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EVOLUTION OF *BORSODIA* (ARVICOLIDAE, MAMMALIA) IN THE VILLANYIAN AND IN THE EARLY BIHARIAN

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Borsodia Janossy and Meulen is a genus of rooted voles belonging to the *Mimomys* group. The genus was a common element of small mammal associations in the Late Pliocene and the beginning of the Early Pleistocene, that is in the Villanyian and the Early Biharian, a period of about 1.5 Ma. The species of *Borsodia* were widely distributed in a latitudinal steppic belt stretching from North China to Central Europe. One of most striking morphological trends in the dental evolution of *Borsodia* was progressing hypsodonty. The rate of hypsodonty increase in *Borsodia* was not constant. It increased in a way close to exponential, having a period of relatively low rise in the Early Villanyian and a period of accelerated rise in the Late Villanyian and the earliest Biharian. This is interpreted as a reflection of the growing aridization. Late species of *Borsodia* gave rise to several rootless lagurine species of the modern fauna in a smooth morphological transition.

INTRODUCTION

In spite of its vast geographical and chronological distribution, the genus *Borsodia* Janossy and Meulen, (1974) remains an insufficiently known microtine genus. Nevertheless, the genus is very important because of its wide distribution, distinct morphology and a very high rate of dental evolution. The genus has a long history covering about 1.5 Ma from the Early Villanyian to the Early Biharian. Geographically the genus had a vast distribution from Northern China, Mongolia and Transbaikalian Russia in the East to Central and Northwestern Europe in the West (Fig. 1). The faunas, where species of *Borsodia* are dominant among small mammals, are distributed in much smaller area that practically coincides with the modern steppic belt. A goal of this article is to give a short review of the problems associated with the study of *Borsodia* and to try to evaluate hypsodonty increase within the genus throughout its existence.

HISTORY OF STUDY AND GENERAL OUTLINE OF TAXONOMY

Borsodia has been studied by many paleontologists (Major, 1902; Mehely, 1914; Kormos, 1938; Erbaeva, 1970; Basarov *et al.*, 1976; Zazhigin, 1980; Rabeder, 1981; Topachevsky and Scorik, 1977; Topachevsky *et al.*, 1987; Topachevsky and Nesin, 1989 and others).

Species of *Borsodia* have long been attributed to either *Mimomys* or *Villanyia*. It is only after the publication of Janossy and Meulen (1974) that the new usage has gradually become widely adopted. In fact, *Borsodia* is a distinct genus of rooted voles, belonging to the *Mimomys* group (sensu Zazhigin, 1980). It is the sister group of *Mimomys* proper. The main diagnostic characters of the genus are: (1) lack of cement, (2) lack of an enamel islet in the anteroconid of the first lower molar and (3) presence of usually only a posterior enamel islet in the third upper molar. *Borsodia* is distinct from *Mimomys* in the absence of cement, absence of an enamel islet in the anteroconid of m_1. It is distinct from *Promimomys* in the absence of an enamel islet in the anteroconid of m/1 and in the first labial fold of m^3/. *Borsodia* differs from *Villanyia*, Kretzoi (1956) in greater dimensions, greater hypsodonty and usually in more complicated molars (Terzea, 1990).

The taxonomy of *Borsodia* is very complicated. More than 20 taxa have been described or named. Many of the described species are apparently synonymous. A taxonomic revision is badly needed. Two major subgenera can be recognized: the nominal subgenus *Borsodia* (Janossy and Meulen, 1974) and an endemic central Asian subgenus named *Shamaromys* by Zazhigin (1989). Only the former group is discussed in this paper. These two major stems separated in the Early Villanyian and differ in third upper molar morphology (Zazhigin, 1980, 1989). The subgenus *Kulundomys* (Zazhigin, 1980) described for the most advanced species of *Borsodia* manifesting many morphological features of rootless lagurines, is probably a younger synonym of *Borsodia* s.l. Though legal and unquestionable, the choice of *B. hungarica* as a type species of the genus *Borsodia* cannot be regarded as very convenient, as *B. hungarica* represents a very advanced stage having lost many primitive characters, but having many derived features. For example, differentiated enamel thickness, noted in the original diagnosis of *Borsodia*, is not typical for most *Borsodia* species that have an undifferentiated enamel wall.

PRINCIPAL STAGES OF DENTAL EVOLUTION

The oldest and most primitive *Borsodia* are associated with the Early Villanyian, MN 16, faunas of the Euro-Siberian province. Two valid species can be recognized among these early forms. The most primitive is *B. steklovi* (Zazhigin, 1980) from the Biteke valley in the Ishim river basin in the south of Western Siberia. The other, later form is *B. novoasovica* (Topachevsky and Scorik, 1977) originally regarded as a subspecies of '*Villanyia petenyii*' from the

FIG. 1. Distribution of Villanyian and Biharian localities of *Borsodia* in Eurasia.

Shyrokino locality on the northern coast of the sea of Azov (Topachevsky and Scorik, 1977; Topachevsky *et al.*, 1987). The conspicuous character of early *Borsodia* is the slightly asymmetric anteroconid of the lower m_1 (Fig. 2). The *Mimomys* ridge is in a very posterior position and an islet fold is rather deep. This structure helps us to understand the mode of enamel islet reduction in the immediate *Promimomys* ancestor of *Borsodia*. The reduction has apparently taken the form of a gradual shallowing of the islet fold. Similar processes led to the appearance of protopliomys morphology in the Late Ruscinian *Promimomys* assemblages of the Euro-Siberian province (Zazhigin, 1980; Topachevsky and Nesin, 1989).

The third upper molar bears a very deep posterior islet, while the plesiomorphic anterior islet condition can be observed only sporadically. However, it is possible that the anterior islet is still constantly present in *B. steklovi* (Zazhigin, 1980). More often the anterior lobe and the first triangle are separate in younger specimens and become more and more confluent with tooth wear (Fig. 2).

The other important character of this early stage is the acrorhyzal position of the posterior root of the lower m_2.

Enamel band thickness is either uniform, or slightly *Mimomys* or of negative type. The histology of the enamel band shows a layer of tangential enamel in the trailing edges of the teeth.

The dentine tracts are very low. To express the hypsodonty stage of the first lower molar, the HH-index introduced by Rabeder (1981) is very convenient. The index is the square root of the sum of squares of the height of the two posterior dentine tracts. The HH-index in primitive *Borsodia* ranges from 1.0 to 2.5.

The second, intermediate stage of *Borsodia* dental evolution is represented in the faunas of the first half of the Late Villanyian, MN 17. The form abundant at this time is *B. praehungarica* (Schevtschenko, 1965). *B. parvisinuosa*, *B. aequisinuosa* and *B. altisinuosa* are apparently younger synonyms of this taxon (Rabeder, 1981). Several important changes had taken place since the Early Villanyian (Fig. 3). The *Mimomys* ridge had shifted anteriorly and the third labial angle become more shallow and the whole anteroconid more integrated, more symmetrical and more *Mimomys*-like. The third upper molars display a much shallower posterior islet, reaching only half of the crown height. Later wear stages still present the anterior confluence. The posterior root of the second lower molar shifts gradually during this stage from

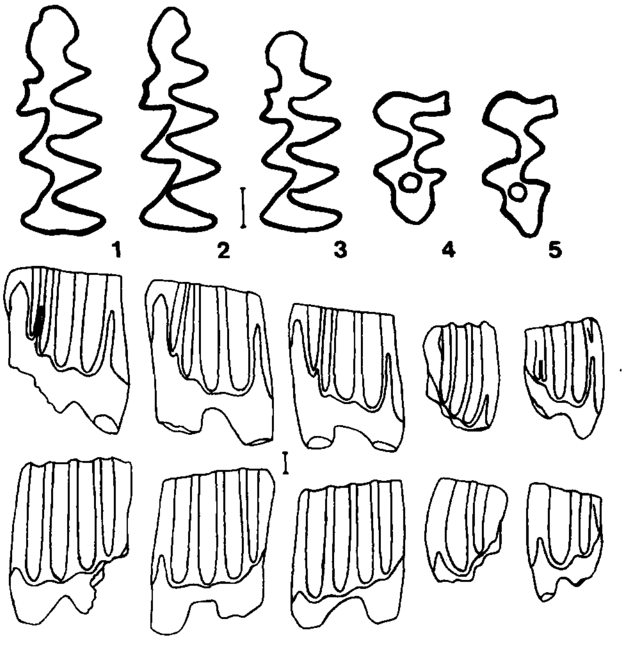

FIG. 2. Early stage of dental evolution in *Borsodia*. 1–2: *Borsodia novoasovica* (Topachevsky and Scoric), Shyrokino. 3: *Borsodia steklovi* (Zazhigin), Biteke, Selety suite. 4: *B.* sp., Biteke, Selety suite. 5: *B.* ex gr. *novoasovica* (Topachevsky and Scoric.), Kryzhanovka-1. 1–3: lower m_1, 4–5: upper m^3; 2,5–inverse. Scale 0.5 mm.

the acrorhyzal to the semipleurorhyzal position on the labial side of the upper surface of the lower incisor. Enamel band thickness remains basically uniform with some thinning in the depth of the folds. The tangential layer of the trailing edges of the triangles is reduced or absent (Rabeder, 1981).

Hypsodonty is markedly higher as compared with the previous stage. The HH-index ranges from 2.5 to 4.5 in successive populations.

The last, advanced stage of *Borsodia* evolution, presents a divergence event. The previously morphologically uniform evolutionary stem ramifies into two distinct branches—*Borsodia arankoides* (Alexandrova, 1976), retaining a distinct *Mimomys* ridge and the *Borsodia fejervaryi* (Kormos, 1934) group, displaying a reduction of this structure. The 'post-divergence' faunas are correlated with the second half of the Late Villanyian.

The taxonomy of these late species of *Borsodia* is most complicated. *Borsodia newtoni* (Major, 1902), *B. petenyii* Mehely, (1914), *B. hungarica* (Kormos, 1938), *B. lagurodontoides* (Schevtschenko, 1965), *B. tanaitica* (Schevtschenko, 1965) and *B. prolaguroides* (Zazhigin, 1980) should be revised to obtain a stable taxonomy, though some very important steps have already been taken (Rabeder, 1981; Mayhew and Stuart, 1986).

Very advanced *Borsodia arankoides* from the Kryzhanovka-4 fauna (Fig. 4) display a morphology transitional to a rootless condition. But even these rootless specimens usually present some signs of future root formation. The well developed *Mimomys* tract causes a separate interruption of the enamel wall.

Borsodia arankoides is usually accompanied by the other closely related advanced species—*Borsodia* ex gr. *fejervaryi* (Fig. 5, 1–3). The anterior prism of the anteroconid is roundish, without the *Mimomys* ridge. However, it may be present in very young specimens.

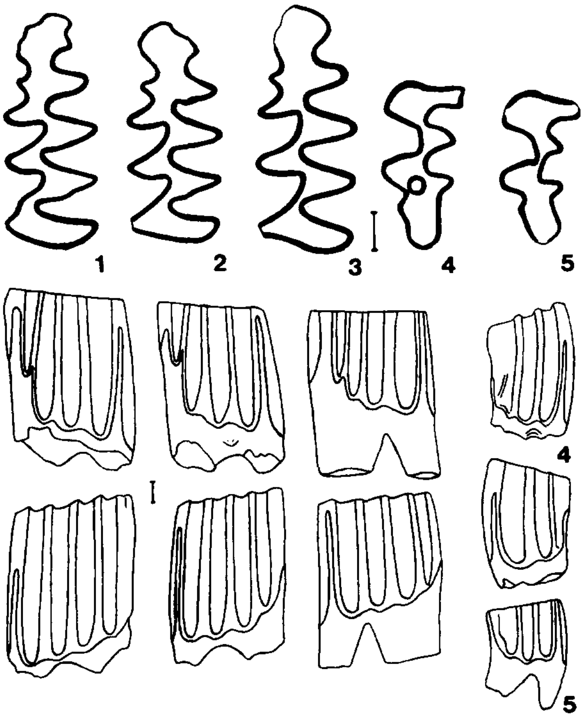

FIG. 3. Intermediate stage of dental evolution in *Borsodia*. 1–5: *Borsodia praehungarica* (Schevtschenko), Kryzhanovka-3. 1–3: lower m_1, 4–5: upper m^3; 3,5–inverted. Scale 0.5 mm.

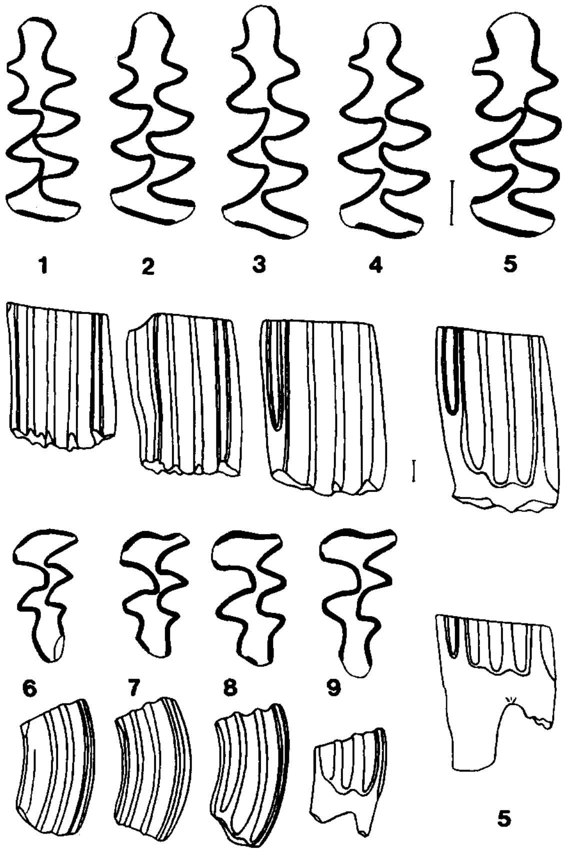

FIG. 4. Advanced stage of dental evolution in *Borsodia*. 1–5: *Borsodia arankoides* (Alexandrova), Kryzhanovka-4. 6–9: *B. arankoides* vel *B.* ex gr. *fejervaryii - prolaguroides*, Kryzhanovka 4. 1–5: lower m_1, 6–9: upper m^3; 6,8,9–inverted. Scale 0.5 mm.

The third upper molars of the two groups of advanced *Borsodia* are very similar (Fig. 4) and it is so far difficult to separate them by any metric or statistical technique. The posterior islet is normally absent, appearing in very young specimens only. Note that the anterior confluence is completely lost in the ontogeny of the tooth.

The high percentage of rootless molars in advanced populations of *Borsodia* originally misled paleontologists, leading to the idea of a migrational appearance of rootless lagurines within *Borsodia* assemblages and of a coexistence of rooted and rootless forms at the beginning of the Biharian (Schevtschenko, 1965; Topachevsky *et al.*, 1987). Now it is clear that many cases of such 'coexistence' can be interpreted within the framework of a single population concept, where ontogenetically younger specimens display a prolonged rootless condition and older specimens still form roots (Fig. 4). Some specimens occurring in fully rootless populations of true early lagurines can sometimes present signs of root formation, as in the molar (Fig. 5, 1) from the early Biharian Tizdar site on the southern coast of the sea of Azov.

In progressive species of *Borsodia* the posterior root of the lower m_2 is situated in a fully pleurorhyzal position, near the labial side of the incisor.

An example of the gradual appearance of lagurine features is, the so called lagurus indentations of the upper molars, or 'lagurine microangles' (Chaline, 1985), which can be observed in advanced species of *Borsodia*, though in very

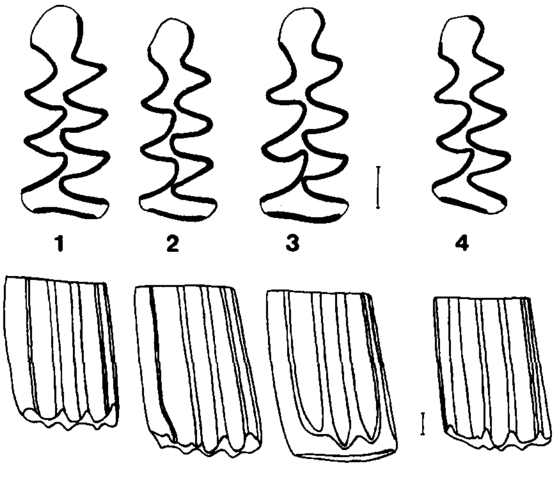

FIG. 5. Advanced stage of dental evolution in *Borsodia*. 1–3: *Borsodia* ex gr. *fejervaryii* (Kormos)–*prolaguroides* (Zazhigin), Kryzhanovka 4. 4: *B.* ex gr. *fejervaryii–prolaguroides* vel *Prolagurus ternopolitanos* Topachevsky, Tizdar. 1–4: lower m_1. Scale 0.5 mm.

low percentages. It is interesting that only up to 50% of individuals in fully rootless populations show these structures (Tesakov, *in press* a).

The enamel differentiation is very well developed, displaying the 'positive' type, with the leading edge of the lower molars thicker than the trailing one.

The schmelzmuster remains more or less unchanged, except for the thinning of the radial layer of the trailing edges of the triangles (Rabeder, 1980).

Hypsodonty reaches its extreme level in this advanced stage of *Borsodia* evolution. After their divergence, the two groups demonstrate very similar and synchronous increases in molar height. The HH-index of the first lower molars increases from 4 to 6 and more and after that level tracts begin to reach the occlusal surface in a rootless stage.

In fact, these two terminal groups of *Borsodia* gave rise to true rootless lagurines in a smooth morphological transition.

HYPSODONTY INCREASE IN *BORSODIA*

For the precise evaluation of any historic process such as the progressing hypsodonty of *Borsodi* an accurate chronology is essential. The chronology of small mammalian faunas of the Villanyian and the lower Biharian of Eastern Europe and Siberia existing today (Vangengeim *et al.*, 1990; Vangengeim and Pevzner, 1991; Zykin *et al.*, 1991 and others) cannot be regarded as very precise. Nevertheless, it enables us to correlate fossil faunas on a geochronological timescale. Samples of *Borsodia* teeth represented by HH-indices of first lower molars are shown in Fig. 6 in a framework of geochronological timescales. The faunas are placed in the table with a precision corresponding to the present state of knowledge. Some faunas might be placed slightly differently. All possible biostratigraphic and geochronologic data have been used. The most important are: paleomagnetic

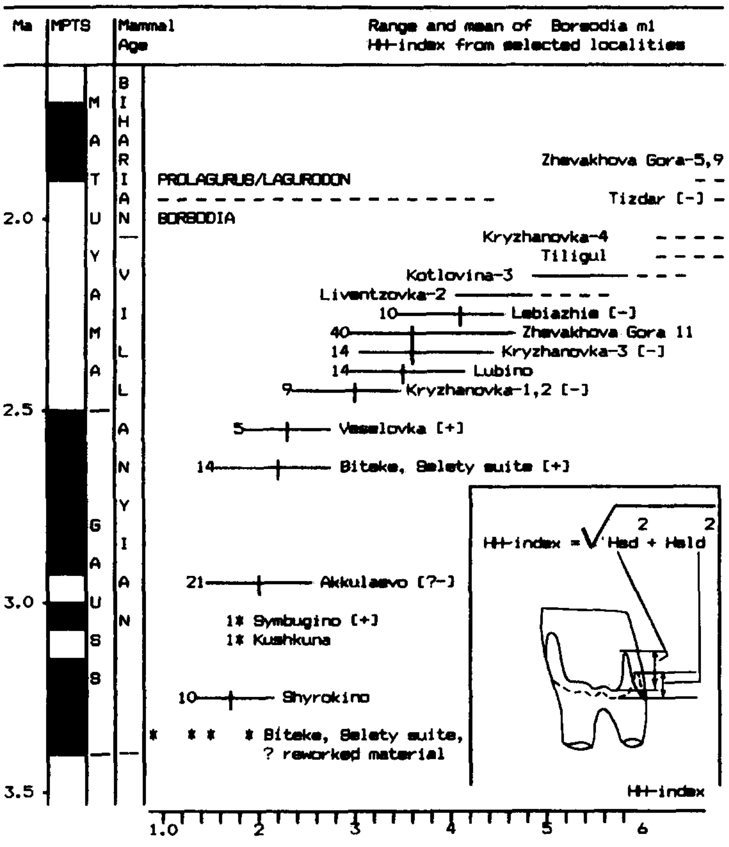

FIG. 6. Hypsodonty increase in several populations of *Borsodia* from the Villanyian and Early Biharian of Eastern Europe and Western Siberia. For each sample, its size, range, mean and data on magnetic polarity (+/-) of the locality is shown where possible.

data (reverse or normal polarity), local stratigraphy and faunal content of each assemblage. The upper limit of the *Borsodia* biozone is determined by the appearance of rootless lagurines and *Allophaiomys*. The new data from the Tizdar locality in the south of European Russia help in pinpointing this event to about 1.9–2.0 Ma (Tesakov, *in press* a). The samples from the Lower Villanyian display relatively gradual increase. The most primitive samples have values of the HH-index close to the Late Ruscinian *Promimomys* values. The youngest *Borsodia* samples from the Early Villanyian are only about two times more hypsodont than the oldest (Fig. 6).

In contrast, the beginning of the Late Villanyian saw an accelerated increase in hypsodonty, until the first rootless lagurines appeared around 2.0 Ma.

How can this irregularity be interpreted? Teeth are only part of the digestive system. It is widely accepted to regard progressive hypsodonty as an adaptation to eating grass. It is an increase in the abrasive properties of green vegetation that makes grass-eaters evolve higher molars to compensate for increased wear. One the other hand, hypsodonty is also caused by the growing consumption of food of low nutritional value.

So a suggestion of increasing aridization leading to the appearance of more abrasive vegetation, that in turn caused the increased hypsodonty in *Borsodia*, seems reasonable.

Some additional evidence of growing aridization can be seen in the small mammal faunas. It is during this time that the bulk of the modern steppic micromammals become common in assemblages. For instance, at about 2.0 Ma ground squirrels appeared, while jerboas became more diverse and numerous (Topachevsky *et al.*, 1987; Tesakov, *in press* b).

SUMMARY

Summing all this up, the following can be said:

(1) Dental evolution of rooted voles of the genus *Borsodia* was very similar to that of other rooted voles and particularly to members of the genus *Mimomys*.

(2) One of the most impressive processes was progressive hypsodonty increase during the course of 1.5 Ma.

(3) The rate of hypsodonty increase in *Borsodia* was not constant. It increased nearly exponentially, having a period of relatively slow increase in the Early Villanyian and a period of accelerating increase in the Late Villanyian.

(4) The genus *Borsodia* gave rise to several rootless lagurine species of the modern fauna in a smooth morphological transition in the huge steppic belt stretching from the Carpathian mountains in the West to Lake Baikal in the East.

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