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INSECTIVORA AND PROTEUTHERIA OF THE LATER EOCENE (UINTAN) OF SAN DIEGO COUNTY, CALIFORNIA

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INSECTIVORA AND PROTEUTHERIA OF THE LATER EOCENE (UINTAN) OF SAN DIEGO COUNTY, CALIFORNIA[1]

By MICHAEL J. NOVACEK[2]

ABSTRACT: A highly diverse fauna of Insectivora and Proteutheria (Mammalia) from Uintan strata (later Eocene) of San Diego County, California, includes at least twelve species representative of a minimum of six families. *Sespedectes singularis,* an adapisoricid erinaceoid, is the most abundantly represented species. *Proterixoides,* a genus closely related to *Sespedectes,* is extremely rare in San Diego localities. A new genus and species, *Cryptolestes vaughni,* is intermediate in some aspects of dental morphology between *Sespedectes* and *Proterixoides* and certain other adapisoricids. *Batodonoides powayensis,* another new genus and species allocated to the Geolabididae, shows strong similarities with *Batodon tenuis* and *Centetodon* spp. The local fauna suggests the presence of a primitive apternodontine and a palaeoryctine. Also present is an aberrant new genus and species, *Aethomylos simplicidens.* There are strong indications of endemism in the San Diego insectivore fauna. Of the 12 taxa described, only *Apatemys, Nyctitherium,* and *Centetodon* are known elsewhere in North America. The local insectivores seem generally more primitive than those of later Eocene faunas from the midcontinent of North America.

INTRODUCTION

The later Eocene (Uintan) terrestrial vertebrate fauna of San Diego County was first studied by Dr. Chester Stock (1937, 1938, 1939). Since the time of Stock's early work, little research on this fauna has been published (see Lillegraven 1973, for a summary of previous work). Such a dearth of literature is a reflection of neither the scarcity nor the insignificance of San Diego Eocene vertebrates. Southern California Uintan terrestrial deposits, which include both strata from the greater San Diego area and the Sespe area north of Los Angeles, are widely separated geographically from all other North American vertebrate fossil bearing deposits of this age. Therefore, the southern California faunas are significant because they represent a later Eocene biogeographic region far removed from midcontinental regions. Furthermore, San Diego Uintan nonmarine beds are in close proximity and, in some cases, even intertongue with marine strata, allowing for chronostratigraphic correlation between marine and nonmarine fossils (see Black and Dawson 1966; Lillegraven 1973, for further discussion).

This report is an early contribution to a long-term project concerned with the salvage and study of later Eocene fossil vertebrates from the San Diego region. It i

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primarily a systematic work and deals with only one aspect of the local vertebrate fauna, the Insectivora (and Proteutheria). Hitherto, only three studies have been published on Eocene insectivores from southern California. Stock (1935) described and named two erinaceid-like insectivores, *Sespedectes singularis* and *Proterixoides davisi* from the Sespe Formation, a unit of late Eocene age located in Ventura County, north of Los Angeles. In the same publication, Stock briefly described a possible leptictid species represented by a lower jaw fragment with a third molar. Gazin (1958) named a new apatemyid species, *Apatemys downsi,* from the Sespe collections. Most recently, Coombs (1971) described *Simidectes,* an insectivore known from the Sespe Formation. Although *Simidectes* is also represented in the "Laguna Riviera" faunal collections made by the University of California Museum of Paleontology (Coombs 1971:18), this genus has not yet been discovered in any Uintan locality in the greater San Diego area.

Not all of the insectivore species represented in the San Diego Uintan collections are described in this paper. Some of the geolabidines recovered will be discussed in a forthcoming review of the Geolabidinae by Lillegraven and McKenna (MS.). There are several specimens referable to *Uintasorex* or a closely related genus. *Uintasorex* has recently been recognized as a member of the Microsyopidae by Szalay (1969*b*), a family which is periodically shifted in its allocation between primates and insectivores (see Szalay 1969a, 1969b, 1971). A thorough consideration of the San Diego *Uintasorex* species has been completed by Lillegraven (In Press). The San Diego genera *Sespedectes* and *Proterixoides* are described in a review of later Eocene erinaceoid insectivores of southern California (MS.).

LOCALITIES

The marine, nonmarine Eocene section in the San Diego area was recently redefined by Kennedy and Moore (1971) who raised the original Eocene Poway Conglomerate to group status. They further subdivided this unit into the basal Stadium Conglomerate, the Mission Valley Formation, and an unnamed formation above the Mission Valley. Occurring stratigraphically below the Stadium Conglomerate is the chiefly nonmarine Friars Formation, the uppermost unit of the La Jolla Group. Uintan vertebrate fossils have been collected from about sixty localities within the Friars Formation, Stadium Conglomerate, and Mission Valley Formation. Detailed descriptions of these localities are on file at the University of California, Berkeley, Museum of Paleontology.

One locality, V-72088, at the northern end of the Camp Pendleton Marine Corps Base near Camp San Onofre, has yielded a significant sample of small vertebrates, including insectivores. The specific stratigraphic position of V-72088 is currently unknown, but the mammalian fauna is Uintan and appears to correspond closely with that of the Mission Valley Formation.

Table 1 summarizes the current distribution of insectivore taxa by locality. Neighboring localities in the same formation are grouped together under "local areas" which correspond to those designated on the map (Fig. 1). It is evident that many taxa are poorly represented, in some instances by only one or two isolated teeth or fragmentary jaws. An exception is observed in the case of *Sespedectes singularis*. Fossils representing this species are abundant and widely distributed. The lower molars of the second most abundant species, *Cryptolestes vaughni*, when severely worn are indistinguishable from those of *Sespedectes singularis*. Consequently, where only lower molars were found, they could not be assigned with great assurance to either species. This is denoted in the table by equal fractions in parentheses put in rows opposite both *S. singularis* and *C. vaughni*. At certain other localities, it was arbitrarily decided that if only diagnostic teeth of one species were found, all specimens including lower molars were referred to that one species. The lack of verification for such an action is signified in Table 1 by question marks preceding the fraction.

While a large sample (243 + specimens) referable to *Sespedectes singularis* has been recovered from locality V-72088, the only other insectivore species known from the locality is *Proterixoides davisi*. A strikingly different insectivore assemblage is represented at locality V-72158. Both *S. singularis* and *P. davisi* are absent, but a closely related species, *Cryptolestes vaughni*, is represented by a large number of specimens (68 +). Even more interesting is the fact that eight different insectivore taxa are represented at V-72158. This difference seems to be consistent throughout the localities listed in Table 1, but only at V-72088 and V-72158 are samples large enough to clearly illustrate the pattern.

The simplest interpretation for the faunal differences between V-72088 and V-72158 is that these localities represent distinctly different microhabitats. Collecting bias is probably a minimal factor as quite large samples of matrix from both localities were washed and sorted for microfossils. The fossiliferous unit from V-72088 is a rather coarse, poorly indurated sandstone. Clayballs present in the unit are rounded or spherical, suggesting that they were transported some distance by water currents. The fossiliferous matrix at V-72158 is predominantly a green silty claystone with minor amounts of sand. These differences suggest that fossils were deposited under relatively higher energy conditions at V-72088 than at V-72158.

It is interesting to note that although V-72088 seems to represent a relatively higher energy depositional environment, insectivore fossils preserved in that locality were less fragmentary than those preserved in V-72158. Twenty-eight mandibles with two or more teeth of *S. singularis* were recovered at V-72088. At V-72158, in contrast, insectivores were mainly represented by isolated teeth or edentulous jaw fragments. Voorhies (1969:22) suggested that the ratio of upper dentitions to lower dentitions of small mammals is inversely related to a greater current energy because maxillae of large and small mammals tend to break up and lose their teeth more readily than mandibles. This generalization is supported by the observation that only three maxillae of *S. singularis* were recovered from V-72088 in comparison to the twenty-eight mandibles recovered. When the total number of teeth both in and out of jaws is counted, the percentage of uppers to lowers is 53%. The ratio of the upper to lower dentitions from V-72158 referable to *Cryptolestes vaughni*, a species nearly the same size as *S. singularis*, is 74%. There might be an explanation to account for both this difference in percentages and the greater number of preserved lower jaws

TABLE I
Distribution of taxa by locality

	UNNAMED FORMATION	MISSION VALLEY FORMATION									
	San Onofre Locality	Poway Localities						Fletcher Hills Localities			
Species[3]	V-72088	V-71180	V-71181	V-71211	V-72157	V-72158	V-72176	LACM 65190	V-6871	V-6893	V-71055
cf. *Apatemys* sp.						$\frac{1}{2}$					
?Palaeoryctine gen. and sp.											
Sespedectes singularis	$\frac{32}{243}$							$\frac{3}{3}$	$\frac{2}{15}$	$\frac{3}{23}$	$\frac{2}{3}$
cf. *Proterixoides davisi*	$\frac{1}{4}$										
Cryptolestes vaughni		$\frac{2}{7}$		$\frac{1}{1}$	$\frac{2}{10}$	$\frac{6}{68}$	$\frac{1}{1}$				
cf. *Nyctitherium* sp.		$\frac{1}{1}$				$\frac{1}{1}$					
Centetodon spp.		$\frac{1}{1}$			$\frac{2}{5}$	$\frac{2}{16}$					
Batodonoides powayensis			$\frac{1}{1}$	$\frac{2}{7}$		$\frac{1}{1}$					
?Apternodontine gen. and sp.											$\frac{1}{1}$
Erinaceoid-like gen. and sp. *incertae sedis*		$\frac{1}{1}$			$\frac{1}{2}$	$\frac{1}{3}$					
Micropternodontine-like gen. and sp. *incertae sedis*						$\frac{1}{1}$					
Aethomylos simplicidens		$\frac{1}{3}$		$\frac{1}{1}$	$\frac{1}{4}$	$\frac{2}{9}$					

	FRIARS FORMATION								
	Mission Gorge Localities			Tierra Santa Localities		Kennedy Locality	Old Mission Locality	Murphy Cyn. 2 Locality	Tecolote Cyn. Locality
Species[3]	V-68116	V-6873	V-71183	V-71175	V-71176	V-71216	V-6840	V-6888	V-6882 (CIT314)
cf. *Apatemys* sp.									
?Palaeoryctine gen. and sp.								$\frac{1}{11}$	
Sespedectes singularis	?$\frac{2}{6}$	$\left(\frac{2}{2}\right)$		$\left(\frac{2}{2}\right)$					
cf. *Proterixoides davisi*	$\frac{1}{1}$								
Cryptolestes vaughni	?$\frac{1}{3}$	$\left(\frac{2}{2}\right)$	$\frac{3}{12}$	$\left(\frac{2}{2}\right)$	$\frac{1}{1}$		$\frac{1}{1}$		$\frac{1}{1}$
cf. Nyctitherium sp.									
Centetodon spp.	$\frac{1}{1}$		$\frac{2}{3}$					$\frac{1}{1}$	
Batodonoides powayensis				$\frac{1}{1}$	$\frac{1}{2}$	$\frac{1}{1}$			
?Apternodontine gen. and sp.									
Erinaceoid-like gen. and sp. *incertae sedis*									
Micropternodontine-like gen. and sp. *incertae sedis*									
Aethomylos simplicidens	$\frac{1}{1}$		$\frac{1}{4}$						

[3] The occurrence of each species at any given locality is indicated by a fraction whose denominator represents the total number of identified specimens from that locality and whose numerator represents the minimum number of individuals necessary to account for the total number of specimens (method after McKenna 1960a).

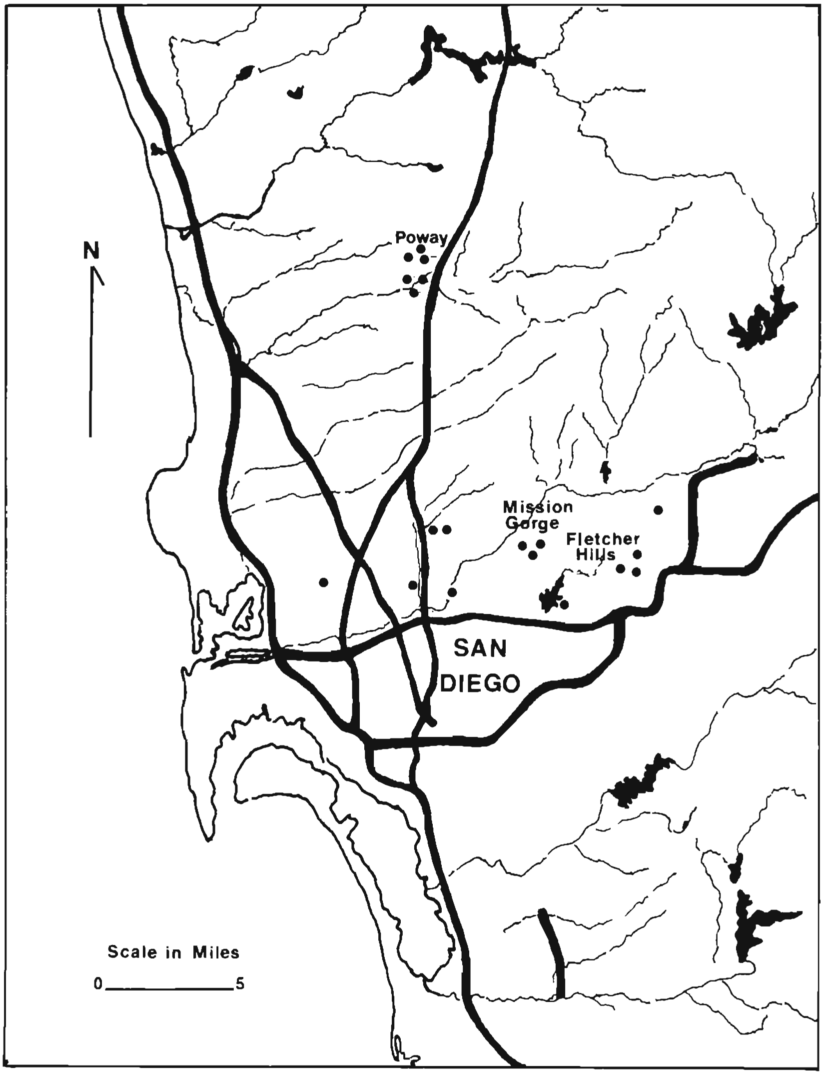


FIGURE 1. Map of the greater San Diego area showing approximate location of all localities (closed circles) except loc. V-72088 listed in Table 1. Heavy black lines represent major highway systems.

of *S. singularis*. Mandibles and maxillae of *S. singularis* from V-72088 may have been carried for only a short distance before they were buried. Maxillae were quickly destroyed, and their teeth were scattered prior to deposition and/or winnowing out by subsequent current action. More durable mandibles successfully resisted initial breakup and subsequent reworking by current action. The situation at V-72158 may have been somewhat different. Many skeletal and dental elements initially fragmented by high energy currents could have collected in the relatively calmer waters represented by the fine-grained matrix at V-72158. If currents were sufficiently strong to fragment both mandibles and maxillae, a random concentration of these scattered elements in current eddies might result in the approach to a 50-50 ratio of upper and lower dentitions of *C. vaughni* observed at V-72158.

There is some evidence that elements of *Sespedectes singularis* were carried for a shorter distance than other small mammalian remains at V-72088. Many isolated rodent teeth of comparable size are scattered throughout the fossiliferous unit; however, rodent mandibles which are at least as strong as those of *S. singularis* are extremely rare. Hence, the rodent material was probably carried a greater distance prior to deposition than bones and teeth of *S. singularis*. Conceivably, remains of *Sespedectes* may have been transported and buried in a site not far from where the animal spent most of its life.

Overall faunal comparisons of a detailed nature between V-72088 and V-72158 have not yet been completed. Excellent lower vertebrate samples from both V-72088 and V-72158 are now being studied by Mr. Richard Schatzinger. It is anticipated that this material will yield significant information on the environments represented. Rather uncommon fish bones and shark and ray teeth are intermixed with terrestrial vertebrate remains at V-72088. Beds containing marine invertebrate fossils are also found in close stratigraphic and lateral proximity to the fossiliferous unit at V-72088. None of these elements are known from V-72158. This suggests that V-72088 may represent an estuarine environment, while V-72158 probably represents an environment further inland.

The "crude" observations presented above do not conclusively prove my interpretation of the microhabitat represented by locality V-72088. The possibilities that 1) *Sespedectes singularis* lived close to the site of burial, and 2) V-72088 may represent an estuarine environment, are merely suggested as hypotheses for future testing by analysis of biological, taphonomic, and sedimentological data.

Another less easily tested hypothetical explanation for the insectivore faunal compositions at V-72088 and V-72158 is that *S. singularis* may have exhibited a broad range of food habits, and thus excluded insectivores competing for the same food resources. I doubt that *S. singularis* would have come into direct competition with most of the kinds of insectivores common to V-72158. There may, however, have been competition between *Cryptolestes vaughni* and *Sespedectes singularis*. The animals are subequal in size, are more abundant than other insectivores in the fauna, and rarely, if ever, are found in the same localities. The dentitions of the two genera are similar in many adaptations, although the molars of *Sespedectes* have more bulbous cusps of lower relief and appear to be better adapted for a crushing mode of occlusion. The difficulty here lies in the lack of predictive value that a particular dental morphology may have for revealing the true feeding habits of the animal with that dental morphology. Many mammals such as rodents possess highly specialized dental and masticatory features yet show natural acceptance of a wide variety of foods (see Landry 1970). Furthermore, analogies presently cannot be drawn from living hedgehog-like forms because the feeding habits of these creatures in their natural habitat are so poorly known.

METHODS

The dental nomenclature employed here follows that of Rich (1971:4) who slightly modified dental terminology proposed by Van Valen (1966:7-9).

All specimens were measured on an Ehrenreich Photo Optical "Shopscope." Measurements were in millimeters and were rounded off to the nearest one-hundredth of a millimeter. The following orientations for measuring cheek teeth (see Fig. 2) were used in this report:

Anteroposterior axis ("A-P" axis):

Lower posterior premolars—long axis of tooth.

Lower molars—line drawn through the apices of the metaconid and the entoconid.

Upper posterior premolars—line extended from anteriormost point of the anterolabial lobe to the posteriormost point of the metastylar lobe.

Upper molars ($M^{\underline{1-2}}$)—line drawn through the apices of the paracone and metacone.

Upper molars ($M^{\underline{3}}$)—line drawn at right angles to a line which divides the tooth into equal anterior and posterior halves.

Length:

Lower posterior premolars—total length of crown; i.e., greatest dimension measured parallel to "A-P" axis.

Lower molars—total distance from the anterior face of the paraconid to the back of the talonid along a line parallel to the "A-P" axis (anterior cingulum not included in measurement).

Upper posterior premolars and upper molars—greatest dimension parallel to the "A-P" axis of tooth.

Width:

Lower posterior premolars—widest part of crown; greatest dimension measured at right angles to "A-P" axis.

Lower molars—two width measurements: trigonid width, talonid width, widest part of each of these sections of the crown measured at right angles to "A-P" axis.

Upper posterior premolars and upper molars—two measurements: anterior width, distance from the labialmost point of the anterolabial corner of the crown to the lingualmost point of the protocone; posterior width, distance from pos-

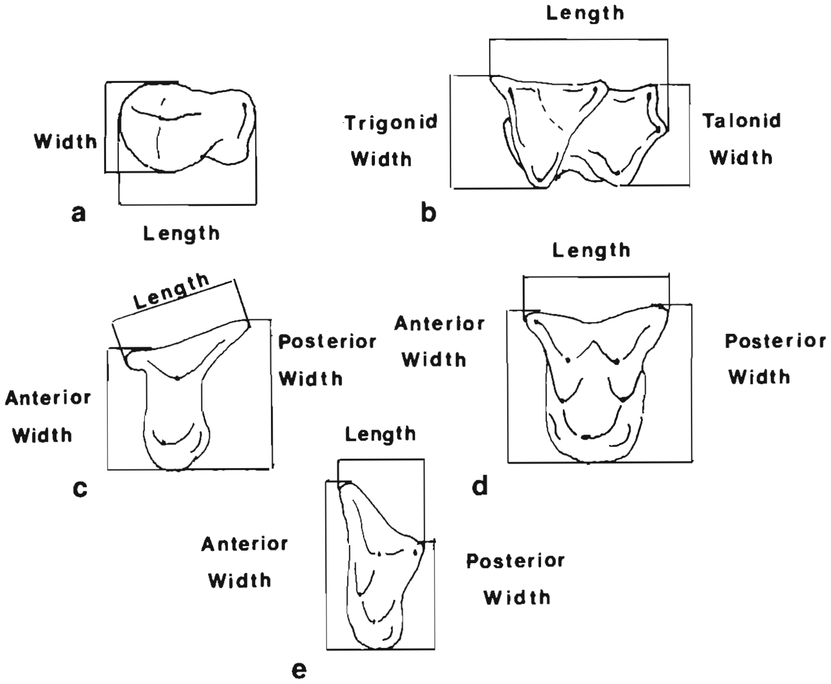


FIGURE 2. Occlusal view of diagramatic cheek teeth showing orientations for measurements; a. lower posterior premolar, b. lower molar, c. upper posterior premolar, d. upper molar (M^1 or M^2), e. upper molar (M^3).

terolabialmost point of metastylar lobe to lingualmost point of protocone; both width measurements taken at right angles to the "A-P" axis.

The following abbreviations appear in this report:

N.	-number of observations (sample size)
O.R.	-observed range of variation
M.	-arithmetic mean
S.D.	-standard deviation
S.E.	-standard error of the mean
C.V.	-coefficient of variation
AMNH	-Department of Vertebrate Paleontology, American Museum of Natural History
CM	-Carnegie Museum
LACM	-Los Angeles County Museum of Natural History
LACM (CIT)	-specimens originally in the California Institute of Technology now housed in Los Angeles County Museum of Natural History
NMNH	-National Museum of Natural History, Smithsonian Institution
UA	-University of Alberta Paleontological Collection
UCMP	-University of California Museum of Paleontology, Berkeley
USNM	-United States National Museum, Smithsonian Institution
YPM	-Yale Peabody Museum

SYSTEMATICS

COMMENTS ON INSECTIVORE CLASSIFICATION

Various authors have noted the acute difficulty in classifying insectivores (see Romer 1968; Butler 1972; Dawson 1967). Due to the great present and past diversity of insectivores, their long evolutionary history, the poor quality and scarcity of fossils from crucial time periods and geographic areas, and the variety of interpretations that have arisen in insectivore taxonomy, the order defies definition and under the present concept is probably an unnatural group (see Butler 1972, for an excellent critical review of the problem).

This report is not intended as a comprehensive review of insectivore systematics. Such a study, which should include an attempt toward a phyletic classification of the order, is sorely needed. However, since the classification endorsed in this paper does not precisely conform to that in any published study, a general discussion of insectivore systematics is required. The following arrangement of higher categories is recognized in this report (taxa described in this paper have been assigned to those families indicated by an asterisk):

Order Proteutheria Romer 1966
Family + Leptictidae Gill 1872
Family + Pantolestidae Cope 1884
Family + Ptolemaiidae Osborn 1908
Family + Apatemyidae* Matthew 1909
Family + Palaeoryctidae* Winge 1917
Order Insectivora Illiger 1811
Suborder Erinaceomorpha Butler 1956, 1972
Family + Adapisoricidae* Schlosser 1887, (Van Valen 1967)
Family Erinaceidae Fischer von Waldheim 1817
Family ? Dimylidae Schlosser 1877
Suborder Soricomorpha Butler 1956, 1972
Superfamily Soricoidea Fischer von Waldheim 1817
Family + Geolabididae McKenna 1960
Family + Plesiosoricidae Winge 1917
Family Solenodontidae Gill 1872
Family + Micropternodontidae Stirton and Rensberger 1964
Family + Nyctitheriidae* Simpson 1928, (Robinson 1968)
Family Soricidae Fischer von Waldheim 1817
Family + Nesophontidae Anthony 1916
Family + Apternodontidae* Matthew 1910
Superfamily Talpoidea Fischer von Waldheim 1917
Family Talpidae Fischer von Waldheim 1917
Suborder Tenrecomorpha Butler 1972
Superfamily Tenrecoidea Gray 1821
Family Tenrecidae Gray 1821
Superfamily Chrysochloroidea Gray 1825
Family Chrysochloridae Gray 1825

Illiger, in 1811, recognized a family Subterranea comprising moles, shrews, and hedgehogs. The name Insectivora was bestowed on this group by de Blainville in 1816.

The original descriptions of *Tupaia, Ptilocercus, Macroscelides, Petrodromus, Rhynchocyon,* and *Cynocephalus* in the first half of the 19th century prompted attempts to subdivide the order into natural categories. Haeckel (1866) created the insectivore suborders Lipotyphla—for those animals (shrews, moles, and hedgehogs) which lacked an intestinal caecum, and Menotyphla—for those animals (tree shrews, elephant shrews, and flying lemurs) in which the caecum was present. The concept Menotyphla (excluding the flying lemurs, separated by Gill in 1872 as the order Dermoptera) carries little, if any phylogenetic meaning. Many similarities between macroscelidids and tupaiids, such as the presence of a caecum, large jugals, fused pubic symphyses, and well-developed orbital wings of the palatine bones are likely primitive eutherian characters and thus are of little use in demonstrating relationships between the two groups. Significant differences between the two families in such features as brain and placental morphology far outweigh any of the above-listed similarities. I endorse Butler's (1972) recognition of the separate orders Macroscelidea and Scandentia (to include tupaiids) as a realistic taxonomic solution.

The lipotyphlan concept, on the other hand, seems well founded. A nucleus of living families, the Erinaceidae, Talpidae, Soricidae, Solenodontidae, Tenrecidae, and Chrysochloridae, comprise what appears to be a natural, though very broad, grouping on the basis of a number of shared-derived characters (cited by Butler 1972). In all these families an intestinal caecum is absent, the jugal bones are small or absent, there is an expansion of the maxillary bones into the orbital region of the skull replacing the palatines in that region, the mobile proboscis is moved by a series of specialized muscles which influence the form of the skull, the basisphenoid bone is the major component of the auditory bulla (although an ossified bulla is not present in soricids), the pubic symphysis is either reduced or absent, and there is no medial internal carotid artery.

A number of fossil groups, the Adapisoricidae, Micropternodontidae, Nesophontidae, Nyctitheriidae, Apternodontidae, Geolabididae, and Plesiosoricidae can, with varying degrees of confidence, be allied with the living lipotyphlans but the evidence for such allocations are mainly dental. A few of these families are, however, represented by excellent cranial material, and an argument for their affinity with Recent forms seems quite tenable.

Butler (1972) recognized the above living and extinct families as members of the order Lipotyphla and relegated several enigmatic insectivore families (Palaeoryctidae, Plagiomenidae, Apatemyidae, Pantolestidae, and Leptictidae) to the order Proteutheria (earlier recognized as a suborder by Romer 1966, and Van Valen 1967). Butler's (1972) action precludes formal usage of the order Insectivora. I see no compelling reason against equating Insectivora with Butler's (1972) Lipotyphla and retaining the former well known in the literature. The Insectivora would thus have a more restricted definition than under former usage, but such action would serve to demonstrate the doubtful ordinal affinities of the proteutherian families.

Order Proteutheria—There is little doubt that the Proteutheria is an artificial and presently indefinable category, and a purely phyletic classification would not recognize the unity of this order. Pending phyletic approach, I have followed Butler (1972) in allocating the Palaeoryctidae, Leptictidae, Apatemyidae, and Pantolestidae to the Proteutheria. Butler (1972) also included the Plagiomenidae in this group, but I regard plagiomenids as provisional members of the Dermoptera in accordance with dental evidence reaffirmed by Rose (1973) and others.

Van Valen's (1967) concept of the Proteutheria differs strongly from the one presented here in his inclusion of tupaiids, zalambalestids, anagalids, paroxyclaenids, and pentacodontids within the suborder and in his recognition of the Palaeoryctidae as a family of his new order of mammals, the Deltatheridia (Van Valen, 1966). As is stated above, there is a case for excluding the Tupaiidae from the Insectivora. Szalay and McKenna (1972) have marshalled evidence for the recognition of a separate order, Anagalida, to include both anagalids and zalambdalestids. Zalambdalestids have specialized features in the cranium, feet, and dentition which suggest a close relationship between this group and lagomorphs (Van Valen 1964, Szalay and McKenna 1971). Whatever their affinities, the Anagalida seems to have diverged very early in the evolution of the Eutheria. In their bunodont molar construction, pentacodontids are more reminiscent of condylarths than insectivores. Pentacodontids are also unique in specializations of the posterior premolars. Van Valen (1967:231) noted the similarities in molar construction between certain pentacodontids and erinaceoids (e.g. *Proterixoides*). Such similarities are likely due to convergence as *Proterixoides, Sespedectes* and some related genera are highly specialized in molar morphology, although their relationship to more generalized adapisoricids can be demonstrated on the basis of other dental features (Novacek, MS.). Crusafont and Russell (1969) dispute Van Valen's (1965) alliance of paroxyclaenids with *Procerberus,* pointing out similarities of these animals with the condylarths, *Promioclaenus, Ellipsodon,* and *Oxyacodon*. Perhaps, as Rich (1971) has suggested, the Paroxyclaenidae should be regarded as Eutheria *incertae sedis*.

MacIntyre (1966), McKenna (1969), Szalay (1968) and others have presented evidence against Van Valen's (1966) placement of the Palaeoryctidae within his order Deltatheridia. The importance of this family in understanding the differentiation of the Eutheria has long been recognized. The Palaeoryctidae as presently regarded is probably an unnatural category whose members are grouped together mainly on the basis of the common possession of dentitions specialized in a shearing or piercing mode of occlusion. There seems little evidence for a close relationship between *Didelphodus* and palaeoryctines. Late Cretaceous North American palaeoryctids *(Cimolestes, Batodon,* and *Procerberus)* contrast strongly in certain dental features, and different species may be related to apatemyids (Szalay 1968), others to geolabidids (McKenna, personal communication), and still others to palaeoryctines, taeniodonts, and creodonts (Lillegraven 1969). Unfortunately, all Cretaceous palaeoryctids (with the exception of some unpublished Mongolian Late Cretaceous forms now under study by Kielan-Jaworowska) are known only from dentitions.

Leptictids contrast broadly with lipotyphlans in a number of important characters: the primary component of the ossified bulla is entotympanic rather than basisphenoid, the medial branch of the internal carotid artery is present, the posterior permanent premolars are molariform, deciduous premolars are retained through much of an individual's lifetime and the leptictid manubrium is uniquely enlarged. Szalay (1968) and others regard the Leptictidae as an isolated group of archaic eutherians not closely related to other insectivores, except for perhaps pantolestids. However, the Leptictidae is the best represented of the early Tertiary insectivores and information derived from such excellent fossil material might provide insight into the morphotypical plan for the Eutheria.

Order Insectivora—The breakdown of the Lipotyphla endorsed in this paper follows Butler's (1972) scheme. The one major departure here is the removal of the Talpidae from Soricoidea to its own superfamily, Talpoidea. This action corresponds with Bugge's (1974) recognition of the phyletic isolation of the talpids based on specializations in the pattern of carotid arterial circulation. Butler (1956) has pointed out many derived similarities between soricids and talpids in cranial morphology, but there is an abundance of anatomical evidence to suggest that talpids diverged very early in the evolution of the Insectivora and may be only remotely related to soricids, though closer than chrysochlorids and tenrecoids (Novacek, unpublished).

Perhaps no insectivore category is as difficult to understand as the Erinaceoidea. This highly heterogeneous superfamily contains many problematic genera. As is the usual case, confusion is greatest regarding primitive members. Two families were recognized by Van Valen, the Erinaceidae and the Adapisoricidae. Adapisoricids are difficult to differentiate from the Erinaceidae, the Hyopsodontidae, the Pentacodontidae, the Tupaiidae, and the Plesiosoricidae. Van Valen did not define this family other than to state (1967:272) that the included genera ". . . are sufficiently different from the Erinaceidae that familial distinction seems useful." Van Valen included four subfamilies within the Adapisoricidae, the Nyctitheriinae, Geolabidinae, Adapisoricinae, and Creotarsinae. He admitted (1967:272) that the assignments of many of the genera within these four subfamilies were provisional.

Robinson (1968) removed the Nyctitheriinae from the Adapisoricidae and raised it to familial rank. Robinson's concept of Nyctitheriidae, however, was notably different from the original one of Simpson (1937) in that the former included within it three subfamilies. The stem subfamily was the Nyctitheriinae consisting of the type genus *Nyctitherium,* its alleged ancestor *Leptacodon,* and a former soricoid, *Saturninia.* To this Robinson added the mole-like (in adaptive specializations, not in affinities) Micropternodontinae and the Geolabidinae. Robinson recognized only two of the eight genera included in the Geolabidinae by Van Valen (1967).

I favor Robinson's (1968) establishment of the family Nyctitheriidae, but I do not agree with his inclusion of the Geolabidinae within that family. Contrary to Robinson's contention (1968:134) the upper molars of geolabidines are not structurally close to those of *Leptacodon tener,* the alleged basal member of the Nyctitheriidae. Also the geolabidine P_4 is strongly contrasting to those of all nyctitheriines. I cannot accept the statement of Szalay and McKenna (1971:288) that nyctitheres (*sensu* Robinson) are derived from Cretaceous palaeoryctid stock via the late Cretaceous genus *Batodon. Batodon* was sufficiently specialized in dental construction to rule out the likelihood of its close relationship with *Leptacodon tener* and related nyctitheriines. *Batodon,* however, may be a primitive geolabidine as suggested by McKenna (personal communication).

The subfamily Geolabidinae has been subjected to major supraspecific revision since the time of Van Valen's classification. Szalay and McKenna (1971) relegated *Opisthopsalis* (a junior synonym of *Sarcodon*) and *Hyracolestes* to the Deltatheridiidae. They regarded *Praolestes* as a zalambdalestid genus belonging to their new order Anagalida. *Stilpnodon* is too poorly represented for assignment to any family with certainty, but its P_4 construction is markedly different from that of all other geolabidine genera recognized by Van Valen. Robinson (1968) has recently reported that the type species of *Myolestes (M. dasypelix)* is referable to a new species of *Nyctitherium.*

The remaining geolabidine genera, *Centetodon, Embassis,* and *Geolabis* are the subjects of a major nomenclature controversy. McKenna has suggested (personal communication) that they are probably all synonymous, but varied opinions have been expressed as to which name has priority (see, for instance, McKenna 1960*b;* Clark 1966). Lillegraven and McKenna are currently reviewing the Geolabidinae and have made progress toward solving this nomenclatorial problem and refining the interspecific taxonomy of the group. One of their suggestions *(personal communication)* is that *Centetodon,* the earliest name, should have priority. Pending results of their study, I have referred to geolabidine material in this report as *Centetodon* sp.

A problem still remains concerning the broader affinities of the Geolabidinae. Although the members of this group (*Centetodon* and closely related, probably synonomous genera) resemble erinaceid-like forms in aspects of the dentition, they show a number of distinctive dental and cranial specializations (see McKenna 1960*b*). McKenna *(personal communication)* has suggested that geolabidines may be closely related to palaeoryctids like *Batodon.* I favor removing the Geolabidinae from the Adapisoricidae and raising the Geolabidinae to familial rank, as Butler has proposed (1972). Butler (1972) has remarked that geolabidines show a number of derived similarities with *Solenodon* and soricids and the allocation of this group to the Soricoidea seems reasonable.

With the exclusion of the above categories, there remains within the Adapisoricidae only the Creotarsinae and the Adapisoricinae. The latter subfamily has been the subject of major modification. Of the six genera included by Van Valen (1967) within the Adapisoricinae, only one, *Adapisorex,* seems to be definitely referable to the subfamily and the validity of this category is doubtful (see Clemens 1973:37, for a recent summary of the problem).

Van Valen (1967:272) conceded that the Creotarsinae lacked unity but could not be subdivided. The Creotarsinae is indefinable on purely morphological grounds, and I do not recognize the subfamily in this report. A subdivision of the Adapisoricidae seems unjustified until better material is available.

ORDER PROTEUTHERIA
FAMILY APATEMYIDAE
SUBFAMILY APATEMYINAE
GENUS *APATEMYS* MARSH
APATEMYS cf. BELLUS MARSH

Figure 3

Referred specimens.—left P_1 (or P_2), UCMP 101440; left lower incisor, UCMP 101623.

Locality.—UCMP loc. V-72158.

Description.—P_1 (or P_2, see West 1973:19) is single-rooted and procumbent with a bladelike crown. The labial face of the blade is strongly concave. A small,

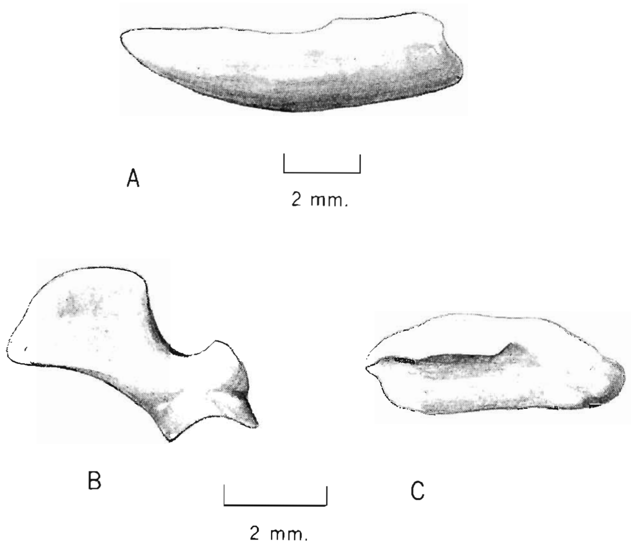


FIGURE 3. *Apatemys,* cf. *A. bellus,* left lower incisor UCMP 101623; a. labial view. Left P_1 (or P_2), UCMP 101440; b. labial view, c. occlusal view.

distinct cusp is present at the posteriormost region of the crown. Dimensions of P_1 (or P_2) are: length = 5.15, width = 1.96; lower incisor (UCMP 101623), length = 9.31, width = 1.91.

Remarks.—the bladelike P_1 (or P_2) (UCMP 101440) is highly characteristic of Eocene-Oligocene apatemyids. It compares closely in size with the homologous tooth of *Apatemys rodens* (described as a P_3 in Gazin 1958: 88-89). West (1973) has recently made all species of *Apatemys,* including *A. rodens* and *A. downsi* from the Sespe Formation (Gazin 1958), junior synonyms of *A. bellus.* The San Diego specimen may represent a geographic extension of *A. bellus.* However, since the major criteria used in apatemyid taxonomy are exclusive of P_1 (P_2) or incisor morphology, there exists the possibility that the San Diego specimens are referable to a new species of *Apatemys.* The P_1 (P_2) of the Oligocene *Sinclairella* differs from UCMP 101440 in lacking a posterior accessory cusp.

FAMILY PALAEORYCTIDAE
SUBFAMILY ?PALAEORYCTINAE
GENUS AND SPECIES *INDET.*

Figure 4

Referred specimen.—left mandible fragment with M_{2-3}, UCMP 96081.

Locality.—UCMP loc. V-6888.

Description.—M_2 has a relatively very tall trigonid. The bladelike paraconid is lower than the protoconid and the metaconid is lingual to the lowest point of the

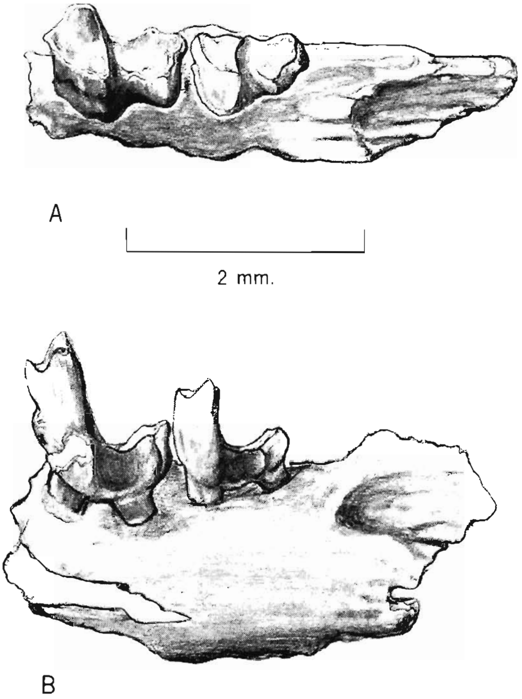


FIGURE 4. Palaeoryctine gen. and sp., left mandible fragment with M_{2-3}, UCMP 96081; a. occlusal view, b. labial view.

protocristid, and is slightly labial to the apex of the protoconid. A narrow anterior cingulum dips steeply ventrolabiad. The talonid is elongate and narrower than the trigonid. The hypoconulid is the highest cusp of the talonid, is situated slightly closer to the entoconid than to the hypoconid, and is strongly produced posteriorly. The laterally compressed entoconid is situated more anteriorly than the hypoconid. The crista obliqua contacts the protoconid labial to the protoconid-metaconid juncture. Dimensions of the M_2 are: length = 1.22, trigonid width = 0.77, talonid width = 0.61.

M_3 is similar in morphology but is considerably reduced relative to M_2. The trigonid is also lower relative to the talonid. The talonid is relatively narrower than that of M_2. The small entoconid is set more posteriorly than the hypoconid. The hypoconulid is more posteriorly produced than in M_2. Dimensions of M_3 are: length = 1.04, talonid width = 0.47.

Remarks.—the lower molars in UCMP 96081, with their high transverse trigonids and low narrow talonids, resemble those of *Palaeoryctes* (Matthew 1913), *Pararyctes* (Van Valen 1966), and *Cimolestes propalaeoryctes* (Lillegraven 1969). They are distinct from the M_2 and M_3's of these genera primarily in that 1) the trigonids are of slightly lower relief; 2) the paraconid is much higher relative to the protoconid and metaconid, as is the lingual opening of the prefossid; 3) the anterolingual face of the protoconid is lower and less steep; 4) the talonid in M_2 is anteroposteriorly more elongated and relatively wider; and 5) the M_3 is considerably less tall and smaller in overall dimensions than the M_2. Although the molars in UCMP 96081 were effective shearing and piercing elements, the above differences suggest that they do not approach the "zalambdodont" condition as closely as do the molars of *Pararyctes, Palaeoryctes,* or *Cimolestes propalaeoryctes.*

The affinities of the San Diego animal are unclear. It is an Eocene form which, despite its late appearance, possesses features in the molars less specialized than Paleocene palaeoryctines and the Cretaceous *Cimolestes propalaeoryctes.* Hypothesized derivation of the species represented by UCMP 96081 from *Palaeoryctes, C. propalaeoryctes* or similar forms would require reversals in trends from those which occurred in the evolution of *Palaeoryctes.* Due to the lack of more complete material, I can only tentatively assign this San Diego insectivore to the Palaeoryctidae as a probable new genus showing affinities most closely with *Palaeoryctes, Pararyctes,* or *Cimolestes (propalaeoryctes).*

While the San Diego animal represented by UCMP 96081 is not excluded from the rather broad definition of the Didelphodontinae (see Van Valen 1966:68), it shows stronger tendencies toward the dental specializations of the Palaeoryctinae. I would refer the San Diego species to the Palaeoryctinae with reservations, acknowledging that more complete evidence may refute this action.

Some students may suggest that the species described here be given a formal taxonomic name. I feel that the assignment of a new generic and specific name on the basis of specimen UCMP 96081 alone could prove to be an impediment to its future study. Insectivore taxonomy is already overburdened with problematic genera represented by one or two teeth.

ORDER INSECTIVORA
SUBORDER ERINACEOMORPHA
SUPERFAMILY ERINACEOIDEA
FAMILY ADAPISORICIDAE
SESPEDECTES STOCK
SESPEDECTES SINGULARIS STOCK

Sespedectes singularis is by far the most abundant insectivore in the San Diego collections. There are, at present, more than 297 isolated teeth and over 43 jaws with two or more teeth referable to this species. Stock (1935) first described *S. singularis* from the Eocene Sespe Formation located north of Los Angeles, in Ventura County, California. No significant morphological differences between specimens from the San Diego localities and the Sespe localities have been recognized. A detailed description and a consideration of the affinities of *Sespedectes* are provided elsewhere (Novacek, MS.).

PROTERIXOIDES STOCK
PROTERIXOIDES DAVISI STOCK

This species is a rarity in San Diego deposits; it is represented by only four specimens. Stock (1935), however, reported that *Proterixoides davisi* was very abundant in the Sespe localities. *P. davisi* bears a strong similarity to *Sespedectes singularis,* differing from the latter only in its much larger size and in details of upper premolar and molar morphology. There is little doubt that the two species are closely related. For a description and analysis of material referable to *Proterixoides,* see Novacek (MS.).

CRYPTOLESTES NEW GENUS

Etymology.—Crypt-G.: hidden, secret; referring to the cryptic identity of material representing this genus. Until the type specimen was recovered, all M^2's were identified as ?leptictid upper molars, and lower teeth were referred to a new species of *Sespedectes.* -lestes G.: robber, following the tradition of the usage of this term to designate small insectivorous animals.

Type species.—*Cryptolestes vaughni.*

Diagnosis of genus.—*Cryptolestes* is distinguished from all other adapisoricid genera by the following combination of characters. DP^4 is three-rooted with a paracone, metacone, protocone, prominent metastylar lobe, and lingual cingula. P^3 is not greatly reduced relative to P^4 and is similar in morphology to it. The upper molars, especially M^2, are transverse teeth with sharp cusps. The paracone and metacone have steep labial faces. The labial lobes, particularly the parastylar lobe of M^2, are prominent. A distinct precingulum is consistently present on M^{1-3} The hypocone of M^{1-2} is well-developed, but lower than the protocone. The paraconule and metaconule are distinct and subequal in size. The postmetaconule wing continues labially as a metacingulum. M^3 has a paraconule. DP^4 is heavily worn by the time the upper molars erupt. There are three mental foramina in the mandible.

CRYPTOLESTES VAUGHNI NEW SPECIES

Figures 5-8, Table 2

Etymology.—named in honor of Peter P. Vaughn, vertebrate paleontologist and teacher.

Holotype.—UCMP 103912, a left maxillary fragment with DP^4 - M^2 and unerupted P^4.

Type locality.—V-71211, Mission Valley Formation.

Referred Specimens.—left mandible with M_{1-3} and alveoli for C - P_4, UCMP 96155; isolated teeth and tooth fragments: P^3, UCMP 101316 and 101437; six P^4's, UCMP 96123, 101128, 101292, 101543, 101605, 101615; 11 M^1's, UCMP 99320, 99427, 101015, 101023, 101322, 101409, 101441, 101531, 101610, 103895, 104407; 22 M^2's, UCMP 96111, 96148, 96439, 96441, 99354, 99387, 99438, 101044, 101120, 101317, 101463, 101473, 101477, 101486, 101505, 101546, 101624, 101636, 101646, 101698, 103904, 104798; 11 M^3's, UCMP 96109, 101049, 101069, 101107, 101124, 101125, 101422, 101499, 101587, 101696, 101744; 9 P_4's, UCMP 96153, 96409, 101411, 101432, 101437, 101502, 101585,

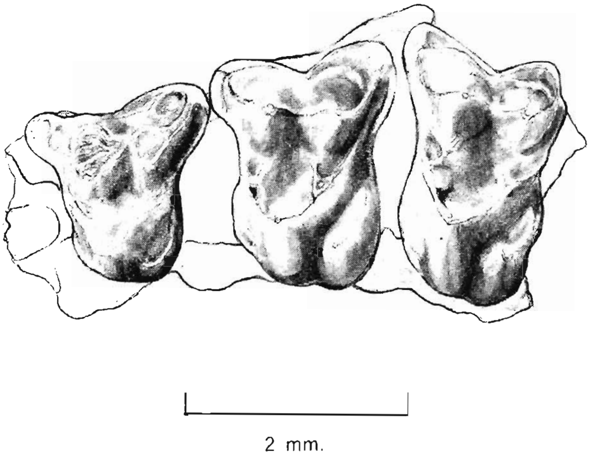


FIGURE 5. *Cryptolestes vaughni,* new genus and species. Holotype, UCMP 103912, left maxillary fragment with DP^4-M^2 and unerupted P^4; occlusal view.

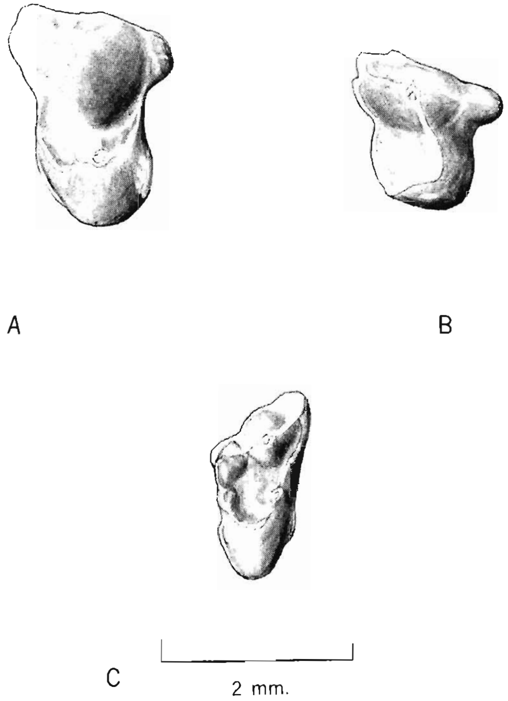


FIGURE 6. *Cryptolestes vaughni,* new genus and species; a. right P^4, UCMP 101128; b. right P^3, UCMP 101437; c. right M^3, UCMP 101587. All views occlusal.

101608, 101609; 9 M_1's, UCMP 96143, 101020, 101051, 101074, 101414, 101429, 101485, 101535, 101606; 16 M_2's, UCMP 101026, 101030, 101039, 101050, 101072, 101088, 101090, 101104, 101323, 101419, 101433, 101462, 101478, 101542, 101618, 103967; 11 M_3's, UCMP 96445, 101034, 101075, 101105, 101108, 101117, 101313, 101328, 101456, 101500, 104409; edentulous jaw fragment, UCMP 104413.

Localities.—UCMP locs. V-6840, V-6873, V-6882, V-68116, V-71175, V-71176, V-71180, V-71183, V-71216, V-72157, V-72158, V-72176, V-73188.

Diagnosis of species.—as for genus.

Description.—DP^4- in the type specimen (UCMP 103912) is a heavily worn three-rooted tooth with a paracone, metacone, and protocone, prominent metastylar lobe, anterior accessory cuspule, and lingual cingula. There is no evidence of a paraconule or metaconule. The presence of a hypocone is suggested by a swelling in the posterolingual corner of the crown and the rise of the postcingulum in this region.

The three-rooted P^3 is slightly wider than long with a high, robust paracone. There is a strong metastylar crest and a minute accessory cuspule at the base of the anterior face of the paracone. The protocone is lower than the paracone and situated lingual and slightly anterior to it. Wear is most notable on the apices of the protocone, paracone, and anterior accessory cuspule, the posterior face of the protocone, and the metacrista.

P^4 is strikingly similar to P^3 in structure differing from the latter only in its larger size and in having a more oblique anterior margin, a relatively more prominent anterior accessory cuspule, and narrow lingual cingula.

The upper molars have bilobate labial margins and sharp, conical cusps. In M^1, the metacone and paracone are well separated and subequal in height. The metaconule and paraconule are well-developed, and the postmetaconule wing continues labiad as the metacingulum. A narrow precingulum is present. The protocone is situated directly lingual to the paracone. There is a distinct hypocone approximately two-thirds the height of the protocone. The postcingulum terminates at the apex of the hypocone. M^2 is similar to M^1 except that it is more transversely elongate and anteroposteriorly compressed, it has a more prominent parastylar lobe, a weaker metastylar lobe, and a more anteroposteriorly compressed hypocone. M^3 differs from M^{1-2} in having a weak metacone situated at the posterolabial corner of the crown and in the absence of a metaconule.

P_4 has a tall protoconid, weak metaconid and vestigial paraconid. The P_4 talonid is a transverse ridge with two minute cuspules.

The lower molars have subequally tall metaconids and protoconids, reduced and blade-like paraconids, and narrow anterior cingula. In M_{1-2} the entoconid and hypoconid are subequal in height and situated directly opposite each other. The hypoconulid is a weak cusp positioned nearly directly between, but slightly posterior to, the entoconid and hypoconid. M_3 is reduced relative to M_{1-2}. The M_3 trigonid is anteroposteriorly elongate. The hypoconulid is produced posteriorly and situated closer to the entoconid than to the hypoconid. The hypoconulid and entoconid are taller than the hypoconid. Wear on the hypoconids precedes that on the other molar cusps.

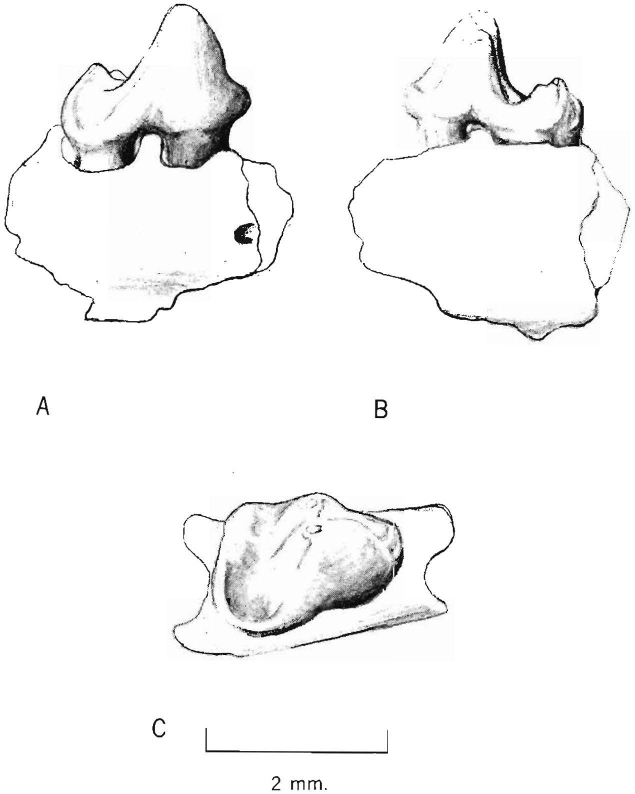


FIGURE 7. *Cryptolestes vaughni,* new genus and species, right mandible fragment with P_4, UCMP 101609; a. labial view, b. lingual view, c. occlusal view.

The mandible has three mental foramina; the anteriormost opening is the largest. The posteriormost mental foramen is situated below the posterior alveolus of P_3.

Remarks.—*Cryptolestes vaughni* and *Sespedectes singularis* show a close similarity in certain dental features. In both forms, P^3 is not greatly reduced relative to the P^4 and is similar in morphology to it. Among erinaceoids in which the upper premolar dentition is known, only *Tupaiodon* (Matthew and Granger 1924), *Litolestes* (Simpson 1936), and the primitive erinaceid *Galerix socialis* (Engesser 1972), possess such a well-developed P^3. The P_4's in both San Diego genera are strikingly similar although *Cryptolestes* differs in having a bicuspid P_4 talonid. P^4 differences between *C. vaughni* and *S. singularis* are truly minor. The lower molars of *Sespedectes* are generally indistinguishable from those of *Cryptolestes*.

Such similarities do not extend to comparisons between the upper molars in both genera. *Cryptolestes* differs markedly from *Sespedectes* in the possession of

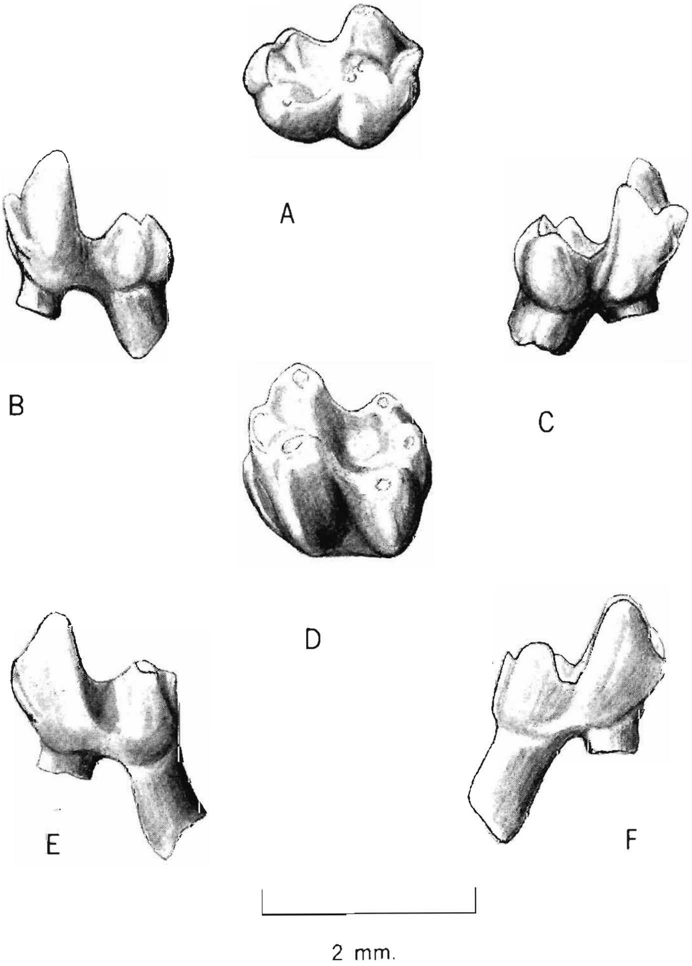


FIGURE 8. *Cryptolestes vaughni*, new genus and species, right M_3, UCMP 101328; a. occlusal view, b. lingual view, c. labial view. Left M_2, UCMP 101542; d. occlusal view, e. labial view, f. lingual view.

the following characters of the upper dentition: 1) the upper molars, especially M^2, are transversely wider and more anteroposteriorly compressed, with sharper cusps; 2) the paracone and metacone are taller, more conical cusps, and their labial faces are clearly steeper than their lingual faces; 3) the labial lobes, particularly the parastylar lobe of M^2, are more prominent; 4) a distinct precingulum is consistently present on M^{1-3}; 5) the hypocone in M^2 is anteroposteriorly more compressed than in

TABLE 2

Measurements of teeth referred to
Cryptolestes vaughni new genus and new species

Element	N.	O.R.	M.	S.D.	S.E.	C.V.
P_4						
length	7	1.75-1.91	1.81	0.058	0.022	3.2
width	7	1.01-1.18	1.09	0.064	0.024	5.9
M_1						
length	9	1.55-1.78	1.66	0.073	0.024	4.4
trigonid width	9	1.12-1.37	1.26	0.066	0.022	5.2
talonid width	8	1.10-1.38	1.24	0.094	0.033	7.6
M_2						
length	15	1.40-1.68	1.57	0.100	0.026	6.4
trigonid width	16	1.23-1.47	1.34	0.077	0.019	5.7
talonid width	17	1.16-1.42	1.27	0.078	0.019	6.2
M_3						
length	13	1.45-1.75	1.55	0.086	0.024	5.6
trigonid width	13	0.89-1.17	1.05	0.151	0.042	14.7
talonid width	12	0.75-1.01	0.86	0.070	0.020	8.2
P^4						
length	4	1.61-1.75	1.65	0.070	0.035	4.3
anterior width	5	1.92-2.04	1.98	0.055	0.025	2.8
posterior width	6	1.72-2.08	1.91	0.123	0.050	6.4
M^1						
length	6	1.50-2.35	1.86	0.334	0.136	17.9
anterior width	3	1.86-2.03	1.95	0.086	0.049	4.4
posterior width	3	2.03-2.23	2.15	0.108	0.062	15.0
M^2						
length	12	1.14-1.48	1.39	0.101	0.029	7.3
anterior width	10	1.99-2.51	2.23	0.203	0.064	9.1
posterior width	15	1.72-2.30	2.11	0.047	0.046	8.4
M^3						
length	10	0.88-1.23	1.08	0.103	0.033	9.6
anterior width	10	1.65-2.07	1.86	0.152	0.049	8.2
posterior width	10	1.06-1.43	1.29	0.026	0.035	8.5

the homologous tooth of *Sespedectes;* 6) the postmetaconule wing continues labially as a metacingulum; 7) DP^4 is heavily worn at the time the upper molars are erupted. These comparisons demonstrate that *Cryptolestes* is closer in upper molar morphology to certain adapisoricids than to *Sespedectes* and *Proterixoides*.

The upper molars of *Cryptolestes, Macrocranion* (Tobien 1962), *Entomolestes (nitens)* (McKenna 1960a), *Messelina* (Tobien 1962), *Litolestes,* and *Scenopagus*

(McKenna and Simpson 1959) are distinguished from those of *Sespedectes* and *Proterixoides* in their common possession of sharper paracones and metacones with steeper labial faces, a relatively lower hypocone, a distinct paraconule, subequal in size to the metaconule, and a metacingulum formed by the labial continuation of the postmetaconule wing.

In all of the above genera except *Scenopagus* and possibly *E. nitens,* the molars are less transversely developed with weaker labial lobes than in *Cryptolestes.*

Macrocranion can be distinguished from *Cryptolestes* by the narrower stylar shelf, more labially situated conules, and weaker precingula in its upper molars. It is separated from both *Cryptolestes* and *Sespedectes* by its reduced P^3 and elongate M_3.

Messelina differs from *Cryptolestes* in much the same features as does *Macrocranion,* but is more clearly separated in its possession of a P_4 with a prominent paraconid and a basined talonid.

The upper molars of *Scenopagus mcgrewi,* noted above, are much more transverse with a stronger parastylar and metastylar lobe than those of *Cryptolestes.* In addition, *Scenopagus* has a smaller hypocone and more lingually situated conules.

Showing a close resemblance with *Cryptolestes* are the upper molars referable to cf. *Entomolestes nitens* by McKenna (1960a: 58-59). Except for the more lingual position of the conules, a slight difference in outline of the labial margin, and a weaker hypocone, the upper molars of *E. nitens* seem hardly different from those of *Cryptolestes.* For the present, cf. *E. nitens* must be distinguished by its possession of a P^4 with an incipient metacone and lower molars with relatively wider talonids.

Litolestes notissimus (Simpson 1936:24) demonstrates a striking resemblance between that genus and *Cryptolestes* in upper molar morphology. The only differences observed are the presence of a stronger parastylar lobe in M^1, weaker parastylar lobes in M^{2-3}, and a weaker precingulum. *Litolestes* is separated by the possession of an incipient metacone on P^4 and a smaller P^3. There is a possible close relationship between *Litolestes, Entomolestes, Cryptolestes,* and *Sespedectes.*

It is evident that in certain dental characters *Cryptolestes* bridges the morphological gap between *Sespedectes* (and *Proterixoides*) and other adapisoricids. Indeed, *Cryptolestes* may be closer to the structure of the morphotypical ancestor of *Sespedectes* and *Proterixoides* than any other primitive erinaceoid known. Evolution of the latter two genera might have involved the loss of primitive characters, such as the second cuspule on the P_4 talonid, and a reduction of cutting elements in the cheek teeth, with an increased development of adaptations for a crushing mode of occlusion. Concomitant with these specializations came a change in the process and timing of tooth eruption. Unlike the condition in *Cryptolestes,* the eruption of the characteristic erinaceoid cutting P^4 is delayed in *Sespedectes.* It is possible to speculate that in *Sespedectes* the molariform DP^3 and DP^4 functioned with the molars as an extensive crushing battery for a significant part of the animal's life span. The evolution of *Cryptolestes* involved none of these modifications and certain primitive dental characters were retained.

Superfamily ?Soricoidea
Family Nyctitheriidae
Subfamily Nyctitheriinae
Genus *Nyctitherium* Marsh 1872
cf. *Nyctitherium* sp.

Figure 9

Referred specimens.—incomplete isolated right upper molars, UCMP 96085 and 101011.

Localities.—UCMP locs. V-71180 and V-72158.

Description.—UCMP 101011 is a damaged right molar missing the entire stylar shelf and most of the metacone. The protocone is nearly as tall as the paracone. The paraconule is situated more lingually than the metaconule. Two distinct wings diverge labially from each conule. The precingulum is narrow but distinct, extending from the anterolingual base of the protocone to a point below the most labial section of the preparaconule wing. A prominent postcingulum is strongly developed into a low hypocone. The apices of the protocone and paracone show slight wear.

A well-developed metacrista is the only notable feature in UCMP 96085 not preserved in UCMP 101011.

Remarks.—UCMP 96085 and 101011 are very close in structure to the upper molars of *Nyctitherium velox* from the middle Eocene (Bridgerian) of North America (Robinson 1968:132, Figs. 2, 6, specimens YPM 15251 and YPM 13515). The

Figure 9. cf. *Nyctitherium* sp., upper right molar, UCMP 101011; occlusal view.

San Diego specimens differ from *N. velox* upper molars only in being more anteroposteriorly compressed and in having a slightly more lingually projecting hypocone (evident in UCMP 101011). In these features UCMP 101011 resembles *Saturninia gracilis,* a former soricid relegated by Robinson (1968) to the Nyctitheriidae. No definite conclusions can be reached concerning this comparison due to the lack of more complete material. In short, UCMP 96085 and 101011 indicate the presence of a nyctithere, possibly congeneric with either *Nyctitherium* or *Saturninia,* in the San Diego Uintan fauna.

FAMILY GEOLABIDIDAE
SUBFAMILY GEOLABIDINAE
GENUS *CENTETODON* MARSH
CENTETODON SP.

Referred specimens.—P^4, UCMP 101306; M^1's, UCMP 101046, 101076, 101301, 101446; M^2's, UCMP 99390, 101082, 101303, 101304, 101307; M^3's, UCMP 101089; P_1, UCMP 101309; P_4's, UCMP 96127, 96137, 99321, 101070, 101081, 101084; M_1's, UCMP 99321, 101055, 101305; M_2's, UCMP 99431, 99434 101123, 101126, 101302; M_3, UCMP 101083.

Localities.—UCMP locs. V-6888, V-68116, V-71180, V-71183, V-72157, V-72158.

Remarks.—The material referable to probably more than one species of *Centetodon* from the San Diego Uintan will be described by Lillegraven and McKenna in their forthcoming discussion of the genus.

BATODONOIDES NEW GENUS

Etymology.—Bato-G., thorn, -don, G. tooth;-oides G., like; referring to the close resemblance to the genus *Batodon.*

Type species.—*Batodonoides powayensis* new species.

Diagnosis.—*Batodonoides* is a diminutive geolabidine significantly smaller than all other members of that subfamily. The lower dentition of *Batodonoides* is not significantly different from that of *Centetodon* except for its smaller size. The upper molars of *Batodonoides* distinguish this genus from all other geolabidines in the possession of the following combination of characters: high piercing cusps, a wide stylar shelf, a strong sharp metacrista, a prominent lingual paraconule, no metaconule, a narrow precingulum and postcingulum not connected across the lingual base of the protocone, a postcingulum developed into a minute hypoconal crest, and a single lingual root.

BATODONOIDES POWAYENSIS NEW SPECIES

Figures 10-12, Table 3

Etymology.—referring to the geologic and geographic origin; all specimens referable to the species found in beds of the Poway Group; type recovered in a locality near the town of Poway, California.

Type.—UCMP 96459, fragment of right mandible with P_4 and M_1.

Type locality.—UCMP loc. V-71211, Mission Valley Formation.

Referred specimens.—fragments of mandibles with P_1, UCMP 96457; P_4's, UCMP 96431, 96432, and 101311; M_1, UCMP 96403; M_{2-3}, UCMP 96448; isolated M_1's, UCMP 96138, 96145; M^1's, UCMP 96126, 96456; edentulous mandible fragments, UCMP 96087, 101458.

Localities.—UCMP locs. V-71175, V-71176, V-71181, V-71211, V-71216, and V-72158.

Diagnosis.—as for genus.

Description.—The anterior edge of the ascending ramus is nearly perpendicular to the horizontal ramus of the mandible. The depth of the jaw below the M_2 is approximately 0.95 mm. The posterior mental foramen is below the anterior root of P_4. An anterior mental foramen is below an alveolus for the posterior root of P_2 in UCMP 101311. A low rounded horizontal ridge extends posteriorly from the base of the anterior border of the median face of the ascending ramus.

P_1 is double-rooted, blade-like, and laterally compressed. The main cusp projects anteriorly, forming a prominent, slightly blunted "nose." A minute posterior accessory cuspule is the most posterior element of the crown.

P_4 has a high trigonid dominated by the protoconid. Most of the labial face of the metaconid is fused to the protoconid, resulting in a steep posterior trigonid wall, broken only at its crest. A steeply descending paralophid extends anterolinguad to the extremely low, well separated paraconid. A blunt shelf descends from the apex of the low paraconid curving around the base of the labial side of the paracristid. The talonid is laterally compressed and lingually shifted, leaving a broad and deep hypoflexid. A posterior cuspule is prominent and close to the center of the back of the talonid. Major wear occurs on the protoconid and the metaconid apices, the protocristid, the entire posterior trigonid wall (except for a narrow labial margin), the hypoflexid, and the anterolabial face of the posterior cuspule.

The trigonid of M_1 is high and curves lingually toward its apex more than does the trigonid of P_4. The protoconid is higher than the metaconid. The median walls of the protoconid and the metaconid are fused nearly to the apex of the metaconid. The paraconid is low relative to the protoconid and the metaconid of M_1 but higher than the paraconid of P_4. The paraconid anterolabial face is much higher than the talonid of P_4. A short cingulum slopes ventrad at a steep angle on the anterolabial face of the paraconid. The talonid is narrower than the trigonid and has a deep basin.

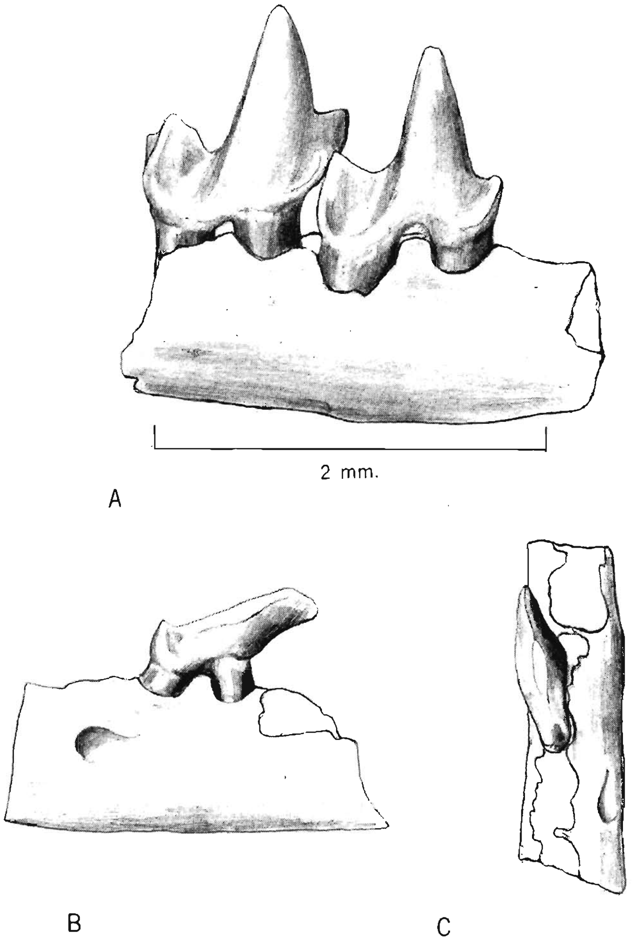


FIGURE 10. *Batodonoides powayensis*, new genus and species, Holotype, UCMP 96459, right mandible fragment with P_4-M_1; a. labial view. Right mandible fragment with P_1, UCMP 96457; b. labial view, c. occlusal view.

The hypoconid and the hypoconulid are subequal in height. The entoconid is the smallest cusp of the talonid. The hypoconulid is situated posterior and central to the hypoconid and entoconid. A crista obliqua joins the base of the posterior trigonid wall far below the lowest point of the protocristid. Wear on M_1 is similar to that on P_4.

Only the talonid of M_2 is preserved (UCMP 96448). At the stage of wear observed, the apices of the closely appressed hypoconulid and entoconid are obscured.

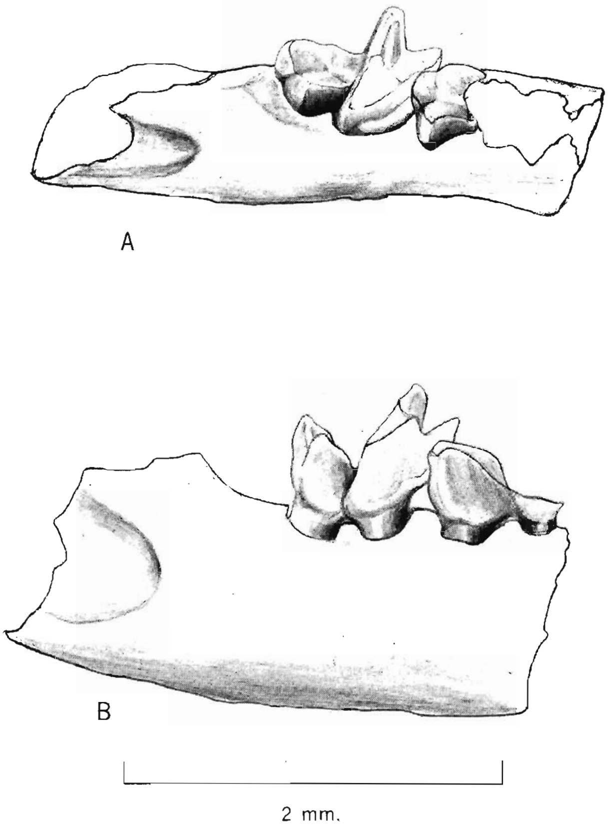


Figure 11. *Batodonoides powayensis,* new genus and species, right mandible fragment with partial M_2 and complete M_3, UCMP 96448; a. occlusal view, b. labial view.

Both cusps are well separated from the hypoconid. The talonid appears to be slightly narrower than the damaged trigonid. There is pronounced wear on the steep labial surface of the entoconid and hypoconulid, and the anterolabial face of the hypoconid. Slight wear exists on the lingual face of the hypoconid.

In the only M_3 preserved (UCMP 96448), the apex of the protoconid is broken away. The talonid is more transversely compressed than those of M_{1-2}. The entoconid is undiscernible, being extremely weak, or possibly absent. The lingual rim of the talonid appears as an unbroken ridge which steeply descends from the apex of the prominent hypoconulid to the base of the posterior metaconid ridge. A hypoconid is present, but it is much lower than the hypoconulid. The trigonid is more acutely triangular in outline than that of M_1. Wear patterns are similar to those in P_4-M_2 mentioned above.

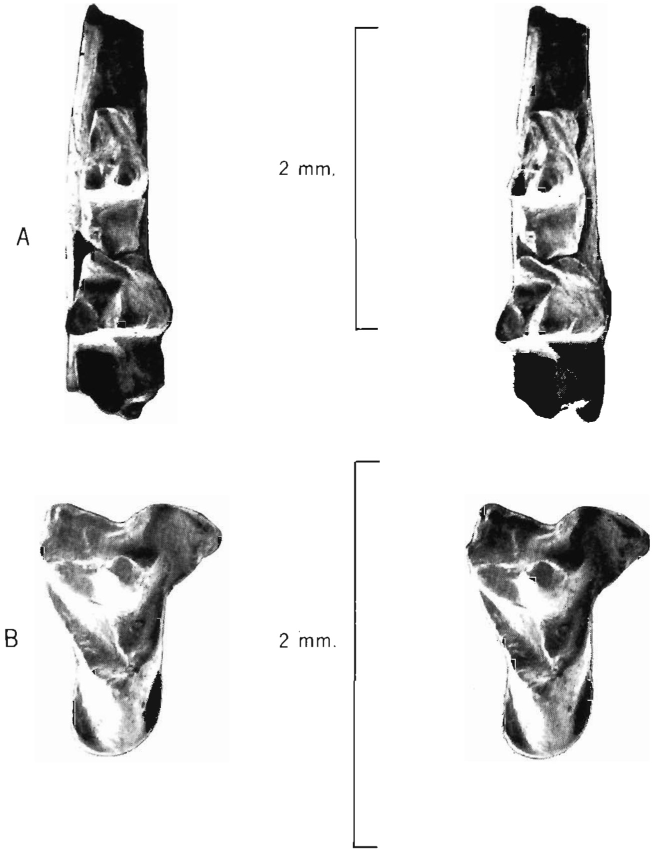


FIGURE 12. *Batodonoides powayensis,* new genus and species, a. Holotype, UCMP 96459, fragment of right mandible with P_4-M_1; b. right M^1, UCMP 96126. All views occlusal. Stereophotographs taken with scanning electron microscope.

The upper molars are transversely wide and anteroposteriorly compressed with high sharp cusps. The paracone is slightly higher than the subequal protocone and metacone. At late stages of wear, the metacone is considerably reduced in height relative to the paracone. The metacone is slightly posteriorly inclined. A very narrow precingulum extends from a point below the paraconule nearly to the lingual edge of the tooth. The postcingulum is developed into a minute hypoconal crest. The labial edge of the wide stylar shelf has an ectoflexus in its mid-region. There is an anteriorly projecting, cuspate parastylar lobe. The paraconule is prominent and lingual, being situated high on the preprotocrista near the upper section of the protocone. A metaconule is absent. The high, sharp metacrista extends to the extreme posterolabial corner of the tooth. The paracrista is low and extends to the apex of the parastylar cusp. There is a vertical trough on the lingual face of the parastylar lobe. Major wear

TABLE 3

Measurements of teeth referred to
Batodonoides powayensis new genus and species

Element	Measurements				
P_1	96457[4]				
length	0.75				
width	0.29				
P_4	96459 (type)	96432	96431	101311	
length	0.90	0.91	0.92	0.93	
trigonid width	0.42	0.41	0.49	0.48	
talonid width	0.30	0.33	0.39	0.39	
M_1	96459 (type)	96432	96138	96145	96403
length	0.99	1.00	1.00	1.04	1.05
trigonid width	0.62	0.61	0.60	0.70	0.65
talonid width	0.48	0.51	0.50	0.52	0.51
$\frac{\text{talonid width}}{\text{trigonid width}}$	0.78	0.83	0.84	0.74	0.79
M_3	96448				
length	0.84				
trigonid width	0.60				
talonid width	0.38				
$\frac{\text{talonid width}}{\text{trigonid width}}$	0.64				
$M^{?1}$	96126	96456			
length	0.95	1.01			
anterior width	1.29	1.15			
posterior width	1.33	1.26			

[4] All numbers are UCMP specimen numbers.

occurs on the apices of the paracone, metacone, the parastylar cusp, the metacrista and centrocrista, preprotocrista, postprotocrista, and labial face of the protocone. Definite shear abrasion can be seen on the anterior and the posterior faces of the trigon cusps, the anterior face of the paraconule, and the posterior wall of the metacrista.

Remarks.—The reference of UCMP 96126 and 96456 (both upper molars) to *Batodonoides powayensis* is not beyond question, but I believe it is supported by several observations. Both upper molar specimens are from localities in which lower teeth of *B. powayensis* were recovered. The only other insectivore teeth collected at these sites were much larger in size. Further, UCMP 96456 was found in the same locality (V-71211) as most of the lower dentitions representing this species, including the type. The teeth are nearly as long and slightly more than twice as wide as the lower molars. Direct manipulation shows that the upper molars occlude adequately with the M_1 of *Batodonoides*.

Functional significance of dental features.—The morphology of the upper and lower molars of *Batodonoides* suggests that occlusion at the beginning of the powerstroke was mainly orthal, followed by lingual movement of the lower molars during the late phases of the powerstroke. This latter movement produced transverse shear against the upper molars.

The relatively lingual position of the paracone and metacone increased the effective shearing surface of the labial prevallum and postvallum. There is a distinct preparaconule wing, providing a second cutting edge opposing the back of the trigonid which functioned in a later phase of the powerstroke. The lingual position of the paraconule in *Batodonoides* served to elongate the preparaconule wing and thus the effective area of this shearing surface. The protocone is transversely wide, anteroposteriorly compressed and transversely aligned with the paracone. Such a condition, as noted by Crompton (1971:70), may be viewed as an extension of the shearing surface of the preparaconule wing, and thus full advantage has been taken of transverse mandibular movement. Because of this specialization, the anterior face of the protocone would be in contact with the back of the trigonid at the end of the powerstroke. The hypoflexid in M_{1-3} of *Batodonoides* is deep and the talonid is laterally compressed, increasing the area of shear surface between the posterior wall of the trigonid and the anterior face of the paracone. This condition would also increase the amount of shear surface between the anterolabial face of the hypoconid and the postparacrista. Deep hypoflexids are often present in mammals in which the paracone is hypertrophied. The narrow precingulum in *Batodonoides* approaches the condition in *Didelphodus* (see Crompton 1971) in which the precingulum is entirely lacking. The precingulum provides an additional cutting edge for shear against the back of the trigonids at the end of the occlusal cycle. That the small hypoconal crest in *Batodonoides* actually ever came in contact with the small hypoconulid and entoconid is highly doubtful. It possibly served as a trap for ingested food. The lack of a metaconule in *Batodonoides* is highly interesting. I feel that the extreme reduction or loss of the metaconule allows for the occlusion of the protocone with the small talonid basin at the end of the powerstroke. It is interesting to note that insectivores with very reduced laterally compressed talonids (e.g., certain tenrecs, apternodontines, etc.) often lack conules.

Affinities.—The lower dentitions of *Batodonoides powayensis* are strikingly similar to those of *Centetodon* (=*Geolabis* see McKenna 1960*b*), differing mainly in their much smaller size. Since disparity in size is nearly always a poor criterion for separating taxa above the specific level, an allocation of *Batodonoides* to *Centetodon* based solely upon lower dentitions seems reasonable. However, upper molars of *Centetodon* differ from those referred to *Batodonoides* in having a narrower stylar shelf and (in latest Eocene and younger species) two lingual roots. Geolabidines show specialized cranial features, including the elongate snout and enlarged lacrimal foramen, which are highly diagnostic of the group (see McKenna 1960b:134). Until associated dentitions and cranial material referable to *B. powayensis* are known, the species cannot be assigned without question to the Geolabidinae. However, based upon the available evidence, the identification of *Batodonoides* as a distinct geolabidine genus seems the most appropriate.

Material referable to the Late Cretaceous species *Batodon tenuis* (see Lillegraven 1969; Clemens 1973) shows very close similarities, both in size and dental morphology, to *Batodonoides powayensis*. The comparative morphology and possible phyletic relationships of these two genera warrant careful consideration.

Examination of AMNH 58777, a lower jaw with P_{2-4}, M_{1-2} referable to *Batodon tenuis*, shows that that species is nearly identical to *Batodonoides powayensis* in morphology of the lower jaws and dentition. The only difference is the position of the posterior mental foramen below the anterior root of P_4 in *Batodonoides* and below the posterior root of P_4 in *Batodon*. An M_3 (UA 4081) tentatively referred to *B. tenuis* by Lillegraven (1969:84) differs from the homologous tooth in *B. powayensis* in its larger size and in its possession of a relatively wider talonid, a prominent entoconid, and a more salient hypoconulid. Regrettably there are no specimens representing either genus in which the M_3 is associated with teeth anterior to the M_1.

Upper teeth of *Batodon tenuis* are poorly known. Lillegraven (1969:84) tentatively referred a maxillary fragment with an M^2 and a partial M^1 (UA 4081) to *B. tenuis* The M^2 in this specimen shows a similarity to the upper molars of *Batodonoides* in having high cusps, a closely appressed paracone and metacone, narrow lingual cingula, a paraconule, a parastylar lobe of similar morphology, a weak paracrista, and a strong metacrista. However, the M^2 in UA 4081 differs from referred M^1's of *Batodonoides* in that 1) the tooth is transversely wider; 2) there is a metaconule; 3) the precingulum is more elongate and is connected to the postcingulum across the lingual base of the protocone; 4) the stylar shelf is narrower; 5) the postcingulum is not developed into a hypoconal crest; 6) the ectoflexus is less deep; and 7) the paraconule is more labial relative to the apex of the protocone. These comparisons suggest that although the putative upper molars of both genera are similar in basic construction, they are easily distinguished.

Batodon was regarded as a didelphodontine palaeoryctid by Lillegraven (1969) and Clemens (1973), but McKenna, who is now restudying the phylogenetic relationships of *Batodon*, has suggested *(personal communication)* that this genus is an early geolabidine. This seems to be a tenable allocation in view of the strong similarities between *Batodon*, *Batodonoides*, and *Centetodon*. Further, I believe that the palaeoryctid like dental characters of these genera (particularly in *Batodon* and *Batodonoides*) are evidence for a close relationship between the Geolabidinae and palaeoryctids.

FAMILY ?APTERNODONTIDAE
SUBFAMILY ?APTERNODONTINAE
NEW GENUS AND SPECIES UNNAMED

Figure 13

Referred specimen.—isolated right M^2, UCMP 96135.

Locality.—UCMP loc. V-71055. Mission Valley Formation.

Description.—The tooth is transversely wide and anteroposteriorly compressed. The metacone is much lower than the paracone and protocone, which are subequal in height. The metacone is fused with the posterior face of the paracone for most of its height, a condition commonly known as "protozalambdotonty." In posterior view, the metacone has the appearance of a shoulder on the steeply rising metacrista. The posterior faces of the metacone and metacrista form the sheer postvallum of the tooth. The labial faces of the paracone and metacone are strongly concave. The stylar shelf is wide, and there is a deep ectoflexus along its labial margin. The parastylar lobe projects anteriorly and is much more prominent than the metastylar lobe. Although the metacrista is somewhat higher than the paracrista, both structures are sharp and prominent. Conules, a precingulum, a postcingulum, and a stylocone are absent. There is a wear facet on the apex of the protocone. Prominent wear is present on the preprotocrista and postprotocrista. The paracone and metacone apices, the paracrista, and the metacrista show only slight wear. Dimensions of UCMP 96135 are: length = 0.75; anterior width = 1.13; posterior width = 1.00.

Remarks.—The above described semi-zalambdodont characters of this tiny specimen suggest a possible affinity with the middle Eocene to middle Oligocene apternodontine genera, *Oligoryctes* Hough (1956:538-541) and *Apternodus* Matthew (1903). However, UCMP 96135 is distinct from the upper molars of those genera in the possession of a weak metacone, the lack of a strong stylocone, the presence of a prominent protocone, and the absence of cingula external to the anterior and posterior faces of the paracone. In addition, *Apternodus* is significantly larger than the animal from the Eocene of San Diego.

McKenna *(personal communication)* brought to my attention a small M^1 (C M 13761) from the Green River Formation, Wyoming, referable to a new middle Eocene apternodontine genus, *Eoryctes* (*nomen nudum* Romer 1966:381 *ex* McKenna MS.), which is being described in his (unpublished) study of the Apternodontinae. The M^1 of this animal is somewhat intermediate in structure between the San Diego specimen and the upper molars of *Oligoryctes* and *Apternodus* in the possession of a large protocone; however, like the latter two genera, it lacks a metacone and it has both an anterior and a posterior paracingulum.

Although the San Diego animal is approximately contemporaneous with other known apternodontines, the protozalambdodont condition of the paracone and metacone suggests that it is structurally primitive in the dentition to forms such as *Oligoryctes*, *Apternodus*, and *Eoryctes*.

Geolabidine upper molars are protozalambdodont in the partial fusion of the paracone and metacone, but they are distinct from UCMP 96135 in their much larger size and in having a hypocone supported by a distinct root (in latest Eocene and later species), a precingulum, weakly developed conules in some forms, and usually a stylocone.

The upper molars of *Palaeoryctes puercensis* differ from UCMP 96135 in the following ways. The upper molars of *Palaeoryctes* are transversely wider and more anteroposteriorly compressed, with relatively higher cusps. The paracone and metacone in *Palaeoryctes* are fused nearly to their apices, and are subequal in height. The stylar shelf is strongly crested in the region of the parastylar and metastylar lobes in the upper molars of *Palaeoryctes* (see Van Valen 1966:140). It is Van Valen's interpretation (1966) that *Palaeoryctes puercensis* and its allies represent an extremely specialized offshoot of the palaeoryctid basal stock, and the alleged affinities between *Palaeoryctes* and living tenrecoids have been seriously questioned by McDowell (1958:208). However, the question of a possible relationship between *Palaeoryctes* and apternodontines requires closer examination. It seems unlikely that *Palaeoryctes* and the species represented by UCMP 96135 are closely related, but such an arrangement cannot be totally dismissed based on the present meager evidence.

Among recent zalambdodont insectivores, the West African tenrecoid genus *Potamogale* shows the closest similarities in morphology of the upper molars to UCMP 96135. Like the latter, *Potamogale* has a weak metacone and a prominent protocone, a feature which is unique among living tenrecoids. However, *Potamogale* seems more specialized toward zalambdodonty than the San Diego specimen in the labial position of the metacone resulting in the V-shaped outline of the ectoloph characteristic of zalambdodont upper molars. There is also a distinct stylocone in *Potamogale*. Whether the presence of a metacone in *Potamogale* represents an advanced specialization or the retention of a primitive ancestral character is a controversial matter (for opposing arguments, see McDowell 1958:180, and Van Valen 1966:footnote,51).

One final statement should be made regarding the size of UCMP 96135. This upper molar approaches the diminutive size of the upper molars of *Suncus etruscus*, the smallest living mammal. UCMP 96135 is representative of a truly tiny insectivore.

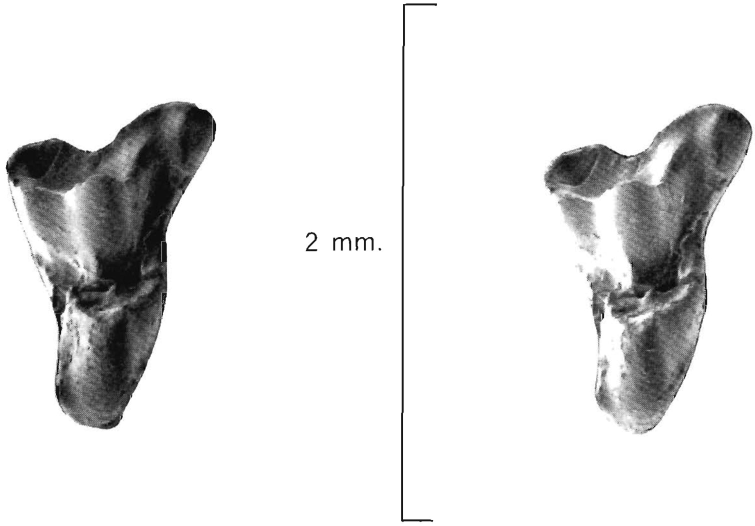


FIGURE 13. ?Apternodontine genus and species, unnamed, right upper molar (M^2?), UCMP 96135; occlusal view. Stereophotographs taken with scanning electron microscope.

INSECTIVORA *INCERTAE SEDIS*
ERINACEOID-LIKE GENUS AND SPECIES

Figure 14, Table 4

Referred specimens.—left M^1, UCMP 101420; fragmentary right M^1, UCMP 101059; right fragmentary M^2, UCMP 101626; right M^3, UCMP 101497; right upper molar fragment, UCMP 101654; right lower molar, UCMP 101617.

Localities.—UCMP locs. V-71180, V-72157, V-72158.

Description.—M^1 is a robust tooth with a conical paracone and metacone which are subequal in height and are well separated by a deep valley. A very prominent metastylar lobe projects labiad and slightly posteriorly. The anteriorly projecting parastylar lobe is much smaller than the metastylar lobe. The metacrista is well-developed. Both the paraconule and the metaconule are distinct and are subequal in basal dimensions. The robust protocone is subequal in height with the paracone and metacone, about twice the height of the hypocone, and is situated directly lingual to the paracone. The precingulum is narrow. The hypocone is a large cusp with a prominent swelling at the posterolingual corner of its base. The apex of the hypocone is positioned well lingual to that of the protocone. UCMP 101626, a probable M^2, differs from M^1 in having a much weaker metastylar lobe.

M^3 (UCMP 101497) is damaged, missing its entire posterior margin. The parastylar lobe projects prominently anterolabiad. The labial tooth margin is straight. There is no metastylar lobe. The paracone is exceedingly higher than the tiny conical metacone. The paraconule is large with a well-developed preparaconule wing but without a postparaconule wing. The metaconule is lower and much more lingually

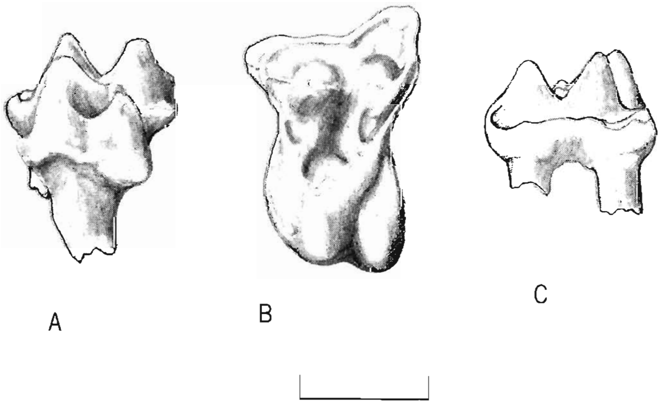


FIGURE 14. Erinaceoid-like genus and species, left M^1, UCMP 101420; a. lingual view, b. occlusal view, c. labial view.

positioned than the paraconule. The protocone is lower than the paracone and is anteriorly recumbent. A narrow precingulum is present.

UCMP 101617, a probable M_2, has an erect trigonid slightly less than twice the height of the talonid. A small anteroposteriorly compressed paraconid is present. A narrow anterior cingulum extends for a short distance along the base of the prevallid. The metaconid is approximately equal in height to the protoconid and is situated directly lingual to it. The crista obliqua contacts the posterior trigonid wall below and slightly labial to the lowest point of the protolophid. The small hypoconulid is situated slightly posterior to and equidistantly between the entoconid and the hypoconid.

Remarks.—The perplexing problems involved in identifying new insectivore species on the basis of a few isolated teeth are fully realized in a consideration of the affinities of the above described material. These specimens resemble homologous teeth of a number of insectivore taxa, but their assignment even at the familial level is unclear.

The molars show the following adapisoricid characters: 1) a large hypocone not connected to the postprotocrista by a ridge; 2) conical paracones and metacones well separated at their bases and subequal in height; 3) a comparatively low trigonid; 4) a weak, anteroposteriorly compressed paraconid; 5) a small, centrally placed hypoconulid; 6) wear patterns which do not suggest a great development of vertical shearing.

TABLE 4

Measurements of teeth referred to
Insectivora *incertae sedis,* Erinaceoid-like gen. and sp.

Element	Measurements	
M^1	UCMP 101420	UCMP 101059
length	3.16	---
anterior width	3.86	4.23
posterior width	4.63	---
M^2	UCMP 101626	
length	---	
anterior width	---	
posterior width	3.55	
M^3	UCMP 101497	
length	1.95	
anterior width	3.10	
posterior width	2.55	
Lower Molar	UCMP 101617	
length	2.71	
trigonid width	2.26	
talonid width	2.14	

The animal represented by the above described specimens shows a close similarity to the adapisoricid genera *Macrocranion tupaiodon* (see Tobien 1962) and *Tupaiodon morrisi* (AMNH 19134, described by Matthew and Granger 1924:1-2), but is easily distinguished from these forms in the prominence of the hypocone and the metastylar spur.

Ankylodon (Patterson and McGrew 1937) from the Oligocene of North America, was placed in Plesiosoricidae by Van Valen (1967:264), but Butler (1972:259) regards this genus as the last surviving member of the Adapisoricidae. The previously unknown upper dentition of *Ankylodon annectens* is now being described by Lillegraven and McKenna *(personal communication).* In the prominence of the metastylar lobe, UCMP 101420 approaches the extreme enlargement of this structure in the M^1 of *Ankylodon.* A resemblance between the two homologous teeth is also seen in the strong, lingually situated hypocone. However, *Ankylodon* is distinct in several major features, including sharper, more anteroposteriorly compressed cusps on the upper molars, taller and sharper lower molar cusps, and evidence of a greater overall emphasis upon vertical shear during occlusion. It is possible that *Ankylodon* arose from an early Uintan adapisoricid-like insectivore with a more generalized morphology resembling that of the above described San Diego teeth.

MICROPTERNODONTINE-LIKE GENUS AND SPECIES

Figure 15

Referred specimen.—a left probable M_2 with the lingual face of the trigonid destroyed, UCMP 101308.

Locality.—V-72158, Mission Valley Formation.

Description.—The trigonid of this tooth is high and quite compressed anteroposteriorly. The protoconid is a sharp cusp, higher than the paraconid, with a steep, slightly overhanging labial edge. A deep prefossid separates the paraconid from the protoconid. A prominent anterior cingulum descends the prevallid at a steep angle. The talonid is elongate with a completely enclosed basin. The hypoconid is more prominent than the entoconid. The hypoconulid and entoconid are approximated but not "twinned." The hypoconulid projects strongly posteriorly. Measurements of the tooth are: length = 1.54; talonid width = 0.89.

Remarks.—UCMP 101308 shows a close resemblance to the M_2 in NMNH (USNM) 186837, a mandible fragment with M_{1-3} from the Little Pipestone Springs localities of the early Oligocene of Montana. Emry *(personal communication)* tentatively identified NMNH 186837 as ?*Micropternodus.* UCMP 101308 differs from NMNH 186837 mainly in having a relatively wider talonid and more extended anterior cingulum.

Geolabidine M_{1-2}'s differ from UCMP 101308 in having less transversely widened prevallids, trigonids which curve lingually toward the apex, a less steeply sloping anterior cingulum, and less posteriorly projecting hypoconulid.

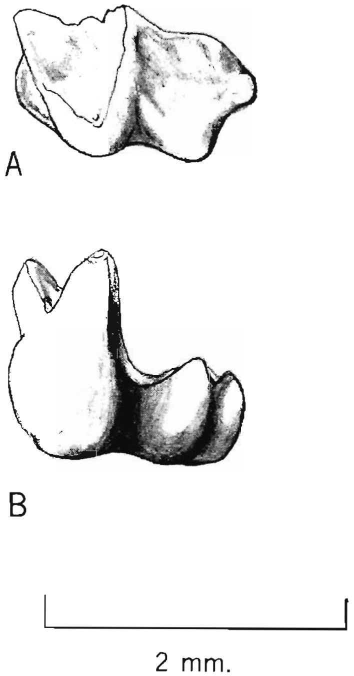


FIGURE 15. Micropternodontine-like genus and species, left M_x, UCMP 101308; a. occlusal view, b. labial view.

The Micropternodontinae (of Stirton and Rensberger 1964) is a specialized insectivore subfamily showing mole-like adaptations and nyctitheriid affinities (see Robinson 1968). The group makes its first appearance in the early Oligocene, or possibly the late Eocene (see Black and Dawson 1966), but it is conceivable that micropternodontine history goes back to early Eocene times. Certain characters in the lower molars of *Micropternodus* as diagnosed by Stirton and Rensberger (1964) are lacking in UCMP 101308. Nevertheless, the latter may, pending more complete material, represent an early Uintan member of the Micropternodontinae.

AETHOMYLOS NEW GENUS

Etymology.—Aeth, Gr., irregular, curious, unusual; mylos, Gr., molar.

Type species.—*Aethomylos simplicidens.*

Diagnosis.—*Aethomylos* is distinguished from all known insectivore genera by the following combination of dental characters. The upper molars are triangular in outline, where viewed from a labial aspect. They have an ectoflexus, a very narrow to absent stylar shelf, a conical paracone, metacone, protocone, and a large deeply excavated protofossa. There are no conules, hypocones, or precingula. The P_4 or DP_4) is an elongate molariform tooth with a large talonid basin and three talonid cusps. There is a "step-like" structure on the back of the trigonid. The lower molars have low trigonids with shelf-like paraconids. There is no anterior cingulum. A sharp turn in the paralophids lends to the trigonids a semi-rectangular outline when viewed from a dorsal aspect. The talonid has a deeply excavated basin bordered by three cusps. The hypoconid is much higher than the hypoconulid.

AETHOMYLOS SIMPLICIDENS NEW SPECIES

Figures 16-19, Tables 5-6

Etymology.—Simplicidens, L., simple tooth; refers to the simplicity of the molar morphology of this species.

Type.—UCMP 96133, left upper molar.

Type locality.—V-71183. Friars Formation.

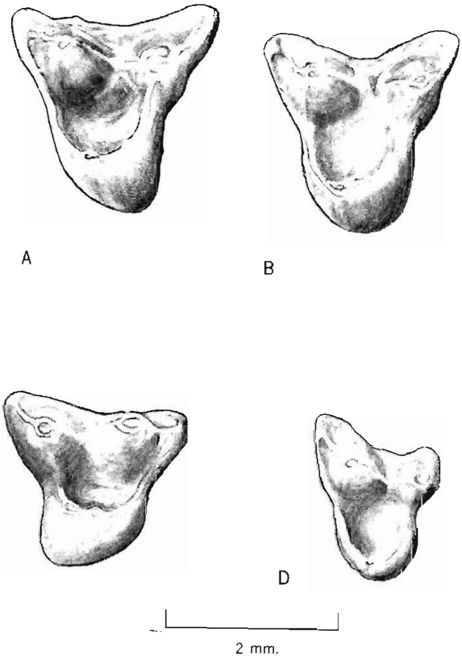
Diagnosis.—as for genus.

Referred specimens.—upper molars (and possibly deciduous premolars), UCMP 96133, 96443, 99428, 101047, 101066, 101068, 101312, 101590, 104178; P_4, UCMP 96088, 101077; M_{1-2}'s, UCMP 96092, 96453, 101067, 101119, 101625, 101645, 101750; M_3, UCMP 101630.

Localities.—UCMP locs. V-68116, V-71180, V-71183, V-71211, V-72157, V-72158.

Description.—All upper teeth listed above show the following morphology. The teeth, in occlusal view, have the vague appearance of an equilateral triangle. An ectoflexus is present. The stylar shelf is extremely narrow to absent. The paracone and metacone are conical cusps with steeper labial faces than lingual faces. The metacone is lower than the paracone and is widely separated from it by a deep valley. The metacone is situated at the posterior edge of the crown and is not bordered posteriorly by a metacingulum. A narrow paracingulum is present. The protofossa is large and deeply excavated. The protocone is anteriorly recumbent and transversely compressed with a steep labial face and a bulbous lingual face. There is no hypocone, but a swelling in the posterolingual corner of the crown is present in most specimens. Lingual cingula are absent. Beyond these basic characters there is marked variation in the morphology of the labial margin of the crown and the metastylar and parastylar spurs among different teeth in the dental arcade.

UCMP 96088 and 101077, both probable P_4's (or DP_4's), are elongate molariform teeth. The paraconid is low and well separated from the protoconid and the metaconid. The protoconid is much higher than the metaconid. The metaconid is situated slightly more posteriorly than the protoconid. There is a step-like structure on the back of the trigonid in UCMP 101077. As a result of wear, the top of the step slants ventrolabiad from a high point behind the lingualmost margin of the posterior face of the metaconid to the base of the crown directly behind the labial margin of the



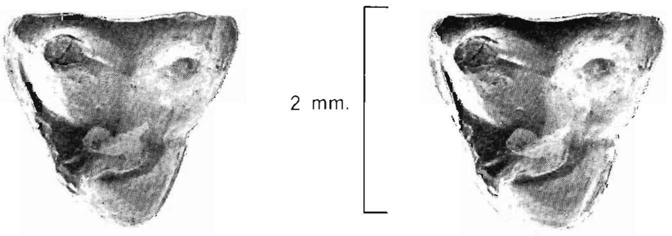


FIGURE 17. *Aethomylos simplicidens,* new genus and species, left upper cheek tooth, UCMP 101066. Occlusal view. Stereophotograph taken with scanning electron microscope.

protoconid. The talonid has a well-developed deeply excavated basin. The three talonid cusps and their connecting ridges form a rim, which, in occlusal view, is rounded rather than sharply angular at the corners.

All lower molars have the following basic features: The trigonid is not exceedingly high in comparison to the talonid and its posterior wall leans forward. The paraconid is shelf-like in appearance. There is no anterior cingulum. The paralophid descends directly anteriorly from the apex of the protoconid for a short distance

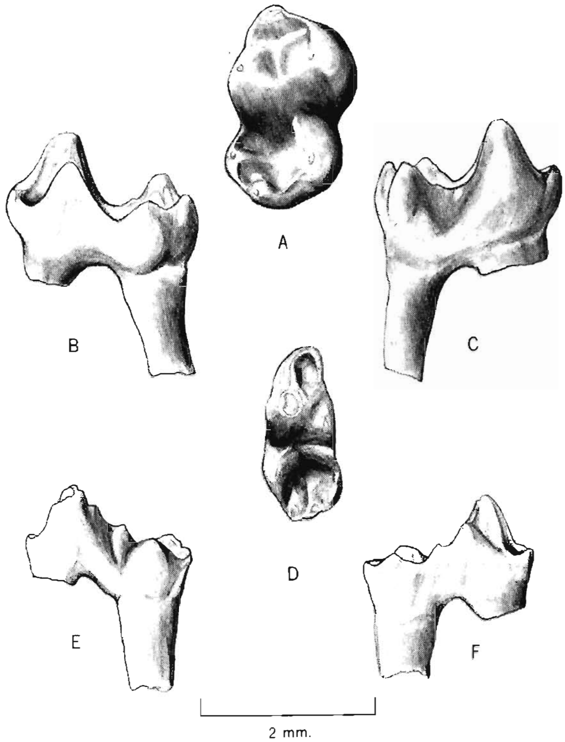


FIGURE 18. *Aethomylos simplicidens,* new genus and species, right lower molar, UCMP 101119; a. occlusal view, b. lingual view, c. labial view. Left $P_{?4}$ (DP_4), UCMP 101077; d. occlusal view, e. labial view, f. lingual view.

before making a nearly 90° linguad turn to contact the apex of the paraconid. The protoconid is higher than the metaconid and is situated farther anteriorly. As a result, the posterior margin of the trigonid is distinctively oblique in occlusal view. The talonid has a broadly excavated basin bordered by three cusps. The hypoconid is much higher than the hypoconulid. In UCMP 101625, the gently sloped lingual face of the hypoconid shows a sculpturing in the form of three or four faint, rounded other lower molar specimens. UCMP 101630, a probable M*3*, differs from all other referred lower molar specimens in having a relatively narrower talonid, a more bulbous hypoconid, and a more transversely compressed entoconid.

Remarks.—Aethomylos simplicidens may not be an insectivore at all; I can find no dental features in this species which indicate a close relationship with any of the presently recognized insectivore families.

Eocene apatemyids show a resemblance to *Aethomylos* in 1) the bowl-shaped structure of the talonid basin, 2) the angular anterolabial corner of the trigonid, 3) the low profile of the trigonids, 4) the forward slant of the posterior trigonid face, and

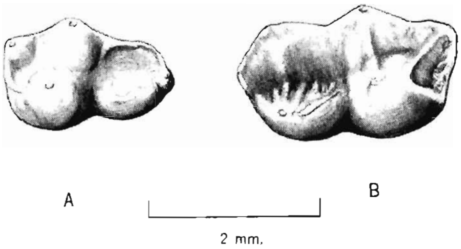


FIGURE 19. *Aethomylos simplicidens,* new genus and species, a. left lower molar (M_3), UCMP 101630; b. right lower molar (M_1 or M_2), UCMP 101625. All views occlusal.

5) the more posterior position of the metaconid relative to that of the protoconid. However, in Eocene apatemyids the anterolabial corner of the trigonid is actually farther forward than the apex of the paraconid, lending to the trigonid a characteristic parallelogram-like outline in occlusal view. No apatemyid known has a well-developed molariform P_4; instead, that tooth is quite reduced compared to M_1. Upper teeth of Eocene apatemyids are poorly known, but most of the existing specimens (see McKenna 1963:34) are broadly different from the upper cheek teeth described above. The upper molar of *Labidolemur* (see West 1972), however, shows a resemblance.

The upper molars of certain oxyaenoid creodonts show a general resemblance to *Aethomylos* upper cheek teeth specimens (see *Oxyaena simpsoni,* Van Valen 1966:80, Plate 8, Figs. 1,2), but the metacone and the paracone are more closely appressed. Oxyaenoid lower molars differ from specimens referred to *Aethomylos* in a number of major features.

Although most members of the Didelphodontinae have transversely extended upper molars, in *Didelphodus altidens* Marsh (early-middle Eocene) and in *D. absarokae* Cope (early Eocene), these teeth are more transversely compressed and approach the equilateral-shaped outline of the upper molars of *Aethomylos*. Didelphodontines are also similar in the lack of a hypocone and lingual cingula, and in having conical paracones and metacones. Despite these superficial similarities, didelphodontine upper molars broadly contrast with those described above in their possession of a wide stylar shelf, a much closer approximation of the paracone and the metacone, both a paraconule and metaconule, and a smaller, less excavated protofossa.

The lower molars of *Didelphodus altidens* and *D. absarokae* show a similarity to the lower molars described here in the low profile of the trigonids, the forward slanting posterior trigonid face, and the talonid which is not sharply cornered. However, lower molars of these didelphodontine species do not show a sharply angular anterolabial corner of the trigonid and have relatively narrower talonids.

McKenna (1960a:88, Fig. 44a) described an isolated upper molar (UCMP 44772 D) from the Wasatchian Four Mile fauna which shows resemblance to the upper molars of *Aethomylos*. Unlike didelphodontines and like *Aethomylos,* UCMP 44772 D does not have a wide stylar shelf, and shows the presence of a broadly excavated protofossa. It differs from upper molars of *Aethomylos* in the possession of a reduced paraconule and a weak mesostyle, characters which could conceivably be present in the structural ancestor of the San Diego genus.

It is obvious from the above comparison that no satisfactory assignment can be made for this new San Diego genus, but it serves as additional documentation of the remarkable diversity of insectivores in the San Diego region during the later Eocene.

TABLE 5

Measurements of the lower cheek teeth referred to *Aethomylos simplicidens*

Element	Measurements	
P_4	UCMP 96088	UCMP 101077
length	1.82	2.24
trigonid width	0.76	0.81
talonid width	0.85	0.92
M_{1-2}	UCMP 101119	UCMP 101625
length	2.27	2.57
trigonid width	1.29	1.32
talonid width	1.25	1.31
	UCMP 101645	UCMP 101750
length	1.91	2.27
trigonid width	1.14	1.30
talonid width	1.48	1.32
M_3	UCMP 101630	
length	1.94	
trigonid width	1.25	
talonid width	0.92	

TABLE 6

Measurements of upper molars and premolars of *Aethomylos simplicidens*

Specimen	Length	Anterior Width	Posterior Width
UCMP 96133 (type)	2.40	2.42	2.41
UCMP 96443	1.85	- - -	- - -
UCMP 99428	2.18	1.81	2.06
UCMP 101047	1.55	1.93	1.55
UCMP 101066	2.00	1.94	1.90
UCMP 101312	1.80	1.75	1.87
UCMP 101590	2.23	2.21	2.27
UCMP 104178	2.31	2.23	2.30

DISCUSSION AND CONCLUSIONS

Insectivora: faunal list.—The following insectivore taxa have been discovered from localities in the Friars and Mission Valley Formations and from UCMP locality V-72088 (unnamed formation) of San Diego County, California:

Class Mammalia
Subclass Theria
Infraclass Eutheria

Order Proteutheria
  Family Apatemyidae
    Subfamily Apatemyinae
      cf. *Apatemys* sp. Marsh 1872

    Family ?Palaeoryctidae
      Subfamily ?Palaeoryctinae
        Genus and species *indet.* probably new

Order Insectivora
  Superfamily Erinaceoidea
    Family Adapisoricidae
        Sespedectes singularis Stock 1935
        cf. *Proterixoides davisi* Stock 1935
        Cryptolestes vaughni n. gen. and sp.

  Superfamily Soricoidea
    Family Nyctitheriidae
      Subfamily Nyctitheriinae
        cf. *Nyctitherium* sp. Marsh 1872

    Family Geolabididae
      Subfamily Geolabidinae
      Centetodon (=Geolabis) sp. Marsh 1872
      Batodonoides powayensis n. gen. and sp.

    Family ?Apternodontidea
      Subfamily ?Apternodontinae
        New genus and species unnamed

Order Insectivora *incertae sedis*
        Erinaceoid-like genus and species
        Micropternodontine-like genus and species
        Aethomylos simplicidens n. gen. and sp.

Comparisons of the local insectivore fauna with those of other Eocene North American vertebrate localities are difficult because the results of recently intensified collecting in the latter areas are largely unpublished. However, at this early stage of research it is evident from the above taxonomic list that insectivores were well represented in the San Diego Uintan fauna. Such a diversity presently equals, if not exceeds, that of any other known North American later Eocene insectivore fauna except that of the Hendry Ranch Member, Badwater Creek localities, Wyoming, in which thirteen insectivore taxa were recognized (Setoguchi 1973, unpublished Master's Thesis, Texas Tech. Univ.; and Black and Dawson 1966).

The scarcity of insectivore remains from later Eocene faunas other than the San Diego or Badwater-Hendry Ranch assemblages is probably a reflection of disparity in collecting technique rather than a reality. Of the localities listed by Black and Dawson (p. 334), only the San Diego and Badwater deposits have been subjected to intensive underwater screening operations (see McKenna 1965, for a description of this collecting procedure).

Age of the San Diego Insectivore Fauna—Insectivore genera which have ranges extending into the Oligocene and later times, such as *Domnina, Ankylodon, Oligoryctes,* and *Apternodus,* are represented in the Badwater faunas but are absent from the San Diego fossil samples. This is not surprising because of the younger age assigned to the Badwater local fauna (see Black and Dawson 1966:344). *Centetodon* is the one San Diego genus that is known also from the North American Oligocene and earliest Miocene, but Lillegraven *(personal communication)* feels that the San Diego species of *Centetodon* are rather primitive forms closely related to Bridgerian species of that genus. Two insectivore taxa, cf. *Nyctitherium* and *Apatemys* sp., suggest a late Bridgerian-early Uintan age for the fauna. *Nyctitherium* is well represented in Bridgerian rocks, but Uintan fossils representing this genus are rare (see Robinson 1968; Black and Dawson 1966). However, such a poor Uintan record may be a function of both inadequate sampling and poor preservation of these diminutive forms. *Apatemys* sp. shows a close resemblance to *A. bellus,* known from both Bridgerian and Uintan faunas. *Sespedectes singularis, Proterixoides davisi,* and *Cryptolestes vaughni* are not known outside the southern California later Eocene, but I regard these genera as closely related to and not particularly advanced over Wasatchian and Bridgerian adapisoricids. Correlation is not yet possible using the remaining insectivore taxa from the San Diego fauna because of their aberrance or poor representation. However, the meager evidence available suggests a primitive aspect for the fauna. If the identification of UCMP 96081 as a possible palaeoryctine is correct, it marks a hitherto unknown Eocene distribution for this specialized late Paleocene subfamily. The possible apternodontine upper molar is of a more primitive structure than the late Eocene-Oligocene genera *Oligoryctes* and *Apternodus.* The upper and lower molars of *Aethomylos* are of primitive morphologies that are reminiscent of certain Paleocene and early Eocene mammals. Animals similar to *Batodonoides powayensis* would not be an unexpected discovery in a Late Cretaceous fauna; the species shows a striking resemblance to *Batodon tenuis* of that age. *B. powayensis* is certainly more primitive than any of the currently recognized species of *Centetodon.*

San Diego mammals on the whole seem more primitive than the Uintan forms of the Sespe region and the largely unstudied Laguna Riviera fauna from Carlsbad (located about forty-five miles north of San Diego). They appear, however, to be advanced over typical Bridgerian mammals from the North American Rocky Mountain region. Thus, an early Uintan age for the fauna is suggested. The fauna has traditionally been considered to represent "late Eocene" time (e.g., Black and

Dawson 1966). Acceptance of Steineck's and Gibson's (1971) arguments would, however, push back the age of the Uintan Mission Valley and Friars Formation mammalian faunas in correlation with the older time intervals represented by ''Ulatisian'' Ardath Shale and the ''Narizian'' Stadium Conglomerate foraminiferal faunas (Lillegraven 1973). Such an action would significantly broaden the concept of the Uintan to include some of the earlier half of the Eocene as well as most of the late Eocene. Consequently, the term ''late Eocene'' as applied to the San Diego Uintan vertebrate fauna would not be strictly appropriate. In acknowledgment of the possibility that the Uintan concept may eventually be broadened, the term ''later Eocene'' has been used throughout this paper in reference to the local fauna.

The primitive nature of the San Diego insectivores certainly does not conflict with a concept of an earliest Uintan age for the local fauna.

Geographical implication of the San Diego Insectivore Fauna.—A certain degree of endemism for the southern California Uintan fauna was suggested by Black and Dawson (1966). Despite the poor documentation of North American Eocene insectivores, there are strong indications that the San Diego insectivore fauna was highly endemic. Of the twelve insectivore taxa described from San Diego in this report, only *Apatemys, Nyctitherium,* and *Centetodon* are known elsewhere in the later Eocene of North America. Black and Dawson (1966:340) stated that the most widespread and best documented insectivore distribution is that of the family Leptictidae. Leptictids are conspicuously absent from the San Diego Uintan fauna. The evidence for this family in southern California faunas consists of a single fragmentary mandible specimen with M*3* (LACM (CIT) 1679, now lost) described by Stock (1935) from locality LACM (CIT) 150 in the Sespe Formation. I am not convinced that Stock's reference of that specimen to the Leptictidae is correct, as an illustration (Stock 1935:216, Fig. 5) of LACM 1679 shows some rather aberrant dental features. The M_3 of *Cryptolestes* shows resemblances to M_3's of many leptictids and it is possible that Stock's specimen is referable to this rather abundant San Diego genus.

Most interesting is the fact that the ubiquitous and abundant southern California insectivore species *Sespedectes singularis* is known from nowhere else in North America. This form is usually found in such large numbers at a given locality that one would likewise expect to have found it by now in some of the midcontinental localities. The restriction of *Sespedectes singularis* and the closely related species, *Proterixoides davisi,* within southern California may be a reflection of a particular environment not represented in known samples from the more continental localities.

The remaining taxa from San Diego have not been found elsewhere in North America. They are also (with the possible exception of *Cryptolestes*) rather aberrant forms which are taxonomically enigmatic, even at the familial level.

I suspect that the seemingly unique nature of the San Diego insectivore fauna is in part due to monographic problems. However, one might venture an intriguing, though purely conjectural, interpretation that some of the insectivores in the San Diego fauna may be part of a more southern, perhaps Central American, radiation. Such a proposition does not seem so farfetched if one considers that southern California may have been opposite western Sonora in the later Eocene prior to significant independent movement as part of the Pacific Plate on the west side of the San Andreas fault system (Minch 1972). This region would thus be much farther removed geographically from the midcontinental Rocky Mountain areas of the United States than it is today. There is no fossil evidence for early Tertiary insectivores in Central America, and there are only two insectivore (soricid) genera found in that region today. However, this does not preclude the possibility that insectivores once flourished in Central America. The present-day insectivore fauna of North America is hardly comparable with the vast diversity that existed there in the earlier Cenozoic.

NOTE ADDED IN PROOF

Since the submission of this paper for publication, several studies have been issued which relate to the later Eocene insectivore fauna from San Diego and warrant mention.

Lillegraven and Wilson (1975) tentatively referred the Camp Pendleton locality (UCMP loc. V-72088) to the Santiago formation (of Woodring and Popenoe, 1945), remarking on the lack of published geologic maps and descriptions of the district encompassing the locality. The views expressed above concerning the "local" and "distal" vertebrate associations represented at locality V-72088 are in agreement with Lillegraven and Wilson's (1975) analysis of the preservation of the rodent *Simimys* at that locality. These authors also noted the reoccurrent association of *Simimys* and *Sespedectes* in localities from Fletcher Hills, Camp Pendleton, and the Sespe Formation, and the interesting absence of these taxa in localities from Rancho de los peñasquitos (the Poway localities listed in Table 1 above). The unique faunal character of the latter region is thus underscored.

In an important review of European adapisoricids, Russell et al.(1975) subdivided the Adapisoricidae into the subfamilies Adapisoricinae (to include *Adapisorex*) and the Dormaalinae (to include *Litolestes, Leipsanolestes, Dormaalius, Entomolestes, Matronella, "Leptacodon" jepseni, Macrocranion, Scenopagus, ?Proterixoides, ?Sespedectes, Talpavus,* and *Ankylodon*).

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