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**Mandibular Musculature and the Origin of the Subfamily *Arvicolinae*  
(*Rodentia*)<sup>1</sup>**

[Pp. 29—72, 10 text-figs.]

**Миёсны зухвы а pochodzenie podrodziny *Arvicolinae* (*Rodentia*)**

**Жевательная мускулатура и происхождение подсемейства *Arvicolinae* (*Rodentia*)**

Abstract. As the fossil record of the arvicoline rodents becomes better known, it has become increasingly difficult to separate primitive genera from similar cricetine rodents on the basis of dental morphology. In search of criteria other than tooth pattern, an examination of the mandibular musculature and its expression in bone structure was made. Several characters of the mandible were found to be more or less typical of the arvicoline and not of the cricetine rodents. Examination of these characters in middle and late Pliocene arvicoline and cricetine rodents of both the Old and New World quite clearly defined the genus *Promimomys* as being arvicoline and the genera *Baranomys* and *Microtodon* as cricetine even though dental patterns are conspicuously similar. A fourth genus, *Microtoseoptes* from the middle Pliocene of both Old and New Worlds, is retained in the subfamily *Arvicolinae*, although both dental and mandibular morphology strongly suggest that it represents a separate lineage of cricetine rodents closely paralleling the arvicolines in some respects but differing in others.

CONTENTS

Introduction. . . . .	30
Mandibular musculature of <i>Microtus</i> . . . . .	32
Masseter group . . . . .	32

<sup>1</sup> Publication authorized by the Director, U. S. Geological Survey. The priority of *Arvicolinae* GRAY, 1821, over *Microtinae* COPE, 1891, has recently been emphasized by KRETZOI (1962b).

Temporalis group . . . . .	36
Pterygoid-Mylohyoid-Hyoid Constrictor group . . . . .	38
Mandibular musculature of <i>Neotoma</i> . . . . .	39
Masseter group . . . . .	39
Temporalis group . . . . .	42
Pterygoid-Mylohyoid-Hyoid Constrictor group . . . . .	43
Notes on mandibular musculature of other rodents . . . . .	43
<i>Onychomys</i> . . . . .	44
<i>Zapus</i> . . . . .	44
<i>Citellus</i> . . . . .	46
Evaluation and characterization of the arvicoline mandible . . . . .	47
Primitive arvicoline and arvicoline-like cricetine rodents . . . . .	54
Family <i>Cricetidae</i> MURRAY, 1866 . . . . .	55
Subfamily <i>Cricetinae</i> MURRAY, 1866 . . . . .	55
Tribe <i>Baranomyini</i> KRETZOI, 1955b . . . . .	55
Genus <i>Microtodon</i> MILLER, 1927 . . . . .	55
<i>Microtodon kowalskii</i> (KRETZOI, 1962) . . . . .	55
Genus <i>Baranomys</i> KORMOS, 1933 . . . . .	57
<i>Baranomys longidens</i> (KOWALSKI, 1960) . . . . .	57
Subfamily <i>Arvicolinae</i> GRAY, 1821 . . . . .	60
Tribe <i>MicrotoscOPTINI</i> KRETZOI, 1955b . . . . .	60
Genus <i>MicrotoscOPTES</i> SCHAU, 1934 . . . . .	60
<i>MicrotoscOPTES disjunctus</i> (WILSON, 1937) . . . . .	60
Tribe <i>Arvicolini</i> GRAY, 1821 . . . . .	62
Genus <i>Promimomys</i> KRETZOI, 1955a . . . . .	62
<i>Promimomys mimus</i> (SHOTWELL, 1956) . . . . .	63
Probable origin of arvicoline rodents . . . . .	67
References . . . . .	69
Streszczenie . . . . .	70
Резюме . . . . .	71

## INTRODUCTION

The voles and lemmings, which make up the *Arvicolinae* are ubiquitous rodents of Holarctica. To date two genera, *MicrotoscOPTES* and *Promimomys*, are known from the middle Pliocene. From one of these, apparently, about 20 living genera have evolved, most of them during the Pleistocene. Thus the arvicolines could be one of the most sensitive indicators of geologic age and of intercontinental correlation throughout the temperate and arctic regions of the northern hemisphere at a time when evolution of many mammals was too slow to be of chronometric value. In comparison with rates of diversification of most mammals throughout the Tertiary period, evolution of the arvicolines has been truly explosive.

HINTON's (1926) monograph of the living and fossil arvicolines is the most significant single contribution to the development of an understanding of the evolution of these rodents. Today, 42 years after HINTON's publication, the study of the arvicolines is still in the discovery stage, and each new fossil tends



to alter and to enlarge, rather than to confirm, existing concepts of both phylogeny and zoogeography.

Fossil data are accumulating at an increasingly rapid rate due to increasing interest and to improvement of collecting techniques. Since the time of HINTON it has become much more obvious that the arvicolines have evolved from cricetine rodents and it is becoming difficult to separate the most primitive known arvicoline from some very arvicoline-like cricetine rodents. Thus some authors (as KRETZOI, 1955b, and SULIMSKI, 1964) have placed the genera *Baranomys* and *Microtodon* in the *Arvicolinae* whereas others have placed them in the *Cricetinae* with question (as SIMPSON, 1945, and STEHLIN and SCHAUB, 1951).

When considering transitional forms, the grade of specialization that defines the morphologic limits of the subfamilies *Cricetinae* and *Arvicolinae* must be arbitrarily selected. Almost all morphologic criteria used to separate arvicoline-like cricetines from cricetine-like arvicolines are based upon teeth. It is desirable to define the morphologic limits on the basis of as many criteria, in addition to dentition, as possible, however. What is an arvicoline or cricetine rodent depends upon the total characters of the entire animal, each of which may evolve at an independent rate. Thus, if we knew only the teeth of *Neotoma* we might justifiably consider it an arvicoline rodent whereas all other characters of the animal are more or less clearly cricetine.

HINTON reviewed the masticatory musculature of the arvicolines and pointed out characters of their skull that were associated with this musculature. He made very little mention of arvicoline characters of the mandible, which conform to the same musculature. It is obvious that this reflected his thinking for, in suggesting that *Brachytarsomys* was a good morphologic representation of what the ancestral arvicoline must have been like, he pointed out presumably arvicoline characters of the skull and of the teeth but failed to note that the mandible of *Brachytarsomys* is basically as cricetine as *Cricetus*.

Skulls of fossil arvicolines are rare, particularly of the most primitive genera, and those of fossil arvicoline-like cricetine rodents are equally rare. Naturally teeth have been used to try to define the subfamily morphology. However, mandibles of these arvicoline-cricetine fossils are relatively common. Because of this, the following review of the masticatory musculature of the *Arvicolinae* was undertaken and mandibular structures characteristic of the arvicolines were identified. Following this review and discussion of the early arvicolines and arvicoline-like cricetines, I have ventured to conclude this report with a section on the probable origin of arvicoline rodents based upon consideration of both dentition and mandibular structures.

Prior to preparing this report I had the pleasure of extended discussions with Claude W. HIBBARD of the United States, Kazimierz KOWALSKI of Poland, Miklós KRETZOI of Hungary, and (unfortunately only by correspondence) Oldřich FEJFAR of Czechoslovakia. Their information and ideas infiltrate the report, and I thank them greatly. In addition, it has been through the generosity of these gentlemen that I have been able to study many of the more

primitive arvicoline rodents. However, all of them would disagree with many of my conclusions.

I am indebted also to J. Arnold SHOTWELL of the University of Oregon for the loan of a mandible of *Promimomys minus*.

In this report the abbreviations used with specimen numbers are as follows: USNM. — — United States National Museum; USGS.-M — — United States Geological Survey comparative collection, Menlo Park (California); and UO — — University of Oregon, Museum of Natural History.

#### MANDIBULAR MUSCULATURE OF *MICROTUS*

(Figures 1 and 2)

The primary purpose of this description of the musculature of *Microtus* is to establish its relationship to the mandibular structures and to serve as a basis for an interpretation of which structures are characteristic of the subfamily *Arvicolinae*. For comparison, the musculature of *Neotoma*, *Onychomys*, *Zapus*, and *Citellus* are described in the pages that follow. *Neotoma* represents a genus of the closely related and ancestral subfamily *Cricetinae* that has evolved mandibular specializations paralleling those of the arvicolines. The others represent genera of rodents more distantly related to the arvicolines and are compared to illustrate those characters of musculature typical of the order and not of the arvicolines.

The following description is based upon the dissection of three specimens of *Microtus longicaudus mordax* from Idaho Springs, Colorado. All specimens were trapped on the first of July and do not represent fully mature individuals. However, the configuration of the mandibular structures, when compared with fully mature mandibles, suggests that changes in musculature with further growth will not seriously alter the conclusions nor descriptions based upon these specimens. Nomenclature of the musculature follows that used by RINKER (1954).

#### Masseter Group

##### *M. masseter superficialis*

Origin. By very strong tendon from small oblong area on low rounded process just below infraorbital foramen.

Insertion. By fleshy attachment on ventral surface of angular process of mandible; ventral surface is flattened for this insertion and has sharp lateral and medial edges which mark, respectively, the boundary between this insertion and those of the *M. masseter lateralis profundus* and *M. pterygoideus internus*. The anterior part of this flattened area faces ventrally. Posteriorly, toward the tip of the angular process, the surface twists to face ventrolaterally. The superficial masseter does not insert along this entire surface to the tip but rather stops short of the tip. The tip of the angular process, including the



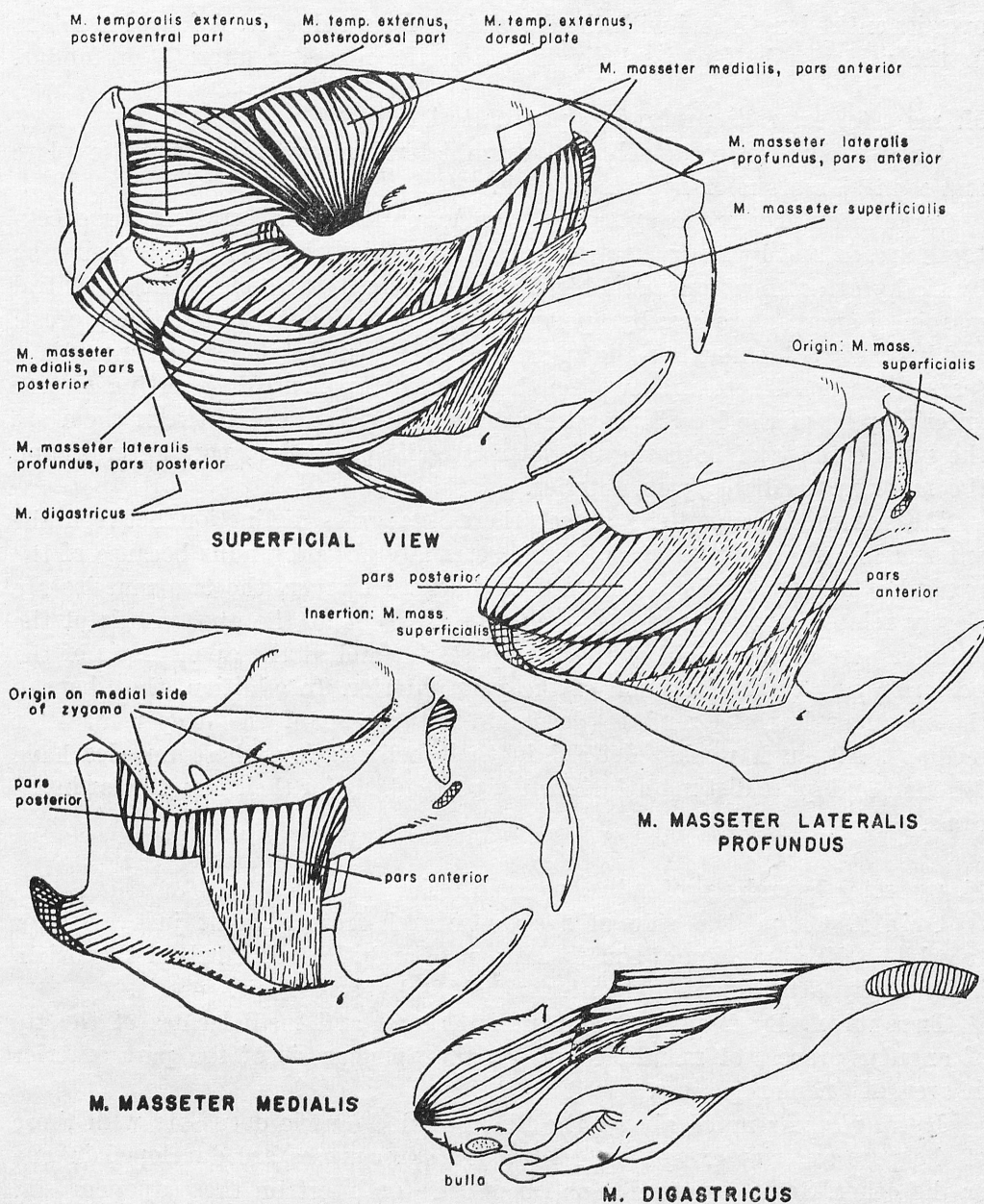


Fig. 1. The mandibular musculature of *Microtus longicaudus*.

flattened ventral surface, is the area of insertion for the M. masseter lateralis profundus, pars posterior.

Remarks. Forward from a point approximately beneath the orbit, this muscle is represented only by a broad aponeurosis which narrows anteriorly to form the tendon of origin. The muscle is quite distinct and separate from the other muscles, although it is in contact with the masseter lateralis profundus



over its entire length and with the digastricus for much of it. A few of its fibers in the posterior half of its belly insert on the masseter lateralis profundus.

*M. masseter lateralis profundus, pars anterior*

**Origin.** By fleshy attachment, from lateral margin of zygomatic plate and ventral margin of zygomatic arch.

**Insertion.** By broad aponeurosis on lower masseteric crest below cheek-tooth arcade and by fleshy attachment of superficial fibers on this aponeurosis; by fleshy attachment on mandible posterior to masseteric crest above ventral margin of angular process; by aponeurosis on posterior end of angular process; and by fleshy attachment on the aponeurosis of the underlying masseter medialis (pars anterior). There are two tough sheets of aponeurosis inserting on the anterior part of the lower masseteric crest, below  $M_1$ , and between them are the muscle fibers of both the masseter lateralis profundus, pars anterior, and the masseter medialis, pars anterior.

**Remarks.** In superficial aspect there is a gross distinction between the anterior and posterior parts of the masseter lateralis profundus because of the somewhat different orientation of their fibers. However, the two muscles are closely related and are not easily separated except at the aponeurosis of the anterior part of the origin of the pars posterior and at the aponeurosis of the posterior part of the insertion of the pars anterior. In addition, the fibers of the masseter lateralis tend to decussate with those of the deeper masseter medialis. Although weakly defined in their belly region, these muscles have different and quite distinct attachments, particularly for their mandibular insertions.

*M. masseter lateralis profundus, pars posterior*

**Origin.** On ventral side of zygomatic arch from a point just posterior to orbit to distal portion of squamosal root of arch. Posterior half of this origin is by fleshy attachment and anterior half is by broad aponeurosis.

**Insertion.** By fleshy attachment on lateral and medial sides of the tip of angular process of mandible and on the aponeurosis of the pars anterior in area of angular process.

**Remarks.** As noted above, the fibers of this muscle decussate with those of the pars anterior except in areas where aponeuroses are developed in one or the other. Some non-tendinous fibers arise or insert on these aponeuroses.

Judging only from skeletal material, there appears to be considerable variation among different arvicoline rodents in the position of the masseter insertions on the angular process. These differences are reflected in the form of the flattened ventral surface of the process, which varies from being entirely ventral (with no lateral rotation), as in *Lemmus*, to being extremely rotated so that the "flattened ventral surface" actually is a flattened lateral surface on the angular process as in *Ondatra*. *Microtus* appears to be intermediate in development. No dissections were performed to substantiate the interpretation,

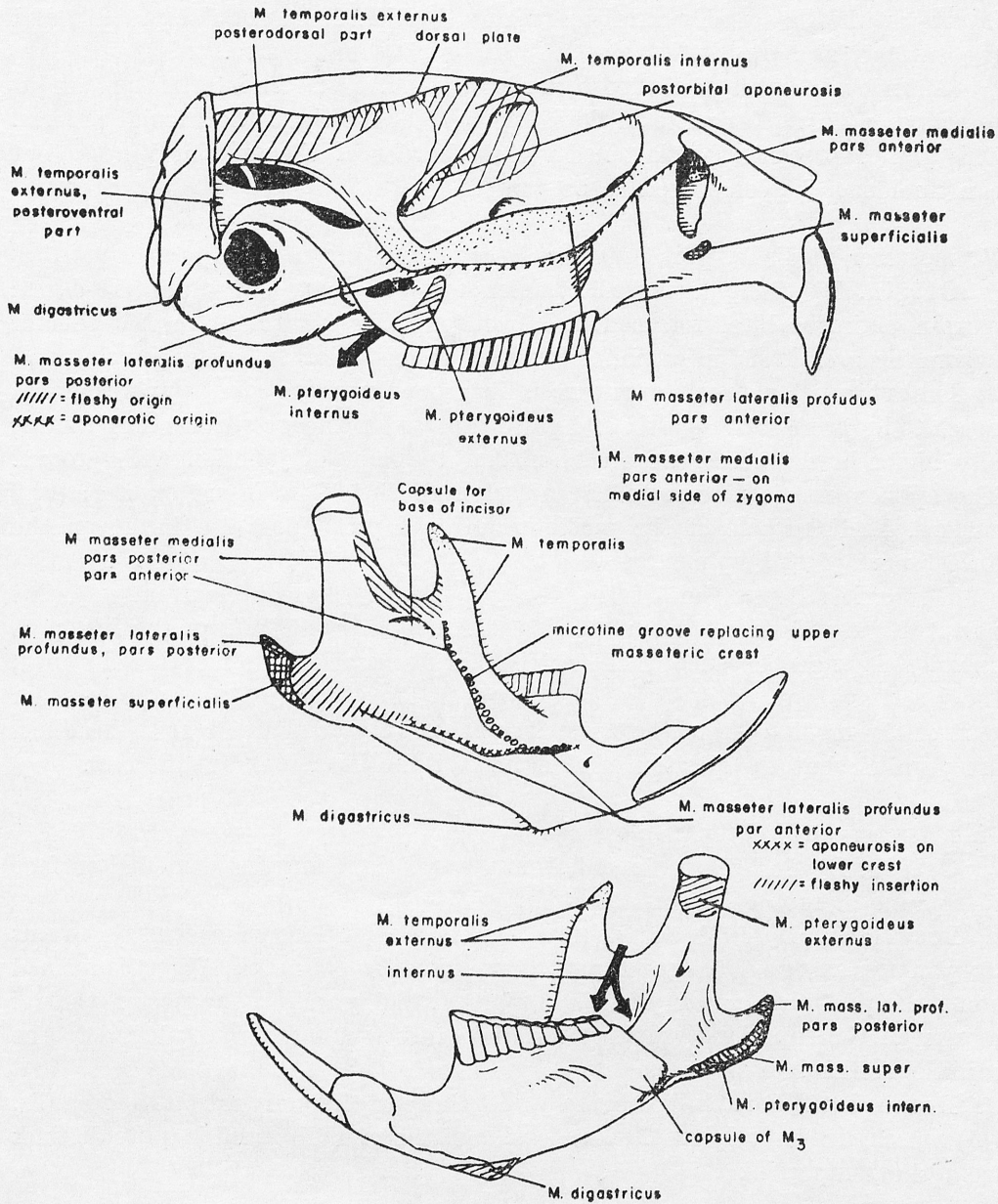


Fig. 2. The mandibular muscle origins and insertions of *Microtus longicaudus*.

but consideration of the mandibular structures involved leads to the following conclusions.

(1) In *Lemmus* no part of the *M. masseter lateralis profundus* inserts on the flattened ventral margin of the angular process.

(2) In *Microtus* part of the posterior part of *M. masseter lateralis profundus*

inserts on the flattened ventral margin at the tip of the angular process, and the surface, as a result, is rotated laterally to some degree.

(3) In *Ondatra* all of the posterior part of *M. masseter lateralis profundus* inserts on a triangular plate on the lateral side of the tip of the angular process. This plate represents the flattened ventral border of the angular process but can no longer be considered to be ventral.

#### *M. masseter medialis, pars anterior*

**Origin.** By fleshy attachment from fossa in maxillary at antero-dorsal margin of infraorbital foramen and from superior margin of medial side of zygomatic arch from infraorbital foramen to posterior suture of jugal.

**Insertion.** By broad aponeurosis in groove running from upper sigmoid notch to lower masseteric crest and paralleling anterior edge of ascending ramus; also along lower masseteric crest anterior to point of junction with groove. The aponeurosis is medial to the muscle and the fibers insert on its lateral surface. Medial fibers of the *masseter lateralis profundus* also insert on the lowest part of this aponeurosis.

**Remarks.** Separation of the fleshy parts of this muscle from adjacent parts of the masseteric group (chiefly the *masseter lateralis profundus, pars anterior*) is vague because of extensive fiber decussation. As mentioned above, the insertions are quite distinctive, however. Also, separation of the anterior part of the *medialis* from the posterior part is very difficult because the fibers are parallel; but the position and nature of the insertions are distinct.

#### *M. masseter medialis, pars posterior*

**Origin.** By fleshy attachment from ventral three-fourths of medial surface of squamosal root of zygomatic arch.

**Insertion.** By fleshy attachment on lateral surface of ascending ramus over an area marginal to deeper part of superior sigmoid notch. A crest is formed along the posterior margin of this insertion which parallels the posteroventral margin of the superior sigmoid notch and outlines a fossa anterodorsal to the capsule of the incisor base.

**Remarks.** Although its fibers parallel those of the more medial *temporalis*, this muscle lies entirely on the lateral side of the mandible and is quite distinct from the *temporalis*.

### Temporalis Group

The temporal muscle of *Microtus* is composed of four fairly distinct units. None of these inserts on the lateral surface of the mandible. Three of these units may be classified as parts of the external temporal muscle. The fourth is the largest single muscle unit and is considered to be the internal temporal. All have distinct origins and fairly distinct insertions but have extensive decussation of their fibers with those of adjacent units in their belly regions. The



muscle units of the external temporal insert chiefly on the tip of the coronoid process and along the anterior edge of the ascending ramus. The internal temporal inserts in the deep, pocketed, internal temporal fossa of the mandible, which is situated between the ascending ramus and the cheek teeth.

#### M. temporalis externus, dorsal plate

**Origin.** By fleshy attachment from temporal crest between a point above posterior root of zygomatic arch and anterior limit of crest (in the immature specimens dissected this anterior limit was well behind the orbit—it is not known whether this head of the external temporal or the internal temporal muscle would continue anteriorly along the temporal crest to its termination which, on mature skulls, is much closer to the premaxillary suture and between the eyes).

**Insertion.** The course of the dorsal plate is obscured by considerable decussation of its belly fibers with those of the internal temporal muscle. However, it seems to insert by a strong tendon on the tip of the coronoid process and by an aponeurosis along the anterior edge of the ascending ramus of the mandible.

**Remarks.** The origin and head of this muscle are superficial to all other elements of the temporalis complex.

#### M. temporalis externus, posteroventral part.

**Origin.** By fleshy attachment from ventral half of lambdoidal crest.

**Insertion.** By strong tendon on tip of coronoid process. This muscle slides, pulley-like, over the squamosal root of the zygomatic arch.

**Remarks.** This muscle is deep to the dorsal plate and superficial to the posterodorsal part of the external temporal.

#### M. temporalis externus, posterodorsal part

**Origin.** By fleshy attachment to dorsal part of lambdoidal crest, posterior half of temporal crest, and much of surface of cranium between these margins.

**Insertion.** With posteroventral part by same tendon to tip of the coronoid process.

**Remarks.** This is the deepest part of the external temporal. The three parts of the external temporal unite in one short lever arm and are concerned chiefly with rapid occlusion and with strength of bite when the jaws are open to a maximum degree and the masseter and deep temporal are stretched beyond their most effective condition. With lesser gape the masseter and the internal temporal muscles have far greater mechanical advantage for strength of bite.

#### M. temporalis internus

**Origin.** By fleshy attachment from side of brain case and posterodorsal wall of orbit. The lower half of the origin from the postorbital process to the root of the zygomatic arch is a particularly strong line of origin and is marked by an aponeurosis.

**Insertion.** By fleshy attachment to bottom of pocketed internal temporal fossa of mandible between ascending ramus and cheek teeth.

**Remarks.** This strong muscle has developed a mechanical advantage equal to the masseter for strength of bite. This seldom-mentioned masseter-like function of the internal temporal muscle is nearly as characteristic of the rodents as is the gnawing incisor. Only in the shrews has the temporal muscle assumed a greater masseter-like function and here it results from a weakening of the masseter system rather than from an overall strengthening of the bite.

#### Pterygoid-Mylohyoid-Hyoid Constrictor Groups

Considered here are only four muscles which seem significant to the structure of the mandible. The two pterygoid muscles are, presumably, not closely related in that the external pterygoid is innervated by the masticatory nerve and the internal pterygoid by the mandibular nerve (RINKER, 1954, p. 15, 18). The two bellies of the digastric muscle are, in the *Cricetinae* at least, also supplied with separate innervation. According to RINKER (idem, p. 19, 36) the anterior belly is supplied by the mylohyoid branch of the mandibular nerve and the posterior belly by the digastric branch of the facial nerve.

##### *M. pterygoideus externus*

**Origin.** By fleshy attachment from oblong area on alisphenoid bone just anterior to foramina ovale and rotundum.

**Insertion.** By fleshy attachment on medial side of condylar process of mandible just below condyle.

##### *M. pterygoideus internus*

**Origin.** By fleshy attachment from pterygoid fossa.

**Insertion.** By fleshy attachment in trough along ventral margin of angular process of mandible. This trough is formed by the medial edge of the flattened ventral border of the process.

**Remarks.** The pterygoid muscles of *Microtus* are very stout, undoubtedly because of the propalinal method of mastication. Except for the deep and enlarged pterygoid fossa on the skull, this is not clearly indicated by bone structure.

##### *M. digastricus*

**Origin.** By fleshy attachment from tip of paroccipital process.

**Insertion.** By fleshy attachment on posterior face of symphyseal eminence.

**Remarks.** The bellies are distinct but are not separated by a tendinous interval nor does the entire muscle thin appreciably in the area of the union of the bellies. The left and right anterior bellies are distinct and do not insert on a mylohyoid raphe. The lateral half of the entire muscle appears to be composed of fibers which are continuous from anterior to posterior bellies. These fibers become aponeurotic at the union of the bellies but are not discontinuous between

the bellies. Medially the aponeurotic condition is greater and the medial one-third of the anterior belly is marked by fibers discontinuous with those of the posterior belly. *Microtus* thus has a digastric intermediate between the hystricomorphine and sciurumorphine condition of PARSON (1894, p. 254).

#### MANDIBULAR MUSCULATURE OF *NEOTOMA*

(Figure 3)

The following description is based upon the dissection of three specimens of *Neotoma mexicana fallax* from Denver, Colorado. As the purpose of this dissection is comparative, the musculature is described only in terms of differences from that of *Microtus*.

##### Masseter Group

##### M. masseter superficialis

Origin. As in *Microtus*. In all specimens seen, in fact in all rodents examined which lacked a hystricomorphine zygoma, the origin is from a point just below the ventral limit of the infraorbital foramen.

Insertion. As in *Microtus* except that an anterior slip continues beneath the mandible and is reflected upward to insert on the medial side along an area posterior and parallel to the base of the incisor, as described by RINKER (1954). The lack of this slip to the medial surface of the mandible in *Microtus* is unusual as it was seen in all other rodents dissected regardless of type.

Remarks. The superficial masseter is closely attached to the posterior part of the masseter lateralis profundus by insertion of some of its fibers on this deeper muscle, particularly in the central belly area. No decussation of fibers were noted, however. From six dissections it appears obvious that the actions of these two muscles must be more closely integrated than in *Microtus*.

##### M. masseter lateralis profundus, pars anterior

Origin. By fleshy attachment, as in *Microtus*. At its anterior limit, the attachment extends slightly farther down the outer side of the lateral wall of the infraorbital foramen than in *Microtus*, but most of the fossa of the zygomatic plate does not serve as an area of origin for the muscle but only separates the muscle from the medial masseter.

Insertion. By broad aponeurosis, as in *Microtus*, with the following exceptions. The lower masseteric crest is proportionately shorter and clearly not so prominently developed as in *Microtus*. The anterior part of the deep lateral masseter does not extend posteriorly to insert on the angular process, as in *Microtus*, but terminates at the posterior margin of the lower masseteric crest, an arrangement characteristic of all rodents examined except the arviculines.

Remarks. The prominence of the lower masseteric crest upon which the anterior part of the masseter lateralis profundus inserts is an obvious character



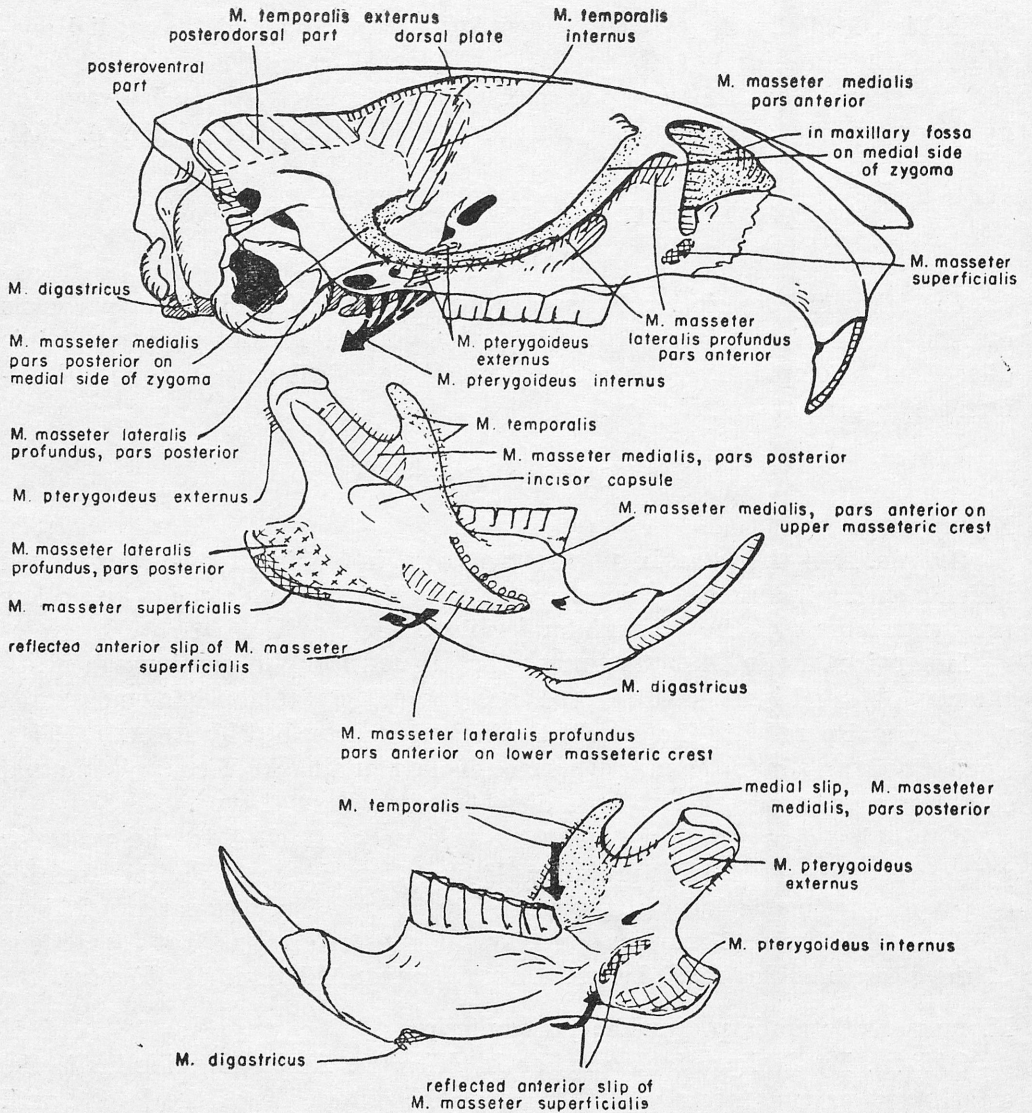


Fig. 3. The mandibular muscle origins and insertions of *Neotoma mexicana*.

of the arvicoline mandible which seems to separate that subfamily from closely related muroid rodents. Although long and far forward in arvicolines, the length and placement are not the distinguishing feature of the crest, for some cricetine rodents (such as *Sigmodon*) exceed some arvicoline rodents in both respects. The arvicoline lower masseteric crest is distinctive because it is remarkably prominent and shelf-like and remains fully prominent from its anterior limit, near the forward edge of  $M_1$ , to a point approximately beneath the posterior margin of  $M_3$ ; this is the posterior limit of the aponeurosis of insertion for this muscle in arvicolines. The crest is similar in *Neotoma* but is not shelf-like,

diminishes in prominence posteriorly, and does not extend as far back as the tooth row does. In most arvicolines the lower masseteric crest is as long or longer than the cheek teeth arcade; in most cricetines it is shorter than the cheek teeth, a glaring exception being *Sigmodon*, in which the lower masseteric crest is continuous with the lateral edge of the flattened ventral border of the angular process.

M. masseter lateralis profundus, pars posterior

Origin. As in *Microtus*.

Insertion. Anteriorly by fleshy attachment and posteriorly by aponeurosis along lateral edge of the ventral margin of angular process or in a band adjacent to ventral margin of angular process if sharp edge not developed; and by fleshy attachment across much of lateral side of angular process.

Remarks. The muscle does not wrap around the tip of the angular process to insert partly on the medial side as in *Microtus*. The three specimens dissected are young adults but have no sharp edge along the insertions of the deep lateral masseter and the superficial masseter. Osteologic specimens of other species of *Neotoma* do have such a sharp edge, and it is not possible to tell from the specimens available whether the lack of the sharp edge on the dissected specimens is a specific character of *N. mexicana* or represents immaturity, although the latter seems more likely.

M. masseter medialis, pars anterior

Origin. As in *Microtus*, except that more of the muscle extends through the infraorbital foramen and that part of its origin which is on the lateral surface of the rostrum is proportionately much larger.

Insertion. As in *Microtus*, except that the medial aponeurosis does not insert in a groove but on a low rounded crest (the upper masseteric crest) running from near the base of the anterior edge of the ascending ramus to the anterior termination of the lower crest. The more posterior fibers have a fleshy insertion on the ascending ramus.

Remarks. Although the general position of the insertion of this muscle is similar in those arvicolines and cricetines examined, the visible structures on the mandible are much reduced in cricetines and are formed differently. The sharp groove running well up the ascending ramus in arvicolines seems very characteristic; in the cricetines it has been seen only weakly developed and only on some specimens of *Neotoma*.

M. masseter medialis, pars posterior

Origin. As in *Microtus*.

Insertion. As in *Microtus*, except that the insertion does not extend as far forward but rather terminates beneath the deepest part of the superior sigmoid notch and is not present on the posterior side of the coronoid process. Although the insertion is entirely fleshy, a prominent ridge, marking the ventral margin of the insertion, extends nearly from the articular condyle to a point

below and slightly anterior to the superior notch, at which point it lies dorsal to the buccal swelling that marks the capsule at the base of the incisor.

▶ A small and separate slip of the posterior part of the medial masseter inserts in the bottom of the superior sigmoid notch and over a small area on the medial surface of the mandible at the base of the notch. This independent slip was not seen in *Microtus*. The fibers parallel those of the temporalis in this area, but they can be recognized as belonging to the masseter group by the fact that the masseteric nerve passes superficial to this slip but deep to the more medial temporalis. This slip originates on the ventral surface of the arch at its squamosal root and on the cranium adjacent and anterior to the zygomatic root in a position directly anterior to the glenoid fossa. Neither origin nor insertion of the slip are recognizable in the configuration of the bone structure.

Remarks. The insertions of the anterior and posterior parts of the medial masseter are much more widely separate in *Neotoma* than in *Microtus*. Because the origins are adjacent on the medial margin of the zygoma of *Neotoma* (as in *Microtus*), the two parts are adjacent in their belly regions, but are much more easily separated than in *Microtus*. Although adjacent and having parallel fibers, the posterior part of the medial masseter is clearly separate from the temporalis.

In both *Neotoma* and *Microtus* the masseteric nerve emerges between the anterior and posterior parts of the medial masseter and serves as a guide for recognition of the boundary between their bellies.

#### Temporalis Group

As in *Microtus*, the temporalis group is composed of four fairly distinct units in *Neotoma*. There are some differences in the position of origin of these units and all units decussate and unite toward their insertion. Most of the three parts of the external temporal insert on the coronoid process and most of the fibers of the internal temporal insert along the anterior edge of the ascending ramus, along the medial surface of this ramus, and in the bottom of the depression between this ramus and the cheek teeth. Only striking difference between *Neotoma* and *Microtus* are noted.

Origins. Approximately as in *Microtus*, except that the internal temporal shows no strong aponeurosis in that part of its origin which lies along the posterior margin of the orbit and, in consequence, *Neotoma* lacks the pronounced postorbital process so characteristic of all arvicoline rodents.

Insertion. As in *Microtus*, except that slightly more of the buccal surface of the coronoid process is involved and fleshy attachment takes place over the entire lingual surface of the ascending ramus anterior to the superior sigmoid notch rather than entirely in the basin between the cheek teeth and the ascending ramus.

Remarks. Concentration of the force of the temporalis in the trough between the ascending ramus and the cheek teeth in *Microtus*, as opposed to



insertion of some fibers over the medial surface of the ascending ramus in *Neotoma*, has resulted in a pocketed internal temporal fossa in the mandible of *Microtus*. This pocketed fossa is not at all developed in *Neotoma* nor in any living cricetine examined. While not always as well developed as in *Microtus*, the tendency is noticeable in many arvicolines. In *Pitymys* and *Lagurus* it is more strongly developed than in *Microtus*.

#### Pterygoid-Mylohyoid-Hyoid Constrictor Groups

##### *M. pterygoideus externus*

Origin and Insertion. As in *Microtus*.

Remarks. Deepening of the palatal region of *Microtus*, because of increased cheek tooth hypsodonty, has resulted in the origin of the external pterygoid lying below the level of the zygomatic arch (fig. 2), whereas in *Neotoma* it lies at the arch level (fig. 3). The positions are otherwise the same.

##### *M. pterygoideus internus*

Origin. As in *Microtus*, but the pterygoid fossa is much less enlarged.

Insertion. As in *Microtus*, although the area of fleshy insertion is greater in proportion to the area of insertion by aponeurosis.

##### *M. digastricus*

Origin and Insertion. As in *Microtus*.

Remarks. Although not expressed in the mandibular osteology, the union of the two bellies is more tendinous in *Neotoma*. Although also intermediate between hystricomorphine and sciurormorphine structure, *Neotoma* is thus more nearly sciurormorphine than is *Microtus*. According to RINKER (1954, p. 37) some other cricetine rodents are typically sciurormorphine in the digastric structure and are less similar to *Microtus* and forms with a typically hystricomorphine digastric muscle.

#### NOTES ON MANDIBULAR MUSCULATURE OF OTHER RODENTS

One specimen each of *Onychomys*, *Zapus*, and *Citellus* was dissected in order to form a basis for interpretation of the differences and similarities between *Neotoma* and *Microtus*. *Onychomys* was selected as a genus related to but not closely comparable with *Neotoma*. *Zapus* and *Citellus* were selected as examples of more distantly related rodents that might show which similarities were of an ordinal nature and which truly indicated affinities between *Microtus* and *Neotoma*. No murine rodents were dissected, but on the basis of comparison of the mandibles of a limited number of murine genera (*Rattus*, *Mus*, and *Apodemus*), I am unable to distinguish between those cricetine and murine mandibular structures that are related to their muscles.

*Onychomys*

The following notes are based on the dissection of one specimen of *Onychomys leucogaster leucogaster* from Aberdeen, South Dakota.

**M. masseter superficialis**

As in *Neotoma*, except that it is less closely associated with the posterior part of the masseter lateralis profundus. Some fibers do insert on this deeper muscle, however. The slip reflected around the ventral margin of the angular process to insert on the medial side is relatively very heavy.

**M. masseter lateralis profundus**

The posterior part is as in *Neotoma* with the exception of less decussation of fibers with the superficial masseter as noted above. The anterior part is as in *Neotoma*.

**M. masseter medialis**

The posterior part lacks the medial slip through the superior sigmoid notch in *Neotoma*. The anterior part shares a common insertion with the masseter lateralis profundus only at the anterior limits of these two muscles. The upper and lower crests of the insertion of these muscles meet only at their anterior terminations and do not merge before this point.

**M. temporalis**

The three divisions of the external temporal muscle are not so clearly seen as in *Neotoma* but otherwise the origin is essentially the same. The insertions are essentially the same except that an unusual slip separates distally and inserts directly behind  $M_3$ . The insertion of the temporalis in the trough between the cheek teeth and the ascending ramus, as a consequence, surrounds the medial, lateral and posterior sides of the posterior end of the origin of those parts of the buccinator originating on the mandible lateral to the cheek teeth. This arrangement is indicated in the bone structure by a small flat area behind  $M_3$  where the slip of the temporalis inserts.

Other muscles are as in *Neotoma*.

Remarks. From the mandibular musculature, *Onychomys* is clearly more closely related to *Neotoma* than *Microtus*, but clearly not the same as *Neotoma*.

*Zapus*

The following notes are based upon the dissection of one specimen of *Zapus princeps princeps* from Denver, Colorado.

**M. masseter superficialis**

In *Zapus* the infraorbital foramen has developed hystricomorphine proportions and, as a consequence, the anteroventral root of the zygoma has moved into

the area of origin of the superficial masseter (or has not moved away from this position, which is the primitive one). Thus, as in the hystricomorphs, this muscle originates from the ventral margin of the ventroanterior buttress of the zygoma rather than from a boss or process on the rostrum below the infra-orbital foramen as in nearly all living non-hystricomorph rodents.

A noticeably great part of the superficial masseter inserts on the deep lateral masseter; the remainder has an insertion not unlike *Microtus* and *Neotoma*.

#### M. masseter lateralis profundus

This muscle is not obviously divided into anterior and posterior parts in *Zapus*. Along that part of the zygomatic arch where the superficial masseter originates, the lateral masseter lies deep to the superficial, as would be expected.

#### M. masseter medialis

About as in *Neotoma*. Anterior and posterior parts were not conspicuous, if present. (The masseteric nerve was not seen in the single dissection). The head of this muscle, which originates on the rostrum and passes through the enlarged infraorbital foramen, is, of course, proportionately larger than in *Neotoma*. However, more obvious than proportionate increase in size is the fact that this head of the medial masseter runs much more nearly ventrad to the mandible than in *Neotoma*, thus greatly increasing the mechanical advantage in mastication.

#### M. temporalis

Not so obviously subdivided as in *Neotoma*. The area of origin is essentially as in *Neotoma*. The insertion is as in *Neotoma* except that the muscle does not extend down the lingual surface of the ascending ramus as far as the trench lateral to the cheek teeth. The temporalis is, therefore, less specialized than in most rodents and has assumed less of the role of the masseter.

#### M. pterygoideus externus and internus

The external pterygoid inserts over the entire medial surface of the articular process above the level of the superior sigmoid notch. This is a larger area than in *Microtus* or *Neotoma* and much larger than in sciurid rodents. The internal pterygoid inserts over the entire medial surface of the angular process.

#### M. digastricus

In contrast to the hystricomorphine pattern of the superficial masseter and the zygoma, the digastric muscle of *Zapus* is clearly of sciuridomorphine pattern with a narrow tendon separating the two bellies.

Remarks. The entire suite of mandibular muscles in *Zapus* is marked by a conspicuous reduction of aponeurotic or tendinous attachments in contrast to both *Microtus* and *Neotoma*. However, this would seem to reflect the smaller size of *Zapus* rather than a taxonomically significant character. The musculature



of *Zapus* is strikingly hystricomorphine in some feature and strikingly sciuro-morphine in others. Because it is different in several respects from either *Neotoma* or *Microtus*, it illustrates the ordinal nature of those features common to all three genera; thus it helps to define, by elimination, those other features that may be of significance at family or subfamily grade.

### *Citellus*

The following notes are based upon the dissection of one specimen of *Citellus lateralis lateralis* from Idaho Springs, Colorado.

#### M. masseter superficialis

This muscle originates from a pronounced masseteric tubercle at the ventral margin of the infraorbital foramen. In position, relative to the infraorbital foramen, this origin is not different than in other rodents examined that not have a hystricomorphine type of zygoma. The superficial masseter inserts on the mandible much as in *Neotoma*; the slip, which is reflected to the medial side and inserts below the base of the incisor, is possibly more prominent than in *Neotoma*. A considerably greater proportion of this muscle inserts on the posterior part of the deep lateral masseter than in *Neotoma*.

#### M. masseter lateralis profundus, pars anterior

Originates from the zygomatic plate over a wider area than in either *Microtus* or *Neotoma* and has none of its origin from the zygoma posterior to the posterior margin of the plate; however, part of its origin is from the aponeurosis of the deep lateral masseter behind the posterior limit of the zygomatic plate. Inserts on the lower masseteric crest much as in *Neotoma*. This muscle is clearly distinct from the medialis but its fibers are closely parallel to the posterior part of the lateralis and the two muscle parts are not easily separable.

#### M. masseter lateralis profundus, pars posterior

Originates from the lateral face of the jugal and inserts over a wide area on the lateral face of the angular process and on the tip of the process.

#### M. masseter medialis, pars anterior

Originates on the ventral and medial surface of the zygoma from the jugal back to the glenoid fossa. No part of this muscle was seen to originate from the orbital surface of the zygomatic plate. However, BRYANT (1945, p. 308) states that it does, and possibly the specimen here dissected is not typical of all squirrels. The muscle has several parts in *Citellus lateralis* and one slip inserts by a strong tendon on the masseteric tubercle of the mandible near the anterior termination of the lower masseteric crest. The two other parts both insert along the upper masseteric crest from  $M_1$  posteriad and along a zone near to but not on the anterior edge of the lateral surface of the ascending ramus. This position of insertion is markedly different than in *Microtus*, where

the insertion is parallel to but more ventral than the anterior edge of the ascending ramus.

#### M. masseter medialis, pars posterior

Originates beneath the squamosal root of the zygomatic arch just lateral to the glenoid fossa. Inserts in a broad area below the upper sigmoid notch and on the temporalis near the tip of the coronoid process. The insertion on the mandible is not nearly so well marked in bone structure as in either *Microtus* or *Neotoma*, possibly because of the position of the incisor base relative to the ascending ramus rather than to any functional difference in musculature.

#### M. temporalis

This muscle is not nearly so clearly subdivided as in either *Microtus* or *Neotoma*, although BRYANT (1945, p. 309) states that it is divisible into three parts. Both origin and insertion are similar to *Neotoma*.

#### M. pterygoideus, external and internal

Essentially as in *Neotoma*, the insertion of the external pterygoid is confined to a very small area just ventral to the mandibular condyle.

#### M. digastricus, anterior and posterior

This muscle (or muscles) is, of course, distinctly sciurumorphine with a long narrow tendon connecting the two bellies. The origin and insertions do not differ greatly from those of other rodents.

### EVALUATION AND CHARACTERIZATION OF THE ARVICOLINE MANDIBLE (Figures 4 and 5)

Those points of similarity between the mandibular structures of arvicoline and cricetine rodents which are shared with other groups of rodents here sampled are not considered significant but rather are assumed to be broad characters of the entire order. In order to determine whether other similarities and differences observed between arvicoline and cricetine rodents are of generic or subfamily importance, a series of osteologic specimens from each subfamily was examined. This series of specimens included the following forms; their subfamily allocation obviously reflects my opinions resulting from this study.

#### *Cricetinae*:

##### (Fossil forms)

- Cricetops dormitor* MATTHEW and GRANGER, Oligocene, Mongolia
- Cricetus runtonensis* (NEWTON), Pleistocene, Czechoslovakia
- Peromyscus pliogenicus* WILSON, middle Pliocene, U. S. A.
- Microtodon kowalskii* (KRETZOI), late Pliocene, Poland
- Baranomys longidens* (KOWALSKI), late Pliocene, Poland

## (Living forms)

*Mesocricetus auratus* WATERHOUSE  
*Cricetus cricetus* LINNAEUS  
*Orozomys palustris* (HARLAN)  
*Onychomys leucogaster* (WIED-NEUWIED)  
*Baiomys taylori* (THOMAS)  
*Reithrodontomys megalotis* (BAIRD)  
*Peromyscus californicus* (GAMBEL)  
     *crinitus* (MERRIAM)  
     *eremicus* (BAIRD)  
     *leucopus* (RAFINESQUE)  
     *maniculatus* (WAGNER)  
     *truei* (SHUFELDT)  
*Sigmodon hispidus* SAY and ORD  
*Neotoma albigula* HARTLEY  
     *fuscipes* BAIRD  
     *lepidota* THOMAS  
     *mexicana* BAIRD  
*Neotomodon altsoni* MERRIAM

*Arvicolinae:*

## (Fossil forms)

*Microscoptes disjunctus* (WILSON), middle Pliocene, U. S. A.  
*Promimomys minus* (SHOTWELL), middle Pliocene, U. S. A.  
*Promimomys insuliferus* (KOWALSKI), late Pliocene, Poland  
*Cseria* new species, middle or late Pliocene, U. S. A.  
*Cseria gracilis* KRETZOI, late Pliocene, Poland  
*Cseria proseki* (FEJFAR), late Pliocene, Czechoslovakia  
*Propliomys hungaricus* (KORMOS), late Pliocene, Poland  
*Ogmodontomys poaphagus* HIBBARD, late Pliocene, U. S. A.  
*Cosomys primus* WILSON, late Pliocene or early Pleistocene, U. S. A.  
*Pliophenacomys primaevus* HIBBARD, late Pliocene, U. S. A.  
*Pliopotamys minor* (WILSON), late Pliocene or early Pleistocene, U. S. A.  
*Mimomys pliocaenicus* MAJOR, early Pleistocene, Poland  
*Mimomys majori* HINTON, middle Pleistocene, Czechoslovakia  
*Mimomys savini* HINTON, middle Pleistocene, Czechoslovakia  
*Pliomys lenki* HELLER, middle Pleistocene, Czechoslovakia  
*Microtus arvalinus* HINTON, middle Pleistocene, Czechoslovakia  
*Microtus ratticepoides* HINTON, middle Pleistocene, Czechoslovakia  
*Pliomys episcopalis* MEHELY, middle Pleistocene, Czechoslovakia  
*Prolagurus pannonicus* KORMOS, middle Pleistocene, Czechoslovakia  
*Pitymys gregaloides* HINTON, middle Pleistocene, Czechoslovakia  
*Pitymys schmidtgeni* HELLER, middle Pleistocene, Czechoslovakia

## (Living forms)

*Lemmus trimucronatus* (RICHARDSON), living and fossil specimens  
*Dicrostonyx torquatus* (PALLAS), living and fossil specimens  
*Synaptomys borealis* (RICHARDSON)  
*Synaptomys cooperi* BAIRD, fossil specimen only  
*Clethrionomys glareolus* (SCHREBER)  
*Clethrionomys gapperi* (VIGORS), fossil specimen only  
*Clethrionomys rutilus* (PALLAS)



*Prometheomys schaposchnikovi* SATUNIN  
*Ondatra zibethicus* (LINNAEUS), living and fossil specimens  
*Arvicola terrestris* (LINNAEUS)  
*Neofiber alleni* TRUE  
*Pitymys pinetorum* (LECONTE)  
*Pitymus subterraneus* (de SÉLYS-LONGCHAMPS)  
*Microtus agrestis* (LINNAEUS)  
*Microtus arvalis* (PALLAS)  
*Microtus californicus* (PEALE)  
*Microtus gregalis* (PALLAS)  
*Microtus longicaudus* (MERRIAM)  
*Microtus miurus* OSGOOD  
*Microtus montanus* (PEALE)  
*Microtus nivalis* (MARTINS)  
*Microtus ochrogaster* (WAGNER)  
*Microtus oeconomus* (PALLAS)  
*Microtus pennsylvanicus* (ORD)  
*Microtus richardsoni* (DEKAY)  
*Microtus xanthognathus* (LEACH)  
*Lagurus lagurus* (PALLAS)  
*Lagurus curtatus* (COPE)

?*Cricetidae* (sensu SIMPSON, 1945) incertae sedis  
 (Living form)

*Ellobius talpinus* (PALLAS)

The most unusual aspect of the above tabulation of specimens examined is that I have removed *Ellobius* from the *Arvicolinae* in line with observations made in this study. Except for the cheek teeth, there are no arvicoline characters of either the skull or mandible. In fact, the extreme anteroposterior shortening of the skull behind the orbits, the lowness of the articular process and height of the coronoid process relative to the mandibular dentition, and the procumbency of the incisors all tend to give *Ellobius* a greater superficial resemblance to such geomyid rodents as *Geomys*. Taxonomically, the teeth are significant, of course, but even the teeth are hardly more arvicoline in appearance than are those of the cricetine *Neotoma*, and I feel that there is no valid reason to include *Ellobius* in the *Arvicolinae*. MATTHEY (1955) has also noted a lack of similarity to the *Arvicolinae* in the cytology of *Ellobius*. I have not attempted to place it in any other cricetid subfamily and, in fact, am not convinced that it belongs in the *Cricetidae* (sensu SIMPSON, 1945).

According to the criteria here considered, *Microtodon* and *Baranomys* belong in the *Cricetinae* and not the *Arvicolinae*, although their cheek teeth (especially those of *Baranomys*) are hardly separable from the most primitive known arvicoline, *Promimomys*.

The following mandibular characters appear to be diagnostic of the arvicoline rodents:

1. The anterior edge of the ascending ramus originates at or anterior to

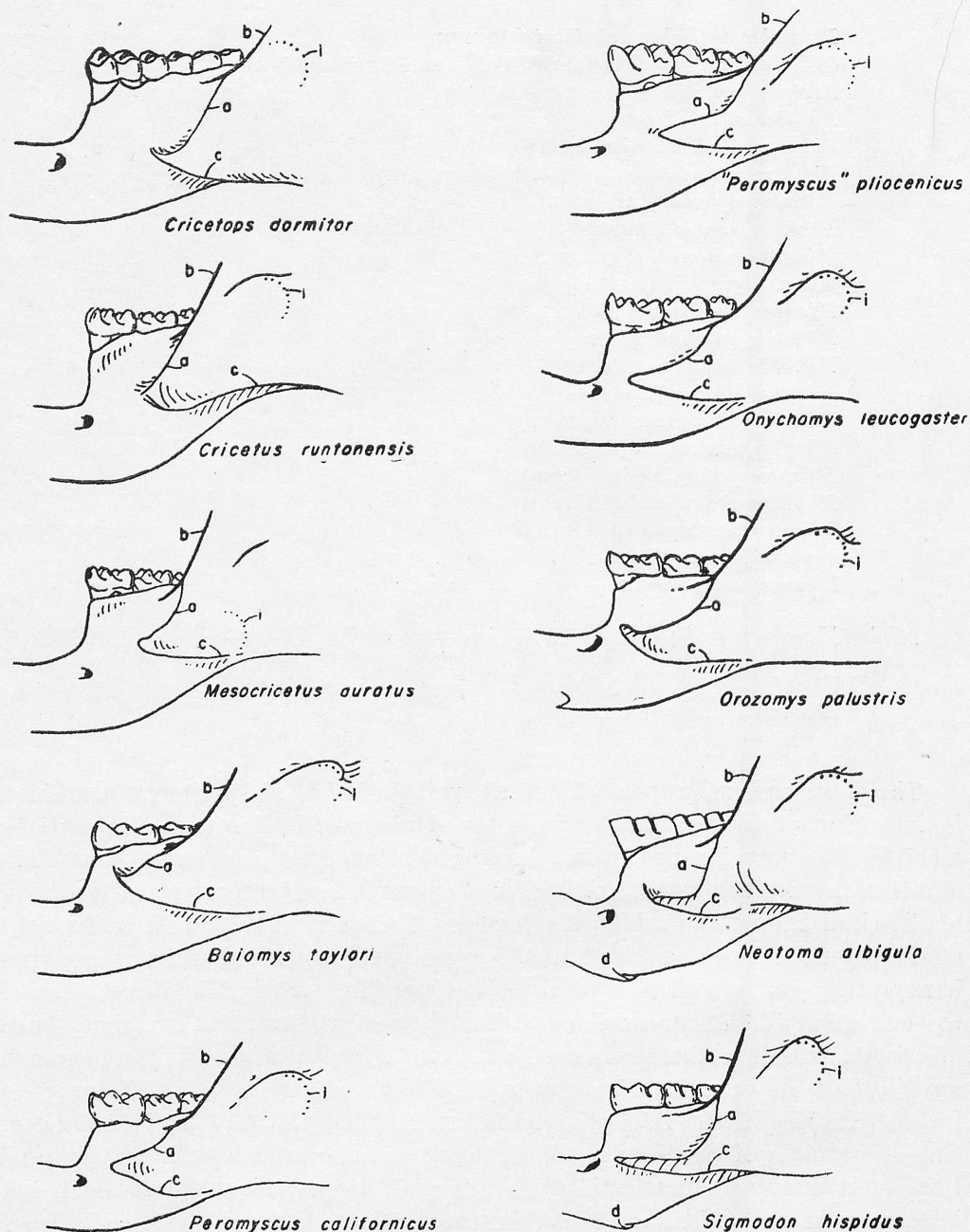


Fig. 4. Mandibular structures of selected cricetine rodents. Letter symbols: a — upper masseteric crest, b — anterior edge of the ascending ramus, c — lower masseteric crest, d — symphyseal eminence for the insertion of the digastric muscle, and i — position of the base of the incisor.

the posterior end of  $M_1$  and ascends steeply, obscuring all or part of  $M_2$  in labial aspect of the mandible.

2. The insertion for the *M. masseter medialis*, pars anterior, is a sharp

narrow groove parallel to, but placed posteroventrally from, the anterior edge of the ascending ramus. This groove is very characteristic and is referred to in the following pages as the "Arvicoline groove".

3. The lower masseteric crest is long, anteriorly placed, and very shelf-like.

4. The internal temporal fossa, in the form of a broad, shallow, elongate depression, separates  $M_2$  and  $M_3$  from the ascending ramus.

Most of these characters are the result of, or result in, a shortening and deepening of the arvicoline mandible, relative to the cricetine mandible, and the obvious effect is a strengthening of the bite.

The anterior position and steep anterior edge of the ascending ramus is a character of nearly all specimens examined, including the most primitive forms here included in the *Arvicolinae*. The single and prominent exception is in North American *Clethrionomys* (*C. rutilus* and *C. gapperi*) (fig. 5). In these species, the anterior edge of the ascending ramus originates at the posterior end of  $M_1$  but forms a low horizontal crest to a point opposite  $M_2$ .  $M_2$  and a small part of  $M_3$  are visible in lateral aspect of the mandible. This is not true of the Old World *C. glareolus*, in which the ascending ramus is typically arvicoline. A somewhat similar condition is found in *Synaptomys* (both *S. borealis* and *S. cooperi*) and, to judge from HINTON'S figure, in *Myopus*. In these lemmings, however, the ascending ramus, even though it begins to rise rather far back, rises so steeply that  $M_3$  is not visible in lateral aspect.

In the cricetine rodents, the anterior edge of the ascending ramus typically originates at or posterior to the posterior end of  $M_1$  and ascends gradually, leaving part or all of  $M_3$  visible in lateral aspect of the mandible. The specialization seen in arvicolines has the effect of moving the resultant of the force of the external temporal muscle anterior from the position in cricetines, thus lengthening the lever arm upon which it acts and strengthening the bite.

In most, but not all, arvicolines, the arvicoline groove meets the lower masseteric crest at a point well behind the anterior termination of the lower crest. In all cricetine examined (except *Microtodon*) there is no arvicoline groove on the ascending ramus. The anterior part of the medial masseter inserts only on the upper masseteric crest, which is approximately in line with the anterior edge of the ascending ramus. In addition, the upper masseteric crest meets the lower masseteric crest at their common anterior termination, marking the anterior extent of the masseteric fossa in unspecialized cricetines.

In many more specialized cricetines, particularly North American forms such as *Neotoma* and *Sigmodon*, an approach to the arvicoline structure is found. In these the upper masseteric crest departs from the anterior edge of the ascending ramus near its origin on the horizontal ramus and curves downward and forward to meet the lower masseteric crest behind its anterior termination. This situation, while paralleling the arvicoline structure, cannot be confused with it because of the lack of the arvicoline groove on the ascending ramus, indicating, in the cricetines, a much shorter line of insertion for the anterior



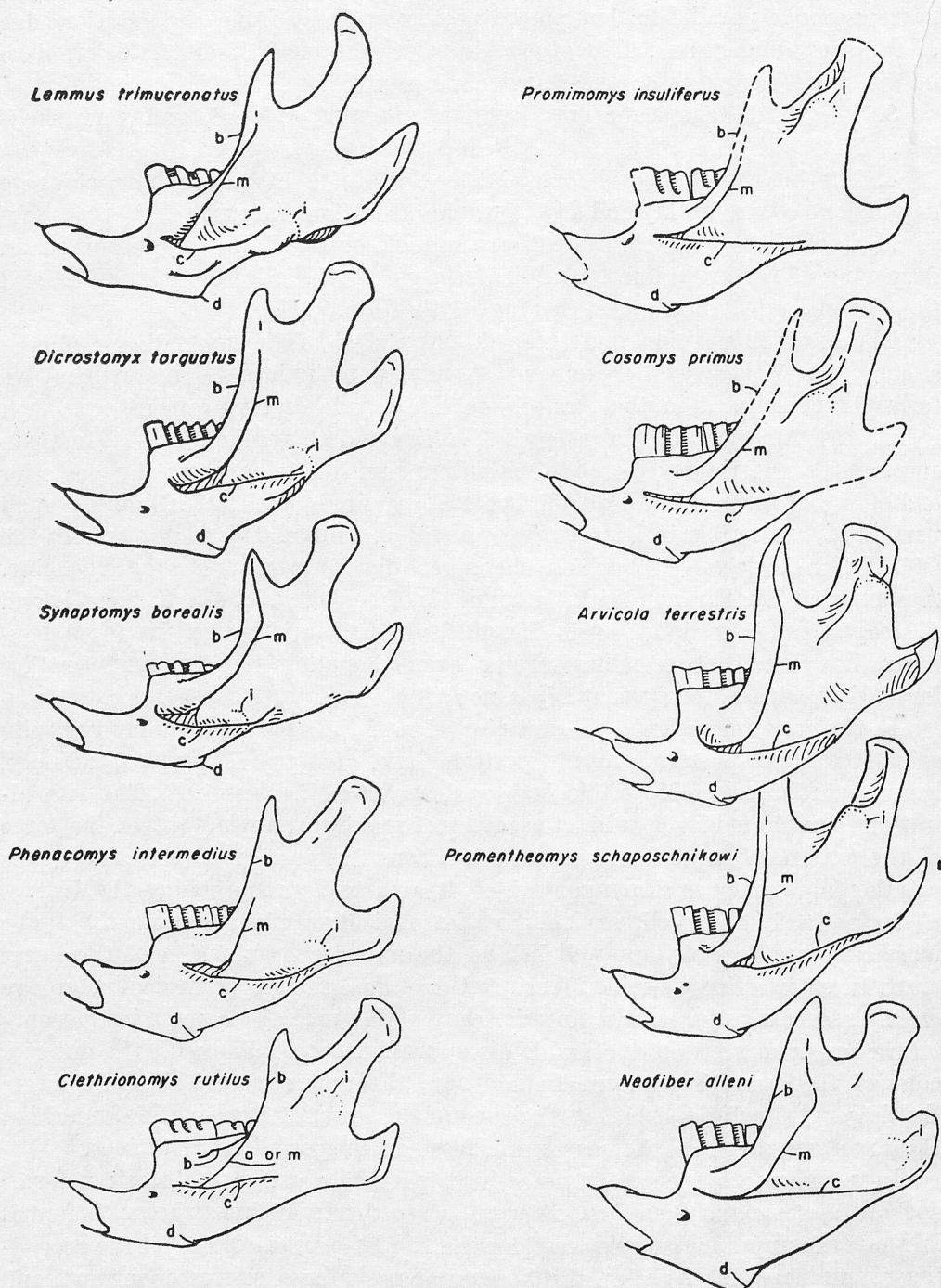


Fig. 5. Mandibular structures of selected arvicoline rodents. Letter symbols: a — upper masseteric crest, b — anterior edge of ascending ramus, c — lower masseteric crest, d — symphyseal eminence for the insertion of the digastric muscle, i — position of the base of the incisor, and m — arvicoline groove.

part of the medial masseter. The reverse is not always true. In some individuals of North American *Clethrionomys rutilus* (not seen in *C. gapperi*) the posterior position of the anterior edge of the ascending ramus has resulted in a coincidence of the arvicoline groove and the anterior edge of the ramus; the arvicoline groove is not in evidence, the anterior part of the medial masseter presumably inserting along the anterior edge of the ascending ramus beside the insertion of the temporalis. Other specimens of *C. rutilus* preserve the arvicoline groove close to, but distinct from, the anterior edge of the ascending ramus, indicating that the anterior part of the medial masseter has an enlarged insertion, as in other arvicolines, and is not limited to the area of the upper masseteric crest, as in cricetines.

The most cricetine-like insertion of the anterior part of the medial masseter in all genera here included in the *Arvicolinae* belongs to the middle Pliocene *Microtoscopes* of Asia and North America. In this genus there is a well developed upper masseteric crest which joins the lower masseteric crest only a short distance behind its anterior termination. This crest is in line with the anterior edge of the ascending ramus, there being no arvicoline groove. The mandibular structures reflecting the insertions of the masseter muscles exactly match those of the late Pliocene *Baranomys longidens* from Poland, but the insertions of the temporal muscle do not.

The shelf-like prominence of the lower masseteric crest on the arvicoline mandible is an obvious result of increasing strength of that part of masseter lateralis profundus, pars anterior, which inserts by a strong aponeurosis on the mandible. It obviously results in a stronger bite. Very few cricetines have the prominent development of the lower masseteric crest found in the arvicolines, but the development of the crest is variable in the arvicolines, being weakest, again, in North American species of *Clethrionomys*.

The union of the upper and lower masseteric crests posterior to their anterior termination in most arvicolines and in some specialized cricetines accentuates the shelf-like prominence of the lower crest, for anterior to this union the crest serves as the point of insertion of two aponeurotic sheets of both medial and deep lateral masseters. The prominence of the lower crest must therefore be judged posterior to this union of insertions.

Of the cricetine rodents examined, excepting the primitive *Cricetops*, the arvicoline-like *Microtodon*, and especially *Baranomys*, approach the *Arvicolinae* most closely in structure of the lower masseteric crest. *Baranomys* also approaches the arvicolines in the development of the internal temporal fossa. This fossa is the mandibular counterpart of the "post-orbital crest or process of the squamosal which is so characteristic of the subfamily" as described by HINTON, (1926, p. 25) and indeed is equally characteristic. Its prominence is due to the fact that that part of the internal temporal muscle which inserts on the anterior-medial side of the ascending ramus in cricetines inserts entirely in the depression of the mandible between the cheek teeth and the ascending ramus in arvicolines, thus strengthening the bite.

Other differences in mandibular muscle are not clearly expressed in the bone structure or do not seem consistent enough to be diagnostic. The loss of the reflected anterior slip of the superficial masseter, which inserts below the incisor on the medial side of the angular process in other rodents dissected, may simply be a result of the hypsodonty of  $M_3$ . In *Microtus* the base of  $M_3$  is enclosed in a bulbous capsule which would clearly obstruct the course of this slip where it bends beneath the mandible and leads dorsoposteriorly towards its insertion. Whether the slip is present in less hypsodont arvicolines as *Ondatra* or *Clethrionomys* is unknown, but the general form of the mandible in this area in these less hypsodont forms suggests that the slip could be present.

Propalinal mastication, which would appear to be universally used in the arvicolines, seems largely to be effected by a strengthening of the pterygoid and hystricomorphine digastric muscles. The posterior extension of the anterior part of the M. masseter lateralis profundus must also aid in propalination. Unfortunately these muscular changes have resulted in little recognizable change in mandibular structure except for a relative increase in the prominence of the symphyseal eminence, a feature of most propalinating rodents as *Castor* and *Neotoma*.

The four arvicoline characters listed above are all specializations which result in greater biting strength while either gnawing or masticating. The first three, all relating to muscular insertions on the buccal side of the mandible, appear to be interrelated and to form a single pattern of specialization. This pattern forms an essentially continuous morphologic gradation in known rodents from the primitive pattern as exhibited by *Cricetops*, through the intermediate cricetine pattern, to the arvicolines.

In summary, this pattern of progressive increase in strength of bite consists of a continued concentration on the anterior parts of the masseter and temporal systems and of a continued shift of both origin and insertion of these systems anteriorly to improve the leverage of the bite. Relative to the position of the cheek teeth, the anterior edge of the ascending ramus (the most anterior insertional area of the temporalis) and the masseteric crest (the insertional areas of the anterior part of the masseter) move forward. The upper masseteric crest (the insertional area of anterior part of masseter medialis) moves forward and, in addition, downward to merge anteriorly with the lower crest so that both medial and lateral masseters apply their most anterior forces to a common insertional area which has maximum effectiveness in occlusal leverage.

#### PRIMITIVE ARVICOLINE AND ARVICOLINE-LIKE CRICETINE RODENTS

Over a decade ago KRETZOI (1955a) pointed out the similarities of some of the rodents here considered and emphasized their close relationship. In the same year (KRETZOI, 1955b) he placed *Baranomys* and *Microtodon* in the subfamily *Baranomyinae* of the family *Arvicolidae*. SULIMSKI (1964, p. 193) followed



this classification and placed the *Baranomyinae* in the *Microtidae* (= *Arvicolidae*). My classification essentially follows SIMPSON (1945, p. 86 and 206) because I believe it more clearly expresses the closer relationship of the arvicoline rodents to the *Cricetinae*, rather than to the murine rodents, and differs from that of KRETZOI in that the *Baranomyini* (see below) are most reasonably included in the *Cricetinae* when overall morphologic similarities are considered.

Family *Cricetidae* MURRAY, 1866

Subfamily *Cricetinae* MURRAY, 1866

Tribe *Baranomyini* KRETZOI, 1955b

Diagnosis. Mandibular structure basically cricetine but with enlargement of insertions of masseter muscles so that lower masseteric crest is somewhat prominent and upper masseteric crest shows some elongation; tendency to lower insertion of temporal muscles relative to occlusal surface present but no indication of anterior shift of these insertions on mandible;  $M_3$  visible in labial aspect of mandible; lower incisor long, passes under  $M_3$ , and originates in capsule in ascending ramus; cheek teeth with moderate development of hypsodont prismatic structure and in arvicoline pattern but anterior cingulum or cap of  $M_1$  and hypoconal complex of  $M_3$  without arvicoline specializations; lingual valleys of lower molars and anterior labial valleys of upper molars rounded and not angular at their apices; lower cheek teeth 2-rooted, upper cheek teeth 3-rooted ( $M^1$  occasionally 4-rooted).

Forms included. *Microtodon atavus* (SCHLOSSER), *Microtodon kowalskii* (KRETZOI), *Baranomys loczyi* KORMOS, *Baranomys longidens* (KOWALSKI), and *Baranomys langenhani* HELLER.

Genus *Microtodon* MILLER, 1927

Genotype. *Sigmodon atavus* SCHLOSSER, 1924 (not seen).

Diagnosis. Anterior cingulum or cap of  $M_1$  small with pronounced postero-labial crest; metaconid of  $M_1$  not triangular to slightly triangular;  $M^3$  lacking arvicoline posterior cingulum;  $M_3$  not known; weak arvicoline groove present.

*Microtodon kowalskii* (KRETZOI, 1962)

(Figure 6)

*Baranomys loczyi* KORMOS. KOWALSKI, 1956, Acta Palaeont. Polonica, v. 1, no. 4, p. 379.  
*Microtodon loczyi* (KORMOS). KOWALSKI, 1960, Acta Zool. Cracoviensia, v. 5, no. 2, p. 457.  
*Baranomys kowalskii* KRETZOI, 1962, Ann. Rept. Hungarian Geol. Institute of 1959, p. 356.  
*Microtodon* sp., possibly new. SULIMSKI, 1964, Acta Palaeont. Polonica, v. 9, no. 2, p. 196.  
*Microtodon loczyi* (KORMOS). KOWALSKI, 1964, Acta Theriologica, v. 7, no. 4, p. 78.

This species is known from the late Pliocene fissure-filling breccia at Podlesice, Poland. Judging from published illustrations of the genotype, *Microtodon atavus* (SCHLOSSER) from the middle Pliocene (Ertemte) of China, *M. ko-*

*walskii* has a larger and more arvicoline-like anterior cap on  $M^1$  and may be somewhat more hypsodont. There are no satisfactory illustrations of the mandible of *Microtodon atavus* published and its structure cannot be compared with that of *M. kowalskii*.

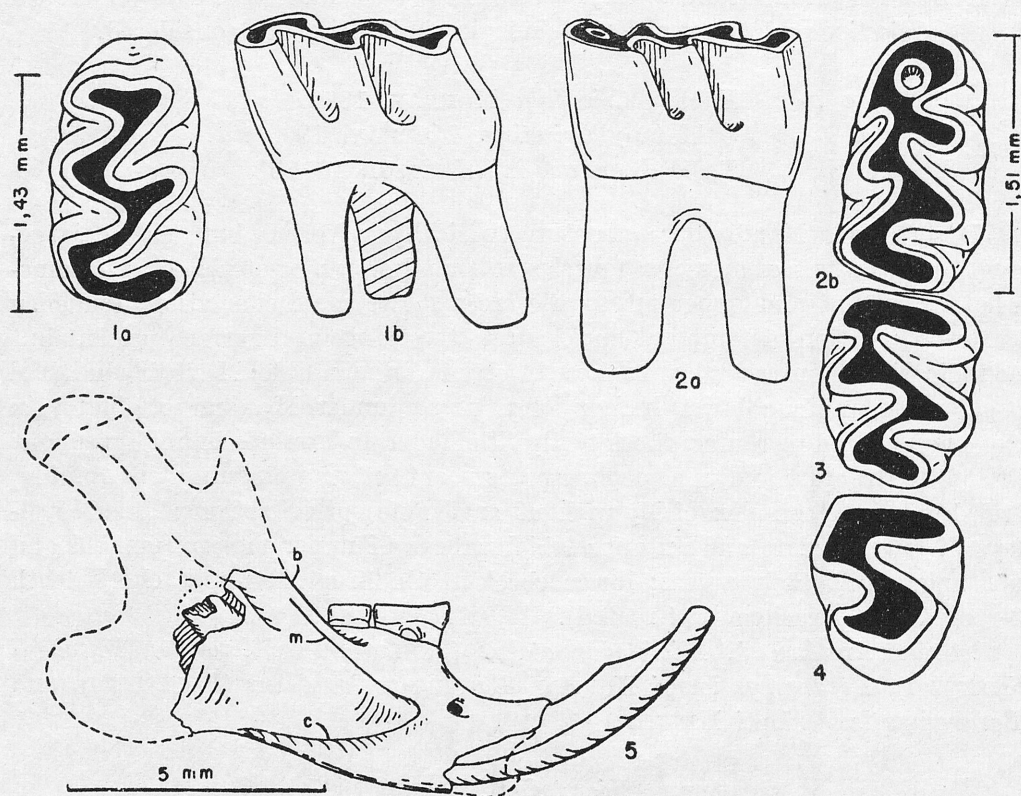


Fig. 6. *Microtodon kowalskii* (KRETZOR). 1. Left  $M^1$ , a — occlusal view, b — labial view. 2. Left  $M^1$ , a — labial view, b — occlusal view. 3. Left  $M^2$ , occlusal view. 4. Left  $M^2$ , occlusal view. 5. Right mandible; reconstruction hypothetical. Teeth and mandible drawn at different scales. USGS-M 6626 from Podlesice, Poland. Letter symbols: b — anterior edge of ascending ramus, c — lower masseteric crest, i — position of the base of the incisor, and m — arvicoline groove.

*Microtodon kowalskii* from Podlesice has a mandibular structure that appears somewhat less arvicoline than *Baranomys longidens*. The valley between the ascending ramus and the cheek teeth is approximately as wide and long as in *Baranomys* but is not as deep below the alveolar border and does not appear to be nearly as well defined as a fossa. It seems reasonable to infer that this area on the mandible was less significant to the insertion of the internal temporal muscle and that therefore much of the muscle must have inserted on the medial face of the ascending ramus as in other cricetine rodents. Similar cricetine features are seen in the masseteric fossa: the lower masseteric crest is less shelf-like than in *B. longidens* and the arvicolines; the upper masseteric crest is straight

and meets the lower crest at its anterior end without even a slight upward curve. The anterior edge of the ascending ramus is in about the same position as in *B. longidens* but here is found a rather remarkable feature — an arvicoline groove for the insertion of the anterior part of the medial masseter is found close to but clearly below and behind the anterior edge of the ascending ramus and persists to about the elevation of the alveolar border. From this, it is clear that the insertion of the anterior part of the medial masseter has enlarged and is approaching an arvicoline condition. It is possible, of course, that similar enlargement of the muscle insertion has taken place in *Baranomys longidens* but is not detectable in bone structure because the insertion has remained on the anterior edge of the ascending ramus. This aspect of the masseteric musculature of *Microtodon kowalskii* is more arvicoline-like than in any other cricetine examined. Only one mandible was available for study, and it is not known if the short arvicoline-groove is present on all specimens.

#### Genus *Baranomys* KORMOS, 1933

Genotype. *Baranomys loczyi* KORMOS, 1933 (not seen).

Diagnosis. Anterior cingulum or cap of  $M_1$  larger than in *Microtodon* and comparable to *Promimomys* but retains prominent posterolabial crest; metaconid of  $M_1$  triangular;  $M_3$  with arvicoline posterior cingulum;  $M^3$  with hypoconal complex often separated from anterior part of tooth; no arvicoline groove but lower masseteric crest fairly prominent.

#### *Baranomys longidens* (KOWALSKI, 1960)

(Figure 7)

*Microtodon longidens* KOWALSKI, 1960, Acta Zool. Cracoviensia, v. 7, no. 11, p. 453.

*Baranomys loczyi* KORMOS (= *Microtodon longidens* KOWALSKI). KRETZOI, 1962, Ann. Rept. Hungarian Geol. Institute of 1959, p. 356.

*Baranomys longidens* (KOWALSKI). SULIMSKI, 1964, Acta Palaeont. Polonica, v. 9, no. 2, p. 193.

*Microtodon longidens* KOWALSKI. KOWALSKI, 1964, Acta Theriologica, v. 7, no. 4, p. 78.

This species is known from the late Pliocene karst-filling bone breccia at Węże I near Działoszyn, Poland. Some uncertainty of the generic assignment exists primarily because of the uncertainty of the diagnosis of *Microtodon atavus* (SCHLOSSER) from the middle Pliocene deposits at Ertemte, China. SULIMSKI (1964, p. 196) has pointed out that the structure of  $M_3$  and of the cap of  $M_1$  of the Węże specimens is similar to that of specimens of *Baranomys loczyi* from Csarnóta 2 in Hungary and different from illustrations of *Microtodon atavus* (SCHLOSSER, 1924, pl. III, fig. 36; SCHAUB, 1934, pl. 1, figs. 16, 17). He has also pointed out that the specimens from the late Pliocene deposits of Podlesice, Poland, do not show this difference and should be referred to *Microtodon*.



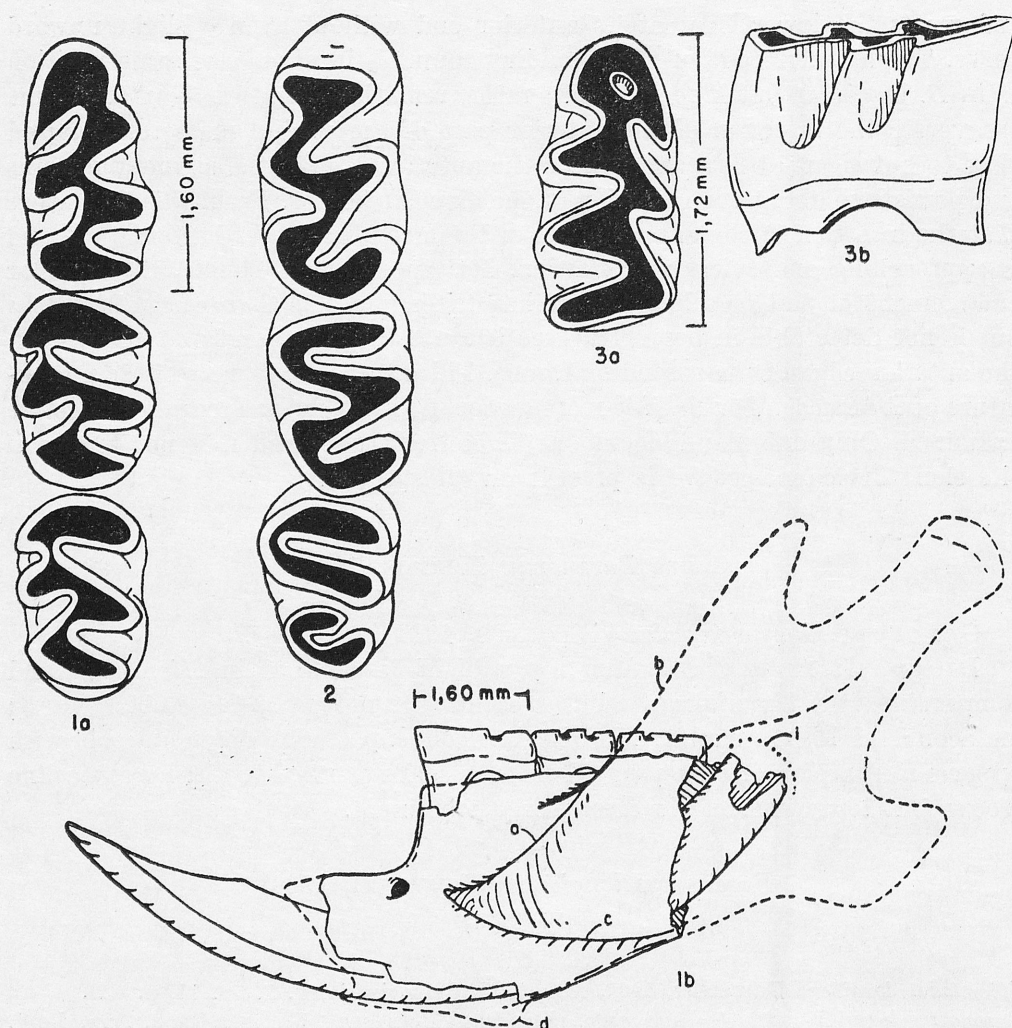


Fig. 7. *Baranomys longidens* (KOWALSKI). 1. Left mandible and dentition, a — occlusal view of dentition, b — lateral view of mandible; reconstruction based upon SULIMSKI (1964, pl. VIII). 2. Occlusal view of left upper dentition drawn from SULIMSKI (1964, pl. VIII). 3. Less worn right  $M_1$ , a — occlusal view, b — labial view. Teeth and mandible drawn at different scales; 1 and 3 are USGS-M 6625 from Weże, Poland. Letter symbols: a — upper masseteric crest, b — anterior edge of ascending ramus, c — lower masseteric crest, d — symphyseal eminence for the insertion of the digastric muscle, and i — position of the base of the incisor.

*Baranomys longidens* from Weże has a mandibular structure intermediate between that typical of the *Cricetinae* and that typical of the *Arvicolinae*. The internal temporal fossa of the mandible is quite long and broad and extends nearly as far forward as the center of  $M_2$ ; this suggest that *Baranomys* was well on its way toward the arvicoline specialization of having all of its internal temporal muscle insert below the occlusal surface of the cheek teeth, rather

than partly on the medial side of the ascending ramus as is seen in cricetine rodents. In addition, the lower masseteric crest is long, strong, and shelf-like and appears to be better developed than in any cricetine observed. However, the upper masseteric crest is a strong, straight ridge in line with the anterior edge of the ascending ramus; it meets the lower crest only at their anterior termination below  $M_1$ , and curves slightly upward just before the meeting point, thus approaching the morphologic stage in which upper and lower crests merge; these crests outline a strong masseteric fossa. In addition, the anterior edge of the ascending ramus originates behind  $M_1$ , approximately opposite the middle of  $M_2$ , and ascends gradually in cricetine fashion, obscuring only part of  $M_3$  in labial aspect of the mandible. There is no arvicoline groove. KOWALSKI (1960, p. 454) notes that the overall appearance of the skull seems more cricetine than arvicoline and classifies the species accordingly. SULIMSKI (1964, p. 195) notes that there is considerable variation in jaw structure, including the position of the anterior edge of the ascending ramus relative to  $M_2$  and  $M_3$  and the anterior termination of the masseteric crests in relation to  $M_1$ . He also notes two distinct groups according to the structure of the teeth. It would seem that two baranomyine species or genera could be represented at Weże. I have only one mandible for study and therefore cannot evaluate the possibility.

The teeth of *Baranomys longidens* have been thoroughly described by SULIMSKI (1964) and KOWALSKI (1960 and 1964). They are very similar to those of both *Microtodon* (Cricetinae) and *Promimomys* (Arvicolinae) and appear to be intermediate between these in both morphology and size. As compared to *Promimomys*, those dental characters of *Baranomys* which are cricetine in nature include:

1. Greater posterior extension of the labial crest of the anterior cingulum of  $M_1$ .
2. More rounded lateral terminations of the lower lingual and upper labial angles.
3. Less hypsodonty, although only slightly less.
4. Greater size of the enamel islet in the cap of  $M_1$  in at least some specimens; this is not the same enamel islet of more typical arvicolines which is formed by pinching off the anterior labial valley, but rather a remnant of the cricetine islet formed by the anterior bifurcation of the anterior cingulum.

These same criteria could be cited to point out the greater cricetine nature of *Microtodon kowalskii* in comparison to *Baranomys longidens* with the addition of the characteristic lack of the arvicoline posterior cingulum on the  $M_3$  of *Microtodon*. *Microtodon*, *Baranomys*, and *Promimomys* have identical root patterns of the cheek teeth: two roots on the lower teeth and three roots on the upper teeth; the  $M^1$  has a large anterior root and smaller lingual middle and central posterior roots (although SULIMSKI [1964, p. 194] notes that a few specimens of *Baranomys longidens* have four roots); the  $M^2$  and  $M^3$  have one posterior and two anterior roots. I have seen no specimen of these genera that have four roots on  $M^2$ , as is often found in *Microtoscopes*.

Subfamily *Arvicolinae* GRAY, 1821  
 Tribe *MicrotoscOPTINI* KRETZOI, 1955b  
 Genus *MicrotoscOPTES* SCHAUB, 1934

Genotype. *MicrotoscOPTES praetermissus* SCHAUB, 1934 (not seen).

*MicrotoscOPTES disjunctus* (WILSON, 1937)

(Figure 8)

*Gomodontomys disjunctus* WILSON, 1937, Carnegie Inst. Washington, Contr. Paleontology, Publ. 487 (1938), no. 1, p. 9.

*MicrotoscOPTES disjunctus* (WILSON), HIBBARD, 1959, Michigan Acad. Sci., Arts, Letters, Papers, v. 44, p. 6.

This species is known from lacustrine deposits of Oregon, Idaho, and Wyoming in the U. S. A. It is slightly larger than the genotypic and only other species, *M. praetermissus*, from China. No upper teeth are known of the species from China as the tooth SCHAUB (1934, p. 38, pl. 1, fig. 14) referred to as an  $M^1$  is an  $M_3$ , as indicated by the fact that the union of the primis is labial to the midline of the tooth (rather than on the midline as in upper teeth), by the presence of only two roots, and by the orientation of the occlusal surface relative to that of the roots.

The teeth of *MicroscOPTES* are unique among the arvicolines, as discussed by SCHAUB (1934, p. 38—39), STEHLIN and SCHAUB (1951, p. 340), and HIBBARD (1959, p. 8). The lower incisor passes beneath the anterior root and labial to the posterior root of  $M_3$ . The cheek teeth seem to be arvicoline in the elaboration and duplication of prisms in the anterior cap of  $M_1$ , by the structure of  $M^3$ , and by the hypsodonty of the teeth. On the other hand, the enamel pattern of the cheek teeth cannot really be compared with any known arvicoline, and about half of the known specimens of  $M^2$  of *M. disjunctus* have four roots, a situation unknown in any arvicoline or arvicoline-like cricetine. Although there are three roots on  $M^1$ , they are arranged differently than in other arvicolines.

The structure of the mandible of *MicrotoscOPTES* is as unique as its dentition. The masseteric insertions are essentially as in *Baranomys longidens*. The upper masseteric crest is straight, in line with the anterior edge of the ascending ramus, and meets the lower crest just behind its anterior termination. The upper crest curves slightly upward as it meets the lower crest. The lower masseteric crest is quite prominent and shelf-like. There is no arvicoline groove. The masseteric musculature of *MicrotoscOPTES* would thus appear to be like that of some arvicoline-like cricetines. However, the structure of the temporal muscles appears to be extremely arvicoline. The fossa for the insertion of the internal temporal muscle is very well developed and it seems very unlikely that any part of this muscle inserted on the medial side of the ascending ramus. In addition, the anterior edge of the ascending ramus is very far forward, ori-



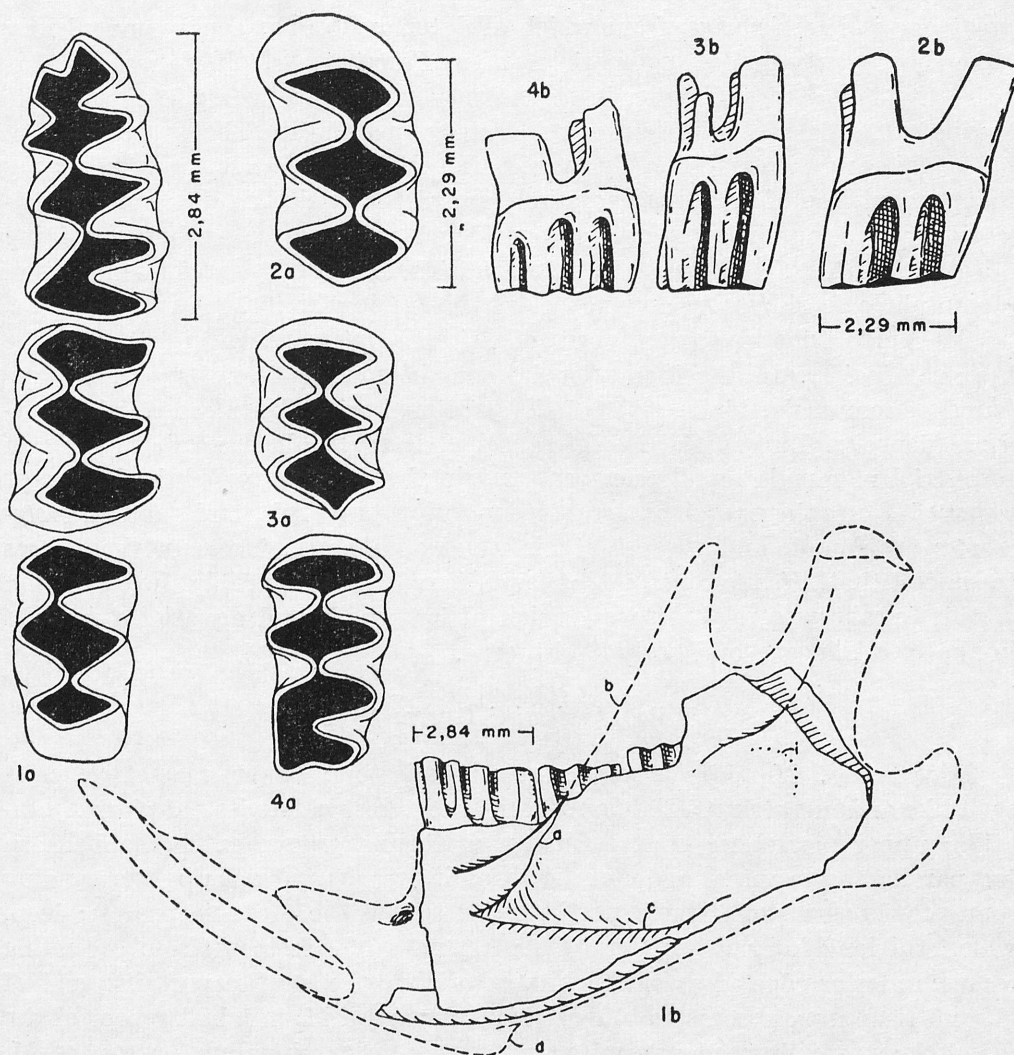


Fig. 8. *Microtoscoptes disjunctus* (WILSON). 1. Left mandible and dentition, USNM 23719; a — occlusal view of dentition, b — lateral view of mandible; reconstruction based upon HIBBARD (1959, fig. 1) and USGS-M 6329. 2. Right  $M^1$ , USNM 23720, a — occlusal view, b — lingual view. 3. Right  $M^2$ , USNM 23721, a — occlusal view, b — lingual view. 4. Right  $M^3$ , USNM 23722, a — occlusal view, b — lingual view. Occlusal views, lingual views, and mandible drawn at different scales. Rome local fauna, Oregon, U.S.A. About half of the known  $M^3$  have a fourth root at the posterointernal corner as shown in 3b. Letter symbols: a — upper masseteric crest, b — anterior edge of ascending ramus, c — lower masseteric crest, d — symphyseal eminence for insertion of the digastric muscle, and i — position of the base of the incisor.

ginating on the horizontal ramus at the back of  $M_1$  and rising quite steeply so that only a small part of  $M_2$  is visible in lateral aspect of the mandible.

A final point to be made is that *Microtoscoptes* is known from the middle Pliocene of North America and China and that the only other arvicoline of this

great age is *Promimomys*, from which all later arvicolines could conveniently have been derived. By comparison with *Promimomys*, *Microtoscopes* has twice the dental specialization in hypsodonty and enamel complications, while having half of the specializations in masticatory musculature. The total characters of the genus now known strongly suggest that *Microtoscopes* represents an early independent line of cricetine evolution toward the arvicoline grade of specialization, precocious in some aspects considered to be arvicoline but remaining cricetine in others. Its inclusion in the *Arvicolinae* is best considered an indication of morphologic similarity and not of phylogenetic affinity.

All North American occurrences of *Microtoscopes* are associated with the beaver *Dipoides*. In the Rome local fauna of southeastern Oregon, a large fauna of mammals, birds, and fish is associated with *Microtoscopes* in near-shore deposits. But as the fossiliferous bed is traced basinward, remains of terrestrial mammals rapidly decrease and in those exposures of the bed most removed from the marginal area of deposition only fish, bird, and *Microtoscopes* are found, and these in their usual abundance. The situation seems to suggest that *Microtoscopes* was an aquatic rodent and possibly the extinction of this lineage was related to evolution of better adapted aquatic arvicolines in the late Pliocene and early Pleistocene.

#### Tribe *Arvicolini* GRAY, 1821

**Diagnosis.** Mandibular structure not cricetine; lower masseteric crest shelf-like and merges with the upper masseteric crest before its anterior termination; upper masseteric crest forms an arvicoline groove extending beneath but parallel to the anterior edge of the ascending ramus and well up the ascending ramus to the superior sigmoid notch, or farther on the coronoid process; deep, wide, and long internal temporal fossa separates cheek teeth from ascending ramus; anterior edge of ascending ramus originates near the posterior end of  $M_1$  and rises steeply so as to obscure  $M_3$  and part of  $M_2$  in labial aspect of the mandible; teeth hypsodont and prismatic; anterior cingulum or cap of  $M_1$  large and showing varying degrees of complication; hypoconal complex of  $M^3$  connected to anterior part of tooth and showing varying degrees of complication; lingual valleys of lower molars angular and tending to curve forward at their apices; anterior labial valleys of upper molars angular and tending to curve backward at their apices; lower cheek teeth two-rooted to rootless; upper cheek teeth three- to two-rooted to rootless; lower incisor long, passing below cheek teeth and originating in a capsule within the ascending ramus in nearly all forms.

#### Genus *Promimomys* KRETZOI, 1955a

**Genotype.** *Promimomys cor* KRETZOI, 1955a (not seen).

**Diagnosis.** Anterior cingulum or cap of  $M_1$  large but uncomplicated, cricetine enamel islet present and persists through much of the tooth wear;

lingual valleys of lower teeth rounded to slightly angular with no tendency to curve forward at their apices; anterior labial valleys of upper teeth rounded to slightly angular with no tendency to curve backward at their apices; hypoconal complex of  $M^3$  simple and in some individuals separated from the anterior part of the tooth until tooth is very worn; all upper teeth three-rooted; teeth without cement; hypsodonty minimum.

*Promimomys mimus* (SHOTWELL, 1956)

(Figures 9 and 10)

*Prosimys mimus* SHOTWELL, 1956, Geol. Soc. America Bull., v. 67, no. 6, p. 732.

*Prosimys mimus* SHOTWELL. KOWALSKI, 1960, Acta Zool. Cracoviensia, v. 5, no. 5, p. 188.

*Microdon mimus* (SHOTWELL). KOWALSKI, 1960, Acta Zool. Cracoviensia, v. 5, no. 11, p. 454.

*Prosimys mimus* SHOTWELL. SULIMSKI, 1964, Acta Palaeont. Polonica, v. 9, no. 2, p. 188.

*Prosimys mimus* SHOTWELL. FEJFAR, 1964, Ustredniho ustavu geol., Rozpravy, no 30, p. 49.

This species is known from two middle Pliocene localities in Oregon, U. S. A.: McKay local fauna in Umatilla County (SHOTWELL, 1956), and the Christmas Valley local fauna in Lake County. Other species of *Promimomys* are *P. cor* KRETZOI, *P. moldavicus* (KORMOS, 1934), and *P. insuliferus* (KOWALSKI, 1958) all from the late Pliocene of central Europe.

*Promimomys cor* is based upon a fragment of a mandible with a well worn  $M_1$ . Because of this, it is difficult to diagnose this species. Aside from age and geography, *P. cor* does not appear to differ significantly from *P. mimus*. KRETZOI (1955a, p. 91) gives the length of  $M_1$  as 2.9 mm, which appears to be considerably larger than the dimension of 1.9 mm given by SHOTWELL (1956, p. 733) for *P. mimus*. However, SHOTWELL's two specimens of  $M_1$  appear to be either very small individuals or to represent a population of small individuals. Forty-nine  $M_1$ 's from the Christmas Valley local fauna (290 kilometers south southwest of McKay) average about 2.5 mm in length of  $M_1$ , with a range of 2.14—2.97 mm. The enamel pattern of the single  $M_1$  of *P. cor* appears identical to that of *P. mimus* except that *P. cor* has a somewhat larger anterior cingulum, suggesting a more progressive species and consistent with its lesser antiquity.

*Promimomys moldavicus* appears to be of the same approximate size; KORMOS (1934, p. 199) cites a range in length of  $M_1$  from 1.8—2.7 mm. KRETZOI (1955a, p. 91) states that *P. moldavicus* shows the beginning of the complication of the anterior cap of  $M_1$  and of the greater hypsodonty that characterize, with further development, the genus *Cseria* and, with still further development of complication of the cap of  $M_1$  and hypsodonty and with the addition of cement to the teeth, the genus *Mimomys*.

*Promimomys insuliferus* is the only European species I have been able to examine. It appears to have slightly greater complexity of the anterior cap of  $M_1$  than *P. mimus* and lingual angles are narrower and more sharply cornered at their apices. It does not appear to have significantly greater hypsodonty and is well within the size range of *P. mimus*; KOWALSKI (1956, p. 376) gives the



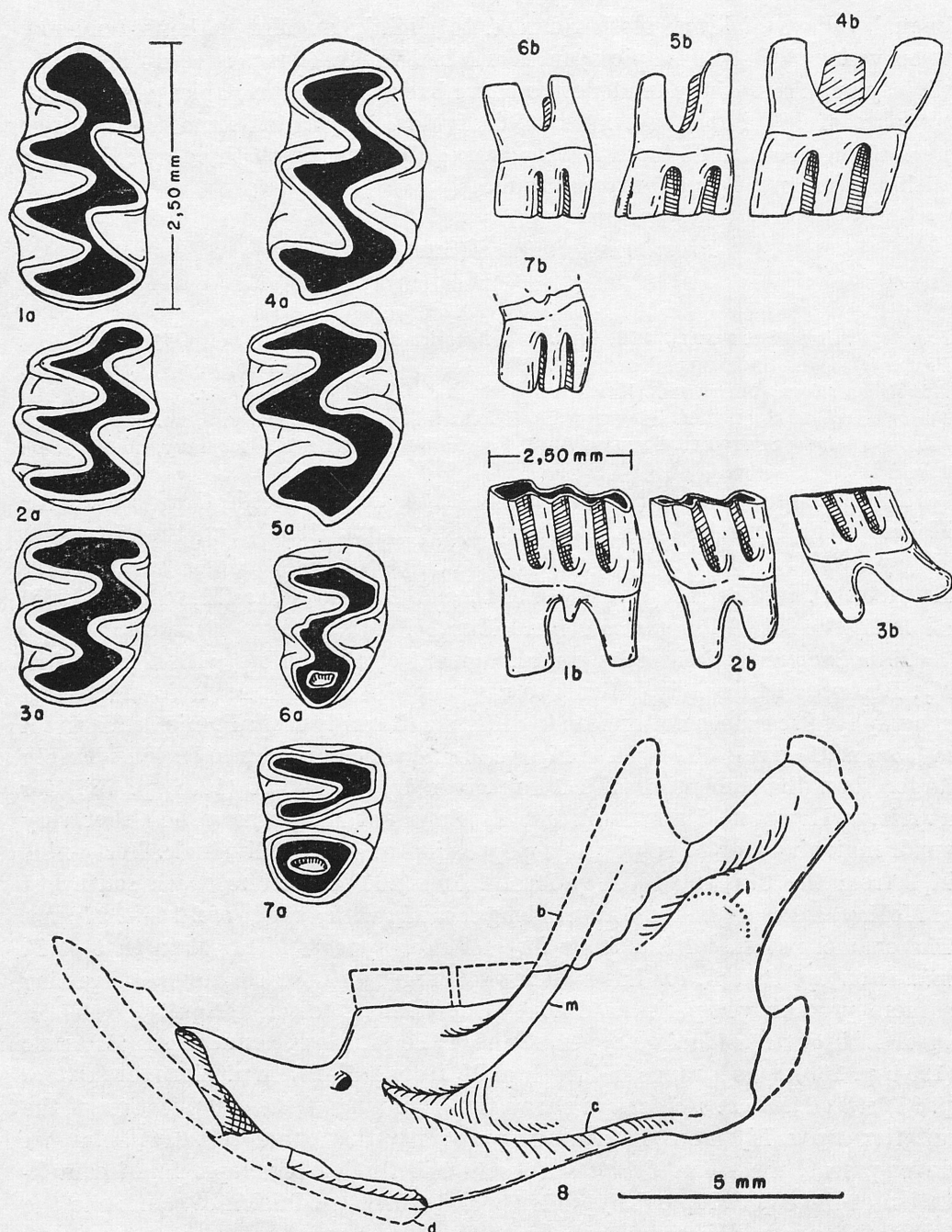


Fig. 9. *Promimomys mimus* (SHOTWELL). 1. Right M<sub>1</sub>, USNM 23712, a — occlusal view, b — lingual view. 2. Right M<sub>2</sub>, USNM 23713, a — occlusal view, b — lingual view. 3. Right M<sub>3</sub>, USNM 23714, a — occlusal view, b — lingual view. 4. Right M<sup>1</sup>, USNM 23715, a — occlusal view, b — labial view. 5. Right M<sup>2</sup>, USNM 23716, a — occlusal view, b — labial view. 6. Right M<sup>3</sup> with hypoconal complex attached to trigon, USNM 23717, a — occlusal view, b — labial view. 7. Right M<sup>3</sup> with hypoconal complex detached from trigon, USNM 23718, a — occlusal

length of two  $M_1$ 's as 2.5 mm and 2.4 mm. KRETZOI (1959, p. 242), while noting that *P. insuliferus* is a true arvicoline intermediate in structure between other arvicolines and *Baranomys*, removes the species from *Promimomys* and places it in a new genus, *Polonomys*, a genus less advanced toward *Cseria* than *Promimomys* as represented by *P. moldavicus*. KRETZOI's concept of morphologic succession is that which I believe most reasonable but he expresses it in generic differences, whereas I feel the differences are more reasonably specific. Thus I would call the morphologic succession *Promimomys mimus* — *P. insuliferus* — *P. moldavicus* whereas KRETZOI would refer to the same succession as *Proso-mys mimus* — *Polonomys insuliferus* — *Promimomys moldavicus*.

The mandible of *Promimomys* is clearly arvicoline and not at all like *Baranomys*. The lower masseteric crest is prominent and long; it extends forward to beneath the anterior root of  $M_1$ . The upper masseteric crest joins the lower just ahead of the posterior root and extends dorsally into a well defined arvicoline groove distinctly posterior to the anterior edge of the ascending ramus. The ascending ramus originates on the horizontal ramus opposite the posterior root of  $M_1$  and rises steeply, obscuring half of  $M_2$  in labial aspect of the mandible. The internal temporal fossa is well developed between the ascending ramus and the cheek teeth alveoli. The symphyseal eminence for the insertion of the digastric muscle is moderately strong. In all respects the masticatory musculature must have been obviously arvicoline.

The teeth of *Promimomys*, in contrast to the very arvicoline-like structure of the mandible, are basically identical to those of *Baranomys* except for size, and differ conspicuously from the next most primitive arvicoline, *Cseria*. A few characters have been mentioned in the discussion of *Baranomys* which tend to make the teeth of *Promimomys* appear more arvicoline, but several characters of cricetine nature are present in its teeth which are lost in most other arvicoline rodents. These are:

1. Retention of the "Cricetine islet" of enamel in the anterior cap of  $M_1$ .
2. Failure of any lower lingual valleys to turn forward near their apices or of the upper anterior labial valleys to turn backward near their apices.
3. Lack of lingual and labial folds in the anterior cingulum complex or cap of  $M_1$ ; in other words, the inclusion in the anterior cap of all parts of the tooth in front of the protoconid and metaconid prisms.
4. Occasional separation of the hypocone complex from the anterior part of  $M^3$ .

view, b — labial view. 8. Left mandible, UO 26694; reconstruction based upon USGS-M 6426. Occlusal views, lateral views of teeth, and mandible drawn at different scales. Christmas Valley local fauna except mandible from McKay local fauna, Oregon, U. S. A. About 1 out of 10  $M_1$ 's from Christmas Valley have the small third root as shown in 1b; about 1 out of 8  $M^3$ 's from Christmas Valley have the hypoconal complex detached from the trigon as shown in 7a. Letter symbols: b — anterior edge of ascending ramus, c — lower masseteric crest, d — symphyseal eminence for insertion of digastric muscle, i — position of the base of the incisor, and m — arvicoline groove.

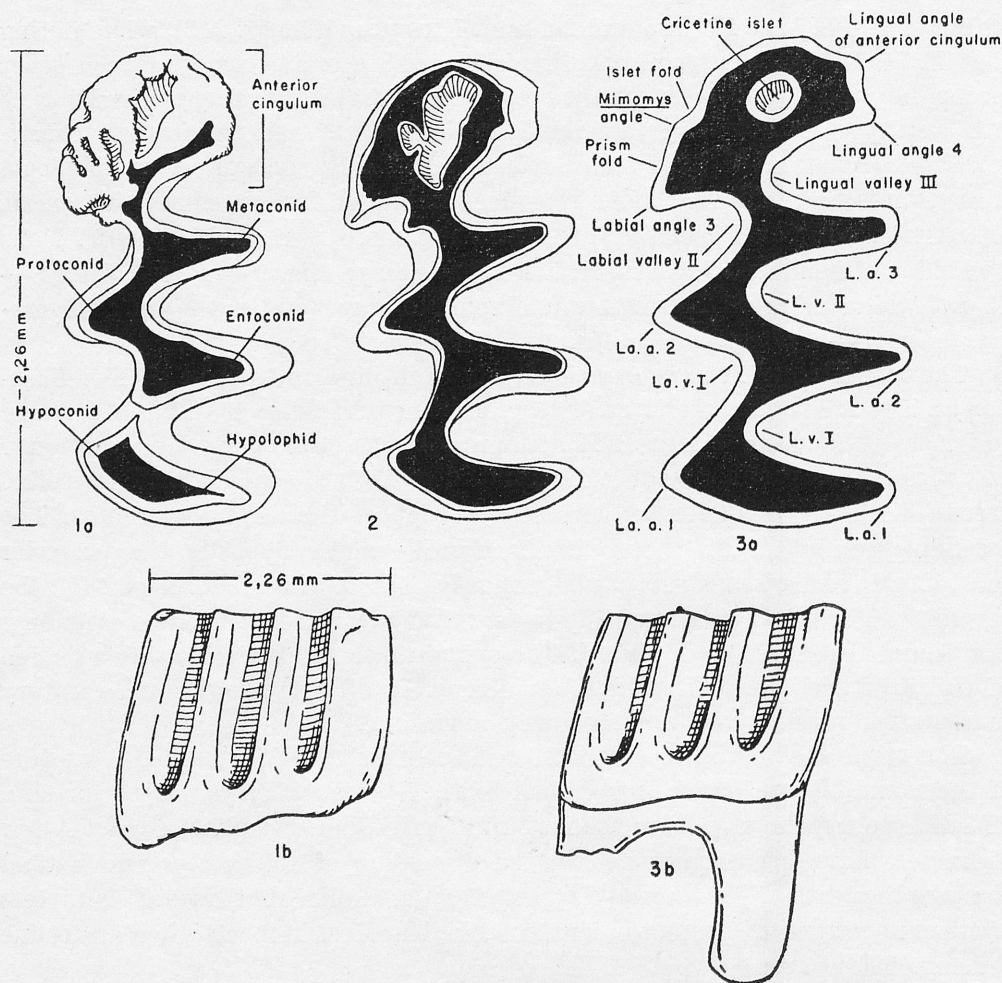


Fig. 10. Little-worn  $M_1$  of *Promimomys mimus* (SHOTWELL). 1. Very slight wear, USNM 23709, a — occlusal view, b — lingual view; terminology shown is conventional for cricetine rodents. 2. Slight wear, USNM 23710. 3. Moderate wear, USNM 23711, a — occlusal view, b — lingual view; terminology shown is conventional for arvicoline rodents. Occlusal views and lingual views drawn at different scales. Christmas Valley local fauna, Oregon, U. S. A.

The islet in the anterior cap of  $M_1$  is derived from the longitudinal emargination of the anterodorsal part of the enamel crown as shown by unworn teeth of *Prosomys mimus* (fig. 10). It is not derived from a pinching off of the lingual fold of the anterior cingulum complex as in most arvicolines having an enamel islet in the cap of the  $M_1$ . This islet appears to be a remnant of the valley splitting the anterior cingulum and of the anterolingual basin behind the anterior cingulum of many cricetine rodents. It persists in at least some arvicoline lineages as longitudinal irregularity in the unworn enamel crown of the anterior cap of  $M_1$  (see, for example, HINTON's fig. 58 of *Ondatra* and *Arvicola*),



but only in *Promimomys* and the arvicoline-like cricetines does it form a conspicuous islet of enamel throughout much of the wear of M<sup>1</sup>.

There are at present 17 M<sup>3</sup>'s of *Promimomys mimus* from the Christmas Valley local fauna. Two of these show a separation of the hypoconal complex from the anterior part of the tooth similar to that described by SULIMSKI (1964, p. 193 and pl. 7, fig. 1), as occurring, presumably, in all individuals of *Baranomys longidens*. In *P. mimus* this separation, if present, persists through most of the wear of the teeth (fig. 9).

Although lingual and labial folds are not present in the anterior cingulum complex of the M<sub>1</sub>, unworn and little-worn teeth show a great complexity of irregularities which obviously include incipient lingual and labial folds as well as other features more prominent in advanced arvicolines. In fact, there are few fossil forms which can so easily be seen to foreshadow such a great variety of more advanced mammals. These incipient arvicoline features are labeled on figure 10.

#### PROBABLE ORIGIN OF ARVICOLINE RODENTS

In summary, there is at present the following fossil record of primitive arvicoline or arvicoline-like cricetine rodents:

Late Pliocene:

*Promimomys*, central Europe

*Baranomys*, central Europe

*Microtodon*, central Europe

Middle Pliocene:

*Promimomys*, North America

*Microtoscopes*, North America and eastern Asia

*Microtodon*, eastern Asia

*Microtoscopes* appears to be arvicoline only by parallelism; if it is derived from a form common also to the lineage leading to true arvicolines, that form would possess both dental and mandibular specializations clearly of cricetine nature, unless the concept of the subfamily *Cricetinae* is greatly restricted, as it would have been if HINTON'S (1926, p. 120) suggestion that *Brachytarso-mys* should be an arvicoline had been accepted.

*Microtodon* and *Baranomys* are close to being arvicoline in both dental structure and mandibular specializations. *Baranomys* in particular has teeth that appear to be arvicoline, and, in the single mandible available for study, appears to be developing an arvicoline-like insertion for the internal temporal muscle. Although more cricetine in other respects, the single mandible of *Microtodon* available for study shows a rudimentary but definite arvicoline groove, indicating that the insertion for the anterior part of the medial masseter extended up the labial side of the ascending ramus, below its anterior edge, is a very typical arvicoline pattern of musculature.

Although it is difficult to judge from the material available, the rapidity with which modification of dental patterns seems to have taken place beyond the evolutionary stage of *Promimomys* casts some doubt upon the concept that a *Baranomys*-like rodent could develop a true arvicoline mandibular musculature without undergoing greater change in its dentition than is observable between *Baranomys* and *Promimomys*. Hence, it seems more likely that *Baranomys* represents, like *Microtoscopes*, a form developing parallel to the true arvicolines in dentition while conservatively retaining a basically cricetine jaw structure. In addition, it also appears more likely that *Microtodon* is morphologically closest to the lineage leading to arvicolines; present data are not sufficient to suggest whether or not the lack of the arvicoline posterior cingulum on the  $M^3$  of *Microtodon* is significant to this suggestion.

The fossil record is obviously incomplete. It does indicate, however, that evolution of *Promimomys* had taken place at least by middle Pliocene time and that arvicoline specializations had not progressed far enough by late Pliocene time to eliminate cricetine rodents with arvicoline specializations from the ecologic scene. The earliest occurrence of *Promimomys* in North America would suggest that this was the continent of origin for the *Arvicolinae*. However, there are no records of *Microtodon* or of other cricetine rodents with the necessary emphasis on the enlargement of the anterior cingulum of  $M_1$  and on hypsodonty in the early and middle Pliocene rocks of North America. Although first appearing in the late Pliocene of Europe, the arvicolines appeared as a flood with a great variety of genera and with both *Baranomys* and *Microtodon*. The arvicoline fauna remained conspicuously more varied in Europe than in North America until the latest Pleistocene time. Only in the early and middle Pliocene rocks of Asia is there record of a variety of cricetine rodents with marked tendencies toward hypsodonty and enlargement of the anterior cingulum of  $M_1$ .

It is not within the purpose of this paper, nor at present within the ability of the author, to review arvicoline genera of an evolutionary grade more advanced than *Promimomys*. However, it appears obvious that many arvicolines may easily be derived from *Promimomys* by accentuation of one or more of the features which separate the dentition of *Promimomys* from *Baranomys*. Among living arvicolines, there are extremes in the selectivity of the features accentuated: *Prometheomys*, which has hardly modified the dental pattern of *Promimomys*, has emphasized hypsodonty; *Clethrionomys*, which has only moderately increased tooth hypsodonty, has considerably modified its dental pattern. Between these extremes is a myriad of variations representing most modern and fossil arvicoline genera.

Reduction in the number of roots in the upper cheek teeth and the addition of cement to the cheek teeth are significant factors in the grade of evolution of arvicolines beyond that achieved by *Promimomys*; I would therefore, prefer to retain the separation of, for example, *Cseria* and *Ogmodontomys* from *Mimomys* and *Cosomys*, respectively. Unless evidence is produced to support the theory of secondary reduction in the length of the lower incisor, we must look elsewhere



than to *Promimomys* for the ancestor of *Phenacomys*, *Neofiber*, and the short-incisored lemmings, as we must for the ancestor of *Microtoscopes*. At present, the subfamily *Arvicolinae* appears to be decidedly polyphyletic, as indicated by KRETZOI in 1955 (1955b, p. 354).

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## STRESZCZENIE

Najdawniejszymi rodzajami norników (*Arvicolinae*) są *Microtoscopes* i *Promimomys*, znane od środkowego pliocenu zarówno ze Starego, jak i Nowego Świata. Budowa zębów u tych rodzajów jest pośrednia między typowymi nornikami i niektórymi gryzoniami z podrodziny chomików (*Cricetinae*). Dwa inne gryzonie, *Microtodon* i *Baranomys*, znane są ze środkowego i późnego pliocenu jedynie w Starym Świecie. Rodzaje te różni autorzy uważali bądź za spokrewnione z chomikami bądź z nornikami. W budowie zębów są podobne do *Promimomys*, choć bardziej od tego rodzaju zbliżone do chomików.

Dla uzyskania danych uzupełniających morfologię zębów, które pozwoliłyby ustalić pokrewieństwo z nornikami w obrębie *Cricetidae*, zbadano muskulaturę żuchwy i jej wpływ na morfologię tej kości. W grupie *musculus temporalis* najbardziej charakterystyczną cechą norników jest przesunięcie jej przyczepów na żuchwie ku przodowi i ku dołowi. Osteologicznym wyrazem tego jest przesunięcie ku przodowi ramienia wstępującego żuchwy i powstanie głębokiego dołu między tym ramieniem i zębami trzonowymi. W grupie *musculus masseter* norniki charakteryzuje rozszerzenie i obniżenie obszaru przyczepu na żuchwie, a także powiększenie struktur kostnych podtrzymujących przyczepy. Tak więc górna listwa mięśnia żwacza rozciąga się daleko na ramię wstępujące i przesunięta jest ku dołowi tworząc charakterystyczny dla norników rów na powierzchni laterałnej i obniża się tak, że łączy się z dolną listwą mięśnia żwacza poniżej zębów trzonowych. W ten sposób m. *masseter lateralis* i *medialis* działają na żuchwę łącznie.

*Baranomys* i *Microtodon*, choć mają niektóre z tych cech, są w zasadzie typowymi chomikami w budowie żuchwy, tak że zaliczono je tutaj do *Cricetinae*. *Microtoscopes* rozwinął niezwykle podobne do *Arvicolinae* przyczepy mięśni z grupy m. *temporalis*, ale typ przyczepu m. *masseter* pozostał u niego

taki, jak u *Cricetinae*. Uważamy, że należy on do *Arvicolinae* na zasadzie rozwoju równoległego, niezależnego od innych form tej podrodziny. *Promimomys* ma umięśnienie żuchwy typowe dla norników i uważamy go za przedstawiciela tej podrodziny, być może wyjściowego dla większości innych jej form, zarówno na podstawie morfologii zębów, jak i muskulatury żuchwy. Choć *Baranomys* bliższy jest *Promimomys* w budowie zębów, to jednak budowa żuchwy *Microtodon* wskazuje, że zbliża się on bardziej do *Cricetinae*, z których rozwinęły się właściwe *Arvicolinae*.

#### РЕЗЮМЕ

Древнейшими родами полевок (*Arvicolinae*) являются *Microtoscopes* и *Promimomys*, известные из отложений среднего плиоцена Старого и Нового Света. По особенностям строения зубов представители этих родов занимают промежуточное положение между типичными полевками и грызунами подсемейства хомяков (*Cricetinae*). Два других грызуна — *Microtodon* и *Baranomys* — известны из среднего и позднего плиоцена лишь Старого Света. Эти роды различными авторами сближались то с хомяками, то с полевками. По строению зубов они приближаются к *Promimomys*, хотя и стоят ближе этого рода к хомякам.

С целью получения дополнительных данных по морфологии зубного аппарата, на основании чего представилась бы возможность определить степень родства полевок с *Cricetinae*, исследовалась жевательная мускулатура и ее воздействие на особенности строения нижней челюсти. Наиболее характерным признаком полевок оказалось значительное смещение кпереди и книзу мест прикрепления к нижней челюсти группы височных мышц. Остеологически это выражается в наклоне вперед переднего края восходящей ветви нижней челюсти и наличием значительного углубления между восходящей ветвью и коренными зубами. Особенностью жевательной группы мышц полевок является расширение и понижение областей прикрепления этих мышц на нижней челюсти, а также усиление костных образований, укрепляющих места прикрепления. Таким образом получается, что верхний жевательный гребень идет далеко кверху по восходящей ветви, будучи смещен несколько книзу от ее переднего угла. Образуется так называемая „арвиколидная“ борозда на латеральной поверхности, а гребень идет книзу настолько далеко, что соединяется с нижним жевательным гребнем. По этой причине усилия, развиваемые латеральной и медиальной жевательными мышцами по отношению к нижней челюсти, складываются.

*Baranomys* и *Microtodon*, хотя и имеют некоторые из приведенных признаков, являются, в сущности, типичными хомяками по особенностям строения нижней челюсти, и в настоящей работе рассматриваются как таковые. *Microtoscopes* отличается чрезвычайно высоким сходством с полевками в типе прикрепления мышц височной группы, но по этим же признакам жевательной мускулатуры он

является типичным хомяком. Допускается его близость с *Arvicolinae*, как результат эволюционного параллелизма. *Promimomys* характеризуется типичным для *Arvicolinae* типом мандибулярной мускулатуры, что дает возможность не только уверенно относить его к этому подсемейству, но и считать предковой формой для большинства других полевок. Кроме жевательной мускулатуры, об этом свидетельствует также тип строения зубов. Хотя *Baranomys* более близок к *Promimomys* по строению зубов, строение нижней челюсти *Microtadon* указывает, что его следует, скорее, сближать с хомяками, от которых и эволюционировали настоящие *Arvicolinae*.

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