

# Anatomy of the arvicoline radiation (Rodentia): palaeogeographical, palaeoecological history and evolutionary data

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Voles and lemmings (Arvicolinae subfamily) diversified throughout the northern hemisphere over five million years into 140 lineages. Attempts have been made to identify relationships within the Arvicolinae on the basis of biochemical, chromosomal and morphological characteristics as well as on the basis of palaeontological data. Arvicolines are thought to have originated from among the Cricetidae, and the history of voles can be divided into two successive chronological phases occurring in Palaearctic and Nearctic areas. The history of lemmings is not well documented in the fossil record and their Early Pleistocene ancestors are still unknown. The arvicoline dispersal is one of the best known and provides an opportunity to test the anatomy of the radiation and more particularly the punctuated equilibrium model. Study of arvicolines reveals three modes of evolution: stasis, phenotypic plasticity and phyletic gradualism. Clearly the punctuated equilibrium model needs to be supplemented by a further component covering disequilibrium in phenotypic plasticity and phyletic gradualism, suggesting a punctuated equilibrium/disequilibrium model. In terms of palaeogeography, study of arvicolines shows that Quaternary climatic fluctuations led to long-range faunal migrations (3 000 km) and study of these patterns is a significant factor in mapping past environments and climates. Some studies attest to the prevailing influence of ecological and ethological factors on skull morphology in arvicoline rodents sometimes inducing morphological convergences.

## 1. Introduction

Voles and lemmings (Arvicolinae, Rodentia) first appeared some 5.5 million years ago and have diversified over this short geological time-span into 140 lineages comprising 37 genera including extinct forms, of which more than a hundred species are extant (Miller 1896, Ellerman 1940, Ellerman & Morrison-Scott 1951, Gromov & Poliakov 1977, Honacki *et al.* 1982, Chaline 1974a, 1987): 143 species in 26 genera (Carleton & Musser 1984, 1993). Modern mammalogists place “microtines” as a subfamily (Arvicolinae) within the Muridae (Carleton & Musser 1993).

### 1.1. Arvicoline characteristics

Arvicolines include voles and lemmings. Voles have a long lower incisor that crosses from the lingual to the labial side of the molars between the bases of the first and second lower molars ( $M_2$  and  $M_3$ ) in the rhizodont forms and then rises in the lower jaw to germinate at or near the articular condyle. In lemmings, by contrast, the lower incisor is very short, entirely lingual relative to the molars and germinates posteriorly ahead of the  $M_3$  capsule. Since the cricetine incisor runs diagonally under the row of molars, the lemming structure seems to be derived and is an apomorphic feature (Kowalski 1975, 1977, Courant *et al.* 1997).

Arvicolines are essentially Holarctic rodents. Their northward distribution is bound by the Arctic Ocean or land ice. Southwards they have rarely reached the subtropical zone: Guatemala, northern Burma, northern India, Israel and Libya. They may have occurred in North Africa in Quaternary times (Jaeger 1988), if *Ellobius* is counted among arvicolines by arguments based on chromosomes (Matthey 1964a), but this is much contested and tends to be refuted by arguments based on lower jaw structure (Repenning 1968).

Historically arvicoline dispersal was controlled by geographical barriers and climate (Repenning 1967, 1980, Fejfar & Repenning 1992, Repenning *et al.* 1990). For example, the high sea levels in Pliocene–Pleistocene times that formed the Bering Strait also flooded low-lying Arctic areas as far away as the Ural Mountains. Before these glaciation-related sea level fluctuations, for-

est cover around the Bering land bridge may have formed an ecological barrier to the migration of these essentially grassland animals.

The deliberate historical focus of this presentation means we must work from palaeontological data in their dated stratigraphical context and discuss and criticize those data in the light of biological data.

The term of “arvicoline” has been here chosen following the classification of Wilson and Reeder (1993).

### 1.2. The morphological approach to palaeontology

Voles are useful palaeoecological, palaeoclimatical, palaeogeographical and evolutionary indicators because they are abundant in fossil and archaeological records and in the wild today where their prismatic teeth are found in pellets regurgitated by birds of prey (Chaline 1972, Andrews 1990 and J. C. Marquet unpubl.). Unfortunately, far too many species have been and still are considered from a typological standpoint with no analysis of variability (Kretzoi 1955, 1956, 1969, Hibbard 1970a, 1972, Rabeder 1981, Fejfar *et al.* 1990). Arvicoline systematics is littered with names that hamper both the establishment of true phylogenetic relationships and our understanding of how the group evolved. Fortunately, with biometric studies, biological populations can be compared by using increasingly comprehensive morphometries (Chaline & Laurin 1986, Brunet-Lecomte & Chaline 1991 and P. Brunet-Lecomte unpubl.). Recent studies have used image analysis of the occlusal surfaces of teeth (Schmidt-Kittler 1984, 1986, Barnosky 1990, Viriot *et al.* 1990). New methods of morphological geometry are now employed (Sneath 1967, Rohlf & Bookstein 1990, Bookstein 1991) using Procrustes 2.0 software (David & Laurin 1992) to quantify phenetic differences and convergence between crania (Courant *et al.* 1997).

New areas of investigation include worldwide systematics and phylogeny based on dental morphology, enamel structures (von Koenigswald 1980, von Koenigswald & Martin 1984a, 1984b and J. Rodde unpubl.), evolutionary modes and stratigraphical data (Chaline 1984, 1986, Chaline

& Farjanel 1990), as well as geographical and climatic distribution patterns (Chaline 1973, 1981, Chaline & Brochet 1989, Montuire 1996, Montuire *et al.* 1997).

### 1.3. Biological approaches

In addition, arvicolines have been the subject of in-depth biological studies — protein differentiation (Duffy *et al.* 1978, Graf 1982, Moore & Janacek 1990), chromosomal formulas (Matthey 1957, Meylan 1970, 1972, Winking & Niethammer 1970, Chaline & Matthey 1971, 1964b, 1973, Winking 1974, 1976, Niethammer & Krapp 1982, Zagorodnyuk 1990a, 1991), reproduction and ecology (Ognev 1964, Gromov & Poliakov 1977, Chaline & Mein 1979, Carleton & Musser 1984, Courant *et al.* 1997) — which have sometimes led to phylogenetic relationships that differ because of the independence of rates of evolution at the various levels of integration of the living world. It has been shown that genetic and morphological data are decoupled to varying extents (Chaline & Graf 1988, Brunet-Lecomte & Chaline 1992, Din *et al.* 1993, Courant *et al.* 1997). A developmental approach has been attempted by using developmental heterochronies in order to analyse their impact on changes in dental morphology over time (Chaline & Sevilla 1990, Viriot *et al.* 1990 and L. Viriot unpubl.). This work has been supplemented by analysis of the dental ontogenesis of the present-day mouse (*Mus musculus*) which is used as an out-group for interpreting heterochronies affecting voles and lemmings (L. Viriot unpubl.).

## 2. Origin of Arvicolines and phylogenetic relationships

### 2.1. Origin of Arvicolines

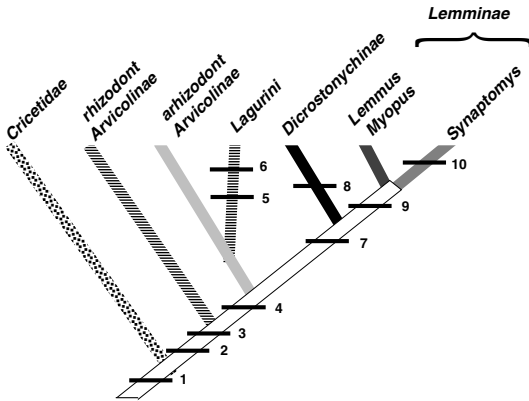
Arvicolines derive from cricetine rodents as evidenced by the difficulty in separating the earliest arvicolines from the arvicoline cricetids. *Baranomys* and *Microtodon*, for example, were classed among the cricetids by Simpson (1945), and Stehlin and Schaub (1951), but placed among arvicolines by Kretzoi (1969) and Sulimski (1964). Repenning (1968) took on the examination of am-

biguous forms on the basis of the characters of lower jaw musculature. He claims that arvicolines are recognised by the following major mandibular characters: (1) the anterior edge of the ascending ramus originates at, or, anterior to the posterior end of  $M_1$  and ascends steeply, obscuring all or part of  $M_2$  in labial aspect; (2) the anterior part of the medial masseter inserts in a narrow groove parallel to the anterior edge of the ascending ramus known as the “arvicoline groove”; (3) the lower masseteric crest is long, located anteriorly and very shelf-like; (4) the internal temporalis fossa forms a broad elongate depression separating  $M_2$  and  $M_3$  from the ascending ramus.

Most of these characters result from shortening and deepening of the arvicoline lower jaw which strengthens the bite.

Repenning's analysis provides the following findings: (1) *Microscoptes disjunctus* (known from the Middle Pliocene of North America and Asia) resembles arvicolines by parallelism and could be considered as an arvicoline “sister group”. L. D. Martin (1975) described a new and very closely related form, *Paramicroscoptes hibbardii*, in the Hemphillian (ca. 6.5 Ma) of Nebraska. A recent revision of material including a study of the enamel structure by W. von Koenigswald (Fahlbusch 1987) confirmed that *Microscoptes* is not an arvicoline but indeed a cricetid; (2) *Baranomys* (from the Uppermost Pliocene of Central Europe), like *Microscoptes* is thought to represent a form that developed in parallel to the arvicolines with respect to dentition (very similar to that of *Prosomys*) while retaining a typically cricetine lower jaw structure; (3) *Microtodon* (from the Middle Pleistocene of Eurasia) belongs with the cricetids although its molars are similar to those of the earliest arvicolines (*Prosomys* from the Middle Pliocene of North America and *Prosomys* of Eurasia). In addition, while very cricetid-like in some respects, *Microtodon* has a rudimentary “arvicoline groove” indicating that the insertion of the anterior part of the medial masseter extended below and behind the anterior edge of the ascending ramus, which is a typically arvicoline arrangement.

Among other fossils that may be included in the search for ancestral cricetine forms are: (1) *Pannonicola brevidens*, a transition cricetine from the Upper Miocene of Zaslady in Hungary de-



**Fig. 1.** Phylogenetic relationships within the main groups of Arvicolinae. Character 1: myomorphic cranial morphology; character 2: occurrence of hypsodont teeth; character 3: variable numbers of alternating or opposing enamel triangles; character 4: absence of dental roots (appearance of arhizodonty); character 5: break in the enamel on triangle 6 of  $M_1$  of *Lagurus*; character 6: "laguroid protuberance" (a small lingual triangle) on the upper molars; character 7: position of the lower incisor; character 8: polyisomery on  $M_1$ ; character 9: lophodont  $M^3$ ; character 10: molars with dissymmetrical structures.

scribed by Kretzoi (1965) with very worn and puzzling teeth; (2) *Rotundomys montisrotundi* followed by *R. bressanus* discovered by Mein (1966, 1975) at Soblay (Ain, France); (3) the micro-cricetid *Microtocricetus molassicus* (Fahlbusch & Mayr 1975) of the Lower Pliocene of Europe with its intriguing microtoid morphology (*Microtus* like) (related to *Democricetodon*?); (4) *Ischymomys* of the Pliocene of NE Asia (*Zazhigin in Gromov & Poliakov 1977*); (5) the species *Celadensia nicolae* Mein et al. (1983) of the Pliocene of Spain as well as *Bjornkurtenia canterranensis* (ex *Trilophomys*) from Terrats (Roussillon) which were considered by Kowalski (1992) to be very primitive voles. Thus there is a wide array of cricetids with arvicoline features but it is currently impossible to specify their involvement in the origin of arvicolines.

## 2.2. Phylogenetic relationships

There are few usable apomorphies because of the frequency of convergence. This parallelism is well documented in various lineages of voles and lem-

mings for cementum appearance in the re-entrant angles of molars (Chaline 1987), for the gradual disappearance of tooth roots (Chaline 1974a, 1977 and L. Viriot unpubl.) and for the appearance of enamel tracts. However, characters that can be polarized divide the Arvicolinae into five groups (Fig. 1) and suggest a first hypothesis for phyletic relations (Courant et al. 1997).

Fossil data show that Cricetidae, like the Arvicolinae, have myomorphic cranial morphology (character 1). In addition, the molar triangles of the Arvicolinae are recognized as homologous to the molar tubercles of the Cricetidae (Stehlin & Schaub 1951). The occurrence of hypsodont teeth (character 2), formed from variable numbers of alternating or opposing enamel triangles (character 3), the appearance of arhizodonty (character 4: absence of dental roots) are the apomorphies used to characterize voles (Arvicolinae) and lemmings (Lemminae and Dicrostonychinae). The plesiomorphic states of these characters in the Cricetidae are low-crowned molars (brachyodont) and alternating tubercles. The position of the lower incisor (character 7) is the main morphological characteristic separating the two arvicoline groups into voles and lemmings (Hinton 1926). In cricetids and voles, the incisor is long and runs diagonally from the lingual to the labial side of the jaw between the  $M_2$  and  $M_3$  roots, terminating relatively high in the ramus of the condylar process (plesiomorphic state). In lemmings, the apomorphic state corresponds to a shorter lower incisor that runs lingually relative to the molars and terminates in line with  $M_3$  (Kowalski 1977). *Lagurus* is easily distinguishable among the voles by two apomorphic features: a localized break in the enamel on triangle 6 of  $M_1$  (character 5) and the "laguroid protuberance" (a small lingual triangle) on the upper molars (character 6), affecting the second tubercle of  $M^1$  or the first tubercles of  $M^2$  and  $M^3$  (Chaline 1972). *Dicrostonyx* is distinctive from other lemmings in having longitudinally complex cheek teeth; this autapomorphic trait corresponds to particularly clear polyisomery on  $M_1$  (character 8) which has more than five triangles (Thaler 1962). *Pliolemmus* shares the same feature (homoplasy) but does not have the major *Pliomys*-like upper  $M^3$  apomorphy. In addition, the *Lemmus-Myopus* group shares a lophodont  $M^3$  with *Synaptomys* (character 9), the derived *Synaptomys* of



North America being further characterized by molars with dissymmetrical structures (character 10).

This cladogram (Fig. 1) is consistent overall with the genetic distance tree established by electrophoresis for 24 arvicoline species (Graf 1982, Chaline & Graf 1988) and with the papers cited above.

### 3. The onset of the Holarctic radiation of voles

The earliest known arvicolines come from the Hemphillian (6–5 Ma) of North America and Ruscianian of Europe. They are *Prosomys mimus* of the Middle Pliocene of Oregon (Shotwell 1956) and *Promimomys insuliferus* of Poland (Kowalski 1956). Agadjanian and Kowalski (1978) classified *Promimomys insuliferus* under the genus *Prosomys* arguing that the genus *Promimomys* described by Kretzoi (1955) was defined from one reworked molar of *Cseria gracilis* at a senile abrasion stage. Agadjanian and Kowalski (1978) conception was adopted by L. Viriot (unpubl.). The *Prosomys* molars maintain certain cricetid characters such as the cricetid enamel islet at the front of the M<sub>1</sub> anterior loop. This *Prosomys mimus* species with identical tooth morphology seems to have ranged throughout Holarctica.

### 4. The Nearctic radiation

Important species are found in Late Hemphillian deposits (Idaho, Wyoming, Nebraska, Kansas): *Ogmodontomys sawrockensis* (Fig. 2) and *Propliophenacomys parkeri*–*P. upteigrovensis* (L. D. Martin 1975, 1979, Repenning & Fejfar 1977, Repenning 1984, Repenning *et al.* 1990). The last two species are uncertain in that the specimens are from the same Pliocene formation and diagnoses are based in one case on lower jaws and in the other case on an upper jaw.

#### 4.1. The first ancestral lineage

*Ogmodontomys sawrockensis* clearly derives from *Prosomys mimus* (Fig. 2) forming an “*Ogmodon-*

*tomys sawrockensis*” stock (L. Viriot unpubl.) that evolves gradually into *O. poaphagus transitionalis* and then *O. poaphagus poaphagus* (Zakrzewski 1967). *Prosomys mimus* also diversified into the following primitive arvicoline lineages:

1. *Pliopotamys minor*–*meadensis*–*idahoensis*–*Ondatra annectens*–*nebrascensis*–*zibethicus*: (Fig. 2) a lineage still represented by *Ondatra zibethicus* that evolved gradually by increased tooth size (Nelson & Semken 1970), hypsodonty, and the proliferation of tooth triangles (polyisomery of Thaler 1962, Viriot *et al.* 1993 and L. Viriot unpubl.). A further form, *Ondatra obscurus* became isolated in Newfoundland from the end of the Pleistocene;
2. *Ophiomys taylori*–*magilli*–*meadensis*–*parvus*–*fricki* (Fig. 2) a lineage that evolved gradually during the Blancan (Hibbard & Zakrzewski 1967);
3. *Cosomys primus* (Fig. 2), a morphologically convergent form of Eurasian *Mimomys* but of large proportions; this species arose from *Ogmodontomys sawrockensis* and remained in morphological stasis for a relatively long time (Lich 1990) before dying out;
4. *Loupomys monahani*, another form morphologically like a European *Mimomys*, but characterized by persistent single radial enamel that seems to form a new instance of parallelism with the European lineage of *Nemausia salpêtrierensis*, a primitive vole of mimomyian morphology (*Mimomys*-like dental morphology) surviving in the South of France at a locality known as Salpêtrière under the famous Gallo-Roman “Pont du Gard” bridge in Upper Palaeolithic strata dated 12 000 B.P. (Chaline & Laborier 1981).

#### 4.2. The second ancestral lineage

A other lineage displays different characteristics that are those of the tribe Pliomyini (M<sup>3</sup> with narrow re-entrant angle in the anterior loop forming the pliomyan fold apomorphy) whose current representatives are exclusively Eurasian. Three possibilities should be envisaged: (1) *Propliophenacomys parkeri* represents the initial stock that became differentiated in North America, while the

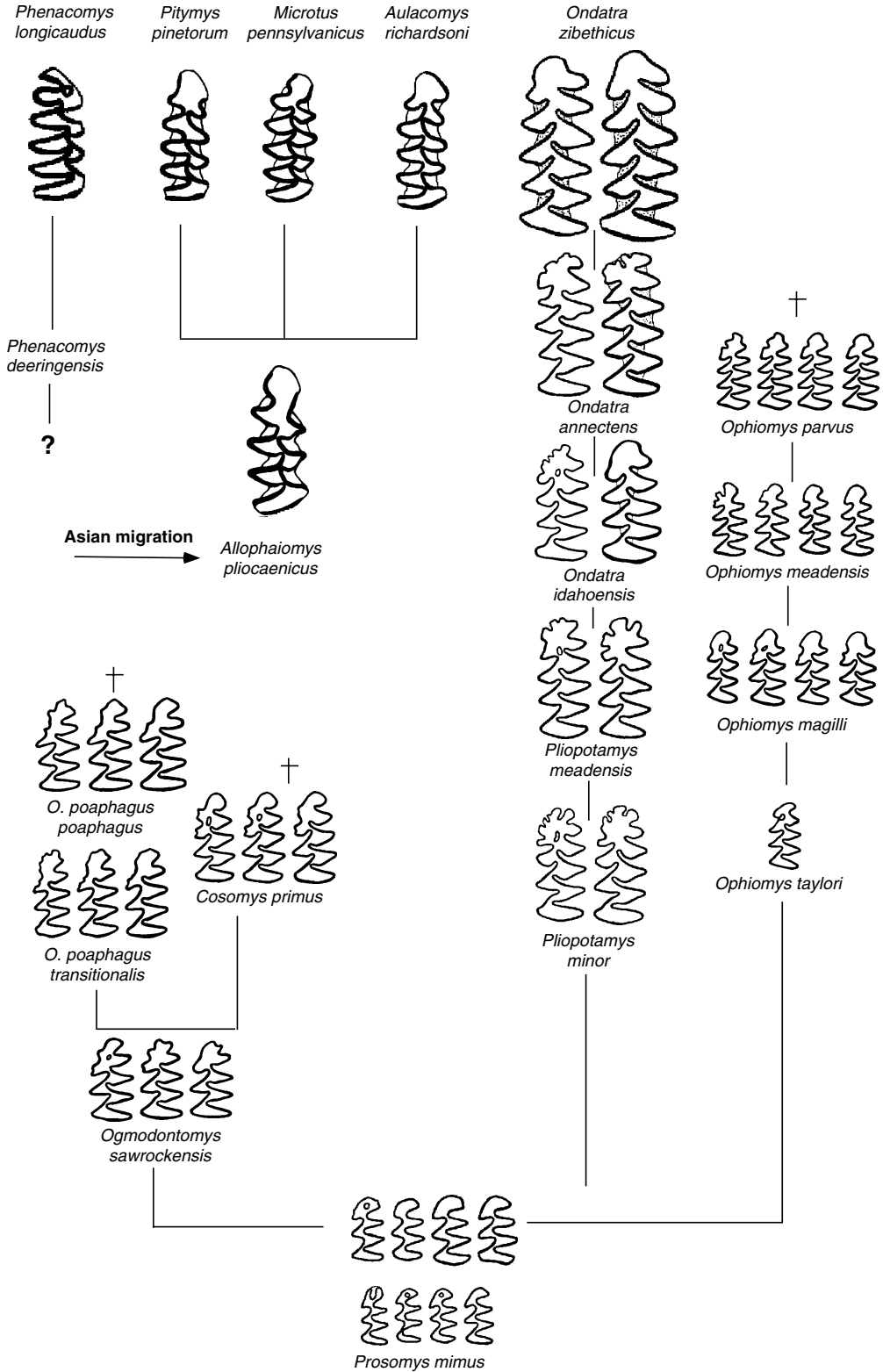


Fig. 2. Nearctic arvicoline radiation based on North American fossil record.

Eurasian forms resulted from later migrations; (2) *Propliophenacomys parkeri* was derived from a Eurasian form that emigrated to North America with *Prosomys*; (3) lastly *Propliophenacomys parkeri* could be Pliomyini by convergence. This last hypothesis is not the most parsimonious. *Propliophenacomys parkeri* evolved gradually into *Pliophenacomys finneyi-primaevus-osborni* by increased hypsodonty and size (Hibbard & Zakrzewski 1967). *Pliophenacomys* may have given rise, during the Irvingtonian, to *Proneofiber* then to *Neofiber* with the acquisition of continuous tooth growth. *Propliophenacomys parkeri* could be the ancestor of two or three other American lineages that share the same apomorphy, one of *Guildayomys hibbaridi* (Zakrzewski 1984), the other of the Pliomyini tribe: *Pliolemmus antiquus*, a particular lineage that was fairly stable for 1.5 Ma, evolving by polyisomery, appearance of interrupted enamel pattern on upper and lower molars in old stage of wear and loss of dental roots.

#### 4.3. The third ancestral lineage

Finally the lineage *Nebraskomys rexroadensis* (Hibbard 1970b)–*Nebraskomys mcgrewi* (Hibbard 1972) seems to maintain a *Prosomys*-like dental morphology with three triangles unlike the derived five-triangle forms. One may wonder whether *Nebraskomys* is not an evolved *Prosomys* as the radial enamel structure (with some lamella) suggests. The only notable difference is that in the  $M_1$  of *Nebraskomys*, triangles 1 and 2 are practically opposite one another, which is an ancestral cricetine character.

#### 5. The first Palaeartic radiation

The ancient Pliocene strata containing *Prosomys insuliferus* are overlain by beds bearing *Dolomys* and *Mimomys*, two genera that can be distinguished from their ancestor, *Prosomys*, by polyisomery (formation of two extra tooth triangles). *Dolomys* and *Mimomys* are closely related, as shown by the *Mimomys occitanus* population of Sète (France) and *Mimomys adroveri* of Orrios 3 (Spain) (Fejfar *et al.* 1990). The juvenile morphology of the earliest forms corresponds to an al-

ternating triangle structure termed the “dolomyan structure” that is conserved through to the present day in *Dolomys (Dinaromys) bogdanovi* (which is actually a cementum-bearing type of *Pliomys*). However, in most fossil lineages, the “dolomyan structure” that consistently appears at the occlusal surface of molars is more or less transient and is superseded with wear by the appearance of a new structure featuring a narrow enamel channel (prism-fold of Hinton) extending along the first outer re-entrant angle of the anterior loop. Another fold plunging into the dentine gives rise by wear to the “mimomyan islet” (innovation). This structure is found not only in *Mimomys* but also in most molars of primitive forms. The *Mimomys occitanus* population of Sète (Hérault, France) is very informative in this respect because, out of 100 specimens, there is continuous variability between the types that preserve “dolomyan structure” (*Dolomys* like dental morphology) along the entire length of the tooth shaft (the rarest: approximately 15%) and those in which the “mimomyan islet” appears by the earliest stages of  $M_1$  morphogenesis and which are accordingly classified with *Mimomys*. The same observation was reported for *Mimomys adroveri* of Orrios 3 where the “mimomyan islet” is represented in about 15% of specimens (Fejfar *et al.* 1990). Identical findings have been made at sites in Poland (Rebيلية Krolewskie) and Hungary with apparently different proportions of the two morphotypes. There, as at Orrios 3 (Fejfar *et al.* 1990), a typological approach “resolved” the problem by describing two species. However, a variability study shows this is a continuous and complex geographical variation that resulted in speciation (Chaline & Michaux 1975). The later view is supported by the study of timing shifts in morphological structures in the lineages *Mimomys davakosi-ostromosensis* and *Kislangia adroveri-cappettai-gusii-ischus* (Agusti *et al.* 1993) where the two structures correspond to two successive ontogenetic phases. This interpretation is supported by the  $M^3$  structure which is typically “mimomyan” and identical to that of *Mimomys occitanus* of Sète. The *Mimomys*  $M^3$  does not have the *Dolomys* structure initially described in Hungary that also appeared in *Prosomys*.

From *Prosomys insuliferus*, rapid diversification led to the individualization of the “dolomyan” and “mimomyan” lineages indicated below.

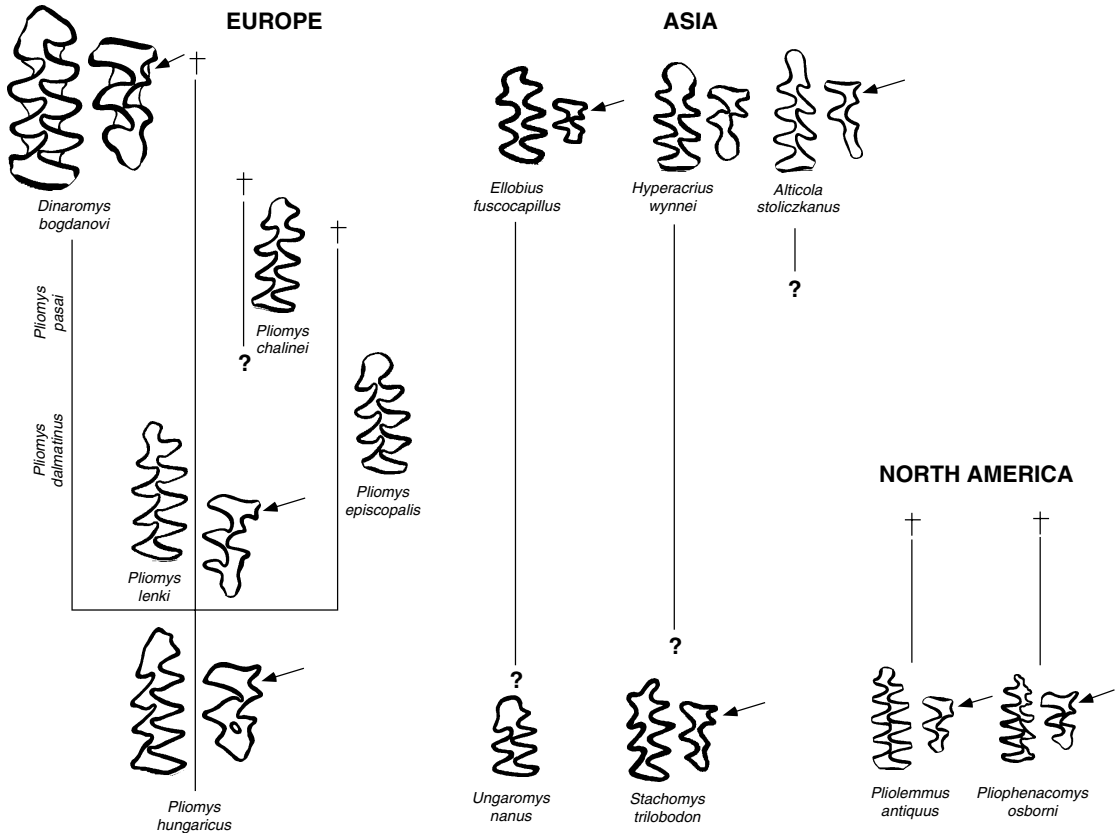


Fig. 3. Holarctic Pliomyine radiation based on the  $M^3$  structure. Arrows indicate the  $M^3$  "pliomyne" structure.

### 5.1. *Pliomys* lineages

The *Dolomys nehringi*–*Pliomys hungaricus* and *Dolomys milleri* lineages need to be considered (Fig. 3). The first was probably the ancestral lineage of the three *Pliomys* lineages: the gradually evolving *Pliomys lenki*–*ultimus*–*progressus* lineage (Bartolomei et al. 1975) and the two species in morphological stasis, *Pliomys episcopalis* and *Pliomys chalinei*. The group first appears in the fossil record in the Italian Villanyan fauna with *D. allegranzi* and later in the Ukraine with the derived *D. topachevskii* (Sala 1996). It is still represented by the relict form of the Balkans, *Dinaromys bogdanovi*. We should also consider the primitive lineages *Villanya exilis*, *Ungaromys weileri*–*nanus*, the first of which died out at the onset of the Pleistocene and the second at the start of the Middle Pleistocene. *Ungaromys weileri*–*nanus* may be related to *Ellobius*, but this is not proved. The same applies to relations between *Sta-*

*chomys* and *Prometheomys* of which an intermediate representative was discovered in Eastern Europe (Agadjanian & Kowalski 1978). Given that the *Dolomys* and *Pliomys* have a "pliomyan"  $M^3$  identical to that of North America *Pliophenacomys* and *Pliolemmus*, it would be worth investigating whether this is due to parallelism or to a common ancestor heritage. In the descendant "pliomyan" lineages, this stage (*Pliomys* structure) is preserved in the adult by the interplay of developmental heterochronies (paedomorphosis). This is fundamental for the systematics of the group. The same evolution prevails for the "pliomyan" forms of the Himalayas and Central Asia of which only extant descendants are known: *Hyperacrius* (*aitchinsoni*, *wynnei*, *fertilis*), *Alticola* (*phasma*, *blandfordi*, *montosa*, *albicauda*, *stracheyi*, *stoliczkanus*, *worthingtoni*, *lama*, *roylei*, *glacialis*, *alliarius*, *strelzowi*) and *Anteliomys* (*wardi*, *chinensis*, *custos*).



## 5.2. *Mimomys* lineages

*Mimomys davakosi*–*ostramosensis* evolution is characterized by the disappearance of “dolomyan” structures and the appearance of “mimomyan” and then “arvicoline” structures. For nearly two million years, the great evolutionary lineage found in Eurasia displayed gradual morphological evolution (Néraudeau *et al.* 1995). This is reflected in the course of evolution by a decrease in the morphological complexity of the anterior part of  $M_1$  (disappearance of the enamel islet, reduced surface area of the anterior loop compared with triangles 4 and 5) accompanied by ejection of the earliest wear stages of the ancestor (“mimomyan” islet stages). But the changes in the occlusal surface are less spectacular than the changes in the lateral aspect. This *Mimomys davakosi*–*ostramosensis* lineage is succeeded in the fossil record by the one extending from *Mimomys coelodus* to the present day *Arvicola terrestris*, via *Mimomys savini*. The transition from the rhizodont stage (rooted teeth; Chaline 1972) to the arhizodont stage (unrooted teeth) greatly increases the crown height and causes substantial changes in the *linea sinuosa* (the lateral enamel dentine junction line). The *Mimomys*–*Arvicola* lineage is the prime example of morphological changes in the occlusal surface of  $M_1$  being controlled by a change in the mode of growth.

The *Mimomys cappettai*–*rex* lineage shows gradual but diachronic evolution parallel to that of the previous lineage (Michaux 1971). The *Mimomys minor*–*medasensis* lineage exhibits parallel gradual evolution, but it is diachronic compared with the previous two lineages (Chaline & Michaux 1982). The history of the *Mimomys reidi* and *Mimomys pusillus* lineages are unknown. The close morphological similarity between *Mimomys burgondiae* of Broin and Labergement (Bresse, France) and fossil *Clethrionomys* (Bauchau & Chaline 1987) suggests their “mimomyan” origin. Comparison of three extant Eurasian species — *Clethrionomys glareolus*, *rutillus* and *rufocanus* — shows that the first two are closely related and form a separate morphological grouping relative to *C. rufocanus* which is a larger species that apparently originated in Eastern Asia. Comparative analysis of morphological distances versus genetic distances shows some congruency between mor-

phological and molecular evolution (Din *et al.* 1993). Fossil molars morphologically close to *Clethrionomys rufocanus* were initially named *rufocanus* by Kowalski and Hasegawa (1976) but were later called *Clethrionomys japonicus* by Kawamura (1988, 1989), who proposed very questionable phylogenetic relationships. *Eothenomys* (*E. olitor*, *E. proditor*) could have evolved from *Clethrionomys*. A Ukrainian form, *C. sokolovi*, could be an early form of *C. glareolus* (Rekovets & Nadachowski 1995, Rekovets 1996, Tesakov 1996).

The lineage history is unknown for *Mimomys petenyi*, *Mimomys pitymyoides*, *Mimomys* (*Cseria*) *gracilis* and *Mimomys* (*Cromeromys*) *tornensis* (Janossy & van der Meulen 1975). However it seems that the last lineage migrates in North America as suggested by the discovery of *Mimomys* (*Cromeromys*) *virginianus* (Repenning & Grady 1988) in the Cheetah Room Fauna (Hamilton Cave, West Virginia) Research in northwestern India (Kotlia 1985, Sahni & Kotlia 1985, Kotlia & von Koenigswald 1992) has shown the presence of primitive voles with rooted teeth: *Kilarcola indicus* and *K. kashmiriensis*. These voles are at a similar evolutionary stage to *Mimomys cappettai* and *occitanus* and might be derived from *Cseria*.

In China, Kormos (1934) described the first *Mimomys* (*Villanya*) *chinensis* on the basis of material collected by Teilhard de Chardin and Piveteau (1930) from Nihewan basin, Hebei. Later numerous *Mimomys* were described (Zheng & Li 1986), some of which are similar to the European species: *Mimomys orientalis* Young, 1935 [including probably *M.* (*Cseria*) *gracilis* and *M. minor*?], *M. banchiaonicus*, Zheng *et al.*, 1975 (= *M. rex*?), *M. gansunicus* Zheng, 1976 (= *M. intermedius*?), *M. heshuunicus* Zheng, 1976, *M. youhenicus* Xue, 1981 (= *M. polonicus*?) and *M. peii* Zheng and Li, 1986 (= *M. pliocaenicus*–*ostramosensis*?).

## 6. The second Palaeartic radiation: modern voles

### 6.1. Origin of the second radiation

The second phase of the vole radiation corresponds to the appearance and diversification of modern voles. The first palaeartic arhizodont voles, grouped with the *Allophaiomys* subgenus (Chaline

1966, 1972, 1987, Chaline *et al.* 1985, Repenning 1992) stem from a still inadequately identified *Mimomys* lineage (*pusillus*, *newtoni*, *lagurodontoides*). For others, the appearance of the *Allophaiomys deucalion/pliocaenicus* group in Central Europe is presumably due to immigration from the Ukraine (Garapich & Nadachowski 1996). The oldest known remains were described as *Allophaiomys deucalion* (van der Meulen 1973, 1978, Horacek 1985), probably a transition form between *Mimomys* and *Allophaiomys* because it is partially rhizodont and arhizodont. *Allophaiomys deucalion* transformed by very rapid stages into *Allophaiomys pliocaenicus*. This species ranged throughout Holarctica some two million years ago, during the Eburonian glacial phase (van der Meulen & Zagwijn 1974, Chaline 1974a) and evolved independently in Palaearctic and Nearctic zones (northern Eurasia, central Asia–Himalayas, and North America), an evolutionary pattern complicated by the interplay of migrations across the Bering land bridge.

## 6.2. History of European *Terricola*

European ground voles belong to the vast Holarctic genus *Microtus* of which they form the subgenus *Terricola* (Chaline *et al.* 1988, Brunet-Lecomte & Chaline 1990, 1991) (Fig. 4). They are found from the Iberian peninsula to the Caucasus Mountains, where 15 biological species are currently identified including for example *M. (T.) subterraneus*, the type species of the subgenus, *M. (T.) multiplex*, *M. (T.) tatricus*, *M. (T.) majori*, *M. (T.) savii*, *M. (T.) pyrenaicus*, *M. (T.) duodecimcostatus*, *M. (T.) lusitanicus* and *M. (T.) thomasi*. European ground voles are characterized by a “pitymyan rhombus” on the first lower molar ( $M_1$ ), a primitive character already found in evolved species of the subgenus *Allophaiomys*. The species *M. (T.) duodecimcostatus* and *M. (T.) lusitanicus* (Brunet-Lecomte *et al.* 1987) which are clearly distinct cytogenetically ( $2n = 62$ ) could be considered as a separate subgenus. These 2 species seem to be indirectly related phylogenetically to the Iberian fossil species *M. (T.) chalinei*.

The Central European forms make up the largest species group. Synthesis of genetic, cytogenetic and odontometric data for this group reveals

two sets of species: (1) the *M. (T.) subterraneus* set with the species *M. (T.) subterraneus*, *M. (T.) majori*, *M. (T.) daghestanicus* and *M. (T.) nasarovi*, and (2) the *M. (T.) multiplex* set with the species *M. (T.) multiplex*, *M. (T.) liechtensteini* and *M. (T.) tatricus* (Zagorodnyuk 1990b). Species of these two sets, especially those of the *M. (T.) multiplex* set, are related phylogenetically to the Cromeirian species (Hinton 1923, 1926, Bourdier *et al.* 1969) *M. (T.) arvalidens* and Middle Pleistocene species *M. (T.) vaufreyi* and *M. (T.) vergrannensis*.

*M. (T.) multiplex* in the Alps and *M. (T.) tatricus* in the Carpathian Mountains seem to be the relict daughter-species of *M. (T.) arvalidens*, *M. (T.) vaufreyi* and/or *M. (T.) vergrannensis*, species which were more widespread than the extant *M. (T.) multiplex* and *M. (T.) tatricus*.

The present-day geographical distribution of the *M. (T.) subterraneus* set, which stretches from the Atlantic Ocean to the Caucasus Mts. for *M. (T.) majori*, seems to argue in favor of the hypothesis by which the species of this set appeared more recently than those of the *M. (T.) multiplex* set which took refuge in the mountainous areas of central Europe.

Italy is occupied by the present-day species *M. (T.) savii*, which is cytogenetically close to the “Middle European group” (Meylan 1970). The morphotype of the  $M^3$  in the fossil species *M. (T.) melitensis* of Malta and *M. (T.) tarentina* of Apulia suggests that *M. (T.) savii* shares a common ancestor with these species. Furthermore, the sporadic occurrence among some *M. (T.) savii* of  $M^3$  of the *subterraneus-multiplex* type suggests close kinship with this group (Contoli 1980, Graf & Meylan 1980). The Pyrenean-Atlantic species *M. (T.) pyrenaicus*, which is similar to *M. (T.) savii* in  $M^3$  morphology, has led to the hypothesis that the two species are closely related, but this relationship is not supported by their  $M_1$  morphology.

The Greek species *M. (T.) thomasi* exhibits morphological convergence of  $M_1$  with those of *M. (T.) duodecimcostatus* and *M. (T.) lusitanicus* (Brunet-Lecomte & Nadachowski 1994), whereas its karyotype is very different ( $2n = 44$ ) as opposed to  $2n = 62$ . This apparent contradiction could be explained by a separation in the Middle

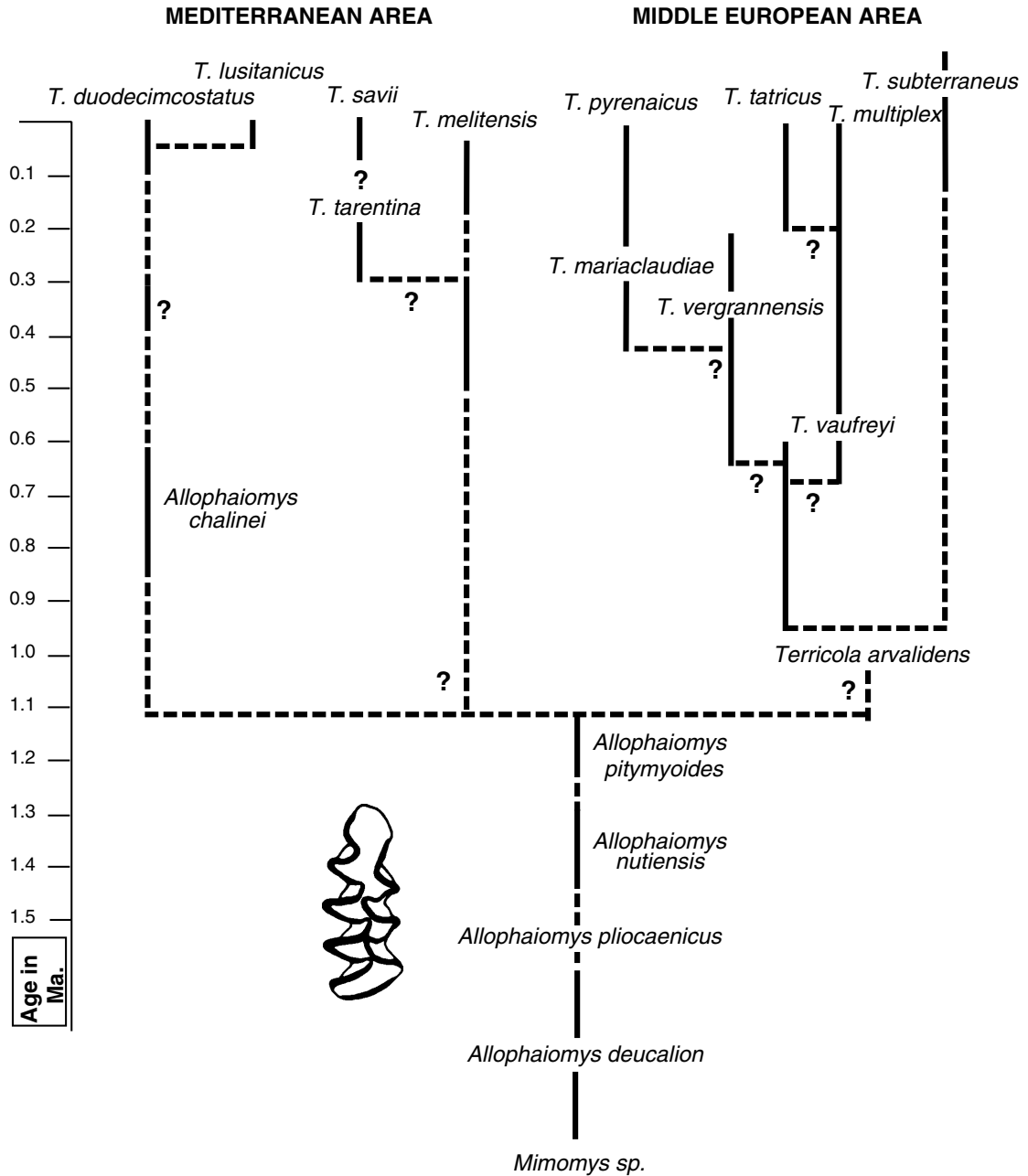


Fig. 4. Stratigraphical distribution and possible phylogenetic relationships of the European *Allophaiomys* and *Terricola*.

Pleistocene leading to extensive cytogenetic differentiation while the Mediterranean biome allowed the continuation of the primitive morphotype of  $M_1$  (which is occasionally identical to that of the ancestral species of *Allophaiomys*).

### 6.3. History of North American *Pitymys*

In North America (Fig. 2) the *Allophaiomys pliocaenicus* that emigrated from Asia during the Eburonian cold period (R. A. Martin 1975, Repenning

1992) gave rise to the *Allophaiomys guildayi-llanensis* lineage, ancestral to *Pitymys cumberlandensis*, a primitive vole viewed as the ancestor of *Pitymys pinetorum* (van der Meulen 1978). *Pitymys pinetorum* and *Pedomys ochrogaster* can be separated by multivariate analysis (Brunet-Lecomte & Chaline 1992) which also shows that *Pitymys pinetorum nemoralis* is morphometrically more closely related to *Pedomys ochrogaster* than to *Pitymys pinetorum pinetorum*. These similarities suggest that the subgenus *Pedomys* is unjustified and should be removed from the literature, and that *nemoralis* should be separated from *pinetorum* and promoted to the rank of a separate species. The *Pitymys quasiater* group appeared in the Irvingtonian and seems to be represented by a *Pitymys meadensis* lineage, the ancestor of *Pitymys mcnowni* that Repenning (1983a) claimed led to *P. nemoralis*. Repenning's phylogenetic reconstruction suggests that the *quasiater* group derived from a second wave of immigration across the Bering land bridge. This idea is inconsistent with the uniform biochemical data (Graf 1982).

#### 6.4. History of other European *Microtus*

In Europe *Microtus* seems to stem from *Microtus (Allophaiomys) nutiensis* and *Microtus (Allophaiomys) burgondiae* of the Early Pleistocene (Chaline 1972, van der Meulen 1973, Chaline et al. 1985). It seems that *Allophaiomys vandermeuleni* shares a common ancestor with the *Chionomys* group, while *A. chalinei* is situated close to the origin of *A. nutiensis* and the European *Terricola* group. Agusti (1991) claimed that *A. burgondiae* can be considered to be the sister-species of *A. jordanicus*, a form from Israel first ascribed by Haas (1966) to *Arvicola (A. jordanica)*. Nadachowski (1990) ascribed the same form to *Chionomys*, but von Koenigswald et al. (1992) believed that *A. jordanicus* ought to be separated from the other *Microtus* under the subgeneric name of *Tibericola*.

On morphological grounds, it seems that *Microtus burgondiae* could be the ancestor of the groups (1) *æconomus* and (2) *nivalis*. However biochemical data show that the snow voles are sufficiently isolated and diversified (Graf 1982) to be treated as a different subgenus, *Chionomys*. This rapid genetic divergence of *Chionomys* shows

that the molecular clock may tick at very different speeds. A study by Nadachowski (1991) showed that the *nivalis* group is differentiated into two subgroups, one in western Europe and the other in the Caucasus Mts. (*Chionomys gud* and *roberti*).

The "gregaloid" forms (*Microtus gregalis*-like dental morphology) that we shall refer to later (comprised of *Stenocranius middendorfi*, *S. miurus* and *S. abbreviatus*), "arvaloid" forms (*Microtus arvalis*-like dental morphology) including *M. arvalis*, *M. rossiaemeridionalis*, *M. montebelli*, *M. mongolicus*, and *M. maximowiczi* and "agrestoid" forms (*Microtus agrestis*-like dental morphology) of *Microtus (M. agrestis, M. pennsylvanicus, M. chrotorrhinus* and *M. xanthognathus*) could derive from *Allophaiomys nutiensis* although it is currently impossible to provide further details about their diversification. Other forms such as *Sumeriomys guentheri* seem to correspond to southern and eastern differentiations of the group.

#### 6.5. History of the *Microtus* of Central Asia, the Himalayas and China

The *Allophaiomys pliocaenicus* morphology currently persists in some species in the Himalayas — *Phaiomys leucurus*, *Blandfordimys bucharensis* and *B. afghanus*, *Neodon juldashi*, *N. sikimensis* and *N. irene* — which differ only in their greater size and have a primitive chromosomal formula that is probably closer (or even identical) to that of *Allophaiomys* (Chaline & Matthey 1971, Nadachowski & Zagorodnyuk 1996). From *Allophaiomys pliocaenicus* stock there were divergences into *Terricola* forms distinguished in these areas by the names of *Neodon sikimensis* and *Blandfordimys afghanus* and into *Microtus* forms termed *Lasiopodomys brandti*, *Proedromys bedfordi*, *Microtus deterrai* (fossil), *M. calamorum*, *M. fortis*, *M. millicens*, and *M. mandarinus*. Ongoing research in China is completing the inventory of eastern forms that consistently exhibit novel geographical traits (Zheng & Li 1990).

A study of *Microtus limnophilus* and *M. oeconomus* populations from all of Eurasia and St. Lawrence Island shows that *M. oeconomus* of Mongolia should be ranked as subspecies (*M. oeconomus kharanurensis*) and that *M. limnophilus*



of Mongolia should be considered as an other subspecies (*M. limnophilus malygini*). *M. limnophilus* of Mongolia is morphologically close to *M. oeconomus*. Dental and cranial analyses indicate the overall morphological homogeneity of the populations of *M. oeconomus* of Europe and especially their proximity with the populations of Buryatia. By contrast, the St. Lawrence Island population differs from the others in size, in particular, but also in shape.

### 6.6. History of other North American *Microtus*

Little is known of the history of North American *Microtus*. The earliest form is *Microtus* from the Wellsch valley not as old as 1.5 Ma in the Saskatchewan Valley. Its morphology is perhaps merely a local variation of *Allophaiomys pliocenicus*. It is similar to the Eurasian form *aeconomus*, the Nearctic fossil *deceitensis* and the extant *M. operarius* now reported to *M. oeconomus* (Repenning 1992).

One very interesting group is that of the upland voles *Stenocranius gregalis*. It is characterized by "gregaloid" type molars and is found in Eurasia (*gregalis* and *middendorfi*) and in North America (*abbreviatus* and *miurus*). Morphologically, *M. middendorfi* is similar to *M. abbreviatus*, whereas *M. gregalis* exhibits marked resemblance to *M. miurus*. However, from karyological data (Fedyk 1970), it is clear that these pairings of species are in fact the result of adaptive convergence. The group's history can be reconstructed as follows. The *gregalis* group individualized from *Allophaiomys* with the *nutiensis* variation whose karyotype should be  $2n = 54$ ,  $FN = 54$ .

The group evolved in the Palaearctic domain by centric fusions leading to the formulas of *M. middendorfi* ( $2n = 50$ ;  $FN = 54$ ) and the yet more derived *M. gregalis* ( $2n = 36$ ;  $FN = 54$ ). *M. middendorfi* is limited to the northern tundra where it survives by dint of substantial physiological adaptations (Schwarz 1963) whereas the more southerly *M. gregalis* group is a steppe species divided into two subspecies, *M. g. major* in the north and *M. g. gregalis* in the south. The subspecies *major* colonized the tundra in recent times without acquiring the specific physiological adaptations of

*M. middendorfi*. Under favorable conditions the steppe form reproduces early before the snow cover disappears (suggesting hypomorphosis).

In the Nearctic domain, the group evolved karyologically by pericentric inversions with *M. abbreviatus* (an endemic form of the St. Matthew Isles in the Bering Sea) and *miurus* ( $2n = 54$ ;  $FN = 72$ ), which implies derivation from a common *Allophaiomys* ancestor and not from the Palaearctic group. Very recently, since post-Wisconsin times, *M. miurus* has migrated to the subarctic tundra where its adaptation to many new habitats has been reflected by substantial subspecies diversification. Fedyk (1970) showed that heterochromosomes probably had a considerable influence on reproductive isolation. The sex chromosomes of *M. abbreviatus* and *M. miurus* are identical (large metacentric X and small telocentric Y) whereas the X chromosomes of *M. middendorfi* and *M. gregalis* are formed by one large metacentric and the Y by one submetacentric in *M. middendorfi* and one large telocentric in *M. gregalis*.

There are "arvaloid" voles in North America forming a uniform group as regards molecules: *M. longicaudus*, *townsendi*, *montanus*, *pennsylvanicus*, *chrotorrhinus*, *xanthognathus*, *canicaudus*, *mordax* and *mexicanus* probably derived from the *Allophaiomys* stock (Chaline & Graf 1988). *Phenacomys*, a vole with an asymmetrical dental pattern, seems to be represented from the Middle Pleistocene by the *deeringensis* form of Alaska, but its origins remain obscure (Chaline 1975). The history of *Aulacomys richardsoni*, *Herpetomys guatemalensis* and *Orthriomys umbrosus* is devoid of fossils.

### 6.7. History of Lagurines

Rabeder (1981) suggested that *Lagurus* originated from *Borsodia petenyi* through the intermediate form *Borsodia hungarica*. This hypothesis is refuted by the morphological variability of the descendant *L. arankae* and the more derived *L. panonicus*. Thereafter two lineages occurred, leading to modern *Lagurus* (in western Eurasia) and *Eolagurus* (in eastern Eurasia). The two lineages evolved in parallel (Chaline 1985, 1987). The *Lagurus* lineage is characterised by the progressive



polyisomeric increase of triangles through *L. pannonicus*–*L. transiens*–*Lagurus lagurus*. The *Eolagurus* lineage evolved by a large increase in size and minor morphological changes through *E. argyropuloi* to *E. luteus*. This lineage migrated to North America where it gave rise to *L. curtatus* which is present in many Irvingtonian and early Rancholabrean localities (Repenning 1992). These early forms also show a less complex morphology than any living *L. curtatus* and a direct descent from *Lagurus* from Eurasia is a tenius suggestion.

## 7. History of lemmings

The earliest known genus is *Synaptomys* from the Upper Pliocene (2.8 Ma) of northern Mongolia. By 2.8 Ma *Synaptomys* had already acquired continuous tooth growth. Its necessarily rhizodont ancestor is still undiscovered. It is found also in the Ural Mts. at 2.45 Ma: *Synaptomys (Pliotomys) mimomiformis* (Sukhov 1970) and in Poland *Synaptomys (Pliotomys) europaeus* (Kowalski 1977). The genus later disappears from Europe but survives in North America where the oldest representative *S. (Pliotomys) rinkerii* is dated to 2.5 Ma ago (von Koenigswald & Martin 1984a). Younger strata contain *Mictomys (Metaxyomys) vetus* (Idaho, Nebraska), *Mictomys (Metaxyomys) anzaensis* (California) and *M. (M.) landesi* (Kansas) and a new *Mictomys (Kentuckomys) kansansensis* lineage (Repenning & Grady 1988). *Mictomys (Mictomys) meltoni* is probably related to the extant *S. borealis*. The species *S. cooperi* related to *S. rinkerii* could be an ancestor of the extant species *Synaptomys (Synaptomys) australis*.

The *Lemmus* which appear in Europe about 2 Ma ago display derived characters of *Synaptomys europaeus* and are probably related to that species. *Lemmus lemmus* ( $2n = 50$ ) is known from the Early Pleistocene in Europe by a slightly smaller form than the extant one and gave rise in the Middle Pleistocene to the taiga lemming, *Lemmus schisticolor* with derived chromosomes:  $2n = 32$  (Chaline et al. 1988, 1989). *Lemmus sibiricus* in Alaska appeared by the start of the Middle Pleistocene, while *Lemmus amurensis* is a living form endemic to Asia that is unknown or unidentified in the fossil record.

As with the previous genera, the history of the genus *Dicrostonyx* is far from clear. A slightly more ancient lineage than the extant one, morphologically simpler, was discovered simultaneously in Alaska (*Predicrostonyx hopkinsi*) (Guthrie & Matthews 1972) and in Burgundy (*Dicrostonyx antiquitatis*) (Chaline 1972). Its relationship with the *D. simplicior–torquatus* lineage is uncertain. The extant *Dicrostonyx hudsonius* is either a relic of *Predicrostonyx hopkinsi* or a recently derived form of *torquatus*. *D. groenlandicus* is probably the product of recent speciation of *D. hudsonius*, as is *D. exul*, a species isolated on the St. Lawrence Islands.

## 8. Analysis of a radiation and evolution

The radiation of arvicolines is one of the best documented for mammals (Repenning 1967, 1980) although only 38 of the 140 lineages (27%) are actually known in the fossil record, probably because of the occurrence of numerous sibling species. This means that 102 lineages (73%) are known only in extant forms; this is notably the case in North American, central Asian and Himalayan species. Lyell's plot of the surviving lineages of the European Quaternary shows that only slightly more than 10% of Early Pleistocene lineages are still represented in the wild today by derived forms, that 65% of extant species appeared in the Middle Pleistocene and that 20% of living species have appeared since the end of the last glaciation or cannot be differentiated from fossil forms (i.e., morphologically they are sibling species). This shows that the "lifespan" of vole species is relatively short, from 0.3 to 1.5 Ma or less.

### 8.1. Structure of the radiation

An overview of the radiation shows that from a Holarctic ancestral stock close to *Prosomys insuliferus*, there were two successive phases corresponding respectively to (1) rhizodont primitive voles and (2) arhizodont modern voles.

The rhizodont character is a plesiomorphy of rodents including murids and cricetids which persists in some voles (*Bjornkurtenia*, *Prosomys*, *Miomys*, *Kislangia*, *Dolomys*, *Pliomys*, *Villanya*,

*Borsodia*, *Cseria*, *Ungaromys*, *Stachomys*, *Nemausia*, *Ogmodontomys*, *Nebraskomys*, *Pliopotamys*, *Pliophenacomys*, *Hibbardomys*, *Ophiomys*, *Cosomys*, *Dinaromys*, *Loupomys*) some of which are still extant (*Clethrionomys*, *Prometheomys*, *Phenacomys*, *Ondatra*). Many rhizodont voles progressively acquired continuous growth (an apomorphy) by the ever later appearance during their development of tooth roots. We shall look at the mechanisms underlying these changes later.

The arhizodont phase similarly involved the spread of an arhizodont form — *Allophaiomys pliocaenicus* — to the entire Holarctic domain whose descendants (*Terricola*, *Microtus*, *Pitymys*, *Chionomys*, etc...) evolved differently in the various regions of the Northern Hemisphere (Eurasia, the Himalayas and North America). Other lineages that arose from rhizodont forms (indicated with \*) later became arhizodont: *Mimomys*\*–*Arvicola*, *Mimomys*\*–*Lagurus*, *Stachomys*\*–*Ellobius*, ?\*–*Hyperacrius*, ?\*–*Alticola*, *Clethrionomys*\*–*Eothenomys*, *Clethrionomys*\*–*Aschizomys*, *Antelionomys*, *Ondatra*\*–*Neofiber*. To this list we should add the lemmings (*Dicrostonyx*, *Lemmus*, *Synaptomys*).

## 8.2. Modes of evolution

Arvicolines are the first group of mammals that can be used for a global assessment of the respective proportions of punctuations, stasis and phyletic gradualism in evolution, i.e. to effectively test the punctuated equilibria model (Chaline 1983, 1987, Devillers & Chaline 1993). Voles include outstanding examples of these three modes of evolution:

1. Phyletic gradualism as in the *Mimomys dava-kosi*–*M. ostromosensis* and *Mimomys savini*–*Arvicola cantiana*–*terrestris* lineage. This lineage is well documented stratigraphically and geographically (Chaline 1984, 1987, Chaline & Laurin 1984, 1986, Chaline & Farjanel 1990, Néraudeau *et al.* 1995) (Fig. 5). Other lineages show gradual parallel, albeit often diachronic, evolution: *Mimomys minor*–*medasensis*, *Mimomys cappettai*–*rex*, *Pliopotamys*–*Ondatra* (Zakrzewski 1969, Nelson & Semken 1970, Schultz *et al.* 1972, L. D. Martin 1984),

- Pliophenacomys*, *Ophiomys* (Hibbard & Zakrzewski 1967 and L. Viriot unpubl.), *Lagurus curtatus* (Barnosky 1987).
2. Morphological stasis is seen in *Cosomys primus* (Lich 1990), *Pliolemmus antiquus*, *Pliomys episcopalis*, *Ungaromys weileri*–*nanus*, *Nemausia salpatriensis* (Chaline 1987), *Loupomys monahani* (von Koenigswald & Martin 1984b) with perhaps an “ecophenotypic stasis” (phenotype plasticity superimposed on genetic stability) or genetic drift variations in a “given morphological spectrum” in *Clethrionomys glareolus* (Corbet 1975, Bauchau & Chaline 1987).
3. Punctuation occurs in all the lineages. All appear “abruptly” in the fossil record, as a consequence of allopatric speciation, such as *Prosomys mimus* and *Pliolemmus antiquus*.

The 52 European lineages whose fossil history is fairly well known all arose by allopatric speciation. Of these lineages, some evolved gradually while others remained in morphological stasis. Evaluation of the respective proportions of gradualism versus stasis shows that phyletic gradualism had been greatly underestimated in arvicoline evolution where it is clearly more common than stasis (Chaline 1983, 1987, Chaline & Brunet-Lecomte 1992, Chaline *et al.* 1993). These data show that the punctuated equilibrium model (Eldredge & Gould 1972, Gould & Eldredge 1977) is inadequate for explaining modes of evolution in arvicolines (Chaline *et al.* 1993).

The model should be refined by including ecophenotypic stasis and phyletic gradualism. We favor a model of equilibria (stasis)/disequilibria (phyletic gradualism), punctuated by the appearance of new lineages (Chaline & Brunet-Lecomte 1992). Finally these modes have been modelled mathematically by two linear functions with a sinusoidal component (Chaline & Brunet-Lecomte 1990):

1. *The linear model.* — The equation  $M = at + b$  (where  $a = 0.516$ ,  $b = 0.512$  and  $t = \text{time}$ ), explains 92% of the morphological change. But the parabolic variation of residuals indicates the inadequacy of the fitting curve which needs a complementary component;
2. *The linear and periodic model.* — The equation  $M = at + b \sin(ct + d) + e$  explains 99% of

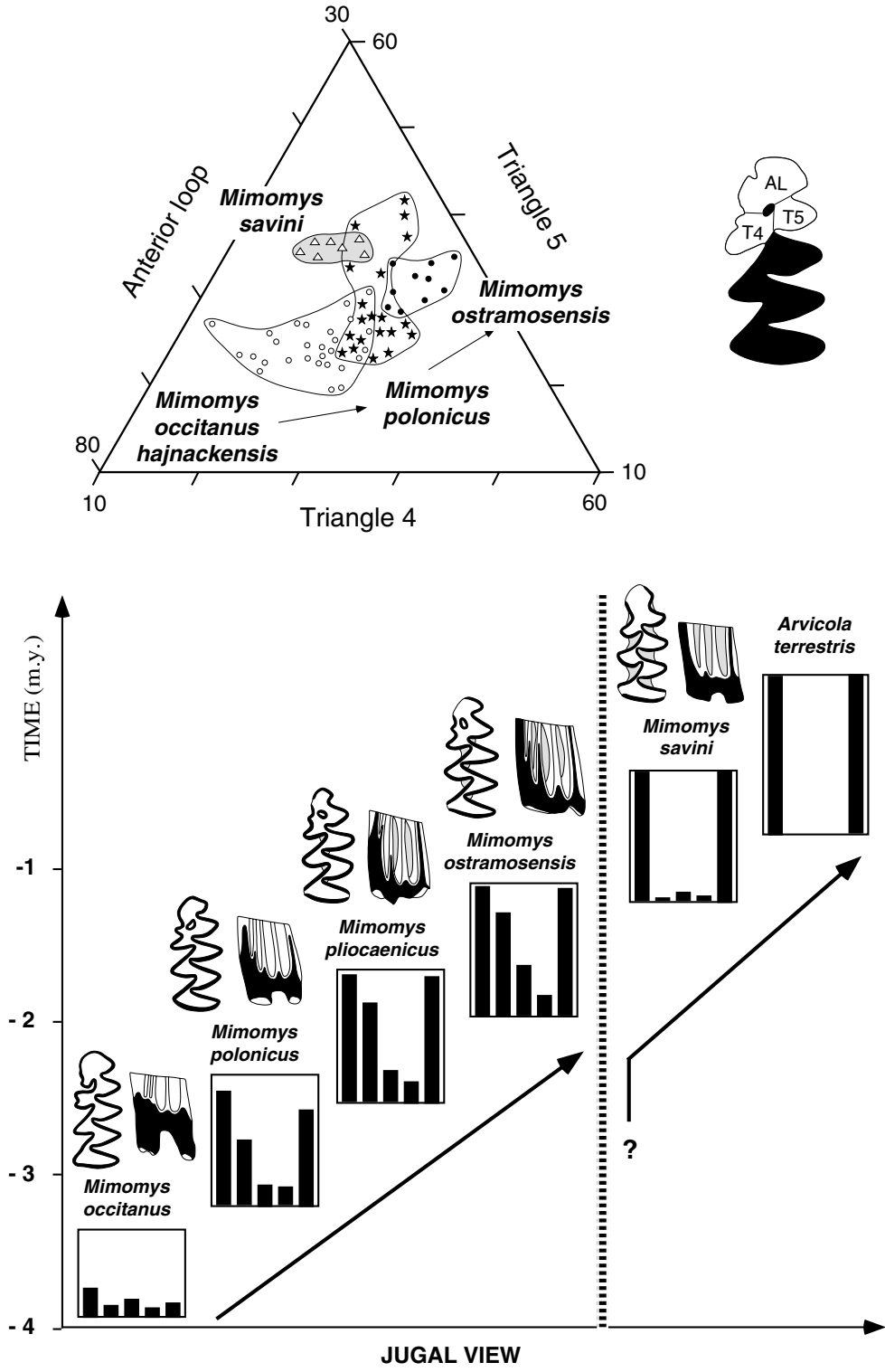


Fig. 5. Phyletic gradualism in *Mimomys*–*Arvicola* and the discontinuity between the two lineages (*Mimomys occitanus*–*ostromosensis* and *Mimomys savini*–*Arvicola terrestris*). The figure in the triangle describes the tridimensional relationships of characters within the lineage (after Viriot et al. 1990, Néraudeau et al. 1995).

the morphological variation ( $a$  is the rate of morphological change by time unit,  $b$  is amplitude and  $c$  permits the calculation of the period  $[6.28/c]$  of the periodic component). Random distribution of residuals shows the fitness and reliability of the model. This equation seems to be a good modeling of phyletic gradualism. Although this model is valid at a short time scale, a Verhulst logistical model can replace it at a larger scale. The period is 2.5 Ma at the million-year time scale, nearly the same observed in the North American mammalian stages (L. D. Martin 1985). In stasis and in ecophenotypism the equation is respectively reduced to  $M = b \sin d + e$  ( $e$  = constant), and to  $M = b \sin (ct + d)$ .

### 8.3. Evolutionary mechanisms: heterochronies

The first evolutionary stage of voles is characterised by the presence of rooted molars. A number of lineages retained roots but most acquired continuous growth and increased hypsodonty. The problem of the transition from limited to continuous growth is a very general phenomenon for mammals and seems to be the result of shifts in the timing of development. In the earliest forms, tooth roots appear very early in ontogeny whereas root development this is retarded in more recent forms (Chaline 1974b). Chaline and Sevilla (1990) showed that for the lineages from *Mimomys* to *Arvicola*, this pattern of evolution was the result of a complex mixture of three types of heterochrony: (1) hypermorphic processes with (2) acceleration of the initial phases and (3) deceleration of the final phases. Von Koenigswald (1993) also saw their evolution as the result of acceleration of early ontogenetic phases and the prolongation of one specific phase within the sequence. He also shows there was decoupling between the morphology and the *schmelzmuster* (apomorphy of lamellar enamel of arvicolines and expansion of lamellar enamel from the basal band over the entire height of the crown), which distinguishes Arvicolinae from the Cricetidae (Cricetids have a radial enamel plesiomorphy). L. Viriot (unpubl.) showed that the appearance of incisor and molar roots (rhizagenesis) was delayed gradually during arvicoline evolution until it was no longer ex-

pressed (Fig. 6). Comparative diagrams of the timing of dental events in cricetids and arvicolines (Fig. 6) show that the appearance of  $M_3$  is obviously pre-displaced in the most derived and hypsodont voles such as *Microtus arvalis*. Some lineages of North American voles (*Ogmodontomys*, *Pliopotamys*–*Ondatra*, *Ophiomys*) show hypsodonty increase before rhizagenesis and polyisomery of triangles (Fig. 7).

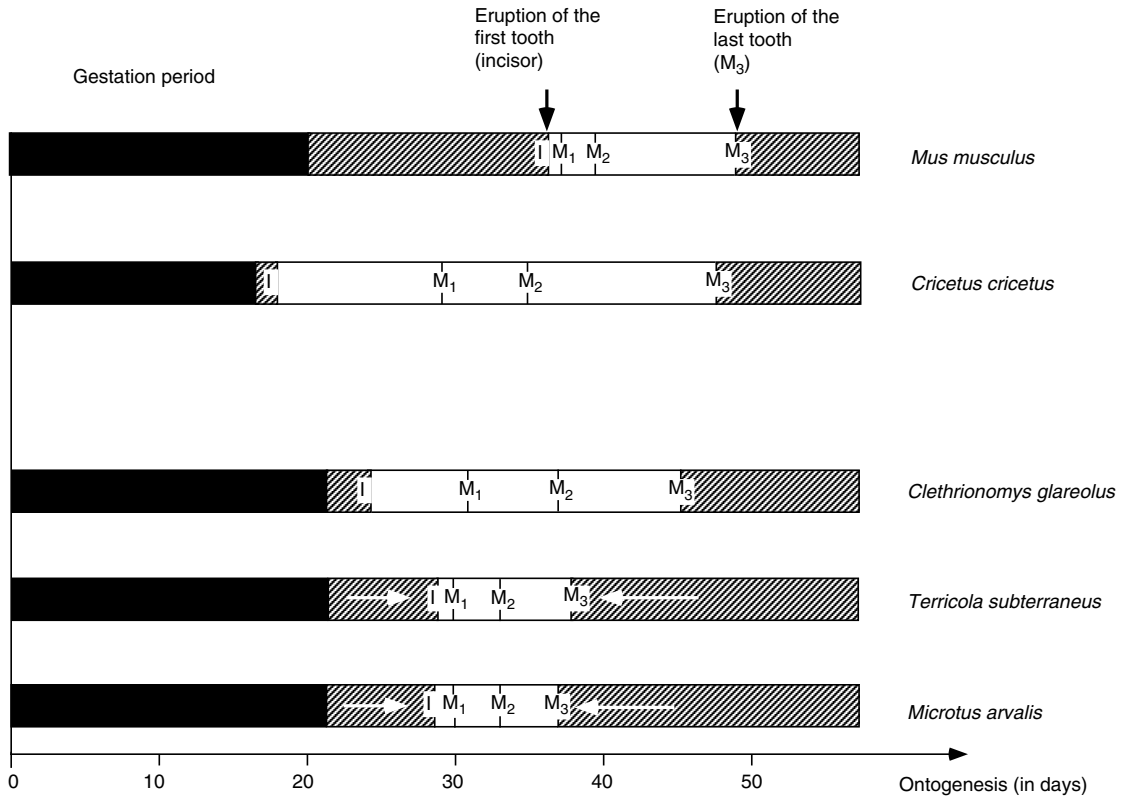
## 9. Morphology and environments

### 9.1. Cranial morphology and environments

A recent study (Courant *et al.* 1997) used superimposition (Procrustes) methods to quantify shape differences and establish phenograms for the three sides of the skull in order to evaluate the respective proportions of genetics and environment in arvicoline cranial morphology. This study indicated a strong connection between skull profile and mode of life: surface-dwelling forms have elongated skulls whereas burrowers have angular skulls. Analysis of the upper sides of the skull revealed a substantial difference between hard-substrate burrowers and other ecological groups. The results of the morphological analyses were compared with the phyletic hypothesis and with ecological data to explore how convergences take place in the evolution of arvicolines. Three cases of convergence have been characterized:

1. The clearest case of convergence in cranial morphology is for the lemming *S. cooperi* (the most derived species), which is classified by Procrustes methods morphologically with the voles, certainly because of its surface-dwelling adaptation;
2. *Lemmus schisticolor* lies outside the set of the other lemmings and is highly convergent with the voles;
3. The vole *Lagurus lagurus* displays similarities that vary with the cranial side concerned. The lower side of the skull presents a highly characteristic “vole” morphology. The lateral side of the skull ranks it among the lemmings.

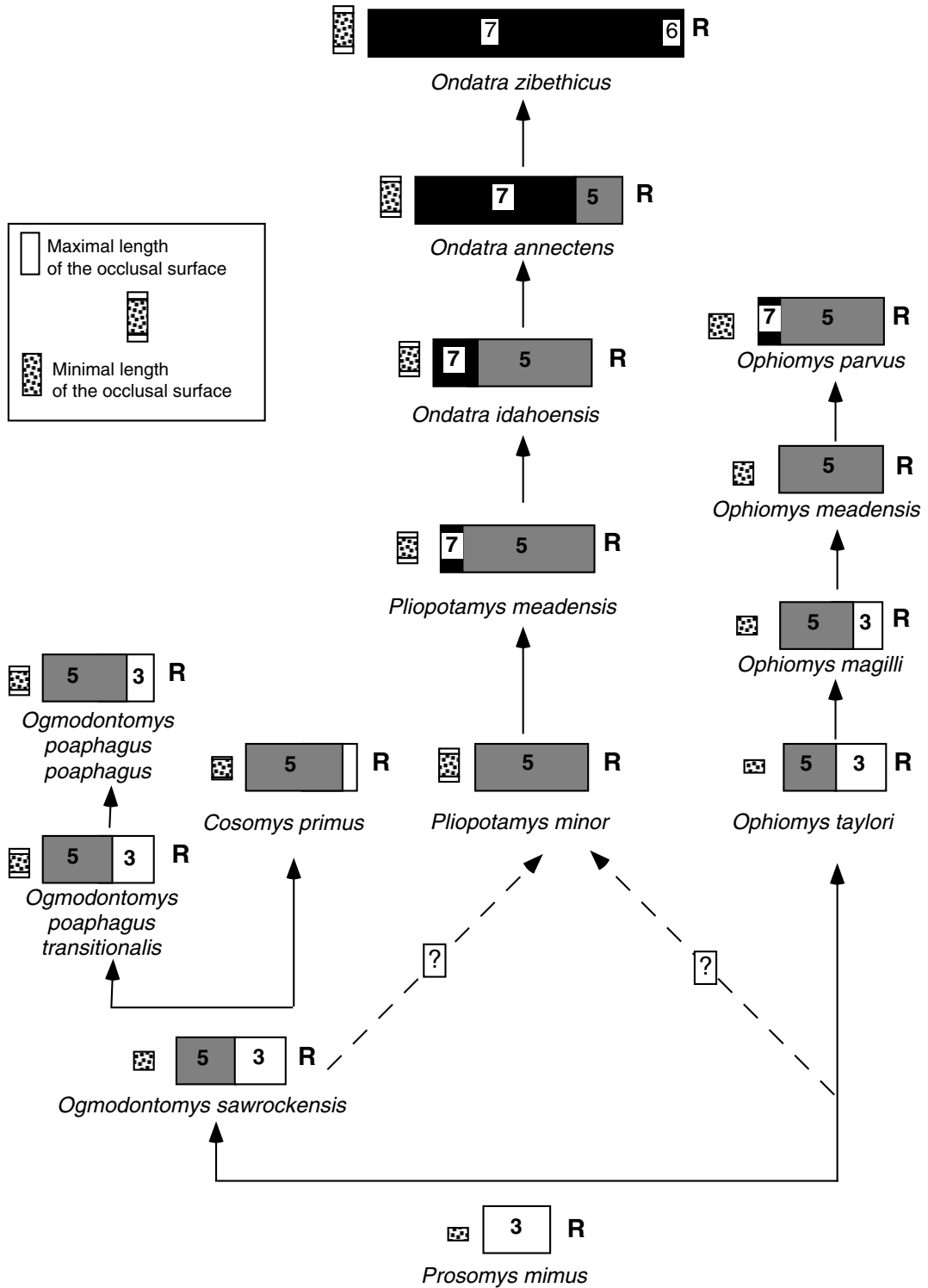
These examples of convergence coincide in part with four ecological events that marked arvicoline history (Fig. 8):



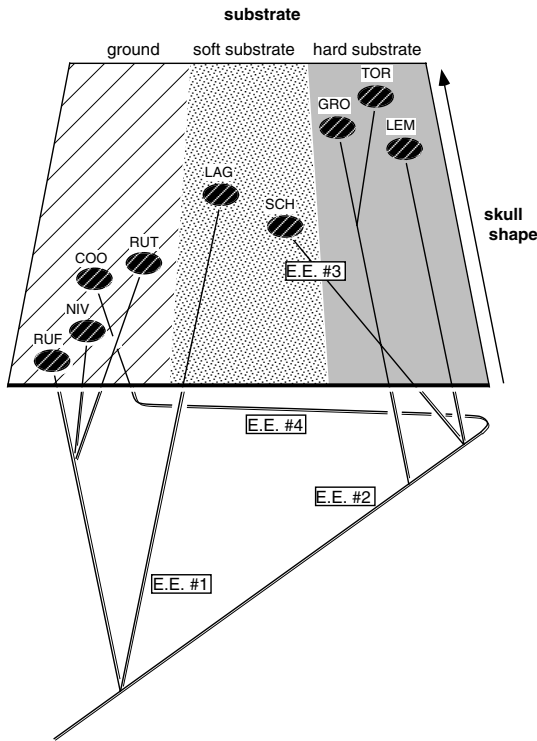
**Fig. 6.** Comparative timing (heterochronies) of dental events in murines, cricetines and arvicolines: incisor appearance is post-deplaced and the appearance of molars is accelerated in voles relative to cricetid.

1. The marked morphological convergence of *S. cooperi* with voles is related to a last ecological event that should mark the return to a surface-dwelling mode of life. If the proposed phyletic pattern is correct, this event may be considered as a reversion to ancestral behavior and the associated skull features. Moreover, its diet is very distinct from the abrasive diet (sedges, tree bark) of the other lemmings, and consists of slugs, snails and green leaves. Thus, *Synaptomys* presents a behavior and a skull morphology close to those of voles;
2. Another ecological event was the lemmings' acquisition of the ability to burrow in hard substrates. The cranial morphology of *L. lemmus* thus reflects an adaptation to life in Arctic climates: an underground mode of life in tundra environments and a diet consisting mainly of hard foods (tree bark, sedges, insects, mosses) requiring robust muscle insertions (massive skull with well-developed processes, marked occipital crest and small interparietal bone allowing for a larger squamosal bone). Fossil evidence suggests this event occurred some 2.8 Ma ago with the advent of first ice age in Praetiglian times;
3. *L. schisticolor* bears witness to another ecological event marking the adaptation to soft-substrate burrowing. This adaptation differs from that of *L. lagurus* as *L. schisticolor* digs galleries not in earth but in the moss cover. This ecological difference is reflected in cranial morphology;
4. If it is accepted that surface dwelling is the standard mode of life of voles, the position of *L. lagurus* can be understood as the result of an ecological event that determined its burrowing mode of life. Living in arid steppes, the species burrows in soft substrates (clay, loams) and differs from the surface-dwelling voles in having higher zygomatic arches and a more thickly set skull.





**Fig. 7.** Comparative diagram of certain dental characters of major North American archaic arvicoline lineages. Lateral evolution of M<sub>1</sub> showing the occlusal structure during abrasion stages (numerals in the bars indicate the numbers of triangles, R: rhizagenesis; the size of the bars are proportionnal to hypsodonty).



**Fig. 8.** Synthetic distribution of arvicolines related to morphological and ecological events. The distribution of selected arvicoline species is shown according to: (1) their phyletic position; (2) morphological position along the “skull shape” axis; (3) ecological behavior. The relative position of the species along the “skull shape” axis is estimated from the sum of morphological distances calculated for each side of the skull. The four small boxes distributed along the tree correspond to major ecological events. Abbreviations: RUF: *Clethrionomys rufocanus*, NIV: *Chionomys nivalis*, COO: *Synaptomys cooperi*, RUT: *Clethrionomys rutilus*, LAG: *Lagurus lagurus*, SCH: *Lemmus schisticolor*, GRO: *Dicrostonyx groenlandicus*, TOR: *Dicrostonyx torquatus*, LEM: *Lemmus lemmus*; E.E.#1; and (4) ecological events (see text).

These results attest to the prevailing influence of ecological and ethological factors on skull morphology in arvicoline rodents.

## 9.2. Parallelism and convergences between Nearctic and Palaearctic forms

In a synthesis covering fossil and extant morphological data together with chromosomes, Chaline (1974a) suggested a spatio-temporal framework

for the Holarctic diversification of modern voles. Research in molecular biology (Graf 1982) and comparison with palaeontological data (Chaline & Graf 1988) and ecological data (M. Salvioni unpubl.) indicate that this framework needs to be corrected because of the numerous instances of morphological parallelism that cannot be detected by palaeontological methods.

The genus *Microtus* includes approximately 60 species distributed among 11 subgenera of which 15 have undergone genetic studies. All the *Microtus* species seem to form a set in which the Nei distance corresponds to  $D < 0.40$ . This distance may be very short in twin species derived from chromosomal speciation. All North American *Microtus* species are closely related, regardless of their division into three subgenera (*Microtus*, *Pitymys* and *Pedomys*). This suggests that they form a monophyletic group derived from the early settler *Allophaiomys pliocaenicus*. As in Eurasia, in North America too there is diversification by parallelism of “Pitymian” forms with a “Pitymian rhombus” and “Microtusian” forms with closed, alternating triangles (*Microtus*). Accordingly the ancient subgenus *Pitymys* is polyphyletic, as Eurasian palaeontology suggested (Chaline 1972). For this reason, North American ground voles alone should be called *Pitymys*, while those of Eurasia should be classed with the subgenus *Terricola* (Chaline et al. 1988).

Morphological comparison of *Pitymys* with *Terricola* shows also spectacular morphological convergences. For example, *Pitymys quasiater* is very close to *Terricola subterraneus* and *T. multiplex*, while *T. duodecimcostatus* is close to *P. nemoralis* and *P. ochrogaster* (Fig. 9; Brunet-Le-comte & Chaline 1992).

## 10. Palaeobiodiversity, paleoenvironments and palaeoclimatology

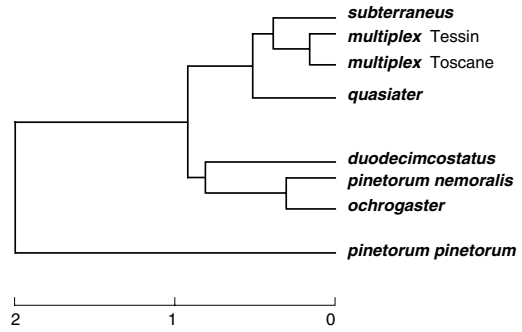
The distribution of voles and lemmings is controlled by environmental parameters (temperature and rainfall) (Hokr 1951, Kowalski 1971). During the Pliocene–Pleistocene, climatic fluctuations brought biological migration waves from north to south and east to west (3 000 km) and vice-versa. Accordingly, analysis of faunal successions of voles and lemmings has become a means of

highlighting changes in climate and environment (Chaline 1973, 1981, Repenning 1984, Chaline & Brochet 1989, Barnosky 1994, Chaline *et al.* 1995, Montuire *et al.* 1997).

The geographical distribution of rodents is a result of their complex history. Arvicolines are distributed holarctically, that is they are found in the temperate and arctic zones of both the Old and New worlds and are diversified in the more northern zones while they are not found in the tropics. Their areas of distribution changed substantially during the Quaternary. They migrated widely in keeping with the extension of their biotopes.

Multivariate analyses (correspondence and component analyses) of rodent associations from stratigraphic sequences are used to characterize the different climatic stages in terms of relative temperature, plant cover and moisture. For example, in the Gigny karst sequence in the French Jura (Chaline *et al.* 1995), faunal analysis can establish positive and negative correlations among the variations of the different species (Fig. 10). The significance of axis 1 in component analysis expresses temperature variations ranging from cold environments with contrasted continental biotopes to more temperate conditions. The significance of axis 2 in the same component analysis reflects vegetation patterns ranging from open to closed habitats. Axis 3 expresses trends in moisture. From the three axes various correlations between faunal and climatic parameters (temperature, plant cover and moisture) can be deduced. Faunal diversity in this sequence (as measured by Shannon index ranging from 0.74 to 2.27) increases with temperature and the complexity of vegetation, but is not sensitive to moisture. Lastly, the comparison of multivariate methods with the weighted semi-quantitative Hokr method (Hokr 1951) shows the two approaches to be complementary. The first method quantifies climatic parameters while the second seems to provide more precise evaluations of the main seasons of rainfall.

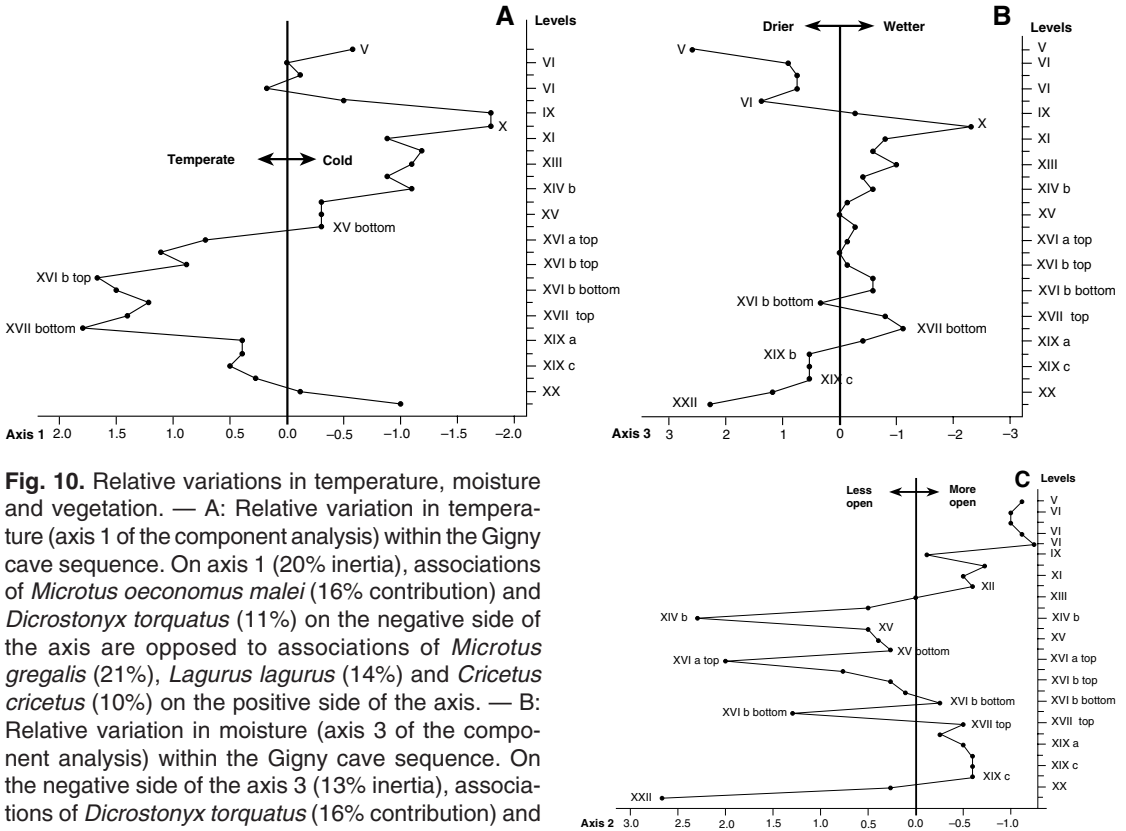
Another new method of estimation developed to evaluate climatic parameters is based on the relationship between climate and species diversity found in arvicolines. This method uses regression techniques (Montuire 1996, Montuire *et al.* 1997 and S. Montuire unpubl.). For further details on these regression techniques, *see* Camp-



**Fig. 9.** Phenogram between European *Terricola* and North American *Pitymys* showing dental convergences and the convergence of *Pitymys quasiater* with *Terricola subterraneus* group as well as the convergence of *Pitymys pinetorum nemoralis* and *Pitymys ochrogaster* within the *Terricola duodecimcostatus* group.

bell (1989), Edwards (1984), Sokal and Rohlf (1981) and Weisberg (1985). The number of species counted for 220 local to regional present-day faunas covering an area of less than 10 000 square kilometres were thus used. For each fauna, the temperature and rainfall parameters were compiled by using data from Wernstedt (1972).

Having completed the various calculations, the highest coefficient can be seen to correspond to the relationship between mean annual temperatures and the number of arvicoline species. This coefficient ( $r$ ) is greater than 0.8 (Fig. 11). In addition, a negative slope can be seen indicating that the greater the number of arvicolines, the lower the temperature is. The good results obtained for correlation coefficients mean that this method of evaluating climatic parameters can be applied confidently to Pliocene–Quaternary faunal sequences in order to reconstruct past climates (Montuire 1996, Montuire *et al.* 1997). Thus, in fossil fauna, given the number of species, it will be possible to determine the corresponding climatic parameter from the regression equation. Different applications have already been made in Hungary, France and Spain. For example, the use of arvicolines from upper Pleistocene deposits of Hungary has given temperature estimates ranging from  $-20^{\circ}\text{C}$  for the coldest fauna to  $24^{\circ}\text{C}$  for the warmest. Arvicolines therefore provide a record of temperature fluctuations over the period under study as suggested by the results of estimates shown in



**Fig. 10.** Relative variations in temperature, moisture and vegetation. — A: Relative variation in temperature (axis 1 of the component analysis) within the Gigny cave sequence. On axis 1 (20% inertia), associations of *Microtus oeconomus malei* (16% contribution) and *Dicrostonyx torquatus* (11%) on the negative side of the axis are opposed to associations of *Microtus gregalis* (21%), *Lagurus lagurus* (14%) and *Cricetus cricetus* (10%) on the positive side of the axis. — B: Relative variation in moisture (axis 3 of the component analysis) within the Gigny cave sequence. On the negative side of the axis 3 (13% inertia), associations of *Dicrostonyx torquatus* (16% contribution) and *Microtus oeconomus malei* (12%) are opposed to associations of *Microtus (Chionomys) nivalis* (14%) and *Microtus arvalis* (13%) on the positive side. — C: Relative variation in vegetation (axis 2 of the component analysis) within the Gigny cave sequence. On the negative side of axis 2 (19% inertia), associations of *Microtus arvalis* (11% contribution) are opposed to associations of *Microtus agrestis* (23%), *Clethrionomys* sp. (23%) and *Eliomys quercinus* (16%).

Table 1. This method, which can be used for other sequences in Eurasia and North America and for other time spans, allows us to compare different regions in terms of climate. It will thus be possible to identify differences between the east and west or the north and south of Europe and to see, for example, what the oceanic or continental influences are. If we compare the results of this method with those of the two previous ones [(1) Multivariate analysis and (2) weighted semi-quantitative Hokr method] applied to a single site at Gigny (Jura), the estimates are apparently contradictory; the biodiversity regression method curve is the reverse of that of temperatures on axis 1 of the component analysis. This apparently paradoxical result could arise because the two methods do not apply at the same scale. The biodiversity regression method is valid for a large geographical

scale whereas the component analysis method can be applied locally. Thus, it is likely that the variations estimated by component analysis at Gigny correspond to a narrow part of the biodiversity graph. This means the biodiversity regression method is more general than component analysis. The two methods are therefore complementary.

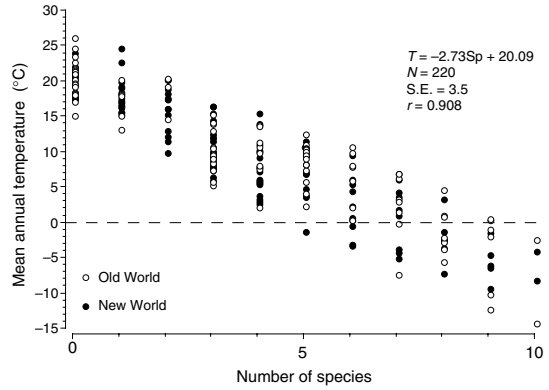
## 11. Conclusion

Voles and lemmings make up one of the best known mammalian radiations in terms of biology and palaeontology. It demonstrates:

1. Two successive phases of evolution corresponding respectively first to rhizodont primitive voles and second to arhizodont modern voles. This pattern of evolution was the result

of a complex mixture of three types of heterochrony: hypermorphic processes, acceleration and deceleration;

2. The existence and respective proportions in arvicolines of phyletic gradualism, stasis and ecophenotypic stasis;
3. The punctuated equilibrium model is inadequate for explaining modes of evolution in arvicolines because phyletic gradualism had been greatly underestimated in arvicoline evolution where it is clearly more common than stasis. Thus the punctuated equilibrium model must be completed into a punctuated equilibria (stasis)/disequilibria (phyletic gradualism) model;
4. The prevailing influence of ecological and ethological factors on skull morphology in arvicoline rodents;
5. The possibility of evaluating Pliocene–Quaternary climatic parameters with arvicolines sequences in order to reconstruct past climates.



**Fig. 11.** Scatter diagram of the number of arvicoline species and mean annual temperatures (after Montuire *et al.* 1997).

Because their radiation and diversification are fairly limited in space and time, it provides source material of a manageable scale to form the basis

**Table 1.** Estimates of mean annual temperature, mean temperature of the coldest month, and mean temperature of the warmest month for Pleistocene Hungarian faunas using arvicolines.

Fauna	Age (Ky)	Number of species of Arvicolines	Annual T (°C)	Min. T (°C)	Max. T (°C)
Baradla 4	5	6	3.1	-11.6	17.9
Kis-Köhat	8	3	11.4	0.7	22.7
Rigo 5	9	4	8.6	-3.4	21.1
Rigo 4	9.2	5	5.9	-7.5	19.5
Rigo 3	9.3	5	5.9	-7.5	19.5
Rigo 2	9.4	4	8.6	-3.4	21.1
Rigo 1	9.5	4	8.6	-3.4	21.1
Rejtek 1	12	8	-2.4	-19.9	14.7
Rejtek 9	13	7	0.4	-15.8	16.3
Petényi Cave	15	8	-2.4	-19.9	14.7
Remetehegy 2	17	7	0.4	-15.8	16.3
Remete Cave b	18	4	8.6	-3.4	21.1
Remetehegy 1	19	5	5.9	-7.5	19.5
Pilisszanto 3	20	8	-2.4	-19.9	14.7
Pilisszanto 2	23	5	5.9	-7.5	19.5
Pilisszanto 1	25	8	-2.4	-19.9	14.7
Bivak Cave	28.7	3	11.4	0.7	22.7
Istalloskö Cave	36	5	5.9	-7.5	19.5
Tokod Nagyberek	36.2	6	3.1	-11.6	17.9
Erd	40	5	5.9	-7.5	19.5
Subalyuk 16–20	50	2	14.1	4.9	24.3
Kalman V	70	4	8.6	-3.4	21.1
Kalman IV	75	5	5.9	-7.5	19.5
Porluyk	80	3	5.9	-7.5	19.5
Süttö -9	90	6	3.1	-11.6	17.9
Süttö 1–2–4	95	2	14.1	4.9	24.3
Horvölgy	100	7	0.4	-15.8	16.3



of a valuable research program. The vole biological/palaeontological model would be complementary to that of mice, which is less developed from the palaeontological standpoint, and so would cover the following issues:

1. Comparison of the hierarchy of divergences and the decoupling at the various levels of organization of living matter (molecular, chromosomal, ontogenetic, morphological);
2. Understanding of the temporal phenomena of speciation, from the origin to the extinction of a particular lineage;
3. Analysis of the impact of chronological changes in dental morphogenesis and understanding in particular of the mechanisms of acquisition of continuous growth, a major evolutionary question in mammals, which should provide a link between genetics and morphology (Ruch 1990);
4. Analysis of the processes and mechanisms of phyletic morphogradualism and progressive size increase;
5. Understanding of the role of internal constraints of development in dental evolutionary parallelism;
6. Understanding of external environmental constraints for morphogenesis which is often convergent with very loosely related groups (marsupials);
7. Appraisal of internal versus external constraints in evolution;
8. Analysis of the colonization of various biotopes and biogeographical zones in the course of a radiation and assessment of the degree of contingency in dispersal and many other issues in terms of physiology, ecology and ethology;
9. Detailed anatomy of a radiation in its well known environmental and palaeoclimatic context.

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