NOTES ON SOME UPPER MIOCENE SHREWS FROM OREGON

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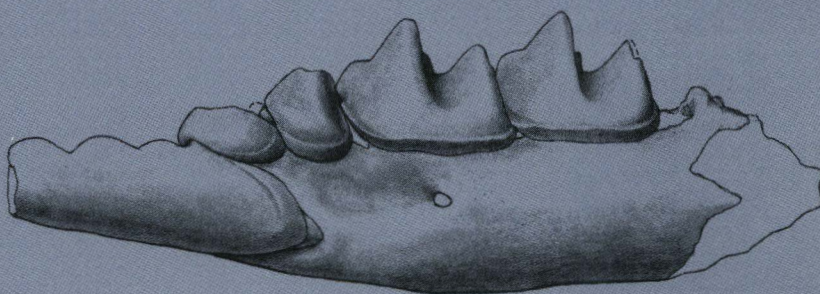# NOTES ON SOME UPPER MIOCENE SHREWS FROM OREGON

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ABSTRACT

Skull Springs and Quartz Basin, two localities of Barstovian (late Miocene) age in Malheur County, Oregon, have produced relatively abundant jaws and teeth of shrews (family Soricidae Gray). The subfamily Heterosoricinae Viret and Zapfe is represented in these localities by *Heterosorex* Gaillard, sp., *Paradomnina relictus* gen. n. et sp. n., and *Ingentisorex tumididens* gen. n. et sp. n. The subfamily Soricinae Murray is represented by the specialized *Alluvisorex arcadentes* gen. n. et sp. n. The subfamily Crocidurinae Milne Edwards is represented by cf. *Limnoecus* Stirton, sp. indet.

INTRODUCTION

Up until the last ten years or so the fossil record of North American late Tertiary shrews was nearly nonexistent. Two shrews, *Limnoecus* and *Heterosorex*, have been described from the late Miocene sediments of the New World, but both are known only from a relatively few specimens. In 1960 and 1961, J. A. Shotwell and students collected and washed matrix from two late Miocene (Barstovian) sites in eastern Oregon. These yielded at least five species of soricids including three new genera.

All the shrews described herein come from only two localities. The Skull Springs site, U.O. locality 2495, is located in Malheur County, Oregon, approximately at the junction of sections 10, 11, 14, and 15, T. 23 S., R. 40 E. (see Shotwell, 1963, map 1, loc. 7). Evernden *et al.* (1964) reported a potassium-argon date from this locality of 15.1 x 10⁶ years b.p. The Quartz Basin site, U.O. locality 2465, is also located in Malheur County about one mile southwest of Ferguson Springs in the center of section 33, T. 24 S., R. 43 E., (see Shotwell, 1963, map 1, loc. 10).

The Skull Springs local fauna was discussed by Gazin (1932) and others. The Quartz Basin local fauna was only recently discovered and worked. Several new Skull Springs localities and the Quartz Basin sites are presently under study by Shotwell.

Although the two localities are relatively close to one another in both space and time, the occurrence of various genera are almost mutually exclusive because of ecological differences. Heterosoricine shrews are the most abundant forms in both localities (Table 1). The discovery of two new genera of heterosoricines in deposits of late Miocene age show that the Heterosoricinae as defined below was a much more diverse and apparently successful group than previously imagined. Heterosorines seem to have been one of the most abundant of the insectovores of the Miocene in some regions of North America. Recent discoveries in the Barstow Formation show that *Paradomnina* was a common shrew in at least one of the localities, whereas *Limnoecus* is the most common (usually the only) shrew in the other sites. As yet, little is understood of the ecological preference of these shrews; although, heterosoricines may have preferred a more moist environment than *Limnoecus*.

TABLE 1

OCCURRENCE OF OREGON BARSTOVIAN SHREWS*

Taxon	Skull Springs UO 2495	Quartz Basin UO 2465
Paradomnina relictus gen. n. et sp. n.	10/2	0
Heterosorex sp.	2/2	0
Ingentisorex tumididens gen. n. et sp. n.	0	82/10
Alluvisorex arcadentes gen. n. et sp. n.	1/1	2/2
cf. *Limnoecus* sp. indet.	1/1	0

* Ratios indicate: number of specimens / minimum number of individuals.

Although *Heterosorex* apparently survived somewhat later in Europe ("Pontian"), there are no heterosoricines known to me from faunas later than Barstovian age in North America. The reason this group fell from relative abundance in such a relatively short period of time is conjectural at present. The occurrence of a specialized soricine (*Alluvisorex*) retaining several primitive characters suggests that this subfamily, too, had become well diversified before the late Miocene, although the meager fossil record does not substantiate adequately this interpretation.

MATERIAL AND METHODS

The method of collection usually determines the abundance and completeness of the specimens and provides an index to the relative abundance of the species within a site. The Quartz Basin site was washed in the field through woven copper wire cloth with 15 x 18 mesh per line inch of 0.0114 inch wire (window screen) in water. The Skull Springs material was recovered from the encasing matrix in the casts of larger specimens. This matrix was dried, soaked in kerosene, and washed through window screen in water at the facilities at the University of Oregon.

All the specimen figures (except Figs. 10 and 17) were drawn with the aid of a camera lucida and binocular microscope unless otherwise stated. All the measurements were taken with a Gaertner measuring microscope accurate to 0.002 millimeters. Scale lines in all the figures represent one millimeter, the scale is not uniform. The length of the fourth upper premolars and upper molars was taken between the extreme anterior (parastyle) and posterior (metastyle) ends of the ectoloph. The length of all other teeth or tooth combinations represents the distance between the antero and posteromost extremities of the tooth (or teeth) with respect to the anteroposterior axis of the tooth (or teeth). In every case the width of a tooth represents the distance between the lingual and labialmost extremities with respect to and perpendicular to the designated length.

Depth of jaw is the perpendicular distance between the alveolar border beneath the metaconid of the first molar to the ventral margin. The height of the coronoid is represented by the distance between the coronoid process and the inflection of the ventral border of the jaw as indicated by the small wedges in Fig. 17.

Abbreviations used throughout this paper are:

L.A.C.M.—Los Angeles County Museum
U.O. (UO)—University of Oregon Museum of Natural History
cf.—to be compared to
sp.—species possibly new but material insufficient for adequate understanding of relationships

Recent specimens of *Myosorex, Suncus, Crocidura, Sorex, Anourosorex, Cryptotis, Blarina*, and *Notiosorex* were available for comparison in addition to the following fossil forms: *Domnina gradata, Heterosorex* (two undescribed species), *Limnoecus tricuspis* (type and others), *L. niobrarensis* (type), *?Hesperosorex chasseae* (type and paratype), and *"Limnoecus" grivensis*.

SYSTEMATICS

Family SORICIDAE Gray 1821

Of late there has been much discontent with the arrangement of the living subfamilies of the Soricidae as listed by Cabrara (1925) and Simpson (1945). James (1963) summarizes much of this discontent with the recognition of the two large subfamilies of shrews, the Soricinae and Crocidurinae. I agree with him in retaining these subfamilies as useful taxonomic divisions with some generic reassignments. Inasmuch as Repenning (in press) has prepared a review of the family, I shall not attempt to present any general review except in those areas where it bears directly upon the fossils under discussion.

There is much confusion over the homology between the antemolar teeth in soricids and the homology of these teeth and those of other placental mammals. James (1963) reviewed the main embryological arguments and I shall follow the scheme he uses. Most of the discussion about homologies hinges upon the designation of the first lower tooth as the I_1, or I_2, or I_3. This question has not been answered beyond dispute by either embryological or paleontological evidence. For convenience, I accept this

TABLE 2

PRESUMED HOMOLOGIES OF THE ANTEMOLAR TEETH OF HETEROSORICINES USED IN THIS PAPER AND ELSEWHERE

	I1	I2	I3	C	P1	P2	P3	P4
UPPER DENTITION								
Paradomnina relictus	I1	I2	....	C	P1	P2	P3	P4
Domnina gradata*	I1	I2	....	I3	P1	P2	....	P4
Heterosorex roperi**	I2	I3	....	C	P2	P3	....	P4
Ingentisorex tumididens	I1	I2	....	C	P1	P2	....	P4
LOWER DENTITION								
Paradomnina relictus***	....	....	I3	C	P1	P2	P3	P4
Domnina gradata*	....	....	I3	P1	P2	P3	....	P4
Heterosorex roperi**	....	....	I	C	P1	P2	....	P4
Ingentisorex tumididens	....	....	I3	C	P1	....	....	P4

* Patterson and McGrew, 1937.

** Wilson, 1960.

*** Same for *D. thompsoni* assuming that Simpson (1941) was correct in suggesting the P4 to be single rooted.

tooth as the I₃. In all the known shrews in which there are more than two teeth between the I₃ and M₁, it is the teeth intermediate to the second tooth and the P₄ that are in the apparent process of reducation. *Domnina thompsoni* and *Paradomnina relictus* appear to have a full complement of five teeth between the I₃ and M₁. The best assignment of these teeth as based on the above assumptions is that they represent the canine, P₁, P₂, P₃, and P₄ respectively (Table 2). Furthermore as is discussed below it is the P₁-P₃ that tend to be reduced and disappear. The same trend seems to be evident in the Crocidurine-Soricine complex thus leaving most of the modern genera with only the canine and fourth premolar in the lower series. I shall follow the scheme suggested above and in Table 2 regardless of how they were designated in the previous literature.

Subfamily HETEROSORICINAE
Viret and Zapfe, 1951

Domnina Cope, 1873 (= *Miothen* Cope, 1873; = *Protosorex* Scott, 1894). L. Olig.-L. Mioc.; N.A.

Paradomnina gen. n. U. Mioc.; N.A.

Heterosorex Gaillard, 1915 (= *Trimylus* Roger, 1885) M. Olig.-U. Mioc.; N.A.: U. Olig. - L. Plioc.; Eu.

Ingentisorex gen. n. U. Mioc.; N.A.

This subfamily was originally proposed by Viret and Zapfe (1951) to emphasize the distinctiveness of the genus *Heterosorex* from the other known (European) shrews. It should be noted that *Trimylus* Roger has priority over *Heterosorex*; however, Viret and Zapfe placed it into synonymy under *Heterosorex* on the grounds that "Cette piece est tout a fait insuffisante pour permettre la creation d'un genre." This is certainly not so at the generic level but may be at the species level. Roger (1885) mentions ". . . der kiefer kraftige, relativ fast plump Formen," the graded size of the molars as shown by the alveoli, and a post-symphyseal foramen (Roger mistook the labial for the lingual side of the jaw—the post-symphyseal for-

amen is probably represented by the middle foramen of Roger's "Aussenseite"). These points are characteristic at the generic level and the latter at the subfamilial level. In addition his figure clearly shows the hypertrophied I₃, posterior position of the mental foramen, and robustness of the ramus that are also characteristic of the genus as now understood. The most compelling reason that I see for the continued retention of *Heterosorex* (and Heterosoricinae) in place of *Trimylus* (Trimylinae) is that *Heterosorex* has been generally accepted by paleontologists and more widely used for this group of species. A name change at this time would only tend to confuse the nomenclature.[2]

Viret and Zapfe apparently overlooked the North American genus *Domnina*, that, as noted by Patterson and McGrew (1937), McDowell (1958), Wilson (1960), and Mawby (1960), shows close relationship to *Heterosorex*. Saban (1958) retained *Domnina* in the Soricinae but included *Amblycoptus oligodon* Kormos (1926) in this subfamily, possibly following the suggestion of Viret and Zapfe that this form might, if better known, be placed here. Saban (p. 844) characterized the subfamily by "grande taille, crane facial large et haut, mandibule sans fossa d'insertion du muscle temporal sur la face interne de l'apophyse coronoide, exodaenodontie dévelopée des molaires." This characterization probably based on *Heterosorex* alone immediately excludes *Amblycoptus* which possesses a very well developed intertemporal fossa. *Amblycoptus* is closely related to *Anourosorex* and is a soricinae.

The Heterosoricinae tend to form one group and the Crocidurinae, Soricinae, and other Oligocene and Miocene shrews such as *Crocidosorex* and *Limnoecus* form another. Thus far only skull and jaw elements of the Heterosoricinae are known. Many characters which may prove to be of subfamilial significance are only

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2 Doben-Florin (Bayerische Akademie der Wissenschaften, 1965) has recently reviewed this synonymy (not seen) and urges the use of the earlier name *Trimylus* Roger.

known in one or two of the genera owing to fragmentary nature of the known remains. Characters which are shared by all of the known heterosoricine genera and serve to distinguish them from all other known shrews are as follows:

1. Absence of a pocketed intertemporal fossa (a shallow depression is usually present).
2. Condyle with one or two articular facets but inferior condylar facet always shifted strongly lingually.
3. Masseteric fossa evident. The dorsal portion of this fossa may have contained the insertion for the lateral division of the temporalis muscle.
4. A well developed posterolingual ridge of the P^4 completely encloses the talon basin. The protocone and hypocone, if present, are usually poorly defined eminences on this ridge.
5. Presence of a small foramen posterior to the mandibular symphysis, here termed the post-symphyseal foramen.

PARADOMNINA RELICTUS gen. n. et sp. n.[3]
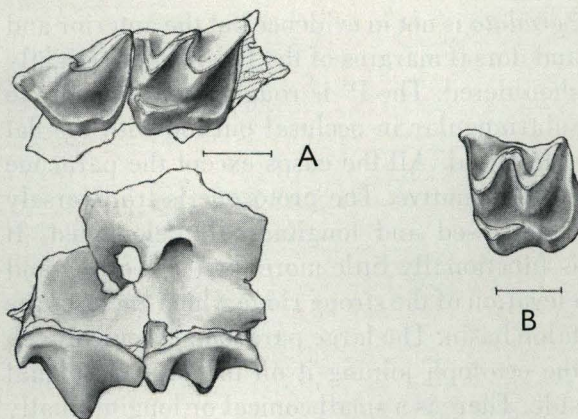
GENOTYPIC SPECIES: *Paradomnina relictus* sp. n.

TYPE: UO 24279, a left mandible with P_3-M_3, root of I_3, and alveoli of C-P_2, lacking the ascending ramus.

HYPODIGM: UO 22605, left maxillary fragment with P^4-M^1; UO 24274, left P^4; UO 24273, left M^1; UO 24271-UO 24272, left M^2's; UO 24275, right mandibular fragment with alveoli of C-P_3 and portions of the I_3 and P_4 alveoli; UO 24276, edentulous left mandibular fragment; UO 24278, left mandibular fragment with talonid of M_2. All specimens from the type locality.

TYPE LOCALITY: Skull Springs, UO loc. 2495

AGE: Barstovian, K/A age 15.1×10^6 years (Evernden *et al.*, 1964, p. 190)

[3] Etymology: From the Greek *para*, near, plus *Domnina* and the Latin *relictus*, forsaken, alluding to the late occurrence of this form.

Figure 1. PARADOMNINA RELICTUS, *gen. n. et sp. n.*, loc. 2495 (Skull Springs). A, UO 22605, left maxilla with P^4-M^1, occlusal and left lateral views. B, UO 24271, left M^2, occlusal view.

DIAGNOSIS: Generic diagnosis same as for the species. *Paradomnina relictus* differs from *Heterosorex* in the more elongate horizontal ramus, narrower lower molars, and relatively weak I_3. It differs from *Ingentisorex* in the lack of exodaenodont P_4-M_1 and presence of the P_2, P_3, and M_3. *P. relictus* most closely resembles the species of *Domnina* but differs from them in the relatively narrower molars, straight hypolophid, and absence of the postentoconid valley. In addition *P. relictus* may be distinguished from the known species of *Domnina* on the following points: from *D. thompsoni* by its relatively shorter lower antemolar length, crowded and transversely elongated antemolar alveoli, and more posterior position of the mental foramen: from *D. gradata* by the presence of the P_3 and smaller size; and from *D. greeni* by the complete and continuous anterior and labial cingula on the lower molars and deeper notch separating the entoconid from the metaconid on the M_1.

DESCRIPTION AND COMPARISON: Only a small fragment of the maxilla retaining the lacrimal foramen and the anterior orifice of the antorbital foramen was preserved in the collection (Fig. 1a). The weak vertical crest on the side of the face just anterior to the lacrimal fora-

men mentioned by McDowell (1958) on *D. ?gradata* is not in evidence but the anterior and and dorsal margins of the foramen are slightly shouldered. The P^4 is roughly semicircular to subtriangular in occlusal outline with the flat side labial. All the cusps except the paracone are diminutive. The protocone is transversely compressed and longitudinally elongated. It is functionally little more than a swelling and elevation of the strong ridge which encloses the talon basin. The large paracone is conical with the ectoloph joining it on the posteriolingual side. There is a small conical or longitudinally compressed parastyle just anterior to the paracone. The labial occlusal outline varies from nearly flat to sinusoidal. The low external cingulum extends from the base of the metastyle forward to the parastyle. The entire lingual border of the tooth from the parastyle to the metastyle is composed essentially of a single heavy ridge upon which the protocone is perched. There is no emargination of the posterior border of the tooth and no indication of a hypocone. The talon basin and the entire tooth are relatively wider in UO 22605 than in UO 24274. There are two strong labial roots, one on each extremity of the tooth. The lingual root was not exposed.

The M^1 and M^2 of *P. relictus* are practically identical to those of *D. gradata*, but perhaps slightly narrower. There is some incipient twinning of the M^1 mesostyle. Patterson and McGrew (1937, p. 249) state that the "M^{1-2} are very similar to corresponding teeth of *Blarina*, the only observable difference being that the strong posterior cingulum extends to a point immediately posterior to the metastyle." Aside from this posterior emargination, *Blarina* differs from *Domnina* and *Paradomnina* primarily in that the teeth are noticeably wider than long, and the protocone is directly connected to the bases of the paracone and metacone by distinct lophs which wear to a crescentic pattern rather than a triangular pattern as in *Domnina* and *Paradomnina*.

The mandible (Fig. 2) is proportioned like that of *D. gradata*, and differs from *D. thompsoni* in the relatively shorter antemolar length. The shallow longitudinal depression below the antemolar teeth on the labial side loses identity beneath the P4. The mental foramen is more posterior than in *D. thompsoni* and falls below the level of the anterior portion of the talonid of the M1. Just posterior to the mandibular symphysis and quite near the ventral border of the jaw there is a small foramen below the trigonid valley of the M1. The ventral anterior portion of the mandible is broken away in the type to reveal the root of the I3, that terminates under the anterior-most part of the M1. Unlike the modern shrews, *P. relictus* apparently lacks the deep longitudinal cleft on the lingual side of the root of the I3. The root is ovate in cross section and flattened or very slightly depressed on the lingual side. The labial border of the I3 alveolus appears to have been just below or anterior to the canine alveolus. The antemolar alveoli are preserved in the type and in UO 24275. There are five alveoli between the incisor and the first molar. These are interpreted as the canine, P1, P2, P3, and P4 respectively. The P3 and P4 are present in the type, thus eliminating the possibility of a double rooted P4. This supports Simpson's (1941) suggestion that the P4 of *D. thompsoni* was single rooted. The rim of the canine alveolus is broken in both specimens, but the root was apparently rather long and nearly paralleled that of the I3. The alveolus of the canine was probably somewhat larger than that of the P1. The roots of the premolars incline progressively toward the vertical from the P1 to the P4. The aveoli of the P1 and P2 are longitudinally compressed and similar in size and shape. The corresponding alveoli in *D. thompsoni* are much less compressed and more rounded in outline. The alveolus of the P3 is smaller than the preceding and suggestive of the diminutive tooth seen in the type. The alveoli of the C-P3 lack the tubercle on the anterior wall of the alveolus that is characteristic of most of the modern shrews. This tubercle, hereafter referred to as the subcoronal tubercle, is present on the P4 alveolus. The subcoronal tubercle is apparently absent
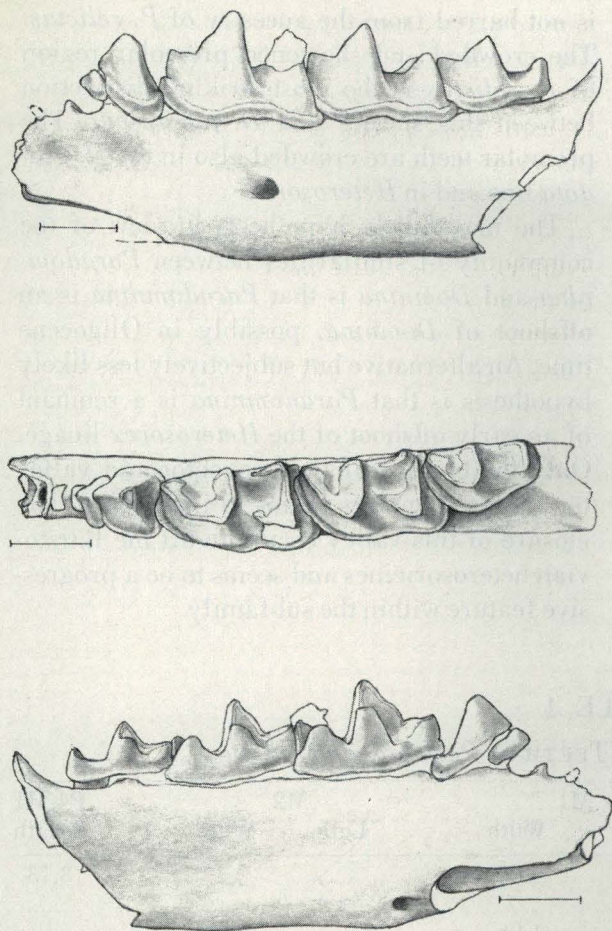
Figure 2. PARADOMNINA RELICTUS, *gen. n. et sp. n.*, UO 24279, *loc. 2495 (Skull Springs), type, left mandible with P^3-M^3, left lateral, occlusal, and right lateral views*

on all the antemolar teeth of *D. thompsoni* and *D. gradata*. It serves as an interlocking device with the tooth that seems to have developed late within the Heterosoricines but earlier within the other shrews. The tubercle may extend well above the enamel margins within the body of the crown (the subcoronal pit). These structures appear to be related to both crowding and coronal procumbency of the antemolar teeth.

The P_3 is diminutive, inflated, longitudinally compressed and devoid of surface structures. It is this tooth that is apparently lost in *D. gradata*. The crown is chevron-shaped in occlu-

sal outline. The tip of the crown is in line with the anterior slope and small beak of the P_4 that overlaps it. In occlusal view the P_4 completely obscures the P_3 alveolus. The P_4 of *P. relictus* is very similar to that of *D. gradata* described and figured by Patterson and McGrew (1937). The lateral cingula do not extend as far forward as in *D. gradata* owing to the anteroventral emargination of the crown where it overlaps the P_3.

The lower molars are not strongly graded in size. All the lower molars of *P. relictus* are relatively narrower than in the species of *Domnina* (Table 3). The post-entoconid valley on the M_1-M_2 is absent thus permitting the hypolophid to join the posterior wall of the entoconid directly. In this respect *P. relictus* more closely resembles *Heterosorex* and *Ingentisorex*. Unlike the other species of *Domnina*, the hypolophid is straight and not deflected posteriorly by the entoconid valley. The entoconid is more posteriorly situated than in *Domnina* and is separated from the metaconid by a relatively broad U-shaped notch. The anterior and labial cingula are continuous around the bases of the protoconid and hypoconid. The cingula tend to be better defined in *P. relictus* than in *D. gradata*. The trigonid valley is not as deeply excavated as in *D. gradata*. *D. greeni* apparently also differs from *P. relictus* in the more poorly developed labial cingula and strong entoconid crest. The M_3 closely resembles that of *D. gradata* but is relatively nar-

TABLE 3

RATIO OF LENGTH OVER WIDTH IN THE LOWER MOLARS OF *Domnina* AND *Paradomnina*

	D. thompsoni*	D. gradata**	D. greeni***	P. relictus
M1	1.5	1.5 - 1.8	1.7	1.9
M2	1.4	1.2 - 1.75	....	1.9
M3	0.7	1.4 - 1.5	....	1.8

  * After Simpson, 1941
 ** After Patterson and McGrew, 1937, plus LACM 5203, 5205, and 5206
*** After Macdonald, 1963

rower. The anterior cingulum is also not as broad as in *D. gradata*. The M₃ talonid of *D. thompsoni* (Simpson, 1941, fig. 1) appears to be relatively wider than in *P. relictus* and *D. gradata*.

RELATIONSHIPS: As a possibly terminal member of the *Domnina* group, *Paradomnina relictus* is probably not closely related to any of the other described forms of *Domnina* on the basis of the closure or lack of the post-entoconid valley. However, this feature could be derived from any of the older species. *D. greeni* is too fragmentary to compare with *P. relictus* but differs from it in comparable features as does *D. gradata*. *D. gradata* would seem to be eliminated from the direct ancestry of *P. relictus* owing to its early loss of the P₃ *D. thompsoni* is therefore the only well known form that

is not barred from the ancestry of *P. relictus*. The crowded and shortened premolar region of *P. relictus* is the most striking distinction between this species and *D. thompsoni*. The premolar teeth are crowded also in the *D. gradata* line and in *Heterosorex*.

The most likely hypothesis in view of the community of similarities between *Paradomnina* and *Domnina* is that *Paradomnina* is an offshoot of *Domnina*, possibly in Oligocene time. An alternative but subjectively less likely hypothesis is that *Paradomnina* is a remnant of an early offshoot of the *Heterosorex* linage. Only the closure of the post-entoconid valley on the lower molars seems to imply this. The closure of this valley occurs in all the Barstovian heterosoricines and seems to be a progressive feature within the subfamily.

TABLE 4

MEASUREMENTS OF THE UPPER TEETH OF *Paradomnina relictus*

Specimen number	P4		M1		M2		P4-M1
	Lgth	Wdth	Lgth	Wdth	Lgth	Wdth	Length
UO 22605	2.01	1.35	1.84	1.67	....	....	3.73
UO 24274	1.92e	1.52	....	....	....	....	....
UO 24273	....	....	1.81	1.86	....	....	....
UO 24371	....	....	....	....	1.58	1.86	....
UO 24272	....	....	....	....	1.60	1.79	....

e Estimated

TABLE 5

MEASUREMENTS OF THE TYPE DENTARY OF *Paradomnina relictus*

Measurement	UO 24279 (Type)
P3: Length	0.43
Width	0.66
P4: Length	0.91
Width	0.88
M1: Length	2.07
Width	1.07
M2: Length	1.91
Width	0.99
M3: Length	1.395
Width	0.78
P4-M3 Length	5.56
M1-M3 Length	4.79
Depth of Jaw	2.07

HETERSOREX sp.

The genus *Heterosorex* was previously reported by Mawby (1960) from Guano Lake, Lake Co., Oregon. A tooth fragment and a fragment of the mandible with the M_1 (Fig. 3) were recovered from the Skull Springs locality. The M_1 of the Skull Springs form is absolutely and proportionately shorter than the Guano Lake form. The mental foramen is also somewhat more posteriorly situated and the groove extending anterior from it is shallower. The Skull Springs form may represent a new species but too little is yet understood about the variation within the species of *Heterosorex* to warrant proposing a new species. The M_1 of UO 24281 is 2.70 mm long and 2.00 mm wide, and the depth of the ramus beneath the M_1 on the lingual side is about 3.5 mm.
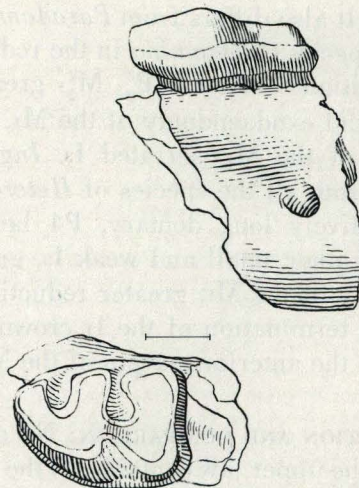

Figure 3. HETEROSOREX *sp., UO 24281, loc. 2495 (Skull Springs), left M_1 with fragment of mandible, occlusal and left lateral views*

INGENTISOREX TUMIDIDENS,
gen. n. et sp. n.[4]

GENOTYPIC SPECIES: *Ingentisorex tumididens,* sp. n.

TYPE: UO 21960, left mandible with P_1-M_2 and basal portion of I_3, lacking angular process and lingual portion on the condyle.

HYPODIGM: UO 22041-UO 22044, UO 22046-UO 22055 isolated I^1's; UO 22303, fragment of upper jaw with I^2 and alveolus of canine; UO 21994-UO 22016, UO 22056-UO 22061, upper teeth fragmentary maxillae; UO 24788, I_3; UO 21958-UO 21959, UO 21961-UO 21993, lower teeth and fragmentary mandibles; all of the above specimens from UO loc. 2465.

TYPE LOCALITY: Quartz Basin, UO loc. 2465

AGE: Barstovian

DIAGNOSIS: Generic diagnosis same as for the species. *Ingentisorex tumididens* differs from all other known heterosoricine shrews in the absence of the third molars, great elongation of the P^4, and great reduction of the maxillary
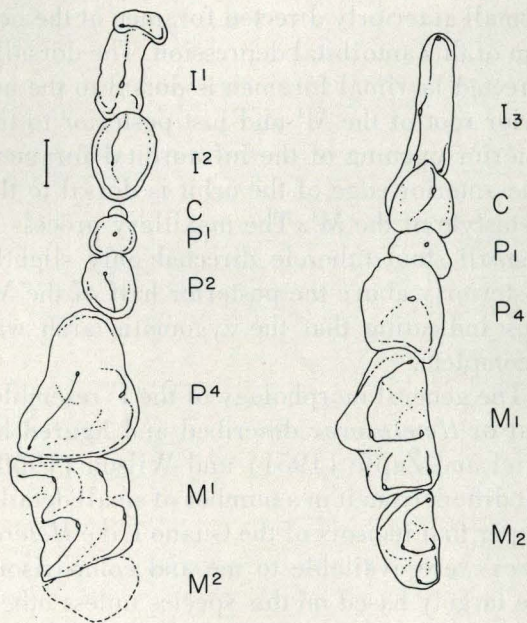
Figure 4. INGENTISOREX TUMIDIDENS, *composite upper right and lower left dentitions. I^1, UO 22054; I^2 (reversed) and canine alveolus, UO 22303; P^2-P^4, UO 22057; M^1, UO 22000; M^2, conjectural; I_3, UO 21472; C, UO 21981; and P_1-M_2, UO 21967*

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[4] Etymology: From the Latin genitive *ingentis*, great, remarkable, large, plus *sorex*, shrew-mouse, and the Latin *tumidus*, swollen, plus *dens*, tooth, alluding to the exodaenodont P_4-M_1.

process. It also differs from *Paradomnina* and all the species of *Domnina* in the reduction of the dentition to 1_1^2, C_1^1, P_2^3, M_2^2, great hypertrophy and exodaendonty of the M_1, great reduction of the M_2, serrated I_3. *Ingentisorex* differs from all the species of *Heterosorex* in the relatively long dentary, P4 larger than canine, rather small and weak I_3, greater hypertrophy of the M_1, greater reduction of the M_2, and termination of the I_1 crown well anterior to the anterior margin of the M_1.

DESCRIPTION AND COMPARISON: No one specimen of the upper jaw contains all the teeth, but the upper tooth row may be reconstructed by matching various specimens that overlap in completeness (Fig. 4). The upper jaw was thus found to contain eight teeth; I^1, I^2, C (alveolus), P^1, P^2, P^4, M^1, and M^2 (alveolus). The infraorbital foramen opens into an oval depression between the roots of the P^4. There is a small anteriorly directed foramen at the bottom of this antorbital depression. The dorsally directed lacrimal foramen is dorsal to the anterior root of the M^1 and just posterior to the anterior opening of the infraorbital foramen. The anterior edge of the orbit is dorsal to the metastyle of the M^1. The maxillary process is a small stout tubercle directed only slightly posteriorly above the posterior half of the M^1 thus indicating that the zygomatic arch was incomplete.

The general morphology of the I^1 resembles that of *Heterosorex* described and figured by Viret and Zapfe (1951) and Wilson (1960) but differs from it in a number of small details. Upper first incisors of the Guano Lake *Heterosorex* were available to me and comparisons are largely based on this species unless otherwise stated. In lateral view the anterior outline of the crown forms a smooth curve in *Ingentisorex* rather than an angle as in *Heterosorex*. In anterior view the axial line of the crown forms a sinusoidal curve rather than a simple arch. The tip of the crown is bifed as in *Heterosorex*, but the cusps are spread farther apart. The posterior basal cusp is more prominent
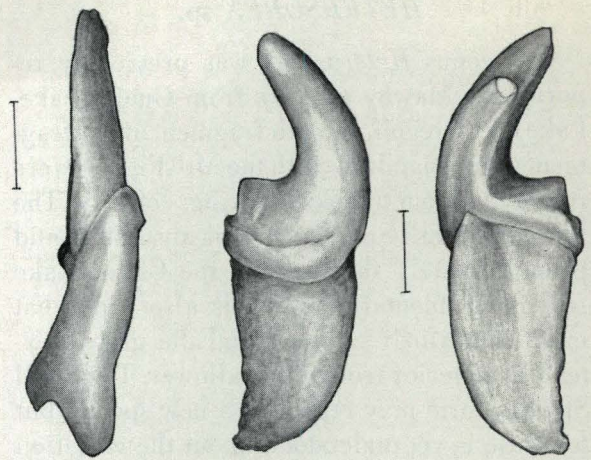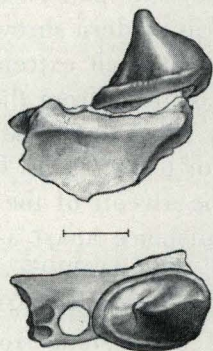

Figure 5. INGENTISOREX TUMIDIDENS, *gen. n. et sp. n., UO 22049, loc. 2465 (Quartz Basin), left I¹ anterior, left lateral, and right lateral views*

and compressed, and the basal labial border of the crown is more nearly perpendicular to the axis of the root. In lateral view the root of *Ingentisorex* does not taper as much as in *Heterosorex*. In general the I^1 of *Ingentisorex* is less robust than that of *Heterosorex*. The greatest diameter of the crown varied fro 2.76 to 3.15 mm in a sample of five.

Only one specimen of the I^2 was represented in the collection. There was, at first, some question as to the association of this tooth with the rest of the dentition. However, in the attached jaw fragment the alveolus directly posterior to the I^2 is identical in size and shape to that of the canine in more complete specimens. The incomplete alveoli anterior to the I^2 and posterior to the canine alveolus are apparently for the reception of the I^1 and P^2 respectively. The subsequent description and figures by Wilson (1963) of the antemolar dentition of *Heterosorex roperi* tend to support this arrangement. In occlusal outline the I^2 is oval. A strong cingulum, devoid of cusps, encircles all but the anterior part of the tooth. The tooth is laterally compressed and culminates in a single, centrally situated, sharp cusp. On the lingual side of the crown there are two low vertical folds; the longer posterior fold is slightly anterior to the apex of the cusp and the anterior one merges

with the anterior slope of the cusp. The I^2 of *Ingentisorex* differs from the comparable tooth in *H. roperi* in a smooth rather than notched posterior basal outline and in the lack of a posterolingual basin and cingular cusps. It is more laterally compressed with a length to width ratio of about 1.5 as compared to 1.1 in *Heterosorex roperi*. The I^2 is single rooted and has an anterior interlocking sulcus on the root that secures it to the maxilla. I^2 is 2.02 mm long and 1.31 mm wide.

Figure 6. INGENTISOREX TUMIDIDENS, *gen. n. et sp. n., UO 22303, loc. 2465 (Quartz Basin), left I^2 and alveolus of canine, occlusal and left lateral views*

The P^2 is a simple tooth, nearly circular in occlusal outline but slightly ovate transversely. The single primary cusp situated anterior to the center of the tooth is surrounded laterally and posteriorly by a robust cingulum. There is a small basin between the principal cusp and the posterior lingual portion of the cingulum as in *H. roperi*. Only a very slight depression marks the anterior face of the root. The crown of the P^2 apparently overlapped the posterior margin of the canine as in *H. roperi*.

Patterson and McGrew's (1937) description and figures of the P^3 (their P^2) of *Domnina gradata* applies almost equally well to that of *Ingentisorex*. The P^3 of *Domnina* and *Ingentisorex* has not experienced the distortion seen in *H. roperi*. The robust root is marked by an anterolabial and a deep lingual cleft. The P^3 encroaches well over the posterior border of the P^2 but may not be overlapped by the P^4.
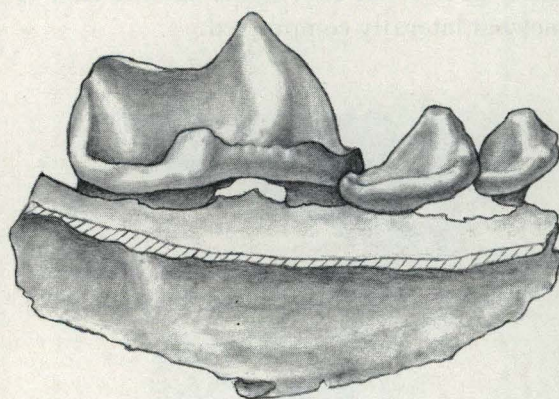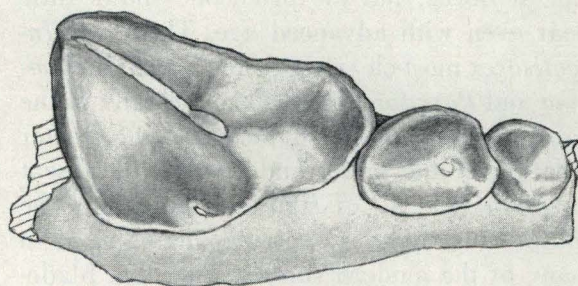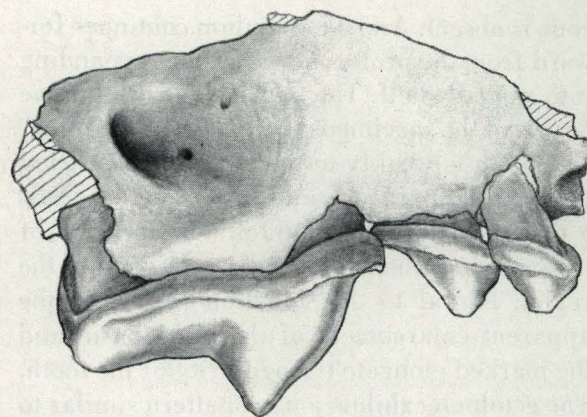
Figure 7. INGENTISOREX TUMIDIDENS, *gen. n. et sp. n., UO 22057, loc. 2465 (Quartz Basin), right maxilla with P^2-P^4, right lateral, occlusal, and left lateral views*

The P^4 is the largest and most striking tooth in the upper jaw. The inflated paracone is the dominant cusp and occupies nearly the entire anterior half of the tooth. A heavy ridge descends lingually from the metastyle and then curves around the talon basin until interrupted by the low but distinct protocone. The hypo-

cone is absent. A weak cingulum continues forward from the protocone sometimes expanding into a small shelf. The parastyle is diminutive on one of the specimens and absent on the other. The tooth is weakly to moderately constricted between the paracone and protocone. There is a distinct external cingulum. The inflation of the paracone anteriorly and constriction of the region lateral to this inflation results in the apparent enlargement of the talon basin and the marked elongate triangularity of the tooth. The ectoloph exhibits a wear pattern similar to that of *Sorex*, but the protocone shows little wear even with advanced age. The P^4 of *Ingentisorex* most clearly resembles that of *Domnina* and *Paradomnina* differing chiefly in the more anterior situation of the paracone, greater inflation of the tooth, and smaller or absent parastyle. The P^4 of *Heterosorex* tends to be equidimensional or even wider than long as in many of the modern shrews. The thin, blade-like metastylar root of *Ingentisorex* is aligned with the margin of the maxilla. The short, compressed protoconal root is the stoutest and is somewhat laterally compressed.

usually concave in occlusal view. The anterior cingulum or a vestige of it continues along the anterior face of the ectoloph in about 70% of the observed specimens. The posterior width is roughly equal to or narrower than the anterior width. This proportion probably reflects the reduction of the M^2. The wear facet of the protocone begins as a line forming a slightly obtuse angle and finally becomes a symmetrical triangle, but even in advanced wear of the protocone, the low hypocone shows only slight wear at its apex. The wear pattern of the ectoloph resembles that in modern shrews. The M^1 has four roots, one at each extremity. Although no M^2 was recognized from the collection, it is indicated by two incomplete alveoli immediately posterior to the M^1 in UO 22056 and UO 22003. The alveoli of the anterior roots are the same distance apart as the posterior roots of the M^1. In UO 22056 (Fig. 8) these are followed by what appears to be a single alveolus about equidistant from the anterolabial and anterolingual alveolus for the M^2, thus suggesting a triangular M^2. The M^3 was undoubtedly absent for there is no place for it to occlude with the lower molars.
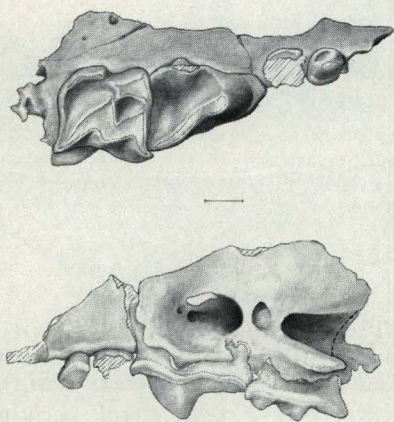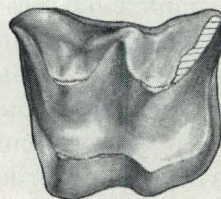

Figure 8. INGENTISOREX TUMIDIDENS, *gen. n. et sp. n., UO 22056, loc, 2465 (Quartz Basin), left maxilla with P^2-M^1, occlusal and right lateral views*

Figure 9. INGENTISOREX TUMIDIDENS, *gen. n. et sp. n., UO 21999, loc. 2465 (Quartz Basin), left M^1, occlusal view*

The M^1 is generally similar to the corresponding tooth in *Domnina, Paradomnina*, and *H. roperi*. It is nearly equidimensional or slightly longer than wide. The labial side is

In the lower jaw only the angular process and lingual portion of the condyle are not represented in the hypodigm. Posterior to the P^4, this jaw closely resembles Simpson's (1941) illustration of *D. thompsoni*; however, the coronoid process is proportionately wider and the ventral border of the ascending ramus is more
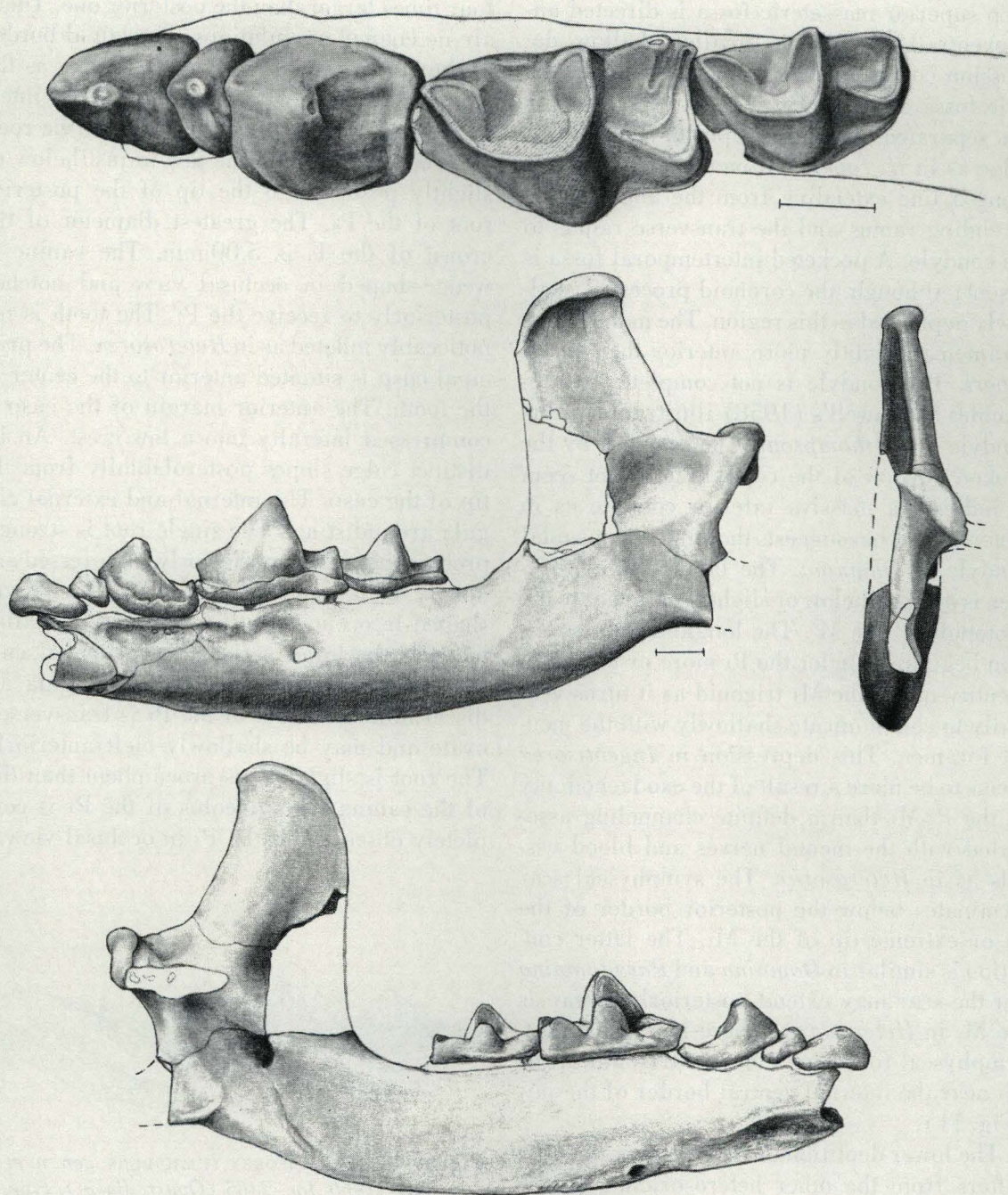
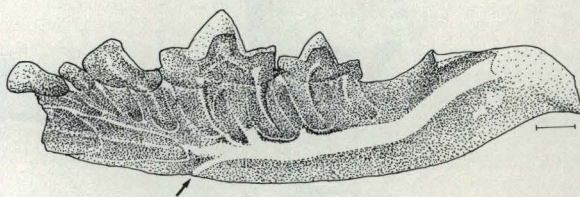**Figure 10.** INGENTISOREX TUMIDIDENS, *gen. n. et sp. n., UO 21960, loc. 2465 (Quartz Basin), type, left mandible with base of I₃ and C-M₂ occlusal, left lateral, posterior, and right lateral views*

dorsally situated than in *D. thompsoni*, thus constricting the inferior sigmoid notch. The deep superior masseteric fossa is directed anteroventrally above the smaller shallow depression corresponding to the inferior masseteric fossa of *H. roperi*. The inferior fossa is not separated from the superior fossa by a ridge as in *H. roperi* but merely drops into it along a line extending from the angle of the ascending ramus and the transverse ramus to the condyle. A pocketed intertemporal fossa is absent; although, the coronoid process is shallowly depressed in this region. The mandibular foramen is slightly more anterior than in *H. roperi*. The condyle is not complete, but resembles McDowell's (1958) illustration of the condyle of *D. thompsoni*. The scar left by the broken portion of the condyle does not seem to indicate a massive inferior condyle as in *Heterosorex*, but suggests the simple sinusoidal condyle of *Domnina*. The large mental foramen is directly below or slightly posterior to the protonoid of the M^1. The longitudinal depression beginning under the P_1 more or less loses identity under the M_1 trigonid as it turns ventrally to communicate shallowly with the mental foramen. This depression in *Ingentisorex* seems to be more a result of the exodaenodonty of the P_4-M_1 than a definite channeling associated with the mental nerves and blood vessels as in *Heterosorex*. The symphyseal scar terminates below the posterior border of the P_4 or extreme tip of the M_1. The latter condition is similar in *Domnina* and *Paradomnina* but the scar may extend posteriorly as far as the M_2 in *Heterosorex*. There is a small postsymphyseal foramen below the trigonid of the M_1 near the internal ventral border of the jaw (Fig. 11).

The lower dentition of *Ingentisorex* not only differs from the other heterosoricines in the absence of the M_3 but also the P_4 in this genus is comparable to the M_2 in size and importance. The I_3 is weak and relatively small when compared to that of *Heterosorex*. The anterior extremity of the crown is upturned; there are two well defined serrations between the an-

terior extremity and the posterodorsal margin of the crown. The anterior serration is about four times larger than the posterior one. There are no enamel crenulations. The labial border of the crown extends posteriorly as far as the anterior tip of the P_4. There is a deep interlocking groove on the lingual side of the root. The root extends into the jaw to just below or slightly posterior to the tip of the posterior root of the P_4. The greatest diameter of the crown of the I_3 is 5.00 mm. The canine is wedge-shaped in occlusal view and notched posteriorly to receive the P_1. The tooth is not noticeably inflated as in *Heterosorex*. The principal cusp is situated anterior to the center of the tooth. The anterior margin of the cusp is compressed laterally into a low crest. An indistinct ridge slopes posterolabially from the tip of the cusp. The internal and external cingula are indistinct. The single root is strongly procumbent, anteroposteriorly compressed and deeply cleft anteriorly. The P_1 is chevron-shaped in occlusal outline and is the smallest tooth of the lower series. The principal cusp is centrally situated and lateral cingula are discernible. The root of the P_1 is transversely ovate and may be shallowly cleft anteriorly. The root is slightly less procumbent than that of the canine. The alveolus of the P_1 is completely obscured by the P_4 in occlusal view.

Figure 11. INGENTISOREX TUMIDIDENS, *gen. n. et sp. n., UO 21960, loc. 2465 (Quartz Basin), type, X-ray of the mandible showing the postsymphyseal branch (arrow) of the mandibular canal*
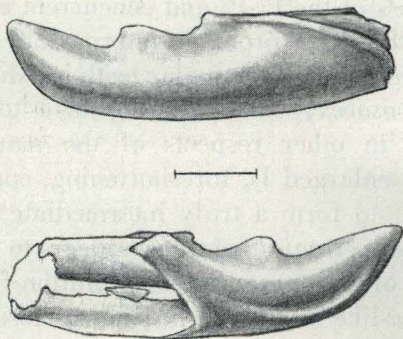
Figure 12. INGENTISOREX TUMIDIDENS, *gen. n. et sp. n., UO 24788, loc. 2465 (Quartz Basin), left I_3, left lateral and right lateral views*

The P_4 is massive and longitudinally subtriangular in occlusal outline. The inflated principal cusp is situated somewhat lingually and far forward. In occlusal view the labial side of the cusp is so greatly inflated that it protrudes beyond the margin of the external cingulum (exodaenodonty). The posterior half of the tooth is shallowly basined. The basin may be accentuated by low ridges curving laterally from the main cusp. A median ridge may also traverse the basin. There is a strong posterior cingulum, but the internal cingulum varies from well defined to nearly absent. There are two somewhat procumbent roots, both are anteroposteriorly compressed. The anterior root is smaller and lies beneath the main cusp; the large posterior root lies beneath the posterior cingulum and basin.

The M_1 is the dominant tooth in the jaw. The talonid is narrower and much shorter than the trigonid. There are narrow posterior and external cingula and an expanded anterior cingulum. The metalophid and paralophid are widely separated and not inflated as in *Heterosorex*. The protoconid is the tallest cusp and its labial wall is inflated greatly as in the P_4 so that it obscures the external cingulum in occlusal view. The paraconid is shorter than the metaconid and about equal to the entoconid. The entoconid is laterally compressed and nearly continuous with the hypolophid so that the post-

entoconid valley is very shallow or absent. The hypoconid is about one-half the height of the protoconid. Wear tends to accentuate the relative height of the protoconid. The two roots of the M_1 are directed slightly posteriorly and are about equal in size.

The M_2 is considerably reduced in comparison to the M_1 and volumetrically smaller than the P_4. It closely resembles the M_3 of *Domnina* and occupies the same functional position as the M_3 of most other shrews. The trigonid is more than half again as long as the talonid. The labial wall of the protoconid does not illustrate the pronounced exodaenodonty seen in the M_1. The M_2 is two rooted, the anterior root being the larger.

All of the specimens are stained black or dark brown thus masking the primary pigmentation that may have been present. Ultra-violet observations were ambiguous. No postcranial elements could be assigned to this form with any degree of assurance, thus nothing is known of the functional morphology of the skeleton.

RELATIONSHIPS: *Ingentisorex tumididens* is not closely related to any known genus but does share a number of characters with *Domnina*
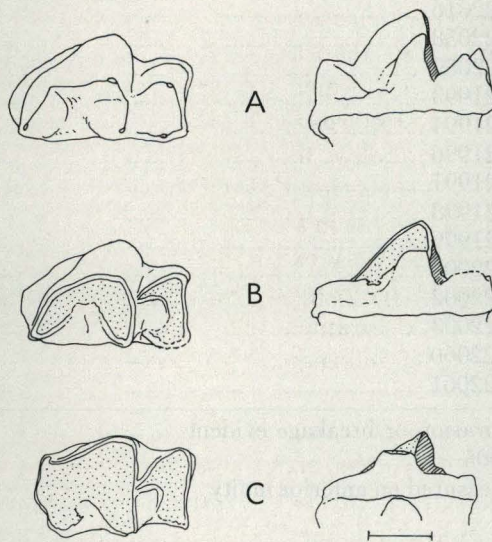
Figure 13. INGENTISOREX TUMIDIDENS, *three progressive wear stages of the right M_1, left lateral and occlusal views. A, UO 21969; B, UO 21992; C, UO 21988*

and *Heterosorex* as mentioned in the characterization of the sub-family. Most of the common traits appear to be a retention of primitive characters seen in *Domnina* and do not help in judging the nearness of relationships of the divergent lines. Unlike *Heterosorex*, however, there are no serious obstacles to the interpretation that *Domnina* is a structural ancestor to *Ingentisorex*. The P_4 is double rooted, proportionately larger and more procumbent than in *Domnina*, but this attribute may be the result

of the loss of the P_2-P_3 and concurrent expansion of the P_4. A probable intermediate stage in the reduction of the molar teeth is exhibited by *Heterosorex*; although, this genus is too specialized in other respects of the mandible (greatly enlarged I_3, foreshortening, complex condyle) to form a truly intermediate form. *Ingentisorex tumididens* thus appears to be the product of a separate line of evolution from a *Domnina*-like stock with no known close relatives.

TABLE 6

MEASUREMENTS OF THE UPPER DENTITION OF *Ingentisorex tumididens*

Specimen Number	P2 Lgth	P2 Wdth	P3 Lgth	P3 Wdth	P4 Lgth	P4 Wdth	M1 Lgth	M1 Wdth
UO 22056	0.99	0.94	......	......	3.46	2.00*	2.54	2.44
UO 22057	0.94	0.97	1.51	1.17	3.40	2.39	......	......
UO 22013	......	......	1.50	1.17	3.51	2.34	......	......
UO 22007	......	......	1.49	1.18	......	......	......	......
UO 22005	......	......	......	......	3.54	2.45	......	......
UO 22006	......	......	......	......	3.51	......	......	......
UO 22008	......	......	......	......	3.47	2.26	......	2.2
UO 22015	......	......	......	......	3.41	2.10	......	......
UO 22016	......	......	......	......	3.39-	2.26	......	......
UO 22058	......	......	......	......	3.46	2.15	......	......
UO 22059	......	......	......	......	3.56	2.39	......	......
UO 21993	......	......	......	......	......	......	2.53	2.16
UO 21994	......	......	......	......	......	......	2.49	2.44
UO 21996	......	......	......	......	......	......	......	2.36
UO 21997	......	......	......	......	......	......	2.50	2.36
UO 21998	......	......	......	......	......	......	......	2.50a
UO 21999	......	......	......	......	......	......	2.72	2.52
UO 22000	......	......	......	......	......	......	2.60	2.30
UO 22002	......	......	......	......	......	......	2.39	2.26-
UO 22003	......	......	......	......	......	......	2.52	2.21
UO 22060	......	......	......	......	......	......	2.61	2.26
UO 22061	......	......	......	......	......	......	2.60	2.43

* Abrasion or breakage evident
− 0.005
a Measured on anterior moity

TABLE 7

MEASUREMENTS OF THE LOWER JAW AND DENTITION OF *Ingentisorex tumididens*

PART I

Specimen	C Lgth	C Wdth	P1 Lgth	P1 Wdth	P4 Lgth	P4 Wdth	M1 Lgth	M1 Wdth	M2 Lgth	M2 Wdth	Depth Jaw
UO 21970	1.55–	1.18	0.90	1.14	2.14	1.54	3.18	1.65	2.10	1.22	2.62
UO 21960	1.53	1.27	0.89	1.20	2.08	1.64	3.01	1.87	2.27	1.33	2.58
UO 21967	......	......	1.00	1.28	2.11	1.74	3.18	1.90	2.20–	1.24	2.86
UO 21981	1.60	1.31	0.88	1.27	2.14	1.70	3.12	1.85	......	......	2.50
UO 21983	......	......	......	......	2.03–	1.59	3.20–	1.85	2.28	1.33	2.49
UO 21990	......	......	......	......	1.87	1.59	3.00–	1.82	2.17	1.24	2.53
UO 21972	1.53	1.22	0.99	1.16	1.96	1.59	......	......	......	......	2.68e
UO 21980	1.56	1.16	0.92	1.11	2.01	1.64	......	......	......	......	......
UO 21988	......	1.22	......	......	......	......	2.81	1.75	......	1.10	2.88
UO 21968	......	......	......	......	1.99	1.54–	......	......	......	......	2.33e
UO 21987	......	......	......	......	2.25	1.83	......	......	......	......	......
UO 21963	......	......	......	......	2.07	1.51	......	......	......	......	......
UO 21992	......	......	......	......	......	1.60–	3.07	1.84	......	......	2.71
UO 21958	......	......	......	......	......	......	2.90	1.80	......	......	......
UO 21964	......	......	......	......	......	......	3.02	1.77	......	......	......
UO 21966	......	......	......	......	......	......	3.08	1.82	......	......	......
UO 21969	......	......	......	......	......	......	3.11	1.78–	......	......	......
UO 21985	......	......	......	......	......	......	2.88	1.63	......	......	......
UO 21989	......	......	......	......	......	......	3.03	1.85	......	......	......
UO 21962	......	......	......	......	......	......	......	......	2.09	1.13	......
UO 21973	......	......	......	......	......	......	......	......	2.19	1.20	......
UO 21975	......	......	......	......	......	......	......	......	2.25	1.18	......

PART II

Specimen	M1-M2 Lgth	M2-P4 Lgth	M2-C Lgth	Height of Coronoid
UO 21960	5.11	7.00	8.83	7.55
UO 21970	5.13	7.03	8.90	7.61
UO 21967	5.13–	7.16	......	7.70
UO 21983	5.37	7.09	......	......
UO 21990	5.05	6.68	......	......
UO 21988	......	......	......	7.38

– 0.005
e estimated

Subfamily SORICINAE Murray, 1866

ALLUVISOREX ARCADENTES, gen. n., sp. n.[5]

GENOTYPIC SPECIES: *Alluvisorex arcadentes*, sp. n.

TYPE: UO 22307, left dentary with I_3-M_2, lacking M_3 ascending ramus and tip of I_3.

HYPODIGM: UO 22308, UO loc. 2465, left ascending ramus lacking ventral margin and tip of the coronoid process.

REFERRED SPECIMENS: UO 24280, UO loc. 2495, mandibular fragment with M_1-M_2.

TYPE LOCALITY: Quartz Basin, UO loc. 2465.

AGE: Barstovian.

DIAGNOSIS: Generic diagnosis same as for the type species. *Alluvisorex arcadentes* is separable from the Heterosoricinae on the construction of the condyle, presence of the intertemporal fossa, and other details of the teeth and ramus (see characterization of Heterosoricinae above). The posterolingual sulcus of the P_4, shape and possibly divided articular surface of the mandibular condyle, stocky lower molars, postmandibular foramen, anterior situation of the entoconid, high entoconid crest, and general robust appearance of the dentary indicate its affinities within the Soricinae. *Alluvisorex* is separable from all the modern and known Pliocene Soricinae on the presence of the P_3. It is distinguishable from other known Miocene soricines by the combination of the compact P_4, rectangular lower molars (occlusal outline), dental formula, posterior position of the mental foramen, and robust jaw.

DESCRIPTION AND COMPARISON: The type mandible is stained dark brown to black thus masking any primary pigmentation. The teeth are in a fairly early stage of wear. All the teeth except the M_3 are represented in the type. The tips of the I_3 and vestigial P_3 are lacking but

enough of the latter is evident to be sure of the dental formula; I1, C1, P2, M3. The horizontal ramus is broken through the posterior alveolus of the M_3 tending to accentuate the stocky appearance of the mandible. In labial view the antemolar region is quite restricted by the posterior location of the I_3 alveolus. The mental foramen is beneath the middle of the M_1, and the symphyseal scar extends posteriorly well beneath the M_1. The I_3 is relatively large and the molars are stocky and not notched on their labial margins. The P_4 is relatively small but has a distinct posterolingual valley or sulcus. These and other characters tend to align *Alluvisorex* with the Soricinae and in several cases with the more advanced soricines.

There are three distinct and laterally compressed serrations on the dorsolabial margin of the I_3. The canine is procumbent and overlaps the base of the crown of I_3. There is a single anteriad cusp from which anterior, posterolabial and posterolingual ridges arise. The posterolabial ridge is somewhat higher and sharper than the others and contributes to the tear-shaped wear pattern of the tooth in the early stages of wear. As on the I_3 there are deep but narrow internal and external cingula. The P_4, P_3, and canine are imbricate. The P_3 is vestigial and nearly all of the crown lies between the posterior ridges of the canine. The crown was apparently featureless except for being more globose centrally. The P_4 is relatively small and nearly equidimensional in occlusal measurements. The labial margins do not or just barely extend below the basal margins of the M_1 in contrast with a vast number of both soricine and crocidurine-like shrews. Ridges radiate from the principal cusp as on the canine, but the posterolabial ridge remains strong and posteriorly turns sharply toward the lingual side, thus forming a distinct but narrow posterolingual sulcus. The anterior margin of the tooth is truncate but the anterior boss, present on the P_4 of modern shrews, is functionally replaced by the small P_3. The molars strongly resemble those of *?Hesperosorex chasseae*, differing chiefly in the somewhat straight-

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[5] Etymology: From Latin *alluvius*, stream or river sediments, plus *sorex*, shrew-mouse, and the Latin *arca*, box, plus *dentes*, teeth, alluding to the rectangular lower molars.
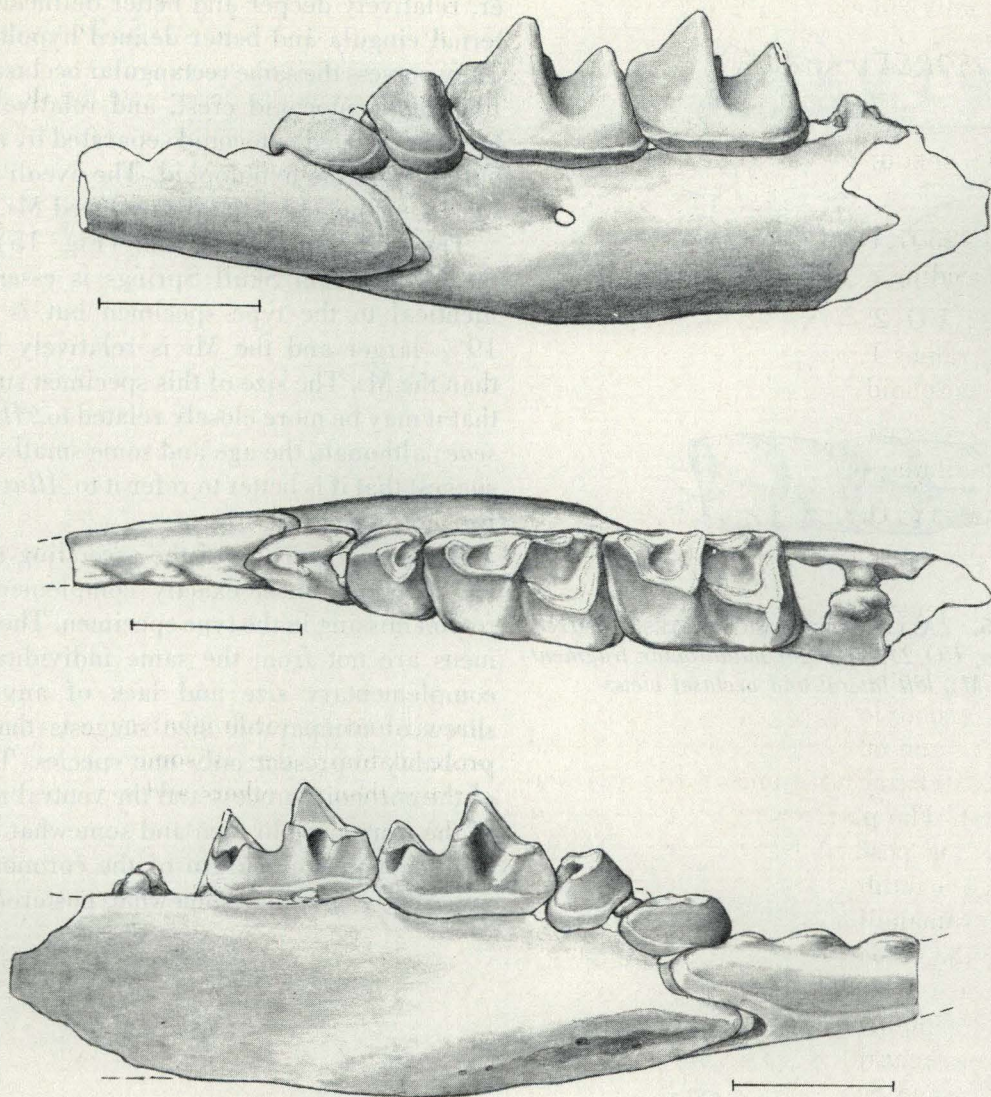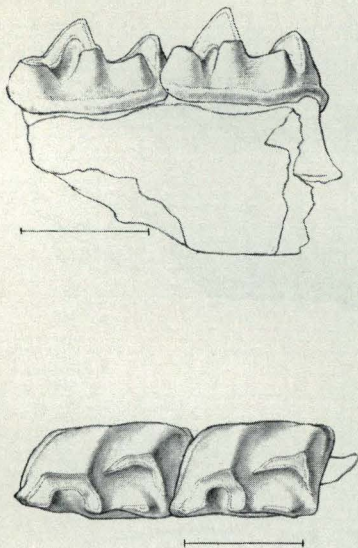
Figure 14. ALLUVISOREX ARCADENTES, *gen. n. et sp. n., UO 22307, loc. 2465 (Quartz Basin), type, left mandible with I₃-M₂, right lateral, occlusal, and left lateral views*

Figure 15. ?ALLUSIVOREX ARCADENTES, *referred specimen, UO 24280, right mandibular fragment with M_1-M_2, left lateral and occlusal views*

er, relatively deeper and better delineated internal cingula and better defined hypolophid. They possess the same rectangular occlusal outline, high entoconid crest, and relatively anteriorly situated entoconid separated by a wide valley from the hypolophid. The aveoli of the M_3 do not suggest a greatly reduced M_3.

The mandibular fragment (Fig. 15) with the M_1-M_2 from Skull Springs is essentially identical to the type specimen but is about 19% larger and the M_1 is relatively longer than the M_2. The size of this specimen suggests that it may be more closely related to *?H. chasseae*; although, the age and some small details suggest that it is better to refer it to *Alluvisorex* for the present.

The major portion of the ascending ramus, UO 22308, almost exactly complements the region missing in the type specimen. The specimens are not from the same individual, but complementary size and lack of any other shrew of comparable size suggests that they probably represent only one species. The tip of the coronoid process and the ventral margin of the ramus are broken and somewhat abraded. The anterior margin of the coronoid was apparently directed somewhat posterodorsal.
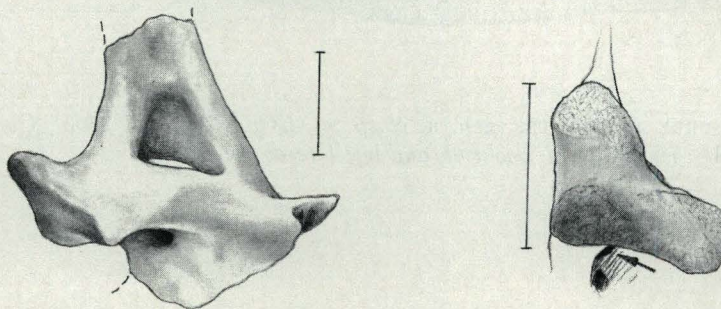
Figure 16. ALLUVISOREX ARCADENTES, *gen. n. et sp. n., UO 22308, loc. 2465 (Quartz Basin), left ascending ramus, right lateral view and posterior view of condyle*

The intertemporal fossa is subtriangular in outline. The condyle is stout and set close to the body of the ramus, but it is not continuous with it as in *Blarina* and *Cryptotis*. There has been some abrasion of the condylar facets so that it is difficult to distinguish with certainty whether the facets were continuous or separated. Slight textural differences suggest that the articular surface was differentiated into superior and inferior facets. The mandibular foramen opens out beneath the neck of the condyle and is nearly but not quite confluent with a small post-mandibular foramen that extends dorsally into the intertemporal fossa. This latter condition is not uncommon within the Soricinae, especially in some of the more specialized forms such as *Blarina, Cryptotis, Blarinella, Petenyia*, etc.

TABLE 8

MEASUREMENTS OF THE LOWER DENTITION
AND JAW OF TYPE OF *Alluvisorex arcadentes*
AND REFERRED SPECIMEN

Measurement		UO 22307	UO 24280
I3:	Length of Crown	2.03	......
	Width	0.51	......
C:	Length	0.75	......
	Width	0.45*	......
P1:	Length	0.19	......
	Width	0.30	......
P4:	Length	0.59	......
	Width	0.54	......
M1:	Length	1.24	1.53
	Width	0.72	0.85
M2:	Length	1.22	1.40
	Width	0.67	0.80
M1-M2 Length		2.29	2.735
C-M2 Length		3.34	......
Depth of jaw below M1		1.1	......
Depth of jaw below M2		1.1	1.3

* Breakage

RELATIONSHIPS: Of the North American fossil shrews, *Alluvisorex arcadentes* compares most closely with *?Hesperosorex chasseae* Tedford (1961). The most marked similarities of these two forms are the position of the mental foramen and the morphology of the molars. The forms differ in a number of important features —some of which may be of ancestor-descendant evolution. *?H. chasseae* lacks the P3, the P4 is relatively longer (in response to the lack of the P3?), and there are fewer and more elongate serrations on the I3. Unfortunately nothing is known of the ascending ramus of *?H. chasseae* so that further comparisons cannot be made. If *Hesperosorex* is as close to *Notiosorex* as Tedford suggests, then *Alluvisorex* should differ quite markedly from *?H. chasseae*. The condyle and ascending ramus of *Notiosorex* is markedly different from that of *Alluvisorex*. I believe that the suggested closeness of *?H. chasseae* is far from demonstrated; in fact, Tedford's own comparisons lead me to think that there are no particularly close relationships between *?H. chasseae* and either *Hesperosorex lovei* or *Notiosorex*. Part of this difficulty may arise because Tedford was not able to compare *?H. chasseae* with the type of *Hesperosorex* and was forced to rely on the somewhat sketchy figures of Hibbard (1957). Repenning (in press) places *?H. chasseae* near *Blarinella* and *Petenyia*; therefore, by extension *Alluvisorex* is also related, but more distantly, to these Eurasian forms.

Subfamily CROCIDURINAE Milne Edwards, 1868-1874

cf. *LIMNOECUS* sp. indet.

A single broken and crushed ascending ramus, UO 24284, of a very small shrew was recovered from the Skull Springs locality. It is too small to be referred to *Alluvisorex*. In the features that may be adequately compared, it is almost identical to *Limnoecus tricuspis* Stirton, although smaller. The superior and inferior condylar facets are confluent lingually as in *L. niobrarensis* Macdonald and *L. vireti* (Wilson). The intertemporal fossa is subtriangular and not ovoid as in Wilson's (1960) illustration of "*Sorex*" *compressus*. The Skull Springs specimen is tentatively referred to *Limnoecus* on the basis of these similarities and proximity of age.
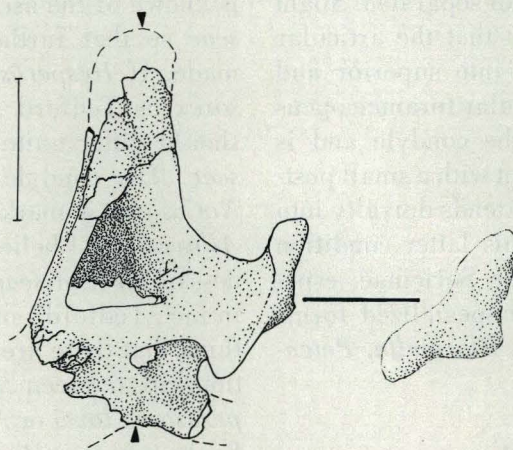
Figure 17. Cf. LIMNOECUS *sp. indet., UO 24284,*
loc. 2495 (Skull Springs), left lateral view of right
ascending ramus and posterior view of condyle

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