FOSSIL TALPIDAE (INSECTIVORA, MAMMALIA) FROM THE LATER TERTIARY OF OREGON

By

J. Howard Hutchison

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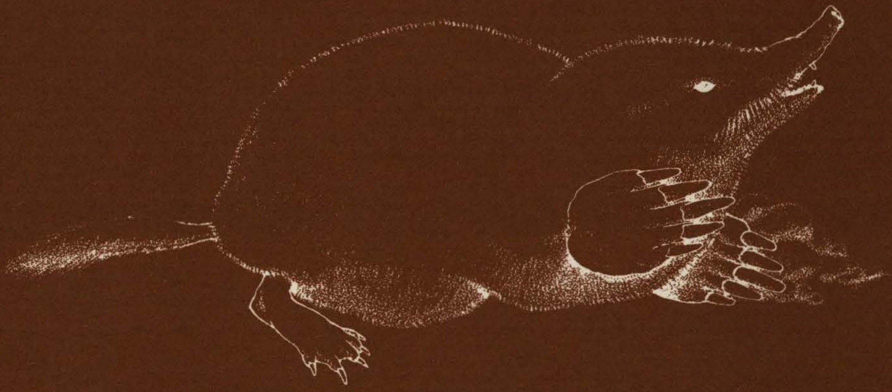

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FOSSIL TALPIDAE (Insectivora, Mammalia) FROM THE LATER TERTIARY OF OREGON

By

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ABSTRACT

The Talpidae of the late Teritary of Oregon are described and their relationships discussed. Two new genera, *Scapanoscapter* and *Achlyoscapter*, a new subgenus, *Xeroscapheus*, and six new species, *Mystipterus pacificus*, *?Neurotrichus columbianus*, *Scalopoides ripafodiator*, *Scapanoscapter simplicidens*, *Scapanus (Xeroscapheus) proceridens*, and *Achlyoscapter longirostris*, are recognized.

INTRODUCTION

The present paper is a continuation of the study of the fossil insectivores of Oregon. The fossil Talpidae of North America were, until recently, poorly known and with few exceptions the same may be said for the Old World members of the family. As compared with the history of other middle and later North American Teritary insectivores, however, the talpid fossil record fares somewhat better. Unquestioned New World moles range in age from Oligocene[2] to Recent and represent four subfamilies, the Uropsilinae, Gaillardinae, Talpinae, and Proscalopinae. Our knowledge of this long record is partly the result of the highly specialized and easily recognized humerus of talpids. Unfortunately, the lack of humeri associated with teeth has led to a confusion as to species, genera and even family assignment of the various elements. The Oregon record is incomplete and does not wholly alleviate this problem but a study of the living genera and well known fossil forms goes a long way toward narrowing the choices available and offers evidence for probable associations.

At the beginning of this study, the necessity of re-examining the postcranial skeletons of recent moles, particularly of the more obscure genera, was recognized and pursued. Although a superficial description and comparison of selected postcranial elements of available living moles is detailed below, a prodigious amount of work remains to be done on the comparative osteology and myology, and the functional morphology of the Recent Talpidae.

The majority of the fossil material described in this paper was recovered by underwater sieving techniques under the direction of J. A. Shotwell (see R. Wilson, 1965). No articulated material was recovered.

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[1] Contribution of the Museum of Paleontology, Univer- of California, Berkeley, and the Paleoecology Laboratory, University of Oregon, Eugene.

[2] Paleocene (Torrejonian) to Recent if the badly broken humerus from Montana described by C. A. Reed (1954) is talpid.

Morphological criteria were the main means of determining association of various elements. However, other criteria may also be useful. Relative abundance of various parts in sieved samples requires the tabulation of each kind of element and the assignment of high abundance elements to one form and low ones to another or others. This method is reasonably reliable in large samples. Another method of determining association relies on the probability that when the same combinations of elements recur in various localities they represent the same species or genus. This method becomes more reliable as the number of samples increases. The latter two methods of determining association necessarily require some degree of taxonomic determination. Recurrent association proved of little use in this study owing to the sparsity of localities. In practice all three means in various combinations were used here to arrive at the assignment of isolated elements to taxa.

The previous literature of New World Tertiary talpids is dispersed and varied. Reed and Turnbull (1956) have surveyed the literature dealing with the Proscalopinae. I shall restrict my review to the other talpids.

Douglass (1903) described and figured the first valid North American Tertiary non-proscalopine talpid under the name *?Talpa platybrachys* on the basis of four humeri from the Late Miocene Flint Creek beds of Montana. After the work of Douglass, no new taxa of talpids were described until 1930, although Merriam (1911) figured and briefly described the humeri of a mole which he referred questionably to *Scapanus* from the middle Pliocene Thousand Creek beds of Nevada, and Matthew (1924) mentioned but did not figure a humerus that he referred to *Scalops* cf. *aquaticus* from his *Hipparion affine* zone of the upper Snake Creek beds of Nebraska. In the same paper Matthew briefly described but did not figure a lower jaw fragment with an M_3 which he named *Talpa incerta*. Hall (1930) described and figured an M_3 and associated dentary fragment from the early Pliocene of Nevada that he considered to be a bat and named it *Mystipterus vespertilio*. Patterson and McGrew (1939) transferred it to the Soricidae and Clark, Dawson, and Wood (1964) suggested other possibilities except Talpidae. Van Valen (1967) aligns *Mystipterus* questionably with the Talpidae. Matthew (1932), in describing new material from the upper Snake Creek beds, figured and briefly described a partly endentulous dentary that he named *Gaillardia thomsoni*. Matthew gave no specific assignment for *Gaillardia*; however, he compared it most closely to members of the Talpidae, excluding it from the Desmaninae on the basis of a difference in dental formula. Wilson (1937) listed but did not describe a *Scapanus* species from the middle Pliocene Rome fauna of Oregon.

Hibbard (1939) described and figured an incomplete humerus from the middle Pliocene Edson Quarry of Kansas. The humerus is that of the advanced fossorial type, such as *Scapanus* and *Scalopus*, to which he compared it. He did not refer to it either of these genera but suggested that it might represent a new genus. Later in a series of papers on the late Pliocene Rexroad fauna of Kansas (1941A, 1941B, 1949 with Riggs, 1953, 1954) he reported a new genus and species of advanced burrowing mole under the name of *Hesperoscalops rexroadi*. Some of the postcranial material assigned to *Scalopus* in the earlier papers was later assigned to *Hesperoscalops*. In 1953, he stated that *Hesperoscalops* was probably the ancestral stock from which *Scalopus* was derived.

During this time Gregory (1942) described but did not figure several humeri from the early Pliocene Big Spring Canyon, Lessert Spring and Minnechaduza localities of South Dakota and Nebraska. He noted the similarity of his fossils with *?Talpa platybrachys* Douglass and the Fort Niobrara material (*Domninoides valentinensis* K. M. Reed, 1962).

Galbreath (1953) in his study of the vertebrate paleontology of northeastern Colorado, mentions several talpid remains from four different faunas. He briefly described but did not figure a "Scalopine sp." humerus from the Cedar Creek member of the White River Oligocene which is "... approximately three-fourths the size of the humerus of *Scalopus aquaticus machrinoides,* but otherwise does not differ in any respect from that of the Recent form." From the Miocene Martin Canyon local fauna, he described a lower molar and suggested that it " ... could well be the structural ancestor of *Hesperoscalops* Hibbard." From the late Miocene Kennesaw and Viv-Peetz faunas, he recorded four incomplete humeri which he designated tentatively cf. *Condylura.*

Shotwell in 1956 and 1963, recorded *Scapanus* sp. from two different Pliocene localities in Oregon. In the earlier paper he also described a new genus and species of desman mole, *Hydroscapheus americanus,* based on a number of postcranial elements. In this same year Green (1956) described and figured the lower jaw of a new genus and species of insectivore from the early Pliocene of South Dakota that he believed to be a shrew and called *Domninoides riparensis.* Littleton and Grosthwaite (1957) listed *Desmana moschata* from the Idaho Formation on teeth identified by J. Hough. Wilson (1960), Tedford (1961), and K .Reed (1962), all pointed out that *Domninoides* is a mole.

Wilson's (1960) paper dealing with the early Miocene rodents and insectivores of northeastern Colorado comprises the most important study of Tertiary North American nonproscalopine moles to date. Two new genera and species of talpid were described. He believed his *Mydecodon martini* compared favorably with the living *Urotrichus* (*Dymecodon*) *pilirostris* (True). His *Scalopoides isodens* did not seem to him to be directly ancestral to any of the Recent New World moles but embodied a combination of characters of both *Neurotrichus* and *Condylura* in the humerus. In discussing the teeth of *Proscalops secundus* Matthew, he noted the similarities of the lower molars with those of *Parascalops* but discounted the likelihood that *Proscalops* was ancestral to either *Parascalops* or *Scalopus* stating that "needed transformation although not impossible suggests that *P. secundus* is aberrant." Throughout his discussions Wilson made thorough comparison (where such is possible) with pertinent Old World fossils, and suggests that *Scalopoides* and *Mydecodon* are represented in the Sansan and La Grive faunas of France.

Contributions to the history and phylogeny of New World talpids have been made in every year since Wilson's paper. Tedford (1961) described and figured a new species of *Scapanus* from the lower Pliocene of the Ricardo Formation of California under the name *Scapanus shultzi.* He suggested that his species is " ... most clearly related to the hypsobrachyodont living species, *S. orarius* and *S. townsendii,* but could conceivably be ancestral to the hypsodont *S. latimanus* and even *Scalopus* (via the Blancan *Hesperoscalops*) as well." In the following year K. Reed described two new species from the great Plains, *Domninoides valentinensis* from the late Miocene of Nebraska and *Hesperoscalops sewardensis* from the late Pliocene Saw Rock Canyon fauna of Kansas, which was previously referred to *H. rexroadi* by Hibbard (1963). In addition to the lower jaw and P^4, the humerus of *D. valentinensis* is figured. No extensive comparison of the humerus with other fossil moles was made and the other limb bones were not described.

Macdonald (1963) described a new species under the name *Domninoides evelynae* based on a couple of fragmentary jaws containing the M_2-M_3, from the lower Miocene Sharps Formation of South Dakota. On the following page he reported *Arctoryctes terrenus* Matthew humeri from the same locality and suggested that *Domninoides* [*evelynae*] may be associated with the humeri. Apparently Macdonald did not see Wilson's (1960) or K. M. Reed's (1961) papers which described the lower teeth of *Proscalops* for there is no mention of these in his paper nor any comparison of his *D. evelynae* teeth with those of *Proscalops.*

In the same year James (1963) reported an undescribed species of *Scalopus* on the basis of three incomplete humeri from the early Pliocene beds of the Cuyama Valley, California. Clark, Dawson, and Wood (1964) in describing some fossil mammals from the early Pliocene of Nevada reported a specimen of *Domninoides* cf. *riparensis* and a toothless jaw fragment that they compared to *Mystiperus vespertilio* Hall. Lewis in the same year listed a *Talpa* sp. from the Barstow Formation of California. Lastly, Firby (1966) in a list prepared by S. D. Webb, reported "?Insectivora, genus undetermined-*Arctoryctes* species." This record from the late Miocene of Nevada is apparently based on the humerus of unknown affinities described by Reed and Downs (1959). Reed and Turnbull (1965) pointed out that this humerus is neither *Arctoryctes* nor a proscalopine mole.

Most of the preceding records need comment in order to orient the reader as to the scope and synonymy of the various genera mentioned in the following discussion and descriptions. I have studied all specimens except those described by Hibbard, Littleton and Grosthwaite, Clark *et al.*, Green, Lewis and the unreferred talpine of Reed and Turnbull.

When Douglass (1903) described *?Talpa platybrachys* he noted that the shaft is narrow and that "The ridge for the insertion of the pectoralis major muscle is well developed on the inner part of the humerus, but does not extend anywhere near so far outward as in *Scalopus*." These features, as well as the general proportions of the humerus, agree very closely with those referred to *Domninoides valentinensis*. Although the species must remain in doubt at present, the assignment of *?Talpa platybrachys* to the genus *Domninoides* seems much more reasonable. Merriam's (1911), Shotwell's (1956, 1963), and Wilson's (1937) records of *Scapanus* from Oregon and Nevada are valid and are discussed further in the systematic section. The humerus described by Matthew (1924) and referred to *Scalops* cf. *aquaticus* certainly agrees closely with the modern *Scalopus* but the species is indeterminate. Mathew considered the reference of his *Talpa incerta* to the genus *Talpa* as provisional. Re-examination and removal of the excess shellac from the M_3 revealed that *Talpa incerta* is neither *Talpa* nor a talpid but an erinaceid. *Mystipterus vespertilio* Hall (1930) appears to be a uropsiline mole. Additional material of this form is described below in the systematic section.

Matthew's (1932) *Gaillardia thomsoni* and Shotwell's (1956) *Hydroscapheus americanus* appear to represent the same species and leave little doubt that this form is an aquatic mole which is best assigned to a new subfamily. I have not seen the humerus which Hibbard (1939) described from the Edson Quarry. It could represent either *Domninoides* or *Scalopus* (*Hesperoscalops*) although I favor the latter judging from its rather stocky appearance (see Addendum). There seems little doubt that *Hesperoscalops rexroadi* Hibbard and *Hesperoscalops sewardensis* K. Reed (1962) are closely aligned with the living *Scalopus* and, as noted by Hibbard (1953), probably form the ancestral stock of the modern *Scalopus*. Indeed the morphological similarities between the specimens of *Hesperoscalops* and *Scalopus* are so great that there is little reason for generic distinction. The characters of the species assigned to *Hesperoscalops* seem consistent enough, however, to retain *Hesperoscalops* as a subgenus and I shall treat it thus in subsequent discussions. The majority, if not all of the specimens described by Gregory (1942) from South Dakota and Nebraska, is assignable to the genus *Domninoides*.

Galbreath's (1953) Scalopine sp. humerus is, as he noted referable to the Recent *Scalopus aquaticus*, although he suggested that this specimen represented the humerus of *Proscalops* and it was so labeled in the University of Kansas collections. Reed and Turnbull's (1965) excellent study of the forearm of *Arctoryctes* allows little doubt that *Arctoryctes* humeri are those of proscalopine moles, and this has been verified by additional associated skeletons of proscalopine moles from both Colorado and Oregon. As far as I can determine from Galbreath's paper, no other specimens were recovered from the same locality as the *Scalopus*-like humerus. On theoretical grounds, I find this occurrence anachronistic and believe it to be incorrectly located or a contaminant from a higher (and younger) stratum. I shall not regard it as a valid age or locality record in further discussions. The humeri of cf. *Condylura* also mentioned by Galbreath are inseparable from those referable to *Domninoides* and are so considered hereafter. The lower tooth of a talpid listed from the Martin Canyon local fauna was not seen but, from Galbreath's description, appears to be either a proscalopine mole or *Domninoides*. The former is more likely in light of Wilson's (1960) discussion.

Quinn (1955) listed *Talpa* in a faunal list from the Late Miocene Lapara Member of the Goliad Formation of Texas. To my knowledge this specimen (not seen) has never been figured or described. Assignment to *Talpa* seems highly unlikely. It is probably a *Domninoides* but is best referred to as a talpine for the present.

Attempts to locate the specimens of *Desmana moschata* (Linnaeus) reported by Littleton and Grosthwaite (1957) from the Idaho Formation were unsuccessful. The identification is highly questionable on geographic grounds and even more dubious in consideration of the known fossil history of talpids in North America. I shall ignore this record in subsequent discussions (see Addendum).

Although *Domninoides riparensis* was soon recognized as a talpid, Tedford (1961) was the only author to note its similarity to *Parascalops* and *Scapanulus*. Unfortunately, these two living genera have been rather neglected in the studies of fossil North American talpids. As will be more fully elaborated upon below, they are important for our understanding of North American talpid phylogeny. *Scapanus shultzi* while still retained within the genus *Scapanus*, is not given the same phyletic position in the phylogeny of the living species as was proposed by Tedford, but is aligned with the new subgenus *Xeroscapheus*. K. M. Reed's (1962) two new species remain unchanged.

Mydecodon martini Wilson (1960) appears to be related to *Mystipterus vespertilio* Hall. I tentatively place *Mydecodon* as a subgenus of *Mystipterus* (see discussion under *M. vespertilio*). Although Wilson aligned his *Scalopoides isodens* most closely with the *Urotrichus*-like moles and *Condylura*, I believe it has closer affinities with *Scapanulus* (which Wilson apparently did not see) and *Parascalops*. A re-survey of the unidentified bone scrap from Martin Canyon Quarry A yielded additional material of *Scalopoides isodens* which is described below. Wilson (p. 49) also described an upper molar under the heading of Soricoid? sp. indet. Re-examination of this specimen reveals that it is an upper molar of a didelphid marsupial. It agrees quite closely with *Peratherium*.

I agree with Macdonald (1963) that *Domninoides evelynae* is a likely candidate for association with *Arctoryctes* humeri from the same locality. In so doing I submit that *D. evelynae* is a proscalopine mole inasmuch as *Arctoryctes* humeri are now known to belong to proscalopine moles. The lower teeth of *Domninoides* are grossly similar in morphology to those of *Proscalops* (compare fig. 4, K. M. Reed 1961, with fig. 2, K. M. Reed 1962). *Proscalops evelynae* (Macdonald) lacks the distinct metastylid of *D. valentinensis* and *D. riparensis*, as pointed out by K. M. Reed (1961) in a footnote, and resembles *Proscalops* in this and other features. That Macdonald confused the lower teeth of *Domninoides* with those of *Proscalops* is evident from K. M. Reed's (1962) mention of a personal communication from Macdonald in which he "suggested that the jaws of his new species may represent the lower dentition of *Proscalops secundus*." Macdonald only discussed some typological problems of the skull of *Proscalops secundus* under the heading of *Domninoides* discussion. The removal of this record restricts the known record of *Domninoides* to the later Miocene and early Pliocene.

The three humeri from the Caliente Formation of California assigned by James (1963) to *Scalopus* are quite unlike *Scalopus* in proportions. James noted the resemblances to humeri now referred to *Domninoides platybrachys* and *D. valentinensis*. The configuration of the pectoral muscle scars is also like that in those species. Apparently much weight is given to the presence of a small foramen in the proximal end of the humerus. He noted its variability in *Scapanus* but indicates that its presence in all his specimens is an indication of relationship to *Scalopus*. I believe that strong similarities with *D. platybrachys* and *D. valentinensis* align it more closely with *Domninoides* than with any other living or fossil talpid.

Lewis (1964) gave no indication where the material ascribed to *Talpa* sp. from the Barstow Formation now resides but the only teeth of a talpid that have been recovered from washing of the Barstow sediments by Tedford are those of *Domninoides* to which Lewis' *Talpa* is probably referable. No other talpid elements are thus far known to me from this formation.

The humerus reported by Reed and Downs (1959) and listed by Webb in Firby (1966) as *Arctoryctes* is apparently the distal end of the humerus of *Meterix latidens*. A list of described moles and the usage as outlined above is summarized in Table 1.

For a group of animals represented by only about two score living species and by about an equal number of fossil forms, the Talpidae has a checkered taxonomic history. There have been almost as many generic names applied as there are living species. C. A. Reed (1951) presented a concise history of the various usages and composition of the proposed subfamilies so that only a brief comment on subsequent classifications is necessary here. The Proscalopine proposed by K. M. Reed (1951) form a close-knit endemic group of North American talpids. The remaining moles have been grouped into two or more subfamilies of varying composition by various authors. Borrowing from Gill (1875) and Weber (1928), C. A. Reed (1951) arrived at a two-fold system of classification comprised of the Desmaninae and the Talpinae. As useful as this may have been for his purposes, his division of Cabrera's (1925) and Simpson's (1945) Scalopinae into desman and non-desman groups seems to be an unwarranted simplification of the relationships among these talpids. The inclusion of *Condylura* in the Desmaninae can only be justified on a few (convergent) features owing to its slight aquatic modifications.

The classification used here resembles that of Campbell (1939) who in turn used a combination of Thomas' (1921) and Winge's (1917) classifications. He used five subfamilies, the Desmaninae, Urotrichinae, Condylurinae, Scalopinae, and Talpinae. Although he did not use the Uropsilinae, this is implied in his work. I have reduced most of his subfamilies to tribal or subtribal level in order to emphasize the more profound differences between the major adaptive and phylogenetic groups of moles. Van Valen (1967) has arrived at an identical classification of subfamilies and a general similarity of the tribes with the notable exception of the composition of the groups of moles included in the Scalopinae of Simpson (1945). Van Valen divides this group into two distinct tribes, the Urotrichini and the Scalopini. His Urotrichini are all of the living Scalopinae of Simpson except *Scalopus* and *Scapanus*, which comprise all of his Scalopini. The characters on which he defines these groups revolve around the presence or absence of an enclosed bulla and features of the molar dentition. The less developed humerus is also used but the distinction beween the humerus of *Scapanus* and that of *Domninoides* or *Parascalops* is certainly much less striking than that between *Neurotrichus* and *Scalopoides* or *Scapanulus*. My impression of this complex of genera is also that there are two major divisions, the Urotrichini and the Scalopini. However, my Urotrichini includes only *Urotrichus* and *Neurotrichus* with the rest falling into the Scalopini. The Scalopini is in turn divided into two subtribes; the Parascalopina, including most of the other genera in Van Valen's Urotrichini, and the Scalopina, which equals Van Valen's Scalo-

TABLE 1

SUMMARY OF ORIGINAL REFERENCES AND PRESENT USAGE OF VARIOUS DESCRIBED NEW WORLD TALPIDS OF THE LATER TERTIARY.

Original Reference	Present Usage
?Talpa platybrachys (Douglass 1903)	_Domninoides_* _platybrachys_
Scapanus (?) sp. (Merriam 1911)	_Scapanus_ sp.
Scalops cf. _aquaticus_ (Matthew 1924)	_Scalopus_ sp.
Talpa incerta (Matthew 1924)	Erinaceidae*
Mystipterus vespertilio (Hall 1930)	unchanged
Gaillardia thomsoni (Matthew 1932)	unchanged
Scapanus (?) sp. (Wilson 1937)	_Scapanus_ sp.
Talpidae (Hibbard 1939)	cf. _Scalopus_* sp.
Hesperoscalops rexroadi (Hibbard 1941A)	_Scalopus_* (_Hesperoscalops_*) _rexroadi_
Scalopus sp. (Hibbard 1941B)	_Scalopus_ (_Hesperoscalops_*) _rexroadi_
Talpidae (Gregory 1942)	_Domninoides_* sp.
Hesperoscalops rexroadi (Hibbard and Riggs 1949)	_Scalopus_* (_Hesperoscalops_*) _rexroadi_
Hesperoscalops rexroadi (Hibbard 1950)	_Scalopus_* (_Hesperoscalops_*) _rexroadi_
Hesperoscalops rexroadi (Hibbard 1953)	_Scalopus_* (_Hesperoscalops_*) _sewardensis_
Scalopine sp. (Galbreath 1953)	_Scalopus_* sp.
Talpid sp. (Galbreath 1953)	Proscalopinae*
Cf. _Condylura_ (Galbreath 1953)	_Domninoides_* sp.
Talpa sp. (Quinn 1955)	Talpini*
Scapanus sp. (Shotwell 1956)	unchanged
Hydroscapheus americanus (Shotwell 1956)	_Gaillardia_* _thomsoni_*
Domninoides riparensis (Green 1956)	unchanged
Desmana moschata (Littleton and Grosthwaite 1957)	?Talpidae*?
Mydecodon martini (Wilson 1960)	_Mystipterus_* (_Mydecodon_*) _martini_
Scalopoides isodens (Wilson 1960)	unchanged
Scapanus shultzi (Tedford 1961)	_Scapanus_ (_Xeroscapheus_*) _shultzi_
Domninoides valentinensis (K. Reed 1962)	unchanged
Hesperoscalops sewardensis (K. Reed 1962)	_Scalopus_* (_Hesperoscalops_) _sewardensis_
Domninoides evelynae (Macdonald 1963)	Proscalopinae*
Scalopus sp. (James 1963)	_Domninoides_* sp.
Domninoides cf. _riparensis_ (Clark _et al._ 1964)	_Scalopus_* (_Hesperoscalops_) _sewardensis_
Talpa sp. (Lewis 1964)	_Domninoides_* sp.

* Asterisk denotes taxonomic name change in this paper.

pini. The osteological survey of the living genera below and the systematic section indicate the reasons for these groupings. The Scaptonychini of Van Valen is accepted here for its utility as a waste basket group for the poorly known European middle Tertiary talpids and reception of the enigmatic _Scaptonyx_.[3]

I have deferred from assigning any of the fossil Eurasian talpids to my classification scheme. The European literature is poor in the osteological descriptions or figures which are significant for my scheme of classification. To assign these forms without re-examination of this material would only tend to obscure the groups as defined upon available material. Furthermore, Van Valen (1967) presents a comprehensive classification of fossil and Recent talpids. Comments on first or second hand knowledge of some of the fossil Eurasian genera are footnoted in appropriate places. The European Talpidae are now under study.

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[3] _Scaptonyx jaegeri_ Seeman (1938), as has been noted by others, is not _Scaptonyx_. Most or all of the European forms referred to _Scaptonyx_ are not referable to this genus and probably belong to other tribes.

CLASSIFICATION OF RECENT AND NORTH AMERICAN FOSSIL MOLES

- Family Talpidae[4]
  - Subfamily Uropsilinae Dobson, 1883.
    - *Uropsilus* A. Milne Edwards, 1871. (=*Rhynchonax* Thomas, 1911; =*Nasillus* Thomas, 1911) Recent; Asia.
    - †*Mystipterus* Hall, 1930. (Including *Mydecodon* Wilson, 1960) Middle Miocene-Early Pliocene; N. Am.
  - †Subfamily Gaillardinae new
    - †*Gaillardia* Matthew, 1932. (=†*Hydroscapheus* Shotwell, 1956) Middle Plioc.; N. Am.
  - †Subfamily Proscalopinae K. M. Reed, 1961. (=Arctoryctinae, C. A. Reed and Turnbull, 1965).
    - †*Cryptoryctes* C. A. Reed, 1954. Early Olig.; N. Am.
    - †*Oligoscalops* K. M. Reed, 1961. Middle Olig.; N. Am.
    - †*Proscalops* Matthew, 1901. (Including †*Arctoryctes* Matthew, 1907) Late Olig.-Early Mioc.; N. Am.
    - †*Mesoscalops* K. M. Reed, 1960. Middle Mioc.; N. Am.
  - Subfamily Desmaninae (Thomas, 1912) Mivart, 1871. (=*Myogalina* Mivart, 1871)
    - *Desmana* Gueldenstaedt, 1777. (†*Mygale* Cuvier, 1800;=*Mygale* Brandt, 1836) Early Plioc.-Recent; Europe. Recent; Asia.
    - *Galemys* Kaup, 1829, Plioc.-Recent; Europe.
  - Subfamily Talpinae Fischer von Valdheim, 1817.
    - Tribe Scaptonychini Van Valen, 1967.
      - *Scaptonyx* Milne Edwards 1872. ?Middle Mioc.; Europe. Recent, Asia
    - Tribe Talpini Fischer von Valdheim, 1817.
      - *Talpa* Linnaeus, 1758 (=including *Mogera* Pomel, 1848; *Parascaptor* Gill, 1875; *Euroscaptor* Miller, 1940; *Eoscalops* Stroganov, 1941; *Asioscalops* [not *Asioscaptor*] Stroganov, 1941) Late Miocene-Recent; Europe. Pleist.-Recent; Asia.
      - *Scaptochirus* A. Milne Edwards. 1867. (=*Chiroscaptor* Heude, 1898) Pleist.-Recent; Asia.
    - Tribe Urotrichini Dobson, 1883.
      - *Urotrichus* Temminick, 1841. (including *Dymecodon* True, 1886) Recent; Japan.
      - *Neurotrichus* Günther, 1880. ?Middle Plioc., Recent; N. Am.
    - Tribe Condylurini Dobson, 1883.
      - *Condylura* Illinger, 1811. Pleist. Recent; N. Am.
    - Tribe Scalopini Dobson, 1883.
      - Subtribe Parascalopina new
        - †*Scalopoides* Wilson, 1960. Middle Mioc.-?Middle Plioc.; N. Am.

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[4] Only some of the newer and more common synonyms are listed—see Van Valen (1967) for more extensive synonymies. Authorship of the groups follows Van Valen except within the Talpinae where I believe some other authors were the first to adequately define the groups with reference to my concept of them.

†*Domninoides* Green, 1956. Late Mioc.-Early Plioc.; N. Am.
Scapanulus Thomas, 1912. ?Middle Plioc.-Recent; Asia.
Parascalops True, 1894. Pleist.-Recent; N. Am.
Subtribe Scalopina (Van Valen, 1967) Winge, 1917.
†*Scapanoscapter* new. Late Mioc.; N. Am.
Scalopus E. Geoffrey Saint Hilaire, 1803 (=*Scalops* Illiger, 1811; includes †*Hesperoscalops* Hibbard, 1941) ?Middle Plioc.-Recent; N. Am.
Scapanus Pomel, 1848. (includes †*Xeroscapheus* new) Early Plioc.-Recent; N. Am.

Talpinae *incertae sedis*
Achlyoscapter new. Late Miocene; N. Am.

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MATERIALS AND METHODS

The rank of subgenus is extensively used throughout this paper. Many of the subgenera used or proposed could be elevated to generic rank based on precedent in the taxonomy of this group. The various genera used here are not

Number of best specimen or institution	Skull and jaws	Manubrium, clavicle, scapula, sternum, and vertebrae	Humerus	Radius and ulna	Innominata and femur	Tibiofibula	Manus and pes	No.†	
USNM 256119	X	X	X	X	X	X	X	1	Uropsilus soricipes
MH 1027	X	X	X	X	X	X	X	1	Urotrichus pilirostris
MVZ	X							10+	Urotrichus talpoides
UO and MVZ	X	X	X	X	X	X	X	10+	Neurotrichus gibbsii
USNM 172374	X	X	X*	X	X	X*		1	Galemys pyrenaicus
YPM 1189	X	X	X	X	X	X	X	2	Desmana moschata
MH 73, MH 115	X	X	X	X	X	X	X	2	Condylura cristata
AMNH	X							2	Scaptonyx fusicaudus
USNM 233838	X	X	X	X	X	X	X	4	Talpa europaea
MVZ 62754	X							1	Talpa occidentalis
USNM 253319	X	X	X	X	X	X	X	2	Talpa micrura
USNM 201318	X		X					1	Scaptochirus moschatus
USNM 240757	X	X	X		X*			1	Scapanulus oweni
MHMH 233	X	X	X	X	X	X	X	1	Parascalops breweri
UO and MVZ	X	X	X	X	X	X	X	40+	Scapanus (all species)
UF and JHH	X	X	X	X	X	X	X	10+	Scalopus aquaticus

† This number indicates the minimum number of specimens in all categories.
* Fragmentary pelvis or proximal end of a long bone only.

so highly diversified at the species level as to warrant the elevation of various subgenera to genus rank. There is, on the other hand, a great utility to the retention of a rather broad generic usage within this family. Thus, limb elements which are unquestionably referable to the *Scapanus* complex may be referred to that genus where further refinement is impossible.

Rather than run the risk of duplicating taxa based on different elements, I have followed the policy of attaching names only to lower jaws and teeth. No taxa are named on isolated teeth, whether upper or lower. At the present rate of collecting, it should not be long before these unnamed forms are known from either more or better material.

Wherever possible, I have attempted to assign isolated upper teeth to species or genera known from lower teeth from the same locality when consistency of size and lack of conflict with more reliable assignments from other samples were met.

Measurements of the larger limb bones were taken with a Vernier caliper. All other measures were taken with either a Gaertner measuring microscope or ocular micrometer. The scale is not uniform and scale lines in all figures are equivalent to one millimeter. All the figures except those of the major limb bones in the osteology section were drawn with the aid of an ocular grid in a binocular microscope. The methods of measurement of the various elements are either illustrated in the osteology section, or explained in the text or in Hutchison (1966).

Abbreviations used throughout this paper are:

AMNH=American Museum of Natural History
CIT=California Institute of Technology (Material now the possession of Los Angeles County Museum)
JHH—Author's collection
M=United States Geological Survey vertebrate locality
MH=Milton Hildebrand Collection, Davis, California
MVZ=University of California Museum of Vertebrate Zoology, Berkeley
UCR=University of California at Riverside
UF=University of Florida, Gainsville
UK=Museum of Natural History, University of Kansas, Lawrence
UO=University of Oregon Museum of Natural History, Eugene
USNM=United States National Museum
YPM=Yale Peabody Museum, New Haven, Connecticut

The recent specimens were assembled from diverse sources and ranged in completeness from skulls to entire skeletons. Since the osteological concept of the various proposed groupings was influenced or dependent upon material available to me, a detailed listing of material is presented.

Oregon localities from which material is discussed in this report range in age from Barstovian to Blancan. The geographic positions are indicated on the map of Figure 1. Other information pertaining to the localities is given in the locality descriptions at the end of the text. Their ages are as follows:

BARSTOVIAN

Quartz Basin UO 2465
Red Basin I UO 2493
Red Basin II UO 2495
M 1040
Beatty Butte M 1041
Guano Ranch M 1042
Snyder Creek M 1043

CLARENDONIAN

Black Butte I UO 2337
West of Riverside UO 2489
Black Butte II UO 2500

HEMPHILLIAN

McKay Reservoir UO 2222
Krebs Ranch I UO 2322
Krebs Ranch II UO 2323
Otis Basin UO 2347
Westend Blowout UO 2349
Bartlett Mountain II UO 2357
Little Valley I UO 2380
Little Valley II UO 2516
Bartlett Mountain UO 2517
Rome CIT 62
Arlington CIT 375

BLANCAN?

Enrico Ranch UO 2223

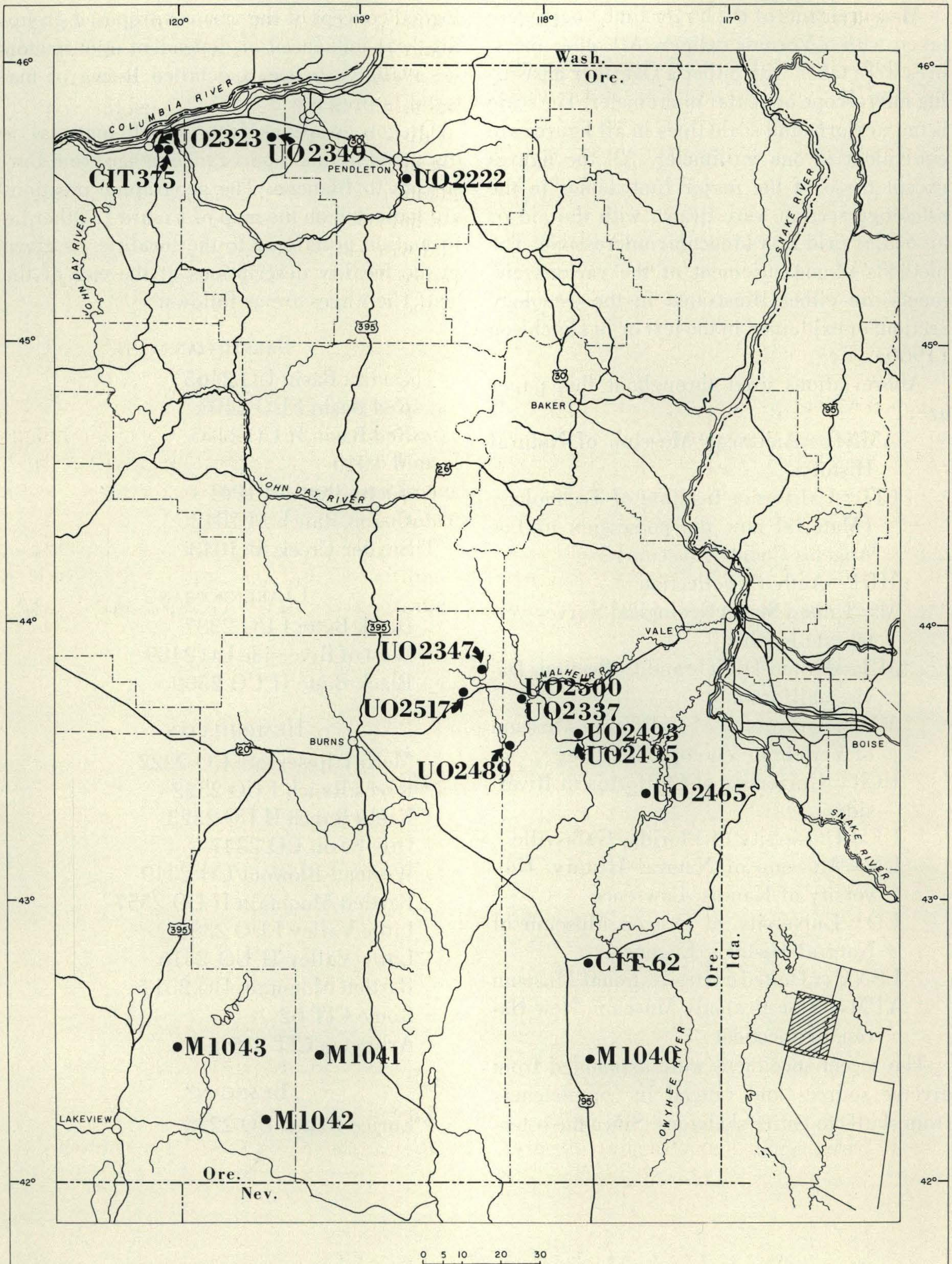

Figure 1. Location of sites from which talpid material is discussed. See text for additional information.

OSTEOLOGY OF LIVING TALPIDAE

Comparative studies on the postcranial skeletons of talpids are rare. The most thorough and useful are those of Campbell (1939) on the comparative shoulder anatomy of the moles and C. A. Reed (1951) on the locomotor and appendicular anatomy in soricoid insectivores. The osteology of the living moles discussed below is not intended to supplant these studies but rather supplement their discussions with brief descriptions of material that was not discussed or not available to them. The following descriptions should be used in conjunction with these papers. No attempt is made to be complete in the following survey but rather to briefly review or cover the general description of those elements which are most commonly recovered as fossils.

The odontological and osteological terminology is derived primarily from C. A. Reed (1951), but also from a number of other sources. A few terms are coined. In order to avoid changes in terminology resulting from the different orientation of the limbs of various talpids in life, I have assumed for purposes of discussion of the individual bones that all the elements are oriented as in a generalized plantigrade mammal. Thus the lateral side of the humerus of *Scapanus* which in life is medial with respect to the axis of the body is still referred to as the lateral side. The plantar side of the foot is considered ventral.

UROPSILINAE DOBSON, 1883

There is only one generally recognized living species of this subfamily, *Uropsilus soricipes*. Since no general osteology of this unique form has been set forth in one place, I shall attempt to mention some of the more salient features.

The skull is generally shaped like that of *Neurotrichus* and the bullae are open both ventrally and dorsally. The lacrimal foramen

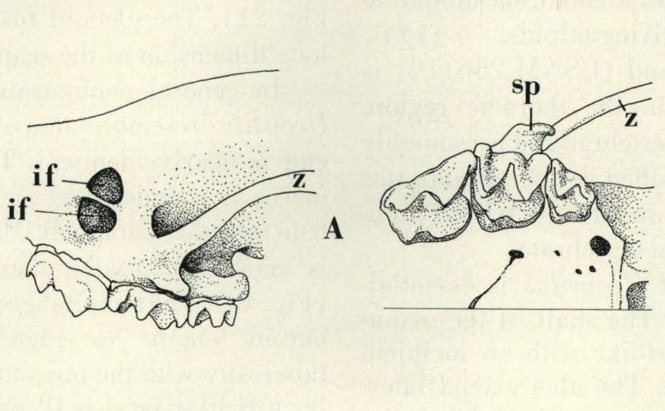

Figure 2. Zygomatic region of the maxilla, left lateral and ventral views. A; *Uropsilus soricipes*, USNM 256119, **B**; *Neurotrichus gibbsii*, JHH 516. **if**—infraorbital foramen; **ims**—insertion of M. masseter superficialis; **lf**—lacrimal foramen; **sp**—subzygomatic process; **z**—zygomatic arch.

is unusually large, being as large as the anterior opening of the infraorbital foramen which is situated immediately below it (see Fig. 2A). The zygomatic arches are strongly dorsad thus descending on the maxilla from above rather than from behind as in other talpids. Just ventral to the zygomatic process of the maxilla is a laterally projecting tubercle, here referred to as the sub-zygomatic process, which apparently serves for the insertion of the M. masseter superficialis. Apparently, this insertion has migrated onto the arch proper in other talpids as the zygomatic arch came to lie more ventrally.

The dentition is reduced and the anterior incisors above and below are enlarged. The postfossid of the lower molars opens out lingually. The upper molars are peculiar in that there is a very well developed shelf extending posteriorly from the metaconule (Fig. 2A) which results in the noticeably concave posterior margin of the teeth, a condition unique to *Uropsilus* among the living talpids.

The specimen in hand (USNM 256119) is somewhat damaged in the thoracic region. There are six lumbar vertebrae and presumably 13 thoracics. Six coossified vertebrae comprise the sacrum, and there are at least 16 and probably a few more caudal vertebrate.

The manubrium of *Uropsilus* is essentially like that of *Sorex*. The shaft of the manubrium (Fig. 3) is rod-like with an incipient ventral midline ridge. The alae extend laterally from the anteriormost end of the manubrium and are not expanded anteroposteriorly as in *Neurotrichus*. The mesosternum consists of three elements.

The clavicle (Fig. 3) is relatively simple, long, slender, and shows a sigmoid flexure comparable to that in man. Campbell (1939) noted that "in the relations of the distal end of the clavicle *Ursopsilus* stands intermediate between the mole type with the articulation limited to the humerus and the shrew type where it is confined to the acromion. *Uropsilus* exhibits an articulation both with the high bifed shrew-like acromion and with the humerus." The scapula also shows a combination of shrew and mole characters. There is a "large bifid acromion, with its distally directed process, on which the clavicle articulates, and the posterior process, the metacromion. . . . ". "The supraspinatus fossa is scarcely represented, the infraspinatus fossa is a minute groove, and the fossae for the subscapularis and for the teres major are unmarked, . . ." (Campbell, 1939, Fig. 21). The glenoid fossa is oblique to the long dimension of the scapula.

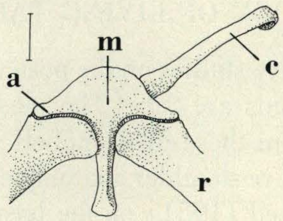

Figure 3. *Uropsilus soricipes*, USNM 256119, ventral view of manubrium and left clavicle. **a**—ala; **c**—clavicle; **m**—manubrium; **r**—costal cartilage.

"In general configuration the humerus of *Uropsilus* resembles that of *Blarina*. The distal end is nearly identical. The head of the humerus is rounded and not elliptical as in the true moles" (Campbell, 1939). The distal end is markedly broader than the proximal end (Fig. 40). The bicipital groove is open throughout its length. No ridge connects the lesser tuberosity with the teres tubercle. The clavicular articular facet is ill defined on the greater tuberosity. There is no fossa for the origin of the M. flexor digitorum profundus ligament.

The ulna of *Uropsilus* shows few if any modifications for burrowing. It is long, slender, and broadly sinusoid with the proximal portion more flexed (Fig. 4). The olecranon process occupies proportionately a very small extent of the length of the ulna. The terminus of the olecranon process is not expanded laterally as in the shrews or other moles. The area of insertion of the triceps muscle is reflected medially. The triceps scar is not well defined and a ridge or crest for the extensor muscles is not developed. The abductor fossa is very narrow and the posterior crest thin. There is no external olecranon crest and the internal crest is simply the continuation of the shaft which forms the olecranon. The processus anconeus is poorly delineated and the coronoid process is not developed. The semilunar notch is correspondingly broadly open anteriorly. The shaft is long and slender, and the relatively narrow distal articular surface forms an oblique angle with the manus.

Like the ulna the radius of *Uropsilus* is also shrew-like. It is long, slender and gently arched (Fig. 4). There is no capitular process. Extending obliquely and distally from the ulnar articulation is a narrow ridge which may be the structural predecessor to the strong crest in this region of the Urotrichini. The distal end of the radius is relatively broader than that of the shrews, even *Blarina*.

The manus of *Uropsilus* shows no specialization for digging. As noted by C. A. Reed (1951) the metacarpals of *Uropsilus* are long, slender, and generally unspecialized as in most shrews. The longest metacarpal is that of digit three (about six times as long as wide). The carpus of *Uropsilus* was not completely prepared but the scaphoid and lunar appear to be fused to form a scapholunar as in soricids. The phalanges are also long and slender. The ungual phalanges are laterally compressed and not bifid. The distal articular surfaces of the metacarpals are flatly cylindrical or slightly convex. There is a median keel as in shrews on the ventral side of the trochlea. Although a radial sesamoid was not noted by previous authors, Reed (1951) has pointed out that this bone is easily lost in preparation. A long, slender radial sesamoid is present in USNM 256119.

In the pelvic girdle there is no pubic symphysis or pseudosymphysis. The ilium is not fused to the sacrum (in the USNM specimen) and only two sacral vertebrae contact the innominate.

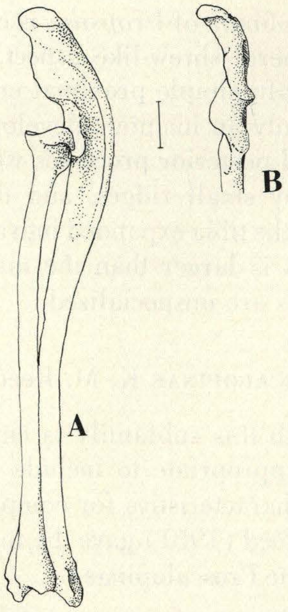

Figure 4. *Uropsilus soricipes*, USNM 256119,**A**; right radius and ulna, right lateral view, **B**; right ulna, anterior view of proximal end.

The femur in shrews may be relatively longer *(Sorex)* or shorter *(Blarina)* than that of the moles. In the shrews the distal margin of the third trochanter is distal to the lesser trochanter thus imparting a rather "long look" to the proximal end of the femur when compared to that of the true moles. In most talpids the third trochanter tends to become aligned transversely with the lesser trochanter thus clustering the insertions of the pelvic muscles near the head and imparting the broad aspect to the proximal end of the femur. The femur of *Uropsilus* is relatively as long as that of *Blarina* and the relationships of the trochanters are shrew-like. *Uropsilus* also differs from the Talpinae in that the proximal articular surface only extends along the dorsal side of the neck toward the greater trochanter, the intertrochanteric crest is evenly curved and well defined, and the third trochanter is below the level of the lesser trochanter.

The tibiofibula of *Uropsilus* is characterized by the general shrew-like aspect, a long and slender shaft, simple proximal end of the fibula with only an incipient development of the lateral and posterior processes which are represented by small ridges, and the falciform process of the tibia expanded into a wide flange.

The pes is larger than the manus and the metatarsals are unspecialized.

PROSCALOPINAE K. M. Reed, 1961

Although this subfamily is entirely extinct it seems appropriate to include a brief summary of characteristics for completeness.

K. M. Reed (1961) gave the following diagnosis for the Proscalopinae:

"Skull chrysochlorid-like; dentition of talpid type. Skull wide and deep in posterior part; flexure in maxillary, between P^3 and P^4, stronger than in *Neurotrichus;* lateral projections on premaxillaries; slight sagittal and occipital crests; palate long relative to skull length; antorbital rim confined to maxillary, not joining main body of zygoma. Wide lingual shelf on upper molars with hypocone [metaconule] varyingly developed; dental formula $I^3_?$ $C^1_?$ $P^3_?$ M^3_3."

Other features of Proscalopinae include the ossified bulla, infraorbital foramen much larger than lacrimal foramen, straight zygomatic arch, anterior incisor above and below (?) enlarged, postfossids open lingually; humerus very broad, distal and broader than proximal end, bicipital groove long and open, head laterally compressed, fossa for ligament of M. flexor digitorum profundus present: ulna with coronoid process well developed, transverse proximal crest; radius short with well developed capitular process; manus broad, scaphoid and lunar separate; ungual phalanges depressed but not bifid; pes probably smaller than manus; rest of skeleton undescribed. See Turnbull and Reed (1965) for more detailed descriptions.

DESMANINAE (Thomas 1912) Mivart, 1871

The Desmaninae form a very compact group at present. All the known members are semiaquatic or amphibious and show corresponding osteological and myological modifications. The desmans show marked modifications of the limbs, being longer proportionately in the distal elements of the limbs than are the other moles. The hind feet are webbed and the metacarpals and phalanges are greatly elongated for support and effectiveness. They also show the characteristic great development of the third trochanter and expansion of the distal end of the femur neither of which are as prominently developed in the other Talpids. The tibia is proportionately very long and deeply grooved for the tendons of the extensor muscles which are characteristic for mammals that use the hind limbs for aquatic locomotion. Dobson's (1882) monograph remains the most complete treatment of the myology and osteology of the Desmaninae *(Desmana)* but Schreuder's (1940) revision of fossil desmans is the best source for separating the various fossil and recent genera from each other on osteological criteria. There has been little confusion in the assignment of desman postcranial elements to the correct subfamily.

The subfamily can be diagnosed as follows: bulla ossified but small; infraorbital foramen much larger than lacrimal foramen; hypocone-like metaconule moderately developed, I^1 and I_2 enlarged; postfossids open lingually; manubrium with expanded anterior alae, ventral keel weak; mesosternum with three elements; clavicle simple and stout, ventral spine and scapular articulation absent; scapula with metacromion, glenoid fossa nearly perpendicular to long dimension, subscapular and teres major fossa present, suprascapular foramen present; humerus (Fig. 40) relatively slender, distal end broader than proximal end, bicipital groove short and partly closed over by fusion of the pectoral process and lesser tuberosity, head laterally compressed, fossa for M.

flexor digitorum profundus ligament present; ulna without coronoid process, transverse proximal crest present; radius with capitular process absent or poorly developed; manus moderately expanded, ungual phalanges bifid, scaphoid and lunar separate; pubic symphysis present, pseudosymphysis absent, ilium fused to sacrum; five caudal vertebrae in sacrum, three vertebrae contacting innominate; tail very long; femur expanded proximally and distally, shaft compressed anteroposteriorly; tibiofibula long and deeply grooved distally, fibula complex proximally; pes larger than manus, metatarsals laterally compressed and at least some twisted.

TALPINAE Fisher Von Valdheim, 1817

SKULL: Complete skulls of fossil moles are seldom found and the discussion of the skull will only be treated lightly here. The general proportions and morphology of the living talpid skulls have been described in numerous other sources. Some of the general trends to be noted within the Talpinae are the general broadening of the cranial cavity, increase in coossification of the roofing bones, and development of the ossified bullae. All these trends are seemingly associated with an increasing degree of fossorial specialization. In such highly fossorial moles as *Scalopus, Scapanus,* and *Talpa,* the ventral floor of the bulla is formed by a ventrolateral flange of the medial arm of the tympanic (ectotympanic) bone. This flange is only slightly developed in *Scaptonyx,* the Urotrichini, *Condylura,* and the Parascalopina, so that the tympanic membrane is visible in ventral view. The tympanic bone is not fused with the surrounding bones in the later genera but becomes completely fused in the Scalopina, *Talpa (Talpa),* and *Scaptochirus.* In *Talpa (Mogera)* the tympanic is overlapped marginally by the bullar wings of the surrounding bones which are not fused with the tympanic.

The stapedial artery and the veins still within the tympanic cavity are enclosed by bony tubes in the highly fossorial moles—Talpini, and Scalopina. The stapedial artery is only partly enclosed or thinly so in *Parascalops* and *Condylura;* a bony tube is absent in the Urotrichini, *Scapanulus,* and *Scaptonyx.*

In none of the species does the stapedial artery or bony tube completely fill the stapedial fenestra and apparently the bony tube does not contact the stapes. Concomitant with the development of an ossified stapedial tube is the closure of the pyriform fenestra. It is open in the Urotrichini, *Scaptonyx,* and *Scapanulus* and closed in the Talpini, *Condylura, Parascalops,* and the Scalopina.

Stroganov (1945), in a comparative study of the auditory ossicles of the living Talpidae, grouped the moles into six taxa; the Desmanidae, Talpinae, Scalopinae, Condylurinae, Urotrichinae and Uropsilinae. It is not clear in his discussion whether he used the terms Urotrichinae and Uropsilinae interchangeably. *Parascalops, Scapanulus* and *Neurotrichus* were not available to him. I have made no dissections of the auditory region of these moles but the form of the malleus is visible in the skulls available. The malleus of *Neurotrichus* resembles that of *Urotrichus* figured by Stroganov. *Parascalops* and *Scapanulus* resemble each other in the form of the malleus being intermediate in morphology between the Scalopina and *Condylura.* Proportionately the manubrium and processus gracilis bear the same angular relationships to the articular surface as in the Scalopina, but the posterior margin of the lamina is sharply angulate as in *Condylura.* The apophysis orbicularis is intermediate in size between *Condylura* and the Scalopina.

DENTITION: There has been much attention given to the dentition, particularly the number of teeth, as a means of classification. This has led to a proliferation of genera which, in its extreme form, resulted in a large number of monotypic genera. Other workers (Osgood, 1937; Jackson, 1915; Palmer, 1937; and Schwartz, 1948) have noted the variability of the number of teeth and have synonymized

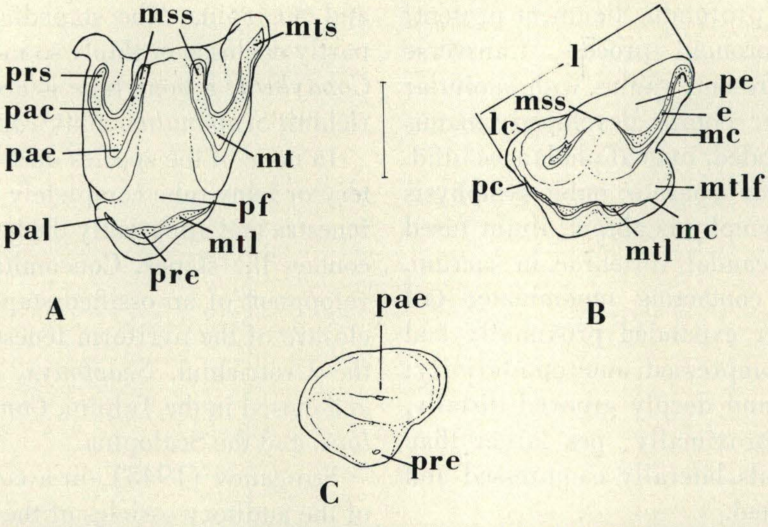

Figure 5. Nomenclature of upper teeth, **A;** *Scapanulus oweni*, left M^2, **B;** *Uropsilus soricipes*, left M^1, **C;** *U. soricipes*, right P^2. **l**—length; **e**—ectoloph; **lc**—labial cingulum; **pac**—paracrista; **pae**—paracone; **pal**—paraconule; **pc**—paracingulum; **pe**—post ectoflexus; **pf**—protofossa; **pre**—protocone; **prs**—parastyle; **mc**—metacingulum; **mss**—mesostyle; **mt**—metacone; **mtl**—metaconule; **mtlf**—metaconule flange; **mts**—metastyle.

many of the named genera. The pendulum swung completely the other way in some groups so that the Talpini is represented by only one living genus, *Talpa* (Schwartz 1948). Ellerman and Morrison Scott (1951) exceeded even Schwartz in that they recognized only three living species of *Talpa* as compared with the six of Schwartz. Valid as this limited approach may be, there are other less variable characteristics of the postcranial skeleton which can be used to evaluate some of the other generic units. These postcranial characters will be touched on under the appropriate category.

I shall not attempt to summarize the dental formulae of the living and known fossil moles except where need be in the systematic discussion; these may be found in the above named sources and elsewhere. There are few gross dentitional modifications exhibited by the talpines as a group. The hypertrophy of the I_2 occurs independently in at least two lineages. The hypertrophy of P_1 seems to be naturally related to the *Talpa* complex as a whole (*Scaptonyx* here included). Extreme molar hypsodonty only develops in two lineages (one extinct) of the Scalopina (those with the hypertrophied I_2) but is incipient in a third (*Scapanus latimanus)*. The reduction in the number of antemolar teeth is invariably associated with a general shortening of the rostrum. This shortening of the rostrum has apparently occurred again and again in divergent lines of moles and is of little taxonomic significance itself but may be very useful in evolutionary progressions when the systematic position of the form can be delineated on other criteria. *Condylura, Parascalops, Scapanus, Talpa,* and *Scaptonyx* all contain species with dentitions of the complete eutherian dental formula. Upper teeth terminology is illustrated in Figure 5.

There are two major molar patterns in the lower dentition which may, in general, be characteristic of a subtribe, tribe, or subfamily. The first type consists of a pattern in which the crista obliqua of the M_2-M_3 joins the trigonid directly or just labial to a well developed metastylid. The postfossid is usually open in this case (see Fig. 6A). In the second case, the crista obliqua joins the protolophid and the metastylid and is usually weak or absent. In this pattern

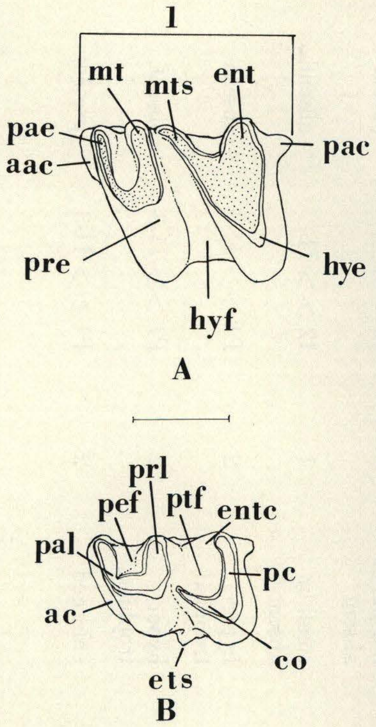

Figure 6. Nomenclature of lower teeth, **A;** *Scapanulus oweni*, left M_2, **B;** *Neurotrichus gibbsii*, left M_2. **l**—length; **aac**—anterior accessory cuspid; **ac**—anterior cingulum; **co**—crista obliqua; **ent**—entoconid; **entc**—entocristid; **ets**—ectostylid; **hye**—hypoconid; **hyf**—hypoflexid; **mt**—metaconid; **mts**—metastylid; **pac**—posterior accessory cuspid; **pae**—paraconid; **pal**—paralophid; **pc**—postcristid; **pef**—prefossid; **pre**—protoconid; **prl**—protolophid; **ptf**—postfossid.

an entocristid is frequently developed which tends to isolate the postfossid (see Fig. 6B). Intergradation between these types is not uncommon, although a tendency toward one or the other is usually discernible in moles with relatively higher crowned (mesodont) teeth.

A comparison of selected dental features is presented in Table 2. It might be inferred from the table that the upper canine is double-rooted and somewhat enlarged. Only *Scaptonyx* and the Talpini have reduced incisors and hypertrophied upper canines.

VERTEBRAE: Vertebrae other than the sacral vertebrae are seldom identified in fossil remains except when associated with an articulated skeleton. The number of vertebrae in the various body regions has been noted to vary. The cervicals invariably number seven. Thirteen thoracic vertebrae bearing functional ribs and six lumbar vertebrae were noted in *Urotrichus, Neurotrichus, Parascalops*, and *Talpa*. Of the two specimens of *Condylura* examined, one had the above condition and the other bore a vestigial and nonfunctional rib on the fourteenth thoracic vertebra, thus leaving only five lumbars. *Scapanus, Scalopus*, and *Talpa (Mogera)* also had five lumbar vertebrae and fourteen thoracic vertebrae with functional ribs. Slonaker (1920) reports six sacral vertebrae for *Scapanus* and *Scalopus* and lists a number of records by others which tend to support his view. C. A. Reed (1951) and others (Leche 1883) observed only five sacral vertebrae and my observations of available talpidines support this view. Gupta (1966) also considered five as the typical talpidian number but noted the variable fusion of the first caudal vertebra to the sacrum in *Scalopus*. The aquatic talpine *Condylura* has seventeen to twenty-one caudal vertebrae, sixteen were counted in *Urotrichus*, and the fossorial moles have the lowest counts: *Parascalops*, thirteen; *Scapanus*, thirteen to fourteen; *Scalopus*, ten to eleven; *Talpa (Talpa)*, ten.

MANUBRIUM: The manubria of *Scaptonyx, Condylura*, and Urotrichini, have large alae originating medially and the ventral ridge forms a deep keel (Campbell, 1939, Figs. 3-5). *Scaptonyx* and the Urotrichini exhibit anterior expansions on the alae which serve as the origin for part of the M. costoscapularis (subclavius of Campbell).

In the Scalopini, "the heightening of the keel and the decrease in width (both real and proportional) is carried still further." (Campbell, 1939, Figs. 6-8). The Parascalopina have a dorsal ridge between the two alae which is lacking in the Scalopina. In the Scalopina and Tal-

TABLE 2

Comparison of Selected Dental Features of Recent Talpid Genera

	Relative size of upr C1 & I1	Size of upper I1	No. of roots on upr canine	No. of roots on upr P4	Lower P1	No. of roots on lwr P1	Relative size of anterior lower antemolars	Metastylid of lower M2
Neurotrichus	I = C	enlarged	2	2	small or absent*	1	A1 > A2	absent
Urotrichus	I > C	enlarged	1	3	small or absent*	1	A1 > A2	absent
Condylura	I2 > I1 > C	enlarged	1	3	normal	2	C > I1 ≧ I2	present
Scapanulus	I >> C	hypertrophied	2	3(?)	normal or absent*	1	I2 > I1	present
Parascalops	I >> C	hypertrophied	1	3(?)	normal	1	I2 > I1	present
Scapanus	I >> C	hypertrophied	1	1	normal or absent	1	I2 ≧ I1	absent
Scalopus	I >> C	hypertrophied	1	1	small or absent	1	I2 >> I1	absent
Talpa	I < C	small	2	3	hypertrophied	2	P1 >> I1-3	absent
Scaptochirus	I < C	small	2	3	hypertrophied	2	P1 >> I1-3	absent
Scaptonyx	I < C	enlarged	2	1	enlarged	2	P1 >> I1-3	present

<—less than
>—greater than
>>—much greater than
A—Antemolars where homologies are questionable—anterior tooth=A1
*—homologies questionable or teeth of variable occurrence within or among species

pini[5] this ridge is replaced by a groove for the anterior vena cava which divides posteriorly. This vein is double in *Parascalops* and *Scapanulus* although the dorsal ridge may be perforated by a foramen. In the Talpini the groove for the vena cava leads off posteriorly to the right instead of dividing and the clavicular facets are inclined at nearly a 45° angle to the shaft, with the ventral margins anteriormost. The reclined articular facets are also typical of *Condylura*, *Scaptonyx*, and the Urotrichini. In the Scalopini the clavicular facets are nearly vertical.

The manubrium of *Scapanulus* has not been previously described. It most closely resembles that of *Parascalops*. As in *Parascalops* there is a dorsal ridge between the two alae. The anterior vena cava is divided by the dorsal ridge, and a foramen perforates the ridge near the alae. The length of the manubrium is relatively shorter than that of *Parascalops*.

It seems appropriate at this point to mention the unique presence in *Scapanulus* and *Parascalops* of a tetrahedral heterotopic bone (Fig. 7) wedged in between the ventromedial spine of the clavicle and anterior basilateral portion of the manubrium. These heterotopic bones are relatively larger in *Scapanulus* and the manubrium is correspondingly narrower anteroventrally than in *Parascalops*. These bones were not observed in any of the other moles examined nor was there any particular space available for them in the articulated skeletons. In *Parascalops* the anteroventral extremity of the manubrium is proportionately wider in response to the relatively smaller heterotopic bones. In *Scapanus* and *Scalopus*, which lack these bones, this portion of the manubrium is still broader. The development of such heterotopic bones may be related to the shift of the clavicle articulation from an oblique to a vertical position with respect to the manubrium. Apparently, there is some ventrally directed force on the proximal end of the clavicle which would, unchecked, tend to disjoint the clavicle. In the non-scalopines this force is nulified by the dorsolateral position of the manubrium articular facet.

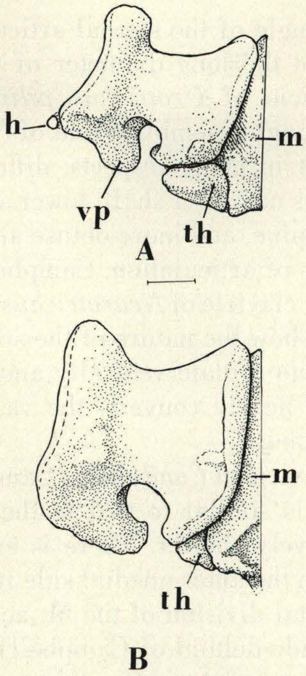

Figure 7. Anterior view of the right clavicle in articulation with the manubrium, **A;** *Scapanulus oweni*, **B;** *Parascalops breweri*. **h**—heterotopic bone; **m**—manubrium (right half); **th**—tetrahedral heterotopic bone; **vp**—ventral process.

MESOSTERNUM: The mesosternum of moles is said by Slonaker (1920) to consist of a variable number of parts. Flower (1870) lists the number of sternebrae as high as five although his figure clearly shows only three. All my observations bear out the fact that there are only three sternebrae in all the moles examined. Three to five sets of ribs may tenuously contact the last sternebra.

CLAVICLE: The clavicle of the Urotrichini and *Scaptonyx* is roughly at least twice as long as deep (Campbell, 1939, Figs. 13-14). There is a well developed ventral process and no reflection of the ventromedial spine. The dorsal prominence is very pronounced owing to the

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[5] The sternum bone of *Scaptochirus primitivus* Zdansky figured by C. C. Young 1934 (Fig. 2A) appears to be the first phalanx of the second digit of a bird.

oblique angle of the sternal articular facet in relation to the long diameter of the clavicle. The clavicle of *Urotrichus pilirostris* (Fig. 8B), although resembling that of *Neurotrichus* (Fig. 8A) in many respects, differs from the latter in its narrower shaft, lower and less complicated spine, and more obtuse angle between the planes of articulation. Campbell's illustration of the clavicle of *Neurotrichus* is too generalized to show the nature of the spine. It is expanded into a plate ventrally and proximally so that it nearly converts the vascular notch into a tunnel.

The clavicle of *Condylura* (Campbell, 1939, Fig. 15) is similar to that in the Urotrichini but relatively shorter. There is an additional process on the anteromedial side for the origin of the distal division of the M. acromiodeltoideus (cleido-deltoid of Campbell). The shortness of the clavicle in *Condylura* compared to the Urotrichini and *Scaptonyx* is the result of the shortening of the distal moiety. The planes of the articular facets are decidedly not parallel.

The clavicle of the Talpini is as variable in morphology as it is in the Scalopini. The articular facets are roughly parallel and the clavicle is quite short, being as long as deep, or less so. There is a prominent hook-like ventral process in *Talpa (Talpa)* (Campbell, 1939, Fig. 19).The process is simple in *Talpa (Mogera)* (Campbell, Fig. 20). The vascular notch which delineates the ventral process from the ventromedial spine is not continued as a gutter posteriorly as in the Scalopini. In *Talpa (Mogera)* the vena cava pierces the clavicle and the ventromedial spine is thus undefined and the vascular notch is absent.

The clavicle of the Parascalopina is longer than in the Scalopina but shorter than the Condylurini. The gutter on the posterior side leading from the vasular notch toward the dorsal prominence is usually well defined. A vascular foramen usually pierces the clavicle within the vascular notch just above the ventral process. The ventromedial spine is deflected laterally in both the Parascalopina and Scalopina by the tetrahedral heterotopic bone in the former and the basilateral buttress of the manubrium in the latter.

The clavicle of *Scapanulus* (Fig. 7A) is shorter and broader than that of *Neurotrichus* and *Condylura* but longer and narrower than in *Parascalops*. As might be expected, *Scapanulus* most closely resembles *Parascalops* in the general aspect of the clavicle. The notch is sharply defined by the ventral process which nearly encloses it ventrally. The ventromedial spine is broadened and reflected laterally so that the articulation of the heterotopic bone is horizontal. In *Parascalops* (Fig. 7B) the ventromedial spine is reflected to about a 45° angle with the horizontal as in *Scalopus* and *Scapanus*. In the latter two genera, however, the ventromedial spine articulates directly with the manubrium rather than with a heterotopic bone. The clavicle of the Scalopina (Campbell, 1939, Figs. 17-18) is even shorter than that of the Parascalopina. The ventral process is reduced to a ridge. In *Scalopus* as in *Talpa (Mogera)* the vena cava pierces the clavicle.

If the living talpines are arranged in a structural progession from the least fossorial to the most, several trends become apparent. As the manubrium increases in length the clavicle shortens and is rotated posterolaterally in relation to the manubrium.[6] However, the humeral articular facet in all the living moles, except *Uropsilus*, continues to face essentially laterally. Therefore, as the clavicle shortens, the sternal and humeral articular facets tend to become parallel. These functional changes are complicated by changes in the clavicular-sternal articulation, but the end result in the advanced burrowing moles is to create a nearly straight bony bridge from humerus to humerus.

SCAPULA: The scapula in the Talpine is very narrow with the glenoid fossa nearly perpen-

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[6] Kistin (1929) figures *Scalopus* and *Galemys* pectoral girdles in ventral view which dramatically illustrates the effect of a lengthening manubrium and shortening of the clavicles. He states "... in the figure shown here, which was drawn from a dried specimen, the clavicle points more anteriorly than it should" (p. 313). In my opinion the angle of the clavicle as he illustrated it is normal.

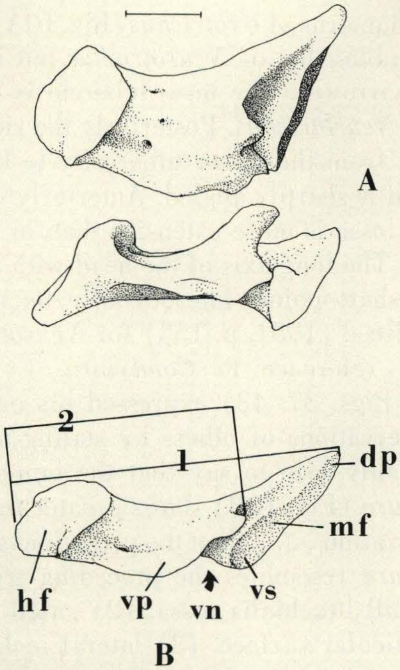

Figure 8. Right clavicle, **A;** *Neurotrichus gibbsii*, posterior and ventral views, **B;** *Urotrichus (Dymecodon) pilirostris*, posterior view. **l**—length; **2**—length of ventral process; **dp**—dorsal prominence; **hf**—humeral articular facet; **mf**—manubrial articular facet; **vn**—vascular notch; **vp**—ventral process; **vs**—ventromedial process or spine.

dicular to its long axis. In the Urotrichini the origins of the M. supraspinatus, M. infraspinatus, and M. teres major are separated on the dorsal side by ridges of bone. The infraspinatus fossa thus appears as a deep groove or channel extending nearly the length of the scapula. The acromion process has a moderately well developed metacromion region (see C. A. Reed, p. 537, for a correction of Campbell's, 1939, Fig. 25). The supra-scapular nerve passes under the acromion process in the usual manner and no foramen is present.

Scaptonyx closely resembles the Urotrichini in the scapula but according to Campbell's Figure 24 lacks the metacromion process and has a more restricted supraspinatus fossa. The scapula of *Condylura* also resembles that in the Urotrichini in major features but is more angulate.

In the Scalopini, "A great development of the teres major fossa and the joining of the upraised dorsal lip of the posterior margin with the vertebral end of the spine has partly covered over the end of the infraspinatus fossa and deepened it in the vertebral half of the bone. The supraspinatus fossa is narrow and defined only on the proximal half of the scapula. The acromion is degenerate as in the Talpinae [my Talpini]. The tuber though small is better rep-

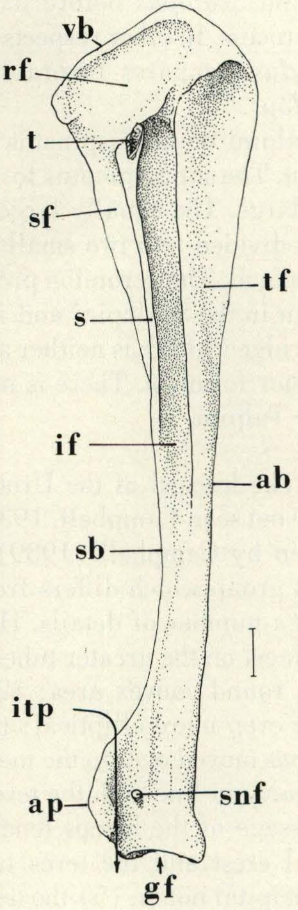

Figure 9.—Dorsal view of the left scapula of *Scapanulus oweni*. **ab**—axillary border; **ap**—acromion process; **gf**—glenoid fossa; **itp**—path of infraspinatus tendon; **rf**—rhomboid fossa; **s**—"spine" of scapula; **sb**—superior border; **sf**—supraspinatus fossa; **snf**—foramen for suprascapular nerve; **t**—tuber of the spine (broken); **tf**—teres fossa; **vp**—vertebral border.

resented than in the . . . " (Campbell, 1939) Talpini. The base of the acromion process is pierced by the supra-scapular nerve. There is a rhomboid fossa between the supraspinatus fossa and the vertebral end.

The scapula of *Scapanulus* (Fig. 9) is a blend of features seen in *Parascalops* and *Scapanus*. The vertebral border is angulate as in *Parascalops*. The rhomboid fossa is separated from the supraspinatus fossa by a low ridge. The walls of the infraspinatus fossa converge anteriorly and thus eliminate the fossa as in *Scapanus* and *Scalopus* before it reaches the acromion process. In other respects the scapula of *Scapanulus* compares favorably with that of *Parascalops*.

In the Talpini the infraspinatus fossa is entirely absent. The supraspinatus fossa is correspondingly large. The equally large teres fossa is partially divided into two small fossae near the vertebral end. The acromion process is even smaller than in the Scalopini and forms a low triangular ridge which has neither a suprascapular notch nor foramen. There is no rhomboid fossa in the Talpini.

HUMERUS: The humeri of the Urotrichini and *Scaptonyx* (not seen-Campbell, 1939, Figs. 35, 41) are said by Campbell (1939) to form a closely knit group which differs from the Desmaninae in a number of details. He lists: (1) clavicular facet on the greater tuberosity is enlarged to a round convex area; (2) the head has become even more elliptical; (3) the pectoral crest has moved over to the medial side of the bone nearly in line with the teres tubercle; (4) the passage of the biceps tendon between the pectoral crest and the teres tubercle has formed a bicipital notch; (5) the teres tubercle forms a long high crest rather than a pointed prominence; (6) a small brachialis fossa is apparent beneath the greater tuberosity; (7) the greater development of the lateral epicondyle; (8) and the humerus is relatively wider. *Scaptonyx* differs according to Campbell from the Urotrichini in the development of a spikelike deltoid process and larger olecranon fossa.

The humerus of *Urotrichus* (Fig. 10A) closely resembles that of *Neurotrichus* but is relatively narrower. The teres tubercle is shorter than in *Neurotrichus*. Posteriorly the ridge extending from the lesser tuberosity to beneath the head is sharply angled. Anteriorly the olecranon fossa is more extensive than in *Neurotrichus*. The long axis of the head with respect to the shaft points laterodistally as pointed out by Reed (1951, p. 154) for *Neurotrichus*.

With reference to *Condylura*, Campbell (1939, Figs. 37, 43) expressed his own and the observations of others by stating that "it is probably safe to say that the humerus of *Condylura* (Fig. 10B) shows greater fossorial specialization . . . " than the preceding groups. *Condylura* resembles the preceding tribes in (1) small brachialis fossa, (2) small clavicular articular surface, (3) lateral inclination of the head, (4) and in comparison with the Urotrichini a distinct notch between the head and the clavicular facet and relatively well developed deltoid and epicondylar processes. However, *Condylura* also resembles the Talpini and Scalopini in (1) the division of the pectoral muscle scar into two distinct regions, the pectoral crest and pectoral ridge, by a right angle bend, (2) large olecranon fossa, and (3) relative width of proximal end.

The humeri of the Talpini (Campbell, 1939, Figs. 50-55) and Scalopini (Fig. 10 D-F) are structurally and adaptively very similar and may be contrasted with the preceding by, (1) the relatively broader proximal ends, (2) heads parallel or medially directed with respect to the long axis of the humeri, (3) large, hemicylindrical clavicular facets not sharply separated from the bases of the heads, (4) large brachialis fossae, and (5) very well developed epicondylar and deltoid processes. Campbell (1939) distinguished the otherwise similar Scalopini from the Talpini by (1) the presence of "a sharp ridge running from the medial side of the scapular facet to the distal end of the lesser tuberosity" accompanied by an abrupt change of plane between the two areas divided by the ridge, and (2) the more

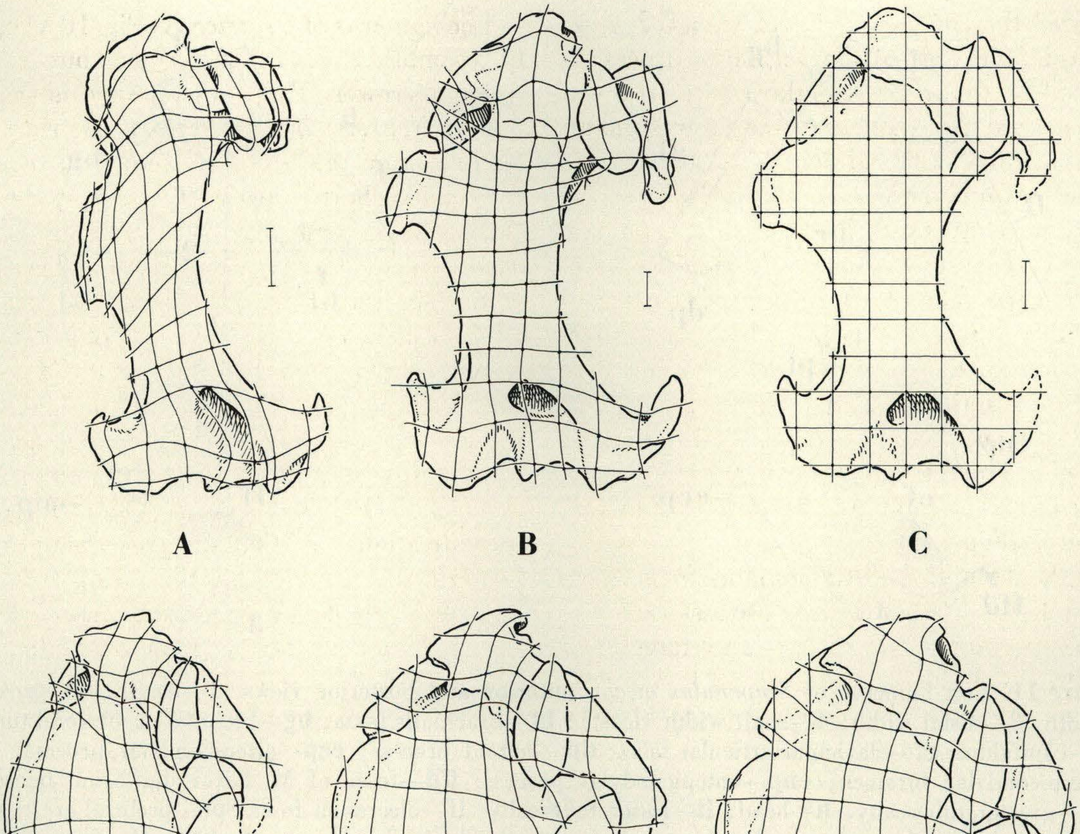

Figure 10. Posterior views of right humeri. Comparison by deformed coordinate method with *Scalopoides isodens* as the standard, **A;** *Urotrichus pilirostris,* **B;** *Condylura cristata,* **C;** *Scalopoides isodens,* **D;** *Scapanulus oweni,* **E;** *Parascalops breweri,* **F;** *Scapanus* sp., UO 4585 (reversed).

pronounced notch between the head and the proximal edge of the lesser tuberosity. These differences Campbell correlates with the greater development of the brachialis fossa in the Talpini.

Scapanulus in part fills the gap in a structural series between *Condylura* and *Parascalops.* Although the humerus of *Scapanulus* (Fig. 11) resembles that of *Condylura* in gross proportions, the details of the humerus are more like those of *Parascalops.* The long axis of the head with respect to the shaft points slightly mediodistally. The deep notch between the trochlea and the fossa for the M. flexor digitorum profundus ligament in *Condylura* is eliminated by the broadening of the trochlea as in *Parascalops,* the Scalopina, and the Talpini. The teres tubercle is relatively longer than

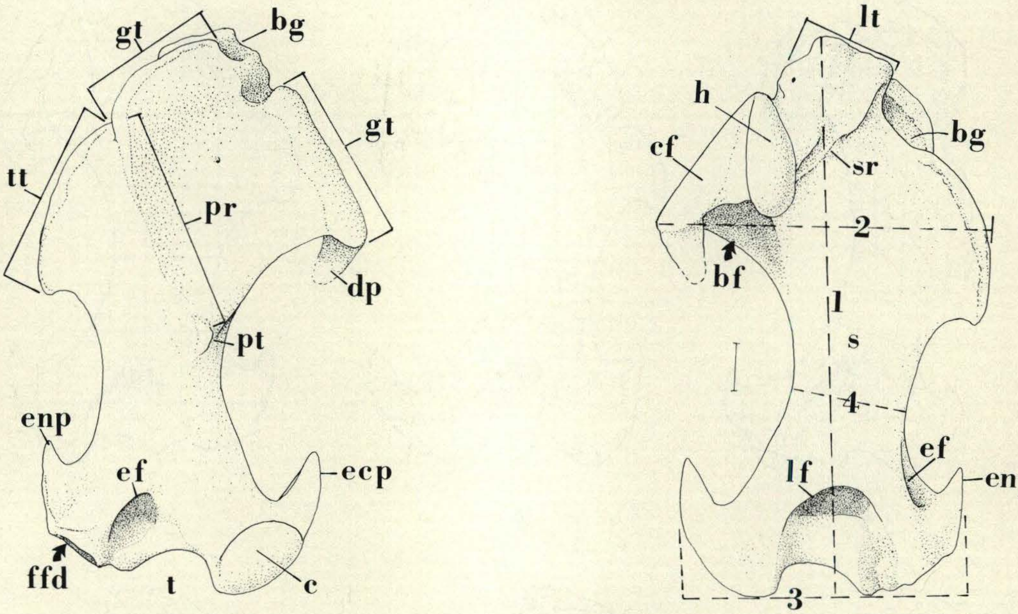

Figure 11. Left humerus of *Scapanulus oweni,* anterior and posterior views. **1**—length; **2**—proximal width; **3**—distal width; **4**—shaft width (least); **bf**—brachialis fossa; **bg**—bicipital groove and tunnel; **c**—capitulum; **cf**—clavicular articular facet; **dp**—deltoid process; **ecp**—ectepicondylar process; **ef**—entepicondylar foramen; **enp**—entepicondylar process; **ffd**—fossa of M. flexor digitorum ligament; **gt**—greater tuberosity; **h**—head; **lt**—lesser tuberosity; **lf**—olecranon fossa; **pc**—pectoral crest; **pr**—pectoral ridge; **pt**—pectoral tubercle; **s**—shaft; **sr**—"scalopine" ridge; **t**—trochlea; **tt**—teres tubercle.

that of *Parascalops.* The angle formed by the plane of the clavicular facet of *Scapanulus* and the axis of the shaft is as in *Parascalops* and the other highly fossorial moles. The plane of the clavicular facet is not parallel to the shaft as in *Condylura.* The shape of the clavicular facet is also of the *Parascalops* type (Fig. 42B). Posteriorly there is a distinct ridge extending from the lesser tuberosity to the head. The notch between the head and the lesser tuberosity is well developed.

ULNA: Reed (1951) discussed the major differences between the foreleg of soricids and talpids as based upon their structure in *Sorex, Neurotrichus,* and *Scapanus.* I shall attempt to fill in a description of some of the more striking osteological features of additional genera and will review some of the features mentioned by Reed. The distal elements of the foreleg seem to remain more plastic to change than does the humerus.

Three major and progressive structural differences may be observed within the Talpinae if the ulnae of moles are arranged in order of fossorial ability (Fig. 13). The manus rotates nearly 90° with respect to the proximal end of the ulna in such a progression. Secondly the ulna progresses from a sinusoidal but relatively delicately built bone in the Urotrichini and *Condylura* to straight but very short-shafted and robust bone in the Scalopini and Talpini. It is interesting to note that the length of the proximal crest of the ulna is relatively as great in *Blarina* as in *Scalopus.* the transversely broadened olecranon process may be considered as a general feature of living soricoids with a few notable exceptions.

In soricids (Fig. 13A) the ulna is relatively long and straight. The olecranon process occu-

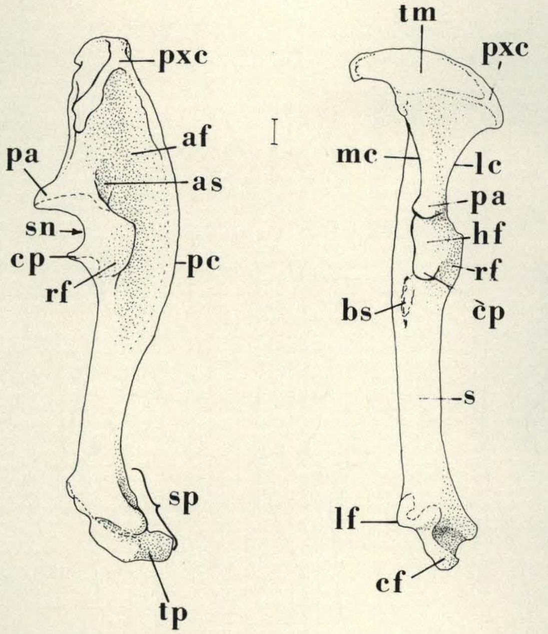

Figure 12. Left ulna of *Talpa europea,* lateral and anterior views. **af**—abductor fossa (M. abductor p. 1.) ; **as**—abductor scar or tubercle; **rbs**—brachialis scar;**cf**—cuneiform articular facet; **cp**—coronoid process; **hf**—humeral articular facet; **lc**—lateral olecranon crest; **lf**—lunar articular facet;**mc**—medial olecranon crest; **pa**—processus anconaeus; **pc**—posterior crest; **pxc**—proximal crest; **rf**—radial articular facet; **s**—shaft; **sn**—semilunar notch; **sp**—styloid process; **tm**—triceps area of insertion; **tp**—terminal process.

pies a proportionately small amount of the length of the ulna. The triceps scar is restricted to the medial side of the olecranon, and is elliptical and perpendicular to the shaft. The abductor fossa is very narrow and the posterior crest is correspondingly thick and close to the semilunar notch. The laterial olecranon crest is short but well defined. The medial olecranon crest is very strong and level with the poorly defined processus anconeus, and the similunar notch is broad. The distal articular surface forms a slight oblique angle with the hand.

The ulna of the Urotrichini (Fig. 13B) is relatively long and sinusoidal in lateral aspect. The olecranon process is proportionately as short or shorter than in the shrews. The triceps scar is transversely elliptical and occupies only the lateral third of the proximal crest. The proximal crest forms a less obtuse angle with the shaft than in the shrews. The apparent expansion of the proximal crest over that in the shrews is partly illusionary owing to the marked narrowing of the anterior platform of the olecranon process. The abductor fossa is greatly expanded over that of the shrews in response to the more posterior position of the posterior crest and a distinct abductor tubercle is present just posterior to the processus anconeus on the lateral side. The lateral and medial olecranon crests are well defined and close together. A distinct processus anconeus is present. The semilunar notch is more restricted than in the shrews. The distal articular surface forms a silghtly more obtuse angle with the hand, but the area of articulation with the hand is almost as small as in the shrews.

In *Condylura* (Fig. 13C) the ulna is still relatively long and sinusoidal, and the olecranon process is still relatively short. The triceps scar is poorly defined and appears to be limited to the internal half of the proximal crest; the scar is very narrow. The proximal crest more nearly aproaches a right angle to the shaft than in the Urotrichini. The relative expansion of the proximal crest is greater than in any of the other talpines. The abductor fossa and posterior crest are about as in *Neurotrichus.* A poorly defined abductor tubercle or scar is present on the base of the lateral olecranon crest. The lateral and medial olecranon crests are well defined. The processus anconeus is distinct and elevated; but the coronoid process is exceedingly low. The semilunar notch is correspondingly very broad and ill defined. The distal articular surface has rotated to nearly a right angle with the hand; and the articular area with the hand is noticeably expanded over that of the Urotrichini.

The ulna of the Scalopina and *Parascalops* (Fig. 13E) bear many features in common and in part may be discussed together. The ulna is relatively short, straight, and quite robust. The proximal crest forms a sharp angle with the

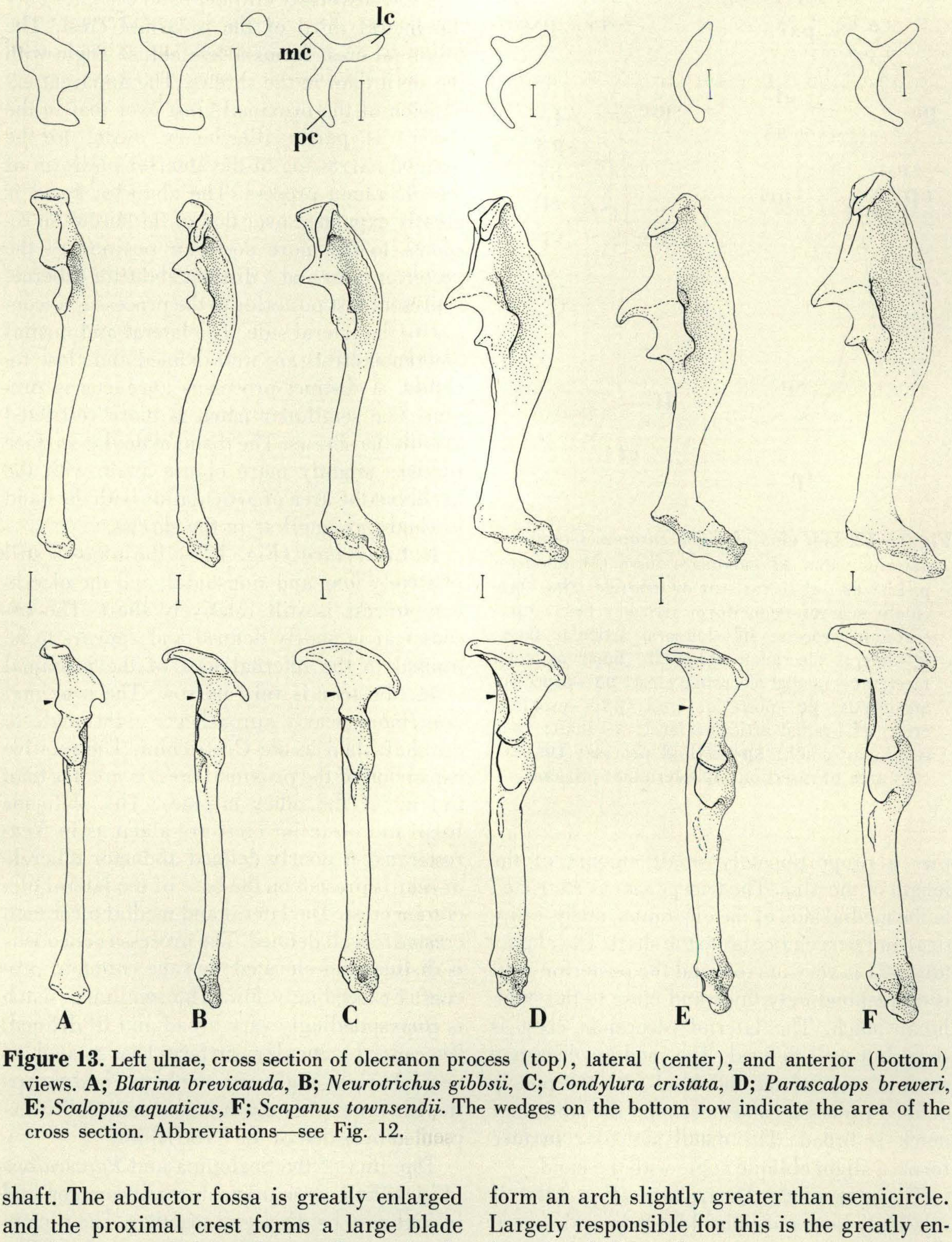

Figure 13. Left ulnae, cross section of olecranon process (top), lateral (center), and anterior (bottom) views. **A**; *Blarina brevicauda*, **B**; *Neurotrichus gibbsii*, **C**; *Condylura cristata*, **D**; *Parascalops breweri*, **E**; *Scalopus aquaticus*, **F**; *Scapanus townsendii*. The wedges on the bottom row indicate the area of the cross section. Abbreviations—see Fig. 12.

shaft. The abductor fossa is greatly enlarged and the proximal crest forms a large blade widely separated from the semilunar notch. The semilunar notch is well defined and may form an arch slightly greater than semicircle. Largely responsible for this is the greatly enlarged and elevated processus anconeus and a smaller but distinct coronoid process. The distal articular surface forms nearly a right angle with the hand and is greatly expanded—primarily posteriorly.

Most of the noticeable differences between the ulnae of these genera are centered around the olecranon process. *Scalopus* (Fig. 13F) may be immediately distinguished from the other two genera and indeed all other talpines by the lack of or suppression of the medial olecranon crest. As in *Neurotrichus* the triceps scar occupies most or all of the central and medial positions of the proximal crest. In *Parascalops* and *Scapanus* the scar is large but it is relatively narrow in *Scalopus*. The abductor scar is elongate and forms part of the base of the lateral crest in *Parascalops* but it is ovoid and lies posterior and internal to the lateral lip of the humeral articular facet in the Scalopina.

The ulnae of *Talpa* (Fig. 12) and *Scaptochirus*[7] are like those of *Parascalops* and *Scapanus* in general features but differ in detail. The triceps scar and medial and lateral ridges of the olecranon are similar to those of *Scapanus*. However, the articular surface for the humerus and radius of the Talpini is displaced laterally so that the radial articular process overhangs the abductor fossa to a greater extent than in the highly fossorial North American moles. The shape of the styloid process in the Talpini differs from that of the Scalopini in shape and relative shortness. The cuneiform articulation is not a long cylindrical articular surface with a small terminal process as in the Scalopini but is formed by a rather short conical to cylindrical internal segment and an equally strong terminal process. The ridge proximal to the cuneiform articular surface is simple in *Scalopus* and *Scapanus* but somewhat swollen terminally in *Parascalops*. In the Talpini this region is developed into a distinct knob.

RADIUS: The radius of talpids is not as complex as the ulna and there are correspondingly fewer outstanding differences between the various genera. The most striking differences, relating to the overall length and robustness of the radius, follow the same pattern as the shaft of the ulna. The radius in all the moles is relatively straight, although there is a gentle broad arching of the radius in the shrews examined. The broadening and torsion of the distal end also follows the pattern seen in the ulna. Reed (1951) noted the significance of the unique development of the capitular process of the radius in talpids.

In the Urotrichini a distinct crest extends distally from the posterodistal margin of the capitular process of the ulna (Fig. 15A). This crest is lacking in all the other Recent moles examined. The radial head of the M. abductor pollicis longis originates on the lateral side of this crest. In *Condylura* (Fig. 15B) the area of origin of this muscle still faces laterally but is on the shaft itself. In all the other more advanced moles, the area of origin forms a shallow posterior facing fossa or flattened area between the ulna facet and the midline of the shaft.

In *Scapanus* (Fig. 15C), *Talpa, Scalopus,* and *Parascalops* (Fig. 14) the lateral surface of the radius is grooved where the tendon of the M. abductor pollicis crosses it. The scars of the retaining ligament for the M. extensor carpi radialis are also well developed in these genera. Neither the grooves nor the scars are developed in *Urotrichus, Condylura, Neurotrichus,* or in the shrews. The angle of the groove for the tendon of the M. abductor pollicis is sharper in relation to the axis of the shaft in *Scalopus* and *Scapanus* than in *Parascalops* and *Talpa*. The proximal extremity of the capitular process culminates in a rounded or arched tuberosity proximal to the level of the ulnar articulation in all the moles examined except *Parascalops* and *Talpa*. In *Parascalops* the process is abruptly terminated at the level of the proximal border of the ulnar articulation. Aside from the distal expansion of the radius as in the ulna, the articular facets for the lunar and scaphoid are better delineated in

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[7] Comments on the skeleton of *Seaptochirus* other than those on the skull and humerus are based on illustrations by Young (1934).

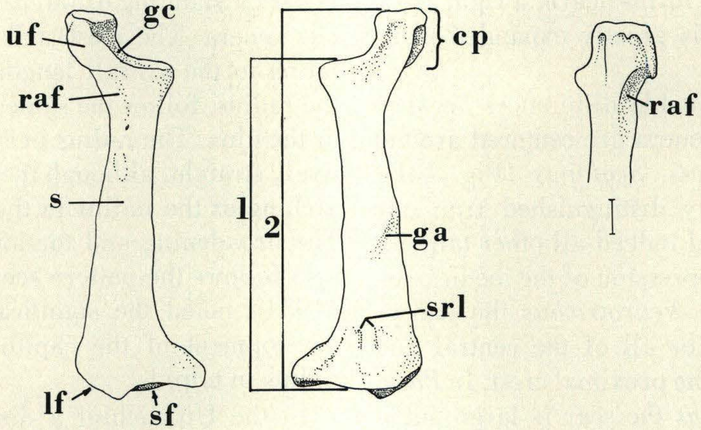

Figure 14. Left radius of *Parascalops breweri*, medial, lateral, and posterior views. **1**—length; **2**—shaft length; **cp**—capitular process; **ga**—groove for tendon of M. abductor pollicis longus; **gc**—glenoid cavity; **lf**—lunar articular facet; **raf**—fossa for radial head of M. abductor p. 1; **s**—shaft; **sf**—scaphoid articular facet; **srl**—scars of retaining ligament for tendon of M. extensor carpi radialis; **uf**—ulnar articular facet.

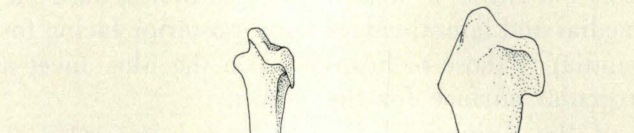

Figure 15. Left radii, posterior view of proximal end (top) and medial view (bottom). **A**; *Neurotrichus gibbsii*, **B**; *Condylura cristata*, **C**; *Scapanus townsendii.*

the more fossorial forms. This is easily seen in the outline of the distal end in medial view. In the Scalopina, *Parascalops* and *Talpa* this outline is distinctly scalloped whereas in *Condylura,* the Urotrichini and the shrews this outline is only a broad convex arch. The increased definition of the distal articular facets in the more fossorial forms is seemingly correlated with the increasing restriction of the hand to one (fore and aft) motion for digging.

SCAPHOID: I believe that virtually every bone in the carpus of the various talpines is distinctive at the generic level and probably at the species level as well in many cases. However, of all the carpals, only the scaphoid was recovered frequently in the fossil samples, so that I shall restrict broad comparisons to it. Other carpals will be discussed in the systematic section.

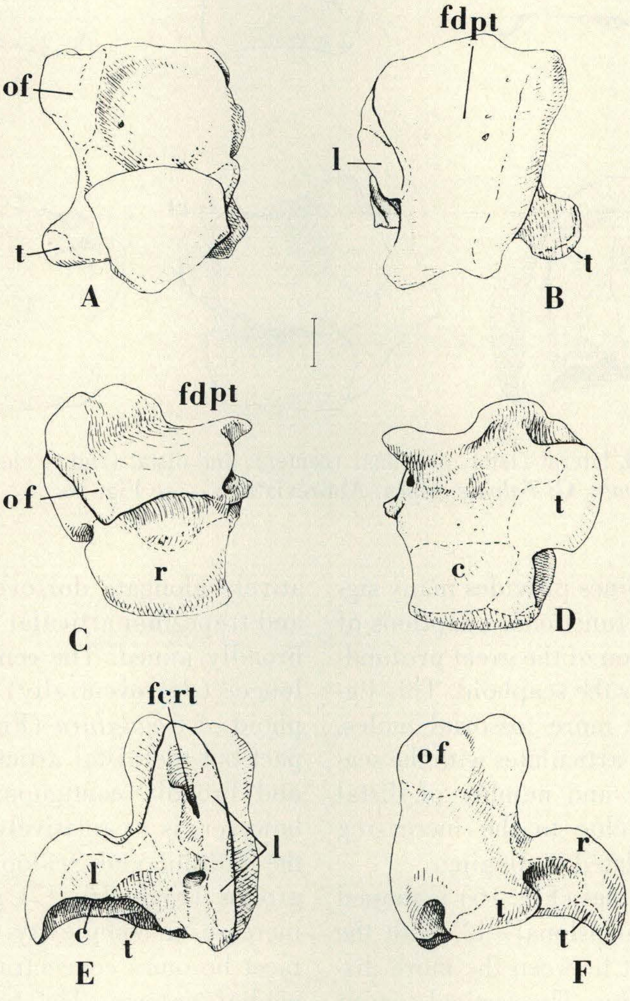

Figure 16. Left scaphoid of *Scapanus townsendii*, **A**; dorsal, **B**; ventral, **C**; proximal, **D**; distal, **E**; lateral, **F**; medial. **c**—central articular facet; **fcrt**—path of M. flexor carpi radialis tendon; **fdpt**—path of M. flexor digitorum profundus ligament; **l**—lunar articular facet; **of**—os falciformis articular facet; **r**—radius articular facet; **t**—trapezium articular facet.

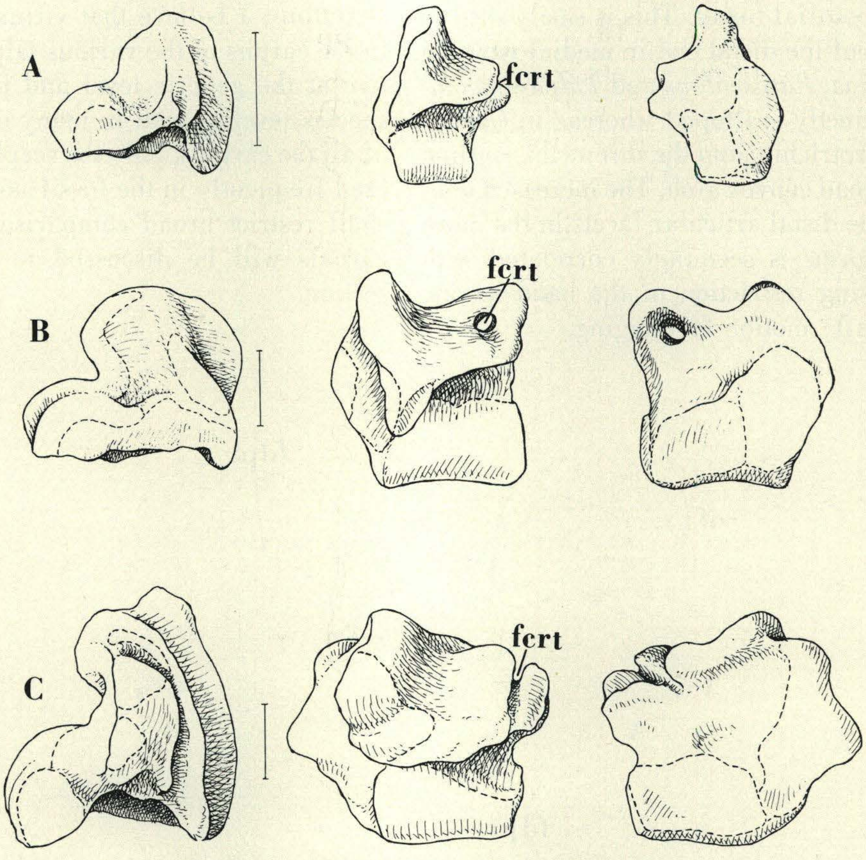

Figure 17. Left scaphoid, lateral (left), proximal (center), and distal (right) views. **A;** *Neurotrichus gibbsii,* **B;** *Condylura cristata,* **C;** *Talpa europea.* Abbreviations—see Fig. 16.

The scaphoid in talpines provides many significant clues as to the functional adaptions of the hand. A large portion of the great profundus ligament passes over the scaphoid. This ligament is larger in the more fossorial moles. The os falciformis also articulates with the scaphoid. The divergence and number of distal articular facets is a clue to the increasing breadth of the hand related to digging.

The scaphoid of talpines (Fig. 16) is shaped like a crude three dimensional "L" with the base being the segment between the more distal carpals and the radius. The vertical arm of the "L" forms the portion of the scaphoid over which the ligament of the M. flexor digitorum profundus rides and to which the os falciformis attaches. The scaphoid of the Urotrichini as exemplified by *Neurotrichus* (Fig. 17A) is relatively elongate dorsoventrally. The centrale and trapezium articular facets are simple and broadly joined. The central articular facet is longer (dorsoventrally) than broad. The scaphoid of *Condylura* (Fig. 17B) is more compact but the distal articular facets are simple and broadly contiguous. The central facet, however, is as relatively broad as it is in all the Talpini and Scalopini. In the latter two groups (Figs. 16, 17C) the trapezium facet increases in complexity. Most of the trapezium facet becomes concentrated on a well defined medial process. The trapezium facet in the Talpini is not distinctly notched as in the Scalopini. The changes in the shape of the centrale and trapezium articular facets reflect both the increase in the breadth of the hand and size of the more distal carpals.

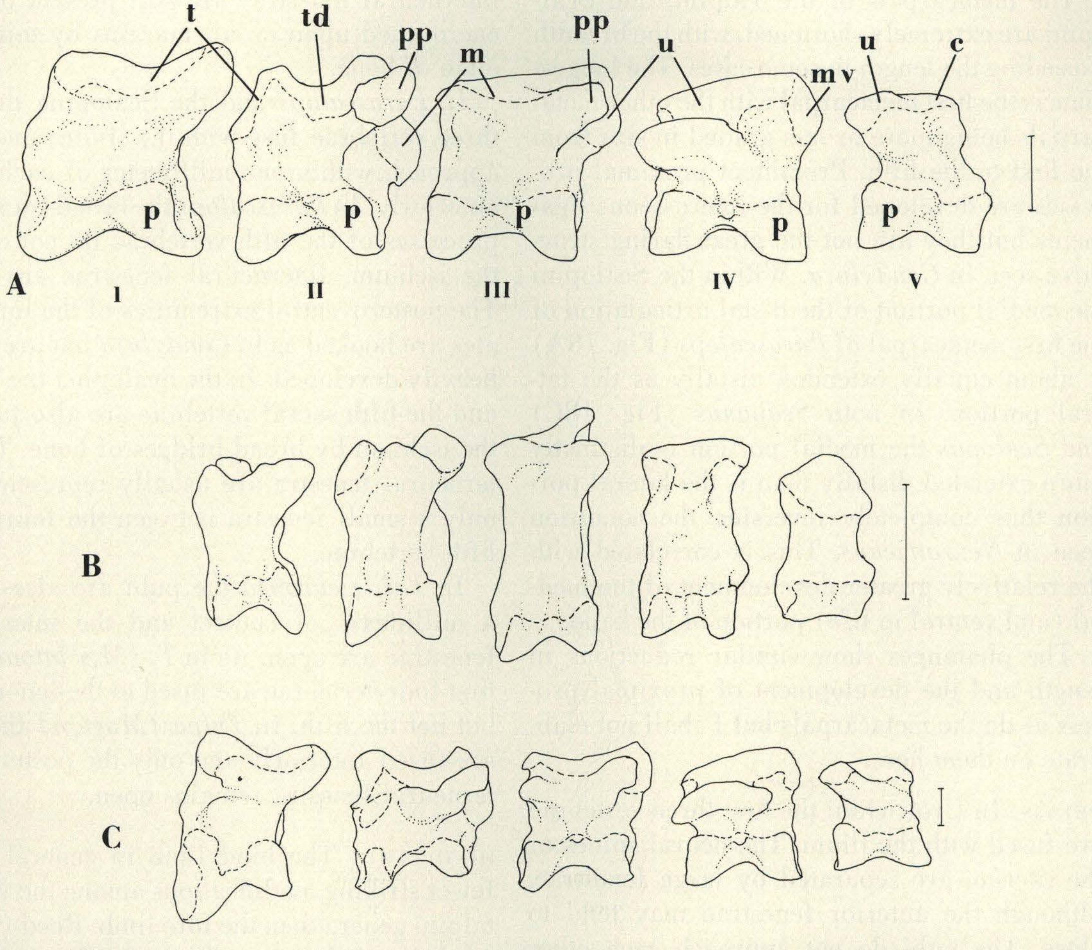

Figure 18. Right metacarpals, ventral view. **A;** *Parascalops breweri,* **B;** *Neurotrichus gibbsii,* **C;** *Scapanus townsendii.* **c**—cuneiform articular facet; **m**—magnum articular facet; **mv**—metacarpal V articular facet; **p**—phalanx articular facet; **pp**—proximal promínces; **t**—trapezoid articular facet; **td**—trapezoid articular facet; **u**—unciform articular facet.

METACARPALS: The metacarpals, like the scaphoid, offer many clues as to the breadth of the hand and in addition offer direct evidence of the shortening of the hand in response to increased fossorial ability.

The metacarpals of *Neurotrichus* (Fig. 18B) are more robust and notably shortend as compared to those of *Urotrichus.* The length of the metacarpals is still more or less symmetrically arranged in decreasing length about the long, third metacarpal. Proximal prominences on the ventral side for interosseous ligaments are poorly differentiated. The lateral moiety of the distal articulation of the first metacarpal is distinctly more distally extended than the medial portion.

The metacarpals of *Condylura* are, on the average, no shorter than in *Neurotrichus.* They are nearly equal in length but are slightly graded in size from the first to the fifth which is the longest metacarpal. The relatively great length of the fifth metacarpal may again be correlated with the semiaquatic habits of *Condylura.* The proximal prominences are more strikingly developed than in other talpines. The medial moiety of the distal articulation of the first digit is more distally extended than the lateral moiety.

The metacarpals of the Talpini, and Scalopini are extremely shortened, with the breadth exceeding the length in some cases. The longest bone is the first metacarpal with the other metacarpals being more or less graded in size from the first to the fifth. Prominent proximal processes are developed for the interosseous ligaments but they are not the great flaring structures seen in *Condylura.* Within the Scalopini the medial portion of the distal articulation of the first metacarpal of *Parascalops* (Fig. 18A) is about equally extended distally as the lateral portion. In both *Scapanus* (Fig. 18C) and *Scalopus* the medial portion is distinctly more extended distally than is the lateral portion thus completely reversing the condition seen in *Neurotrichus.* This is correlated with the relatively greater development of the medial (and ventral in life) portion of the hand.

The phalanges show similar reductions in length and the development of proximal process as do the metacarpals but I shall not elaborate on them here.

PELVIS: In Urotrichini the first three vertebrae are fused with the ilium. The neural spines of the sacrum are separated by large fenestrae, although the anterior fenestrae may tend to close. The pubi do not approach each other closely anteriorly. The fifth vertebra has well developed transverse processes.

In *Condylura* the first three and perhaps the anteriormost part of the fourth vertebrae fuse with the ilium. The neural spines are separated by moderately large fenestrae. Anteriorly the pubi come to within one millimeter of each other. The posteroventral extremity of the innominate is strongly hooked ventrally as in the Desmaninae, providing increased insertion and leverage of the M. adductor brevis et magnus. The transverse processes of the fifth vertebra are ligamentously joined to the ischium.

In *Scapanulus* the available innominate was severely damaged so the degree of pseudosymphysis was not determinable. The first three vertebrae are fused with the ilium. Slight bridges of bone apparently extended from the fourth and fifth vertebrae to the ischium. The interneural fenestrae are still present but are encroached upon on all margins by thin lamellae of bone.

In *Parascalops* and the Scalopina the first three vertebrae fuse with the ilium; and pubi approach within one millimeter of each other anteriorly. In *Parascalops* the broad transverse processes of the fifth vertebrae do not contact the ischium. Interneural fenestrae are large. The posteroventral extremities of the innominates are hooked as in *Condylura* but are not so heavily developed. In the Scalopina the fourth and the fifth sacral vertebrae are also fused to the ischium by broad bridges of bone. The interneural fenestra are usually represented by only a small fenestra between the fourth and fifth vertebrae.

In *Talpa europea* the pubi are also within a millimeter of contact and the interneural fenestrae are open. As in *T.* (*M.*) *latouchi* the first four vertebrae are fused to the innominate but not the fifth. In *Talpa (Mogera)* the pubi are fused anteriorly and only the posterior interneural fenestra remains open.

HIND LIMB: The hind limb in general shows fewer striking modifications among the various talpini genera than the fore limb. Reed (1951) gave detailed descriptions and figures of the hind limbs of *Neurotrichus* and *Scapanus.* Fortuitously these genera represent the two main morphological groups that I was able to distinguish among the genera examined.

FEMUR: In the femur of the Talpinae the proximal articular surface, besides extending toward the greater trochanter, also fans out posteriorly to approach the intertrochanteric notch and terminate near it in a ridge. This ridge usually causes an inflection in the intertrochanteric crest or results in the poor definition of the crest in its midregion.

The femur in the Urotrichini is relatively long and delicate. The femur in the Talpini and Scalopini resembles that of the Urotrichini except that the shaft is shorter and the whole femur is stouter. With one exception, in all Talpinae the condyles of the femur are convergent distally. In *Condylura,* however, the long axis of the lateral condyle has rotated so that it is parallel to that of the medial condyle. Elsewhere in the Talpidae, I have only seen this feature within the Desmaninae.

TIBIOFIBULA: The tibiofibulae fall into two well defined types. The Urotrichini type is characterized by a slender shaft and falciform process expended into a wide flange. Additionally the lateral process of the fibula is slender and bar-like with its dorsal extremity expanded into a hatchet-shaped structure. *Condylura* conforms to this type. The Scalopini type is characterized by the relatively stout shaft, narrow and hook-like falciform process, and the lateral process of the fibula expanded into a triangular plate just after leaving the body of fibula. *Scalopus, Scapanus, Talpa,* and *Parascalops* exhibit this type of tibiofibula. *Parascalops* retains a slightly expanded dorsal process on the fibula which is undoubtedly the homologue of the hatchet-shaped process in *Neurotrichus* but in overall construction the lateral process is more like that of *Scapanus.*

The elements of the foot were infrequently found in the fossil record of Oregon and thus the descriptive osteology of modern moles is not presented here.

SYSTEMATICS

TALPIDAE

Brief osteological diagnoses of the tribes of the Talpinae and subfamilies which include Oregon species are presented below. The other subfamilies are diagnosed in the osteological section.

Subfamily UROPSILINAE Dobson, 1883

Zygoma arched dorsally, bulla not expanded; manubrium simple; clavicle long and slender with articulations for humerus and scapula; humerus narrow, head rounded, open bicipital canal, no fossa for ligament of M. flexor digitorum profundus; ulna slender and without transversly expanded olecranon process; radius slender, no capitular process; feet elongate and shrew-like, ungual phalanges not bifid; pelvic girdle and hind limb shrew-like.

MYSTIPTERUS Hall, 1930

TYPE: *Mystipterus (Mystipterus) vespertilio* Hall, 1930;

INCLUDED SPECIES: *Mystipterus(Mydecodon) martini* Wilson, 1960. *Mystipterus (Mystipterus) pacificus*, n. sp.

KNOWN DISTRIBUTION: Middle Miocene (Hemingfordian) of Colorado, Late Miocene (Barstovian) of Oregon, and Early Pliocene (Clarendonian) of Oregon and Nevada.

AMENDED DIAGNOSIS: Small shrew-moles with dental formula; $\frac{?\ ?\ ?\ ?}{2\ 1\ 3\ 3}$ and/or $\frac{?\ ?\ ?\ ?}{3\ 1\ 3\ 3}$. P_1 (?) absent, P_2 single or double-rooted, P_3-P_4 double-rooted, P_2-P_4 graded in size, largest posteriorly. Lower molars with moderately brachyodont crowns, anterior, posterior and labial cingula present, entrocristid of M_2-M_3 extending to or near to bases of metaconids with concomitant basining of the postfossids. Trigonid cusps of M_1 crowded together, protoconid very low. Two mental foramina in lower jaw, posterior foramen beneath M_1. Posterior margins of upper molars concave, P^2 double-rooted and larger than P^3. *Uropsilus*-like humerus.

Mystipterus vespertilio Hall, 1930, was erected on the basis of a single worn and slightly damaged lower third molar and associated dentary fragment. Described originally as a vespertilionid bat by Hall, it was transferred to the Soricidae by Patterson and McGrew in 1939. The characters they used for placement within the Soricidae are characteristic of the Heterosoricinae only. Clark, Dawson and Wood (1964) pointed out that the features of the dentary used by Patterson and McGrew were not unique to the Soricidae, and would just as well serve to align *Mystipterus* with such diverse insectivores as *Nyctitherium*, *Micropternodus* or cf. *Myloestes*. It is indeed curious that these authors did not suggest affinities with the Talpidae, which in the light of the geologic age is more reasonable than some of the archaic early Tertiary insectivores. Van Valen (1967) independently arrived at alignment with the Talpidae but was (understandably) in doubt as to its affinities within the group.

Additional material of *Mystipterus vespertilio* from Fish Lake Valley, Nevada, was recently collected by J. A. Suthard and described in an unpublished Masters thesis. With his kind consent, this material was borrowed and is described below. Suthard noted the similarity between *Mystipterus vespertilio* and *Mydecodon martini* and considered them as congeneric although actual specimens of *M. martini* were not available to him at the time.

Wilson (1960) noted the similarity of *M. martini* with the shrew-moles comprising the Uropsilinae and Urotrichina. Although in reference to these groups, he stated that "it is hardly possible in the absence of both upper dentition and the humerus to state to which *Mydecodon* shows the closest affinities", he favored the Urotrichina on the basis of the construction of the talonid valleys. With both of the above restrictions now removed, at least in part, it is now possible to ascertain with greater certainty the relationships of these two moles as well as the third one described below.

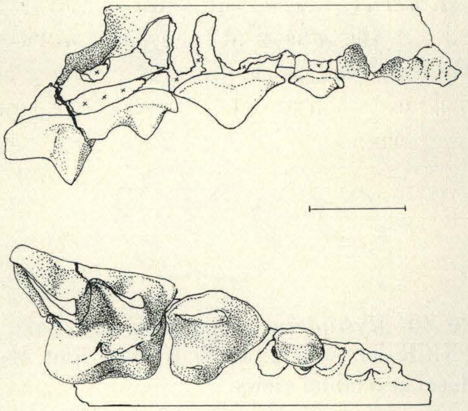

Figure 19. *Mystipterus vespertilio*, Fish Lake Valley, UCR loc V6302, UCR 10048, right maxillary fragment with P^3-M^1, occlusal and labial views.

The three species discussed below comprise the first avowed fossil Uropsiline moles either in the Old or New World. *Mystipterus vespertilio* is not assuredly known from Oregon, but its taxonomically important position to the New World uropsilines and relationship to the Oregon uropsilines in particular necessitate the description of the new and possibly topotypic material from the Esmeralda Formation of Nevada.

Mystipterus (Mystipterus) vespertilio Hall, 1930

(Figs. 19 and 20)

TYPE: UCMP 29604 from UCMP loc. V-2804.

REFERRED MATERIAL: UCR loc. V-6302 site 1. UCR 10048, maxilla fragment with P^3-M^1; UCR 10249, ectoloph of M^1; UCR 10246 and UCR 10248, M_1's; UCR 10044, M_2-M_3; UCR 10247, M_2 and trigonid of M_3; UCR 10245, dentary fragment with fragment of the M_3.

AMENDED DIAGNOSIS: Small shrew-mole with dental formula; $\frac{?\ ?\ ?\ ?}{?\ ?\ ?\ 3}$. Upper teeth brachyodont, P^2 double-rooted and larger than P^3, M^1 transversely broader than *Uropsilus*, well developed metaconule flange, anteriorly situated metacone and concave posterior margin. Lower molars like *Mystipterus martini* except with more cylindrical entoconids on M_1-M_2.

DESCRIPTION: Aside from the teeth, the maxilla fragment, UCR 10048, also retains three alveoli anterior to the P^3 (Fig. 19). The anteriormost alveolus is small and is followed by two larger alveoli apparently for a double-rooted P^2. The P^3 is small and ovate in occlusal outline. It is double-rooted. The single cusp is situated just anterior to the center of the tooth and is entirely enclosed by a narrow cingulum. If alveoli are a reliable indication of size, the P^2 was larger than the P^3. The three-rooted P^4 is subtriangular in occlusal outline with a low but prominent and elongate protocone. The principal cusp, the paracone, is centrally situated on the labial moiety. It is connected with the posterior extremity of the tooth by a broad sloping ridge. The cingulum is poorly preserved in places but appears to have enclosed the entire tooth except for the lingual margin of the protocone. Both premolars are very low crowned. The M^1 is also quite brachyodont and subquadrate in occlusal outline except for the typically extended metastylar region. The metaconule is situated anterior to and near the level of the metacone but the posterolingual margin of the metaconule is greatly extended posteriorly as in the soricids. This results in a deeply concave posterior margin on the tooth. The paraconule is only vaguely defined and is little more than a slight thickening of the anterior cingulum which connects the parastyle to the protocone. The metastyle shows an incipient twinning. Narrow labial cingula connect the mesostyle to the parastyle anteriorly and to the distal portion of the metacone-metastylar crest. The posterior cingulum is well defined on the labial moiety of the tooth but becomes poorly defined lingually.

Only the small part of the dentary that is associated directly with the molars is preserved, thus nothing is known of the antemolar dentition. Patterson and McGrew (1939) and Hall (1930) have already mentioned that the masseteric fossa extends downward nearly to the ventral margin of the jaw. There is a mental foramen below the middle of the trigonid of the M_1. The M_1 is very similar to that of *M. martini* except in the construction of the talonid. The entoconid of *M. vespertilio* is more cylindrical in cross section than in *M. martini,* and the postcristid instead of connecting with the tip of the entoconid joins the posterolabial margin of that cusp at the same level as the posterior accessory cusp. The entoconid and postcristid tend to form a continuous wear surface in most moles, but this peculiar arrangement in *M. vespertilio*, as in the majority of the soricids, delays the development of a continuous pattern until late wear. The specimens of the second molar differ somewhat from each other. UCR 10044 (Fig. 20) strongly resembles the corresponding tooth in *M. martini* except that the talonid differs, although less strikingly, as does the M_1. Additionally the talonid of the M_2 is relatively longer than in *M. martini.* The other specimen, UCR 10247, is somewhat larger (see Table 3) and the entocristid joins the protolophid a little more labially at the midpoint of the protolophid. The entire M_3 is preserved in the type and UCR 10044. The tip of the metaconid of the type specimen has apparently been broken off since the time of Hall's description (1930). The U.C. Riverside specimen compares favorably with the type in both size and morphology. The posterior cingulum tends to be better defined in *Mystipterus vespertilio* than in *M. martini.*

RELATIONSHIPS: As noted by Suthard (unpublished thesis) *Mystipterus vespertilio* bears a close relationship to *Mydecodon martini* of Wilson (1960) in the construction of the lower molars. Suthard considered the two forms to be congeneric on this basis; this arrangement is tentatively accepted. Wilson (1960) while noting a strong similarity between *Mydecodon martini* and *Uropsilus* nevertheless believed that *M. martini* bore a closer relationship to *Urotrichus* (*Dymecodon*) *pilirostris* (True) and *Urotrichus talpoides* Temminck based on the construction of the lower molar talonids. Judging from the material from other talpids on the whole, this was a good assumption. The upper teeth of *Mystipterus vespertilio,* however, indicate a strong degree of affinity with *Uropsilus.* The expanded metaconule shelf is unique to *Uropsilus* (Fig. 2A, 5C) within the living talpids. Unfortunately, the lack of preserved antemolar dentition prevents further comparison between *M. martini, M. pacificus,* and *Uropsilus.*

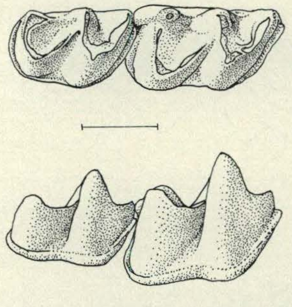

Figure 20. *Mystipterus vespertilio,* Fish Lake Valley, UCR loc V6302, UCR 10044, right M_2-M_3, occlusal and labial views.

Uropsilus and *Mystipterus* resemble each other in the morphology of the P^4, and overall shape, brachydonty, expanded metaconule shelf, labial cingulum, and concave posterior margin of the M^1. These characters in combination are unique to *Uropsilus* among the living moles. *M. vespertilio* differs from *Uropsilus* in the more brachyodont upper and lower teeth, shorter P^4, relatively smaller P^3, double-rooted P^2, larger P^2 than P^3, well developed entocristids and more lingual extensions of the cristae obliquae on the lower molars. The latter two characters, those noted by Wilson (1960) in *M. martini,* tend to make basins of the talonid crowns. It was also these two features which disuaded him from aligning *Mydecodon* with *Uropsilus.* Despite these differences from *Uropsilus,* I believe the character of the M^1 to be the single most significant feature upon which to align *Uropsilus* with *Mystipterus.* The occurrence, described below, of *Mystipterus-Mydecodon* lower teeth along with a uropsiline maxillary fragment and undoubted uropsiline humerus tend to substantiate this otherwise tenuous conclusion.

TABLE 3

Comparative Measurements of the Lower Dentition of *Mystipterus vespertilio, M. pacificus* and Related Forms

Specimen	P2		P4		M1		M2		M3		M1-M3	Depth of
	Lgth	Wdth	Lgth	Wdth	Lgth	Wdth	Lgth	Wdth	Lgth	Wdth	Length	Jaw
M. pacificus												
UO 22437	....	....	....	....	....	....	1.79	1.18	1.47	0.92	....	1.67
UO 22438 (Type)	....	....	1.04	0.66	1.64	1.18	1.71	1.11	1.35	0.82	4.55	1.72
UO 22345	....	....	....	....	....	....	1.82	1.16	1.43	0.91	....	1.65
UO 22346	....	....	....	....	....	....	....	....	1.44	0.73	....	....
UO 22350	0.71	0.50	1.02	0.75	....	....	....	....	....	....	....	....
UO 22567	....	....	....	....	1.60	1.12	....	....	....	....	....	....
UO 22570	....	....	....	....	1.62	1.19	....	....	....	....	....	....
UO 22577	....	....	....	....	1.73	1.18	....	....	....	....	....	....
M. cf. *M. pacificus*												
UO 24336	....	....	....	....	1.50	0.99	....	....	....	....	....	....
USNM 23771	....	....	....	....	1.60	1.13	1.67	1.17	1.40	1.00	4.80	1.67
USNM 23770	....	....	....	....	1.51	1.17	....	....	....	....	....	1.93
Mystipterus sp.												
UO 24786	....	....	....	....	1.70	1.20	....	....	....	....	....	1.82
UO 24787	....	....	....	....	....	....	....	....	....	....	....	1.60
M. vespertilio												
UCR 10246	....	....	....	....	1.53	0.93	....	....	....	....	....	....
UCR 10248	....	....	....	....	1.33	1.00	....	....	....	....	....	....
UCR 10247	....	....	....	....	....	....	1.57	0.97	....	....	....	....
UCR 10044	....	....	....	....	....	....	1.50	0.93	1.33	0.80	....	....
UO 29604 (Type)	....	....	....	....	....	....	....	....	1.18	0.77	....	....

Mystipterus (Mystipterus) pacificus,[8] n. sp.
(Figs. 21-27)

TYPE: UO 22438, an incomplete left dentary with P_4-M_3, roots of P_3 and the posterior root of the P_2.

HYPODIGM: UO 22437, UO 22345, UO 22346, UO 22350, UO 22601, fragmentary jaws and teeth; UO 22567, UO 22570, UO 22577, isolated M_1's; UO 22510, maxillary fragment with left M^2; UO 22309, right humerus lacking distal extremity; UO 26801, proximal extremity of left humerus. All specimens from the type locality.

REFERRED SPECIMENS: UO 22418, maxillary fragment with P^2-P^4; UO 22516, DP.^{4} Both from type locality.

TYPE LOCALITY: UO loc. 2465. Quartz Basin.
AGE: Barstovian.

DIAGNOSIS: Differs from the other species of the genus in larger size, relatively longer antemolar region, additional antemolar tooth, P_2 double-rooted, anterior mental foramen beneath P_2, paralophid more transversely aligned. Metaconule of M^2 posteriorly situated. P_4 relatively more massive than in *M. martini* and there is no pronounced expansion of the heel. Lower molars similar to those of *M. (Mydecodon) martini* except with more cylindrical entoconids.

DESCRIPTION: A single upper second molar, UO 22510, seems to be referable to *M. pacificus* on the basis of size and occlusal comparability with the lower molars of this species. It is too large for association with *Achlyoscapter*, n. gen., and too small for *Domninoides*. Since upper molars ascribed to *Scalopoides* with a high degree of certainty are also known from the same locality, this leaves *Mystipterus* the probable associate. The tooth (Fig. 21) is roughly rectangular in occlusal outline being wider than long. The cusps are heavily worn and the metastyle is broken off. The ectoloph is W-shaped and the mesostyle may have been twinned but, if so, this is obscured by wear. The paraconule, protocone, and metaconule are united in wear but all are easily distinguishable. The protocone is the largest of the labial cusps. The paraconule is about half the size of the protocone and separated from it by a deep lingual furrow. The metaconule is situated posteriorly slightly posterior to the level of the center of the metacone. The base of the metacone is expanded to such an extent that this cusp and the metastyle form the posteriormost extremities of the tooth while contributing to the concave posterior margin of the tooth. A narrow paracingulum extends from the paraconule to the parastyle and a faint metacingulum is present posteriorly. The labial root is very broad anteroposteriorly originating from the base of the protocone to the metaconule. The distal extremity of this root is expanded still further into a hatchet-shaped structure. The root is transversely compressed. The M^2 is about 1.5 mm. long and 1.94 mm. wide.

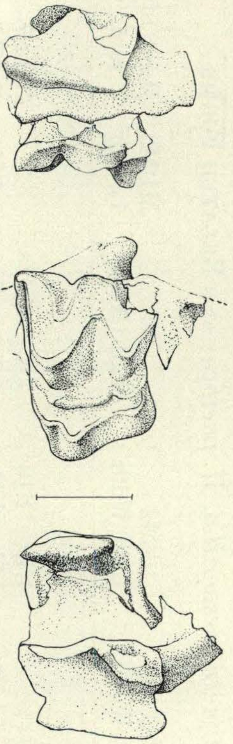

Figure 21. *Mystipterus pacificus* n. sp. Quartz Basin, UO loc 2465, UO 22510, left M^1 and maxillary fragment, labial, occlusal, and dorsal views.

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[8] From the Latin *pacificus*, alluding to its Pacific Coast occurrence.

Although only a small fragment of the maxilla is adhering to the M^2, several significant features are preserved. A blade-like process terminating dorsal to the metastylar region of the M^2 extends laterally from the maxilla. The process apparently originated in part anterior to the M^2. I believe this process to be homologous to the subzygomatic process of the maxilla in *Uropsilus* (see Fig. 2A). A low crest extends from the posterior margin of the subzygomatic process dorsally to the posterior edge of a dorsally directed process. This latter process is transversely compressed. Its longitudinal breadth is not surely determinable on this specimen but it does not appear to have extended anterior to the level of the M^2. A sharp ridge of bone extends anterior from the base of the dorsally directed process and forms along with it part of the external wall of the infraorbital canal. Very little of this ridge is preserved and its crest appears to be broken off so that I was not able to determine whether it is simply a ridge or part of the base of the infraorbital bridge. There are two probable interpretations of the above structures. One is that the root of the dorsally directed process is that of the infraorbital bridge as in the Talpinae, Desmaninae, and Proscalopinae, and the other that this structure is the base of a dorsally arched zygomatic arch as in *Uropsilus.* The latter interpretation seems more likely to me in the light of the following facts: (1) there is no other apparent process suggested or evident from the specimen which would give rise to a posteriorly projecting root of the zygomatic process, (2) the position and fragility of the root of the alleged zygomatic process is extremely similar in development and position to that of *Uropsilus,* (3) the well defined infraorbital canal shows no indication of fanning out anteriorly as in the non-uropsiline moles, (4) and the short ridge preserved in this specimen anterior to the zygomatic root suggests that another process, the infraorbital ridge, is present anteriorly.

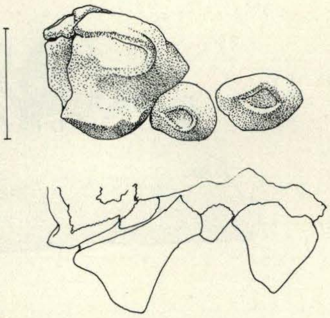

Figure 22. *Mystipterus pacificus* n. sp. Quartz Basin, UO loc 2465, UO 22318, right P^2-P^4, occlusal and labial views.

Like the other specimens referred to this species, a fragment of the snout with P^2-P^4, UO 22418, is referred to *M. pacifiicus* by elimination and by general size agreement. The three teeth are crowded together so that about half of the P^3 is concealed in lateral view by the P^2 and P^4 (Fig. 22). The P^3 is smaller than the P^2. The P^2-P^3 are simple single cusped teeth. The P^2 has a relatively higher and sharper cusp than the P^3. The P^2 is double-rooted. The P^4 is badly damaged by crushing. It has the same general form and morphology as *Scalopoides ripafodiator* but is smaller.

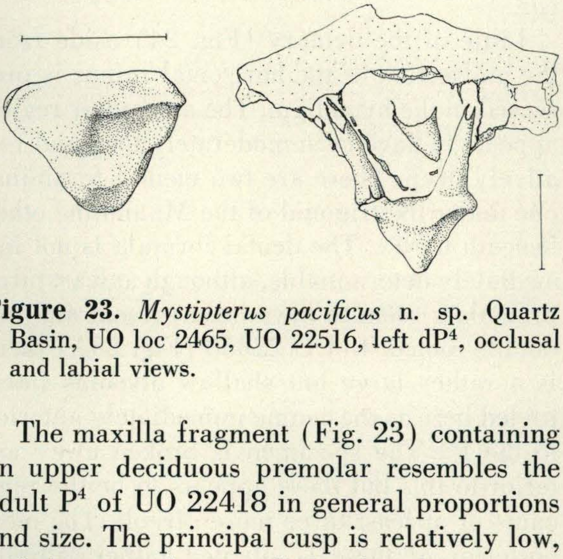

Figure 23. *Mystipterus pacificus* n. sp. Quartz Basin, UO loc 2465, UO 22516, left dP^4, occlusal and labial views.

The maxilla fragment (Fig. 23) containing an upper deciduous premolar resembles the adult P^4 of UO 22418 in general proportions and size. The principal cusp is relatively low, and there is a large well developed protocone lingually. A cingulum encompasses the tooth except for the protocone. The three roots diverge strongly as is commonly the case in deciduous teeth. The apex of an incompletely formed adult P^4 is discernible in the cavity

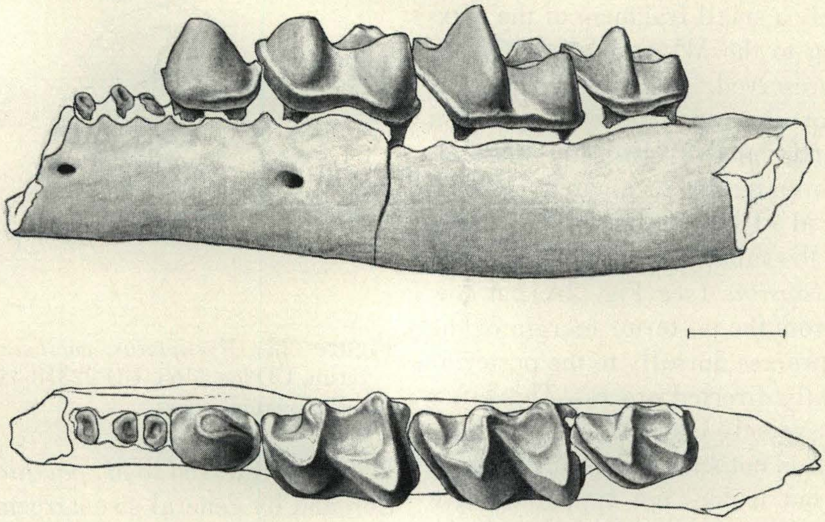

Figure 24. *Mystipterus pacificus* n. sp. Quartz Basin, UO loc 2465, Type specimen UO 22438, labial and occlusal views.

between the roots of the dP^4. There is usually a general similarity between the permanent tooth and its deciduous predecessor in talpids in both size and morphology and it is for this reason that UO 22516 is referred to *M. pacificus*.

Little of the dentary (Fig. 24) aside from the midsection of the horizontal ramus is preserved in the hypodigm. The antemolar region appears to have been moderately long and relatively deep. There are two mental foramina, one under the trigonid of the M_1 and the other beneath the P_2. The dental formula is not immediately determinable, although at least three premolars seem to have been present and are double-rooted. In UO 22350 (Fig. 25A) there is a rather large but shallow alveolus interpreted here as the canine immediately anterior to the P_2. The specimen is broken away anterior to this but there appears to be the remnants of at least three more alveoli. The most posterior of these is situated rather labially and is flanked anterolingually by the remains of a second alveolus. Ventrally on the broken anterior surface of this specimen, the posterior extremity of still another alveolus may be seen. The tooth was apparently rather procumbant and is interpreted as the I_1. These three anterior alveoli are assumed to represent the I_1 to I_3. There are several other interpretations for the four anterior alveoli. The two alveoli in front of the P_2 may have held an enlarged P_1 as in the Talpini. The P_1 may be single-rooted. The P_1 may be single or double-rooted and there were additional alveoli not in evidence. However, for the sake of description and for subjective reasons, I shall consider the dental formula to be I3, C, P3, M3.

The P^2 is dominated by a high protoconid encircled by a small cingulum with a very small paraconid. The roots of the P_2 are longitudinally aligned but compressed anteroposteriorly as are those of the succeeding premolars. The P_4 is a larger version of the P_2. The protoconid is very sharp. There is no pronounced expansion of the posterior cingulum into a heel; although the most posterior part of the cingulum is somewhat cuspidate. A distinct groove descends the posterior slope of the protoconid which in *M. martini* is either absent or effaced by wear or breakage.

The M_1 is rather wedge-shaped with the trigonid shorter and narrower than the talonid. There are narrow anterior, labial and posterior cingula. The anterior cingulum is incomplete lingually. There is a prominent postero-

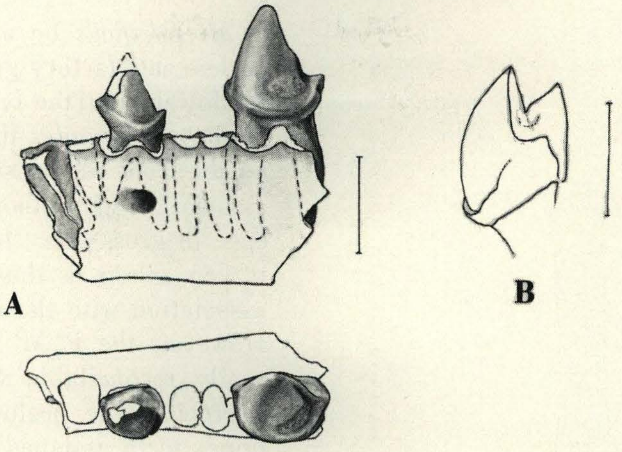

Figure 25. *Mystipterus pacificus* n. sp. Quartz Basin, UO loc 2465, **A;** UO 22350, left dentary fragment with P_2 and P_4, labial and occlusal views, dashed outlines of roots restored from X-ray photograph, **B;** UO 22577, unworn right M_1, anterior view.

internal accessory cuspule. The protoconid is the tallest cusp followed by the equally tall hypoconid, entoconid and metaconid. The paraconid is exceedingly low (Fig. 25B), small and more transversely aligned than in *M. martini* or *M. vespertilio.* The crista obliqua intersects the protolophid about midway along its length. There is no metastylid but a low distinct entocristid extends to the base of the metaconid thus enclosing the postfossid. The labial cingula are interrupted by the hypoconid in the M_2-M_3. The M_2 is more rectangular than the M_1 and the trigonid and talonid are about equal in length and breadth. The morphology of the M_2 of *M. pacificus* closely resembles that of *M. martini* and *M. vespertilio* except that the trigonid is somewhat more compressed anteroposteriorly and the anterior cingulum is not as relatively large. The entrocristid abuts against the base of the metastylid which is more or less fused with the metaconid. The M_3 of *M. pacificus* is not significantly different from that of the other species.

The two incomplete humeri (Fig. 26) are referable to the Uropsilinae. The Quartz Basin specimens are a little longer and somewhat more robust than the humerus of *Uropsilus* but otherwise correspond in morphology to nearly the finest detail.

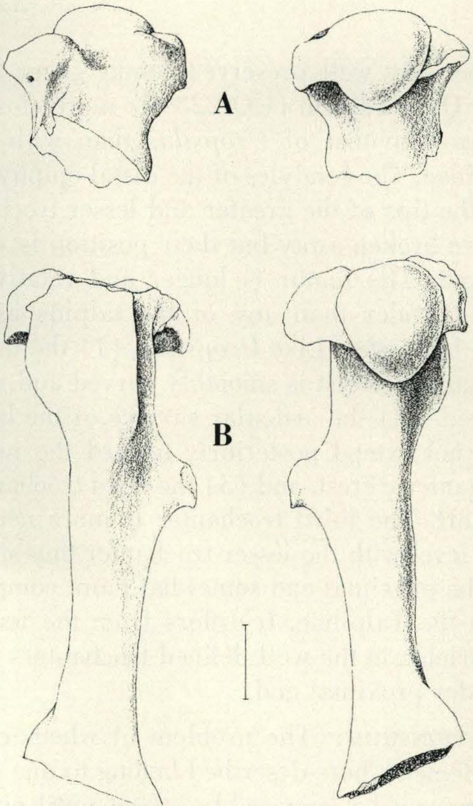

Figure 26. *Mystipterus pacificus* n. sp. Quartz Basin, UO loc 2465, **A;** UO 26801, left proximal portion of an uncrushed humerus, anterior and posterior views, **B;** UO 22309, right humerus with proximal end fractured and rotated postero-distally, anterior and posterior views.

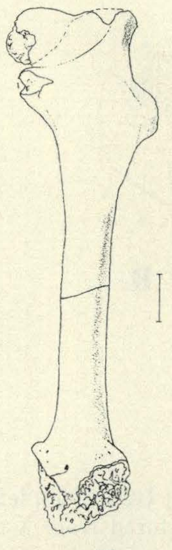

Figure 27. *Mystipterus pacificus* n. sp. Quartz Basin, UO loc 2465, UO 22399, right femur, posterior view.

The only well preserved femur (Fig. 27) from Quartz Basin (UO 22399) more closely agrees with that of *Uropsilus* than with the Talpinae. The condyles of the distal epiphysis, and the tips of the greater and lesser trochanter are broken away but their position is well marked. The femur is longer and relatively more slender than any of the talpids aside from *Uropsilus*. Like *Uropsilus*, (1) the intertrochanteric crest is smoothly curved and well defined, (2) the articular surface of the head does not extend posteriorly toward the intertrochanteric crest, and (3) the third trochanter is short. The third trochanter is more nearly on a level with the lesser trochanter thus making the proximal end somewhat more compact as in the Talpinae. It differs from the femur of soricids in the well defined trochanters and broader proximal end.

RELATIONSHIPS: The problem of whether all the elements here described belong to one species cannot be irrevocably solved until either an articulated skeleton or a number of large samples become available. The similarity of the maxilla and humerus to *Uropsilus* indicate that these elements, at least, belong to the same species. The femur is likewise assigned to *M. pacificus* on a similar basis although on less satisfactory grounds. This leaves only the lower jaw (the type specimen) in serious doubt. *Scalopoides* may be easily eliminated on the basis of the sampling which indicates association with other limb bones and difference in gross size. *Achlyoscapter longirostris* n. gen. et. sp. is thus the last possibility for association with the maxilla and limb bones. However, the P^4-M^1 of *Achlyoscapter* is not easily reconcilable with M^2 assigned to *M. pacificus*. The occlusal relationships of the upper teeth assigned to *A. longirostris* agree very well with the type jaw of *Achlyoscapter* but not with that of *M. pacificus*. The M^1 *of A. longirostris* and the M^2 of *M. pacificus* do not compare well serially as one would expect if they represented the same species. The M^2 assigned to *M. pacificus* occludes well with lower teeth of this species. Lastly, the occurrence of *Mystipterus* lowers with uropsiline upper teeth in the two Clarendonian localities tends to support my conclusion that *Mystipterus* is a uropsiline mole.

The referred humerus alone is sufficient to situate *M. pacificus* within the Uropsilinae. The possession of a submaxillary process, dorsally directed zygomatic process and concave posterior margin of the M^1 which are otherwise unique to *Uropsilus* offer further confirmation of uropsiline relationships. The presence of three double-rooted premolars in the lower jaw as compared to only two in the *Uropsilus* examined is nearer the theoretically more primitive condition than either *M. martini* or *Uropsilus*. The presence of rather transversely elongate upper molars may likewise represent something nearer to the primitive condition. The development of the transversely shorter M^1 of *M. vespertilio* represents a further step toward the condition in *Uropsilus*.

M. pacificus differs in the lower jaw from *M. martini* and *Uropsilus* in its probable greater number of teeth, presence of three double-rooted premolars, and relatively longer and deeper antemolar region. It is further distinguishable from *Uropsilus* by the convergence of the entocristid and crista obliqua on the metastylid, transversely longer M^2 with a more posteriorly situated metaconule, and bladelike subzygomatic process. *M. pacificus* is distinguishable from both *M. vespertilio* and *M. martini* by its larger size and more convergent entocristid and crista obliqua on the lower molars. On the basis of serial analogy the M_2 of *M. pacificus* would seem to differ from that of *M. vespertilio* (as deduced from the M_1) in its relatively greater width and more posterior metaconule and concomitantly less developed metaconule flange. If the maxillary fragment, UO 22418, is properly assigned to *M. pacificus*, additional differences between *M. pacificus* and *M. vespertilio* include higher crowned teeth and reduced cingula on the P^2-P^3.

M. pacificus, while not the earliest record of the uropsiline moles, appears to be the most primitive on the whole. A similar situation with regard to the Quartz Basin moles is exemplified by *Scalopoides ripafodiator* n. sp. described below.

Mystipterus cf. *M. (Mystipterus) pacificus*

Specimens from four Barstovian localities are referable to *M.* cf. *M. pacificus* and are described below. A single M_1, UO 24336, from Red Basin loc. 2495 is indistinguishable from that of *M. martini* except for its slightly larger size. A jaw fragment containing the M_1-M_3, USNM 23771, from Guano Ranch USGS loc. M 1042 is the size of the Quartz Basin species but has the molar morphology and relative molar size of *M. martini.* Another jaw fragment, USNM 23770, from the same locality retains a well worn M_1 and has a deeper jaw than USNM 23771, but this is probably an allometric feature.

The variation noted in the molar patterns and sizes (Table 3) of the specimens of *Mystipterus* from Quartz Basin, Red Basin, and Guano Ranch, could well be that encompassed within a single species. The lack of sufficient material from the last three localities precludes any such definite assignment. The upper dentition, variation, and morphology of the antemolar region remains the best known criterion for distinguishing the species of *Mystipterus.* Size (used broadly), geologic age, and geographic distribution argue for tentative assignment of eleven of these specimens to *M.* cf. *pacificus* until better material demonstrates otherwise.

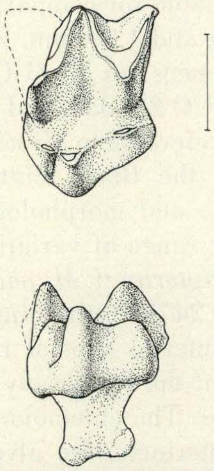

Figure 28. *Mystipterus* sp. Black Butte II, UO loc 2500, UO 24780, left M^2, occlusal and lingual views.

Mystipterus (Mystipterus) sp.
(Fig. 28)

An upper M^2, UO 24780, very similar to the one referred to *M. pacificus* was recovered from Black Butte, UO loc. 2500. The anterolabial extremity is broken away but the tooth is little worn and therefore has some features not directly observable in the *M. pacificus* specimen. The pronounced difference between the two specimens is that the lingual sulcus which separates the paraconule and protocone is much deeper in the Black Butte specimen. The paraconule, protocone, and metaconule are distinct. The tooth is lower crowned than *Scalopoides* or *Neurotrichus* but in agreement with *Uropsilus.* The base of the metaconule has the same extended base as in the Quartz Basin specimen and has a concave posterior margin. The parastyle is only minutely developed but a narrow paracingulum is present. The mesostyle shows no particular indication of division. The lingual root is similar to the Quartz Basin specimen although somewhat twisted. A small papiliform root somewhat labial to the center of the tooth is also preserved. The metacone crests of the ectoloph are equal in length and both shorter than the paracone crests of the ectoloph as in *Uropsilus*. The morphology of the paraconule is nearly identical to that of the *Uropsilus pilirostris* specimen available for comparison. The M^2 is 1.80 mm. long and 1.99 mm. wide.

Three specimens, an M_1 (UO 24786), talonid of an M_2 (UO 25183), and a jaw fragment (UO 24787) referable to *Mystipterus* were recovered from the Black Butte UO locality 2500. The size and morphology of the teeth fall within the range of variation of those referred to *Mystipterus* cf. *M. pacificus*. The jaw fragment (UO 24787) retaining all the alveoli between the anterior root of the M_2 and the anterior root of the P_2, closely resembles that of *M. pacificus*. The antemolar portion shows little taper anteriorly, the alveoli are not so crowded together anteroposteriorly, and the antemolar length may have been relatively longer than that of *M. pacificus*.

Again the serial comparison of the M^2 of *Mystipterus* sp. with the M^2 of *M. vespertilio* tends to distinguish these species. These specimens and *M. vespertilio* constitute the latest known record of the genus.

Summary of *Mystipterus* relationships

Wilson (1960) compared *Mystipterus (Mydecodon)* with nearly all the reasonably well known and possibly related genera from Europe. I, like he, have been handicapped in comparing the North American material with the European by the lack of sufficiently detailed descriptions and figures or the lack of suitable comparative material. *Mystipterus* may be distinguished from all the described European small talpids where upper molars or humeri are known or are nominally associated. No assuredly uropsiline moles are yet known as fossils from Europe, but it is possible that some material has been misassigned as in the American genera.

Aside from the lower molars and possibly a few upper premolars, *M. (Mystipterus) vespertilio* and *M. (Mystipterus) pacificus* are not comparable by direct means. *M. vespertilio* appears to be specializing in the direction of *Uropsilus* in the upper dentition and the lower dentition of *M. martini* has already achieved the antemolar reduction characteristic of *Uropsilus*. The construction of the lower molars alone serves to distinguish *Mystipterus vespertilio* from *Uropsilus*. The development of the more open talonid of *Uropsilus* is not an insurmountable barrier to the interpretation that *Uropsilus* is a descendant of *Mystipterus*, even if only American forms are considered.

All the species here assigned to the genus *Mystipterus* are so referred on the basis of the similar morphology of the lower molars. To assign them all to the same genus without recognition of subgenera would tend to obscure the marked differences between antemolar regions of *M. (Mydecodon) martini* and *M. (Mystipterus) pacificus*.

M. vespertilio is tentatively aligned with *M. pacificus* under the subgenus *Mystipterus* but the largely uncomparable material of *M. vespertilio* make this arrangement largely one of convenience.

The more primitively generalized and less reduced antemolar dentition of *M. pacificus* would tend to remove it as a direct descendant of *M. martini* but the sharing of at least an early Miocene common ancestor seems probable. The phyletic position of *M. vespertilio* must remain in doubt until the acquisition of more material.

Subfamily GAILLARDINAE, new

INCLUDED GENERA: *Gaillardia* Matthew, 1932.

KNOWN DISTRIBUTION: Middle Pliocene (Hemphillian) of Oregon and Nebraska.

DIAGNOSIS: (Based on *Gaillardia*): An aquatic desman-like mole; lower molars with anteroposteriorly compressed trigonids and talonids, wide separation of the metaconids and metastylids; dentary with small coronoid and angular processes, angular process buttressed by anterior ascending ridge of bone; clavicle long but moderately robust; humerus with open bicipital canal, no fossa for the ligament of M. flexor digitorum profundus, ovate head, lesser tuberosity lower than head, deltoid process separated from greater trochanter, prominent teres tubercle; femur with third and greater trochanters fused together, intertrochanteric crest extends laterally to third trochanter, medial epicondyle spikelike, lateral epicondylar sesamoid fused to epicondyle; distal end of tibiofibula with two anterior and three posterior tendonal grooves; calcaneum and cuboid relatively short and compact; metacarpals long and twisted.

GAILLARDIA Matthew, 1932

GENOTYPE: *Gaillardia thomsoni* Matthew, 1932.

KNOWN DISTRIBUTION: Same as for subfamily.

DIAGNOSIS: Same as for subfamily.

Gaillardia thomsoni Matthew, 1932 (Fig. 29-38)

Hydroscapheus americanus Shotwell, 1956, p. 724.

TYPE: AMNH 20508, right lower jaw with P_3-P_4 and M_3 preserved.

REFERRED SPECIMENS: UO 9415, UO 26827, two edentulous mandible fragments; UO 24810 M_1; UO 25125, M_2; UO 24815; trigonid of a lower molar; UO 26824 and UO 26825, two upper premolars; UO 3206, clavicle; UO 3185, UO 3505, UO 4101, UO 24811, UO 26829, three complete and two partial humeri; UO 26830, proximal portion of an ulna lacking the end of the olecranon process; UO 26831, third metacarpal; UO 4102, damaged sacrum; UO 2412, UO 2443, UO 2888, UO 2902, UO 3682, UO 3814, caudal vertebrae; UO 2698, UO 3200, UO 10381, UO 25125, two complete and two partial femora; UO 2456, UO 3792, UO 24808, UO 24809, UO 26832, distal ends of tibiofibulae; UO 3815, midshaft of tibiofibula; UO 3376, UO 3414, UO 24807, UO 26833, calcanea; UO 26834, cuboid; UO 25127, UO 26836, two fourth metatarsals; UO 2400, UO 2415, UO 26837, distal ends of metatarsals; all of the above from UO locality 2222.

Subsequent to Shotwell's (1956) original collections and description of *Hydroscapheus americanus*, additional specimens were collected among which is an edentulous incomplete mandible, UO 9415. The specimen (Fig. 29) lacks the portion of the jaw anterior to the P_3 and the extremities of the coronoid process, condyle, and angular process. The remaining portion of the dentary is essentially identical to that of *Gaillardia thomsoni* Matthew from the Upper Snake Creek beds of Nebraska. The two forms here are considered as conspecific.

In comparison to Desmaninae (see Schreuder, 1940) the lower jaw of *Gaillardia thomsoni* exhibits a number of differences. The whole ascending ramus slants posterodorsally rather than directly dorsal. The coronoid process is relatively shorter and much more slender and delicate. Conversely, the condylar process is longer and relatively stronger. The condylus is small, slightly ovate, and not transversely expanded. The angular process is dorsoventrally compressed, transversely expanded, and relatively smaller and shorter than in the Desmaninae. The posterior mental foramen is below and a little posterior to the posterior root of the M_1. The anterior mental foramen is below the alveolus of the canine (P_1 of Matthew). On the labial side a ridge of bone extends from the angular process to a region somewhat above the angle of the horizontal

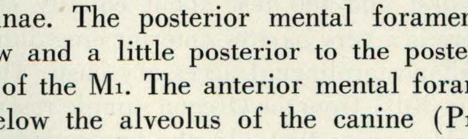

Figure 29. *Gaillardia thomsoni*, McKay Reservoir, UO loc 2222, UO 9415, left mandible, left lateral view.

TABLE 4

MEASUREMENTS OF THE DENTARY OF *Gaillardia thomsoni*

	Type	UO 9415
Length P_1-M_3 alveoli	12.3	.....
Length M_1-M_3 alveoli	6.8	7.3
Height of ramus (internal) behind M_1	3.5	3.8
Posterior border of jaw to anterior border of ascending ramus	4.9	5.4
Width of condylus	1.4	.....

and ascending rami; this ridge is entirely absent in the Desmaninae. The mandibular foramen is situated in about the same position as in *Galemys*. The lower dental formula of *G. thomsoni* is here considered to have been complete with all the teeth anterior to the P_3 single-rooted. The anterior incisor was probably hypertrophied.

In the type of *Gaillardia* the P_3 is slightly larger than the P_4 which is simpler in form than in *Desmana*. In the Oregon specimen of the M_1 (Fig. 30A), the crista obliqua unites with a metastylid which is not joined to the metaconid. This feature relates to the greater anteroposterior compression of the talonid and more spacious hypoflexid. The degree of expression of the major cusps is about the same as in the Desmaninae with the paraconid the smallest and the rest about equally strong. There is a very narrow anterior cingulum and small posterolingual accessory cusp. The M_2 (Fig. 30B) from the Oregon sample resembles the M_1 except that (1) the trigonid is more compressed, (2) the anterior cingulum is absent, (3) the trigonid is wider than the talonid, (4) there is a well developed anterolingual accessory cusp. The M_3 of the type of *Gaillardia* is heavily worn but shows the compressed trigonid of the preceding teeth and large hypoflexid. All the molars lack ectostylids.

Of the isolated antemolars referred to this form, two closely resemble the P^2 of *Galemys* in proportions. They have a large principle cusp (Fig. 30C) with anterior and posterior accessory cuspules and narrow internal cingulum.

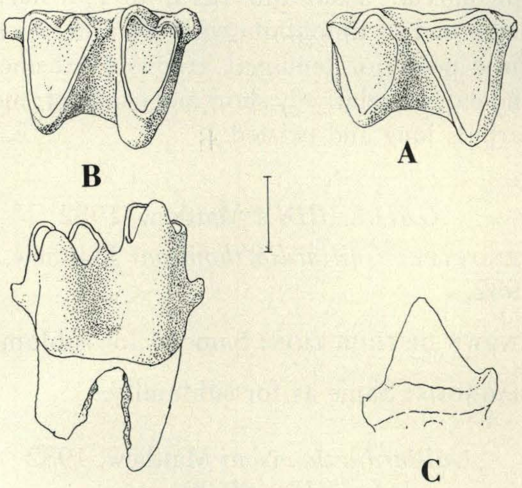

Figure 30. *Gaillardia thomsoni*, McKay Reservoir, UO loc 2222, **A;** UO 24810, left M_1, occlusal view, **B;** UO 25125, right M_2, occlusal and labial views, **C;** UO 26825, left upper premolar, lingual view.

TABLE 5

MEASUREMENTS OF THE LOWER TEETH OF *Gaillardia thomsoni*

	length	width
P_3 (Type)	1.65	1.06
P_4 (Type)	1.60	1.00
M_1 (UO 24810)	2.45	1.90
M_2 (UO 25125)	2.59	1.90
M_3 (Type)	2.24	1.66

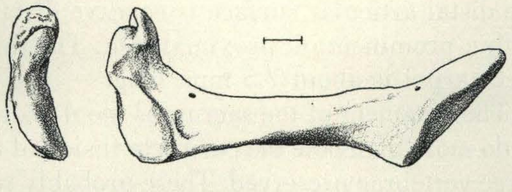

Figure 31. *Gaillardia thomsoni*, McKay Reservoir, UO loc 2222, UO 3206, left clavicle, posterior and distal views.

Shotwell (1956) previously described most of the postcranial elements of *Gaillardia*; however, I wish to call attention to additional features not specifically mentioned by Shotwell, and in contrast to the Desmaninae. The clavicle (Fig. 31) of *Gaillardia* differs from the Desmaninae in that (1) the distal end is as wide or wider than the proximal end, (2) the humeral articular surface is relatively smaller, and (3) there is a prominent dorsally directed process on the distal end. This process is terminated by a peculiar callosity, possibly anomalous, but also possibly the remnant of the scapular artculation which is present in this position in *Uropsilus*.

The humerus (Fig. 32) differs from that of the Desmaninae in a number of features already listed by Shotwell (see diagnosis of subfamily) and additionally in (1) head not separated from greater tuberosity by a deep channel, (2) deltoid process separated from the greater tuberosity by a broad concavity, (3) shape of pectoral process closer to *Uropsilus*, (4) area of muscle attachment on teres tubercle strongly oblique to shaft, (5) lesser tuberosity lower than head, (6) broader distal end, and (7) no deep notch sharply separating trochlea from the ventral margin medially.

The ulna fragment (Fig. 33) preserved few features except those in the immediate vicinity of the semilunar notch. As preserved the ulna resembles that of the Desmaninae in its narrowness, undeveloped coronoid process, narrow articular surface, and proximal third bowed

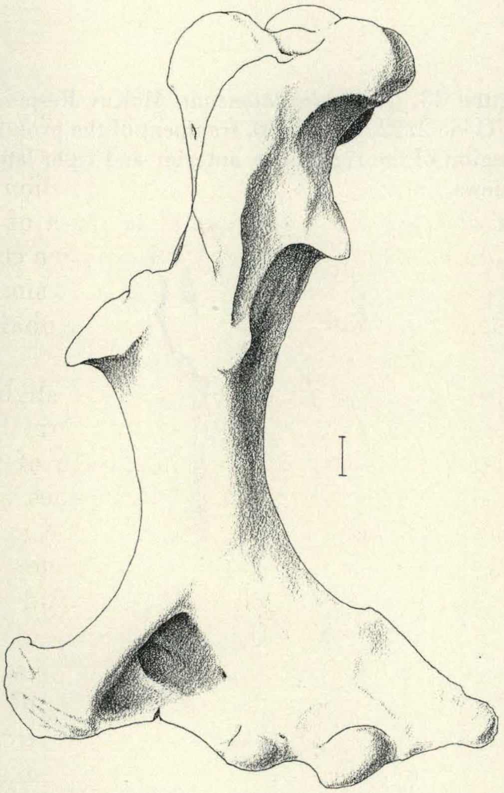

Figure 32. *Gaillardia thomsoni*, McKay Reservoir, UO loc 2222, UO 26829, left humerus, anterior view.

TABLE 6

MEASUREMENTS OF THE HUMERI OF *Gaillardia thomsoni*

	UO 4101	O 24811	UO 26829
Length	18.6	18.0	20.1
Width of proximal epiphysis	5.0	5.7	6.25
Minimum shaft width	2.9	3.0	3.35
Width of distal epiphysis	10.0*	11.3e	12.9

e Estimated measurement

* Noticeable abrasion or breakage tending to reduce measurement

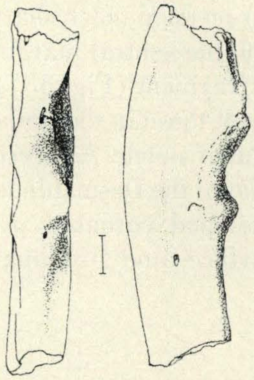

Figure 33. *Gaillardia thomsoni*, McKay Reservoir, UO loc 2222, UO 26830, fragment of the proximal region of the right ulna, anterior and right lateral views.

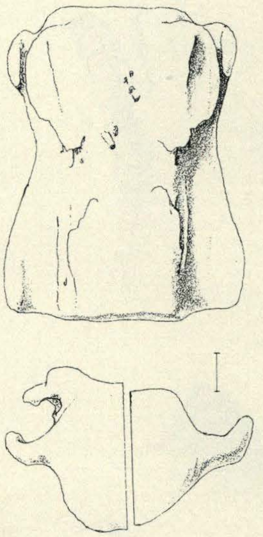

Figure 34. *Gaillardia thomsoni*, McKay Reservoir, UO loc 2222, UO 2443, caudal vertebra, dorsal, anterior (left) and posterior (right) views.

posteriorly. The ulna of *Gaillardia* differs from the Desmaninae in that the processus anconeus is flush with anterior margin of the olecranon process, the proximal articular surface is narrower and more strongly convex transversely, and the abductor fossa is open and shallow.

The third metacarpal resembles that of *Desmana* in general but is relatively somewhat longer and the distal articular surface is convex transversely with only a shallow depression just proximal to it dorsally. In *Desmana* the distal articular surface is concave distally with a prominent pit proximal to it. The third metacarpal is about 7.5 mm. long.

The fragment of the sacrum is too damaged to do more than note the complete fusion of the three vertebrae preserved. These probably represent the third to the fifth sacral vertebrae and apparently had thin transverse processes such as in *Galemys*. The caudal vertebrae (Fig. 34) more closely resemble those of *Desmana* than *Galemys* except that the prezygopophyses are more horizontally aligned.

The femur of *Gaillardia* (Fig. 35) while functionally related to those of the Desmaninae differs from them in a number of features as noted by Shotwell and in that the (1) ligamentum teres scar is not surrounded laterally by the articular surface of the head, (2) lesser trochanter is more widely separated from the head, (3) third trochanter is fused with greater trochanter to form a large plate, (4) intertrochanteric crest extends to the third rather

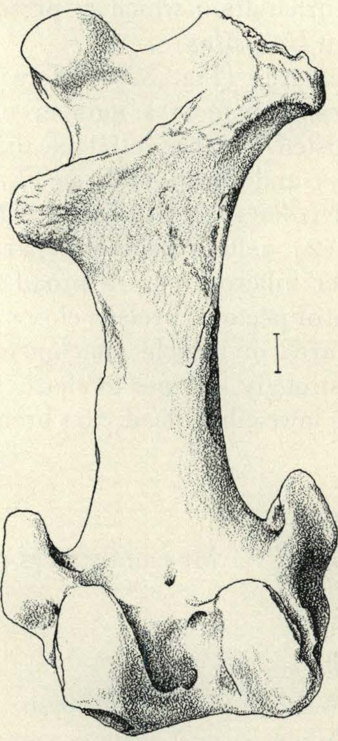

Figure 35. *Gaillardia thomsoni*, McKay Reservoir, UO loc 2222, UO 2698, right femur, posterior view.

TABLE 7

MEASUREMENTS OF THE FEMORA OF *Gaillardia thomsoni*

	UO 2698	UO 10381
Maximum length	19.0	16.6*
Maximum width of proximal end across trochanters	8.25	......
Minimum width of shaft	3.1	2.6
Width of distal end	8.7	7.3e

e Estimated measurement

than greater trochanter, (5) position of the M. adductor brevis et magnus is marked by a prominent scar opposite the lesser trochanter on the posterolateral margin of the femur, (6) medial epicondyle is extended into a thick, dorsally projecting spike, (7) lateral epicondylar sesamoid is fused to epicondyle, and (8) patellar surface is broader.

As noted by Shotwell (1956) the tibia and fibula are fused distally and the posterior side of the distal end of the tibiofibula (Fig. 36) has three rather than two grooves. The large anterior groove for tendons of the M. extensor digitorum longis and tibialis anticus is divided distally by a prominent tubercle on the medial side of the fibula thus causing the M. extensor digitorum longus tendon to lie entirely on the fibula and more posterior than the groove for the M. extensor digitorum tibialis anticus tendon. The prominent lateral crural tuberosity is located near the lateral and distal extremity of the lateral malleolus. On the posterior surface the groove for the M. flexor digitorum tibialis and tibialis posticus has retracted posteriorly and the tendons are restrained from slipping anteriorly by a well developed ridge which extends laterally from the shaft. The groove for the tendon of the M. flexor digitorum fibularis is separated from the above by a low narrow ridge for about a third of the length of the tibiofibula shaft. As in the desmans the large deep groove for the peroneus muscle tendons is distinct along the entire length of the combined shafts of the tibiofibula. The peroneus groove is bifurcated distally as in *Desmana* by a laterally compressed tubercle. The more lateral groove is slightly larger in contrast to that in *Desmana*. The fragment of the midportion of the tibiofibula resembles *Desmana* in proportions except that the falciform plate is slightly concave rather than convex distally.

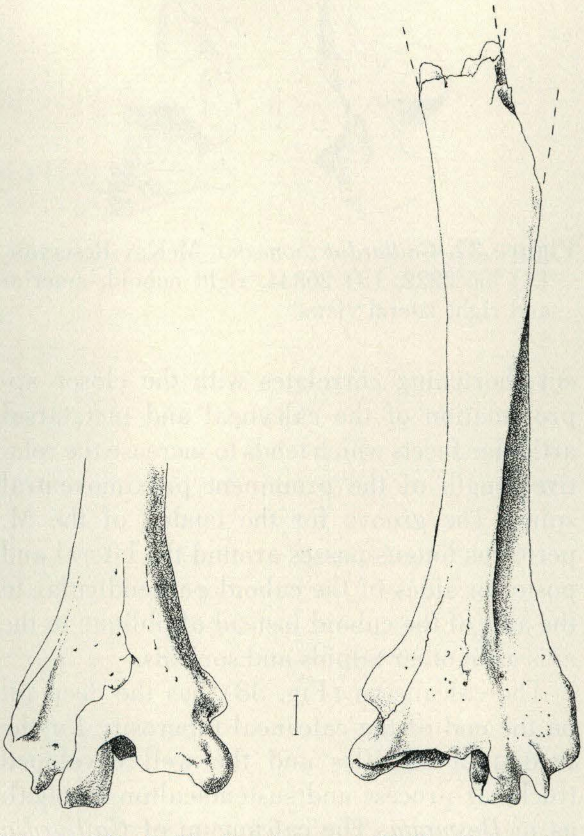

Figure 36. *Gaillardia thomsoni*, McKay Reservoir, UO loc 2222, UO 26832, distal portion of right tibiofibula, anterior and posterior views.

The cuboid (Fig. 37) retains all the major features of the Desmaninae and Talpinae except that it is much more compact. The appar-

TABLE 8

MEASUREMENTS OF THE TIBIOFIBULA OF *Gaillardia thomsoni*

	UO 3792	UO 24809	UO 2456	UO 24808	UO 26832
Length of coossified portion to base	18+	.....	.....	.....	18.7
Distal width	6.6	5.8	6.75	5.8e	6.25
Minimum width of shaft	2.6	2.4*	2.4	.....	2.1

e Estimated measurement

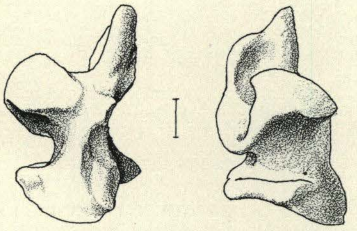

Figure 37. *Gaillardia thomsoni*, McKay Reservoir, UO loc 2222, UO 26834, right cuboid, anterior and right lateral views.

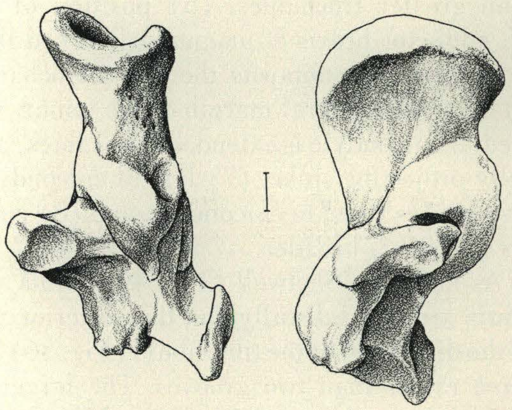

Figure 38. *Gaillardia thomsoni*, McKay Reservoir, UO loc 2222, UO 26833, right calcaneum, dorsal and right lateral views.

TABLE 9

MEASUREMENTS OF THE CALCANEA OF *Gaillardia thomsoni*

	Length	Width across sustentaculum
UO 3376	.....	3.8e
UO 24807	7.8	4.0
UO 26833	9.1	4.7

e Estimated measurement

ent shortening correlates with the closer approximation of the calcaneal and metatarsal articular facets which tends to increase the relative length of the prominent proximoventral spine. The groove for the tendon of the M. peroneus longus passes around the lateral and posterior sides of the cuboid perpendicular to the axis of the cuboid instead of oblique to the axis as in other talpids and soricids.

The calcaneum (Fig. 38) has the deep pit on the end of the calcaneal tuberosity for the tendon of Achilles and the well developed trochlear process and sustentaculum astragali as in *Desmana*. The calcaneum of *Gaillardia* differs from *Desmana* in the longitudinally elongate posterior articular surface, laterally and posteriorly displaced cuboid facet, and lack of a continuous ridge or backbone extending from the end of the calcaneal tuberosity to the cuboid facet ventrally.

The fourth metatarsal (Fig. 39) is elongate with the distal end rotated medially about 45° with respect to the proximal end as in the Desmaninae. The metatarsal differs from that of *Desmana* in the narrower proximal articular surface, transversely concave distal articular surface and relatively weak ventral keel on the distal end. The transverse compression of the metatarsal is not as great as in *Desmana*. The two specimens (UO 25127, UO 26836) of the fourth metatarsal are 18.0 mm. and 16.2 mm. long respectively.

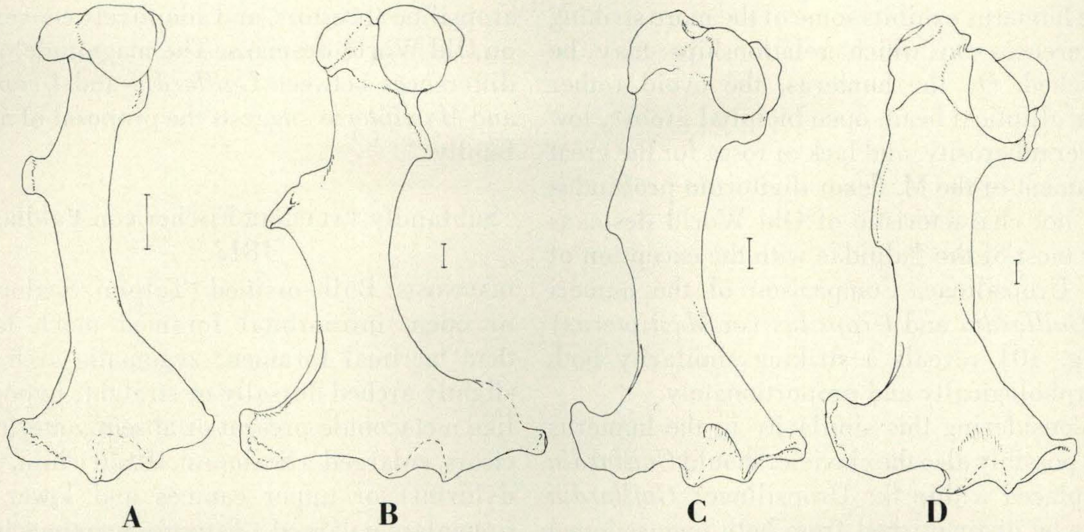

Figure 40. Left humeri, posterior views, **A;** *Uropsilus pilirostris,* **B;** *Gaillardia thomsoni,* UO 26829, **C;** *Desmana moschata,* **D;** *Galemys pyrenaicus.*

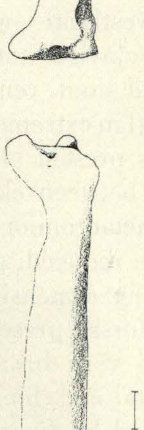

Figure 39. *Gaillardia thomsoni,* McKay Reservoir, UO loc 2222, UO 25127, right metatarsal, proximal and dorsal views.

RELATIONSHIPS: In the original description of *Gaillardia thomsoni* Matthew (1932) did not specifically include it within the Talpidae but this is implied by the nature of his comparisons. He assumed on the basis of the alveoli that the P_2 and canine were double-rooted and thus excluded it from relationship with the desmans while noting that "*Condylura* perhaps comes nearest, . . ." My examination of the type revealed no particular reasons for assuming that the canine or P_2 were double-rooted and indeed the converse is suggested by the size relationships of the alveoli. In my opinion the lower jaw of *Gaillardia* retained a complete dental formula as in the desmans.

The postcranial skeleton of *Gaillardia* belongs unquestionably to that of an aquatic insectivore in which the hind feet and tail were the main locomotor organs in water. This feature and the humeroclavicular articulation immediately suggest relationships with the desmans. However, the functional adaptation of *Gaillardia* to aquatic locomotion does not necessarily indicate relationships with the Desmaninae. While sharing a number of functional similarities with the Old World desmans, *Gaillardia* has a great number of dissimilarities in every element available for comparison, and these differences are of greater degree than the differences within the Desmaninae.

The humerus exhibits some of the more striking differences on which relationships may be weighed. On the humerus, the ovoid rather than elliptical head, open bicipital groove, low lesser tuberosity, and lack of fossa for the great ligament of the M. flexor digitorum profundus are not characteristic of Old World desmans nor most of the Talpidae with the exception of the Uropsilinae. Comparison of the humeri of *Gaillardia* and *Uropsilus* (or *Mystipterus*) (Fig. 40) reveals a striking similarity both morphologically and proportionately.

Considering this similarity in the humerus and possibly also the clavicle, should *Gaillardia* be placed within the Uropsilinae? *Gaillardia* may be distinguished from both unquestioned desmanines and unquestioned uropsilines at least at the tribal level. Systematic assignment hinges on the question of whether burrowing adaptions of the humerus seen in the Desmaninae were inherited from a semifossorial ancestor or developed independently after semiaquatic or aquatic adaptations had been initiated. There would be no great difficulty in deriving the *Desmana* type of humerus from a urotrichine type, a view favored by Gill (1888) and Reed (1951). Campbell (1939) postulated that fossorial moles must have had an aquatic ancestor to survive a nonadaptive stage in the transition between ambulatory and fossorial stages. I agree with Reed (1951) that Campbell's hypothesis is unnecessary. The development of fossorial features from a uropsiline-like or shrew-like ancestor has happened at least twice according to Reed and Turnbull (1965). The Proscalopinae and Talpinae both develop an elliptical humeral head, fossa for the great ligament of the M. flexor digitorum profundus, large olecranon fossa, etc., but other functional and chronological data suggest that both groups were independently derived from a uropsiline-like stock. The same may be true for the Desmaninae whether or not *Gaillardia* is a relic of an early adaptive stage in the evolution of the Desmaninae.

My conclusion is that *Gaillardia* represents a separate lineage of talpids derived from uropsiline ancestors, and adaptively convergent on Old World desmans. The magnitude of the differences between *Gaillardia* and *Uropsilus* and *Mystipterus* suggests the proposal of a subfamily.

Subfamily TALPINAE Fischer von Valdheim, 1817

DIAGNOSIS: Bulla ossified (Talpini, Scalopina) or open, infraorbital foramen much larger than lacrimal foramen; zygomatic arch only slightly arched dorsally or straight; hypocone-like metaconule present or absent, anterior incisors enlarged (Scalopini, Urotrichini, Condylurini) or upper canines and lower first premolars enlarged (Talpini, Scaptonychini), postfossid of molars open or closed lingually; manubrium with greatly developed ventral keel, dorsal keel present or absent, alae large and expanded, (Scaptonychini, Urotrichina, Condylurini) or vestigial—when expanded the alae are medial; clavicle not articulating with scapula, short and stout, ventral spine present —may be vestigial in extremely short clavicles; heterotopic bones present (Parascalopina) or absent ventrally between clavicle and manubrium; scapula-metacromion present or absent, acromoin may be reduced, glenoid fossa perpendicular to long dimension, subscapularis and teres major fossae present; humerus relatively slender to very broad, proximal end broader than distal end, bicipital groove long and partly covered by fusion of the pectoral crest with lesser tuberosity, fossa for the M. flexor digitorum profundus ligament present, head laterally compressed; ulna with coronoid process moderately to strongly developed, transverse proximal crest present; radius with capitular process weak to strong; manus relatively narrow to very broad; ungual phalanges bifid, scaphoid and lunar separate, either M. extensor carpi ulnaris sesmoid or os falciformis present; pubic symphysis absent, pseudosymphysis present or absent; five vertebrae in sacrum, three to five vertebrae fused to innominate; femur moderately expanded proximally, shaft normal; tibiofibula long to short, only moderately grooved distally, fibula complex proximally; pes larger to smaller than manus, metatarsals unspecialized.

Tribe Scaptonychini Van Valen, 1967

DIAGNOSIS: Unexpanded bulla; I_1^1 not enlarged, upper canine and P_1 enlarged, manubrium with large alae and articular facets for clavicles strongly inclined; clavicle long; scapula with infraspinatus and rhomboid fossae, no metacromion process or suprascapular foramen.

No New World genera known.

Tribe Talpini Fischer von Valdheim, 1817

DIAGNOSIS: Bulla expanded; I_1^1 not enlarged, upper canine and P_1 enlarged; manubrium with small alae, groove for anterior vena cava undivided, articular facets for clavicles inclined anteriorly; clavicle short, articular facets roughly parallel; scapula without infraspinatus fossa, rhomboid fossa, metacromion process, or suprascapular foramen, teres fossa partly divided; humerus broad with head directed distally or mediodistally, great excavation of brachialis fossa; pubi close together.

No New World genera known.

Tribe Urotrichini Dobson, 1883

DIAGNOSIS: Bulla not expanded, I_1^1 enlarged, upper canine and P_1 not enlarged; manubrium with large alae, articular facets for clacivles inclined; clavicle long with converging articular planes; scapula with metacromion process, infraspinatus fossa and rhomboid fossa, no suprascapular foramen; humerus narrow, brachialis fossa shallow, head directed laterodistally; ulna long, sinuous; radius long and with a capitular process crest; third metacarpal longest; pubi widely separated.

?Neurotrichus columbianus[9] n. sp.

(Fig. 41)

TYPE: UO 24816, a nearly complete right mandible lacking only the tip of the coronoid and angular processes and the teeth preceding the P_4.

HYPODIGM: UO 26826, P_4; UO 24814, M_1; UO 24832, UO 25129, M_2's. All of the above from type locality.

TYPE LOCALITY: McKay Reservoir, UO loc. 2222.

AGE: Hemphillian.

DIAGNOSIS: Small mole with dental formula: $\frac{?\ ?\ ?\ ?}{3\ 1\ 3\ 3}$. Mandible with noticeable taper to antemolar region, anterior teeth procumbent, P_3-P_4 double-rooted; molars brachyodont, resemble *N. gibbsii* but crista obliqua of M_2-M_3 usually joins protolophid more lingually and labial cingula better developed, molars proportionately larger; anterior margin of ascending ramus straight and at right angles to the horizontal ramus, longer condylar process and more posteriorly situated mandibular foramen than in *Neurotrichus*.

DESCRIPTION: The dentary (Fig. 41) is similar in general shape to that of the shrew-moles. The ascending ramus forms a sharp right angle with the horizontal ramus. Posterior to the level of the coronoid process the mandibular foramen is situated on the ventral margin of the mylohyoid ridge. The masseteric fossa is rather deeply excavated. Although the angular process is broken off, the broken surface suggests that it was rather platelike as in *Scapanulus*. The coronoid process is also broken but was definitely rather short anteroposteriorly. The antemolar region is relatively short and tapered. There is one mental foramen beneath the P_3 and another below the M_1 trigonid. The symphysial scar extends to the level of the P_4. The three most anterior teeth, here interpreted as incisors, are represented only by their alveoli, all of which are quite procumbent. The borders of the two anterior alveoli are damaged so that the relative diameters are difficult to interpret. The I_3 seems to be the smallest and is arbitarily considered here to be the tooth lost in *N. gibbsii*. The I_3 is followed by two equally large alveoli for the C and P_1. I consider the succeeding two alveoli, a small anterior one followed by a somewhat labially situated larger one, to represent a double-rooted P_3. It might be ar-

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[9] After Columbia River.

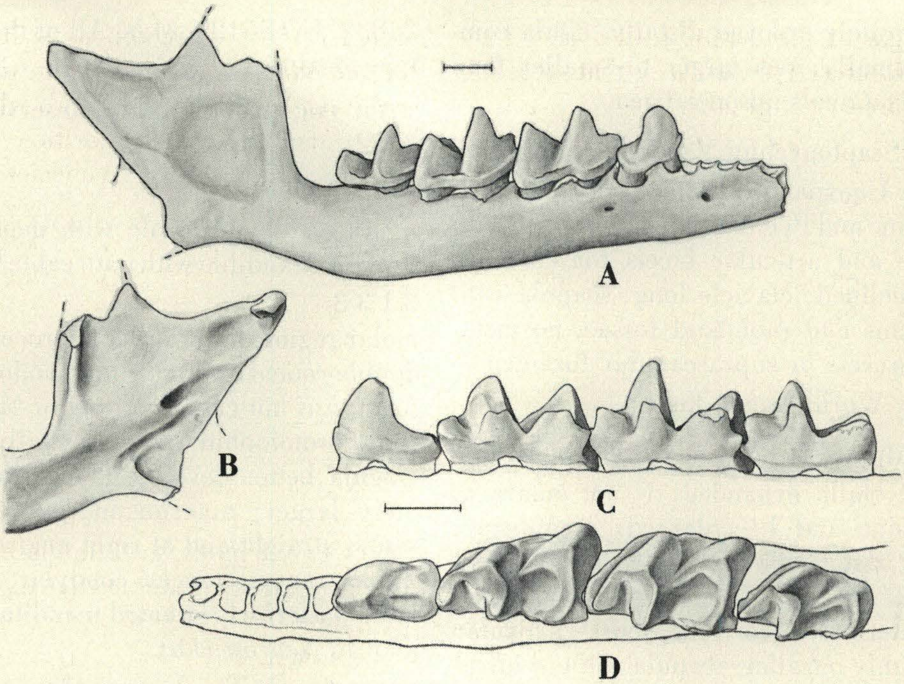

Figure 41. *?Neurotrichus columbianus* n. sp. McKay Reservoir, UO loc 2222, Type specimen UO 24816, right mandible with P_4-M_3, **A**; labial view, **B**; lingual view of ascending ramus, **C**; lingual view of P_4-M_3, **D**; occlusal view alveoli and P_4-M_3.

TABLE 10

Measurements of the Lower Dentition of *?Neurotrichus columbianus*

		UO 24816 (Type)	UO 24814	UO 24832	UO 25129	UO 26826
P_4:	Length	1.40	------	------	------	1.56
	Width	0.83	------	------	------	0.81
M_1:	Length	2.07	1.90	2.00	------	------
	Width	1.32	1.33	1.23	------	------
M_2:	Length	2.13	------	------	2.00	------
	Width	1.30	------	------	1.17	------
M_3:	Length	1.80	------	------	------	------
	Width	0.97	------	------	------	------
M_1-M_3 Length		5.9	------	------	------	------
C-P_4 Alveolar		3.0	------	------	------	------
P_2-P_4 Alveolar		2.5	------	------	------	------
Length M_3 to Condylus		6.5	------	------	------	------

gued in light of the dentition of some of the other shrew-moles (*Urotrichus*) that these two alveoli represent individual teeth, but their relative size and arrangement to each other and to the anterior mental foramen is so like that found in *N. gibbsii* that any other interpretation seems less likely.

The P_4 is elongate with a well developed heel which is the widest part of the tooth. The protoconid is inflated and centered over the anterior root. There is no evidence of a metaconid on the type but the isolated specimen has a small metaconid about half way up the posterolingual side of the protoconid. A narrow anterior cingulum surrounds part of the protoconid and a somewhat heavier cingulum encloses the heel posteriorly and laterally. A deep short groove divides the heel longitudinally. A similar groove or arrangement of flanking enamel folds is present in *N. gibbsii, Uropsilus, Mystipterus, Urotrichus,* and *Scalopoides*. The anterior root is smaller than the posterior one.

The molars are brachyodont and proportionately similar to *Uropsilus*, and other Urotrichini. The molars appear to be relatively larger in proportion to the jaw than the above. Labial cingula bridge the hypoflexid. The crista obliqua of the M_2-M_3 contact the middle of the protolophid, or the base of the metaconid. The other features of the molars fall within the variation of those of *N. gibbsii*.

RELATIONSHIPS: Size and general proportions of ?*N. columbianus* seem to align it with the shrew-moles. The crowded and reduced antemolar dentition tends to remove it from *Achlyoscapter* as well as a number of other differences. The known uropsilines all possess posterior cingula on the M_1-M_2 and differ in morphology of the P_4, low situation of the mandibular foramen, and in the shrew-like angular process. ?*N. columbianus* lacks the well developed metastyles of the M_2-M_3 of *Scalopoides*, and the arms of the M_2-M_3 trigonids diverge more. Among the Urotrichini ?*N. columbianus* differs from the species of *Urotrichus* in dental formula, proportionately larger P_4, double-rooted P_3, and more robust M_1 trigonid. ?*N. columbianus* resembles *N. gibbsii* in the general morphology of the P_4-M_3, double-rooted P_3, and mental foramina position. It can be distinguished from the living species by the sharp angle of the horizontal and ascending rami, proportionately larger molars, additional antemolar tooth, and more posterior mandibular foramen and condyle.

The above comparisons are similar to those of Wilson (1960) in comparing *Mystipterus* (*Mydecodon*) *martini* to the shrew-moles. Here, as there, the dental formula and small differences in molar form may give a false impression of relationship. The morphology of the lower antemolar teeth in these groups is of little use without corroborative postcranial material in determining the relationships of the various small moles. On the jaw material available, ?*N. columbianus* seems to be closely related to *N. gibbsii*. However, convergence in molar and premolar morphology has been demonstrated in other moles (e.g. *Scalopus-Scapanus, Domninoides-Proscalops*) and can be documented in a number of other undescribed forms. Features of the ascending ramus and crowding of the antemolar teeth lead me to suspect that ?*N. columbianus* is related to *Scalopoides*. None of the features of the teeth are so strange that they could not be derived from *Scalopoides. S. isodens* has already achieved the same dental formula and root reduction seen in ?*N. columbianus*. Also the ?*Scalopoides* material from McKay would tend to support such a view. On the other hand ?*N. columbianus* would make a good temporal and structural ancestor for *N. gibbsii* on the basis of assigned material. The poor record of *Scalopoides*-like dentitions in the Clarendonian and Hemphillian does not give any clues as to the dental evolution or trends of this complex. The general relationship of the reduction in rostrum length and increasing fossorality exhibited by several lineages would suggest such an end product, but this generalization cannot as yet be demonstrated within the *Scalopoides* complex.

If some of the *Scalopoides*-like postcranial material and the ?*N. columbianus* material represent the same group of animals, then a new genus would probably be in order. Since this association cannot be adequately demonstrated and inasmuch as there is no means evident to determine if the similarities signify homology or analogy, I have sought to treat the various elements separately and let the weight of the morphological features determine taxonomic assignment for each element.

Tribe Condylurini Dobson, 1883

DIAGNOSIS: Bulla not expanded, I_1^1 enlarged; upper canine and P_1 not enlarged; manubrium with large alae, articular facets for clavicles inclined anteriorly; clavicle moderately long with distinct process for origin of M. acromiodeltoideus muscle, articular planes converge; scapula with metacromion process, rhomboid fossa, and infraspinatus fossa, no suprascapular foramen; humerus moderately broad, head directed laterodistally, brachialis fossa shallow; ulna long and sinuous, very broad proximal crest; metacarpals slightly graded in size from the fifth, the longest, to the first; pubi close together.

No Tertiary fossils known.

Tribe Scalopini Dobson, 1883

DIAGNOSIS: I_1^1 or I_2^1 enlarged, upper canine and P_1 not enlarged; manubrium with small alae, articular facets for clavicle vertical, groove for anterior vena cava divided posteriorly; clavicle moderately long to short, articular facets convergent to roughly parallel; scapula with infraspinatus fossa, rhomboid fossa, and suprascapular foramen, metacromion process absent; humerus moderately to very broad, head directed distally to mediodistally, brachialis fossa moderately deep; ulna and radius moderately long to short; pubi close together.

Subtribe Parascalopina new

DIAGNOSIS: Metastylids of molars usually present; bulla not expanded; stapedial tube incompletely or poorly ossified; manubrium with dorsal ridge and paired anterior venae cavae; heterotopic bones may occur between clavicles and manubrium; humerus generally narrower and pectoral ridge terminates more laterally than in the Scalopina, concavity surrounded by pectoral ridge, pectoral crest and greater tuberosity of humerus deep; capitular process of radius flattened proximally.

SCALOPOIDES Wilson, 1960

GENOTYPE: *Scalopoides isodens* Wilson, 1960

KNOWN DISTRIBUTION: Middle Miocene (Hemingfordian) of Colorado, Late Miocene (Barstovian) to Middle Pliocene ? (Hemphillian) of Oregon.

AMENDED DIAGNOSIS: Small fossorial moles of dental formula: $\frac{?\ ?\ ?\ ?}{3\ 1\ 3\ 3}$ or fewer. I_2 moderately enlarged, P_2 single or double-rooted, P_3-P_4 double-rooted. Molar crowns more or less mesodont, protoconids and hypoconids angulate, prominent metastylids present on flanks of metaconids in M_2-M_3, crista obliqua extending to bases of metaconids, entocristids help enclose postfossids lingually. M_1-M_2 subequal. M_3 smaller but robust. Dentary talpine-like in shape. Two mental foramina, posterior one beneath or just posterior to P_4. P_4 subtriangular and compact. Upper molars tritubercular, protoconule small or absent, metaconule relatively small and close to protocone, mesostyles slightly or not twinned. Clavicle intermediate in length between *Condylura* and *Scapanulus*, details closer to *Scapanulus*, faint to moderate reflection of the ventromedial spine. Humerus with gross proportions similar to *Condylura* but details nearer *Scapanus*, axis of the head parallels humeral axis, clavicular articular facet crudely ovate, prominent "scalopine ridge". Ulna *Parascalops*-like but more slender. Radius more robust than in Urotrichini or *Condylura*, capitular process well developed, distal end scalloped. Metacarpals much shorter than in the Urotrichini or *Condylura* but longer than living Scalopini.

Scalopoides isodens Wilson, 1960

(Figs. 42-45)

Although *Scalopoides isodens* is not known from Oregon, as the genotypic species it figures prominently in any discussion of the relationships of the genus and referred species. The following descriptions are based upon Wilson's (1960) original material and additional material sorted from the original collection residue.

In the description of the humerus Wilson (1960) stated that the "humeri of *S. isodens*, in addition to proportions, agree except for minor details with those of *Condylura*."

In the details of the humerus a much better match is found within the Scalopini (Fig. 10). Wilson did not see the humerus of *Scapanulus*, so a detailed comparison is called for here as well as a re-evaluation of the similarities and dissimilarities between *Condylura* and *Scalopoides*. Of the living Scalopini , *Scapanulus* has the longest humerus in relation to its width and is comparable to *Condylura* in this respect. *Scalopoides* resembles *Scapanulus* in that (1) the axis of the head is nearly parallel to the axis of the humerus, (2) the "scalopine ridge" of Campbell (1939) is present and generally similar, (3) the clavicular articular facet is strongly angled with respect to the axis of the humerus (about 30°), (4) the large deep channel separating the head from the greater tuberosity is absent, (5) the trochlea is relatively broad, (6) the fossa for the ligament of the M. flexor digitorum profundus has only a very slight anterior component, and (7) the proximal end of the bicipital tunnel is visible anteriorly. *Scalopoides* differs from *Scapanulus* in that (1) the plane of the head is more nearly parallel to the humeral axis, (2) the teres tubercle is shorter, and (3) the pectoral crest is shorter. *Scalopoides* resembles *Condylura* in the relatively wide gap between the medial rim of the trochlea and the fossa for the ligament of M. flexor digitorum profundus and the pectoral crest is more nearly comparable in length. *Condylura* differs from *Scalopoides* in that (1) the head is directed strongly laterally, (2) the scalopine ridge is absent (3) the clavicular articular facet is nearly parallel to long axis of humerus, (4) a deep, wide channel separates the head from the clavicular facet, (5) the trochlea is relatively narrower, (6) the teres tubercle is relatively shorter, (7) the fossa for the M. flexor digitorum profundus ligament has a strong anterior component and (8) the proximal end of the bicipital tunnel is not visible anteriorly. The subovate shape of the clavicular facet (Fig. 42) in *Scalopoides* shows a much closer relationship to *Scapanulus* and thus to the Parascalopina on the humerus than it does to *Condylura* or any more generalized form. However, in many respects the humerus of *Scalopoides* may be thought of as intermediate in form between *Condylura* and the Recent Scalopini.

The clavicle is relatively longer than in the living Parascalopina but shorter than in *Condy-*

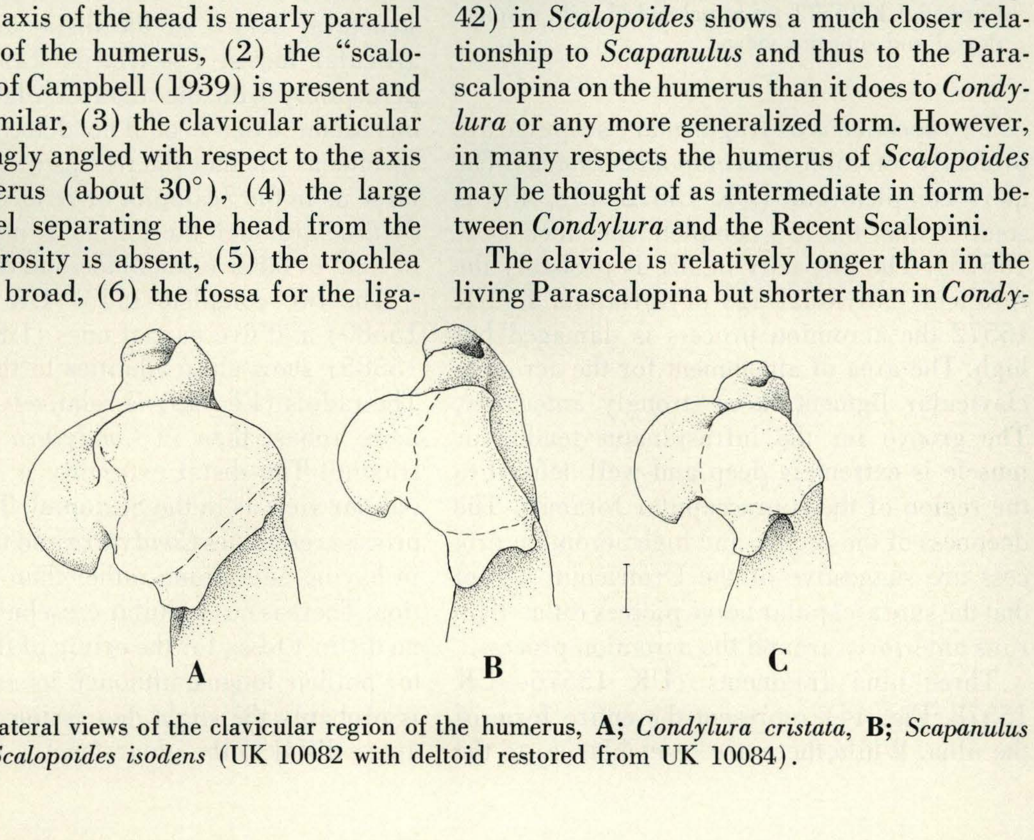

Figure 42. Lateral views of the clavicular region of the humerus, **A;** *Condylura cristata,* **B;** *Scapanulus oweni,* **C;** *Scalopoides isodens* (UK 10082 with deltoid restored from UK 10084).

lura. The ventral process is damaged on both available specimens, UK 15570 and UK 15571. The ventral process seems to have been bladelike and unelaborated. There is a ventral articular facet on the ventromedial spine for articulation of a small heterotopic bone. The humeral facet faces strongly posteriorly and slightly ventrally rather than slightly dorsally as in the living Scalopini. The gutter leading from the vascular notch to the dorsal prominence is only moderately developed. The clavicle has none of the extra processes seen on the clavicle of *Condylura.*

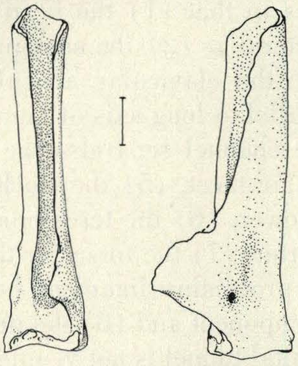

Figure 43. *Scalopoides isodens*, Quarry A Martin Canyon, UK 15572, proximal end of right scapula, dorsal and superior views.

Two specimens of fragmentary scapulae are probably referable to *Scalopoides isodens.* The more complete one (UK 15572, Fig. 43) is smaller than the less complete specimen (UK 15573). The disparity in size is probably the result of individual age or variation. In UK 15572 the acromion process is damaged but high. The area of attachment for the acromioclavicular ligment faces strongly anteriorly. The groove for the infraspinatus tendon or muscle is extremely deep and well defined to the region of the suprascapular foramen. The deepness of the groove and high acromion process are suggestive of the Urotrichini except that the suprascapular nerve pierces rather than runs anteriorly around the acromion process.

Three ulna fragments (UK 15576—UK 15578, Fig. 44) represent the entire form of the ulna. While there are resemblances to the

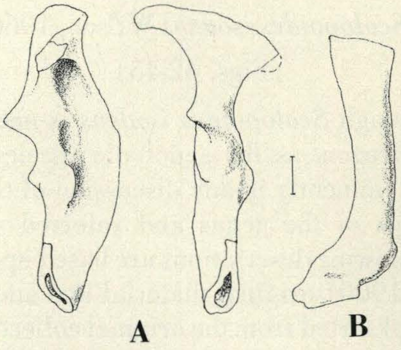

Figure 44. *Scalopoides isodens*, Quarry A Martin Canyon, **A;** UK 15576, proximal end of right ulna, lateral and medial views, **B;** UK 15577, distal end of right ulna, lateral view.

Urotrichini, the majority of features place it well within the Scalopini. The ulna of *S. isodens* resembles the Urotrichini and *Condylura* in (1) the relative shortness of the olecranon process, (2) the very slight sinuousness of the shaft, (3) and the somewhat obtuse angle between the distal end of the shaft (in the Urotrichini) and the anterior moiety of the distal epiphysis. *S. isodens* resembles *Parascalops* and *Domninoides* in the short and robust shaft and the structural details of the distal and proximal articular facets. The triceps scar merges imperceptibly with the anterior platform of the olecranon so that I could not determine on these specimens whether the triceps insertion was as large as in the Scalopini or reduced as in *Condylura;* although the former is more probable in light of other resemblances to the Scalopini.

The two complete radii (UK 15579, UK 15580) and five partial ones (UK 15581-UK 15585) show close affinities to the Scalopini. The radius (Fig. 45) is relatively shorter and more robust than in *Condylura* or the Urotrichini. The distal extremity is scalloped in palmar view as in the Scalopini. The capitular process resembles *Condylura* and the Scalopina in having an oblique rather than flat termination. There is no capitular crest but there is also no distinct fossa for the origin of the M. abductor pollicis longus, although its area of origin is probably the slight depression immediately anterodistal to the ulnar facet.

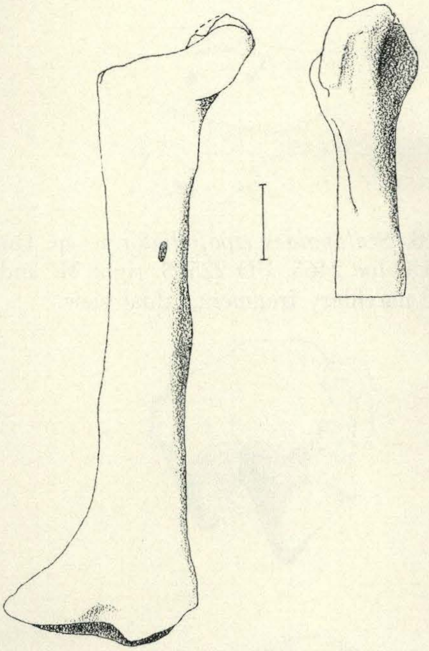

Figure 45. *Scalopoides isodens*, Quarry A Martin Canyon, UK 15579, right radius, medial view and posterior view of proximal end.

A single proximal phalanx II or III, UK 15586, of the manus is relatively longer than that of *Parascalops* or the Scalopina but much too short to be confused with Urotrichini. It is definitely that of a burrowing mole.

The three ungual phalanges, UK 15587, of the manus are bifid and tranversely broadened distally as in other Talpinae. The subungual process is rather deep as compared to those of the living burrowing moles but not as deep and globular as in the Urotrichini. The lateral blades of the claw extend more posteriorly as in the burrowing moles.

Only one poorly preserved specimen (UK 15588) of the distal end of the tibiofibula was recovered from Martin Canyon. It resembles the better known *S. ripafodiator* described below except that the groove for the peroneus tendons is not well developed and the crural ligament is not prominently ossified.

RELATIONSHIPS: The relationships of *S. isodens* to other species and the affinities of the genus are considered in the discussion of *S. ripafodiator* and summary below.

Scalopoides ripafodiator[10] n. sp.

(Figs. 46-60)

TYPE: UO 22488, a right mandible with I_2 and P_1-M_3, lacking the ascending ramus, tip of the jaw anterior to the I_2, and trigonid of the M_1. Molars heavily worn.

HYPODIGM: UO 22504—UO 22509, UO 22511—UO 22515, UO 22517-UO 22518, UO 22520—UO 22524, UO 22527—UO 22543, UO 22578, UO22580, UO 22582—UO 22589, UO 26314, UO 26322—UO 26324, UO 26339, upper teeth and maxillary fragments including 11 P^4, 2 P^2, 20 M^1, 17 M^2, 2 M^3; UO 22342, UO 22482—UO 22485, UO 22490, UO 22492, UO 22494—UO 22496, UO 22499—UO 22501, UO 22545—UO 22546, UO 22548—UO22551, UO 22566, UO 22568—UO 22569, UO 22571—UO 22576, UO 22590—UO 22592, UO 22595, UO 22598—UO 22600, UO 26303, lower teeth and fragmentary mandibles; UO 22414, anterior portion of manubrium; UO 22415—UO 22417, UO 22427, UO 22431, UO 22436, UO 24839—UO 24842, complete and incomplete clavicles; UO 22354—UO 22373, UO 22375—UO 22384, UO 22387—UO 22394, UO 24844-UO 24846, humeri and fragments thereof; UO 22339, UO 22451—UO 22469, UO 24847—UO 24848, fragmentary ulnae; UO 22336, UO 22420—UO 22425, UO 22428—UO 22429, UO 22433—UO 22434, UO 26800, one complete and ten fragmentary radii; UO 22444—UO 22450, UO 24833—UO 24834, scaphoids; UO 24239—UO 22440, UO 22443, third metacarpals; UO 22441—UO 22442, ungual phalanges of manus; UO 22552—UO 22557, UO 22559—UO 22563, fragmentary innominata; UO 22395—UO 22396, UO 22398—UO 22399, UO 22402—UO 22408, UO 22411, UO 24836, fragmentary femora; UO 22470—UO 22471, UO 22473—UO 22479, UO 22481, tibiofibula fragments—three proximal epiphyses and seven distal ends; UO 22401, astragalus; UO 22404, UO 22410, UO 24837, calcanea. All from type locality.

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[10] From the Latin *ripa*, stream bank, and *fodiator*, a digger.

TYPE LOCALTY: UO loc. 2465. Quartz Basin.

AGE: Barstovian.

DIAGNOSIS: Small mole about the size of *S. isodens,* and dental formula $\frac{?\ ?\ ?\ ?}{3\ 1\ 3\ 3}$. Lower molars generally similar to *S. isodens.* I_3 less spatulate, P_2 double-rooted, antemolar region more robust and longer. Metaconule of upper molars present, paraconule low but evident and persistent with wear, M^2 with slight division of the mesostyle. Clavicle, humerus, radius and ulna generally similar to *S. isodens,* humerus relatively narrower, longer pectoral ridge, radius and ulna proportionately more slender.

DISCRIPTION: Only a small portion of the maxilla of *Scalopoides ripafodiator* is preserved in the sample; however, UO 22515, (Fig. 46) clearly shows the nature of the base of the zygomatic process of the maxilla. The relationships of this region are most like those of *Parascalops breweri* among the living moles and to a lesser extent like those of *Scalopus aquaticus.* There are two distinct crests for the insertion of the M. masseter that extend anterior from the dorsal and ventral margins of the zygomatic arch. The dorsal crest is either absent or fused with the ventral crest in other talpines examined.

The P^3 is a simple tooth (Fig. 47). The crown is essentially a single connate cusp with a small posterior cingulum. It is double-rooted with the round anterior root inclined anteriorly. The transversely wider posterior root projects vertically into the maxilla. The P^4 is a symmetrically triangular tooth (Fig. 47) with the labial side the longest. The paracone is centered over the center of the tooth. The posterior moiety of the cusp is somewhat compressed transversely into a stout crest. The protocone is relatively small but usually a well defined cusp. It is transversely compressed and essentially an enlargement of the narrow cingulum which encloses the posterior moiety of the tooth. This cingulum may connect by way of a very narrow labial cingulum with the short anterior cingulum which forms the anteriormost extremity of the tooth.

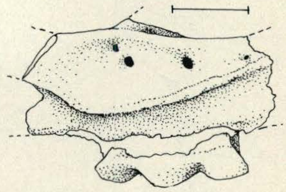

Figure 46. *Scalopoides ripafodiator* n. sp. Quartz Basin, UO loc 2465, UO 22515, right M^2 and associated maxillary fragment, labial view.

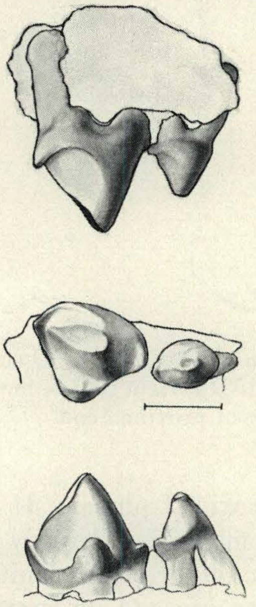

Figure 47. *Scalopoides ripafodiator* n. sp. Quartz Basin, UO loc 2465, UO 22580, right P^3-P^4, labial, occlusal, and lingual views.

The M^1 of *S. ripafodiator* (Fig. 48A) resembles that in the Urotrichini in general shape and morphology. The protocone is large and flanked by a smaller but distinct metaconule. The paraconule is minute and just anterior to the apex of the protocone on the protocrista. All evidence of the paraconule is usually eliminated during the initial stages of wear. Narrow paracrista are present. The metastyle is elongate but only weakly divided. There is a small and well defined parastyle. The four roots are situated under the metacrista, paracone and protocone and a filiform one below and a little labial to center of the tooth. The root under the metacrista is strongly compressed anteroposteriorly while the others are oblate in cross-section.

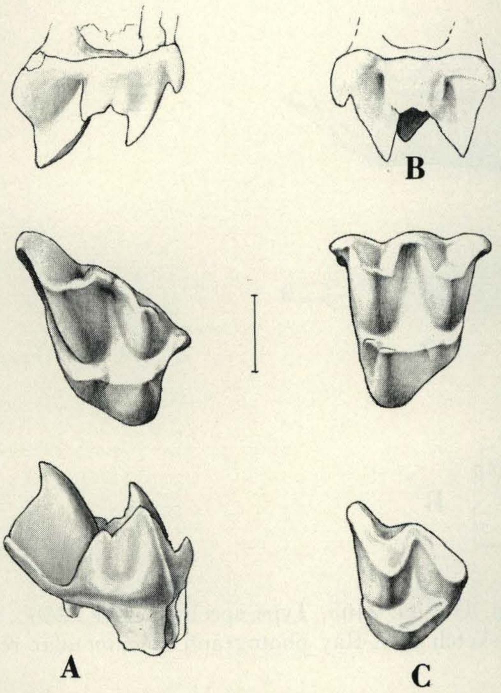

Figure 48. *Scalopoides ripafodiator* n. sp. Quartz Basin, UO loc 2465, **A**; UO 22537, right M^1, labial, occlusal, and lingual views, **B**; UO 22506, left M^2, labial and occlusal views, **C**; UO 22520, left M^3, occlusal view.

The M^2 of *S. ripafodiator* (Feb. 48B) strongly resembles that of *S. isodens* in most respects. The metaconule is larger and more distinct than in *S. isodens*. The parastyle which is not present in Wilson's material (possibly abraded off) is a distinct cusp. Some vestige of a labial cingulum may be sporadically present in the reentrant folds between the protocone and metaconule and between the protocone and the paraconule. The paraconule, although about as prominent as in *S. isodens,* is slightly more removed from the apex of the protocone and less likely to be completely obliterated by wear. The paracingulum and metacingulum (with one exception in the case of the latter) do not extend to the stylar cusps. The M^2 has four roots in analogous position as the M^1. Interradicular crests are absent in all the molars.

Only two worn third upper molars (Fig. 48C) of a small mole were recovered from Quartz Basin, both appear to be referable to *S. ripafodiator*. They strongly resemble those of *S. isodens*. The paraconule is not discernible in the worn Quartz Basin specimens and the metaconule is somewhat better developed. The M^3 is three-rooted with one root under each extremity.

The mandible (Fig. 49) is more robust especially anteriorly than *S. isodens*. There is little taper to the jaw anteriorly and it is about as deep beneath the P_2-P_3 as under the M_3. There are two mental foramina, one under the P_4 and a larger one under the P_3 or between the roots of the P_2 and P_3. The symphysis extends posteriorly beneath the P_4. There is one antemolar tooth absent in *S. ripafodiator*. Wilson (1960) listed the lower dental formula for *S. isodens* as complete based on analogy with *Proscapanus sansaniensis* Lartet. He had previously thought the formula was 3, 1, 3, 3. Comparison of *S. ripafodiator* and *S. isodens* indicates that Wilson's earlier determination was the correct one and that both species have the same dental formula.[11] The antemolar region is relatively longer and the teeth are not as crowded as in *S. isodens*. The length of the I_2 to P_4 comprises 82 % of the M_1-M_3 alveolar length in *S. ripafodiator* as compared with only 68% in *S. isodens*. The I_1-I_2 are inclined about 45° to the axis of the jaw and the succeeding teeth progressively less so. The P_2-P_4 are double-rooted. An X-ray of the antemolar region (Fig. 49B) reveals a long and strong I_2 root extending posterior to the level of and beneath the P_2. Consequently, the roots of the canine and I_3 are quite short. The single-rooted antemolars (Fig. 50) are of uneven size ranked in the following order from smallest to largest, I_3, C, I_1, I_2. The I_1 is incisiform and closely appressed to the I_2. The I_2 is enlarged as in *Scapanulus* and bears a similar relationship to the I_1. Posteriorly the crown is rounded but anterolingually it narrows to an edge thus imparting a tear-shaped cross-section to the crown. The I_3 and C are peg-like or slightly premolariform teeth. The roots of the P_2 are somewhat oblique in the

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[11] The homologies of the two teeth between the I_2 and P_2 are not presently demonstrable. The designation of the missing tooth as the P_1 is an arbitrary one.

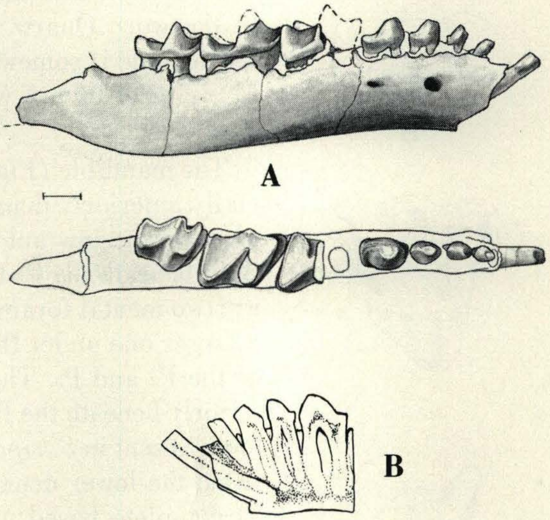

Figure 49. *Scalopoides ripafodiator* n. sp. Quartz Basin, UO loc 2465, Type specimen UO 22488, right mandible, **A;** labial and occlusal views with I^2-M^3,**B;** sketch of X-Ray photograph of antemolar region.

jaw with the posterior root lingual to the anterior one. The large protoconid is centered over the anterior root. As in the rest of the premolars the protoconid slants somewhat anteriorly. There is a very small posterior cingulum with an incipient ridge extending anterodorsally toward the apex of the protoconid. The roots of the P_2 of *S. ripafodiator* are not as closely appressed as in *S. isodens*. The P_3 resembles the P_2 but is larger, the roots are better aligned longitudinally and the posterior cingulum and ridge are better developed. The P_4 of *S. ripafodiator* generally resembles that of *S. isodens* except in the following details: (1) it is broader, (2) the protoconid is more inflated, (3) the posterior cingulum extends transversely the width of the protoconid before curving anteriorly, (4) paraconid and anterior cingulum are absent or weakly developed, (5) the metaconid is not discernible or very weakly so.

The molars (Fig. 51) closely resemble those of *S. isodens* but in general have a somewhat more inflated appearance and the labial cingula are less distinct. In the M_1 the paralophid is not straight as in *S. isodens*. The lingual moiety of the paralophid is bent lingually rather than anterolingually thus imparting a more compact aspect to the tooth. The anterior cingulum is variable in occurrence and expression. The M_2 is similar to *S. isodens* except as noted above and in the construction of the talonid. The entoconid is usually more massive and columnar than in *S. isodens*. The M_3 closely resembles *S. isodens* except as noted above.

Only the anteriormost extremity of the manubrium (Fig. 52) was recovered. In the features preserved it shows closest similarities with the manubrium of *Scapanulus* and *Parascalops*. The bases of the alae are more dorsally situated and merge posteriorly with the broad and poorly differentiated dorsal keel. The alae were apparently rather broad although probably not much more so than in *Scapanulus*. The anterior margin and clavicular articular surfaces are nearly vertical. The

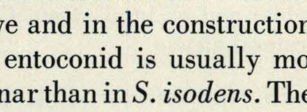

Figure 50. *Scalopoides ripafodiator* n. sp. Quartz Basin, UO loc 2465, UO 22499, anterior end of right mandible with I_1-C, labial view.

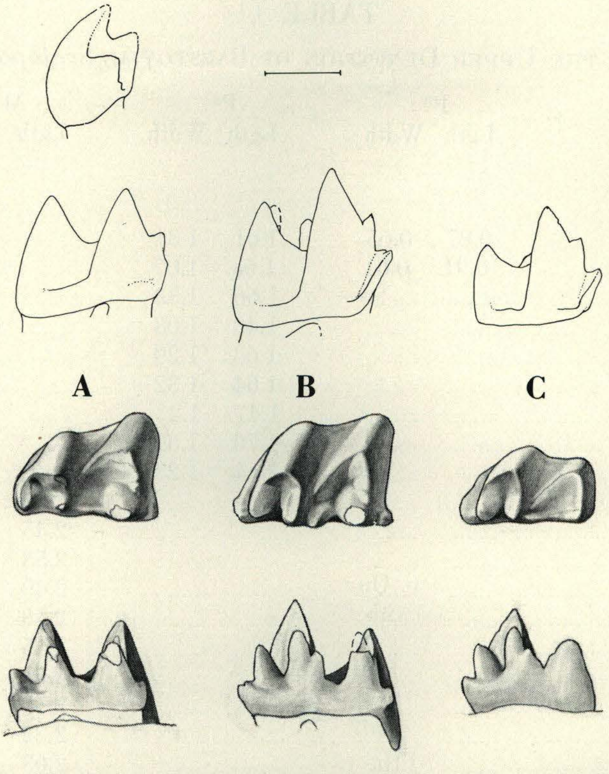

Figure 51. *Scalopoides ripafodiator* n. sp. Quartz Basin, UO loc 2465, **A;** UO 22484, right M_1, anterior, labial, occlusal, and lingual views, **B;** UO 22573, right M_2, labial, occlusal, and lingual views, **C;** UO 22490, right M_3, same views as B.

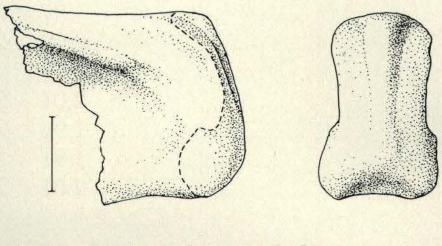

Figure 52. *Scalopoides ripafodiator* n. sp. Quartz Basin, UO loc 2465, UO 22414, anterior part of manubrium, right lateral and anterior views.

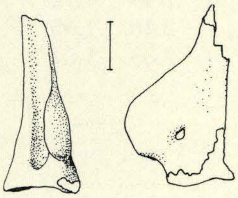

Figure 53. *Scalopoides ripafodiator* n. sp. Quartz Basin, UO loc 2465, UO 22432, right scapula, dorsal and superior views.

anterior ventrolateral bosses are not anterolateral projections, situated to contact the ventromedial borders of the clavicles as in *Scapanus*, *Scalopus*, and *Talpa*, but are rather posteriorly situated, suggesting that they served for the articulation of a tetrahedral heterotopic bone or cartilage as in *Scapanulus* and *Parascalops*. This is verified by the morphology of the ventromedial spine of the clavicle as well as the gap between the ventral articular surfaces of the clavicle and manubrium when articulated.

Only a small region of the proximal area of the scapula (Fig. 53) was preserved in the sample, and its construction strongly resembles that of *Parascalops*. The suprascapular nerve pierces the acromion. The path of the infraspinatus tendon is well marked by a pronounced groove extending from the infraspinatus fossa to the region of the suprascapular foramen but this groove is possibly not as deep as in *S. isodens*. The area for insertion of the

TABLE 11

MEASUREMENTS OF THE UPPER DENTITION OF BARSTOVIAN *Scalopoides* FROM OREGON

	P^3		P^4		M^1		M^2	
Specimen	Lgth	Wdth	Lgth	Wdth	Lgth	Wdth	Lgth	Wdth
Scalopoides ripafodiator								
Quartz Basin								
UO 22580	0.87	0.65	1.61	1.31				
UO 22582	0.91	0.61	1.6e	1.07				
UO 22578			1.66	1.33				
UO 22579			1.48	1.08				
UO 22584			1.68	1.29				
UO 22585			1.64	1.32				
UO 22587			1.47	1.2*				
UO 22588			1.70	1.32				
UO 22589			1.64	1.23				
UO 22528					2.55	1.67		
UO 22530					2.45	1.70		
UO 22532					2.53	1.78		
UO 22534					2.40	1.72		
UO 22535					2.58	1.72		
UO 22536					2.45	1.73		
UO 22537					2.62	1.65		
UO 22538					2.50	1.75		
UO 22540					2.52	1.73		
UO 22541					2.63	1.69		
UO 22543					2.65	1.85		
UO 22504							1.88	2.35
UO 22506							2.12	2.36
UO 22507							1.98	2.22
UO 22509							1.97	2.35
UO 22511							2.09	2.40
UO 22514							1.79	2.37
UO 22515							2.01	2.37
UO 22518							1.96	2.27
UO 22523							1.91	2.36
UO 22524							2.01	2.37
Scalopoides cf. *S. ripafodiator*								
Red Basin								
UO 24311	0.77	0.54	1.56	1.12				
UO 24319			1.54	1.10		1.52		
UO 24312			1.53	1.08				
UO 24316					2.46	1.55		
UO 24317					2.44	1.72		
UO 24318					2.46	1.65		
UO 24320					2.33	1.57		
UO 24321							1.82	2.03
UO 24322							1.90	2.22
UO 24324							1.76	1.78
UO 24325							1.69	2.05
UO 24328							1.62	2.06
UO 24329							1.70	2.17
UO 24330							1.67	2.04

e Estimated measurement.

* Noticeable abrasion or breakage tending to reduce measurement.

TABLE 12

MEASUREMENTS OF SELECTED LOWER DENTITIONS OF BARSTOVIAN *Scalopoides*

Measurement		*S. ripafodiator*					*S.* cf. *S. ripafodiator*		
		UO 22488 (Type)	UO 22501	UO 22550	UO 22548	UO 22499	UO 24300	UO 24301	UO 23766
I_1:	Length	....	....	....	....	0.39	....	....	....
	Width	....	....	....	....	0.32	....	....	....
I_2:	Length	0.49	....	....	....	0.50	....	....	....
	Width	0.43	....	....	....	0.45	....	....	....
I_3:	Length	....	....	....	....	0.33	....	....	....
	Width	....	....	....	....	0.33	....	....	....
P_1:	Length	0.38	....	....	....	0.37	0.28*	....	....
	Width	0.37	....	....	....	0.37	0.34	....	....
P_2:	Length	0.58	0.54	....	....	....	0.54	....	....
	Width	0.50	0.48	....	....	....	0.38	....	....
P_3:	Length	0.72	0.81	....	0.74	....	0.53	0.71	....
	Width	0.60	0.60	....	0.59	....	0.42	0.50	....
P_4:	Length	1.16	1.20	1.13	1.06	....	0.86	1.15	1.30
	Width	0.81	0.85	0.78	0.76	....	0.65	0.67	0.85
M_1:	Length	....	1.92	1.85	....	....	1.47	....	1.82
	Width	....	1.50	1.44	....	....	1.33	....	1.45
M_2:	Length	2.12	2.16	....	....	....	....	....	....
	Width	1.45	1.46	....	....	....	....	....	....
M_3:	Length	1.83	....	....	....	....	....	....	....
	Width	1.16	....	....	....	....	....	....	....

acromioclavicular ligament faces dorsolaterally as in the living Scalopini with only a slight anterior component.

The clavicle of *S. ripafodiator* closely resembles that of the *S. isodens*. The sample from Quartz Basin shows a considerable variation in size (Table 14). The smaller specimens more closely resemble those of *S. isodens* in details and proportions (Fig. 54B) but the larger specimens (UO 24415, UO 22431, UO 22482) are proportionately longer than the others. The difference in length occurs entirely in the distal moiety thus resulting in a long plate-like ventral process (Fig. 52A). The gutter leading from the vascular notch toward the dorsal prominence is better developed than in *S. isodens*.

The humerus of *S. ripafodiator* (Fig. 55) while strongly resembling *S. isodens* in most features differs in a few small details. The clavicular articular facet is somewhat saddle-shaped compared to the simple curved articular facet in *S. isodens*. The trochlea is relatively wider. The pectoral ridge is straight, extends farther distally, and ends in a more vertically oriented and elongate tubercle, whereas in *S. isodens* the ridge scar tends to be curved or broken, does not extend as far distally and terminates in a stout, prominent and more transversely oriented tubercle. On the whole the humerus is relatively more slender than *S. isodens*.

The radius of *S. ripafodiator* (Fig. 56), represented by one complete and twelve incomplete

TABLE 13

MEASUREMENTS OF THE LOWER MOLAR TEETH OF BARSTOVIAN *Scalopoides*

	M^1		M^2		M^3	
	Length	Width	Length	Width	Length	Width
S. ripafodiator						
Quartz Basin						
UO 22494	1.80	1.15	2.30	1.15	....	....
UO 22546	....	....	2.01	1.26e	1.82	1.17
UO 22549	....	....	2.09	1.29	1.86	0.96
UO 22551	1.90	1.43	....	....	1.82	1.13
UO 22500	1.94	1.36	....	....	....	....
UO 22484	1.88	1.45	....	....	....	....
UO 22568	1.88	1.42	....	....	....	....
UO 22571	1.87	1.42	....	....	....	....
UO 22572	1.92e	1.43	....	....	....	....
UO 22576	1.93	1.45	....	....	....	....
UO 22600	1.81	1.35	....	....	....	....
UO 22573	....	....	2.04	1.40	....	....
UO 22575	....	....	2.01	1.38	....	....
UO 22342	....	....	....	....	1.81	1.07
UO 22485	....	....	....	....	1.83	1.12
UO 22490	....	....	....	....	1.79	1.07
UO 22496	....	....	....	....	1.84	1.05
UO 22590	....	....	....	....	1.81	1.09
UO 22591	....	....	....	....	1.79	1.12
UO 22595	....	....	....	....	1.79	1.09
UO 22598	....	....	....	....	1.81	1.07
S. cf *S. ripafodiator*						
Red Basin						
UO 24304	....	....	1.93	1.19	1.56	0.91
UO 24305	....	....	1.94	1.29	....	....
UO 24310	....	....	2.00	1.31	....	....
UO 24298	1.69	1.28	....	....	....	....
UO 24299	1.75	1.31	....	....	....	....
Guano Ranch						
USNM 23767	1.89	1.36	2.20	1.42	....	....
Beatty Butte						
USNM 23761	....	....	2.20	1.26	1.78	1.00

e Estimated measurement.

radii, resembles that of *S. isodens* in most details but differs in general proportions. It is relatively more slender than *S. isodens* (Table 16) in the shaft and terminal epiphysis.

While the number of specimens is greater than that from Martin Canyon, none of the ulnae from Quartz Basin are as well preserved. In features that can be compared, *S. ripafodiator* differs from *S. isodens* in that the lateral olecranon crests are not as well defined but closer together and the medial crest is not higher than the lateral crest.

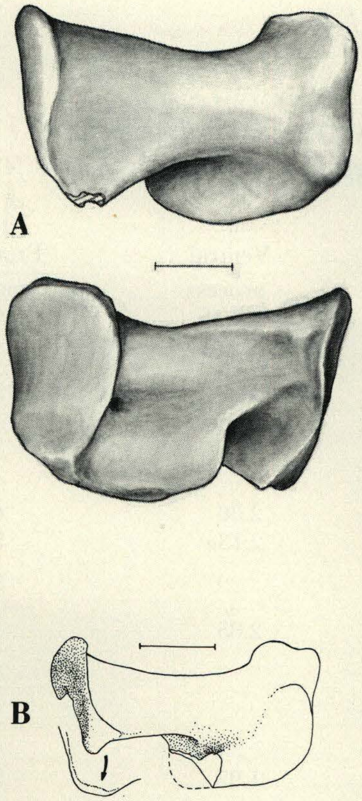

Figure 54. *Scalopoides ripafodiator* n. sp. Quartz Basin, UO loc 2465, **A;** UO 22415, left clavicle, anterior and posterior views, **B;** UO 22416, right clavicle, anteroventral view and anterior view of ventromedial spine.

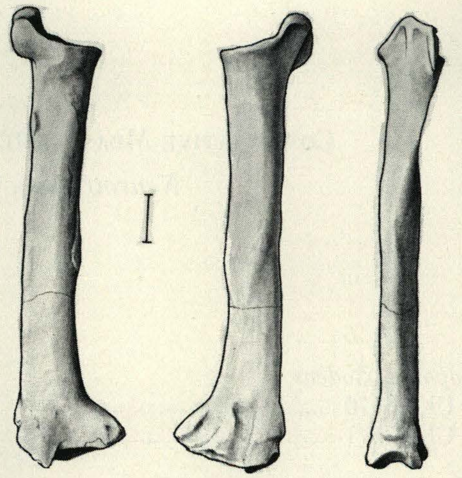

Figure 56. *Scalopoides ripafodiator* n. sp. Quartz Basin, UO loc 2465, UO 22428, left radius, medial, lateral and posterior views.

Of the moles available for comparison, the scaphoid of *S. ripafodiator* (Fig. 57) most closely resembles that of *Parascalops* in morphology and general proportions. There are three notable differences: the groove for the tendon of the M. flexor carpi radialis is bridged by bone to form a short tunnel, the facet for the os falciformis is more distally situated like that in *Scapanus*, and the posterior crest is relatively broader.

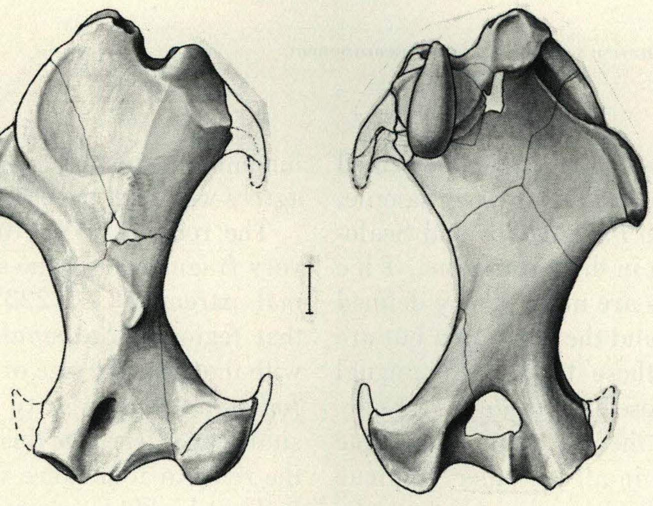

Figure 55. *Scalopoides ripafodiator* n. sp. Quartz Basin, UO loc 2465, UO 22366, left humerus, anterior and posterior views, unshaded areas with solid lines restored from other specimens.

TABLE 14

Comparative Measurements of the Clavicles of *Scalopoides*, *Neurotrichus*, *Condylura*, and *Scapanulus*

	Maximum length	Ventral process length	Process lg. / max. lg. %
Scalopoides isodens			
UK 15570	3.60	1.80e	50
UK 15571	3.98	....	....
Scalopoides ripafodiator			
UO 22415	4.50	2.88	64
UO 22416	3.61	2.13e	59
UO 22417	3.17	....	....
UO 22427	4.21	....	....
UO 22431	....	2.85	....
UO 22436	3.69	....	....
UO 24840	3.24	....	....
Scalopoides sp. A			
UO 24761	3.58e	1.95	54.5
?*Scalopoides* sp. C			
UO 25106	2.80*	1.45e	....
UO 25107	2.96*	....	....
Neurotrichus gibbsii	4.08	3.17	78
Condylura cristata	6.00	3.12	52
Scapanulus oweni	3.52	2.27	65

e Estimated measurement.
* Noticeable breakage or abrasion tending to reduce measurement.

The third metacarpal (Fig. 58), represented by three specimens in the Quartz Basin sample, is more elongate than *Parascalops* and Scalopina but shorter than in the Urotrichina. The proximal tuberosities are more poorly defined than in *Parascalops* and the Scalopina but are specialized toward these types. The ungual phalanges are like those of *S. isodens.*

In the innominate there are three vertebrae fused to the ilium as in all the other Talpinae but there is no bony connection between the acetabular region and the fourth sacral vertebra as in the Scalopina. In general robustness and other details preserved in the fragmentary innominata in the sample, *S. ripafodiator* agrees well with the other Parascalopina.

The remains of the femur (Fig. 59A) are very fragmentary. One specimen of the proximal extremity (UO 22395) closely resembles that region in *Scapanulus* and agrees closely with the expected size of the femur for *S. ripafodiator*. The majority of the specimens are similarly referred to this species on the basis of the relative abundance within this locality.

The tibiofibula is represented only by proximal and distal end fragments. The distal end of the tibiofibula (Fig. 59B) while closely resembling the common scalopine type has a

TABLE 15

COMPARATIVE MEASUREMENTS OF THE HUMERI OF *Scalopoides* AND *Scalopoides*-LIKE MOLES FROM OREGON AND COLORADO

Specimen	Total length	Prox. width	Shaft width	Distal width
S. isodens				
Martin Canyon Quarry A				
UK 10081	......	......	2.06	4.91
UK 10084	9.52	6.31	2.31	4.95
UK 10085	8.96	6.23	2.31	4.95
UK 10086	......	......	2.29	5.18
UK 10087	......	......	2.16	4.74
UK 10088	......	......	2.28	5.30
UK 10089	......	......	2.01	......
UK 10090	......	......	2.33	4.52
S. ripafodiator				
Quartz Basin				
UO 22355	......	......	2.26	4.54
UO 22361	......	......	2.17	......
UO 22366	9.75	......	2.24	4.62
UO 22370	......	......	2.26	4.33*
UO 22377	......	......	2.21e	4.56
UO 22387	9.23	......	2.06	......
S. cf. *S. ripafodiator*				
Red Basin				
UO 24343	......	......	......	3.91
UO 24249	......	......	......	3.87
Guano Lake				
USNM 23765	......	......	2.15	4.50
USGS loc. M. 1041				
USNM 23752	......	......	1.40	3.20
USNM 23754	......	......	......	4.95
USNM 23755	......	......	1.85	4.10
USNM 23756	......	......	1.85	......
USNM 23757	......	......	1.80	......
Scalopoides sp. A				
Black Butte				
UO 24764	......	......	2.24e	......
UO 24765	......	6.09	......	......
Scalopoides sp. B				
Black Butte				
UO 24784	......	......	1.66	3.67
?*Scalopoides* sp. D				
McKay Reservoir				
UO 24817	......	......	2.18	4.73
?*Scalopoides* sp. E				
McKay Reservoir				
UO 22606	7.81	......	1.73	......

* Noticeable breakage or abrasion tending to reduce measurement.

e Estimated measurement.

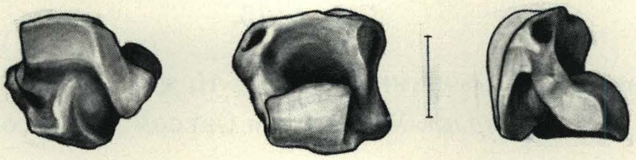

Figure 57. *Scalopoides ripafodiator* n. sp. Quartz Basin, UO loc 2465, UO 22446, right scaphoid, distal, dorsal, and lateral views.

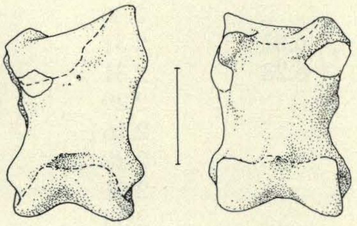

Figure 58. *Scalopoides ripafodiator* n. sp. Quartz Basin, UO loc 2465, UO 22439, left third metacarpal, dorsal and ventral views.

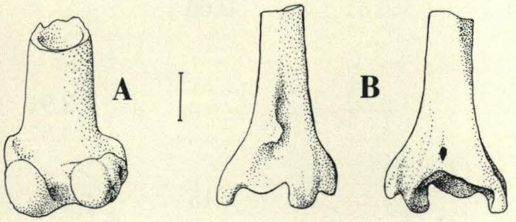

Figure 59. *Scalopoides ripafodiator* n. sp. Quartz Basin, UO loc 2465, **A;** UO 22398, distal end of right femur, posterior view, **B;** UO 22471, distal end of left tibiofibula, anterior and posterior views.

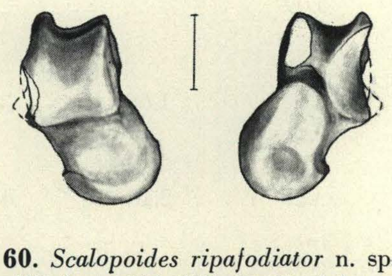

Figure 60. *Scalopoides ripafodiator* n. sp. Quartz Basin, UO loc 2465, UO 22401, left astragalus, dorsal and ventral views.

rather deep groove for the peroneous tendons as in *Condylura.* The fused portion of the tibiofibula is relatively long compared to the known Scalopini. The ossified portion of the transverse crural ligament is usually quite prominent and the ligament may ossify for more than half its length in some individuals (UO 22470). Of the three proximal epiphyses (UO 22481, UO 22475, UO 22479) assigned to this species on size, none of the significant diagnostic features of the falciform process are well enough preserved to enable a meaningful comparison with the other moles.

The calcaneum and astragalus are not significantly different from that in other known scalopines to warrant description. Unlike the other genera, the astragalus (Fig. 60) has a very broad neck as in *Scalopus.*

RELATIONSHIPS: Wilson (1960) in his discussion of the relationships of *Scalopoides isodens,* compared *Scalopoides* with various European genera and concluded that although it could be separated from the better known European genera, unidentified, or incompletely identified, specimens in the Sansan and La Grive faunas may be referrable to *Scalopoides.* He notes however that such similarity is only observable in the molars since the antemolar dentition was not preserved in the sample he examined. Convergence in molar form or in many of the limb bones is not uncommon in the talpids. Although re-examination of described and undescribed European materials may yet reveal similarities between North American and European talpids at the generic level, the differences cited by Wilson between *S. isodens* and various described European genera will also serve to separate *S. ripafodiator* from these forms.

TABLE 16

COMPARATIVE MEASUREMENTS OF THE RADII OF *Scalopoides*, *Condylura* AND *Neurotrichus*

	Shaft length (1)	Distal width (2)	Capitular process (3)	3/1 %	2/1 %
Scalopoides isodens					
Martin Canyon					
UK 15579	7.70	2.55	0.85	11	33
UK 15580	7.85	2.40	0.55*	......	31
UK 15581	......	2.05	......	......	......
UK 15583	......	2.30	......	......	......
UK 15584	......	......	0.70*	......	......
UK 15585	......	......	0.85	......	......
Scalopoides ripafodiator					
Quartz Basin					
UO 22428	8.40	2.23	0.76	9	27
UO 22421	7.34	2.14	......	......	29
UO 22433	7.85	2.07	......	......	26
UO 22424	......	......	0.75	......	......
UO 22425	......	......	0.77	......	......
UO 22429	......	......	0.72	......	......
UO 26800	......	......	0.74	......	......
UO 22420	......	2.21	......	......	......
UO 22422	......	2.04*	......	......	......
UO 22423	......	2.06	......	......	......
UO 22434	......	2.18	......	......	......
Scalopoides cf. *S. ripafodiator*					
Red Basin					
UO 24337	7.47	1.92	0.74	10	26
UO 24339	......	2.12	......	......	......
UO 24340	......	2.03	......	......	......
UO 24341	......	......	0.85	......	......
UO 24342	......	......	0.75	......	......
Neurotrichus gibbsii	7.55	1.57	0.55	7	21
Neurotrichus gibbsii	8.40	1.71	0.53	6	20
Neurotrichus gibbsii	7.84	1.84	0.53	7	23
Condylura cristata	11.55	2.84	0.96	8	14

* Noticeable abrasion tending to reduce measurement.

While the conservative nature of the dentition and relatively long clavicle with converging planes tend to align *Scalopoides* with the Urotrichini, the more fossorially specialized humerus, radius, ulna, and manubrium tend to situate it adaptively nearer *Condylura* and *Scapanulus*. The details of humerus ("scalopine" ridge, angle of the head, angle of the clavicular articular facet, etc.), manubrium (vertical anterior margin), clavicle (evidence of heterotopic bones, simple construction), ulna (prominent coronoid process, angle and detail of distal articular surface), radius (scalloped distal margin), metacarpals (robust and relatively simple construction), and generalized dentition and premolar construction serve to segregate *Scalopoides* from the Condylurini and align it with the Scalopini, especially the Parascalopina.

Scalopoides is readily distinguishable from all the living North American Scalopini in its less specialized foreleg, double-rooted premolars, and a number of smaller details. In foreleg specialization, it compares better with the only Eurasian living scalopine *Scapanulus* than with any of the North American forms, however, this is primarily an adaptive similarity. *Scapanulus* closely approaches *Scalopoides* in the construction of the lower molars but lacks the entocristids. The incisors are similar in form and the I_2 is enlarged in *Scapanulus* to approximately the same degree as in *Scalopoides;* however, *Scapanulus* retains a complete lower dental formula and all the premolars are single-rooted. The upper molars of *Scapanulus* (Fig. 5) also differ from *Scalopoides* in the prominently twinned mesostyles and relatively smaller protocones. On the humerus the teres tubercle and clavicular articular facet are relatively larger in *Scapanulus*. *Scalopoides* does not exhibit the twisting of the greater tuberosity and head medially as in *Scapanulus* and *Parascalops* (Figs. 10 D, E). The clavicle of *Scapanulus* while showing many similarities to *Scalopoides* in overall morphology and the presence of a facet for a heterotopic bone is relatively shorter than that of *Scalopoides* and the planes of articular facets are more nearly parallel. The articular planes of the clavicle of *S. isodens* and *S. ripafodiator* converge both posteriorly and ventrally to a greater degree than in any of the living Scalopini. The manubria of *Scalopoides* and *Scapanulus* strongly resemble each other in the slight degree of lateral expansion of the anterobasal extremity. The heterotopic bones of *Scalopoides,* however, appear to have been much smaller than those in *Scapanulus.*

Parascalops is a step further removed from *Scalopoides* in all of the above features. Moreover, in *Parascalops* upper molars, the metaconule and paraconule are very prominent and form a nearly rectangular lingual shelf. In the lower molars *Parascalops* has distinct mesostyles separated from the metaconids. The antemolars are all present and all the premolars are single-rooted. Also, the clavicle is much shorter and the humerus much broader than in either *Scapanulus* or *Scalopoides*. The base of the manubrium is expanded anteriorly with consequent reduction of the heterotopic bones.

Scapanus, while seemingly remote from *Scalopoides,* differs in some ways to a lesser degree from it than do *Scapanulus* or *Parascalops.* The mesostyles of upper molars are only slightly twinned and the paraconule and metaconule are subservient to the large protocone. The humerus, although broader and shorter shafted than *Scalopoides,* does not exhibit the twisting of the head and greater tuberosity of *Scapanulus* and *Parascalops.* The lower molars are higher crowned than in *Scalopoides* and lack metastylids. The lower antemolar dentition is usually complete, and premolars are single-rooted but the molars have entocristids.

Scalopus is still further removed morphologically from *Scalopoides* owing to its much broader humerus, shorter clavicle,, radius, ulna, and metacarpals, greatly reduced dentition, and hypsodont teeth.

At the species level, *S. ripafodiator* closely resembles *S. isodens* in most details. The two moles may, however, be segregated on a number of features which I interpret as more primitive in *S. ripafodiator*. The longer and more robust antemolar region, double-rooted P_2, peglike I_3, and relatively longer humerus, ulna and radius all indicate the retention of a primitive feature and a more generalized species than *S. isodens.* Assuming that the relative time occurrence of these two species is correct, then *S. isodens* does not form an ideal ancestor for *S. ripafodiator*. That they shared a common ancestor within the genus *Scalopoides* seems quite probable; however, such an ancestral form seemingly would be Arikareean in age.

Scalopoides cf. *S. ripafodiator*

Several specimens of *Scalopoides* were recovered from the Red Basin and southern Oregon localities. They are probably best referred tentatively to *S. ripafodiator* on gross features but differ from the type sample in their smaller size (Red Basin) and details of some teeth. All of the Red Basin specimens except the distal end of one tibiofibula come from UO loc. 2495. Specimen UO 24311 from Red Basin preserves two P^2 alveoli anterior to the P^3; this single P^3 has a small third root on the labial side between the two main roots. The P^3-M^1 differ in no consistant respects from the Quartz Basin sample except in their somewhat smaller size. The M^2 may, on the average, have a slightly more distinct paraconule, slightly deflated protocone and relatively narrower labial moiety than in the Quartz Basin *Scalopoides*.

Only one Red Basin specimen, UO 24300, preserves a substantial part of the lower antemolar region. Heavily worn C-M_1 are preserved, although the bone of the dentary, minutely fractured and splintered, may be distored strongly. The dental formula as preserved is like *S. ripafodiator* and all the premolars are likewise double rooted. There appears to be a mental foramen under the P_3 and a smaller one under the P_2. The jaw is very shallow in the antemolar region and is similar to *S. isodens* but the paralophid of the M_1 is bent as in *S. ripafodiator*. The shallowness of the jaw may be due in part to the advanced age of the individual or post depositional distortion (a common phenomenon in this locality) or both. The relationship of the posterior cingulum of the P_4 to the protoconid is more like that of *S. isodens* than *S. ripafodiator*. In another specimen, UO 24301, from the same locality, the P_3-P_4 are well preserved. A mental foramen is present beneath the P_4 in this specimen. Again the P_4 is very similar to that of *S. isodens*, although the paraconid is not as well defined and the protoconid is not as angulate. The molars are like those of *S. ripafodiator* except in size.

Two specimens from Guano Ranch preserved in one the P_4-M_1 (USNM 23766) and the M_1-M_2 in the other (USNM 23767). Another specimen (USNM 23761) from USGS loc. 1041 preserved the M_2-M_3. The molars are like those of *S. ripafodiator* but the one P_4 is relatively larger and longer than those from Quartz Basin. The morphology of the tooth resembles that of the Red Basin sample more than the type material.

No complete humeri were recovered from Red Basin. The fragmentary ones—mostly distal ends—are smaller than those of *S. ripafodiator* but are not otherwise easily comparable to any of the better known *Scalopoides* in detail.

The distal or mid-portions of six humeri (USNM 23752—USNM 23757) from USGS loc. M 1041 and one from Guano Ranch (USNM 23765) agree closly with those of *S. ripafodiator* in detail. One specimen (USNM 23752) is smaller (Table 15) than all the others and is comparable in size to the small *Scalopoides* from Black Butte to which it may be related if there are indeed more than one species of *Scalopoides* in this sample.

Aside from Quartz Basin other foreleg elements of Barstovian *Scalopoides* from Oregon are known only from Red Basin. The few ulna fragments are not observably different from those of *S. ripafodiator* from Quartz Basin.

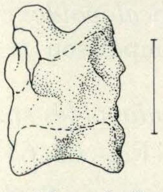

Figure 61. *Scalopoides* cf. *S. ripafodiator*, Red Basin, UO loc 2495, UO 24376, left second metacarpal, posterior view.

The one complete and five partial (UO 24337—UO 24342) radii, although smaller, are similar to those of the hypodigm.

The scaphoid (UO 24364, UO 24365), metacarpal III (UO 24379), ungual phalanx of the manus (UO 24374), and astragali (UO 24369—UO 24370) are also like those from the Quartz Basin sample. The metacarpal II (UO 24376, Fig. 61) which was not represented in the other sample is shorter than the metacarpal III from Quartz Basin and relatively narrower and longer than the metacarpal II in *Parascalops* and the Scalopina but considerably shorter than that in the Urotrichini or *Condylura*. The proximal tuberosities are damaged but better developed than in the Urotrichini.

The distal ends of the tibiofibula from Red Basin are essentially identical to those from Quartz Basin except for smaller size. However, the crural ligament is extensively ossified in the majority of the specimens from the Red Basin collection. The three distal ends of the tibiofibula (USNM 23758—USNM 23760) from USGS loc. 1041 fall within the range of *S. ripafodiator* in morphology and size.

Two extreme alternatives dealing with the above specimens are that at least three species are represented in the Barstovian samples of *Scalopoides* from Oregon or that there is considerable interdeme variation (including geography and time) particularly in regard to the P_4. The latter view is accepted here until such time that larger samples from these and other localities are available to adequately appreciate the population differences which may be used in differentiating grossly synchronous and geographically proximate populations or species. All the above material is thus referred to *Scalopoides* cf. *S. ripafodiator* until further comparison is possible.

Scalopoides sp. A
(Figs. 62, 63)

Several specimens of a *Scalopoides*-size mole were recovered from the Black Butte locality, UO loc. 2500. They are grouped together under a single heading largely on the basis of size and similarity to better known *Scalopoides*.

Nearly the entire proximal half of the humerus (UO 24765) and fragments of the shaft (UO 24764) and condyle (UO 24766) of two others attest to the presence of a *Scalopoides*-like mole, about the size of *S. ripafodiator* and *S. isodens*, in the Black Butte fauna. Although similar to the Miocene *Scalopoides* in most comparable details, the narrow groove between the head and clavicular articular facet is obliterated. There is some slight difference in the shape of the lesser tuberosity anteriorly although this is variable in structure; and the margin of the teres tubercle appears to be better aligned with the axis of the humerus. The pectoral muscle scars are too poorly preserved for comparison.

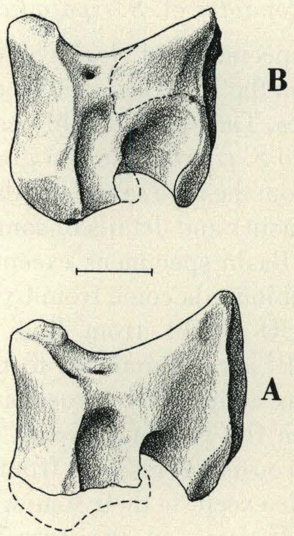

Figure 62. Left clavicles, posterior view, **A;** *Scalopoides* sp. A, Black Butte, UO loc 2500, UO 24761 (reversed right clavicle), **B;** *?Scalopoides* sp. **C;** Bartlett Mountain, UO loc 2517, UO 25106, dorsal prominence restored from UO 25107.

A single clavicle (UO 24761, Fig. 62B) lacking the ventral border of the ventral process and the clavicular articulation represents a mole about the size of that expected for the humeri described below. The clavicle represents a mole about the size of *S. ripafodiator* except that it is markedly shorter. Most of the shortening compared with that of *S. ripafodiator* occurs in the lateral moiety of the shaft, thus the ventral process forms a short plate rather than a long blade. In general appearance this clavicle resembles the clavicle of Scalopini sp. A from Red Basin discussed below. There is no prominent reflection of the ventromedial spine for a heterotopic bone. The relative shortness of clavicle is comparable to that in *Scapanulus*.

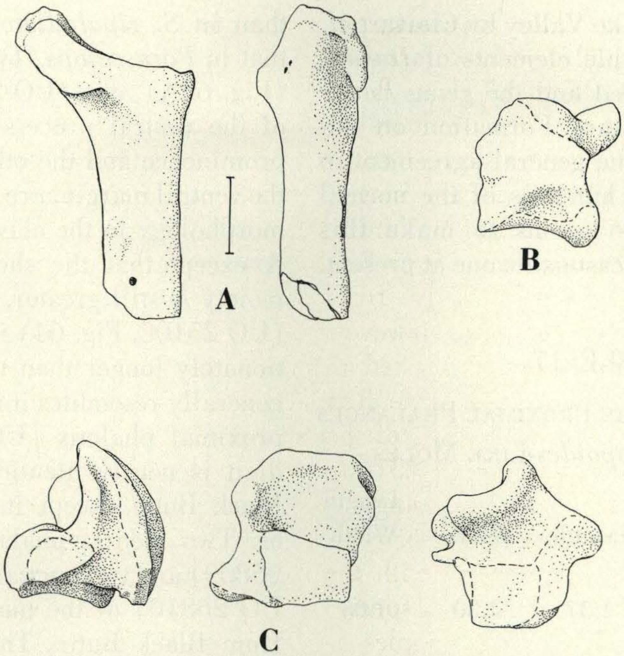

Figure 63. *Scalopoides* sp. A, Black Butte, UO loc 2500, **A;** UO 24759, proximal end of left radius, medial and posterior views, **B;** UO 24774, left first metacarpal, dorsal view, **C;** UO 24760, left scaphoid, lateral, dorsal and distal views.

Two ulna fragments (UO 24767, UO 24768) preserve neither extremity but resemble those of *S. ripafodiator* in comparable features. A specimen of the proximal end of a radius (UO 24759, Fig. 63A) differs from the Miocene species of *Scalopoides* in that the capitular process is drawn out more and supported as in *Parascalops* by a strong rib posteriorly resulting from the excavation of the shaft below the ulnar articular facet for the origin of the M. abductor pollicis longus as in *Scapanus*. The ulnar articular facet is elongated and well removed from the body of the shaft.

The scaphoid (UO 24760, Fig. 63C) resembles that of *Parascalops* even more closely than that of *S. ripafodiator* in the more proximal position of the os falciformis attachment, unbridged groove for the tendon of the M. flexor carpi radialis and the narrower posterior crest. However, there are a number of small difficultly described proportional and morphological differences which prevent this form from being a perfect miniature of *Parascalops*. The two small first metacarpals (UO 24774, UO 25181) are definitely those of a burrowing mole. They are as relatively compact as in *Parascalops* and most closely resemble this genus except that the lateral moiety of the distal articular surface is still more distally extended (Fig. 63B) than the medial one and not equal as in *Parascalops* or longer than the medial one as in the Scalopina. The three proximal phalanges (UO 24763, UO 24777, UO 25180) representing possibly as many digits of the manus, strongly resemble the phalanx of Scalopini sp. A from Red Basin in size and proportions, although, the Black Butte specimens are still slightly but relatively longer (Table 17). The middle phalanx (UO 26803) of the manus is short and of the burrowing type. The ungual phalanges of the manus (UO 24769, UO 25179) are like those of other *Scalopoides*.

The bones of the manus indicate a mole better adapted for digging than *S. ripafodiator* or *S. isodens* which is consistent with the shortened clavicle. The bones of the manus could belong to a small *Domninoides* such as that reported from Fish Lake Valley by Clark *et al.* (1964), but comparable elements of *Domninoides* are not recorded and the genus is unknown from the Juntura Formation on unequivocal material. The general agreement in expected size for the humerus of the normal *Scalopoides*-like mole seems to make this assignment the more reasonable one at present.

TABLE 17

Measurements of the Proximal Phalanges of Various *Scalopoides*-Like Moles

	Length	Width	Length/Width
Scalopoides isodens			
UK 15586	1.37	1.30	1.05
Scalopoides sp. A			
UO 24763	1.43	1.20	1.19
UO 24777	1.57	1.30	1.21
UO 25180	1.72	1.13	1.52
?*Scalopoides* sp. C			
UO 26807	1.40	1.27	1.10
?*Scalopoides* sp. D			
UO 27144	1.50	1.13	1.33

Scalopoides sp. B

A single humerus (UO 24784) from Black Butte loc. 2500 lacking most of the proximal end except the teres tubercle would seem to be well beyond the range of variation in size represented by *Scalopoides* sp. A from the same locality. The pectoral scars are not sharply defined but do not differ greatly from those of *S. ripafodiator*.

?*Scalopoides* sp. C

(Figs. 62, 64)

A few postcranial elements of a small mole about the size of *Scalopoides ripafodiator* were recovered from the Bartlett Mountain locality. Two scapula fragments (UO 24800, UO 26805) resemble the scapulae of *Parascalops* and the Miocene *Scalopoides*. The infraspinatus groove while well defined is narrower than in *S. ripafodiator* but quite similar to that in *Parascalops*. Two incomplete clavicles (Fig. 62A), one (UO 25106) lacking the tip of the ventral process and all of the dorsal prominence and the other (UO 25107) all of the ventral margin, are very similar in size and morphology to the clavicle of *Scalopoides* sp. A except that the shortening of the lateral moiety is still greater. The fourth metacarpal (UO 25108, Fig. 64) is narrower and proportionately longer than that of *Parascalops* but generally resembles it in structural detail. The proximal phalanx (UO 26807) of a manus digit is nearly identical to UO 24763 from Black Butte except it is very slightly shorter. Two medial phalanges (UO 26808, UO 26809) and two ungual phalanges (UO 24798, UO 26810) of the manus are also like those from Black Butte. The proximal end of the femur (UO 26806) is comparable to that of other *Scalopoides*. The astragalus (UO 26812) is like that of *S. ripafodiator* but the neck is narrower as in *Scapanus*.

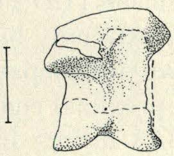

Figure 64. ?*Scalopoides* sp. C, Bartlett Mountain, UO loc 2517, UO 25108, right fourth metacarpal, posterior view.

Because of the great time gap between the better known *Scalopoides* (Barstovian) and the Hemphillian moles, assignment of various elements to *Scalopoides* becomes more tenuous. Nevertheless the similarities in morphology of the above postcranial elements and general agreement in size still point to closer relationship to *Scalopoides* than to other comparably represented moles. ?*Scalopoides* sp. C and ?*Scalopoides* sp. D may be synonymous but since they are each known from different elements and are nearly four hundred miles apart geographically, it seems best to treat them separately.

?Scalopoides sp. D
(Fig. 65)

The distal portion of a humerus (UO 24817) and a shaft fragment of another (UO 25128) indicate the presence of a *Scalopoides* grade of mole about the size of *S. ripafodiator* in the McKay Reservoir locality. The shaft is more robust and the anterior orifice of the entepicondylar foramen is more extensively pocketed than in the other species of *Scalopoides*. The pectoral crest terminates more proximally than in *S. ripafodiator*.

This humerus appears to be somewhat better fossorially specialized judging from its robustness and pectoral crest position. This specimen and the jaw and teeth provisionally assigned to "*Neurotrichus*" may represent a single species. This possibility is discussed further under *?Neurotrichus columbianus*.

The proximal phalanx of the manus (UO 27144) assignable to this or the following species, is intermediate in proportions between *Parascalops* and Scalopina sp. A.

?Scalopoides sp. E
(Fig. 66)

Four specimens from McKay of a *Scalopoides*-like mole appear to be too small to assign to *?Scalopoides* sp. D. The humerus (UO 22606) is complete except for the radial condylus, head, deltoid process, and part of the lesser tuberosity. It resembles *S. ripafodiator* in most details except on the obliteration of the groove between the head and clavicular facet, configuration of the pectoral muscle scars, more pocketed anterior orifice of the entepicondylar foramen, and small size. There is a vertical raised ridge anteriorly in the middle of the shaft which is part of the pectoral muscle scar complex. This is not prominently developed or present on the other *Scalopoides*-like humeri seen, although its expression is probably age dependent.

Part of the semilunar notch and shaft of the ulna (UO 26819, UO 27145) agree in the detail of the distal margin the semilunar notch with *Scalopoides* especially *S. ripafodiator* and *Scalopoides* sp. A rather than *Neurotrichus* or Urotichini. These specimens could be part of *Scalopoides* sp. D but size seems to favor a smaller mole.

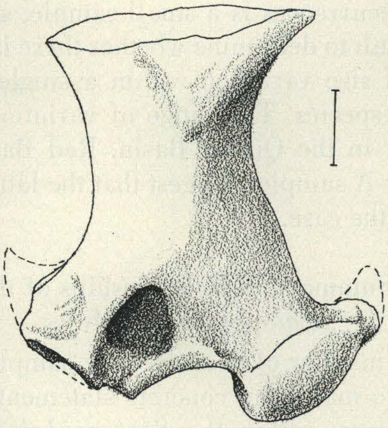

Figure 65. *?Scalopoides* sp. D, McKay Reservoir, UO loc 2222, UO 24817, shaft and distal end of left humerus, anterior view.

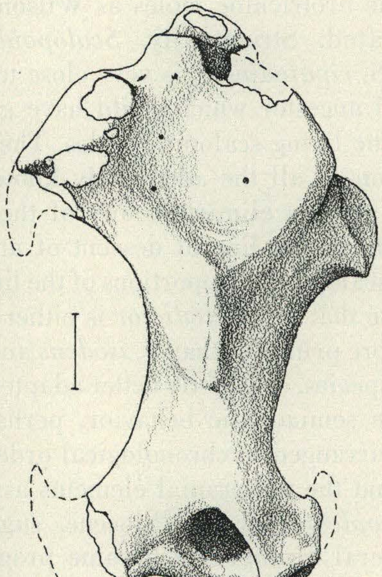

Figure 66. *?Scalopoides* sp. E, McKay Reservoir, UO loc 2222, UO 22606, right humerus, anterior view.

This represents the second or third occurrence of a small *Scalopoides*-like mole with a larger *Scalopoides*-like mole. Each of these joint occurrences is a small sample, so that it is difficult to determine whether there is a great deal of size variation within a single species or two species. The range of variation of the humeri in the Quartz Basin, Red Basin, and Quarry A samples suggest that the latter situation is the case.

Summary of Relationships of the *Scalopoides*-like Moles

The number of good locality samples is too small to make any concrete statements on the phylogeny within the *Scalopoides* complex. The increased knowledge of the postcranial skeleton does align *Scalopoides* with the more specialized moles, the Scalopini, rather than with the urotrichine moles as Wilson (1960) postulated. Structurally, *Scalopoides*, especially *S. ripafodiator*, is very close to a hypothetical ancestor which could have given rise to all the living scalopine moles. The reduced dentition of all the adequately known *Scalopoides* species eliminates any of these forms from the direct line of descent of any of the living scalopines. Proportions of the limb bones indicate that *S. ripafodiator* is either structurally more primitive than *S. isodens* and the Pliocene species, or slightly better adapted for facultative semiaquatic behavior, perhaps both. When arranged in chronological order, *S. isodens* and the postcranial elements assigned to *Scalopoides* from the Pliocene, suggest that in general *Scalopoides* became progressively better adapted for burrowing with time. This may have occurred at various times in different regions and thus may not be used as a means of correlation outside the Great Basin until equally good or better sequences can be demonstrated in other areas.

DOMNINOIDES Green, 1956

Domninoides (sensu lato) is turning up with increasing frequency in middle and later Tertiary deposits of North America, but little is yet known about its systematic position with respect to the living genera. Only Tedford (1961) has attempted a careful comparison of *Domninoides* with the Recent American genera. He concluded, rightly, that *Domninoides* is more closely related to *Parascalops* than to any other Recent American mole.

PROVISIONAL DIAGNOSIS: Burrowing moles with reduced antemolar dentition; P_4 and P_2 double-rooted; P_3 single-rooted. Lower molars moderately high crowned (mesodont), postfossids open lingually and crista obliqua of M_2-M_3 joining metastylid as in *Parascalops*, metastylids not as posteriorly situated as in *Parascalops*. Humerus *Parascalops*-like in morphology and proportions, except in the pectoral muscle scar V-configuration.

Domninoides sp.

(Figs. 67-69)

Domninoides is known from teeth in two Barstovian localities in Oregon, Guano Ranch and Quartz Basin. Two incomplete jaws each containing the M_1-M_2, USNM 23768 andUSNM 23769 (Fig. 67), from Guano Ranch closely approach the *Scalopoides* species from the same locality in size. They may be distinguished from the *Scalopoides* on (1) the absence of an entocristid, (2) the extension of the crista obliqua of the M_2 to the metastylid and its more lingual extension on the M_1, (3) and relatively

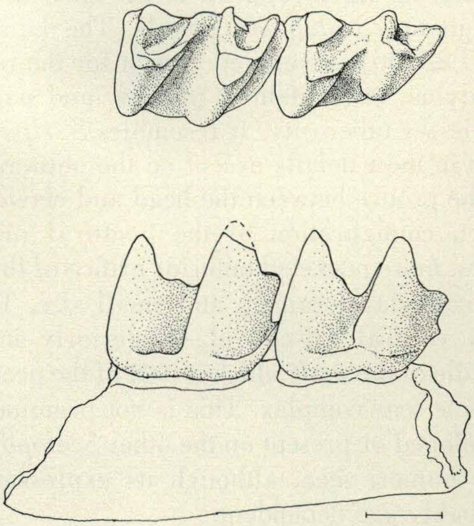

Figure 67. *Domninoides* sp. Guano Ranch, USGS loc M1042, USNM 23769, right dentary fragment with M_1-M_2, occlusal and labial views.

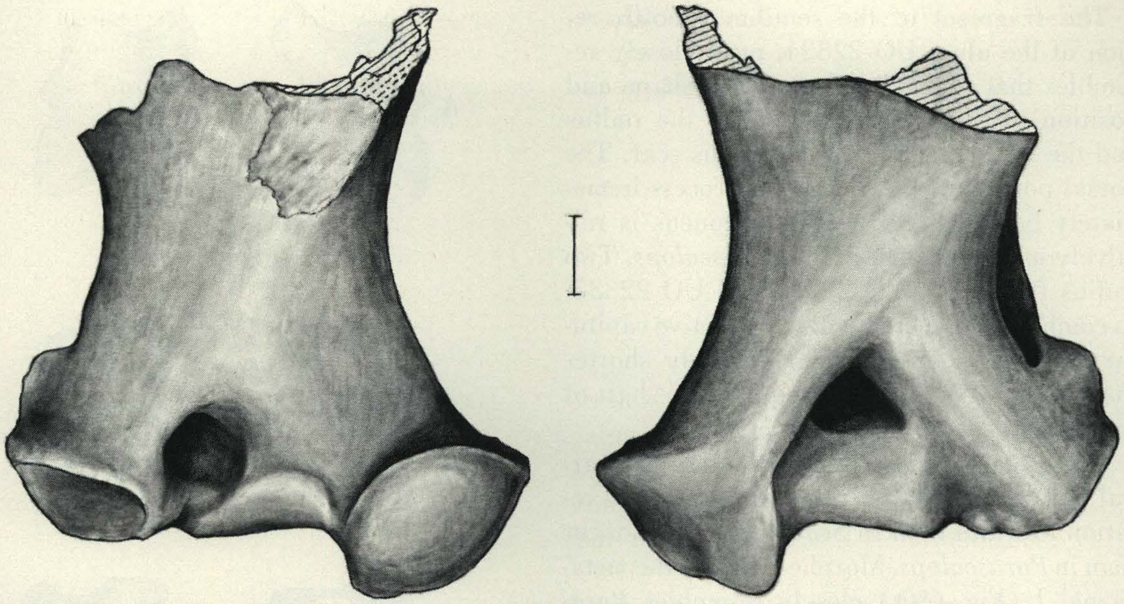

Figure 68. *Domninoides* sp. Quartz Basin, UO loc 2465, UO 22333, distal end of left humerus, anterior and posterior views.

wider molars. All of these features are characteristic of *Domninoides*. A single, somewhat eroded M_2, UO 22498, from Quartz Basin closely resembles the Guano Ranch forms in size and morphology.

Several postcranial elements, mostly incomplete, of a burrowing mole were also recovered from Quartz Basin. They are included here largely on the grounds of expected relative size and the lack of any conclusive evidence to the contrary that there is another burrowing mole in the fauna. The distal end of the humerus, UO 22333 (Fig. 68), has a very stout and inflated shaft. The pectoral tubercle is very well developed and elongate as in the Scalopina, but the lateral edge of the tubercle is more vertically oriented than in *Scapanus* or *Scalopus*. Unfortunately, the actual surface of the tubercle is eroded to the extent that the details of the muscle scars are obscured. The teres tubercle does not approach the epicondyle as closely as in *Scapanus* and *Scalopus* and is thus more like the condition in *Parascalops*, *Domninoides*, and Scalopina sp. A.

TABLE 18

MEASUREMENTS OF THE LOWER TEETH AND JAWS OF *Domninoides* SP.

		UO 22498	USNM 23768	USNM 23769
M_1:	Length	....	2.00	2.13
	Width	....	1.37	1.40
M_2:	Length	2.36	2.30	2.23
	Width	1.20*	1.47	1.50
Depth of jaw below M_1 metaconid		....	1.87	1.73

* Abraded.

The fragment of the semilunar notch region of the ulna, UO 22334, most closely resembles that of *Parascalops* in the shape and position of the articular facet for the radius and the M. abductor pollicis longus scar. The dorsal portion of the olecranon process immediately behind the processus anconeus is relatively narrower than in the *Parascalops*. Two radius fragments, UO 22340 and UO 22335, in combination lack only the distinctive capitular process. The radius is relatively shorter than in *Parascalops*. The length of the shaft of UO 22340 is 7.2 mm.

The metacarpal I, UO 22338, and metacarpal IV, UO 22341, are relatively shorter in relation to width than in *Scalopoides* but longer than in *Parascalops*. Morphologically the metacarpal I (Fig. 69A) closely resembles *Parascalops* except for the presence of a shallow groove on the dorsal side immediately distal to the proximal articular facet. The metacarpal IV (Fig. 69B) has a smaller articular facet for metacarpal V than in *Parascalops* which results in a more angulate proximolateral extremity. The medial phalanx, UO 22337 (Fig. 67C), of the second or third digit of the manus is relatively short and resembles *Parascalops*, *Scapanus orarius* and *S. townsendii* in proportions. An ungual phalanx, UO 24835, was also recovered.

RELATIONSHIPS: The dentulous elements fall within the reasonable variation in size and morphology of that of *D. riparensis* or of the *D.* cf. *riparensis* reported from the Clarendonian Fish Lake beds of Nevada. Differences in the configuration of the antemolar teeth will probably prove to be useful in delineating the species of *Domninoides*, but this region is not preserved in any of the Oregon specimens. The specific relationships of *D. platybrachys* will be in doubt until more material is found. specific reference to these or any of the other Barstovian and Clarendonian records of *Domninoides* seems unwarranted in the light of the meager material thus far published.

The postcranial elements pose different problems. More than one burrowing mole may be represented in the Quartz Basin. Some of the features of the humerus and radius suggest possible relationships to the Scalopina while other elements more closely resemble those of the Parascalopina. If the association of these elements with each other and the *Domninoides* tooth is valid, then we are dealing with a small burrowing mole which is more specialized in some aspects of the humerus and shortness of the radius and phalanges than *Parascalops* but less specialized in the relative shortening of the metacarpals.

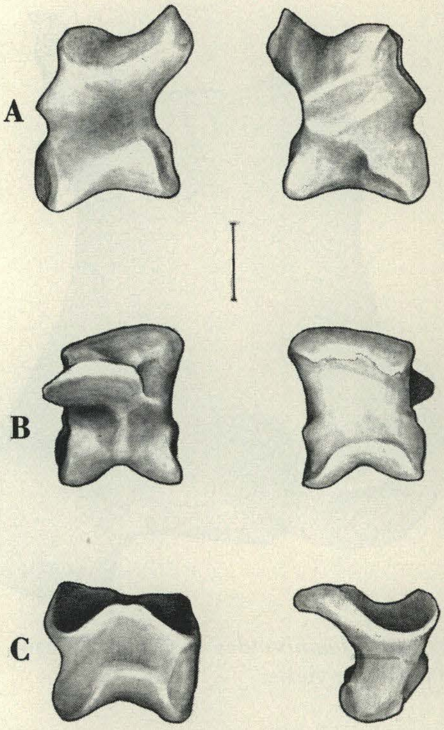

Figure 69. *Domninoides* sp. Quartz Basin, UO loc 2465, **A;** UO 22338, metacarpal I, dorsal and ventral views, **B;** UO 22341, metacarpal IV, dorsal and ventral views, **C;** UO 22337, left proximal phalanx of digit II or II, dorsal and right lateral views.

Subtribe Scalopina (Van Valen, 1967) Winge, 1917

No metastylids on lower molars; bulla expanded, stapedial tube strongly ossified; manubrium without dorsal ridge, anterior vena cava divided posteriorly; no heterotopic bones between clavicles and manubrium; humerus

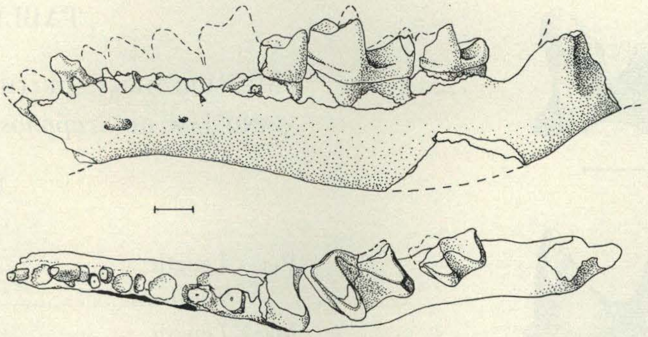

Figure 70. *Scapanoscapter simplicidens* n. sp., n. gen., Red Basin UO loc 2495, Type specimen UO 24286, left mandible with I_3, P_3, talonid of M_1, and M_2-M_3, labial and occlusal views.

broad, pectoral ridge terminates medially, area surrounded by pectoral ridge, pectoral crest, and greater tuberosity shallow; capitular process of radius rounded or pointed.

SCAPANOSCAPTER[12] n. gen.

GENOTYPE: *Scapanoscapter simplicidens*, n. sp.

KNOWN DISTRIBUTION: Late Miocene (Barstovian) of Oregon.

DIAGNOSIS: Scalopine mole about the size of *Scapanus latimanus* with dental formula: $\frac{?\ ?\ ?\ ?}{3\ 1\ 4\ 3}$. I_2 is not hypertrophied, P_1-P_4 double-rooted, prominent heel on all (?) lower premolars. Molars brachyodont, trigonids anteroposteriorly compressed. M^1 metacingulum well-developed and extends posteriorly around base of metacone.

Scapanoscapter simplicidens[13] n. sp.

(Figs. 70-72)

TYPE: UO 24286, fractured left mandible with heavily worn P_1, talonid of M_1, and M_2-M_3; mandible broken just posterior to beginning of ascending ramus and anterior to middle of the I_2 alveolus.

HYPODIGM: UO 24289, UO 24290, worn and unworn M^1's; UO 24291 lingual moiety of M^2 (?); UO 24287, UO 24288 trigonid of M_2, unworn M_1; UO 24294 proximal end of scapula; UO 24292, ulna fragment; UO 24296 scaphoid; UO 23295, third metacarpal; UO 24285, UO 24377, one proximal phalanx, two medial phalanges and an ungual phalanx of manus; UO 24386, astragalus. All from type locality.

REFERRED SPECIMEN: USGS loc. M 1040; USNM 23751, humerus lacking ulnar articular region.

TYPE LOCALITY: Red Basin, UO loc. 2495.

AGE: Barstovian.

DIAGNOSIS: Same as genus.

DESCRIPTION: The dentary of *Scapanoscapter* (Fig. 70) is shaped like that of *Scapanus (Scapanus)*, *i.e.*, the Recent species. There are two mental foramina, one ventral to the P_4, and the larger anterior one ventral to the P_2-P_3. The anterior tip of the jaw is broken but the dental formula was apparently complete. The jaw is broken through the I_2 alveolus. The remains of the I_2 alveolus do not indicate a notably enlarged tooth. The I_3 is a peg-like tooth and the smallest tooth in the jaw. The alveolus of a larger, single-rooted canine follows the I_3. This alveolus is obliquely ovate. Of the premolars only the P_1 is preserved but the alveoli of the remaining teeth indicate that the premolars increased regularly in size from the P_1 to P_4. All the premolars are distinctly double-rooted. The roots of the first two premolars are obliquely aligned in the jaw with the anterior root more labial. The crown of the P_1 consists of a simple

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[12] From the Greek *skapane,* digging tool, and *skapter,* digger.

[13] From the Latin *simplis,* simple, and *dens,* tooth.

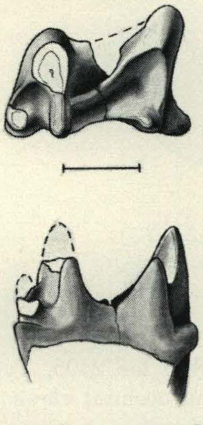

Figure 71. *Scapanoscapter simplicidents* n. sp., n. gen., Red Basin, UO loc 2495, UO 24287, right M_1, occlusal and lingual views.

connate cusp centered over the anterior root. A simple heel forms the posterior moiety of the tooth.

The M_1 (UO 24287, Fig. 71) resembles *S. shultzi* in many respects but differs as follows: (1) it is lower crowned, (2) the trigonid is slightly less compressed anteroposteriorly, (3) a narrow cingulum is present around the anterior and labial base of the protoconid. The M_2 also closely resembles that of *S. schultzi* except that (1) a poorly defined metastylid and long tapering anterior cingulum are present, (2) the crista obliqua and entocristid more closely approach each other anteriorly, and (3) there is no suggestion of an ectostylid. The M_3 is heavily worn and damaged in the type but it also apparently resembled *S. schultzi* except in the presence of a narrow anterior cingulum and lack of an ectostylid.

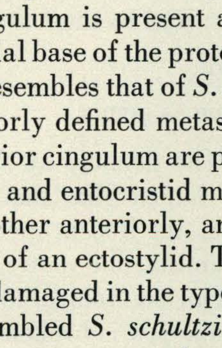

Figure 72. *Scapanoscapter simplicidens* n. sp., n. gen., Red Basin, UO loc 2495, UO 24289, right M^1 (posterolabial part restored from UO 24289), occlusal view.

TABLE 19

Measurements of the Lower Dentition and Jaw of *Scapanoscapter simplicidens*.

		UO 24286 (Type)	UO 24287
P_1:	Length	0.76	....
	Width	0.48	....
M_1:	Length	....	2.46
	Width	....	1.72
M_2:	Length	2.33*	....
	Width	1.87	....
M_3:	Length	1.83e	....
	Width	....	....
I_2-M_3 alveolar length		12.1	....
P_1-P_4 alveolar length		4.0	....
M_1-M_3 alveolar length		7.0	....
Depth of jaw below M_1		2.55	....

* Noticeable abrasion tending to reduce measurement.
e Estimated measurement.

The M^1 (Fig. 72) resembles that of *Scalopoides* more than *Scapanus* in most features other than size. It is relatively brachyodont with a distinct metaconule. The paraconule is a well developed cusp adjacent to the apex of the protocone in the unworn condition, and there is a paracingulum. In the position of the filiform root of *Scalopoides* there is a raised transverse ridge. The other roots are similar to those in *S. ripafodiator*. The living species of *Scapanus* do not possess prominences between the roots of the molars. The M^1 is about 2.8 mm. long and 2.64 mm. wide.

Only the region immediately forming the glenoid cavity of the scapula is preserved. The acromion process appears to arise directly from the glenoid rim rather than removed from it by a small gap as in *Scapanus* and *Parascalops*. The foramen for the suprascapular nerve is correspondingly nearer the glenoid border than in the aforementioned genera. However, in these features UO 24294 closely resembles *Scalopus*. The biceps tubercle appears to arise directly from the glenoid rim.

TABLE 20

COMPARATIVE MEASUREMENTS OF THE HUMERI OF THE *Scapanus*-LIKE MOLES FROM OREGON

	Total length	Proximal width	Distal width	Shaft width
Scapanoscapter simplicidens				
USGS Loc. M1040				
USNM 23751	12.5e	10.0	......	4.2
Scapanus (*Xeroscapheus*) cf. *S.* (*X.*) *shultzi*				
Black Butte I				
UO 24632	......	......	......	4.2
UO 24633	......	......	8.2	......
West of Riverside				
UO 23075	......	......	8.1	4.4
Loc. ? Juntura Fm.				
UO 23074	......	......	9.0	4.8
S. (*X.*) *proceridens*				
Krebs Ranch II				
UO 8476	16.1	11.7	9.7	5.3
UO 8474	......	......	8.5	4.6
UO 8475	......	......	9.0	4.8
UO 22603	......	......	8.8	4.6
Krebs Ranch I				
UO 4585	16.2	12.1	9.8	4.8
Westend Blowout				
UO 7960	14.5e	10.5+	9.0	4.7
UO 5959	......	......	9.4	4.8
CIT 375				
LACM 16765	14.6	10.9	8.6	5.0
Little Valley I				
UO 10816	......	......	9.7	4.7
S. cf. *S.* (*X.*) *proceridens*				
McKay Reservoir				
UO 3506	......	......	7.8	3.8
Scapanus sp.				
Rome				
LACM 6499	......	......	4.4	2.3e
LACM 6499	......	7.7+	4.1	......
Scapanus nr ? *S. latimanus*				
Enrico Ranch				
UO 4585	16.2	12.1	9.8	4.8

e=Estimated measurement.
+=Broken measurement as preserved.

The humerus from USGS loc. M 1040 lacking the ulnar articular region is about the size of that of *Scapanus orarius* and is nearly identical to that of the living species of *Scapanus* in morphology and proportions except that the fossa for the brachialis muscle is not as deeply excavated. Reference to this genus and species is provisional.

A fragment of the semilunar notch region of the ulna resembles that of the modern *Scapanus* except that the coronoid process is rather poorly developed.

The scaphoid is broken and lacks all of the posterior and medial crests. The medial process is smaller than in *Scapanus (Scapanus)* but relatively larger than in *Parascalops*. The pit for the scapholunar tendon is small and restricted to the lateral moiety. As in *Scapanus* the central facet occupies a large majority of the radial trochlea distally.

The metacarpal III is essentially the same as in *S. townsendii* and *S. orarius* in morphology and proportions except that the lateral proximal process is somewhat more heavily developed and thus resembles *Parascalops* in this feature. The third metacarpal is proportionately shorter than in *Parascalops*. The proximal phalanx and two medial phalanges of the manus (UO 24285 collectively) and ungual phalanx are proportionately and morphologically like those of *S. orarius* and *S. townsendii*. The astragalus is similar to that in *S. (Scapanus)* except that the tibial facet is more saddle-shaped as in *Parascalops*.

Scapanoscapter simplicidens appears to be referable to the Scalopina on the construction of the talonid and close similarity of the teeth to those of *S. shultzi*. The upper teeth and antemolar teeth suggest a very primitive member of the *Scapanus* complex which retains many *Scalopoides*-like features. Postcranially the skeleton seems to have achieved a structural grade near that of *S. orarius* and *S. townsendii*. The double-rooted premolars are considered as a primitive character which will serve to distinguish it from all the living and known fossil North American highly fossorial talpids. Temporally and functionally it is in a position to be a structural ancestor to either *Scapanus* and *Scalopus*, although the former is more probable based upon known distributions.

SCAPANUS Pomel, 1848

DIAGNOSIS: Scalopine moles with usually complete dental formulae. Clavicle usually not pierced by vena cava. Humerus not as broad as in *Scalopus*.

Subgenus *SCAPANUS* Pomel, 1848

GENOTYPE: *Scalops townsendii* Bachman, 1839.

INCLUDED SPECIES: *Scapanus townsendii* (Bachman) 1839. *S. orarius* True, 1896. *S. latimanus* (Bachman), 1842.

KNOWN DISTRIBUTION: Middle Pliocene (Hemphillian) to Recent of Western North America.

DIAGNOSIS: Medium to large moles with relatively long antemolar regions, P_1-P_4 single-rooted, I_2 only moderately enlarged. Clavicle not pierced by vena cava. Scapula with infraspinatus fossa extinguished well before reaching acromion process.

Scapanus cf. *S. (Scapanus)* sp.
(Fig. 73)

Three teeth and some hand bones of a moderately large mole from Bartlett Mountain, UO loc. 2517, are probably referable to *Scapanus*.

The lower M_3 (UO 24803) is so heavily worn that the cusp morphology is obscured. The anterolabial accessory cusp is large and rectangular. The anterior cingulum extends part way along the paralophid from the accessory cusp. There is a labial cingulum bridging the hypoflexid. The tooth is therefore not referable to *S. proceridens*. The M_3 is 2.13 mm. long and 1.47 mm. wide. An upper M^2 (UO 24804) and M^3 (UO 26341) fall within the variation of the teeth of *S. orarius* or *S. townsendii* in every detail except for size in which they are intermediate between these two species. The metaconule is not as isolated from the lingual base of the metacone by a deep notch as in *S. lati-*

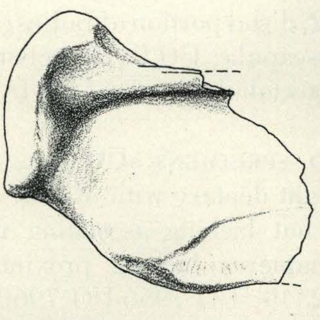

Figure 73. *Scapanus (Scapanus)* sp. Bartlett Mountain, UO loc 2359, UO 9664, anterior portion of the manubrium, left lateral view.

manus. The M^2 is 2.58 mm. long and an estimated 2.4 mm. wide; the M^3 is about 1.7 mm. long and 1.7+ mm. wide (ectoloph damaged).

The anterior third of the manubrium (UO 9664) from Bartlett Mountain loc. 2357 closely resembles that of the living species except that the depth of the area for insertion of the M. pectoralis superficialis posticus is deeper, i.e., more extensive than in the modern forms.

Two fifth metacarpals (UO 25102, UO 26935) are essentially identical to that in *S. orarius.* The three ungual phalanges of the manus (UO 25110, UO 26936, UO 26937) are also present in the sample.

The sample is small but there is not a single morphological feature which would exclude the Bartlett Mountain species from inclusion in the subgenus *Scapanus* or forming a possibly ancestoral species to the living forms. The M_3, in extreme wear, is not unlike *S. shultzi* except for the lack of an ectostylid. The material is too sparse to eliminate the possibility that these specimens represent a primitive member of *Xeroscapheus*, although their assignment to the subgenus *Scapanus* seems more likely to me.

Scapanus nr.? *S. latimanus*

(Fig. 10 F)

An isolated humerus, UO 4585, from Enrico Ranch, Lake Co., is about the same size as that of the living *S. latimanus* and is otherwise not distinguishable from the humeri of Recent *Scapanus.* The range of *S. latimanus* includes the site of the fossil locality. The age of the Enrico Ranch material is in doubt but is at least as old as Blancan.

XEROSCAPHEUS[14] n. subgen.

SUBGENOTYPE: *Scapanus (Xeroscapheus) proceridens,* n. sp.

KNOWN DISTRIBUTION: Early Pliocene (Clarendonian) of California and Oregon, Middle Pliocene (Hemphillian) of Oregon.

DIAGNOSIS: Medium to large moles with hypsobrachyodont to hypsodont lower molars, and crowded antemolar teeth. Trigonids of lower molars anteroposteriorly compressed, P_1-P_3 single-rooted, P_4 double-rooted or suggestion of fused roots, I_2 enlarged. Scapula with a narrow infraspinatus fossa which extends as a deep groove to the acromion process. Radius, ulna, and non-terminal phalanges relatively shorter than in living *S. (Scapanus).*

Scapanus (Xeroscapheus) cf. *S. shultzi*

MATERIAL: Black Butte II, UO loc. 2500: UO 24662, dentary fragment; UO 24749, about two-fifths of the proximal portion of the scapula; UO 24751, UO 24753, two humerus fragments; UO 24747, metacarpal IV; UO 24758, ossified palmer ligament; UO 24743, UO 24744, UO 24756, ungual phalanges of the manus; UO 24745, UO 24754, calcanea. Black Butte I, UO loc. 2337: UO 24632, UO 24633, distal ends of two humeri. West of Riverside, UO loc. 2489: UO 23075, humerus lacking proximal end; UO 23076, distal end of radius. Juntura Formation, exact locality unknown; UO 23074, humerus lacking most of proximal end.

About two-fifths of the proximal portion of the scapula was recovered. The acromion process originates slightly more anterior than in the modern species. The infraspinatus fossa continued forward as a deep gutter until passing anterior to the posterior margin of the acro-

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[14] From the Greek *xeros,* dry, and *skapheus,* digger.

mion process. The biceps tubercle is developed just posterior to the glenoid rim as in *Parascalops* and is contiguous with it. In size and the above mentioned features, UO 24749 closely resembles a similarly preserved scapula from the Ricardo Formation in the UCMP collections.

The humeri closely resemble the modern *Scapanus* in details and proportions. The notch between the teres tubercle and the epicondyle is small and not like the relatively large notch in the specimen referred to *S. shultzi* from the Ricardo Formation.

The somewhat eroded metacarpal IV is about at the structural grade and morphology of *S. orarius, S. townsendii,* and *Parascalops.* The proximal phalanx of the second or third digit of the manus and median phalanx are proportionately slightly shorter in relation to their respective widths than *S. latimanus* and approach *Scalopus* in this respect. The ossified palmer ligament, ungual phalanges of the manus, and calcaneum show no consistent differences from those of the living *Scapanus.*

The described material of *Scapanus shultzi* is largely not comparable to the material from the Juntura Formation. The humerus referred to *S. shultzi* by Tedford (1961) is crushed and broken so that comparisons between the incomplete but well preserved humeri from Oregon are difficult. Additional material of *Scapanus* from the Ricardo Formation of California is coming to light through screen washing efforts of Mr. David Whistler at the University of California at Berkeley. Although this material has not been studied, cursory examination suggestions that the Oregon material may be referable to *S. shultzi.*

Scapanus (Xeroscapheus) proceridens[15] sp. n.

(Figs. 74, 75)

TYPE: UO 22508, right mandible with I_2, P_1, M_1-M_2, but lacking ascending ramus and tip of horizontal ramus.

HYPODIGM: UO 8474, UO 8476, UO 22603, one complete and three fragmentary humeri; UO 22602, distal portion of radius; UO 26839, complete scapula; UO 8429, pelvic girdle anterior to acetabular region; all from type locality.

REFERRED SPECIMENS: UO loc. 2380: UO 26921, right dentary with M_1-M_2, and alveoli of I_2-M_3 but lacking ascending ramus; UO 10816; humerus lacking proximal portion. UO loc. 2349: UO 7956-UO 7960, two damaged humeri. CIT loc. 375: LACM 16764, edentuluous dentary fragment; LACM 16765, humerus lacking head. UO loc. 2322: UO 8643, dentary fragment; UO 26890, poorly preserved distal end of radius. UO loc. 2516: UO 26922, dentary fragment with M_2-M_3; UO 26923, head of humerus; UO 26924, ulna fragment; UO 26925, scaphoid; UO 26926, lunar; UO 26927, medial phalanx II or III of manus; UO 26928-UO 26929, ungual phalanges.

TYPE LOCALITY: Krebs Ranch II, UO loc. 2323.

AGE: Late Hemphillian.

DIAGNOSIS: Deep jawed species with dental formula $\frac{?\ ?\ ?\ ?}{3\ 1\ 4\ 3}$. I_2 hypertrophied, I_3 vestigial; P_4 with fused double (?) root, P_1-P_3 single-rooted; molars hypsodont with extensive os cementum. Antemolar length proportionately more reduced than in other species. Scapula with infraspinatus fossa extending beneath acromion process. Humerus as in living species of *Scapanus.* Radius and ulna relatively shorter than in living species (?). Phalanges of manus shorter than living species.

DESCRIPTION: The mandible (Fig. 74) is deep and relatively short. The mandibular symphysis extends posteriorly to the level of the P_4. Of the two mental foramina, one is located ventral to the P_2 and the other under the P_4. The tip of the type dentary is lacking but the dental formula appears to have been complete based on the referred material from Little Valley and by analogy with other scalopine moles. The I_2 is hypertrophied, incisiform and rather rodent-like. The anterior leading edge of the root is sheathed in os cementum which also extends up the posterior moiety of the crown. Crowded

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[15] From the Latin *procerus,* high, and *dens,* tooth.

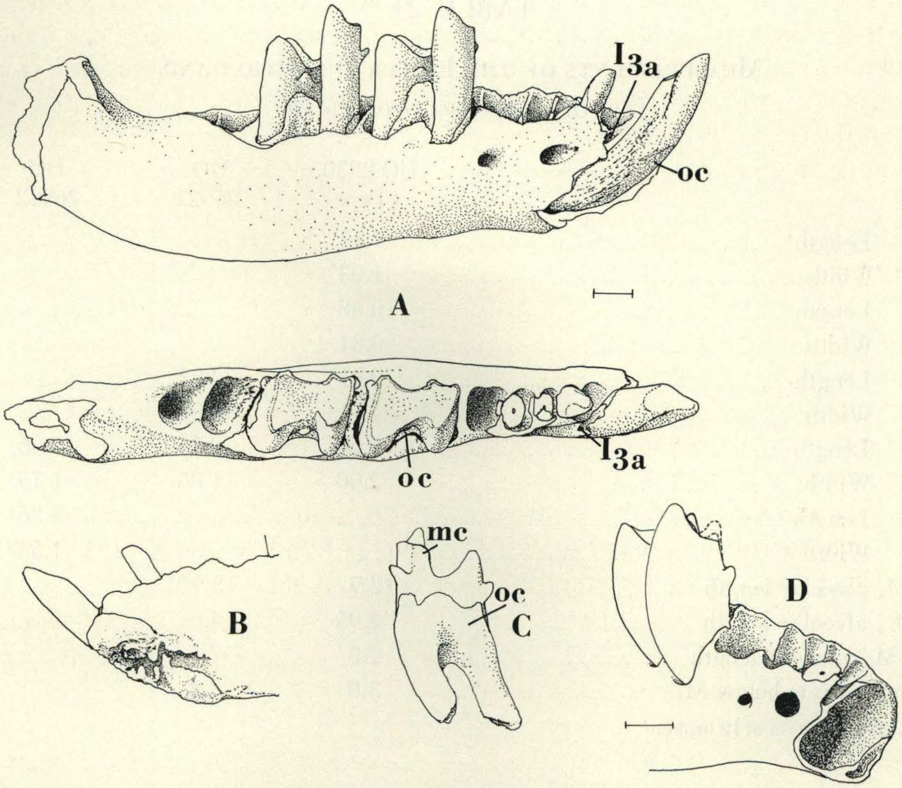

Figure 74. *Scapanus (Xeroscapheus) proceridens* n. sp., **A**; Krebs Ranch II, UO loc 2323, Type specimen UO 22508, right mandible with I_2, P_1, and M_1-M_2, labial and occlusal views, **B**; Type specimen, lingual view of antemolar region, **C**; Type specimen, M_2, lingual view, **D**; Little Valley I, UO loc 2380, UO 26921, anterolabial view of antemolar region. I_{3a}-I_3 alveolus; **mc**—metaconid; **oc**—os cementum.

between the labial margins of the I_2 and canine is what appears to be the remnant of a tiny alveolus presumably for a vestigial I_3. The crown of the canine is broken off but the root indicates that it was a simple peg-like tooth, anteroposteriorly compressed like the P_1. The P_1 is a simple sharply pointed tooth. All the premolars were apparently single-rooted. The antemolar teeth were all tightly appressed. The P_2 root indicates a tooth the size and shape of the preceding. The alveolus of the P_3 is larger than the preceding but similarly constructed. The alveolus of the P_4 is nearly square in transverse outline. It may have housed two closely appressed roots but more likely contained a single fused root.

The molars differ from all other talpids, except *Scalopus*, in two salient features; they are truly hypsodont (taller than long with enamel extending below alveolus rim) and they are partly enclosed by os cementum. The occlusal pattern is essentially the same as that of *S. (X.) shultzi* except that the connection between the trigonid and talonid is broader (this may be owing to the more advanced stage of wear); the trigonids are slightly more compressed anteroposteriorly. There is no cingulum bridging the hypoflexid, and the anterior and posterior accessory cusps are relatively smaller in size.

The referred mandibles from Little Valley differ little from the type specimen. The P_2 and canine alveoli are narrower and the os cementum is not as extensive on the molars. There is a small remnant of the I_1 alveolus also in UO 26921 (Fig. 74C).

A complete scapula (Fig. 75) lacking only the tip of the scapular spine tuber and a chip out of the auxilliary border was recovered from

TABLE 21

Measurements of the Lower Dentition and Jaw of *Scapanus proceridens*

		UO 22503 (Type)	UO 26921	UO 26922
I_2:	Length	1.13	....	....
	Width	1.03	....	....
P_1:	Length	0.58	....	....
	Width	0.81	....	....
M_1:	Length	2.41	2.82	....
	Width	1.91	2.00	....
M_2:	Length	2.64	2.76	2.66
	Width	2.00	1.86	1.75
M_3:	Length	....	....	2.36
	Width	....	....	1.53
I_2-M_1 alveolar length		12.9	13.9*	....
P_1-P_4 alveolar length		2.95	4.0	....
M_1-M_3 alveolar length		7.8	7.7	....
Depth of jaw below M_1		3.8	3.2	....

* Anterior margin of I2 broken

the type locality. It closely resembles the living species in the extent and development of the acromion process and the posterior position of the biceps tuberosity. The infraspinatus fossa continues forward as in *S.* cf. *S. shultzi.* Unlike the living species the dorsal opening of the infraspinatus fossa is very narrow, tapering only slightly anteriorly, and does not flare out posteriorly. The scapular spine tuber tends to isolate the posteriormost portion of the fossa opening from the rest. Of the material examined this feature is partly developed in *S. latimanus* and *S. townsendii* but absent in *S. orarius* owing to the more posterior situation of the spine tuber.

A proximal fragment of the scapula from Little Valley is smaller and differs from the Columbia River specimen. In this specimen the walls of the infraspinatus fossa converge to extinguish the fossa slightly posterior to the acromion process. In this specimen all of the superficial lamellar bone has been dissolved away which may in part account for these discrepancies.

The humeri fall within the range of variation of the recent species of *Scapanus* in proportions and morphology. The brachialis fossa is deeply excavated as in the modern species. The ulna fragment resembles that of *Scapanoscapter simplicidens* from Red Basin (Barstovian) in the relatively weak coronoid process; although, in this instance, this may be owing to the evident erosion of the specimen. The distal ends of two radii resemble the modern species of *Scapanus* except that the groove for the tendon of the abductor pollicis longus appears to be more distally situated. The more distal position of this groove is usually an indication of a relatively short radius as exemplified by *Scalopus aquaticus.*

The perfectly preserved scaphoid has a short and relatively broad proximal crest as in *Scalopus.* The part of the trapezium facet on the trochlear process is very small and faces distomedially as in *S. latimanus* and *Scalopus.* Laterally nearly the entire groove for the tendon of the M. flexor carpi radialis is roofed over by bone to form a long tunnel. The lunar

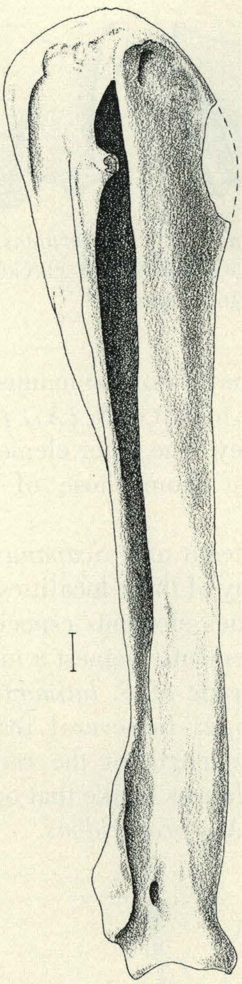

Figure 75. *Scapanus (Xeroscapheus) proceridens* n. sp., Krebs Ranch II, UO loc 2323, UO 26839, left scapula, dorsal view.

more closely resembles that of *Scalopus* in the general proportions and stockiness but in the details of the carpal articulations it also resembles the modern *Scapanus.* The medial phalanx II or III of the manus is proportionately very short in relation to its width and is therefore quite comparable to *Scalopus* in this respect.

The sacrum and innominata of the pelvic girdle as preserved are fully as fused anteriorly as in the living *Scapanus.*

RELATIONSHIPS: *Scapanus (Xeroscapheus) proceridens* exhibits a number of features characteristic of only the most advanced North American burrowing moles. The mandible strongly resembles *Scalopus aquaticus* in (1) the short antemolar region, (2) hypertrophied I_2, (3) hypsodont molars, (4) presence of os cementum, (5) reduction of cingula and accessory cuspids, and (6) compressed trigonids. However, *Scalopus (Hesperoscalops) rexroadi* or *S. (H.) sewardensis,* presumably (and admittedly) ancestral to *S. aquaticus,* primitively possess better developed cingula and accessory cuspids than *S. proceridens.* The I_1 and I_3 are greatly reduced in *S. proceridens* but it is the canine and a premolar that are reported lost in *S. rexroadi* (Hibbard, 1953). The cf. *Scalopus* sp. from the Hemphillian Edson Quarry of Kansas described by Hibbard (1939) suggest that the *Scalopus* lineage was already well established by Hemphillian time.

Of the modern species of *Scapanus, S. latimanus* most closely resembles *S. proceridens* in (1) the shortening of the antemolar region, (2) high crowned or hypsodont teeth, (3) absence of anterior cingula and reduction of the labial cingula, and (4) hypertrophy of the I_2. *S. latimanus* also differs from *S. proceridens* in the (1) relatively longer antemolar region and mandibular sympysis, (2) lack of os cementum, (3) presence of large accessory cuspids, (4) remnants of labial cingula, and (5) more open trigonids. The possibly somewhat older material from Little Valley, UO loc. 2516, approaches *S. latimanus* in the presence of larger accessory cuspids and vestiges of the labial cingula.

The humerus and scapula of *S. proceridens* indicate close affinity with *Scapanus (Scapanus).* The humerus does not show the extensive broadening as in *Scalopus.* The striking resemblances to *Scalopus* may be considered as an example of parallelism. The proximal elements of the foreleg do not differ greatly from those of *S. (Scapanus)* but the distal elements tend to more closely resemble *Scalopus* in their functional shortness.

In conclusion, *S. (X.) proceridens* can not be considered as ancestral to any of the living *Scapanus* but rather an offshoot of the primitive

Scapanus stock via *S. shultzi* which roughly paralleled *Scalopus* in several structural modifications.

Scapanus cf. *S. (Xeroscapheus) proceridens*

(Figs. 76, 77)

MATERIAL: Otis Basin UO loc. 2347: UO 26930, edentulous dentary fragment; UO 26931, clavicle; UO 26932, ulna fragment lacking the proximal crest, posterior crest and distal end; UO 26933, radius lacking capitular process; UO 26934, ungual phalanx of manus. McKay Reservoir UO loc. 2222: UO 3508, proximal end of scapula; UO 3506, humerus lacking proximal end; UO 24818, metacarpal I; UO 24819, proximal phalanx II or III of manus; UO 24818, ungual phalanx of manus.

The clavicle (Fig. 76) from Otis Basin is fully of the modern type. I could see no consistent differences between the various living species and the fossil with the sample available except that the ventral process is relatively shorter proximodistally and the clavicular (vascular) notch correspondingly is wider than in the living species. There is also a nutrient foramen dorsal to the ventral process on the anterior face of the clavicle which was not observed in the modern sample.

The humerus from McKay is small, about the size of that in *S. orarius,* but the scapular fragment is that of a mole about the size of the Krebs Ranch mole. The ulna from Otis Basin is too fragmentary for much comparison but the shaft appears to have been relatively shorter than in *S. orarius* or *S. townsendii.* The much better preserved radius (Fig. 77) from this locality is definitely shorter than either of the above species and is relatively as short or shorter than that in *S. latimanus* or *Scalopus aquaticus.* In details the radius (position of the groove for the tendon of M. abductor pollicis longus, etc.) more closely resembles *Scapanus,* especially *S. latimanus.*

The metacarpal I from McKay strongly resembles that of *S. latimanus* but is proportionately somewhat shorter, although not closely approaching *Scalopus* in this respect.

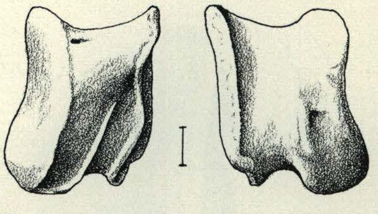

Figure 76. *Scapanus* cf. *S. proceridens,* Otis Basin, UO loc 2347, UO 26931, left clavicle, posterior (left) and anterior views.

The proximal phalanx of the manus is proportionately similar to that of *S. (X.) proceridens* from Little Valley. The other elements are not notably different from those of the living *Scapanus.*

Although no teeth of a *Scapanus*-like mole were found at any of these localities, advanced features of various elements especially in the distal foreleg elements, suggest a mole beyond the structural grade of *S. latimanus* and approaching *Scalopus* in several respects. The reduction in the length of the radius, metacarpals and phalanges is like that occurring or expected in *S. (X.) proceridens.*

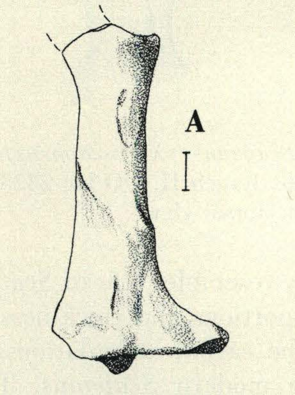

Figure 77. *Scapanus* cf. *S. proceridens,* **A;** Otis Basin, UO loc 2347, UO 26933, right radius, lateral view, **B;** McKay Reservoir, UO loc 2222, UO 24819, right second or third proximal phalanx of manus. **1**—length; **2**—width.

Scapanus sp.

The two partial humeri (LACM 6599) from Rome (CIT loc. 62) are about the size and morphology of *S. orarius* but assignment even to subgenus is of little meaning based on the material available.

Summary of Relationships of the *Scapanus*-like Moles

The oldest of the *Scapanus*-like moles, *Scapanoscapter simplicidens*, is in the position of providing a good structural and temporal (Barstovian) ancestor to the genus *Scapanus*. The low crowned molars, complete dental formula, and double-rooted premolars pose no special problems to deriving all the species of *Scapanus* from this genus. Likewise, *Scalopus* could also be derived from such an ancestral form, although there is no direct indication of this. The phalanges and metacarpals of the manus essentially achieved the same degree of shortness as in the Recent *S. orarius* and *S. townsendii*. Indeed, on the basis of the known material, *S. simplicidens*, provides the latest species which could serve as a common ancestor for all the species of *Scapanus*.

Tedford (1961), on the basis of teeth, postulated that the Clarendonian *S. shultzi* constitutes a reasonable common ancestor for the living species; however, the referred Oregon material and as yet unstudied postcranial material from the Ricardo Formation indicate that *S. shultzi* is off the direct lineage of the Recent species. The shortening of the distal forearm elements in *S. shultzi* has proceeded beyond that of the most fossorially specialized of the Recent species, *S. latimanus*. *S. shultzi* is thus well on the way toward the development of the brevirostrine *S. (Xeroscapheus) proceridens* of the Hemphillian.

While some hypsobrachyodont moles may still occur in the Hemphillian faunas, the hypsodont *S. proceridens* seems to be the dominant species in the Great Basin and is strikingly convergent with *Scalopus* in many features, although surpassing it in the devolpment of os cementum.

The living species all seem rather closely related with *S. latimanus* being the most distinctive. This species occupies the largest range and variety of habitats and in many ways seems to be heading down the same structural pathway as *S. shultzi*. *S. latimus* has the greatest crowding of the antemolars (one lost in some southern populations—see Palmer, 1937), most compressed trigonids, highest crowned teeth, and shortest metacarpals and phalanges of all the living species of *Scapanus*. The more open trigonids in *S. townsendii* and *S. orarius* may be derived from the compressed condition in *Scapanoscapter*.

Scalopina sp. A
(Figs. 78-81)

A few isolated teeth and skeletal elements recovered from USGS loc. M. 1043 at Snyder Creek seem to represent one species and probably a new genus of advanced burrowing moles thus far undescribed. Additional matrix in the form of anthill accumulations has been collected but had not been picked at the time of this writing. Since available material seems in-

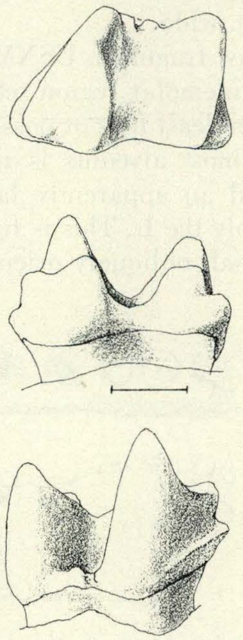

Figure 78. Scalopina sp. A, Snyder Creek, USGS loc M1043, USNM 23773, occlusal, lingual and labial views.

sufficient to me for useful characterization of this form, I shall restrict my discussion to the description of the material at hand and tentative relationships.

The M^1, USNM 23775, closely resembles that of the living *Scapanus townsendii* or *S. orarius* except that the protocone is more robust and inflated basally. Unlike *Scapanoscapter,* the paraconule is not distinguishable and the metaconule is small and not particularly distinct. The tooth is 3.12 mm. long and 2.33 mm. wide.

The M_2, USNM 23773 (Fig. 78), is brachyodont. The trigonid is wider but shorter than the talonid and the anterior cingulum tapers and vanishes labially. The tooth is moderately worn but the entocristid was either very low or absent so that the postfossid opens lingually. The crista obliqua intersects the middle of the protolophid, and there is no metastylid. These last two mentioned features distinguish it from all the other North American highly fossorial moles. The trigonid is about as compressed as in *Scapanoscapter*. There is a weak cingulum bridging the hypoflexid and a strong posterior accessory cuspid. This tooth is 2.88 mm. long and 1.93 mm. wide.

A lower jaw fragment, USNM 23774 (Fig. 79), of the antemolar region retains the roots or alveoli of at least four or possibly five teeth. The anteriormost alveolus is inclined about 45° and held an apparently large and long tooth, probably the I_2. This is followed by the roots of a small obliquely oriented premolar. There are a number of possible interpretations for the succeeding four alveoli. There are two mental foramina on this fragment of jaw. Regardless of the dental formula, the antemolar region was at least somewhat crowded. If the first alveolus preserved is that of the I_2, then at least two teeth have been lost between the I_2 and the first recognizable premolar.

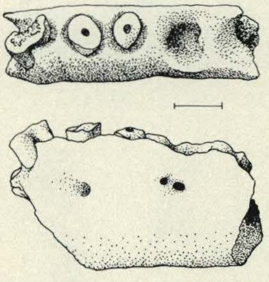

Figure 79. Scalopina sp. A, Snyder Creek, USGS loc M1043, USNM 23774, fragment of the antemolar region of the left mandible, occlusal and labial views.

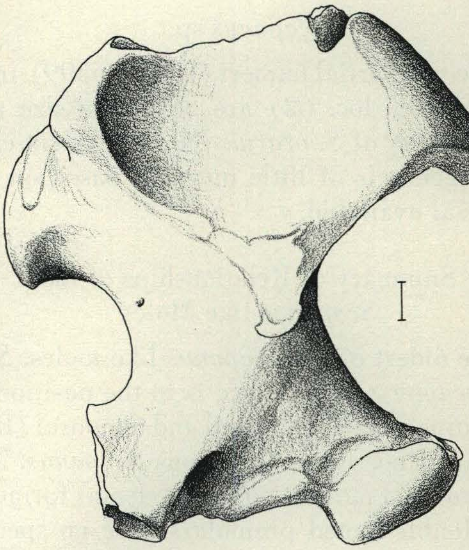

Figure 80. Scalopina sp. A, Snyder Creek, USGS loc M1043, USNM 23776, left humerus lacking proximal extremity and epicondyles, anterior view.

The humerus, USNM 23776 (Fig. 80), is devolped to about the same structural grade as *Parascalops* and *Domninoides.* It also resembles these genera in several structural details such as the basining of the area between the pectoral muscle scars, and relatively narrow clavicular facet. On the other hand the relationship of the pectoral muscle scars is roughly intermediate between that of *Scapanus* and *Domninoides.*

The second and fourth metacarpals, USNM 23777 and USNM 23778, are proportionately longer than in either *Parascalops* or the Recent Scalopina. The fourth metacarpal resembles the same element from Quartz Basin referred to *Domninoides,* except in greater size, less expanded proximal tubercle and slightly longer proportions.

The medial phalanx of the second, third, or fourth digit, USNM 23779 (Fig. 81), is ex-

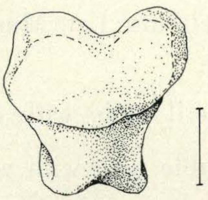

Figure 81. Scalopina sp. A, Snyder Creek, USGS loc M1043, USNM 23779, medial phalanx from manus, dorsal view.

tremely short in relation to its width and is comparable to or shorter than that in *Scalopus*.

The development and lateral situation of the pectoral tubercle of the humerus, lack of the metastylid and labial situation of the crista obliqua on the second lower molar, small size of the conules on the upper first molar, and the highly fossorial specializations of the forearm suggest affinities with the Scalopina.

Scalopini sp. A
(Figs. 82, 83)

Four postcranial elements, a clavicle, two metacarpals, and a phalanx of a small burrowing type mole were recovered from Red Basin, UO loc. 2495. They are either too small or too large to be adequately assigned to any of the other moles known from this site with perhaps the exception of *Scalopoides*. The elements are only slightly larger than those of *Scalopoides ripafodiator* from Quartz Basin but differ strikingly in proportions. Inasmuch as the *Scalopoides* from Red Basin is smaller but otherwise closely resembles the Quartz Basin *Scalopoides*, it seems unlikely that these elements belong to this genus.

The clavicle, UO 24388 (Fig. 82), is proportionately shorter than any of the known Miocene *Scalopoides*, although it does resemble the short clavicle of *?Scalopoides* sp. C. The shape of the ventral process is similar to that in *Scapanulus* although somewhat more broadly based. There is no obvious lateral reflection of the ventromedial spine. A span of bone bridges the vascular notch from the base of the ventromedial spine to the dorsal margin of the ventral process thus forming a foramen. The presence or absence of this bridge may be individually variable if a larger sample were known. A nutritive foramen also pierces the clavicle within the vascular notch. Posteriorly the notch continues dorsally as a deep gutter extending to the dorsal prominence. The long axes of the articular facets are more nearly parallel than they are in the Talpini.

The two metacarpals are relatively shorter in relation to their width than those of *Scalopoides* although slightly longer than in *Scapanoscapter simplicidens*. The third metacarpal, UO 22439 (Fig. 83A), is about at the same structural grade as in *Parascalops*. The fourth metacarpal, UO 24375, is nearly identical to the fourth metacarpal referred to *Domninoides* from Quartz Basin except that it may be very slightly shorter. The proximal tuberosities are well defined on both specimens. A single proximal phalanx of the manus, UO 24378 (Fig. 83B), is essentially identical to that of *S. isodens* except for its slightly larger size. It is 1.43 mm. long and 1.33 mm. wide.

The structure and details of the clavicle indicate that Scalopini sp. A is referable to the Scalopini. The high degree of specialization in the clavicle and hand bones eliminates the Urotrichini as here interpreted. Among the Parascalopina, the Miocene *Scalopoides* are

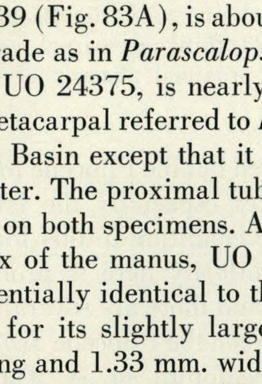

Figure 82. Scalopini sp. A, Red Basin, UO loc 2495, UO 24388, left clavicle, posterior and ventral views.

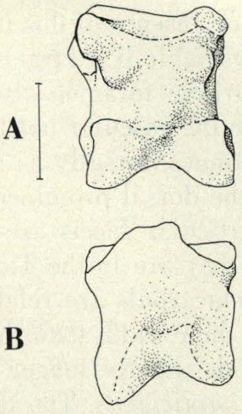

Figure 83. Scalopini sp. A, Red Basin, UO loc 2495, **A**; UO 24373, third metacarpal, ventral view, **B**; UO 24378, proximal phalanx of manus, dorsal view.

less specialized but the Pliocene forms referred to *Scalopoides* especially the later members approach the condition in this form. The proportional similarity here is probably one of convergence and there are several detailed differences between the Pliocene *Scalopoides*-like moles and Scalopini sp. A. The discernible lateral deflection of the ventromedial spine of the clavicle for the tetrahedral sesamoid in *Scapanulus* and *Parascalops* is absent in Scalopini sp. A. *Domninoides* is not certainly represented by any of the elements known from the Red Basin. There is a similarity of the manus bones to those referred to *Domninoides* from Quartz Basin, but the Quartz Basin specimens are only tenuously grouped together. There is so much structural convergence in various lineages of burrowing talpids, that I believe it is more realistic to leave these elements unassigned especially in view of the lack of any associated *Domninoides* teeth (or any other available mole) from the locality. General similarity to *Scalopoides*, *Scapanulus*, and *Parascalops* tends to align Scalopini sp. A with the Parascalopina.

TALPINAE *incertae sedis*

ACHLYOSCAPTER [16] gen. n.

GENOTYPE: *Achlyoscapter longirostiris*, sp. n.

KNOWN DISTRIBUTION: Late Miocene (Barstovian) of Oregon.

DIAGNOSIS: Small mole with dental formula $\frac{?\,?\,?\,?}{3\,1\,4\,3}$. Mandible long with very little taper to antemolar region; antemolars uncrowded; I_3 to P_4 roughly graded in size, largest posteriorly; all premolars double-rooted and laterally compressed; P^2 (?) and P^3 double-rooted; P^4 elongated posteriorly, prominent protocone; M^1 with three discernible labial cusps and well defined paracrista and metacrista.

Achlyoscapter longirostris[17] n. sp.

(Figs. 84-88)

TYPE: UO 22412, left mandible with I_3-M_1 and the alveoli of I_1-I_2 and M_2-M_3, most of the ascending ramus lacking.

HYPODIGM: UO 22419, fragment of right dentary with P^4-M^1 and alveoli of P^2-P^3; UO 22583 and UO 22344, P^4's; UO 22343, left mandible fragment with M_1-M_2 and alveoli of P_4 and M_3; right mandible fragment with alveoli of M_1-M_3. All specimens from the type locality.

REFERRED SPECIMENS: UO loc. 2465: UO 22351, fragment of upper jaw with two antemolars; UO 22352, UO 22353, two scaphoids. UO 24335, right mandible fragment with damaged M_1 and alveoli of P_1-P_4.

TYPE LOCALITY: UO loc. 2465, Quartz Basin.

AGE: Barstovian.

DESCRIPTION: One specimen, UO 22419, (Fig. 84A) preserves the P^4-M^1, alveoli of the P^3 and posterior root of the P^2. A downward flexure of the snout is evident in the area of the P^4. The posterior alveolus of the P^2 suggests that the tooth was slightly oblique in the maxillary with the anterior moiety more medial. The P^3 was apparently larger but similarly arranged. The P^4 (Fig. 88B) is a narrow elongate tooth with a prominent protocone which imparts a distinct triradiate aspect to the tooth. The high sharp

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[16] From the Greek *achlys*, mist, dimness, darkness, and *skapter*, a digger.

[17] From the Latin *long*, long, plus *rostrum*, snout.

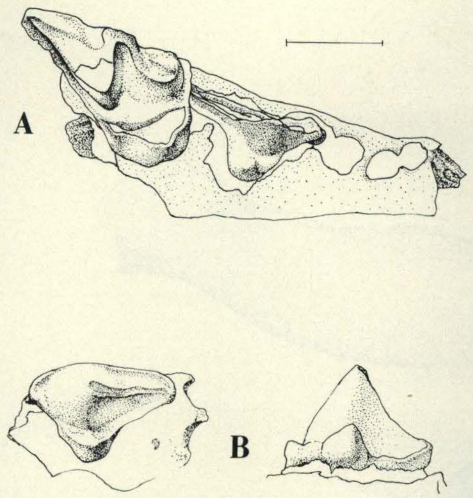

Figure 84. *Achlyoscapter longirostris* n. sp., n. gen., Quartz Basin, UO loc 2465, **A;** UO 22419, right maxillary fragment with half of P_4 and M^1, occlusal view, **B;** UO 22583, left P^4, occlusal and lingual views.

TABLE 22

Measurements of the Upper Dentition of *Achlyoscapter longirostris*

		Length	Width
P^4:	UO 22344	1.41	0.89
	UO 22583	1.56	1.04
	UO 22419	1.46	....
M^1:	UO 22419	....	1.40

paracone is situated anterior to the center of the tooth. A long concave crest extends from the apex of the paracone to the posterior extremity of the tooth. The tooth is enclosed in a narrow cingulum which expands somewhat at the anterior tip and is contiguous with the protocone. The protocone extends medially and slightly anterior to the center of the tooth. There are three roots, one beneath each extremity. The lingual roots diverge from each other.

The M^1 is subtriangular in occlusal outline. The protocone, paraconule, and metaconule are all distinguishable on the worn tooth. The metaconule is situated close to the base of the metacone as is the paraconule to the paracone. Well defined paracingula and metacingula are present. The parastyle is either not developed or abraded away in the specimen, probably the latter.

In UO 22351 (Fig. 85) part of the anteriormost lateral wall of the narial opening and two associated teeth are preserved. Immediately below the narial flange there is a round alveolus presumably for a single tooth. This alveolus is followed by a single-rooted tooth with a high transversely compressed cusp which is slightly recurved. Immediately posterior to this tooth is a larger double-rooted tooth somewhat less compressed and with the beginnings of a posterior cingulum but otherwise similar in form to the preceding tooth. Part of another alveolus follows this. The tall, compressed and uncrowded nature of these teeth as well as the size of the specimen suggest that they may be P^1 to canine inclusive of *A. longirostris.*

The dentary is long and not strongly tapered anteriorly (Fig. 86). There are two mental foramina, one beneath the P_2 and the other under the P_4. The symphysis extends back as far as the P_2. The dental formula is complete: I3, C, P4, M3. All the teeth anterior to the P_1 are single-rooted and the P_1 and all succeeding teeth are double-rooted (Fig. 86A). The I_1 is inclined about a 45° angle to the axis of the

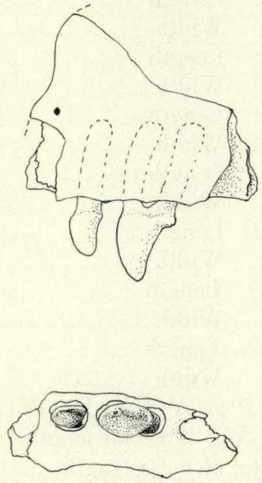

Figure 85. *Achlyoscapter longirostris* n. sp., n. gen., Quartz Basin, UO loc 2465, UO 22351, rostral fragment with ?C-P^1, labial and occlusal views.

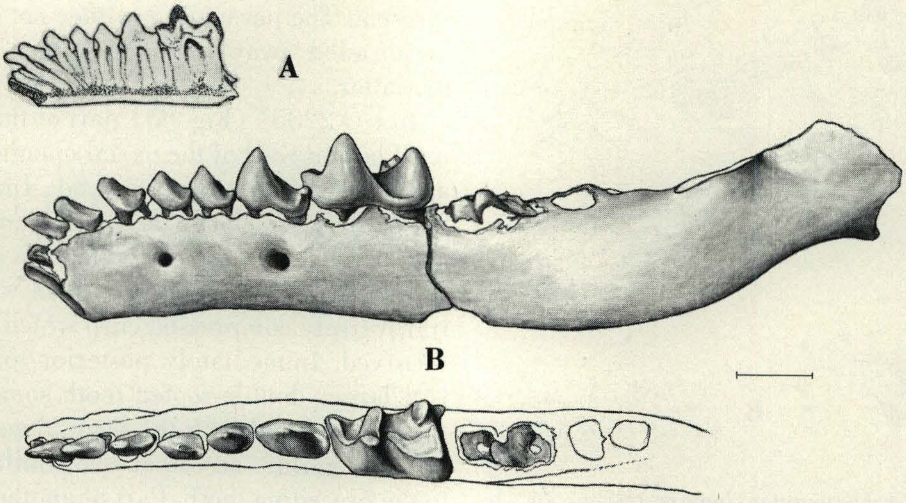

Figure 86. *Achlyoscapter longirostris* n. sp., n. gen., Quartz Basin, Type specimen UO 22412, left mandible with I_3-M_1, **A;** sketch of X-Ray photograph, **B;** labial and occlusal views.

TABLE 23

Measurements of the Lower Dentition and Jaw of *Achlyoscapter longirostris*

		UO 22412	UO 22343	UO 24335
I_3:	Length	0.59	......	......
	Width	0.30	......	......
C_1:	Length	0.64	......	......
	Width	0.31	......	......
P_1:	Length	0.60	......	......
	Width	0.33	......	......
P_2:	Length	0.60	......	......
	Width	0.35	......	......
P_3:	Length	0.67	......	......
	Width	0.39	......	......
P_4:	Length	0.98	......	......
	Width	0.51	......	......
M_1:	Length	1.61	1.58	......
	Width	0.98	1.03	......
M_2:	Length	......	1.64	......
	Width	......	0.99	......
P_1-P^4:	Alveolar length	2.63	......	2.45
M_1-M_3:	Alveolar length	4.36	4.43	......
Total alveolar length		8.32e	......	......
Depth of mandible below M_1 (internal)		1.59	1.56	1.57

e Estimated length.

jaw and the succeeding teeth become progressively more vertically aligned to about the P_2-P_3. The I_1 and crown of the I_2 are missing but both possessed long roots, although neither seems to have been especially enlarged. The rest of the antemolars progress in size from the I_3 to the P_4. The crown of the I_3 is procumbent and strongly compressed transversely. The posterior base of the crown suggests an incipient heel. The canine is similar to though larger than the I_3. The root of the canine extends posteriorly beneath both the roots of the P_1. The P_1 is not so compressed as in preceding teeth, and there is a small posteriobasal cuspule flanked by weak cingula which extend ventrally and anteriorly a short distance on either side. The basal cuspule is joined to the base of the protoconid by a short ridge. The crown of the P_1 is still rather procumbent and the apex of the protoconid is situated slightly anterior to the level of the anterior root. The roots of the P_1 are relatively and absolutely shorter than those of the other premolars. The P_2 is about the same size as the P_1 but is more compact, and the heel is no more developed. The protoconid is centered squarely over the anterior root. The P_3 is oval in occlusal outline and has lost the wedge-shaped outline of the preceding teeth. There is a slight basining of the heel on either side of the ridge connecting the base of the protoconid and the posterior cuspule. There is a very faint suggestion of the metaconid on the P_3. The P_4 in turn resembles the P_3 but is more elongate. The heel is relatively larger but its features are no better defined than on the P_3.

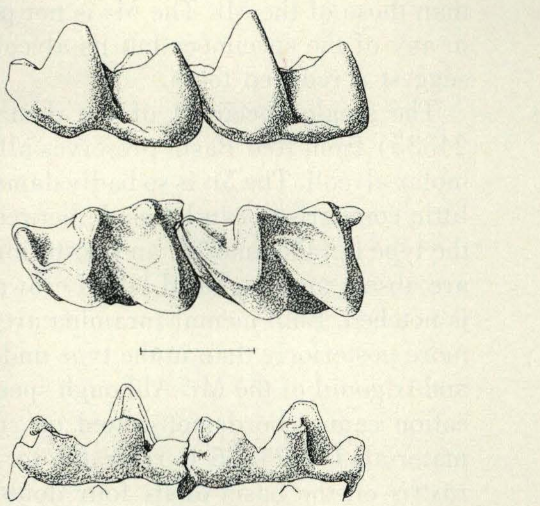

Figure 87. *Achlyoscapter longirostris* n. sp., n. gen., Quartz Basin, UO loc 2465, UO 22343, left M_1-M_2, labial, occlusal and lingual views.

The molars (Fig. 87) are brachyodont. The M_1 is rather wedge-shaped in occlusal view and the trigonid is slightly longer but narrower than the talonid. The anterior cingulum is poorly developed or absent. A short cingulum covers the base of the paraconid anterolingually and lingually. The labial cingulum is incompletely developed bridging only the hypoflexid. There is no posterior cingulum but a small posterointernal accessory cuspid is present. The basilabial margin of the tooth is notched. The profossid is deep and cuts anterolabially thus restricting the paralopid to a low sharp ridge deeply notched between the parconid and protoconid. The paraconid is the lowest cusp but well formed. The protoconid is the tallest cusp and the remaining cusps are of about equal height. The entoconid is connate without an entocristid or only a very small one; however, the lingual rim is somewhat raised so that the shallow postfossid is enclosed. There is no metastylid and the crista obliqua joins the middle of the protolopid.

The M_2 is only preserved in UO 22343. The tooth is more rectangular than the M_1. The anterior cingulum is well developed but the labial cingulum as in the M_1 is only developed across the hypoflexid. Also, like the M_1, there is a small anterolingual cingulum around the base of the paraconid and a posterior accessory cuspid. The trigonid is more compressed anteroposteriorly than in the M_1, and the talonid is slightly longer and wider than the trigonid. A metastylar ridge is fused to the metaconid and is connected to the entoconid by a low but distinct entocristid. The crista obliqua extends more lingually than in the M_1 to terminate just before the juncture between the metastylid ridge and the metaconid. The labial edges of the protoconid and hypoconid are more angular than those of the M_1. The M_3 is not preserved in any of the specimens but its alveoli do not suggest a reduced tooth.

The single specimen of the dentary (UO 24335) from Red Basin preserves all the premolar alveoli. The M_1 is so badly damaged that little comparison can be made between it and the type but the anterior and posterior cingula are absent and the basal labial crown margin is notched. Both mental foramina are situated more posteriorly than in the type under the P_3 and trigonid of the M_1. Although specific allocation cannot be demonstrated on such poor material, UO 24335 is referable to *A. longirostris* on the basis of its four double-rooted premolars and construction of the M_1.

Two scaphoids (Fig. 88) from a mole about the size of *Achlyoscapter* were recovered from the type locality. They are about 13 per cent smaller than those of *Scalopoides ripafodiator* and presumably quite different from those expected for *Mystipterus*. In general the two specimens resemble the scaphoid of *S. ripafodiator* but are transversely narrower, dorsoventrally longer, and possess a prominent spur which projects posteriorly from the center of the posterior crest. The general features of the scaphoid suggest a manus nearly comparable to that of *Scalopoides*.

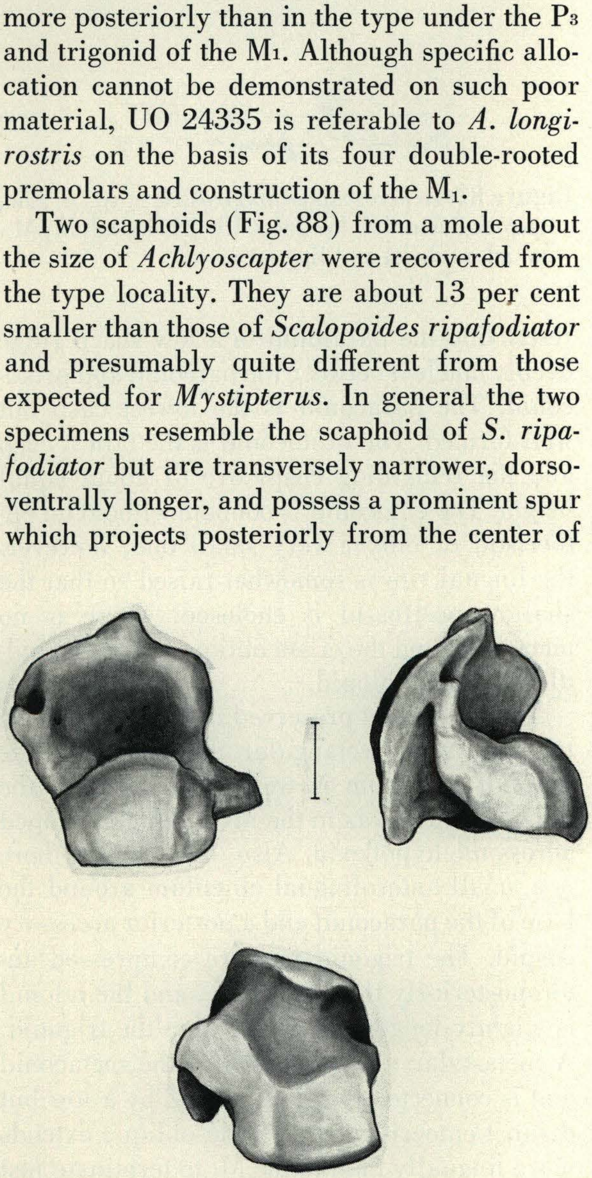

Figure 88. *?Achlyoscapter longirostris* n. sp., n. gen., Quartz Basin, UO loc 2465, UO 22353, right scaphoid, dorsal, medial and distal views.

RELATIONSHIPS: *Achlyoscapter longirostris* may be distinguished from all of the North American fossil and living moles by a combination of its small size, brachyodont molars, complete lower dental formula, narrow double-rooted lower premolars, and elongate upper fourth premolar. There is no evident hypertrophy of the anterior lower incisors as in all the Recent Urotrichini, Scalopini, and Uropilinae, nor is the P_1 double-rooted or enlarged as in Recent *Scaptonyx* or Talpini.

Among the Eurasian fossil moles in which comparable material is available, "*Scaptonyx*" *jaegeri* Seeman (1938) most closely approaches *Achlyoscapter* in having the same number of teeth, little antemolar specialization, and elongate M_1 with open prefossid. Notable differences of "*S.*" *jaegeri* from *Achlyoscapter* include (1) the single-rooted P_1, (2) more posterior location of both mental foramina, (3) well developed anterior and labial cingula on the lower molars, and (4) crista obliqua of M_1 extending much further labially (if Seeman's 1938 figures are accurate).[18] Regardless of these differences *A. longirostris*, as known, shows its greatest general similarity to "*S.*" *jaegeri*, however, the types of these two species must be more closely compared than is possible with the existing literature before actual relationship or simple retention of generalized characters can be evaluated.

The structure of the lower molars and the small size of this species suggest affinities with the Urotrichini. The lower dental formula is unlike any Recent urotrichine but this is to be expected in a possible primitive member. Reduction of the antemolar dentition except the anterior incisors, increase in molar crown height, and compaction of the P^4 and other small dental modifications could situate *Achly-*

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[18] In Seeman's illustrations (Figs. 12-15) all the molars show the same structure. This seems highly unlikely in any detailed sense for a brachyodont mole.

loscapter on the line to any of the Recent Urotrichini. On the other hand the scaphoid, if associated with this mole, would tend to align *Achlyoscapter* with the Scalopini or at least place it beyond the structural grade of the Urotrichini as used here. The conservative nature of the dentition suggests a structural notch below that exemplified by *Scalopoides.*

Of the North American fossil talpids, *Achlyoscapter* provides the best available ancestor for *Condylura*. Like *Achlyoscapter*, *Condylura* has a complete set of brachyodont teeth, elongate antemolar region, double-rooted premolars, and elongate P^4. However, *Condylura* is far removed from *Achlyoscapter* and other moles by its molariform lower premolars separated by diastemata. The lower molars of *Condylura* also have prominent metastylids with the crista obliqua joining directly to the metastylid rather than the protolophid as in *Achlyoscapter*. These features cannot be considered primitive in *Condylura* and could be developed directly from such a form as *Achlyoscapter*. Unfortunately, no moles which might bridge the gap between these two forms are yet known.

TALPIDAE AND TALPINAE *incertae sedis*

Several localities have yielded isolated upper teeth which, owing to their rarity in the samples or to the small size of the sample, are difficult to assign to a particular genus. They are therefore discussed under general headings and arranged by locality. There is sufficient variability within genera and species and a general similarity between many genera with otherwise widely divergent postcranial skeletons to make specific assignments meaningless without a more complete series of the dental and skeletal material.

Talpinae *incertae sedis*

BLACK BUTTE: UO loc. 2500 (Fig. 89). The upper P^4, UO 24779, of a small mole closely resembles that of *Scalopoides ripafodiator* in most details. Although much of the enamel has been stripped away, the paracone appears to have been joined to the anterior extremity of the tooth by a cingulum.

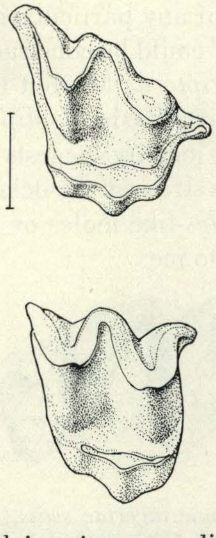

Figure 89. Talpinae *incertae sedis*, Black Butte, UO loc 2500, **A;** UO 24781, right M^1, occlusal view, **B;** UO 24782, right M^2, occlusal view.

An M^1, UO 24781 (Fig. 89A), is a brachyodont tooth with a distinct protocone, paraconule, and metaconule. Well developed paracingulum and metacingulum are present as well as a strong parastyle. The mesostyle is elongate and was probably partly divided before wear. The structure of the lingual moiety of the tooth approaches *Parascalops* in the reduction of the protocone and prominence of the conules. This imparts a rather rectangular outline to the lingual moiety rather than a V-shaped one as in *S. ripafodiator*. The roots are like those of *S. ripafodiator*. The tooth is 2.39 mm. long and 1.61 mm. wide.

The M^2, UO 24782 (Fig. 89B), is not unlike *Scalopoides* except that the protocone is reduced in volume thus imparting a flatter outline to the lingual margin. The metaconule although worn was not greatly separated from the protocone as it is in the M^2 specimen referred to *Mystipterus* from this locality. The roots are broken but were apparently like those of *S. ripafodiator*. The tooth is 1.87 mm. long and 2.00 mm. wide.

In size the M^1 could belong either with UO 24782 or the referred *Mystipterus* M^2. I believe the former association more probable on the basis of the analogous similarity of the lingual cusps and lack of any particularily uropsiline features. The M^2 could be construed as a variation of the *Mystipterus* M^2, but the similarity between the Quartz Basin *Mystipterus* M^2 and the one from this locality suggests a consistency of the characters stressed. Association with one of the *Scalopoides*-like moles or *Domninoides* seems probable to me.

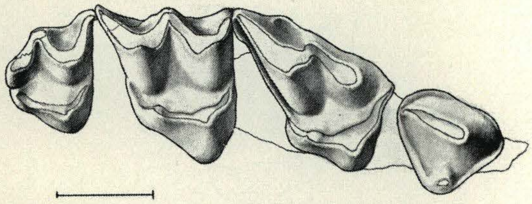

Figure 90. Talpinae *incertae sedis*, Bartlett Mountain, UO loc 2517, UO 26804 right P^4-M^3, posterolingual tip of M^2 restored from opposite side, occlusal view.

BARTLETT MOUNTAIN: UO loc. 2517 (Fig. 90). The most complete associated upper dentition, UO 26804, of all the fossil moles studied comes from this locality. Unfortunately no lower teeth of a mole of comparable size were recovered so that its affinities remain in doubt. The specimen consists of a right upper tooth series with the P^4-M^3 and a left series with P^4-M^2. All the teeth were recovered as isolated specimens in a single screen of washed matrix. Since they are all in the same state of preservation and wear and two of the teeth retain a bony contact, there is no doubt that only one individual is represented. An additional P^4, UO 26841, was also recovered from the site. The molar teeth indicate an animal about the size of *Achlyoscapter*.

The P^4 nearly forms an equilateral triangle in occlusal outline except that the labial side is somewhat longer than the others. The paracone is transversely compressed posteriorly as in *Scalopoides* but the cusp as a whole is not as relatively large. A cingulum encloses the tooth except around the lingual base of the protocone and the posterior extremity and narrows anterolabially as in *Scalopoides*. The protocone is a low but well defined connate cusp. Three prominent roots are present.

TABLE 24

MEASUREMENT OF THE TEETH OF TALPINAE *incertae sedis* FROM BARTLETT MOUNTAIN

		Length	Width
UO 26841			
P^4		1.21	0.97
UO 26804			
P^4:	right	1.23	1.00
	left	1.27	0.97
M^1:	right	1.88	1.17
	left	1.90	1.13
M^2:	right	....	1.63
	left	1.47	1.60
M^3:	right	1.20	1.05

The M^1 resembles that of the Urotrichini and small parascalopine moles. The protocone, paraconule, and metaconule are all discernible even with wear. Paracingulum and metacingulum are present. The parastyle forms a prominent shelf-like anterolabial extension of the paracrista. The posterior ectoflexus is unusual in its shallowness, and there is a short cingulum which fills in even what little concavity there is basially.

The lingual cusps of the M$_2$ resemble those of the M^1 but the lingual sulcus separating the protocone and paraconule is better developed. The paracingulum and metacingulum do not extend to the stylar cusps. The mesostyle shows no incipient twining and the parastyle and metastyle are not strongly curled as in many other moles. There are four roots as in *Scalopoides* but they are interconnected to the central root by low thread-like interradicular ridges. The lingual root is transversely compressed and longitudinally broadened as in *Mystipterus* and *Neurotrichus*, but it is more obliquely oriented.

The M^3 resembles that of *S. ripafodiator* in most details except that the anterior ectoflexus is longer and broader. There are three roots.

General features suggest affinities of these specimens with the *Scalopoides*-like moles but the urotrichine moles also show many of these same features.

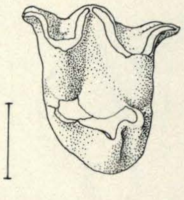

Figure 91. Talpinae *incertae sedis,* McKay Reservoir, UO loc 2222, UO 24812, right M^2, occlusal view.

MCKAY RESERVOIR: UO loc. 2222 (Fig. 91). Four upper teeth of small moles were recovered from McKay. Two of these teeth are upper second molars, both different. The heavily worn P^4, UO 26817, is transversely compressed so that the posterior crest of the paracone must have been quite sharp-edged. The cingula are similar to those of *Scalopoides ripafodiator* except that there is no cingulum on the anterior extremity and the anterolabial side of the tooth. The protocone has been sheared away with wear. The lingual root is situated close to and almost between the labial roots. The tooth is 1.50 mm. long and 1.00 mm. wide.

One of the second molars, UO 24813, strongly resembles *S. ripafodiator* in detail except that the protocone has a shorter lingual slope, is less angulate lingually, and is enclosed by an irregular narrow cingulum. It lacks the metacingulum of *Neurotrichus gibbsii* and has a small cuspidate paraconule like *S. ripafodiator. N. gibbsii* either lacks the paraconule or it may be expressed by a small noncuspidate elevation of the protocrista. The roots are like those of *Scalopoides.* The lingual root of *N. gibbsii* is similar to that of *Mystipterus.* In addition to the major roots there are two papillate roots, one centrally situated and the other between the lingual and postirolabial roots. The tooth is 1.80 mm. long and 2.02 mm. wide.

The other second molar, UO 24812 (Fig. 91), differs from the first in the following features: larger size, large distinct paraconule as in *Mystipterus* sp. from Black Butte, lack of a lingual cingulum, lack of the posterior papillate root, and somewhat more divided mesostyle. It is 2.10 mm. long and 2.26 mm. wide.

The M^3, UO 26818, resembles that of *Neurotrichus* in almost every detail except that the paraconule is discernible and similar to that in the M^2 of *S. ripafodiator* in position and expression. No cingula are present and the metaconule does not bulge posteriorly as prominently as in many specimens of *N. gibbsii.* It is 1.40 mm. long and 2.37 mm. wide.

It seems likely that most or all of the above teeth might be assigned to one or both of the small moles known from McKay, *?Scalopoides* or *?Neurotrichus.* There is a significant amount of time separating the McKay fossils from the latest well known *Scalopoides* (*S. ripafodiator,* Barstovian) and the living *Neurotrichus gibbsii.* The molar teeth of talpines are basically conservative but may develop many small transient or convergent modifications to obfuscate assignment without the benefit of a large sample or an articulated specimen. In the case of the small McKay sample, both the moles (if indeed there are two) are similar enough in size to cause confusion of similar teeth and I will thus refrain here from making arbitrary assignments.

GUANO RANCH, USGS loc. M 1042 (Fig. 92). A single M^2, USNM 23772, appears to belong to a mole smaller than *Scapanus* but larger than *Scalopoides ripafodiator.* Although generally similar to *Scalopoides* in morphology, it is higher crowned. The labial moiety is relatively smaller and the ectoloph is very sharp with more deeply excavated ectoflexi and protofossa. The tooth is 2.06 mm. long and 2.58 mm. wide. A cuspidate mesostyle is absent. This may represent the M^2 of *Domninoides* but is hardly demonstrable on the small sample available.

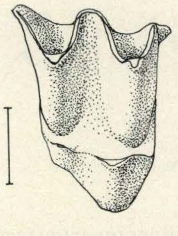

Figure 92. Talpinae *incertae sedis,* USGS loc M1042, USNM 23772, right M^2, occlusal view.

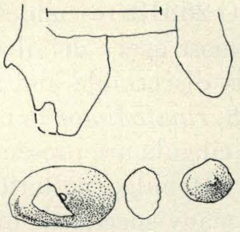

Figure 93. Talpinae *incertae sedis,* Quartz Basin, UO loc 2465, UO 25289, two upper right antemolar teeth, labial and occlusal views.

Talpidae *incertae sedis*

QUARTZ BASIN: UO loc. 2465. An upper jaw fragment, UO 2258 (Fig. 93) anterior to the P^4 from Quartz Basin preserves two antemolars. The anterior tooth is simple with a moderately tall and slightly inflated cusp. This is followed by an alveolus apparently for a tooth of similar nature which in turn is followed by a large double-rooted tooth four times the size of the first. The large tooth is regularly ovate in occlusal view with a large double-rooted tooth about four times the size of the first. The large tooth is regularly ovate in occlusal view with a simple large cusp and small posterior cingulum. The general appearance of the teeth would suggest a small mole other than *Achlyoscapter* but this would still leave *Scalopoides*, *Mystipterus*, and *Domninoides* and possibly one of the other nonsoricid insectivores as possible candidates for association.

The proximal epiphysis of the tibiofibula, UO 22304 (Fig. 94), from the same locality represents a mole smaller than *Scalopoides ripafodiator.* The falciform process is damaged but appears to have had a large flange. In proximal view there is a small spur off the lateral condyle that is not visible in this view in any of the moles or shrews examined. The specimen could belong to *Achlyoscapter* or *Mystipterus* but there is no definite evidence as to which it should be assigned—if either.

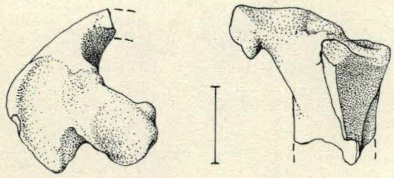

Figure 94. Talpidae *incertae sedis,* Quartz Basin, UO loc 2465, UO 22304, proximal end of right tibia, proximal and anterior views.

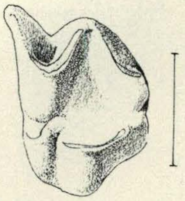

Figure 95. Talpidae *incertae sedis,* Bartlett Mountain, UO loc 2517, UO 24799, left M^3, occlusal view.

BARTLETT MOUNTAIN: UO loc. 2517 (Fig. 95). An isolated M^3, UO 24799, about the size of *Scalopoides ripafodiator* was recovered from this locality. It differs from the M^3 of several other small moles studied in the presence of a very strong lingual sulcus separating the large distinct protocone from the paraconule. The paracingulum is very short and does not extend labially beyond the base of the paracone. There are no other cingula. The mesostyle is elongate but not noticeably divided. In size and analogus morphology of the entire lingual moiety this tooth strongly resembles the form represented by Talpinae *incertae sedis* M^2, UO 24812, from McKay. It also agrees with the ?Talpidae *incertae sedis* from this locality in size.

?Talpidae *incertae sedis*

(Figs. 96, 97)

Three lower teeth of questionable talpid affinities from two localities of different age were recovered from the Juntura Basin. An M_1, UO 25289, from Black Butte locality 2500, is strikingly different from any of the tapids, living or extinct, examined. The tooth (Fig. 96A) is wedge-shaped in occlusal outline. The trigonid and talonid are about equal in length but the talonid is wider than the trigonid. The

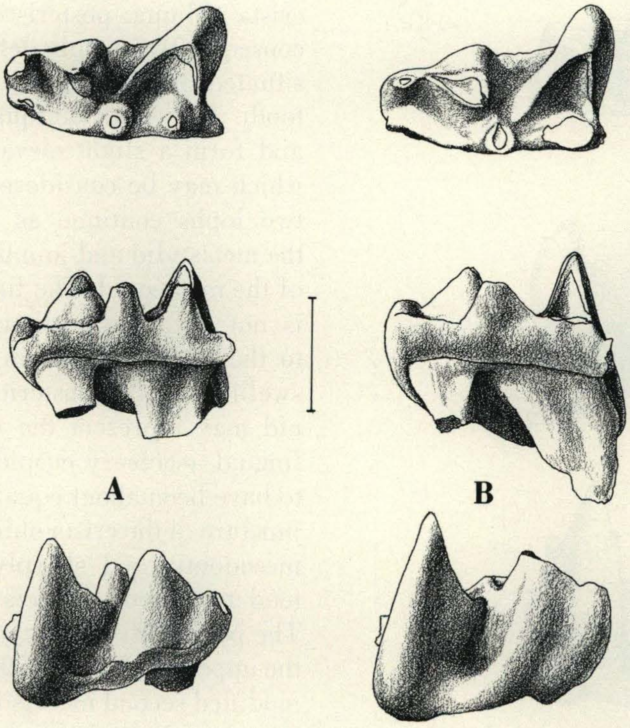

Figure 96. ?Talpidae *incertae sedis*, lower right first molars, occlusal, lingual and labial views, **A;** Black Butte, UO loc 2500, UO 25289, **B;** Bartlett Mountain, UO loc 2517, UO 25124.

trigonid is very peculiar. The protoconid is the largest trigonid cusp. It is either fused with a labially displaced metaconid or somewhat transversely elongated. There is a low connate paraconid anteriorly and labially which is connected to the protoconid by a narrow paralophid. The paralophid arches anterolabially from the anterior side of the protoconid to connect to the labial side of the paraconid. A ridge extending from the level of the protoconid to the level of the paraconid along the lingual side of the trigonid serves to enclose the prefossid lingually so that it opens outwardly at the anterior extremity of the tooth. The metaconid is either absent, fused with the protoconid or displaced posteriorly into the normal position of the metastylid. For the sake of discussion I will consider the latter to be the case. The metaconid is a tall, sharply connate cusp displaced posterior to the level of and not joined to the protoconid. The crista obliqua and short low entocristid join the base of the metaconid thus enclosing the postfossid. The hypoconid is the largest cusp of the tooth and more or less normal in shape for a talpid. The entoconid is like the metaconid in shape. The postcristid joins the base of the entoconid posteriorly. There is a distinct posterior accessory cuspid but no posterior cingulum. A narrow labial cingulum extends from the anterolabial face of the hypocond to beneath the paraconid. There is a tiny ectostylid on the cingulum at the base of the hypoflexid. The labial side is nearly mesodont but the lingual side is very shallow thus the entoconid, metaconid, protoconid and hypoconid are all about the same occlusal level but the latter two are much deeper. There is a rather small cross-sectionally ovate anterior root and a much larger subtriangular posterior root.

Of the two unassigned lower molars from Bartlett Mt. UO loc. 2517, one is an M_1, UO 25124 (Fig. 96B). This specimen resembles UO 25289 from Black Butte in all essential

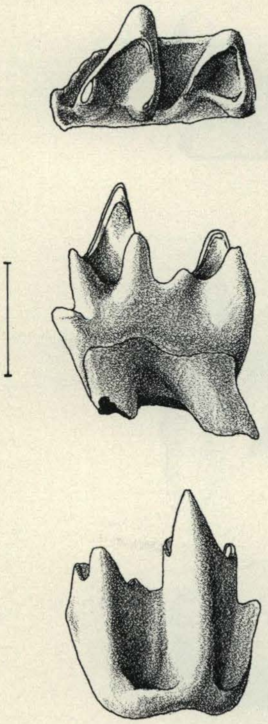

Figure 97. ?Talpidae *incertae sedis*, Bartlett Mountain, UO loc 2517, UO 25105 right M_3, occlusal, lingual and labial views.

features but differs in detail (1) the tooth is higher crowned labially, (2) the labial cingulum is greatly reduced and absent around the protoconid, (3) the roots slant more posteriorly, and (4) the talonid is proportionately wider.

An M_3, UO 25105 (Fig. 97), probably represents part of the same species as UO 25124 on the basis of size. The trigonid and talonid are about equal in length but the talonid is narrower. There is a wide and sharply defined anterior cingulum which is expanded somewhat labially into an accessory cuspid. A labial cingulum bridges the base of the hypoflexid. The trigonid is rather compressed anteroposteriorly and the protoconid is sharply angulate labially. The prefossid is deep and opens out between the paraconid and the metaconid. The protoconid is the tallest cusp, followed by the metaconid and then by the equally tall paraconid, entoconid, and hypoconid. The hypoflexid and postfossid are very deep and the crista obliqua, postcristid and entocristid are consequently sharply defined. The entoconid is situated in the posterolingual extremity of the tooth. The crista obliqua and entocristid join and form a slight elevation at their juncture which may be considered the metastylid. The two lophs continue as one loph anterior to the metastylid and join the posterolingual base of the metaconid. The lingual side of the tooth is not as disproportionately short compared to the labial side as in UO 25124. A slight swelling on the posterior side of the entoconid may represent the remains of a posterolingual accessory cuspid. The two roots seem to have been about equally strong. The remote juncture of the crista obliqua and enterocristid, mesodonty, and sharply angulate hypoconid tend to support association with UO 25124. The possibility exists that M_3, UO 25105, and the upper M^3, UO 24799, from this locality are modified second molars in a reduced dentition.

RELATIONSHIPS: Little can be said as to the relationships of the animals represented by these three teeth. The morphology of the talonid and posterior accessory cuspules on the first molars is suggestive of talpids. The bizarre structure of the trigonid, however, is not present in any of the known talpids. The Chiroptera also have lower molars which closely resemble taplids in general morphology and isolated molars may be relatively easily confused with those of talpids (*e.g. Mystipterus*). No attempt was made to survey all of the genera of Chiroptera but the spot checking of various bat genera did not reveal any more structural similarity of the fossils with bats than with the talpids. The trend toward hypsodonty is more characteristic of the Talpidae than of the Chiroptera.

Among the other insectivora there are numerous possibilities of relationship, however none of the North American or better known Eurasian erinaceids or soricids show any particular similarity with these fossils. These teeth are thus provisionally referred to the Talpidae.

Assuming that the development of hypsodonty or trends in that direction are usually not reversed, the Black Butte specimen indicates an older age (as do other elements of the fauna) than the specimens from Bartlett Mountain. The rarity of these forms precludes much utility in relative dating at present.

TABLE 25

MEASUREMENTS OF THE LOWER TEETH OF ?TALPIDAE *incertae sedis*

	M_1 UO 25289	M_1 UO 25124	M_3 UO 25105
Length	1.98	2.06*	1.77
Width trigonid	0.87	0.93	0.77
Width talonid	1.20	1.33	1.07
Height metaconid	0.67	0.67*	0.77
Height hypoconid	1.38	1.80	1.93

* Accessory cuspid broken and metaconid worn.

SUMMARY

The history of the talpids is perhaps more poorly understood than is warranted by the material at hand; however, tremendous gaps in our knowledge of the group allow a wide margin of error and chance for misinterpretation. No one has yet postulated a general hypothesis of the history of the North American moles, largely because the published record is poor and in some cases misleading. I do not pretend to present a complete or cohesive picture of the paleogeographic and phyletic history of the group, but the new material discussed herein, as well as much additional material under study, does suggest a picture or rather an imperfect mosaic which allows a closer approximation of that history than was hitherto possible.

The earliest talpids known from North America are the Proscalopinae. Reed and Turnbull (1965) suggest that the Proscalopinae, the only assuredly endemic subfamily, were derived from a generalized basal stock independently of that which gave rise to the rest of the moles sometime in the Eocene. If such a generalized stock was Holarctic in its distribution in the Eocene or earlier then none of its members have been identified as such. The earliest form known from limb material, *Cryptoryctes* C. A. Reed, from the Chandronian of Colorado is already highly specialized toward a fossorial existence. The Proscalopinae remain the only known moles in North America during the Oligocene. In Europe during this time, the "true" moles or Talpinae appear and enjoy a similar freedom from competition with members of other talpid subfamilies. The Proscalopinae continue on into Hemingfordian (early Middle Miocene) time, but by the close of this land mammal age they had become extinct.

Before the extinction of the Proscalopinae, two other subfamilies of moles, the Talpinae and Uropsilinae, appear in the fossil record from the early Hemingfordian of Colorado (Wilson, 1960). I postulate that representatives of these two groups dispersed from Asia during the Arikareean (Early Miocene). Significantly, the two new genera, *Mystipterus* and *Scalopoides*, are ambulatory and only moderately fossorially specialized and thus offer seemingly little competition to the highly fossorially specialized proscalopines which occur at the same locality. In the absence of the proscalopines, several different and highly specialized moles all within the Talpinae appear during the Barstovian (late Middle Miocene). *Scalopoides* and *Mystipterus* continue and are joined by still another talpid (*Achlyoscapter*) of unknown fossorial ability but probably structurally between the afore-mentioned genera. The highly adapted burrowing moles known from at least three genera are not uncommon in Barstovian microvertebrate assemblages. At least one of these, *Domninoides*, continues on into the Clarendonian (Late Miocene-Early Pliocene). *Scapanus* and probably *Scalopus* arise from one or more of the pre-Clarendonian genera. *Mystipterus* and *Scalopoides* still survive at least in the western faunas.

The Hemphillian (Middle Pliocene) talpids from the Great Plains are not yet well known but relatives of most of the Clarendonian forms from the Great Basin with the possible exception of *Mystipterus* continue on into Hemphillian time. In addition, a single genus referred to a new subfamily, *Gaillardia*, appears in both the Great Basin and Great Plains.

By the close of the Hemphillian and possibly earlier, the diversity of the talpids decreased, leaving only forms related or ancestral to Recent genera. The ancestors or Tertiary representatives of *Neurotrichus* and the unique *Condylura* are not unquestionably known. The nearest living relatives of *Neurotrichus* are in Japan, and may represent the latest talpid dispersal into North America.

The temporal ranges and postulated relationships of the better known North American talpids are illustrated in Figure 98.

The later Tertiary records of talpids described here indicate several related trends. There is a general but uneven decrease in diver-

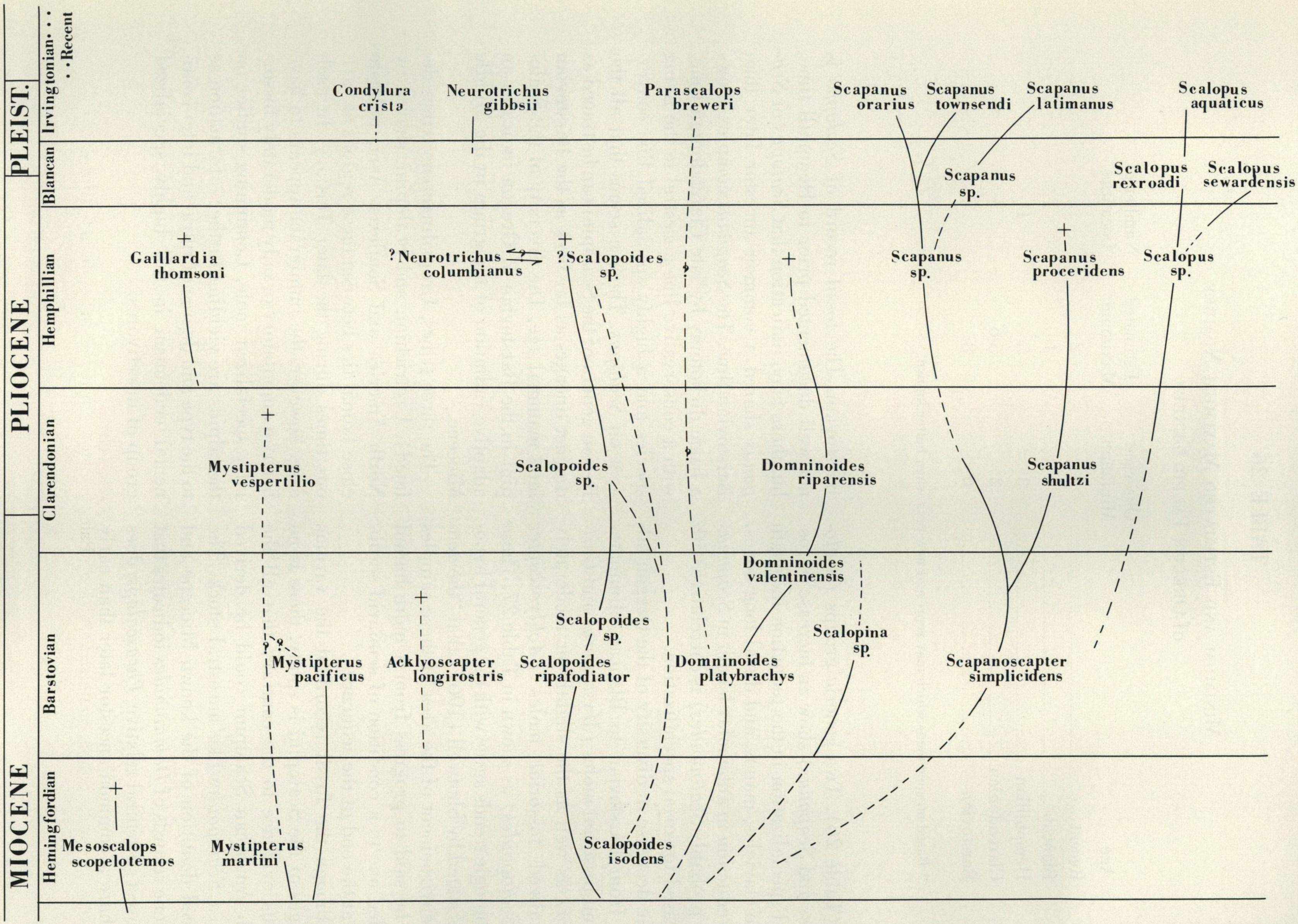

Figure 98. Tentative phylogeny of later Cenozoic Talpidae from North America.

TABLE 26

MINIMUM AND ESTIMATED MAXIMUM NUMBER of OREGON TALPID GENERA

Age	Observed Minimum	Estimated Maximum*	Number of Localities
Recent	2	2	....
Blancan	1	1	1
Hemphillian	3	5	11
Clarendonian	3	5-6	3
Barstovian	6	8	7

* Based on specimens which may represent new taxa when better known.

sity (Table 26). Two generic groups *(Scalopoides* and *Scapanus)* show an increase in fossorial specialization in the reduction in length of the clavicles, manus, and distal long bones. The reduction in antemolar length in *Scapanus* (and probably *Scalopoides*) is correlative with increased fossorial specialization.

The decrease in diversity of the Oregon talpids from Barstovian to Blancan eliminates the non-fossorial moles *(Mystipterus* and *Gaillardia)* as well as the slightly or moderately specialized fossorial moles *(Achlyoscapter* and *Scalopoides)* as shown in Table 27. These chronologic trends agree with the general hypothesis stated by Shotwell (1967) that "the general environment of the area of these samples may be said to progress from a more humid wooded one to a condition of semiarid scrubland at the end of the sequence".

Although the fossil record of the various lineages of the Scalopini is spotty, there is no serious evidence to the contrary that all the North American Scalopini could be derived from a *Scalopoides*-like ancestral stock. The reduced dentition of the known Miocene and Pliocene records of *Domninoides* indicates that its closest structural relative, *Parascalops*, does not share a common ancestor later than early Barstovian. The fossil record of *Scalopus* is not well documented prior to Hemphill time, but there is no indication that *Scalopus* or *Scapanus* shared a common ancestor later than Barstovian time. The *Scapanus* complex shows a basic dichotomy by late Clarendonian time, with a conservative line ancestral to the living species and a highly specialized line convergent on *Scalopus*. Thus, it seems that all the Recent genera of the Scalopini can be traced as distinct lineages as far back as the Barstovian land mammal age. The diversity of the Scalopini in the Barstovian of Oregon indicates an adaptive radiation of the group in the Middle Miocene.

The three tribes, Uropsilinae (no tribes defined), Urotrichini, and Scalopini, shared by North America and Southeast Asia, indicate close faunal ties between these regions at various times during the later Tertiary. In each case, however, the immigrant appears to have been an ambulatory or only moderately fossorially specialized mole. Continuing studies on the talpids are yielding further information as to the type and degree of intra- and inter-continental endemism in this highly specialized group of insectivores.

TABLE 27

Approximate Adaptive Grade of Oregon Talpidae

	Ambulatory	Aquatic	Semiaquatic	Semifossorial	Fossorial	
Recent				*Neurotrichus*		*Scapanus*
Hemphillian		*Gaillardia*			*?Scalopoides*	*Scapanus*
Clarendonian	*Mystipterus*				*Scalopoides* *Domninoides**	*Scapanus*
Barstovian	*Mystipterus*		*Achlyoscapter?*		*Scalopoides* *Domninoides*	*Scapanoscapter* Scalopina sp. A

* From Nevada.

TABLE 28

Occurrence and Abundance of Oregon Late Tertiary Moles

TAXON	BARSTOVIAN							CLARENDONIAN			HEMPHILLIAN										BLANCAN	
	UO 2465	UO 2495	UO 2493	M 1040	M 1041	M 1042	M 1043	UO 2500	UO 2337	UO 2489	UO 2222	UO 2323	UO 2347	UO 2349	UO 2380	UO 2516	UO 2517	UO 2357	CIT 62	UO 2322	CIT 375	UO 2223
*Mystipterus pacificus**	12/3																					
M. cf. *M. pacificus*		1/1				2/2																
M. (Mystipterus) sp.								4/1														
Gaillardia thomsoni											42/3											
*?Neurotrichus columbianus**											4/2											
*Scalopoides ripafodiator**	227/14																					
S. cf. *S. ripafodiator*		71/7	1/1		10/4	2/2																
Scalopoides sp. A								17/2														
Scalopoides sp. B								1/1														
?Scalopoides sp. C																	12/2					
?Scalopoides sp. D											2/2											
?Scalopoides sp. E											4/2											
Domninoides	9/1					2/2																
Scapanoscapter simplicidens**		15/2		1/1																		
Scapanus cf. S *(Scapanus)* sp.																	8/1					
S. cf. *S. shultzi*								16/2	2/2	1/1												
*Scapanus proceridens**												8/2		2/2	2/1	8/1				1/1	1/1	
S. cf. *S. proceridens*											5/1		5/1					1/1				
Scapanus sp.																			2/2			
S. nr. ? *S. latimanus*																						1/1
Scalopina sp. A							7/1															
Scalopini sp. A		4/1																				
Acklyoscapter longirostris**	9/2	1/1																				
Talpidae *incert. sed.*						1/1		3/1								2/2						
Talpidae *incert. sed.*	2/1										4/2					1/1						
?Talpidae *incert. sed.*								1/1								2/1						
Unassigned Talpidae	11/5															2/1						

* New species or genus.

LOCALITY DESCRIPTIONS

The following described localities are listed by institution and then numerical order. Localities are described only to the level of section. More precise information is on file in the respective institutions and the University of California Museum of Paleontology, Berkeley.

Method of collection is also given for each locality as an indication of sampling reliability. The designation of fine screen refers to industrial woven wire cloth with 24 by 24 mesh per line inch of 0.0128 inch wire, and standard screen refers to woven wire cloth with 15 by 18 mesh per line inch of 0.0114 inch wire. (UO= University of Oregon Museum of Natural History; M=United States Geological Survey locality; CIT=California Institute of Technology—these collections now the property of Los Angeles County Museum).

UO 2222—McKay Reservoir, Umatilla Co., sec. 35, T.2 N., R.32 E., and to sec. 2, T.1 N., R.32 E. Surface collected, quarried, and approximately a ton of matrix washed through fine screen.
AGE: Hemphillian
REFERENCES: Shotwell, 1955, 1956, 1958 A-B, 1967; Brodkorb, 1958.

UO 2223—Enrico Ranch, Klamath Co., sec. 28, T.40 S., R.9 E. Surface collected.
AGE: Blancan?

UO 2322—Krebs Ranch I, Gilliam Co., sec. 30, T.3 N., R.22 E. Surface collected.
AGE: Late Hemphillian
REFERENCES: Shotwell, 1958 A.

UO 2337—Black Butte I, Malheur Co., sec. 11, T.21 S., R.37 E. Quarried and roughly one and one half tons of matrix washed in the field through standard screen.
AGE: Clarendonian
REFERENCES: Brodkorb, 1961; Shotwell and Russell, 1963.

UO 2347—Otis Basin, Harney Co., sec. 18, T.20 S., R.36 E. Surface collected and from ant hills.
AGE: Hemphillian
REFERENCES: Shotwell, 1963.

UO 2349—Westend Blowout, Morrow Co., on line of sec. 7 and 8, T.3 N., R.27 E. Surface collected.
AGE: Late Hemphillian
REFERENCES: Shotwell, 1958 B, 1961.

UO 2357—Bartlett Mountain II, Harney Co., sec. 22, T.21 S., R.35 E. Surface collected.
AGE: Hemphillian
REFERENCES: Shotwell, 1958 B, 1963

UO 2380—Little Valley I, Malheur Co., sec. 33, T.20 S., R.43 E. Surface collected, quarried, and washed with standard screen.
AGE: Late Hemphillian

UO 2465—Quartz Basin, Malheur Co., sec. 33, T.24 S., R.43 E. Quarried, about three tons of matrix washed in field with standard screen, and about 400 pounds washed through fine screen.
AGE: Early Barstovian
REFERENCES: Shotwell, 1963, 1967; Hutchison, 1966.

UO 2489—West of Riverside, Malheur Co., approximately sec. 9, T.24 S., R.37 E. Surface collected.
AGE: Clarendonian

UO 2493—Red Basin I, Malheur Co., approximately at junction of sections 10, 11, 14, and 15, T.23 S., R.40 E. Surface collected and quarried for large vertebrates, residue from casts washed through standard screen.
AGE: Barstovian
REFERENCES: Gazin, 1932; Shotwell, 1963.

UO 2495—Red Basin II, Malheur Co., about 30 yards east of UO 2493. Same method of collection as UO 2493.
AGE: Barstovian, K/A date 15.1×10^6 years b. p.
REFERENCES: Gazin, 1932; Shotwell, 1963; Evernden *et al.*, 1964; Hutchison, 1966.

UO 2500—Black Butte II, Malheur Co., approximately at junction of sec. 10, 11, 14 and 15, T.21 S., R.37 E. Surface collected and about one and three quarters tons of matrix washed through fine screen.
AGE: Clarendonian
REFERENCES: Shotwell, 1963, 1967.

UO 2516—Little Valley II, Malheur Co., sec. 33, T.19 S., R.43 E. Surface collected, quarried, and washed through fine screen.
AGE: Late Hemphillian
REFERENCES: Shotwell, 1967.

UO 2517—Bartlett Mountain, Malheur Co., sec. 9, T.21 S., R.35 E., part of UO 2239, and CIT 107. About one and one quarter tons of matrix washed through fine screen.
AGE: Hemphillian
REFERENCES: Shotwell, 1963, 1967

M 1040—Malheur Co., sec. 25, T.35 S., R.42 E. Anthill collection.
AGE: Barstovian
REFERENCES: Repenning, 1967.

M 1041—Beatty Butte, Harney Co., sec. 14, T.36 S., R.29 E. Anthill collection.
AGE: Barstovian
REFERENCES: Wallace, 1946; Repenning, 1967.

M 1042—Guano Ranch, Lake Co., sec. 34, T.38 S., R.27 E. Anthill collection.
AGE: Barstovian
REFERENCES: Repenning, 1967.

M 1043—Snyder Creek, Lake Co. ,sec. 32, T.35 S., R.23 E. Anthill collection.
AGE: Barstovian
REFERENCES: Repenning, 1967.

CIT 62—Rome, Malheur Co., sec. 7, R.32 S., R.51 E. Surface collected.
AGE: Hemphillian
REFERENCES: Wilson, 1934, 1937.

CIT 375—Arlington, Gilliam Co., near junction of sections 30, 31, 32, and 29, T.3 N., R.22 E. Surface collected.
AGE: Late Hemphillian

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ADDENDUM

After the completion of this manuscript, unseen talpid material from previously mentioned localities was examined. Dr. C. E. Ray located and sent to me the alleged *Desmana moschata* listed in Littleton and Grosthwaite (1957) from Idaho. The specimens are not mammalian but the pharyngeal teeth of a cyprinid (Cypriniformes, Osteichthyes), probably *Sigmopharyngodon* Uyeno 1961. The talpid reported by Hibbard (1939 from the Edson locality in Kansas is referable to *Scalopus*.

PUBLICATIONS

Museum of Natural History
University of Oregon
Eugene, Oregon

Bulletins	*Titles*	*Price*
No. 1	Cenozoic Stratigraphy of the Owyhee Region, Southeastern Oregon; Kittleman, L. R. *et al.*, 45 pp., 9 plates 11 figures, (December 1965)	$1.50
No. 2	Notes on some Upper Miocene Shrews from Oregon, Hutchison, J. H., 23 pp., 17 figures, (March 1966)	$1.25
No. 3	A New Archaic Cetacean from the Oligocene of Northwest Oregon, Emlong, D., 51 pp., 15 figures, (October 1966)	$1.50
No. 4	The Archaeology of a Late Prehistoric Village in Northwestern California; Leonhardy, Frank C., 41 pp., 17 figures, (March 1967)	$1.00
No. 5	*Peromyscus* of the Late Tertiary in Oregon; Shotwell, J. Arnold, 35 pp., 11 figures, (June 1967)	$1.25
No. 6	Ethnomalocology and Paleoecology of the Round Butte Archaeological Sites, Deschutes River Basin, Oregon; Roscoe, E., 20 pp., 4 figures (July 1967)	$ .75
No. 7	Its Own Story, The Museum of Natural History; 16 pp.	no charge
No. 8	Geologic Map of the Owyhee Region, Malheur County, Oregon; Kittleman, L., and others, scale 1:125,000 (September 1967)	$2.00
No. 9	Late Tertiary Geomyoid rodents of Oregon; Shotwell, J. Arnold, 28 figures (November 1967)	$1.25
No. 10	Refinements in Computerized Item Seriation; Craytor, W.B., and LeRoy Johnson Jr., (March 1968)	$ .75
No. 11	Fossil Talpidae (Insectivora, Mammalia) from the Tertiary of Oregon; Hutchison, J.	$1.25
No. 12	Plants of the Three Sisters Region, Oregon Cascade Range; Ireland, O. 130 pp.	$3.75