Subfamilies and Genera of the Soricidae

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By CHARLES A. REPENNING

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Classification, historical zoogeography,
and temporal correlation of the shrews

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CONTENTS

Diagnoses and contents of subfamilies—Continued

ILLUSTRATIONS

[Figs. 1–41 are drawings of the Soricidae]

SUBFAMILIES AND GENERA OF THE SORICIDAE

By Charles A. Repenning

ABSTRACT

The shrews constitute a distinct and uniform but phylogenetically diverse family in which five subfamilies, one subdivided into three tribes, can be recognized by consistent morphologic differences. These differences are traceable back through the late and middle Tertiary shrews and point to a hypothetical common ancestor. The trends of the morphologic change within the subfamilies rather clearly indicate what this ancestor should look like. Because the great majority of fossil shrews are represented only by teeth and mandibles, the morphologic characters here used to classify most shrews pertain to these parts of the animals.

The extinct subfamily Heterosoricinae is known from the Oligocene to the Pliocene and in both the Old and the New Worlds. Four genera are recognized in North America; one of them is known also from the Old World. At least 12 species are included in these genera. The subfamily is not closely related to other shrews, and all shrews in the subfamily lack an internal temporal fossa on the mandible, have extreme lingual offset of the lower mandibular articulation, and retain at least some pigmentation in the teeth.

The living subfamily Crocidurinae is known from the middle Miocene to the Recent in the Old World. In the subfamily are 11 to 13 fossil species and 10 living genera. The subfamily appears most likely to be of Austro-Tethyan origin (mainly Ethiopian Africa and peninsular India) and is not well represented in the known fossil record. It is characterized by an internal temporal fossa on the mandible, by little or no separation of the articular facets on the mandibular condyle with a labial emargination of the interarticular area, by the retention of a primitive triangular P_4, and by no pigmentation of the teeth.

The extinct subfamily Limnoecinae is known from the early Miocene to the middle Pliocene in North America and closely parallels the Old World crocidurines in morphology. Two genera and three species are recognized. The subfamily is characterized by crocidurine features except that P_4 is modified from a triangular tooth to one in which a central crest runs from the apex of the single cusp to the posterior cingulum; at least some pigmentation is present in the teeth.

The living subfamily Soricinae is known from the late Oligocene to the Recent in the Old World and from the early Miocene to the Recent in North America. It is characterized by an internal temporal fossa on the mandible, by little to great separation of the articular facets on the condyle of the mandible with a lingual emargination of the interarticular area, by the modification of the primitive triangular cusp of P_4 into a labial shearing blade with a posterolingual basin, and by retention of tooth pigmentation in most, but not all, genera. This subfamily is very large and is divisible into three tribes largely on the basis of masticatory modifications; this basis of separation is supplemented by characters in the teeth. The tribe Soricini contains at least 3 extinct genera, about 30 extinct species, and 4 living genera. It is characterized by little modification of its mandibular articulation or teeth and by a prominent entoconid crest on M_1. The tribe Blarinini contains at least 4 extinct genera, 10 extinct species, and 2 living genera. It is characterized by slight to great modification of its mandibular articulation with a broad interarticular area, no entoconid crest on M_1, and by a trapezoidal M^2. The tribe Neomyini contains 4 fossil genera, 13 fossil species, and 9 living genera. It is characterized by great modification of its mandibular articulation with a narrow interarticular area, an entoconid crest on M_1 in most forms, and a prominent bifid upper incisor in most Old World forms.

The extinct subfamily Allosoricinae is known from the late Miocene to the late Pliocene in Europe. It is characterized by unusual carnivorelike cheek teeth that are unequaled in specialization by any other shrew. Two genera (one unnamed) are included in this subfamily.

INTRODUCTION

The living shrews are generally placed in two subfamilies with the exception of the African armored shrew *Scutisorex*, which some workers (for example, Allen, 1917) have placed in a separate subfamily. The Soricinae are holarctic in distribution, and the Crocidurinae are entirely of Old World distribution and largely tropical. As stated by Ellerman and Morrison-Scott (1951, p. 41), this division into two subfamilies "seems to be based chiefly on the Soricinae having teeth pigmented at the tips, and the Crocidurinae having teeth entirely white." These authors, Friant (1947), and several others have pointed out that, although the Soricinae normally have pigmented teeth, pigmentation in the subfamily is variable—very light in several genera and entirely missing in a few genera. Because of this variability, several zoologists, including Ellerman and Morrison-Scott (1951) and Heim de Balsac and LaMotte (1956, p. 141–142), have not recognized subfamilies of the Soricidae; however, others, including Friant, have recognized them.

In considering fossil shrews, there has been a similar tendency to abandon the subfamilies of living shrews (Hibbard, 1950, p. 129; and Viret and Zapfe, 1951, p. 414). With the study of fossil shrews, however, greater attention has been directed toward additional criteria to recognize suprageneric taxa within the Soricidae. Although he preferred to consider his groups as of less than subfamily rank, Stirton (1930, p. 223–225) reviewed and grouped many of the living shrews to evaluate a Miocene fossil. He selected five divisions of the family, which he called groups, on the basis of eight features (10 features for the *Anourosorex* group). Those features that Stirton used to distinguish his groups include tooth pigmentation, shape of the internal temporal fossa of the mandible (fossa pterygoidea, intertemporal fossa, or posterointernal ramal fossa of authors), degree of separation of the condyles of the mandible (or articular facets on the condyle), height of tooth cusps, separation of the tips of the protoconid and the metaconid, position of the foramen ovale, form of the talonid of M_3, and nature of the entoconid and basin of the talonid of M_1 and M_2.

Earlier Schlosser (1924, p. 5) suggested that the absence of secondary cuspules on the cutting edge of the lower incisor and the shape of the ascending ramus of his species *Crocidura kormosi* were distinctive of the genus. Still earlier Miller (1912, p. 30, 86) pointed out that the Crocidurinae could be separated from the Soricinae on the basis of the structure of P_4. Lavocat (1951, p. 23–24), following Miller's criterion, seems to have been one of the first to place much significance on the morphology of P_4 in fossil shrews. He regarded his *Crocidosorex piveteaui* as intermediate between *Crocidura* and *Sorex* largely on the basis of the form of P_4. Wilson (1960, p. 35, 36, 38) also placed emphasis on the form of the P_4 in *Sorex*. The slightly more anterior average position of the mental foramen in the Crocidurinae has also been mentioned by several authors as of possible value in distinguishing this subfamily from the Soricinae.

Therefore, it seems that there are a large number of dental and mandibular features that may be useful in separating the Crocidurinae from the Soricinae besides tooth pigmentation, which has been considered to be a fallible criterion. Cranial and postcranial skeletal features, as well as criteria based upon the soft parts, may also be useful, but with very few exceptions these are not known in the fossil record. A review of the above features, of the dental formulae, and of the morphology of P^4 and M^1 in most fossil species and in most living genera leads to the conclusion that subfamilies are recognizable in both living and fossil shrews. Five subfamilies are clearly recognizable in the fossil record: the Crocidurinae and the Soricinae, representing the surviving subfamilies; and the Heterosoricinae, the Allosoricinae, and the Limnoecinae (new name), representing extinct groups of subfamily rank. The living subfamilies are of approximately equal size; there are 21 soricine species and 21 crocidurine species in the Palearctic and Indian regions (Ellerman and Morrison-Scott, 1951), no soricines occur in Africa, and there are no crocidurines in North America.

Specimens of nearly all North American fossil shrews older than Pleistocene were examined during this review as were specimens representing all but two[1] living genera of the world; however, specimens of only six Old World fossil species were examined. In this review the description of Old World fossil forms is largely from published accounts. Such a review has obvious disadvantages as the criteria here utilized are not always discussed or clearly figured in published descriptions. For this reason little attempt to revise the nomenclature of the Old World fossil shrews is made, although they are placed in the subfamilies which seem most appropriate as based upon published descriptions. The specimens examined are listed in the discussion of the taxa they represent.

Subfamily, tribe (where applied), genus, and many extinct species diagnoses are given in terms of the criteria here used. For many shrews, particularly for the living genera, other criteria are available in the literature to enlarge the diagnoses but these criteria are not mentioned here because they cannot be applied uniformly to both living and fossil shrews. This does not imply that other criteria are not valid or useful.

The illustrations are somewhat stylized but were done carefully with a camera lucida attached to a microscope. There is an advantage in having all forms illustrated by the same technique and by one person. The illustrations are not drawn to a uniform scale because size has appeared to be of no more than specific significance. When possible, P_4, M_1, and M_3 are shown in both occlusal and buccal view; P^4 and M^1 in occlusal view. M_2 almost always parallels the development of M_1 and hence is not shown in the illustrations, even of types. In the few shrews where M_2 shows noticeable difference from M_1, the difference is noted in the text. The mandible is drawn in lingual view, and the condyles of the mandible are shown in posterior view.

Embryological studies to determine the dental formulae of the soricids in terms of incisor, canine, premolar, and molar teeth (Ärnbäch-Christie-Linde,

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[1] *Feroculus* and *Solisorex* from Ceylon. Photographs of British Museum (Natural History) specimens of these genera were examined.

1912; Kindahl, 1960) are not in entire agreement and the formulae seem to vary with the genus under study. Although this work is certainly important in evaluation of the phylogeny of the Soricidae, it has not been considered in this review. Dental formulae given in this report are arbitrarily based upon the frequent use of the term "antemolar" in published descriptions of shrews. The term applies to those teeth between the soricid incisor and the molars. The formula used is:

$$\text{Total}=\frac{\text{soricid incisor–antemolars including } P^4\text{–molars}}{\text{soricid incisor–antemolars including } P_4\text{–molars}}$$

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EVALUATION OF CHARACTERS

Of the features observed in the dental and mandibular morphology during this review, the structure of the P_4 is most useful in the recognition of subfamilies. (See fig. 1.) The structure of the mandibular condyle is nearly as useful, and pigmentation of the teeth seems significant but is subject to exceptions. The absence of the internal temporal fossa is a subfamily character of the Heterosoricinae. The other morphologic characters, when considered singly, appear to be of taxonomic value only after the identity of the subfamily has been established. In combination, most characters may be mutually supporting of subfamily assignment, and some are of subfamily importance when developed to an extreme degree. Most appear to represent evolutionary trends in several shrew lineages that are parallel in direction but not equal in rate of change.

During this review it has been found that in the characters here examined the shrews are remarkably stable in comparison with other mammals. Unless otherwise noted, the reliability of these characters does not seem to be reduced by individual variability. Atavism is rather rare although it does occur in living and presumably in fossil forms.

Structure of P_4

Domnina gradata Cope (Patterson and McGrew, 1937) is, in several respects, including the structure of the P_4, ideal as the prototype of all soricids. In other respects it is clearly a heterosoricine shrew. In occlusal view the P_4 of *D. gradata* has a simple equilaterally triangular outline and a single large triangular cusp (figs. 1, 3). There is a posterior basal cingulum that extends nearly to the anterior corner of the tooth on both the lingual and the labial sides. Although the cingulum is prominent at the posterolabial corner, it does not overhang the root and cover the alveolus as in most modern shrews. The posterior surface of the crown slopes uniformly to the cingulum and is slightly concave between the posterolateral corners of the crown. The posterolateral corners of the triangular cusp are sharp so that slight ridges run from the apex of the cusp to the cingulum at the posterolabial and posterolingual corners of the tooth. The P_4 is the largest tooth of the antemolar series with the exception of the procumbent incisor and possibly the first antemolar, which is unknown. The antemolar alveoli of some species of *Trimylus* are similar to those of *Domnina gradata*, but P_4 is not the largest post-incisor antemolar in *Trimylus*.

Domnina is here placed in the subfamily Heterosoricinae on the basis of features other than the crown of P_4. The P_4 in the genera *Trimylus* and *Ingentisorex* appear to be similar to that of *Domnina* except that details of the cingulum and cusp morphology have been lost in the development of a rounded, bulbous tooth. The P_4 of *Paradomnina* is like that of *Domnina*.

The basic triangular pattern that is retained in the Crocidurinae differs only slightly from that in *Domnina*. In the Soricinae, however, the crown is converted into an oblique blade by emphasis of a crest connecting the anterior cusp with the cingulum at the posterolabial corner of the tooth and by suppression

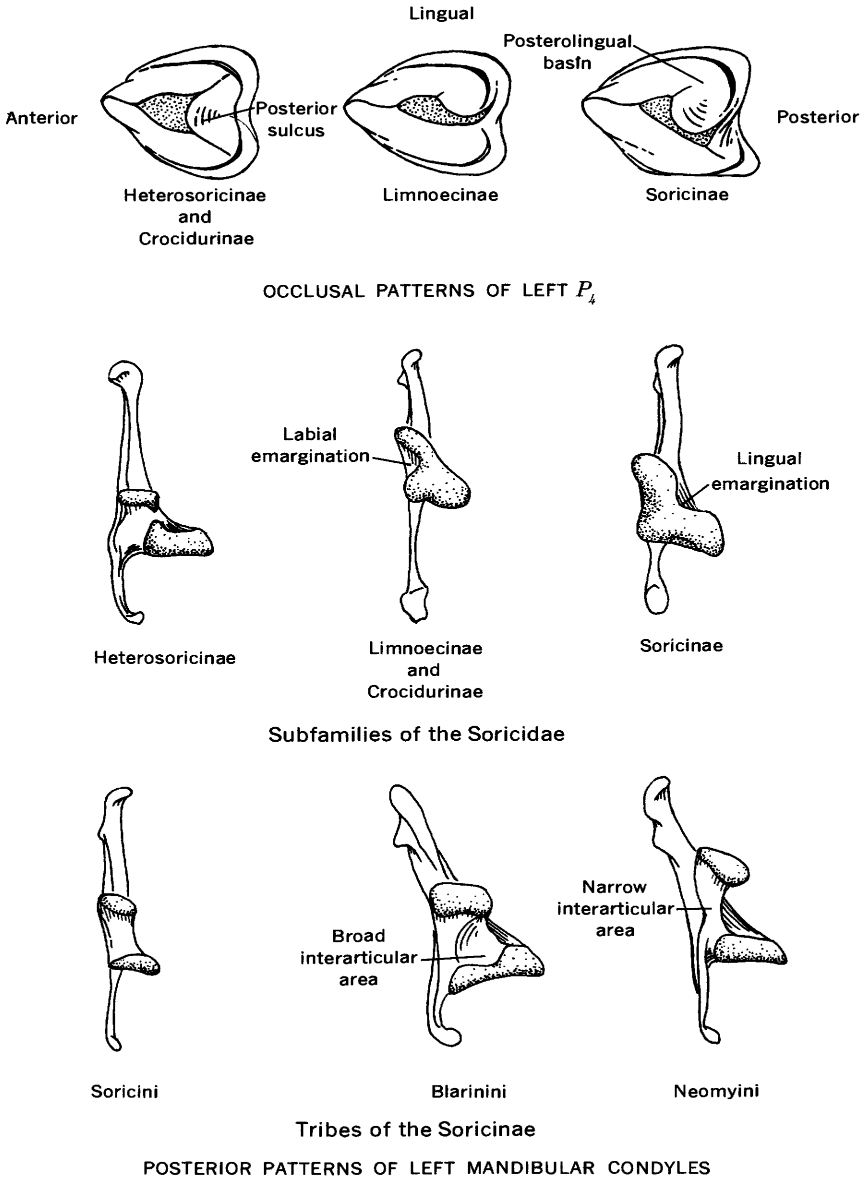

FIGURE 1.—Taxonomically significant differences in structure of P_4 and mandibular condyles.

of the anteroposterior lingual crest and development of a basin in its place. In most soricines the labial blade combines with the posterior cingulum to form a continuous L-shaped crest which encloses the posterolingual basin on both labial and posterior sides. The labial crest of the triangular P_4 is also accentuated in the Limnoecinae, but it has shifted lingually nearly to a median position. The lingual crest of the triangle is almost completely suppressed but no posterolingual basin has formed because of the medial position of the labial crest.

These basic patterns of the P_4 are diagrammatically shown in figure 1. With few exceptions these patterns are clearly recognizable in all shrews considered in this review. The exceptions are all within the group of heavy-toothed and stout-jawed soricines where other characters, such as widely separated mandibular condyles, leave no doubt of subfamily affinity.

No soricid has ever developed a molariform P_4, and for this reason the late Eocene *Saturninia gracilis* Stehlin (1940), which has a well-developed trigonid and talonid in its P_4, cannot be considered ancestral to any shrew; as recognized by Stehlin (1940, p. 306), *Saturninia* appears to be an erinaceoid similar to *Leptacodon*.

Pigmentation

Pigmentation in soricid teeth seems to be remarkably stable insofar as fossilization is concerned and is usually preserved even in Oligocene specimens. It may be obscured, however, by coloration of the entire tooth during fossilization or altered to such a degree that it is not visible in normal light. In some genera, when its presence is not detectable in ordinary light, it can be seen under ultraviolet light as described by Patterson and McGrew (1937, p. 247). Hibbard (1950, p. 128) noted that reaction of pigmentation to ultraviolet light is not consistent in either Recent or fossil specimens that he examined.

In many shrews, pigmentation is present only at the tips of the cusps and along the crests of the lophs so that heavy wear removes all pigmented parts of the tooth. Although pigmentation is usually of a very conspicuous color, the teeth of some shrews, like *Nectogale*, are pigmented over much of their surface, but the pigmentation is of such a light value and slight saturation that it may be overlooked. Apparent lack of pigmentation in a fossil shrew, therefore, must be evaluated cautiously, particularly if the teeth have been darkened by fossilization.

Nevertheless, pigmentation is an important character in the recognition of the subfamilies of the Soricidae. The teeth of *Domnina gradata* are extensively pigmented (the pigment is a pale yellowish orange), indicating that pigmentation was acquired early in the history of the Soricidae (Patterson and McGrew, 1937, p. 247) or was inherited from the soricoid ancestor of the family. In *Trimylus*, pigmentation is present but restricted; it is certainly present on the lower incisor, on P_1, and on the upper incisor. In the Crocidurinae and in the Allosoricinae, tooth pigmentation is lost. In the Limnoecinae it seems to be present in most specimens, but Macdonald (1947, p. 125) and also Hibbard (1957, p. 329) stated that *Limnoecus niobrarensis* Macdonald shows no pigmentation. James (1963, p. 36) pointed out, however, that in Macdonald's type the teeth are worn to a level beneath the base of the pigmented area on other specimens of the genus. In the Soricinae, pigmentation is characteristic but is very light in some genera and absent in a few; some soricines have been classified as crocidurines because of the lack of tooth pigmentation.

Internal temporal fossa of the mandible

This fossa (also called *fossa pterygoidea*, intertemporal fossa, and posterointernal ramal fossa by other authors) is not pocketed in the Heterosoricinae (fig. 2). It is deeply pocketed in all other subfamilies (figs. 8–41), and in these groups its form seems to be of no more than generic importance as far as diagnosis of most shrews is concerned.

The soricid internal temporal fossa is a consequence of the loss of the zygomatic arch and much of the masseter muscle. The internal part of the temporal muscle assumes the function of the masseter in this situation, and its insertion on the medial side of the coronoid process is enlarged and is shifted ventrally, to a level approximating that of the masseter in other mammals, for a more masseterlike force and leverage. Loss of the zygomatic arch and development of the internal temporal fossa also are associated with loss of the masseteric fossa on the lateral side of the mandible, for the same reason. With the exception of heterosoricines, no shrew has a masseteric fossa; also, the heterosoricines do not have a soricine internal temporal fossa and have retained a reduced zygomatic arch.

Patterson and McGrew (1937, p. 256–257), apparently in a lapse of memory while thinking of the internal temporal fossa, stated that a deep masseteric fossa "extending downward much nearer the ventral margin of the jaw" (than in the bat *Miniopterus*) is a soricid character. This and several other features led them to place the genus *Mystipterus* Hall in the Soricidae rather than in the Chiroptera. The deep masseteric fossa of *Mystipterus* clearly indicates, however, that the animal has a normal mammalian masseter system because the fossa cannot form without the masseteric muscle.

Hall's illustration (1930, pl. 38b) shows that the masseteric fossa of *Mystipterus* is well developed, and his opinion that the genus is a bat seems much more reasonable than other opinions which label it a shrew. The lack of reduction in the size of the talonid of M_3 (the only tooth known) and the full development of the V-shaped pattern on the talonid and on the trigonid of M_3 suggest, however, that *Mystipterus* may be a talpid. It resembles *Mydecodon martini* Wilson (1960, fig. 32) and is somewhat less like the living *Neurotrichus*.

Mandibular condyle

Domnina (*D. thompsoni* Simpson, see McDowell, 1958, p. 181–182, fig. 30E) has virtually one broad mandibular condyle which is constricted and offset in its center foreshadowing the doubled articular facets of later soricids. Separation, to form two articulations, has chiefly taken place in the early Miocene shrews although in some the articular facets may still be joined. This situation is little changed in the later limnoecines and in the modern crocidurines. Some of the living soricines and the extinct allosoricines have greatly accentuated the separation of the facets.

On many mandibular condyles it is difficult to clearly distinguish the extent of the articular facets. Compare, for example, the variations in interpretation of the facets on *Limnoecus niobrarensis* made by Hibbard (1957, fig. 3A), by James (1963, fig. 9c), again by James (1963, fig. 11), and in this report (fig. 18). All were made by careful examination of the same specimen.

There are three basic patterns to be seen in the mandibular condyles of the shrews (fig. 1). In nearly all shrews these are recognizable regardless of the degree of separation of the articular facets, regardless of the vagueness of the limits of the articular surfaces, and regardless of the antiquity of the shrew considered insofar as the present record is known.

In the subfamily Heterosoricinae the lower articular facet of the mandibular condyle is not much offset ventrally from the upper facet (more so in *Trimylus* than in *Domnina*) but is placed lingually to an extreme degree so that virtually no part of the lower facet lies below the upper facet. This situation is not found in any other subfamily.

In the subfamilies Crocidurinae and Limnoecinae, the lower facet of the mandibular condyle is beneath the upper, and the two facets are continuous along the lingual side of the posterior face of the condyle. If separated, an elevated and usually rounder bridge on the lingual side of the posterior face of the condyle, the interarticular list of Sulimski (1959, p. 128–129), connects the two facets, and there is an excavation of the interarticular area on the labial side of the posterior face of the condyle. This condylar structure is invariable in these two subfamilies but in a few shrews, as in the giant species of *Suncus*, the articulating surface connecting the upper and lower facets is so broad that it is impossible to decide whether the interarticular excavation is on the lingual or labial side of the posterior face of the condyle.

In the subfamily Soricinae the lower facet is below the upper in posterior view, and the two facets are continuous along the labial side of the condyle. If separated, as they are in all known forms younger than middle Miocene, the two articular facets are connected by an interarticular list that is on the labial side of the posterior face of the condyle, and the lingual side of the interarticular area is excavated. This pattern is also invariable, but the position of the articular surfaces is otherwise greatly variable in the subfamily, largely in degree of anterior placement of the lower facet. This variation in articulation is not known in other subfamilies, the most extreme exceptions being in the extinct crocidurine *Diplomesodon fossorius* Repenning (1965) and on the extinct allosoricine *Allosorex stenodus* Fejfar (1966).

Height of cusps

There is a general trend throughout the soricids to increase the crown height in the evolution of the separate lineages, except in the Heterosoricinae; however, relative cusp height is difficult to judge. In this review it has been found easier, in most shrews, to estimate the stage of evolution by observing the relative height above the labial cingulum at which the bottom of the reentrant valley between the protoconid and the hypoconid opens on the labial side of M_1. In *Domnina* and the many earlier Miocene shrews, this reentrant opens at or very close to the level of the cingulum. In many of the more advanced forms, there is an appreciable distance between the reentrant and the cingulum. In many living shrews, however, this is not so and the value of this character is quite variable with different lineages. Although partly related to cusp height, this feature may also be related to a tendency of the metalophid-protolophid junction to shift slightly labially in geologically later genera.

Heel of M_3

Reduction of the talonid of the M_3 in *Crocidura* to a single trenchant cusp has frequently been cited as a character distinctive of the crocidurines. It is prevalent in this subfamily but is also found in some soricines, like *Cryptotis*. It also occurs in the Limnoecinae but not in the Heterosoricinae. The heel of M_3 is virtually lost in a few shrews, and the entire M_3 is missing in five genera.

Position of the mental foramen

The mental foramen lies beneath the middle of M_1 or the anterior root of M_2 in the Heterosoricinae; beneath P_4 to beneath the anterior root of M_1 in the Crocidurinae; beneath or slightly ahead or behind the anterior root of M_1 in the Limnoecinae; and in the Soricinae beneath the middle of M_1 in most Miocene to Recent species examined but beneath the P_4 in *Crocidosorex* and in *Antesorex*, new genus, of the late Oligocene to early Miocene. In all lineages it tends to have shifted posteriorly in geologically younger forms. The position of the foramen seems fairly constant within the subfamilies but the overlap in position between subfamilies is great. In addition there have been a very few individuals of living shrews noted during this review that have either doubled mental foramina or have the mental foramen significantly anterior to its position in other individuals from the same local population.

In the figures, the mental foramen is usually shown with the labial view of the lower teeth. These teeth are generally separated for clearer illustration, and a line is shown between the foramen and the tooth (either P_4 or M_1) with which it is properly oriented.

Closeness of the protoconid to the metaconid on M_1

Stirton (1930, p. 244) cited the closeness of these two cusps in his "Crocidura group" as being distinctive. Although it seems that it might reflect the height of cusp to some degree, it does appear to be characteristic of the living crocidurines and particularly of the extinct limnoecines. I have had considerable difficulty in making the comparison with even moderately worn teeth and consider it virtually impossible to judge the closeness of these cusps in figures of worn teeth. As a consequence, the character has not been considered to be of much value in this review except where the two cusps are obviously close. In many shrews where it seems of importance, an anterior view of M_1 is figured.

Structure of P^4 and M^1

There appears to be no subfamily distinctiveness in these teeth other than for the Heterosoricinae. This subfamily is alone in the absence of an emargination of the posterior basal outline of the tooth in all forms and in the consequent failure to develop a posterior projection of the hypoconal flange. This structure is otherwise characteristic of most, but certainly not all, genera of the Soricidae.

Miscellaneous features

Secondary cuspules on the cutting edge of the lower incisor seem to have no significance in subfamily characterizations or in evolutionary patterns. The dental formulae show a broad trend toward reduction in number of antemolars, but the trend cannot be correlated with subfamily distinctions. Overlap of the alveolus and part of the ramus by the labial cingulum of P_4 is most extreme in some soricine genera but is present to some degree in both limnoecine and crocidurine shrews. A prominent entoconid on M_1 is characteristic of most shrews, but its variation in prominence and in position seems to be a tribal or generic character. A depression on the labial surface of the horizontal ramus in the region of the mental foramen is also a generic character in the Heterosoricinae and in some Soricinae. A bifid or fissident upper incisor is conspicuous in the Heterosoricinae and in the tribe Neomyini; and is slightly developed in many incisors in the tribe Soricini. It is known in only one genus of the Crocidurinae. This feature is formed by a smaller cusp branching from the medial side of the principal (anterior) hooklike cusp of the falciform first upper soricid incisor. The occlusal outline of M^2, and the position of the zygomatic process of the maxillary relative to M^2, the nature of development of the superior pterygoid fossa of the mandible, the extent of the external temporal fossa of the mandible, and a few other features are characters of tribal significance in the Soricinae.

DIAGNOSES AND CONTENTS OF SUBFAMILIES

Subfamily HETEROSORICINAE Viret and Zapfe, 1951

P_4 has triangular cusp, little or no posterior sulcus on cusp, and root transversely broadened or even doubled in most species; M_1 low cusped—reentrant between protonid and hypoconid opens at level of cingulum; M_3 has double-cusped or crescentic talonid (this tooth is absent in *Ingentisorex* from the late Miocene of Oregon); P^4 and M^1 have no emargination of posterior basal outline and no posterior projection of hypoconal flange; in *Trimylus*, M^2 is trapezoidal and the zygomatic process of maxillary originates opposite it, but in the less specialized *Domnina*, M^2 is rectangular and the zygomatic process originates behind this tooth; tooth pigment present at least to some degree; masseteric fossa well developed; internal temporal fossa lacking or very shallow and never pocketed; ventral condyle of mandible offset lingually much farther from plane of mandible at lower sigmoid notch than in any other subfamily of shrews and at approximately right angles to vertical axis of horizontal ramus; mental foramen below middle of M_1 to below anterior root of M_2 and usually associated with depressed area on labial face of mandible or with groove running anterodorsad from foramen to region of P_4, or both; a small foramen of unknown function (Mawby, 1960, p. 955) on lingual face of mandible near inferior margin below M_1 or M_2; medium to very large size; early Oligocene to late Miocene, North America; middle Oligocene to early Pliocene, Europe. "*Sorex*" *kinkelini* Zinndorf (1901) appears to be from middle Oligocene (Rupelian) deposits. The specimen is a lower incisor that clearly represents *Trimylus*, but the species is not definable. As noted by Zinndorf (p. 134), it is closest to *Trimylus neumayrianus*.

Genus DOMNINA Cope, 1873

Genotype: *Domnina gradata* Cope, 1873

P_4 triangular in occlusal view with sharp-cornered triangular cusp; M_1 has very prominent entoconid distinctly separated from hypolophid and united to metaconid by high ridge (entoconid crest); teeth not bulbous; cingulum strong but not inflated; mental foramen below middle of M_1 and associated only with minor depression on labial face of mandible. Dental formula 1-5-3/1-5-3 or 1-5-3/1-4-3.

Domnina is the oldest and most primitive shrew here recognized. In form of P_4, height of crown of M_1, relatively slight reduction of the heel of M_3, little separation of the mandibular condyles, lack of a deep and pocketed internal temporal fossa, lack of a posterior emargination on P^4 and the upper molars, pigmentation of the teeth, and other features related to the structure of the skull (see McDowell, 1958, p. 182–184, and Patterson and McGrew, 1937, p. 255), *Domnina* could easily be considered ancestral to most other shrews. *Domnina* is precocious, however, in the posterior position of the mental foramen and in the extreme lingual placement of that part of the mandibular condyle homologous to the lower condyle of other shrews. It is atypical, in comparison with genera of the other subfamilies, in its transversely broadened or double-rooted premolars. These last features clearly indicate that *Domnina* is a specialized shrew belonging in the Heterosoricinae and not a generalized ancestor to all shrews.

Domnina thompsoni Simpson, 1941

Figure 2

A species of *Domnina* with lower antemolars not crowded anteroposteriorly; five(?) antemolars in addition to soricid incisor; roots of antemolars not transversely broadened; somewhat smaller size than *D. gradata.* Early Oligocene (Chadronian) of Montana.

This is the only known specimen of *Domnina* on which the mandibular condyles are well preserved. They are drawn apart but not separated (see McDowell, 1958, fig. 30D, E). It is interesting to note, even in this early stage of evolution of the soricid doubled condyle, that the lower anticular facet is well displaced lingually in the heterosoricine fashion and to a far greater extent than in any other subfamily. The presumed reduction in number of antemolars in *D. gradata*, their conspicuous crowding between the molars and the insicor, and the transversely broadened or doubled roots of these antemolars are marked differences between these two species.

Specimen examined.—The type, American Museum of Natural History 32647.

Domnina gradata Cope, 1873

Figure 3

A species of *Domnina* with dental formula 1–5–3/1–4–3; lower antemolars crowded together, four in number, with transversely broadened or incipiently doubled roots; somewhat larger size than *D. thompsoni;* heavily pigmented teeth—nearly all of M_1 above cingulum is pigmented. Middle Oligocene (Orellan) of Colorado and Nebraska and Oligocene of Wyoming.

This is a very well-known shrew (see Patterson and McGrew, 1937). The first postincisor antemolar of the lower dentition is not known. The similarity in alveolar pattern between this species and *Trimylus* from the late Miocene of Oregon suggests that the P_4 of *D. gradata* may not be larger than the first postincisor antemolar. The second and third lower antemolars are of a form similar to, but much smaller than, P_4.

The P^4 is typically soricid but differs in certain characters. The protocone, typically small in most shrews, is either not present or is represented by a small bladelike elevation on the hypoconal cingulum. The paracone is more prominent and of a more conical form than in most shrews. The parastyle is minute and hardly more than a cingular irregularity. Finally, there is no emargination of the posterior basal outline

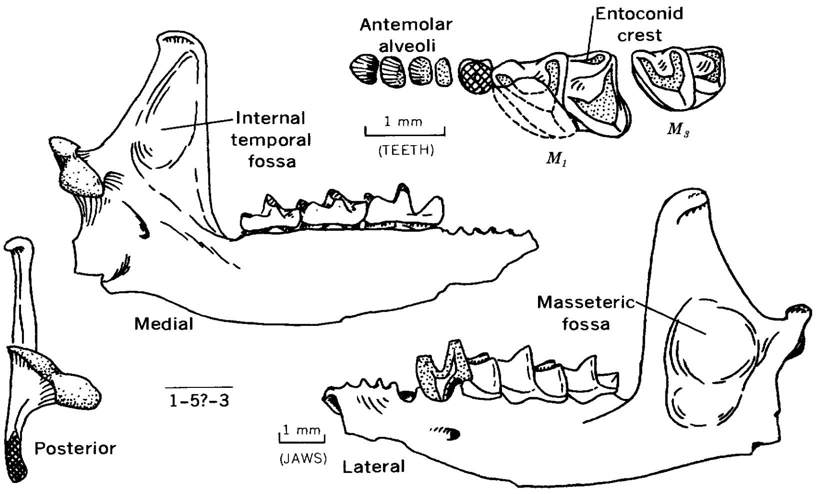

FIGURE 2.—*Domnina thompsoni* Simpson, type, AMNH 32647. Left mandible. Medial view from Simpson (1941); posterior view from McDowell (1958).

although the basin between the parametaconal blade and the hypoconal cingulum is very deep. The P^4 is known only on USNM 12841.

The M^1 is typically soricid except that it lacks the posterior emargination and the protruding hypoconal flange which results from this emargination.

Consistent with its slightly younger geologic age, the mental foramen is slightly posterior of the position in *D. thompsoni* and is a little behind the midpoint of M_1 rather than a little behind the anterior root of M_1.

On the basis of USNM 12841 from Wyoming, McDowell (1958, fig. 30B, C) concluded that *Domnina gradata* lacked the zygomatic arch as do most shrews. Further preparation of the damaged skull of this specimen leads me to feel not only that the lack of an arch is not demonstrable on this specimen but that the size and shape of the broken end of the maxillary root of the zygoma suggests that a relatively large and horizontally broad arch or zygomatic process was present. This conclusion is almost mandatory when one considers the very large, deep, and extensive masseteric fossa on the mandible. It should be noted, also, that McDowell's illustration (fig. 30C) shows a slight posterior emargination on P^4 and M^1. This emargination is not present on the specimen, but its absence could not be established until some matrix and a thick coating of glue were removed from the teeth.

Specimens examined.—Chicago Natural History Museum P25750, P15320, P25754, and P25749; U.S. National Museum 12841.

Domnina greeni Macdonald, 1963

According to Macdonald (1963, p. 168), the ridge (the entoconid crest) connecting the entoconid to the metaconid is lower than in *D. gradata*, and the labial cingulum is not present below the protoconid (although his fig. 5A seems to show that it is). His measurements indicate a shrew the size of *D. gradata.* Early Miocene (Arikareean) of South Dakota.

This specimen was not seen.

Domnina n. sp.

Figure 4

Material.—U.S. National Museum 23095, isolated left P_4 and M_1 with posterior half of the talonid missing. These two teeth were found in situ within 3 inches of each other and have the same degree of wear; it is assumed that they belong to the same individual. Collected by C. A. Repenning in 1959.

Locality and age.—U.S. Geological Survey vertebrate loc. M1033, eastern Caliente Range, San Luis Obispo County, Calif. Early Miocene. Found in association with *Archaeolagus* and *Parahippus* in beds which contain, in the same area, mammals believed to belong in the Arikareean North American Provincial Age (Repenning and Vedder, 1961).

Diagnosis.—A small species of *Domnina* with P_4 that has transversely broadened root; size one-fourth smaller than *D. gradata;* pigment reduced to only tips of cusps.

Description.—USNM 23095 is a shrew differing from *Domnina gradata*, in the parts represented, only by its size and the amount of pigmentation of its teeth. P_4 is a triangular tooth with a single triangular cusp and a posterior cingulum which extends forward on both sides nearly to the anterior apex of the tooth. The cingulum does not overhang the root and would not have hidden either the root or the alveolus. The root of this speci-

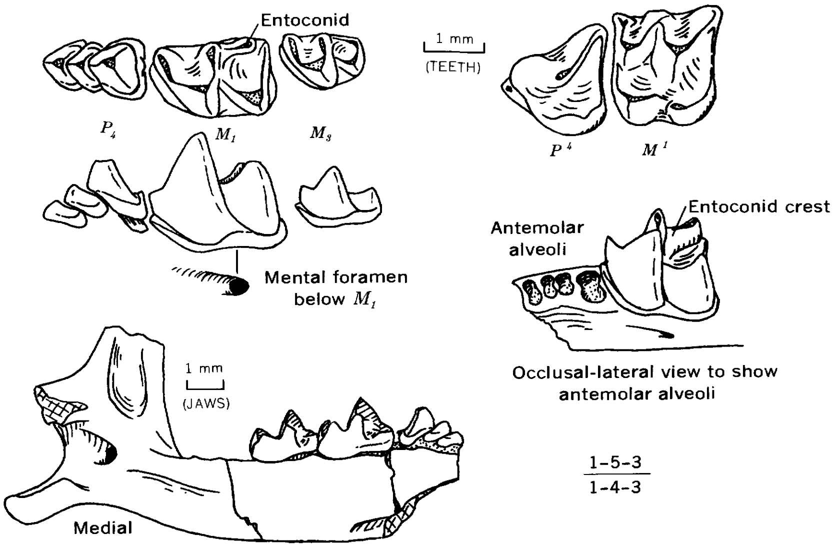

FIGURE 3.—*Domnina gradata* Cope, USNM 12841. Left mandibles; P^4 and M^1. M_3 is from CNHM P15320, and lower antemolar alveoli are from CNHM UC 1552.

men was lost, but on the basis of the area of attachment P_4 was either double rooted or at least transversely widened and anteroposteriorly compressed to about half of the width. Only a faint trace of yellowish pigment can be seen near the cusp apex. Maximum width of P_4 is 0.8 mm, and the anteroposterior length is about 1.0 mm. There is a cavity formed by caries on the cingulum near the posterolingual corner of the tooth.

The posterior half of the talonid is missing from the M_1, and the tooth is well worn. The cingulum is strong from the paraconid to its termination at the fracture across the talonid. The entoconid is prominent and is connected to the metaconid by a crest that appears to be relatively as high as that in *D. gradata.* The metalophid joins the protolophid slightly labial of the midline of the tooth. The reentrant between the protoconid and the hypoconid opens on the labial side of the tooth at the cingulum and actually blends with the cingulum as in *D. gradata.* A faint trace of yellowish pigment is detectable on the labial face of the paralophid. The M_1 is about 1.5 mm in length (including an estimation of the missing part of the talonid) and about 1.0 mm wide across the protolophid. *D.* n. sp. (USNM 23095) is about as much smaller than *D. thompsoni* as *D. thompsoni* is smaller than *D. gradata:*

M_1	D. *n. sp.*	D. thompsoni*	D. gradata* *(mean)*
Length	1.5±	1.8	2.3
Width	1.0	1.2	1.5

*Data from Simpson (1941, p. 2).

The closer approach in size of *D.* n. sp. to *D. thompsoni* would suggest a closer relationship. The anteroposteriorly compressed root of the P_4 of *D.* n. sp., however, and the relative age of the three species indicates a closer relationship between *D.* n. sp. and *D. gradata.* Except for its alveolus, P_4 is not known in *D. thompsoni.*

Genus **PARADOMNINA** Hutchison, 1966

Genotype: *Paradomnina relictus* Hutchison, 1966

A heterosoricine shrew resembling *Domnina* but lacking a prominent entoconid crest joining the entoconid to the metaconid on M_1 and M_2; postentoconid valley lacking on M_1 and M_2 so that hypolophid unites with entoconid; five postincisor antemolars including P_4 in the mandible; antemolar roots compressed anteroposteriorly as in most heterosoricines; cheek teeth elongate and not bulbous, mandible elongate in contrast to *Trimylus.* Late Miocene (Barstovian) of Oregon. Only one species, the genotype, is known.

Specimens examined.—The type and referred specimens listed by Hutchison (1966, p. 5).

Genus **TRIMYLUS** Roger, 1885 [2]

Genotype: *Trimylus schlosseri* Roger, 1885 =
Sorex sansaniensis Lartet, 1851

P_4 triangular in occlusal view (lacking other details because of bulbous form), smaller than first antemolar behind incisor (but first antemolar known only in late Miocene and early Pliocene forms); M_1 very low crowned, swollen, with inflated cingulum, these characters increasing in prominence in geologically younger forms; entoconid present on M_1 in earlier forms but more detached from metaconid than in *Domnina* and closely attached to hypolophid, decreasing in importance and becoming a distal part of hypolophid in geologically youngest forms; talonid of M_3 with crescentic loph and not distinctly bicuspid as in *Domnina;* mental foramen below middle of M_1 to middle of M_2 (more posterior than in any other shrew) and placed in a depression on labial face of mandible which leads anterodorsally to premolar region; horizontal ramus massive and increasingly so in geologically younger forms; mandibular condyles widely separated in heterosoricine pattern (lower condyle displaced more lingually than ventrally); pigmentation reduced and in most forms only on incisors and anterior antemolars. Dental formula 1-5-3/1-4-3 or 1-4-3/1-3-3.

There are at least three species of *Trimylus* in Europe and at least four in North America. The relationship between these is obscure but suggests two lineages. One is confined to North America, and the other to Europe. If two lineages are represented, they are not readily recognizable because of parallel, but not identical, evolutionary trends on each continent. The presence of two

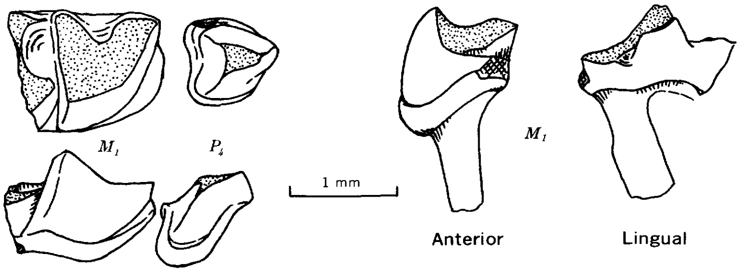

FIGURE 4.—*Domnina* n. sp., USNM 23095. Right P_4 and M_1.

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[2] In a recent publication, Doben-Florin (1964, p. 15–16) traced the history of the names *Heterosorex* Gaillard (1915) and *Trimylus* Roger (1885) and unquestionably established the priority of *Trimylus.* See synonomy under *Trimylus sansaniensis.*

lineages is suggested by the position of the conspicuous mental foramen which is below the trigonid of M_2 in all European forms for which illustrations have been seen. In North American forms the foramen is below the talonid of M_1 except in *Trimylus roperi* in which it is below the trigonid of M_2 as in the European forms. Progressive changes throughout the genus include increase in massiveness of the mandible, increase in bulbousness of the molars, increase in fusion of the entoconid to the posterior loph of the talonid of M_1 and M_2 with ultimate loss of this cusp as a distinct feature in geologically youngest forms, and decrease in the space for the lower antemolars between the incisor and M_1, which results in reduction in size of the posterior antemolars and (in European forms) loss of an antemolar in both upper and lower jaws. The suggested relationships cannot be further evaluated without study of the European specimens.

Trimylus compressus (Galbreath), 1953

Figure 5

Domnina compressa Galbreath, 1953, Kansas Univ. Paleont. Contr., no. 13, Vertebrata, art. 4, p. 46–49, fig. 14.
Heterosorex compressus (Galbreath). Mawby, 1960, Jour. Paleontology, v. 34, no. 5, p. 954–956, fig. 2.

A little specialized species of *Trimylus* with molars distinctly more bulbous and cingula more inflated than in *Domnina* but less so than in other North American species of *Trimylus;* entoconid prominent on M_1, connected to posterior lophid (or hypolophid) of talonid and separated from metaconid; lower antemolars not greatly crowded between incisor and M_1 although more so than in *D. gradata;* mental foramen below talonid of M_1. Middle Oligocene (Orellan) of Colorado and middle or late Oligocene of Nebraska.

Only two specimens are known, both right mandibles. The type, University of Kansas 8154, has been described by Galbreath (1953, p. 46–49) and by Mawby (1960, p. 954–955, text fig. 2). The referred specimen is Chicago Natural History Museum UM400 and was collected north of Pine Ridge, Sioux County, Nebr. Neither specimen has the antemolars, but the type shows the alveoli of the posterior two and part of a third (Mawby, p. 955) from which an estimate of the crowding between the incisor and M_1 can be made. The Nebraska specimen shows a very light orange pigmentation on the upper half of the paraconid blade of M_1, and, thus, indicates greater tooth pigmentation than is present in younger species. *T. compressus* has been compared to *T.* aff. *neumayrianus* (described by Viret and Zapfe, 1951, p. 425–426) by Mawby (1960, p. 955). Perhaps the most significant comparison that can be made between the two is the slight crowding between the incisor and M_1 relative to later species on both continents.

Specimen examined.—Chicago Natural History Museum UM400.

Trimylus aff. neumayrianus (Schlosser), 1887

Heterosorex aff. *neumayrianus* (Schlosser). Viret and Zapfe, 1951, Eclogae geol. Helvetiae, v. 44, no. 2, p. 425–426, fig. 12.

Viret and Zapfe described a mandible of *Trimylus* from upper Oligocene (upper Stampian) rocks of Rickenbach, Switzerland. Their illustration shows three antemolar alveoli that are not at all crowded between the incisor and M_1. The posteriormost alveolus is long anteroposteriorly and, as suggested by Wilson (1960, p. 31), may have held the roots of two antemolars, which would bring the antemolar count to four. *Domnina gradata* and all North American species of *Trimylus* in which the premolar count is reasonably well established have four antemolars behind the incisor. Insofar as I am aware, however, this is the only *Trimylus* of Europe that may have had four antemolars. Wilson's suggestion that there were roots of two antemolars in the last alveolus of *T.* aff. *neumayrianus* is supported by the strong anteroposterior compression of

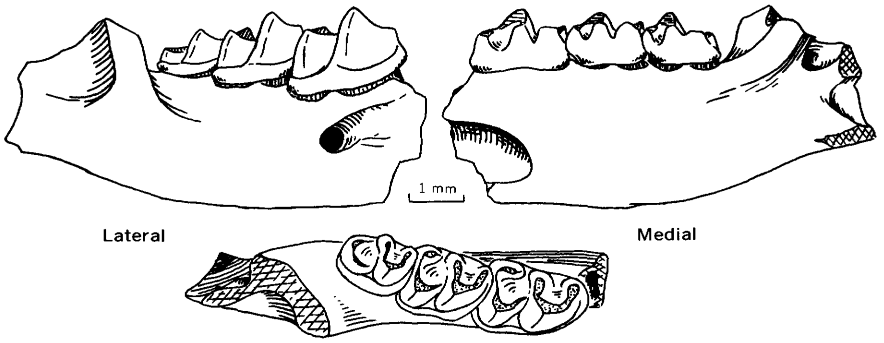

FIGURE 5.—*Trimylus compressus* (Galbreath), CNHM UM400. Right mandible and dentition.

the roots of all heterosoricines except *D. thompsoni*—that the elongate alveolus should have held just one root seems contradictory to a very well established character of the subfamily.

Trimylus aff. *neumayrianus* is also characterized by a very posterior mental foramen, a characteristic of all European species of the genus but not of any American species except *T. roperi.* In size *T.* aff. *neumayrianus* is comparable to *T. compressus* but it has a stouter horizontal ramus. Viret and Zapfe's illustration seems to show low teeth on the cutting edge of the lower incisor, a characteristic of earlier European species.

This specimen was not seen, and the only illustration and description seen are those of Viret and Zapfe.

Trimylus neumayrianus (Schlosser), 1887

Sorex neumayrianus Schlosser, 1887, Beitr. Paläontologie Geologie Österreich-Ungarns, v. 6, p. 122, pl. 2, figs. 46–50.

Heterosorex neumayrianus (Schlosser). Gaillard, 1915, Soc. linnéene Lyon Annales, v. 62, p. 83.

Heterosorex neumayrianus (Schlosser). Viret and Zapfe, 1951, Eclogae geol. Helvetiae, v. 44, no. 2, p. 425.

Viret and Zapfe have compared their Stampian *Trimylus* with Schlosser's description of his Aquitanian species as well as possible from the published record. The lower antemolars, as well as their alveoli, according to Schlosser (1887, p. 122), are unknown. To judge from his figure 60 of plate 2, however, the proximal termination of enamel on the labial side of the lower incisor seems to be very nearly below the anterior edge of M_1, a fact indicating greater anteroposterior compression of the antemolars than in *Trimylus* aff. *neumayrianus* from Rickenbach. The incisor to M_1 relationship seems to be very close to that in the Arikareean specimen from South Dakota, and there is less anteroposterior compression of the antemolars than in the late Arikareean *Trimylus roperi* from Colorado. The incisor bears two prominent cusps along its cutting edge.

The masseteric fossa (Schlosser, 1887, plate 2, fig. 50) seems to be larger, deeper, and more extensive than in any other shrew, including the Arikareean and older species from North America, but the fossa is not preserved in the earlier European specimens. The mental foramen is below the trigonid of M_2 as in all Old World forms. Early Miocene (Burdigalian) from Germany (Weisenau and Wintershof-West) and possibly middle Oligocene (Rupelian) as "*Sorex*" *kinkelini* Zindorf, 1901. No specimen seen.

Trimylus dakotensis Repenning, n. sp.

Figure 6

Heterosorex. Macdonald, 1951, Soc. Vertebrate Paleontology [Guide Book], 5th Field Conf., p. 72.

Heterosorex. Mawby, 1960, Jour. Paleontology, v. 34, no. 5, p. 951, 952, 955, 956.

Holotype.—University of California Museum of Paleontology 37270; a nearly complete left mandible lacking the angular process and the antemolars. Collected by R. A. Stirton, 1934.

Type locality and age.—University of California Museum of Paleontology loc. V 3417, Flint Hill fauna, Bennett County, S. Dak. Early Miocene (Arikareean).

Diagnosis.—A small species of *Trimylus* with mental foramen below talonid of M_1; M_1 has entoconid flush against but not confluent with hypolophid, labial cingulum heavy and inflated but absent anterior to protoconid; M_3 has inflated cingulum and tooth unreduced in contrast to late Miocene species; all cheek teeth moderately bulbous and low crowned.

Description.—*T. dakotensis* is comparable in size to *T.* aff. *neumayrianus* and *T. compressus;* it is smaller than *T. mawbyi*, n. sp., and slightly smaller than the smallest specimens of *T. roperi* described by Wilson (1960, p. 32). Although the antemolars and that part of the mandible containing their alveoli are destroyed, the distance from the incisor to M_1 would indicate con-

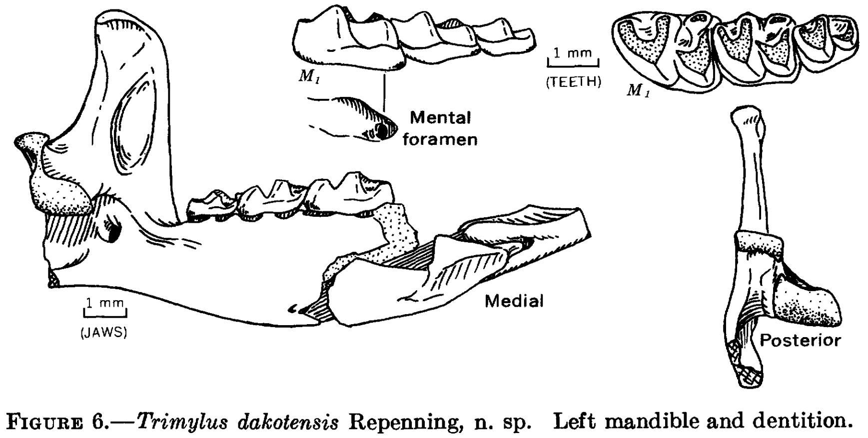

FIGURE 6.—*Trimylus dakotensis* Repenning, n. sp. Left mandible and dentition.

siderably greater anteroposterior compression of the antemolars than is evident in either *T.* aff. *neumayrianus* or *T. compressus*. *T. dakotensis* differs from *T. compressus* in greater inflation of the labial cingula and in greater bulbousness of the cheek teeth. These same characters are further accentuated in the late Miocene species to be described in the following pages. *T. dakotensis* differs only slightly, however, from the nearly contemporaneous *T. roperi*. The chief differences appear to be the somewhat smaller size, the absence of a labial cingulum anterior of the protoconid of M_1, slightly less massive mandible below the molars, and, perhaps most importantly, the anterior position of the mental foramen in *T. dakotensis*. Measurements of the type specimen have been given by Mawby (1960, table 1, column e).

The coronoid and articular processes of the mandible of *T. dakotensis* are very well preserved. In typical heterosoricine fashion the lower articular facet is offset lingually so that no part of it lies beneath the upper facet. Although similar in pattern to *Domnina thompsoni*, the articular facets are separated and this pattern matches all known species of *Trimylus* for which the articular structure is known.

The type of *Trimylus dakotensis* appears to be the first specimen of this genus found in North America (there is no record of the date of discovery of CNHM UM400). Certainly it was the first *Trimylus* to be recognized from North America and was described in manuscript many years ago by Joseph T. Gregory. Unfortunately, the manuscript was never published and thanks are here given to Dr. Gregory for permission to describe the specimen in this report.

Trimylus roperi (Wilson), 1960

Heterosorex roperi Wilson, 1960, Kansas Univ. Paleont. Contr., Vertebrata, art. 7, p. 27–33, figs. 14–22.

A large species of *Trimylus* with dental formula 1–5–3/1–4–3; four antemolars closely appressed between the lower incisor and M_1; entoconid of M_1 distinct in lingual view but completely fused to hypolophid in occlusal view; M_1 lower crowned than Oligocene and early Miocene forms and higher crowned than late Miocene forms from North America; mental foramen below or slightly behind trigonid of M_2—in North America a character unique to this form; P^4 and M^1 very similar to *Domnina gradata* but more massive; size large, comparable to *T. sansaniensis* and *T. mawbyi*, n. sp. (see measurements in Mawby, 1960, and Wilson, 1960). Late early Miocene (late Arikareean) of Colorado.

This is the earliest *Trimylus* in which the upper teeth are known (Wilson, 1963). They are also known from the late Miocene *T. sansaniensis* and *T. mawbyi*, n. sp. All are strikingly like *Domnina*, and all have bifid upper incisors similar to the living genus *Neomys*.

These specimens were not seen but are well illustrated and described by Wilson.

Trimylus mawbyi Repenning, n. sp.

Figure 7

Heterosorex sp. Mawby, 1960, Jour. Paleontology, v. 34, no. 5, p. 950–956, text fig. 1.

Type.—University of Oregon 10486, right mandible with incisor, antemolars 1 and 4, M_{1-3}, and part of the ascending ramus. Collected by F. B. Van Houten in about 1955.

Type locality and age.—Five miles southwest of the south end of Guano Lake and about 24 miles southwest of Beatty Butte, Lake County, Oreg. The exact locality is not known to me; however, there are many outcrops in the general area that could represent the locality, and all are of the same strata. The referred material comes from these strata at localities from within 10 miles to about 40 miles from the type locality.

Late Miocene (Barstovian). The associated fauna is virtually identical to that from the Mascall Formation.

Referred material.—U.S. National Museum 23096, a left mandible with incisor, alveoli for four antemolars, and M_1 and M_2, U.S. National Museum 23097, a right M^1; both from U.S. Geological Survey loc. M1041, Beatty Butte fauna. Also five lower incisors, three upper incisors, and a mandible fragment with M_1 from the following localities: Beatty Butte (loc. M1041), Harney County; Guano Ranch (loc. M1042), Lake County, 15 miles southwest of Beatty Butte; and Snyder Creek (loc. M1043), Lake County, which is 37 miles west-northwest of Beatty Butte. All referred specimens were associated with Barstovian mammals.

Diagnosis.—Of all known species of *Trimylus*, *T. mawbyi* has the greatest reduction of M_3 relative to M_1, the greatest bulbousness of M_1, the greatest inflation of the cingulum of M_1, the lowest cusp height of M_1, and the greatest massiveness of the mandible relative to the molar size. The metalophid joins the protolophid of M_1 far more labially than in any other species. Also conspicuous is the fact that the stout molars are farther to the rear, relative to the anterior edge of the ascending ramus, than in any other heterosoricine.

Description.—In addition to the above characters, *T. mawbyi* has the mental foramen below the talonid of M_1, a position typical of most American members of this subfamily. The entoconid of M_1 is a blunt cuspid thoroughly merged with the hypolophid. The upper incisor is bifid. The M^1 is quite comparable to *T. roperi* only more stout and bulbous. The antemolar alveoli of

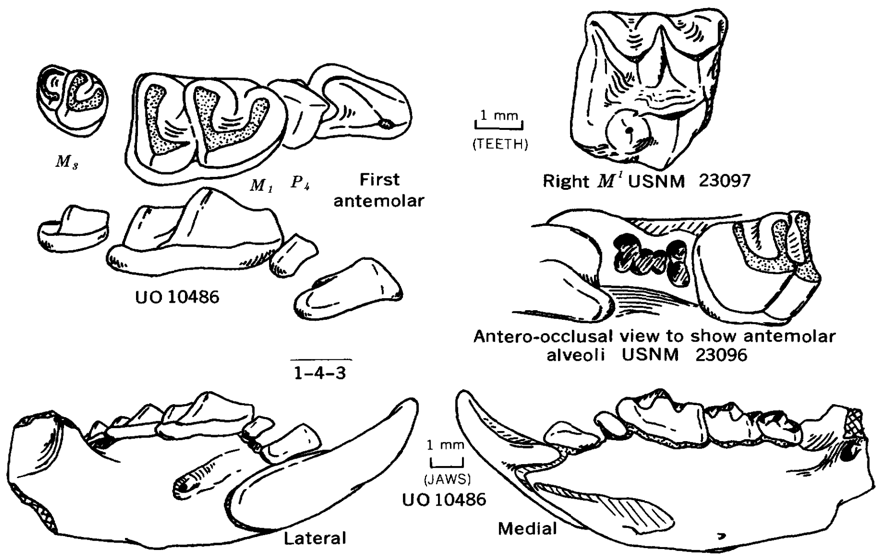

FIGURE 7.—*Trimylus mawbyi* Repenning, n. sp., type UO 10486 and referred specimens. Type: right mandible and dentition. USNM 23096: left mandible and dentition. USNM 23097: right M^1.

the lower jaw, USNM 23096, show clearly that four transversely widened or doubled roots were present much as in *Domnina gradata* only more closely compressed between the incisor and M_1. The alveoli of the first and last antemolars are nearly the same size and much larger than the intervening two. The type specimen, however, shows that the crown of P_4 was much smaller than that of the first antemolar. These alveoli are nearly identical to those shown by Wilson for *T. roperi* (1960, fig. 20), which he feels (p. 31) are indicative of four antemolars behind the incisor. Measurements of the type have been given by Mawby (1960, table 1, column d).

The general mandibular and dental structure of *T. mawbyi* immediately gives the impression of a nutcracker type of action rather than the usual soricid condition which could be compared to the weak but quick action of chopsticks. Perhaps the heterosoricine mandibular characters in general reflect a molluscan, crustacean, or thick elytrum coleopterous diet. In addition, many of the mandibular characters are very similar to the living Chinese Mole- or Burrowing-Shrew, *Anourosorex;* thus fossorial habits are implied.

The type of *T. mawbyi* was described in detail by Mawby (1960) with excellent illustrations. He felt (p. 954) that a new species was represented but preferred not to name it until other specimens were known. Now that these are known, the species is named in his honor.

Specimens examined.—The type and referred specimens mentioned above, which include all known specimens.

Trimylus sansaniensis (Lartet), 1851

Sorex sansaniensis Lartet, 1851, Annuaire dépt. Gers, Auch, p. 13.

Trimylus schlosseri Roger, 1885, Naturw., Ver. Schwaben u. Neuburg Ber., v. 28, p. 106–107.

Heterosorex delphinensis Gaillard, 1915, Soc. linnéene Lyon Annales, v. 62, p. 14.

Trimylus schlosseri Roger. Stromer, 1928, Bayer. Akad. Wiss. Abh., Math.-naturw. Abt., v. 32, no. 1, p. 13 (= *S. sansaniensis* and *H. delphinensis*).

Heterosorex sansaniensis (Lartet). Viret and Zapfe, 1951, Eclogae geol. Helvetiae, v. 44, no. 2, p. 419.

Trimylus sansaniensis (Lartet). Doben-Florin, 1964, Bayer. Akad. Wiss. Abh., Neue Folge, v. 117, p. 15.

A species of *Trimylus* with postincisor antemolars reduced to three in the lower jaw, of which the most anterior is largest (Crusafont Pairó, 1957), and tightly compressed between incisor and M_1; entoconid of M_1 completely fused to hypolophid; mental foramen below trigonid of M_2; size comparable to *T. roperi;* molars not so bulbous and not placed so far posteriorly relative to ascending ramus as in *T. mawbyi;* four upper postincisor antemolars (including P_4) are clearly indicated in figure 11 of Viret and Zapfe (1951, p. 423). The lower incisor does not have subsidiary cusps along its cutting edge (Zapfe, 1951, p. 464, fig. 7). Later Miocene (Vindobonian) and early Pliocene (early Pontian) of Europe.

No specimens were seen. The Vindobonian specimens from La Grive St. Alban are well described and illustrated by Viret and Zapfe (1951, p. 419–424, figs. 10, 11), and those from the Vindobonian of Vallés-Penedés by Crusafont Pairó (1957).

Genus **INGENTISOREX** Hutchison, 1966

Genotype: *Ingentisorex tumididens* Hutchison, 1966

A heterosoricine shrew with bulbous dentition like *Trimylus* except $M\frac{3}{3}$ missing; P_4 very large and larger than first postincisor antemolar; lower incisor short, not stout at base, one very prominent cusp on its cutting edge; labial cingulum of M_1 and M_2 strong but not greatly swollen; trigonid of M_1 and M_2 noticeably wider than talonid; mandible slender and not massive. Late Miocene (Barstovian) of Oregon. Only one species, the genotype, is known.

Specimens examined.—The type and referred specimens listed by Hutchison (1966, p. 9).

Subfamily **CROCIDURINAE** Milne-Edwards, 1868–1874

P_4 has triangular cusp and a sulcus down posterior face of cusp, slight or no overhang of labial cingulum over root and alveolus, one or two roots; pigmentation absent; dental formula 1–6–3/1–4–3 to 1–6–3/1–3–3 in late Miocene and 1–3–3/1–2–3 to 1–5–3/1–3–3 in modern forms; articular facets of mandibular condyle separated but not widely, articulation surfaces usually united either along lingual side of the condyle with a labial interarticular depression or across most of the interarticular surface; internal temporal fossa of mandible present; mental foramen below P_4 in Miocene forms and below anterior root of M_1 in Pliocene to Recent forms; very small to very large size (the smallest and largest living shrews are included). Middle Miocene to Recent, Europe and Africa; early(?) Pliocene to Recent, Asia.

Although the Crocidurinae resemble *Domnina* in the structure of the P_4 and are closely paralleled in other features by the North American Limnoecinae, there are no specimens outside of the Old World that appear to represent this subfamily. In many features this subfamily is a primitive group, and it is somewhat surprising, therefore, to find that the earliest shrews of the Old World are only soricine and heterosoricine; the earliest crocidurine shrews are from the Burdigalian of Europe (Doben-Florin, 1964, "*Sorex*" *pusilliformis*, and *Soricella discrepans*) and Africa (Butler and Hopwood, 1957, *Crocidura* sp.). The living shrews of Africa, Peninsular India, and Ceylon, all belong in the Crocidurinae (including *Scutisorex*), and possibly their earlier record is to be found in this area.

Many Old World fossil species of shrews are here included in the Crocidurinae and conform to the above diagnosis. The two most distinctive crocidurine characters exhibited by all these are the triangular P_4 (shared only with the Heterosoricinae) and the lingual union of the mandibular articular facets, with a labial interarticular depression (shared only with the Limnoecinae). The first species discussed are those included in noncrocidurine genera in previous publications but whose subfamily affinities appear to be crocidurine. These are not reassigned to crocidurine genera, however, because the present review has been detailed enough to establish subfamily rank only, and all available specimens should be examined before generic reassignment is made. The remainder of both fossil and living species are discussed under their appropriate genera, in alphabetical order.

"**Sorex**" **pusilliformis** Doben-Florin, 1964

"Small shrew, tooth cusps unpigmented * * * M_2 about as large as M_1. Incisor toothed [cutting edge of lower incisor scalloped], first scallop located far from the tooth base. Two antemolars in the lower jaw, the posterior one [P_4] two-rooted, its crown bearing two small secondary cuspids. M_1 and M_2 with hypoconulid [entoconid separated from hypolophid], talonid of M_3 one- to two-cusped * * * Mental foramen below the second antemolar [P_4]. Condyle with unseparated, *Crocidura*-like articular surface." (Doben-Florin, 1964, p. 32, part of diagnosis). P_4 has a triangular cusp with well-developed posterolabial and posterolingual crests and "concave posterior face"; small accessory cuspulids are present on each of the posterior crests (Doben-Florin, p. 33). The articular structure of the mandible is distinctly crocidurine, as stated in the original diagnosis and as shown in Doben-Florin's illustrations (pl. 4, fig. 1b). The species clearly is not *Sorex.*

The dental formula is 1–?–3/1–2–3, and the species differs from *Miosorex grivensis* also in smaller size and cusp height (see Doben-Florin, 1964, p. 41). This appears to be one of the oldest crocidurine shrews known from Europe and is from the older Burdigalian locality of Wintershof-West. Doben-Florin reviewed the problem of the identity of *Sorex pusillus* von Meyer which seems, at present, to be irresolvable. At least some of the Aquitanian shrews assigned to this species have pigmented teeth and appear to be assignable to the soricine shrew *Crocidosorex antiquus* (Pomel); the others are not assignable to subfamily on the basis of published descriptions.

"**Sorex**" **dehmi** Viret and Zapfe, 1951

Dental formula 1–6–3/1–4–3; P_4 has two roots longitudinally placed in mandible, both posteroexternal and posterointernal crests of triangular cusp have subsidiary cuspules along them much as in the living *Sylvisorex*, posterolabial cingulum of P_4 slightly overhanging posterior root; M_1 has moderate cusp height, talonid wider than trigonid so that metalophid units with protolophid (protoconid-metaconid crest) very near to protoconid; M_3 has remnant of basin remaining in talonid as in *Miosorex grivensis* and not trenchant as in modern crocidurines; mental foramen below P_4; dental foramen usually far forward; P^4 and M^1 have slight emargination of the posterior border quite comparable to *Miosorex grivensis*, according to Mein (1958, figs. 20, 21). Late Miocene (Vindobonian) or possibly somewhat earlies (late Burdigalian) (Mein, 1958, p. 106) of Europe.

No specimens were seen. They are, however, well figured and described by Viret and Zapfe (1951, p. 415–417) with a description of the upper dentition by Mein (1958, p. 25–26). This species is as distinct from other known fossil and living shrews as the living genera are distinct from each other. It should be placed in a new crocidurine genus or with *Miosorex grivensis* as a separate species. This should not be done without study of the large sample now available (Mein stated that he has 100 mandibles and 14 maxillaries from Vieux-Collonges). "*Sorex*" *dehmi* has an interesting combination of features, some of which seem more progressive than *M. grivensis* and most of which seem more primitive than its contemporary.

Genus **CROCIDURA** Wagler, 1832

Figure 8

Genotype: *Sorex leucodon* Hermann, 1780

Dental formula 1–4–3/1–2–3; lower incisor short to moderate length and curving upward, cutting edge slightly serrate to smooth, groove along length of medial side curves downward below notch in basal border; first upper antemolar larger than equal-sized second and third antemolars, all unicuspid. Late Miocene(?) to Recent, Africa; early Pleistocene to Recent, Europe; Pleistocene to Recent, Asia.

During this review no characters were noted which would serve to separate *Crocidura* from *Suncus* on the basis of lower dentition or structure of the mandible. Prof. P. M. Butler (written commun. 1964) suggested that there appears to be taxonomic value in the "cingulumlike groove running along the length of the medial side of the first lower incisor. In all *Suncus* except *S. lixus*, this continues above the notch in the basal border of the tooth as a posterolingual cingulum. This does not happen in *Crocidura*." The additional upper antemolar in *Suncus* is, of course, diagnostic. Ellerman and Morrison-Scott (1951, p. 65) stated that in their opinion *Suncus* is no more than a subgenus of *Crocidura*. Throughout the Soricidae, dental formula is a significant character of generic stature, and the opinion held in this review is that *Crocidura* and *Suncus* must be retained as distinct genera on this basis or else an immense amount of synonomy is in order throughout all living shrews.

It is not so easy to defend the generic distinctiveness of *Crocidura* and *Praesorex* by proclaiming custom to be guiding dogma of soricid taxonomy. In this comparison the above diagnosis is not diagnostic. *Crocidura* differs from *Praesorex* in smaller size (which is variable), in having an inflated pterygoid region on its skull, in having great interorbital skull breadth relative to the rostral breadth at the infraorbital foramina, and in having a basined fossa for the in-

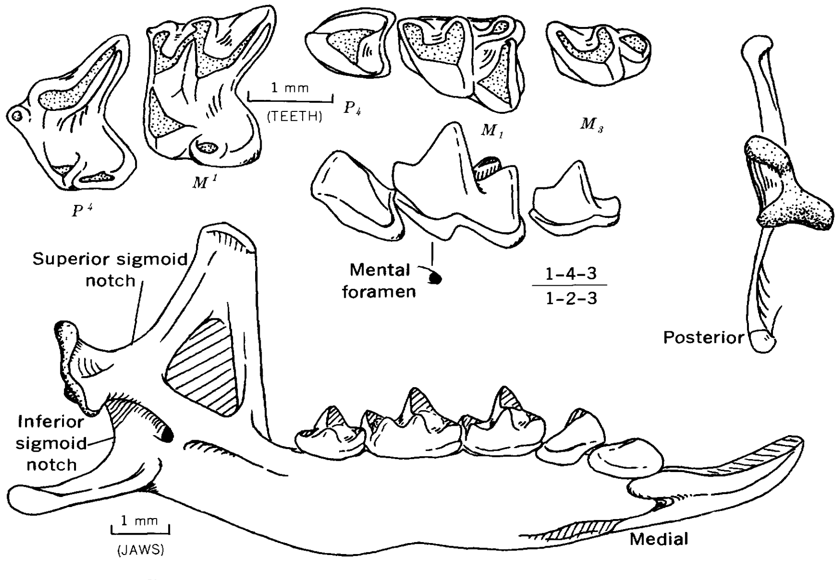

FIGURE 8.—*Crocidura russula* Hermann, Belgium, author's collection 60186. Left mandible and dentition and left upper dentition.

sertion of the superior pterygoid muscle on the mandible (all of which can easily be shown to vary with size). There are two characters which may be constant differences between the genera but which have not been checked for consistency in this review nor, as far as I am aware, in any study because of the lack of an adequate sample of *Praesorex*. These are the more anterior position of the mental foramen and the shorter, more velvety, fur of *Crocidura*. In *Crocidura* the mental foramen lies below the P_4 to below the protoconid of M_1. In the two available specimens of *Praesorex*, it lies below the hypoconid of M_1. According to Meester (1953, p. 213), who had only two specimens of *Praesorex* but a large series of *Crocidura*, the difference in pelage is diagnostic. For this review, therefore, *Praesorex* is retained as a separate genus, and the above characters are considered diagnostic of *Crocidura*.

Crocidura sp., Butler and Hopwood, 1957

This specimen (Butler and Hopwood, 1957, p. 2) seems too incomplete to defend the generic assignment. Late Miocene, Kenya.

Crocidura wongi Pei, 1936

More primitive than any living crocidurine in that the talonid of M_3 is not reduced to a single trenchant cusp although it is practically so, according to Pei (1936, p. 22). No specimen was seen. It is well illustrated by Pei (figs. 10,11). Pleistocene of China.

Crocidura taungsensis Broom, 1948

A small species lacking the anterior cusp present on the P^4 of living species, according to Meester (1955, p. 274–275). Early Pleistocene, South Africa.

Crocidura kornfeldi Kormos, 1934

More delicate than living *C. suaveolens*, according to Friant (1947, p. 264). No specimen was seen. Early Pleistocene of Europe.

Crocidura obtusa Kretzoi, 1938

Elongate first lower antemolar and "blunt" P_4 with dimensions comparable to living *C. leucodon*, according to Kretzoi (1938, p. 92). No specimen was seen. Pleistocene of Europe.

Crocidura zorzii Pasa, 1948

Citation from Sulimski (1962, p. 484). No specimen seen. Middle Pleistocene of Italy.

Genus DIPLOMESODON Brandt, 1853

Figure 9

Genotype: *Sorex pulchellus* Lichtenstein, 1823

Dental formula 1–3–3/1–2–3; first upper antemolar larger than second; M^2 trapezoidal; lower incisor without or with single accessory cuspule on cutting edge; P_4 slightly larger than preceding antemolar, crocidurine posterolingual crest very weak; posterolabial crest virtually lacking; M_1 has longitudinally shortened talonid, entoconid present and either com-

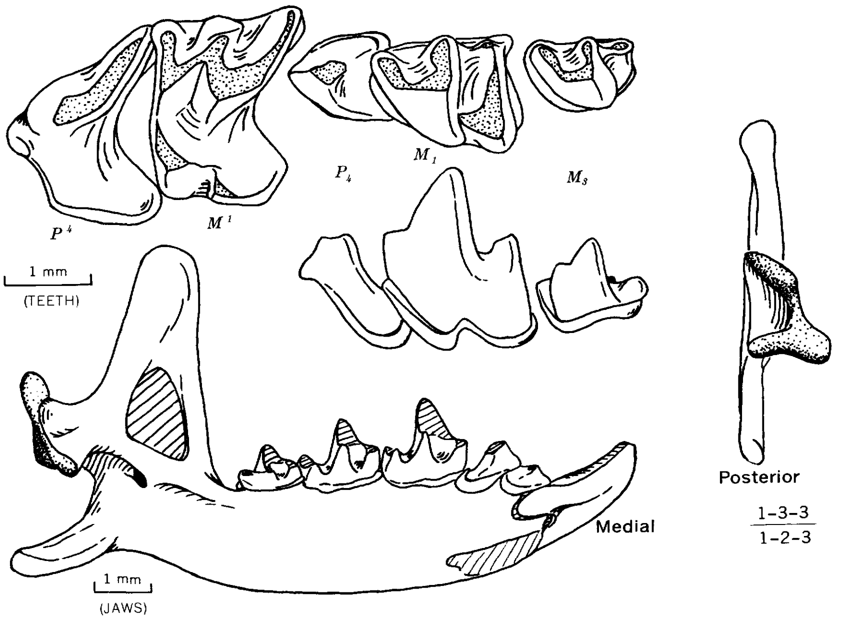

FIGURE 9.—*Diplomesodon pulchellum* (Lichtenstein), Kazakhstan, U.S.S.R., AMNH 206558. Left mandible and dentition and left upper dentition.

pletely fused with hypolophid or very close to this lophid, entoconid crest very low, labial cingulum continuous from paraconid to behind hypoconid but not inflated or enlarged; M_1 and P_4 distinctly anteroposteriorly compressed to adjust to short snout (in upper dentition this adjustment is made by loss of antemolars rather than by marked anteroposterior compression of teeth); trigonid of M_3 slightly reduced but talonid greatly reduced to single cusp with entoconid crest leading directly to metaconid or entirely lost; zygomatic process of maxillary originates just behind parastyle of M_2 to opposite metastyle of M_1; mental foramen below protoconid of M_1 to below anterior tip of M_1 and posterolabial corner of P_4; ascending ramus high, vertical and narrow; internal temporal fossa triangular and rather small; mandibular condylar process and articular facets somewhat more widely separated than in *Crocidura* to extreme separation for subfamily, articular surfaces continuous (or nearly so) along lingual margin of interarticular area. Recent of south-central U.S.S.R. (Aral Sea area) and early Pleistocene of South Africa.

Specimen examined.—American Museum of Natural History 206558, a male *Diplomesodon pulchellum* from west Kazakstan, U.S.S.R.

Diplomesodon fossorius Repenning, 1965

A large species with greatly reduced $M\frac{3}{3}$ and with extreme specialization of the mandibular articulation, paralleling that of many soricine shrews. Type and referred specimens listed by Repenning were seen. Early Pleistocene, South Africa.

Genus FEROCULUS Kelaart, 1852

Genotype: *Sorex feroculus* Kelaart, 1852

Dental formula 1–5–3/1–2–3; lower incisor with two lobes on cutting edges as in *Sylvisorex* but inclined forward rather than rounded; foreclaws enlarged. Specimens of this shrew are very scarce. Through the kindness of R. W. Hayman I have been able to examine photographs of the specimen in the British Museum (Nat. History) (BM 28.10.27.6). The similarity to *Sylvisorex* is striking. From the photographs I am unable to see any differences that would appear significant except possibly one less cusp and the forward inclination of the cusps on the cutting edge of the lower first incisor of *Feroculus*. The posterolingual emargination of the P^4 and M^1 is broader and deeper in *Feroculus*. No specimen was seen. Recent, Ceylon.

Genus MIOSOREX Kretzoi, 1959

Figure 10

Genotype: *Sorex pusillus* var. *grivensis* Depéret, 1892

Dental formula 1–6–3/1–3–3; P_4 has slight overhang of labial cingulum over root and secondary cuspule along posterolabial crest; M_1 with moderate cusp height—reentrant between the protoconid and hypoconid emerges on labial face a short distance above cingulum; talonid of M_3 not as reduced as in modern crocidurines but retains slight basin enclosed by high labial and very low lingual ridge; P^4 with only slight emargination of posterior border; M^1 with moderate emargination; mental foramen below root of P_4. Late Miocene (Vindobonian) of Europe.

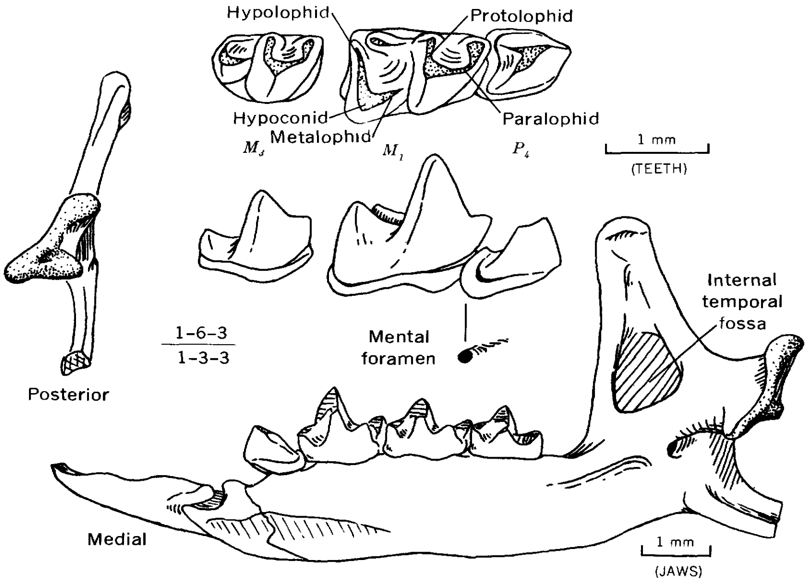

FIGURE 10.—*Miosorex grivensis* (Depéret), UC 24859 with P_4 and incisor restored from Viret and Zapfe (1951). Right mandible and dentition.

The slightly reduced and basined talonid of M_3, the slight emargination of P^4 and M^1, the retention of six upper antemolars, and possibly the lesser height of crown of M_1 are all that separate this crocidurine shrew from related living genera.

Miosorex grivensis (Depéret), 1892

Sorex pusillus, var. *grivensis* Depéret, 1892, Mus. d'histoire nat. Lyon Archives, v. 5, mém. 2, p. 48.

Sorex (s.l.) *grivensis* (Depéret). Viret and Zapfe, 1951, Eclogae geol. Helvetiae, v. 44, no. 2, p. 411–412, figs. 1–3.

Miosorex grivensis (Depéret). Kretzoi, 1959, Vertebrata hungarica, v. 1, no. 2, p. 248, footnote 1.

This is the only species assigned to the genus.

Specimens examined.—University of California Museum of Paleontology 42672, a right mandible with M_2 and M_3, and University of Colorado 24859, a right mandible with M_1 to M_3 from La Grive St. Alban. More complete material is well figured and described by Viret and Zapfe.

Genus MYOSOREX Gray, 1838

Figure 11

Genotype: *Sorex varius* Smuts, 1832

Dental formula 1–5–3/1–3–3; lower incisor short and curving upward, cutting edge smooth or has two low cuspulids; first upper antemolar larger than following ones except P^4, second very small, third nearly as large as first, and fourth minute (lost in *Myosorex polli* Balsac and LaMotte, 1956, p. 155–157), all bicusped with cusps forming parallel longitudinal blades; posterior lobe of falciform upper incisor also bilobed so that two rows of lobate cusps run from nipping part of incisor back to P^4; P_4 with accessory cuspule on both posterolingual and posterolabial crests; P_3 minute and on the lingual side between the two major lower antemolars; early Pleistocene to Recent, Africa.

Ellerman, Morrison-Scott, and Hayman (1953, p. 19) stated that the P_3 is so vestigial as to be very rarely present and so considered *Myosorex* a subgenus of *Suncus*. Eleven specimens of *M. varius* from Cape Province, South Africa (three localities), are in the Museum of Vertebrate Zoology, University of California, Berkeley. Of these 11 specimens, 9 have the vestigial P_3 on both mandibles, 1 (UCMVZ 117080, a male) has it on one mandible only, and 1 (UCMVZ 117085, a very old male) has the P_3 missing on both mandibles although the upper antemolars are as described above. I am inclined to feel that the tendency to have three postincisor lower antemolars is very strong in this species and that this tendency, combined with the unique structure of the upper antemolars, is of generic importance and comparable in magnitude to differences found between other genera.

Specimens examined.—*Myosorex varius*, 11 specimens in the University of California Museum of Vertebrate Zoology. Also, early and late Pleistocene specimens of *Myosorex* in the University of Colorado Museum from Cave of Hearths and Limeworks, Makapansgat, Transvaal, South Africa.

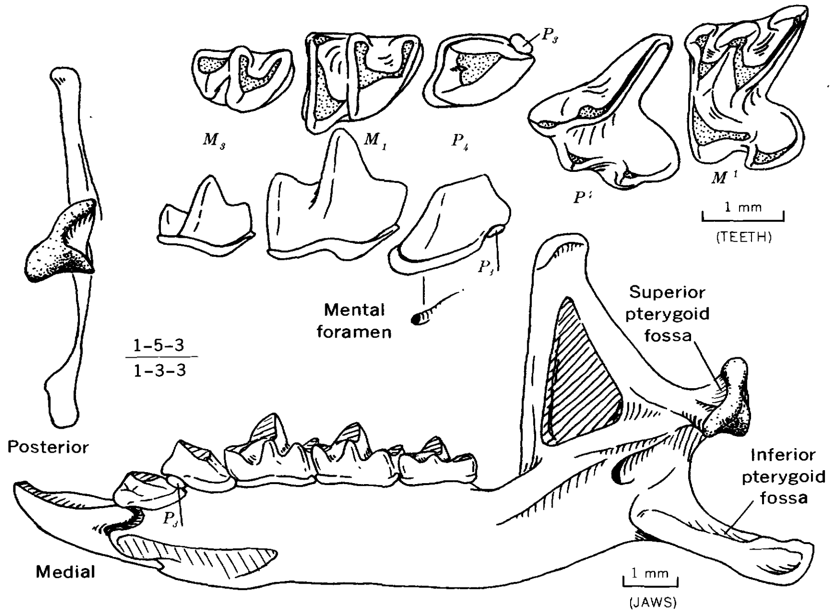

FIGURE 11.—*Myosorex varius* (Smuts), Cape Province, Union of South Africa, UCMVZ 17086. Right mandible and dentition and left upper dentition.

Myosorex robinsoni Meester, 1955

According to Meester (1955, p. 272–273), this species lacks subsidiary cuspules on the posterolabial and posterolingual crests of P_4. Several specimens were examined. Early Pleistocene, South Africa.

Genus PARACROCIDURA Balsac, 1956

Genotype: *Paracrocidura schoutedeni* Balsac, 1956

Dental formula 1–4–3/1–2–3; upper incisor with expansion of anterointernal border producing chisel-like cutting edge rather than point as in most shrews; P^4, M^1, and M^2 with squared posterior borders lacking any emargination; first lower postincisor antemolar very large and longitudinally bicuspid. Recent, Africa.

Relative to soricine shrews, most crocidurine shrews tend to have enlarged and elongate first lower postincisor antemolars. The elongation of this tooth in *Paracrocidura* exceeds any shrew examined during this review, however, and greatly exceeds the most closely comparable genera, *Sylvisorex* and *Feroculus*. The structure of P^4, M^1, and M^2 is unique for the subfamily. The development of medial crests on the tip of the upper incisors is also unique for the subfamily and appears to be comparable to the fissident incisor found in the Heterosoricinae and in most Old World genera of the tribe Neomyini (new name; see p. 45). The structure of the P_4, which has both posterolabial and posterolingual crests (with prominent secondary cuspules), indicates that *Paracrocidura* is a crocidurine shrew. The structure of the mandibular condyle has not been described. No specimen was seen.

Genus PRAESOREX Thomas, 1913

Figure 12

Genotype: *Crocidura goliath* Thomas, 1906

Dental formula 1–4–3/1–2–3; largest known shrew; teeth as in *Crocidura;* pterygoid region of skull not inflated; interorbital breadth not great relative to rostral breadth at infraorbital foramina; mandibular insertion of superior pterygoid muscle not basined and pterygoid spicule developed; mental foramen below hypoconid of M_1; fur long, coarse, with prominent guard hairs. Recent of equatorial Afria.

This ermine- to weasel-sized genus is the largest known shrew, living or extinct. It is not, however, greatly larger than the giant species *Suncus caeruleus*. Except for size it is hardly more than a species of *Crocidura*, and some species assigned to *Crocidura* are nearly as large. With the exception of the position of the mental foramen and the nature of the pelage, all characters listed in the above diagnosis are known to vary with size in other shrews. Its similarity to *Crocidura* is discussed under that genus. Balsac and LaMotte (1957, p. 29) consider *Praesorex goliath*, the only species included in this genus, to be a species of *Crocidura*.

Specimens examined.—Harvard University Museum of Comparative Zoology 14718, a female *Praesorex*

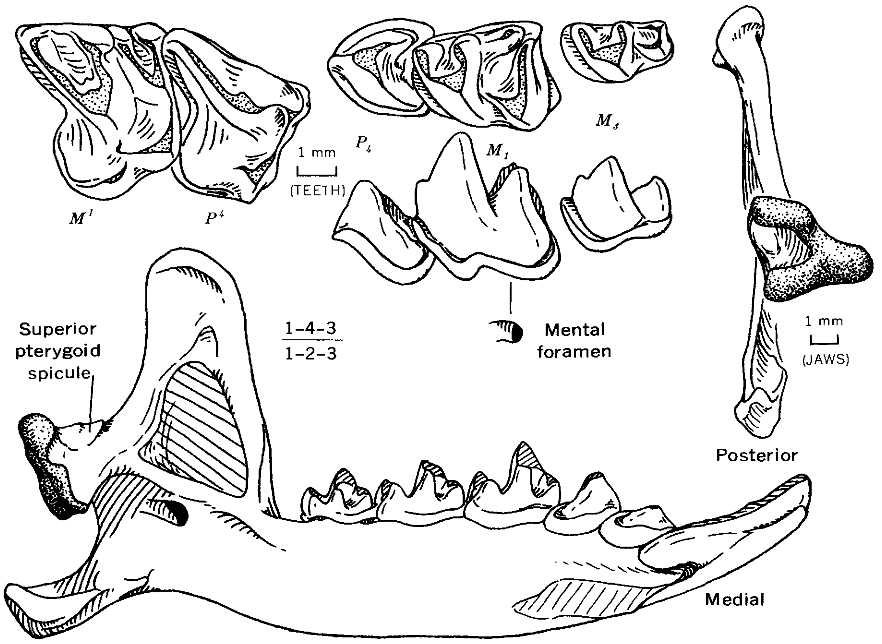

FIGURE 12.—*Praesorex goliath* (Thomas), Cameroons, MCZ 14718. Left mandible and dentition and right upper dentition.

goliath from Cameroons; British Museum (Nat. History) BM. 11.5.5.7, a male *Praesorex goliath* from Cameroons.

Genus SCUTISOREX Thomas, 1913

Genotype: *Sylvisorex somereni* Thomas, 1910

Dental formula 1–5–3/1–2–3; first upper antemolar slightly larger than subequal following three; lower incisor short, curving upward at tip, with smooth upper margin; in dorsal aspect articular facets of mandibular condyle much closer to being normal to longitudinal axis of the mandible than in other crocidurines; angular process of mandible enlarged, stout, and attenuated posteriorly in comparison with other crocidurines; vertebral column with remarkable specialization (Allen, 1917). No specimen was seen. It is well illustrated by Allen. Recent, Africa.

Genus SOLISOREX Thomas, 1924

Genotype: *Solisorex pearsoni* Thomas, 1924

Dental formula 1–4–3/1–2–3; lower incisor with smooth cutting edge as in *Suncus;* foreclaws enlarged. The more significant parts of the description of *Solisorex* given by Thomas (1924, p. 94) are as follows: "Articulation with lower jaws unusual in various aspects. Most noticeable is the great size and transverse extent of the mandibular condyles, each of these being broader than the space which separates them from each other across the middle line * * * Teeth large and heavy * * * Upper 'unicuspids' only three in number, of which the anterior one is almost unique in the family by being slightly bicuspid, in size the first is much the largest, the second about one-sixth its bulk, and the third rather more than twice the size of the second. First two molars more square than in *Pachyura* [*Suncus*]. * * * with less salient posterointernal lobes * * * Lower molars also simplified, without accessory basal lobes or ledges, the posterior (M_3) remarkably reduced, consisting only of a smooth lunate cuspless crest corresponding to the tuberculo-sectorial trigonid of the other shrews, the unusual heel completely aborted."

Solisorex is distinct from all known shrews. It is unique among the crocidurines in the loss of the labial cingulum on the lower teeth; the reduction of M_3 and the specialization of the mandibular articulation is matched only by the extinct *Diplomesodon fossorius;* the dental formula and other features of the dentition are similar to *Praesorex.*

Through the kindness of R. W. Hayman, I have been able to examine photographs of a specimen in the British Museum (Nat. History), BM.31.8.14.4. No specimen was seen. Recent, Ceylon.

Genus SORICELLA Doben-Florin, 1964

Genotype: *Soricella discrepans* Doben-Florin, 1964

The following quotations are from Doben-Florin (1964, p. 48):

Diagnosis.—"Middle-sized soricid, teeth appear unpigmented."

Lower dentition.—"Doubly-scalloped incisor, scallops inclined forward, the first [most posterior] near the tooth base. Three single-cusped antemolars, the last [most posterior or P_4] two rooted, the middle tooth smaller. Molars decreasing in size from front to back. M_1 and M_2 without hypoconulid [entoconid fused to the hypolophid], M_3 rather large with double-cusped talonid. Labial cingulum strong."

Upper dentition.—"Incisor with posterior accessory cusp, four antemolars, all well visible; the second smaller than the rest. Between the last [most posterior] and P^4 lies a small diastem. M^1 and M^2 are concavely emarginate on their posterior side; their trigonbasins closed posteriorly for the most part by a flat enamel border."

Condyle.—"Rather small with wide, almost straight, undivided articular surface."

From Doben-Florin's illustration of the posterior view of the mandibular condyle (pl. 5, fig. 5: the condyle of specimen 11702, shown on table 34, p. 53, to be a left mandible), the articular structure is distinctly crocidurine and has prominent lingual confluence of the two articular surfaces. Her figures of the occlusal view of P_4 are not clear enough for me to be certain that they have the crocidurine triangular cusp. The high dental formula, 1–5–3/1–3–3, the uniquely sharp cusps on the cutting edge of the lower incisor, and the tall, narrow coronoid process of the mandible, which is very reminiscent of *Diplomesodon,* appear to be the most distinctive characters of this genus.

One species, *Soricella discrepans* Doben-Florin, has been described. It is from the older Burdigalian of Wintershof-West. No specimen was seen.

Genus SUNCUS Ehrenberg, 1832

Figure 13

Genotype: *Suncus sacer* Ehrenberg, 1832

Dental formula 1–5–3/1–2–3; lower incisor short to moderate length and curving upward, cutting edge only very slightly serrate at most; groove along length of medial side curves above notch in basal border and forms posterolingual cingulum; first upper antemolar larger than subequal second and third, fourth antemolar much smaller, all unicuspid. The genus contains the smallest and the next to largest living shrews. Early Pleistocene to Recent, Africa; Recent, Europe and Asia.

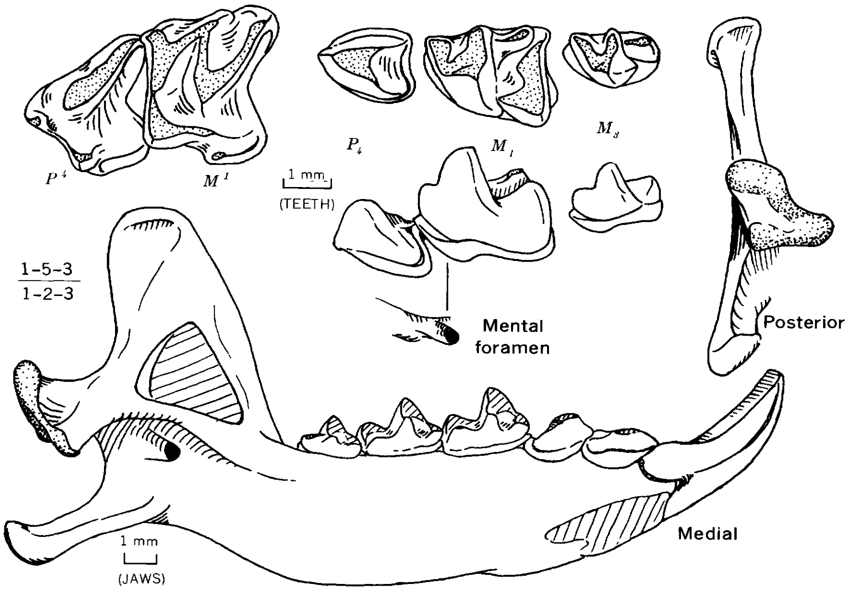

FIGURE 13.—*Suncus caeruleus* Kerr, Ceylon UCMVZ 81267. Left mandible and dentition and left upper dentition.

Ellerman and Morrison-Scott (1951, p. 65) stated that in their opinion this genus is no more than a subgenus of *Crocidura.*

Specimens examined.—A small series including *Suncus caeruleus* and *S. etruscus* in the University of California Museum of Vertebrate Zoology.

Suncus sp., Meester, 1955

The genus has been reported from several South African localities. Several specimens have been seen. Early Pleistocene, South Africa.

Genus SURDISOREX Thomas, 1906

Figure 14

Genotype: *Surdisorex norae* Thomas, 1906

Dental formula 1–4–3/1–2–3; upper antemolars as in *Crocidura* except P^4 distinctly more elongate (also seen in *Myosorex blarina zinki* Balsac and LaMotte, 1956, fig. 2); lower antemolars elongate; first lower antemolar with two-cusped crest; P_4 two rooted with accessory cuspule on both posterolabial and posterolingual crests, posterolingual crest incomplete behind accessory cuspule, posterolabial crest normal for subfamily to accessory cuspule but behind this cuspule crest swings lingually and merges with posterior cingulum at midpoint of tooth or even as far lingually as posterolingual corner of tooth; metalophid-protolophid junction of M_1 placed remarkably close to labial side of tooth; other dental characters as in *Crocidura;* ascending ramus very broad; articular condyle of mandible of crocidurine pattern but unique in closeness of upper and lower articular surfaces and basically a single, triangular, posteriorly convex articular surface with labial emargination. Recent, Africa.

Although the structure of P_4 of this shrew closely parallels that of the soricine shrews, other features, particularly the mandibular condyle, clearly indicate that it is a crocidurine shrew. The condyle itself is also interesting in that it more closely approaches the normal mammalian single condyle than does that of any other living shrew examined in this review, although in *Myosorex* the articular surfaces are only slightly separated.

Specimens examined.—U.S. National Museum 182593, a male of *S. norae,* from Kenya; American Museum of Natural History 187262, a female from Kenya.

Genus SYLVISOREX Thomas, 1905

Figure 15

Genotype: *Crocidura morio* Gray, 1862

Dental formula 1–5–3/1–2–3; lower incisor long and projecting straight anteriorly (except *S. megalura,* see Heim de Balsac and LaMotte, 1957, fig. 10c), cutting edge serrate with three prominent notches separating rounded cuspate lobes comparable to those of many species of *Sorex;* first upper antemolar behind incisor larger than equal-sized second, third, and fourth, all unicuspid; P_4 with accessory cuspule on the posterolingual crest only. Recent, Africa.

Ellerman, Morrison-Scott, and Hayman (1953, p. 19) treated *Sylvisorex* as a synonym of *Myosorex,* and *Myosorex* as a subgenus of *Suncus.* The construction of the lower incisor alone would indicate that *Sylvisorex*

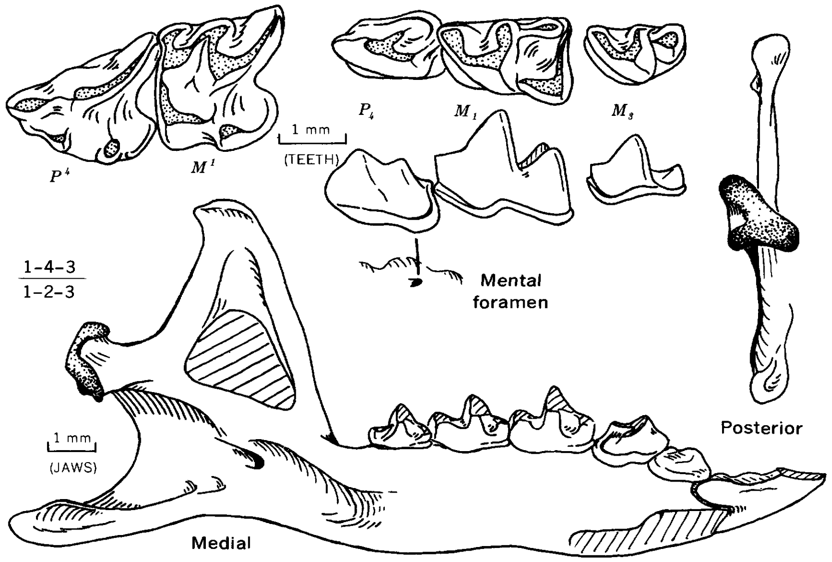

FIGURE 14—*Surdisorex norae* Thomas, Kenya USNM 182593. Left mandible and dentition and left upper dentition.

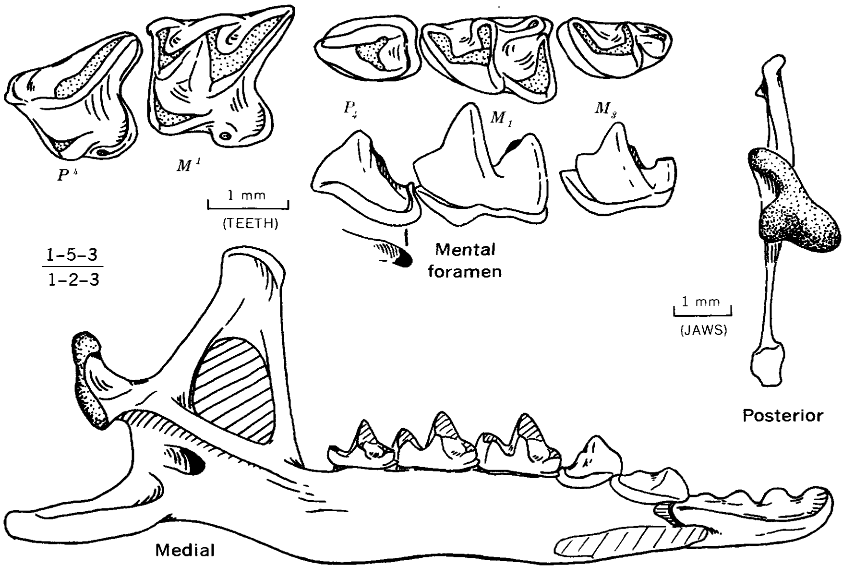

FIGURE 15.—*Sylvisorex lunaris* Thomas, Uganda, CNHM 26260. Left mandible and dentition and left upper dentition.

is distinct and possibly closer to *Feroculus* than to *Suncus*.

Specimen examined.—Chicago Natural History Museum 26260, *Sylvisorex lunaris*, from Uganda.

Crocidurinae? Incertae Sedis

"Limnoecus" micromorphus Doben-Florin, 1964

"Very small shrew, teeth probably pigmented, similar to *L. niobrarensis* [on which no pigment is visible] * * * M_3 with a single-cusped talonid. M_1 and M_2 with a hypoconulid [hypolophid separated from entoconid] and very strongly developed entoconid. In the M_1 the metaconid stands slightly behind the protoconid. All three molars with a delicate, but distinct labial cingulum * * * Two antemolars, the posterior one two rooted. Mental foramen below the trigonid of M_1, condyle with undivided articular surfaces, *Crocidura*-like. Mandibular foramen behind the middle of the internal temporal fossa." (Doben-Florin, 1964, p. 44).

In her description of the holotype, Doben-Florin further stated (p. 45) that a "pronounced, somewhat concave chewing surface, on the three-cornered outline [of P_4] slopes from the tooth cusp [apex]." On page 48, she makes the following comparison: "The chewing surface of the two antemolars are stretched out in *L. niobrarensis* and run to a median, small, posterior cusp. In the Wintershof form, however, the chewing surface is three cornered, somewhat concavely excavated, the elevated posterior margin allows the tooth to appear two cusped from the labial side; there is, however, no corner behind the cusp as formed for example, in the Recent *Sorex alpinus*." From this description, as well as from what can be seen from the single illustration of the occlusal surface of P_4 (pl. 4, fig. 9a), the P_4 of "*L.*" *micromorphus* appears to be crocidurine rather than limnoecine.

Although difficult to judge from figure 9a of plate 4, the distance between the protoconid and metaconid of M_1 appears relatively much greater than in any known limnoecine shrew.

Doben-Florin's statement about possible pigmentation and the posterior position of the mental foramen suggest that the species is not crocidurine, however. It seems, therefore, that no conclusive subfamily assignment can be made from the published description. The species is here questionably referred to the Crocidurinae because of the form of the P_4. The objections to this referral may be reduced by noting that Doben-Florin was not certain that the teeth were pigmented.

"*L.*" *micromorphus* is from the older Burdigalian fauna of Wintershof-West. No specimen was seen.

"Sorex" collongensis Mein, 1958

To judge from Mein's figure 22, this shrew has a crocidurine P_4. Its teeth have no pigmentation, and the mental foramen is below P_4, which also suggest the crocidurine shrews, in late Miocene or more recent time at least. Mein (1958, p. 26) stated that the species also has a mandibular articulation that is enormous for the size of the mandible but does not figure the articulation or further describe it. His description of the internal temporal fossa as "semicircular" suggests the Soricinae. Based upon the criteria of the present review, this shrew is only questionably placed in the Crocidurinae.

According to Mein, it has an anteriorly placed dental foramen—comparable to "*S.*" *dehmi*—and four lower antemolars. No specimen was seen. Late middle or late Miocene of France.

Crocidura?, Mein, 1958

Only two maxillary fragments are reported (Mein 1958, p. 27). According to Mein, they resemble "*Sorex*" *dehmi* from the same fauna but have fewer antemolars. Based upon the criteria considered in the present report, these specimens are not assignable to a subfamily. No specimens were seen. Late middle to early late Miocene, France.

Three living genera which are customarily placed in the Crocidurinae are not included in this subfamily in this review. The main criteria used to remove them from the Crocidurinae and to place them in the Soricinae are structure of P_4 and structure of the mandibular condyles. In addition, some have pigmented teeth, at least in some individuals. In one genus, pigmentation is only at the very tips of the cusps and is removed in early wear; in another, it is of a very light color so that it is sometimes unnoticed. One genus is unpigmented. In the past few decades many people have noticed the fact that some crocidurines have pigmented teeth, and there have been two distinct reactions: One is that the subfamily criteria break down and hence the subfamily classification is not real; the other is that the shrews in question have pigmented teeth and are not crocidurine by definition.

The first reaction is typified by Ellerman and Morrison-Scott (1951, p. 41) who made note of the inconsistencies in pigmentation and abandoned subfamily classification without further investigation. The second reaction is perhaps best typified by Bate (1945, p. 761), who removed those shrews with pigmented teeth from the Crocidurinae but also cited several other skull and skeletal differences that suggest closer relationships to the Soricinae.

Genera which have been included in the Crocidurinae (for example, by Simpson, 1945, p. 51–52) but are included in the Soricinae in this review are: *Anourosorex; Chimarrogale; Nectogale.*

In addition, North American fossil shrews generally assigned to the genus *Limnoecus* are removed from the Crocidurinae and placed in a new subfamily, the Limnoecinae, on the basis of the structure of P_4, pigmentation, structure of M_3, and position of the mental foramen; the mandibular articulation of the Limnoecinae appears identical to that of the Crocidurinae.

Subfamily **LIMNOECINAE** Repenning, new name

P_4 with little or no lingual segment or posterolingual ridge of primitive triangular cusp, labial segment of primitive cusp and its posterolabial crest form a medially shifted longitudinal ridge, labial shearing blade (as in Soricinae) not developed, posterolingual basin (as in Soricinae) little or not developed, single root, slight overhang by labial cingulum over root and alveolus but never as extreme as in most soricines; M_1 with protoconid and metaconid as close or closer together in unworn teeth than in any other known shrew, entoconid strong, entoconid crest low; M_3 lacking double-cusped talonid in earliest form and an appreciable talonid basin lost through emphasis of metalophid by late Miocene time, becoming very nearly a simple trenchant heel like that in modern crocidurine shrews and more trenchant than in late Miocene crocidurines; upper teeth unknown except for incisor and M^3; pigmented heavily in earliest form but only at tips of cusps in later forms; lower dental formula 1–3–3 to 1–2?–3; articular facets of mandibular condyle as in Crocidurinae, internal temporal fossa present; mental foramen below trigonid of M_1 (more posterior than in most crocidurine shrews of comparable age). Early Miocene (Arikareean) to middle Pliocene (Hemphillian),[3] North America.

This is a small but nevertheless distinct subfamily. It is rather well known in the Miocene and early Pliocene faunas of western United States and is represented from faunas of both ages in California (Stirton, 1930; James, 1963, p. 31–47), from the Miocene of Colorado (Wilson, 1960, p. 33–35), Wyoming (Reed, 1960, p. 6–7), and Nebraska (Macdonald, 1947), and from the early Pliocene of Nevada (J. E. Mawby, oral commun., 1963) and middle Pliocene, Oregon.

Genus ANGUSTIDENS Repenning, n. gen.

Genotype: *Sorex vireti* Wilson, 1960

Diagnosis.—P_4 triangular in occlusal view and basically crocidurine in pattern except strong posterolabial crest meets (but does not merge with) cingulum distinctly medial of posterolabial corner and posterolingual crest reduced and detached from apex of primary cusp, sulcus on posterior face of cusp between crests; M_1 with protoconid and metaconid distinctly close together, entoconid strong and detached from hypolophid but connected to metaconid by very low entoconid crest, reentrant between protoconid and hypoconid emerges on labial face of tooth just above cingulum, labial cingulum very subdued to absent below protoconid of M_1 but strong both anteriorly and posteriorly from this point; M_3 with reduced talonid but still retaining minute basin and low entoconid crest; mental foramen below trigonid of M_1; pigmentation extensive, comparable to *Sorex;* lower dental formula 1–3–3 or possibly 1–4–3, in which case P_3 was vestigal and represented in type mandible by a minute alveolus on anterior margin of alveolus of P_4.

Etymology.—Latin: Angustidens, narrow tooth; refers to the closeness of the protoconid to the metaconid.

Angustidens vireti (Wilson), 1960

Figure 16

Sorex vireti Wilson, 1960, Kansas Univ. Paleont. Contr., Vertebrata, art. 7, p. 33–35 and 37–38.

Limnoecus vireti (Wilson). James, 1963, California Univ. pub. Geol. Sci., v. 45, p. 36.

A fairly large shrew slightly smaller than living *Blarina brevicauda.* Size, location of the mental foramen in a depression that leads anterodorsally to the antemolar region, location of the dental foramen about on midline of and well below internal temporal fossa, and weakness or absence of the labial cingulum of M_1 below protoconid may prove to be of specific importance when other shrews are found that belong to this genus. Early Miocene (Arikareean) of northeastern Colorado.

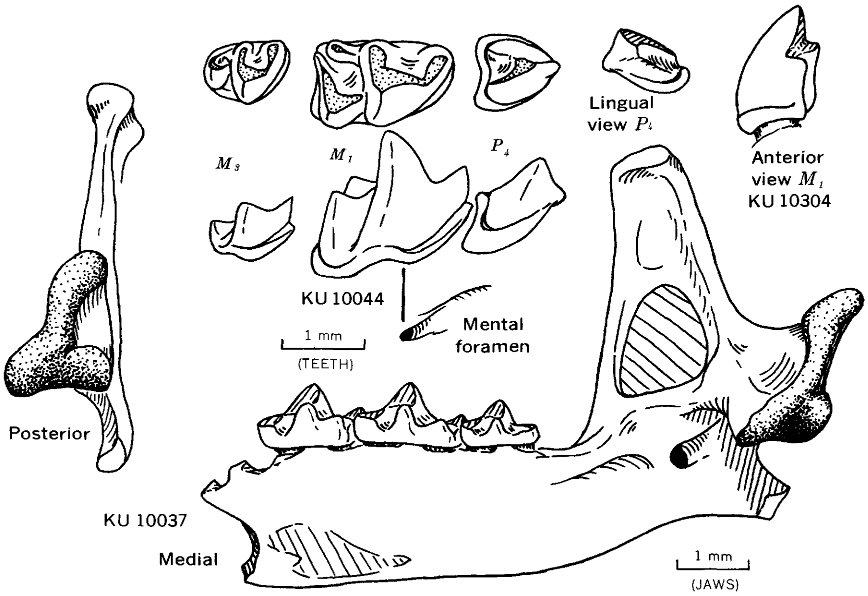

FIGURE 16.—*Angustidens vireti* (Wilson), type KU 10037 and referred specimens KU 10044 and 10304. Right mandible and lower dentition.

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[3] A right mandible of *Limnoecus* sp. cf. *L. tricuspis,* bearing unworn M_1 to M_3, was collected by the author from the Hemphillian fauna at Rome, Oreg. This represents the only known middle Pliocene record.

James (1963, p. 39) placed this species in the genus *Limnoecus*. The relationship is clear but the differences between *Limnoecus* of the late Miocene and Pliocene and this species seems to be greater than comparable differences between living shrew genera, as between *Sorex* and *Microsorex*. Wilson's species, therefore, is placed in a new genus. In the form of P_4 and M_3, *Angustidens vireti* is exactly intermediate between the condition believed to have been present in a hypothetical soricid progenitor (typified in these two teeth, at least, by *Domnina*) and *Limnoecus*.

Specimens examined.—The type, University of Kansas Museum of Natural History 10037, and paratypes listed by Wilson (1960, p. 33).

Genus LIMNOECUS Stirton, 1930

Genotype: *Limnoecus tricuspis* Stirton, 1930

P_4 with posterolabial crest of primitive triangular P_4 forming medial crest which hooks lingually where it merges with posterior cingulum, posterolingual crest nearly or entirely lost; reentrant valley between protoconid and hypoconid of M_1 emerges on labial face well above cingulum; talonid of M_3 reduced to trenchant heel formed by posteriorly directed metalophid and hypoconid, talonid basin virtually lost although faint trace of entoconid crest (not continuous with hypoconid) usually present on lingual edge of talonid in unworn teeth; pigment reduced to tips of cusps or at most to upper half of paraconid blade of M_1; lower dental formula 1–3–3 to 1–2?–3.

Limnoecus tricuspis Stirton, 1930

Figure 17

Medium-sized shrew comparable in size to living *Sorex araneus;* teeth more slender in occlusal view and more delicate than *L. niobrarensis;* P_4 retaining slight remnant of posterolingual crest; M_3 retaining slight talonid basin and entoconid crest with trenchant metalophid curving posterolingually to merge with hypoconid; lower dental formula 1–2?–3. Late Miocene (Barstovian), early Pliocene (Clarendonian), California, and middle Pliocene (Hemphillian), Oregon.

This is the genotypic species. In the type description Stirton (1930, p. 218) considered the lack of a metaconid on M_3 to be a diagnostic feature of *Limnoecus*. James (1963, p. 31–47) reprepared and restudied the type and concluded that the metaconid had been broken off of the specimen. He also described new material from the early Pliocene. Known material is not adequate to rule out the possibility of a vestigial P_3 being present.

Specimens examined.—The type, University of California Museum of Paleontology 31047; topotypic material in the University of California at Riverside; and referred specimen, University of California Museum of Paleontology 55515, from Cuyama Valley, Calif. Uncataloged specimen from USGS vertebrate loc. M1078, Rome, Oreg.

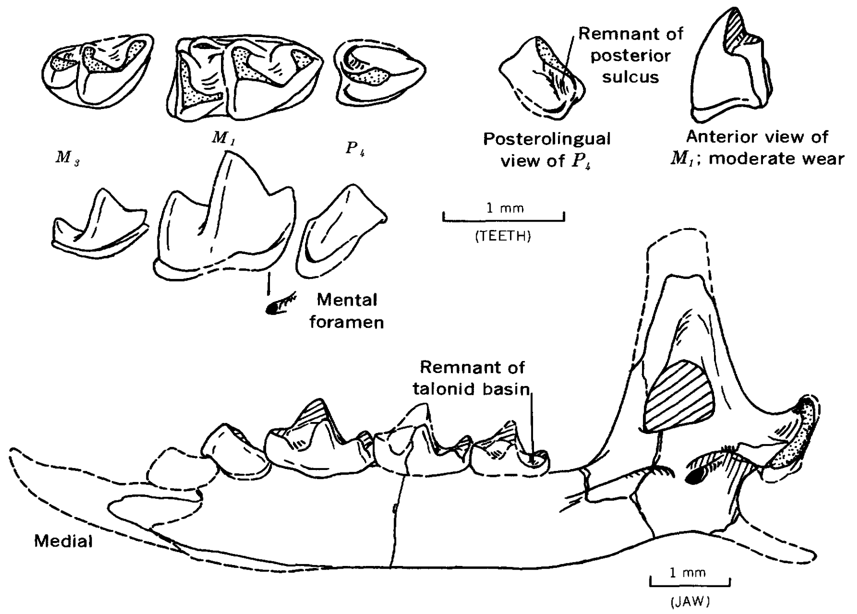

FIGURE 17.—*Limnoecus tricuspis* Stirton, type, UCMP 31047. Right mandible and lower dentition.

Limnoecus niobrarensis Macdonald, 1947

Figure 18

Medium-sized shrew with teeth broader in occlusal view, bearing stouter cusps, than those of *L. tricuspis;* P_3 minute, vestigial, and largely overlapped by P_4; P_4 nearly square in occlusal outline with no trace of posterolingual crest; M_3 with metalophid directed posteriorly to hypolophid, very slight remnant of entoconid crest but no trace of talonid basin; mandible stouter than in *L. tricuspis;* lower dental formula 1–3–3. Late Miocene (Barstovian), Nebraska.

The differences between *L. tricuspis* and *L. niobrarensis* are slight but are of the same sort and of same magnitude as are observable in the mandibles of living species of *Sorex*, for example, between *Sorex cinereus* and *Sorex merriami.* Based on this analogy with living species, these differences seem to be of specific value. Many of the specific characters given by Macdonald (1947, p. 124–125) were based upon features that James (1963, p. 32–33, tables 6, 7) pointed out resulted from damage of the type of *L. tricuspis* not known to Macdonald. James further concluded that the differences in tooth proportions between the two species could represent those of sex rather than species and synonymizes *L. niobrarensis* with *L. tricuspis.* The possibility that the differences are sexual rather than specific has not seemed great enough in the present review to abandon Macdonald's species, and it is here retained until a larger sample of both species can shed more light on their variation.

Specimens examined.—The type and paratype, University of California Museum of Paleontology 36171 and 36172.

Subfamily SORICINAE Fischer von Waldheim, 1817

P_4 with no lingual segment of primitive triangular cusp, labial segment of primitive cusp and its posterolabial crest retained as labial shearing blade, in more advanced forms this blade is continuous with elevated posterior cingulum forming L-shaped crest enclosing posterolingual basin (which has evolved from posterior sulcus between crests of primitive triangular cusp of P_4), posterolingual crest greatly reduced or absent (more usual in advanced forms), cingulum overhangs root and lateral surface of mandible below posterolabial corner of P_4 in most genera more than in contemporary forms of other subfamilies, single rooted except in atypical Miocene form; molars variable; pigmentation usually present, sometimes extreme, but absent in some genera of one tribe; dental formula 1–6–3/1–4–3 in early Miocene forms (higher than in *Domnina*) and 1–6–3/1–2–3 to 1–3–3/1–2–3 in modern forms (1–4–2/1–2–2 in *Amblycoptus*); mental foramen in many genera farther back than in contemporary crocidurines and limnoecines; articular facets of condyles little separated (or even joined in earlier forms) to extremely separated in most living genera, facets are joined along labial side of condyle, rather than along lingual side as in crocidurine-limnoecine pattern, with lingual emargination of interarticular area; internal temporal fossa present. Late Oligocene

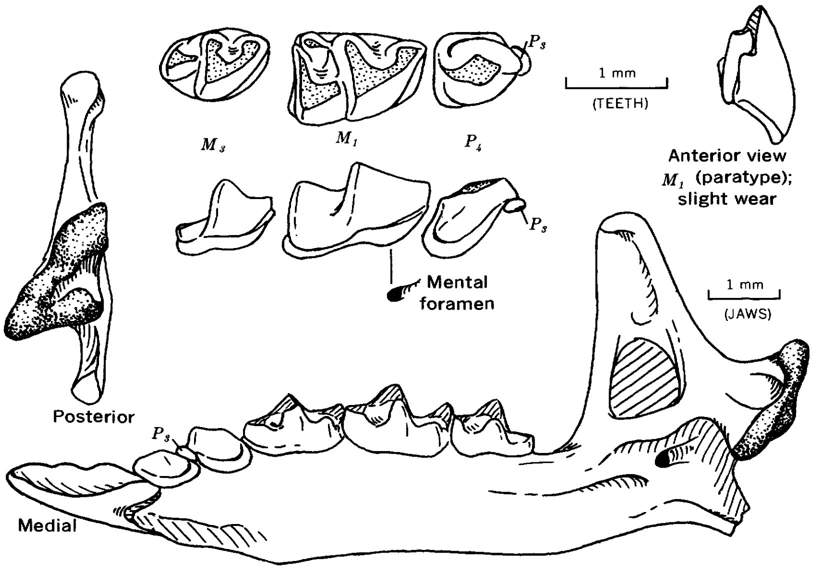

FIGURE 18.—*Limnoecus niobrarensis* Macdonald, type and M_1 of paratype, UCMP 36171 and 36172. Right mandible and lower dentition.

(Stampian) to Recent, Europe; early Miocene (Arikareean) to Recent, North America; early(?) Pliocene to Recent, Asia; Recent, South America; not known from Africa or peninsular India. Romer (1928, p. 100) stated that *Sorex vulgaris* (= *Sorex araneus*) now lives in Mediterranean Algeria but is not known in the late Pleistocene deposits of that area; however, this is the only publication I have found that mentions soricines from Africa.

A diagnosis of this subfamily is difficult to outline briefly because of great evolutionary change and because of remarkable differences in contemporaneous genera of the subfamily, particularly later in the history of the subfamily. Consideration of the subfamily as a whole and throughout its history leaves only two criteria which are entirely definitive: the structure of P_4 and of the articular condyle or condyles. In some genera even these are difficult to recognize but never has there been any question of subfamily recognition when more variable criteria have been used in support of the characters of P_4 and of the condyles. It should be emphasized, however, that other characters vary with the stage of evolution and with separate lineages within the subfamily Soricinae.

Although the number of living species of crocidurine shrews about equals that of the soricine shrews, there are twenty-nine soricine genera recognized in this review and only ten crocidurine genera. To review this large subfamily with some system comparable in detail to that used for the other subfamilies, the Soricinae have been broken down into three tribes. These subdivisions are based on the structure of the mandibular articulation and associated musculature which appears to remain constant within the tribes despite the presence of genera otherwise very diverse in form. The subfamily is readily classified into two tribes on the basis of the mandibular articulation. A third tribe is set up for those few genera (but many species) that are of primitive structure in their articulation and cannot easily be assigned to either of the two more specialized tribes. In varying degrees other features support this tribal grouping.

Within the tribes further subdivision, of a subtribe magnitude, is suggested by features found to be exclusive in only part of a tribe, and these features seem to have geographic significance, at least on a continental scale. These subtribes are discussed and serve as a basis for the order of discussion of genera where such lesser subdivisions seem to be present. They are not sharply defined, however, and are not formally set up as classification units.

The modification of the mandibular articulation is developed to increase the strength of the bite. To do this the lower articular facet, on which the mandible is hinged, is moved forward to shorten the lever arm of the horizontal ramus. The temporal muscle is also strengthened, and its area of origin is spread upward and forward over the cranium. Its greater and more transverse force increases the tendency for the posterior part of the mandible to be pulled into the side of the braincase when biting. Consequently, the upper articular facets, the single function of which is to counteract the transverse force of the temporal muscle, is changed in orientation in order to remain approximately normal to the average force resultant of the temporal muscle. As the upper articulation does not function as a hinge but rather slides back and forth over a strong articular boss on the cranium, this does not impair the hinge action of the mandible which is controlled by the position of the lower condylar facet.

Primitively the condyloid process supporting the upper articular facet is a thin plate of bone alined with the plane of the ascending and horizontal rami, as in *Sorex*. As the force of the temporal muscle increases, the plane of the condyloid process curves away from the plane of the horizontal ramus and toward the braincase in order to parallel the force resultant of the temporal muscle to attain greatest possible strength in resisting the tendency of this muscle to pull the mandible into the braincase. This is actually accomplished by an outward warping of only the ascending ramus rather than of the entire proximal part of the mandible.

The most readily recognized changes in the proximal part of the mandible resulting from a strengthening of the bite area are, therefore, separation of the articular facets by the forward placement of the lower facet and outward deflection of the ascending ramus to allow the inward curving of that part of the condyloid process that supports the upper facet.

As these changes take place, an emargination of the lingual side of the interarticular area develops and the insertion of the superior pterygoid muscle on the lingual side of the condyloid process, between the two articular condyles, becomes basined. This condition is found in *Neomys* and is the articular structure which characterized the tribe Neomyini (fig. 1). The action of the superior pterygoid muscle upon the mandible is directly forward, consequently the lingual condylar emargination weakens its insertion and a pterygoid spine or boss is developed to strengthen it in many forms. The spine is at the dorsal margin of the superior pterygoid fossa just below the upper sigmoid notch. The tribe Neomyini is also characterized by a bifid upper incisor and a prominent entoconid crest on M_1 of most forms, as well as several other dental and cranial features.

In other shrews the insertion of the superior pterygoid muscle is strengthened by the development of a bone plate across the lingual condylar emargination which also strengthens the condylar process supporting the upper condyle. Except in forms where the bone plate is weakly formed, no pterygoid spine is required or developed. In posterior view the intercondylar area appears to lack any emargination although the area filled by the bone plate behind the basined insertion of the superior pterygoid muscle is usually depressed from the rest of the interarticular area. This is the condition found in *Blarina* and is the articular structure that characterized the tribe Blarinini (fig. 1). The tribe Blarinini is also characterized by an uncleft upper incisor and by no entoconid crest on the M_1, as well as several other dental and cranial features.

The articular structure is unmodified in the tribe Soricini (fig. 1). The articular facets are not far apart and the condylar process, the coronoid process, and the horizontal ramus all lie in the same plane. An entoconid crest is present on M_1, and a bifid upper incisor, generally a feature of a variant individual, may or may not be present.

Tribe SORICINI Fischer von Waldheim, 1817

Articular facets of mandibular condyle continuous or only slightly separated, both facets approximately normal to longitudinal axis of cranium; when facets are separate, interarticular area broad with no conspicuous lingual emargination seen in posterior view, lower facet not offset lingually beyond plane of mandible at lower sigmoid notch or shifted appreciably forward (fig. 1); superior pterygoid fossa of the mandible a shallow pit; external temporal fossa of mandible extends no lower on ascending ramus than upper sigmoid notch; internal temporal fossa of mandible large and triangular; coronoid process not deflected labially but in plane of horizontal ramus and of condyloid process; zygomatic process of maxillary originates to rear of M^2; M^2 rectangular in occlusal view; M_1 with strong entoconid crest; M_3 unreduced or with only talonid reduced, roots separate by distance equal to or greater than transverse diameter of anterior alveolus; teeth pigmented.

This tribe includes four living genera; one is *Sorex*, containing by far the largest number of species of any genus of shrew and the only truly holarctic genus now living. The tribe also contains the oldest fossil representatives of the subfamily Soricinae because, by definition, it has the least specialized mandibular articulation. Among living genera of this tribe, there are two distinct lineages. The first lineage, exemplified by the living *Sorex*, is primitive in nearly all respects in addition to the articular structure and has a known history dating from the late Oligocene of Europe and the early Miocene of North America. The second lineage, exemplified by the living *Blarinella*, is advanced in most respects except in the articular structure and has a known history dating from the middle Pliocene of eastern Asia, and from the late Pliocene of Europe.

Genus CROCIDOSOREX Lavocat, 1951

Genotype: *Crocidosorex piveteaui* Lavocat, 1951

Dental formula 1–6–3/1–4–3, including a minute vestigial P_3; P_4 with soricine labial shearing blade which bears a secondary cuspule but (in contrast to *Sorex*) does not merge with posterior cingulum and does not enclose posterolingual basin, overhang by cingulum at posterolabial corner of tooth very slight and single root not covered; M_1 with cingulum only along paraconid blade and with reentrant valley between protoconid and hypoconid emerging on labial face of tooth well above enamel base in marked contrast to contemporary *Domnina;* M_3 as in *Sorex* and *Domnina* with unreduced talonid enclosed lingually by entoconid crest; mental foramen below P_4; mandibular condyle with facets only slightly more separated than in *Domnina* but lower facet placed more ventrally than in heterosoricines and not offset lingually beyond plane of mandible at lower sigmoid notch, condyle with soricine pattern of labial connection between upper and lower facets and lingual emargination between facets rather than opposite as in crocidurines and limnoecines (see pl. 2, fig. 73, in Schlosser, 1887, for illustration of condyle); internal temporal fossa deep and narrowly triangular; masseteric fossa absent; P^4 and M^1 with moderate emargination of posterior basal outline between hypoconal flange and metastyle.

Crocidosorex piveteaui Lavocat, 1951

Medium-sized shrew comparable in size to living *Sorex araneus;* M_1 with prominent entoconid connected to metaconid by relatively low entoconid crest; upper teeth unknown; teeth unpigmented according to Lavocat (1951, p. 24). No specimen was seen. Late Oligocene (upper Stampian) of France according to René Lavocat (oral commun., 1963).

Crocidosorex antiquus (Pomel), 1853

Sorex antiquus Pomel, 1853, Annales sci., litt., indus. [Auvergne], v. 26, p. 81–229.

Sorex antiquus, Stehlin, 1940, Eclogae geol. Helvetiae, v. 33, p. 298, figs. 1b, 2b, 3, 4b, and 5b.

Small shrew, smaller than *C. piveteaui* and comparable in size to living *Microsorex hoyi;* M_1 with prominent entoconid connected to metaconid by well-developed entoconid crest; teeth pigmented; upper teeth and mandible as described for genus. No specimen seen. Excellent material is well illustrated and described by Stehlin (1940, p. 298–301). Early Miocene (Aquitanian) of France (Montaigu-le-Blin) and Germany (Weisenau).

C. piveteaui and *C. antiquus* are similar shrews, but the differences in pigmentation and in the entoconid crest seem to warrant their retention as separate species until such time as the specimens can be compared directly. Lavocat (1951, p. 23–24) makes no comparison between the two.

"*Sorex pusillus* von Meyer" of Tobien (1939, p. 165) may belong to this genus, but the published description is not adequate for certain assignment. Stehlin (1940, p. 299, footnote 4) stated his opinion that "*Sorex*" *pusillus* and "*Sorex*" *ambiguus* are probably about the same as "*Sorex*" *antiquus.* The same possibility is also expressed by Kretzoi (1959b, p. 247); however, Kretzoi also noted that "*Sorex*" *pusillus* von Meyer was preoccupied by *Sorex pusillus* Gmelin, and he replaced the name with a new genus and species (ibid., p. 247, 248, footnote 1) *Oligosorex meyeri* to apply to the shrew from Weisenau (without reference to other shrews he would include in the genus) Kretzoi's diagnosis for the genus *Oligosorex* is "late Oligocene and Miocene Soricids of small dimensions, retaining three unicuspids between P_4 and the relatively small and primitive front incisor in the lower jaw"; this diagnosis basically conforms to that here used for *Crocidosorex.* Study of the specimens, however, could well lead to the conclusion that the two genera are distinct.

Crocidosorex is structurally suitable as an ancestral form for all later soricine shrews. It differs little from living *Sorex,* the differences being those cited in the generic diagnosis.

Genus ANTESOREX Repenning, n. gen.

Genotype: *Sorex compressus* Wilson, 1960

Diagnosis.—P_4 and mandibular condyle as in Soricinae. P_4 with weak shearing blade that merges with posterior cingulum, shearing blade with slight secondary cuspule, posterolingual basin not developed, two roots arranged longitudinally, labial cingulum slightly overhangs anterior root and not posterior root; M_1 with reentrant valley between the protoconid and metaconid emerging on labial face of tooth well above cingulum (much higher than in the limnoecine shrew *Angustidens vireti* which was collected in the same deposits as the genotype of *Antesorex*), well-developed entoconid connected to metaconid by a high entoconid crest, labial cingulum fairly strong along paraconid blade but very weak and difficult to see along remainder of labial side of tooth; M_3 as in *Sorex* with talonid basin completely enclosed by the entoconid crest; emargination of posterior basal outline of P^4 about as in *Crocidosorex* but possibly slightly greater in M^1; teeth pigmented; mental foramen below posterior root of P_4; internal temporal fossa strong and narrowly triangular as in *Crocidosorex*;

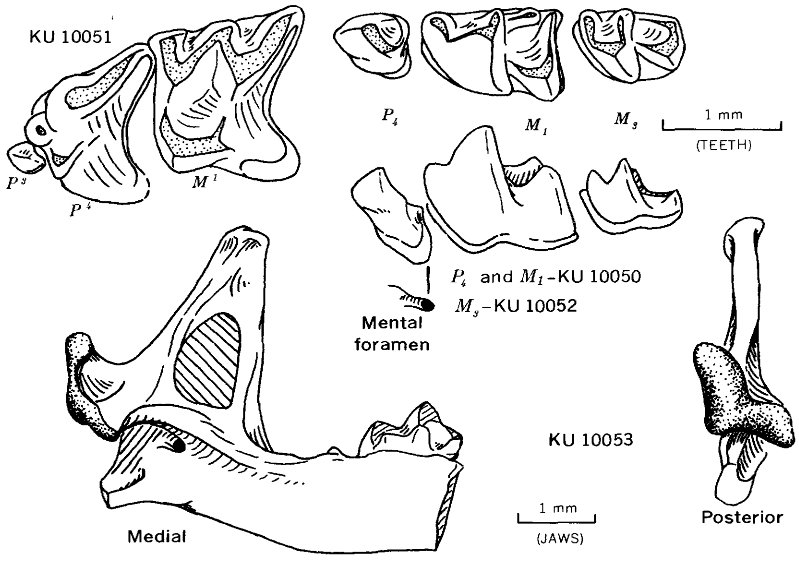

FIGURE 19.—*Antesorex compressus* (Wilson), type KU 10050 and referred specimens. Left mandible and lower dentition and referred left upper dentition.

masseteric fossa absent; mandibular condyle with facets only slightly more separated than in *Domnina* but lower facet placed more ventrally than in heterosoricines, articular surfaces of facets continuous along labial side of condyle and not along lingual side of condyle as in limnoecines and crocidurines; number of antemolars unknown.

Etymology.—Latin: Ante, before, and the genus *Sorex.*

Antesorex compressus (Wilson), 1960

Figure 19

Sorex compressus Wilson, 1960, Kansas Univ. Paleont. Contr., Vertebrata, art. 7, p. 35–38, figs. 29–31.

Small shrew comparable in size to *Microsorex hoyi;* P_4 anteroposteriorly compressed and with constriction around crown that may have been deformity during growth; M_1 with protoconid remarkably close to the metaconid in unworn teeth. Late early Miocene (late Arikareean), northeastern Colorado.

The genus *Antesorex* from North America is very close to *Crocidosorex* from Europe, and *A. compressus* is most like *C. antiquus. Antesorex* is slightly more advanced in the union of the labial shearing blade to the posterior cingulum of P_4, in the continuous (although weak) cingulum along the labial side of M_1, and in the somewhat greater emargination of the posterior basal outline of M^1. It seems less advanced in the retention of two roots on P_4, a feature that may be an atavism.

Specimens examined.—The type, University of Kansas, Museum of Natural History 10050, and paratypes listed by Wilson (1960, p. 35).

Genus SOREX Linnaeus, 1758

Figure 20

Genotype: *Sorex araneus* Linnaeus, 1758

Dental formula 1–6–3/1–2–3; lower incisor usually with ventral margin having little dorsal curve toward tip (all Old World species appear to have three well-developed scalloped cusps on cutting edge of lower incisor, but there are exceptions to this in New World species); M_1 with entoconid crest connecting entoconid to metaconid; M_3 as in *Domnina* and *Crocidosorex* with unreduced and basined heel; P^4 and M^1 with strong emargination of posterior basal outline; protocone of P^4 not as lingual in position as hypoconal flange; teeth pigmented; articular facets of mandibular condyle slightly to moderately separated, lower facet extends labially to or beyond plane of mandible at lower sigmoid notch; interarticular area of condyle not appreciably constricted in posterior view in most species but extremely variable and approaching the pattern of other tribes in some species; mental foramen usually below protoconid of M_1 or anterior of this point.

The genus is the most generalized and, in many respects, the most primitive of living soricine shrews. No species are known that are unquestionably of early Pliocene age, but there are a large number of fossil species included in the genus of later Pliocene and Pleistocene age. These have been briefly reviewed (mostly from published accounts) for conformity to the generic diagnosis but not for synonymy or for

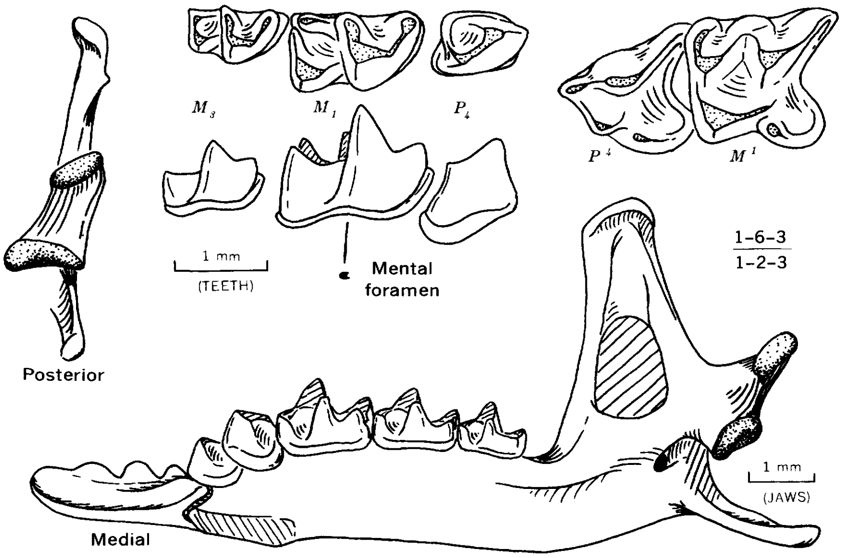

FIGURE 20.—*Sorex araneus* Linnaeus, Belgium, author's collection 60182. Right mandible and lower dentition and left upper dentition.

specific diagnosis. The following list is of species here included in the genus, some questionably:

Pliocene and earliest Pleistocene species

Sorex dixonensis Hibbard, 1956. To judge from the published illustrations, the low-crowned molars, the wide lower mandibular condyle, the narrow interarticular area, and the very strong entoconid crest on M_2 are exceptional for the genus. The generic and tribal assignment is here considered doubtful. No specimen was seen. Earliest Pleistocene (late Blancan), Kansas.

Sorex alpinoides Kowalski, 1956. Poland. No specimen was seen.

Sorex leahyi Hibbard, 1956. The lower condyle is more elongate lingually than in most species of *Sorex*. Generic and tribal assignment here considered in doubt. No specimen was seen. Earliest Pleistocene (late Blancan), Kansas.

Sorex minutus Linnaeus, 1776, central Europe, late Pliocene (Sulimski, 1962, p. 461) to living. Recent specimens seen.

Sorex rexroadensis Hibbard, 1953. No specimen was seen. Late Pliocene (early Blancan), Kansas.

Sorex sandersi Hibbard, 1956. No specimen was seen. Earliest Pleistocene (late Blancan), Kansas.

Sorex subminutus Sulimski, 1962. No specimen was seen. Late Pliocene (pre-Villafranchian), Poland.

Sorex taylori Hibbard, 1937. No specimen was seen. Late Pliocene and middle Pleistocene (early Blancan and Irvingtonian), Kansas.

Early Pleistocene species

Sorex araneoides Heller, 1930. Germany. No specimen was seen.

Sorex cinereus Kerr, 1792. Kansas (Hibbard, 1944, p. 719–720). A living species. Only Recent specimens were examined.

Sorex cudahyensis Hibbard, 1944. Kansas. The type, University of Kansas Museum of Natural History 6513 was examined.

Sorex fallax Heller, 1936. Germany. No specimen was seen.

Sorex kennardi Hinton, 1911. (?)Germany (Heller, 1958, p. 18–19); the type, from England, is late Pleistocene. No specimen was seen.

Sorex lacustris (Hibbard), 1955 [*Neosorex lacustris* Hibbard]. Kansas. No specimen was seen.

Sorex praealpinus Heller, 1930. Germany and Poland. No specimens were seen.

Sorex praearaneus Kormos, 1934. Hungary, Germany, and Poland. No specimen was seen.

Sorex runtonensis Hinton, 1911. Austria, Czechoslovakia, England, Germany, and Poland. Two specimens, author's collection 6235 A and C from Czechoslovakia were examined.

Sorex subaraneus Heller, 1959. Germany. No specimen was seen.

Species known only from the late Pleistocene

Sorex perminutus Kretzoi, 1959b, equals *Sorex minutissimus* Heim de Balsac, 1940, France. No specimen seen.

Sorex frankstownensis Peterson, 1926. Pennsylvania. No specimen was seen.

Many living species have been reported from late Pleistocene deposits.

Genus DREPANOSOREX Kretzoi, 1941

Genotype: *Sorex* (*Drepanosorex*) *tasnadii*
Kretzoi, 1941

Diagnosis as *Sorex* except that the upper soricid incisor is fissident in all known examples (Miklós Kretzoi, oral commun., 1966); lower molars stout with heavy cusps that are lower crowned than those of *Sorex*; teeth with pale-orange-yellow pigment rather than dark red; mandibular condyles large with greater vertical separation than in *Sorex*, and dorsal condyle extended much farther back approximating

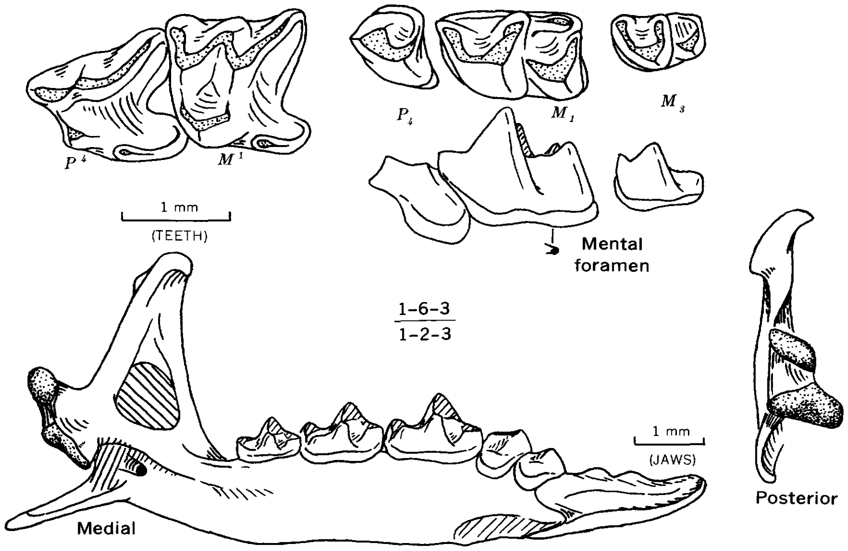

FIGURE 21.—*Microsorex hoyi* (Baird), Alaska, author's collection 6059. Left mandible and dentition and left upper dentition.

the condition found in *Blarinella*. Middle Pleistocene of Europe. Four species have been named:

Drepanosorex margaritodon (Kormos), 1935. Middle Pleistocene, Hungary. No specimen seen.

Drepanosorex savini (Hinton), 1911. Middle Pleistocene, Austria, Czechoslovakia, and England. One specimen seen, author's collection 6234 from Czechoslovakia.

Drepanosorex tasnadii (Kretzoi), 1941. Middle Pleistocene, Hungary and Germany. No specimen seen.

Drepanosorex pachyodon (Pasa), 1948. Original designation *Sorex pachyodon*. Middle Pleistocene, Italy. No specimen seen.

Genus MICROSOREX Baird, 1877

Figure 21

Genotype: *Sorex hoyi* Baird, 1858

Dental formula as in *Sorex* 1–6–3/1–2–3, but third and fifth upper antemolars minute; relative to trigonid, talonid of M_3 somewhat more reduced than in *Sorex*; because shortening of upper antemolar arcade is reflected in lower antemolars, P_4 somewhat broader in occlusal view than in *Sorex*; in contrast to nearly all species of *Sorex*, P_4 with curving J-shaped labial crest rather than an angulate L-shaped crest, slight posterolingual basin; M_1 as in *Sorex*; mental foramen rather far to rear and nearly beneath hypoconid of M_1. Only Recent specimens examined. Two fossil species have been named:

Microsorex pratensis Hibbard, 1944. Middle Pleistocene (Irvingtonian), Kansas.

Microsorex minutus Brown, 1908. Late Pleistocene (Rancholabrean), Arkansas.

The five genera just discussed are the known representatives of the unspecialized lineage of the tribe Soricini. In addition to the unspecialized mandibular articulation, they have dental characters that do not differ greatly between the Oligocene forms and the living forms. Nor do the dental characters differ greatly from those found in the earliest members of other subfamilies, like the heterosoricine *Domnina*, the crocidurine *Miosorex grivensis*, and the limnoecine *Angustidens*, although these earliest members of the other subfamilies clearly show the beginnings of dental modification characteristic of their subfamilies. The remaining genera of the tribe Soricini, in contrast, have considerable dental modification from the primitive pattern although the mandibular articulation is still clearly primitive.

Genus ALLUVISOREX Hutchison, 1966

Figure 22

Genotype: *Alluvisorex arcadentes* Hutchison, 1966

A soricine shrew with primitive mandibular articulation comparable to that of *Antesorex* in outline but with small interarticular area separating upper and lower articular facets; dental formula ?/1–3–3 (in *A. arcadentes*) to 1–6–3/1–2–3 (in *A. chasseae*); cheek teeth stout and low cusped; mandible heavy; lower incisor with three low rounded cusps on cutting edge; P_3 minute when present; M_1 with entoconid very close to metaconid and connected to it by a high and prominent entoconid crest, postentoconid valley very wide, metalophid joins protolophid close to protoconid, labial cingulum prominent but not inflated; occlusal outline of M_1 and M_2 distinctly rectangular; M_3 with reduced talonid consisting of longitudinal metalophid ter-

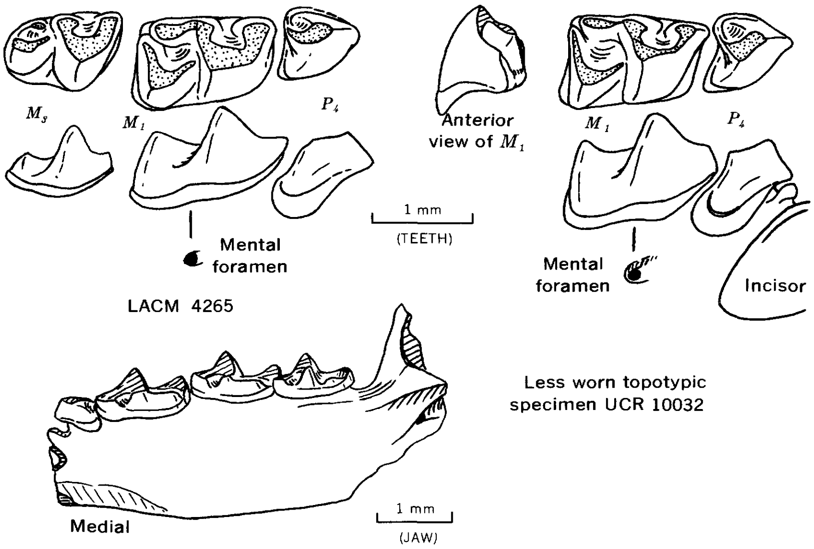

FIGURE 22.—*Alluvisorex chasseae* (Tedford), paratype, LACM 4265 and topotype UCR 10032. Right mandible and lower dentitions.

minating in strong hypoconid, no entoconid, very low entoconid crest, more on the lingual side of the talonid than on the occlusal surface and missing on one specimen of *A. chasseae* from Nevada (UCR 10237); mental foramen below metalophid of M_1; upper incisor not fissident; P^4 and upper molars intermediate between *Sorex* and *Blarinella.* Late Miocene (Barstovian) of Oregon and early Pliocene (Clarendonian) of Nevada and California.

Two species have been named:

Alluvisorex arcadentes Hutchison, from the late Miocene of southeastern Oregon. This species retains a minute P_3. The type and referred material listed by Hutchison (1966, p. 18) were seen.

Alluvisorex chasseae (Tedford), originally described from the lower Pliocene of California (Tedford, 1961) and subsequently described from the lower Pliocene of Nevada (Suthard, 1966). The paratype, Los Angeles County Museum 4265, and topotypes in the University of California, Riverside, as well as the specimens from Fish Lake Valley, Nev., in the same institution were seen.

Genus PETENYIA Kormos, 1934

Figure 23

Genotype: *Petenyia hungarica* Kormos, 1934

Dental formula 1–5–3/1–2–3; lower incisor with two low cuspules on its cutting edge; M_1 with prominent entoconid crest about as in living species of *Blarinella*, labial cingulum strong but not inflated and continuous to posterior margin of tooth behind hypoconid; talonid of M_3 greatly reduced and no trace of entoconid crest; third upper antemolar reduced, fourth very reduced, fifth upper antemolar absent in *Petenyia* (present but minute in *Blarinella quadraticauda*); P^4 and M^1 with slight emargination of posterior basal outline; hypoconal crest of M^1 and M^2 united to protocone to form a continuous endoloph; M^2 rectangular with zygomatic process of maxillary originating posterior to M^2; teeth pigmented and stout; mandible heavy; mental foramen below hypoconid of M_1; articular structure of mandible as in *Blarinella*; coronoid spicule is well formed and virtually as in living *Blarinella.* Late Pliocene to middle Pleistocene of central Europe.

Four species, *Petenyia hungarica* Kormos, *Petenyia suavensis* Pasa (1948), *Petenyia neglecta* Kretzoi (1943), and *Petenyia stehlini* Kretzoi (1943) are known. The genus is very close to the living *Blarinella* and differs chiefly in its loss of minute fifth upper antemolar.

Specimens examined.—Central Geological Survey of Czechoslovakia SÚÚG, OF 65566, a complete right lower jaw, and SÚÚG, OF 65565, a complete left lower jaw, both from the earliest Pleistocene (Villafranchian) of southern Slovakia.

Genus BLARINELLA Thomas, 1911

Genotype: *Sorex quadraticauda* Milne-Edwards, 1872

Dental formula 1–6–3/1–2–3; lower incisor relatively shorter than typical *Sorex*, upward curving, with two low scalloped cusps on upper cutting edge; lower cheek teeth stout with deep cingula not inflated, M_1 and M_2 with entoconid close to metaconid and both cusps connected by high entoconid crest that is more prominent than in any other shrew; M_3 with trigonid unreduced in size but talonid reduced to single low nearly conical but slightly bladelike hypoconid; P^4 with very slight emargination of posterior basal outline and with lingual cingulum very prominent medial to protocone; M^1 with very slight posterior

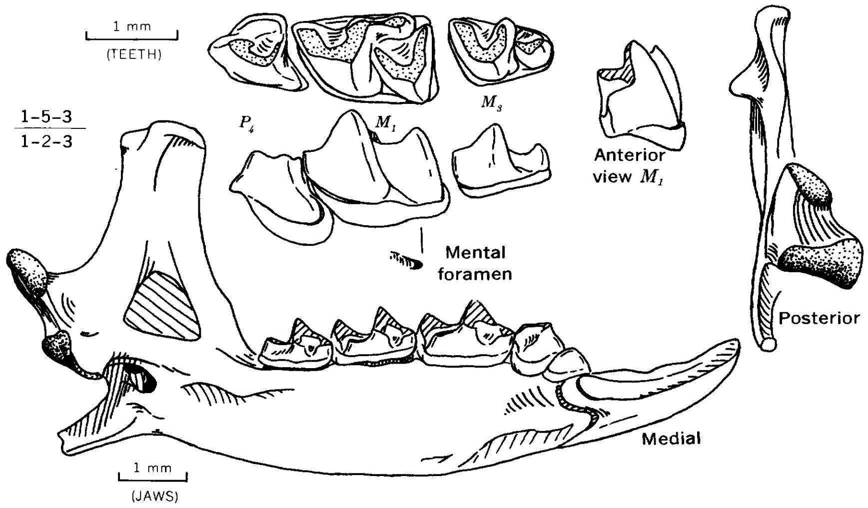

FIGURE 23.—*Petenyia hungarica* Kormos, SÚÚG, OF 65565. Left mandible and dentition.

emargination; M^2 rectangular; teeth heavily pigmented as in *Blarina;* zygomatic process of the maxillary originates posterior to M^2; mental foramen beneath middle of M_1; mandible stout; internal temporal fossa tending to be oval; condylar process and articular facets relatively large but otherwise as in *Sorex.*

One fossil and one living species have been named. They range from the middle Pliocene to Recent in China. The genus *Petenyia* from the late Pliocene and early Pleistocene of Europe is very closely related and differs chiefly in the loss of one upper antemolar.

Blarinella kormosi (Schlosser), 1924

Crocidura kormosi Schlosser, 1924, Palaeontologia sinica, ser. C, v. 1, no. 1, p. 5–6, pl., figs. 1, 2.

Blarinella kormosi (Schlosser). Miller, 1927, Palaeontologia sinica, ser. C, v. 5, no. 2, p. 8–9.

From Schlosser's description and illustrations (1924, p. 5–6; pl. 1, figs. 1, 2) and from Miller's discussion (1927, p. 8–9), I am not sure that the very distinctive entoconid crest of M_1 and single-cusped talonid of M_3 are on this species. Photographs of *Crocidura kormosi* on file in the U.S. National Museum, which were sent by Professor Wiman to Dr. Miller and served as a basis for Miller's revision, show that between the time of Schlosser's study and the time of Wiman's photograph the specimen had lost its M_3. In addition, although the photographs are not clear in this respect, the entoconid crests on M_1 and M_2 appear to be rather low, if present at all. The species could be a member of the tribe Blarinini and related to "*Sorex*" *kretzoii* Sulimski, a possibility further discussed under "*S.*" *kretzoii.* The mandibular structures shown on Schlosser's illustration seem typical of the genus, as Miller pointed out. The talonid of M_1 does not seem anteroposteriorly shortened as in the Blarinini nor does the mental foramen appear to be far enough back on the mandible for this tribe. Middle Pliocene (Ertemte fauna) of Mongolia. No specimen seen.

Blarinella quadraticauda (Milne-Edwards), 1872

Figure 24

This living species of *Blarinella* bears considerable superficial resemblance to *Blarina* in its dental formula, reduction of upper antemolars, pigmentation, stoutness of lower teeth, depth of cingula of lower teeth, and in the stoutness of mandible. It clearly differs from *Blarina* in its exceedingly prominent entoconid crest and posterior continuation of the labial cingulum to the rear of the hypoconid on M_1 and M_2, manner of reduction of the talonid of M_3, lack of anteroposterior shortening of the talonid of M_1 and M_2, development of a cingulum medial to the protoconid of P^4, rectangular M^2, more anterior mental foramen, origin of the zygomatic process of the maxillary behind M^2, and most importantly it differs from *Blarina* in its *Sorex*-like mandibular articulation and features of the posterior part of the mandible and of the cranium related to this type of articular structure.

Specimen examined.—Chicago Natural History Museum 36217, a male from Szechwan, China.

Soricini Incertae Sedis

"Sorex" stehlini Doben-Florin, 1964

"Small *Sorex*, tooth cusps lightly colored yellowish orange. $M_1 - M_3 = 3.13 - 3.25$ mm; M_2 somewhat

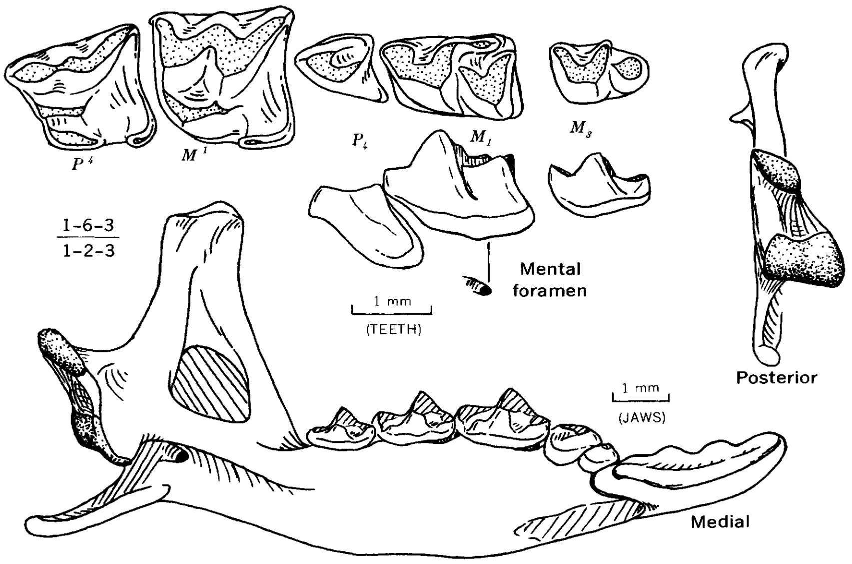

FIGURE 24.—*Blarinella quadraticauda* (Milne-Edwards), China, CNHM 36217. Left mandible and dentition and left upper dentition.

smaller than M_1. *I* [lower incisor] doubly scalloped, first scallop quite close to the tooth base. Three single-rooted antemolars [including P_4] in the lower jaw, the second and third very steeply placed. Molars with wide cingulum and massive cusps. M_1 and M_2 with hypoconulid [entoconid separated from hypolophid] and a lingual metaconid placed behind the protoconid. M_3 single-cusped in its talonid. Mental foramen beneath to behind the protoconid of M_1. Condyles with large articular surfaces." (Doben-Florin, 1964, p. 41).

The articulation of the mandible is primitive and similar to that of *Antesorex* or *Crocidosorex*. Hence, the species appears to belong in the tribe Soricini. Unlike these two earlier Miocene genera, "*Sorex*" *stehlini* has three quite specialized features: the talonid of M_3 is reduced to a single cusp, suggestive of the talonid of *Petenyia*, *Blarinella*, or some genera in the tribe Blarinini; the mental foramen is far to the rear in comparison to the other two earlier Miocene Soricini genera; and the teeth as a whole are massively constructed and have much heavier cingula than in these two genera. These specializations, three antemolars, and the more primitive mandibular articulation, relative to that on *Sorex*, all indicate that the species does not belong in *Sorex*. It would be possible to infer an ancestral relationship to *Petenyia* for this species except that Doben-Florin's illustrations do not seem to indicate the presence of the prominent entoconid crest characteristic of *Petenyia* and related genera. The absence of the entoconid crest would suggest a relationship to the largely North American tribe Blarinini and possibly an ancestral relationship to late Miocene *Adeloblarina* through shortening of the relative anteroposterior length of the talonid of M_1 and M_2 and specialization of the mandibular articulation.

"*Sorex*" *stehlini* is from the older Burdigalian fauna of Wintershof-West. No specimen was seen.

"Sorex" hibbardi Sulimski, 1962

Lower incisor has the two strong scalloped cusps on upper cutting edge more strongly developed than in *Blarinella*, and the incisor is relatively longer; cingula on lower molars strong and of uniform thickness rather than deepened; M_1 and M_2 with entoconids well developed but without very prominent entoconid crest of *Blarinella* and *Petenyia;* M_3 with reduced talonid lacking entoconid as in earlier species of *Blarinella;* coronoid process low and curved backward at tip; condyloid process very heavy with articular structures similar to *Blarinella;* teeth distinctly pigmented; internal temporal fossa large and triangular but with well-developed limula; late Pliocene (lower part of Węże Breccia), Poland.

This shrew is intermediate between *Sorex* and *Blarinella* in almost all its characters. To judge from Sulimski's description, the species should be assigned to a new genus rather than be used as the basis for major enlargement of the definition of either established genus. This genus should not be described, however, without study of the specimens. No specimen was seen.

Genus ZELCEINA Sulimski, 1962

Genotype: *Neomys soriculoides* Sulimski, 1959

Dental formula 1-5-3/1-2-3; upper incisor not bifid; P^4 and M^1 appear to have moderate posterior emargination; M^2 rectangular, and zygomatic process of maxillary originates posterior to M^2; lower incisor short with two low scalloped cusps on cutting edge much as in *Neomys*; M_1 with strong labial cingulum, but no published information indicates presence or absence of entoconid crest; M_3 described as one-half smaller than M_1, strongly reduced talonid without entoconid; teeth pigmented at tips; mental foramen below hypoconid of M_1.

The P^4 is described by Sulimski (1959, p. 150; 1962, p. 476) as having a posteriorly projecting protocone—the only published illustration of this tooth (1959, fig. 5C) suggests to me that the protocone is anteriorly placed close to the parastyle but has a prominent cingular shelf posteromedial to the protocone as in *Blarinella*. There is no published figure of the occlusal view of the lower teeth, and it is not possible to say whether the M_3 has both talonid and trigonid reduced as in some species of *Soriculus* or has only the talonid reduced as in *Petenyia*—Sulimski's (1959) figures 4a and 4b of plate 3 seem to show that just the talonid is reduced. The posterior part of the mandible is distinctly more like *Blarinella* than *Neomys* except that the interarticular area is a little too narrow for *Blarinella*; it is clearly too broad for *Neomys*, and in addition to the labial edge seems swollen in Sulimski's (1962) figure 3b of text-plate 2, much as in living *Blarinella*.

Definite assignment of this genus to any tribe is dependent upon the presence or absence of the entoconid crest on M_1, the nature of reduction of M_3, and considered study of the articular structure of the mandible. Assignment to the tribe Neomyini seems questionable because of the lack of the bifid upper incisor in an Old World form of this little specialization and because of the posterior position of the mental foramen and the two cusps on the lower incisor. Assignment to the tribe Blarinini is not supported by the rectangular M^2, the position of the zygomatic process of the maxillary, and the narrowness of the interarticular area of the mandible. Assignment to the tribe Soricini near the genus *Petenyia* is favored by the general similarity of all features that have been described or illustrated but is left uncertain because of those features not described or illustrated.

If *Zelceina* is related to *Petenyia*, in which there is a strong entoconid crest and only the talonid of M_3 is reduced, it probably should be recognized as a distinct genus, at least on the basis of differences in the articular structure of the mandible.

One species has been named *Z. soriculoides* (Sulimski) from the late Pliocene (lower part of Węże Breccia), Poland. No specimen was seen.

Tribe BLARININI Stirton, 1930

Articular condyles of the mandible widely separated; lingual condylar emargination at least partially filled by a bony plate so that interarticular area is broad; lower condyle enlarged, offset lingually, moved anteriorly, and facing more ventrally relative to *Sorex*; condylar process supporting upper condyle curved toward skull; coronoid process deflected outward (fig. 1); superior pterygoid fossa moderately basined but with little or no pterygoid spicule; internal temporal fossa of the mandible small and oval or with a well-developed limula; external temporal fossa of mandible high and extending down coronoid process no farther than upper sigmoid notch or less, coronoid spicule prominent but very high on ascending ramus; mental foramen varies in position but usually beneath hypoconid of M_1; zygomatic process of maxillary originates opposite posterior part of M^2 in all forms; M^2 trapezoidal in occlusal view in most forms; most conspicuously M_1 with no trace of an entoconid crest but strong entoconid (with one exception), talonid anteroposteriorly shortened; entire M_3 reduced, talonid tending to be further reduced to form crescentic crest with V of hypoconid weak or absent and reduced to minute shelf with small cusp in one genus; roots of M_3 separated by distance less than transverse diameter of anterior alveolus; teeth heavily pigmented and very stout.

Blarina and *Cryptotis* are the only living genera included in this tribe. *Blarina* contains only 2 species (Hall and Kelson, 1959, p. 52) confined to the eastern part of the United States; *Cryptotis* contains at least 25 species (p. 55–56) in the eastern half of North America and in Central America. It is the only shrew to have entered South America. The tribe contains a fair number of extinct genera in both North America and Eurasia and is known back to the late Miocene.

Genus ADELOBLARINA Repenning, n. gen.

Genotype: *Adeloblarina berklandi*, n. sp.

Diagnosis.—A soricine shrew with stout molars comparable to *Blarina* but with mandibular structures more like those in *Sorex*; lower dental formula 1–2?–3; M_1 with crown having stout base, dense pigmentation, talonid shortened anteroposteriorly, entoconid distinctly separated from hypolophid and relatively close to metaconid but separated from metaconid by a pronounced valley, hypolophid extends past the entoconid to the lingual cingulum, posterolabial part of labial cingulum (near hypoconid) enlarged and attenuate posteriorly as in *Paracryptotis* and not as in *Blarina* so that labial embrasure between M_1 and M_2 would be less open than in *Blarina;* alveoli for M_3 are close together; mandible moderately stout with depressed area that leads anterodorsally from mental foramen to region of the antemolars; mental foramen below middle of M_1; coronid process narrow, its anterior edge forming a 90° angle with alveolar plane of horizontal ramus and its tip not deflected buccally as in *Neomys* or *Blarina;* inferior condyle oriented 90° from verticle axis of horizontal ramus and 45° from longitudinal axis, articular facet facing ventrally and offset lingually from plane of mandible at inferior sigmoid notch, anterior displacement of inferior condyle not as extreme as in *Blarina*, *Cryptotis*, or *Notiosorex*, slightly less than in *Chimarrogale*, about equal to *Neomys*, greater than in *Sorex*; interarticular area presumably with moderate lingual emargination not filled with bone plate, but condyloid process anterior to interarticular area transversely thickened more than in most genera of the Neomyini; base of condyloid process, at its junction with ascending ramus, vertically narrow in comparison with all soricine shrews not included in tribe Soricini; superior pterygoid fossa of mandible has very shallow basin with poorly developed boss for insertion of superior pterygoid muscle; external temporal fossa of mandible not extended down coronid process as far as superior sigmoid notch; internal temporal fossa of mandible narrowly triangular with well-developed limula.

Etymology.—Greek: Adelos [ἄδηλος], obscure, and *Blarina*; related to *Blarina* to an unknown degree.

Adeloblarina berklandi Repenning, n. sp.

Figure 25

This species was named in honor of James O. Berkland, who found the type specimen while collecting with the author in southeastern Oregon during the summer of 1963.

Holotype.—U.S. National Museum 23098; a right mandible lacking the superior mandibular condyle and bearing M_1. Collected by J. O. Berkland.

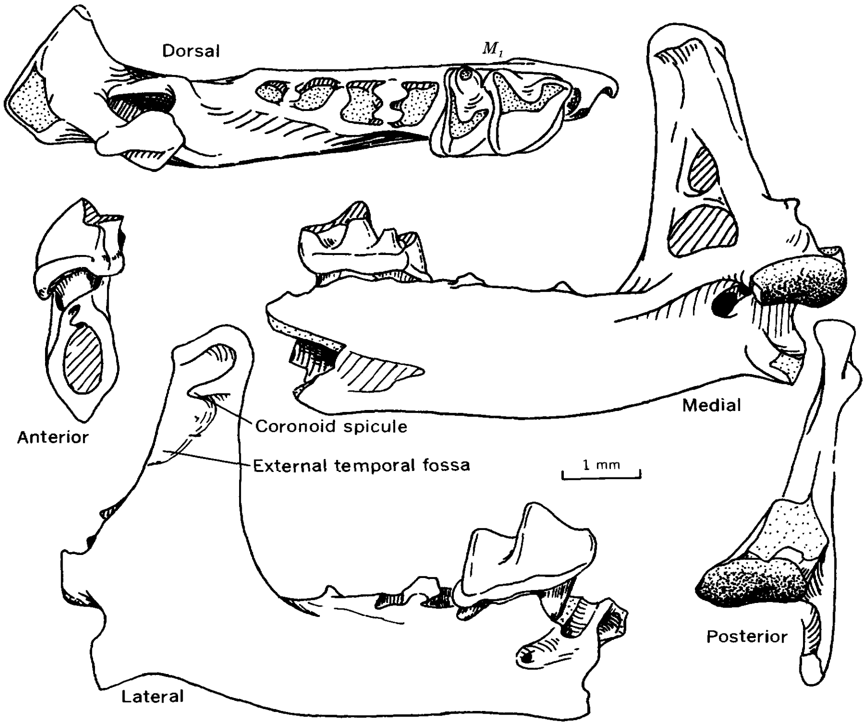

FIGURE 25.—*Adeloblarina berklandi* Repenning, n. gen. and n. sp., USNM 23098. Right mandible and M_1.

Type locality and age.—U.S. Geological Survey vertebrate loc. M1040; in poorly exposed and sparsely fossiliferous orange tuffaceous mudstone at the south end of the Bowden Hills, Malheur County, Oreg. Late Miocene (Barstovian, possibly late Barstovian).

Diagnosis.—A species of *Adeloblarina* of a size greater than *Cryptotis parva*, smaller than *Blarina brevicauda*, and about equal to *Neomys fodiens*. Other than size, the postmandibular canal connecting the bottom of the pocketed internal temporal fossa with the dental foramen and the position of the mental foramen just behind the anterior root of M_1 may prove to be of specific importance when other shrews are found that belong to this genus.

Discussion.—At first impression it might seem impossible to identify a fossil shrew from so incomplete a specimen as the type of *Adeloblarina berklandi*. The internal temporal fossa, however, shows that it is a soricid and not a heterosoricine shrew; the separation of the articular condyles and the degree of pigmentation show that the shrew belongs in the subfamily Soricinae; the anterior placement and lingual offset of the lower condyle, as well as the total lack of an entoconid crest on M_1, eliminate the tribe Soricini; the total lack of a entoconid crest on M_1, the stoutness of M_1 in association with a strong cingulum and heavy pigmentation, the closeness of the alveoli of M_3, and the association of moderate articular modification with these features strongly suggest assignment to the tribe Blarinini; the shallow basin of the superior pterygoid fossa, the width of the interarticular area, where preserved, just above the lower condyle, and the elevation of the bottom of the external temporal fossa above the upper sigmoid notch are evolutionary modifications of the Blarinini not found in the Neomyini.

Within the tribe Blarinini, *Adeloblarina* is clearly distinct in minimum separation of the articular condyles, in vertical narrowness of the base of the condyloid process, in lack of labial deflection of the coronoid process, in anterior position of the mental foramen, and in slenderness of the horizontal and ascending rami. All these features that separate *Adeloblarina* from other genera of the tribe Blarinini are clearly to be considered as primitive and approaching the condition observed in more primitive members of the tribe Soricini. Conversely, all other genera here included in the tribe Blarinini could be derived from *Adeloblarina* by further specialization of these same features.

The articular structure of the mandible of *Adeloblarina* is hardly more modified from the primitive articulation of *Sorex* than is the structure found in *Blarinella*; however, the modifications are those which lead to the more typical articulation of the tribe Blarinini. It would appear possible, therefore, that the tribe diverged from a *Sorex*-like ancestor shortly before the time of *Adeloblarina* in the latter part of the Miocene.

Genus CRYPTOTIS Pomel, 1848

Genotype: *Sorex parvus* Say, 1823

Dental formula 1–5–3/1–2–3 in all but one species which is 1–6–3/1–2–3; trigonid of M_3 not greatly reduced relative to M_1, but talonid greatly reduced to very small heel with single small conical cusp in living forms (somewhat less reduced in late Pliocene species); P^3 much smaller than preceding upper antemolars (except P^2 in species still retaining this tooth); P^4 and M^1 have moderate to slight posterior emargination, varying with species, and strong broadly curving hypoconal cingulum; M^2 rectangular or very nearly so, but zygomatic process of maxillary originates opposite the metacone or metastyle; pigment less than in *Blarina*; mental foramen beneath hypoconid of M_1; mandibular articulation as in *Adeloblarina* except with lower articular facet placed somewhat more forward but well to rear of lower sigmoid notch, variable development of bone plate filling the lingual excavation of interarticular area but never developed to extent found in *Blarina*, in some species (as *C. parva*) bone plate not noticeably more developed than in *Adeloblarina*; coronoid process slightly deflected labially and condyloid process supporting upper articular facet slightly curved toward cranium; coronoid process broader at level of superior sigmoid notch and condyloid process somewhat vertically deeper where it merges with ascending ramus than in *Adeloblarina*; internal temporal fossa triangular about as in *Adeloblarina*; external temporal fossa deeper, reaching superior sigmoid notch as in *Paracryptotis.* Middle Pliocene to Recent, North America.

In the mandibular structure and in the position of the zygomatic process, *Cryptotis* is a primitive member of the Blarinini and is less specialized than all other genera of the tribe except *Adeloblarina.* It appears precocious and distinct in that there is extreme reduction of the heel of M_3. The interarticular area of the mandible in some species (as *C. parva*) has a strong resemblance to the Neomyini (new name), but this is less true of other species in which the bone plate filling the lingual emargination of the interarticular area is better developed. In addition, the lower articular facet is not offset as far lingually as in the Neomyini so that there is no groove separating the facet from the lower sigmoid notch; the absence of an entoconid crest in as unspecialized a shrew as *Cryptotis* seems very contradictory to the condition found in the Neomyini or, for that matter, in the Soricini. The zygomatic process is farther forward (relative to the tooth row) than in comparable shrews of the Neomyini or any shrew of the Soricini.

Cryptotis adamsi (Hibbard), 1953

Figure 26

Blarina adamsi Hibbard, 1953, Jour. Paleont. v. 27, no. 1, p. 29–31, figs. 2B, 3C, 4B, C, and D, and 5B.

Assignment of this species to *Blarina* or *Cryptotis* is a matter of definition. The species is virtually identical in mandibular structure and lower and upper dentition to living *Cryptotis.* It does, however, retain the minute P^2 lost in the living species of the genus

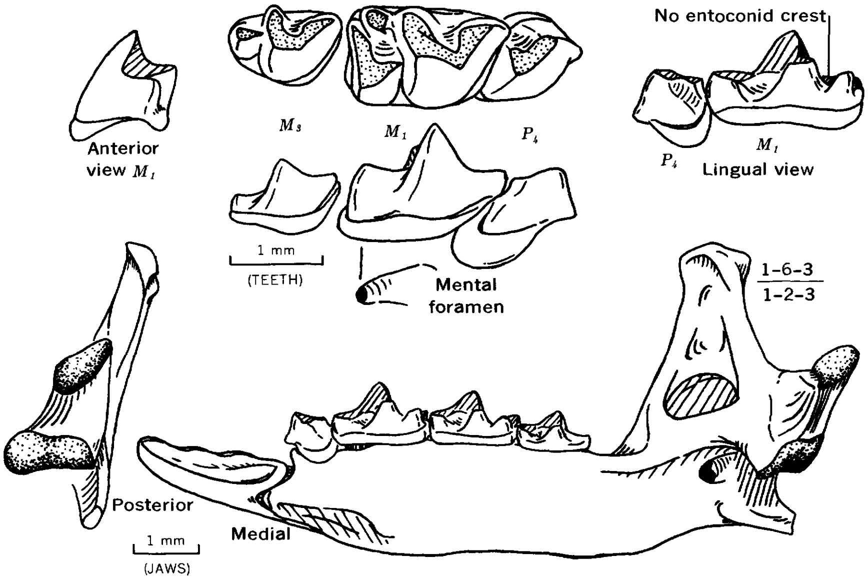

FIGURE 26.—*Cryptotis adamsi* (Hibbard), topotype, UM 28411. Right mandible and dentition.

and, hence, has the dental formula of living *Blarina*. The assignment of this species to *Cryptotis* in this report is based upon the belief that the following differences between it and Blarina represent phylogenetically significant characters and that the presence of P^2 is an expectable primitive feature. From species assigned to *Blarina*, *Cryptotis adamsi* differs in (1) greater anteroposterior shortening of the talonid of M_1, (2) more posterior placement of the metaconid of M_1, relative to the position of the protoconid, (3) greater reduction of the heel of M_3, (4) retention of a primitive blarinine mandibular articulation and associated jaw structure, and (5) a rectangular M^2. Items (4) and (5) could be considered primitive characters that represent an ancestral condition in the *Blarina* lineage, but items (1), (2), and (3) are clearly specializations in the late Pliocene species not yet achieved in the living species of the *Blarina* lineage.

A fragmentary specimen assigned to this species has been found in the middle Pliocene (Hemphillian) Christmas Valley local fauna of Lake County, Oreg. (U.S. Geol. Survey vertebrate loc. M1061). The geologic range is, therefore, middle Pliocene (Hemphillian) of Oregon and late Pliocene (early Blancan) of Kansas.

Specimens examined.—Topotypes, University of Michigan Museum of Paleontology 28411, 24352, and 27310, all well-preserved mandibles from the Rexroad local fauna, Kansas, and USGS M6511, a fragmentary mandible from the Christmas Valley local fauna, Oregon.

Cryptotis? meadensis Hibbard, 1953

Less reduced heel on M_3, more lingual metalophid-protolophid junction, and somewhat less forward placement of lower articular facet than in living *Cryptotis*.

These features appear less advanced but related to those of the living forms. *C.? meadensis*, however, is very unusual in not having a distinctly isolated entoconid on M_1 and in having a P_4 that is very similar to the P_4 in the Limnoecinae. The articular structure of the mandible of *C.? meadensis* clearly could not belong to a limnoecine shrew. Late Pliocene (early Blancan) of Kansas.

Specimen examined.—University of Michigan Museum of Paleontology 27266, the type, from the Rexroad fauna of Kansas.

Cryptotis kansasensis Hibbard, 1957

The teeth and mandible, as determined from published descriptions of both species, are similar to those in the living species *C. magna*. No specimens of either species have been examined during this review, and I am unable to see how the two species differ. From the living *Cryptotis parva*, they differ in greater size, lack of a posterior emargination of the upper molars and P^4, more trapezoidal form of M^2, a more rounded anterointernal corner of P^4, stouter lower molars, and greater filling by bone of the lingual emargination of the interarticular area of the mandible. *C. kansasensis* is from the early Pleistocene of Kansas.

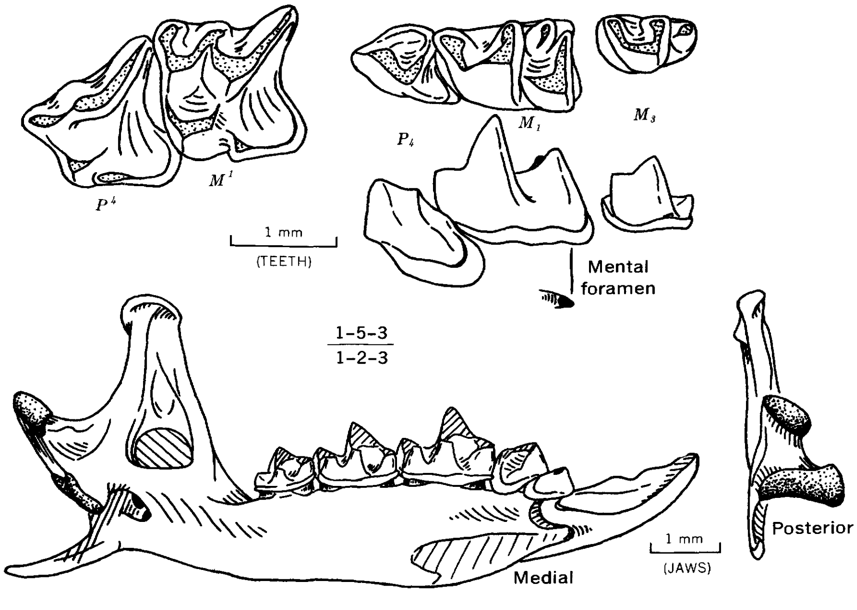

FIGURE 27.—*Cryptotis parva* (Say), Kansas, UCMVZ 40144. Left mandible and dentition and left upper dentition.

Cryptotis parva (Say), 1823

Figure 27

This living species has also been reported as fossil from the middle Pleistocene deposits of Kansas (Hibbard, 1963, p. 203–204). Only Recent specimens were seen.

Cryptotis mexicana (Coues), 1877

This living species has been reported as fossil from late Pleistocene deposits of Mexico (Findley, 1953, p. 633–639). No specimen was seen.

Genus PARACRYPTOTIS Hibbard, 1950

Figure 28

Genotype: *Paracryptotis rex* Hibbard, 1950

Dental formula 1–5–3/1–2–3; M_3 well reduced relative to M_1 with well-developed crescentic talonid crest; M_1 with deep labial cingulum from protoconid to posterior part of tooth (behind hypoconid), where it is better developed than in living *Blarina*, metalophid joins protolophid slightly labial to position of this junction in *Adeloblarina* but well lingual to position of junction in living *Blarina*, base of crown broad, hypolophid does not extend lingually as far as in living *Blarina*, and entoconid is slightly more posterior; P^3 smaller than preceding upper antemolars; P^4 and M^1 with no posterior emargination; M^2 trapezoidal and zygomatic process of maxillary originating opposite metacone; pigmentation slightly less than in *Blarina;* mental foramen from beneath center of M_1 to below posterior root of M_1—anterior to average position in living *Blarina* but overlapping most of range found in living *Blarina*; mandibular articulation as in *Blarina* with broad interarticular area, but inferior facet not placed as far forward and slightly visible behind lower sigmoid notch in labial view; superior pterygoid fossa a shallow basin with no pterygoid spicule; internal temporal fossa small and circular; external temporal fossa reaching superior sigmoid notch; coronoid process moderately deflected labially. Hibbard (1950, p. 122–127) compared this genus with *Cryptotis* and with *Blarina*. *Paracryptotis* appears to be closely related to *Blarina* on the basis of the reduction in size of the entire M_3, and the trapezoidal occlusal outline of M^2, in addition to the articular structure of the mandible and other similarities to *Blarina* mentioned by Hibbard. In the dental formula and possibly in the structure of the talonid of M_3, *Paracryptotis* is more closely related to *Cryptotis*. In the lingual position of the metalophid-protolophid junction and the development of the cingulum on M_1, *Paracryptotis* is less advanced than living *Blarina* but is about equal in this feature to the late Pliocene *Blarina gidleyi* and to *Cryptotis*. In the mandibular articulation, *Paracryptotis* is somewhat less advanced than *Blarina* but more advanced than *Cryptotis*.

The genus includes only one species, *Paracryptotis rex* Hibbard, from the late Pliocene (early Blancan) Rexroad fauna of Kansas and the middle Pliocene (Hemphillian) Rome fauna of Oregon.

Specimens examined.—Two topotypic mandibles labeled University of Michigan Museum of Paleontology 47760. Uncataloged specimen from USGS vertebrate loc. M1078, Rome local fauna, Oregon.

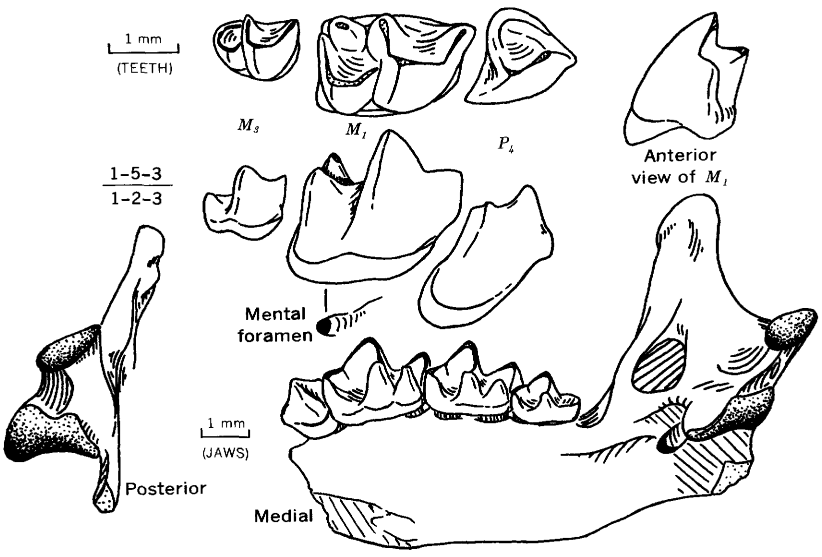

FIGURE 28.—*Paracryptotis rex* Hibbard, topotype, UM 47760. Right mandible and dentition.

Genus SHIKAMAINOSOREX Hasegawa, 1957

Genotype: *Shikamainosorex densicingulata*
Hasegawa, 1957

Articular structure typical of Blarinini; differs from *Paracryptotis* in greater inflation of labial cingulum of M_1 to M_3, greater reduction of heel of M_3, and greater anterior displacement of lower articular facet of mandible.

The advancement of the lower articular facet, which is hidden behind the mandible in labial view, suggests a greater similarity to *Blarina*. The other points of difference between *Shikamainosorex* and *Paracryptotis*, however, are an accentuation of those features which separate *Paracryptotis* from *Blarina*. In addition, the junction of the metalophid to the protolophid is as in *Paracryptotis* and early Pleistocene *Blarina* and far more lingually located than in living *Blarina*. Middle Pleistocene, Totigi Prefecture, Japan.

The differences between *S. densicingulata* Hasegawa and *Paracryptotis rex* are of no greater magnitude than those between *Blarina gidleyi* from the late Pliocene of Idaho and the living *Blarina*. It would seem, by comparison, either that Hasegawa's species *densicingulata* should be included in the genus *Paracryptotis* or that Gazin's species *gidleyi* should be placed in a new genus ancestral to *Blarina*. This should not be done, however, without comparison of the specimens.

Sulimski (1962, p. 472–473) suggested that *Shikamainosorex densicingulata* may be related to *Anourosorex*. The very prominent cingula on the lower molars, the lesser reduction of M_3, as well as the type of reduction seen on the talonid of M_3, the height of the inferior border of the external temporal fossa of the mandible (which is as in *Paracryptotis* and *Blarina*), and most importantly the articular structure of the mandible rule out a relationship with *Anourosorex*. *Anourosorex*, with characteristic development of its features, is known from deposits in Japan of the same age as those that contained *S. densicingulata* (Shikama and Hasegawa, 1958). No specimen was seen.

"Sorex" dehneli Kowalski, 1956

This shrew seems close to *Paracryptotis* and to *Shikamainosorex*. As far as can be judged from published accounts, the M_1 is as in *Paracryptotis* and *Blarina gidleyi*; the M_3 is well reduced (at least on the holotype) and has a reduced, crescentic talonid; the mental foramen is as in the two American genera.[4] The mandibular articulation compares favorably with *Paracryptotis* in form and stage of advancement. The knoblike structure of the apex of the coronoid process seems unique. Because of the mandibular articulation and the tooth structure, the species seems, at least, to belong in the tribe Blarinini and not to the genus *Sorex*. Kowalski (1960, p. 170) noted similarities with *Blarinoides mariae* Sulimski and suggested that they are probably congeneric. The species is known from the late Pliocene of Poland. No specimen was seen.

Genus BLARINA Gray, 1838

Figure 29

Genotype: *Sorex talpoides* Grapper, 1830

Dental formula as in *Sorex* 1–6–3/1–2–3; talonid of M_1 and M_2 shortened; M_3 least reduced of tribe (possibly excepting *Adeloblarina*), but with talonid shortened and intraspecifically variable in development of crescentic crest, alveoli close together; P^4, M^1, and M^2 with only slight emargination of posterior basal outline; M^2 trapezoidal and zygomatic process of maxillary originates opposite this tooth; teeth stout and heavily pigmented; mandible stout; mental foramen varying from beneath protoconid of M_1 to between M_1 and M_2 (farther to the rear than in any other shrew besides *Trimylus*; articular facets of mandibular condyle widely separated, lower facet placed well forward and hidden behind mandible at lower sigmoid notch in labial view, interarticular area broad; superior pterygoid fossa as shallow basin with no spicule; external temporal fossa extends downward to superior sigmoid notch and follows its ventral margin to upper condyle.

Of all living shrews for which a reasonable sample was examined during this review, the genus *Blarina* stands out as being the most variable intraspecifically. Most notable are the variations in the structure of the talonid of M_3, the position of the mental foramen, and the form of the cingulum on the lower cheek teeth. In the living species *B. brevicauda*, the talonid of M_3 varies from a considerably reduced and rounded heel that has a well-developed crescentic crest similar to *Paracryptotis* to a rectangular heel that has a reasonably sharp V on the hypoconid, a conspicuous entoconid elongated to form a short entoconid crest separated from the hypolophid by a valley, and a fairly angulate posterolingual cor-

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[4] Although Kowalski (1956, p. 346) stated that the mental foramen is below P_4, his figures (pl. 1, figs. 5, 6) clearly show it below the middle of M_1. The talonid of M_1 in the holotype is broken, and the isolated trigonid resembles, at first glance, a P_4; this situation suggests that Kowalski inadvertently mistook this talonid for P_4 while describing the position of the mental foramen. He is not alone, for Sulimski, who prepared Kowalski's illustration of the type, apparently took Kowalski's statement at face value without referring to the specimen or his own artistry because he (1962, p. 471) made the same mistake in thinking the trigonid of M_1 was the P_4 when he compared his *"Sorex" kretzoii* with *"Sorex" dehneli*.

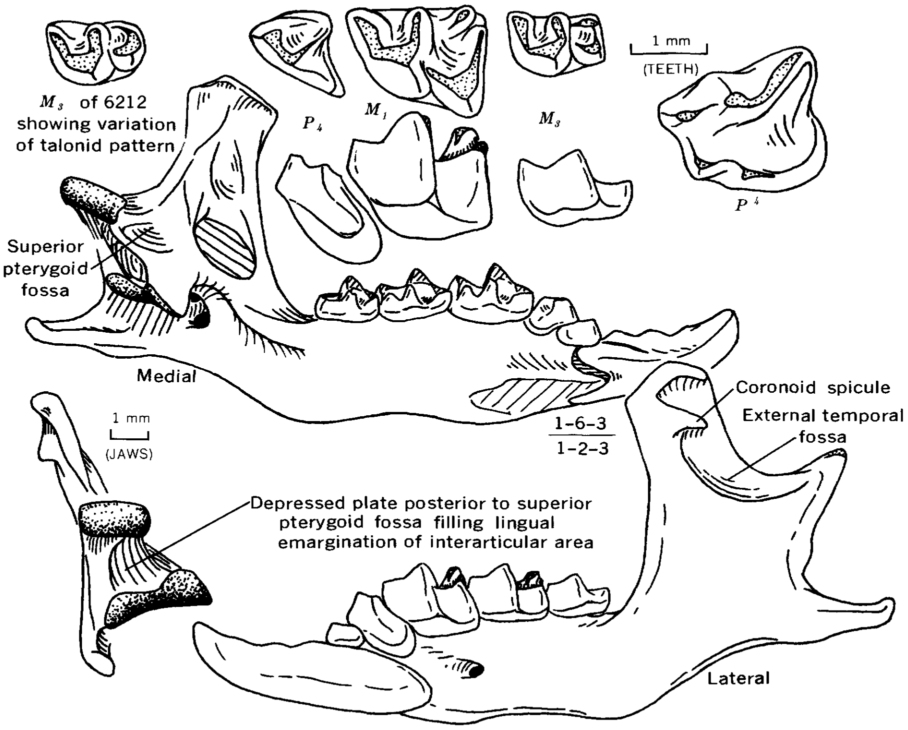

FIGURE 29.—*Blarina brevicauda* (Say), author's collection 6188 from Michigan and M_3 of 6212 from New Jersey. Left mandible and dentition and left P^4.

ner in occlusal view not greatly different from that in *Sorex*. The range in position of the mental foramen in the species *Blarina brevicauda* is nearly as great as that seen within the subfamilies throughout their geologic history. Other features, as the position of the junction of the metalophid with the protolophid on M_1, the posterior emargination of P^4 and M^1, or the structure of the mandibular articulation seem as stable as in any other shrew genus. Four species have been recognized as fossil.

Blarina gidleyi Gazin, 1933

Figure 30

M_3 within more *Sorex*-like variation of living *Blarina brevicauda*; pigmentation of the teeth and structure of mandibular articulation identical to those features in living species; M_1 with metalophid-protolophid junction placed far lingual to position in living species and similar to *Paracryptotis*, hypolophid does not extend as far lingual as in living species, and cingula as in *Paracryptotis* and *Adeloblarina* rather

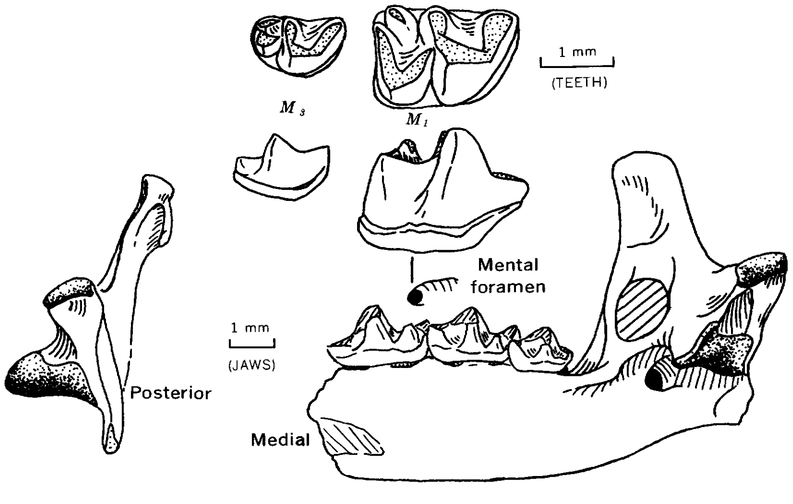

FIGURE 30.—*Blarina gidleyi* Gazin, topotype, UM 3304. Right mandible and dentition.

than reduced in region of hypoconids and deepened below protoconids as in living species; upper teeth unknown; mental foramen below midpoint of M_1; horizontal ramus without sharply angulate inferior border of living species but possibly stouter throughout.

Most of these characters are clearly primitive, and the species is intermediate between the living species and *Adeloblarina* on the basis of these differences. It is possible the differences are of generic importance and that, therefore, this species should not be included in *Blarina*.

Late Pliocene (early Blancan) Hagerman fauna of Idaho.

Specimen examined.—University of Michigan Museum of Paleontology 3304, as well preserved mandible.

The other species of *Blarina* reported as fossil are all from the late Pleistocene. None of these were seen.

Blarina fossilis Hibbard, 1943. Kansas.
Blarina simplicidens Cope, 1899. Pennsylvania.
Blarina brevicauda (Say), 1823. A living species in the eastern half of North America and reported from the late Pleistocene from Oklahoma and Kansas.

Genus BLARINOIDES Sulimski, 1959

Genotype: *Blarinoides mariae* Sulimski, 1959

Dental formula 1-6-3/1-2-3; P_4 very large and inflated; M_3 greatly reduced but talonid not reduced relative to trigonid, distinct entoconid; P^4 and M^1 with moderate emargination of posterior basal outline as in *Blarina; M^2* trapezoidal and zygomatic process originating opposite metacone as in *Blarina*; teeth pigmented and stout; mandible very heavy; mental foramen between roots of M_1; articular facets of mandible widely separated and about as in *Blarina*.

Although very similar to *Blarina*, according to Sulimski (1959, p. 147) *Blarinoides* differs in its larger size, weaker coronoid spicule, inflated P_4, presence of entoconid on M_3 of all individuals, and relative sizes of the upper antemolars. In labial position of the metalophid-protolophid junction and development of the cingulum on M_1, *Blarinoides* appears much closer to the living *Blarina* than to the late Pliocene *Blarina gidleyi*.

One species named: *Blarinoides mariae* Sulimski. Known from the late Pliocene of Poland and Hungary (Sulimski, 1962, p. 483). Kowalski (1960, p. 170) suggested that his species "*Sorex*" *dehneli*, from the early Pleistocene of Poland, may belong in the genus *Blarinoides*, a possibility that seems logical to me from a review of the published accounts. No specimen was seen.

Kretzoi (1962, p. 353) placed this species in the genus *Shikamainosorex*. Kowalski and Li (1963, p. 143) did not agree with such a generic assignment and pointed out that *Shikamainosorex* has a greater reduction of M_3 and a broader cingulum than *Blarinoides*. These differences appear real to me and in addition the M_3 of *Blarinoides* clearly retains a small entoconid that is not present on the reduced talonid of M_3 of *Shikamainosorex*. From the published descriptions it appears that *Shikamainosorex* is clearly related to *Paracryptotis* and that *Blarinoides* is related more to *Blarina*, as the authors of both genera originally supposed.

Blarinini? Incertae Sedis

"Sorex' kretzoii Sulimski, 1962

This shrew appears, from Sulimski's description and illustrations, to have a heavy lower articular facet on the mandible that is basically horizontal and notched in its upper edge and is shifted forward only slightly from its position in *Sorex*, a reasonably broad interarticular area, an upper articular facet that is rotated well toward the longitudinal axis of the mandible, a labially deflected coronoid process, no entoconid crest on the lower molars, and a relatively little reduced M_3. The combination of these features suggests the tribe Blarinini, but unfortunately most of the characters cannot be clearly verified in the published description. The vagueness results not so much from the fault of the description, which is better than the description of many fossil shrews, but from the generalized nature of "*Sorex*" *kretzoii*. This is particularly so in its mandibular articulation, which could be either a *Blarinella*-type in the tribe Soricini or a very primitive articulation in the tribe Blarinini. From Sulimski's figures (text-pl. 2, figs. 9, 10), the articulation appears to belong in the Blarinini, but if so it is closer to the Soricini in lacking a forward shift of the lower articular facet than is any member of the Blarinini except *Adeloblarina* from the late Miocene.

Tribal assignment must be decided on the basis of the lingual offset of the lower articular facet from the lower sigmoid notch, rotation of the upper articular facet toward the longitudinal axis of the mandible, degree of curvature toward the skull of the condyloid process supporting the upper facet, labial deflection of the coronoid process, position of the origin of zygomatic process of the maxillary, and the occlusal outline of M^2. None of these are determinable from the published description. One strong point in favor of assignment to the Blarinini is the positive statement of Sulimski (1962, p. 469) that the entoconid crest ("crest between the entoconid and metaconid") is lacking; no shrew assigned to the Soricini is yet known that lacks the entoconid crest.

There is a rather striking resemblance between Schlosser's (1924) figure 1 of plate 1 of *Blarinella kormosi* (Schlosser) and Sulimski's (1962) figure 9a of text-plate 2 of "*Sorex*" *kretzoii* Sulimski. If *Blarinella kormosi* does not have the very distinctive entoconid crest on M_1 and M_2 and the reduced talonid on M_3 of *Blarinella*, as Schlosser's illustrations suggest and as might be implied by Miller's (1927, p. 9) words "the characters in which * * * *Blarinella kormosi* differs from the living Chinese *B. wardi* appear to approach, in every instance, those of *Blarina* * * *" (*Blarina* does not have the entoconid crest or reduced talonid of *Blarinella*), it seems probable that *Blarinella kormosi* is very closely related to "*Sorex*" *kretzoii*, and is not *Blarinella*.

"*Sorex*" *kretzoii* is from the late Pliocene (lower part of the Węże Breccia), Poland. No specimen was seen.

Peisorex pohaiensis Kowalski and Li, 1963

The authors of this genus and species do not mention whether the entoconid crest is present or absent on the $M_{1\text{-}2}$ of the single known mandible, but it appears to be absent in their illustrations. The unusually specialized mandibular articulation could belong to either the tribe Blarinini or the tribe Neomyini, to judge from the published description and illustrations. The deep pit (superior pterygoid fossa) in the area just anterior to the superior condyle of the mandible, however, strongly suggests that *Peisorex* belongs in the tribe Blarinini.

According to the authors (Kowalski and Li, 1963, p. 142), *Peisorex pohaiensis* is a large shrew characterized by a connection between the internal temporal fossa (their "fossa pterygoidea") and the mandibular (dental) foramen, by a simple coronoid process lacking any spicule, and by the prominent basin of the superior pterygoid fossa. The shrew is known from the middle Pleistocene of China. No specimen was seen.

Tribe NEOMYINI Repenning, new name

Diagnosis as for tribe Blarinini except as follows: Lingual condylar emargination of mandible open, consequently interarticular area very narrow; lower condyle elongate, offset lingually from plane of lower sigmoid notch to greater extent than in Blarinini, more anteriorly placed and facing more ventrally than in Soricini, separated in many specimens from lower sigmoid notch by groove because of extreme lingual offset (fig. 1); superior pterygoid fossa deeply basined with pterygoid spicule in most forms; external temporal fossa of mandible low with ventral margin varying from level of superior sigmoid notch to level of lower articular facet; coronoid spicule high to very low; coronoid process with very strong tendency to curve anteriorly at tip but tip spatulate in a few forms; mental foramen beneath middle of M_1 as in *Sorex* and not placed so far to rear as in many genera of Blarinini; M^2 rectangular in occlusal view and zygomatic process of maxillary originates posterior to M^2 in nearly all forms except those having extreme reduction of last molars; protocone of P^4 tends to be farther separated from parastyle and placed farther medially than in *Sorex*; upper incisor bifid or fissident, as in *Trimylus*, in most Old World forms; bifid upper incisor not present in New World forms; M_1 with prominent entoconid crest in most forms but weak in some and missing in those having extreme reduction of last molars; M_3 variable and may be unreduced as in *Sorex*, with talonid only reduced as in *Blarinella*, greatly reduced as in *Blarina*, or entirely lost; labial cingula on lower molars never deep as in *Blarina*, well developed to absent; teeth pigmented over less extensive area or lightly pigmented relative to *Sorex* or colorless, slim to stout.

The Neomyini include nine living genera, more than any other tribe of the subfamily Soricinae; however, each of these genera include very few living species, many only one. The fossil record of the tribe is clearly very incomplete. The oldest specimens are of early Pliocene age, and some of these are the most specialized forms known, a situation illustrating how far the history of the Soricidae is from being completely documented. Because the bifid upper incisor is also known in the Heterosoricinae, is sometimes present in the Soricini, and is found in one crocidurine shrew, it would seem to be a primitive character inherited from a common ancestor.

The Neomyini are largely a Palearctic tribe although there are three genera from North America. Except for the living *Anourosorex* and fossil relatives of this genus, most Old World forms have bifid upper first incisors; the New World genera do not although they are very close to the eastern Asian *Chodsigoa* in many other characters. Two lineages are thus suggested. Within the Old World forms no suggestion of further phylogenetic breakdown has been noted, but rather, the known forms fit rather neatly into a uniformly gradational series from the little specialized *Neomys* to the extremely specialized *Anourosorex*. This graded series is entirely morphologic and is not related to an evolutionary sequence insofar as the present fossil record reveals.

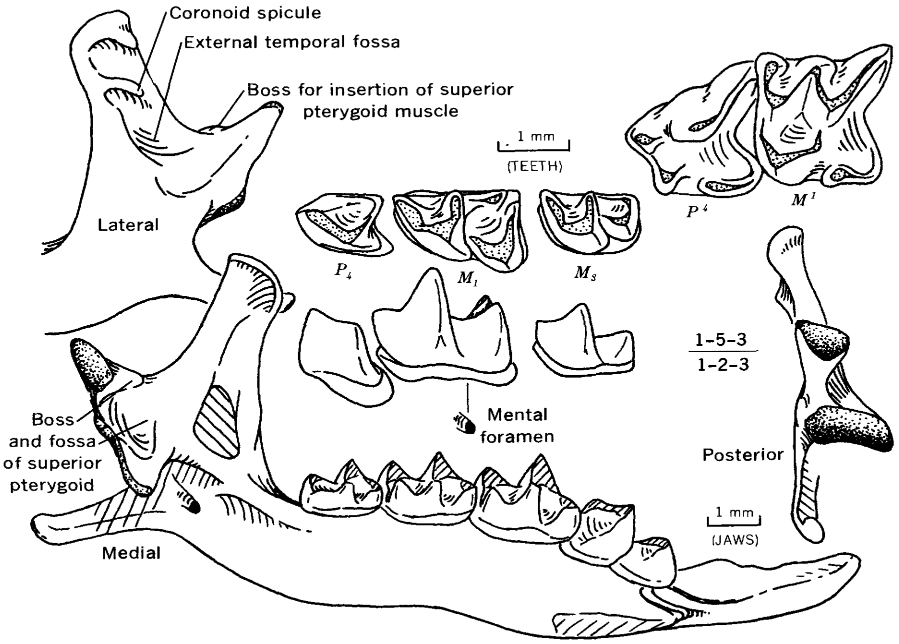

FIGURE 31.—*Neomys fodiens* (Pennant), France, UCMVZ 30044. Left mandible and dentition and left upper dentition.

Genus NEOMYS Kaup, 1829

Figure 31

Genotype: *Sorex daubentonii* Erxleben, 1777

Dental formula 1–5–3/1–2–3; upper incisor bifid in about half of the specimens examined; fourth upper antemolar small; P^4 with protocone shifted more medial from parastyle than in *Sorex*; lower incisor with one weakly defined and irregular cusp on cutting edge; labial cingulum strong on lower molars; pigment extensive for tribe but less so than is typical of *Sorex*; pterygoid boss of mandible moderately developed; upper articular facet of mandible oval; lower articular facet not placed so far forward that it is hidden in labial view; coronoid spicule high; external temporal fossa high and terminating at superior sigmoid notch; tip of coronoid process narrow with prominent anterior curve. Early Pleistocene to Recent of Europe, Recent of Asia.

Except for dental formula, upper and lower incisor, and P^4, there appears to be no way to separate *Neomys* from *Sorex* on the basis of dentition alone. Among European species of *Sorex*, *Neomys* appears distinguishable by the higher cusps in unworn teeth (Miller, 1912, p. 68).

Five species have been reported as fossil:

Neomys browni Hinton, 1911. Late Pleistocene, England. No specimen was seen.

Neomys fodiens (Pennant), 1771. Late Pleistocene, England; a living species. Only Recent specimens were seen from the Museum of Vertebrate Zoology, University of California.

Neomys newtoni Hinton, 1911. Early Pleistocene, England and Czechoslovakia. One specimen was seen, author's collection 6340, from Czechoslovakia. The specimen was returned to the Czechoslovakian Geological Survey since preparation of this report; the new catalog number is unknown.

Neomys intermedius Brunner, 1952. Middle Pleistocene, Germany. No specimen seen.

Neomys castellarina Pasa, 1948. Middle Pleistocene, Italy. No specimen seen.

One living species other than *N. fodiens* is recognized by Ellerman and Morrison-Scott (1951, p. 61).

Genus PETENYIELLA Kretzoi, 1956

Genotype: *Sorex gracilis* Petényi, 1864

This genus was named in a footnote (Kretzoi, 1956, p. 160), and *Sorex gracilis* Petényi (1864, p. 70) was cited as the genotype. Kretzoi (1959a, p. 239) gave a brief diagnosis.

Sulimski (1962, p. 479–480, 483) recognized the genotypic species *Petenyiella gracilis* and a new species *Petenyiella zelcea* from the Węże Breccia on the basis of direct comparison with the Hungarian specimens. Unfortunately most of his description is in comparison to the genotype, which is poorly described and illustrated in available publications. From Sulimski's discussion (1962, pages just cited, and 1959, p. 157–159 under the genus *Suncus*), the following features place the genus *Petenyiella* in the Neomyini.

Condyles fairly widely separated, lower facet elongate, and interarticular area narrow; lower incisor with two rather indistinct lobes on its cutting edge;

M_1 "similar in structure" (Sulimski, 1959, p. 158) to *Suncus* and therefore assumed to have well-developed entoconid crest; M_3 "strongly reduced talonid with poorly recognized hypoconid" also similar in structure to *Suncus* in which the talonid is more reduced than in *Crocidura* in European forms of *Suncus* and *Crocidura* (Miller, 1912, p. 84); teeth pigmented at tips; size very small.

Kretzoi (1959a, p. 239) gave the following characters in diagnosis of *P. gracilis*: soricine of *Suncus* size with four upper unicuspids which are comparable in form to the unicuspids of *Sorex*, two-lobed lower incisor, and delicate yellow pigmentation.

Kormos (1934, p. 306, fig. 38) gave a good illustration of the mandible under the new name *Pachyura pannonica*. He also suggested that the species might be considered a new genus, for which possibility he provided the new generic name *Allopachyura*. Because he did not apply this name to the species, it would appear to have no validity, and *Petenyiella* is here used.

As Kretzoi said (1962, p. 353), the genus is close to *Soriculus* [*Episoriculus* as here used]. It is a Neomyini shrew characterized by its small size, by its rather unspecialized mandibular condyles with the small lower condyle farther to the rear than in *Neomys*, and by a greatly reduced and single-cusped talonid on M_3.

There appear to be significant differences in the development of the upper condylar process in *Petenyiella*. *P. zelcea* from the Węże Breccia (Sulimski, 1959, pl. 3, fig. 2, and pl. 4, fig. 1; 1962, pl 2, fig. 1, and text-pl. 2, fig. 1) most closely resembles *P. gracilis* [*P. pannonica* of Kormos, 1934, fig. 48] and has the upper articular facet well above the upper sigmoid notch and the lower facet well posterior to the lower sigmoid notch. The specimens which Sulimski referred to *P. gracilis* from the Węże Breccia (Sulimski, 1959, pl. 3, fig. 1, and pl. 4, fig. 2) have the upper articular facet below the level of the upper sigmoid notch and the lower facet well forward and almost hidden behind the lower sigmoid notch in lateral view. This is a much greater difference than has been observed in any other genus of shrew. The possibility that two genera are represented and also that Sulimski has referred the wrong one to *P. gracilis* is here suggested.

The genus is known from the late Pliocene of Hungary and from the late Pliocene and Pleistocene of Poland (mostly from the lower part of the Węże Breccia, according to Sulimski, 1962, p. 483). No specimen was seen.

Genus EPISORICULUS Ellerman and Morrison-Scott, 1951

Figure 32

Genotype: *Sorex caudatus* Horsfield, 1851

Dental formula 1–5–3/1–2–3; upper incisor bifid as in *Neomys*, fourth upper antemolar very small; P^4 with protocone placed close to parastyle as in *Sorex*; lower incisor as in *Neomys* but shorter; labial cingulum on lower molars as in *Neomys*; M_3 with heel very slightly reduced relative to *Neomys* and V of hypo-

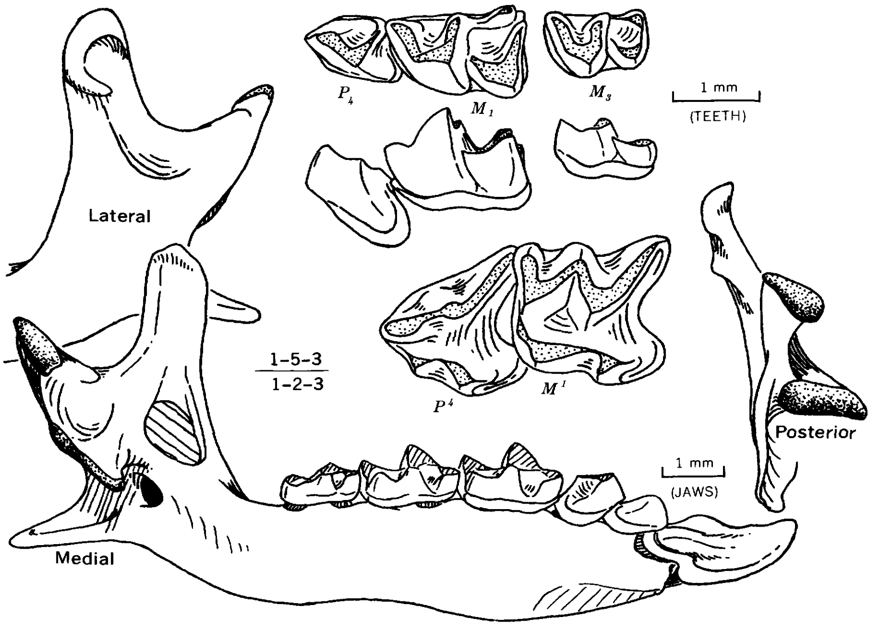

FIGURE 32.—*Episoriculus caudatus* (Horsfield), India, CNHM 35415. Left mandible and dentition and left upper dentition.

conid not so acute; pigmentation less than in *Neomys* lacking on M_3 and only at very tip of hypoconid on talonid of M_1 and M_2; pterygoid boss of mandible almost undetectable; upper articular facet of mandible oval as in *Neomys*; lower articular facet placed farther forward than in *Neomys* and barely visible behind lower sigmoid notch in labial view; coronoid spicule lower than in *Neomys* and directed posteroventrally toward lowest point of upper sigmoid notch rather than above it as in *Neomys*; external temporal fossa slightly lower than in *Neomys* and extending well below upper condyle. Recent of eastern Asia and late Pliocene of Europe.

Episoriculus was proposed as a subgenus of *Soriculus* by Ellerman and Morrison-Scott (1951) because of marked differences between species previously included in *Soriculus*. They pointed out (p. 57) that the external differences between these species are greater than those between *Sorex* and *Blarinella*. Following Osgood's suggestion of the subgeneric importance of the extra tooth in *Chodsigoa*, they also considered this genus a subgenus of *Soriculus*. In the present review, mandibular and dental characters also seem to separate these three subgenera to a significant degree. Although these differences are not as great as those between *Sorex* and *Blarinella*, they are as great as those that separate many genera of the Neomyini. Because of these differences the three subgenera which Ellerman and Morrison-Scott placed in the genus *Soriculus* are here given full generic status for the sake of maintaining the degree of morphologic distinctiveness noted between genera of the Neomyini and between most genera of the Soricidae.

Episoriculus differs from *Chodsigoa* in having one more upper antemolar, in more extensive pigmentation, in a less anterior pitch of the tip of the coronoid process, in a lesser width of the coronoid process at the level of the superior sigmoid notch, and in its oval upper articular facet. These differences are not great but are of the same sort and magnitude that separate *Episoriculus* from *Neomys*. If *Chodsigoa* and *Episoriculus* are to be considered subgenera under one genus, it should be under the genus *Neomys*; the characters of *Episoriculus* and *Chodsigoa* differ much more from those of *Soriculus*.

Ellerman and Morrison-Scott recognize two living species of *Episoriculus*.

Specimens examined.—Two specimens of *E. caudatus* (Horsfield): Chicago Natural History Museum 39632, a male from Szechwan, China, and 35415, a male from Sikkim, India. These represent two subspecies.

Episoriculus gibberodon (Petényi), 1864

Equals *Crocidura gibberodon* Petényi, 1864; *Soriculus kubinyi* Kormos, 1934; *Soriculus gibberodon* (Petényi) of Kretzoi, 1956; and *Asoriculus gibberodon* (Petényi) of Kretzoi, 1959. Elevation of the subgenera of *Soriculus* to generic stature necessitates reevaluation of the generic assignment of this fossil species. The following characters bar its assignment to either *Soriculus* or to *Chodsigoa* and indicate its affinity with living *Episoriculus*: dental formula 1–5–3/1–2–3; lower incisor short; M_3 only slightly reduced with distinct entoconid; complete labial cingulum on lower molars; pigment present on tips of cuspids of the lower molars; no anterior inclination of tip of coronoid process; relative narrowness of ascending ramus at level of upper sigmoid notch; coronoid spicule higher than in *Chodsigoa* or *Soriculus*; lower articular facet not placed as far forward as in *Soriculus* (not as far as in the living *Chodsigoa* or *Episoriculus*); and upper articular facet oval.

Late Pliocene of Hungary and Poland. No specimen was seen.

Genus CHODSIGOA Kastschenko, 1907

Figures 33, 34

Genotype: *Soriculus hypsibius* deWinton, 1899

Dental formula 1–4–3/1–2–3; upper incisor bifid as in *Neomys*; upper antemolars of uniform size; P^4 with protocone as in *Sorex* and with extreme emargination of posterior basal outline—one species, at least, exceeding all other shrews in this feature except *Notiosorex jacksoni*; emargination of M^1 and M^2 also extreme; lower incisor as in *Episoriculus*; P_4 variable in angularity of junction of labial shearing blade with crest formed by posterior cingulum; M_3 variable in reduction of talonid from nearly unreduced (fig. 34) as in *Episoriculus* to noticeably reduced (fig. 33) with talonid shortened, hypolophid crescentic, entoconid lost as distinct cuspid, and entoconid crest almost lost but present as very low lingual crest; pigmentation very reduced but present on tips of antemolars, tip of paracone of P^4 and in one species on very tip of protoconid of M_1; pterygoid spicule moderately developed on ridge running from internal temporal fossa to superior condyle well below upper sigmoid notch; upper articular facet triangular as in *Anourosorex* and *Notiosorex;* lower articular condyle as in *Episoriculus* and slightly visible behind lower sigmoid notch in labial view; coronoid spicule low—entirely at or below level of upper sigmoid notch; external temporal fossa lower than in *Episoriculus* and terminating downward closer to level of lower condyle than to upper condyle. Pleistocene and Recent of eastern Asia.

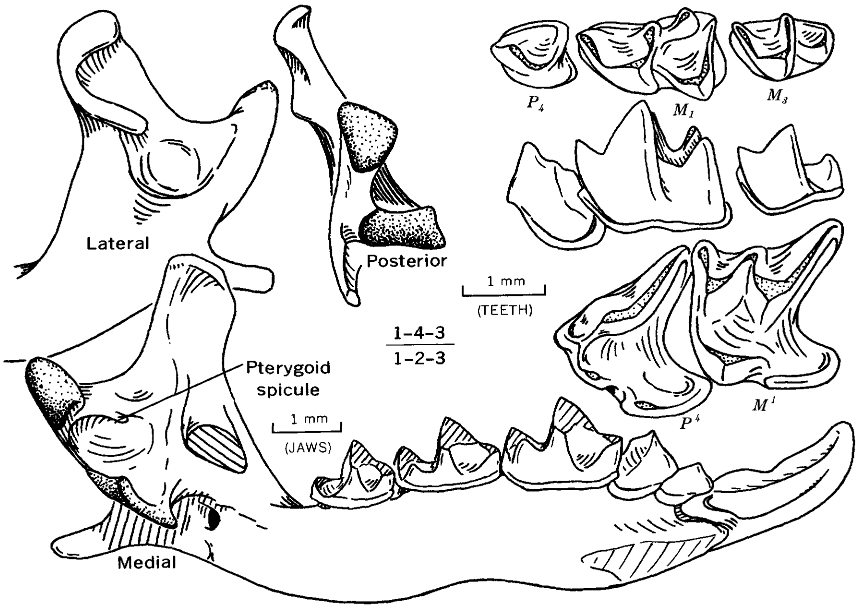

Figure 33.—*Chodsigoa hypsibia* (deWinton), China, CNHM 35760. Left mandible and dentition and left upper dentition.

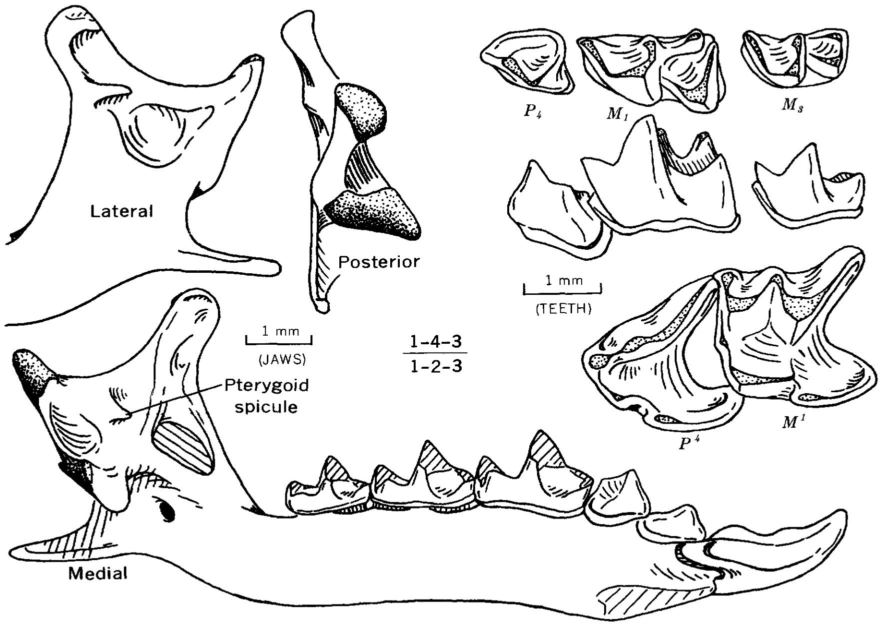

Figure 34.—*Chodsigoa salenskii* (Kastschenko), China, CNHM 39614. Left mandible and dentition and left upper dentition.

Three species in this group are recognized by Ellerman and Morrison-Scott (1951, p. 60–61) of which only two have been seen. *Chodsigoa hypsibia*, with a uniformly curving labial crest of P_4 and a reduced heel on M_3, is almost indistinguishable from the living *Notiosorex crawfordi* of North America on the basis of its dentition. Typical of the Old World Neomyini, the trigonid of M_1 is longer relative to the talonid than in *Notiosorex*, and the upper incisor is bifid. There is pigment on the very tip of the protoconid of M_1 in *N. crawfordi* and none on the specimen of *C. hypsibia* available for study, but there is pigment on the tip of the M_1 protoconid of *C. salenskii*. Both species of *Chodsigoa* have greater emargination of P^4 and the upper molars than *N. crawfordi* but not greater than the late Pliocene *Notiosorex jacksoni*. There is also great similarity in the mandibular structures although the coronoid spicule is clearly lower and the ascending ramus noticeably broader at the level of the upper sigmoid notch in *Chodsigoa.* Hibbard (1950), p. 128) made note of this similarity.

Specimens examined.—Chicago Natural History Museum 35760, a female *C. hypsibia* (deWinton) from Shansi, China, and 39614, a female *C. salenskii* (Kastschenko) from Szechwan, China.

Chodsigoa bohlini (Young), 1934

Neomys bohlini Young, 1934, Palaeontologia sinica, ser. C, v. 8, no. 3, p. 16–18, pl. 1, figs. 9–11.

Pei (1936, p. 18–19) stressed the point that this fossil differs from *Neomys* in that pigment is found only on the lower incisor and antemolars and not on the lower molars and that the talonid of M_3 "is reduced to one single pointed cusp." From Pei's illustrations the lower condyle appears too far forward, the external temporal fossa appears much too low, and the coronoid spicule also appears too low to be *Neomys.* The M_3 appears to match that of *Chodsigoa hypsibia.* All these features are those that separate *Chodsigoa* from *Neomys*, and therefore the species is here placed in *Chodsigoa.* The coronoid spicule is too low, the paraconid-metaconid distance on M_1 appears to be too great, and the geographic distribution does not indicate that it should be classified as *Notiosorex.* The species itself could stand on the basis of the narrowness of the ascending ramus at the level of the upper sigmoid notch. The questionably associated upper dentition (figured by Pei) seems to be indeterminate; it does not seem to belong to either *Chodsigoa* or *Neomys* because of the lack of pigment and the minimal emargination of M^1. Kowalski (1958, p. 14) also noted that this species is not *Neomys.*

Pleistocene of China (Choukoutien, loc. 3). No specimen was seen.

Genus BEREMENDIA Kormos, 1934

Figure 35

Genotype: *Crossopus fissidens* Petényi, 1864

Dental formula 1–5–3/1–2–3; upper incisor bifid; third upper antemolar small, fourth very small; P^4 about as in *Soriculus* with parastyle placed somewhat farther forward than in *Neomys*, and posterior emargination moderate to strong; lower incisor without irregularities on its cutting edge; P_4 with somewhat inflated cingulum; M_1 stout with complete and inflated labial cingulum, entoconid crest high and prominent; M_3 with unreduced trigonid but talonid very reduced, lacking entoconid and entoconid crest as in *Chodsigoa hypsibia*; teeth with dark red to black pigment about to same extent as *Blarinella*, about equal in area to *Soriculus* or *Nectogale* but much darker in color; upper articular facet oval; lower facet placed farther forward than in any other genus of Neomyini except *Anourosorex* and its allies and not visible in labial view; interarticular area very broad for Neomyini and very similar to *Blarina*, except superior pterygoid fossa is a deep pit and has not filled in with bone to thicken the condyloid process as in *Blarina*; coronoid spicule high; external temporal fossa moderately low below upper sigmoid notch and meets superior condyle; anterior curve

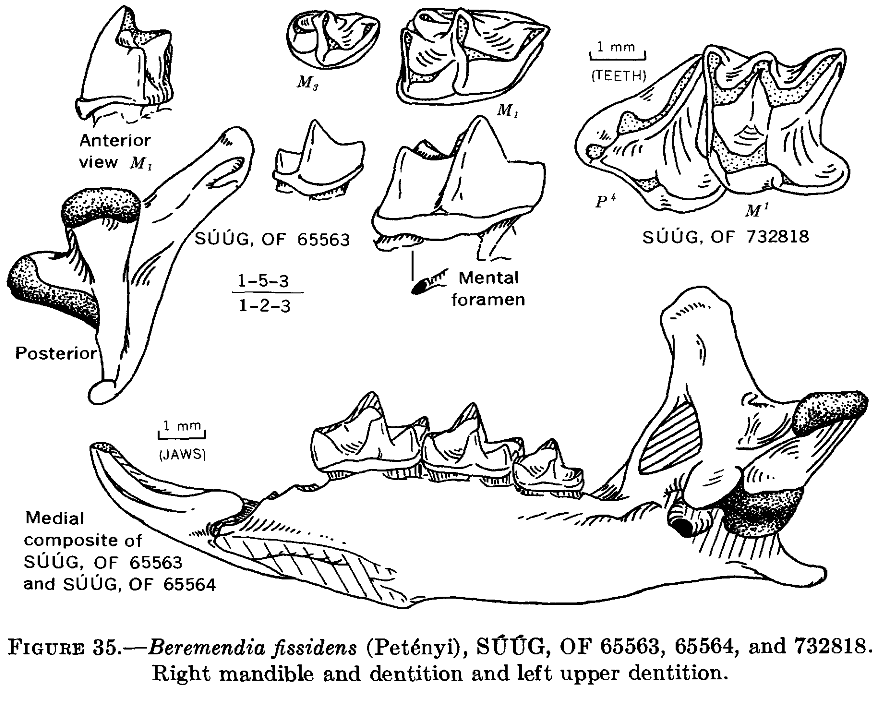

FIGURE 35.—*Beremendia fissidens* (Petényi), SÚÚG, OF 65563, 65564, and 732818. Right mandible and dentition and left upper dentition.

on tip of coronoid process extreme. Late Pliocene to middle Pleistocene of Europe (where it is a very common fossil) and probably Pleistocene of China.

In several features, *Beremendia* closely parallels *Blarina* and *Blarinoides.* The stout teeth with very dark pigment, the large size, and the articular structures of the mandible seem to show, at first glance, a very close relationship between these genera. The bifid upper incisor, the entoconid crest on M_1, anterior flex of the tip of the coronoid, and even details of the condylar structure clearly indicate, however, that *Beremendia* belongs in the tribe Neomyini. Three species have been named:

Beremendia fissidens (Petényi), 1864. Europe. The following specimens have been examined: Central Geological Survey of Czechoslovakia, and SÚÚG, OF 732815, 732816, 732817, and 732818, all from west Slovakia, and SÚÚG, OF 65563 and 65564 from south Slovakia. These specimens include most of the upper and lower dentition with complete mandibles.

Beremendia sinensis (Zdanski), 1928. Choukoutien fauna of China (generic assignment by Kretzoi, 1956). No specimen was seen.

Beremendia ucrainica (Pidoplichko), 1953. Middle Pleistocene of Europe (generic assignment by Miklós Kretzoi, oral commun., 1966). No description or specimen seen.

Genus NESIOTITES Bate, 1945

Genotype: *Nesiotites hidalgo* Bate, 1945

Dental formula 1–5–3/1–2–3 or 1–4–3/1–2–3; upper incisor bifid; fourth upper antemolar minute when present; P^4 and M^1 with moderate emargination of posterior basal outline; lower incisor with one or two low cusp on cutting edge; P_4 paralleling that in Limnoecinae with labial blade centrally located on tooth, posterolingual basin present; teeth with or without pigment; articular structure of mandible as in *Neomys*; coronoid process relatively low and neither spatulate nor curved forward.

No specimen of this genus has been seen, and this diagnosis is based upon Bate's description and illustrations but is not the same as hers. Her diagnosis also included the following: Extinct; medium size; deep snout; P^4 and M^{1-3} as in *Sorex*, and M_3 larger than in Recent *Chimarrogale* or *Soriculus.* She made no note of the conspicuously less emargination of the posterior border of P^4 and M^1 or of the relatively great lingual shift of the protocone of P^4, in comparison with *Sorex*, that seems to be indicated in her figure 7b.

Three species are described, all from the Pleistocene of the Mediterranean Islands:

Nesiotites hidalgo Bate, 1945. Mallorca and Minorca.
Nesiotites corsicanus Bate, 1945. Corsica.
Nesiotites similis (Hensel), 1855. Sardinia.

Genus NECTOGALE Milne-Edwards, 1870

Figure 36

Genotype: *Nectogale elegans* Milne-Edwards, 1870

Dental formula 1–4–3/1–2–3; upper incisor bifid; P^4 with protocone fairly close to parastyle; lower teeth as in *Neomys* except stouter cuspids and secondary cuspids present on P_4 and M_1; no cuspids on cutting edge of lower incisor; labial cingulum absent on P_4 and present only at base of paraconid blade of lower

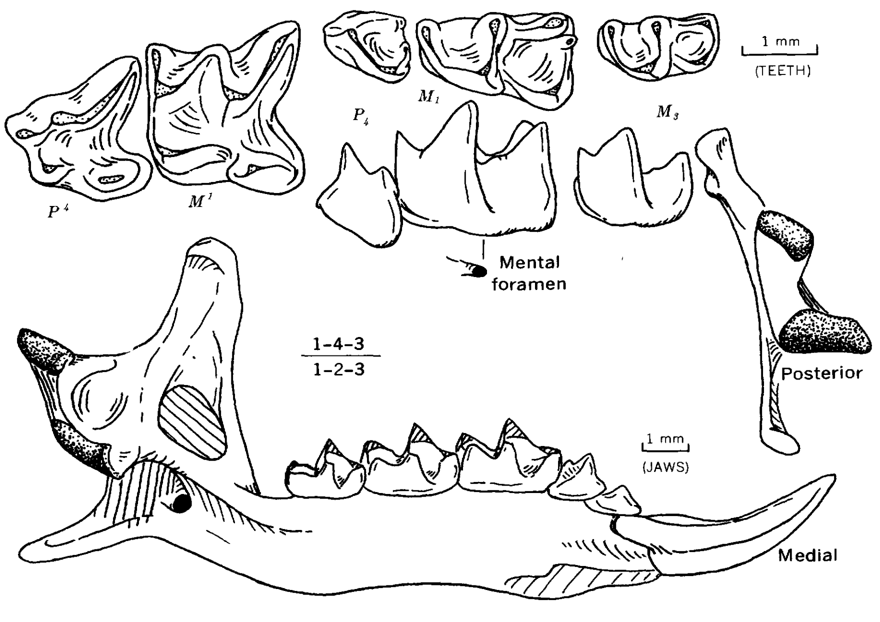

FIGURE 36.—*Nectogale elegans* Milne-Edwards, China, USNM 254812. Left mandible and dentition and left upper dentition.

molars; entoconid crest continuous between entoconid and metaconid on molars; pigmented enamel extreme in extent, covering about three-fourths of labial side of M_1, but very pale flesh color that contrasts very little with unpigmented enamel—pigment more obvious in ultraviolet light; mandibular condyles as in *Neomys* except lower articular facet not as long.

This genus is unique in the great extent of its very light pigment, equaled in extent by *Beremendia*, and the accessory cuspids of the P_4 and lower molars; *Nectogale*, *Nesiotites*, and *Hesperosorex* appear to be the only genera in the tribe that do not exhibit either a spatulate or anteriorly deflected tip to the coronoid process. This is the first genus of the Neomyini discussed which shows a reduced labial cingulum, a feature characteristic of *Anourosorex* and its allies. There is no fossil record of this genus and only one living species, *Nectogale elegans* from eastern Asia, according to Ellerman and Morrison-Scott (1951, p. 88).

The genus has been considered a crocidurine shrew.

Specimen examined.—U.S. National Museum 254812, a male from Szechwan, China.

Genus SORICULUS Blyth, 1854

Figure 37

Genotype: *Cosira nigrescens* Gray, 1842

Dental formula 1–5–3/1–2–3; upper incisor bifid; fourth upper antemolar small; P^4 with protocone shifted medially and parastyle shifted anteriorly away from paracone to lengthen tooth, posterior emargination moderate; lower incisor with one cusp on cutting edge; P_4 elongate with labial cingulum; labial cingulum of lower molars reduced, moderately strong below parastylid, weak below protoconid, and absent posterior to protoconid; entoconid crest very low on M_1 but still present (in contrast to tribe Blarinini); entire M_3 somewhat reduced and talonid further reduced as in pattern of *Blarina;* pigment varying from somewhat more extensive than in *Neomys* to undetectable but when present light orange (as in *Domnina* and some other ancient shrews) rather than dark reddish brown as in *Sorex* and *Blarina*; no pterygoid spicule or boss in specimens seen and superior pterygoid fossa a shallow basin because of thickening of condylar process; upper articular facet of mandible oval; lower facet barely visible behind lower sigmoid notch in labial view; coronoid spicule prominent and low on ascending ramus; external temporal fossa about as in *Chodsigoa* but with deep basin beneath coronoid spicule; tip of coronoid process broadly spatulate with little to no anterior deflection. Recent of eastern Asia.

Ellerman and Morrison-Scott (1951, p. 58) recognized only one living species that would be in this genus as recognized here. In addition to a reduction of the labial cingulum of the lower molars, this genus is the first discussed in the tribe Neomyini to show a significant reduction of the entire M_3 and of the entoconid crest on M_1 and is the first discussed to show a strongly spatulate tip of the coronoid process; all these trends reach maximum development in *Anourosorex* and its allies. There is no known fossil species

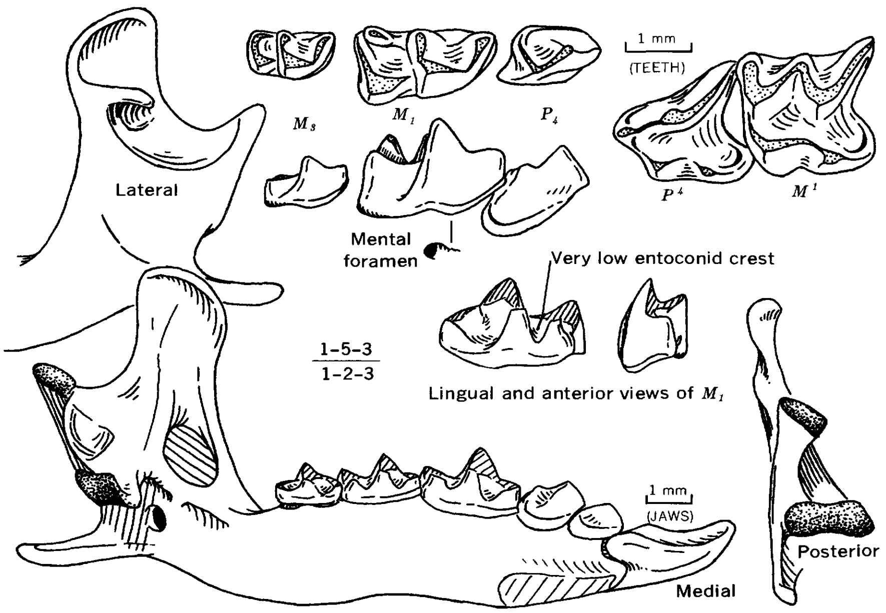

FIGURE 37.—*Soriculus nigrescens* (Gray), India, CNHM 82563 (teeth) and 82565 (mandible). Left mandible, right lower dentition, and left upper dentition.

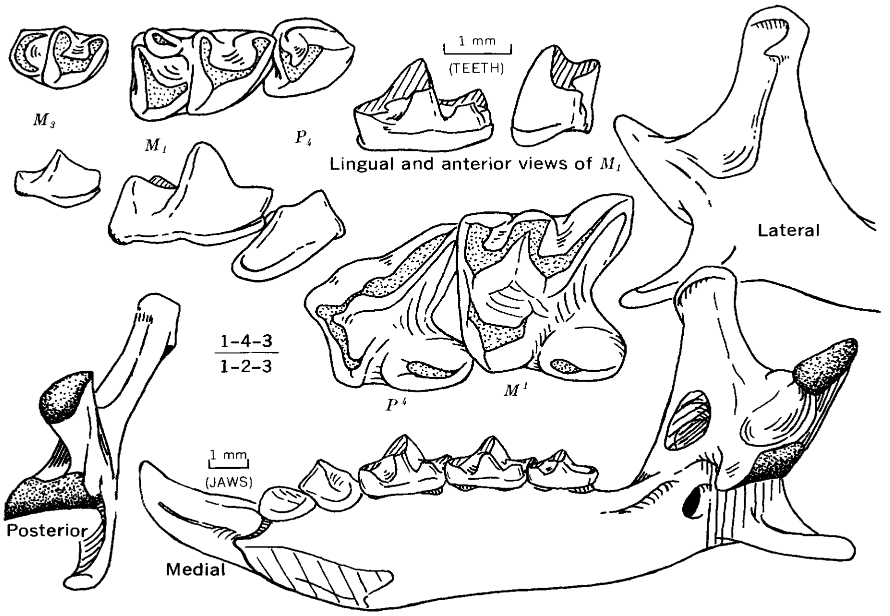

FIGURE 38.—*Chimarrogale himalayica* (Gray), India, UCMVZ 119400. Right mandible and lower dentition and left upper dentition.

which could be assigned to this genus as here understood.

Specimens examined.—*Soriculus nigrescens* (Gray), Chicago Natural History Museum 82363, a female from Lachen, India; 82564, a male from Lachen, India; and 82565, a female from Ghoom, India. These specimens represent two subspecies.

Genus **CHIMARROGALE** Anderson, 1877

Figure 38

Genotype: *Crossopus himalayanus* Gray, 1842

Dental formula 1–4–3/1–2–3; upper incisor sometimes bifid; P^4 with protocone placed far medially from parastyle, posterior emargination strong; M^2 trapezoidal; lower incisor with smooth cutting edge but with raised crest of edge in position of cusp of *Neomys*; P_4 with weak labial cingulum and not elongate; M_1 with moderate labial cingulum below paraconid but very thin and weak, almost unnoticeable, posterior to protoconid and not present on posterior face of tooth by hypoconid; entoconid crest very low on M_1 about as in *Soriculus;* entire M_3 reduced and talonid further reduced to a *Blarina*-like crescent; teeth rather stout and pigment not visible under normal light but under either long- or short-wave ultraviolet light pigment can be seen to be somewhat less extensive than in *Neomys*; zygomatic process of maxillary originates opposite metacone of M^2 as in Blarinini ; area of insertion of superior pterygoid muscle not basined at all but somewhat swollen because of thickening of condylar process (this feature is unique in the Neomyini although approached by *Soriculus*); pterygoid boss moderately prominent just below upper sigmoid notch; upper articular facet oval; lower facet slightly visible in labial view but offset lingually from lower sigmoid notch by groove as in *Chodsigoa*, *Notiosorex*, and *Megasorex;* coronoid spicule slight and very high on process; external temporal fossa fairly low, dropping to about midway between condyles with a relatively deep basin in lower part opposite pterygoid insertion on medial surface and partly responsible for lack of basined pterygoid fossa; tip of coronoid process small and knoblike, with moderate anterior curve. Recent of eastern Asia.

Ellerman and Morrison-Scott (1951, p. 87–88) listed one living species, *Chimarrogale platycephala* (Temminck), 1842, which is possibly better known as *Chimarrogale himalayica* (Gray), 1842. There is no known fossil species that could belong to this genus. The genus has been considered a crocidurine shrew.

Specimens examined.—University of California Museum of Vertebrate Zoology 119400, a male from Nepal, and U.S. National Museum 240167, from Yunnan, China.

Genus **ANOUROSOREX** Milne-Edwards, 1870

Figure 39

Genotype: *Anourosorex squamipes*
Milne-Edwards, 1872

Dental formula 1–3–3/1–2–3; upper incisor not bified in specimen seen; first upper antemolar larger than second; P^4 with protocone shifted medially and para-

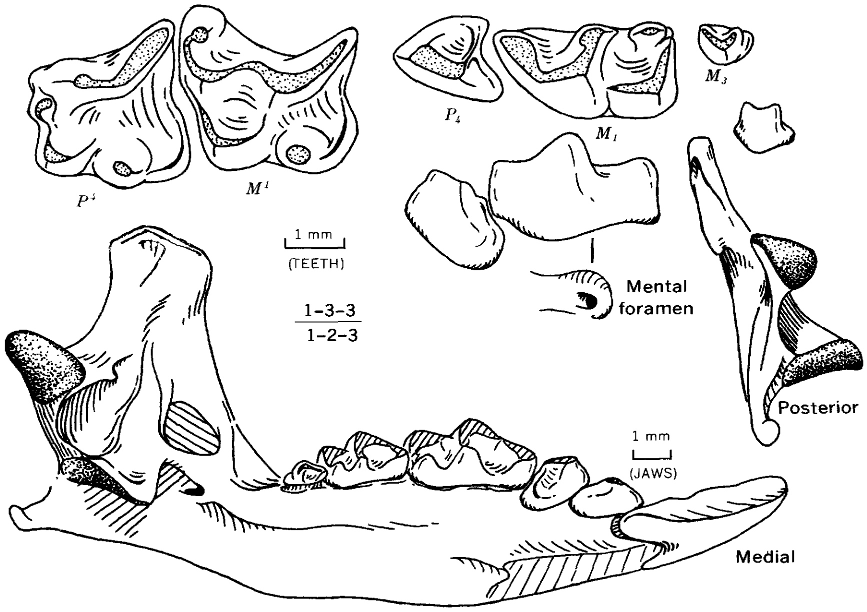

FIGURE 39.—*Anourosorex squamipes* Milne-Edwards, China, CNHM 36970. Left mandible and lower dentition and left upper dentition.

style subdued, consequently anterior and medial basal outlines form approximately a right angle, emargination of posterior basal outline very slight; M^1 with exaggerated parastyle and subdued mesostyle; M^2 reduced and almost triangular; M^3 minute; lower incisor with smooth or very slightly irregular upper cutting edge; M_1 with exceptionally elongate trigonid, entoconid crest lacking, metalophid-protolophid junction located very labially and comparable to *Blarina*, labial cingulum totally lacking as on all lower teeth; M_2 reduced; M_3 minute with very slight talonid remaining; teeth unpigmented and bulbous; zygomatic process of maxillary originates opposite M^2; mental foramen in depression below middle of M_1; coronoid process broad and spatulate, very broad at level of upper condyle; coronoid spicule strong and fairly low; external temporal fossa of mandible low, extending about to level of lower condyle; superior pterygoid fossa of mandible as deep basin with prominent pterygoid spicule; upper articular facet triangular as in *Chodsigoa;* interarticular area very narrow; lower condyle placed well forward of lower sigmoid notch. Middle Pliocene to Recent, eastern Asia.

In dental and mandible structures, this is the most specialized of living shrews. *Nectogale*, *Soriculus*, and *Chimarrogale* all have features that suggest a relationship to *Anourosorex*, but it does not seem possible to decide which is most closely related from the characters considered in this review. Although all these are eastern Asian shrews of the modern fauna, close relatives are also found in the Pliocene record of North America (J. H. Hutchison, written commun. 1964) and Europe.

Ellerman and Morrison-Scott (1951, p. 87) recognized only one species, *Anourosorex squamipes* Milne-Edwards, although some authors appear to still consider *A. assamensis* Anderson as a distinct species.

Specimen examined.—Chicago Natural History Museum 36970, a male from Szechwan, China.

There are two fossil species included in the genus:

Anourosorex inexpectatus (Schlosser), 1924. Placed in the genus *Neomys* by Schlosser and compared with *Beremendia fissidens* from Europe. As Miller (1927, p. 10) noted, the species agrees well with living *Anourosorex*. From Schlosser's illustration (1924, pl. 1, fig. 4), the presence of M_3 is indicated by its alveolus and thus eliminates assignment of the species to the genus *Amblycoptus*. Middle Pliocene of Mongolia (Ertemte fauna). No specimen was seen.

Anourosorex japonicus Shikama and Hasegawa, 1958. M^2 triangular; M^3 and M_3 further reduced than in living species. Middle Pleistocene of Japan (Siraiwa fauna). No specimen was seen.

Genus **AMBLYCOPTUS** Kormos, 1926

Genotype: *Amblycoptus oligodon* Kormos, 1962

Dental formula 1-4-2/1-2-2; differs from *Anourosorex* in the following characteristics: One more upper antemolar; M^1 with greater emphasis of parastyle; M^2 completely reduced to triangle and resembling M^3 of other shrews; $M\frac{3}{3}$ missing; jaw stouter; interarticular area somewhat broader with oval upper articular facet. Early Pliocene (Polgardi fissure–*Hipparion* fauna), Hungary. One species named, *Amblycoptus oligodon* Kormos. No specimen was seen.

Genus HESPEROSOREX Hibbard, 1957

Genotype: *Hesperosorex lovei* Hibbard, 1957

Labial cingulum of M_1 prominent, somewhat inflated, not deepened, and continuous around hypoconid to posterior border of tooth; entoconid of M_1 prominent, close to metaconid (closer than on M_2) and connected to metaconid by an entoconid crest of moderate height; hypolophid of M_1 (inadvertently called the paraconid by Hibbard) well developed and extending past the entoconid to the lingual cingulum (not so extensive lingually on M_2 to judge from Hibbard's figure); M_1 and M_2 stout and "tips of the molars show evidence of pigmentation," suggesting noticeably less pigmentation than in *Blarina*; mental foramen below middle of M_1; coronoid spicule[5] not well developed and fairly low, as in *Chodsigoa;* tip of coronoid process narrow, not curved anteriorly and not spatulate; articular structures most generalized of tribe; upper facet narrowly oval; lower facet broadly oval and placed only moderately forward but offset far lingually (characteristic of Neomyini) and separated from lower sigmoid notch by a groove; interarticular area broad relative to all other genera of Neomyini except *Beremendia* and comparable in general development to specialized Soricini as *Blarinella* or generalized Blarinini as *Cryptotis* and *Adeloblarina.* Middle Pliocene (Hemphillian) of North America.

This genus is somewhat questionably referred to the Neomyini because the genotypic specimen, a mandible with M_1 and M_2, was not available for examination. Classification with the Soricini seems to be eliminated by the condyloid and coronoid structures but not by great or obvious differences. The tribe Blarinini is eliminated by the entoconid crest of M_1 and by the extreme offset of the lower condyle. The absence of a lingual emargination of the interarticular area is the chief objection to placing *Hesperosorex* in the tribe Neomyini, but this objection seems to be outweighted by the distinctive lingual offset of the lower condyle and the resulting groove between the condyle and the lower sigmoid notch. The absence of the emargination of the interarticular area seems to be due to a minimal lingual shift of the superior condyle resulting from minimal curvature toward the cranium of the condyloid process supporting the superior condyle and thus suggests that the coronoid process is not deflected labially as in more typical members of the Neomyini. If these suggestions are true, the mandibular structures could represent a primitive condition, not far removed from the Soricini, that could be expected in the Neomyini. These suggestions, however, cannot be evaluated from the published descriptions.

The genotypic species, *Hesperosorex lovei* Hibbard, is from the middle Pliocene Teewinot Formation of Wyoming. No specimen was seen.

Genus NOTIOSOREX Baird, 1877

Figure 40

Genotype: *Sorex* (*Notiosorex*) *crawfordi* Coues, 1877

Dental formula 1–4–3/1–2–3; upper incisor not bifid; P^4 with protocone about as in *Sorex*, posterior emargination strong to extreme; M^2 rectangular; lower incisor short with one low cusp on cutting edge; P_4 with curving junction of labial blade and crest of posterior cingulum; M_1 with metaconid and paraconid close together relative to *Chodsigoa*, labial cingulum strong, entoconid and entoconid crest strong; M_3 with reduced heel, entoconid lost, entoconid crest suppressed, V of hypoconid not developed, and metalophid and hypoconid form curved trenchant crest; tip of protoconid of M_1, of paracone of P^4, and tips of more anterior teeth pigmented; teeth slender; zygomatic process of maxillary originates opposite metastyle of M^2; mental foramen below middle of M_1; tip of coronoid process narrow and inclined slightly forward; coronoid spicule moderately low; external temporal fossa of mandible moderately low and extending down to about midway between condyles; superior pterygoid fossa of mandible deeply basined, pterygoid spicule strong or barlike; condyloid structure as in *Chodsigoa* with triangular upper facet and groove labial to lower facet. Late Pliocene (early Blancan) to Recent, North America.

One living species, *Notiosorex crawfordi* (Coues), is recognized and is also known from the late Pleistocene of Kansas and California. The one extinct species, *Notiosorex jacksoni* Hibbard, is known from the late Pliocene (early Blancan) of Kansas (Hibbard, 1950) and possibly from the middle Pleistocene (Irvingtonian) of California (Vallecito Creek fauna, unpub. record, J. A. White, oral commun., 1963) and differs in being intermediate in size between living *Notiosorex* and *Megasorex* and in having extreme emargination of the posterior basal outline of P^4 and the upper molars, thus resembling *Chodsigoa salenskii.*

Specimens examined.—Four specimens of the living species from Texas and California in the University of California Museum of Vertebrate Zoology; one specimen possibly of *N. jacksoni* from the Pleistocene of California in the Los Angeles County Museum.

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[5] As here used; Hibbard reserved the term, possibly correctly, in the sense used by Gaugrahn, for a needlelike projection rather than a ridge.

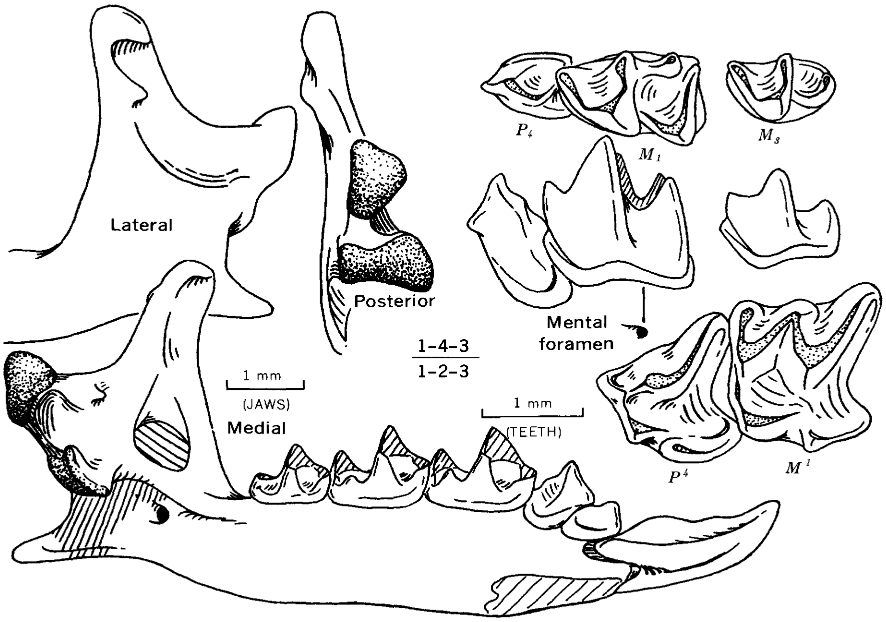

FIGURE 40.—*Notiosorex crawfordi* (Coues), Texas, UCMVZ 98040. Left mandible and dentition and left upper dentition.

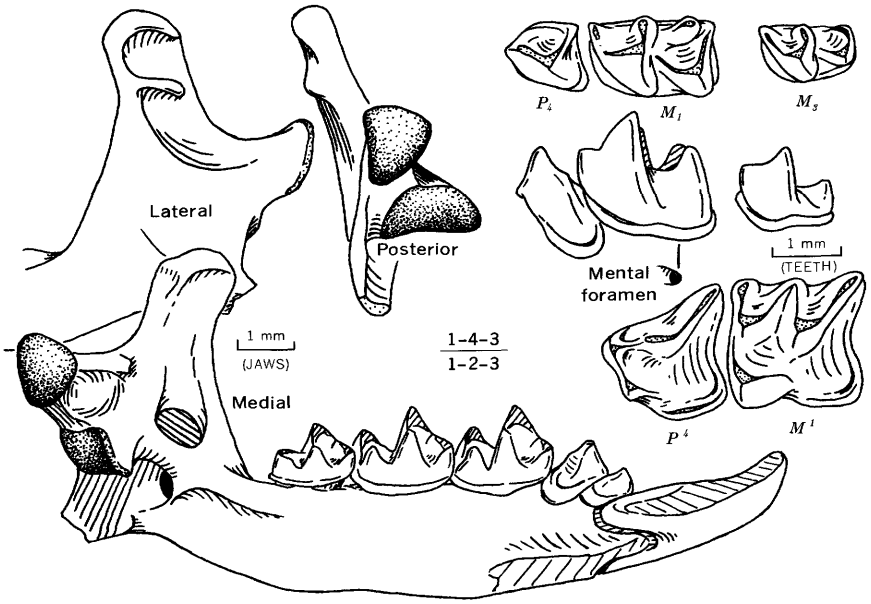

FIGURE 41.—*Megasorex gigas* (Merriam), Mexico, LACM 13568. Left mandible and dentition and left upper dentition.

Genus **MEGASOREX** Hibbard, 1950

Figure 41

Genotype: *Notiosorex gigas* Merriam, 1897

Dental formula 1-4-3/1-2-3; upper incisor not bifid; P^4 about as in *Notiosorex* but with only slight posterior emargination; M^2 rectangular; lower incisor as in *Notiosorex*; P_4 with more angulate junction of labial shearing blade with crest of posterior cingulum than in *Notiosorex* and more like *Chodsigoa salenskii*; entoconid crest of M_1 very low; talonid of M_3 little reduced and as in *Chodsigoa salenskii;* zygomatic process of maxillary originates behind M^2; mandibular structures virtually as in *Notiosorex* and *Chodsigoa* except tip of coronoid more inclined anteriorly and more spatulate than in *Notiosorex*; one living species, *Megasorex gigas* (Merriam), Recent of Mexico.

Specimen examined.—Los Angeles County Museum 13568, a female from Colima, Mexico.

Neomyini? Incertae Sedis

Deinsdorfia franconia Heller, 1963

This genus and species was defined (Heller, 1963, p. 5–7) on the basis of a toothless right mandible from the Pleistocene fauna of Deinsdorf. In Heller's photographs it is characterized by rather extreme posterior placement of the mandibular condyles but otherwise appears not unlike *Neomys.* Heller's (fig. 2c) drawing of the posterior view of the condyles, however, does not appear similar to *Neomys* at all. Fejfar (1966, p. 243) interpreted Heller's drawing as indicative of the tribe Soricini, but I have some question about the accuracy of the drawing. If the drawing is correct then I suspect that *Deinsdorfia* belongs in the Blarinini. In any event, I am unable to place the genus in any soricid tribe from published descriptions but feel that it most likely belongs in the Neomyini.

Subfamily ALLOSORICINAE Fejfar, 1966

This subfamily was recently established by Fejfar to include a most unusual shrew, *Allosorex stenodus.* In his discussion of this shrew, Fejfar (1966, particularly p. 240–241) pointed out the similarities of *Allosorex* to "*Sorex*" *gracilidens* and suggested that the latter could well be the late Miocene ancestor of *Allosorex.* He did not, however, include "*Sorex*" *gracilidens* in his new subfamily. To me, the similarities are strong, however, and, being faced with a problem of subfamily assignment that Fejfar did not have, I include "*Sorex*" *gracilidens* in the family Allosoricinae, rather than in "Soricidae, Incertae Sedis," for it clearly does not belong in any other subfamily of shrews. The following diagnosis of the subfamily Allosoricinae is revised from Fejfar (p. 223) with modifications to allow inclusion of "*Sorex*" *gracilidens.*

Lower antemolars high cusped with conspicuous sectorial adaptation, P_4 apparently derived from a crocidurinelike triangular crown but a clear tendency to form a high sharp anteroposterior shearing blade with no overhang of alveoli by enamel cap; lower molars narrow and high cusped, very carnivorelike, trigonid much longer than talonid, paralophid blade knife edged and conspicuously oriented anteroposteriorly in comparison to most shrews, metaconid close to and much lower than protoconid, metalophid united to protoconid and forming a continuous crest with hypolophid, hypolophid united with entoconid, entoconid crest absent and talonid basin open lingually between entoconid and metaconid particularly in *Allosorex,* cingulum weak to not present; coronoid process low and anteroposteriorly wide; mandibular condyles separated and upper one placed far posteriorad; upper incisor fissident, teeth not pigmented. The unpigmented, carnivorelike lower teeth are most characteristic of this subfamily.

"*Sorex*" *gracilidens* Viret and Zapfe, 1951

P_4 with single, narrow, high cusp that has narrowly triangular occlusal section surrounded by a basal cingulum, anteroposteriorly two rooted; M_1 very suggestive of P_4 in *Martes:* narrow, paralophid nearly parallel to axis of mandible, metaconid reduced and fused to protoconid; metalophid nearly parallel to axis of mandible, hypoconid and entoconid strong and forming square corners on posterior border of short talonid; M_3 also similar but reduced and talonid reduced to rounded heel apparently with only one cusp; mental foramen below P_4, internal temporal fossa well developed; upper and lower articular facets clearly formed and fairly widely separated, but there appears to be no interarticular excavation. Late Miocene (Vindobonian) of Vienna Basin.

From published descriptions, this shrew does not clearly belong to any subfamily except the Allosoricinae. No specimen was seen. Fejfar (1966, p. 240–241, figs. 13, 14) described new material and discussed the possible ancestral position of "*Sorex*" *gracilidens* to the genus *Allosorex.*

Genus ALLOSOREX Fejfar, 1966

Genotype: *Allosorex stenodus* Fejfar, 1966

Large; dental formula 1–?–?/1–2–3; sectorial development of cheek teeth extreme, paralophid and metalophid parallel to axis of mandible; lower incisor with hooked tip and trough along lingual side of cutting edge; upper incisor very weakly fissident; coronoid process very low; condyles very large and widely separated so that they are not connected by an interarticular area. Late Pliocene, Czechoslovakia.

This genus is, easily, the most specialized and unusual shrew known.

Specimen seen.—SÚÚG, OF 652366, a toothless mandible, and SÚÚG, OF 652370, a mandibular fragment with M_1, both topotypes from Ivanovce, near Trenčín, Czechoslovakia.

SORICIDAE Incertae Sedis

Podihik kura Deraniyagala, 1958

This living shrew was defined on the basis of two specimens from Ceylon and was considered to be a soricine shrew because the teeth were pigmented pale reddish gray. I am informed by Dr. Deraniyagala (written commun., 1965), however, that the coloration of the teeth has entirely disappeared in both preserved specimens. This suggests to me that the reddish color was a stain rather than actual tooth pigment, which is very stable. From published descriptions and supplemental notes provided by Dr. Deraniyagala I am unable to assign this shrew to a subfamily. If it is a soricine shrew, its occurrence would be most unusual, and the only one in peninsular India or Ceylon and the only one south of the ancient Tethys seaway.

Names of fossil genera not used in text

Allopachyura Kormos, 1934; included in *Petenyiella.*
Asoriculus Kretzoi, 1959; included in *Episoriculus.*
Heterosorex Gaillard, 1915; included in *Trimylus.*
Miothen Cope, 1873; included in *Domnina.*
Oligosorex Kretzoi, 1959 (*Oligosorex meyeri*); possibly valid; in *Crocidosorex* (*Crocidosorex antiquus*).
Plesiosorex Pomel, 1848, not a soricid.
Protosorex Scott, 1895; included in *Domnina.*

ANCESTRY OF THE SORICIDAE

In this review it has been shown that the Soricidae is a family of diverse phylogeny and that subfamilies can be recognized by consistent morphologic differences which are traceable back through the late and middle Tertiary toward a common ancestry. The family is, however, distinctly differentiated from all other mammals. There is no shrew known that is sufficiently generalized morphologically to be this common ancestor. The dental and mandibular characters of the oldest known member of each of the four subfamilies and the directions of modification of these characters in younger forms suggest what this original shrew should look like. Its diagnosis may be about as follows:

Dental formula 1–6–3/1–5–3; upper incisor falciform and bifid; upper antemolars except P^4 small, simple in form, equal in size or anterior ones larger, only slightly crowded; P^4 nearly equilaterally triangular in occlusal view, protocone close to anterior apex of triangle and close to incipient parastyle at anterior apex, posterior emargination very slight or lacking; M^1 square in occlusal view with W-shaped ectoloph, protocone strong, hypoconal shelf and cingulum strong, emargination of posterior outline slight or lacking, no protoconule or metaconule; M^2 square and similar to M^1; M^3 triangular, metastyle and hypoconal shelf lacking; lower incisor large with extreme procumbency typical of Soricidae, possibly with two rounded cuspules on upper cutting edge; lower antemolars with a single triangular cusp, the first and last (P_4) largest, only slight tendency to be crowded; P_4 not even slightly molariform and clearly single cusped, posterior and lateral cingula prominent, two rooted; M_1 with trigonid and talonid well developed, metaconid and paraconid more widely separated than on M_2, metalophid meeting protolophid at midline of tooth or possibly closer to the metaconid, entoconid clearly separated from hypolophid and connected to metaconid by a high and well-formed entoconid crest, no hypoconulid, labial cingulum probably strong, labial reentrant between the protoconid and hypoconid emerges at level of cingulum; M_2 like M_1 but paraconid closer to metaconid; M_3 with trigonid like that on M_2 but talonid reduced (to condition as in *Sorex*), entoconid connected to hypolophid; all teeth pigmented light orange; zygomatic process of maxillary originates behind M^2; zygomatic arch probably incomplete but maxillary process strong; mental foramen below P_4 or P_3; internal temporal fossa of mandible strong but not pocketed; external temporal fossa of mandible weak and confined to tip of coronoid process, its posterior margin above upper sigmoid notch; masseteric fossa of mandible moderately strong, insertion on angular process marked by crest; superior pterygoid fossa of mandible on anterior side of condylar process; condylar process delicate; condyle small and single, articular facet probably covers dorsal, posterior, and ventral sides of condyle to fit into pocketed glenoid; small size.

This hypothetical ancestor would unquestionably resemble a shrew despite the lack of the pocketed internal temporal fossa, of the doubled mandibular condyle, of the emargination of the posterior border of P^4 and the upper molars, and of the reduced number of antemolars. The characters that would make it appear shrewlike, together with the occurrence of these characters in mammals with similar dentition, are as follows:

1. Procumbent and enlarged lower incisor. Perhaps this is the most typically soricid feature. It is shared with no similar mammal.
2. Falciform upper incisor. This is shared to a slight degree by some erinaceoids, as *Saturninia*, but still is a typical soricid feature. In connection with this tooth, it should be noted that the bifid upper incisor found in the Heterosoricinae, in the tribe Neomyini, and in some members of the tribe Soricini is also found in some Chiroptera but has not been noted in any other mammal with closely comparable dentition.
3. Entoconid separated from the hypolophid (except on M_3). This is a typical soricid feature but is found in a few Chiroptera and also in erinaceoids when the hypoconulid breaks the continuity of the hypolophid. In the erinaceoids, however, the presence of the hypoconulid is a far greater dissimilarity than the separation of the entoconid is a similarity to the shrews.

4. Entoconid crest on M_1 (and M_2). This is a typical soricid feature but is shared with most Chiroptera and with *Nesophontes.*
5. A strong hypoconal shelf and cingulum depressed from the level of protocone and no distinct hypocone on M^1 and M^2. This is a typical soricid feature that is shared in typical development only by the Chiroptera. The Talpidae either lack hypoconal structures or have a hypoconal shelf that is on a level with the protocone and has a fairly distinct hypocone. The same can be said for most forms included in the Erinaceoidea.
6. Protoconule and hypoconule absent. This is a character that is shared with the Chiroptera, Talpidae, and *Nesophontes.*
7. W-shaped ectoloph. This is a character that is shared with the Chiroptera, Talpidae, and perhaps *Nesophontes*, as well as many other dialambdont insectivores.
8. M^3 reduced by loss of metastyle and hypoconal structures. This is a character shared with the Chiroptera and Talpidae but not with typical Erinaceidae.
9. P_4 not molariform. This is a character shared with the Chiroptera, Talpidae, and *Nesophontes.*
10. No hypoconulid on M_1 and M_2. This is a character shared with the Chiroptera and Talpidae, as well as with some erinaceoids and possibly *Nesophontes.*
11. Zygomatic arch (or process of the maxillary) originates behind M^2. This is a character shared with the Chiroptera and the Talpidae.
12. Metalophid-protolophid junction near the metaconid of M_1 and M_2. This is a character shared and exceeded by the Talpidae and shared by the Chiroptera.
13. Metaconid farther from paraconid on M_1 than on M_2. This character is found in some forms of most insectivore groups. It is mentioned here because it has not been seen in the Chiroptera during this review.

Although it represents only an approximation based upon the inferred dental characters of the hypothetical ancestor of the four subfamilies of the Soricidae, it is interesting to note the relative degree of resemblance of the shrews to other insectivores and bats. Of the 13 characters listed as shrewlike, the Chiroptera share 11, the Talpidae share 7, the Erinaceoids share 4+, and the problematic sub-Recent genus *Nesophontes* from the West Indies shares 4+. Of course consideration of other morphologic characters, as in the forelimbs of bats, may outweigh dental similarities.

It appears, therefore, that Soricidae were certainly represented in the Oligocene by the subfamilies Heterosoricinae and Soricinae. The subfamily Crocidurinae and the Limnoecinae have features that could not have been entirely derived from either the Soriciniae or the Heterosoricinae, as these subfamilies are here understood from their earliest known records; the features appear to have been inherited from an ancestral form possessing some characters of both Oligocene subfamilies. Therefore it has to be assumed that the Crocidurinae and Limnoecinae were also present in the Oligocene or that an unknown group was present from which both diverged. The geographic isolation of these two subfamilies, the Crocidurinae in the Old World and perhaps only south of the Tethys seaway before the Miocene (Repenning, 1965, p. 195) and the Limnoecinae in the New World after the early Miocene, suggests that they were derived from the native soricid stock sometime before the earliest record of the soricines. This would certainly be in the Oligocene for the origin of the Crocidurinae of the Old World and probably in the Oligocene for the origin of the Limnoecinae in the New World.

The Oligocene subfamilies of the Soricidae diverged from an unknown, preearly Oligocene, very shrewlike soricid ancestor. This common ancestor appears to have evolved, along with the Chiroptera and the Talpidae, from an unknown soricoid. If one assumes that the slow rate of morphologic change evidenced in the middle to late Tertiary fossil record of the shrews reflects earlier rates of change, divergence of these groups from the unknown soricoid must have taken place before the Eocene. It would seem the Soricoidea-Chiroptera stock could not have diverged from the remaining insectivores after these had a molariform P_4, and this may well take the ancestry of the Soricoidea (at this point including the Chiroptera) back to the Mesozoic and possibly to the origins of placental mammals.

PALEOZOOGEOGRAPHY AND CORRELATION

Before the late Pliocene the fossil record of the shrews is quite inadequate. Even after that time the known specimens are not abundant except from a few localities where either the manner of fossil accumulation or the method of collection has been favorable. Furthermore, most shrews are highly endemic animals not only geographically limited in both living and fossil species but tending to remain so throughout appreciable spans of their evolutionary histories. Finally, rates of evolution vary greatly as illustrated by the conservatism of the tribe Soricini contrasted with the exorbitant adaptive modification and variety seen in the tribe Neomyini, both within the subfamily Soricinae. These conditions all indicate that interpretation of the significance of a fossil shrew should be made with caution.

The small subfamily Heterosoricinae contains only four known genera and is characterized by little ramification of its phylogeny. *Domnina* is known only from North America, where it ranges through the Oligocene and early Miocene. During this time it tends to increase the crowding of its antemolars and possibly to reduce its pigmentation, but stages of evolution cannot be clearly defined on the basis of the known material. Unless a specimen can be identified with a known species, it appears that it may be useful in establishing geologic age only in terms of closeness to one limit of the temporal range of the genus rather than to the other.

The genera *Paradomnina* and *Ingentisorex* are known only from the late Miocene of North America.

Trimylus is better represented in number of species and in greater temporal and geographic range. In North America and possibly in Europe the evolution of this genus appears to be almost straight line with a uniform rate of change. It seems quite possible at present to recognize middle or late Oligocene and early, middle, and late Miocene stages of evolution in North American *Trimylus*. The possibility of similar usefulness in the European forms cannot be evaluated without examination of the specimens.

Although *Trimylus* is known only back to the middle Oligocene, it seems reasonable to assume that the genus became a part of the fauna of both North America and Europe during the early Oligocene mammalian interchange. Oligocene species show a greater similarity than do more recent species of both hemispheres; since the beginning of the Miocene, possibly since the early Oligocene, endemic Old and New World lineages appear to have been in existence. *Trimylus roperi* from the early Miocene of Colorado may represent an immigration of the European stock during the early Miocene mammalian exchange or may be a part of the American stock that has an otherwise unrecognized variability in the position of the mental foramen. The Heterosoricinae is unique in several features and seems much more distantly related to the other soricid subfamilies than all the other subfamilies are to each other.

The fossil record of the Crocidurinae is very meager. The oldest specimens known are of middle Miocene age from Europe (Doben-Florin, 1964) and Africa (Butler and Hopwood, 1957, p. 2). The subfamily is characterized by the retention of primitive characters, and the modern forms differ from those of the late Miocene in the loss of one, two, or three upper and lower antemolars, in greater reduction of the talonid of M_3, and in a greater emargination of the posterior basal outline of P^4 and M^1. In all other features, morphologic differences seem to be greater between living crocidurines than between living forms and late Miocene forms.

The Crocidurinae are largely tropical Old World forms and are the only shrews, fossil or living, known from Africa, peninsular India, and Ceylon. In Africa the subfamily shows its greatest diversity in living genera. The apparently late appearance of the crocidurines in the Tertiary scene in Eurasia and their obvious African affinities suggest that they may have evolved largely in Africa. Their distinctly soricid features, however, do not suggest that they are derived from independent African sources but rather that they are descendant from the same stem as all other shrews and in many features are not far removed, morphologically, from this ancestry.

Closely paralleling the Crocidurinae in lack of specialized morphology but entirely distinct in distribution, the small New World subfamily Limnoecinae is known by a few species from the early Miocene to the middle Pliocene. The earliest known species is associated with soricine shrews from which it is clearly distinct on the basis of all subfamily criteria. These earliest forms are clearly intermediate between the late Miocene to middle Pliocene *Limnoecus* and the hypothetical soricid ancestor. Thus, stage of evolution within the Limnoecinae is recognizable to the extent of distinguishing a late Miocene to middle Pliocene species from an early to middle Miocene one. Assuming comparable rates of evolution, earlier (but now unknown) forms should be equally as definitive of geologic age, although perhaps not distinguishable from the Crocidurinae except in their geographic distribution.

The similarity of the dental and mandibular characters of the Crocidurinae and the Limnoecinae result largely from the retention of those features believed to have been typical of the hypothetical soricid ancestor. It appears to be reasonable that both of these subfamilies evolved in isolation, removed from the competitive pressure of the closely related Soricinae. Although the earliest known limnoecine genus, *Angustidens*, is associated with the earliest known North American soricine genus, *Antesorex*, it seems likely both that the Limnoecinae had an older history in North America and that *Antesorex* represented a recently introduced stock closely similar to *Crocidosorex* of comparable and even greater age in Europe. Furthermore, the extinction of the North American Limnoecinae in the middle Pliocene was at the time

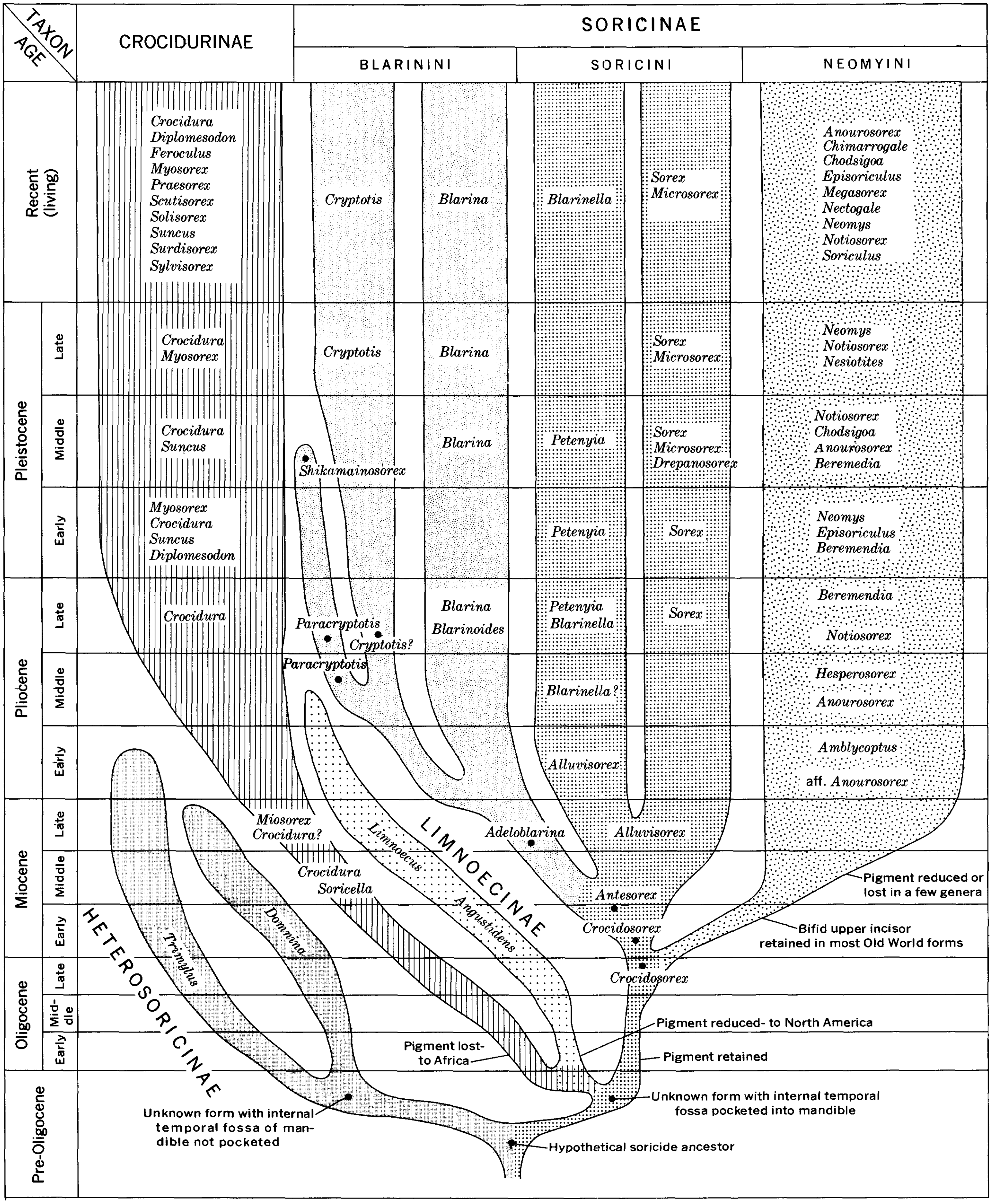

FIGURE 42.—A phylogeny of the Soricidae.

of apparently explosive diversification of the Soricinae. This may also coincide with the approximate time of extinction of the Heterosoricinae in both the Old and New Worlds, although there is no record of this subfamily younger than late Miocene in North America. In the Old World the Crocidurinae have survived. With the exception of a few species of *Suncus* and *Crocidura*, however, the Crocidurinae of Africa and peninsular India and the Soricinae of Palearctica (excluding Mediterranean Africa and including northern India, Burma, and Indochina) are mutually exclusive in their ranges. Those species of *Suncus* and *Crocidura* which have successfully invaded Palearctica seem to have done so by being adaptable to a great diversity of environments from dry grasslands to damp forests and shores; many are commensal with humans.

The boundary between those areas occupied entirely by the living crocidurine shrews and those areas occupied largely by the living soricine shrews coincides with the position of the Miocene Tethys seaway to a remarkable degree and suggests an incredible degree of endemism with these shrews.

The Soricinae is the largest subfamily of the shrews and has a fossil record known from the late Oligocene of Europe and from the early Miocene of North America. The earliest members of the subfamily are very generalized, and this primitive condition persists today in *Sorex* and closely related genera, here included in the tribe Soricini. Two other tribal lineages diverge from this unspecialized stem: the tribe Neomyini, apparently of Old World origin and still largely of Old World distribution, and the tribe Blarinini, apparently of New World origin and now confined to this area. Morphologically this subfamily is so diverse that the stage-of-evolution concept has no meaning at more than tribal level and in many groupings is apparent only in smaller taxonomic units, here informally referred to as generic groups. In the tribe Neomyini the fossil record is inadequate to chronologically define any evolutionary picture although the tribe is rather well represented in the fossil record.

The tribe Soricini includes two generic groups: the genus *Sorex* and closely related forms and the genus *Blarinella* with fossil genera related to it. The *Sorex* group is conspicuously unspecialized and uniquely successful among all shrews, as exemplified by *Sorex*, the only living holarctic genus. Except for the Heterosoricinae, the earliest known shrews belong in the *Sorex* group by virtue of their lack of specialization. These early soricines (*Crocidosorex* and *Antesorex*) differ from the living *Sorex* in their greater number of teeth, more anterior position of the mental foramen, a more primitive P_4, less emargination of the posterior border of P^4, M^1, and M^2, and in the slightly less separation of the articular facets on the mandibular condyle. These early soricines are also believed to be ancestral to other shrews of the Soricinae.

The *Blarinella* generic group diverged from those with this primitive pattern presumably in the Miocene by enlargement of the mandibular condyle (but with no relative increase in separation of the facets as was done in other tribes), accentuation of the entoconid crest of M_1 and M_2, and reduction of the talonid of M_3. This generic group is represented in the late Miocene and early Pliocene of North America, in the middle Pliocene of China, and the late Pliocene of Europe (where *Petenyia* continues until the middle Pleistocene), and now lives in the Chinese highlands.

The tribe Blarinini is first known from the late Miocene in the genus *Adeloblarina* of North America. This genus is not far removed from the basic stock of the Soricinae, which is first known in North America from the early Miocene, but has several features clearly indicative of the Blarinini. The middle Pliocene to living *Cryptotis* is not much advanced over this stage in several respects, but the living *Blarina* is greatly specialized in most characters except for its retention of five upper antemolars. The number of upper antemolars, the nature of reduction of the M_3, and the degree of specialization of the mandibular articulation seem to indicate that the tribe is divisible into three generic groups: Two are represented by the living genera *Blarina* and *Cryptotis* and the third by the extinct *Paracryptotis* from the Pliocene.

Blarina and related shrews are derived from a form similar to *Adeloblarina* by retention of five upper unicuspids, by lack of reduction of the talonid relative to the trigonid of M_3 (although the entire tooth may be reduced), and by extreme separation of the mandibular condyles. Only two genera have this characterization: *Blarinoides* from the late Pliocene of Europe and *Blarina* from the late Pliocene to Recent of North America.

Cryptotis and *Paracryptotis* are derived also from a form similar to *Adeloblarina* by the retention of only four upper unicuspids except the earliest known species and by the reduction of the talonid of M_3 relative to the trigonid. In *Cryptotis*, reduction of the M_3 talonid is greatest but separation of the mandibular condyles is relatively slight. The genus is known from the middle Pliocene to the Recent in North America. *Paracryptotis* has a somewhat less reduced talonid on M_3 but has much greater separation of the mandibular condyles, nearly as extreme as in *Blarina*, and is known from the middle and late Pliocene of North America. *Shikamainosorex* from the middle Pleistocene of Japan is very closely related to *Paracryptotis* but is somewhat more advanced in reduction of the talonid of M_3 and in separation of the mandibular condyles. "*Sorex*" *kretzoii* and "*Sorex*" *dehneli* from the late Pliocene of Poland may be related to *Cryptotis* or *Paracryptotis*, but published information is not sufficient to clearly indicate that these generic groups are represented in the Cenozoic of Europe.

Although largely a North American tribe, the Blarinini clearly were introduced once, and possibly twice, into the fauna of the Old World, where they do not seem to have been too successful. Possibly they found the Old World Neomyini strong competition. *Cryptotis* is the only shrew which has entered South America.

The tribe Neomyini is first known from the early Pliocene of Europe and North America. The earliest known European form, *Amblycoptus*, is the most specialized shrew of the tribe. Therefore, it appears that no pattern of evolutionary stages is detectable from the information available for this review, but more likely that the diversification in morphologic types of the tribe Neomyini was as great in the early Pliocene as it is today.

The tribe is also represented in North America by *Hesperosorex* from the middle Pliocene, by *Notiosorex* from the late Pliocene to the Recent, and by the living *Megasorex*. These genera differ from most of the Old World Neomyini in their lack of a bifid upper incisor. Inasmuch as the bifid falciform upper incisor is also found in the Heterosoricinae, it is considered to be a primitive feature inherited from a common ancestor. It therefore seems more reasonable to postulate that the Eurasian Neomyini, with its great diversity of forms, represents the parental stock and that a few forms entered North America before the early Pliocene and were also separated from the Eurasian population before that time.

In establishing the subfamily Heterosoricinae, Viret and Zapfe (1951, p. 426) suggested that the genus *Amblycoptus* may belong to that subfamily because of mandibular similarities. Although clearly not a heterosoricine shrew, *Amblycoptus* and fossil and living *Anourosorex* do closely parallel *Trimylus* in the massive masticatory structures. The suggested similarity of habits and the presence of this specialized member of the Neomyini in the lower Pliocene of the Old World, at the approximate time of the extinction of *Trimylus*, seems to provide a plausible explanation for the extinction of the Heterosoricinae in that area. Within the Crocidurinae the extinct *Diplomesodon fossorius* and to some extent the living *Solisorex* have also made comparable adaptations of their masticatory structures.

In summary, the shrews are useful in correlation of geologic age, but the degree of their usefulness depends on the lineage represented and on the geographic considerations involved in such correlation. The subfamily Limnoecinae clearly originated in North America. The subfamily Crocidurinae almost certainly is of Indo-African origin although it must have been derived from a soricid stock of holarctic distribution which was also the source of the Limnoecinae and the Soricinae. The large subfamily Soricinae seems to be of Eurasian origin although diversification of the subfamily into tribes took place throughout Holarctica: the tribe Blarinini of New World origin, the tribe of Neomyini of Old World origin, and the tribe Soricini representing the primitive Old World stock.

The Soricidae offer, with varying certainty, evidence of intercontinental faunal exchanges. Tentatively, these may be listed as follows:

1. Late Eocene or earliest Oligocene. Dispersal of *Trimylus* between North America and Eurasia; possible dispersal of ancestral Limnoecinae from Eurasia to North America; possible dispersal of ancestral Crocidurinae from Eurasia to Africa.
2. Early Miocene. Dispersal of Soricinae from Eurasia to North America; possible dispersal of *Trimylus* to North America.
3. Middle Miocene. Dispersal of some Crocidurinae from Africa to Eurasia.
4. Late(?) Miocene. Dispersal of Neomyini from Eurasia to North America.
5. Middle and late Pliocene. Dispersal of Blarinini from North America to Eurasia.
6. Late Pleistocene or Recent. Dispersal of Blarinini from North America into adjacent South America; introduction of some crocidurines to Pacific islands by man.

KEY TO LIVING AND FOSSIL GENERA OF THE SORICIDAE

[Based on mandible and lower dentition]

1a. Internal temporal fossa of the mandible not pocketed (Subfamily HETEROSORICINAE), p. 7
  2a. Entoconid crest present; teeth delicate_ *Domnina*, p. 7

1a. Internal temporal fossa of the mandible not pocketed—Con.

2b. Entoconid crest absent.

3a. Teeth delicate, cingulum not inflated; talonid of M_3 not reduced and with rectangular crest through hypoconid and entoconid *Paradomnina*, p. 10

3b. Teeth stout to bulbous, cingulum inflated; talonid of M_3 reduced with crescentic crest through hypoconid------------------------ *Trimylus*, p. 10

3c. Teeth stout, cingulum strong but not inflated; M_3 lost----------------------- *Ingentisorex*, p. 15

1b. Internal temporal fossa of the mandible pocketed.

4a. Interarticular area of mandible prominent lingually, or articular facets confluent lingually, and excavated labially.

5a. Teeth not pigmented; P_4 tetrahedral with prominent anterior, posterolateral, and posterolingual crests radiating from apex of principal cusp; range Old World (Subfamily CROCIDURINAE), p. 15

6a. Mandibular dental formula 1–4–3. *"Sorex" dehmi*, p. 15

6b. Mandibular dental formula 1–3–3.

7a. P_3 nearly as large as P_4; talonid of M_3 unreduced, double-cusped with well-developed basin; incisor short, curved, with two sharp, anteriorly inclined cusps on its cutting edge----- *Soricella*, p. 21

7b. P_3 minute; talonid of M_3 slightly reduced, single-cusped but with entoconid crest and weak basin; incisor with two very low, rounded cusps on cutting edge *Miosorex*, p. 18

7c. P_3 minute; talonid of M_3 reduced to single cusp; incisor short----- *Myosorex*, p. 19

6c. Mandibular dental formula 1–2–3.

8a. Mental foramen beneath P_4 to paraconid of M_1.

9a. Incisor with prominent scallops on cutting edge.

10a. Three rounded scallops as in *Sorex* *Sylvisorex*, p. 22

10b. Two anteriorly inclined pointe cusps as in *Soricella* *Feroculus*, p. 18

9b. Incisor not prominently scalloped.

11. Talonid of M_3 virtually lost, no cingulum on molars, condyles very specialized *Solisorex*, p. 21

12. P_4 very elongate, condyles united *Surdisorex*, p. 22

13. Talonid of M_1 anterosposteriorly compressed, minute P_3 present in some individuals *Myosorex*, p. 19

14. First antemolar behind incisor elongate relative to P_4 as in *Sylvisorex*----*Scutisorex*, p. 21

15. P_4 two-rooted *"Sorex" pusilliformis*, p. 15

1b. Internal temporal fossa of the mandible pocketed—Con.

4a. Interarticular area of mandible prominent lingually—Con.

5a. Teeth not pigmented—Continued

6c. Mandibular dental formula 1–2–3—Continued

8b. Mental foramen beneath protoconid of M_1.

16a. Cingulumlike groove along medial side of incisor continues above notch in basal border of tooth *Suncus*, p. 21

16b. Cingulumlike groove along medial side of incisor continues below notch in basal border of tooth.

17. Talonid of M_1 moderately compressed anteroposteriorly; coronoid process broad at base *Crocidura*, p. 16

18. Talonid of M_1 greatly compressed anteroposteriorly; coronoid process narrow at base *Diplomesodon*, p. 17

19. First post-incisor antemolar very elongate and anteroposteriorly double-cusped *Paracrocidura*, p. 20

8c. Mental foramen beneath hypoconid of M_1, size gigantic---------*Praesorex*, p. 20

5b. Teeth pigmented at tips; P_4 a longitudinal blade or tending that way, posterolingual crest from cusp apex reduced or lost; range North America (Subfamily LIMNOECINAE), p. 24

20a. Posterolabial crest of P_4 terminates against posterior cingulum midway between posterolabial corner of tooth and midline of tooth-----------------*Angustidens*, p. 25

20b. Posterolabial crest of P_4 terminates against posterior cingulum at midline of tooth *Limnoecus*, p. 26

4b. Interarticular area of mandible prominent labially or facets confluent labially, interarticular area excavated lingually; P_4 with prominent anterior and posterolabial crests radiating from apex of principal cusp but posterolingual crest essentially lacking, posterolabial crest curves lingually and merges with posterior cingulum of tooth enclosing a posterolingual basin (Subfamily SORICINAE), p. 27

21a. Condyles of mandible not widely separated and lower condyle not moved greatly forward on the mandible; entoconid crest present on M_1-----------------(Tribe SORICINI), p. 29

22a. Mandibular condyles confluent.

23a. Posterolabial crest of P_4 does not merge with posterior cingulum *Crocidosorex*, p. 29

23b. Posterolabial crest of P_4 merges with posterior cingulum------*Antesorex*, p. 30

22b. Mandibular condyles separated.

24a. M_3 unspecialized, virtually as in *Domnina* with distinct entoconid on rectangular hypolophid; pigmented dark red; considerable variation in pattern of mandibular condyles ----*Sorex*, p. 31

1b. Internal temporal fossa of the mandible pocketed—Con.

4b. Interarticular area of mandible prominent labially or facets confluent labially—Continued

21a. Condyles of mandible not widely separated and lower condyle not moved greatly forward on the mandible—Continued

22b. Mandilar condyles separated—Continued

24b. M_3 unspecialized, teeth heavy and low cusped; pigment orange; pattern of mandibular condyles as in *Sorex araneus* but large, stout, and dorsal condyle extended further back *Drepanosorex*, p. 32

24c. M_3 slightly reduced with entoconid lacking and crescentic hypolophid; pigmented dark red; P_4 somewhat compressed anteroposteriorly; condyles relatively large and close together *Microsorex*, p. 33

24d. M_3 with greatly reduced talonid; teeth stout, entoconid crest very prominent and postentoconid valley very wide on M_1.

25a. Metalophid of M_3 forms median crest with only minor remnant of entoconid crest; mandibular condyles separated but pattern not greatly different than in *Antesorex* *Alluvisorex*, p. 33

25b. Metalophid of M_3 forms single elongate cusp on talonid, faint trace of entoconid crest; labial cingulum on M_1 deep below protoconid; mandibular condyles well separated---------*Petenyia*, p. 34

25c. Metalophid of M_3 forms single conical cusp on talonid, no trace of entoconid crest; labial cingulum on M_1 deep below protoconid; mandibular condyles widely separated-----------*Blarinella*, p. 34

21b. Condyles of the mandible widely separated and lower condyle moved conspicuously forward on the mandible, interarticular area broad; entoconid crest lacking on M_1 (Tribe BLARININI), p. 37

26a. Lower condyle not hidden behind lower sigmoid notch in labial aspect.

27a. Mental foramen below protoconid of M_1------------ *Adeloblarina*, p. 37

27b. Mental foramen below hypoconid of M_1--------------- *Cryptotis*, p. 39

26b. Lower condyle meets lower sigmoid notch and is barely visible in labial aspect *"Sorex" dehneli*, p. 42, and *Paracryptotis*, p. 41

26c. Lower condyle entirely anterior to lower sigmoid notch and not visible in labial aspect.

28a. P_4 bulbous; entoconid present on M_3; labial cingulum on M_1 inflated *Blarinoides*, p. 44

1b. Internal temporal fossa of the mandible pocketed—Con.

4b. Interarticular area of mandible prominent labially or facets confluent labially—Continued

21b. Condyles of the mandible widely separated—Con.

26c. Lower condyle entirely anterior to lower sigmoid notch and not visible in labial aspect—Continued

28b. P_4 not bulbous; entoconid present or absent on M_3—when absent hypolophid crescentic; labial cingulum on M_1 deep but not inflated------- *Blarina*, p. 42

28c. P_4 not bulbous; entoconid and hypolophid absent on M_3—talonid reduced to metaconid crest; labial cingulum on M_1 inflated------ *Shikamainosorex*, p. 42

21c. Condyles of mandible widely separated and lower condyle moved conspicuously forward on the mandible and located lingually so that groove separates lower condyle from lower sigmoid notch, interarticular area narrow; entoconid crest present on M_1 except in *Anourosorex* and *Amblycoptus*------ (Tribe NEOMYINI), p. 45

29a. Upper mandibular articulation with oval facet.

30a. M_3 unreduced, entoconid present, hypolophid rectangular.

31. Incisor long; pigment conspicuous *Neomys*, p. 46

32. Incisor short; pigment slight *Episoriculus*, p. 47

33. Incisor short; pigment variable and light orange; entoconid crest very low on M_1; labial cingulum not continuous around hypoconid on M_1 *Soriculus*, p. 52

34. Incisor short to intermediate; pigment slight to absent; labial shearing blade of P_4 on longitudinal midline of tooth--------- *Nesiotites*, p. 51

35. Incisor long; pigment very light but widespread; labial cingulum present only below paraconid of M_1 *Nectogale*, p. 51

30b. M_3 reduced with crescentic hypolophid.

36a. Pigment not visible in ordinary light; labial cingulum weak on M_1 behind protoconid *Chimarrogale*, p. 53

36b. Pigment prominent; labial cingulum strong and deep around M_1 *Beremendia*, p. 50

30c. M_3 reduced with single cusp on talonid *Petenyiella*, p. 46

29b. Upper mandibular articulation with triangular facet.

37a. M_3 unreduced.

38a. Pigment prominent; entoconid crest of M_1 strong------*Neomys*, p. 46

38b. Pigment slight; entoconid crest of M_1very low-----*Megasorex*, p. 56

1b. Internal temporal fossa of the mandible pocketed—Con.

4b. Interarticular area of mandible prominent labially or facets confluent labially—Continued

21c. Condyles of mandibles widely separated—Con.

29b. Upper mandibular articulation with triangular facet—Continued

37a. M_3 unreduced—Continued

38c. Pigment slight; entoconid crest of M_1 strong-----------*Chodsigoa*, p. 48

37b. M_3 reduced.

39a. Entoconid lacking but entoconid crest and talonid basin present on M_3; very little pigment.

40a. Tip of coronoid process massive, coronoid spicule large *Chodsigoa*, p. 48

40b. Tip of coronoid process slight, coronoid spicule small *Notiosorex*, p. 55

39b. Entire talonid of M_3 virtually lacking-----------*Anourosorex*, p. 53

39c. M_3 lacking------*Amblycoptus*, p. 54

4c. Mandibular articulations widely separated and upper articulation placed very far to the rear; teeth unpigmented and high cusped with carnivorelike appearance; M_1 with trigonid very long, talonid very short, paralophid oriented essentially anteroposteriorly, metaconid close to protoconid, metalophid unites protoconid to hypoconid, hypolophid rectangular with no post entoconid valley, entoconid crest lacking and talonid basin opens lingually between metaconid and entoconid (Subfamily ALLOSORICINAE), p. 57

41a. Mandibular condyles not extremely separated; labial cingulum present on cheek teeth "*Sorex*" *gracilidens*, p. 57

41b. Mandibular condyles extremely separated; labial cingulum lacking on cheek teeth *Allosorex*, p. 57

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INDEX

[Italic page numbers indicate both major references and descriptions]

U.S. GOVERNMENT PRINTING OFFICE : 1967 O—240-305