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EARTH SCIENCES

THE BIOSTRATIGRAPHY OF ARVICOLINE RODENTS IN NORTH AMERICA

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Arvicoline rodents are presently the most useful biostratigraphic tools in North America for the correlation of continental sediments that are Blancan in age or younger. Recent work in the Central Great Plains suggests that they also may have value for intercontinental correlations. About one-third of the Blancan genera of arvicolines became extinct at the end of Blancan time, while the earliest post-Blancan faunas contain very few arvicolines. The fauna from beneath the "type-S Pearlette Ash" at the type section of the Sappa Formation (1.2 million years B.P.) contains the earliest dated record of a *Microtus*-like microtine (*Allophaiomys*) from North America. Essentially the same arvicoline occurs beneath the Kansas Till in Doniphan County, Kansas. This arvicoline may well be an immigrant from Eurasia which entered North America in the Early Pleistocene and may be of considerable use in correlation with the European sequence. A zonation for the Late Cenozoic in North America based on arvicolines is proposed, and evolution within the Ondatrini is discussed.

† † †

Arvicoline rodents are widely distributed, evolve rapidly, and can be recovered in large numbers from most continental Late Pliocene and Pleistocene sites in the Northern Hemisphere. These attributes make them useful biostratigraphic tools, and their usefulness has been enhanced by detailed studies of evolutionary trends in various lineages (Nelson and Semkin, 1970; Chaline, 1972; Van der Meulen, 1973). Most work has centered on progressive changes in size, crown complexity, hypsodonty, height of dentine tracts, and development of cement in the re-entrant angles of the molars. These characters can usually be best studied in M_1 , and most of the classification of fossil arvicolines has centered around that tooth.

The earliest record of the Arvicolinae is a single tooth referred to *Microtoscopes* from the Clarendonian of Oregon (Shotwell, 1970). However, arvicolines are now well known from the Kimballian and Hemphillian of North America (Martin, 1975) with five genera (*Microtoscopes*, *Paramicrotoscopes*, *Prosomys*, *Ogmodontomys*, *Propliophenacomys*)

present. All of these early arvicolines have rooted teeth, lack dentine tracts, and lack cement in their re-entrant angles. They also have relatively simple crown patterns on their cheek teeth. M_1 has in all cases a posterior loop, three alternating triangles, and an anterior loop (except in *Propliophenacomys* where a fourth triangle is separating off of the anterior loop). *Prosomys* and *Microtoscopes* occur in Eurasia as well as in North America. But it would appear that the North American records of this genus tend to be somewhat older. *Prosomys minus* is more primitive than the Eurasian species (Repenning, 1968). This distribution is somewhat surprising, as it has been generally accepted that the arvicolines arose in Eurasia (based on the presence there of related cricetines). Mein (1975) has reported a cricetine, *Rotundomys bressanus*, from the Upper Vallesian (Miocene) of Soblay in France, which he regards as close to the ancestry of later arvicolines. At the end of the Kimballian in North America, the Microtoscoptini became extinct, but the other arvicolines underwent a dramatic radiation in the Hemphillian and Blancan. The Blancan arvicolines parallel the evolutionary trends of those from the Villafranchian, but represent a separate radiation. Because of this we can only correlate on the basis of evolutionary grade. The North American Blancan arvicoline rodents may be derived from *Prosomys* (Martin, 1975). Three and possibly four major radiations are represented: (1) the *Ogmodontomys* group, (2) the *Nebraskomys* group, (3) the *Pliophenacomys* group, and (4) the bog lemming group. All taxa (except *Synaptomys*) in these groups are thought to be restricted to North America. The lemmings are probably an Asiatic radiation with subsequent immigration to North America.

The *Ogmodontomys* group includes microtines that are very conservative in terms of hypsodonty, and none of them develops truly ever-growing cheek teeth. The unworn M_1 has a prism fold and an enamel islet in *Ogmodontomys*, *Pliopotamys*, *Cosomys*, and *Ophiomys*. "*Mimomys*" *monahani* does

not appear to have the enamel islet. All of these taxa are confined to the Blancan. The most primitive member of the group, *Ogmodontomys*, represents a very conservative line that is known from the Hemphillian Saw Rock Canyon local fauna, and had changed only slightly some three or four million years later when it occurred as *Ogmodontomys poaphagus* in the Rexroad and Sand Draw local faunas. *Ogmodontomys* itself does not appear to occupy the central position I have given it in the past (Martin, 1975). *Cosomys* is known from California and Idaho, but it has not been found in the Central Great Plains. It could be related to "*Mimomys*" *monahani* from the Mullen Assemblage (Martin, 1972) in north-central Nebraska. "*Mimomys*" *monahani* is a very interesting species, as it is the only known North American form that may actually belong in the Eurasian genus, *Mimomys*, sharing with species of that genus a large anterior loop on M_1 with a prism fold, rooted teeth, and cement. The lack of an enamel islet on the anterior loop for M_1 is unusual for *Mimomys*, but this feature is variable on some of the more advanced Eurasian species. "*Mimomys*" *monahani* is very advanced for a species of *Mimomys* with relatively high-crowned teeth and high dentine tracts (Martin, 1972).

Ophiomys is the most diverse genus in the *Ogmodontomys* group, as it includes five species, *Ophiomys taylori*, *O. meadensis*, *O. magilli*, *O. fricki*, and *O. parvus*. *Ophiomys taylori* is a small species lacking obvious dentine tracts and having a simple pattern on M_1 , with only three alternating triangles. *Ophiomys magilli* also has a simple crown pattern on M_1 , but is larger and has higher dentine tracts than *O. taylori*. The remaining three species of *Ophiomys* have five alternating triangles, with the anterior two confluent with the anterior loop. *Ophiomys meadensis* is larger than *O. fricki*, although both have low dentine tracts. *Ophiomys parvus* of the Grandview local fauna is the only species with relatively high dentine tracts.

The only living member of the *Ogmodontomys* group is the muskrat, *Ondatra*. Its Blancan ancestor is placed in the genus *Pliopotamys*, and its evolutionary history (summarized later in this paper) is one of the best known and most interesting in vertebrate paleontology. *Pliopotamys* is relatively low crowned, without well developed dentine tracts and cement. Two species of *Pliopotamys* are recognized. *P. minor* occurs in the Hagerman local fauna, and *P. meadensis* is known from the Deer Park, Broadwater, and Sand Draw local faunas. These two taxa differ in size, with *P. meadensis* being the larger. The earliest records of *Ondatra* are from the Grandview, White Rock, and Seneca local faunas and the Mullen assemblage, all of which contain *Ondatra idahoensis*. *Ondatra* differs from *Pliopotamys* primarily in having higher dentine tracts and cement in the re-entrant angles.

The *Nebraskomys* group contains only two genera, *Nebraskomys* and *Atopomys*. They are small arvicoline which have persistently low-crowned molars, simple crown patterns,

and a relatively small anterior loop which is crenulated and bears a small enamel islet on slightly worn teeth. The alternating triangles on the lower molars and M^1 of *Nebraskomys* tend to be opposite to each other so that they are broadly confluent. This type of pattern also occurs in the Microscoptini and *Trilophiomys*. However, this similarity is probably due to parallelism. *Nebraskomys* is a relatively rare microtine. The largest sample is from the Broadwater local fauna, and its stratigraphic usefulness is somewhat limited. Hibbard (1970) recognized two species on the basis of height of the dentine tracts: *N. rexroadensis*, with very low tracts from the Rexroad local fauna, and *N. mcgrewi*, with slightly higher tracts from the Sand Draw local fauna. Material from the Broadwater local fauna seems to be *N. mcgrewi*. *Nebraskomys* presently is restricted to the Blancan, but it probably gave rise to *Atopomys* from younger deposits in Texas, and Cumberland Cave (Zakrzewski, 1975).

The *Pliophenacomys* group always has at least four alternating triangles on M_1 and lacks the enamel pit on the anterior loop. It may be derived from the Hemphillian genus, *Propliophenacomys* (Martin, 1975). They develop hypsodont teeth with high dentine tracts, but do not develop cement in the Blancan. Three species of *Pliophenacomys* are known, based to a large extent on progressively increasing height of dentine tracts, with *P. finneyi* having the lowest, leading to *P. primaevus* and then to *P. osborni* with the highest dentine tracts. *Pliophenacomys osborni* is similar to the Eurasian genus *Pliomys*, and Eshelman (1975) has recently discussed the possibility of its actually belonging in that genus. According to Hibbard and Dalquest (1973), *Pliophenacomys* gave rise to *Proneofiber*, which is ancestral to the round-tailed water rat *Neofiber*. However, the species *Pliophenacomys osborni* is too specialized in its molar enamel to have given rise to *Neofiber*. The only other member of this radiation is *Pliolemma*, a microtine with evergrowing teeth, but with low dentine tracts and no cement in the re-entrant angles. It occurs in the Dixon, Benders, and Sand Draw local faunas and may be the earliest known arvicoline with ever-growing molars.

The lemmings have an interesting history in North America. The absence of any related forms that lack cement or have rooted teeth argues against their origin here. Their sudden appearance in the Late Blancan may result from a simple crossing of Beringia to North America, or could represent a southern shift from a very northern center of radiation which may have been holarctic in scope. Certainly they were already full-fledged lemmings when they first appear in the fossil record. Probably the oldest known North American lemming is *Synaptomys* (*Synaptomys*) *rinker* from the Dixon local fauna. This subgenus retains a primitively simple dental pattern with large, pointed, lingual, alternating triangles on the lower molars. A derived condition, with the lingual triangles very much reduced, occurs in *Synaptomys* (*Mictomys*). *Mictomys* does not occur in the Blancan, but a subgenus that shows distinct tendencies towards it does. This subgenus,

Metaxyomys, is known from the Grandview, Seneca, and Borchers local faunas, and Zakrzewski (1972) has also named a species from the Anza-Borrego Irvingtonian. The species *Synaptomys (Metaxyomys) vetus* occurs in the Grandview local fauna, while *S. (M.) landesi* occurs in the later Borchers local fauna.

Lemmings are the earliest arvicolines in North America that show both rootless molars and cement in the re-entrant angles. By the time of the Sappa and Wathena local faunas we have true Northern bog lemmings. *S. (Mictomys)* is also a common component of the later Cudahy faunas. The earliest known North American occurrences of the lemmings *Lemmus* and *Dicrostonyx* are from the Cape Deceit local fauna in Alaska where Guthrie and Matthews (1971) described *Predicrostonyx hopkinsi*. I regard this fauna as being in the general age range of the Cudahy faunas, because of the relatively advanced dental pattern found in *Microtus deceitensis*, although it may be slightly older.

With the end of the Blancan (about two million years B.P.) there is a dramatic turnover in the character of the North American microtine fauna. *Pliolemmus*, "*Mimomys*," *Ogmodontomys*, and *Ophiomys* became extinct, and the dominant small rodents in the next younger faunas were heteromyids and cricetids rather than arvicolines. The oldest faunas that probably post-date the extinction are the Borchers and Curtis Ranch local faunas. The Borchers contains *S. (Metaxyomys)* and a primitive *Ondatra*. The volcanic ash below the Borchers has been dated at about 1.9 million years B.P. Zakrzewski (1972) reports the co-existence of a *Microtus*-like microtine and *S. (Metaxyomys)* in the Late Cenozoic of the Anza-Borrego desert. The next earliest faunas are the Wathena, Java, Kentuck, and Sappa local faunas. The Wathena fauna underlies Kansan till, and the Sappa local fauna underlies the type-S Pearlette ash, which has been dated at 1.2 million years B.P. All of these faunas contain a primitive *Microtus*-like arvicoline. R. Martin (1975) has assigned the Java and Kentuck specimens to the European species *Allophaiomys pliocaenicus*. The anterior loop is of the arvicolid type (Van der Meulen, 1973, Fig. 21). The only other arvicolines in these localities are *Ondatra* and *S. (Mictomys)*. If R. Martin's assignment is correct, we have a fairly firm correlation with the lower part of the Biharian (L. D. Martin, 1977). The earliest record of *Microtus*-like rodents in Eurasia is *Allophaiomys deucalion* from the Upper Villanyan of Hungary. This would make it slightly older than the earliest certain occurrence of a *Microtus*-like microtine in North America. Although possible records of such a microtine exist for the Vallecito local fauna (Zakrzewski, 1972) and the Curtis Ranch local fauna (Lammers, MS., 1970), these two faunas date around 1.8 million years and may thus actually predate the Eurasian occurrences.

The Cape Deceit fauna in Alaska contains *Predicrostonyx hopkinsi*, *Microtus deceitensis*, and "*Pliomys*" *deeringensis*.

This suite of arvicolines suggests that the Cape Deceit local fauna is also correlative with part of the Biharian. However, the identification of *Pliomys* in this fauna has been doubted by Chaline (personal communication, 1977), who regards "*Pliomys*" *deeringensis* to be assignable to *Phenacomys*.

The Cudahy faunas that underlie the type-O Pearlette ash (0.6 million years B.P.) show a marked radiation of arvicolines. They still have *Ondatra* and *S. (Mictomys)*, and also contain several species of *Microtus*, including *M. paroperarius*, *M. llanensis*, and *M. meadensis* in the Central Great Plains. Chaline (1966, 1972) has shown a similar sequence in Europe with early faunas containing only *Allophaiomys pliocaenicus*, followed by a marked radiation. It would appear that European and North American radiations fall within the same time framework. We do have a heavy regional sampling bias with most fossil microtines known from the western United States and the Central Great Plains. Our knowledge of the sequence in the North and East is limited. This was aptly demonstrated by the discovery of the Cape Deceit fauna in Alaska. Prior to that discovery, *Dicrostonyx* and *Lemmus* were unknown in North America until the Wisconsinan. Cape Deceit showed us that *Dicrostonyx* and *Lemmus* have about as early a record in North America as they have elsewhere. In other words, we had a boreal radiation in Alaska that was totally unrepresented south of the continental ice sheet until *Dicrostonyx* appeared there in the Late Pleistocene. The eastern faunas are also somewhat unique with their own species suites, although a good review comparing them with the plains species might clarify their relationships.

We now have a sequence of arvicolines (Figs. 1 and 2) that we can relate to the traditional North American scheme of Land Mammal Ages (see Schultz, et al., 1978). In fact, this sequence has the potential of providing a refined biostratigraphy. In attempting this, I have divided the arvicoline sequence in North America into seven arvicoline "zones" as follows:

Zone I contains the first appearance of arvicoline rodents in North America (? Clarendonian) and includes the following species: *Microtoscoptes disjunctus* (Wilson), *Paramicrotoscoptes hibbardi* (Martin), *Prosomys mimus* (Shotwell), *Ogmodontomys sawrockensis* Hibbard, *Propliophenacomys uptegevovensis* Martin, and *Propliophenacomys parkeri* Martin. It is characterized by microtines with simple, rooted teeth that lack cement, and by the last appearance of the *Microtoscoptini*. It may be possible to subdivide this zone as the *Microtoscoptini* seem restricted to older (Kimballian) faunas while *Propliophenacomys* and *Ogmodontomys* may occur in later (Hemphillian) ones.

Zone II contains the first appearance of microtine rodents with rootless teeth (*Pliolemmus*), and muskrats (*Pliopotamys*). It includes the following species: *Ogmodontomys poaphagus* Hibbard, *Nebraskomys rexroadensis* Hibbard, *N. mcgrewi* Hibbard, *Cosomys primus* Wilson, *Ophiomys taylori* Hibbard,

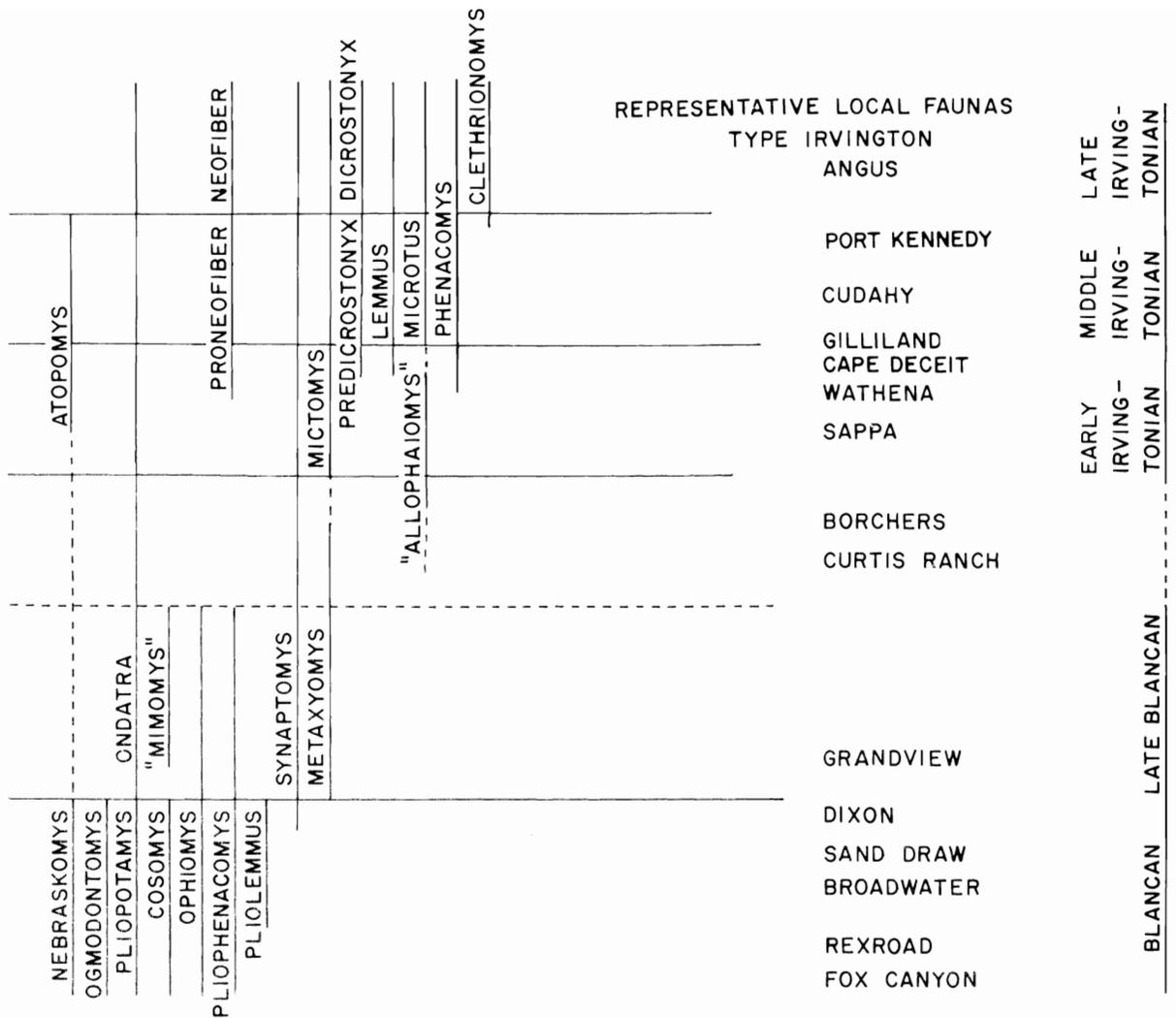


Figure 1. Biostratigraphic distribution of North American Blancan-Irvingtonian arvicoline genera.

O. meadensis Hibbard, *Pliophenacomys finneyi* Hibbard and Zakrzewski, *P. primaevus* Hibbard, *Pliopotamys minor* (Wilson), *P. meadensis* (Hibbard), and *Pliolemmus antiquus* Hibbard.

Zone III contains the first records of bog lemmings and the last records of *Mimomys*, *Ophiomys*, *Ogmodontomys*, and *Pliolemmus* in North America. It includes the following taxa: *Ogmodontomys* sp., *Nebraskomys mcgrewi* Hibbard, *Ophiomys parvus* Wilson, *Ophiomys fricki* Hibbard, *Pliophenacomys osborni* Martin, *Ondatra idahoensis* Wilson, *Pliolemmus antiquus* Hibbard, "*Mimomys*" *monahani* Martin, *Synaptomys (Synaptomys) rinkeri* Hibbard, and *Synaptomys (Metaxyomys) vetus* Wilson.

Zone IV contains the first appearance of round-tailed water rats, the northern bog lemming *Synaptomys (Mictomys)* and *Microtus*-like microtines, "*Allophaiomys*." Faunas of this age show the lowest arvicoline diversities of the last four

million years in North America. Microtine Zone IV includes *Ondatra* cf. *annectens* Brown, *Synaptomys (Mictomys) kansasensis*, "*Allophaiomys*" sp., and *Proneofiber guildayi* Hibbard and Dalquest.

Zone V contains a wide range of microtines, including *Phenacomys* sp., *Clethrionomys*, *Ondatra annectens* Hibbard, *Synaptomys (Mictomys) meltoni* Paulson, *Microtus paroperarius* Hibbard, *Pitymys meadensis* Hibbard, and *Pedomyllanensis* Hibbard.

Zone VI contains *Ondatra nebracensis*, *Neofiber leonardi*, *Microtus pennsylvanicus* (with five alternating triangles), and *M. ochrogaster*. These were microtines of generally modern aspect, but were still slightly less advanced than the living forms. For instance, the *Microtus pennsylvanicus* from this zone has a slightly more primitive M_1 (fewer alternating triangles) than most modern populations of that species, and *Ondatra nebracensis* is smaller than the modern *Ondatra zibethicus*.

ERA and MAMMAL AGE	CALIFORNIA	ARIZONA	IDAHO	KANSAS	NEBRASKA	SOUTH DAKOTA	TEXAS	PENNSYLVANIA	N.A. ARVICOLINE ZONES	EUROPEAN LOCALITIES	
PLEISTOCENE "IRVINGTONIAN"	Local Fauna										
	Sheridanian			Sandahl Rezabek Adams	Mullen ^a Hay Springs Angus	Rushville			VI		
		Irrington									
					Cudahy - 6 my.				Cumberland Port Kennedy	V	
				Kentuck Kansan Till Wathena	Sappa - 1.2 m.y.	Java		Gilland	IV		
	Vallecito Creek	Curtis Ranch - 1.86 m.y.		Borchers - 1.9 m.y.						Le Coupet 1.9 m.y.	
	PLIOCENE BLANCAN			Grandview	White Rock Dixon	Mullen ^b Seneca				III	Tegelen
		Coso Mountain	Wolf Ranch - 2.45 m.y.		Sanders Deer Park Spring Creek	Lisco Broadwater	Sand Draw	Delmont	Cita Canyon Blanco	II	Lower Valdarno
			Benson - 3.08 m.y.								
				Hagerman - 3.4 m.y.	Benders Rexroad Keefe Canyon Fox Canyon						Etouaires 3.4 m.y.
										Villafranca d'Asti	
				Sawrock Canyon	Devi's Nest Santee Uplegrove Lemoine				I	Samos	

Figure 2. Correlation of North American arvicoline zones with selected local faunas.

Zone VII. This is essentially the modern arvicoline fauna of North America and corresponds to the Rancholabrean Land Mammal Age.

These zones are based on progressive evolution as well as first and last appearance of taxa, but it is the clarity of progressive evolutionary trends in microtine teeth that provides much of their usefulness and interest. Most microtines consume grass in one form or another, and this abrasive diet has resulted in directional changes for increased hypsodonty and crown complexity. Very early arvicolines like *Prosomys* have an anterior loop, three alternating triangles, and a posterior loop on M_1 . These correspond to the anteroconid, metaconid, protoconid, entoconid, and hypoconid plus the posterior cingulum in a cricetine M_1 . The grinding surface is modified primarily by increasing the length and complexity of the anteroconid. A good example of this is *Dicrostonyx*, which now has the anteroconid of M_1 expanded into four alternating triangles and an anterior loop composing one-half the length of the tooth. Most of the variability and taxonomic usefulness is concentrated on the evolving anterior end of the anteroconid, while the posterior portion of the tooth remains relatively stable. This is a result of the fact that the anterior portion is not constrained by an adjacent tooth, and in M^3 , the other taxonomically useful molar, evolution

proceeds posteriorly while the anterior portion of the tooth remains stable. In the lower dentition, the M_1 becomes progressively larger as compared to the other molars as its anterior end is elaborated (Martin, 1975). The elaboration of the crown pattern takes place by selection on crenulations of the anterior loop. In young individuals of early arvicoline species, the anterior loop is highly crenulated, and some of the crenulations occupy the form and position of incipient triangles. As the re-entrants of these crenulations become larger, additional alternating triangles are "budded" off. In many early microtines one of the re-entrants in the anterior loop is very large and with wear closes off a distinct enamel islet (Hinton, 1926). In later microtines with more hypsodont teeth, this islet tends to be lost. Primitively, the incisor is short in microtines and remains so in lemmings, but several other lineages have independently lengthened the incisors so that the capsular process is labial rather than lingual (as in *Microtus*). This is probably a reflection of rapid incisor growth needed to compensate for increased abrasion.

Like all grass-eating mammals, microtines show progressive hypsodonty in the evolution of their molars until most forms have ever-growing teeth. As the crowns of their teeth become higher, the roots become smaller and appear later ontogenetically. This means that as the tooth becomes higher and exerts

more leverage on its socket, the roots that anchor it become smaller. This is compensated for by the development of shallow grooves in the enamel of the crown which expose the dentine thinly covered with root cement. These grooves are called dentine tracts, and the peridental ligaments that anchor the tooth to its socket follow them up the crown (Martin, 1975) so that the dentine tracts move up the crown, taking over the function of the diminishing roots. This same response to hypsodonty has occurred in numerous other mammals, including gophers and beavers. In all cases it is a good measure of hypsodonty. Another result of increased hypsodonty is the addition of cement to the re-entrant angles. This occurs gradually, with the cement restricted to small pockets in the bases of the re-entrant angles of old individuals in primitive forms, and with the re-entrant angles completely filled in advanced forms like *Microtus*. The development of both dentine tracts and cement seems to have occurred independently in most of the major lineages of microtines.

The most extensively studied group of arvicolines in terms of progressive evolution and, hence, the most biostratigraphically useful, is the muskrats, *Ondatrini*. Their evolution in North America has been summarized in some detail (Nelson and Semkin, 1970; Schultz, Tanner, and Martin, 1972; Zakrzewski, 1974).

The following four evolutionary trends have been well documented: (1) increase in size; (2) increase in hypsodonty

and, thus, in dentine-tract height; (3) increase in crown complexity on M_1 ; and (4) addition of cement to the re-entrant angles. The oldest known (Arvicoline Zone II) muskrats belong to the genus *Pliopotamys*, which is characterized by the lack of cement. The oldest known (Arvicoline Zone III) species of *Ondatra*, *O. idahoensis*, has small amounts of cement in the base of the re-entrant angles, and by the time we reach *Ondatra annectens* in Arvicoline Zone V, the re-entrant angles are filled with cement. A simple phylogeny can be suggested for muskrats (Schultz, et al., 1972; Nelson and Semkin, 1970): *Pliopotamys minor* (Arvicoline Zone II lower part) → *Ondatra idahoensis* (Arvicoline Zone III) → *Ondatra annectens* (Arvicoline Zone V) → *Ondatra nebracensis* (Arvicoline Zone VI) → *Ondatra zibethicus* (Arvicoline Zone VII). Along this lineage we see increasing crown complexity (Fig. 4b). *Pliopotamys minor* has a posterior loop, five alternating triangles, and a highly-crenulated anterior loop with a deep infold that becomes an enamel islet with wear. The fourth and fifth triangles are better separated from the anterior loop in *P. meadensis* and *Ondatra idahoensis*. In *O. annectens*, *O. nebracensis*, and *O. zibethicus*, the posterior portion of the anterior loop opens broadly into the sixth and seventh triangles. Along this same lineage we can also see a marked chronocline for progressive size increase (Fig. 3). This chronocline is somewhat complicated by a north-south decline in size in the modern muskrats, with the northern forms being somewhat larger (Nelson and Semkin, 1970). These facts complicate the stratigraphic interpretation, making populations near the continental ice

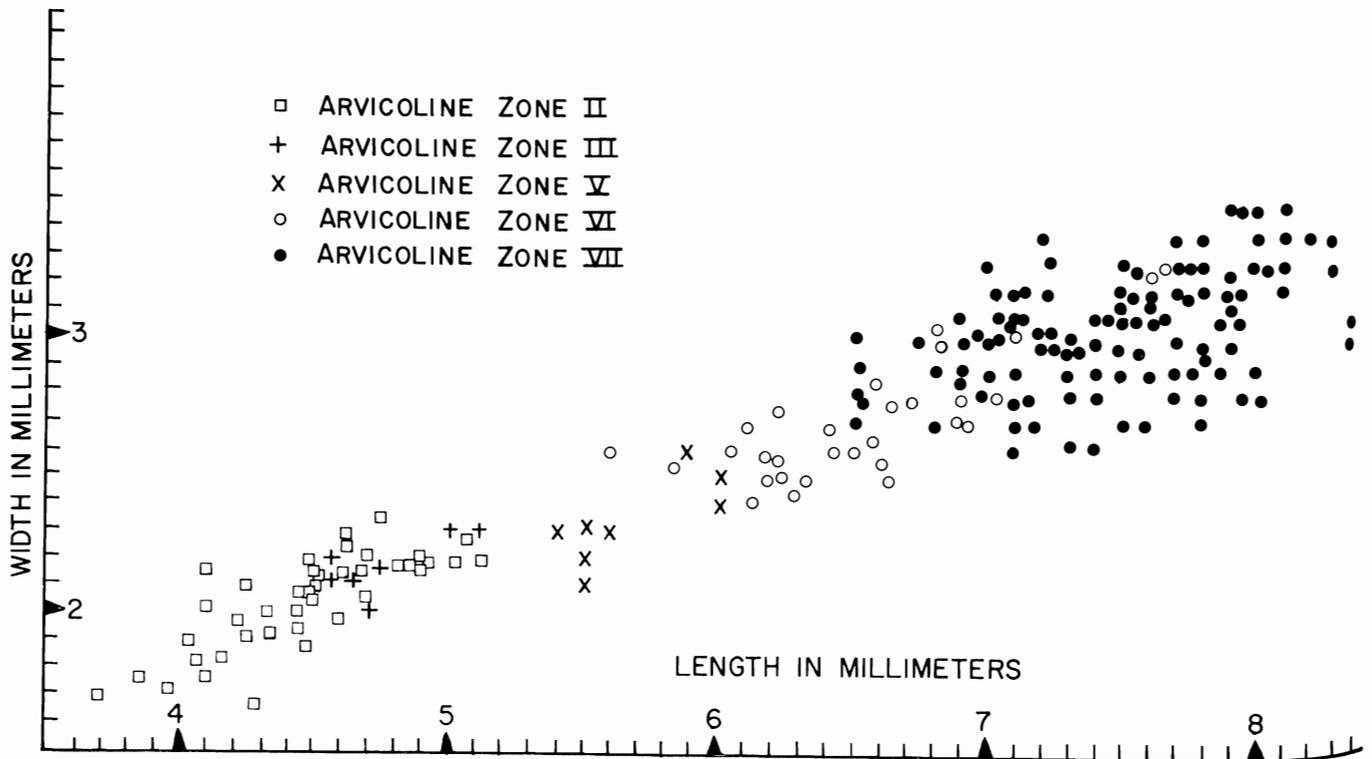


Figure 3. Length and width of lower first molars of muskrats showing increase in size from older to younger arvicoline zones. (Adapted from Nelson and Semkin, 1970; Zakrzewski, 1969; Schultz, et al., 1972)

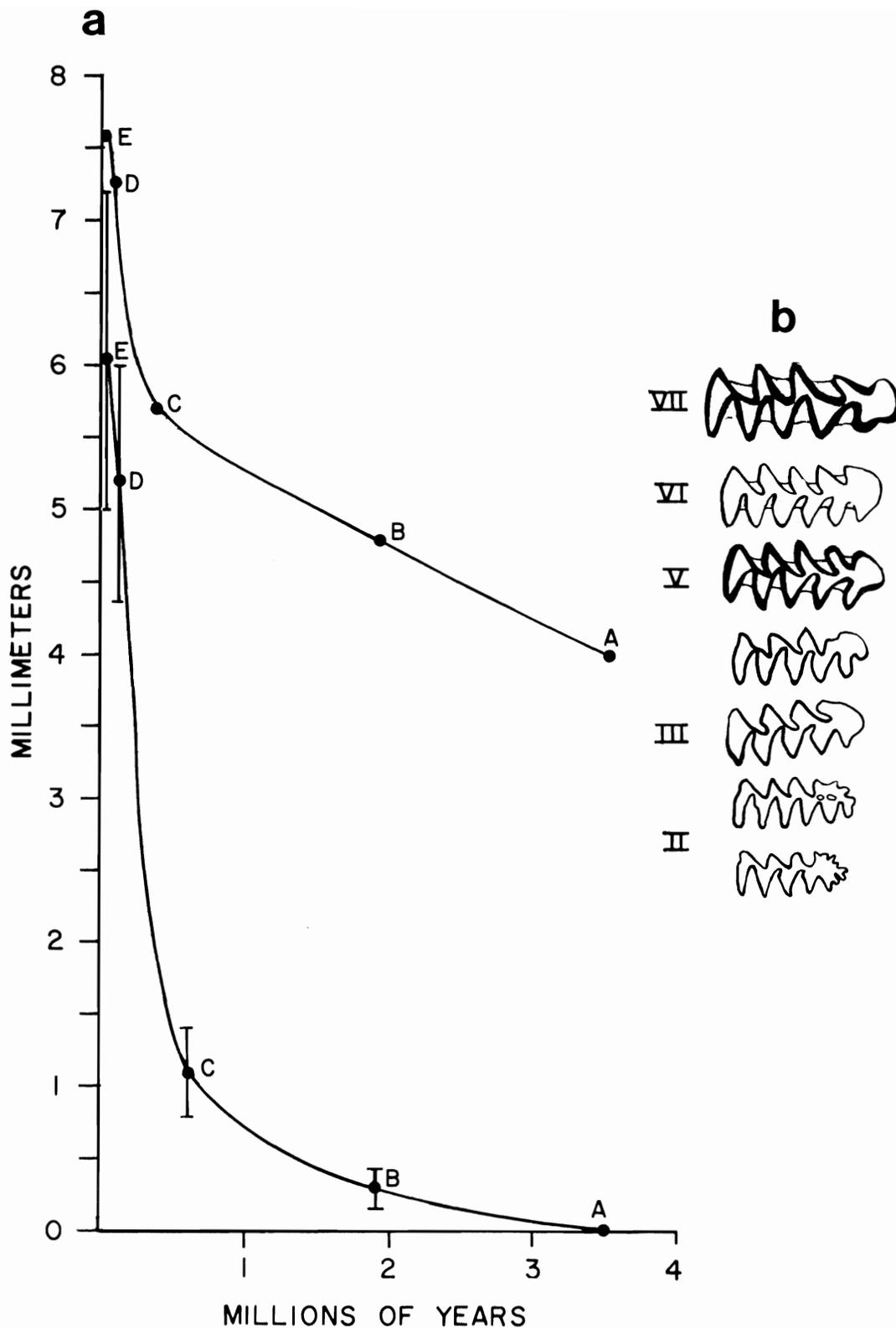


Figure 4. **a** Graph showing change in dentine tract height on M_1 (upper curve) and length of M_1 (lower curve) for muskrats (measurements adapted from Nelson and Semkin, 1970); (A) Hagerman local fauna, (B) Borchers and Grandview local faunas, (C) Cudahy local faunas, (D) Wisconsinan faunas, and (E) modern muskrats.

b Left M_1 's of muskrats arranged in stratigraphic sequence with the oldest at the bottom and North American arvicoline zone listed on the left. From bottom to top: *Pliopotamys minor*, *P. meadensis*, *Ondatra idahoensis*, *O. cf. annectens*, *O. annectens*, *O. nebracensis*, *O. zibethicus*. (All X5).

appear younger than contemporaneous populations further away from it. This appears to be the case with the muskrats from the Wathena Local Fauna, which are anomalously large for their stratigraphic position. However, on a whole the chronocline works remarkably well, with substantial overlap in successional species.

Dentine tracts as a measure of hypsodonty have also proven very useful in studying the muskrat succession (Nelson and Semkin, 1970). In a sense these are more reliable than size since the tracts seem not to be found out of sequence with respect to stratigraphic position. *Pliopotamys minor* has been described as lacking dentine tracts, but very low ones are sometimes present (Zakrzewski, 1969).

Many workers on fossil mammals were surprised when radiometric dates became available for the Blancan Land Mammal Age, and it was shown to be relatively much longer than had been expected. The reason appears to be the common expectation that evolutionary rates are constant. Semkin's muskrat chronoclines provide a remarkable opportunity to test this expectation. Four of his fossil samples have radiometric dates associated with them: Hagerman, 3.5 m.y.; Borchers, 1.9 m.y.; Cudahy, 0.6 m.y.; and the Wisconsinan samples, all of which probably date less than 100,000 B.P. The Borchers and Grandview specimens are lumped together by Semkin and Nelson (1970); although this may not be quite appropriate (Borchers is probably younger than Grandview), the grouping is so tight that the analysis should not be affected. Semkin also does not give dentine tract data for *Pliopotamys*. This is not serious, because dentine tracts in this genus are very low or absent, and I have taken zero as the starting point for the Hagerman sample. We see immediately (Fig. 4a) that there is a fairly slow, steady increase in both size and dentine tract height from the Hagerman to the Cudahy faunas, but after the Cudahy faunas we see a precipitous increase in dentine-tract height. When we look at M_1 length over the same sample, we see exactly the same effect. Clearly evolutionary rates were not constant for these characters, and insofar as we have assumed that it was, we have been led into error. The reasons for this post-Cudahy increase in evolutionary rate is not presently clear, but it appears to have occurred in other North American Pleistocene mammals (Martin, MS.).

It is possible to place most North American Blancan and later faunas stratigraphically using arvicoline zones and to correlate those zones with Eurasia (Fig. 2). However, some problems exist. Arvicoline Zone II might actually be split into two zones or subzones, the older of which would contain *Pliophenacomys fineyi* and *Nebraskomys rexroadensis*, rather than *Pliophenacomys primaevus* and *Nebraskomys mcgrewi*. Faunas with *Pliopotamys minor* (Hagerman) are also older than faunas with *P. meadensis* (Broadwater). It is also not clear if the Dixon Local Fauna belongs to Zone II or III. I have put it in Zone III in the chart because Eshelman points out the

close similarity (including presence of cement) of the teeth of the muskrat from that locality with those of *Ondatra idahoensis*. The Curtis Ranch, Borchers, and Vallecito Creek local faunas are a special problem. They lack both characteristic Blancan and Irvingtonian genera, thus putting them in a sort of biostratigraphic limbo, and they have been assigned both to the Blancan (Zakrzewski, 1975) and to the Irvingtonian (Lindsay et al., 1975; Schultz and Martin, 1977). I presently place them in Zone IV, but they might also be placed in Zone III or perhaps placed in their own category, as they lack *Ogmodontomys*, *Pliophenacomys*, *Mimomys*, *Pliolemmus*, and *Ophiomys*, all of which occur in Zone III, and may contain a *Microtus*-like rodent (*Allophaiomys?*). They differ from other faunas in Zone IV in having *Metaxomys* rather than *Mictomys* and a smaller, more primitive muskrat.

The Gilland fauna is hard to place, as it contains only a single endemic microtine, *Proneofiber guildayi*; however, this low microtine diversity is in itself suggestive of Zone IV, and true *Neofiber* occurs in Zone V.

Zone V includes a number of eastern faunas, including Cumberland Cave, Port Kennedy Cave, and the Conard fissure. These localities contain microtines at the same stage of evolution as those in the Cudahy faunas, which are mostly placed in different species. It may prove that some of this is due to lack of adequate comparison with the Cudahy taxa, or it may represent faunal provincialism. The latter interpretation seems likely, as strong provincialism can be shown for North America in the Wisconsinan (Martin, Neuner, and Well, MS.).

Zones VI and VII are closely related and are differentiated primarily on progressive evolution in muskrats. It is worth noting that the duration of an arvicoline zone becomes progressively less as we approach the present, a reflection of the change in evolutionary rates discussed earlier.

The sequence of arvicoline zonation in North America and Eurasia can be utilized to address the position of the Neogene/Quaternary boundary. One suggested boundary has been the base of the Blancan (Schultz and Martin, 1977; Schultz and Stout, 1961). This boundary would lie between microtine Zones I and II. In Europe it would probably lie somewhere between Turolian and the Ruscinian, as some Blancan faunas (Rexroad, Fox Canyon) are probably older than any Villafranchian faunas, as shown by Berggren and Van Couvering (1974). Hibbard's (1972) placement of the Pliocene/Pleistocene boundary lies between the lower and upper faunas of Microtine Zone II and corresponds to the Pliocene/Pleistocene boundary between the lower and middle Villafranchian published by Tobien (1970). Tobien shows this boundary at above 3 m.y., which he also takes to be the Astian/Calabrian boundary. Berggren and Van Couvering (1974) place the base of the Calabrian much higher (1.7-1.8 m.y.) and draw the boundary there. This would be between the lower and upper parts of Microtine Zone IV. Lindsay et al.

(1975) and Schultz and Martin (1977) have argued that the boundary should be drawn at the top of the Blancan. This may be the same as Berggren and Van Couvering (1974) or may be slightly lower (the top of Arvicoline Zone III as shown in Fig. 4). If the boundary is taken to be between the Villafranchian and the Biharian as those land mammal ages are presented in Berggren and Van Couvering (1974), it would lie between Arvicoline Zones IV and V. Thus, all of the proposed European boundaries seem to be recognizable in North America, and no problem exists in placing the Neogene/Quaternary boundary in North America if agreement can be reached as to its position in Europe.

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