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Notes on the Anterior Dentition and Skull of *Proterixoides* (Mammalia: Insectivora: Dormaaliidae), and a New Dormaaliid Genus from the Early Uintan (Middle Eocene) of Southern California

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ABSTRACT.—The anterior dentition and the anterior part of a skull of the dormaaliid lipotyphlan *Proterixoides davisi* have been recovered from late Uintan (middle Eocene) deposits in San Diego County, California. *Proterixoides* and other sespedectines are incipiently diprotodont, i. e., they have moderately enlarged, closely appressed, chisel-shaped first and second lower incisors that probably functioned together with the similarly enlarged corresponding upper incisors. Sespedectines are also characterized by having relatively small subequal lower third incisors and canines, relatively small buttonlike third upper incisors, and relatively small double-rooted upper first canines. The distinctive antemolar morphology of *Crypholestes*, *Sespedectes*, and *Proterixoides* corroborates the morphological integrity of the subfamily Sespedectinae.

Patriolestes novaceki is a new genus and species of dormaaliid from the early Uintan of San Diego County. It is characterized by a relatively large second lower incisor and lower canine, a usually single-rooted and relatively small third lower premolar, a bulbous trigonid on the fourth lower premolar not differentiated into separate cusps, the fourth lower premolar slightly longer anteroposteriorly than the first lower molar, lower molars with erect anteroposteriorly compressed trigonids, first lower molars with trigonids averaging wider than talonids, a relatively large double-rooted upper canine, single-rooted first and second upper premolars, deciduous and permanent third upper premolars much smaller than the fourth, and relatively sectorial upper molars. *Patriolestes* can be excluded from the Sespedectinae but is not readily assignable to either the Dormaaliinae or Scenopaginae. Pending collection of more complete material of its presumed relatives, *Patriolestes* is best classified as Dormaaliidae, *incertae sedis*.

INTRODUCTION

Insectivores from the Eocene of southern California were first described by Stock (1935). These early collections were obtained from the middle member of the Sespe Formation of Ventura County, representing the later part of the Uintan and the Duchesnean North American Land Mammal "ages" (NALMAs). See Krishtalka et al. (1987), Prothero (1996), Walsh (1996), and Lucas (1992) for discussions of the Uintan and Duchesnean NALMAs, and Kelly (1990) and Kelly et al. (1991) for a revised biostratigraphy of the Sespe Formation. Stock (1935) named the erinaceomorph genera *Proterixoides* and *Sespedectes*, and also tentatively referred a mandible fragment to the Leptictidae. The Erinaceomorpha (hedgehogs, gymnures, and their extinct relatives) and Soricomorpha (shrews, moles, solenodons, and possibly golden moles and their extinct relatives) together comprise the "true" insectivores, or Lipotyphla. See Novacek (1986a), Butler (1988), and MacPhee and Novacek (1993) for discussions of the names "Lipotyphla," "Proteutheria," and "Insectivora."

Novacek (1976) described several new lipotyphlan and "proteutherian" taxa from early and late Uintan localities in San Diego County. The most common early Uintan lipotyphlan from San Diego is the dormaaliid erinaceomorph *Crypholestes vaughni* (see Novacek 1976, 1980, 1985), which is morphologically similar to the late Uintan and Duchesnean *Sespedectes* and *Proterixoides* but retains a few more primitive dental features. A new, relatively large species of *Crypholestes* and a small species of the scenopagine dormaaliid *Scenopagus* were also recorded from the early Uintan of San Diego by Walsh (1996, table 1), and their description is planned for a future report. *Crypholestes*, *Sespedectes*, and *Proterixoides* are assigned to the dormaaliid subfamily Sespedectinae (Novacek 1985). New specimens of *Proterixoides davisi* allow a revised diagnosis of the Sespedectinae based on the complete anterior dentition and a partial skull.

Novacek (1976) assigned six isolated teeth from the early Uintan of San Diego to a relatively large "erinaceoid genus and species." He (1976, 1982) compared this material with various erinaceomorph taxa and suggested that the unnamed genus was most closely related to *Scenopagus* and *Ankylodon*, a conclusion reiterated by Novacek et al. (1985). The latter two genera were assigned to the dormaaliid subfamily Scenopaginae by Novacek (1985). Since 1976, a few additional specimens of the "erinaceoid genus and species" have been recognized in UCMP and LACM collections from the Friars Formation (for abbreviations see Table 1). Several mandibular and maxillary fragments and many isolated teeth have also been collected in San Diego County by SDSNH personnel. The present material is sufficient to justify the formal naming of the "erinaceoid genus and species," and a more detailed discussion of its phylogenetic position is now possible.

The lithostratigraphic ranges of several dormaaliid taxa in southwestern San Diego County are shown in Fig. 1. Novacek's (1976) specimens of the "erinaceoid genus and species" were col-

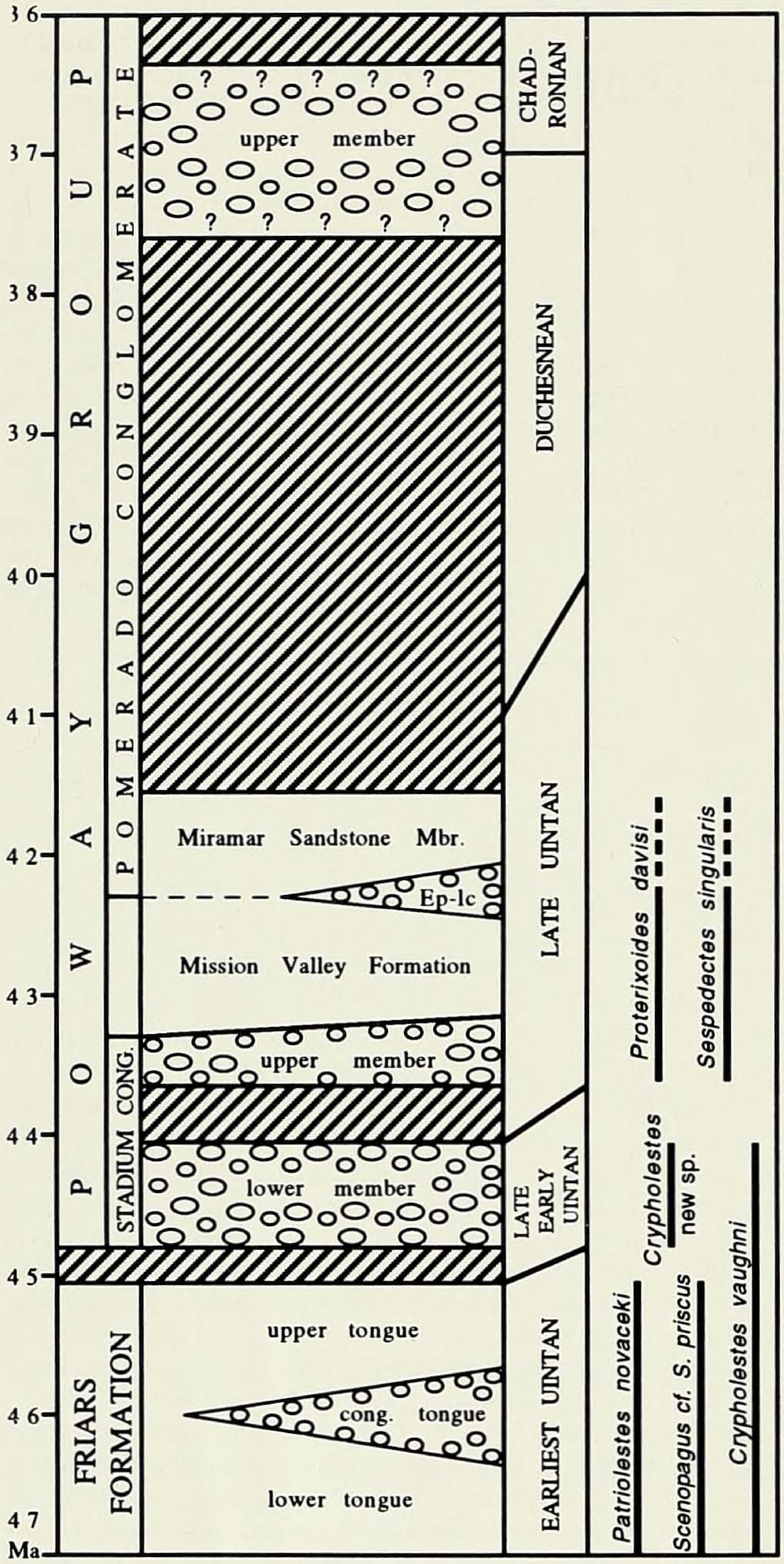


Figure 1. Known lithostratigraphic ranges in southwestern San Diego County of several erinaceomorph taxa discussed in this paper. Dashed upper parts of the ranges of *Sespedectes singularis* and *Proterixoides davisi* represent the inferred extent of their biochronozones (see Walsh, in press). Estimated numerical ages of the Friars Formation and Poway Group are based on information in Walsh (1996), Walsh et al. (1996), and an unpublished late Duchesnean or early Chadronian mammal assemblage from the upper member of the Pomerado Conglomerate (SDSNH Locs. 4041–4042). Ep-lc, lower conglomerate member of the Pomerado Conglomerate.

lected from the Rancho Peñasquitos district in the northern part of the city of San Diego, from strata mapped as the Mission Valley Formation by Kennedy and Peterson (1975). However, these strata actually pertain to the upper tongue of the Friars Formation, according to the stratigraphic revision of Walsh et al. (1996). Walsh (1996) discussed the profound faunal differences between the early Uintan Friars Formation and late Uintan Mission Valley Formation, and the relationships of these assemblages to those from Wilson's (1972) members "B" and "C" of the Santiago Formation in northwestern San Diego County.

METHODS

Important specimens are often introduced in the form "XXXX/YYYYY," where "XXXX" represents the locality number, "YYYYY" the specimen number. Several Eocene local faunas and geographic collecting districts of San Diego County are discussed by Golz and Lillegraven (1977), Walsh (1996), and Walsh et al. (1996).

Teeth from I1/i1 to P2/p2 are referred to as antemolars, while teeth from P3/p3 to M3/m3 are referred to as cheek teeth. Cheektooth terminology largely follows that of Rich (1981). The first upper and lower premolars of the dormaaliid taxa discussed herein are designated as "DP1" and "dp1," following the observation that in eutherians these loci are usually not replaced by permanent teeth (Butler 1948:463; Ziegler 1971). Thus, for the purpose of assigning isolated antemolars to particular loci, I assume that DP1 and dp1 are not replaced in the taxa described below (no convincing evidence cur-

TABLE 1. Abbreviations used.

AMNH	American Museum of Natural History, New York
AP	anteroposterior length
AW	anterior width of DP4 and P4–M3
C	upper canine
c	lower canine
CM	Carnegie Museum of Natural History, Pittsburgh
CV	coefficient of variation
D	upper deciduous tooth
d	lower deciduous tooth
I	upper incisor
i	lower incisor
L	left
LACM(CIT)	Original collections of the California Institute of Technology, now housed at the Natural History Museum of Los Angeles County
M	upper molar
m	lower molar
M	arithmetic mean
N	sample size
OR	observed range of variation
P	upper premolar
p	lower premolar
PW	posterior width of DP4 and P4–M3
R	right
SD	standard deviation
SDSNH	San Diego Society of Natural History
UCMP	University of California Museum of Paleontology, Berkeley
USGS	United States Geological Survey
W	maximum transverse width of upper and lower teeth (for p4 and teeth anterior to P3/p3 inclusive)
WTAL	maximum width of talonid of dp4 and m1–3
WTRI	maximum width of trigonid of dp4 and m1–3
YPM	Yale Peabody Museum, New Haven, Connecticut

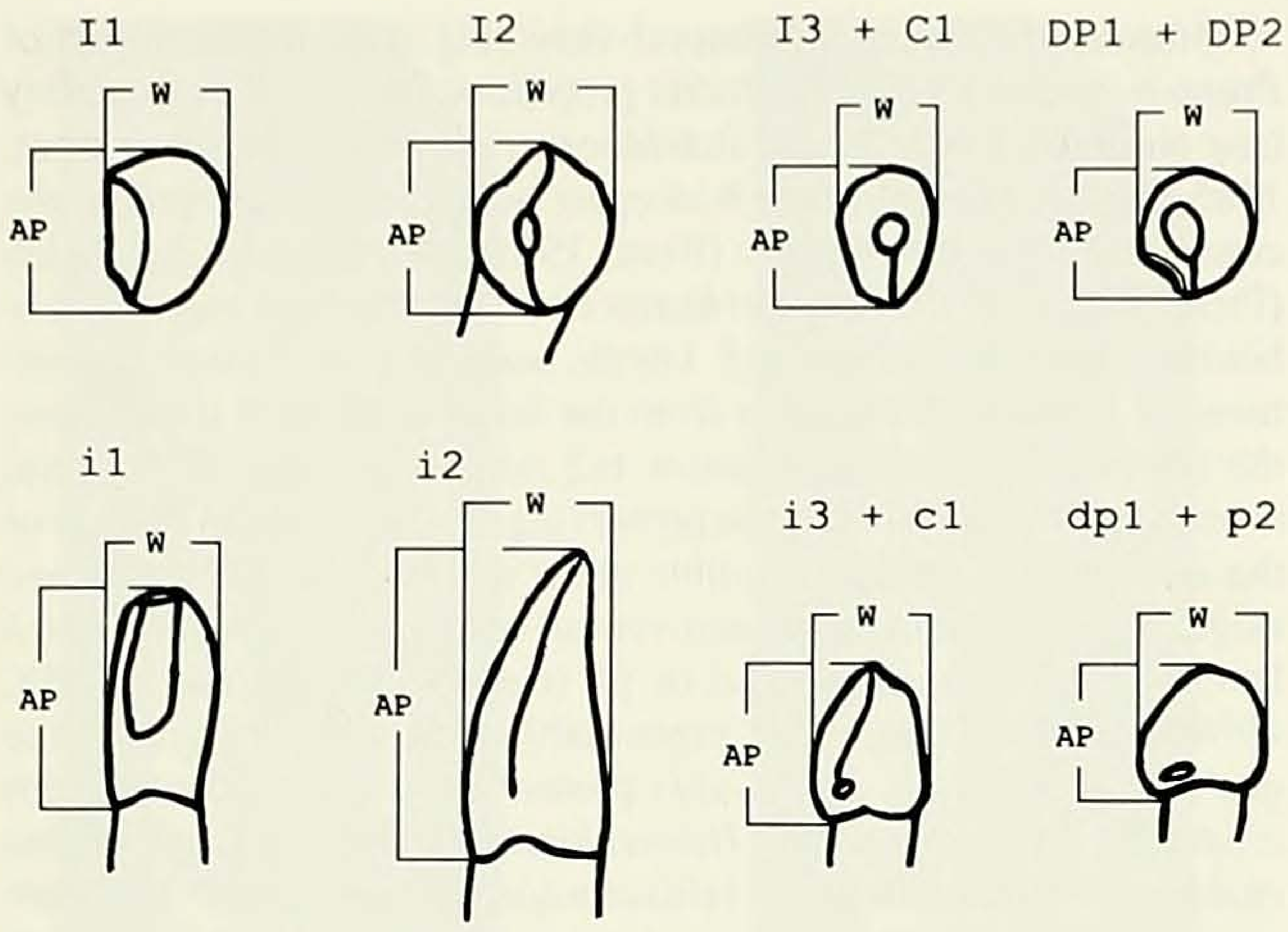


Figure 2. Generalized occlusal views of upper and lower left antemolars of *Proterixoides davisi* showing orientations for measurements used in this paper.

rently suggests otherwise). For the sake of clarity in comparisons within the Lipotyphla, I use the traditional four-premolar primitive eutherian tooth formula in preference to the five-premolar terminology advocated by McKenna (1975) and Schwartz and Krishtalka (1976) and further discussed by Novacek (1986b).

Measurements of teeth are in millimeters (mm) and were made on an Ehrenreich Photo-Optical Industries "Shopscope" to the nearest 0.01 mm. Orientations and endpoints for the measurements of antemolars are illustrated in Fig. 2. For I1-P2, I defined the AP axis as a line that bisects the crown of the tooth into equal lateral and medial halves as seen in occlusal view. The AP length of I1-P2 was taken parallel to the AP axis and measured the maximum anteroposterior length of the crown as seen in occlusal view. The width of I1-P2 was taken perpendicular to the AP axis and measured the maximum transverse width of the crown as seen in occlusal view. The anteroposterior length of i1-2 was measured parallel to the root, from the base of the enamel on the lateral side of the tooth to the anterodorsal tip of the crown, as seen in postero-occlusal view. This dimension is inherently variable owing to occlusal wear, so only essentially unworn i1-2s were included in the measurements for AP. The width of i1-2 measured the maximum transverse width of the crown as seen in postero-occlusal view. For i3-p3, the AP plane was defined to be the vertical plane that passes through the apex of the main anterior cusp and bisects the the area of the crown into two equal halves as seen in occlusal view. The AP length was then measured within this plane, but parallel to the maximum elongation of the crown as seen in lateral view. The width of i3-p3 was taken perpendicular to the AP plane and measured the maximum width of the crown as seen in occlusal view.

Measurements of DP3/P3-M3 and dp4/p4-m3 were taken according to the instructions given by Novacek (1976:8-9), with the following clarifications. The labial endpoint for the width of DP3 was always located at the labial base of the paracone even though the metastylar lobe sometimes extended even farther labiad. The anteroposterior lengths of P4s were taken as indicated by Novacek (1976, fig. 2). The corresponding width measurements for P4 are not perpendicular to the AP axis but are parallel to a line that passes through the paracone apex and bisects the lingual lobe into equal anterior and posterior halves. The anterior width of P4 was measured along an axis that passes through the apex of the parastyle, while the posterior width of M3 was measured along an axis that passes through the apex of the metacone.

Two different terms have been used to designate a tooth that leans anteriorly relative to the dorsal surface of the mandible. Stock (1935) used the term "proclivous" to describe the attitude of i2 in *Proterixoides*. I use it here to describe lower incisors whose crowns are elongated essentially parallel to the root (i. e., the angle between them is 175-180 degrees) and whose roots are implanted at a relatively low angle into the end of the mandible. The term "procumbent" describes antemolars whose crowns are elongated anteriorly at a distinct angle to the axis of the root as seen in lateral view (e.g., i3-p2 of *Proterixoides*). Degrees of procumbency may be characterized as follows: Slightly procumbent, root/crown angle 165-175 degrees. Moderately procumbent, root/crown angle 150-165 degrees. Highly procumbent, root/crown angle 120-150 degrees. "Trenchant" describes antemolars whose crowns are anteroposteriorly elongated, with a sharp anteroposterior ridge or keel as seen in occlusal view. "Bulbous" refers to a tooth crown (or part of a crown) that is convex and broadly rounded, without any prominent cusps or significant ridges. "Globular" designates upper anterior premolars whose crowns are essentially spherical or ellipsoidal and situated atop a single root of smaller diameter. Finally, "transverse" specifies upper cheek teeth whose labiolingual widths are much greater than their anteroposterior lengths. Higher-level taxonomy used in this paper follows that of Novacek (1985).

SYSTEMATICS

Mammalia Linnaeus, 1758
Eutheria Gill, 1872
Insectivora Illiger, 1811
Lipotyphla Haeckel, 1866
Erinaceomorpha Gregory, 1910 (Saban, 1954)
Dormaalioidea Novacek, 1985
Dormaaliidae Quinet, 1964
Sespedectinae Novacek, 1985

Included Genera.--Sespedectes Stock, 1935; *Proterixoides* Stock, 1935; *Crypholestes* (Novacek, 1976; 1980).

Known Distribution.—Early Uintan to Duchesnean of southern California. Krishtalka and Stucky (1984) reported *Crypholestes* in the early Bridgerian of Utah, while Storer (1996) reported *Sespedectes* in the late Uintan of Saskatchewan.

Emended Diagnosis.—Dormaaliids with moderately enlarged, proclivous, chisel-shaped i1 and i2, closely appressed to one another. Lower i3 and c1 single-rooted, moderately procumbent, virtually identical in size and shape, both much smaller than i1-2. Lower dp1 and p2 single-rooted, with small, moderately procumbent, triangular, heart-shaped crowns; p2 slightly larger than dp1, but both distinctly smaller than c1. I1 moderately enlarged, with curved, transversely compressed root and oval crown developing a concave lingual wear surface, resulting in a shovel-like appearance; I2 subequal in size to I1 but with more bulbous crown and shorter root. Size and occlusal relationships of upper and lower first and second incisors showing an incipiently diprotodont condition. I3 with single, short, straight, cylindrical root and buttonlike crown much smaller than I1-2, identical in shape to that of C1 but about 10% smaller in linear dimensions. C1 double-rooted or with incompletely fused roots; crown small, buttonlike, anteroposteriorly elongate, only slightly longer than P2. DP1 and P2 single-rooted, with small globular crowns, much smaller than P3. Skull poorly known, but snout apparently relatively long and narrow; nasals unfused; postorbital process absent; weak sagittal crest present; palate not fenestrated; lacrimal foramen situated on anterior dorsal border of orbit; anteroventral face of zygomatic root distinctly concave. Cheek-tooth characters diagnostic of the Sespedectinae are discussed by Novacek (1985).

Discussion.—The revised diagnosis of the Sespedectinae is based largely on the anterior dentitions of *Proterixoides* described below. That this diagnosis is also applicable to *Sespedectes* and *Crypholestes* is demonstrated by a nearly complete mandible of *Sespedectes singularis* (SDSNH 3755/56171), numerous isolated antemolars of *S. singularis* from SDSNH Loc. 3564, and numerous isolated antemolars of *Crypholestes vaughni* from various SDSNH localities in the Friars Formation. Once observed in place, the antemolars of sespedectines are quite distinctive, and isolated teeth can usually be allocated to specific loci with some confidence.

Proterixoides Stock, 1935
Proterixoides davisi Stock, 1935
Figs. 3, 4, 8c, 12b, 12d

Diagnosis.—Sespedectine much larger than *Crypholestes* or *Sespedectes*; morphological differences between *Proterixoides* and *Sespedectes* are minor; see Novacek (1985:15).

Known Distribution.—Late Uintan to Duchesnean (middle Eocene) of southern California.

Stratigraphic Units, Localities, and Referred Specimens.—

Santiago Formation, Member C: Jeff's Discovery local fauna (SDSNH Locs. 3276 and 3560-3564): Mandible fragments with i2 + p4: 42710. i3-dp1 + p3-4: 42804. dp1-m3: 48303. p3-4: 49696, 52800. p3-m1: 46627. p3-m2: 42636, 54942. p3-m3: 42709, 42802, 47458, 48309. dp4: 47181. p4-m1: 47682, 47683, 48980. p4-m3: 42639, 42806, 47728, 48401. m1-2: 52682. m1-3: 42805, 47461, 48135, 48728, 49661, 52205. m2-3: 46986, 48448, 48643, 52206. Palatal fragment with LP2-3 + RC1: 47699. Maxillary fragments with: P2-3: 42711. P2-M2: 42638. P3-M3: 47657. P4-M1: 48117. P4-M2: 47180, 47457. M1-2: 54562. M2-3: 48139. 303 isolated batch-catalogued antemolars and 180 isolated individually catalogued cheek teeth are also known from Jeff's Discovery.

Rancho del Oro local fauna: SDSNH Loc. 3445/58944: Partial skeleton with partial skull containing LI3-M3 and RI1-2 + P3-4 + M2-3, associated mandibles containing Lp4-m3 and Rc1-m3, plus another mandible fragment from a different individual containing Lc1 + p3-m3.

Stadium Conglomerate, upper member: SDSNH Loc. 3536: 12 isolated teeth.

Mission Valley Formation: SDSNH Loc. 3273: 13 isolated cheek teeth, plus several isolated antemolars. SDSNH Loc. 3426: two isolated cheek teeth. One isolated cheek tooth each from SDSNH Locs. 3537, 3627, and 3742. SDSNH Loc. 3870: Mandible fragments with p3-4: 54434. p3-m1: 54594, 54745. p3-m2: 54430. p3-m3: 54427-54429, 54596. m1-3: 54431: m2-3: 54433. Maxillary fragments with: C1 + P3-M3: 54597. P3-M1: 54436. P3-M2: 54598, 54599. M1: 54435. Numerous additional uncurated jaw fragments and isolated teeth are also present in the collections from SDSNH Locs. 3870, 4020, and 4038.

Pomerado Conglomerate, lower member: SDSNH Loc. 3755/56165: Mandible fragment with i1-2 + p3-m3.

Discussion.—At the time of Novacek's (1985) report on southern California sespedectines, only three published specimens of *Proterixoides davisi* were known from San Diego County, all from UCMP V-72088 (Santiago Formation, Camp San Onofre local fauna). Golz and Lillegraven (1977) had also recorded *Proterixoides* sp. from the latest Uintan or earliest Duchesnean Laguna Riviera local fauna (Santiago Formation, Member C). Since then, hundreds of specimens of *P. davisi* have been collected from Member C, as well as three different late Uintan stratigraphic units of the Poway Group in southwestern San Diego County. See Novacek (1985) for a detailed description of the cheek teeth of this genus. The following descriptions address only the mandible, skull, and antemolar dentition of *Proterixoides*. F. S. Szalay and I are currently studying isolated tarsal bones referable to *Proterixoides*.

Mandible.—As seen in lateral view (Fig. 3B), the mandible of *Proterixoides* is similar in general proportions to that of *Sespedectes* (see Novacek 1985, fig. 2) and *Macrocranion* (see Novacek et al. 1985, fig. 1). The mandible is deepest below m2-3, and unlike the condition in brachyericines (Rich, 1981) and modern erinaceids (Frost et al., 1991), there is no distinct decrease in depth immediately below the posterior end of m3. On the basis of 16 measurable specimens of *Proterixoides davisi* from the Jeff's Discovery local fauna, the depth of the mandible below m2 ranges from 4.7 to 7.2 mm, averaging 5.8 mm. Specimens preserving an intact ventral margin of the anterior part of the mandible show a strong medially concave ridge extending from the posteroventral corner of the symphysis to a level below the posterior end of p4 (e.g., SDSNH 42636, 47458, 49696, 54942). This ridge presumably marks the origin of the genioglossus muscle and is also present in at least some modern erinaceids (e.g., *Erinaceus*, *Hemiechinus*). The distribution of this character in other Paleogene erinaceomorphs is uncertain. There are usually three mental foramina, the most anterior of which occurs below p2, the most posterior below the middle of p4. As in *Sespedectes* (see Novacek, 1985, fig. 2), the posterior margin of the symphysis ends below p1, the dorsal ridge of the masseteric fossa is strong, and the coronoid process is high and anteroposteriorly broad (e.g., SDSNH 58944, mandibles not figured).

Lower antemolar dentition.—The complete anterior dentition of *Proterixoides davisi* is now known from several mandibles and a partial skull. On the basis of these specimens, many isolated antemolars of *P. davisi* have been identified in the large screenwashed sample of microvertebrates from the Jeff's Discovery local fauna. Prior to the collection of this new material, the only antemolar of *P. davisi* known was the i2 in LACM(CIT) 1676 (Stock 1935, fig. 4).

The i1 of *Proterixoides davisi* is proclivous, with a long, robust, slightly curved, gradually tapering, transversely compressed root (SDSNH 56165, Figs. 3A-B). The crown is chisel-shaped, transversely narrow, anteroposteriorly elongate, and dorsoventrally compressed at the tip. As seen in anteroventral view, the crown flares out laterally from the root, again giving the appearance of a chisel. As seen in posterodorsal view, the medial tip of the crown is taller than the lateral tip. The anteroventral face of the crown is slightly convex. The posterodorsal face of the crown is also convex, but it bears a large, blunt, central ridge that extends from the base of the crown nearly to the tip. Occlusal wear facets form at the tip of the crown and along the posterodorsal ridge. No interdental wear facets have been observed on the medial side of any i1, suggesting that left and right i1s of *Proterixoides* were not closely appressed to one another. Sixteen isolated i1s are known from SDSNH Loc. 3564 (SDSNH 58945), and 13 deciduous i1s also seem to be present (SDSNH 58947). The latter have crowns smaller than the permanent i1, with thin root walls that are usually broken just below the base of the crown.

The lower i2s of *Proterixoides* are similar in size and morphology to the i1s but are oriented in the mandible in such a way that their roots are dorsoventrally compressed (Fig. 3). The crown of i2 has a more rounded tip and a stronger dorsal ridge than i1, and also has the appearance of being given a distinct counterclockwise helical twist relative to the flat crown of i1. Six isolated i2s are known from SDSNH Loc. 3564 (SDSNH 58946), and 26 deciduous i2s also seem to be present (SDSNH 58948). Like the putative di1s, the di2s have crowns smaller than the permanent i2, with thin root walls that are usually broken just below the base of the crown. As seen in occlusal view, the lateral side of the crown of i1 is eclipsed by the medial side of the crown of i2 (Fig. 3A). A distinct interdental wear facet is almost always present on the lateral side of the posterodorsal face of the crown of i1 and the ventral face of the tip of i2, indicating that these two teeth were closely appressed.

The i3 and c1 of *Proterixoides* are preserved in place in SDSNH 42804 (Figs. 3C-D). The crowns of both teeth are much smaller than

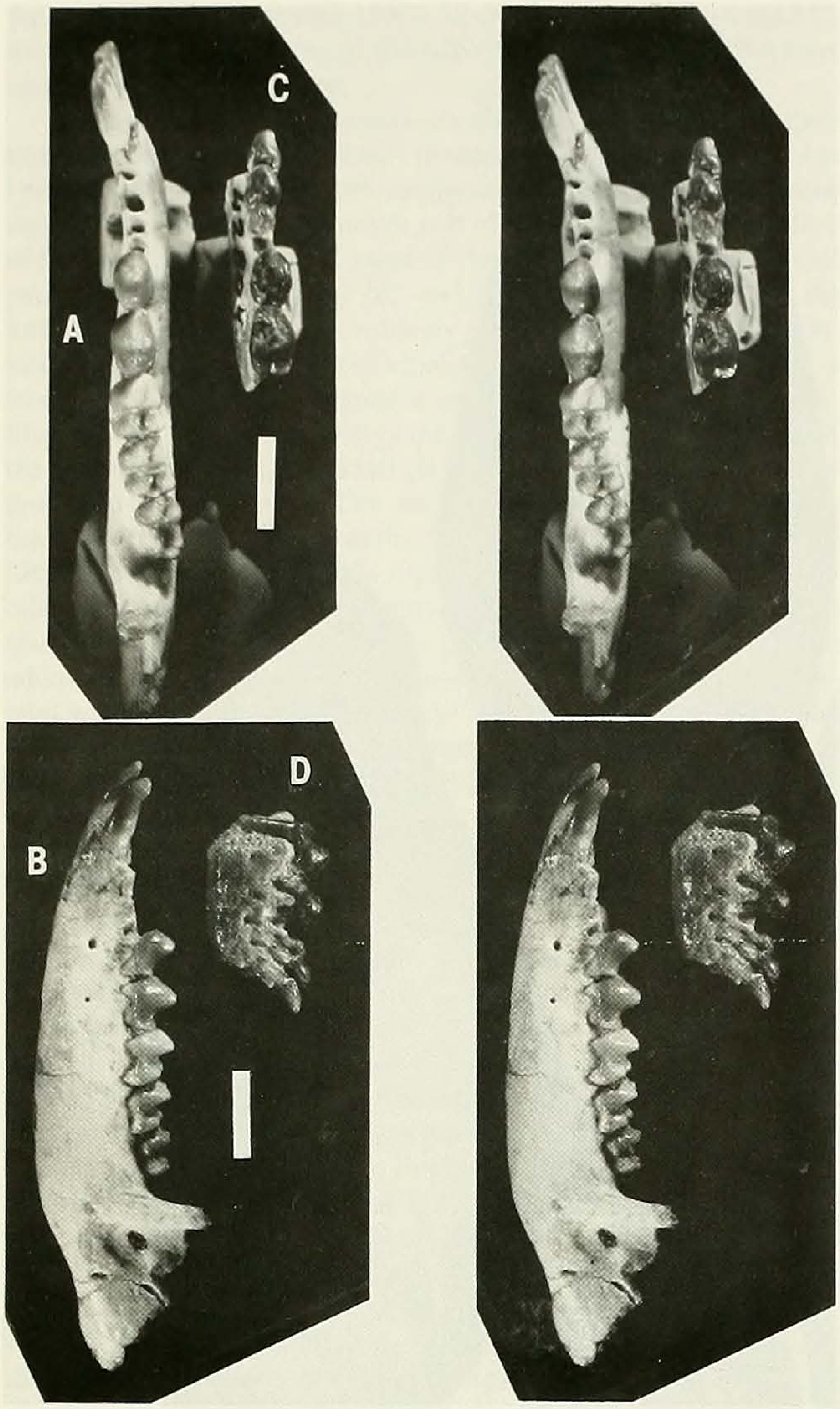


Figure 3. Stereophotographs of mandibular specimens of *Proterixoides davisi*. (A), Occlusal, and (B), lateral views of SDSNH 56165, L mandible with i1-2 + p3-m3. (C), Occlusal, and (D), lateral views of SDSNH 42804, R mandible fragment with i3-dp1 + p3-4. Scale bars, 5 mm.

i1-2 and are virtually identical in size and morphology. Both are moderately procumbent, nontrenchant, and have the appearance of an anteroposteriorly elongate rounded triangle in occlusal view. The crown of i3 is anteroposteriorly slightly more elongate than c1 but is dorsoventrally slightly thinner. Both teeth are single-rooted, with the root of i3 being smaller in diameter than that of c1 (see also the emtpy alveoli for these teeth in SDSNH 56165; Fig. 3A). Twenty-eight isolated i3s and 25 isolated c1s are also known from SDSNH Loc. 3564 (SDSNH 58949 and 58950), but no di3s or dc1s have been recognized.

Stock (1935) assumed that *Proterixoides* had a double-rooted p2 and had lost (d)p1. As in *Sespedectes* and *Crypholestes*, however, *P. davisi* retains single-rooted dp1 and p2 (Novacek 1985). The dp1 is preserved in SDSNH 42804 (Fig. 3C-D), and dp1-p2 are both preserved in SDSNH 48303 (not figured). Twenty-seven isolated dp1s and 19 isolated p2s are also known from SDSNH Loc. 3564 (SDSNH 58951 and 58952, respectively). Both dp1 and p2 are distinctly smaller than i3 and c1 but have similar triangular occlusal outlines and moderately procumbent crowns with weak dorsal ridges. The crown and root of p2 are slightly larger than those of dp1. Eight isolated teeth from SDSNH Loc. 3564 are tentatively identified as dp2s of *P. davisi* (SDSNH 58953). They are slightly smaller and dorsoventrally thinner than the p2 but are relatively more elongated anteroposteriorly, have stronger dorsal ridges, and have a deeper indentation in the occlusal outline of the posterior end of the tooth.

Skull.- The partial skeleton of *Proterixoides davisi* represented by SDSNH 58944 includes the anterior part of a laterally compressed skull. Both premaxillaries were found "floating" in the matrix and have been reattached to the skull in their approximately correct anatomical position. On the basis of substantial wear on the permanent premolars, the individual was a mature adult. At least in part for this reason, few cranial sutures are detectable.

In dorsal view (Fig. 4A), even allowing for lateral distortion and fragmentary preservation, the snout seems to be relatively long and narrow and thus more similar in this respect to extant hylomyine erinaceids than to erinaceines (Frost et al. 1991). The main skull fragment preserves the transversely thin left nasal, most of which has broken away from the frontal and been tilted upward so as to appear as if standing vertically on its lateral edge. The posterior parts of the unfused left and right nasals are deeply embayed into the anterior part of the frontal. The rest of the right nasal, most of the right maxillary, and all of the right lacrimal have been broken away. The anterior portion of the frontal has been pushed ventrally downward, thus tearing itself away from the left nasal. The metopic suture is barely discernible. The temporal ridges on the frontal converge posteriorly at the same anteroposterior level as the constriction. There is no indication of a postorbital process. A very weak sagittal crest is present at the posterior end of the skull fragment. Part of this crest presumably extends to the frontal, but whether any of it is formed by the parietals cannot be determined, as the suture between these bones cannot be identified. As in *Ankylodon* (see Fox 1983, fig. 1), a weak ridge extends ventrolaterad from the lateral edge of the frontal, just anterior to the constriction. This ridge quickly swings anteriad to merge with the dorsal rim of the orbit, but unlike *Ankylodon*, does not develop into a strong antorbital crest. As in *Brachyerix* (see Rich 1981, fig. 8), a knob of bone (lacrimal tubercle) on the most anterior part of the dorsal rim of the orbit marks the location of the lacrimal foramen.

In left lateral view (Fig. 4B), the skull appears to be relatively compressed dorsoventrally, more similar to modern hylomyines than to erinaceines (Frost et al. 1991). The left premaxilla is nearly complete. The ventral margin of the premaxilla is relatively long anteroposteriorly compared to its dorsoventral height, and the posterodorsal process appears to have extended posteriad almost to the level of the infraorbital foramen. *Proterixoides* is more similar in these respects to *Ankylodon* (see Fox 1983, fig. 1) and *Brachyerix* (see Rich 1981, fig. 8) than to *Macrocranion* (see Maier 1979, fig. 6A). The anterior opening for the infraorbital canal occurs immediately dorsal to P3, as in *Sespedectes* (see Novacek 1985, fig. 4A), *Ankylodon* (see Fox 1983, fig. 1), *Brachyerix* (see Rich 1981, fig. 8), and *Macrocranion* (see Novacek et al. 1985, fig. 1). The dorsoventral and transverse diameters of the infraorbital foramen in SDSNH 58944 are 2.2 and 1.1 mm, respectively. The minimum length of the infraorbital canal is 5.1 mm.

The maxillary-lacrimal, maxillary-frontal, and frontal-parietal sutures cannot be identified on the snout or orbital wall. As in various lipotyphlan taxa, there are two different dorsoventral levels of the palate as seen in lateral view. In *Proterixoides*, the transition between them is gradual and occurs largely between P2 and P3. This differs somewhat from the condition in *Ankylodon*, in which the transition apparently occurs between P3 and P4 (see Fox 1983, fig. 1). Short lengths of the anterior part of both zygomatic arches are preserved in SDSNH 58944. Although a jugal-maxillary suture cannot be discerned on either arch, it is likely that the region where these sutures occurred is not preserved (compare with *Brachyerix*; Rich and Rich 1971, fig. 1). The anterolateral face of the zygomatic process is strongly concave, forming a distinct antorbital fossa for the origin of

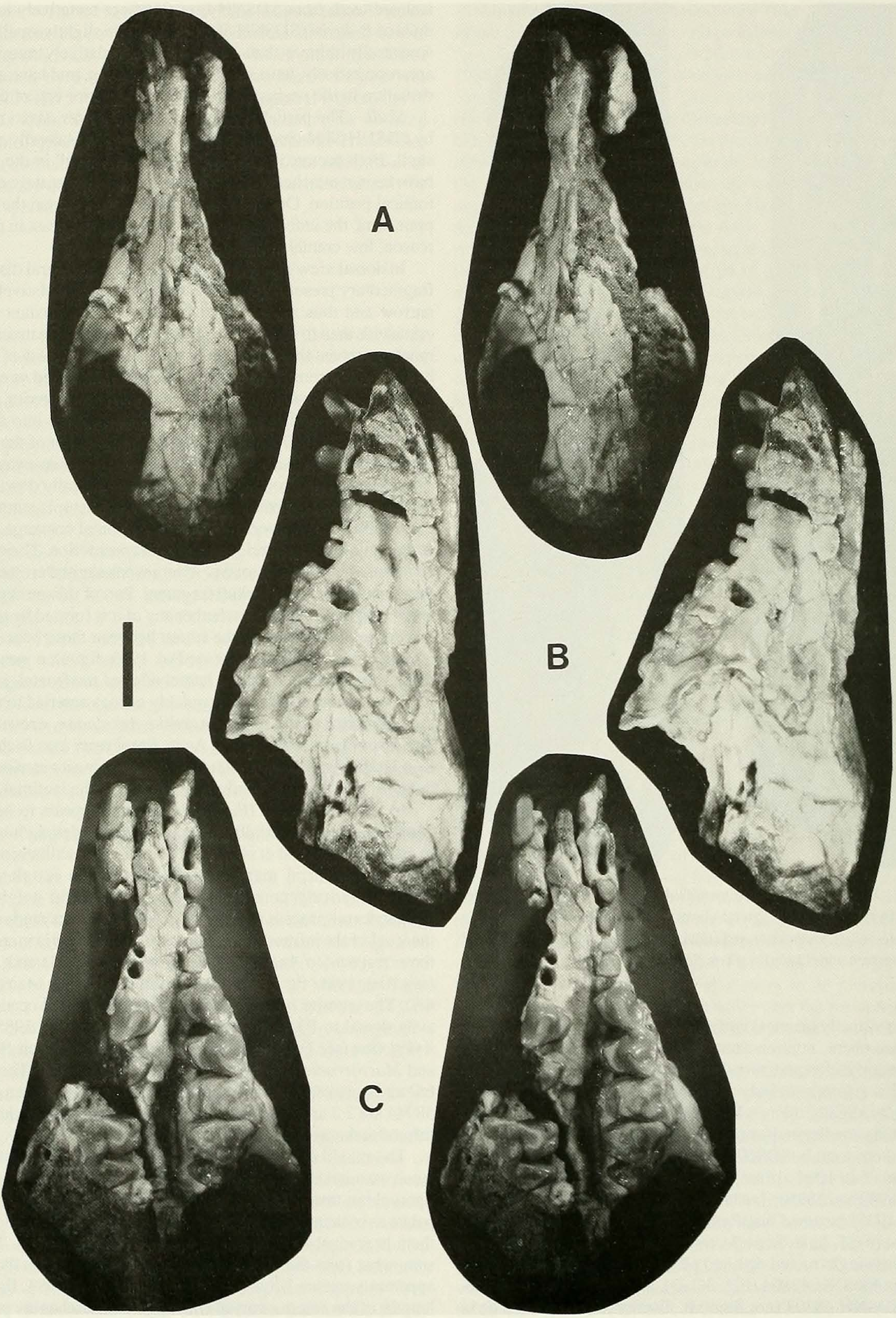


Figure 4. Stereophotographs of SDSNH 58944, partial skull of *Proterixoides davisi* preserving LI3–M3 and RI1–2 + P3–4 + M2–3. Scale bar, 5 mm. (A), Dorsal view; (B), left lateral view (apparent concavity of skull roof is due to crushing); (C), ventral view.

the snout muscles (Novacek 1986a:30–31). As measured behind M2, the dorsoventral thickness of the left zygomatic process is 3.8 mm, and its dorsal edge is sharp.

The left orbital wall reveals several structures, although their identities are generally uncertain because the sutural boundaries between the frontal, parietal, orbitosphenoid, alisphenoid, and palatine cannot be located. In the anterior part of the orbit, the dorsal surface of the maxillary comprises most of the floor and shows the dorsal ends of the lingual roots of M2 and M3. The posterior end of the infraorbital canal opens immediately above the floor of the most anterior part of the orbit. No postpalatine foramen is evident, but a small foramen seems to be present on the posterior edge of the maxillary behind LM3. Immediately dorsomedial to the posterior end of the infraorbital canal is a small pit at the anterior end of a shallow groove in the orbital wall. This pit is located in the same place relative to the infraorbital canal as the pit for the inferior oblique muscles identified by Novacek (1986a, fig. 9) in the orbit of *Leptictis*. Another, larger pit occurs at the ventral base of the lacrimal foramen. It also occurs at the anterior end of a groove in the orbital wall. Three additional, parallel grooves are present in the ventral part of the orbital wall. The most ventral of these lies immediately dorsal to the dorsal surface of the palatine and runs from the lingual root of M3 back to the posterior end of the skull fragment. The middle of these grooves ends anteriorly in a small pit or foramen (orbitonasal foramen?) and ends posteriorly below what is presumably the sphenorbital and/or suboptic foramen (compare with the orbit of *Brachyerix*; Rich and Rich 1971, fig. 15). Another distinct pit immediately anterodorsal to the latter foramen may represent the optic foramen. Immediately posterior to the sphenorbital (?) and/or suboptic (?) foramen, a small bridge of bone may define the anterior and posterior openings of a very short alisphenoid canal. The broken outline of what may be the anterior rim of the foramen ovale is doubtfully present at the posterior end of the skull fragment.

In ventral view (Fig. 4C), the palate has been pulled upward relative to the crowns of LC1–P2, and the left and right cheek teeth are compressed quite close together. The left maxillary preserves C1–M3, while the right maxillary preserves alveoli for C1–P2, intact P3, the lingual half of P4, and intact M2–3. The width of the snout narrows appreciably but gradually from P4 to C1. The maxillary root of the zygomatic arch originates lateral to M2, as in *Macrocranion* (see Maier 1979), *Ankylodon* (see Fox 1983), and many other lipotyphlans. At least part of both palatines contribute to the hard palate, but the maxillary–palatine sutures cannot be identified. There is no obvious postpalatine torus, and there does not appear to be any fenestration of the palate as in *Ankylodon* (see Fox 1983, fig. 2) or *Brachyerix* (see Rich 1981, fig. 10). The skull is preserved back to the posterior part of both palatines, but the basicranium was broken away prior to burial, and there is no indication of the palatine–alisphenoid sutures. The internal narial opening is present but distorted.

Upper antemolar dentition.—Combining teeth from the left and right sides of SDSNH 58944 completes the upper dentition of *Proterixoides* (Fig. 4C). I1–2 are present in a fragment of the right premaxilla and are the largest upper anterior teeth (just as i1–2 are the largest lower anterior teeth). I1 has a dorsoventrally elongated crown, with a relatively flat lingual face and an asymmetrically convex labial face. The flat lingual face becomes concave with wear, assuming a characteristic shovel-like appearance. The wear facet is presumably caused by occlusion with the chisel-shaped tip of i1. The large transversely compressed root of I1 curves gently posteriad into the premaxilla. There is a short diastema of about 1 mm between I1 and 2. I2 is subequal in size to I1 but has a transversely wider, less dorsoventrally elongate crown whose labial and lingual faces are both uniformly convex. I2 develops a relatively flat wear facet on the tip of the crown. The root is robust as in I1 but is shorter and curves more strongly into the premaxilla. Twelve isolated I1s and 21 isolated I2s of *Proterixoides* are known from SDSNH Loc. 3564 (SDSNH 58954 and 58955, respectively). In addition, 43 isolated mitten-shaped teeth with thin root walls probably represent deciduous I1–2s (SDSNH 58958).

The occlusal relationships of the lower and upper first and second incisors in *Proterixoides* and other sespedectines were probably similar to the relationships documented by Butler (1980:173–175) in extant tupaiids. As discussed by Butler (1980:173) in reference to *Ptilocercus*, the arrangement of the anterior incisors in sespedectines may best be termed "incipiently diprotodont."

The left premaxilla of SDSNH 58944 is essentially complete. It contains a crushed alveolus for I1, an intact but empty alveolus for I2, and a moderately worn complete I3 (Fig. 4B–C). The crown of I3 is much smaller than those of I1–2 and differs morphologically from the anterior incisors in that it is short and buttonlike, very similar to the C1 preserved in the same specimen but about 10% smaller in linear dimensions. Twelve isolated I3s from SDSNH Loc. 3564 (SDSNH 58956) show that the crown apex is located near the anterior end of the tooth and sends a weak dorsal ridge to the posterior base of the crown. The anterior part of the crown is wider than the posterior part and develops a flat posterodorsally dipping wear facet. The cylindrical root of I3 is short, straight, and rapidly tapering.

C1 is preserved in place in the partial skull of SDSNH 58944 (Fig. 4C). It has a small buttonlike crown that is anteroposteriorly slightly longer but distinctly narrower transversely than P2. As in I3, the anterior part of the crown of C1 is taller and wider than the posterior part. The C1 in SDSNH 58944 misleadingly appears to have a single anteroposteriorly elongate root. However, 3 of 12 isolated C1s of *Proterixoides* from SDSNH Loc. 3564 have separate anterior and posterior roots (SDSNH 58957). In the remaining nine C1s, the roots are incompletely fused into a single root, bearing distinct longitudinal constrictions on their labial and lingual faces. Novacek (1985) described the C1 of *Sespedectes stocki* as being single-rooted. However, many isolated C1s of *Sespedectes*

TABLE 2. Measurements of antemolars in SDSNH 58944, partial skull and associated mandibles of *Proterixoides davisi*.

	I1		I2		I3		C1		DP1		P2	
	AP	W	AP	W	AP	W	AP	W	AP	W	AP	W
L premaxilla + maxilla	—	—	—	—	1.31	0.97	1.66	1.10	0.98	1.06	1.36	1.37
R premaxilla	1.88	1.34	2.03	1.56	—	—	—	—	—	—	—	—
	i1		i2		i3		c1		dp1		p2	
	AP	W	AP	W	AP	W	AP	W	AP	W	AP	W
L mandible	—	—	—	—	—	—	2.34	1.69	—	—	—	—
R mandible	—	—	—	—	—	—	2.36	1.67	—	—	1.62	1.56

singularis from SDSNH Loc. 3564 are double-rooted (SDSNH 60036), as are many isolated C1s of *Crypholestes vaughni* from the Friars Formation.

Heavily worn DP1s and P2s are preserved in place in SDSNH 58944 and are much smaller than P3. Nineteen isolated DP1s and 16 isolated P2s from SDSNH Loc. 3564 (SDSNH 58959 and 58960) show that both teeth are single-rooted, with globular crowns consisting of a single apical cusp and a weak posterodorsal ridge. P2 is distinctly larger than DP1 and has a short postcingulum not present in DP1. One of the P2s included in SDSNH 58960 may be deciduous, as it has thin root walls and lacks a postcingulum. The upper anterior premolars of *Proterixoides* are morphologically very similar to the much smaller homologous teeth of *Sespedectes* (see Novacek 1985, fig. 3).

Measurements.—Measurements of antemolars of *P. davisi* preserved in the associated mandibles and partial skull of SDSNH 58944 are given in Table 2, while standard statistics for measurements of antemolars and cheek teeth of *P. davisi* from the Jeff's Discovery local fauna are given in Table 3. The latter provides a good indication of the expected size variation in a dormaaliid species based on a large sample collected from a single site.

Novacek (1985, table 5) presented standard statistics for measurements of cheek teeth of *P. davisi* from the Sespe Formation. It will be seen from Table 3 that linear dimensions of the Jeff's Discovery teeth average between 5% and 15% smaller than the Sespe teeth. However, the latter sample is stratigraphically and temporally heterogeneous, and some tooth positions are represented by just a few specimens. An analysis of whether more than one species of *Proterixoides* is recognizable in the middle Eocene deposits of southern California is beyond the scope of this paper but certainly feasible. The phylogenetic position of the Sespedectinae is discussed below under Evolutionary Relationships.

TABLE 3. Standard statistics for teeth of *Proterixoides davisi* from the late Uintan Jeff's Discovery local fauna, Member C of Santiago Formation, San Diego County.

Tooth		*N*	OR	*M*	SD	CV
I1	AP	6	1.59-1.79	1.67	0.078	4.7
	W	6	1.49-1.64	1.58	0.056	3.5
I2	AP	11	1.94-2.33	2.12	0.159	7.5
	W	11	1.46-1.80	1.61	0.112	7.0
I3	AP	10	1.23-1.44	1.34	0.082	6.1
	W	10	0.94-1.08	1.00	0.042	4.2
C1	AP	8	1.40-1.64	1.55	0.090	5.8
	W	8	1.07-1.26	1.12	0.065	5.8
DP1	AP	16	0.94-1.15	1.08	0.057	5.3
	W	16	0.93-1.09	0.99	0.055	5.5
P2	AP	13	1.33-1.61	1.45	0.080	5.6
	W	13	1.26-1.50	1.36	0.075	5.5
P3	AP	10	2.87-3.46	3.10	0.221	7.2
	W	11	2.65-3.31	2.96	0.207	7.0
DP3	AP	4	2.91-3.08	2.98	0.079	2.6
	W	4	2.31-2.35	2.33	0.023	1.0
P4	AP	12	2.86-3.31	3.09	0.109	3.5
	AW	14	2.71-3.59	3.07	0.242	7.9
	PW	12	3.35-3.95	3.68	0.184	5.0
DP4	AP	5	2.98-3.25	3.10	0.127	4.1
	AW	5	2.65-3.27	2.93	0.266	9.1
	PW	5	2.99-3.51	3.28	0.225	6.7
M1	AP	18	2.80-3.22	2.98	0.119	4.0
	AW	19	3.69-4.14	3.89	0.132	3.4
	PW	19	3.92-4.55	4.20	0.189	4.5
M2	AP	15	2.54-2.89	2.71	0.109	4.0
	AW	15	3.92-4.61	4.21	0.201	4.8
	PW	15	3.46-4.06	3.77	0.187	5.0
M3	AP	17	1.68-2.14	1.92	0.123	6.4
	AW	15	2.86-3.51	3.08	0.196	6.4
	PW	18	2.09-2.66	2.27	0.142	6.2
i1	AP	3	2.70-3.02	2.87	0.160	5.6
	W	15	1.19-1.39	1.26	0.053	4.2
i2	AP	5	3.25-3.64	3.43	0.158	4.6
	W	5	1.63-1.88	1.75	0.105	6.0
i3	AP	19	1.84-2.32	2.07	0.110	5.3
	W	19	1.32-1.65	1.46	0.090	6.2
c1	AP	15	2.04-2.24	2.15	0.055	2.5
	W	20	1.50-1.86	1.64	0.092	5.6
dp1	AP	10	1.33-1.49	1.39	0.053	3.8
	W	13	1.14-1.33	1.23	0.053	4.3
p2	AP	13	1.47-1.94	1.65	0.151	9.2
	W	17	1.35-1.60	1.48	0.076	5.1
dp2	AP	7	1.52-1.82	1.70	0.101	5.9
	W	7	1.17-1.22	1.20	0.017	1.4
p3	AP	19	2.70-3.07	2.87	0.097	3.4
	W	19	1.78-2.22	1.94	0.107	5.5
dp3	AP	12	2.36-2.59	2.50	0.074	3.0
	W	14	1.50-1.78	1.63	0.079	4.8
p4	AP	29	2.93-3.75	3.36	0.154	4.6
	W	29	1.97-2.61	2.24	0.131	5.9
dp4	AP	11	2.99-3.34	3.12	0.125	4.0
	WTRI	10	1.49-1.77	1.63	0.082	5.0
	WTAL	11	1.83-2.13	1.98	0.103	5.2
m1	AP	26	2.90-3.34	3.10	0.120	3.9
	WTRI	25	2.30-2.71	2.44	0.096	3.9
	WTAL	25	2.31-2.72	2.51	0.105	4.2
m2	AP	37	2.71-3.13	2.92	0.107	3.7
	WTRI	38	2.36-2.80	2.57	0.091	3.5
	WTAL	37	2.27-2.60	2.41	0.078	3.2
m3	AP	28	2.53-3.22	2.94	0.167	5.7
	WTRI	28	1.75-2.31	2.03	0.128	6.3
	WTAL	28	1.51-1.89	1.70	0.106	6.3

Dormaaliidae, *incertae sedis*

Patriolestes gen. nov.

Etymology.—Named for the Friars Formation, in reference to the Franciscan friars (Kennedy and Moore 1971:717). *Patrio-*, father; *-lestes*, robber (Greek).

Type Species.—*Patriolestes novaceki*, sp. nov.

Diagnosis.—*Patriolestes* differs from all known Eocene erinaceomorph genera in having the following combination of characters (putative autapomorphies within Dormaaliidae indicated by **boldface**). No diastemata in lower anterior dentition; i1 proclivous, chisel-shaped, apparently somewhat smaller than i2; i2 proclivous, with anteroposteriorly elongate, chisel-shaped crown, distinctly larger than i3; i3 moderately procumbent and trenchant; c1 single-rooted, slightly procumbent, bulbous, with largest crown of the lower anterior teeth; dp1 single-rooted, with moderately procumbent triangular crown, smaller than p2–3; p2 single-rooted with moderately procumbent triangular bulbous crown subequal to that of p3; p3 usually single-rooted, with slightly procumbent, bulbous crown, somewhat pentagonal in occlusal outline, and much smaller than p4; p4 slightly longer than m1, double-rooted, bulbous, **without differentiation of trigonid cusps or paracristid**, and with single small cusp at posterolingual corner of short talonid; lower molars with erect anteroposteriorly compressed trigonids and bladelike paraconids; lower and upper molars relatively sectorial; **m1 trigonid width averaging slightly greater than talonid width**; I1–2 moderately enlarged, with shovel-like crowns. I3 much smaller than I1–2, with dorsoventrally short, anteroposteriorly elongate crown with distinct dorsal ridge. **C1 double-rooted, with large, bulbous crown**; DP1–P2 single-rooted, with small, globular, slightly anteroposteriorly elongate crowns with weak dorsal ridges; DP3 triple-rooted, with very strong metastylar lobe, distinct metacone, but no hypocone; DP3 much smaller than the triple-rooted, large, molariform DP4; P3 subtriangular in occlusal outline, without metacone or hypocone, and much smaller than P4; P4 triple-rooted, large, transverse, with strong posterolabially directed metastylar crest but without hypocone or metacone; M1 with hypocone extending further linguad than protocone. M2 transverse, usually with protocone extending further linguad than hypocone. M1-3 generally with strong pre- and post-paraconular and metaconular wings. See below for detailed character-by-character comparisons of *Patriolestes* with other erinaceomorph taxa.

Patriolestes novaceki sp. nov.
Figs. 5-7, 8a, 8b, 9-11

"Erinaceoid-like genus and species" (Novacek 1976:36).

"cf. *Proterixoides davisi*" (Golz and Lillegraven 1977:53).

"cf. *Proterixoides* sp." (Golz and Lillegraven 1977:53).

"Erinaceid-like genus and species" (Novacek et al. 1985:5).

Proterixoides davisi (Novacek 1985:15, in part).

"Dormaaliidae, new genus and species" (Walsh 1996:84).

Etymology.—Species named after Dr. Michael J. Novacek, for his contributions to vertebrate paleontology.

Type Specimen.—SDSNH 49250, right mandible fragment with p4-m3.

Type Locality.—SDSNH Loc. 3784, "Stonecrest Square Site 4." Friars Formation (undifferentiated), west wall of Murphy Canyon, San Diego County, California.

Diagnosis.—Morphology as for genus; size as indicated by measurements in Tables 4-6.

Known Distribution.—Early Uintan of San Diego County, California (Friars Formation and Member B of Santiago Formation).

Localities and Referred Specimens.—See Appendices 1-2.

Mandible.—There are 13 mandible fragments (none preserving the coronoid or condyle) containing at least one tooth in LACM, SDSNH, and UCMP collections. The most dentally complete of these is the type specimen (Fig. 5), but other mandibles preserve more complete anterior alveoli (Fig. 6). From the few specimens showing an intact ventral surface of the mandible anterior to p4, there does not appear to be a distinct ridge for the origin of the genioglossus muscle, unlike the condition in *Proterixoides*. The lateral side of the mandible consistently has two small mental foramina. In most cases, the most anterior of these is located below p3, and the posterior foramen is located below the middle of p4 (e.g., SDSNH 56725). In UCMP 133966, however, the two foramina are situated below p2-3, and SDSNH 54912 has three small foramina below p2-4. The masseteric fossa ends anteriorly below the m3 hypoconulid, as in *Proterixoides*. The dorsal ridge defining the fossa is much stronger than the ventral ridge. The mandibular symphysis ends posteriorly below p2. The dorsal margin of the symphysis is defined by a ridge of variable strength and is quite pronounced below c1. The observed depth of the mandible below m2 ranges from 5.1 to 5.4 mm ($N = 5$).

SDSNH 56725 preserves p3-4 and at least portions of the alveoli for i1-p2 (Fig. 6A). All alveoli are crowded closely together and show that i1-p2 were single-rooted. The alveolus for i1 is heavily damaged, but the tooth had a proximally slender root, oriented at a relatively low angle into the mandible. The i2 alveolus was distinctly larger in diameter than the i1 and i3 alveoli. In SDSNH 56725, the round canine alveolus is much larger than the i3 and dp1 alveoli. In SDSNH 54912, however, the c1 alveolus is only slightly larger than the adjacent alveoli (Fig. 6D). In all available specimens, the p2 alveolus is significantly larger than the dp1 alveolus and is subequal in size to the p3 alveolus.

Lower Dentition.—Lower antemolars of *Patriolestes* are not preserved in available mandibles, and upper incisors of *Patriolestes* are not preserved in the only available premaxillary. However, many isolated antemolars of *Patriolestes* have been collected from several SDSNH localities in the Friars Formation, and their allocation to specific loci is aided by comparison to the dentition of *Proterixoides davisi* described above. In addition, the few other lipotyphlan and "proteutherian" taxa in the Poway fauna whose antemolars might be confused with those of *Patriolestes* are relatively rare (Walsh 1996).

The least confidently identified antemolar of *Patriolestes* is i1, in part because the anterior diameter of the i1 alveolus is not preserved on any available mandible. Eight isolated teeth, varying greatly in size, are tentatively assigned to this locus. Their crowns are similar to that of the i1 of *Proterixoides* in being anteroposteriorly compressed and chisel-shaped (e.g., SDSNH 58919, Fig. 7). However, most of these teeth are relatively small compared to the i2s of *Patriolestes* described below, whereas the crowns of i1-2 in *Proterixoides* are subequal in size. Furthermore, the roots of the putative i1s of *Patriolestes* are cylindrical, whereas the i1 root of *Proterixoides* is more robust and distinctly compressed transversely. Finally, unlike the condition in *Proterixoides*, most of these teeth have distinct interdental wear facets on their medial sides, indicating close appression of the left and right i1s. Suspiciously, most of the putative i1s of *Patriolestes* seem to be too small to occlude properly with the relatively large I1s described below. Perhaps only SDSNH 58919 is an i1, and the remaining smaller teeth are di1s or do not pertain to *Patriolestes*.

Ten isolated teeth from the Friars Formation are identified as i2s of *Patriolestes* (e.g., SDSNH 58732, Fig. 7). They are very similar to the homologous teeth of *Proterixoides davisi* but are distinctly smaller. Six of the i2s have an appression facet on the ventral side of the tip of the crown, caused by interdental wear with i1. As in i1, occlusal wear facets are developed on the tip and dorsal ridge of the crown. Six isolated teeth are tentatively identified as di2s (Appendix 1). They are similar in size and morphology to the permanent i2s but have sharper dorsal ridges and a small posterodorsal cuspule.

On the basis of the relatively small alveolus for i3 in several mandibles, 12 isolated teeth with relatively slender roots are identified as i3s of *Patriolestes* (e.g., SDSNH 27628, Fig. 7). They have moderately procumbent, anteroposteriorly elongate, trenchant crowns that are distinctly smaller than those of i2 or c1. The dorsal keel runs from the posterolabial corner of the crown forward to the sharp anterior tip. A very weak posterolabial cuspule is sometimes present at the posterior end of the keel. The i3s often have an appression facet on the ventral side of the tip of the crown (caused by interdental wear with i2) and another appression facet at the posterolingual corner of the crown (caused by interdental wear with c1). The i3 of *Patriolestes* is relatively larger and much more trenchant than that of *Proterixoides* but appears to be similar in morphology to the i3 of *Macrocranion nitens* (see Novacek et al. 1985, figs. 1-2). An additional 11 isolated teeth are identitifed as di3s of *Patriolestes*. They are very similar in size and occlusal outline to the i3s, with much weaker dorsal ridges but a stronger posterolabial and anterodorsal cuspule.

In *Proterixoides davisi*, c1 is only slightly larger than i3, and the two teeth are very similar in crown morphology. In contrast, the 15 isolated c1s of *Patriolestes* are distinctly larger than the i3s and slightly larger than the i2s. They have relatively broad, anteroposteriorly elongate, slightly procumbent, nontrenchant crowns with a rather bulbous overall appearance (e.g., SDSNH 58828, Fig. 7). No dc1s have been recognized.

Sixteen isolated teeth are identified as dp1s of *Patriolestes*, and 14 isolated teeth are identified as p2s (e.g., SDSNH 58936 and 58720, Fig. 7). They are similar to the homologous teeth of *Proterixoides davisi* in that they are single-rooted, moderately procumbent, and have triangular crowns with a weak dorsal ridge and a weak posterolabial cuspule. A slight indentation in the posterior margin of the crown makes the occlusal outline of dp1 appear "upside-down heart-shaped" in postero-occlusal view. Again as in *P. davisi*, referred p2s of *Patriolestes* are slightly larger than dp1s. Nine isolated teeth are identified as dp2s of *Patriolestes*. They are similar to p2 in size and in their roughly triangular slightly to moderately procumbent crowns. However, the deciduous teeth have more anteroposteriorly elongate crowns, their posterior margin forms a more oblique angle with the AP axis, and they usually have a distinct posterior cingulid and distinct posterolabial cuspule.

TABLE 4. Measurements of upper cheek teeth of *Patriolestes novaceki* from the early Uintan of San Diego County.

	(DP3)/P3[a]		P4			M1			M2			M3		
Specimen	AP	W	AP	AW	PW	AP	AW	PW	AP	AW	PW	AP	AW	PW
Friars Fm., undifferentiated														
SDSNH 58776	(2.45)	(1.54)	—	—	—	—	—	—	—	—	—	—	—	—
SDSNH 51258	—		3.44	3.32	4.28	—	—	—	—	—	—	—	—	—
LACM(CIT) 55933	—	—	3.45	2.92	4.23	—	—	—	—	—	—	—	—	—
LACM(CIT) 56119	—	—	3.49	3.33	4.46	—	—	—	—	—	—	—	—	—
UCMP 101690	—	—	—	2.95	—	—	—	—	—	—	—	—	—	—
SDSNH 51293	—	—	3.31	3.19	4.16	—	—	—	—	—	—	—	—	—
SDSNH 49350	—	—	—	—	—	3.13	4.29	4.72	—	—	—	—	—	—
SDSNH 41353	—	—	—	—	—	—	—	—	—	—	—	2.12	3.16	2.64
Friars Fm., upper tongue														
SDSNH 27011	(2.17)	(1.64)	—	—	—	—	—	—	—	—	—	—	—	—
SDSNH 38150	(2.37)	(1.66)	—	—	—	—	—	—	—	—	—	—	—	—
SDSNH 38122	1.76	2.07	—	—	—	—	—	—	—	—	—	—	—	—
SDSNH 38149	1.89	1.86	—	—	—	—	—	—	—	—	—	—	—	—
SDSNH 43963	1.93	2.00	—	—	—	—	—	—	—	—	—	—	—	—
SDSNH 54857	1.85	1.87	3.65	3.42	4.44	3.48	4.61	5.19	2.86	5.52	4.86	—	—	—
SDSNH 31767	—	—	—	—	—	2.90	3.70	4.11	—	—	—	—	—	—
SDSNH 37998	—	—	—	—	—	3.00	3.93	4.28	—	—	—	—	—	—
SDSNH 37999	—	—	—	—	—	3.12	4.09	4.45	—	—	—	—	—	—
UCMP 101420	—	—	—	—	—	3.08	4.19	4.69	—	—	—	—	—	—
UCMP 133967	—	—	—	—	—	3.17	4.10	4.51	—	—	—	—	—	—
UCMP 154719	—	—	—	—	—	2.85	3.94	—	—	—	—	—	—	—
SDSNH 37616	—	—	—	—	—	—	—	—	—	—	4.09	—	—	—
SDSNH 38004	—	—	—	—	—	—	—	—	2.62	4.19	3.98	—	—	—
SDSNH 31765	—	—	—	—	—	—	—	—	—	—	—	—	—	2.37
SDSNH 31766	—	—	—	—	—	—	—	—	—	—	—	—	—	2.27
SDSNH 38005	—	—	—	—	—	—	—	—	—	—	—	1.72	3.11	2.24
SDSNH 38006	—	—	—	—	—	—	—	—	—	—	—	—	—	2.40
Friars Fm., cong. tongue														
SDSNH 56950	(2.46)	(1.96)	—	—	—	—	—	—	—	—	—	—	—	—
SDSNH 58835	(2.32)	—	—	—	—	—	—	—	—	—	—	—	—	—
SDSNH 43083	1.99	1.67	—	—	—	—	—	—	—	—	—	—	—	—
SDSNH 56951	1.93	2.05	—	—	—	—	—	—	—	—	—	—	—	—
SDSNH 56952	1.74	1.96	—	—	—	—	—	—	—	—	—	—	—	—
SDSNH 56953	2.01	2.04	—	—	—	—	—	—	—	—	—	—	—	—
SDSNH 56965	1.73	1.67	—	—	—	—	—	—	—	—	—	—	—	—
SDSNH 60053	1.83	1.90	—	—	—	—	—	—	—	—	—	—	—	—
SDSNH 56185	1.82	1.56	3.81	3.33	4.38	—	—	—	—	—	—	—	—	—
SDSNH 43081	—	—	3.43	3.12	4.19	—	—	—	—	—	—	—	—	—
SDSNH 55679	—	—	—	—	—	3.09	4.03	4.48	—	—	—	—	—	—
SDSNH 56956	—	—	—	—	—	3.12	—	—	—	—	—	—	—	—
SDSNH 58639	—	—	—	—	—	3.12	—	—	—	—	—	—	—	—
SDSNH 60055	—	—	—	—	—	—	—	4.41	—	—	—	—	—	—
SDSNH 60056	—	—	—	—	—	3.14	3.85	4.51	—	—	—	—	—	—
SDSNH 56957	—	—	—	—	—	—	—	—	2.70	4.30	4.02	—	—	—
Friars Fm., lower tongue														
SDSNH 39748	(2.29)	(1.72)	—	—	—	—	—	—	—	—	—	—	—	—
SDSNH 58721	(2.12)	(1.58)	—	—	—	—	—	—	—	—	—	—	—	—
SDSNH 39747	1.68	1.83	—	—	—	—	—	—	—	—	—	—	—	—
SDSNH 39761	1.72	1.73	—	—	—	—	—	—	—	—	—	—	—	—
SDSNH 46139	1.94	1.90	—	—	—	—	—	—	—	—	—	—	—	—
SDSNH 39335	—	—	—	—	—	2.52	3.49	3.89	—	—	—	—	—	—
SDSNH 39683	—	—	—	—	—	—	—	3.94	—	—	—	—	—	—
SDSNH 46373	—	—	—	—	—	2.98	3.94	4.38	—	—	—	—	—	—
SDSNH 45802	—	—	—	—	—	2.65	3.51	3.91	—	—	—	—	—	—
SDSNH 39682	—	—	—	—	—	—	—	—	—	—	3.80	—	—	—
SDSNH 37400	—	—	—	—	—	—	—	—	—	—	—	1.55	2.77	2.10
SDSNH 39685	—	—	—	—	—	—	—	—	—	—	—	—	—	2.16
SDSNH 46274	—	—	—	—	—	—	—	—	—	—	—	1.68	3.06	2.33

[a] Values in parentheses are for DP3; others are for P3.

TABLE 5. Measurements of lower cheek teeth of *Patriolestes novaceki* from the early Uintan of San Diego County.

	(dp3)/p3[a]		p4		m1			m2			m3		
Specimen	AP	W	AP	W	AP	WTRI	WTAL	AP	WTRI	WTAL	AP	WTRI	WTAL
Friars Fm., undifferentiated													
SDSNH 56725	—	1.85	3.75	2.57	—	—	—	—	—	—	—	—	—
SDSNH 49250 (holotype)	—	—	3.41	2.37	3.27	2.68	2.53	2.93	2.63	2.30	2.80	2.04	1.58
SDSNH 49207	—	—	—	—	3.26	2.81	2.62	—	—	—	—	—	—
SDSNH 49436	—	—	—	—	3.33	2.56	2.62	—	—	—	—	—	—
SDSNH 50589	—	—	—	—	3.07	2.62	2.55	—	—	—	—	—	—
SDSNH 51259	—	—	—	—	3.12	2.60	2.53	—	—	—	—	—	—
SDSNH 49611	—	—	—	—	—	—	—	—	—	—	2.73	1.91	1.49
LACM(CIT) 55935	—	—	3.22	2.30	3.20	2.56	2.60	—	—	—	—	—	—
LACM(CIT) 55936	—	—	3.22	2.33	3.07	2.52	2.51	—	—	—	—	—	—
LACM(CIT) 55937	—	—	—	—	3.21	2.71	2.68	2.96	2.66	2.34	—	—	1.55
LACM(CIT) 56189	—	—	—	—	—	—	—	—	—	—	2.63	—	1.67
Friars Fm., upper tongue													
SDSNH 58723	(2.04)	(1.40)	—	—	—	—	—	—	—	—	—	—	—
SDSNH 58743	(2.03)	(1.40)	—	—	—	—	—	—	—	—	—	—	—
SDSNH 58744	(2.08)	(1.46)	—	—	—	—	—	—	—	—	—	—	—
SDSNH 58808	(2.13)	(1.50)	—	—	—	—	—	—	—	—	—	—	—
SDSNH 60026	(2.13)	(1.46)	—	—	—	—	—	—	—	—	—	—	—
SDSNH 32004	2.04	1.66	—	—	—	—	—	—	—	—	—	—	—
SDSNH 32080	1.88	1.60	—	—	—	—	—	—	—	—	—	—	—
SDSNH 58747	1.84	1.53	—	—	—	—	—	—	—	—	—	—	—
SDSNH 58748	1.91	1.58	—	—	—	—	—	—	—	—	—	—	—
SDSNH 58749	2.08	1.67	—	—	—	—	—	—	—	—	—	—	—
SDSNH 58791	1.78	1.66	—	—	—	—	—	—	—	—	—	—	—
SDSNH 37609	—	—	3.35	2.31	—	—	—	—	—	—	—	—	—
SDSNH 37987	—	—	3.02	2.10	—	—	—	—	—	—	—	—	—
SDSNH 37988	—	—	3.27	2.25	—	—	—	—	—	—	—	—	—
SDSNH 42428	—	—	3.40	2.24	—	—	—	—	—	—	—	—	—
SDSNH 45160	—	—	3.40	2.42	—	—	—	—	—	—	—	—	—
SDSNH 46436	—	—	3.49	2.50	—	—	—	—	—	—	—	—	—
SDSNH 31764	—	—	—	—	2.96	2.24	2.15	—	—	—	—	—	—
SDSNH 37610	—	—	—	—	3.10	2.31	2.32	—	—	—	—	—	—
SDSNH 37992	—	—	—	—	3.15	2.60	2.52	—	—	—	—	—	—
SDSNH 45161	—	—	—	—	3.60	2.85	2.78	—	—	—	—	—	—
SDSNH 56717	—	—	—	—	—	—	—	3.04	2.57	2.44	—	—	—
SDSNH 37993	—	—	—	—	—	—		2.73	2.55	2.42	—	—	—
SDSNH 47865	—	—	—	—	—	—	—	—	—	2.45	—	—	—
SDSNH 37612	—	—	—	—	—	—	—	—	—	—	2.58	2.05	1.63
SDSNH 37613	—	—	—	—	—	—	—	—	—	—	—	—	1.56
SDSNH 37994	—	—	—	—	—	—	—	—	—	—	2.50	1.89	1.53
SDSNH 37995	—	—	—	—	—	—	—	—	—	—	—	—	1.79
SDSNH 46555	—	—	—	—	—	—	—	—	—	—	2.56	1.92	1.55
SDSNH 46556	—	—	—	—	—	—	—	—	—	—	3.00	2.11	1.65
SDSNH 54858	—	—	3.75	2.65	3.37	2.71	2.95	3.34	2.91	2.82	3.34	2.38	1.96
UCMP 101617	—	—	—	—	—	—	—	2.82	2.23	2.09	—	—	—
UCMP 133966	—	—	3.40	2.39	3.24	2.44	2.45	—	—	—	—	—	—
Friars Fm., cong. tongue													
SDSNH 60042	(2.10)	(1.43)	—	—	—	—	—	—	—	—	—	—	—
SDSNH 60041	2.06	1.82	—	—	—	—	—	—	—	—	—	—	—
SDSNH 58830	1.95	1.69	—	—	—	—	—	—	—	—	—	—	—
SDSNH 58837	1.94	1.67	—	—	—	—	—	—	—	—	—	—	—
SDSNH 55498	—	—	3.72	2.49	—	—	—	—	—	—	—	—	—
SDSNH 55825	—	—	3.66	2.50	—	—	—	—	—	—	—	—	—
SDSNH 60043	—	—	3.31	2.38	—	—	—	—	—	—	—	—	—
SDSNH 55499	—	—	3.38	2.24	3.20	2.53	2.50	—	—	—	—	—	—
SDSNH 55500	—	—	3.40	2.46	3.20	2.59	2.39	—	—	2.18	—	—	—
SDSNH 54912	—	—	—	—	3.09	2.40	2.54	2.91	2.55	2.34	—	—	—
SDSNH 54926	—	—	—	—	3.32	2.56	2.52	—	—	—	—	—	—
SDSNH 43276	—	—	—	—	—	—	—	—	2.55	2.35	—	—	—
SDSNH 56947	—	—	—	—	3.08	2.47	2.47	3.00	2.54	2.40	2.83	—	1.76
SDSNH 60044	—	—	—	—	3.18	2.64	2.65	—	—	—	—	—	—
SDSNH 60045	—	—	—	—	3.24	2.58	2.70	—	—	—	—	—	—
SDSNH 60046	—	—	—	—	—	—	—	2.96	2.54	2.30	—	—	—
SDSNH 56948	—	—	—	—	—	—	—	—	—	—	—	—	1.55
SDSNH 56949	—	—	—	—	—	—	—	—	—	—	2.78	2.00	1.67
SDSNH 60047	—	—	—	—	—	—	—	—	—	—	2.70	2.22	1.81

(*Continued*)

TABLE 5 *(Continued)*.

	(dp3)/p3[a]		p4		m1			m2			m3		
Specimen	AP	W	AP	W	AP	WTRI	WTAL	AP	WTRI	WTAL	AP	WTRI	WTAL
Friars Fm., lower tongue													
SDSNH 58935	(1.96)	(1.48)	—	—	—	—	—	—	—	—	—	—	—
SDSNH 58971	(1.90)	(1.30)	—	—	—	—	—	—	—	—	—	—	—
SDSNH 58927	1.77	1.55	—	—	—	—	—	—	—	—	—	—	—
SDSNH 58972	1.63	1.64	—	—	—	—	—	—	—	—	—	—	—
SDSNH 45799	—	—	3.19	2.34	—	—	—	—	—	—	—	—	—
SDSNH 45800	—	—	—	—	2.77	2.27	2.24	—	—	—	—	—	—
SDSNH 54995	—	—	—	—	2.65	2.18	2.20	—	—	—	—	—	—
SDSNH 39680	—	—	—	—	—	—	—	2.39	2.18	2.02	—	—	—
SDSNH 54996	—	—	—	—	—	—	—	2.51	2.18	1.94	—	—	—
SDSNH 39681	—	—	—	—	—	—	—	—	—	—	—	1.75	1.42
SDSNH 45801	—	—	—	—	—	—	—	—	—	—	2.39	1.80	1.48
SDSNH 46272	—	—	—	—	—	—	—	—	—	—	2.48	1.97	1.52
Santiago Fm., Member B													
SDSNH 36576	—	—	—	—	—	—	—	—	—	—	2.72	2.09	1.58

[a] Values in parentheses are for dp3; others are for p3.

SDSNH 56725 contains the only permanent erupted p3 preserved in a mandible (Fig. 6A). It is fully premolariform and much smaller than the p3 of *Proterixoides*. Eleven isolated p3s show a bulbous crown with a rounded pentagonal occlusal outline (e.g., SDSNH 58837, Fig. 7). They lack a dorsal ridge but generally retain a weak posterolabial cuspule. Although the p3 appears to be single-rooted in SDSNH 56725, two isolated p3s from SDSNH Loc. 3483 show that a short distance below the base of the crown, the trunk root bifurcates into two separate but closely appressed anterior and posterior branches (e.g., SDSNH 58749). Of the remaining six isolated p3s with an intact single root, four have a distinct longitudinal indentation running down the lingual side. Crown morphologies of the double-rooted and single-rooted morphs are indistinguishable, being similar to, but slightly larger and dorsoventrally thicker than p2.

Eight isolated teeth are identified as dp3s of *Patriolestes* (e.g., SDSNH 60026; Fig. 8A). There is no differentiation of the trigonid,

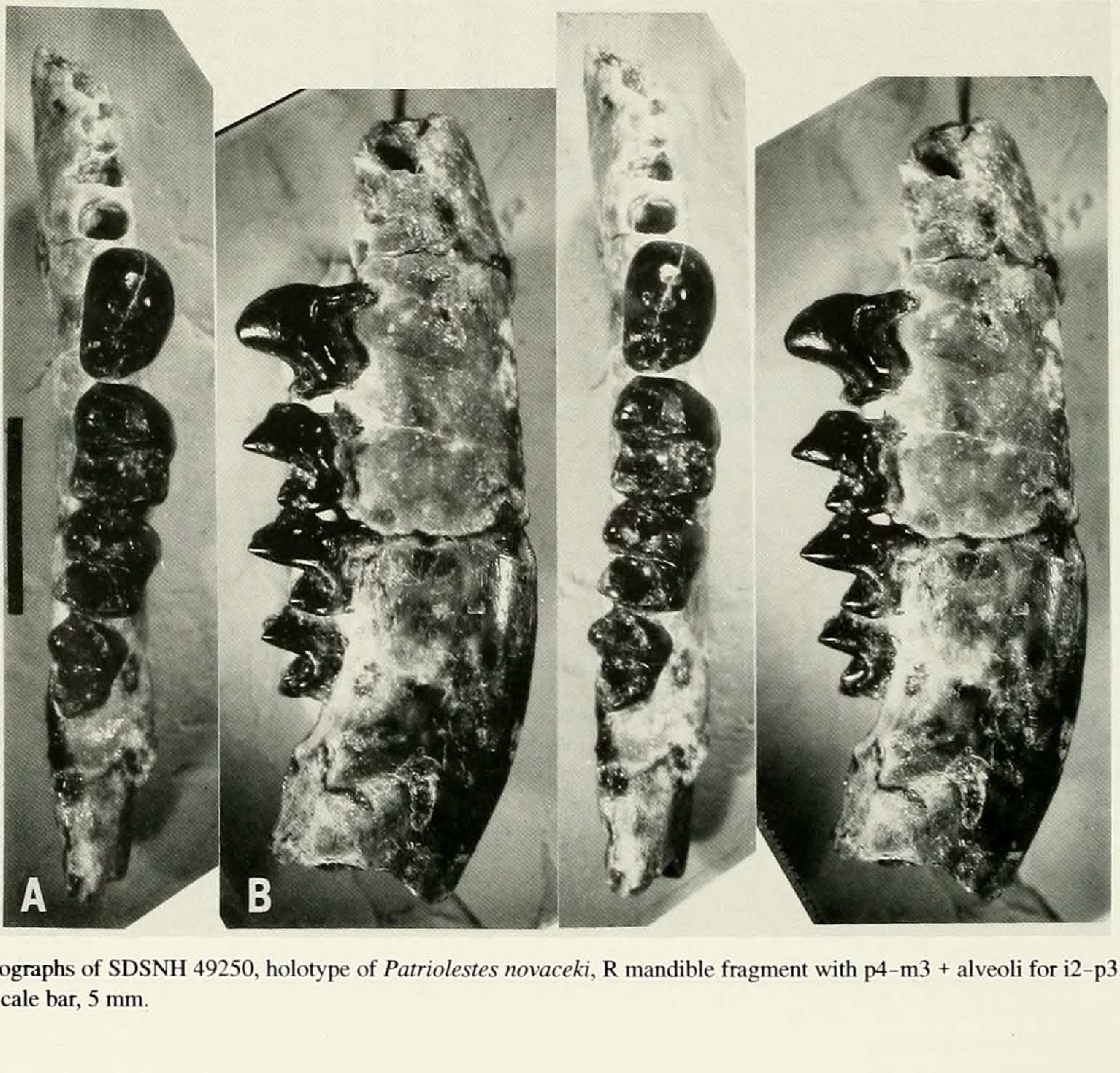


Figure 5. Stereophotographs of SDSNH 49250, holotype of *Patriolestes novaceki*, R mandible fragment with p4–m3 + alveoli for i2–p3. (A), Occlusal view; (B), lateral view. Scale bar, 5 mm.

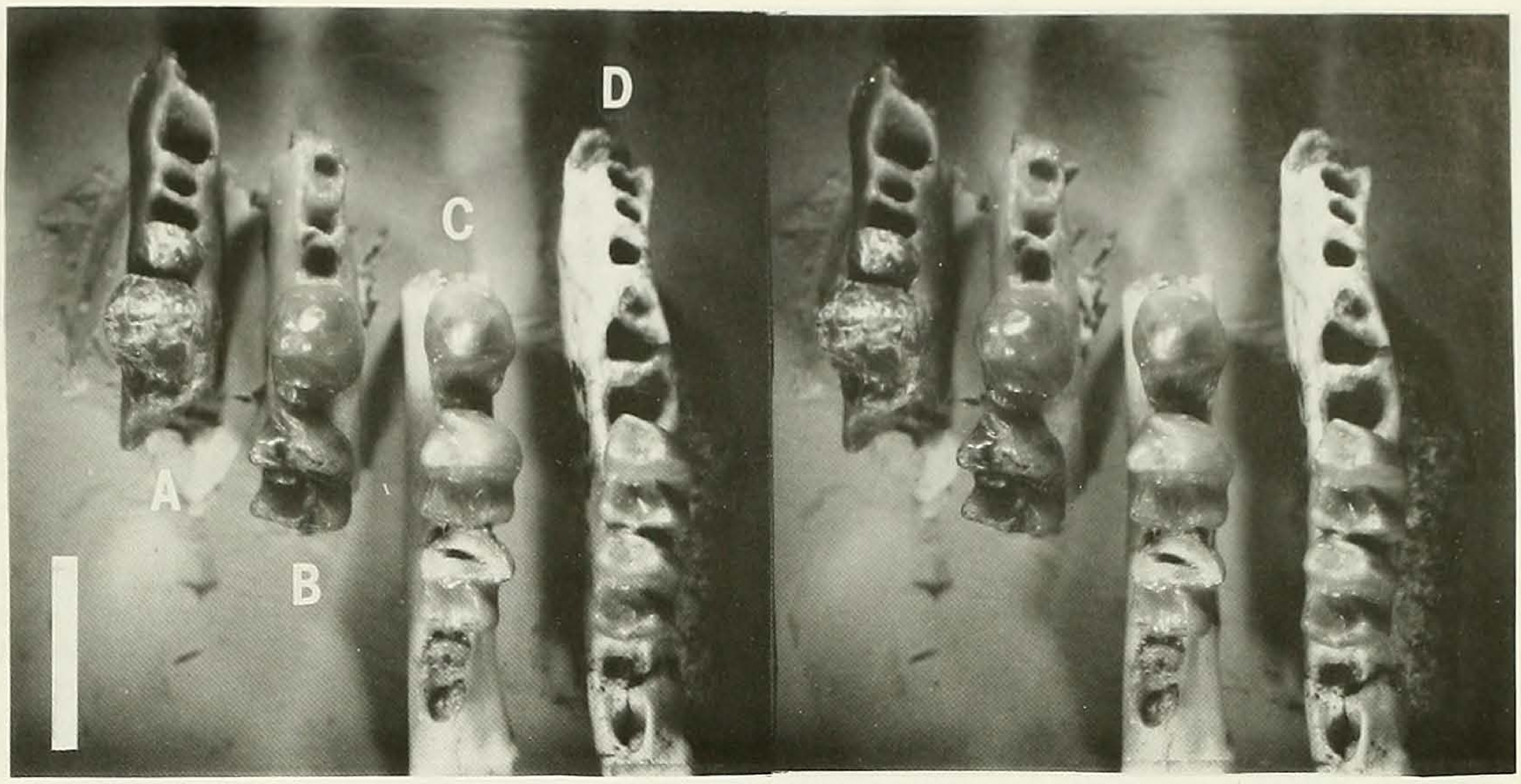


Figure 6. Stereophotographs in occlusal view of four right mandible fragments of *Patriolestes novaceki*, showing anterior alveoli and composite p3–m2. (A), SDSNH 56725; (B), UCMP 133966; (C), SDSNH 55500; (D), SDSNH 54912. Scale bar, 5 mm.

and only a very weak paracristid. The dp3 differs from p3 in the same way that dp2 differs from p2 (i.e., the deciduous teeth are more anteroposteriorly elongate, their posterior margins make a more oblique angle with the AP axis, and they usually have a distinct posterior cingulid and a distinct posterolabial cuspule). The single root of dp3 is cylindrical in cross-section. Only SDSNH 60026 preserves enough of the root to show that a weak longitudinal indentation was present on the lingual side. The dp3 of *Patriolestes* differs from the previously undescribed dp3 of *Proterixoides* (e.g., SDSNH 46624; Fig. 8C) in that the latter is larger (both absolutely and relative to dp4), has a stronger paracristid and postmetacristid, lacks a posterior cingulid and posterolabial cuspule, and has a posterior margin whose occlusal outline is essentially perpendicular to the AP axis.

Several isolated p4s show two essentially cylindrical roots of subequal diameter. The p4 is also present in several mandible fragments (Figs. 5–6) and is unique among known dormaaliids in having a bulbous trigonid, with no differentiation of metaconid or paraconid and no paracristid (in this respect, the p4 of *Patriolestes* is similar to the p3 of *Proterixoides*). The p4 is also wide transversely relative to the p4 in most other dormaaliid taxa. The labial side of the tooth is uniformly convex in occlusal outline, while the lingual side is slightly concave. The talonid is relatively short, lacks a cristid obliqua, and

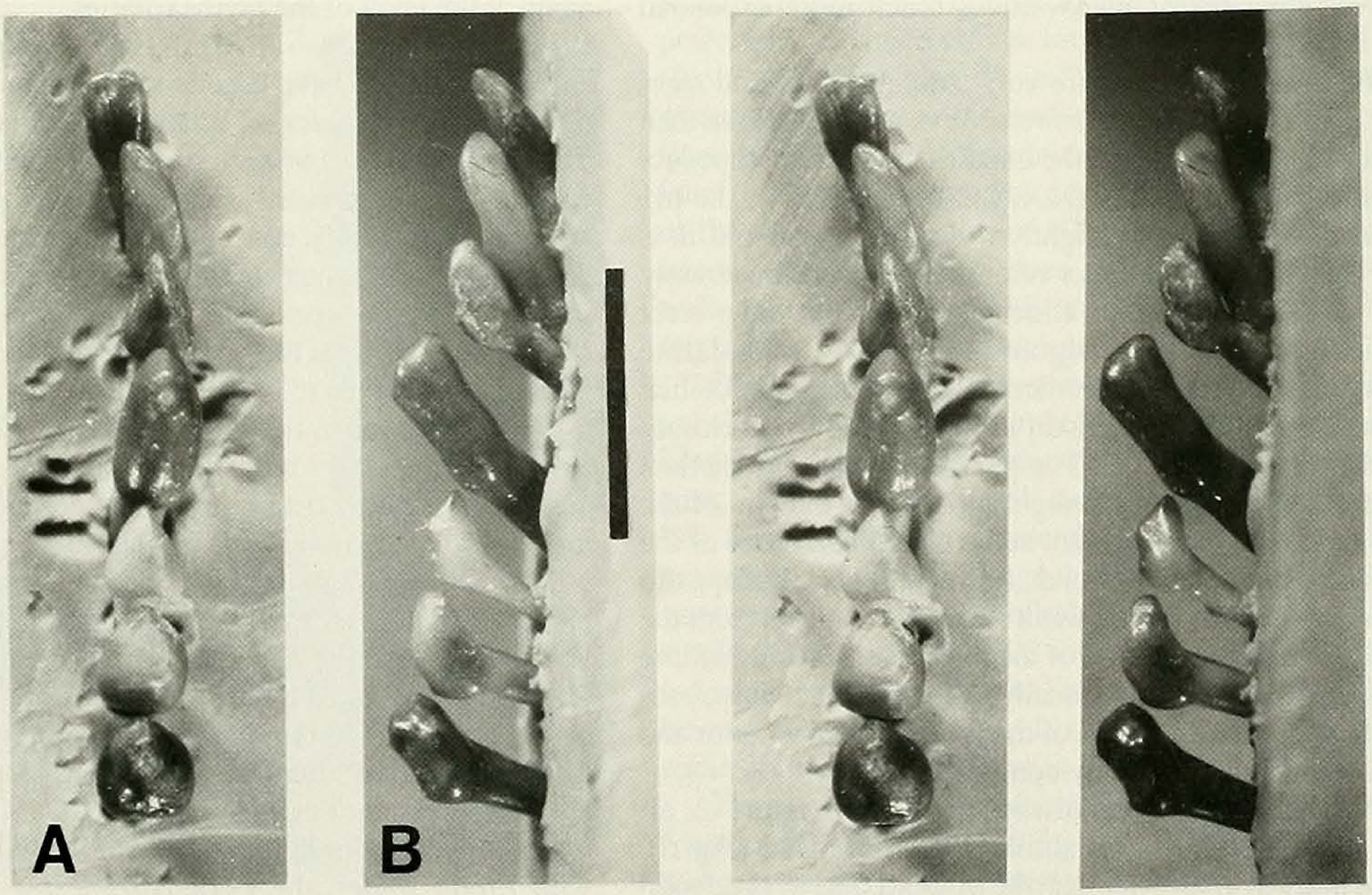


Figure 7. Stereophotographs of composite Ri1–p3 of *Patriolestes novaceki*. (A), Occlusal view; (B), lateral view. i1: SDSNH 58919. i2: SDSNH 58732. i3: SDSNH 27628. c1: SDSNH 58828. dp1: SDSNH 58936. p2: SDSNH 58720. p3: SDSNH 58837. Scale bar, 5 mm.

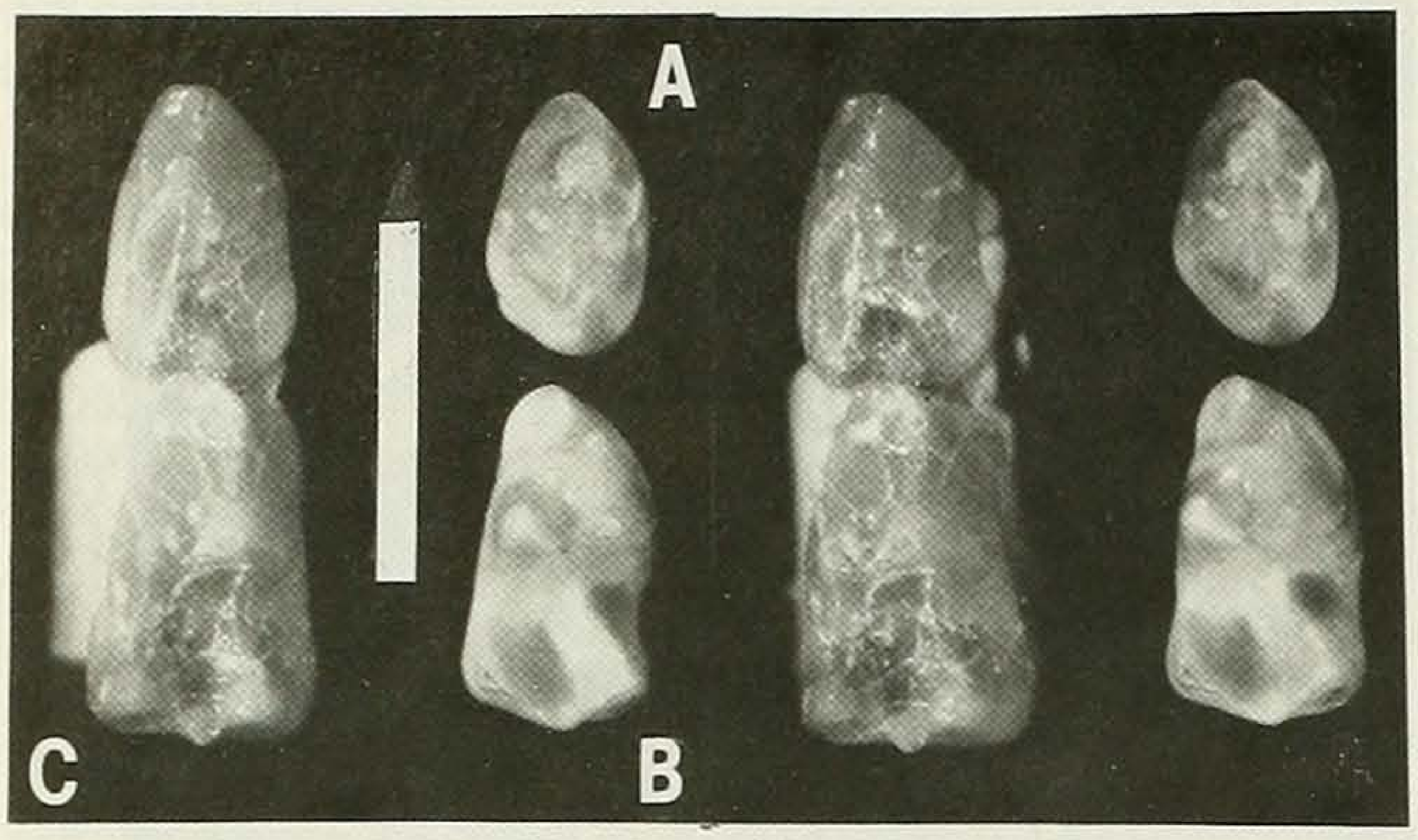


Figure 8. Stereophotographs in occlusal view of (A), SDSNH 60026, isolated Rdp3 of *Patriolestes novaceki*; (B), SDSNH 45798, isolated Rdp4 of *Patriolestes novaceki*; (C), SDSNH 46624, associated Rdp3-4 of *Proterixoides davisi*. Scale bar, 3 mm.

invariably bears one small anteroposteriorly compressed cusp at the posterolingual corner of the crown. A short ridgelike postcingulid usually extends from the apex of the talonid cusp to the posterolabial corner of the crown.

Two dp4s of *Patriolestes* are known (e.g., SDSNH 45798, Fig. 8B). They are molariform, anteroposteriorly elongate teeth, with a distinct metaconid, protoconid, paraconid, cristid obliqua, and hypoconulid. The talonid basin is completely enclosed. The protoconid is slightly larger and taller than the metaconid and lies slightly anterior to the latter cusp. It should be noted that SDSNH 60026 is the largest of the eight known dp3s of *Patriolestes novaceki*, while SDSNH 45798 is distinctly smaller than the only other known dp4. Thus, the teeth illustrated in Figs. 8A-B are probably closer in size than would be the case in most individuals of this species. The dp4 of *Patriolestes* differs from the previously undescribed dp4 of *Proterixoides davisi* (e.g., SDSNH 46624, Fig. 8C) in that the latter has slightly more rounded cusps, a relatively smaller talonid basin, a weaker cristid obliqua, a relatively narrower trigonid whose labial face is concave rather than convex, and a much more expanded paraconid region.

The m1 and 2 of *Patriolestes* are very similar in size and morphology. In a given mandible, m1s are always slightly larger than m2s (Figs. 5 and 6). In contrast to the condition found in sespedectines and most other dormaaliids (Novacek et al. 1985:4), the m1 trigonid of *Patriolestes* is usually slightly wider than the talonid, as is invariably the case in m2. This fact often makes even moderately worn isolated m1-2s difficult to allocate. Both teeth have erect anteroposteriorly compressed trigonids with a low bladelike paracristid that extends from the protoconid apex to the anterolabial base of the metaconid. The paracristid is weaker and more closely appressed to the metaconid in m2. The paraconid is never a distinct cusp and is represented by only a slight swelling at the end of the paracristid. A short cingulid is present at the anterolabial base of the teeth. The weak cristid obliqua extends from the hypoconid apex to the extreme base of protoconid. A weak ridge also extends from the entoconid apex to the extreme base of the metaconid, closing off the talonid basin. The hypoconulid is usually a small distinct cusp, centrally located at the posterior magin of the talonid. Both anterior and posterior roots are anteroposteriorly compressed.

The m3 is usually shorter and always narrower than m1-2, although the trigonid morphology is similar to that of m1-2 (Fig. 5). The m3 talonid is always narrower than the trigonid. The hypoconulid is of variable strength but is always stronger than in m1-2, often extending well posterior to the entoconid. The anterior root is anteroposteriorly compressed, while the posterior root is anteroposteriorly elongate.

Skull.—Very little of the skull of *Patriolestes* is known. SDSNH 55497 is a palatal fragment consisting of part of the left maxillary and premaxillary and part of the right maxillary (Fig. 9). As seen in ventral view, a right-lateral "fault" running through the midline has sheared the right maxillary about 9 mm anterior to the left maxillary. At the level of DP1-P3 is a distinct ridge on the medial edge of each maxillary, possibly not attributable to distortion, since a similar ridge is present in SDSNH 56185. The left premaxilla fragment preserves damaged alveoli for I1-3, and the alveolus for I2 retains the dorsal end of the root. The left maxillary fragment preserves a double-rooted complete C1, single-rooted complete DP1 and P2, the alveoli for triple-rooted P3, and the lingual alveolus for a triple-rooted P4. The right maxillary preserves the broken roots of C1, the alveolus for DP1, a complete P2, and the alveoli for P3. There are no diastemata between any of the upper teeth. However, the left maxillary-premaxillary suture has pulled apart slightly and filled with matrix, giving the false impression of a short diastema between C1 and the empty I3 alveolus. The dorsal side of SDSNH 55497 preserves fragments of the nasals, but their original shape and contact relationships to other bones cannot be determined.

SDSNH 54857 and 56185 are maxillary fragments of *Patriolestes* whose teeth are described further below. They show that the anterior opening for the infraorbital canal was dorsal to a point between P3 and 4. This position is similar to that seen in *Scenopagus* (Butler 1972, fig. 5) but perhaps slightly more posterior than in *Proterixoides*, *Macrocranion*, or *Ankylodon*. The dorsoventral diameter of the infraorbital foramen is 2.1 and 2.4 mm in SDSNH 54857 and 56185, respectively, which are about the same as in *Proterixoides*. The exact length of the infraorbital canal in SDSNH 54857 and 56185 is not currently measurable owing to obscuring matrix but appears to be comparable to that of *Proterixoides*. As in a variety of lipotyphlan taxa, the ventral side of the zygomatic root originates lateral to M2. The anteroventral surface of the zygomatic arch is distinctly concave in SDSNH 54857 and 56185, as in *Proterixoides*. As seen in SDSNH 56185, the magnitude and rate of descent of the level of the palate from M1 to C1 is moderate and gradual. The width of the snout narrows distinctly from P4 to P3, widens slightly at C1, then narrows again at the level of the premaxillaries.

Upper Dentition.—In SDSNH 55497, the alveolus for I1 is damaged but seems to have been at least as large as that for I2. By analogy with *Proterixoides*, 17 relatively large isolated incisors are identified as I1s of *Patriolestes* (e.g., SDSNH 58973, Fig. 10). They have transversely compressed slightly curved roots and tall oval crowns developing lingually concave shovel-shaped wear facets. Unworn I1s have a weak anterior ridge and a stronger posterior ridge descending from the apex of the crown. Some of these putative I1s are mitten-shaped in that they possess a small posterior cusp or "thumb" but seem too robust to be deciduous teeth.

From the broken root in SDSNH 55497, I2 of *Patriolestes* was also a relatively large tooth, though slightly smaller than I1, and had a cylindrical rather than transversely compressed root. Ten isolated incisors seem to possess this morphology (e.g., SDSNH 56714, Fig. 10). They have slightly curved roots and transversely compressed crowns similar in morphology to I1. However, the crowns of putative I2 are dorsoventrally and anteroposteriorly shorter than the putative I1s. Thirteen isolated incisors are tentatively identified as DI1s and/or DI2s (Appendix 1). They have erect mitten-shaped crowns with distinct posterior "thumbs" and slightly curved roots that are variably compressed or cylindrical.

The alveolus for I3 is damaged in SDSNH 55497, but by analogy with *Proterixoides*, the I3 of *Patriolestes* is probably a relatively small tooth with a short, straight, cylindrical root. The 29 teeth so identified here have anteroposteriorly elongate, slightly procumbent

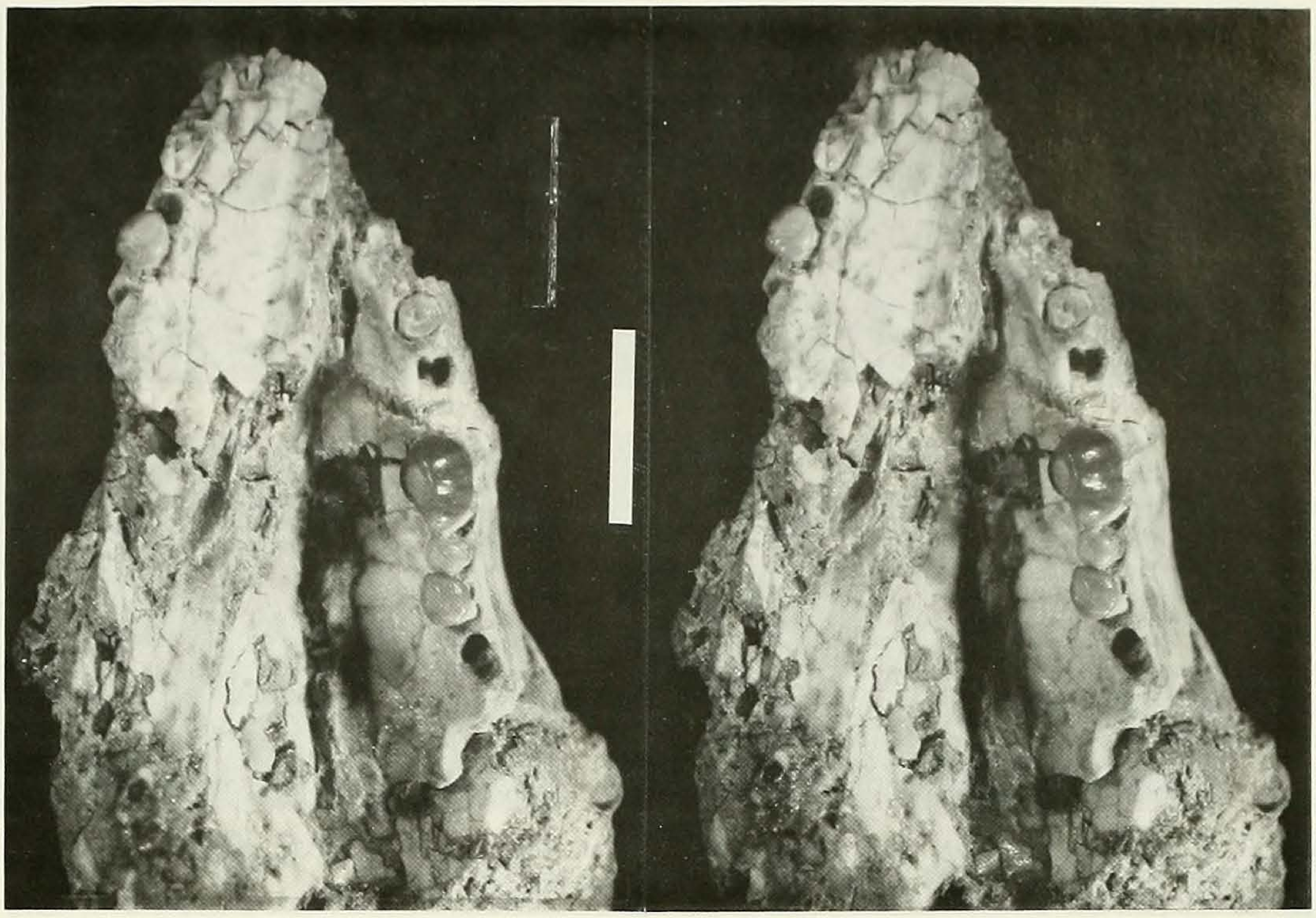


Figure 9. Stereophotographs in occlusal view of SDSNH 55497, palatal fragment of *Patriolestes novaceki* with alveoli for LI1–3, complete LC1–P2, partial alveoli for LP3–4, broken roots of RC1, alveolus for RDP1, complete RP2, and alveolus for RP3. Scale bar, 5 mm.

crowns, which consist of a tall anterior cusp, a central dorsal ridge, and a very weak posterior cuspule (e.g., SDSNH 58760, Fig. 10). Twenty-one additional isolated teeth are similar to the putative I3s but have stronger posterior cuspules and are tentatively identified as DI3s. Both putative I3 and DI3 develop a steeply dipping planar wear facet on the lingual face of the crown, presumably caused by occlusion with the trenchant crown of i3. The relatively large number of teeth identified as I3 and DI3 is suspicious. Perhaps the currently unrecognized DP2 of *Patriolestes* is morphologically indistinguishable from I3 and/or DI3, resulting in an artificially high abundance of the latter teeth.

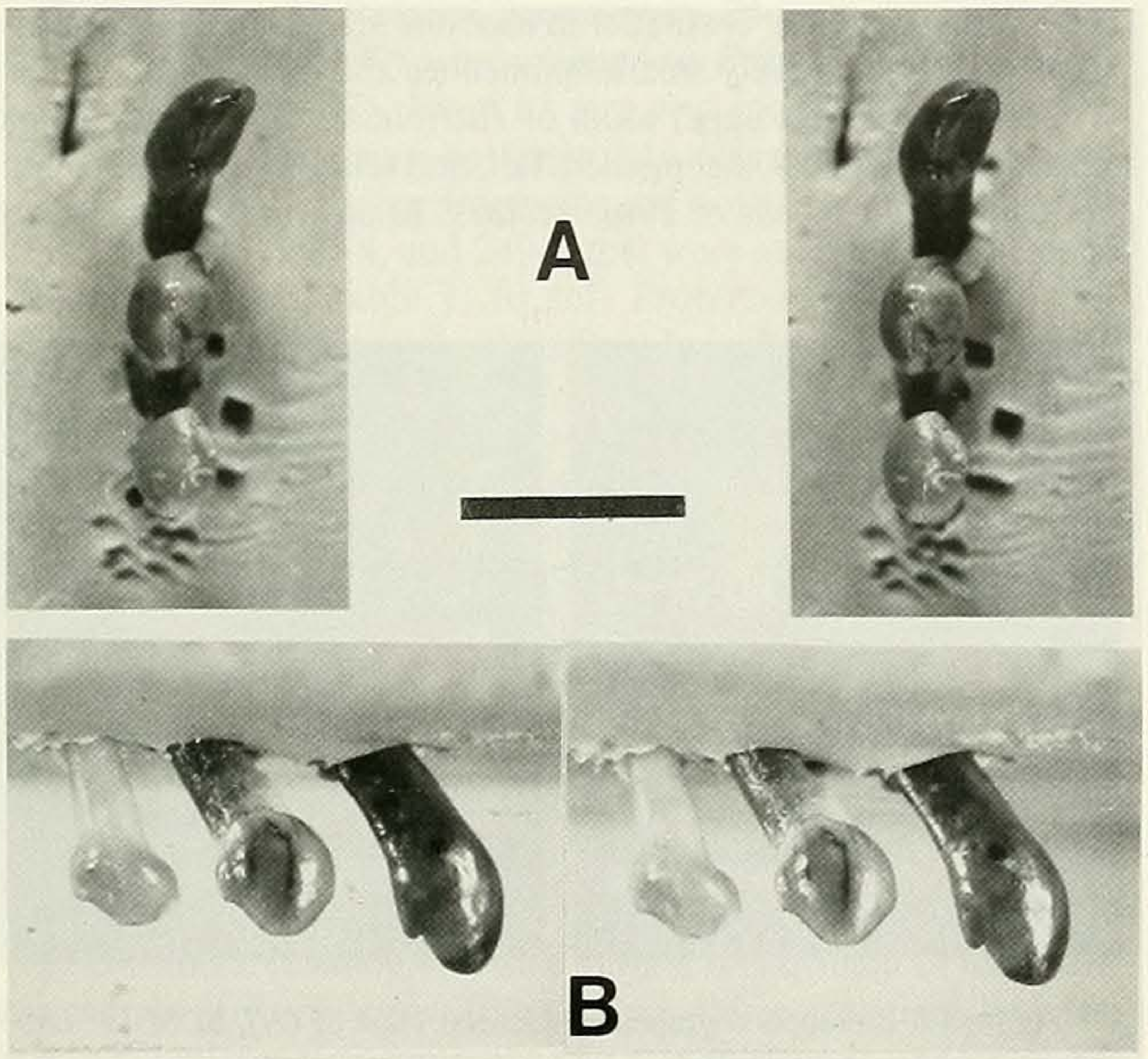


Figure 10. Stereophotographs of composite RI1–I3 of *Patriolestes novaceki*. (A), Occlusal view; (B), lateral view. I1: SDSNH 58973. I2: SDSNH 56714. I3: SDSNH 58760. Scale bar, 3 mm.

The C1 of *Patriolestes* is preserved in place in SDSNH 55497 (Fig. 9) and SDSNH 56185 (Fig. 11A) and is also represented by 13 isolated teeth. C1 is double-rooted, with a large, bulbous, anteroposteriorly elongate crown, much larger than I3, DP1, and P2, and also much larger than C1 in *Proterixoides davisi*. A weak ridge is sometimes present on the posterodorsal part of the crown, sometimes terminating in a weak posterior cuspule. A posteriorly dipping wear facet (presumably caused by occlusion with c1) develops on the apex of the crown. Both roots of C1 are cylindrical in cross-section. No unequivocal DC1s have been recognized. SDSNH 58800 has resorbed (?) roots and very thin enamel but does not differ significantly in size or morphology from undoubted permanent C1s.

DP1 and P2 are preserved in place in SDSNH 55497 (Fig. 9) and are similar in size and morphology to their homologs in *Proterixoides*. The DP1 crown is semiglobular, slightly anteroposteriorly elongate, and has a weak ridge running anteroposteriorly down the midline. Isolated DP1s have a slender cylindrical root with no longitudinal indentation on their lingual side (e.g., SDSNH 58820). The P2 is very similar in crown morphology to DP1 but distinctly larger. The single cylindrical root of P2 sometimes bears a distinct longitudinal indentation running down its lingual side (e.g., SDSNH 58823). DP2s have not been recognized, although as noted above it is possible that some of the teeth identified as I3s/DI3s are actually DP2s.

The permanent P3 of *Patriolestes* is preserved in two maxillary fragments (SDSNH 56185, Fig. 11A; SDSNH 54857; Fig. 11B) and is also represented by 12 isolated teeth. It is always much smaller than P4 and than the P3 of *Proterixoides*. All P3s are triple-rooted, but in three specimens (SDSNH 31996, 56185, and 56965) the lingual and posterolabial roots are partially fused. Most P3s have an occlusal out-

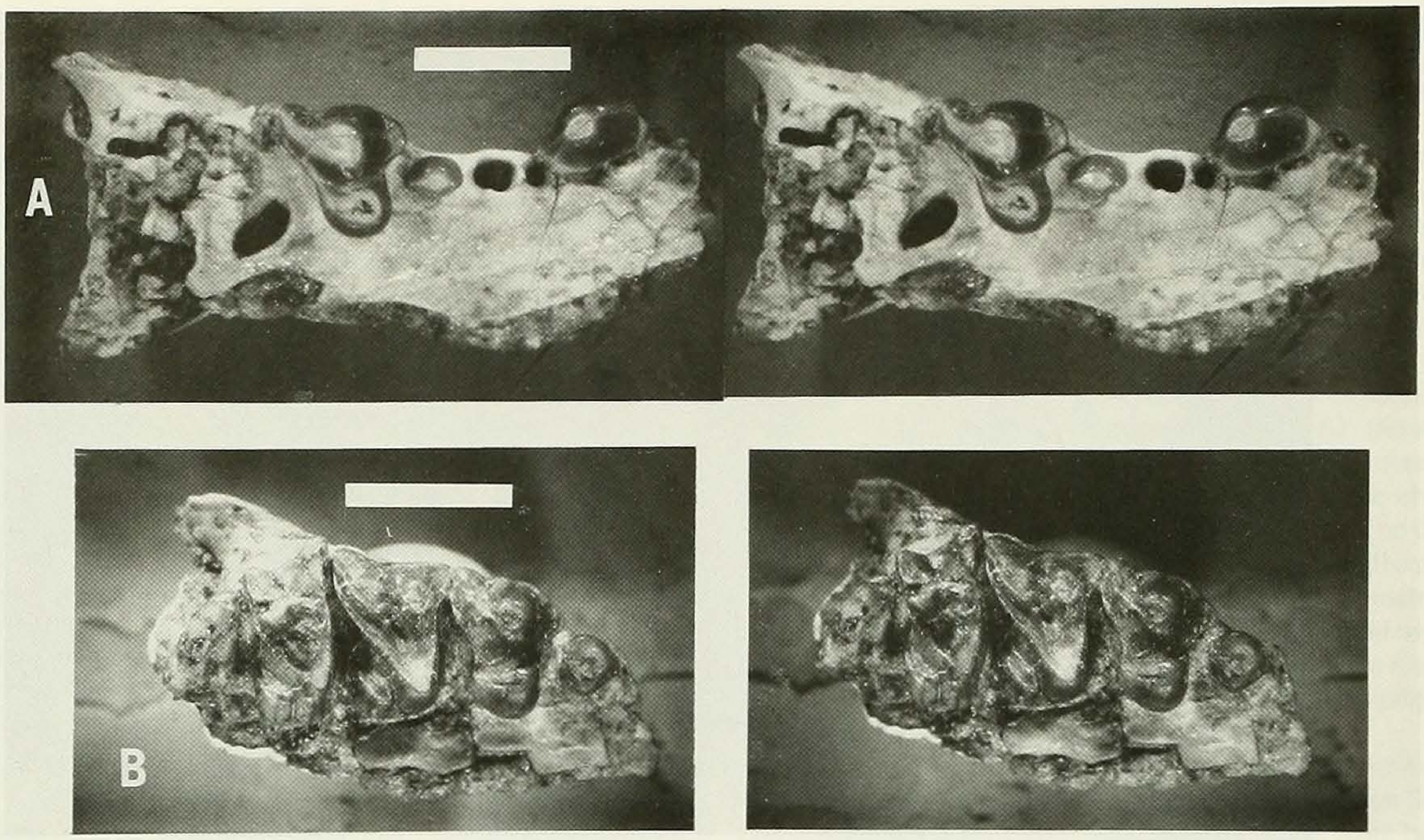


Figure 11. Stereophotographs in occlusal view of maxillary fragments of *Patriolestes novaceki*: (A), SDSNH 56185, R maxillary fragment with C1, alveoli for DP1-P2, and P3-4. (B), SDSNH 54857, R maxillary fragment with P3-M2. Scale bars, 5 mm.

line approximating a rounded equilateral triangle. The crown is dominated by a large conical paracone and never shows a distinct parastylar lobe or parastyle. The protocone lobe ranges from virtually absent (SDSNH 43083) to relatively strong (SDSNH 56951). The protocone ranges from absent (SDSNH 56953) to weak (SDSNH 46139) to moderately developed (SDSNH 56951). There is no metacone or hypocone. The metastylar lobe ranges from weak (SDSNH 56952) to strong (SDSNH 56951). A weak labially concave metastylar crest connects the apex of the paracone to the metastylar region. A distinct metastyle is present only on SDSNH 39761.

The permanent P4 is preserved in place in SDSNH 56185 and SDSNH 54857 (Fig. 11) and is also represented by 12 isolated teeth. The labial half of the crown is dominated by a large conical paracone, which sends a sharp metastylar crest sweeping posterolabiad to the end of a strong metastylar lobe. A metacone and metasyle are absent. The parastylar lobe is relatively weak but occasionally bears a tiny parastyle. The protocone is conical, and from its apex a postprotocrista of variable strength extends posteriad to merge with a weak posterior cingulum, which in turn extends to the metastylar area. There is no hypocone. A short posterolingual cingulum is usually present, but there is never an anterolingual cingulum.

Seven isolated DP3s are known (e.g., SDSNH 56950; Fig. 12A). All are triple-rooted, with the posterolabial root being the largest. All have a very small protocone lobe and protocone, a very small parastylar lobe, no parastyle, and no hypocone. The anterior half of the tooth is similar to P3 in that it is dominated by a large conical paracone. However, the posterior half of DP3 consists of a very large metastylar lobe, upon which sits a distinct metacone. A cingulum connects the posterior base of the protocone lobe to the lingual base of the metastylar lobe. The DP3 of *Patriolestes* differs from the previously undescribed DP3 of *Proterixoides* (e.g., SDSNH 43584, Fig. 12B) in that the latter is much larger relative to DP4, lacks a metacone, has a transversely very wide parastylar lobe with a distinct parastyle, and has a much stronger protocone lobe, with a distinct protocone and hypocone.

A single damaged DP4 of *Patriolestes* is known (UCMP V-73138/154720; Fig. 12C). The parastylar lobe, metacone, and most of the metastylar lobe have been broken away, but enough of the crown remains to show that the tooth was fully molariform. The paracone is conical and much larger than in M1-2. A large, posteriad-jutting metastylar lobe is present. Weak pre- and post-paraconular wings are present, along with stronger pre- and post-metaconular wings. A distinct hypocone sends a strong posthypocrista labiad to the posterior base of the crown. The hypocone extends slightly more lingually than the protocone. A short anterior cingulum is present at the anterior base of the protocone. Measurements: AW = 3.57 mm; PW = 3.72 mm (min.). The DP4 of *Patriolestes* differs from the previously undescribed DP4 of *Proterixoides* (e.g., SDSNH 46638, Fig. 12D) in that the latter is smaller in absolute size, is much less transverse, and has relatively smaller paracones and metacones.

M1 is the largest upper tooth of *Patriolestes*. The paracone and metacone are conical, steep-sided, tall, and relatively small in diameter compared to those of *Proterixoides*. In unworn specimens, the

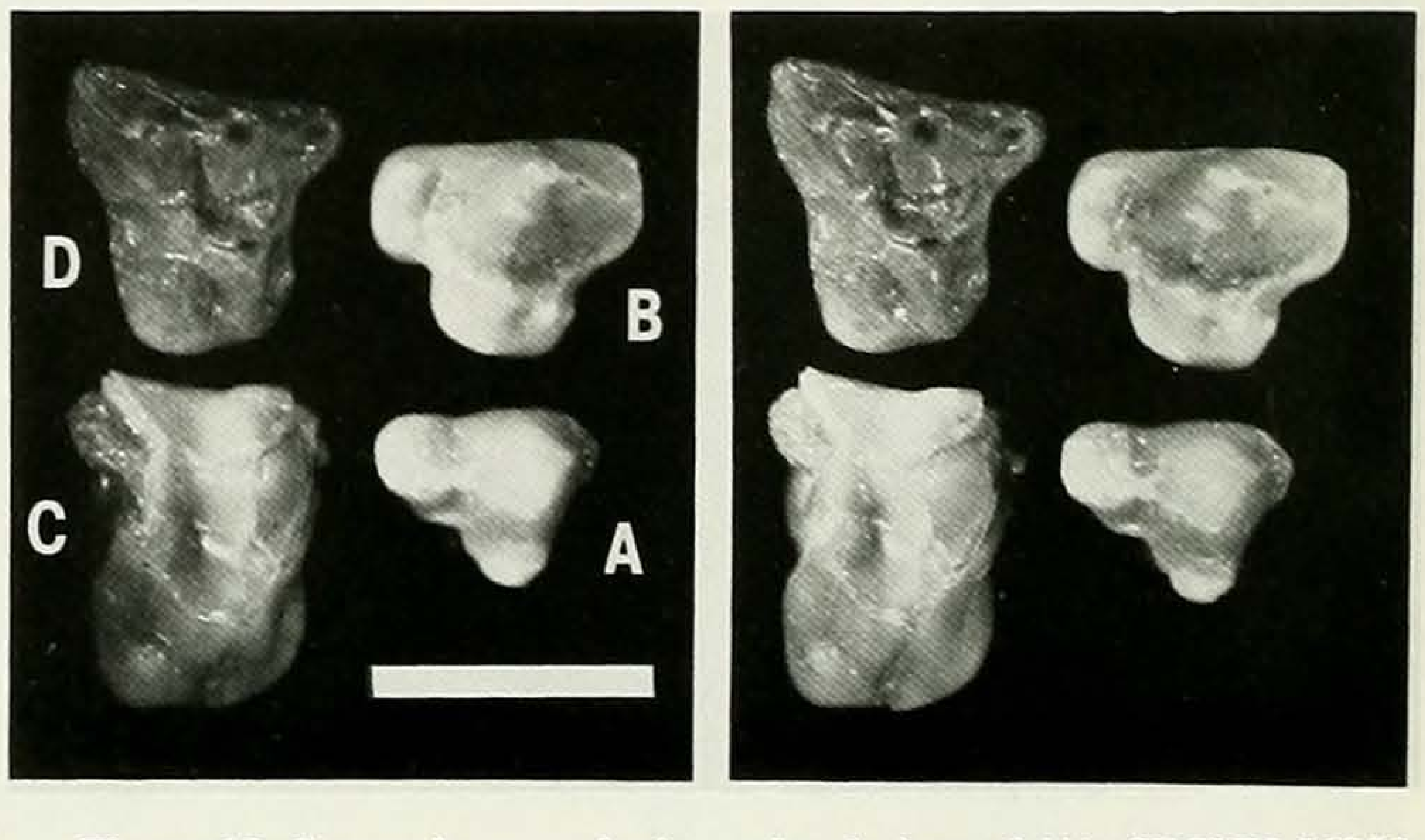


Figure 12. Stereophotographs in occlusal view of (A), SDSNH 56950, isolated RDP3 of *Patriolestes novaceki*; (B), SDSNH 43584, isolated LDP3 of *Proterixoides davisi*; (C), UCMP 154720, isolated RDP4 of *Patriolestes novaceki*; (D), SDSNH 46638, isolated RDP4 of *Proterixoides davisi*. Scale bar, 3 mm.

paracone is slightly taller than the metacone. The parastylar lobe is weak, with a weak parastyle but no parastylar crest. The metastylar lobe is well developed, with no metastyle but with a strong metastylar crest. There is a weak continuous ectocingulum along the labial border of the tooth. The strong protocone bears strong pre- and postprotocristae. The preprotocrista branches into a preparaconular wing (which extends to the anterior base of the paracone) and a postparaconular wing (which extends to the lingual base of the paracone). The postprotocrista branches into a premetaconular wing (which extends to the anterolingual base of the metacone) and a postmetaconular wing (which extends to the end of the metastylar lobe as a posterior cingulum). The protocone is much taller than the hypocone, but the latter always extends further linguad than the former. A strong posthypocrista extends labiad to the posterior base of the tooth. A short anterior cingulum is present at the anterior base of the protocone. The tooth has three roots. The lingual root is somewhat compressed transversely (see empty alveolus in SDSNH 56185; Fig. 11A), and is much larger than the cylindrical labial roots.

M2 is similar to M1 with the following exceptions. The parastylar lobe extends labiad much more than the metastylar lobe, and the resulting ectoflexus is much deeper than in M1. A weak parastylar crest is present in M2 (absent in M1). The hypocone usually does not extend lingually past the protocone (one exception is SDSNH 39682). Both the lingual and labial halves of M2 are anteroposteriorly shorter than in M1, giving M2 a relatively transverse appearance. The lingual root in M2 is smaller and more cylindrical than in M1.

M3 (not figured) is much smaller than M1-2 and has the triangular occlusal outline typical of most dormaaliids. The paracone is conical and much larger and taller than the metacone. A prominent parastylar lobe extends anterolabiad, and is connected to the base of the paracone by a weak parastylar crest. There is no parastyle. A weak paraconule is present, along with a weak preparaconular wing. The postparaconular wing is sometimes absent (SDSNH 38005) and weak when present (SDSNH 45162). A weak metaconule on the postprotocrista is sometimes present (SDSNH 31766), sometimes absent (SDSNH 38005). There is no premetaconular wing. Weak to moderately strong anterior and posterior cingula are always present but never complete around the lingual face of the protocone. There is no hypocone. The lingual root is relatively large and transversely compressed, while the two labial roots are small and cylindrical.

Discussion.—An isolated, fragmentary P4 from the Friars Formation (UCMP 101690) was assigned to *Proterixoides davisi* by Novacek (1985:16-17). From its size and morphology, however, UCMP 101690 can now be positively referred to *Patriolestes novaceki*. Similarly, the jaw fragments and isolated teeth from LACM (CIT) Locs. 249, 249-S, and 249-P that were assigned by Golz and Lillegraven (1977, table 1) to "cf. *Proterixoides* sp." and "cf. *Proterixoides davisi*" are clearly referable to *Patriolestes novaceki*. As a result of these revised identifications, the genus *Proterixoides* is unknown from the Friars Formation and is restricted to the late Uintan and Duchesnean. Finally, UCMP 101059 was included by Novacek (1976:36-37) in the original sample of the "erinaceoid-like genus and species." This fragmentary M1 has a lingual root that is extremely compressed anteroposteriorly, unlike the more cylindrical roots of undoubted upper molars of *Patriolestes*. I assign UCMP 101059 to a probable new leptictid genus, which is represented by more complete material from the Friars Formation (e.g., SDSNH 3483/43811).

Correlation of Size and Stratigraphic Occurrence

A considerable amount of size variation is evident in the available sample of *Patriolestes*. To reveal possible correlations between size and stratigraphic occurrence, the raw measurements for cheek teeth are segregated by stratigraphic unit (Tables 4 and 5). Selected measurements for p4-m3 and P4-M1 are illustrated in the bivariate plots of Figs. 13 and 14. The few available teeth from the lower tongue of the Friars Formation (collected from two districts, Santee and South Creek) usually fall at the small end of the range for each tooth position. Teeth from the conglomerate tongue of the Friars Formation (one district—Scripps Ranch North) consistently fall in the middle of the range for each tooth position. Teeth from strata considered by Walsh et al. (1996) to pertain to the upper tongue of the Friars Formation show the most size variation. As discussed by Walsh et al. (1996), localities in the upper tongue of the Friars Formation along State Route 52 (SDSNH Locs. 3611, 3612, 3685, 3883) are roughly equivalent stratigraphically to localities from the upper part of the undifferentiated Friars in the lower end of Murphy Canyon (San Diego Mission district; SDSNH Locs. 3784, 3785; LACM(CIT) Locs. 249, 249-S, 249-P). This stratigraphic similarity is reflected by teeth from these nearby districts tending to be relatively large. Indeed, the largest examples of p4, m2, m3, M1, and M2 of *Patriolestes novaceki* are represented by two specimens from a single locality in the upper tongue of the Friars in the State Route 52 district (SDSNH 54857 and 54858). Interestingly, however, teeth from the upper tongue of the Friars Formation in the Rancho Peñasquitos and Carmel Mountain Ranch districts show a wide range in size variation, and a few of them are even smaller than teeth from the lower tongue of the Friars. Finally, the single measurable tooth from Member B of the Santiago Formation falls in the middle of the range of m3s from the Friars Formation (Fig. 13D).

To use m1 and 2 to illustrate the maximum size variation in the sample, the longest m1 (SDSNH 45161) is 36% longer than the shortest m1 (SDSNH 54995), and the longest m2 (in SDSNH 54858) is 40% longer than the shortest m2 (SDSNH 39680). The holotype specimen of *Patriolestes novaceki* was collected from the undifferentiated Friars Formation in the San Diego Mission district, which yields relatively large specimens. Given this considerable variation in size, it is possible that a smaller species of *Patriolestes* may eventually be recognizable. However, more specimens should be collected from the lower tongue of the Friars Formation for the relatively small size of individuals comprising this "population" to be corroborated. Additional collections from the upper tongue of the Friars are also needed to document further the apparent geographic variation in the size distribution of individuals preserved therein. Finally, as noted above, the relative size of c1 was apparently variable in *Patriolestes* (e.g., SDSNH 56725 vs. 54912), and the possibility that sexual dimorphism accounts for some of the size variation should not be discounted. For the present, I regard all specimens as pertaining to a single variable species evolving through time. Therefore, statistics for the entire pooled sample of *Patriolestes* teeth are given in Table 6.

Trigonid/Talonid Proportions of m1-2

Based on the data in Table 5, Fig. 15A plots talonid width vs. trigonid width for all measurable m1s of *Patriolestes*. Most points plot above the line of equal widths, showing that the m1 trigonid is often slightly wider than the talonid. This condition is unusual for most Eocene dormaaliids, in which the m1 trigonid is usually slightly narrower than the talonid (Novacek et al. 1985:4). Figure 15B plots m2 talonid width vs. trigonid width and shows that all points fall well above the line of equal widths. Both figures again show the relatively small size of teeth fom the lower tongue of the Friars Formation, while teeth from the upper tongue of the Friars are more variable in size.

Interdental Proportions of Lower Cheek Teeth

Trends in the relative anteroposterior lengths of the lower cheek teeth of *Patriolestes* are shown in Table 7, which is based on the data in Table 5 but incorporates only associated teeth or teeth in mandibles. The length of m1 is normalized to 1.00, and the corresponding relative lengths of p4 and m2-3 are indicated. The p4 of *Patriolestes* is always slightly longer than m1, and m2 is always

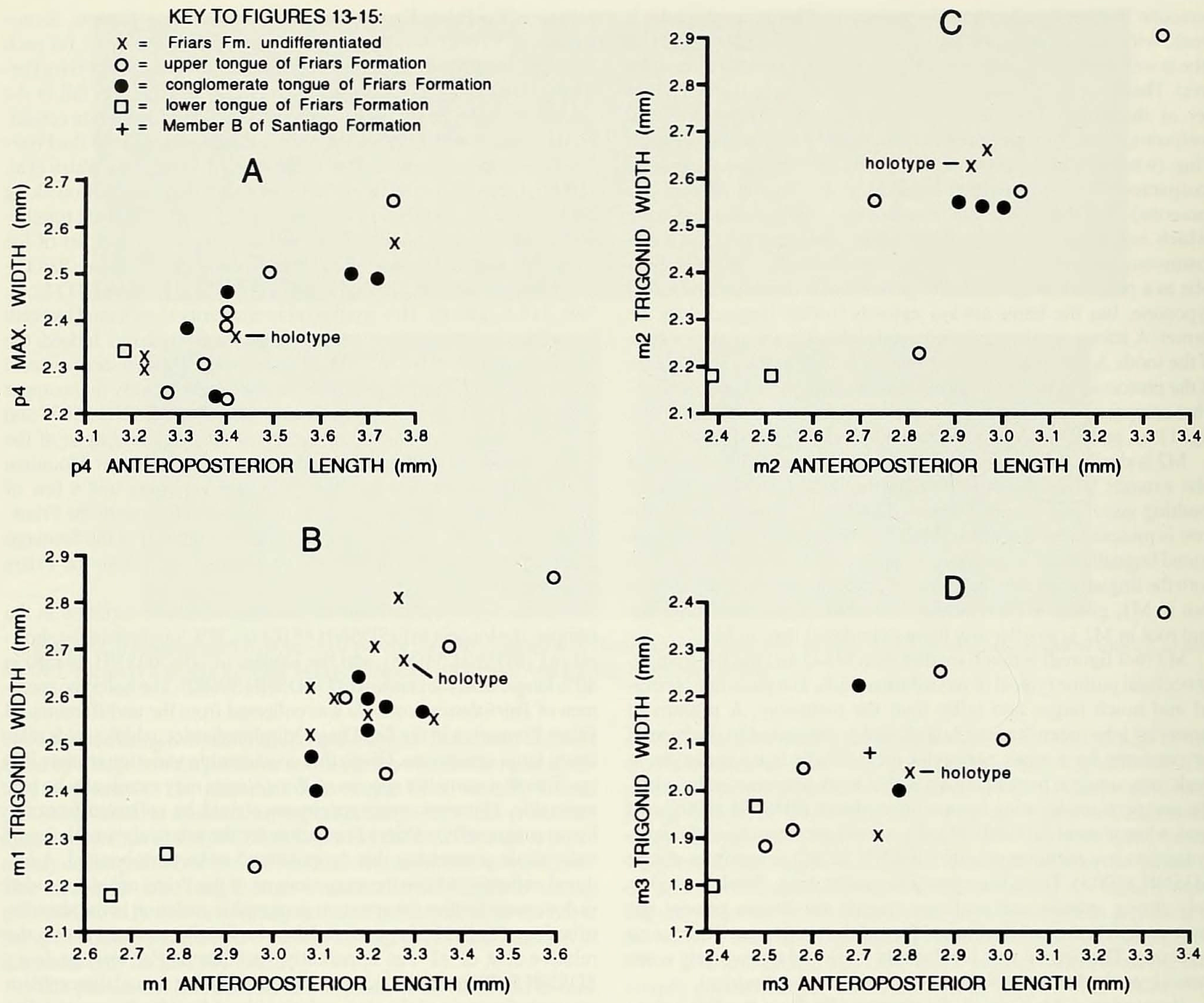


Figure 13. Plots of anteroposterior length vs. trigonid width for p4-m3 of *Patriolestes novaceki*. (A), p4; (B), m2; (C), m1; (D), m3.

slightly shorter than m1. The m3 is usually distinctly shorter than m1 but was equal to m1 in one specimen. For comparative purposes, mean values for the relative anteroposterior lengths of p4-m3 for *Patriolestes* and several other dormaaliid genera are presented in Table 8, and discussed further below.

TAXONOMIC COMPARISONS

Patriolestes is similar to middle Eocene sespedectines (*Sespedectes*, *Proterixoides*, and *Crypholestes*; Novacek 1976, 1985) in having a moderately enlarged proclivous chisel-shaped i2, a p4 slightly longer than m1 (Table 8), and relatively small single-rooted DP1-P2. Sespedectines differ from *Patriolestes* in having a relatively larger i1, a relatively smaller nontrenchant i3 subequal in size to c1, a double-rooted relatively large p3, a differentiated p4 trigonid, more anteroposteriorly elongate m1-2s, a trigonid narrower than the talonid on m1, a relatively much smaller C1 whose two roots are sometimes partially fused, a relatively much larger P3, and less tranverse M1-2.

Patriolestes is similar to the early-to-middle Eocene dormaaliine *Macrocranion* (e.g., Bown and Schankler 1982, plate 5; Novacek et al. 1985, fig. 2; MacPhee et al. 1988) in having a small single-rooted p2, a very small usually single-rooted p3 (a specimen with a double-rooted p3 was assigned to *M. nitens* by Bown 1979, fig. 42d), a relatively simple p4 trigonid, and a very small P3. *Macrocranion* differs from *Patriolestes* in having relatively small lower incisors and canines, a p4 with a distinct paracristid, a p4 consistently shorter than m1, a slight progressive increase in anteroposterior length from m1 to m3 (Table 8), longer m1-3 trigonids, an m1 talonid wider than trigonid (Krishtalka 1976), a single-rooted C1, a double-rooted P2, a less transverse M1-2, and a relatively larger M3.

Patriolestes is similar to certain European Eocene "amphilemurids" (e. g., *Pholidocercus*; von Koenigswald and Storch 1983) in its reduced single-rooted p2-3, simplified p4 trigonid, and relatively small P3. *Pholidocercus* differs from *Patriolestes* in having i2 smaller than i3, c1 smaller than dp1, dp1-p2 larger than p3, a relatively small single-rooted C1, a double-rooted P2, and more bunodont molars. Novacek et al. (1985) considered the Amphilemuridae to be a family separate from the Dormaaliidae, but Novacek (1985) regarded this taxon as a tribe of the Dormaaliinae.

Patriolestes is similar to various species of the early-to-middle Eocene scenopagine *Scenopagus* in having relatively anteroposteriorly compressed m1-2 trigonids, a very small P3, relatively transverse M1-2, and relatively sectorial molars (e. g., McKenna and Simpson 1959; Robinson 1966, plate III; McGrew and Sullivan 1970, fig. 6A; Krishtalka 1976, figs. 4-6; Bown 1982, plate 2A,B). Interestingly,

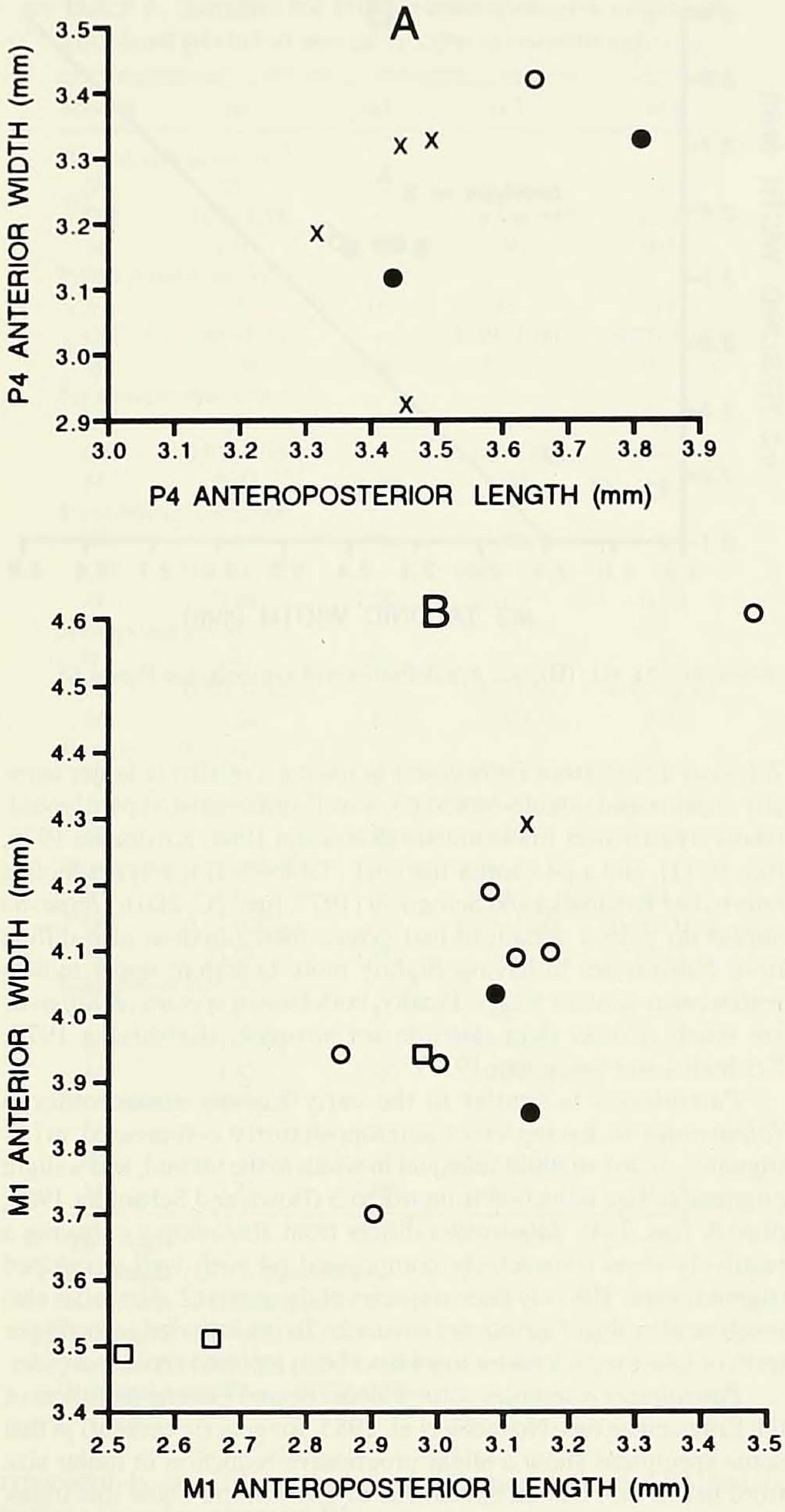


Figure 14. Plots of anteroposterior length vs. anterior width for P4–M1 of *Patriolestes novaceki*. (A), P4; (B), M1. For definitions of symbols, see Figure 13.

TABLE 6. Standard statistics for teeth of *Patriolestes novaceki* from the early Uintan of San Diego County.

Tooth		*N*	OR	*M*	SD	CV
I1	AP	16	1.53-2.05	1.77	0.172	9.7
	W	16	1.07-1.48	1.30	0.143	11.0
I2	AP	9	1.51-1.96	1.66	0.150	9.0
	W	10	1.04-1.45	1.24	0.116	9.4
I3	AP	27	1.23-2.04	1.51	0.185	12.2
	W	27	0.89-1.43	1.09	0.127	11.7
C1	AP	10	2.60-3.17	2.85	0.197	6.9
	W	11	1.55-2.11	1.85	0.177	9.6
DP1	AP	8	1.01-1.30	1.15	0.093	8.1
	W	9	0.89-1.15	1.02	0.101	9.9
P2	AP	16	1.49-1.84	1.62	0.103	6.3
	W	17	1.19-1.56	1.41	0.107	7.6
P3	AP	14	1.68-2.01	1.84	0.107	5.8
	W	14	1.56-2.07	1.87	0.158	8.5
DP3	AP	7	2.12-2.46	2.31	0.130	5.6
	W	6	1.54-1.96	1.68	0.149	8.9
P4	AP	7	3.31-3.81	3.51	0.166	4.7
	AW	8	2.92-3.42	3.20	0.187	5.8
	PW	7	4.16-4.46	4.31	0.121	2.8
M1	AP	15	2.52-3.38	3.02	0.229	7.6
	AW	13	3.49-4.61	3.97	0.307	7.7
	PW	14	3.89-5.19	4.39	0.386	8.1
M2	AP	3	2.62-2.86	2.73	0.122	4.5
	AW	3	4.19-5.52	4.67	0.738	15.8
	PW	5	3.80-4.86	4.15	0.411	9.9
M3	AP	4	1.55-2.12	1.77	0.246	13.9
	AW	4	2.77-3.16	3.03	0.175	5.8
	PW	8	2.10-2.64	2.31	0.167	7.2
i1	AP	5	1.39-2.34	1.84	0.352	19.1
	W	8	0.84-1.13	1.00	0.120	12.0
i2	AP	7	2.25-2.47	2.39	0.078	3.3
	W	10	1.00-1.39	1.21	0.129	10.6
i3	AP	11	1.69-2.26	2.02	0.159	7.9
	W	12	1.04-1.43	1.20	0.122	10.1
c1	AP	12	2.08-3.07	2.61	0.302	11.6
	W	11	1.39-1.82	1.60	0.153	9.6
dp1	AP	15	1.37-1.78	1.61	0.110	6.8
	W	16	1.21-1.67	1.39	0.118	8.5
p2	AP	9	1.71-1.92	1.84	0.068	3.7
	W	12	1.44-1.67	1.56	0.074	4.8
dp2	AP	7	1.85-1.99	1.91	0.053	2.8
	W	7	1.31-1.53	1.39	0.081	5.8
p3	AP	11	1.78-2.08	1.92	0.105	5.4
	W	12	1.53-1.85	1.66	0.096	5.8
dp3	AP	7	1.90-2.13	2.04	0.086	4.2
	W	7	1.30-1.50	1.43	0.068	4.8
p4	AP	17	3.19-3.75	3.43	0.184	5.4
	W	18	2.10-2.65	2.38	0.135	5.7
dp4	AP	2	2.98-3.09	3.04	0.055	1.8
	WTRI	2	1.56-1.84	1.70	0.140	8.2
	WTAL	2	1.72-1.97	1.85	0.125	6.8
m1	AP	23	2.65-3.60	3.16	0.193	6.1
	WTRI	23	2.18-2.85	2.54	0.173	6.8
	WTAL	23	2.15-2.95	2.52	0.183	7.3
m2	AP	11	2.39-3.34	2.87	0.259	9.0
	WTRI	12	2.18-2.91	2.51	0.214	8.5
	WTAL	14	1.94-2.82	2.31	0.216	9.3
m3	AP	14	2.39-3.34	2.72	0.241	8.9
	WTRI	13	1.75-2.38	2.01	0.170	8.4

Robinson (1968:4) reported an enlarged lower incisor in *S. priscus* (YPM 15254; assigned to *S. curtidens* by Krishtalka 1976:14). If corroborated, this could prove to be a significant similarity shared with *Patriolestes*. A complete lower jaw from the Wind River Formation (Wasatchian) was identified as *Scenopagus* sp. by Stucky et al. (1990, fig. 9). This specimen apparently has a double-rooted p2–3, a slightly enlarged c1, and a small i3, but the nature of i1–2 is unclear. *Scenopagus* differs from *Patriolestes* in having a relatively larger double-rooted p3 with a "paraconid flange," a differentiated p4 trigonid (Krishtalka 1976, figs. 4A–B), and a p4 consistently shorter than m1 (Table 8). Some specimens of *Scenopagus* show a slight progressive decrease in anteroposterior length from m1 to 3, whereas others do not (e.g., Krishtalka 1976, fig. 6A vs. fig. 4B).

The upper dentition of *Scenopagus* anterior to P3 is apparently unknown. McKenna and Simpson (1959) noted that empty alveoli on the type maxilla of *S. mcgrewi* (AMNH 56035) suggest a double-rooted P2. If substantiated, this condition in *Scenopagus* would be a primitive similarity shared with *Macrocranion* rather than *Patriolestes*. However, Novacek (1985, table 7) implied that *Scenopagus* had a single-rooted P2. The possibility also exists that the most anterior preserved alveolus in AMNH 56035 is the posterior alveolus for a

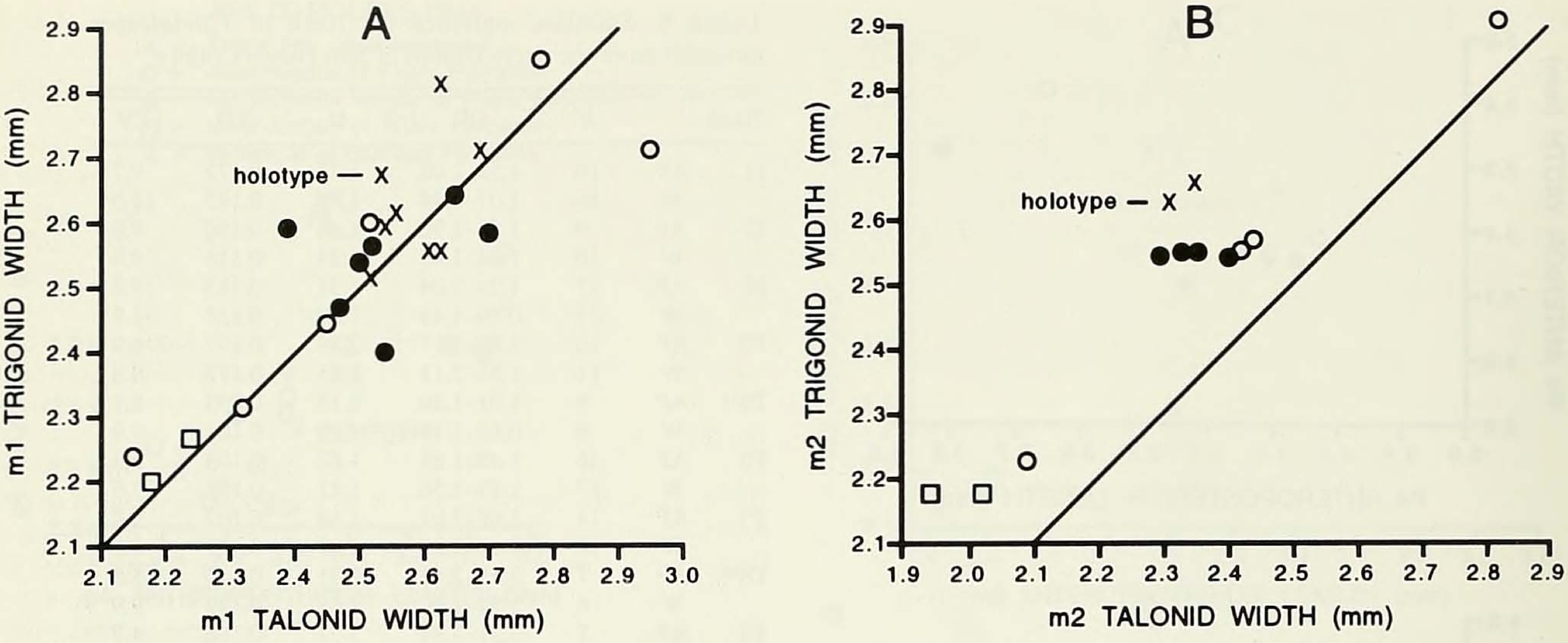


Figure 15. Plots of talonid width vs. trigonid width for m1-2 of *Patriolestes novaceki*. (A), m1; (B), m2. For definitions of symbols, see Figure 13.

large double-rooted C1, as in *Patriolestes*. Stucky et al. (1990:177) indicated that skull material of *Scenopagus* is available from the Wind River Formation, so these questions should eventually be resolved. Finally, characters of the lower dentition assumed for *Scenopagus* are based on species other than the type species *S. mcgrewi* (see Krishtalka 1976) and should therefore be viewed with caution. Krishtalka (1976) tentatively considered *S. mcgrewi* to be a junior synonym of *S. edenensis*, but Novacek et al. (1985) retained the former as a distinct species.

Patriolestes is similar to the middle Eocene to early Oligocene lipotyphlan *Ankylodon* in having relatively sectorial molars, anteriorly compressed trigonids, and relatively transverse upper molars. *Ankylodon* differs from *Patriolestes* in having a relatively large double-rooted p3 and a differentiated p4 trigonid, greatly hypertrophied m1-3 entoconids, a relatively large P3, a hypocone on P4, much stronger M1-2 hypocones, and much stronger metastylar and parastylar lobes on M1 and M2, respectively (Lillegraven et al. 1981, figs. 49-51). Given Fox's (1983) reinterpretation of the dental formula of *Ankylodon*, this genus also differs from *Patriolestes* in the subequal size of i3 and c1, the loss of dp1, the greatly enlarged fanglike I1 and smaller but still fanglike I2, a relatively small single-rooted C1, the loss of DP1, and a fenestrated palate.

Patriolestes is similar to the early-to-middle Eocene erinaceomorph *Talpavus* in having relatively sectorial lower molars with erect anteroposteriorly compressed trigonids and bladelike paraconids. *Talpavus* differs from *Patriolestes* in having a relatively larger laterally compressed double-rooted p3, a well-differentiated p4 trigonid, relatively narrower lower molars (Robinson 1968; Krishtalka 1976, figs. 9-11), and a p4 shorter than m1 (Table 8). If the upper molars referred by Krishtalka and Setoguchi (1977, figs. 2C, 2D) to *Talpavus duplus* do indeed pertain to that genus, then *Talpavus* also differs from *Patriolestes* in having slightly more bunodont upper molars with weaker conular wings. Finally, both known species of *Talpavus* are much smaller than *Patriolestes novaceki* (Krishtalka 1976; Krishtalka and Setoguchi 1977).

TABLE 7. Relative anteroposterior lengths of associated p4-m3 of *Patriolestes novaceki*. Length of m1 normalized to 1.00.

Specimen	p4	m1	m2	m3
LACM (CIT) 55935	1.01	1.00	—	—
LACM (CIT) 55936	1.05	1.00	—	—
LACM (CIT) 55937	—	1.00	0.92	—
SDSNH 49250	1.04	1.00	0.90	0.86
SDSNH 54858	1.11	1.00	0.99	1.00
SDSNH 54912	—	1.00	0.94	—
SDSNH 55499	1.06	1.00	—	—
SDSNH 55500	1.06	1.00	—	—
SDSNH 56947	—	1.00	0.97	0.92
UCMP 133966	1.05	1.00	—	—

Patriolestes is similar to the early Eocene erinaceomorph *Talpavoides* in having erect anteroposteriorly compressed m1-2 trigonids, an m1 trigonid subequal in width to the talonid, and a slight progressive size reduction from m1 to 3 (Bown and Schankler 1982, plate 6, figs. 3-4). *Talpavoides* differs from *Patriolestes* in having a relatively short transversely compressed p4 with well-developed trigonid cusps. The only known species of the genus (*T. dartoni*) is also much smaller than *Patriolestes novaceki*. To my knowledge, no upper teeth or lower teeth anterior to p4 have been reported for *Talpavoides*.

Patriolestes resembles some Paleocene and Eocene members of the Erinaceidae (see Novacek et al. 1985, for generic content) in that some specimens show a slight progressive reduction in molar size from m1 to m3. Not all specimens of *Patriolestes* show this trend, however. Further, early erinaceids such as *Entomolestes*, *Litolestes*, and the unnamed Tepee Trail Formation taxon (AMNH 88288; cf. *Ocajila* of McKenna 1980; Novacek et al. 1985:11) differ from *Patriolestes* in having a double-rooted p2, a more anteroposteriorly elongate p3, and differentiated p4 trigonids (Krishtalka and West 1977; Novacek et al. 1985). *Litolestes* also differs from *Patriolestes* in having small bilobate or trilobate lower incisors (Schwartz and Krishtalka 1976). Lower incisor crowns are apparently unknown for *Entomolestes*. Although the early Uintan Tepee Trail Formation taxon is similar to *Patriolestes* in having a slightly enlarged i1-2 and a moderately enlarged bunodont double-rooted C1, the former differs from *Patriolestes* in having double-rooted DP1-P2, a strong P4 hypocone, and much more quadrate upper molars with reduced parastylar and metastylar lobes.

Patriolestes resembles the aberrant Oligocene erinaceoid *Proterix* in having a relatively small single-rooted p2-3, a simplified p4 trigonid, a large double-rooted bunodont C1, and a small triangular P3 (Gawne 1968; Bjork 1975). *Proterix* differs from *Patriolestes* in having a greatly enlarged i1, more bunodont molars, in lacking

TABLE 8. Statistics for relative anteroposterior lengths of associated p4–m3 of several Eocene erinaceomorph taxa.

Species	p4	m1	m2	m3
Patriolestes novaceki[a]				
N	7	10	5	3
OR	1.01–1.11	—	0.90–0.99	0.86–1.00
M	1.05	1.00	0.94	0.93
Proterixoides davisi[a]				
N	9	18	16	11
OR	1.01–1.11	—	0.89–1.00	0.91–1.06
M	1.06	1.00	0.95	0.98
Scenopagus edenensis[b]				
N	3	6	4	1
OR	0.91–0.95	—	1.00–1.09	—
M	0.93	1.00	1.04	1.14
Scenopagus curtidens[b]				
N	4	7	5	1
OR	0.83–0.88	—	0.95–1.00	—
M	0.84	1.00	0.99	0.89
Scenopagus priscus[b]				
N	6	9	4	2
OR	0.80–0.93	—	0.93–1.07	0.67–0.93
M	0.88	1.00	1.02	0.80
Macrocranion nitens[c]				
N	6	9	9	3
OR	0.84–0.95	—	0.95–1.05	1.05–1.05
M	0.91	1.00	1.02	1.05
Talpavus cf. *T. nitidus*[d]				
N	5	6	4	4
OR	0.71–0.86	—	0.85–1.00	0.86–1.00
M	0.81	1.00	0.89	0.93
Talpavoides dartoni[e]				
N	4	5	2	—
OR	0.77–0.92	—	0.88–0.95	—
M	0.82	1.00	0.92	—
Entomolestes grangeri[f]				
N	6	9	5	1
OR	0.67–0.80	—	0.87–1.00	—
M	0.72	1.00	0.92	0.87

[a] This study.
[b] Krishtalka (1976), appendix A.
[c] Krishtalka (1976), appendix C.
[d] Krishtalka (1976), table 6.
[e] Bown and Schankler (1982), table 6.
[f] Krishtalka and West (1977), table 1.

hypoconulids, and DP1, in the loss or aberrant structure of P2, and in having a large hypocone on P4.

Finally, *Patriolestes* differs from several Paleogene erinaceomorphs of uncertain phylogenetic position (*Dormaalius*, *Diacodon*, *Eolestes*, *Litocherus*, and *Diacocherus*; see Gingerich 1983; Novacek et al. 1985) in that these taxa, where known, all have a double-rooted p2 and/or p3, and/or differentiated p4 trigonids, and/or relatively anteroposteriorly elongate bunodont lower molars, and/or single-rooted upper canines.

EVOLUTIONARY RELATIONSHIPS

I use the term "evolutionary relationship" to include ancestor-descendant and cladistic relationships. The higher-level relationships of early erinaceomorphs and other insectivorans are by no means settled. At the most basic level, there is no consensus on the identity of the sister group of the Lipotyphla. Novacek (1986a) and MacPhee and Novacek (1993) favored a sister-group relationship between lipotyphlans and leptictids, allying them together in a superorder Insectivora. In contrast, Stucky and McKenna (1993), closely following McKenna (1975), assigned the Leptictidae and their allies to a separate superorder Leptictida and regarded the Lipotyphla as a grandorder within the superorder Preptotheria. Under this view, possible sister taxa of the Lipotyphla might include the Carnivora and Tubulidentata (MacPhee and Novacek 1993).

More disagreement exists concerning relationships within the Erinaceomorpha. The most comprehensive treatments available are those of Novacek et al. (1985) and Novacek (1985). These authors recognized a basic dichotomy within Erinaceomorpha corresponding to the superfamilies Erinaceoidea and Dormaalioidea (spelled Dormaaleoidea by Novacek, though based on *Dormaalius*). Nevertheless, many of the nodes on Novacek's (1985) cladogram are defined by relatively minor features of the dentition, and significant changes to this arrangement may be expected as better specimens of various poorly known taxa are collected.

In a competing hypothesis of lipotyphlan relationships, Butler (1988) raised the Scenopaginae (containing *Scenopagus* and *Ankylodon*) to family rank, regarding it as the sister taxon of the Erinaceidae. Butler also transferred the Sespedectinae from the Dormaaliidae to the Scenopagidae and tentatively excluded *Macrocranion* from the Lipotyphla, greatly altering the concept of the Dormaaliidae envisioned by Novacek et al. (1985) and Novacek (1985). Another classification of lipotyphlans was proposed by Stucky and McKenna (1993), who abandoned the family name Dormaaliidae, used the name Amphilemuridae for Novacek's (1985) concept of the Dormaaliinae, raised the Sespedectinae to family rank, and included within it *Scenopagus* and *Ankylodon*. Neither Butler (1988) nor Stucky and McKenna (1993) recognized the dormaalioid–erinaceoid dichotomy fundamental to the classifications of Novacek et al. (1985) and Novacek (1985).

These divergent opinions stem largely from the relatively incomplete materials representing many relevant taxa. Since the cladistic structure of various potential dormaaliid and erinaceomorph outgroups is debatable, the polarity of many relevant characters is also uncertain. Although the reality of the dormaalioid–erinaceoid dichotomy requires additional corroboration, it seems premature to attempt a comprehensive revised parsimony analysis of the relationships of these taxa. Nevertheless, the following comments are based on the general classification and proposed character polarities of Novacek (1985), with some modifications.

Novacek's (1985, fig. 9) cladogram shows the Dormaaliidae diagnosed by the following putative autapomorphies that may separate them from early erinaceids: (1) p2 small and procumbent or peglike and single-rooted; (2) p4 with short bicuspid or unicuspid heel; (3) P2 peglike and single-rooted; (4) M1–2 hypocones relatively large. Novacek et al. (1985) and Novacek (1985) noted that this diagnosis is problematical in that some of these characters also occur in certain putative Paleogene erinaceids (e. g., a short p4 talonid is present in *Entomolestes*). In addition, the upper dentition is unknown for many of these taxa (e. g., *Entomolestes*, *Leipsanolestes*, *Eolestes*, and *Dartonius*). Note that character (3) should not be regarded as an autapomorphy for the Dormaaliidae because a double-rooted P2 is retained in *Macrocranion* (see Novacek et al. 1985, fig. 1), *Pholidocercus* (see von Koenigswald and Storch 1983), and possibly *Scenopagus* (see McKenna and Simpson 1959). Accordingly, a double-rooted P2 is included in a list of proposed dormaaliid plesiomorphies (Fig. 16).

Sespedectinae

The moderately enlarged upper and lower first and second incisors of *Proterixoides* somewhat resemble the enlarged incisors of several extant erinaceid genera (e.g., Frost et al. 1991). However, incisor enlargement is prone to parallelism within the Lipotyphla and other eutherians (Butler 1980:173). Thus, the incipiently diprotodont condition of the Sespedectinae seems to be insufficient evidence for a close relationship with the Erinaceidae, and the former subfamily is tentatively retained in the Dormaaliidae. Consistent with this decision is the apparent lack of incisor enlargement in the Paleogene erinaceids *Entomolestes* and *Litolestes* (as noted, the Tepee Trail Formation taxon had slightly enlarged i1-2, but the upper incisors are apparently unknown).

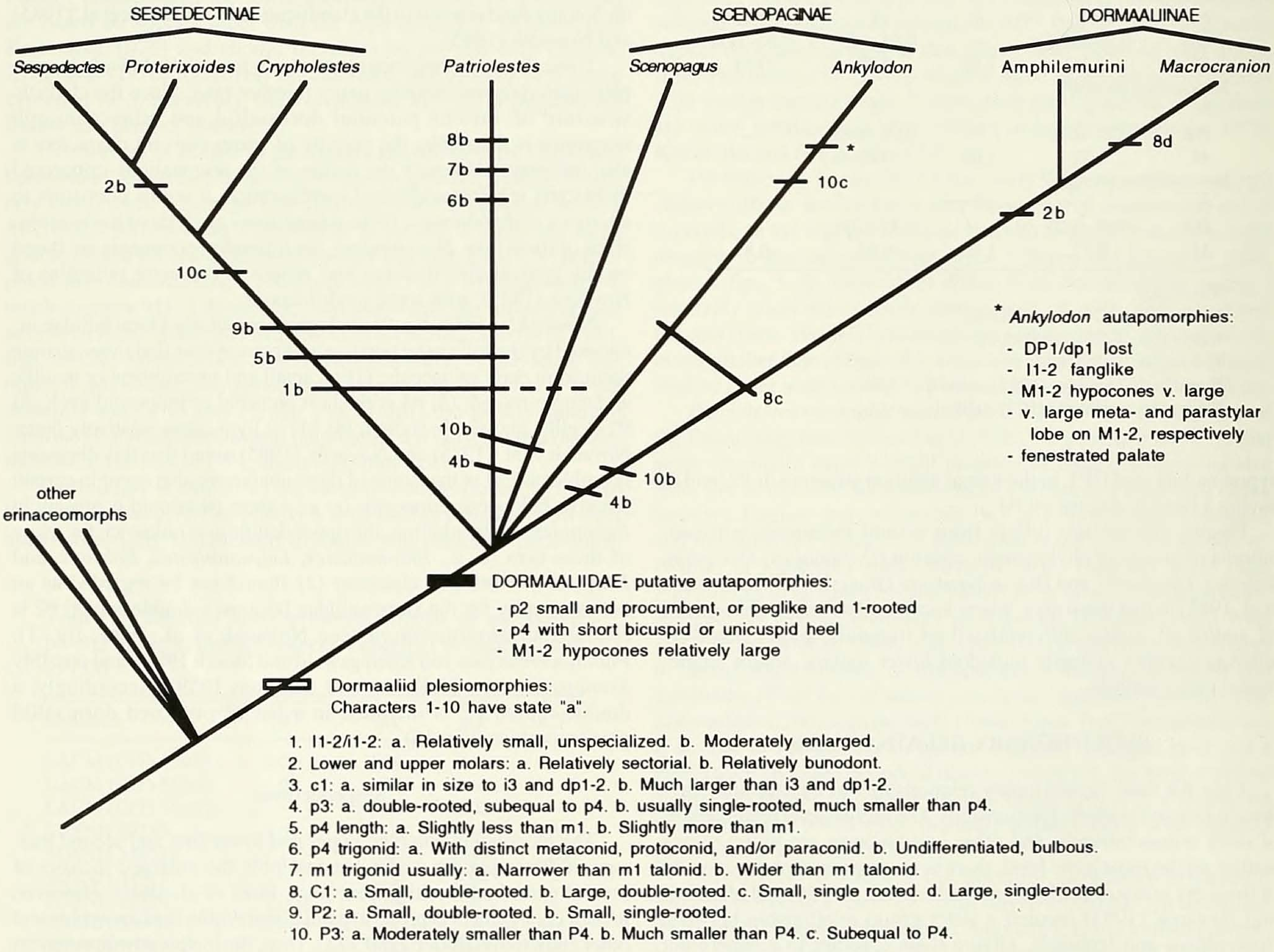
Robinson (1966:29) suggested that *Scenopagus* is a logical ancestor for *Proterixoides*. Although this remains a possibility, the immediate ancestor of both *Proterixoides* and *Sespedectes* was probably *Crypholestes* (cf. Novacek 1976:24). *Crypholestes* has somewhat more sectorial molars than *Proterixoides* or *Sespedectes*, which helps to bridge the morphological gap between the latter two genera and *Scenopagus*. Nevertheless, derivation of *Crypholestes* from *Scenopagus* requires that the very small P3 of the latter genus is primitive, capable of evolving into the large P3 of sespedectines (see further discussion below).

Another possible ancestral morphotype for the Sespedectinae is represented by the Paleocene erinaceomorph *Litocherus* (see Gingerich 1983). As noted by Novacek (1976:24), the upper cheek teeth of *Litocherus notissimus* are remarkably similar in morphology to those of *Crypholestes vaughni* (see Simpson 1936:24). The p4 of *Litocherus* is also similar to that of sespedectines in being slightly longer than m1, although p3-4 of *Litocherus* have sharper cusps than p3-4 of sespedectines (Gingerich 1983, fig. 1). According to Simpson (1936:25), (D)P1 and P2 of *L. notissimus* have relatively small, simple crowns (apparently like sespedectines) but are both double-rooted (unlike sespedectines). An important difference between these taxa is the large recurved single-rooted C1 and large c1 in *Litocherus* (Simpson 1936, 1937), as opposed to the small double-rooted C1 and small c1 in sespedectines.

Patriolestes

Patriolestes has all three of the characters that currently diagnose the Dormaaliidae and is thus assigned to this family. Novacek (1985) recognized three subfamilies of the Dormaaliidae (Sespedectinae, Scenopaginae, and Dormaaliinae). *Patriolestes* can be excluded from the Sespedectinae on the basis of its enlarged c1 and C1, its relatively small usually single-rooted p3, and its very small P3.

Existing diagnoses of the Scenopaginae and Dormaaliinae are not entirely satisfactory. The Scenopaginae (containing *Scenopagus* and *Ankylodon*) were diagnosed as having large, distinct P4 hypocones and large and posterolingually situated hypocones on M1-2 (Novacek 1985, fig. 9). However, the M1-2 hypocones of *Scenopagus* are approximately as large, relatively, and posterolingually situated as those of *Macrocranion* (e. g., Krishtalka 1976, figs. 4C and 7C; Bown and Schankler 1982, plate 5) and do not approach the hypertrophied condition of *Ankylodon* (Lillegraven et al. 1981, fig. 49). The Dormaaliinae were diagnosed by Novacek (1985, fig. 9) as having the derived characters of a small single-rooted p3 and a very small peglike or triangular P3. However, *Scenopagus* also has a



* *Ankylodon* autapomorphies:
- DP1/dp1 lost
- I1-2 fanglike
- M1-2 hypocones v. large
- v. large meta- and parastylar lobe on M1-2, respectively
- fenestrated palate

DORMAALIIDAE- putative autapomorphies:
- p2 small and procumbent, or peglike and 1-rooted
- p4 with short bicuspid or unicuspid heel
- M1-2 hypocones relatively large

Dormaaliid plesiomorphies:
Characters 1-10 have state "a".

1. I1-2/i1-2: a. Relatively small, unspecialized. b. Moderately enlarged.
2. Lower and upper molars: a. Relatively sectorial. b. Relatively bunodont.
3. c1: a. similar in size to i3 and dp1-2. b. Much larger than i3 and dp1-2.
4. p3: a. double-rooted, subequal to p4. b. usually single-rooted, much smaller than p4.
5. p4 length: a. Slightly less than m1. b. Slightly more than m1.
6. p4 trigonid: a. With distinct metaconid, protoconid, and/or paraconid. b. Undifferentiated, bulbous.
7. m1 trigonid usually: a. Narrower than m1 talonid. b. Wider than m1 talonid.
8. C1: a. Small, double-rooted. b. Large, double-rooted. c. Small, single rooted. d. Large, single-rooted.
9. P2: a. Small, double-rooted. b. Small, single-rooted.
10. P3: a. Moderately smaller than P4. b. Much smaller than P4. c. Subequal to P4.

Figure 16. Cladogram showing distribution of selected morphological characters of various dormaaliid taxa. Polarities and topology modified from Novacek (1985).

very small, triangular P3, yet its alleged sister taxon *Ankylodon* has a P3 nearly as large as P4 (Lillegraven et al. 1981, fig. 49). Indeed, the P3 in the holotype specimen of *Scenopagus mcgrewi* (McKenna and Simpson 1959) and one specimen of *S. curtidens* (Bown 1982, plate 2B) are just as small relative to P4 as the P3 in one skull of *Macrocranion nitens* (USGS 3676; Novacek et al. 1985, fig. 2).

Novacek (1985, table 7) suggested that a P3 "small to moderate, triangular, at least 2-rooted," is primitive for erinaceomorphs (e.g., *Diacodon*; see Novacek 1982) and that the states "very small, peglike or triangular" and "large with several cusps, similar to P4" are both derived. I tentatively follow this proposal here, but note that there is considerable doubt concerning the polarities of the various states of the character "P3 size relative to P4" (cf. Fox 1983:975).

Patriolestes lacks a hypocone on P4, which might exclude it from the Scenopaginae. However, the P4 hypocones on the type specimen of *Scenopagus mcgrewi* (AMNH 56035) and a referred specimen of *S. edenensis* (CM 6433; Krishtalka 1976, fig. 4C) are quite small, so the absence of this cusp in *Patriolestes* need not bar a close relationship between the two genera. Like *Scenopagus* and *Ankylodon*, *Patriolestes* has relatively sectorial molars, anteroposteriorly compressed trigonids with bladelike paraconids, and relatively tranverse M1-2s. Although these characters may be primitive for the Dormaaliidae (Novacek et al. 1985:3-4), they seem to exclude *Patriolestes* from the Dormaaliinae, which are characterized by cheek teeth with more bulbous cusps. However, *Patriolestes* also has a very small usually single-rooted p3, which is diagnostic of the Dormaaliinae (Novacek 1985, fig. 9). In view of this equivocal evidence (Fig. 16), an assignment of *Patriolestes* to either the Scenopaginae or Dormaaliinae is unjustified, and I prefer to classify it as Dormaaliidae, *incertae sedis*.

Patriolestes is unique among known dormaaliids in having a relatively large double-rooted bunodont C1, and in this respect it resembles the aberrant Oligocene erinaceoid *Proterix* (see Matthew 1903; Gawne 1968; Bjork 1975). Novacek (1985:19) implied that the large double-rooted C1 in *Proterix* was more "conservative" than the small single-rooted C1 in sespedectines (as noted above, C1 in sespedectines is actually two-rooted, with frequent incomplete fusion). The issue of C1 character-state polarity is further complicated by the presence of a large single-rooted C1 in the Paleocene erinaceomorph *Litocherus* (see Simpson 1936, 1937) and the early Eocene putative dormaaliid *Macrocranion* (see Novacek et al. 1985, fig. 1). Although many of the characters in which *Patriolestes* differs from *Proterix* are clearly primitive, the similarity in C1 morphology shared by the two genera seems to be convergent in view of the presumed erinaceoid status of *Proterix*.

Given the limited material of *Patriolestes* then available, Novacek (1982) suggested it to be the sister taxon of *Ankylodon*, on the basis of the enlarged M1-2 hypocones and enlarged M1 metastylar spurs allegedly shared by these taxa. However, the new specimens of *Patriolestes* described above generally do not have M1-2 hypocones or the M1 metastylar lobes significantly enlarged relative to those in at least some specimens of *Macrocranion* (e. g., Krishtalka 1976, fig. 7C) and *Scenopagus* (e. g., Krishtalka 1976, fig. 4C). Although UCMP 101420 does have a relatively large metastylar lobe (Novacek 1976, fig. 14), this structure is not significantly expanded in most other available M1s of *Patriolestes* (e. g., SDSNH 37999 and 54857). The parastylar lobe of M2 of *Patriolestes* is also variable in its degree of expansion (e.g., SDSNH 38004 vs. 54857).

To complicate matters, Fox (1983) described the upper anterior dentition and portions of the skull of *Ankylodon* and concluded it is actually a soricomorph insectivore, rather than an erinaceomorph as generally supposed (e.g., Lillegraven et al. 1981). With the exception of the fanglike I1, Novacek et al. (1985) questioned the validity of the skull characters in *Ankylodon* cited by Fox to indicate soricomorphan relationships. Novacek et al. (1985) and Novacek (1985) therefore retained *Ankylodon* in the Erinaceomorpha and included it with *Scenopagus* in the subfamily Scenopaginae. Butler (1988) did not comment on Fox's classification of *Ankylodon* but supported an ancestor-descendant relationship between *Ankylodon* and *Scenopagus*.

Since the higher-level position of *Ankylodon* has not been settled, I address only the possibility of its being a direct descendant of *Patriolestes*. Evolution of *Ankylodon* from *Patriolestes* requires several character reversals, including a re-enlargement of the small usually single-rooted p3 into a large double-rooted tooth, a re-differentiation of the bulbous p4 trigonid, a re-enlargement of the small P3, and a re-reduction of the large double-rooted C1 into a small single-rooted tooth. Butler's (1988) derivation of *Ankylodon* from *Scenopagus* also requires a re-enlargement of the small P3 in the latter genus. On the other hand, *Patriolestes* is a plausible descendant of *Scenopagus* in that where known, *Scenopagus* retains the primitive condition of the derived character states of *Patriolestes* (excepting the small P4 hypocone). Discovery of the anterior dentitions and upper teeth of *Scenopagus*, *Talpavus*, and *Talpavoides* should clarify the relationships of these and other dormaaliid taxa.

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APPENDIX 1.
ALL KNOWN SPECIMENS OF *PATRIOLESTES NOVACEKI*, ARRANGED BY ELEMENT.

i1(?): SDSNH 27600, 32487, 58729, 58919, 58980, 58997, 60008, 60024.

i2: SDSNH 56968, 58732, 58788, 58789, 58807, 58826, 58964, 58998, 60013, 60037.

di2(?): SDSNH 58731, 58810, 58812, 58925, 58933, 58965.

i3: SDSNH 27628, 56970, 56971, 58730, 58825, 58921, 58966, 58981, 58983, 58984, 58990, 60019.

di3: SDSNH 37528, 58811, 58824, 58920, 58926, 58932, 58982, 58999, 58797, 58813, 58967.

c1: SDSNH 31922, 31936, 48043, 56967, 58733-58735, 58814, 58827, 58828, 58968, 58969, 60004, 60038, 60039.

dp1: SDSNH 31883, 31913, 31934, 31935, 32000, 56964, 58641, 58736-58739, 58798, 58816, 58936, 58985, 58986, 60040.

p2: SDSNH 31876, 31990, 56966, 58640, 58720, 58740-58742, 58790, 58829, 58836, 58937, 60014. UCMP 154722.

dp2: SDSNH 31983, 32006, 58722, 58745, 58746, 58934, 58970, 58971, 59000.

p3: SDSNH 32004, 32080, 58747-749, 58791, 58830, 58837, 58927, 58972, 60041.

dp3: SDSNH 58723, 58743, 58744, 58792, 58808, 58935, 60026, 60042.

p4: LACM(CIT) 55934. SDSNH 37609, 37987, 37988, 39679, 42428, 45160, 45799, 46436, 47240, 49612, 55825, 60043.

dp4: SDSNH 45798, 56946.

m1: SDSNH 31764, 37610, 37992, 45161, 45800, 46271, 49207, 49436, 50589, 51259, 54926, 54995, 60044, 60045.

m1 or 2: SDSNH 37989, 37991, 39680.

m2: SDSNH 32039, 37611, 37993, 42429, 43230, 51069, 54996, 56717, 60046. UCMP 101617.

m3: LACM(CIT) 56189. SDSNH 37612, 37613, 37994, 37995, 39678, 39681, 45801, 46272, 46555, 46556, 49611, 56724, 56948, 56949, 60047. UCMP 109514, 109536.

mandible fragments with (or associations of):

p3-4: SDSNH 56725.

unerupted p3 + m1-2: SDSNH 54912.

p4: SDSNH 55498.

p4-m1: LACM(CIT) 55935, 55936. UCMP 133966.

p4-m2: SDSNH 55499, 55500.

p4-m3: SDSNH 49250, 54858.

m1 or 2: SDSNH 46554.

m2: SDSNH 43276.

m1-3: LACM(CIT) 55937. SDSNH 56947.

m2-3: SDSNH 47865.

I1: SDSNH 31979, 56972, 58726, 58727, 58757, 58941, 58943, 58973, 58992, 60005, 60015, 60025, 60027, 60048-60050. UCMP 154721.

I2: SDSNH 37512, 43251, 56714, 56969, 58796, 58809, 58831-58833, 60017.

DI1-2 (?): 32491, 32494, 58725, 58751, 58753, 58755, 58793, 58799, 58817, 58930, 58938, 60007, 60017.

I3: SDSNH 31920, 31929, 37523, 42484, 56973, 58719, 58752, 58760, 58761, 58794, 58805, 58806, 58821, 58834, 58923, 58929, 58939, 58942, 58974-58977, 58991, 58993, 60009, 60010, 60020, 60022, 60051.

DI3 (?): 32500, 37506, 37511, 37530, 58750, 58754, 58756, 58818, 58922, 58928, 58987-58989, 58994-58996, 60001, 60006, 60011, 60021, 60028.

C1: SDSNH 27650, 31998, 43250, 51367, 58758, 56960-56963, 58724, 58800, 58924, 60002.

DP1: SDSNH 27587, 58819, 58820, 60003, 60012, 60018, 60023.

P2: SDSNH 32050, 58762-58766, 58660, 58795, 58801-58804, 58823, 58931, 58979, 60052. UCMP 109546, 110041.

P3: SDSNH 38122, 38149, 39747, 39761, 43083, 43963, 46139, 56951-56953, 56965, 60053.

DP3: SDSNH 27011, 38150, 39748, 56950, 58721, 58823, 58835.

P4: LACM(CIT) 55933, 56119. SDSNH 37614, 43081, 51258, 56954, 56955, 59637, 58638, 60054. UCMP 101690, 106355.

DP4: UCMP 154720.

M1: SDSNH 31767, 36578, 37998-38001, 38003, 39335, 39683, 39684, 43082, 43231, 45802, 46373, 49350, 51070, 51102, 55679, 56718, 56956, 58639, 58768, 60055, 60056, 60057. UCMP 101420, 133967, 154719.

M1 or 2: LACM(CIT) 55945. SDSNH 45163, 60058. UCMP 101654, 101626.

M2: LACM(CIT) 55944. SDSNH 31768, 37615, 37616, 38002, 38004, 39682, 42430, 45552, 46066, 46273, 56957, 58769.

M3: SDSNH 31765, 31766, 36579, 37400, 38005, 38006, 39685, 41353, 45162, 46274, 51103. UCMP 101497, 109796.

palatal fragment with LC1-P2 + RP2: SDSNH 55497.

maxillary fragments with:

C1 + P3-4: SDSNH 56185.

P3-M2: SDSNH 54857.

P4-M1: SDSNH 51293.

APPENDIX 2.

ALL KNOWN SPECIMENS OF *PATRIOLESTES NOVACEKI*, ARRANGED BY STRATIGRAPHIC UNIT, INSTITUTION, AND LOCALITY.

Friars Formation, undifferentiated.—**SDSNH Loc. 3414**: 41353. **Loc. 3430:** 58942. **Loc. 3784**: 49207, 49250, 49350, 49436, 49611, 49612, 50589, 51258, 51259, 51293, 56724, 56725. **Loc. 3785**: 50786, 51069, 51070, 51102, 51103, 58810-58822. **Loc. 3832:** 51367.

LACM (CIT) Loc. 249: LACM(CIT) 55933, 55934. 55935, 55936, 55937, 55944, 55945, 55949. **Loc. 249-S**: 56119. **Loc. 249-P**: 56189.

UCMP Loc. V-68116: UCMP 101690.

Upper tongue of Friars Formation.—**SDSNH Loc. 3254:** SDSNH 27011, 27628, 27650, 27600, 27623, 27587. **Loc. 3373**: 31764-31768, 31876, 31883, 31885, 31913, 31920, 31922, 31924, 31929, 31934-31936, 31964, 31979, 31983, 31990, 31996, 31998, 32000, 32004, 32006, 32039, 32050, 32080, 60013-60016. **Loc. 3380**: 42428, 42430, 58719, 58720, 60017. **Loc. 3391**: 32487, 32491, 32494, 32500, 56717, 56718. **Loc. 3482**: 37609-37616, 58722-58728, 60018. **Loc. 3483**: 37987-37989, 37991-37995, 37998-38006, 38149, 38150, 58729-58770, 58943, 60019-60023, 60028. **Loc. 3484:** 58776-58777. **Loc. 3591:** 43963. **Loc. 3611**: 45160-45163, 58788-58796, 60024-60025. **Loc. 3612**: 45552, 47865, 58797-58806. **Loc. 3681**: 46554-46556, 58807-58809. **Loc. 3685**: 46436. **Loc. 3771**: 47240. **Loc. 3883**: 54857, 54858, 60026-60027.

UCMP Loc. V-71180: 101654. **V-72157**: 101420, 106355, 109514, 109536, 109546, 110041. **V-72158**: 101497, 101617, 101626, 154719. **V-73138**: 109796, 133966, 133967, 154720-154722.

Conglomerate tongue of Friars Formation.—**SDSNH Loc. 3615:** 42484. **Loc. 3616:** 60004. **Loc. 3617**: 43081-43083, 43276, 58824-58837, 60005-60007. **Loc. 3620**: 43230-43231, 43250-43251. **Loc. 3621**: 55497-55500, 55825, 56946-56973, 58637-58642, 58659-58660, 60008-60012. **Loc. 3730:** 48043. **Loc. 3739**: 54912, 54926. **Loc. 3824**: 56185, 60037-60058.

Lower tongue of Friars Formation.—**SDSNH Loc. 3494**: 37400. **Loc. 3496:** 37506, 37511-37513, 37523, 37528, 37530. **Loc. 3503**: 39335, 58990-58991. **Loc. 3505**: 39678-39685, 39747, 39748, 39761, 58964-58989. **Loc. 3655**: 46066, 46139, 58919-58924, **Loc. 3656**: 46271-46274, 58925-58931, 58992-58994. **Loc. 3657**: 46373. **Loc. 3658**: 45798-45802, 58932-58941, 58995-58996. **Loc. 3828:** 56714. **Loc. 3893**: 54995-54996, 58823, 58997-59000, 60001-60003.

Member "B" of Santiago Formation.—**SDSNH Loc. 3440**: 36576-36579.