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Status of *Simidectes* (Insectivora, Pantolestidae) of the Late Eocene of North America

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INTRODUCTION

In 1919 Peterson described specimens of *Pleurocyon magnus* found near Myton, Utah, "horizon C" of the Uinta Formation, and of *Pleurocyon medius* of the White River pocket, "Uinta B." The material on which the two species were based was incomplete, *P. magnus* being represented primarily by part of a left mandible with P₃-M₂, an isolated upper molar, a right ramus with canine in place, and various postcranial fragments including limb bones and a fairly complete pes. *Pleurocyon medius* was even more scantily represented by an edentulous lower jaw, a lower jaw fragment with M₁ in place, and various limb pieces. The material was not adequate for any extended study and was considered to be of a miacine miacid with affinities to *Vulpavus* and *Oodectes*. The only criteria for distinguishing the two species of *Pleurocyon* were the differences in size and the fact that they came from two different stratigraphic horizons.

In 1933 Stock described additional specimens, a number of upper and lower jaws with teeth, as belonging to *Pleurocyon* (*Simidectes*) *merriami*, a new subgenus and species. These specimens came from Pearson Ranch, Locality 150, of the lower Sespe Formation, upper Eocene of California and were somewhat larger than any *Pleurocyon* described by Peterson.

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Stock noted a few small differences in the construction of P_3 and P_4 between *P. merriami* and *P. magnus* but was convinced that they belonged to the same genus and that they were related to *Oodectes* and *Vulpavus*.

Kraglievich, in a paper published in 1948, but apparently written without knowledge of Stock's publication, noted the preemption of the name *Pleurocyon* by a canid genus and suggested the generic name *Petersonella* for the specimens described by Peterson.

In an unpublished manuscript written in 1959 or 1960 Mac Intyre pointed out that *Simidectes* rather than *Petersonella* is the correct name for Peterson's *Pleurocyon* because, according to article 23e of the International Code (1961), a prior subgeneric name becomes the generic name when the original generic name is invalid. Usage of the name *Simidectes* by Van Valen (1965) is probably explained by his access to Mac Intyre's manuscript.

As *Simidectes* has been more and more seriously studied there has been an increasing tendency for students to question placement of the genus in the Miacidae. This paper will attempt to evaluate the possibilities of relationship to various higher groups and to determine what can and cannot be said about the affinities of *Simidectes*.

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ABBREVIATIONS

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

A.M.N.H.:C.A., the American Museum of Natural History, Comparative Anatomy

C.M., Carnegie Museum

K.U., University of Kansas Museum of Natural History

L.A.C.M., Los Angeles County Museum

P.U., Princeton University

U.C.M.P., University of California Museum of Paleontology, Berkeley

U.C.R., University of California, Riverside

Y.P.M., Yale University, Peabody Museum of Natural History

SYSTEMATICS

ORDER INSECTIVORA

SUPERFAMILY PANTOLESTOIDEA COPE, 1887, *INCERTAE SEDIS**SIMIDECTES* STOCK, 1933¹

Pleurocyon PETERSON, 1919, p. 52, *nec* Mercerat, 1917,² p. 13.

Pleurocyon (*Simidectes*) STOCK, 1933, p. 481.

Petersonella KRAGLIEVICH, 1948, p. 162.

Simidectes: VAN VALEN, 1965, p. 394.

TYPE SPECIES: *Simidectes magnus* (Peterson, 1919).

INCLUDED SPECIES: The type species, *Simidectes medius*, and *S. merriami*.

KNOWN DISTRIBUTION: Late Eocene (Uintan through Duchesnean of Wood et al., 1941) of North America.

GENERIC DIAGNOSIS: Dentition full placental number; canine large, recurved, and transversely compressed (especially in *S. magnus*); little or no diastema between canines and P_1^1 ; P_1^1 and P_2^2 small, P_1 single rooted and P_2 double rooted but with roots close together; P_3^3 premolari-form; P_4^4 premolariform to semi-molariform and as large as molars; molars decreasing in size from M_1^1 – M_3^3 ; extremely reduced cingula on both upper and lower molars; paracone larger than metacone on upper molars, paracone and metacone close together; no hypocone; trigonid of lower molars low crowned; talonid trenchant between hypoconid and small entoconid on M_1 and M_2 , no entoconid on M_3 ; mental foramina below posterior end of P_2 and below posterior end of P_3 ; abruptly slanted, large coronoid process with deep masseteric fossa; articular process of mandible transversely wide and rolled into a semi-cylindrical shape; angular process incurved and strongly developed; entepicondylar foramen present on humerus, large deltoid crest; third trochanter present on femur; pes with five metatarsals and no fusion of tarsals.

DESCRIPTION AND DISCUSSION: The preceding descriptive characters are modified from Peterson (1919) and Stock (1933) with a few additions. In several cases characters are known from material available for only one species and could become diagnostic for only that species if conflicting characters are later discovered in other species of *Simidectes*. The large number of common characters shared by specimens referred to

¹ *Pleurocyon* is a preempted name; hence by Article 23e of the International Code (1961) *Simidectes*, proposed as a subgenus of *Pleurocyon* by Stock (1933), is the valid generic name and by Article 50b is attributable to Stock. As shown on a succeeding page there is no subgeneric distinction between *Pleurocyon* (*Pleurocyon*) and *Pleurocyon* (*Simidectes*).

² *Pleurocyon* Mercerat, 1917, is, according to Kraglievich (1948), referable to *Theriodictis*, which Kraglievich believed to be a subgenus of the genus *Canis*.

TABLE 1
MEASUREMENTS (IN MILLIMETERS) OF THE LENGTHS OF LOWER PREMOLARS AND
LOWER MOLARS IN *Simidectes*

| | P ₁ | P ₂ | P ₃ | P ₄ | M ₁ | M ₂ | M ₃ |
|--------------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|
| L.A.C.M. No. 935 | 3.3 | 6.0 | 9.6 | 11.3 | 10.5 | — | 6.8 |
| L.A.C.M. No. 1208 | 3.5 | 6.9 | 9.7 | 12.3 | 10.3 | 10.2 | 7.3 |
| L.A.C.M. No. 1228 | — | 5.8 | 8.3 | — | — | 11.0 | — |
| L.A.C.M. No. 150/ | — | — | — | — | 11.0 | — | — |
| L.A.C.M. No. 938 | — | — | — | 11.1 | 11.1 | 9.7 | — |
| L.A.C.M. No. 940 | — | — | 9.3 | 10.4 | 10.6 | — | — |
| L.A.C.M. No. 936 | — | — | 10.6 | 11.5 | 10.1 | 8.8 | — |
| L.A.C.M. No. 1358 | 4.6 | — | 9.4 | 11.6 | 10.9 | — | 6.6 |
| L.A.C.M. No. 1139 | — | — | 9.2 | 11.5 | 11.1 | 10.1 | 6.6 |
| U.C.M.P. No. 83680 | | | | | | | |
| Right side | — | — | 8.4 | 10.1 | 11.0 | 9.6 | — |
| Left side | — | — | — | — | 11.2 | — | — |
| U.C.M.P. No. 83681 | — | — | — | — | — | 9.9 | — |
| U.C.M.P. No. 83682 | — | — | — | — | — | — | 6.4 |
| U.C.R. No. 14110 | — | — | — | — | 11.2 | — | — |
| U.C.R. No. 14111 | — | — | — | — | — | 10.0 | — |
| C.M. No. 2928 | — | — | 7.6 | — | 9.5 | 8.4 | — |
| C.M. No. 3006 | — | — | — | 10.5 | — | — | — |
| A.M.N.H. No. 1966 | — | — | — | — | 8.3 | — | — |
| P.U. No. 14657 | — | — | — | — | — | 7.9 | — |
| K.U. No. 16114 | — | — | 9.4 | — | — | 8.2 | — |

this genus and the relatively few features distinguishing the species (see below, especially the similarities between *Simidectes medius* and *S. merriami*) make the division of *Simidectes* into subgenera unnecessary, and they are accordingly abandoned here.

Measurements of upper and lower teeth and the jaws of known *Simidectes* specimens are included in tables 1–5. The measuring procedures used follow those of Mac Intyre (1966, pp. 126–127) with the following modifications: (1) measurements were made to the closest 0.1 mm.; (2) premolar lengths include the measurement of labial length of P⁴; a lingual length for P⁴ and a P⁴ metastyle measurement are not included because the tooth is not a carnassial; (3) as M₃ has no entoconid the posterior molar width for this tooth is the maximum talonid width; (4) the talonid length for the lower molars was taken to be the distance from the most posterior edge of the tooth to the junction of the cristid obliqua with the trigonid, but in worn teeth this measurement was only approximate; (5) the jaw depth was invariably taken below M₁; (6) because the upper molars have no hypocone, the anterior and posterior upper molar

widths were taken respectively from parastyle to protocone and from metastyle to protocone; (7) premolar width, grind widths, shear length, and angle γ were omitted.

Lower incisors are known only in L.A.C.M. No. 1358, an old individual judged from the extreme wear on all its teeth. All three incisors are small and peglike, increasing in size from I_1 to I_3 . They are closely crowded and procumbent and most worn on the tips. All three lower incisors seem to be slightly labiolingually compressed; this compression

TABLE 2
MEASUREMENTS (IN MILLIMETERS) OF THE LENGTHS OF UPPER PREMOLARS AND
UPPER MOLARS IN *Simidectes*

| | P ¹ | P ² | P ³ | P ⁴ | M ¹ | M ² | M ³ |
|--------------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|
| L.A.C.M. No. 1211 | | | | | | | |
| Right side | 3.8 | 4.6 | 9.3 | 10.4 | 9.4 | 6.9 | 4.5 |
| Left side | — | 4.5 | 9.5 | 10.5 | 9.3 | 7.3 | 5.2 |
| L.A.C.M. No. 1212 | — | — | 8.5 | 11.1 | 9.2 | 7.7 | — |
| P.U. No. 11317 | — | — | — | — | — | 5.8 | 5.1 |
| L.A.C.M. No. 927 | | | | | | | |
| Right side | — | 4.9 | 10.3 | — | — | 8.5 | 5.5 |
| Left side | — | 4.8 | 9.5 | — | — | 9.2 | 5.4 |
| U.C.M.P. No. 83752 | — | — | — | 9.9 | — | — | — |
| K.U. No. 16114 | — | — | 8.6 | — | — | — | — |

is most noticeable on I_2 and I_3 on the left side. On I_3 there is a slight posterior and lingual cingulum, which ends posterolabially in a tiny basal cusp.

The only upper incisor of *Simidectes* known is a right I^3 of L.A.C.M. No. 927, but the roots for I^1 and I^2 in this specimen prove that all three upper incisors were originally present. There is a wear surface on the tip of I^3 and another oval-shaped one on the lingual surface where I_3 probably rubbed against it. A cingulum passes along the posterior and lingual base of I^3 .

Between the upper canine and I^3 is a diastema, which allowed reception of the lower canine when the mouth was closed. A ridge from I^3 posterodorsally onto the maxillary and then ventrally to the antero-lateral border of the canine delineates the area that received the tip of the lower canine.

As recorded in the generic diagnosis, both upper and lower canines are recurved and transversely compressed. The enamel of most *Simidectes* canines (and the enamel of some of its other teeth also) shows fine crenu-

lations. Both upper and lower canines may have a very shallow groove posterior to a small ridge running from base to tip along the antero-lingual surface of the tooth.

The first and second upper premolars are simple peglike teeth in both upper and lower jaws, but the second premolar is slightly larger than the first. In the lower jaw both P_1 and P_2 have small lingual cingula. P_2 has an incipient talonid cuspid. In the upper jaw P^2 has a small lingual cingulum.

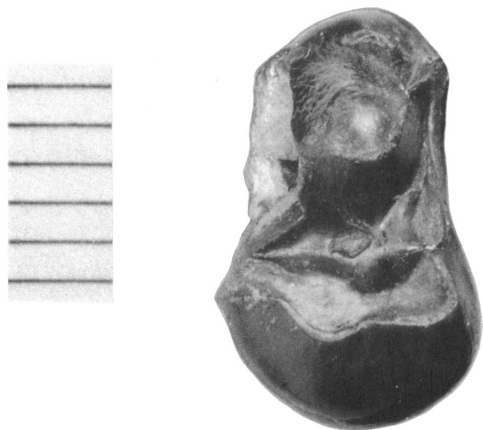


FIG. 1. Upper molar (? M^1) of C.M. No. 3006, paratype of *S. magnus*, from the Myton Member of the Uinta Formation, Uintan. Posterolabial surface (upper left) is broken. Each scale division equals 1 mm. $\times 5$.

The degree of molarity of the third and fourth premolars is described in the preceding diagnosis according to the criteria of Szalay (1969a, p. 199). P_3 has a protoconid and an elongated, single-cusped talonid. Differences in P_3 and P_4 among the three species will be discussed under species characteristics. P^4 is the most molariform of the premolar teeth, having well-defined metacone, protocone, and parastyle, although the paracone is by far the best developed cusp. On P^3 there is a small metacone and parastyle, and the protocone is variably developed in different specimens, appearing on a well-defined lingual cingulum.

The reduction of molar cingula is particularly great on the upper molars. Stock (1933) stated that the upper molar (the only upper tooth known, see fig. 1) of C.M. No. 3006, the paratype of *Simidectes magnus*, has an ectocingulum, but this statement is somewhat misleading. The remaining labial surface of this broken tooth is barely differentiable from

a similar part of an upper molar of *S. merriami* and has little more of a cingulum. The unbroken labial surface of this tooth is the anterior surface, not the posterior surface as was stated by Peterson (1919, p. 53).

A paraconule and metaconule are present on both M^1 and M^2 but appear to be lacking on M^3 . Similarly the small parastyle and the metacone decrease in size from M^1 to M^3 until there is barely a sign of them on M^3 . Although the upper molars have no hypocone, the metaconule has the approximate position of a hypocone on M^1 and M^2 , but it is not on a cingulum. The protocone of M^1 and M^2 has a labial slant.

The lower molars are narrow compared to their lengths (greatest width three-fourths or less the length in 28 out of 29 lower molars measured and two-thirds or less in 25 out of 29). The talonids of all three lower molars are narrower than the trigonids. The morphology of the trigonid is of great interest. The protoconid is the tallest cusp of the trigonid, but it is only slightly taller than the metaconid and is almost directly medial but slightly posterior to it. The paraconid is greatly reduced compared to the protoconid and metaconid and is in a central position at the anterior border of the lower molar. On M_1 and M_2 the paraconid is a low twinned or indistinct cusp. On M_3 the paraconid may be a distinct low cusp, but in several specimens, for example L.A.C.M. No. 935, there are in place of the single paraconid at least two tiny indistinct cusps in a circle around the border of the tooth anterior to both protoconid and metaconid. On both upper and lower molars the cusps are low and blunt even on comparatively unworn specimens. These cusps present very little area for orthal shear.

The large coronoid process, deep masseteric fossa, and well-developed angular process suggest that the temporalis, masseter, and internal pterygoids were important chewing muscles. The mechanism of action of these muscles and their sizes relative to each other is not precisely known and might be profitably studied in a project dealing with mandibles of a number of carnivorous, omnivorous, and herbivorous mammals. The transversely wide semi-cylindrical condyle of the lower jaw mentioned earlier is approximately at the level of the tooth row when the tooth row is held horizontal, and it is not set off on a neck from the rest of the mandible.

The anterior part of the skull is preserved in two specimens, L.A.C.M. No. 927 and L.A.C.M. No. 1211, but both are distorted by crushing. The internal nares are approximately medial to M^3 . The palate slants antero-dorsally from the tooth row and has at least two longitudinal ridges on its surface. The anterior palatine foramina are large and are postero-medial to I^3 and about 2 mm. from the midline. The orbital part of the

palatine is not known in either specimen, nor are the pterygoids and lacrimals, for the skulls are cut off posteriorly at approximately the level of the orbits.

The premaxillaries are fused in the midline. The diastema between I^3 and the upper canine was described along with these elements of the upper dentition. In the maxillaries the infraorbital foramen is large



FIG. 2. Anterior view of snout of L.A.C.M. No. 927 showing left and right broken canines and right I^3 . Specimen is from Locality 150, Sespe Formation, Duchesnean. Snout is distorted due to crushing, but dorsoventral elongation of nasal passage is evident. Small scale divisions are in millimeters. $\times 0.9$.

and is above M^1 (the infraorbital foramen is easily distinguishable only in L.A.C.M. No. 1211 and even here is distorted in shape because of crushing). The boundary between the maxillaries and the nasals is well above the canines and not far from the middorsal line of the snout. The posterior termination of the nasals by the frontals is difficult to determine but appears to be posterior to the infraorbital foramen and anterior to the orbit. The snout is large and appears to be dorsoventrally increased in size by a middorsal ridge (fig. 2) running longitudinally along the top of the snout. No frontals are preserved in *Simidectes* except in L.A.C.M. No. 1211 where only the anterodorsal part of these bones remains. Here the frontals are flattened between the orbits and are surrounded both posteriorly and laterally by a thickened ridge of bone (see fig. 3). The entire flattened area has a shieldlike outline. The function of the flat-

tened area is uncertain, but the posterolateral ridges could have been continuous with a sagittal crest if one existed in *Simidectes*. The existence of a sagittal crest cannot be ascertained because the dorsal part of the skull posterior to the orbits has not been preserved. The posterolateral ridges of the frontal bone referred to here have been partially recon-



FIG. 3. Dorsal view of antorbital portion of skull of L.A.C.M. No. 1211 from Locality 150, Sespe Formation, Duchesnean, showing flattened frontal bones between orbits and posterior and lateral ridges around flattened area. Small scale divisions are in millimeters. $\times 0.9$.

structed with plaster in this specimen so that the exact dimensions may not be represented, but the flattened shieldlike area was an actual structure with approximately the outlines shown.

Only two *Simidectes* specimens retain any material posterior to the orbits, and this material is limited. K.U. No. 16114 has two glenoid fossae and L.A.C.M. No. 927 a fragmentary squamosal and alisphenoid and possibly a mastoid (see fig. 4). The glenoid fossa is almost entirely lateral to the external auditory meatus and mastoid process. The pre-glenoid and postglenoid processes are both well developed, though the latter is thicker than the former. The strong development of these processes is particularly visible on L.A.C.M. No. 927 and must have restricted



FIG. 4. Fragmentary squamosal and alisphenoid of L.A.C.M. No. 927 from Locality 150, Sespe Formation, Duchesnean. Ventral view with anterior at top. Small scale divisions are in millimeters. $\times 0.9$.
Abbreviations: AS, alisphenoid-squamosal suture; EAM, external auditory meatus; GF, glenoid fossa; MP, mastoid process; SM, suprameatal fossa.

fore-aft movement of the mandible. From preglenoid process to postglenoid process the glenoid fossa is gently curved (this shape is more obvious in L.A.C.M. No. 927 than in K.U. No. 16114, largely because of the breakage of the postglenoid process in the latter). The glenoid fossa appears to be on the same frontal plane as the ventral surface of

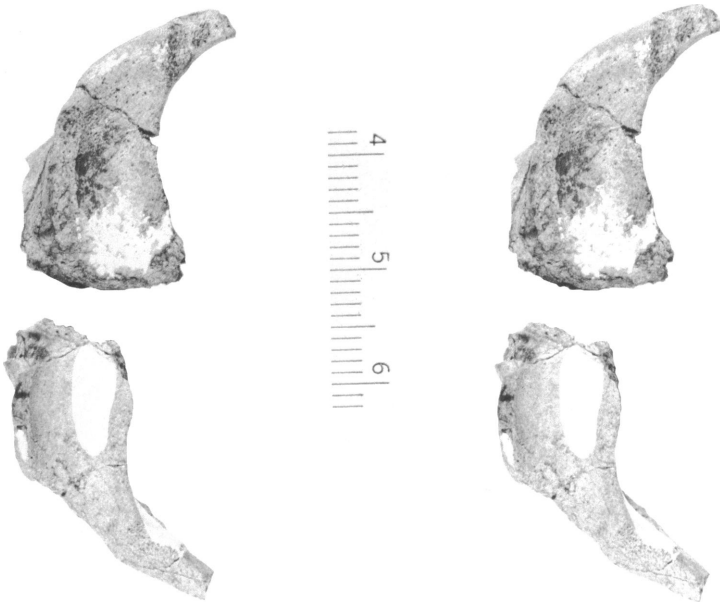


FIG. 5. Ventral view of glenoid fossae of K.U. No. 16114 from Wagonhound Member of the Uinta Formation, Uintan, with right fossa uppermost. Anterior is at the right of the figure. Postglenoid process is broken on both sides. Postglenoid foramen is visible on the right fossa just posterior to postglenoid process. Small scale divisions are in millimeters. $\times 1.5$.

the basicranium (i.e., the condyle is not dependent). In both specimens the glenoid fossa is broken off medially, but in each the Glasserian fissure may be seen medial to and not perforating the postglenoid process. The chorda tympani probably passed through the Glasserian fissure and then almost directly anteriorly along a groove in the squamosal. In L.A.C.M. No. 927 the suture of the alisphenoid with the squamosal runs nearly parallel and approximately 4 mm. medial to the Glasserian fissure. Just lateral to the Glasserian fissure is the postglenoid foramen, fully preserved only on the right side of K.U. No. 16114 (see fig. 5). The postglenoid foramen is of moderate size and perforates the posterior

surface of the postglenoid process, slightly dorsal to the plane of the glenoid fossa.

The dorsal parts of the squamosal are missing, and therefore the border with the parietal cannot be delineated. Posteriorly the squamosal is probably closely appressed onto the mastoid, but sutures are not visible above the mastoid process or crossing the external auditory meatus. The mastoid process is moderately developed but is not enlarged. It is not large enough to constrict the auditory meatus, which is laterally short. An unusual feature in *Simidectes* is a suprameatal fossa posterodorsal to the lateral end of the external auditory meatus and anterodorsal to the mastoid process. The fossa excavates the mastoid process and is quite similar in location and size to that in modern procyonids such as *Potos* and *Nasua*. No counterpart for this structure was seen in any Paleocene or Eocene mammals examined.

Only the lateral part of the alisphenoid is present in L.A.C.M. No. 927. The anteromedial part containing the foramen ovale is missing. Just medial to the alisphenoid-squamosal suture is a depression in the alisphenoid bone possibly for the inferior ramus of the stapedia artery running forward to the alisphenoid canal. The inferior ramus of the stapedia artery could also have run through the Glasserian fissure in company with the chorda tympani. The groove for the chorda tympani is sufficiently large to have housed both the artery and the nerve. Just medial to the above described depression in the alisphenoid the ventral surface of the skull is broken off and the external surface of the alisphenoid can no longer be traced. However, dorsal to the break the alisphenoid can be traced into the brain cavity. A longitudinal groove running just dorsal to the ventral surface of the alisphenoid and separated from the brain cavity by a lamina appears to end anteriorly in the area of the foramen ovale. Several additional small grooves on the internal walls of the braincase are probably for cerebral arteries.

The postcranial material of C.M. No. 3006 was described by Peterson (1919) and is the only postcranial material known to be associated with *Simidectes* cranial material. Most of the postcranial material of C.M. No. 3006 is so badly crushed that little more information can be extracted from it than Peterson originally gave. Among the Los Angeles County Museum material collected from Locality 150, Pearson Ranch, are a number of well-preserved limb bones which according to size criteria could be referable to *Simidectes*. However, each of these bones has its own specimen number, and none of these numbers corresponds with the numbers of specimens known from cranial material. Judged from the humeri, of which ten specimens are available, two or possibly

three different kinds of animals are represented. Several humeri have a strong deltoid crest and well-developed supinator crest. Others have a weak to moderate deltoid crest and weak supinator crest. Both kinds have an entepicondylar foramen. Other limb bones in the collection also indicate more than one kind of animal, but differences are less obvious. Comparison of limb bones from Locality 150 (particularly the humeri) with bones of C.M. No. 3006 yields no unequivocal impression of which bones represent *Simidectes*. No unassociated humeri correspond exactly to the humerus of C.M. No. 3006, but those humeri with strong deltoid and supinator crests are closest and may in fact be referable to *Simidectes*. The humeri with weaker deltoid and supinator crests possibly belong to hyaenodonts of the Pearson Ranch fauna (see Stock, 1948). At any rate the solution to the problem of what material represents *Simidectes* requires a careful study of the Pearson Ranch fauna as a whole, a project which is beyond the scope of this paper.

Simidectes magnus (Peterson, 1919)

Pleurocyon magnus PETERSON, 1919, p. 52.

Petersonella magna: KRAGLIEVICH, 1948, p. 162.

TYPE: C.M. No. 2928, fragmentary left mandible with P_3 - M_2 in place (P_3 and P_4 are broken) and roots for C, P_1 , P_2 , and M_3 (see fig. 6).

PARATYPE: C.M. No. 3006, fragment of right maxilla with jugal, right mandible with canine in place, isolated upper and lower teeth and tooth fragments, postcranial fragments including some limb bones and a semi-complete right pes.

?REFERRED SPECIMEN: K.U. No. 16114, fragmentary left mandible with M_2 in place, part of right mandible with P_3 , isolated P^3 , glenoid fossae of skull (fig. 5).

TYPE LOCALITY: Six miles southeast of Myton, Uinta County, Utah.

HORIZON: Uinta Eocene, "horizon C, near base" (horizon of type specimen as given by Peterson, 1919) and ?"horizon B" (reported horizon of K.U. No. 16114).

SPECIFIC DIAGNOSIS: Intermediate in size between *Simidectes medius* and *S. merriami*; canines more transversely compressed than in *S. merriami*; P_3 with a small cuspid anterior to the protoconid and separated from it by a furrow; P_4 with a lingual ledge (?entocingulid) on the talonid, P_3 with a comparable but smaller ledge; ectocingulum on the only known upper molar (fig. 1) slightly more developed than that of *S. merriami* but barely distinguishable; metaconule on upper molar larger and more lingually



FIG. 6. Left, occlusal view of C.M. No. 2928, the type of *S. magnus*, a left ramus. Right, occlusal view of isolated P_4 of C.M. No. 3006, the paratype of *S. magnus*. Both specimens are from the Myton Member of the Uinta Formation, Uintan. Small scale divisions are in millimeters. $\times 1.5$.

located than in *S. medius* or *S. merriami*, has the approximate position and probable function of a hypocone.

DISCUSSION: K.U. No. 16114 is provisionally referred to *S. magnus* by virtue of its size (see table 1) and the morphology of P_3 , although it could well fall into *S. medius*. The specimen has no P_4 or upper molars preserved. If referable to *S. magnus* the University of Kansas specimen extends the range of the species downward to the "Uinta B horizon" (Wagonhound Member of the Uinta Formation).

Simidectes medius (Peterson, 1919)

Pleurocyon medius PETERSON, 1919, p. 59.

Petersonella media: KRAGLIEVICH, 1948, p. 162.

TYPE: A.M.N.H. No. 1966 [A.M.N.H. No. 1966 is without doubt the



FIG. 7. Lateral and occlusal views of A.M.N.H. No. 1966, the type of *S. medius*, a partial right ramus with M_1 in place, from the Wagonhound Member of the Uinta Formation, Uintan. Small scale divisions are in millimeters. $\times 1.5$.

specimen erroneously reported by Peterson (1919) as A.M.N.H. No. 1969. A.M.N.H. No. 1969 is, according to American Museum records, the skull and foot bones of ?*Triplopus*, a rhinocerotoid.], fragmentary right ramus of mandible with M_1 in place (see fig. 7).

PARATYPE: A.M.N.H. No. 1992, fragmentary right ramus and very incomplete postcranial material.

REFERRED SPECIMENS: P.U. No. 11317, left and right maxillary fragments with M^2 and M^3 on both sides and part of M^1 on the left side

(see fig. 8), various cranial and postcranial fragments; P.U. No. 14657, left ramus with M_2 .

TYPE LOCALITY: White River pocket, Utah.

HORIZON: Uinta Eocene, "horizon B."

SPECIFIC DIAGNOSIS: Smaller species than *Simidectes magnus*; M^3 less reduced compared to M^2 than in *S. merriami*; ectocingula on upper molars



FIG. 8. Occlusal view of left maxillary fragment of P.U. No. 11317 from the Wagonhound Member of the Uinta Formation, Uintan, referred to *S. medius*, showing M^2 , M^3 , and roots of M^1 . Small scale divisions are in millimeters. $\times 1.5$.

similar to *S. magnus*, slightly more developed than in *S. merriami*; metaconule labial to, and much smaller than, protocone as in *S. merriami*.

DISCUSSION: No lower premolars are known for *Simidectes medius*. For this reason the species cannot yet be diagnosed according to the criteria of P_3 and P_4 used to separate *S. magnus* from *S. merriami*.

Peterson (1919) did not specifically designate a type for *Simidectes medius*, but he implied (p. 59) that the type and paratype were as above. In my opinion Peterson should not have named the species *S. medius* for the incomplete material he described from the White River pocket, "Uinta B." Resolution between *S. medius* and *S. magnus* was inadequate because of the small sample size and the absence of known morphological distinctions between these species.

Recently additional specimens of *Simidectes* were found among the Uinta materials of Princeton University. These specimens are all from the White River pocket of the Uinta Basin, "Uinta B horizon." P.U. No.

14657 is even smaller than the type of *S. medius*, whereas the upper molars of P.U. No. 11317 are smaller than the only known upper molar of *S. magnus* and have a more labially positioned metaconule. If these two specimens are referred to *S. medius*, the species then consists of animals differing from both *S. magnus* and *S. merriami* in smaller size and details of dental morphology. Both *S. medius* and *S. magnus* are still incompletely known, and considerable discussion is possible concerning their separation. They are regarded here as separate species. The morphological differences between *S. medius* and *S. merriami* (diagnosed below) are small, but significant differences in size are sufficient to insure classification into two species. Because *S. medius* shares characteristics of both *S. magnus* and *S. merriami* it may be ancestral to both.

Simidectes merriami Stock, 1933

Pleurocyon (*Simidectes*)¹ *merriami* Stock, 1933, p. 481.

TYPE: L.A.C.M. No. 1139, left mandibular ramus with C, P₃-M₃ (figured in Stock, 1933, p. 483).

PARATYPE: L.A.C.M. No. 1212, maxillary fragment with C, P⁴-M² (see fig. 9).

REFERRED SPECIMENS: L.A.C.M. No. 934, right ramus of mandible; it has since been reconstructed with L.A.C.M. No. 1208, a left mandibular ramus which is similar to it in dimensions and is probably part of the same individual (figs. 11, 13, and 14); L.A.C.M. No. 1211, antorbital part of skull with P²-M³ on right side, C-M³ on left side (figs. 3, 10); L.A.C.M. No. 1228, fragmentary left ramus with C, P₂-M₁; L.A.C.M. No. 940, left partial ramus with C, P₃-M₁; L.A.C.M. No. 935, right partial ramus with C-M₁, M₃ (figs. 11, 12); L.A.C.M. No. 936, right partial ramus with C, P₃-M₂ (fig. 10); L.A.C.M. No. 938, partial right ramus with P₄-M₂; L.A.C.M. No. 1358, left and right partial rami with I₁-C on both sides and all teeth through M₁ present on one side or the other; L.A.C.M. No. 927, antorbital part of skull having right I³, left canine, and on both sides P²⁻³ and M²⁻³ (fig. 2), partial squamosal and alisphenoid (fig. 4); additional more fragmentary Los Angeles County Museum material including possible postcranial material; U.C.R. No. 14111, a right M₂; U.C.R. No. 14110, a right M₁; U.C.M.P. No. 83680, left mandible with M₁, right fragmentary mandible with P₃-M₂ and erupting canine (figs. 11, 12); U.C.M.P. No. 83681, a left

¹ In a plate legend Stock (1933, p. 482) used the term *Pleurocyon* (*Sespecyon*) *merriami* in referring to the illustrated material, which included the specimen he had just named the type of *P. (Simidectes) merriami*. Since the subgenus name *Sespecyon* appears nowhere in his text, it is here considered to be a *nomen nudum*, not to be applied to *Simidectes*.

M₂; U.C.M.P. No. 83752, a left P₄; and U.C.M.P. No. 83682, a left M₃.

TYPE LOCALITY: North of Simi Valley, Ventura County, California, Locality 150 (of California Institute of Technology), Pearson Ranch.

HORIZON: Sespe Formation, Duchesnean, latest Eocene (horizon of

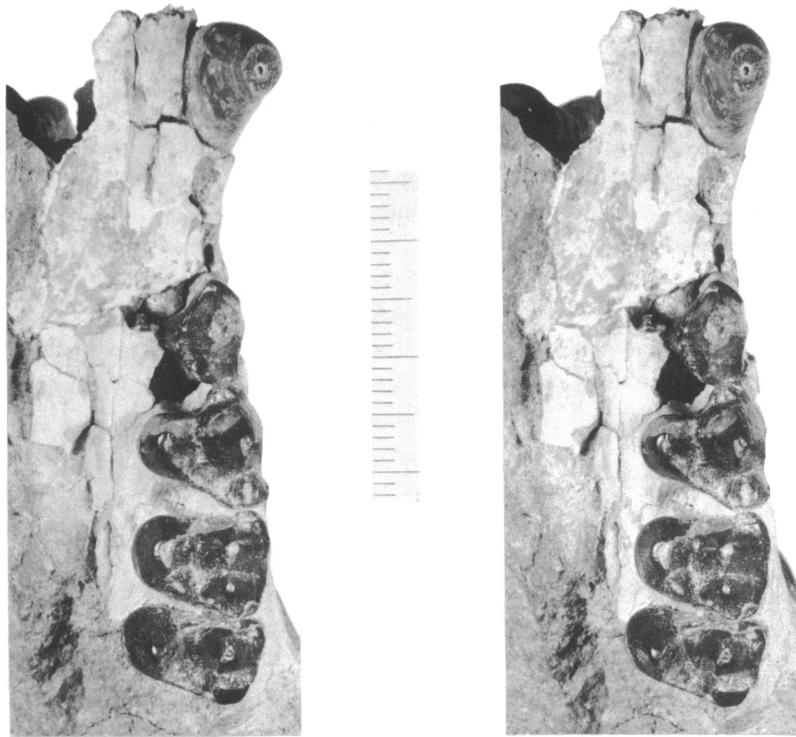


FIG. 9. Occlusal view of L.A.C.M. No. 1212, the paratype of *S. merriami* from Locality 150, Sespe Formation, Duchesnean, showing canine and P₃-M₂. Small scale divisions are in millimeters. $\times 1.5$.

type and other Locality 150 specimens); "Carlsbad [California] unnamed formation" of Waters (ms) and David J. Golz (personal commun.), ?Uintan (horizon of material from the University of California, Berkeley and Riverside).

SPECIFIC DIAGNOSIS: Largest species of *Simidectes*; no development of ectocingula on upper molars; metaconule of upper molars small and less lingual in location than the metaconule in *S. magnus*; P₃ with no small cuspid anterior to the protoconid; P₃ and P₄ with only hypoconid on the talonid and no lingual ledge.

DISCUSSION: Although the referred specimens differ somewhat from each other in the depth of the jaw relative to the size of the teeth, a variation due probably to age and possibly also to the sex of the individuals, they have no significant morphologic distinctions and are hence assigned to a single species. Specimens of *Simidectes merriami* may have a variably developed small cuspid anterior to the protoconid of P_4 , contrary to Stock's diagnosis of the species.

The teeth of specimens from the lower (probably Uintan) horizon are slightly smaller than those of most specimens from Locality 150. The variation is, however, considered to be within the range of a single species.

STRATIGRAPHY

The stratigraphy of beds from which *Simidectes* specimens have come is still incompletely known. The type locality of *S. magnus* is in the Myton Member of the Uinta Formation ("Uinta C") and stratigraphically higher, according to Wood et al. (1941), than the White River pocket (type locality of *S. medius* and locality of the Princeton University specimens of *S. medius* collected by Hatcher), which is in the Wagonhound Member ("Uinta B"). K.U. No. 16114, collected by Dr. Robert W. Wilson, was considered by him to be from beds in the Wagonhound Member by lithologic and color evidence. The specimen itself is quite similar to *S. magnus*, known otherwise only from the Myton Member, but it could be referable to *S. medius*.

Locality 150 of the Sespe Formation was considered by Wood et al. (1941, p. 10) to be correlative with the Duchesne River Formation of northeastern Utah and thus of Duchesnean (latest Eocene) age. Locality 150 is the latest occurrence of *Simidectes* known. The *Simidectes* specimens at the University of California, Berkeley, and the University of California, Riverside, are from localities V-6839 and V-6830 respectively at Laguna Riviera, San Diego County, California. The fauna of the "Carlsbad unnamed formation" at Laguna Riviera is currently under study by students at these institutions, but according to Waters (ms) and Golz (personal commun.) it is probably of Uintan age and thus earlier than the fauna from Locality 150. Exactly how the beds at Laguna Riviera correlate with strata in the Uinta Basin is as yet uncertain.

TOOTH OCCLUSION AND MASTICATION

Although both Peterson and Stock homologized the cusps of *Simidectes* teeth with those of *Vulpavus*, *Oodectes*, and other miacids, apparently no one has occluded the teeth to discover how the animal really chewed.

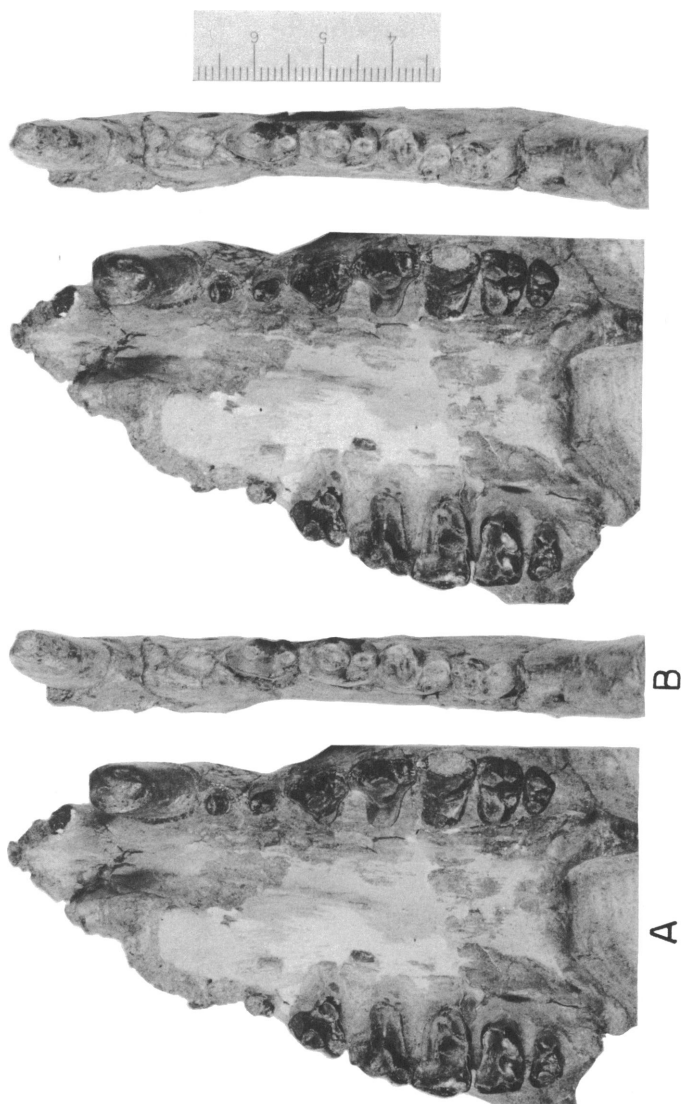


FIG. 10. Occlusal views. A. L.A.C.M. No. 1211. B. L.A.C.M. No. 936, showing wear surfaces. Both specimens are from Locality 150, Sespe Formation, Duchesnean. The right teeth (p^3 - M^3) of L.A.C.M. No. 1211 were compared with L.A.C.M. No. 936, a right ramus, in a study of occlusal relationships. Small scale divisions are in millimeters. $\times 0.9$.

Although small shear facets are present on the teeth, the cusp tips of both premolars and molars are first worn.

Among the specimens of *Simidectes merriami*, L.A.C.M. No. 1211, an upper jaw, and L.A.C.M. No. 936, a right lower jaw, occlude quite closely and have approximately the same degree of wear. They suffice for a study of occlusal relationships (see fig. 10). In the lower jaw the canine and P_3 - M_2 are in place, and there are alveoli, for P_1 , P_2 , and M_3 . On the right side of L.A.C.M. No. 1211 P^2 - M^3 are in place.

The anterior lingual surface of the paracone of P^3 has a worn groove through which the posterior worn surface of P_3 slides as the jaw opens and closes. The talonid of P_3 and the tip of the paracone of P^3 are worn as they occlude with each other.

The prevallum surfaces of P^4 , M^1 , and M^2 are worn transversely before any other surface of these teeth is worn (note L.A.C.M. No. 1212, the paratype of *S. merriami*, which has less worn teeth than those presently under discussion). On P^4 this surface is apparently worn by contact with the tip and posterior slope of the protoconid of P_4 . On M^1 and M^2 the prevallum wear surfaces are formed by occlusion with the postvallids of M_1 and M_2 respectively. In a young individual the wear surfaces mentioned above are the only ones in evidence because the embrasure between the upper molars is small and the trigonid cuspids of M_1 and M_2 (and the protoconid of P_4), all moderately tall, are braked by the anterior surface of the opposing upper tooth (where the wear surfaces are found). As the trigonids become more worn the talonids of P_4 , M_1 , and M_2 (and to some degree the prevallids of M_1 and M_2) begin to grind against a transverse area along the posterior surfaces of P^4 , M^1 , and M^2 respectively. Eventually, as wear continues, the cusps of P^4 , M^1 , and M^2 are worn down to the level of the rest of the tooth. The anterior surface of the upper molars continues to be slightly more worn than the posterior. Since most of the teeth on specimens of *S. merriami* are worn to this condition it may be that wear to this grinding sort of tooth occurred fairly rapidly during the life of the individual (see figures 9, 10, 11, 12, 13 for teeth showing varying amounts of wear). In early stages, where there is apparently both slight shearing as well as grinding, these actions are not confined to any particular set of teeth that might be designated carnassials, although wear is often greater on P^4 and M^1 and their opposing lower teeth. However, in some specimens the main wear is displaced either slightly anteriorly or posteriorly to these teeth. The small M^3 of L.A.C.M. No. 1211 is worn in at least two places, but since the right M_3 is not in place in L.A.C.M. No. 936 it is difficult to determine how this wear occurred. Because the M_3 protoconid is worn in several specimens,

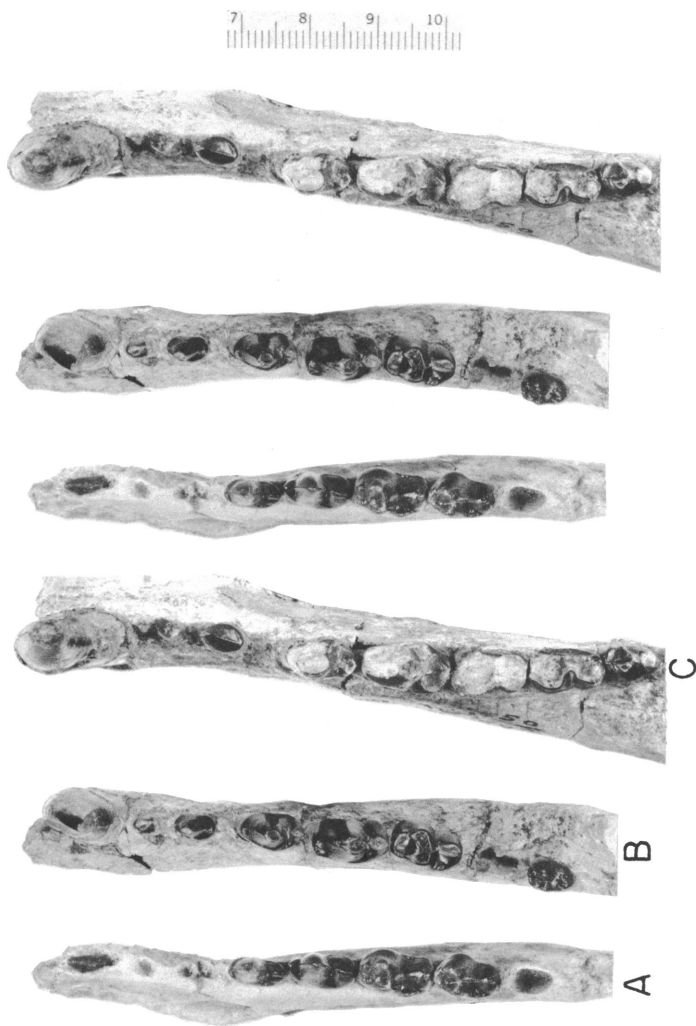
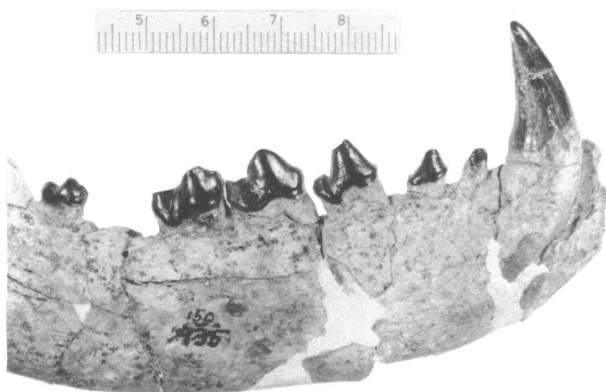


FIG. 11. Occlusal views. A. U.C.M.P. No. 83680, a right ramus from Laguna Riviera, California, "Carlsbad unnamed formation," ?Uintan. B. L.A.C.M. No. 935, a right ramus from Locality 150, Sespe Formation, Duchesnean. C. L.A.C.M. No. 1208, a left ramus from Locality 150. There is progressive tooth wear from A to C. Small scale divisions are in millimeters. 1×0.9 .



A



B

FIG. 12. Lateral views. A. U.C.M.P. No. 83680, Laguna Riviera, "Carlsbad unnamed formation," ?Uintan. B. L.A.C.M. No. 935, Locality 150, Sespe Formation, Duchesnean. Figures 12A, 12B, and 13 are in a series showing progressive tooth wear. Small scale divisions are in millimeters. $\times 0.9$.

it may be responsible for much of the wear on M^3 . The small M_3 of L.A.C.M. No. 935 has tiny wear surfaces on the posterolabial surface of the trigonid and extending onto the talonid which may be caused by shear against the paracone of M^3 before this cusp is worn down.

The fact that there is shear from the paracone to the protocone on the upper molars suggests that *Simidectes* was capable of some ectental chewing motion, since the width of the lower teeth is less than the width of the area worn on the opposing upper teeth. The deep masseteric fossa and the well-developed, incurved angular process on the mandible for the insertion of strong masseter and internal pterygoid muscles (see figs. 13, 14) give further evidence that ectental jaw motion was possible. The



FIG. 13. Lateral view of L.A.C.M. No. 1208, Locality 150, Sespe Formation, Duchesnean, showing tooth wear and the posterior part of the mandible. Small scale divisions are in millimeters. $\times 0.9$.

tall coronoid process and the articular process at the level of the tooth row suggest that the temporalis muscle was large and that orthal jaw movement was also important. The transversely wide, semi-cylindrical articular condyle would have allowed ectental movement, but the preglenoid and postglenoid processes would have prevented propalinal movement of the mandible.

Studies of the chewing mechanisms in recent and fossil mammals



FIG. 14. Posterior view of L.A.C.M. No. 1208, Locality 150, Sespe Formation, Duchesnean, showing the coronoid process, articular condyle, and angular process. Small scale divisions are in millimeters. $\times 0.9$.

(Sicher, 1944; Davis, 1964; Scapino, 1965; Van Valen, 1969; Szalay, 1969b) are helpful for interpretation of mastication in *Simidectes*. A comparison with ursids is particularly illuminating. Although the mandibles of *Simidectes* and *Ursus* are not identical in shape they share many common characteristics, among them a tall coronoid process, deep masseteric fossa, well-developed incurved angular process, and transversely wide, semi-cylindrical articular condyle, not positioned on a neck and at approximately the level of the tooth row. The teeth of each, though morphologically quite different, are used for grinding. *Ursus* has progressed farther than *Simidectes* in increasing the surface area of the molars and reducing the anterior cheek teeth. These developments are in many, though not all, mammals adaptations to an omnivorous mode of life. *Simidectes*, like most early mammals, apparently had an unfused mandibular symphysis. Scapino described the mandibular symphysis of ursids

as fused, whereas Davis considered the symphysis of *Ursus* to be unfused. From my own observations the degree of symphyseal fusion in ursids varies. The mandibles of *Ursus americanus*, A.M.N.H.: C.A. No. 2520 and others, are not totally fused at the symphysis but have much less movable symphyses with greater areal extent than do mandibles of *Simidectes*. The significance of the difference in symphyseal fusion is that in *Ursus* the ectental movement of the jaws is probably more coordinated in both mandibles, whereas in *Simidectes* lateral movement of one ramus could take place without significant side movement of the other ramus. Side movement of the anterior part of the mandible may have been small compared to that of the posterior part.

DISCUSSION

The affinities of *Simidectes* to other early Tertiary mammals are far from obvious. Among the paleontologists who have examined *Simidectes* there are numerous conflicting hypotheses concerning the origin of the animal. I have examined these possibilities and have tried to determine the relationships as far as possible.

MIACIDS: Both Peterson (1919) and Stock (1933) placed *Simidectes* among the miacine miacids and in particular compared it with *Vulpavus*, *Oodectes*, and *Palaeoarctonyx*. In my opinion there is some justification for their having done so, considering the amount of material available to them, but neither *Vulpavus* nor *Oodectes* nor *Palaeoarctonyx* could have been an ancestor of *Simidectes*. Most of my miacid comparisons with *Simidectes* were made using *Vulpavus*, since this genus is well represented by specimens at the American Museum of Natural History. The main similarities between these two genera are: three molars with a decrease in size from M_1^1 to M_3^3 ; lower molar trigonids not tall; no distinct shear developed between the typical carnivore carnassials; some embrasure present between P^4 and M^1 ; lower molars three-fourths or less as wide as they are long; talonid narrower than trigonid; paracone larger than metacone; and a well-developed deltoid crest on the humerus. The presence of an entepicondylar foramen on the humerus, the third trochanter on the femur, and the undifferentiated elements of the pes are not characters that give a clue to miacid affinities, for they are present in a number of other early mammals as well. A similarity between miacids in general and *Simidectes* is the lack of a hypocone. In the upper molars of *Simidectes* there is some tooth squaring but the metaconule is involved, not a hypocone. *Simidectes* differs in several points from *Vulpavus*, among them the trenchant talonids (the talonids of *Vulpavus*, are basined, although those of *Oodectes* are trenchant) and enlarged P_3^3 and P_4^4 . Although *Vulpavus*

lacks the strong P^4 - M_1 shear characteristic of many other miacids it has much more shear between these teeth than does *Simidectes*. In *Vulpavus* the embrasures between P^3 and P^4 , P^4 and M^1 , and M^1 and M^2 are large enough so that shear takes place without much direct occlusion of the primary cusps. There is essentially no development of carnassiality in *Simidectes*, but the size of the embrasure between P^4 and M^1 does not make it impossible for *Simidectes* to have had ancestors with a high M_1 trigonid. However, such ancestors are not necessary. Unlike those of all miacids examined, the upper teeth of *Simidectes* essentially lack styler shelves and cingula; reduction of the ectocingulum is particularly apparent. It is possible for these structures to be lost in evolution but not too likely that they should be lost rapidly from a line which had evolved as long as the Bridgerian Miacidae.

Comparisons of the alisphenoid-squamosal fragments of *Simidectes* with the corresponding portions of miacid skulls can be made also. In miacids the inferior ramus of the stapedial artery, if present, probably does not run in a groove medial to the alisphenoid-squamosal suture but probably does accompany the chorda tympani. The Glasserian fissure is well defined. As described previously, *Simidectes* may have retained the inferior ramus of the stapedial artery, which would have run either through the groove medial to the alisphenoid-squamosal suture or through the Glasserian fissure. In *Simidectes* the alisphenoid-squamosal suture is on an anteroposteriorly oriented prominence. The corresponding area is flat in all the miacids examined except *Vulpavus profectus*, A.M.N.H. No. 12626, where the suture is on a prominence which is not oriented in an anteroposterior direction. Of course many difficulties remain in the comparison of the *Simidectes* ear region. If entire skulls of early mammals are at hand, discrimination between groups may be possible. With only limited material available, however, the task is very difficult, for in many parts of the auditory region differentiation among groups is not yet very great.

The conclusion reached from comparisons of *Simidectes* with miacids is that the original placement of *Simidectes* among the miacids, although not to be wholly discounted, is doubtful. Better reasons can be found for allying *Simidectes* with other groups.

OXYAENIDS AND HYAENODONTIDS: Numerous oxyaenids (*Palaeonictis*, *Patriofelis*, *Oxyaena*, and others) were examined and shown to be not closely related to *Simidectes*. Many of these genera were discussed by Osborn and Wortman (1892), Matthew (1909), Matthew and Granger (1915), Sinclair and Jepsen (1929), and Denison (1938). A striking similarity between *Simidectes* and these animals is the shape of the articu-

TABLE 3
MEASUREMENTS (IN MILLIMETERS) OF ANTERIOR WIDTH AND POSTERIOR
WIDTH OF LOWER MOLARS IN *Simidectes*

| | Anterior Width | | | Posterior Width | | |
|--------------------|----------------|----------------|--------------------|-----------------|----------------|----------------|
| | M ₁ | M ₂ | M ₃ | M ₁ | M ₂ | M ₃ |
| L.A.C.M. No. 935 | 7.0 | — | 4.6 | 5.5 | — | 3.6 |
| L.A.C.M. No. 1208 | 6.7 | 6.6 | 5.9 | 5.6 | 5.1 | 4.1 |
| L.A.C.M. No. 1228 | 6.9 | — | — | 6.3 | — | — |
| L.A.C.M. No. 150/ | 6.2 | — | — | 5.8 | — | — |
| L.A.C.M. No. 938 | 6.2 | 5.9 | — | 5.8 | 5.4 | — |
| L.A.C.M. No. 940 | 6.7 | — | — | 5.3 | — | — |
| L.A.C.M. No. 936 | 7.4 | 5.9 | — | 6.4 | 5.7 | — |
| L.A.C.M. No. 1358 | 6.9 | — | (3.1) ^a | 5.9 | — | 3.9 |
| L.A.C.M. No. 1139 | 6.5 | 6.5 | 4.4 | 5.4 | 5.2 | 3.8 |
| U.C.M.P. No. 83680 | | | | | | |
| Right side | 7.2 | 6.7 | — | 6.2 | 4.8 | — |
| Left side | 6.8 | — | — | 6.0 | — | — |
| U.C.M.P. No. 83681 | — | 6.1 | — | — | 4.5 | — |
| U.C.M.P. No. 83682 | — | — | 4.8 | — | — | 3.1 |
| U.C.R. No. 14110 | 6.1 | — | — | 5.3 | — | — |
| U.C.R. No. 14111 | — | 5.9 | — | — | 5.2 | — |
| C.M. No. 2928 | 5.2 | 5.5 | — | 4.0 | 4.1 | — |
| A.M.N.H. No. 1966 | 4.9 | — | — | 4.3 | — | — |
| P.U. No. 14657 | — | 4.9 | — | — | 4.3 | — |
| K.U. No. 16114 | — | 4.7 | — | — | 4.1 | — |

^a Measurement is approximate.

lar and angular processes of the mandible. The transversely wide, semi-cylindrical articular condyle is admittedly very similar to that found in *Palaeonictis*, *Oxyaena*, and many other oxyaenids. It is, however, also characteristic of modern ursids and to some extent of such omnivorous Carnivora as *Nandinia*, *Nasua*, and *Procyon*. The miacid *Vulpavus* is also quite similar in this respect. No arctocyoniid was seen to have an articular condyle of this type, but in almost all specimens studied this part of the mandible was not preserved. The semi-cylindrical condyle, the well-developed, incurved angle, and other such features are apparently not completely indicative of a phylogenetic relationship nor of a particular way of chewing, but they are probably more indicative of the latter than the former. They are often correlated with a large coronoid process and a deep masseteric fossa. In the case of *Simidectes* the shape of the angular and articular processes (as well as of the glenoid fossa) were probably of more masticatory than phylogenetic significance. Denison (1938, p. 238) suggested that *Palaeonictis* was an indiscriminate feeder with reduced

molar shear. The posterior jaw morphology described could have been an adaptation here to a less strictly predatory mode of life. However, since some highly predaceous oxyaenids had a semi-cylindrical articular condyle this characteristic must have been in some cases either transmitted through phylogenetic lines or adapted to an extremely different mode of life from that of *Simidectes*. *Patriofelis*, while having the semi-cylindrical condyle, combines it with a short, very deep jaw, the mechanics of whose closing must have been very different from that for the long, more

TABLE 4
MEASUREMENTS (IN MILLIMETERS) OF ANTERIOR WIDTH AND POSTERIOR
WIDTH OF UPPER MOLARS IN *Simidectes*

| | Anterior Width | | | Posterior Width | | |
|-------------------|-------------------|----------------|----------------|-----------------|----------------|----------------|
| | M ¹ | M ² | M ³ | M ¹ | M ² | M ³ |
| L.A.C.M. No. 1211 | | | | | | |
| Right side | 12.2 | 10.6 | 7.7 | 12.4 | 10.5 | 7.4 |
| Left side | 12.1 | 10.8 | 7.0 | 13.2 | 10.5 | 6.1 |
| L.A.C.M. No. 1212 | 12.2 | 12.9 | — | 12.7 | 12.6 | — |
| P.U. No. 11317 | — | 10.6 | 8.2 | — | 10.5 | 7.7 |
| L.A.C.M. No. 927 | | | | | | |
| Right side | — | 12.7 | 8.4 | — | 12.0 | 7.5 |
| Left side | — | 12.5 | 9.1 | — | 12.2 | 8.2 |
| C.M. No. 3006 | 10.6 ^a | — | — | — | — | — |

^aNot certain whether this tooth is M¹ or M².

slender *Simidectes* mandible. Another similarity between *Simidectes* and oxyaenids is the closely apposed paracone and metacone on the upper molars, but this characteristic is more extreme in both oxyaenids and hyaenodontids than in *Simidectes*.

Other characteristics preclude an oxyaenid ancestry for *Simidectes*. The size of the embrasure between P⁴ and M¹ of *Simidectes* might admit an ancestor with a high trigonid on M₁, but the spaces between the upper molars are very small. Oxyaenids typically have high trigonids on M₁ and M₂ (the trigonids of *Ambloctonus* are admittedly somewhat lower, but the primary shearing nature of the teeth is still obvious and the metaconid is reduced). The same difficulties apply to hyaenodontids (for example, *Sinopa*), which develop the trigonid of M₃ as a tall shearing surface. Moreover, there is no hyaenodontid with the round-edged molars characteristic of *Simidectes*. Oxyaenids and hyaenodontids are for the preceding reasons eliminated as close relatives of *Simidectes*.

MESONYCHIDS: A comparison of *Simidectes* with even the earliest known

mesonychid, *Dissacus*, indicates that *Simidectes* could not be derived from this group. Although the lower molars of *Dissacus*, particularly the talonids, are narrow like the molars of *Simidectes* (and usually narrower), they suggest a more shearing carnivorous habit. There is already a tendency toward premolarization of the lower molars and to the bulbous sort of teeth so characteristic of *Pachyaena*, *Mesonyx*, and the other mesonychids whose modes of feeding were analyzed by Szalay and Gould (1966). Unlike *Simidectes*, *Dissacus* has the articular condyle of the mandible on a neck. The foot structure even of *Dissacus* is beginning to be specialized to a cursorial mode of life. In *Dissacus* the pes is pentadactyl, but the hallux, though complete, is considerably smaller than the other metatarsals (Matthew, 1937). The tarsus, despite lacking the later mesonychid specializations of astragalus and calcaneum, is narrowed and deepened. The metatarsals are long and compact, the phalanges shortened. *Simidectes magnus* is definitely pentadactyl (although metatarsal V is missing in C.M. No. 3006), and the metatarsals are not elongated. Although metatarsal I is the smallest of the four metatarsals known, the decrease in size appears to be gradual from metatarsal IV to I. The tarsals are unfused and generalized, not unlike those of many condylarths and miacids. It is impossible to tell whether the ungual phalanges of *Simidectes* were fissured, because none is available for study. To put it briefly, *Simidectes* could not be derived from any known mesonychid.

ARCTOCYONIDS: A first glance at the shape of the jaw and the large snout of *Simidectes* suggests arctocyonid affinities. There are few early mammalian carnivores with a mandible as stout and deep as that of *S. merriami*, while the majority of arctocyonids have one that is thicker and deeper. The snout of *Simidectes* has a large opening for the external nares, similar in shape to the narial opening of many arctocyonids. The lower incisors are somewhat procumbent and suggest a browsing or nipping use. The thickened flat area on the frontal bones between the orbits has no counterpart on any arctocyonid examined, but such elaborations are more characteristic of the ungulate suite of mammals in general than of miacids and other carnivores. The principal arctocyonids examined were *Triisodon*, *Goniacodon*, *Eoconodon*, *Oxyclaenus*, *Anacodon*, and *Deltatherium*. In addition, casts of several small arctocyonids (for example, *Arctocyon*) were examined. Illustrations of *Paratriisodon*, an Asiatic contemporary of *Simidectes*, were also checked from the description by Chow (1959). The teeth, particularly the lower molars, of these animals differ in several respects from those of *Simidectes*: M_2 ordinarily larger than M_1 ; lower molars transversely widened, as wide as they are long; talonids as wide as trigonids and typically carrying three cusps; and upper molars

with a cingulum and usually some development of a hypocone (*Triisodon* is unusual in its lack of a hypocone). *Simidectes* is like many arctocyonids in that the paracone is slightly larger than the metacone. The chewing mechanism, however, probably differed greatly between *Simidectes* and arctocyonids. In *Eoconodon*, for example, the primary worn area on the upper molars is lingual to the paracone and metacone and approximately equal in width to the width of the opposing lower molars. Ectental jaw movement was limited, but propalinal grinding did occur, evidenced by anteroposterior lines on the molars which suggest the direction of movement of the teeth against each other.

Comparison of the squamosal and alisphenoid of *Simidectes* with the same bones of A.M.N.H. No. 16329, *Eoconodon heilprinianus*, a triisodontine, was aided by Hunt's (ms) study of the basicranium of *Loxolophus* and *Eoconodon* and Russell's (1964) study of *Arctocyon*. Both similarities and differences between the skulls of *Simidectes* and *Eoconodon* occur. As is the case in *Simidectes* the glenoid fossa in *Eoconodon* is on the zygomatic arch, largely lateral to the rest of the skull. In contrast to that of *Simidectes*, however, the condyle is dependent, that is, the glenoid fossa is on a plane about one-half centimeter ventral to the basicranium. The preglenoid process is missing in *Eoconodon*, and the articular surface for the mandibular condyle is flat, allowing the mandible to move forward and back as previously described, stopped only by the postglenoid process. The glenoid fossa of *Simidectes* is curved, and both preglenoid and postglenoid processes are well developed. The large, tubular postglenoid foramen of *Eoconodon* is on the posterior slope of the glenoid region on approximately the same plane as the rest of the basicranium, not on the same plane as the surface of the glenoid fossa. In *Simidectes* the postglenoid foramen is similar in size and shape to the above but is only slightly dorsal to the plane of the glenoid fossa, which is very close also to the plane of the basicranium. Medial to the glenoid fossa and lateral to the alisphenoid-squamosal suture are two grooves in *Eoconodon*. The more lateral of these grooves (missing in *Loxolophus* and *Arctocyon*, two other arctocyonids known from basicrania) ends anterolaterally on the surface of the glenoid fossa. Its function is unknown. The other, more medial groove is quite deep and runs almost directly in a posterior to anterior line. Probably this groove carries both the chorda tympani and the inferior ramus of the stapedia artery, the latter almost certainly present. The supposed presence of this artery is a similarity to *Simidectes*, where, as discussed in an earlier section, its passage may or may not be in company with the chorda tympani. In *Eoconodon* there is no suggestion of a groove medial to the alisphenoid-squamosal suture. In both *Simi-*

dectes and *Eoconodon* the suture between alisphenoid and squamosal is on a small prominence. The external auditory meatus and mastoid process appear to be quite similar in shape and composition in *Simidectes* and

TABLE 5
MEASUREMENTS (IN MILLIMETERS) OF TRIGONID LENGTH AND TALONID
LENGTH OF LOWER MOLARS AND OF JAW DEPTH BELOW M_1 IN
Simidectes

| | Trigonid Length | | | Talonid Length | | | Jaw Depth |
|--------------------|-----------------|-------|--------------------|----------------|-------|--------------------|---------------------|
| | M_1 | M_2 | M_3 | M_1 | M_2 | M_3 | |
| L.A.C.M. No. 935 | 6.3 | — | 4.3 | 4.1 | — | 2.8 | 24.7 |
| L.A.C.M. No. 1208 | 5.6 | 5.4 | 4.3 | 4.3 | 4.5 | 2.5 | 31.5 |
| L.A.C.M. No. 1228 | 6.9 | — | — | 4.0 | — | — | 25.8 |
| L.A.C.M. No. 150/ | 5.8 | — | — | 4.4 | — | — | 26.3 |
| L.A.C.M. No. 938 | 7.0 | 5.3 | — | 4.4 | 4.3 | — | 32.5 |
| L.A.C.M. No. 940 | 6.0 | — | — | 4.5 | — | — | 23.7 |
| L.A.C.M. No. 936 | 6.7 | 5.2 | — | 3.8 | 3.7 | — | 24.2 |
| L.A.C.M. No. 1358 | 7.0 | — | (3.4) ^a | 4.3 | — | (2.8) ^a | 26.4 |
| L.A.C.M. No. 1139 | 7.0 | 5.6 | 3.7 | 3.9 | 4.5 | 2.9 | 19.7 |
| U.C.M.P. No. 83680 | | | | | | | |
| Right side | 6.3 | 5.2 | — | 4.2 | 4.1 | — | 29.5 |
| Left side | 6.8 | — | — | 3.8 | — | — | 29.7 |
| U.C.M.P. No. 83681 | — | 5.8 | — | — | 3.6 | — | — |
| U.C.M.P. No. 83682 | — | — | 3.7 | — | — | 2.9 | — |
| U.C.R. No. 14110 | 6.3 | — | — | 4.5 | — | — | — |
| U.C.R. No. 14111 | — | 5.7 | — | — | 4.3 | — | — |
| C.M. No. 2928 | 5.6 | 4.8 | — | 3.8 | 3.7 | — | 23.5 |
| C.M. No. 3006 | — | — | — | — | — | — | (23.8) ^a |
| A.M.N.H. No. 1966 | 4.8 | — | — | 2.9 | — | — | 18.9 |
| P.U. No. 14657 | — | 4.8 | — | — | 3.2 | — | 16.3 |
| K.U. No. 11614 | — | 4.4 | — | — | 3.3 | — | (18.4) ^a |

^a Measurement is approximate.

Eoconodon, though unlike *Eoconodon* there is no distinct groove posterior to the mastoid in *Simidectes*.

The pes and limb bones of *Simidectes* could easily belong to an arctocyonid, but they give little positive evidence for a relationship to arctocyonids.

Morphologically there is no convincing evidence against deriving *Simidectes* from arctocyonids. The majority of arctocyonids are Puercan and Torrejonian genera [*Protungulatum*, the earliest known arctocyonid, described by Sloan and Van Valen (1965), is latest Cretaceous], and very few cross the Paleocene-Eocene boundary. Even those that are known to

cross could not be the ancestors of *Simidectes*, for they are all too specialized. It is possible that arctocyonids, particularly triisodontines but possibly oxyclaenines, could have given rise to *Simidectes* or a *Simidectes*-like creature, but this branching would have had to have occurred at least prior to Torrejonian times, millions of years before the first *Simidectes* specimen appears in the fossil record. Prior to Torrejonian times, there were triisodonts capable of giving rise to mesonychids with their reduced talonids and lack of hypocones. If morphologically more similar relatives could not be found for *Simidectes*, arctocyonids might be suitable ancestors. However, since greater similarities between *Simidectes* and another group can be shown (see below), the chance of close relationship between *Simidectes* and arctocyonids is slight.

PAROXYCLAENIDS: There are among early mammals a number of groups whose affinities, like those of *Simidectes*, are still in question. Among these mystery mammals are paroxyclaenids, *Ptolemaia*, and pantolestids (including both pantolestines and pentacodontines). It is worthwhile to examine the affinities of *Simidectes* to these groups.

In a comparison with paroxyclaenids, a cast, A.M.N.H. No. 55956, of the type of *Paroxyclaenus lemuroides* and casts of specimens of genera related to *Paroxyclaenus* (for example, *Russellites*) were particularly useful. Helpful also were discussions by Russell and McKenna (1961) and Van Valen (1965). There are numerous similarities between *Paroxyclaenus* and *Simidectes*. In both, P¹ and P² are small and are probably vestigial teeth. The teeth are low crowned, and the cingula on the molars are greatly reduced. The molars decrease in size from M₁¹ to M₃³. The upper molars are somewhat transversely elongated and have no hypocone. The canines are grooved in both genera, but in *Paroxyclaenus* there are both posterolabial and posterolingual grooves, and these are both better defined than the single anterolingual groove in *Simidectes*. Some important differences between *Simidectes* and *Paroxyclaenus* follow. *Paroxyclaenus* has a diastema between P¹ and P², whereas *Simidectes* has none. On P³ *Simidectes* has the beginning of a metacone, but the protocone is relatively undeveloped. In contrast, *Paroxyclaenus* has a well-developed protocone on P³, but the metacone is barely visible. A similar situation pertains in the case of P⁴, for in *Paroxyclaenus* the tooth has the form of M¹ with large protocone and even a metaconule, but no metacone. The P⁴ in *Simidectes* has metacone, protocone, and parastyle, and the border of the tooth from metacone to protocone is slanted anterolingually, an embrasure occurring between this border and M¹. On the upper molars *Paroxyclaenus* has a larger styler shelf than does *Simidectes*, and the paracone and metacone are farther apart on M¹ and M². In *Paroxyclaenus* the metaconule

is on a straight line between protocone and metacone on M^1 and M^2 , whereas in *Simidectes* the metaconule is posteriorly displaced from this line. On the lower molars the metaconid of *Paroxyclaenus* is not so close in height to the protoconid as it is in *Simidectes*, nor does the paraconid occupy a central position on the anterior border of the tooth. The talonid is basined, not trenchant as in *Simidectes*.

Paroxyclaenids have been compared with many early mammalian groups such as pantolestids, mioclaenine hyopsodontids, and others. On the basis of the evidence given above *Paroxyclaenus* cannot be excluded as a possible relative of *Simidectes*. However, its geographical separation from *Simidectes* and the fact that no paroxyclaenids are known from North America suggests the possibility that the similarities between paroxyclaenids and *Simidectes* could be the result of convergence in two groups of different ancestry. The problem cannot be resolved with the amount of material presently available.

Ptolemaia: *Ptolemaia lyonsi* was first described from the Egyptian Fayum deposits by Osborn in 1908, and since that time affinity has been claimed between it and several other mammalian groups. A history of the genus was recounted by Van Valen (1966), who said he followed Matthew in suggesting relationship to the Pantolestidae. McKenna (personal commun.) places Osborn's Ptolemaiidae within the Pantolestoidea. My comparison with *Simidectes* was based upon A.M.N.H. No. 13269 (the type of *Ptolemaia lyonsi* with P_3 and M_{1-3} in place) and Y.P.M. No. 18117, an undescribed mandible with canine, P_2 , and M_1 in place. Dr. Elwyn L. Simons kindly allowed me to examine the latter specimen, and he will discuss it more fully.

On both specimens of *Ptolemaia* the M_1 is strongly worn on the occlusal surface and comparison with *Simidectes* is difficult. The crown of this tooth in A.M.N.H. No. 13269 is much higher than that of the same tooth in *Simidectes*. Also, the furrows on the sides of the tooth between trigonid and talonid are weaker than in *Simidectes*. The M_2 and M_3 are less worn than M_1 and therefore are more easily interpretable. On these teeth the paraconid does not appear to be reduced or to be placed in the center of the anterior border of the tooth as occurs in *Simidectes* (the M_3 of the type of *Ptolemaia* is broken in this area). On M_3 in *Ptolemaia* the talonid is only about three-fourths as tall as the trigonid, whereas in *Simidectes* the trigonid and talonid are approximately the same height.

Judged from the alveoli, P_4 in *Ptolemaia* was a large tooth. The P_3 , like that of *Simidectes*, is worn on the occlusal surface and slightly posterior to the tips of the cusps. Unlike *Simidectes* there are on P_3 two cuspids posterior to the protoconid. The single small cuspid (or possibly just a cingu-

lum) anterior to the protoconid has a counterpart in *S. magnus*. The two-rooted P_2 in Y.P.M. No. 18117 has both trigonid and talonid and has the same shape as the P_2 of *Simidectes* but is larger compared to P_3 than the *Simidectes* P_2 . The canine, like that of *Simidectes*, is recurved and has crenulations of the enamel. On both *Ptolemaia* specimens there is one mental foramen just anterior to the anterior root of P_3 compared with the two mental foramina of *Simidectes*, one below the posterior root of P_2 and the other below the posterior root of P_3 . The posterior part of the jaw is not well preserved in the *Ptolemaia* specimens, but the degree of slant of the anterior part of the coronoid process is less than in *Simidectes*. A cast of the young specimen referred by Schlosser in 1910 to *Ptolemaia* but almost certainly not referable to this genus was examined and found to have general but not special resemblance to *Simidectes*.

Briefly, *Ptolemaia* does not have enough common characteristics with *Simidectes* to indicate close relationship, and because of the large spatial distance separating the two genera and the fact that no upper teeth of *Ptolemaia* are known one must be careful in interpreting the similarities that do exist. The main similarities are in the general shape of the lower teeth, the type of wear on them, and the shape and enamel of the canines. There is no characteristic known, however, that would make a general relationship between *Ptolemaia* and *Simidectes* impossible.

PANTOLESTIDS: The family Pantolestidae is known from the Paleocene through early Oligocene of Europe, from the late Eocene of Asia, and from the Paleocene through mid-Oligocene of North America. Although the group has a reasonably large degree of uniformity, the various genera within it have numerous differentiating characters, some of which are quite similar to characteristics of *Simidectes* and some of which are not. The genera examined either by specimens, illustrations, or descriptions are as follows: the pentacodontines *Coriphagus*, *Pentacodon*, *Aphronorus*, *Bisonalveus*, and *Amaramnis* and the pantolestines *Pantolestes*, *Chadronia*, *Propalaeosinopa* [= *Bessoecetor*], *Palaeosinopa*, *Cryptopithecus*, and *Dyspterna*. Descriptions and discussions of most of these genera are available in Matthew (1909), Hopwood (1927), Simpson (1935), Cook (1954), Gazin (1956, 1962), Van Valen (1966, 1967), and Clark (1968).

Some general characteristics shared by *Simidectes* and most pantolestids are the grinding occlusal wear on the molars, the high-cusped lower premolars (in relation to the lower molars), the tall coronoid process and deep masseteric fossa, the crenulation of the enamel on the canines and some other teeth, the recurved canine, and the transversely broad articular condyle. An important difference is the location of mental foramina. The most posterior mental foramen in *Simidectes* is below P_3 , whereas the

single mental foramen of pantolestids is ordinarily below M_1 . However, in *Coriphagus* and *Cryptopithecus* the mental foramen is below P_4 , so the location of mental foramina may not be too important. Also, on the upper molars of most pantolestids there is a large posterolingual cingulum and often a hypocone. The molar cusps are often more sharply connate than those of *Simidectes*, but this sharpness varies. The upper molar cusps of *Chadronia* and *Pantolestes*, for example, though less bulbous than the cusps of *Simidectes*, are considerably less connate than those of *Pro-palaeosinopa*.

The lower molars of *Simidectes* are very similar to those of a number of pantolestids, particularly to the pentacodontines. In all the pantolestids examined there is a size decrease from M_1 to M_3 . In *Coriphagus* the paraconid is reduced to a comparable degree to the paraconid in *Simidectes* and has a similar position on the trigonid. *Coriphagus* also approaches *Simidectes* in the narrow, trenchant nature of its talonid, though its entoconid is slightly more developed compared to the hypoconid than in *Simidectes*. However, in most other pantolestids the tendency is toward a wide, basined talonid with hypoconid and entoconid about equally developed. The lower premolars of pantolestids have considerable variation between genera. Some are small, but many have high cusps compared to the cusps on the molars, a situation reminiscent of *Simidectes*. In *Pentacodon*, for example, P_4 is a large tooth with morphology quite similar to P_4 in *Simidectes*. However, the wear on this tooth is not occlusal, and the tooth was apparently used quite differently from the same tooth in *Simidectes*. *Aphronorus*, another pentacodontine with a *Simidectes*-like P_4 , has, however, more wear on the tips of the cusps than does *Pentacodon*.

The upper molars of pantolestids differ more sharply from those of *Simidectes* than do the lower molars. There is a decrease in size from M^1 to M^3 , but in many cases these teeth are strongly elongated transversely in relation to the anteroposterior length. However, in *Pantolestes* and *Chadronia* these teeth have approximately the same outline as upper molars of *Simidectes* except that there is a posterolingual cingulum. The metacone is reduced on M^3 in both pantolestids and *Simidectes*, a situation which in many pantolestid genera is also accompanied by a strong development of the parastyle. Except for the posterolingual cingulum, the cingula are reduced on the upper molars of most pantolestids. The upper premolars vary in size in relation to the molars through the various genera of pantolestids. In *Coriphagus*, for example, all of the premolars are much smaller than the molars, but in *Aphronorus* P^4 is as large as, or larger than, M_1 and the morphology of the tooth is similar to that of P^4

of *Simidectes* except that the metacone is small and that there may be an incipient hypocone.

Where the posterior part of the mandible is preserved in pantolestid specimens it is generally similar to that of *Simidectes*. The articular condyle is transversely broadened and the angle is enlarged, though it may not be incurved and is often connected to the rest of the mandible by a narrow necklike region. The coronoid process is very tall and generally much more abruptly slanted than the coronoid of *Simidectes*. Some pantolestids may have chewed in a manner quite close to the mastication of *Simidectes*, but some, like *Chadronia* with its articular condyle at a peculiar angle to the rest of the jaw, almost certainly did not.

Where known, as in *Pantolestes* and *Chadronia*, the snout of pantolestids is rounded and not dorsoventrally expanded as in *Simidectes*. Two basicrania of pantolestids are available for comparison, the type of *Chadronia* and Y.P.M. No. 13525, a specimen of *Pantolestes longicaudus*. McKenna's (MS) study of these basicrania was helpful in the comparison with *Simidectes*. In the squamosal-alisphenoid area an important feature in *Chadronia* is the foramen caroticum alisphenoidi, from which the inferior ramus of the stapedia artery emerges to the ventral surface of the skull and then runs anteriorly in a small groove medial to the alisphenoid-squamosal suture toward the alisphenoid canal. The region of the foramen caroticum alisphenoidi is missing in L.A.C.M. No. 927 (*S. merriami*) and as mentioned in the generic description, it is questionable whether the inferior ramus of the stapedia artery ran in a groove medial to the alisphenoid-squamosal suture or through the Glasserian fissure in company with the chorda tympani. Although the passage of this artery in *Simidectes* has important diagnostic implications, the question at present cannot be resolved. The alisphenoid-squamosal suture in both *Simidectes* and *Chadronia* is on a raised area medial to the glenoid fossa. The glenoid fossa of *Chadronia*, like that of *Simidectes*, has both preglenoid and postglenoid processes. It is on the same frontal plane as the rest of the basicranium. The postglenoid foramen is small in *Chadronia* but larger in *Pantolestes longicaudus*. Its position on the posterior slope of the glenoid area on approximately the same plane as the glenoid fossa is generally similar to the position in *Simidectes*. No tympanic bone remains in the area of the alisphenoid-squamosal suture in *Simidectes*, but it cannot be ascertained whether this bone was never present or whether it was lost in preservation. In the region posterior to the glenoid fossa the mastoid process is greatly enlarged in *Chadronia* and constricts the external auditory meatus. The mastoid process is not well preserved in *P. longicaudus* but is probably enlarged to a lesser degree than in *Chadronia*. In *Simidectes*

the mastoid process is only of moderate size and does not constrict the external auditory meatus.

As a summary of the comparison between *Simidectes* and pantolestids it must be stated that if all pantolestids are taken together the number of common characteristics with *Simidectes* is great. However, no single pantolestid genus shows particularly close relation to *Simidectes*. There is no evidence to negate a connection between *Simidectes* and pantolestids. Within the family Pantolestidae are several Eocene representatives which attained relatively large size. These larger pantolestids, although probably not themselves ancestral to *Simidectes*, could well have paralleled another not distantly related line that gave rise to *Simidectes*.

At this point I am unable to demonstrate conclusively a relation between *Simidectes* and any mammalian group. From the point of view of total morphologic similarities combined with temporal and spatial proximity the pantolestids have the greatest chance of relationship with *Simidectes*. However, because of differences between *Simidectes* and pantolestids I hesitate to include *Simidectes* in the family Pantolestidae. McKenna (personal commun.) includes within the superfamily Pantolestoidea the Pantolestidae, Apheliscidae, and Ptolemaiidae. These probably related families have always been mysteries within the mammalian classification. Within the superfamily Pantolestoidea I also place *Simidectes* because this genus is probably related in some way to the included groups. The difficulty of classifying *Simidectes* stems from the fact that it is unspecialized in relation to most mammals and therefore does not share a large number of specializations with any single group.

SUMMARY

Simidectes, the correct generic name for *Pleurocyon* of Peterson (1919) and Stock (1933), is considered (primarily from lack of evidence to the contrary) to consist of three species: *S. magnus*, *S. medius*, and *S. merriami*. No subgeneric distinctions are maintained. These species are known largely from upper and lower teeth, limited cranial material, and some postcranial material. These mammals were probably browsing omnivores whose teeth did more grinding than shearing. Affinities with numerous early mammal groups are dismissed, and though present evidence is slight, *Simidectes* is placed with the pantolestids, apheliscids, and ptolemaiids in the superfamily Pantolestoidea, to which its probability of affinity is greatest.

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