The Sespedectinae, a New Subfamily of Hedgehog-like Insectivores

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ABSTRACT

A new subfamily of erinaceomorph insectivorans, the Sespedectinae, is defined to include Sespedectes, Proterixoides, and the more dentally conservative Crypholestes. All three genera are confined to the middle Eocene of southern California. A new species of Sespedectes, S. stocki, from the San Onofre area (? Santiago Formation) of northern San Diego County is recognized on the basis of size parameters of the lower molars. Dental evidence favors the placement of sespedectines within the dormaaliids. The subfamily is distinguished from other dormaaliids by its large, complex P3, bunodont molar cusp pattern, and several other dental features. The bunodont molar construction of sespedectines is reminiscent of the European “amphilemurids.” There is evidence to suggest, however, that some of the special similarities between these two groups were independently derived. Contrary to some theories, sespedectines are not erinaceids, nor are they hyopsodontid condylarths. In a classification that reflects the pattern of relationships preferred here, the Dormaaliidae comprises three subfamilies, the Dormaaliinae (including Dormaalius, Macrocarnion, and the tribe Amphilemurini), the Scenopaginae (Scenopagus and Ankyodon), and the Sespedectinae.

INTRODUCTION

So little is known about Early Tertiary insectivorans . . . that speculations on the origin and history of the group must be based largely on existing structures and conditions and consequently the distinguishing of palaeotelic from caenotelic or adaptive conditions confronts us at every turn. (Gregory, 1910, p. 287)

Erinaceomorph insectivorans played a crucial role in early attempts to develop a higher-level classification of placental mammals. Gregory (1910) claimed, for example, that these forms comprised an ancestral stock for many orders of mammals. This venerable notion much later fell prey to criticisms of insectivorans as archetypical placental ancestors (Van Valen, 1967; Novacek, 1982). Nevertheless, fossil erinaceomorphs show
features that suggest potential relationships with a wide variety of mammalian taxa. It is widely acknowledged that the resolution of relationships within the Erinaceomorpha directly bears on the problems of monophyly and affinities for other insectivoran clades as well as putative fossil primates, condylarths, and carnivorans (Saban, 1958; Russell, 1964; Van Valen, 1967; Novacek, 1982).

Erinaceomorphs are also distinguished by a comparatively rich fossil record. These are among the most abundant mammals in Early Tertiary faunas of North America and Europe, an abundance more effectively sampled through the recent emphasis of washing and sorting of matrix for small fossil bones and teeth. In this sense, Gregory’s (1910) above-quoted remarks on the miserable fossil record of insectivorans no longer seems appropriate. Yet Gregory’s statement holds true for at least one aspect of this record. Most early fossil insectivorans are represented only by isolated teeth or partial jaws. The incomplete anatomical data promote a sketchy picture of homologous characters and taxic relationships. Living insectivorans provide the primary evidence for monophyletic groups. The fossils are often relegated to paraphyletic, “waste-basket” categories that have been associated with other mammalian taxa in virtually any fashion imaginable (see Van Valen, 1967, fig. 7).

It is worthwhile, then, to review the rapidly increasing list of fossil erinaceomorphs for meaningful groupings. Presumably, even the partial anatomical sampling represented by fossil teeth can be used as evidence for a predictive classification of monophyletic taxa. Such a classification was the aim of several recent reviews (Krishtalka, 1976; Novacek, 1982; Novacek, Bown and Schankler, 1985; Koenigswald and Storch, 1983). The purpose of this paper is to identify the relationships of two of the better represented, but more problematic, fossil erinaceomorphs, the Eocene genera Sespedectes and Proterixoides. This purpose requires a more explicit hypothesis of erinaceomorph relationships (fig. 9) than previously proposed.

Stock (1935) first described Proterixoides and Sespedectes from the Uintan (=middle-late Eocene) of the Sespe Hills area in southern California. Stock remarked on the resem-

blance and possible close affinity of Proterixoides to Tertiary Erinaceidae, a view supported by several authors (e.g., Butler, 1948; McKenna and Simpson, 1959). Subsequently, these genera suffered a fate similar to that noted above for many other early Tertiary insectivorans. They were dispatched to the confusing and dentally diverse Erinaceomorpha and their relationships were left unclarified. It has even been suggested (Russell, 1964; Russell, Louis, and Savage, 1975) that Sespedectes and Proterixoides are primitive hyopsodontid condylarths.

Many additional specimens of erinaceomorphs were recovered from middle Eocene assemblages of San Diego County in the early 1970s. These efforts, by field parties from U.C. Berkeley and San Diego State University, led to the description of a third taxon, Crypholestes (Novacek, 1976), that appeared closely related to Sespedectes. Unfortunately, much of the original material of Proterixoides and Sespedectes collected by Stock could not be relocated and further study of the taxa was abandoned.

Two subsequent developments made feasible a renewed consideration of the southern California Eocene “hedgehogs.” Dr. David Golz relocated and carefully curated Stock’s original collection (acquired from California Institute of Technology by the Natural History Museum of Los Angeles County). This allowed comparison of the large Sespe samples of Sespedectes and Proterixoides with additional material from the San Diego Eocene. Secondly, several recent revisions of erinaceomorph groupings (Russell, Louis, and Savage, 1975; Krishtalka, 1976; Bown and Schankler, 1982; Novacek, 1982; Gingerich, 1983; Koenigswald and Storch, 1983; Novacek, Bown, and Schankler, 1985) provide a general framework for comparisons of the southern California taxa and the basis for a more highly resolved classification of the Erinaceomorpha.

Acknowledgments

I thank J. A. Lillegraven for his initial advisement on my graduate research of the southern California Eocene and for organizing and leading the field parties that collected the specimens from San Diego described in
this report. D. E. Savage provided useful criticism, spiritual guidance, and friendly field support. D. Golz, through his outstanding curatorial efforts, made this study possible. Raphael Delveccio assisted in the measurement and statistical analysis. Otto Simonis prepared some of the specimens. Illustrations were made by Lorraine Meeker, Lisa Lomapa, Chester Tarka, and Lauren Duffy. I thank L. Flynn, J. Flynn, M. C. McKenna, G. Musser, and A. Wyss for comments on the manuscript. The National Science Foundation (NSF GB-30519 awarded to Lilligraven) supported the field recovery and curation of the San Diego specimens. Support was also provided by the University of California, Museum of Paleontology, Berkeley, and the Frick Laboratory Endowment Fund, American Museum of Natural History.

**ABBREVIATIONS**

AW, anterior width  
L, maximum anteroposterior length  
PW, posterior width  
W, maximum width  
W-TAL, talonid width  
W-TRI, trigonid width  
C.V., coefficient of variation  
M, arithmetic mean  
N, number of observations (sample size)  
O.R., observed range of variation  
S.D., standard deviation  
LACM, Los Angeles County Museum of Natural History  
LACM (CIT), specimens or localities originally in the California Institute of Technology now housed in Los Angeles County Museum of Natural History  
UCMP, University of California Museum of Paleontology, Berkeley

**DENTAL TERMINOLOGY AND CRITERIA FOR MEASUREMENTS**


All specimens were measured on an Ehrenreich Photo Optical "Shopscope." Measurements are in millimeters rounded off to the nearest one-hundredth of a millimeter. Orientations of cheek teeth for measurements follow those given in Novacek (1976).

**SYSTEMATICS**

CLASS MAMMALIA LINNAEUS, 1758  
ORDER INSECTIVORA CUVIER, 1817  
SUBORDER DORMAALIIDAE QUINET, 1964  
SUBFAMILY SESPEDECTINAE, NEW

**TYPE GENUS:** Sespedectes Stock, 1935.  
**INCLUDED GENERA:** Proterixoides Stock, 1935; Crypholestes Novacek, 1976.

**DIAGNOSIS:** Shares with the dormaaliids Scenopagus, Ankylodon, Dormaalius, and Macroramnion the following derived dental features: P₁₋₂ reduced, single-rooted, peglike, or procumbent; P₄ premolariform (with large protoconid, small metaconid and paraconid, and short weakly basined or unbasined talonid with one or two minute cuspsules); paraconids on M₁₋₃ transverse, sharp, crestiform (but worn to a lophid appearance), and closely approximated to metaconids; trigonids on M₁₋₃ distinctly canted anteriorly and anteroposteriorly compressed in occlusal view; P₄ with sweeping metastylar crest, vestigial or absent metacone, and weak posterolingual expansion of cingulum or hypocone; well-developed hypocone on M₁₋₂. Differs from above genera in having a P₃ with a well-developed protoconid and a short heel; a P₃ well developed and similar in structure to P₄ with a prominent metastylar crest, paracone, protocone and posterolingual cingulum; a marked inflation of molar cusps giving the crowns a "bunodont" appearance; and large swollen hypocones and distinct conules on upper molars. Differs from (primitive) Erinaceids in the small and simple structure of P₁₋₂ and P₄, more crestiform paraconids, more canted lower molar trigonids, less progressively reduced dimensions from M₁ to M₃, and less salient paraconid on M₁. Similar to "amphilemurids" (Amphilemur, Pholidocercus, Alisaticipithecus, Gesneropithex) in having bunodont crowns of cheek teeth but differs from this group in having large, double-rooted P₃ with expanded protoconid (small, procumbent, and single-rooted in "amphilemurids"), weaker paraconid on P₄, a well-developed P₃ similar to P₄ in morphology, a less symmetrical P₄ with a strong, posteriorly extended metastylar crest, and...
more semirectangular and transverse upper molars (semiquadrat in amphilemurids) with stylar shelves and spurs (stylar shelves and para- and metastylar spurs greatly reduced or absent on M1-3 in "amphilemurids").

**DISTRIBUTION:** Middle–later Eocene (Uintan), southern California.

**DISCUSSION:** The distinctive features shared by the southern California Eocene dormaaliids warrant recognition of a separate subfamily for these taxa. *Sespedectes*, by far the best represented form, is designated the nominal genus for the group. *Crypholestes* is the most conservative sespedectine; *Proterixoides*, in some aspects, the most derived.

The above diagnosis clarifies the inclusion of sespedectines within the Dormaaliidae (see also Novacek, 1982) but distinguishes them from more generalized dental taxa (*Scenopagus*) or divergently specialized forms. Confusion is likely to arise with comparisons of "amphilemurids" (see Koenigswald and Storch, 1983) and sespedectines. The two groups share the distinctly bunodont crown pattern that is a departure from the more sectorial dentition of primitive Erinaceomorpha. "Amphilemurids" are, however, like *Macrocranion* and unlike sespedectines in the small size of P3, the more symmetrical structure of P4, and the more quadrate outline of the upper molars. These comparisons suggest a possible close affinity with *Macrocranion*. Koenigswald and Storch (1983) excluded this and other close associations for "amphilemurids," but their conclusion rests mainly on the observation that "amphilemurids" are extremely specialized in cheek tooth and certain cranioskeletal features. In the reduction of P1-3, *Macrocranion* and *Dormaalius* show a greater special similarity to amphilemurids than to other Erinaceomorpha. Perhaps amphiblemurids shared a close common ancestry with *Macrocranion* but diverged radically from an ancestor with a "Macrocranion-like" cheek tooth morphology. Under this scheme, the bunodont construction of the molar cusps was derived independently in "amphilemurids" and sespedectines.

These conclusions are based on detailed comparisons of sespedectines with an array of taxa that have been transferred to and fro among Erinaceidae, "adapisoricids," dormaaliids, primates, and Hyopsodontid condylarths. Essential aspects of these comparisons are given below.

**Genus Sespedectes** Stock, 1935

**TYPE SPECIES:** *Sespedectes singularis* Stock, 1935.

**INCLUDED SPECIES:** *Sespedectes stocki*, new species.

**DIAGNOSIS:** Differs from *Proterixoides* in its significantly smaller size and in having a less excavated P4 talonid basin; a more crestiform paraconid on M1-3, a less semiquadrat outline of M1-3; a relatively more transverse P3 of closer structure to P4; a less rounded, more "squared" lingual border of P3-4; more bulbous molar cusps; a distinct metacrista on M2, and a greatly expanded metaconule on M1-2. Differs from *Crypholestes* in having less transverse, more antero-posteriorly lengthened upper molars (especially M2); more bulbous molar cusps; greatly expanded metaconules on upper molars; less prominent labial spurs on M1-2; weak or absent precingulum on M1-3; more inflated hypocone on M2; later retention of DP4; and only one small cusp (rather than two) on the P4 talonid.

**DISTRIBUTION:** Friars, Mission Valley Formations, San Diego. ? Santiago Formation, Camp San Onofre. Sespe Formation, Ventura County. Middle–later Eocene (Uintan) southern California.

**DISCUSSION:** *Sespedectes* is the most abundant insectivoran in the southern California Eocene. The genus is known only from dentitions but there are possibly associated skeletal remains from UCMP locality V-72088 at Camp San Onofre. Although remains of *Crypholestes* in the San Diego sequence are slightly more abundant than *Sespedectes* (Table 1 in Novacek and Lillegaen, 1979), the former genus is not known from the Camp San Onofre or Sespe localities (Novacek, 1976, Table 1).

**INTRAGENERIC VARIATION:** No distinct, qualitative morphological differences were detected among specimens of *Sespedectes* from San Diego, Sespe, and San Onofre localities. Nevertheless, the large sample referable to this genus permits an assessment of morphometric variation. Raw dental measurements (tables 1, 2, 3) were statistically
analyzed according to the following procedure.

Each isolated tooth or isolated jaw was treated as an individual. The alternative practice of testing only the minimum number of individuals (the greatest number of a particular tooth from only one side of the jaw) is, in this case, an underestimate of sample size. Right and left rami were never found in association or even in close proximity. Isolated teeth were widely scattered throughout a given sampling of rock. It is doubtful that a significant percentage of complementary teeth from opposite sides of the jaw represent the same individual.

Large samples of cheek teeth were recovered from the Camp San Onofre locality (UCMP V-72088) but samples from other localities were smaller. Thus, certain neighboring samples of the same formation were grouped. This grouping was straightforward in the case of the Sespe localities, as locality LACM (CIT) 180 accounted for a large percentage of Sespedectes from that region. Grouping was more problematical for the San Diego—Fletcher Hills localities, where sample sizes were much smaller. "Lumping" data in this manner increases sample size, but lessens the confidence of identifying homogeneous populations (Rensberger, 1971, p. 11). Nevertheless, lumped samples showed coefficients of variation that were generally close to 5 or 6 (Simpson, Roe, and Lewontin, 1960) and grouped samples showed variances often homogeneous with that of the large, normally distributed sample of V-72088. These results justify the organization of data used in this statistical comparison.

Only lower molars were recovered in sufficient numbers for comparison. Three samples were recognized: sample 1 comprised only UCMP V-72088 from Camp San Onofre (table 1); sample 2 included four proximate localities in the Mission Valley Formation exposed in the Fletcher Hills area of San Diego proper (UCMP V-6893, UCMP 6871, LACM 65190, UCMP V-71055) (table 2); sample 3 comprised four localities from the Sespe Formation in canyons of the Sespe Hills of Ventura County, California (LACM [CIT] 150, LACM [CIT] 180, LACM [CIT] 202, LACM [CIT] 207) (fig. 1, table 3).

It is likely that both samples 1 and 2 represent rock sections more restricted temporally than sample 3. There was, however, no evidence of variation in tooth dimensions among samples of the Sespe Formation that could lead one to infer marked temporal change.

An "F max" test (Sokal and Rohlf, 1969, pp. 375–376) revealed that within-group variances of the three samples were homogeneous for all linear dimensions (antero-posterior length, trigonid width, talonid width). The null hypothesis that geographic location had no effect on tooth size was then tested. Results of a Student's T-test showed

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<th>M.</th>
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TABLE 2
Measurements of Cheek Teeth of *Sespedectes singularis* from UCMP V-6893, V-6871, V-71055, and LACM 65190 ("Fletcher Hills" Mission Valley Formation)
Symbols are defined under Abbreviations. Raw measurements are in millimeters.

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<td>M¹ L</td>
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<td>0.015</td>
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...that the null was rejected only in comparisons of trigonid width of M₁, between sample 1 and 2 and 1 and 3; talonid width of M₁ between 1 and 2; trigonid width of M₂ between 1 and 2 and 1 and 3; and talonid width of M₂ between 1 and 2 and 1 and 3 (table 4). In short, the San Onofre sample (inferred population) is distinctive in several molar dimensions from the Fletcher Hills and Sespe "populations."

These statistical results are corroborated by the observation that M₃s of *Sespedectes* from UCMP V-72088 were relatively larger than M₃s of the same genus from other localities (fig. 1, A and B). In this case neither sample 2 nor 3 was large enough for statistical comparison with sample 1. Hence the former two samples were nested. This procedure is not intended for comparisons of inferred "local populations" but merely as a test of the apparent discreteness of M₃s from UCMP V-72088. Lumping samples 2 and 3 yielded CVs ranging between 4 and 6 for all dimensions of M₃. Combining these with sample 1
yielded CVs greater than 7 and, in the case of trigonid width, as high as 11.

This indication of heterogeneity was supported by Student's T-test, which revealed significant differences between sample 1 and the nested samples 2 and 3 in all M₃ parameters. Scatter diagrams also show, albeit some overlap, a cluster of M₃ dimensions from the V-72088 sample that are clearly separated from M₃ dimensions of other samples (fig. 1).

What do these statistical comparisons mean for taxonomy? The debate over the nature of a fossil species reflects a desire to recognize something comparable to "reproductively isolated populations." Fossil taxa can only be identified by their structural characters and, as such, variation in these characters—morphological differences—must be taken seriously. The sample of Sespedectes from V-72088 is homogeneous, yet it is significantly different in size parameters of M₁⁻³ from other samples. The individuals from the San Onofre locality are therefore recognized as a new species of Sespedectes (see diagnosis and discussion below).

**Sespedectes singularis** Stock, 1935

**Type Specimen:** LACM (CIT) 1785, left mandible complete from anterior side of canine alveolus to slightly posterior of anterior

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**Fig. 1.** Plots of trigonid width (A) and talonid width (B) against anteroposterior length for M₃'s of *Sespedectes*. Open circles, sample 1 (locality UCMP V-72088). Solid circles, combined samples 2 and 3 (localities UCMP V-6893, 6871, 71055, LACM 65190, LACM (CIT) 150, 180, 202, 207). See text for locality information.

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**TABLE 4**

<table>
<thead>
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<th>Elements and Dimensions</th>
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<td>2-3</td>
<td>2.02</td>
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* C.L. is critical t value for rejection of the null hypothesis (H₀) that there is no significant difference between sample means, at P (level of significance) = 0.05 and DF (degrees of freedom) = N - 1. tₚₜ is calculated t value derived from sample means.
border of coronoid process, with \( P_3-M_3 \) (Stock, 1935, plate 1, figs. 6, 6a).

**Type Locality:** LACM (CIT) 150, “Pearson Ranch,” Brea Canyon Section, Sespe Formation. North of Simi Valley, Ventura County, California.

**Diagnosis:** Differs from *Sespedectes stocki* in having slightly (but significantly) narrower trigonids and talonids on \( M_{1-2} \) and smaller \( M_3 \)s (tables 1–4, fig. 1).

**Localities and Referred Specimens:** Locality LACM (CIT) 150. “Pearson Ranch,” Sespe Formation between Brea and Alamos Canyons, Ventura County, California: mandible fragments with \( P_3-M_3 \), LACM 42628; \( P_4-M_1 \), LACM 42625; \( M_{1-3} \), LACM 42626; \( M_{1-2} \), LACM 42625.

Locality LACM (CIT) 180. “Tapo Canyon,” Sespe Formation, Ventura County, California: Mandible fragments with \( P_3-M_3 \), LACM (CIT) 1892; \( P_2-M_2 \), LACM (CIT) 1893; \( P_4-M_1 \), LACM 39970; \( M_3 \), LACM 39971, 39972, 39995, LACM (CIT) 5198, 5199; maxillary fragments with \( M_{1-2} \), LACM 39982; \( M_{2-3} \), LACM 39983; isolated \( P_3 \), LACM 39969, 39976; isolated lower molars, LACM 39973–39975, 39977–39980, 39991–39995, 39997–39999, 40177, 40181, 40186, 40192; isolated upper molars, LACM 39984, 39985, 40189.

Locality LACM (CIT) 202. “Brea Canyon,” Sespe Formation, Ventura County, California: Mandible fragments with \( P_3-M_3 \), LACM (CIT) 1483; \( P_4-M_1 \), LACM (CIT) 1891; \( P_2-M_2 \), LACM (CIT) 5197, 5200; \( P_3-M_1 \), LACM 37955, 37956, 37959, 37965, 42386; \( M_{1-3} \), LACM (CIT) 5196; \( M_{1-2} \), LACM 37958, 37967, 42388; \( M_{2-3} \), LACM 37960, 37994; maxillary fragments with \( M_{1-3} \), LACM 37942; \( M_{1-2} \), LACM 37943; \( M_{2-3} \), LACM 37944; isolated \( P_3 \), LACM 37957, 37964, 37969, 37993, 37995, 37996, 37998, 42387; isolated lower molars, LACM 37940, 37941, 37962, 37963, 37968, 37971, 37977–37985, 37987–37990, 37992, 42389; isolated \( P_4 \), LACM 37954; isolated upper molars, LACM 37946–37953.

Locality LACM (CIT) 207. “Brea Canyon,” approximately 75 ft stratigraphically below and 400 ft west of locality LACM (CIT) 202. Sespe Formation, Ventura County, California. Mandible fragment with \( P_2-M_3 \), LACM (CIT) 1890; maxillary fragment with \( P_1, P_3-M_3 \), LACM (CIT) 1889; \( P_4-M_2 \), LACM 42615; \( M_1 \), LACM 42616; \( M_2 \), LACM 42617; \( M_3 \), LACM 42618.

Locality UCMP V-6893. “Jack-in-the-Box,” Fletcher Hills District. Mission Valley Formation, San Diego County, California. Mandible fragments with \( P_3-M_3 \), UCMP 95865; \( P_4-M_1 \), UCMP 96188; \( M_{1-2} \), UCMP 96146; \( M_{1-3} \), UCMP 96150; maxillary fragment with \( D_3-M_2 \), UCMP 96161; \( P_4-M_1 \), UCMP 96151; \( P_4-M_3 \), UCMP 85681; isolated lower molars, UCMP 96125, 96143, 96177, 96162, 96434; isolated \( P_3 \), UCMP 96126; isolated upper molars, UCMP 96093.

Locality UCMP V-6871. “Fletcher Parkway.” Fletcher Hills District. Mission Valley Formation, San Diego County, California. \( P_4 \), UCMP 101333; \( M_1 \), UCMP 99330. Several additional isolated teeth.

Locality LACM V-65190. “Fletcher Hills.” Mission Valley Formation, San Diego County, California. Mandible fragments with \( P_4 \), \( M_{1-2} \), UCMP 15955, 15959; \( M_{2-3} \), UCMP 15956.

 Locality UCMP V-71055. “Baltimore Locality.” Fletcher Hills District. Mission Valley Formation, San Diego County, California. Maxillary fragments with \( P_4 \), \( M_{1-2} \), UCMP 96150; \( M_{1-2} \), UCMP 96144.


Locality UCMP V-71175. “Soiset’s Surprise.” Friars Formation, San Diego County, California. \( M_2 \), UCMP 96134.

**Description:** Other than the morphometric differences noted above, *Sespedectes singularis* and *S. stocki* are essentially identical. This description applies to both taxa. The mandible is slender, tapering anteriorly from a point below \( M_1 \). The masseteric fossa is bordered anteriorly by a prominent ridge. The coronoid process is high, and anteroposteriorly broad. The condylid process is higher than the tooth row and is closer to the dorsal crest of the coronoid process than to the angular process. There is a horizontal ridge on the medial surface of the angular process, which curves slightly upward in its anterior
section. The inferior dental foramen (preserved in UCMP 96584) is located directly above the anterior section of the angular process about the level of the tooth row. The symphysis of the jaw terminates at a point below P₁. The anterior mental foramen is below P₂, the posterior mental foramen below the anterior root of P₄. All the teeth of the lower jaw, particularly the anterior premolars, are crowded.

None of the jaws was preserved with incisors, but roots and alveoli indicate that I₂ was enlarged and I₃ was much smaller. Isolated incisors from UCMP V-72088 have a mitten-shaped profile with long, transversely flattened roots. These are probably referable to *Sespedectes stocki* and are comparable to those of *S. singularis*.

Alveoli also indicate that the lower canine is single-rooted and not greatly enlarged.
P$_{1-2}$ are not definitely known in *S. singularis*, but in *S. stocki* these teeth are procumbent, reduced, and single-rooted with a single, rounded cusp (fig. 2).

P$_3$ is double-rooted and, from comparisons with alveoli in *Sespedectes singularis* and known teeth in *S. stocki*, is much larger than P$_1$ and P$_2$. The crown is essentially a large, rounded cusp and a very small heel separated by a shallow trough. There is sometimes a minute cuspule on the transverse ridge of the posterior heel. Slightly lingual and anterior to this cuspule is an even smaller cuspule, discernible in slightly worn or unworn teeth. There is a shallow hypoflexid (fig. 2).

P$_4$ varies considerably in appearance with wear. In the type and in most other specimens this tooth is quite worn and the paralophid makes an unbroken descent from the apex of the protoconid. In unworn P$_4$s, the paralophid protrudes anteriorly in a rounded shoulder about midway down its length. The paraconid varies in form from a small, low cusp to a worn ridge representing the transverse spur of the paralophid. The metaconid is much lower than the protoconid and is situated labial and slightly posterior to it. The labial face of the metaconid coalesces with the protoconid for most of its height. A deep posteroventrally sloping trough separates the talonid ridge from the back of the protoconid and metaconid. The talonid is an oblique ridge with a single cusp often obscured by wear. The apices of the metaconid, protoconid, and the crest of the paralophid are often worn to a single, continuous wear facet (figs. 2, 5).

M$_1$ is slightly longer than wide with a low, anteriorly canted trigonid. The protoconid and metaconid are swollen at their bases and are subequal in height. A short paralophid curves anterolingually from the apex of the protoconid, terminating in a low paraconid. In unworn teeth, the paraconid is anteroposteriorly compressed, bladelike, and inclined forward. The paraconid is located directly anterior and labial to the metaconid. There is a short anterior cingulum. In most specimens, the talonid is slightly wider than the trigonid. The cristae obliqua is a blunt ridge that contacts the post-vallid wall slightly labial to the protoconid-metaconid juncture. The hypoconid and entoconid are subequal in height and are much higher than the hypoconulid. The hypoconulid is not lingually positioned but is situated roughly midway between the hypoconid and entoconid and slightly posterior to them (figs. 2, 5).

Circular wear facets appear early on apices of all cusps of M$_1$, except the paraconid. On the latter, an elliptical wear facet develops which is continuous with that on the paralophid. Heavy wear on the protoconid usually precedes that on the metaconid. Late stages of wear show a confluent facet linking all trigonid cusps and connecting lophs. The sequence of wear is as follows: (1) circular wear facets on the three talonid cusps, (2) a confluent facet joining hypoconid and hypoconulid, (3) extensive wear on the hypoconulid and hypoconid until these cusps are worn level with the talonid basin, while the entoconid remains prominent and cuspate (a diagnostic Erinaceomorph wear pattern), (4) extensive wear of the entoconid and confluent facets joining all three cusps.

M$_2$ is similar in structure and wear pattern to M$_1$, except that it is relatively wider with a talonid slightly narrower than the trigonid and a smaller paraconid less separated from the metaconid.

M$_3$ is smaller than M$_{1-2}$ with a much narrower and more elongate talonid. Unlike M$_{1-2}$ the hypoconulid is a prominent, more posteriorly and lingually positioned cusp. Wear on the hypoconulid precedes that on the hypoconulid and entoconid. In later stages of wear the latter two cusps form a distinct crest with a confluence of their steep lingual faces.

Maxillary fragments rarely preserve teeth anterior to P$_3$. An upper canine is unknown in *Sespedectes singularis*, but this tooth in *S. stocki* is small and single-rooted with a button-shaped crown that resembles P$_1$–P$_2$ (fig. 4A).

The latter teeth are preserved in UCMP 85681 (from UCMP V-6893). They are single-rooted and essentially identical in appearance. P$_1$ is slightly smaller than both C and P$_2$ (fig. 3, A, B, and C).

The three-rooted DP$_3$ is much longer than wide (fig. 3E). Its principal feature is a high paracone. Sloping posteroabially from the paracone is a distinct crest that lacks a metacone. The labial face of the paracone is flat and steep; the lingual face, more gently sloping. There is no distinct styloal shelf. The parastylar spur is prominent and rounded in oc-
Fig. 3. *Sespedectes singularis*. (A) labial; (B) occlusal; (C) lingual views of UCMP 85681, right P\(^1-4\). (D) labial; (E) occlusal; (F) lingual views of UCMP 96161, DP\(^3-4\), M\(^1-2\). Both specimens from locality UCMP V-6893.

cuspal view and is developed into a small, bulbous cusp (parastyle). The protocone is much lower than the paracone. Its posterior face is worn to a flattened slope inclined at about 45° (fig. 3F) to the horizontal plane of the tooth row. A swelling in the posterolingual corner of the crown suggests the presence of a low, weak hypocone (fig. 3).

DP\(^4\) is molariform and is more transverse than DP\(^3\); its posterior width is nearly equal to its anteroposterior length. Both a paracone and metacone are present, the latter being lower than the former. The paracone of DP\(^4\) is significantly lower than the paracone of DP\(^3\) and the latter seems to have functioned as a puncturing cusp similar to posterior premolar paracones of more modern Erinaceids. A weak metacrista is present and protrudes slightly beyond the labial margin of the more anterior section of the crown. In DP\(^3\) there is no appreciable stylar shelf and the protocone is much lower than the paracone. The preprotocrista extends to the parastyle. The hypocone is well developed and situated more lingually than the higher protocone. It is separated from the wall of postprotocrista by a shallow trough. There is a distinct metacrista but no paracone. A precingulum is absent. As in DP\(^3\), the lingual root is anteroposteriorly broader than the labial roots (fig. 3, D, E, and F).

The three-rooted P\(^3\) is slightly wider than long with a high, triangular (in labial view) paracone. There is a strong, sweeping metastylar crest but no evidence of a metacone. There is a minute parastyle opposite the anterolabial corner of the paracone which projects slightly beyond the straight, anterior margin of the crown. The labial margin is slightly convex opposite the paracone. There is no appreciable stylar shelf. The low protocone is bordered posteriorly by a weak bulge that may be a hypocone. The posterior face of the protocone tends to wear to an inclined slope similar to that in DP\(^3\) (figs. 3, 4, 5, 8).

P\(^4\) is essentially identical to P\(^3\) in structure, differing only in its slightly larger size and more transverse proportions, a more oblique anterior margin, and a more prominently projecting parastyle (figs. 3, 4, 5, 8).
M1 is rectangular to semiquadrat with its length equal to or greater than three-fourths its width. There is a weak ectoflexus and stylar shelf. All the molar cusps are low and rather bulbous in construction. The paracone and the metacone are well separated and are subequal in height. The strong metacrista extends labially and slightly posteriorly from the apex of the metacone. The protocone is anteroposteriorly compressed with a rounded lingual face. The protocone is lower than the paracone and metacone and only slightly higher than the well-developed and slightly more lingual hypocone. The hypocone is separated by a narrow trough from the posterior faces of the protocone and postprotocrista. A crest curves from the apex of the hypocone to a point at the posterior base of the crown below the metaconule. It continues labially as a wide metacingulum. The very prominent, bulbous metaconule occupies most of the area between the protocone and the lingual face of the metacone. In some specimens there is a weak premetaconule wing, but there is never a postmetaconule wing. The paraconule is much smaller than the metaconule and becomes obscured at early stages of wear. Some specimens show a short, very narrow precingulum. As in the posterior premolars, the lingual root is anteroposteriorly broad (figs. 3, 4, 5, 8).

M2 is similar to M1 except for its much more prominent parastylar spur, less posterolingually expanded hypocone, and slightly lower more lingually positioned metacone. No M2 shows a precingulum (figs. 3, 4, 8).

M3 is much smaller than M1-2, with a strong oblique labial margin and a very prominent parastylar spur. There is no metastylar lobe; the metacone occupies the extreme posterolabial corner of the crown. The paracone is much higher than the protocone and both cusps are higher than the metacone. The preprotocrista extends to the parastylar spur, forming a narrow cingulum along the anterior base of the paracone. Some specimens show a very small precingulum and postcingulum. The lingual root of M3 is not anteroposteriorly broadened as in M1-2 (figs. 4, 5, 8).
Nothing is known of the skull of Sespedectes singularis aside from a few partial maxillary fragments associated with the upper dentitions described above. In these specimens the large anterior opening of the infraorbital canal is located above a point on the alveolar border between the labial roots of P3 (fig. 4A). The anterior “root” of the zygoma begins at the level of M1. The anterolateral surface of the zygomatic arch is strongly concave.

**DISCUSSION:** Sespedectes singularis co-occurs with Crypholestes vaughni in certain San Diego localities (Novacek, 1976, table 1; Golz and Lillegraven, 1977, table 1). The two species differ distinctly in upper molar structure (fig. 8), but not in size or morphology of the lower cheek teeth. The P₄ talonid of C. vaughni is bicuspid rather than unicuspid as in S. singularis, but other differences between lower teeth are few and subtle. Isolated lower molars from some of these problematic localities (e.g., UCMP V-6873) are not included in the measurement analysis of Sespedectes.

Sespedectes but not Crypholestes is present in the Fletcher Hills localities of the Mission Valley Formation, while the latter alone is present in Poway localities north of San Diego, representing the same formation. Both species, as noted above, coexist in localities between these two areas which represent Friars and Mission Valley facies. All other things being equal—namely approximate time, elevation, and habitat—it is conceivable that this is an example of contiguous to slightly overlapping ranges of two closely related species. However, the equality of the properties mentioned has not been established.

An interesting difference between Crypholestes and Sespedectes relates to the ontogeny of tooth replacement. In the latter the eruption of the characteristic trenchant P₄ of erinaceomorphs is delayed, whereas Crypholestes exhibits the more typical pattern of an earlier replacement. Thus it is inferred that Sespedectes retained for a prolonged period a more extensive “crushing battery” comprising DP₃-₄, M₁-₃ (Novacek, 1976, p. 24).

**Sespedectes stocki,** new species

**ETYMOLOGY:** Named after the late Chester Stock, who provided the original descriptions.
of insectivores and many other mammals of the southern California Eocene.

**TYPE SPECIMEN:** UCMP 99391, right mandible with P1-M3 (fig. 2).

**TYPE LOCALITY:** UCMP V-72088 “Onofre Locality One.” Sandstone lens near northern extreme of Camp Pendleton Marine Corps Base at Camp San Onofre. Santiago Formation, northwest corner of San Diego County. Possibly significantly younger than the Friars–Mission Valley Formation assemblage of greater San Diego and roughly equivalent to older parts (Tapo and Brea Canyon) of the Sespe Formation in Ventura County (Golz, 1976; Golz and Lillegraven, 1977).

**DIAGNOSIS:** Differs from *Sespedectes singularis* in having wider talonids and trigonids on M1-2 and larger, broader M3s (tables 1-4, fig. 1).

**LOCALITY AND REFERRED SPECIMENS** (partial listing): All referable specimens from the type locality: Fragments of mandible with P3-M3, UCMP 98654, 99353; P4-M2, UCMP 99411, P4-M3, UCMP 98655, 98656, 99394, 99399; P4-M2, UCMP 101406; P4-M1, UCMP 98653, 99407, 101329; M1-2, UCMP 99402, 99412, 101371; M2-3, UCMP 98652, 99406, 99408, 99413, 99470; maxillary fragment with C, P3-M3, UCMP 99401; M1-3, UCMP 96461; isolated I3s ?, UCMP 99452, 99492, 101341, 101353, 101391; I3s ?, UCMP 99286, 99493, 101348, 101374, 101402; P3s, UCMP 99361, 99396, 101363, 101365, 101400, 101405; P4s, UCMP 99279, 99345, 99392, 99473, 101368, 101380, 101394; M1s, UCMP 99404, 99416, 99472, 99656, 101349, 101387, 101390, 101395, 101406; M2s, UCMP 98656, 99326, 99393, 99395, 99403, 99412, 99479, 101340, 101346, 101347, 101361, 101369, 101371, 101406; M3s, UCMP 99275, 99353, 101372, 101376; P3s, UCMP 99398, 99474, 101415; P4s, UCMP 99355, 99397, 101350, 101351, 101356, 101357, 101381, 101408; M1s, UCMP 99469, 101384, 101392; M3s, UCMP 99490, 101377, 101383, 101385.

**DISCUSSION:** *Sespedectes* has also been reported from UCMP V-6883 (“Half-Day Pocket”) and LACM 68102 (“Laguna Riviera Quarry”) in the Santiago Formation near Carlsbad, California (Golz and Lillegraven, 1977, table 1). Specimens were tentatively assigned to *S. singularis*, but reference to *S. stocki* may be more appropriate. The Laguna Riviera material is currently under study by workers at the LACM, UCMP, and U.C. Riverside.

The San Onofre locality shows a curious
dominance of diversity by two taxa, *Sespepectes stocki* and the rodent *Simimys simplex*. Other San Diego County localities generally show more even relative abundances of several small insectivorans and rodents. The composition of the San Onofre sample may be influenced by certain taphonomic and sedimentary factors discussed in Novacek (1976, pp. 3–7).

**Genus Proterixoides Stock, 1935**

**Type and Only Species:** *Proterixoides davisi* Stock, 1935.

**Diagnosis:** Differs from *Sespedectes* in its much larger size and in having a more excavated P₄ talonid basin; more lophid, rather than crestiform, paraconid on M₁₋₃, more quadrate outline of M₁₋₃; a less transverse, more triangular P₃ that is similar but does not match P₄ in outline and construction; a more evenly convex outline of the lingual border of P₃₋₄; more conical, slightly less bulbous molar cusps; very weak or no metacrista on M²; a less inflated metaconule on M². Differs from *Crypholestes* in being much larger and in having more quadrate upper molars and more swollen molar cusps (tables 5, 6; figs. 6, 7).

**Distribution:** Sespe, Santiago, and Friars Formations, southern California. Uintan (middle–later Eocene).

**Proterixoides davisi** Stock, 1935

**Type Specimen:** LACM (CIT) 1673, right maxillary fragment with P₃₋₄ (Stock, 1935, plate 1, fig. 1).

**Type Locality:** LACM (CIT) 150 “Pearson Ranch,” Brea Canyon Section, Sespe Formation. North of Simi Valley, Ventura County, California.

**Diagnosis:** Same as for genus.

**Localities and Referred Specimens** (localities are described under listing for *Ses-
TABLE 5
Measurements of Cheek Teeth of Proterioxoides davisi from LACM (CIT) 150, 150E, 180, 202, and 207 (Sespe Hills, Sespe Formation)
Symbols are defined under Abbreviations. Measurements are in millimeters.

<table>
<thead>
<tr>
<th>Element and Dimensions</th>
<th>N.</th>
<th>O.R.</th>
<th>M.</th>
<th>S.D.</th>
<th>C.V.</th>
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<tbody>
<tr>
<td>P₃ L</td>
<td>6</td>
<td>3.16-3.96</td>
<td>3.54</td>
<td>0.347</td>
<td>9.8</td>
</tr>
<tr>
<td>W</td>
<td>6</td>
<td>1.82-2.27</td>
<td>2.40</td>
<td>0.401</td>
<td>16.7</td>
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<td>P₄ L</td>
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<td>2.95-4.19</td>
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<td>9.5</td>
</tr>
<tr>
<td>W</td>
<td>21</td>
<td>2.04-2.84</td>
<td>2.45</td>
<td>0.230</td>
<td>9.4</td>
</tr>
<tr>
<td>M₁ L</td>
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<td>2.95-4.16</td>
<td>3.35</td>
<td>0.281</td>
<td>8.4</td>
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<tr>
<td>W-TRI</td>
<td>23</td>
<td>2.16-3.11</td>
<td>2.55</td>
<td>0.218</td>
<td>8.5</td>
</tr>
<tr>
<td>W-TAL</td>
<td>23</td>
<td>2.32-3.38</td>
<td>2.69</td>
<td>0.051</td>
<td>9.1</td>
</tr>
<tr>
<td>M₂ L</td>
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<td>3.02-3.96</td>
<td>3.30</td>
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<tr>
<td>W-TRI</td>
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<td>2.75</td>
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<td>W-TAL</td>
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<td>2.60</td>
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<tr>
<td>P₁ L</td>
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<td>3.20-3.69</td>
<td>3.41</td>
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<tr>
<td>W-TRI</td>
<td>8</td>
<td>2.08-2.43</td>
<td>2.25</td>
<td>0.124</td>
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<tr>
<td>W-TAL</td>
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<td>1.65-2.07</td>
<td>1.86</td>
<td>0.151</td>
<td>8.1</td>
</tr>
<tr>
<td>P₄ L</td>
<td>6</td>
<td>3.03-3.40</td>
<td>3.26</td>
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<tr>
<td>AW</td>
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<td>3.52-4.16</td>
<td>3.79</td>
<td>0.263</td>
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</tr>
<tr>
<td>PW</td>
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<td>4.00</td>
<td>0.218</td>
<td>5.4</td>
</tr>
<tr>
<td>M₁ L</td>
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<td>3.22</td>
<td>0.173</td>
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</tr>
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<td>3.54-4.37</td>
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<td>0.244</td>
<td>8.4</td>
</tr>
<tr>
<td>M₃ L</td>
<td>2</td>
<td>2.20-2.43</td>
<td>2.32</td>
<td>0.163</td>
<td>7.0</td>
</tr>
<tr>
<td>AW</td>
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<td>3.57-3.78</td>
<td>3.68</td>
<td>0.148</td>
<td>4.0</td>
</tr>
<tr>
<td>PW</td>
<td>2</td>
<td>2.55-2.98</td>
<td>2.77</td>
<td>0.304</td>
<td>11.0</td>
</tr>
</tbody>
</table>

TABLE 6
Measurements of Cheek Teeth of Proterioxoides davisi from San Diego County Localities UCMP V-68116 and V-72088
Symbols are defined under Abbreviations. Measurements are in millimeters.

<table>
<thead>
<tr>
<th>Element</th>
<th>L</th>
<th>W-TRI</th>
<th>W-TAL</th>
</tr>
</thead>
<tbody>
<tr>
<td>M₁ (UCMP 106078)</td>
<td>3.33</td>
<td>2.48</td>
<td>2.56</td>
</tr>
<tr>
<td>M₂ (UCMP 106078)</td>
<td>3.18</td>
<td>2.54</td>
<td>2.44</td>
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<tr>
<td>M₃ (UCMP 101335)</td>
<td>3.2ₗ</td>
<td>2.₇ₗ</td>
<td>2.₄ₗ</td>
</tr>
<tr>
<td>P₄ (UCMP 101690)</td>
<td>2.₉ₗ</td>
<td>3.₁₂</td>
<td>3.₄ₗ</td>
</tr>
<tr>
<td>M₁ (UCMP 99363)</td>
<td>3.₁ₗ</td>
<td>—</td>
<td>—</td>
</tr>
</tbody>
</table>

ₗ Damaged specimen.

pedectes singularis): Locality LACM (CIT) 150, type locality. Mandible fragments with P₃-M₃, LACM 42602; P₄-M₃, LACM 42599; P₄-M₁, LACM 42620; M₁, LACM (CIT) 1677 (Stock, 1935; plate 1, fig. 2); M₁-M₂, LACM 42600; maxillary fragments with P₃-M₃, LACM (CIT) 1674; P₄, M₂-M₃, LACM (CIT) 1675 (Stock, 1935; plate 1, fig. 3); isolated lower molars, LACM 42601, 42603; P₄, LACM 42603, 42621; P₄, LACM 42622.

Locality LACM (CIT) 150E. “Pearson Ranch.” Mandible fragments with P₃-M₂, LACM (CIT) 1678, LACM 42594; M₁-M₂, LACM 42596; M₁-M₃, LACM 42593, 42597; M₂-M₃, LACM 42595, isolated lower molars, LACM 42598.

Locality LACM (CIT) 180. “Tapo Canyon.” Mandible fragments with P₃-M₁, LACM 39939; P₄-M₁, LACM 39938; P₄-M₂, LACM (CIT) 1886; P₄-M₂, LACM (CIT) 1887; M₂-M₃, LACM (CIT) 1874, 1888; maxillary fragments P₃-M₃, LACM (CIT) 1873; isolated P₃, LACM 39936, 39937, 39964; P₄, LACM 39940–39945, 39965–39967; lower molars, LACM 39946–39963, 39968; P₄, LACM 39920, 39922; P₄, LACM 39921; upper molars, LACM 39924–39935.

Locality LACM (CIT) 202. “Brea Canyon.” Mandible fragment with P₄-M₁, LACM (CIT) 1885; P₄, LACM 37939.

Locality LACM (CIT) 207. “Brea Canyon.” Mandible fragment with P₃-M₂, LACM (CIT) 1883; P₄-M₂, LACM 42607; P₃-M₁, LACM 42612; P₂-M₁, LACM (CIT) 1884, LACM 42608; P₃, LACM 42613; P₄, LACM 43614; lower molars, LACM 42609–42611; upper molars (M₂), LACM 42605–42606.

Locality UCMP V-72088. “San Onofre” and Locality UCMP V-68116 “Dog Spring Three.” Mandible fragment with M₁-M₂, UCMP 106078; M₂, UCMP 101335; P₄, UCMP 101690; M₃, UCMP 99363.

DESCRIPTION: Stock (1935) provided a brief, comparative description of this taxon. The features of Sespedectes singularis generally apply for Proterioxoides davisi with the obvious exception of diagnostic differences specified above. Unfortunately, the anterior dentition is very poorly known in Proterioxoides.
DISCUSSION: Stock (1935, p. 218) reported that Sespedectes singularis was less abundant in CIT 150 collections than Proterixoides davisi but he did not publish sample sizes for either species. The relatively large samples of Proterixoides from the Sespe localities show high variation in certain tooth dimensions (e.g., P4 length, width; M1 talonid width; M1 anterior width; M3 posterior width; see table 5). Some of these parameters are difficult to measure with consistency (upper molar widths), and a large sample of M3s shows low coefficients of variation for all parameters measured (table 5). If heterogeneity is present, there is no obvious pattern for it. Thus, all Sespe samples are referred to one species, Proterixoides davisi.

A small number of isolated teeth from the Santiago and Friars Formation of San Diego County are morphologically indistinguishable from the Sespe specimens. Measurements of these teeth fall within the range represented by the Sespe samples (table 6).


Type and Only Specie: Crypholestes vaughni Novacek, 1976.

Diagnosis: Significantly smaller than Proterixoides with more transverse molars and less bulbous cusps. Very close in size and lower molar structure to Sespedectes but differs in having a bicuspid P4, talonid; more transverse upper molars with more conical, less bulbous cusps; more prominent labial spurs (particularly parastylar spur of M2); a consistently present precingulum on M1-3; less swollen hypocone on M2; labial extension of the postmetaconule wing as a metacingulum on M1-2; DP4 heavily worn at the time the molars are erupted (fig. 8B).


Discussion: Detailed description of Crypholestes was provided elsewhere (Novacek, 1976), but this systematic review prompts a revised diagnosis. Crypholestes is dentally the least specialized member of the Sespedectinae. The genus, represented only by C. vaughni, is not known from the Sespe or other areas outside of the San Diego County Eocene.

Fig. 8. Comparisons of occlusal views of (A) Sespedectes singularis, LACM (CIT) 1889, right P3-4, M1-3 (image reversed) from locality LACM (CIT) 207 and (B) Crypholestes vaughni, UCMP 103912, left P4, M1-2 from locality UCMP V-71211.

Relationships of the Sespedectinae

The bunodont appearance of the cheek teeth in sespedectines has been the source of some confusion. Russell (1964) and Russell, Louis, and Savage (1975) have suggested, for example, that these southern California taxa, at least Proterixoides, are possibly primitive hypsodontid condylarth rather than Erinaceomorpha. This claim can be disputed on several grounds.

First, hypsodontids are so poorly defined that any small mammal with a rather generalized, nonsectorial dentition may find itself dispatched to this group. Nevertheless, Gingerich (1983) has recently provided some cogent arguments for distinguishing primitive Erinaceomorpha from primitive Hypsodontid. In contrast to the latter, Erinaceomorpha typically have sharper-cusped cheek teeth, a strong postmetacrista on P4, M1-3, more crestiform paracynids, and lack distinct labial cingula on the lower molars.

This demarcation, though generally useful, does not clearly establish the more bunodont Proterixoides, Sespedectes, and "amphilemurs" as Erinaceomorpha. For this purpose,
additional characters are needed. Unlike hyopsodontids, these taxa have single-rooted, crowded anterior premolars; P₄s with weaker metaconids and short talonids with only small basins and cusps. (The P₄ talonid is generally large with a distinct basin in Hyopsodontinae, but reduced in the Mio-
claeninae.) The latter subfamily is, however, easily distinguished from Proterixoides, Ses-
pedectes, and amphilemurids.) M₁ paracon-
ids, though small and lophid in construc-
tion, are more salient; upper P⁴ has a strong, sweeping metastyalar crest typical of "mod-
ern" erinaceids, and the upper molars have stronger labial spurs, less inflated paracones, and more strongly developed hypocones.

These comparisons are discrepant with Russell's (1964) association of Proterixoides (and Sespedectes) and Pascatherium dolloi as closely related members of the Hyopsodon-
tidae. Russell, Louis, and Savage (1975) ex-
cluded Pascatherium from Erinaceomorpha because of its double-rooted premolars, bunodont molars, vestigial or absent paraconids, mental foramen below or slightly an-
terior to M₁, and the lack of a postmetaconule 
crista. Only the last condition and the buno-
dont "gestalt" of the molars are shared with Proterixoides and Sespedectes. Moreover, variation in metaconule development is seen among generally similar upper molars of Ses-
pedectes, Proterixoides, and Cryptolestes. 
Only in Sespedectes is the development of a postmetaconule crest completely obscured by inflation of the metaconule (fig. 4). To sum, sespedectines show diagnostic erinaceo-
morph traits lacking in Pascatherium and more typical hyopsodontids.

The inclusion of sespedectines within Erinaceomorpha still leaves open several pos-
sibilities for relationships. These reflect inter-
pretations in the literature that date back to Stock (1935). Sespedectines might qualify as erinaceids or "amphilemurids," or special-
ized dormaaliids, or a fourth clade of Erinaceomorpha separate from these groups. The alternatives will be briefly considered.

Stock (1935) regarded both Proterixoides and Sespedectes as erinaceids and noted the affinity of the former with the Oligocene gen-
us Proterix. Butler (1948) in his compre-
hensive review of the Erinaceidae suggested that Proterixoides might have been an early

offshoot of the Erinaceinae while also being "transitional" between dentally more primiti-
ve galericines (= echinosoricines) and Pro-

terix.

How valid are these associations? Table 7 
summarizes dental comparisons of sespedec-
tines with Recent Erinaceinae and Galerici-
nae. In most features, sespedectines seem 
more primitive. Notably lacking in sespedec-
tines are the marked elongation of the M₁, 
the progressive reduction in size from M₁ to 
M₂, the crest linking the hypocone with the 
postprotocrista, and the more quadrate di-
mensions of the upper molars—features which 
clearly define erinaceids.

The well-developed P₃ in sespedectines 
(character 13) is of phylogenetic interest. Most 
early erinaceomorphs do not show this con-
dition and it is likely that the erinaceomorph P₃ is primitively a simple, small, and some-
what triangular tooth as in Diacodon and 
Scenopagus (Novacek, 1982). Most erina-
ceids, certainly Recent ones, retain this latter 
condition, but at least two early members of the family show the derived sespedectine 
trait of a large P₃ that is closely similar to P₄. Re-
semblance is most striking with Galerix so-
cialis from the Miocene of Europe (see En-
gesser, 1972, p. 44). However, this genus 
departs from sespedectines in having the 
characteristic erinaceid features noted above 
and in table 7.

Another putative galericine, Tupaiodon 
Matthew and Granger (1924) from the Oli-
gocene Hsanda Gol Formation of Mongolia 
(see Butler, 1948), bears a close similarity to 
sespedectines in the P₃, P₄ condition. In ad-
in, the Asian genus departs from typical erinaceids and resembles sespedectines in 
having a small, premolariform upper canine 
and a very small or absent paraconule on 
M₁-₃. Tupaiodon does, however, show char-
acteristic erinaceid traits lacking in sespedec-
tines. Closer comparison with the original 
material is warranted.

As for other early galericines, the case for 
close relationships with sespedectines seems, 
if anything, weaker than for the abovementi-
tioned candidates. Other species of Galerix 
(including Pseudogalerix) have a very small 
P₃ (see Engesser, 1972). Tetracus (early Oli-
gocene, Europe) is poorly known but appears 
to have a double-rooted P₂ not notably small-
er than P3 (Butler, 1948; Saban, 1958). *Lanthanotherium* (middle–late Miocene, Europe; late Miocene–early Pliocene, North America) has a more specialized dentition seen in galericines (two lingual roots on M1–2 and a swollen posteriorly expressed hypocone in M3). Although the metaconule is swollen in *Lanthanotherium* in a manner similar to that in *Sespedectes*, not all sespedectines share this trait. It seems likely that the character was independently derived in the two genera. *Neurogymnurus* (late Eocene–middle Oligocene, Europe) has large double-rooted canines and anterior premolars, a small triangular P3, and several of the diagnostic dental traits of erinaceids.

From the discussion above, it is clear that most of the “evidence” for the alleged affinity between sespedectines and early galericines resides in primitive resemblance. Only the well-developed P3 in *Galerix socialis* and *Tupaiodon* and the inflated metaconule in *Lanthanotherium* suggest special relationships.

Other subfamilies of erinaceids fail to show special traits that link them with sespedectines. Brachyericines have greatly enlarged lower incisors, shortened face, reduced P4 trigonid, greatly elongated shearing crest on P4, and very small M3 that seem to be more specialized expressions of the basic erinaceid condition (see Rich, 1981). *Anmpechinus* (early Oligocene–late Miocene, Europe; late Oligocene–early Miocene, Asia; Miocene, Africa; late Miocene, North America) basically differs from sespedectines in the features it shares with other erinaceines (table 7). *Palaeoscaptor* (Oligocene, Asia) is dentally more primitive than *Anmpechinus*, but shows that even early members of the Erinaceinae are easily distinguished.

A final comparison of sespedectines with putative erinaceids concerns *Proterix* Matthew (1903). As the name implies, *Proterixoides* was originally allied with *Proterix* by Stock (1935), and Butler (1948) and others supported his argument. McKenna and Simpson (1959) remarked, for example, that *Proterixoides* was near to the structural ancestry of *Proterix*. The latter genus is, however, peculiar in many dental and cranial traits and its relationships within the Erinaceomorpha remain uncertain (Rich, 1981).

*Proterix* resembles sespedectines primarily in the lack of specializations of molars and premolars characteristic of erinaceids—namely the lack of a marked M1, prevallid and a progressive, posterior reduction in size of the lower molars; and the presence of a less developed “cutting” crest (metacrista) on the P4, smaller paraconids on the lower molars, and smaller, less isolated hypocones.

*Proterix* does, however, seem more conservative than sespedectines in having a large, double-rooted upper canine, a small, triangular-shaped P3, and a weaker metaconule on M1. It seems more derived in the greatly shortened snout, the loss of P1, the loss or aberrant structure of P2, a more distinct hypocone on P4, more quadrate molars, and the lack of hypoconulids on M2,3. Only the bunodont morphology of the molar cusps and the small, single-rooted P2 suggest a special relationship between sespedectines and *Proterix*.

These comparisons leave unresolved the problem of affinities of *Proterix*. The genus does not fit well within the Erinaceidae, and it should perhaps be formally excluded from that group (Rich, 1981, p. 109). *Proterix* may be related to sespedectines (though not to *Proterixoides* specifically), but it does not share many of the dental specializations that define that subfamily. It may, alternatively, be a close relative of “amphilemurids.” Resemblances to brachyericines in tooth reduction and skull shape seem independently derived.

The dental evidence reviewed above does not support the allocation of the subfamily Sespedectinae to the Erinaceidae. The simplification and reduction in size of the anterior premolars is a departure from the basic condition in erinaceids. This departure is also characteristic of specialized dormaalids (see Novacek, 1982). The bunodont construction of the molars is most like *Proterix*, a genus whose assignment to the Erinaceidae is equally suspect. The large, complex P3 is matched only by the galericines *Galerix socialis* and *Tupaiodon*. Most importantly, sespedectines lack many of the important specializations of the dentition that define more “modern” erinaceids. These characters are present, though less developed, in the late Paleocene, early Eocene members of the group (e.g., *Litolestes, Cedrocherus, Entomolestes*, see Krishtalka,
### Table 7

**Comparative Dental Characteristics in Sespedectines and other Erinaceomorphs**

<table>
<thead>
<tr>
<th>Characters</th>
<th>Sespedectes</th>
<th>Cryptodectes</th>
<th>Protocrocidus</th>
<th>Protorolinus</th>
<th>Macrocranion</th>
<th>Geogaleorhinus</th>
<th>Amphiferus</th>
<th>Pholidocercus</th>
<th>Alatacoticus</th>
<th>Selenop杭tus</th>
<th>Leptocyon</th>
<th>Talapothus</th>
<th>Didelphodon</th>
<th>Didelphomyinae</th>
<th>Micromyinae</th>
<th>Echinosorex</th>
<th>Neorufous</th>
<th>Erinaceinae</th>
<th>Erinaceomorphs</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. (a) P1, P2, P3 present; (b) P1, P3 absent; (c) P1, P2, P3 absent.</td>
<td>a a a1 a1 a ? a a a a a ? ? a a1 a a ? ? a a a ? a ? ? ? a a b c</td>
<td></td>
<td></td>
<td></td>
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<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>2. (a) P2 moderate size, double-rooted; (b) P2 small, procumbent, or peglike, single-rooted; (c) P2 absent.</td>
<td>b b' b b b ? b b b b b ? b a a a1 ? a ? b ? ? ? a a c</td>
<td></td>
<td></td>
<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>3. (a) P3 moderately large, double-rooted; (b) P3 small, procumbent, or peglike, single-rooted; (c) P3 absent.</td>
<td>a a a b b ? b b b a a ? ? a a a ? a ? b2 b2 ? ? ? a c c</td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td>4. (a) P4 with elongate talonid, talonid basin; distinct cusps; (b) P4 with short bicuspid or unicuspid heel.</td>
<td>b b b b b b b b b a a a a a ? b b a a b b b b b b b b b</td>
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<td>5. M1,3 (a) subequal in size; (b) moderate; or (c) marked progressive reduction in size from M1 through M3.</td>
<td>a a a a a a a a a a a a a a a c b c b b b b c c</td>
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<td>6. (a) M1 trigonids semi-compressed, paraconid crestiform, or lophid; (b) moderately; or (c) marked elongation of prevalid shear on M1, paraconid crestiform or connate.</td>
<td>a a a a a a a a a a a a a a a a a a b b b b b b b b b b b b b b c c</td>
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<td>7. Lower molar exodontal denty (a) absent; (b) present.</td>
<td>b b b a a b b b a a a a a a b b b b b b b b b b b b b b b b b b</td>
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<td>8. M1,3 trigonids (a) taller, erect; (b) lower, canted.</td>
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<td>9. Distinct ectocingulum on labial M1,3 (a) absent; (b) present.</td>
<td>a a a a a a a a a a a a a a a b b b a a a a b ? a b b b</td>
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<td>10. Hypoconids on M1,2 (a) moderate size; (b) small.</td>
<td>a a a a a a a a a a a a a a a a a a b b b b b b b b b b b b b b</td>
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<td>11. Molar cusps (a) connate or sectorial; (b) slightly swollen; (c) very swollen, bulbous or bunodont.</td>
<td>c b c a a c c c c c a a a a a a a a a a a a a a a a a a a a a a a a</td>
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TABLE 7—(Continued)

| Characters | Sepedectes | Cryolophodon | Proterotherium | Deltatherium | Gomphotherium | Amphimeryx | Pholidotheres | Mammuthus | Scepocepahus | Eriauchenia | Eosalodon | Taipanodon | Taipanovides | Diacodon | Mckennaiatherium | Dacocherus | Carphodon | Loxochelys | Lapidosaurus | Eototherium | Adapisorox | Neomaranella | Eolestes | Darotus | Galerix | Eremitinae | Brachytherinae |
|------------|------------|--------------|---------------|--------------|---------------|------------|---------------|-----------|-------------|-------------|-----------|------------|--------------|------------|---------------|-------------|-----------|-------------|-------------|-----------|---------|--------|------------|--------|--------|
| 12. P3 (a) caniniform, two-rooted; (b) peglike, one-rooted; (c) absent. | b b b | b b' | b | ? | b | ? | b | b | a | ? | a | a | a | a | a | ? | ? | ? | ? | ? | a3 | a | a | a | a | a | a3 | c |
| 13. P3 (a) small to moderate triangular, at least two-rooted; (b) very small, peglike, or triangular; (c) large with several cusps, similar to P4. | c c c | b b | ? | b b | a | ? | a | a | a | a | ? | b b | a | ? | a | a | a | ? | ? | ? | ? | a3 | b | b |
| 14. P4 hypocone (a) absent, very weak; (b) large, distinct. | a3 | a3 | a3 | ? | a | ? | a a | b b | ? | b | ? | a | a | a | ? | a | ? | ? | ? | a3 | ? | ? | ? | b | b |
| 15. P4 metacone (a) absent; (b) present. | a a a | a | ? | a a | a b | b b | ? | b | a b | ? | a | a | ? | b | b | ? | a | a a | a |
| 16. M3-2 hypocones (a) small; (b) larger; (c) larger and situated postero-lingually. | b b b | b b b | b b b | b b | c c | ? | a | b | a | b | ? | b | b | ? | b b | ? | b b | ? | b b |
| 17. M3-2 stylar spurs (a) moderately developed; (b) weak or absent; (c) very prominent. | a a a | a b b b a c c | ? | a | a a | ? | a | ? | b b | ? | a a | ? | b b | ? | a a a | a |
| 18. M3-2 (a) semirectangular; (b) subquadrate; (c) semi-quadrate. | a a a | a b b c b a a | ? | a | a | ? | a | a | ? | b b | ? | b b | ? | c c |
| 19. M3-2 hypoconid crest (a) absent; (b) present. | a a a | a a a a a a a a | a | ? | a | a | a | a | ? | a | a | ? | a | ? | a | a | ? | b b b |
| 20. M3 (a) transverse, semi-triangular with distinct parastylar spur, hypocone weak or absent; (b) heart-shaped, weak or absent parastyle and hypocone; (c) transversely oval, hypocone; (d) posteriorly expanded, usually with enlarged hypocone; (e) M3 absent. | a a b | ? | a | ? | b b | ? | a | ? | a | a | ? | ? | ? | b a | ? | ? | d4 | c | e |

1 Inferred from alveoli and partial or isolated teeth.
2 Tooth small, but double-rooted.
3 P3 small, but connate and double-rooted.
4 Galerix shows (secondary) enlargement of P3.
5 Hypocone vestigial or easily worn but posterolingual ("hypoconal") cingulum distinct.
6 Greatly expanded with large hypocone in most galericines, but not in Galerix.

The other candidates for relationship to the sespedectines belong to a group traditionally dubbed the Adapisoriciidae. The nominal character...
taxon for this group, *Adapisorex*, is, however, more likely a member of the Erinaceidae (Krishtalka, 1976; Novacek, Bown, and Schankler, 1985). Typical “adapisorids” differ markedly from *Adapisorex*. A recent proposal is the recognition of two specialized erinaceomorph families in addition to the Erinaceidae (Novacek, Bown, and Schankler, 1985). These are the Amphilemuridae and the Dormaaliidae (see also Koenigswald and Storch, 1983). Several erinaceomorphs whose generalized dental condition precludes their assignment to the foregoing families (e.g., *Diacodon, Adunator, Diacotherus*, and *Litocherus*) are regarded as Erinaceomorpha incertae sedis (Novacek, Bown, and Schankler, 1985; table 1).

Table 7 summarizes comparisons of sespedectines with a variety of erinaceomorphs, including “amphilemurids,” dormaaliids, and early, more dentally conservative, members of the Erinaceidae. Arguments for homologies and polarities of most of these dental characters are presented in Novacek (1982). Unlike more primitive *incertae sedis* taxa (e.g., *Diacodon*), sespedectines have small P\(_{1-2}\) with single roots and simplified crowns; P\(_4\) with short, simple talonids; at least an incipient hypocone on P\(_4\); lower, more canted trigonids on M\(_{1-3}\); and reduced, crestiform to lophid paraconids. These characters support the affinity of sespedectines with dormaaliids and “amphilemurids.” This is reflected in the scheme of relationships portrayed in a cladogram (fig. 9).

Within dormaaliids, sespedectines show somewhat closer resemblance with *Dormaalius* and *Macrocranion* than with the *Scenopagus-Ankylodon* grouping. Like the former, but unlike the latter, P\(_{1-2}\) are more reduced (P\(_{1-2}\) are poorly known in *Scenopagus*) and the lower molar trigonids are less erect. Like *Macrocranion*, but unlike *Scenopagus* and *Ankylodon*, the upper molars of sespedectines are more quadrate (upper molars are unknown in *Dormaalius*). However, these differences are subtle and the relevant characters are unknown in some critical taxa. It seems best to recognize sespedectines, the *Scenopagus-Ankylodon* group, and the *Dormaalius-Macrocranion* group as three separate clades within Dormaaliidae.

The remaining possibility—that sespedectines are more closely related to “amphilem-
urids”—is even more difficult to assess. The crucial dental evidence is lacking in some referred “amphilemurids.” At present, the preferred organization of the character evidence is reflected in the cladogram (fig. 9). Although the bunodont crown pattern is strikingly similar in Sespedectes, Proterixoides, and “amphilemurids,” this condition is not comparably developed in the sespedectine Crypholestes. To retain the integrity of the sespedectines based on specializations of the P3-P4 condition (fig. 3; table 7) requires the independent development of the bunodont condition in amphilemurids and sespedectines. Moreover, the reduced, single-rooted P3, and more quadrate upper molars in “amphilemurids” are more closely matched by Macrocranion, suggesting a close affinity between these taxa. Discoveries of more developed P3s in certain “amphilemurids” where this tooth is presently unknown (e.g., Gesneropithex) would weaken this hypothesis.

If the scheme of relationships portrayed in figure 9 is accepted, it would certainly not be reflected in a family-level rank for the Amphilemuridae. A phylogenetic classification that better represents the higher-level branching in the cladogram would take the following form:

Order Insectivora
  Suborder Erinaceomorpha
    Superfamily Dormaalioidea
      Talpavus
      Talpavoidea
    Family Dormaaliiidae
      Subfamily Scenopaginae
        Scenopagus
        Ankylodon
    Subfamily Dormaaliiinae
      Dormaalius
      Macrocranion
    Tribe Amphilemurini
      Amphilemur
      Gesneropithex
      Alsaticopithex
      Pholidocercus
    Subfamily Sespedectinae
      Crypholestes
    Tribe Sespedectini
      Sespedectes
      Proterixoides

Superfamily Erinaceoidea
  Erinaceoidea incertae sedis
    Eolestes
    Dartonius
    Neomatronella
    Adapisorex
    Leipsanolestes

Family Erinaceidae
  Entomolestes
  Cedrocherus
  Litolestes

  Subfamily Galericininae (see Butler, 1948)
  Subfamily Brachyericininae (see Rich, 1981)
  Subfamily Erinaceinae (see Butler, 1948; Rich, 1981)

Erinaceomorpha incertae sedis
  Diacodon
  Diacocherus
  Mckennatherium = Adunator
  Litocherus

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