suggests that that genus is too advanced in its morphology

to serve as a structural ancestor for apatemyids.

Correspondence in the upper and lower molar construction of the second molars (probably the most primitive in the molar row) of *Jepsenella*, on one hand, and of such palaeoryctids as *Cimolestes*, *Puercolestes*, and *Didelphodus*, on the other, is astonishingly close.

In fact, the only major differences between the upper molars of *Didelphodus absarokae* (A.M.N.H. Nos. 4228, 15700, 15010) and M² of *Jepsenella praepropera* is the presence of a primitive preparacrista with a prominent carnassial notch on *Didelphodus*. These differences are barely generic in kind when the molars alone are examined. The lower molars of *Didelphodus* (A.M.N.H. Nos. 4229, 16825) and those of *Jepsenella* are as similar in morphology as the upper molars. The lower molars of *Jepsenella* resemble those of *Didelphodus* much more than they do of any erinaceoid known to me, including *Leptacodon tener*.

Although the upper dentition of *Leptacodon tener* (McKenna, 1968) and that of *Jepsenella* share such primitive characters as the fairly broad parastyle-lobe, the protocone and the hypocone of *Leptacodon tener* are relatively larger and more advanced by the late Paleocene. Nevertheless, an advanced character shared between the two genera is the transverse shortening of the upper molars compared with the primitively wide molars of palaeoryctids and leptictids. The sharing or retention of primitive features is not a sufficient basis for postulating close relationships, although the single advanced feature noted (the transverse shortening of the upper molars) for both apatemyids and some erinaceoids may prove to be more significant than it seems at present.

If the loss of the protocone of the third premolar and a general transverse constriction of this tooth occurred in the Paleocene, as in *Leptacodon tener*, then they may be considered additional advanced features shared by the apatemyids and erinaceoids.

Although it is possible that apatemyids evolved their specializations of incisor and molar construction prior to the late Cretaceous palaeoryctids, from earlier, more primitive placental stocks, the best interpretation based on the present evidence favors palaeoryctid origins for the Apatemyoidea at some time during the late Cretaceous.

Independent or common origin with erinaceoids from the same or closely related stocks of palaeoryctids is not improbable. I consider leptictid origins for either the Apatemyoidea or the Erinaceoidea unlikely. Cretaceous and Paleocene leptictids have several characters more advanced than the molar construction in both apatemyids and erinaceoids.¹

¹ Van Valen's (1967) concept of the stem-erinaceoid family Adapisoricidae Schlosser

If erinaceoids originated independently from leptictids, from either Cretaceous or early Paleocene palaeoryctids (which I consider probable), then the separation of leptictoids and erinaceoids on the ordinal or subordinal level may become necessary. Whether mixodectids originated from palaeoryctids independently or were derived from a stock of stem-erinaceoids at some time during the early Paleocene is presently an insoluble dilemma.

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was not defined, and many of the genera allocated to the four subfamilies (Geolabidinae, Adapisoricinae, Creotarsinae, Nyctitheriinae) undoubtedly represent unnatural groupings, as Van Valen (1967, p. 272) admitted. Until the various erinaceoid genera are thoroughly studied and documented, an uncritical acceptance of an ill-defined (or rather non-defined) concept of the Adapisoricidae will only create further taxonomic confusion. On the other hand, the use of the four subfamily groupings of Van Valen, until the necessary revisions are undertaken, can be heuristically sound practice for the poorly known early erinaceoids.

