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MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN, NO. 86

**The Anatomy of the Diastemal Palate  
in Microtine Rodents**

BY

WILBUR B. QUAY

ANN ARBOR  
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## THE ANATOMY OF THE DIASTEMAL PALATE IN MICROTINE RODENTS\*

### INTRODUCTION

THE diastemal palate is that part of the palate which lies between the incisors and the molariform teeth. Its variations are striking within the rodents of the subfamily Microtinae and raise questions concerning anatomical relations, functions, and ontogenetic and phylogenetic trends. The variations here noted are primarily of two sorts: (1) variations in the surface structures and (2) variations in the foramina of the bones of the diastemal palate. These structures were found to vary taxonomically and to present an interesting trend within the Microtinae. Their description in the literature is incomplete and confused because of the multiplicity of names applied to the same or similar structures in different rodents and also because of the lack of a thorough comparative study of their occurrence in rodents. The variations in the foramina of the diastemal palate, most notably in the incisive or anterior palatine foramina, are obvious in any comparative study of rodent skulls and have been the subject of much interest since they are often used as taxonomic characters. The amount of variation found in the foramina has been studied previously, but the correlation of the variations with other biological and anatomical features has not been made beyond the stage of casual speculation. It became apparent that variations in the superficial and osseous aspects of palatal anatomy might be correlated, and that a comparative study of their anatomical relationships might aid in interpreting their functional and evolutionary significance.

The structures discussed in this report will concern primarily the superficial integumentary features, the blood vessels, and the bones with their foramina. The other structures of anatomical interest in the diastemal palate have somewhat different relationships. They include (1) muscles which extend into the palatal area, but which are best studied with the other muscles of the head, (2) nerves which, since they are of small size, require special methods and can be more profitably studied over a larger area of the head, and (3) cartilages and other structures in the nasopalatine area which require special techniques and which are more closely related to anatomical features in the nasal chambers. It is hoped that these other structures will be described in later publications.

I am most grateful to W. H. Burt and Emmet T. Hooper for the use of the collections and facilities in the Museum of Zoology, University of Michigan. Hearty thanks go also to the curators of other collections from which specimens were borrowed. I am grateful to William A. Brudon, artist for the Museum of Zoology, University of Michigan, for the expertly made plates of the bones and foramina of the diastemal palate.

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### Materials and Methods

Materials used in this study include (1) 75 specimens preserved in 10 per cent formalin or other fluids, representing 10 genera and 30 species; (2) about 750 skulls which are in museum collections and which represent 17 genera and 40 species; and (3) five specimens, representing five genera, the heads of which were serially sectioned for microscopic examination.

In the following text, museum numbers for particular specimens are given. In these instances the abbreviations for the collections concerned are: CNHM, Chicago Natural History Museum; MCZ, Museum of Comparative Zoology, Harvard University; UMMZ, University of Michigan Museum of Zoology; QC, W. B. Quay (private collection).

The specimens preserved in fluids were examined with the dissecting microscope for the superficial features of the diastemal palate. From these specimens the following measurements were taken with vernier calipers: alveolobasilar length, length of the diastemal palate, and distance from the nasopalatine canal openings in the palate to the posterior edge of the incisive alveoli. To demonstrate the patency of the nasopalatine canals, red latex was injected into the external nares of 14 of the fluid-preserved specimens. To demonstrate the arteries and veins, red latex was injected caudally into the carotid arteries or into the right ventricle, and blue latex was injected cephalically into the jugular veins of anesthetized or recently killed specimens. These specimens were then fixed for a few hours in 10 per cent formalin acidified with acetic acid to harden the latex. They were then washed in water and preserved in one part glycerine to four parts of 10 per cent neutral buffered formalin. The 10 per cent neutral buffered formalin is made with a neutral solution of formalin (40 per cent formaldehyde in water) in distilled water in a ratio of one part formalin to nine parts water. To every liter of 10 per cent solution of neutral formalin is added 3.50 grams of anhydrous acid sodium phosphate ( $\text{NaH}_2\text{PO}_4$ ) and 6.50 grams of anhydrous disodium phosphate ( $\text{Na}_2\text{HPO}_4$ ) to buffer the solution to a pH of 7.0 (see Lillie, 1948:26). Other sodium or potassium phosphates could have been substituted.

The heads of five specimens were studied microscopically in serial sections. Four of these specimens had been fixed in Bouin's fluid shortly after death and had been so preserved for about one year. The fixing solution that had been used by the collector of the fifth specimen is not known, but the sections of the head showed considerable tissue distortion. The specimens fixed in Bouin's fluid were entirely satisfactory. The heads of the five specimens were washed in water and then decalcified for five months in an aqueous solution of equal parts of 50 per cent formic acid and 20 per cent sodium citrate. This period was longer than necessary, but did not cause any undesirable effects. The completion of decalcification was checked by fluoroscopic examination of the heads. The heads were then washed in water, dehydrated through ethyl alcohol solutions of increasing strength, cleared in cedar oil for about ten days, washed in benzene, and embedded in paraffin (melting point  $60^{\circ}$ - $62^{\circ}$ ) for about 36 hours. Serial sections, each 10 microns thick, were cut and mounted on two- by three-inch slides. These were stained with the standard Ehrlich's acid

hematoxylin and 1 per cent eosin in 95 per cent ethyl alcohol technique (Bensley and Bensley, 1938:73).

The skulls of microtines which are in museum collections were examined microscopically for morphological features of interest in the diastemal palate, particularly in the foramina. For each specimen examined a set of measurements was made. The measurements are: condylobasilar length of skull (from articular surface of condyle to posterior edge of incisive alveolus); (2) alveolobasilar length (from the posterior end of  $m^3$  to the posterior edge of the incisive alveolus); (3) diastemal length (from anterior edge of the alveolus of  $m^1$  to the posterior edge of the incisive alveolus); (4) length of the incisive foramina; (5) length of the part of the diastemal palate anterior to the anterior tip of the incisive foramina (from the anterior edge of the incisive foramina to the posterior edge of the incisive alveolus); and (6) length of the part of the diastemal palate anterior to the posterior end of the incisive foramina (from the posterior edge of the incisive foramina to the posterior edge of the incisive alveolus). In some species it was possible to take additional measurements owing to the presence of well-defined landmarks within the incisive foramina. These measurements are: (7) length of the anterior part of the incisive foramina (from the constriction in the foramina near the premaxillary-maxillary suture, or from the suture itself, to the anterior edge of the foramina); (8) length of the posterior part of the foramina (7 subtracted from 4); (9) width of the incisive foramina, (a) maximum width of the anterior or premaxillary part, (b) width at the premaxillary-maxillary suture or at the constriction near it, (c) maximum width of the posterior or maxillary part; (10) length of the part of the diastemal palate lying anterior to the level of the nasopalatine canal openings in the palate (from the widest point in the anterior or premaxillary division of the incisive foramina, from the suture, or from the adjacent constriction, to the posterior edge of the alveolus of the incisor). In instances where there are several points of reference possible for one measurement, the points used for particular examples will be stated. The justification and the meaning of some of these measurements will become more apparent from the discussion of measurements in the section on the bony structure and foramina of the diastemal palate.

Measurements of 2.0 mm. or greater were made with a vernier caliper under a stereoscopic microscope with an accuracy of roughly  $\pm$  0.2 mm. Measurements less than 2.0 mm. were made with a micrometer eyepiece vertically located in azimuth in a stereoscopic microscope with an accuracy of roughly  $\pm$  0.03 mm.

#### List of Species and Subspecies

Listed below are the names and authorities of all microtines that are mentioned, figured, or for which data are presented in this report. In most instances the taxonomy follows Ellerman's usage (1941) and is one of general, although tentative, acceptance. Subspecific names are used only where they may serve to define more exactly series of specimens that

were used in the study. Subgeneric names are used where certain peculiarities of the diastemal palate or its foramina appear to be characteristic (tentatively) of particular subgenera rather than of the genera or species concerned.

Tribe Lemmi (lemmings)

- Dicrostonyx hudsonius* (Pallas)  
     *groenlandicus* (Traill)  
*Synaptomys cooperi* Baird  
*Myopus schisticolor saianicus* Hinton  
*Lemmus lemmus* Linnaeus  
     *trimucronatus alascensis* Merriam  
     *harroldi* Swarth

Tribe Microti (voles)

- Clethrionomys glareolus* Schreber  
     *rufocanus* Sundevall  
     *rutilus* Pallas  
     *gapperi gapperi* (Vigors)  
         *proteus* (Bangs)  
     *brevicaudus* (Merriam)  
     *californicus obscurus* Merriam  
*Phenacomys intermedius* Merriam  
     *longicaudus* True  
     *silvicola* A. B. Howell  
*Eothenomys melanogaster* Milne-Edwards  
     *proditor* Hinton  
*Antelionomys custos rubelius* G. M. Allen  
*Alticola* (*Alticola*) *roylei semicanus* G. M. Allen  
     (*Platycranius*) *strelzowi* Kastschenko  
*Arvicola terrestris* Linnaeus  
*Microtus* (*Chilotus*) *oregoni* Bachman  
     (*Aulacomys*) *richardsoni richardsoni* DeKay  
         *macropus* Merriam  
     (*Microtus*) *pennsylvanicus* Ord  
         *montanus* Peale  
         *longicaudus* Merriam  
         *californicus* Peale  
             *eximius* Kellogg  
         *mexicanus* Saussure  
         *mogollonensis* Mearns  
         *arvalis* Pallas  
         *agrestis* Linnaeus  
         *oeconomus* Pallas  
             *operarius* Nelson  
             *immutus* Merriam  
     (*Chionomys*) *nivalis* Martins  
         *roberti* Thomas  
     (*Pedomys*) *ochrogaster* Wagner  
     (*Stenocranius*) *gregalis* Pallas  
         *abbreviatus* Miller  
         *miurus* Osgood  
*Phaiomys leucurus* Blyth  
*Lasiopodomys brandti* Radde  
*Neodon sikimensis* Hodgson  
     *irene* Thomas  
*Pitymys subterraneus* de Selys-Longchamps  
     *pinetorum* Le Conte  
     *quasiater* Coues

*Lagurus (Lagurus) luteus* Eversmann  
(*Lemmiscus*) *curtatus* Cope  
*Neofiber alleni* True  
*Ondatra zibethica* Linnaeus  
*Prometheomys schaposchnikowi* Satunin  
*Ellobius talpinus larvatus* G. M. Allen

## SURFACE FEATURES

### General Description

Features of the mucous membrane. — In most rodents the diastemal palate is covered by a mucous membrane which forms a number of folds and ridges. In some microtines the most anterior part of the mucous membrane of the diastemal palate forms an anterior longitudinal ridge (Fig. 1). In others this ridge is obscure or lacking (Fig. 2). The anterior longitudinal ridge or its remnants in all species of microtines so far examined rises and broadens posteriorly, buttressing an incisive or palatine papilla, which thus forms the posterior end of the ridge. On each side of the papilla is an opening of one of the paired nasopalatine canals, which extend dorsad through the paired anterior palatine (incisive) foramina. These canal openings are present in all microtines examined. Behind the palatine papilla there are several, typically three, transverse palatine ridges in microtines. To distinguish these from the fainter ridges occurring between the molariform tooth rows, they may be termed transverse diastemal ridges.

Inflexed areas of the lip. — The lips of microtines are furred and are notable for their medial lobes which extend within the oral cavity between the incisors and the molariform teeth (Figs. 1 and 2). Most frequently such furred extensions of the lips have been described only casually in works on rodents and have not been given specific names. Such names, when they have been given to the labial lobes, do not correspond to those used for the same structures in other species. One of the earliest studies, and the most extensive concerning the lips of mammals, is that which is contained in the series of articles by Schulze (1912-16). Only one of these articles (1916) concerns rodents, and this is devoted to the sciuriforms. The medial lobe of the upper lip of sciuriforms is designated in this article as the *inflexum pellitum der Oberlippe*. Since inflexus is the Latin (masculine) noun used in this name, in the present study of microtine lips the name "inflexus of the upper lip" is used for the medial or palatal lobe of that lip. The Latinized equivalent is inflexus(i) pellitus(i) labii superioris.

The inflexi of the upper lip have been given various names by different authors. In the wood rat they were called "oral sphincter pads" by Howell (1926:90), since they effect complete closure of the mouth when the buccinator muscles are in normal tone. The inflexi of the upper lip in *Microtus arvalis* were called "implexi(um) pelliti(um) labii superioris" by Sulc (1929); however, the use of implexi in place of inflexi does not seem

correct, since in *Microtus arvalis* and all other rodents which I have examined the medial or palatal lobes of the upper lip are truly infoldings (inflexi) rather than twistings (implexi) of the upper lip. In the pocket gopher (*Thomomys*) these structures were called "palatal lobes" of the upper lip by Hill (1937:83). In various microtines they were called "labial lobes" by Vinogradov (1926*a,b*) and "lobi labiales" by Ognev (1948:418, 484, 552).

The lower lip of microtines is furred and externally appears to be short and simple in form. But actually its internal configuration is more complex than that of the upper lip, since there is a ventral pair of inflexi (inflexi [us] ventralis labii inferioris) extending medially toward each other over the base of the lower incisors and a dorsal pair of inflexi (inflexi [us] dorsalis labii inferioris) extending medially toward each other behind the inflexi of the upper lip (Figs. 1 and 2). The skin of the ventral inflexi is not greatly modified, but that of the dorsal inflexi of the lower lip in all species examined is greatly modified by the presence of long, stiff, posteromedially directed hairs which arise from crater-like openings in follicles that also give rise to greatly enlarged sebaceous-type glands.

The dorsal inflexi of the lower lip in microtines appear to correspond to the structure figured and described in *Aplodontia* as an *Insel* by Schulze (1916). Schulze considered this to be an extension of the inflexus of the upper lip as did Richardson (1829:211) in a description of the species. But Schulze stated further that it is separated from the inflexus of the upper lip by a bare "zona intermedia." The relation of the *Insel* to the lower lip and its infoldings was not stated and should be re-examined in *Aplodontia*. The haired and narrow inner boundary of the lower lip in sciuriforms was called *inflexum pellitum der Unterlippe* by Schulze. In *Microtus arvalis* Sulc (1929) found that the *Insel* (or insula) of Schulze was not an isolated part of the upper lip, but was an infolding of the lower lip. This he then called "implexum pellitum labii inferioris." In summary it should be noted that: (1) the term "dorsal inflexus of the lower lip" as used in the present study corresponds both to the *Insel* of Schulze and to the "implexum pellitum labii inferioris" of Sulc, and (2) that the term "ventral inflexus of the lower lip" does not correspond to any of the names or structures described by Schulze or Sulc.

The furrow lined with mucous membrane between the inflexus of the upper lip and the dorsal inflexus of the lower lip was called the "sulcus interimplexialis" by Sulc (1929) and corresponds to the "zona intermedia" of Schulze. In the present report it is called the interinflexal sulcus (sulcus interinflexalis), which should be a more appropriate term.

Nasopalatine canals. — The nasopalatine canals are narrow passages lined with stratified squamous epithelium. They are patent in adult specimens of *Synaptomys cooperi*; *Lemmus trimucronatus*; *Clethrionomys*; *Phenacomys intermedius* and *longicaudus*; *Arvicola terrestris*; *Microtus oregoni*, *richardsoni*, *pennsylvanicus*, and *californicus*; *Pitymys pinetorum*; *Neofiber alleni*; and *Ondatra zibethica*, since in these specimens colored latex which was injected into the external nares flowed freely through the nasopalatine canals. Patency of the nasopalatine canals is also seen in all of the heads of adult microtines which were serially sectioned and

microscopically examined. The sectioned heads are of *Synaptomys cooperi*, *Lemmus trimucronatus harroldi*, *Clethrionomys californicus obscurus*, *Phenacomys longicaudus*, and *Microtus mogollonensis*. It is of interest to note that in a serially sectioned head of a fetal (30 mm. crown-rump length) *Synaptomys cooperi* the nasopalatine canals are present, but are firmly plugged with epithelial cells. Thus, it appears that the adult patency of the canals may result from a secondary opening of the nasopalatine epithelial cords rather than from a continual nasopalatine hiatus from early embryonic stages.

The adult nasopalatine canals have the form of laterally compressed funnels passing ventrally and somewhat posteriorly from the floor of the nasal chambers to the sides of the incisive papilla. In the adult microtines, whose nasopalatine canals were injected with latex via the external nares, dissections show that these funnel-like canals pass through the premaxillary region of the incisive foramina and that the widest area of the premaxillary region of the foramina corresponds to the passage of the more ventral part of the funnel. This is also evident in the sectioned heads.

Associated with the nasopalatine canals and the incisive papilla are certain glands, cartilages, muscles, and sensory structures. These form a rather complex nasopalatine apparatus, which differs considerably from one group of rodents to another. The serial sections of microtine heads show that the cartilages supporting the nasopalatine canals and the incisive papilla differ from one microtine genus to the next. The morphology of the nasopalatine apparatus is a topic that will be discussed in a later publication, since it leads to considerations of functions and structures extending beyond the limits of the present report. It will suffice to say that the size and the position of the premaxillary part of the incisive foramina appear to be reflections of the size and position of the nasopalatine canals themselves rather than of any of their glands or other accessory structures.

#### Characteristics of Genera and Species

The features discussed under each genus in the following paragraphs will be limited to those that show a significant amount of difference from the same features in other genera of the subfamily and to those that vary significantly from species to species within the genus. The species and number of specimens examined are given in parentheses. The specimens of each genus examined always included at least one adult.

*Dicrostonyx* (*D. hudsonius*, 2; *D. groenlandicus*, 3)

(Fig. 1)

The most striking characteristic in the diastemal palate of this genus is the breadth and exposure of the anterior longitudinal ridge. The nasopalatine canal openings are spaced far apart and are directed laterally; they cannot be seen in Figure 1 since they are hidden under the lateral folds of the incisive papilla in both the juvenile and adult specimens.

The inflexi of the upper lip are the least developed of all those seen in the subfamily. Only in adults do they extend far medially, and then there is only a small fleshy lobe extending to each side of the incisive papilla. These lobes cover the nasopalatine canal openings and very little else. The medial extent of the edges of the upper lip inflexi varies somewhat according to the amount of muscular contraction at the time of death. In the adult specimen figured the inflexal lips are farther apart than might be usual, but in other specimens, as well, the inflexal lips never reach the median ridge of the papilla. Ognev (1948:484) has given a brief description of the inflexi of the upper lip in *Dicrostonyx*.

TABLE I

A. Percentage of the Diastemal Palate Which Lies Anterior to the Nasopalatine Canal Openings, a Measure of the Anterior-posterior Location of the Nasopalatine Canal Openings

B. Percentage of Alveolobasilar Length Formed by the Diastemal Palate

N = number of specimens.

Genus	Species	N	A		B	
			Mean	Range	Mean	Range
<i>Dicrostonyx</i>		3	42	39-45	57	55-60
<i>Synaptomys</i>	<i>cooperi</i>	3	37	35-40	53	50-58
<i>Lemmus</i>		4	36	31-39	55	52-57
<i>Clethrionomys</i>		8	42	39-46	58	56-61
<i>Phenacomys</i>	<i>intermedius</i>	2	46	45-47	54	52-56
	<i>longicaudus</i>	1	40	40	54	54
<i>Arvicola</i>	<i>terrestris</i>	2	53	50-56	61	61
<i>Microtus</i>	<i>oregoni</i>	2	46	45-47	58	57-58
	<i>richardsoni</i>	3	56	53-58	62	61-63
	<i>pennsylvanicus</i>	5	45	43-47	57	55-59
	<i>montanus</i>	2	45	42-48	58	57-59
	<i>longicaudus</i>	5	45	41-46	56	54-58
	<i>californicus</i>	2	44	44	55	55
	<i>mexicanus</i>	1	47	47	55	55
	<i>arvalis</i>	3	48	46-49	56	55-58
	<i>agrestis</i>	7	44	41-46	54	51-56
	<i>oeconomus</i> (Europe)	3	47	45-49	57	57-60
	<i>nivalis</i>	1	44	44	56	56
	<i>ochrogaster</i>	1	46	46	58	58
	<i>miurus</i>	1	49	49	61	61
<i>Pitymys</i>	<i>subterraneus</i>	1	45	45	56	56
	<i>pinetorum</i>	2	45	44-45	57	54-59
<i>Neofiber</i>	<i>alleni</i>	3	54	49-57	58	55-60
<i>Ondatra</i>	<i>zibethica</i>	3	56	55-58	59	57-62

*Synaptomys* (*S. cooperi*, 4)

(Fig. 1)

The anterior longitudinal ridge in *Synaptomys* is much slenderer than it is in *Dicrostonyx*, and it has a median longitudinal furrow in adults.



The openings of the nasopalatine canals are exposed on the roof of the mouth of a young specimen (Fig. 1), but in adults the openings are turned anterolaterally, with the result that they are invisible ventrally and that they come in contact with the margins of the inflexi of the upper lip. The anterior longitudinal ridge is very short in this genus, and the nasopalatine canal openings are placed more anteriorly in the diastemal palate than they are in most of the other microtines examined (Table I).

The inflexi of the upper lip are more extensive medially than those in *Dicrostonyx*, but less so than those in *Lemmus*. In the young specimen of *Synaptomys* the medial edges of the inflexi of the upper lip extend much closer to the mid-line than do those of the juvenile specimen of *Dicrostonyx*.

*Lemmus* (*L. lemmus*, 4; *L. trimucronatus*, 3)

(Fig. 1)

The anterior longitudinal ridge in *Lemmus* is much more constricted and depressed in its mid-region than it is in *Synaptomys*. In *Lemmus* it bears a median furrow, a character shared only by *Synaptomys*. In a few specimens of *Lemmus lemmus* there is an incipient fourth diastemal ridge just anterior to the first molariform tooth.

The inflexi of the upper lip are more extensive anteriorly and medially in *Lemmus* than in *Dicrostonyx* or *Synaptomys*, and they are more densely haired. Ognev (1948:418) briefly described them. There is only a trace of ventral inflexi of the lower lip.

*Clethrionomys* (*C. glareolus*, 4; *C. rufocanus*, 1;  
*C. rutilus*, 2; *C. gapperi*, 3; *C. brevicaudus*, 2)

(Fig. 1)

The anterior longitudinal ridge is constricted and depressed in its mid-region, but it is not so greatly constricted and depressed as that of *Lemmus*. It is, therefore, more conspicuous in *Clethrionomys* than in *Lemmus*. The anterior hillock on the longitudinal ridge is not furrowed, as it is in *Synaptomys* and *Lemmus*.

The inflexi of the upper lip do not extend so far medially as they do in *Lemmus*. They have been described and figured by Vinogradov (1926 b) for *C. glareolus*.

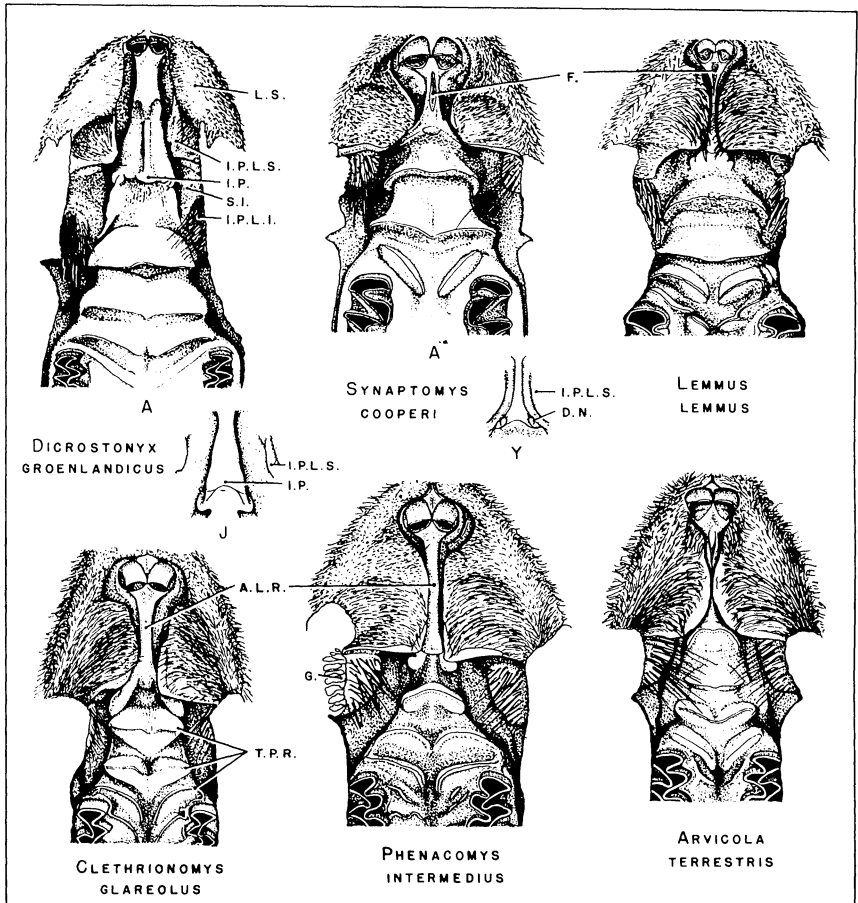


Fig. 1. The diastemal palate in six microtine genera, viewed from below (not drawn to same scale).

*Dicrostonyx groenlandicus*. A. adult ♀ (QC 3-C-112), Baffin Island, Canada; J. juvenile ♂ (QC 3-C-114), Bernard Harbor, N.W.T., Canada.

*Synaptomys cooperi*. A. adult ♂ (UMMZ 53799), Washtenaw Co., Michigan, U.S.A.; Y. young (UMMZ 60651), Washtenaw Co., Michigan, U.S.A.

*Lemmus lemmus* ♂ (UMMZ 57798), Mjösen Lake, Norway.

*Clethrionomys glareolus* ♀ (QC 3-C-473), Furstenwalde, Spree, Germany.

*Phenacomys intermedius* ♀ (QC 3-C-310), Teton Co., Wyoming, U.S.A.

*Arvicola terrestris* ♀ (UMMZ 97683), Sipoo (near Helsinki), Finland.

A.L.R., anterior longitudinal ridge; D.N., nasopalatine duct opening; F., furrow on anterior longitudinal ridge; G., sebaceous glands in dorsal inflexus of lower lip; I.P., incisive papilla; I.P.L.I., dorsal inflexus of lower lip; I.P.L.S., inflexus of upper lip; L.S., upper lip; S.I., interinflexal sulcus; T.P.R., transverse palatine ridges.

*Phenacomys* (*P. intermedius*, 6; *P. longicaudus*, 2)

(Fig. 1)

The slender anterior longitudinal ridge is similar to that of *Clethrionomys* and is constricted and depressed in its middle area. In the specimens examined the ridge is somewhat shorter and stouter in *P. longicaudus* than in *P. intermedius*. Also, the inflexi of the upper lip in these specimens appear to be more extensive in adult *intermedius* than in adult *longicaudus*; in *P. intermedius* they cover the incisive papilla, but in *P. longicaudus* more of the medial area of the palate is exposed, and the incisive papilla is not covered. In both species the openings of the nasopalatine canals are covered by the smooth medial surfaces of the inflexi. In a young *P. longicaudus* the medial extent of the upper lip inflexi is similar to that shown for the young *Synaptomys*.

In specimens of *P. intermedius* the dorsal inflexi of the lower lip are large. In an old adult *P. longicaudus* the dorsal inflexi of the lower lip are smaller, not swollen, have fewer hairs, smaller sebaceous glands, and a black pigmentation concentrated around the openings of the follicles. Noticeable black or melanin deposits could not be found in the inflexi of the young specimen examined.

*Arvicola* (*A. terrestris*, 2)

(Fig. 1)

The anterior longitudinal ridge is lacking because of the extreme constriction and depression in what would be its mid-region. Anteriorly, there is a small remnant, bearing a median furrow inclosing a small ridge extending back from the gums of the incisors. Posteriorly, the incisive papilla remains.

The inflexi of the upper lip meet but do not fuse. Posteriorly, they cover the openings of the nasopalatine canals and the sides of the palatine papilla.

*Microtus* (*M. oregoni*, 2; *M. richardsoni*, 3; *M. pennsylvanicus*, 6; *M. montanus*, 2; *M. longicaudus*, 5; *M. californicus*, 2; *M. mexicanus*, 1; *M. arvalis*, 3; *M. agrestis*, 7; *M. oeconomus* (Europe), 3; *M. o. inuitus*, 1; *M. nivalis*, 1; *M. ochrogaster*, 1; *M. miurus*, 1)

(Fig. 2)

In all specimens examined, the anterior longitudinal ridge is lacking, and the inflexi of the upper lip either meet or come very close together; they are never fused. They have been described by Vinogradov (1926b) and Sulc (1929). Ventral inflexi of the lower lip are discernible in some specimens.

*Pitymys* (*P. subterraneus*, 1; *P. pinetorum*, 2)

(Fig. 2)

A true anterior longitudinal ridge is lacking; however, there is an exposure of mucous membrane shown in this area. The inflexi of the upper lip are well developed, as in *Microtus*. They are relatively larger and closer together in *P. subterraneus* than in *P. pinetorum*. Ventral inflexi of the lower lip are sometimes discernible.

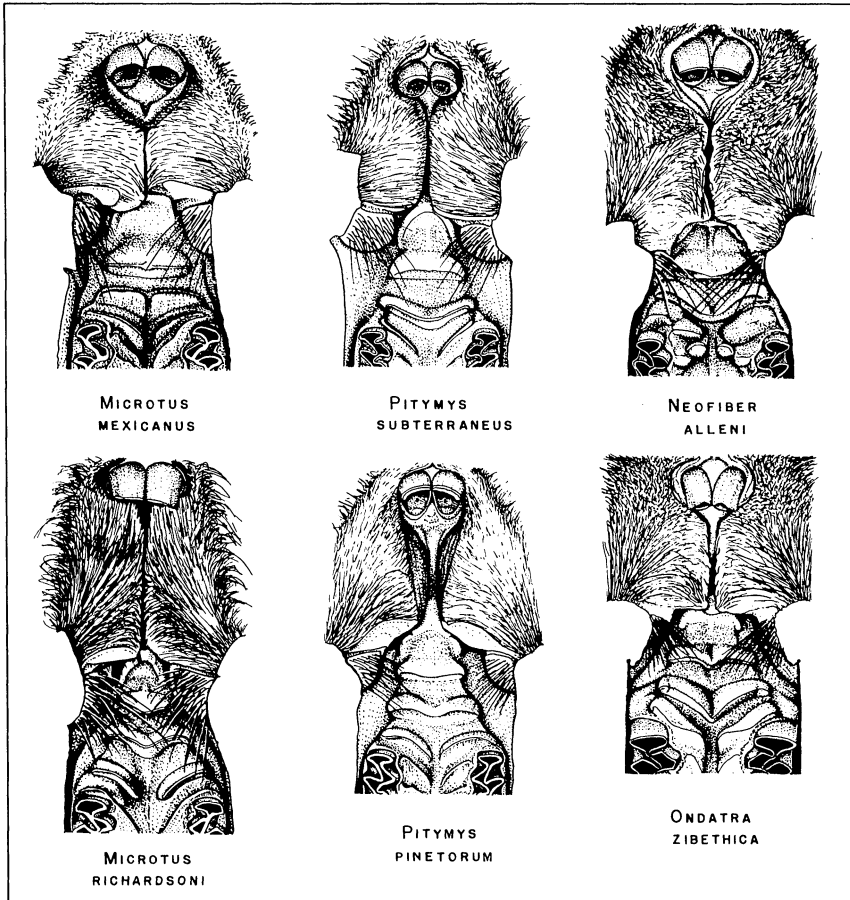


Fig. 2. The diastemal palate in six microtine species, viewed from below (not drawn to same scale).

*Microtus mexicanus* ♀ (QC 3-C-169), Distrito Fed., Mexico.

*Pitymys subterraneus* ♂ (UMMZ 97685), Esztergom, Hungary.

*Neofiber alleni* ♂ (QC 3-C-418), Dade Co., Florida, U.S.A.

*Microtus richardsoni* ♂ (UMMZ 80219), Teton Co., Wyoming, U.S.A.

*Pitymys pinetorum* ♀ (QC 3-C-54), Accomack Co., Virginia, U.S.A.

*Ondatra zibethica* ♀ (QC 3-C-374), Washtenaw Co., Michigan, U.S.A.

*Neofiber (N. alleni, 3)*

(Fig. 2)

An anterior longitudinal ridge is lacking. The inflexi of the upper lip are highly developed; they meet along the mid-line of the diastema, but they are not joined. Ventral inflexi of the lower lip are present.

*Ondatra (O. zibethica, 3)*

(Fig. 2)

The superficial features of the diastemal palate in this genus are much the same as those in *Neofiber*. Baird (1859:561) and Ognev (1948:534) have briefly described the inflexi in this species.

*Prometheomys*

According to Vinogradov (1926*a, b*) and Ognev (1948:552-53), the inflexi of the upper lip and the ventral inflexi of the lower lip are highly developed. The inflexi of the upper lip meet but do not fuse, and the ventral inflexi of the lower lip are not as greatly developed as those in *Ellobius*, according to these authors.

*Ellobius*

In this genus occurs the greatest development of the inflexi of the upper lip and the ventral inflexi of the lower lip (Vinogradov, 1926*a, b*; Ognev, 1948). The inflexi of the upper lip are even fused to each other across the mid-line. In the figure by Vinogradov (1926*b*) there are three transverse diastemal structures shown behind the fused inflexi. The most anterior of these appears to be the incisive papilla, and the two more posterior structures are undoubtedly transverse diastemal ridges. Also visible in the illustration are the dorsal inflexi of the lower lip. Whether the nasopalatine canals are present or patent in this genus is not known. If they lie at the sides of the incisive papilla, they are situated more posteriorly in the diastemal palate of *Ellobius* than they are in all other microtine genera studied to date, according to Vinogradov's illustration.

## Functional and Evolutionary Significance

Inflexi of the upper lip.—It is generally believed that maximal development of the inflexi of the upper lip in rodents serves to separate the posterior, or masticatory, part of the oral cavity from the anterior area around the incisors, so that the material being worked on by the incisors or finding access to them does not fall into the rear of the mouth. This idea

was first expressed by Merriam (1895) for the Geomyidae. In rodents that are highly specialized for fossorial life, especially those that dig with the incisors, the inflexi of the upper lip are of maximal development and are fused to each other across the mid-line of the palate. This has been reported for the following: the bathyergid genera *Georychus* (Tullberg, 1899), *Heliophobius* and *Heterocephalus* (Vinogradov, 1926b), the hystricomorph genus *Ctenomys* (Pocock 1922a), the Geomyidae (Merriam, 1895; Bailey, 1915; Vinogradov, 1926b; Hill, 1937), and the microtine genus *Ellobius* (Vinogradov, 1926b; Ognev, 1948). Whether the same situation is present in other rodents of extreme fossorial specialization has not been ascertained. It is known that the inflexi of the upper lip are greatly developed and fused in some hystricomorph genera (*Myocaster*, *Chinchilla*, *Lagostomus*, and *Dinomys*) which are not known to be fossorial or which are only slightly so (Pocock, 1922a, 1926) and that they are moderately or well developed, but not fused, in a great variety of rodents of diverse habits (Pocock, 1922a,b,c).

In the Microtinae the inflexi of the upper lip are always present, but their extent or amount of development shows great intergeneric differences and lesser intrageneric differences. In *Dicrostonyx*, considered by Hinton (1926:35) to be fundamentally the most primitive of the lemmings and of the Microtinae, the inflexi are the least developed. In *Synaptomys* they are more developed and in *Lemmus* still further developed. *Synaptomys*, considered by Hinton (1926:38) to be more primitive than *Lemmus*, lacks the specializations for fossorial habits shown by Recent species of *Lemmus*. This is interesting since the extent of the development of the upper lip inflexi in the three genera of lemmings examined parallels Hinton's ideas concerning their relatively primitive or advanced phylogenetic positions and also suggests a correlation with fossorial habits. In the voles (Tribe Microti) there is no condition comparable with that seen in *Dicrostonyx*. The development of the upper lip inflexi in voles is least in *Clethrionomys* and *Phenacomys*, corresponding roughly to the stage present in *Synaptomys* among the lemmings; it is greater in the genera *Arvicola*, *Microtus*, *Pitymys*, *Neofiber*, *Ondatra*, and *Prometheomys*, corresponding roughly to that in *Lemmus*; and it is greatest in the genus *Ellobius*, of extreme fossorial specialization.

Whether the amount of development of the upper lip inflexi in all voles is related to the extent to which the incisors are used in digging is difficult to decide. It seems likely, however, that in some genera or species the inflexal flaps may serve to exclude foreign materials from the back of the mouth and throat whether fossorial life is involved or not. In some instances there may be a correlation with aquatic habits, since in the aquatic microtines (*Arvicola*, *Microtus richardsoni*, *Neofiber*, and *Ondatra*) the inflexal flaps are well developed. This is also true for the aquatic rodents *Myocaster* and *Castor* (Pocock, 1922a,c). Even in microtines with weakly developed upper lip inflexi, the inflexal flaps may serve as protective covers for the nasopalatine canal openings in the palate. These flaps, even when very weakly developed, may also aid in the handling of materials being gnawed or ingested. Sulc (1929) stated that these structures in *Microtus arvalis* may be used to lubricate and cleanse the forefeet.

Ventral inflexi of the lower lip.—These structures appear in a great variety of rodents (Tullberg, 1899; Pocock, 1922*a,b,c*; Vinogradov, 1926*b*), but they are most strongly developed in fossorial forms and seem to parallel the upper lip inflexi in the extent of their development in each form. This is seen in the microtines examined. According to Vinogradov (1926*b*), these inflexi may be seen rather clearly in *Lagurus*, more so in *Prometheomys*, and very distinctly in *Ellobius*. It is likely that they are more purely specializations for excluding materials in the incisor area from the back of the mouth than are the inflexi of the upper lip, since the functions of the latter may involve food handling and protection of the nasopalatine canal openings.

Dorsal inflexi of the lower lip.—These structures occur in a variety of rodents (*Aplodontia*, Schulze, 1916; *Castor*, Pocock, 1922*c*; *Neotoma*, Howell, 1926), and their known distribution within the order gives no clue to their function. They are present in all microtines examined here or reported upon in the literature. There is some variation in the size of the dorsal inflexi of the lower lip in microtines, but this variation is so slight that correlations between the size of the inflexi and habits do not appear possible in this subfamily. Although their function is obscure, Howell's (1926:90) belief that they serve to allow entrance of particles of food and to hinder their egress seems plausible.

Anterior longitudinal ridge.—This structure is reduced or lost in those microtines in which the inflexi of the upper lip are well developed. Thus, it is best seen in the genera *Dicrostonyx*, *Synaptomys*, *Clethrionomys*, and *Phenacomys*, which Hinton (1926) considered very primitive structurally.

Position of the nasopalatine canal openings.—The percentage of the diastemal length which lies anterior to the nasopalatine canal openings in the palate is a suitable index for comparing the anteroposterior position of the canal openings in different microtines. This is shown in Table I for all of the microtines dissected. The ranges in percentages obtained for each species indicate considerable variation and limit the significance of the differences between means. There appears, however, to be a distinct and significant correlation of relatively more posteriorly situated nasopalatine canal openings with aquatic habit, as exemplified by *Arvicola terrestris*, *Microtus richardsoni*, *Neofiber alleni*, and *Ondatra zibethica*. As has been mentioned above, if there are patent nasopalatine canals emerging at the sides of the incisive papilla, shown in *Ellobius* by Vinogradov, they certainly are the most posteriorly located of any of those in the subfamily. This trend is associated with the trend in the separation of the incisive area from the masticatory area by the upper lip inflexi and the ventral inflexi of the lower lip. But the association is imperfect in some genera, such as *Synaptomys* and *Lemmus*, in which the upper lip inflexi are fairly well developed and the nasopalatine canal openings are relatively the most anteriorly located in the subfamily.

The more posterior position of the nasopalatine canal openings in the aquatic microtines could be achieved merely by a disproportionate increase in the length of the anterior part of the diastemal palate with respect to the length of the entire palate. That such is not the case in all aquatic

microtines is suggested in Table I, B, where the percentage of the alveolobasilar length made up by the diastemal palate is given. In *Neofiber*, *Ondatra*, and *Arvicola* the percentage of the palate comprised in the diastemal palate does not appear to be significantly different from that of unspecialized species in other genera.

Transverse diastemal ridges.—In nearly all microtines there are three transverse diastemal ridges, but in *Lemmus* there is sometimes a fourth, and in *Ellobius*, as portrayed by Vinogradov (1926b), there appear to be only two. If it is recalled that (1) the nasopalatine canal openings and the incisive papilla which supports them are situated most anteriorly in *Lemmus* (Table I) and most posteriorly in *Ellobius* and that (2) their antero-posterior position directly limits the length of the diastemal palate between them and the molariform teeth, it can be seen that the number of transverse diastemal ridges may be correlated with the relative length of the space provided for them by the position of the nasopalatine canal openings and the incisive papilla.

Variations in the configuration of the ridges in different microtines have not given any clues to the functional significance of the structures.

#### OSTEOLOGICAL FEATURES

Three features in the osseous structure of the diastemal palate were found to be of particular interest: (1) the relative length of the diastemal palate itself, (2) the incisive (anterior palatine) foramina, and (3) the small premaxillary and the interpremaxillary nutritive foramina.

After preliminary studies it was decided that in the first two of these the changes which take place with age should be appraised to determine whether they are the same in all species. It became desirable, then, to compare these age changes quantitatively in adequately represented species. Since the actual ages of the specimens were not known, it was necessary to find some quantitative criterion that would approximate relative age. A satisfactory criterion in morphological studies of microtines is the condylobasilar length of the skull (Howell, 1924). This measurement, however, could not be taken accurately for many of the specimens in my series, owing to injury of the occipital area; therefore, the alveolobasilar length was used instead. This measurement has been shown by Howell (1924), to be closely correlated with the condylobasilar length in *Microtus montanus*, and the same correlation in six other microtines is shown by the graphs in Figure 3. In these graphs each dot represents a small sample of specimens whose alveolobasilar length lies within a certain arbitrary range. The arbitrary ranges are the same in length but not in number of representative specimens. The dots on the graph represent the mean alveolobasilar length and the mean condylobasilar length for each sample of specimens. In all six species there appears to be a linear relationship between alveolobasilar and condylobasilar length.

No significant differences could be found that might be correlated with sex, although an intensive search was made for these during the preliminary phase of the work; therefore, in the preceding and following



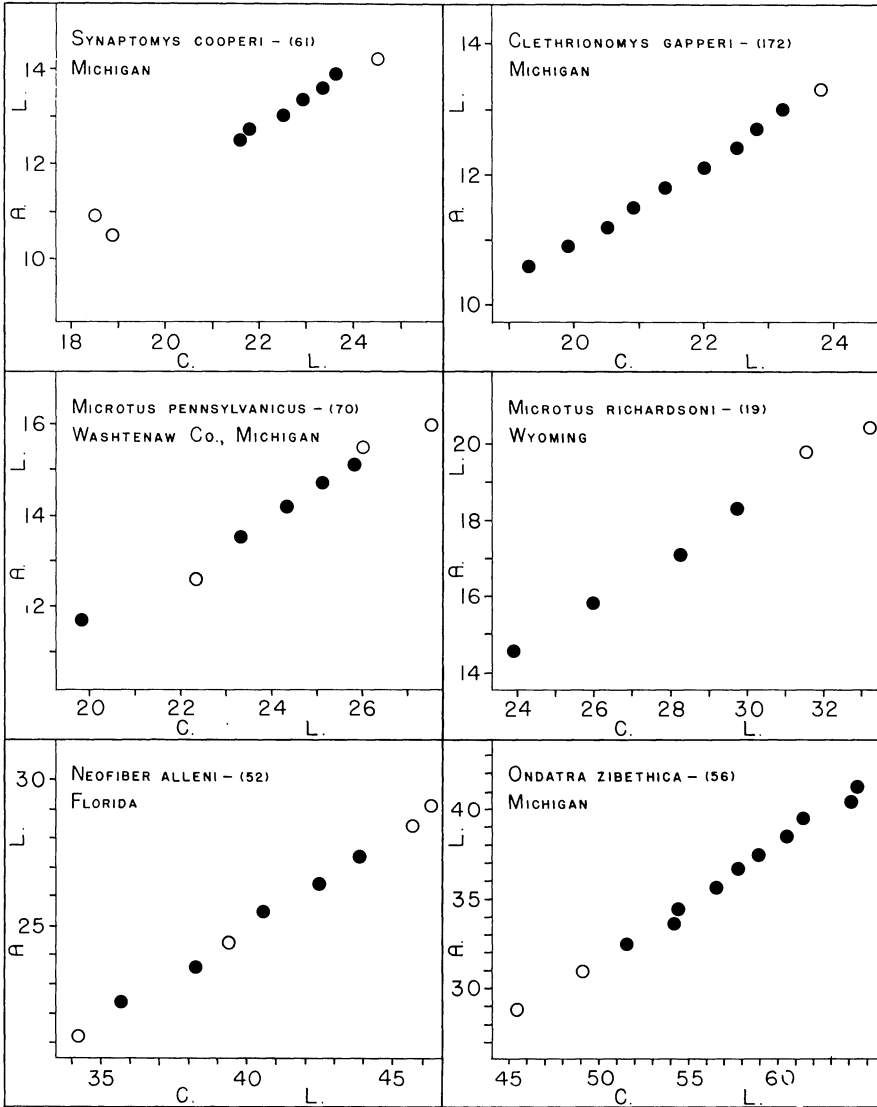


Fig. 3. Correlation between alveolobasilar length and condylobasilar length in six species. Each dot represents the mean alveolobasilar length (A.L.) and the mean condylobasilar length (C.L.) of a sample of specimens whose alveolobasilar length lies within a certain range, equal in length to that of other samples in the same graph. Hollow dots indicate samples of one or two specimens; solid dots, samples of three or more specimens. The species, total number of specimens, and locality are given at the upper left corner.

discussions the sexes are grouped together. It should be realized, however, that if more specimens were available, statistically significant differences would probably become apparent. Gould and Kreeger (1948:145),

in a study of 158 male and 199 female muskrats, found that the means of all skull measurements used were greater for the males than for the females. Of these measurements the mean diastemal length, of particular interest in this study, differs by 0.64 mm. and has a standard error of  $\pm 0.11$ . Goin (1943:221), in a study of 104 *Microtus pennsylvanicus* skulls, found that the males averaged slightly larger and more variable than the females.

#### Relative Length of the Diastemal Palate

The alveolobasilar length and diastemal length increase as the condylobasilar length increases in each of the six species examined. If the percentage of the increase should be the same in both diastemal length and alveolobasilar length, the relative length of one to the other would remain the same during increase in size. In some of the microtines, however, the percentage of increase of the diastemal length is greater than that of the alveolobasilar length, with the result that in larger and presumably older individuals the proportion diastemal length to alveolobasilar length is greater than in smaller and presumably younger individuals. This is shown in Figure 4, in which the proportion diastemal length to alveolobasilar length is plotted against alveolobasilar length, which is an approximation of relative size and age. In *Synaptomys cooperi* the proportional length of the diastema presents no clear trend with increase in size and age, but in the other microtines the proportional length of the diastema appears to increase with increase in size and age. It seems likely, as is suggested by the results shown in Figure 4, that the proportional increase in diastemal length during the life span indicates differences between species. If the age ranges represented by the alveolobasilar lengths were the same for each species, the species differences in the proportional increase in the diastema could be quantitatively compared. Although the age ranges represented by the data for each species are similar, they are not precisely known and prevent further analysis of species differences in the proportional increase of the diastemal length within each species.

The proportion diastemal length to condylobasilar length of the skull was calculated and plotted for the same species used in Figure 4. The results are essentially similar to those shown in the figure, with the primary difference being that the proportional increase in diastemal length with respect to increased condylobasilar length is not as great as that with respect to increased alveolobasilar length. The statement by Gould and Kreeger (1948), that the relative diastemal length with respect to skull length remains almost constant with increasing skull length in the muskrat, may possibly be attributed to the fact that their "measurements have been made on a selected sample of skulls representing animals in an advanced period of life."

The length of the diastema with respect to the alveolobasilar length in the 41 microtine species examined ranges from 46 to 64 per cent. The range of variation within each species is so great that most of the species overlap with respect to this character. Nevertheless, it is of interest to note that the mean value is lowest in *Myopus* (49 per cent), *Synaptomys*

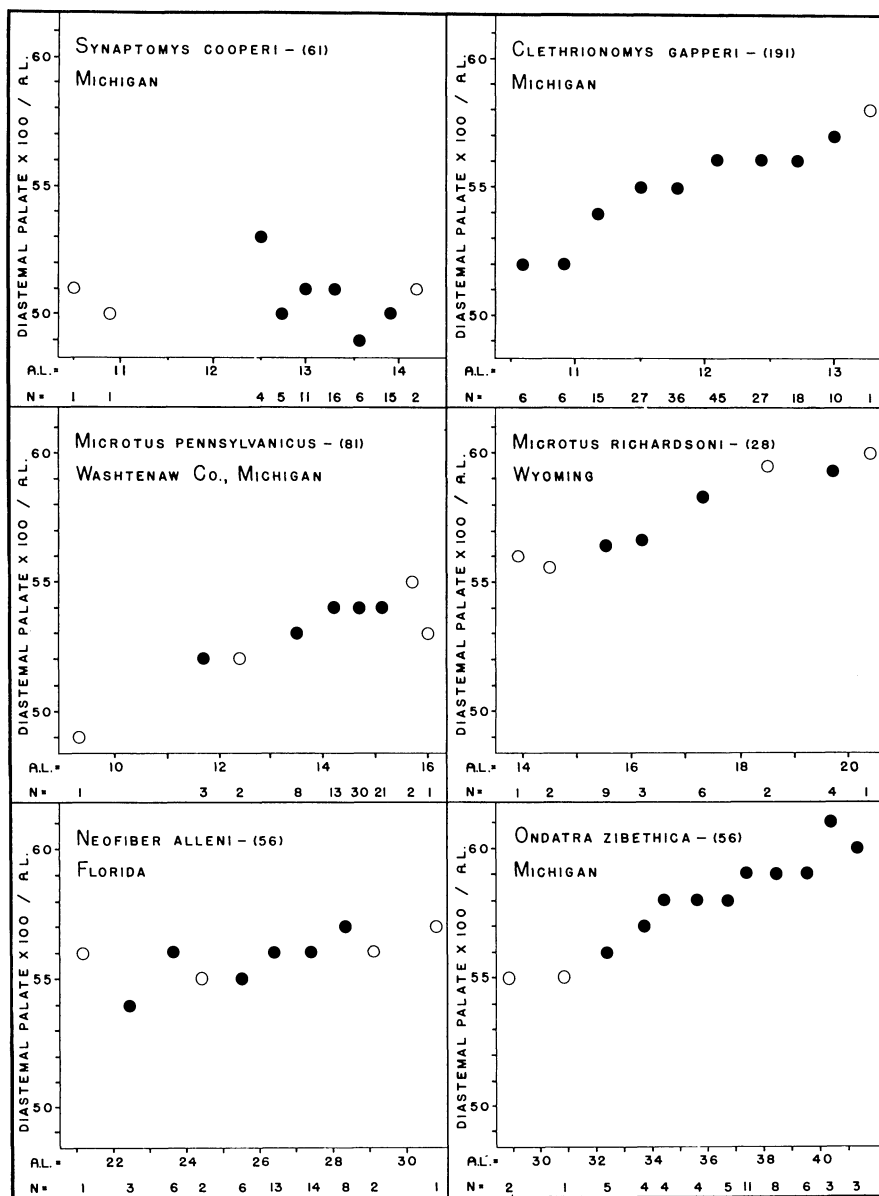


Fig. 4. Species differences in the relative increase of the diastemal part of the palate over the molariform tooth-bearing part of the palate with increased alveolobasilar length (A.L.) and age. Each dot represents the mean values obtained for a sample whose alveolobasilar length lies within a certain range, equal in length to that of other samples in the same graph. N—number of specimens in each sample. The species, total number of specimens, and locality are given at the upper left corner.

(50 per cent), and *Phenacomys* (50 per cent), genera that are considered by Hinton (1926) to be among the most primitive microtines. At the other end of the series it is difficult to decide which genera illustrate the maximum relative diastemal length, since interspecific overlap is so broad. This is in large measure caused in many species at this end of the series by the continual increase of the relative diastemal length throughout life.

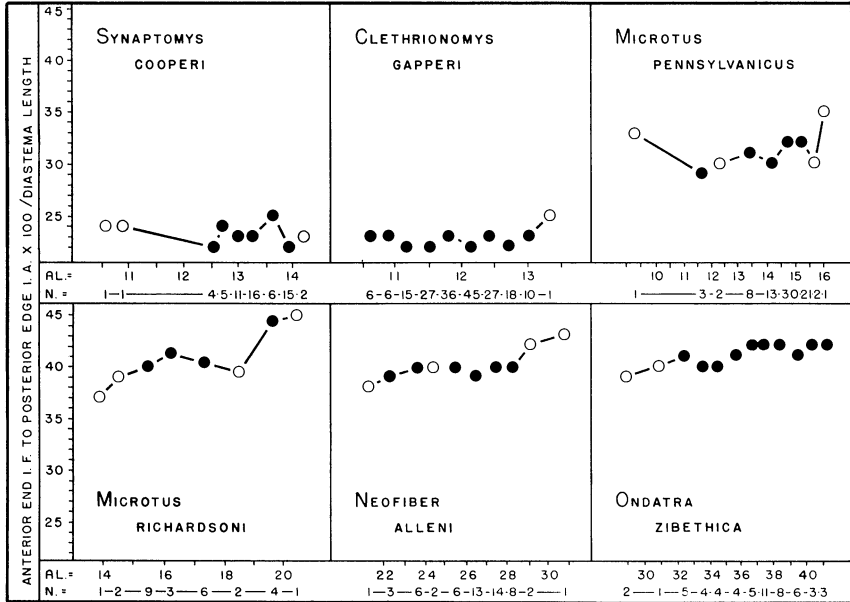


Fig. 5. The anteroposterior position of the anterior edge of the incisive foramina during the continual growth of the palate in six microtine species. The anteroposterior position is determined by the percentage of the diastemal length which lies between the most anterior edge of the incisive foramina and the posterior edge of the incisive alveolus (anterior end i. f. to posterior edge i. a. x 100/d.l.). A.L. — alveolobasilar length in mm. N — number of specimens in each sample. The localities represented are the same as those in Figures 3 and 4.

Although there is frequent intergeneric and interspecific overlap in relative diastemal length, this measurement may often be useful in characterizing certain genera and species, especially if the age changes are plotted and compared. In my data the usefulness of this measurement for species characterization applies particularly to species in the genera *Clethrionomys* and *Microtus*.

### Incisive (Anterior Palatine) Foramina

The variations of interest in the incisive foramina concern the position, size, and shape of the foramina. These will be discussed in that order.

The anteroposterior position of the incisive foramina in the diastemal palate is judged by the percentage of the diastemal length that is anterior to the foramina. Instead of determining the percentage of the palate lying anterior to the middle of the foramina, it is more practical to determine the percentage of the palate lying anterior to particular landmarks in the foramina, such as their posterior and anterior limits and the premaxillary-maxillary suture. The anteroposterior position of the anterior and posterior

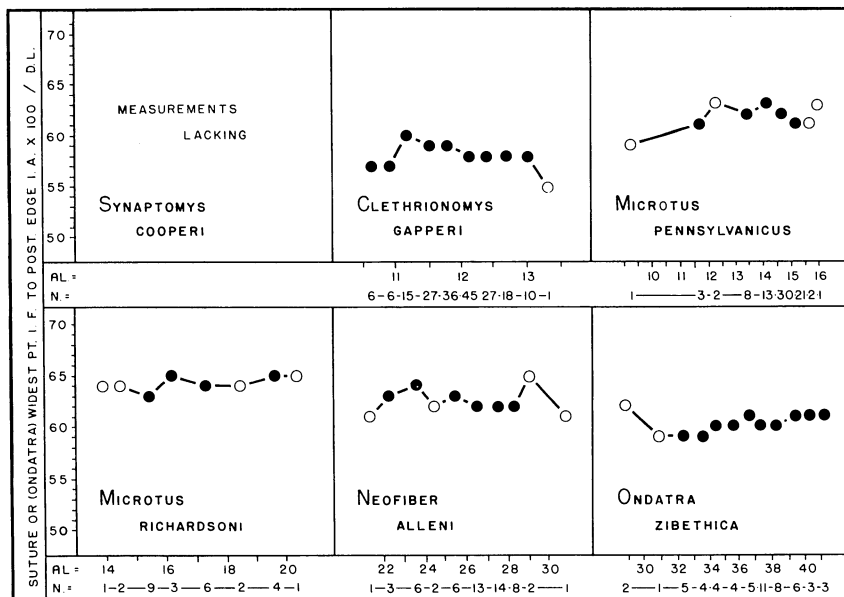


Fig. 6. The anteroposterior position of the premaxillary-maxillary suture (or in *Ondatra* the widest point) of the incisive foramina during the continual growth of the palate in five microtine species. The anteroposterior position is determined by the percentage of the diastemal length which lies between the suture (or in *Ondatra* the widest point) in the incisive foramina and the posterior edge of the incisive alveolus (suture or in *Ondatra* widest point i.f. to posterior edge i.a. x 100/d.l.) A.L. — alveolobasilar length in mm. N — number of specimens in each sample. The localities represented are the same as those in Figures 3 and 4.

limits of the incisive foramina do not vary greatly with age in most microtines. As can be seen in Figures 5 and 7, however, there is a trend in some species for the anterior limit to be more posteriorly situated and the posterior limit to be more anteriorly situated in older specimens. But the premaxillary-maxillary suture maintains a relatively constant position regardless of age changes and is the most constant value (Fig. 6). Its serrate pattern, however, often hinders its use as a landmark in precise measurements. The variation in the position of the anterior and posterior limits of the incisive foramina, as seen in Figures 5 and 7, may be construed as a result of size changes in the foramina themselves rather than as shifts in their position. Developmentally, the incisive foramina thus appear to be relatively constant in position in the six species intensively studied.

The interspecific differences in the location of the limits of the foramina and of the premaxillary-maxillary suture may be seen in Table II. One of the most interesting trends shown in this table is the posterior shift of the anterior limit of the foramina in *Ellobius*, *Ondatra*, *Microtus richardsoni*, *Lagurus*, *Neofiber*, and *Arvicola*, microtines that dig with their incisors or that are aquatic. This posterior shift of the anterior limit of the foramina is probably correlated in large part with the posterior shift of the nasopalatine ducts. When this same trend is sought in the

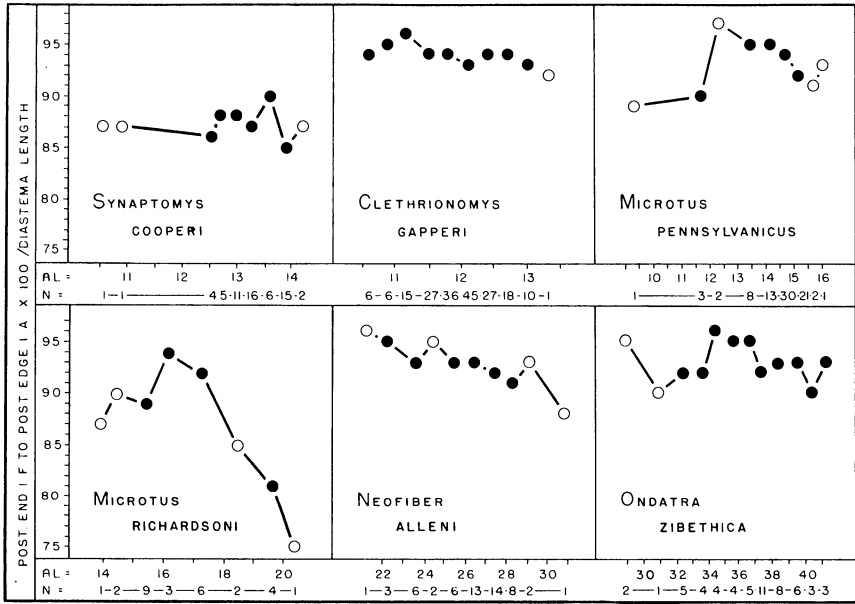


Fig. 7. The anteroposterior position of the posterior edge of the incisive foramina during the continual growth of the palate in six microtine species. The anteroposterior position is determined by the percentage of the diastemal length which lies between the most posterior edge of the incisive foramina and the posterior edge of the incisive alveolus (posterior end i.f. to posterior edge i.a. x 100/d.l.) A.L. — alveolobasilar length in mm. N — number of specimens in each sample. The localities represented are the same as those in Figures 3 and 4.

position of the premaxillary-maxillary suture, it is discovered that the posterior shift is reduced in amplitude. In the position of the posterior limit of the foramina there is no trend suggestive of correlation with the posterior shift in the position of the nasopalatine ducts.

The list of species in Table II may be separated roughly into two groups according to the position of the anterior limit of the incisive foramina. The lemmings (Lemmi) and more primitive voles (Microti) have 30 per cent or less of the diastemal palate lying anterior to the anterior limit of the incisive foramina. The voles (Microti) frequently considered more advanced or specialized have 30 per cent or more of the diastemal palate lying anterior to the anterior limit of the incisive foramina.

TABLE II

Anteroposterior Position of the Incisive Foramina Indicated by the Percentage of the Diastemal Length Lying Anterior to (A) the Anterior Tip of the Incisive Foramina, (B) the Premaxillary-Maxillary Suture, and (C) the Posterior Tip of the Incisive Foramina

N = number of specimens,  $\bar{x}$  = mean, s = standard deviation.

Genus, Species, Subspecies	N	A		B		C	
		$\bar{x}$	s	$\bar{x}$	s	$\bar{x}$	s
<i>Dicrostonyx groenlandicus</i>	5	28.8	2.17			88.6	3.65
<i>Synaptomys cooperi</i>	61	23.0	2.26			86.5	8.04
<i>Myopus schisticolor saianicus</i>	4	22.8	2.06			89.3	0.96
<i>Lemmus lemmus</i>	2	28.0				79.5	
<i>Lemmus trimucronatus alascensis</i>	15	26.6	2.29			86.2	2.62
<i>Clethrionomys glareolus</i>	9	22.7	2.65			93.7	3.46
<i>Clethrionomys rutilus</i>	6	19.7	2.16			88.8	1.33
<i>Clethrionomys gapperi gapperi</i>	191	22.4	1.80			93.9	3.39
<i>Clethrionomys gapperi proteus</i>	5	22.8	2.17			88.4	2.07
<i>Phenacomys intermedius</i>	20	30.3	3.39	63.0	4.62	90.6	3.47
<i>Phenacomys longicaudus</i>	4	26.3	4.03			96.0	1.41
<i>Phenacomys silvicola</i>	1	26.0				96.0	
<i>Eothenomys melanogaster</i>	21	30.2	3.00	65.6	3.21	96.4	2.24
<i>Eothenomys proditor</i>	8	29.5	1.60	66.0	2.72	97.1	2.36
<i>Antelionomys custos rubelius</i>	7	27.1	2.48	64.4	1.40	96.7	2.14
<i>Alticola roylei semicanus</i>	7	26.7	2.63	61.0	2.52	94.6	2.51
<i>Alticola stelzowi</i>	1	28.0		57.0		104.0	
<i>Arvicola terrestris</i>	6	37.2	3.06	63.7	1.86	84.7	5.09
<i>Microtus oregoni</i>	15	33.5	1.81	62.6	2.75	100.0	2.03
<i>Microtus richardsoni macropus</i>	28	40.9	2.53	63.7	1.56	88.5	5.35
<i>Microtus pennsylvanicus</i>	81	31.4	2.59	61.7	2.69	93.5	2.59
<i>Microtus californicus eximius</i>	19	32.7	1.97			96.8	1.83
<i>Microtus mexicanus</i>	16	32.9	2.20	65.6	3.26	94.5	1.75
<i>Microtus nivalis</i>	4	29.8	1.50	62.8	1.71	92.3	0.50
<i>Microtus roberti</i>	3	33.3	1.15	60.3	0.57	87.0	1.73
<i>Microtus ochrogaster</i>	12	34.5	3.26	62.2	2.52	89.7	3.39
<i>Microtus gregalis</i>	8	32.6	1.30	60.4	2.33	91.6	2.06
<i>Microtus abbreviatus</i>	3	32.7	4.04	62.7	4.04	90.3	3.05
<i>Microtus miurus</i>	3	32.7	0.58	60.7	1.15	92.0	2.00
<i>Lasiopodomys brandti</i>	8	32.9	0.98	66.3	2.12	92.4	2.45
<i>Neodon sikimensis</i>	7	34.3	1.60	67.1	2.91	93.9	2.12
<i>Neodon irene</i>	4	31.0	2.71	65.8	4.62	97.0	1.41
<i>Pitymys subterraneus</i>	7	34.6	2.07	67.7	2.69	93.6	3.05
<i>Pitymys pinetorum</i>	9	36.3	3.02	63.4	3.33	89.7	2.24
<i>Pitymys quasiater</i>	10	33.7	2.06	65.1	3.66	94.1	2.23
<i>Lagurus luteus</i>	3	40.3	4.16	60.7	3.79	84.3	1.53
<i>Lagurus curtatus</i>	9	37.0	2.69	68.2	3.83	97.9	3.33
<i>Neofiber alleni</i>	56	39.7	1.95	62.3	1.99	92.5	2.43
<i>Ondatra zibethica</i>	57	41.5	2.08			93.1	2.83
<i>Prometheomys schapschnikowi</i>	3	29.7	0.58	65.7	0.58	86.0	2.65
<i>Ellobius talpinus larvatus</i>	3	57.3	4.16	72.7	3.05	83.7	4.16

The size of the incisive foramina was determined by measurements of length and width. The length was measured as the greatest length of the foramen on either side. The lengths of the premaxillary and of the maxillary regions of the foramina were measured in species having a distinct premaxillary-maxillary suture. The width measurement was made from the lateral edge of one foramen to the corresponding lateral edge of its mate on the opposite side, and thus equals the width across both foramina.

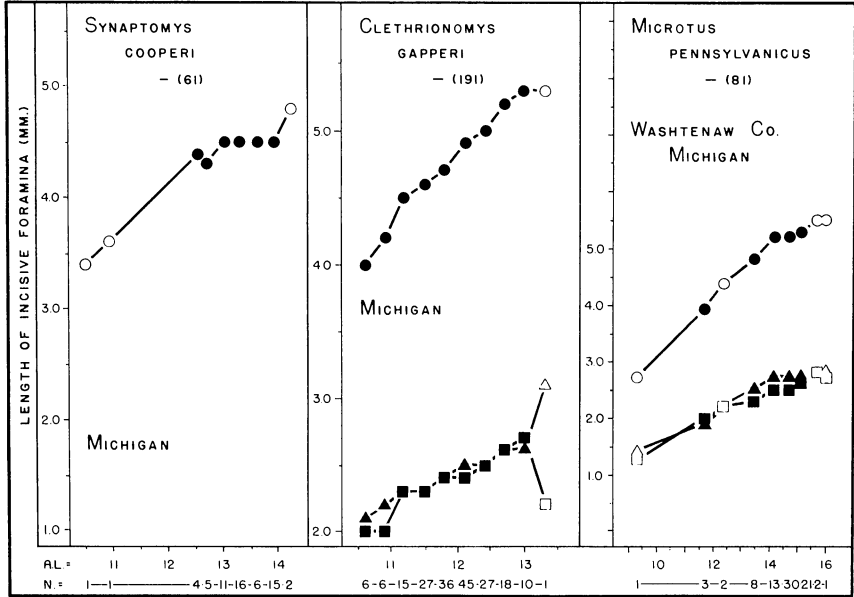


Fig. 8. The length of the incisive foramina (circles) and the lengths of their premaxillary (squares) and maxillary (triangles) regions during the continual growth of the palate in three microtine species. A.L. — alveolobasilar length in mm. N — number of specimens in each sample.

Width was measured at three different places when landmarks were constant enough to allow their use as end points. A width measurement was made for all species across the widest area enclosed by the premaxillary bones. In many species width was measured also across the mid-point of the region enclosed by the maxillary bones and across the foramina at the level of the suture.

The age changes in the length and width of the incisive foramina were examined in all species, but they were graphed for only a few as examples. These may be seen in Figures 8, 9, and 10.

The length of the incisive foramina in most microtines increases with age. In *Microtus richardsoni*, however, and usually to a lesser extent in a few other species, the length of the foramina decreases sharply in adulthood (Fig. 9; Pl. IV, A-D). When the lengths of the premaxillary- and



maxillary-enclosed parts of the foramina are examined separately, it is found that in most species the two parts increase at the same rate. In *Microtus richardsoni*, on the other hand, the premaxillary region increases at a normal rate throughout the life span, whereas the maxillary region in early life lengthens and then in later life shortens.

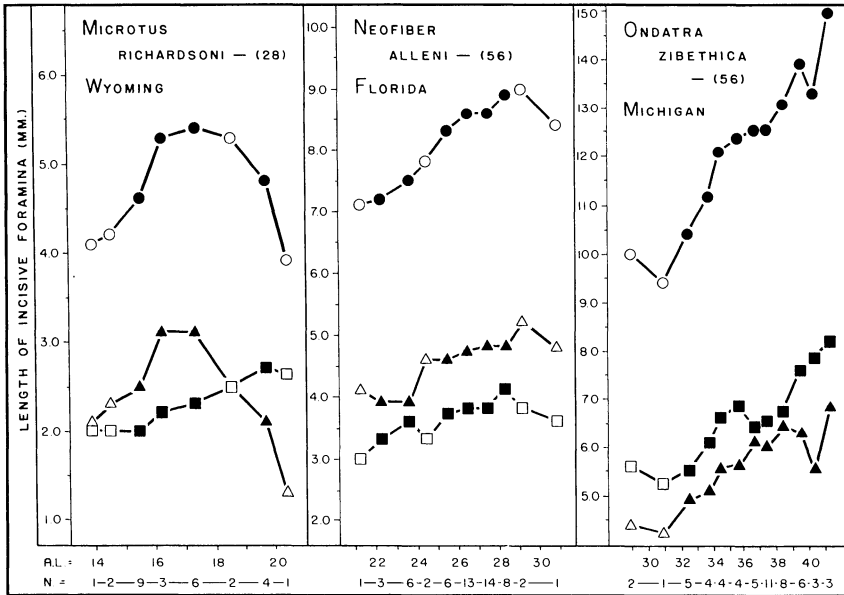


Fig. 9. The length of the incisive foramina (circles) and the lengths of their premaxillary (squares) and maxillary (triangles) regions during the continual growth of the palate in three microtine species. A.L. - alveolobasilar length in mm. N - number of specimens in each sample.

The width of the incisive foramina in many microtines increases with age. This increase is graphed for *Clethrionomys gapperi* in Figure 10. In this species both the maximum width in the premaxillary region of the foramina and the width at the level of the suture increase.

In *Microtus pennsylvanicus* (Fig. 10) the maximum width in the premaxillary region increases, the width at the suture is variable, and the width at mid-level in the maxillary region of the foramina decreases. In *Microtus richardsoni* (Fig. 10) this trend is carried still further. The maximum width in the premaxillary region decreases slightly, and the width at the suture decreases greatly. The width at mid-level in the maxillary region is reduced to nothing in adults, as the sides of the maxillary part of the foramina fuse (Pl. IV, A-D). Thus, in microtines there is a trend in some species for reduction in the size of the incisive foramina during the life span. This reduction occurs primarily in the posterior or maxillary part of the foramina and is detectable first as a reduction in the

width of this area. The shortening of the posterior part of the foramina in *Microtus richardsoni* is a by-product, due to the increasing extent of the contact between the lateral surfaces of the foramina. The functional or developmental significance of this trend is not known.

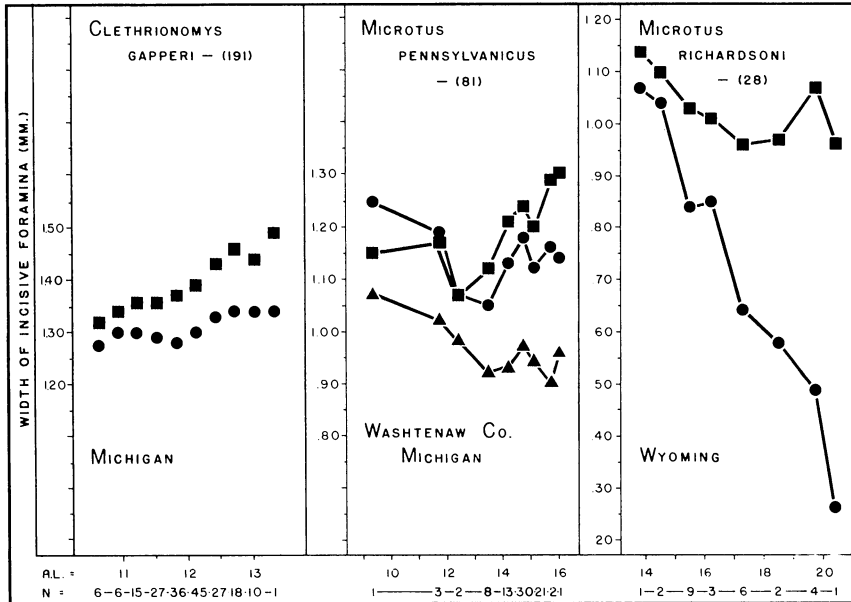


Fig. 10. The width of the incisive foramina at the widest point in their premaxillary region (squares), at the level of the premaxillary-maxillary suture (circles), and at mid-length in their maxillary region (triangles) during the continual growth of the palate in three microtine species. A.L. — alveolobasilar length in mm. N — number of specimens in each sample.

The length of the incisive foramina is frequently used as a taxonomic character. It often has been shown, however, to be the most variable of the usual cranial measurements. In *Ondatra* its coefficient of variation was found to be  $9.98 \pm 0.46$  (Latimer and Riley, 1934) and in *Microtus pennsylvanicus*,  $17.07 \pm 1.09$  in males and  $14.60 \pm 1.01$  in females (Goin, 1943). Examination of this measurement in 40 species of microtines has shown that it differs greatly from species to species and that in many cases it can still be used to distinguish particular genera or species.

It was noted by Hinton in his review of the Microtinae (1926:15) that the incisive foramina are usually moderately large, but in forms showing marked fossorial specialization of the skull they are much reduced in size. Among microtines this is most clearly seen in *Ellobius* (Pl. III, H). Extreme reduction in the size of the foramina in fossorial, incisor-digging rodents is apparent also in species of the families Bathyergidae, Geomyidae, and Spalacidae and in the genus *Tachyoryctes* (Muridae). In the species of

the families Bathyergidae and Geomyidae and in the genera *Tachyoryctes* and *Ellobius* the extreme reduction in the size of the foramina is associated with an extreme posteriad shift in their position. In contrast, the markedly fossorial species among the sciuromorph and hystricomorph rodents do not show these trends.

The shape and size relationships of the premaxillary and maxillary parts of the incisive foramina are illustrated in Plates I-IV for various microtines exemplifying particular conditions. The size and shape of the premaxillary part are generally rather constant. Variability within and between species is centered in the maxillary part of the foramina. The widest area in the foramina is nearly always in the posterior half of the premaxillary part, the area traversed by the nasopalatine ducts. The constancy of this part of the foramina may well be a reflection of the constancy of the relationship with, and the importance of, the nasopalatine canals. There is usually a constriction of the foramina at the premaxillary-maxillary suture. Maximal breadth of the maxillary part of the foramina is seen in *Myopus* (Pl. I, B). Maximal length of this part is seen in *Alticola* (*Platycranius*) (Pl. II, B), in which subgenus the posterior tips of the foramina lie behind the anterior edge of the first molariform tooth on each side. Narrowing of the maxillary part of the foramina in old age is seen in the genera *Lemmus* (*trimucronatus* and *lemmus*), *Arvicola* (*terrestris*), and *Ondatra* (*zibethica*), in the subgenera of *Microtus*, *Aulacomys* (*richardsoni*) and *Stenocranius* (*gregalis*, *miurus*, and *abbreviatus*), and to a lesser extent in certain species of the subgenus *Microtus* (*pennsylvanicus*, and *oeconomus operarius*). Within the subgenus *Stenocranius* the trend is most marked in *abbreviatus*. In all of these microtines which show narrowing of the maxillary part in old age, the constriction at the suture is especially prominent. As noted above, foramina of minimal size within the Microtinae are found in the extreme fossorial and incisor-digging form *Ellobius*. It is difficult to decide whether narrowing of the foramina in adulthood in the above-named forms represents an incipient modification following an adaptational pattern similar to that already well developed in *Ellobius*, or whether it is a token of nonadaptive physiological changes during adulthood or of some other condition.

In microtines I have been unable to find any support for correlation between "small size of the incisive foramen and high degree of humidity in the environment." Nor have I found any evidence to support the idea that "animals which live far away from large rivers usually have larger foramina than animals which live close to rivers." These two ideas were proposed by Moojen (1948:327) to explain the size variation of the incisive foramen in Brazilian spiny rats (*Proechimys*). On the generic level in microtines the smallest foramina do not occur in aquatic genera (*Ondatra*, *Neofiber*, *Arvicola*), but in *Ellobius*, a genus that is found only in the deserts and steppes of Central Asia (Allen, 1940; Berg, 1950; Ognev, 1950). *Lagurus*, another genus found in dry areas, has foramina of the same size as those found in certain species of *Microtus* and in other genera typical of moister environments (Pl. III, E). On the subspecific level there is the same lack of correlation. Without extensive data on habits and microhabitat throughout the year, however, it is difficult to decide with any

accuracy whether the microclimate of one subspecies is more humid than that of another.

#### Premaxillary and Interpremaxillary Nutritive Foramina

A careful examination of these foramina was made in the species and specimens listed in Table II. In many species these foramina were found to be extremely variable in position and number, but in some they were found to be invariable enough to have diagnostic significance. The variability and patterns of these foramina in microtines are stated for each group examined, with the hope that the diagnostic characters provided will aid in the identification of fragmentary microtine remains. Plates I-IV, showing the diastemal palate, should also be examined.

*Dicrostonyx groenlandicus*.—One symmetrical bilateral pair of premaxillary foramina is present in all examined specimens; an interpremaxillary foramen between the premaxillary foramina is sometimes present, but is usually small or lacking.

*Synaptomys cooperi*.—Similar to *Dicrostonyx*.

*Myopus schisticolor*.—Two symmetrical bilateral pairs of premaxillary foramina are present, one pair lying medial to the other, its foramina almost fusing in the mid-line; sometimes present also is a minute interpremaxillary foramen considerably posterior to the premaxillary foramina.

*Lemmus (lemmus and trimucronatus)*.—Similar to *Dicrostonyx* and *Synaptomys*, but premaxillary and interpremaxillary foramina are usually of equal prominence.

*Clethrionomys (glareolus, rufocanus, rutilus, and gapperi)*.—Foramina are variable in number and arrangement, but most specimens have three arranged in the same pattern as those in *Dicrostonyx* and *Synaptomys* and situated about one-third of the way back from the incisors to the incisive foramina.

*Phenacomys intermedius*.—Foramina are close to the incisors, but are highly variable in number and distribution.

*Eothenomys* and *Antelionomys*.—Foramina variable.

*Alticola roylei*.—In all adult specimens there are three foramina of equal size: a symmetrical bilateral pair of premaxillary foramina anterior to a single interpremaxillary foramen.

*Arvicola terrestris*.—In most specimens there are three foramina of nearly equal size: a symmetrical bilateral pair of premaxillary foramina and a single interpremaxillary foramen between them.

*Microtus oregoni*.—In most specimens there are three foramina: a symmetrical bilateral pair of premaxillary foramina and a single interpremaxillary foramen between or behind them.

*Microtus richardsoni*.—In at least 65 per cent of the specimens there is a distinctive and constant pattern; in the other 35 per cent of the specimens there are suggestions of the same pattern which is obscured by increase or decrease in number of foramina and shifts in their relative positions. In the basic pattern there are five foramina: two bilateral pairs of premaxillary

foramina, of which the members of the anterior pair are 0.7 to 0.9 mm. apart and the members of the posterior pair are very close together, and a still more posterior interpremaxillary foramen.

*Microtus pennsylvanicus*.—In at least 60 per cent of the specimens there is a distinctive and constant pattern; in 27 per cent the basic arrangement is the same, but there are modifications in number or position; in 13 per cent the basic pattern could not be demonstrated. Typically, there are four premaxillary foramina arranged in pairs, one of which is usually more posterior and is represented by larger and more medial foramina.

*Neofiber alleni*.—Typically, there are one or two large interpremaxillary foramina midway between the incisors and the incisive foramen. There are four patterns: (1) In 42 per cent of the specimens there is a pair of interpremaxillary foramina, a large anterior one and a smaller posterior one as far as 1.1 mm. away; (2) In 39 per cent of the specimens there is a single large interpremaxillary foramen which bifurcates dorsally into a large anterior branch and a smaller posterior branch; (3) In 17 per cent of the specimens there is a single large interpremaxillary foramen without visible branching; (4) In 2 per cent of the specimens the pattern is similar to (1) except for the fact that the anterior interpremaxillary foramen is represented by a bilateral pair of premaxillary foramina. Smaller or accessory foramina may occur in a fan-shaped zone anterior and lateral to the above-mentioned foramina.

*Ondatra zibethica*.—Foramina are highly variable in number and arrangement, but in many specimens the three most prominent foramina are arranged in the same pattern as those in *Clethrionomys*.

## CIRCULATORY FEATURES

The blood vessels of the diastemal palate were studied most extensively in three specimens of *Ondatra zibethica* collected at Ann Arbor, Washtenaw County, Michigan. In these the arteries were injected with red latex, the veins with blue. Study of the vessels in these specimens was carried on through gross dissections viewed with a stereomicroscope. Since the vessels of the muskrat were most thoroughly studied because of their larger size and the availability of fresh specimens for injection of vessels, they will be described in detail below, and subsequently the variations found in other microtines will be compared with the pattern in the muskrat.

### Arterial System

(Fig. 11)

The arterial supply to the palate is furnished primarily by the paired palatine arteries which arise from the internal maxillary artery, pass through the palatine canals, and, with the palatine nerves, emerge on the surface through the paired posterior palatine foramina. Just after emerging from the foramen each artery sends a branch posteriorly under the palatine mucosa. This branch, in turn, sends twigs to the adjacent gums

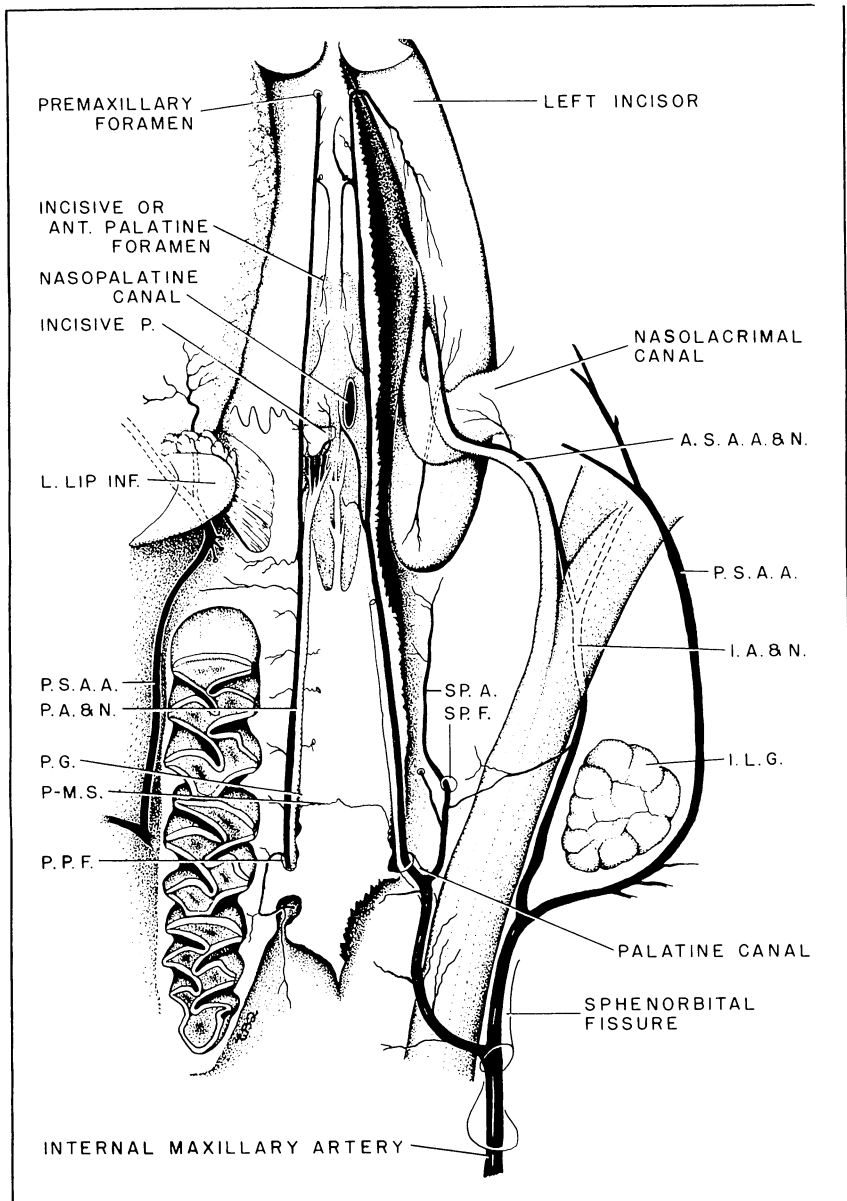


Fig. 11. The arterial system of the diastemal palate in the muskrat (*Ondatra z. zibethica*. QC 3-C-617, Washtenaw Co., Michigan, U.S.A.). A.S.A.A. & N. — anterior superior alveolar artery and nerve, I.A. & N. — infraorbital artery and nerve, I.L.G. — intra-orbital lacrimal gland, Incisive P. — incisive papilla, L.Lip.Inf. — dorsal inflexus of the lower lip, P.A. & N. — palatine artery and nerve, P.G. — palatine groove, P-M.S. — pre-maxillary-maxillary suture, P.P.F. — posterior palatine foramen, P.S.A.A. — posterior superior alveolar artery, SP.A. — sphenopalatine artery, SP.F. — sphenopalatine foramen.

and a branch dorsally through a deep groove in the palatine bones; it also sends branches posteriorly into the glandular mucosa of the adjacent soft palate. The palatine arteries extend forward with the nerves in the deep palatine grooves and give off small branches on either side to the adjacent gums and palatine mucosa. Just anterior to the first molariform tooth small branches are sent laterally; these closely approach branches of the posterior superior alveolar artery. In the rat (*Rattus*) Greene (1935:185) reported an anastomotic branch between these elements.

At or near the posterior end of the incisive foramina the palatine artery on each side divides into two branches of nearly equal size. The medial one sends several branches dorsad through the incisive foramen to the nasal chambers and passes other branches to the incisive papilla. The lateral one extends along the lateral edge of the incisive foramen and sends branches to the highly vascular tissue of the incisive papilla. One small branch passes laterally over the premaxillary-maxillary suture. The main branch continues anteriorly along the side of the incisive foramen and sends small branches medially to the mucosa of the nasopalatine duct and to the anterior part of the diastemal palate. The main branch of the palatine artery on each side ends in small vessels which pass dorsad in or between the premaxillary bones. The larger and more lateral of these vessels pass through the bone to the alveoli of the incisors and follow them posteriorly along their medioventral edge to the vicinity of the nasolacrimal duct crossing. Anterior terminal branches of the palatine arteries could not be traced into the nasal chambers in the specimens examined.

Contributing slightly to the palatine arterial supply is the posterior superior alveolar artery, which arises from the internal maxillary artery in the sphenorbital fissure and passes ventrally and then anteriorly along the lateral surface of the alveolar ridge. Anterior to the first molariform tooth, small branches are sent into the bone; these closely approach lateral branches of the palatine arteries noted above. More anteriorly, branches are sent to the inflexi peiliti of upper and lower lips.

### Venous System

(Fig. 12)

The veins of the diastemal palate can be separated into two major categories, those lying anterior or rostral to, and those lying posterior to, the nasopalatine canals. The anterior palatine veins consist of a pair of lateral veins and a single median vein. The lateral anterior palatine veins originate near the nasopalatine canals and then course forward along with the palatine arteries on each side. The median anterior palatine vein arises from a weakly developed anterior nasopalatine venous plexus in the tissue within and around the most anterior part of the incisive foramina. It then leads forward in the midline of the diastemal palate and is followed on each side by small branches of the palatine arteries. Near the alveoli of the incisors the median vein bifurcates; the resulting branches lead into the lateral veins on their respective sides. Small branches of the median and lateral veins

pass into the premaxillary and interpremaxillary foramina along with small arterial branches from the palatine arteries. In the gums behind the incisors the lateral veins break up into small anastomosing branches which are continuous with small labial veins leading to the anterior facial vein near the angle of the mouth.

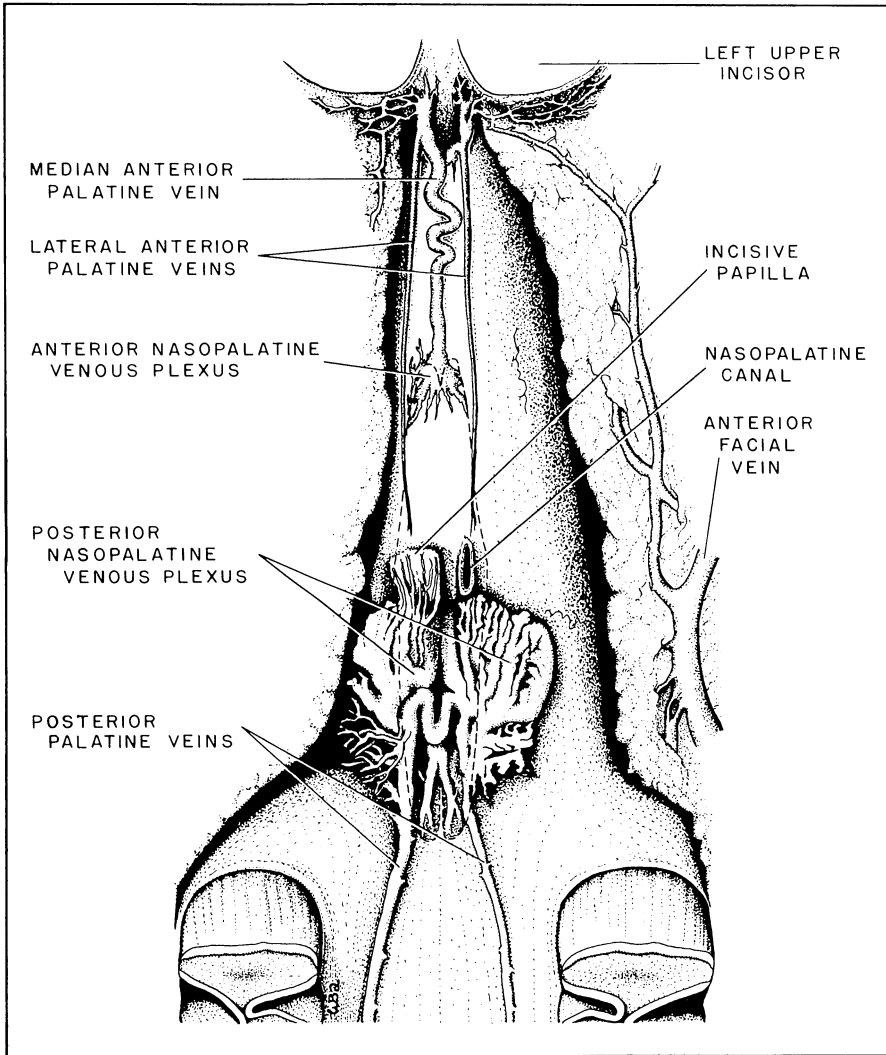


Fig. 12. The venous system of the diastemal palate in the muskrat (*Ondatra z. zibethica*. QC 3-C-616 and 3-C-619, Washtenaw Co., Michigan, U.S.A.).

The posterior palatine veins are paired and lie in the palatine grooves with the paired palatine arteries and nerves. At the posterior end of the



incisive foramina they enter a large venous plexus which is continuous dorsally with venous channels in the nasal chamber. From this posterior nasopalatine venous plexus a rich network of branches extends into the incisive papilla. The concentrated mass of vessels that forms the plexus itself extends laterally, covering, or passing ventrally over, the palatine arteries and nerves on each side. The plexus does not extend anteriorly beyond the level of the nasopalatine canals and is, therefore, confined to the posterior part of the incisive foramina, or that part supported by the maxillary bones.

#### Comparisons with Other Microtines

Gross dissections of two latex-injected *Microtus pennsylvanicus* specimens failed to show any significant differences in the major vessels of the palate from those described above for *Ondatra*. Small branches, however, were not traced as extensively as they were in *Ondatra*. Likewise, in serial sections of heads of *Lemmus*, *Synaptomys*, *Phenacomys*, *Clethrionomys*, and *Microtus* significant differences in the major vessels of the diastemal palate were not seen; however, minor variations were commonly found. A special study was made only of such minor variations as involve the small anterior terminations of the anterior palatine vessels which pass dorsad through the small premaxillary and interpremaxillary foramina. These vessels are of interest in considerations of the function and importance of the foramina and their different patterns and sizes in diverse microtines.

In the specimen of *Lemmus trimucronatus* a set of medial vasa passes through a rather large interpremaxillary foramen and enters the blood spaces beneath the ventral lining of the nasal passages. Pairs of lateral vasa enter premaxillary foramina, a medium-sized one on each side slightly anterior to the interpremaxillary foramen. These vasa join vessels of the marrow spaces in the premaxillae, and vessels from these spaces pass to the alveoli of the incisors.

In the specimen of *Phenacomys longicaudus* vasa penetrate the premaxillae via bilateral foramina and join extensive marrow spaces within the bone.

In the specimen of *Synaptomys cooperi* vasa penetrate the premaxillae via bilateral premaxillary foramina and a median interpremaxillary foramen to join the vessels of the extensive marrow spaces.

In the specimen of *Clethrionomys californicus* blood vessels enter an interpremaxillary foramen. They then pass forward in a median bony canal, and between the anterior parts of the two incisive alveoli join the vessels of the marrow spaces on each side.

In the specimen of *Microtus mogollonensis* the vasa that pass dorsad into the premaxillae are paired. They first enter a median interpremaxillary foramen. Within the bone the canal leading from the foramen bifurcates, and the paired vessels diverge into these canals. These vessels extend anteriorly in bony canals and pass beyond the level of the anterior ends of the incisive alveoli; enroute, they come to lie in the loose tissue under the

ventral nasal mucosa. They finally terminate in the ventrolateral region of the external nares.

In the specimens mentioned above, as a general rule, the penetrating vessels are artery and vein complements, although often the arteries are very small and difficult to trace. It should be noted that in these specimens there are extensive networks of vessels in the premaxillary marrow cavities and that these may be followed to vessels of the incisive alveoli and those of the nasal mucosa. Where distinct vessels are described for these areas, they are independent and pass without deviation to the alveolar or nasal regions concerned. It is easy, however, to visualize how they probably developed from the more indirect and irregular vessels passing through the marrow spaces.

#### Significance of Vessels in the Palatine Foramina

The functional significance of many of the palatine foramina may be related to the blood vessels which pass through them. In this regard, the posterior part of the incisive foramina, or that part embraced by the maxillary bones and lying behind the nasopalatine canal, is of great interest. Although it transmits small branches of the palatine arteries and nerves, it appears to be primarily concerned with the transmission of the vessels of the posterior nasopalatine venous plexus. The posterior part of the incisive foramina could be much reduced in size without affecting nerve and artery passage, but the venous transmission between nasal and palatine areas would be greatly curtailed. It might be inferred that the size of the posterior part of the incisive foramina is a reflection of the development of the nasopalatine venous connection, and this probably is frequently the case. It should be remembered, however, that although reduced nasopalatine venous passage seems assured when the posterior part of the incisive foramina is small, increased nasopalatine venous passage is not necessarily consequential when it is large.

The premaxillary and interpremaxillary foramina are of small size and are probably not of great functional significance. Nevertheless, their variations in number, size, and location are of some interest since they sometimes appear to be species characters, although rather variable ones. The lateral premaxillary foramina in microtines are concerned with the passage of vessels to the marrow spaces or sometimes directly to the incisive alveoli. The median or interpremaxillary foramina in microtines are concerned with passage of vessels to the marrow spaces or sometimes directly to the nasal chambers. Thus, these foramina are concerned with blood vessel transmission, but the routes of passage and the locations of the terminations of these vessels cannot be correlated with the positions of the foramina through which they pass. Attempts, therefore, at homologizing particular premaxillary or interpremaxillary foramina between species are not practical.

## SUMMARY AND CONCLUSIONS

In rodents of the subfamily Microtinae there are three paired inflexi (infoldings) of the lips. A dorsal pair of inflexi of the lower lip is present and has nearly the same appearance in all species. A ventral pair of inflexi of the lower lip and a pair of inflexi of the upper lip are highly developed in certain specialized species. Within the subfamily the increased inflexal development is accompanied by: (1) a reduction and loss of the anterior longitudinal ridge of palatal mucous membrane; (2) an increase in the relative length in the diastemal palate, due in part to increase in relative length during life; (3) a posteriad shift of the nasopalatine canals and their palatal openings; (4) a posteriad shift of the premaxillary region of the incisive foramina; and (5) a reduction in the number of transverse diastemal ridges of palatal mucous membrane. These trends are most marked in incisor-digging genera.

The incisive foramina increase in size with age in some species and decrease in others. The decrease begins as a narrowing of the area embraced by the maxillary bones and may lead to its eventual closure. The premaxillary area of the incisive foramina is occupied primarily by the nasopalatine canals, which are present and patent in all adult specimens examined. The maxillary area of the foramina is occupied primarily by the posterior nasopalatine venous plexus. Small premaxillary and inter-premaxillary foramina are variable and transmit arteries and veins.

The arterial supply of the diastemal palate is furnished by paired palatine arteries passing rostrally from the internal maxillary artery. The venous drainage is divisible into anterior and posterior systems at the level of the nasopalatine canals. In the posterior system are the large posterior nasopalatine venous plexus and the paired posterior palatine veins. In the anterior system are the small anterior nasopalatine venous plexus and three anterior palatine veins.

The results of this study stress the fact that measurements of the diastemal palate and the incisive foramina can be used as taxonomic characters, but that their valid use for a particular species or genus is dependent on analyses of their individual variation and modification during growth and aging. Furthermore, by such studies are differences in growth and aging processes made apparent; these may well be more definitive and significant in the characterization of particular taxonomic units than are measurements alone. When anatomical differences between animals are analyzed, correlations with ontogenetic, phylogenetic, functional, and adaptational relationships should be sought, for these are clues to the mechanism of evolution.

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PLATE I

The diastemal palate and incisive foramina of adult microtines in selected examples to illustrate generic characteristics (not drawn to same scale).

- A. *Dicrostonyx groenlandicus* ♀ (CNHM 7079); Pt. Barrow, Alaska.
- B. *Myopus schisticolor* ♀ (CNHM 30494); 15 mi. N. of Urga, Mongolia.
- C. *Clethrionomys gapperi* ♀ (UMMZ 86206); Presque Isle County, Michigan, U.S.A.
- D. *Phenacomys longicaudus* ♀ (UMMZ 97575); Sonoma County, California, U.S.A.
- E. *Synaptomys cooperi* ♂ (UMMZ 82737); Presque Isle County, Michigan, U.S.A.
- F. *Lemmus lemmus* ♂ (UMMZ 92711); Enontekiö, Fjeld Saana, Finland.
- G. *Phenacomys intermedius* ♂ (UMMZ 67889); Teton Park, Wyoming, U.S.A.
- H. *Eothenomys proditor* ♀ (CNHM 33004); Nguluko, Yunnan, China.

PLATE I

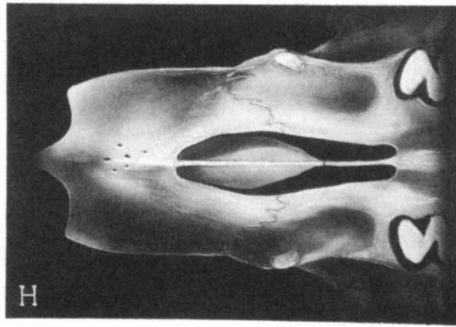
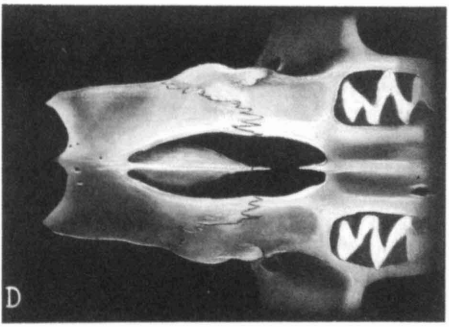
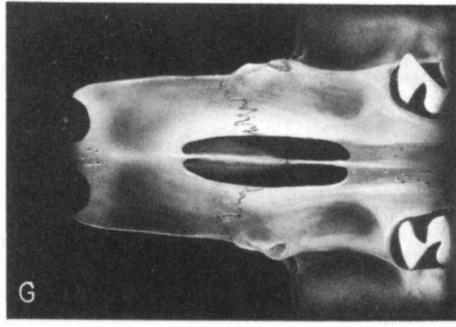
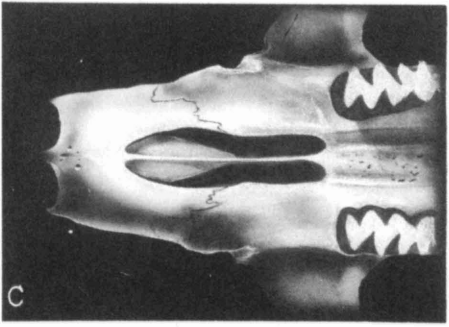
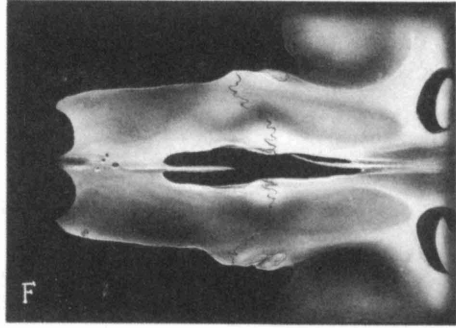
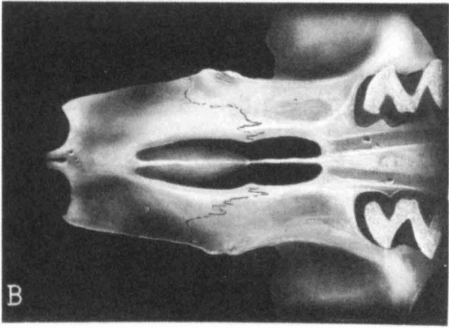
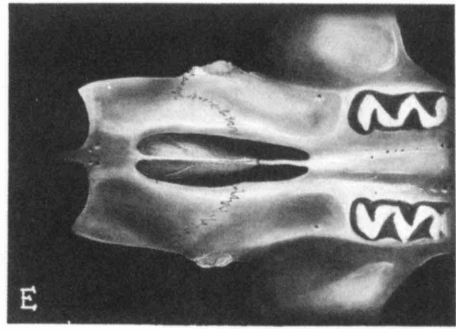
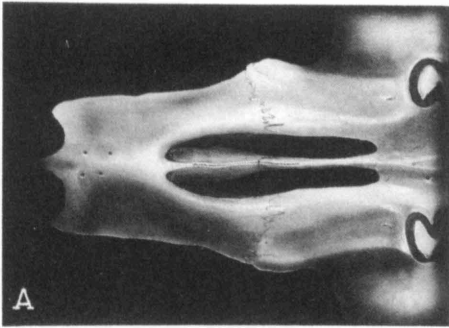


PLATE II

The diastemal palate and incisive foramina of microtines. A through D show the typical characters of particular subgenera. E and F show the latitude of the individual variation that occurs in one species. G and H show the age changes that occur in *Microtus oeconomus operarius*. All specimens except G are adults (not drawn to same scale).

- A. *Alticola (Alticola) roylei semicanus* ♂ (CNHM 31687); Sain Noin Khan, Mongolia.
- B. *Alticola (Platycranius) strelzowi* ♀ (CNHM 34033); Tchegan-Burgaz, Altai, Siberia.
- C. *Microtus (Chilotus) oregoni* ♂ (UMMZ 81934); Pierce County, Washington, U.S.A.
- D. *Microtus (Microtus) pennsylvanicus* ♂ (UMMZ 90407); Pennington County, South Dakota, U.S.A.
- E. *Microtus (Microtus) californicus* ♀ (UMMZ 80400); Marin County, California, U.S.A. Alveolobasilar length, 15.4 mm.
- F. *Microtus (Microtus) californicus* ♀ (UMMZ 80410); Marin County, California, U.S.A. Alveolobasilar length, 15.8 mm.
- G. *Microtus (Microtus) oeconomus operarius* ♀ (UMMZ 94078); 7 mi. N. of Bettles, Alaska. Alveolobasilar length, 12.8 mm.
- H. *Microtus (Microtus) oeconomus operarius* sex? (UMMZ 94068); Kiana, Kobuk River, Alaska. Alveolobasilar length, 16.4 mm.



PLATE II

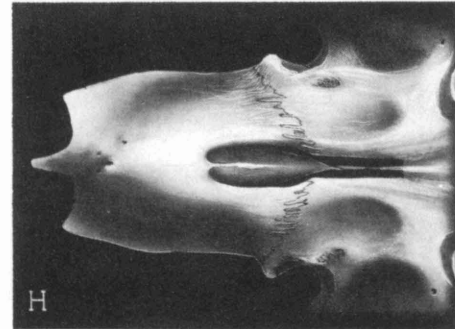
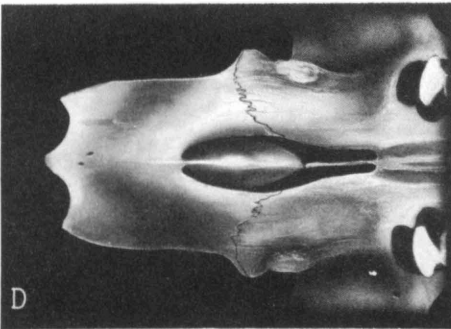
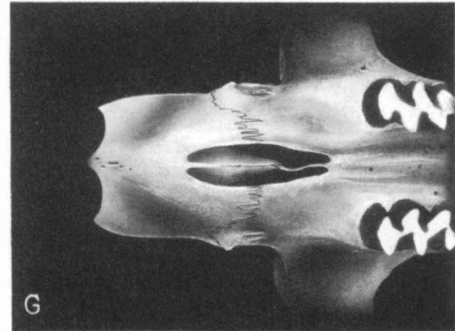
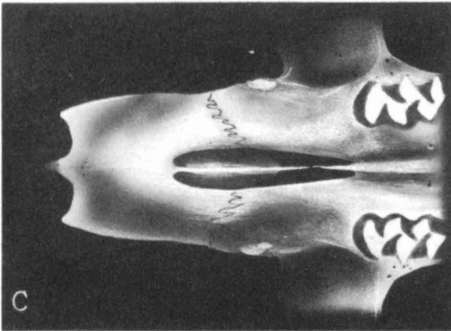
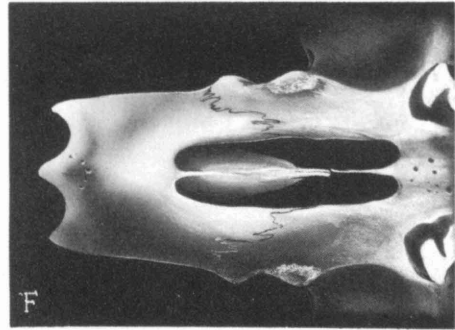
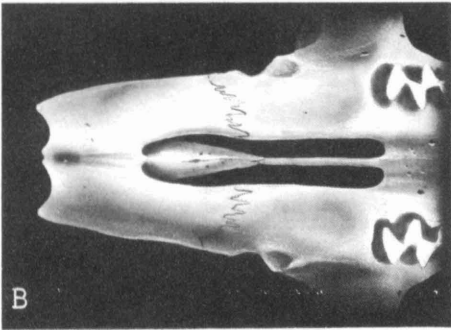
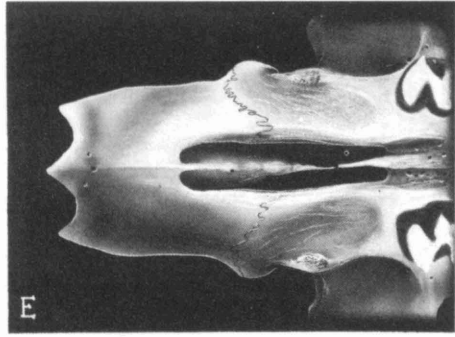
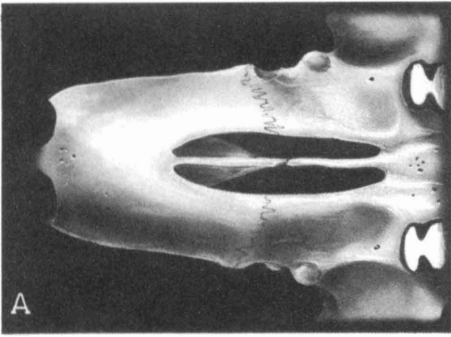


PLATE III

The diastemal palate and incisive foramina of adult microtines in selected examples to illustrate generic characteristics (not drawn to same scale).

- A. *Microtus (Pedomys) ochrogaster* ♂ (UMMZ 95769); Meade County, Kansas, U.S.A.
- B. *Microtus (Stenocranius) miurus* ♂ (CNHM 20063); Sheep Creek, Kenai Peninsula, Alaska. Note particularly the constriction of the maxillary part of the incisive foramina.
- C. *Phaiomys leucurus* ♀ (UMMZ 75183); Rupshu-Tsokar, Kashmir, India.
- D. *Pitymys pinetorum* ♂ (UMMZ 92628); Campbell County, Virginia, U.S.A.
- E. *Lagurus (Lemmiscus) curtatus* ♀ (UMMZ 78206); Blaine County, Idaho, U.S.A.
- F. *Neofiber alleni* ♀ (UMMZ 83575); Alachua County, Florida, U.S.A.
- G. *Prometheomys schaposchnikowi* sex? (MCZ 25971); N. Osetia, N. Caucasus, U.S.S.R.
- H. *Ellobius talpinus larvatus* sex? (MCZ 24454); Mongolia. Note particularly the extreme posteriorward shift in the position of the incisive foramina and their reduced size.

PLATE III

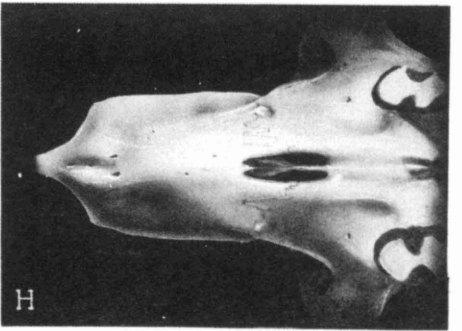
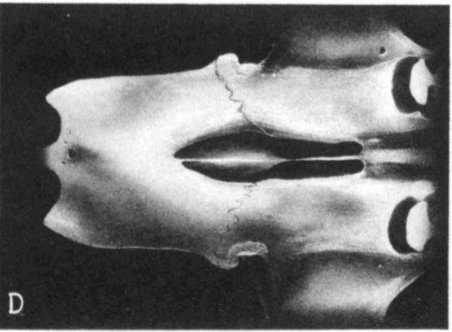
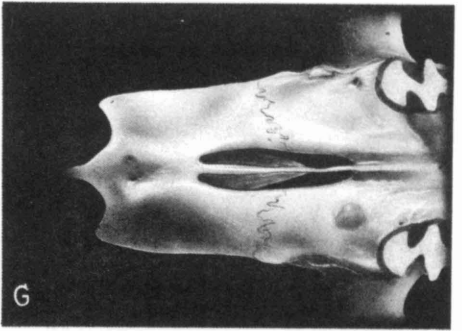
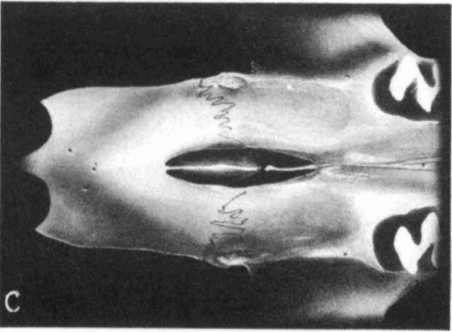
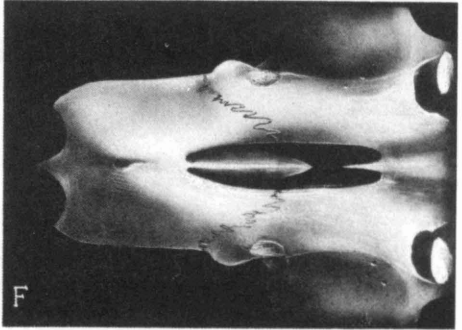
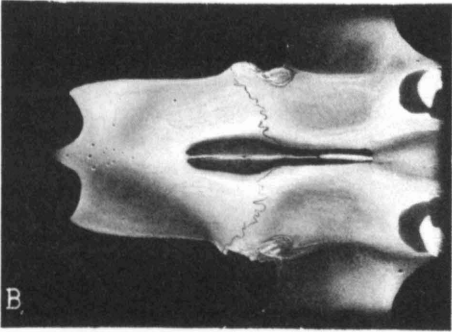
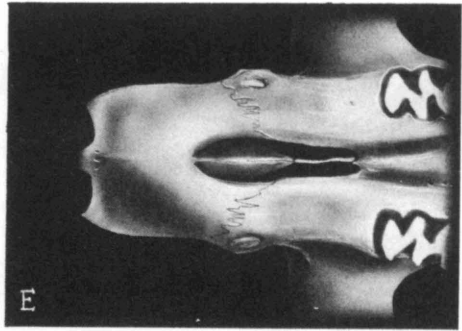
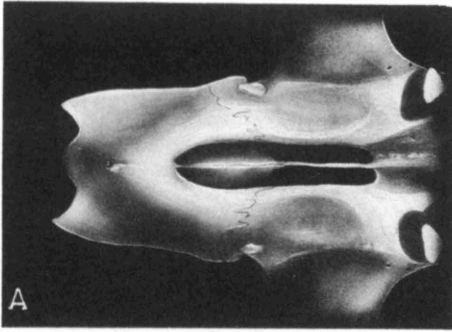
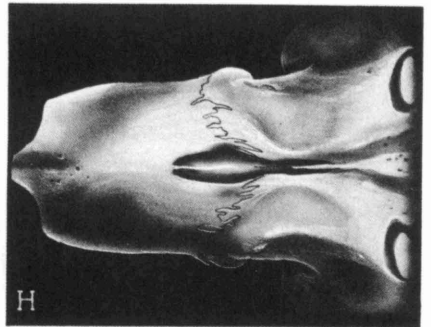
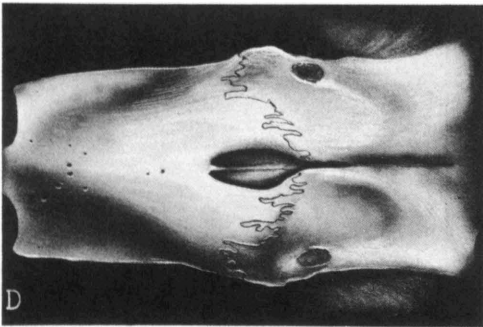
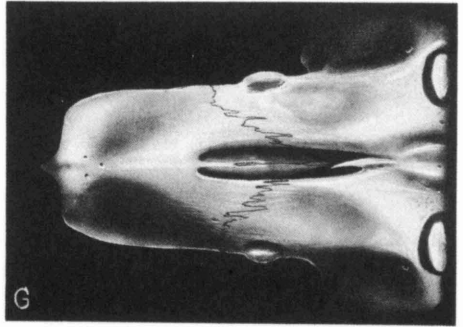
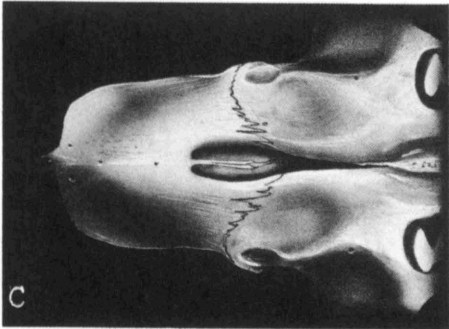
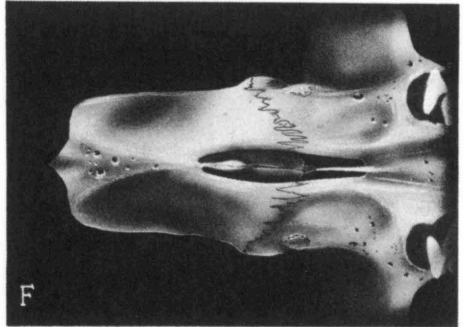
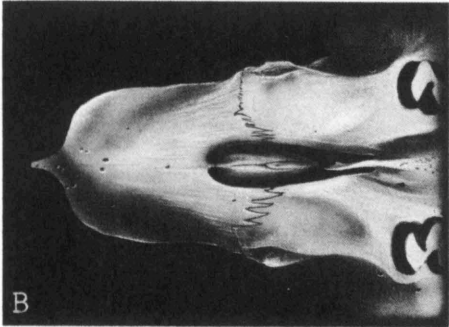
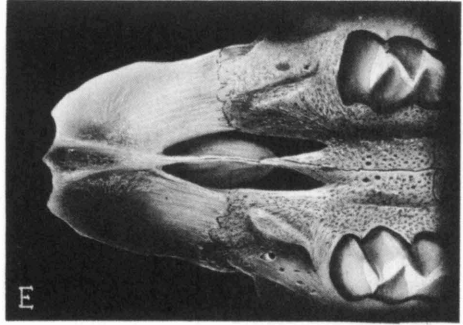
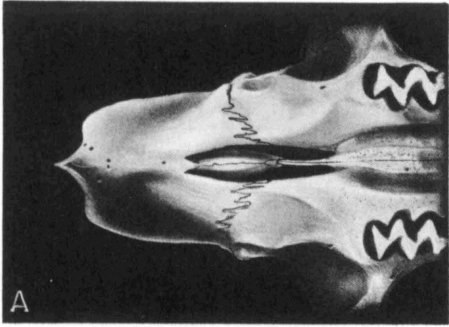


PLATE IV

The diastemal palate and incisive foramina of three aquatic microtines, showing the changes that occur with age. Note particularly the reduction of the maxillary part of the incisive foramina in *Microtus richardsoni* and *Arvicola terrestris* and the apparent absence of this reduction in *Ondatra zibethica* (not drawn to same scale).

- A. *Microtus (Aulacomys) richardsoni* ♀ (UMMZ 67971); Teton Park, Wyoming, U.S.A. Alveolobasilar length, 13.9 mm.
- B. *Microtus (Aulacomys) richardsoni* ♂ (UMMZ 67975); Teton County, Wyoming, U.S.A. Alveolobasilar length, 15.9 mm.
- C. *Microtus (Aulacomys) richardsoni* ♂ (UMMZ 67977); Teton County, Wyoming, U.S.A. Alveolobasilar length, 17.0 mm.
- D. *Microtus (Aulacomys) richardsoni* ♂ (UMMZ 62078); Teton County, Wyoming, U.S.A. Alveolobasilar length, 20.4 mm.
- E. *Ondatra zibethica* ♀ (QC 3-C-573); Jackson County, Michigan, U.S.A. About 22 days old. Alveolobasilar length, 23.3 mm.
- F. *Ondatra zibethica* ♀ (UMMZ 77836); Livingston County, Michigan, U.S.A. Old adult. Alveolobasilar length, 40.0 mm.
- G. *Arvicola terrestris* ♂ (CNHM 6436); Meiringen, Switzerland. Alveolobasilar length, 17.6 mm.
- H. *Arvicola terrestris* ♂ (CNHM 63850); Ob. Bayern, Germany. Alveolobasilar length, 21.3 mm.

PLATE IV





No. 30. The Darters of the Genera <i>Hololepis</i> and <i>Villora</i> . By Carl L. Hubbs and Mott Dwight Cannon. (1935) Pp. 93, 3 plates, 1 figure . . . . .	\$0.50
No. 31. Goniobasis of the Coosa River, Alabama. By Calvin Goodrich. (1936) Pp. 60, 1 plate, 1 figure . . . . .	\$0.35
No. 32. Following Fox Trails. By Adolph Murie. (1936) Pp. 45, 6 plates, 6 figures . . . . .	\$1.00
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