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**A REVIEW OF
PHYLOGENY AND CLASSIFICATION
OF GERBILLINAE
(MAMMALIA: RODENTIA)**

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ОБЗОР ФИЛОГЕНИИ И
КЛАССИФИКАЦИИ GERBILLINAE
(MAMMALIA: RODENTIA)

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To the memory of
W. G. Heptner

Igor Ya. Pavlinov

A REVIEW OF PHYLOGENY AND
CLASSIFICATION OF GERBILLINAE
(MAMMALIA: RODENTIA)

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Under consideration are modern concepts of phylogeny and taxonomy of a rodent subfamily Gerbillinae (gerbils and jirds). Principal pathways of morphological evolution of the masticatory apparatus (mainly cheek teeth) and the ossean middle ear (mainly mastoid part of the auditory bulla) in Gerbillinae are characterized. Fossil genera referred to Gerbillinae are briefly reviewed, the genera *Epimerionaes* and *Pseudomeriones* are shown to be non-gerbillines. Predominating hypotheses about both phylogenetic position of Gerbillinae within Muroidea and genealogical relationships among its genera are outlined. Principal points of both agreements and disagreements between morphology-based and DNA-based phylogenies are indicated. Previous and current classifications of Gerbillinae are exposed, with most attention being paid to the one developed by the author. Suprageneric taxa and genera recognized in the latter are described: each taxon is characterized in respect to its major morphological features, principal fossils, various versions of its contents and relationships, and nomenclature upon a need. The identification keys for the genera and subgenera are provided. Ill. 26. Bibl. 133.

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Рассмотрены современные представления о филогении и систематике грызунов подсемейства Gerbillinae (песчанки). Охарактеризованы основные направления специализации жевательного аппарата (главным образом щёчных зубов) и костного среднего уха (главным образом мастоидного отдела слухового барабана) песчанок. Представлен краткий обзор ископаемых родов, относимых к Gerbillinae; показано, что роды *Epimerionaes* и *Pseudomeriones* должны быть исключены из этого подсемейства. Изложены основные гипотезы о положении подсемейства среди Muroidea, структура филогенетических связей между его родами; отмечены основные точки согласия и расхождения морфологических и молекулярно-генетических генеалогических схем. Кратко рассмотрены прежние и существующие классификации Gerbillinae; основное внимание уделено системе, разработанной автором. Охарактеризованы признанные в этой системе надродовые группы и роды современных песчанок: для каждого таксона указаны основные морфологические признаки, ключевые ископаемые представители, изложены разные версии состава и родственных связей, при необходимости затронуты вопросы номенклатуры. Представлены ключи для определения родов и подродов современных песчанок. Илл. 26. Библ. 133.

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INTRODUCTION

Phylogeny and taxonomy of the rodent subfamily Gerbillinae was subjected to a serious reconsideration during the last two decades. This was due to active incorporation of modern phylogenetic methodology into researches on gerbilline classification. As a matter of fact, this subfamily appeared to be one of the first family-group taxa of the Old World muroids which taxonomy was studied on the basis of the modern phylogenetic approach (Pavlinov, 1982a); in this respect it could be compared with the New World neotomines and peromyscines (Carleton, 1980). Under explorations were both relationships of gerbillines to other muroids and those among gerbillines themselves. Respective researches were at first based on morphological data (Pavlinov, 1982a; Tong, 1989; Pavlinov et al., 1990) and were supplemented subsequently with molecular findings (Chevret, Dobigny, 2005). Their cumulative efforts have led to several phylogenetic and classificatory schemes which agree in some important details and disagree in others.

As far as taxonomic relationships of gerbillines to other muroid rodents are concerned, one of the most important findings appeared to be their “shift” from cricetids, where they have traditionally been placed, to murids. To be true, this has been preceded by realization of phylogenetic heterogeneity of the classical taxon “Muridae”. Within gerbillines themselves, several principal supposedly monophyletic groups became reconized based on both morphological and molecular data: taterillines (or gerbillurines), gerbillines proper, and rhombomyines; the two latter forming a monophyletic group of higher rank. However, some points of significant disagreements revealed between those two kinds of data concerning phylogenetic position of several genera that affect entire phylogenetic and classificatory schemes for this subfamily. Some enigmatic gerbilline taxa remain for which either status or position remain quite unclear.

It is evident that such inconsistencies have great impact on understanding of gerbillines’ evo-

lutionary history including pathways of their morphological specialization, dispersion over continents and penetration into the desert biotas, etc.

There are several important causes of disagreements between explorers of gerbilline phylogeny and taxonomy which are to be taken into account when the entire situation is being observed.

One of them is that, among complex morphological structures available, masticatory apparatus and middle ear appeared to be of most use in elaborating phylogenetic classification for Gerbillinae (Pavlinov et al., 1990). They are under evident environmental control which makes quite clear their evolutionary transformations and character polarities, on the one hand. The problem is that, on the other hand, this prevents unambiguous identification of homogenies and homoplasies for each of these structures and, as a consequence, unambiguous recognition of holophyletic and paraphyletic groups defined by respective characters. However, because the selection pressures for the masticatory and hearing organs are evidently quite different, their simultaneous use in the phylogenetic reconstruction warrants that the resulting consensus tree contains a significant phylogenetic signal.

Another cause is very limited molecular data still available for phylogenetic reconstruction in the subfamily Gerbillinae. Indeed, the only comprehensive molecular study so far completed was based on just two fragments of mitochondrial DNA (Chevret, Dobigny, 2005). Although these authors insist upon priority of molecular over morphology-based phylogeny, there is however an opinion that mtDNA behaves as a solitary unit in the evolution and so it should be treated as a single character in phylogenetic reconstructions (Doyle, 1992). Therefore, the molecular-based phylogenetic reconstruction of Chevret and Dobigny looks pretty weak in its factological background. This conclusion, because of shortage of the reliable fossil records in gerbillines, seems to be true also for unconditional application of mo-

lecular clock hypothesis to the genetic distance data in the particular case under consideration.

At last, an important source of the above disagreements is concealed in different taxonomic philosophies, each treating its own way the phylogeny proper, its correct representation by classification, and the character weighting strategy. Earlier classifications of Gerbillinae/Gerbillidae were evidently gradistic (e.g. Heptner, 1933), the subsequent pretended to be phylogenetic in its “classical” (Haeckelian) sense (e.g. Chaline, Mein, 1979), while most recent belong to cladistic (Hennigian) branch of phylogenetics predominating in the contemporary taxonomic studies (Pavlinov, 1982a, 2001; Pavlinov et al., 1990; Chevret, Dobigny, 2005). However, the cladistics itself is not a uniform theoretical construction, which becomes more than apparent when methodological backgrounds of morphological and molecular trees for Gerbillinae, all declared being phylogenetic (or, more strictly, cladistic), are compared.

It is evident that, in order to proceed more effectively with exploration in phylogeny and taxonomy of the subfamily Gerbillinae, a kind of summary of preceding studies is needed. It would make more evident the points of both agreement and disagreement between different approaches. The former would mean a reliable consensus about monophyly of respective taxa. The latter would indicate the focal points of further researches, aimed not at contraposition of these approaches but at search of the other points of consensus.

So the main task of the present contribution is to provide a review of modern ideas about the phylogeny-based gerbilline taxonomy. In doing so, I shall expose principal versions of the latter offered so far by zoologists, paleontologists and genetists. Recent taxa will be under most close consideration whereas fossil genera will be just briefly discussed. More attention will be paid to the ideas have being developed by myself during last two decades or so (which explains and, to a degree, excuses an extensive self-citation). Principal diagnostic features will be indicated for the genera and presumable monophyletic groups of higher ranks recognized by me. Points of agreements and disagreements between different classifications based on different characters and classificatory approaches will be highlighted.

As it follows from the above consideration, any discussion of differences between existing classifications of Gerbillinae would be superficial without taking into account their theoretical backgrounds, be they explicitly declared or just presumed. However, comparison of the “philosophical” matters lying behind particular classifications to be considered here goes far beyond the scope of my issue; they should be left for the future investigations (maybe upon a time when the nowadays predominating numerical phyletics, like its phenetic predecessor, is no longer a kind of taxonomic fashion, and limitations of molecular evidence become more clear). Instead, I shall give few words about theoretical background of my own taxonomic approach and its resulting classification to make it more transparent and open to criticisms.

This approach could be defined, if any formal label is requested, as a kind of evolutionary cladistics (Hill, Crane, 1982; Saether, 1983; Pavlinov, 1990, 1998). Very briefly, it implies that a) phylogenetic analysis should be based, as much as possible, on the biologically sound evolutionary scenarios for morphological and eventually other traits allowing to estimate at least some of the character polarities (Hennig, 1966), and b) monophyletic groups could be defined not only by “true” but also by “underlying” (in the sense of Saether, 1983) synapomorphies resulting from parallel evolution of closely related groups. This approach was initially elaborated for morphological characters, but nowadays most popular maximum likelihood principles of molecular phylogenetics also fit demands of the evolutionary cladistics as far as they presume “evolutionary scenarios” for molecular structures (Felsenstein, 2003). It is acknowledged also that discrimination between the above two principal kinds of synapomorphies is based on probabilistic judgments dependent on the entire context of phylogenetic reconstructions and, thus, cannot be ultimate (Pavlinov, 2005). And, at last and most, it is acknowledged that any phylogenetic scheme is but a particular hypothesis which is consistent with both its theoretical background and observed facts, and is to be tested properly by other facts (which however are by no means “ultimate falsifiers” being dependent on respective theoretical background).

EVOLUTIONARY TRENDS AND MORPHOLOGICAL FEATURES

Gerbillines possess certain morphological traits in common with other desert/semidesert dwellers, such as heteromyids and, to a less extent, specialized dipodoids. Among these traits, before all, most noticeable is enlarged and eventually hypertrophied auditory bulla. At the same time, gerbils are interesting in that they retained rather generalized external appearance as compared with jerboas whose bipedal locomotory adaptations are usually considered as most typical for desert rodents (Mares, 1980). As a matter of fact, the most specialized desert gerbils, such as *Pachyuromys* or *Desmodilliscus*, are least similar to jerboas in their locomotion habits and respective morphological adaptations. Instead, the gerbils of otherwise generalized genus *Gerbillus* share some features of the pedal desert specialization with if not jerboas but with at least pocket mice (subfamily Perognathinae).

The scope of the present contribution does not allow to consider in details an interesting evolutionary phenomenon of existing of two conspicuously recognizable life forms of small desert rodents, one of which is represented by highly specialized jerboas and their analogues (such as the Australian *Notomys*) and another by more generalized gerbils and similar species (such as the Asian *Calomyscus*). At least some of the differences between them are supposed to be correlated with the way the rodents dwell the desert landscape (Shenbrot et al., 1999). For instance, it was shown that the well known negative ratio between the size of pinna and auditory bulla in specialized desert rodents could be explained by the way of their escaping from predation which, in its turn, depends on the size and patchy structure of their home ranges (Pavlinov, Rogovin, 2000).

In the present chapter, I shall concentrate on consideration of those pretty limited morphological features that allow discussing phylogenetic relationships and taxonomic status of extant gerbils. These are basically elements of the masticatory apparatus (both bony structures and dentition) and the ossean middle ear. Other cranial por-

tions, such as alisphenoid region, though quite informative in certain family-group rodent taxa, are very modified due to enlarged auditory bulla in many gerbillines and appeared to be of no great value in this group (Pavlinov et al., 1990). Alisphenoid and palatal morphology is useful to discriminate particular genera (such as *Desmodilliscus*, *Taterillus*, *Microdillus* with enlarged posterior palatal foramina) but is of far less significance in recognizing their sister-group relationships. Male genital morphology bearing an important phylogenetic information in several rodent families (e.g. Arata, 1964; Carleton, 1980; Pavlinov, Shenbrot, 1983) appeared to be quite uniform in gerbillines studied so far (Pavlinov, 1986; Pavlinov et al., 1990) and is also omitted here (but see account of the genus *Desmodilliscus* below). At last, museum postcranial skeletons are preserved for just few gerbilline genera, so their more extensive collecting and detailed phylogenetic study is a task for the future works.

BONY ELEMENTS OF MASTICATORY APPARATUS

Gerbillinae are characterized by so called myomorph type of masticatory apparatus; they differ from more generalized (in this respect) members of Muroidea by dominance of the anterior portions of *musculus masseter* over *m. temporalis*. Respective modifications of the bony structures constituting masticatory apparatus in gerbillines include a strong tendency toward enlargement of the anterior portion of zygo-masseteric construction (zygomatic arc + masseteric plate) correlated with reduction of temporal plate of the braincase and coronoid process of the mandible.

As far as gerbilline zygo-masseteric construction is concerned (Fig. 1), the most spectacular is the anterior outgrowth of the masseteric (= zygomatic) plate that is elongated to form a so called masseteric keel. So, in the gerbillines this plate consists of two clearly identifiable parts, of which

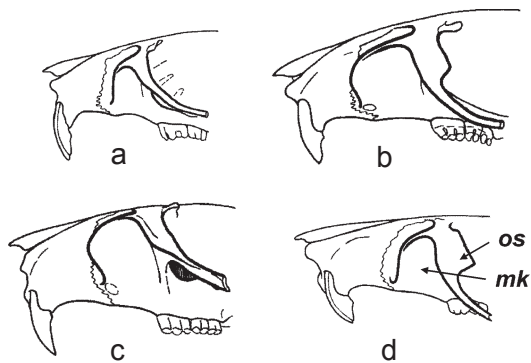


Fig. 1. Zigo-masseteric construction (lateral view) in some Gerbillinae (not to scale, after Pavlinov et al., 1990):

Рис. 1. Зиго-массетерная конструкция (вид сбоку) у некоторых Gerbillinae (не в масштабе, по Pavlinov et al., 1990):

mk – masseteric keel (киль массетерной площадки), *os* – orbital shield (орбитальный навес)

a – *Desmodilliscus*, *b* – *Gerbilliscus*, *c* – *Rhombomys*, *d* – *Ammodillus*

the posterior one, which is typical for all muroids, is situated at the base of the anterior zygomatic root proper, whereas the anterior one, the keel specific for gerbillines (and occurring occasionally in some other muroids), expands forward along the rostrum. This construction is most generalized in *Desmodilliscus* and *Gerbillus*, which are characterized by the least developed masseteric plate among extant gerbillines (Fig. 1a). Two principal, though not quite distinct, trends could be identified in progressive evolution of the masseteric plate. Its keel is strongly elongated in taterillines (especially in *Gerbilliscus*, Fig. 1b), while it becomes rather high in rhombomyines (especially in *Rhombomys*, Fig. 1c). Dorsal expansion of anterior portion of zygomatic arc leads to formation of a conspicuous orbital shield in some genera (such as *Ammodillus*, Fig. 1d). All these differences occur as general trends only and no sharp distinctions could be traced among phylogenetic lineages. But at least taterilline-like elongation of the masseteric keel could be considered as a synapomorphy for taterillines.

These two trends in development of the zygomatic-arterial construction are correlated with certain transformation of temporal plate of the braincase delimited dorsally by parasagittal ridges (Pavlinov et al., 1990). It becomes narrower with the

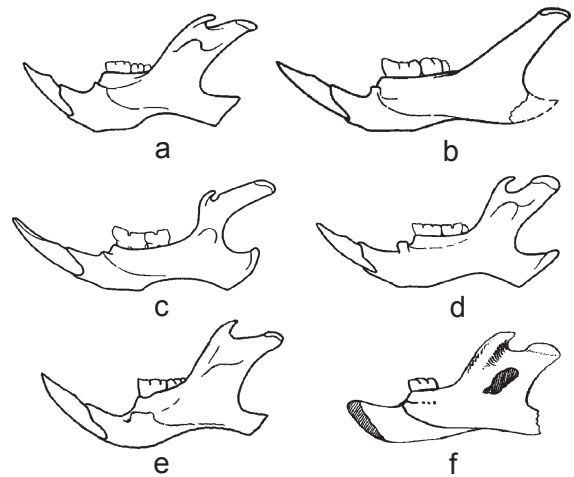


Fig. 2. Mandible (lateral view) in some Gerbillinae and their relatives (not to scale, after Pavlinov et al., 1990):

Рис. 2. Нижняя челюсть (вид сбоку) у некоторых Gerbillinae и близких к ним (не в масштабе, по Pavlinov et al., 1990):

a – *Gerbillus*, *b* – *Ammodillus*, *c* – *Desmodilliscus*, *d* – ?*Monodia*, *e* – *Pachyuromys*, *f* – *Myocricetodon*

taterilline-like keel elongation, and expands in most advanced rhombomyines. The latter feature reflects parallel evolution of the masticatory apparatus in rhombomyines and arvicolines and may serve as additional support for phylogenetic specificity of the so-called “higher gerbils” (genera *Meriones*, *Rhombomys* and their allies).

Changes of the mandible (Fig. 2) are partly correlated with evolution of the auditory bulla and partly with changes in proportions of the masticatory muscles. There are certain reasons to suppose that it is the bullar pneumatization (considered below) that initiated all these transformations of the masticatory apparatus in gerbillines (Potapova, 1990). This “bullar effect” is most evident, if compared to muroids with generalized bulla, in that ascending ramus of the mandible takes more vertical position and becomes narrower and the posterior curvature between this ramus and angular process becomes deeper, while the latter process becomes less vertical.

It is to be noticed that all these intercorrelated features are evident even in the gerbils with relatively small auditory bulla (Fig. 2a). So they may serve as an important indirect evidence of pneumatization of the auditory bulla when no data on morphology of the latter is available. In particular, these features seem to discriminate extant ger-

billines from extinct myocricetodontines for which quite typical “murid” mandible was reported (Fig. 2f). However, this correlation is not very strong; in *Pachyuromys* with its inflated auditory bulla the ascending ramus of mandible is very wide, though taking more vertical position than usual for the “typical” gerbils (Fig. 2e).

Ascending ramus of the mandible completely lost coronoid process in *Ammodillus* (Fig. 2b), a feature unique among Muroidea. This is correlated with most narrow temporal plate and maximal orbital shield. Another very specific ascending ramus morphology is observed in *Desmodilliscus* that differs by long and narrow *pr. articularis* and very wide *pr. angularis* (Fig. 2c). This morphotype found in *Desmodilliscus*, like the one in the genus *Ammodillus*, is an autapomorphy and is of minute cladistic significance as it does not indicate any sister-group relationships. However, another gerbil genus close to *Gerbillus*, here called tentatively *?Monodia*, possesses a mandibular morphology (Fig. 2d) resembling the one observed in *Desmodilliscus*. Such an intriguing similarity could hardly indicate close relationships between these two tiny gerbils but, as it is shown in the account of the subtribe Gerbillina below, may indicate a generic status of *?Monodia*.

DENTITION

Gerbiline dentition is pretty specific and constitutes one of several predominating types within the rodent order (Shevyreva, 1976). Due to this, molars of the gerbils are easily recognizable among Recent Old World Muroidea, on the one hand. But it provides certain problems with allocation of some extinct muroid rodents to this subfamily by isolated teeth alone, on the other hand.

In general, gerbilline molars are initially quite simple, though not to an extent observable in such muroids as specialized hydromyines (see Missonne, 1969), and their further simplification is one of the principal trends of dental evolution in the subfamily (Petter, 1975; Pavlinov, 1984a). It involves reduction of particular elements of the molar crown, decrease of the last molars (lower M3 disappeared in *Desmodilliscus*, see Fig. 2c), and partial reduction of the molar roots. It is to be stressed that all these manifestations of the overall trend peculiar to gerbillines are intercorrelated, so the gerbils most specialized in respect to crown pattern are also most advanced in respect to reduction of both the entire M3 and the roots on M1 and M2 (Pavlinov, 1984a; Pavlinov et al.,

1990). This correlation bears on recognition of non-gerbilline nature of several extinct rodent genera not infrequently allocated to Gerbillinae (see the chapter on paleontology below).

In characterizing the evolution of gerbilline dentition, it is to be stressed that its tendencies are better understandable by analyzing not the definitive crown patterns observed in the well worn teeth but rather the age variation beginning with the minimally worn molar crowns. The latter appeared to be most important in revealing accessory elements of the dental crown and sequences of fusion of the cusps with the age that are quite specific for different types of the crown pattern in Gerbillinae (Pavlinov, 1979a, 1984a, 1985; Pavlinov et al., 1990).

Detailed nomenclature of the gerbil dental crown was elaborated by C. Robbins (1971) based on that had been developed by P. Hershkovitz (1962) for the New World Cricetidae. After that, several new cusplets were discovered in living gerbillines (Pavlinov, 1981a, 1985). The complete set of molar crown elements known to occur in the Recent members of this subfamily (Pavlinov 1984a; Pavlinov et al., 1990) is shown in Fig. 3. I use the informal term “longitudinal bridgelet” in the subsequent descriptions instead of the formal “mur” or “murid” of Hershkovitz for the longitudinal connections between laminae. This is because the interlamina “murid” on lower molars could be confused terminologically with the accessory “murid” cusplets on the same teeth.

The ancestral condition of gerbilline dentition is characterized by moderately high (mesodont) crown bearing isolated main cusps and few accessory cusplets. Anterocone of upper M1 was most probably solid, as no one case of its splitting into a pair of cones is known in extant gerbillines. Anteroconid of lower M1 was splitted into two separate elements, extero- and intero-anteroconids, this condition is observed on minimally worn teeth in Asian *Tatera*. Subsequently, they are fused to form the solid anteroconid (see below). There are two additional isolated cusplets occurring on lower M1 and M2, protoconulid and hypoconulid: the both are preserved in living *Ammodillus* and disappeared in others. Anteroloph of upper M2 (not shown in Fig. 3) was initially small and usually becomes fused with the first lamina in more advanced gerbils (remained conspicuous in extant *Microdillus*). Just traces of hypoconule are evident in living gerbils with most generalized dentition, usually as an outgrowth of the

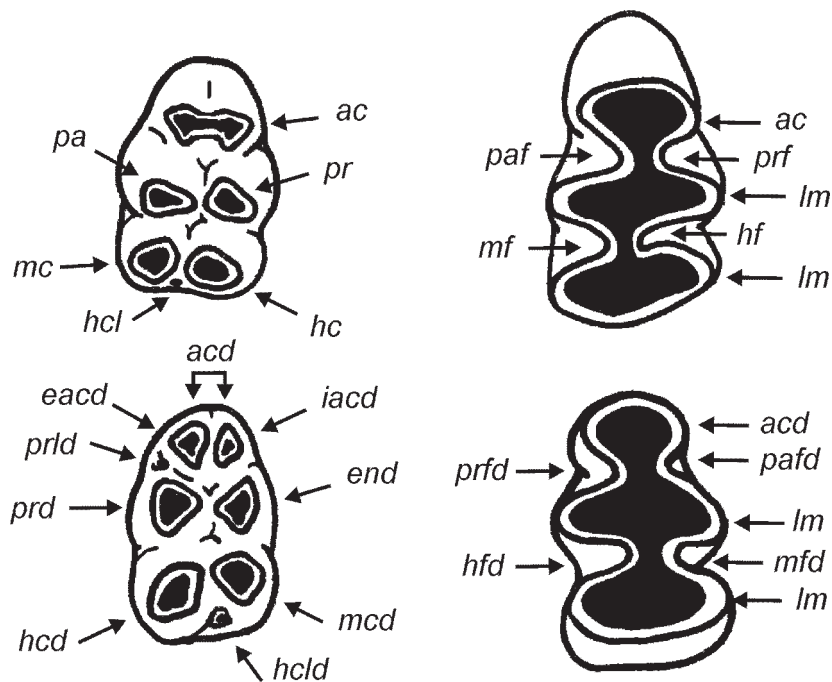


Fig. 3. Nomenclature of upper (above) and lower (below) bunodont (left) and prismatic (right) molars in Gerbillinae (after Pavlinov et al., 1990, modified). Abbreviations:

ac – anterocon, *acd* – anteroconid, *eacd* – exteroanteroconid, *end* – entoconid, *iacd* – interoanteroconid, *hc* – hypocone, *hcd* – hypoconid, *hcl* – hypoconule, *hcd* – hypoconulid, *hf* – hypoflexus, *hfd* – hypoflexid, *lm* – lamina, *mc* – metacone, *mcd* – metaconid, *mf* – metaflexus, *mfd* – metaflexid, *pa* – paracone, *paf* – paraflexus, *pafd* – paraflexid, *pr* – protocone, *prd* – protoconid, *prf* – protoflexus, *prfd* – protoflexid, *prld* – protoconulid

Рис. 3. Номенклатура верхних (вверху) и нижних (внизу) бунодонтных (слева) и призматических (справа) коренных у Gerbillinae (по Pavlinov et al., 1990, с изменениями). Обозначения:

ac – антерокон, *acd* – антероконид, *eacd* – экстероантероконид, *end* – энтоконид, *iacd* – интероантероконид, *hc* – гипокон, *hcd* – гипоконид, *hcl* – гипоконул, *hcd* – гипоконулид, *hf* – гипофлексус, *hfd* – гипофлексида, *lm* – ламина, *mc* – метагон, *mcd* – метаконид, *mf* – метфлексус, *mfd* – метафлексид, *pa* – паракон, *paf* – парафлексус, *pafd* – парафлексида, *pr* – протокон, *prd* – протоконид, *prf* – прототфлексус, *prfd* – прототфлексида, *prld* – протоконулид

hypocone. The upper M3 was initially with four cusplets (preserved in *Microdillus* and several other genera), while its lower homologue was most probably bicuspid. They both tend to become very simple in most advanced gerbillines.

The molar roots are much reduced as compared to other muroid rodents with non-evergrowing cheek teeth. There are two main (anterior and posterior) roots on both upper and lower M1 and M2 whereas M3 are always with one root each in all living members of Gerbillinae. The main roots are added with much smaller median rootlets on both lower and upper M1 and on upper M2, the lower M2 always lacking any additional root. In the upper toothrow, M1 bears one or two median rootlets and M2 possesses no more than one such rootlet. It is important to stress that, in extant gerbillines, the median rootlets are present on the least

advanced molars, and they tend to disappear with increase of the molar crown height. In one genus, *Rhombomys*, cheek teeth became evergrowing and completely lost roots.

Awareness of these principal trends is important for taxonomic allocation of some extinct genera with dental crown pattern superficially similar to that in most advanced Recent gerbils. For instance, *Leakeymys*, which is similar by the overall molar crown morphology to advanced taterillines, possesses a bi-lophed lower M3 (Lavocat, 1964). Thus, it does not fit the trend leading to the most evolved lophodont taterillines in which the lower M3 is much simpler. The genus *Epimeriones* with prismatic molars similar to those of the “higher gerbils” (*Meriones* etc.) is characterized by the presence of a large median root on all M1 and M2 and by two-rooted M3 (Daxner-Hock,

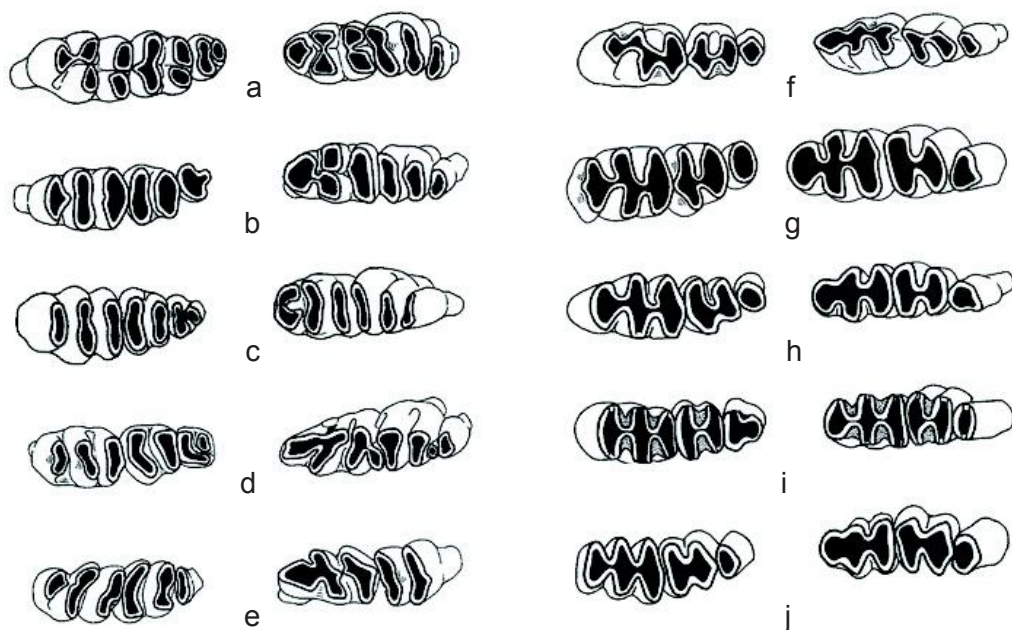


Fig. 4. Principal molar crown types in Gerbillinae (after Pavlinov, 1984a, not to scale). For each taxon, upper tooththrow is on the left, and lower tooththrow is on the right:

Рис. 4. Основные типы строения коронки коренных у Gerbillinae (по Pavlinov, 1984a, без масштаба). Для каждого таксона верхний зубной ряд слева, нижний зубной ряд справа: a – *Gerbillus*, b – *Gerbillurus*, c – *Gerbilliscus*, d – *Ammodillus*, e – *Desmodilliscus*, f – *Dipodillus*, g – *Sekeetamys*, h – *Meriones*, i – *Rhombomys*, j – *Brachiones*

1972), which altogether puts it outside the evolutionary trend of the entire gerbillines. The problems with inclusion of some extinct rodents in the subfamily Gerbillinae by dental traits are considered in more details in the paleontological chapter below.

Molar crown types (Fig. 4) start their evolution in gerbillines, as in all other rodents, with the bunodont condition. This initial type is characterized by separateness of the main cusps and by primary asymmetry of the crown pattern (Fig. 4a). This asymmetry may be characterized in several ways: by slightly alternating main cusps; by small but conspicuous differences in size of both those cusps (metacone is the smallest) and flexuses (paraflexus and hypoflexus on the upper M1 are the widest). Due to the latter, the dentine field of moderately worn upper teeth is S-shaped on M1 and C-shaped on M2 in Gerbillinae with bunodont dentition. Connections between cusps tend to appear quite late and succession of their formation is not strictly fixed, so it is the longitudinal bridgelets and not the transverse laminae that may first

to appear with the tooth wear.

Two principal directions of the molar crown transformations from the bunodont condition are observed in the subfamily, one leading to the lophodont crown and another to the prismatic crown pattern (Pavlinov, 1984a; Pavlinov et al., 1990). The both are similar in rising the crown height and in forming transverse laminae due to fuse of the opposite main cusps which always or usually (depending on degree of specialization) occur already on the minimally worn teeth. The major difference between these two patterns includes development of the longitudinal interlaminal connections (mures and murids) which are characteristic of prismatic molars and are absent in lophodont molars.

The transformation of the bunodont type in both principal directions is usually (but not always) accompanied by the crown symmetrization, that is, by gradual disappearance of the primary asymmetry. However, the supposedly secondary asymmetry did evolve in several genera with more advanced lophodont molars while prismatic teeth always tend to be symmetrical.

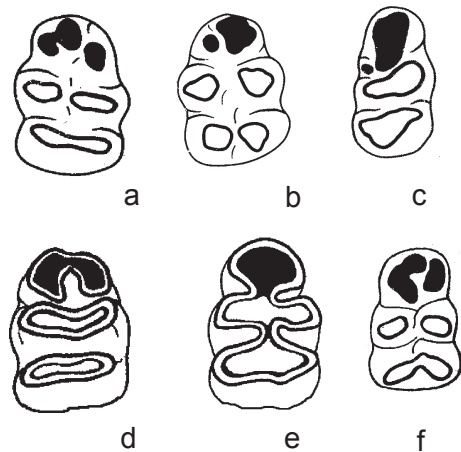


Fig. 5. Anteroconid (shaded) of the 1st lower molar in some Gerbillinae (after Pavlinov, 1984, not to scale): a – *Tatera*, b – *Desmodillus*, c – *Ammodillus*, d – horseshoe type in *Gerbilliscus*, e – rhomboid type in *Sekeetamys*, f – rare horseshoe variant in *Dipodillus*

Рис. 5. Антерококонид (затемнен) 1го нижнего коренного у некоторых Gerbillinae (по Pavlinov, 1984, не в масштабе):

a – *Tatera*, b – *Desmodillus*, c – *Ammodillus*, d – подковообразный тип у *Gerbilliscus*, e – ромбовидный тип у *Sekeetamys*, f – редкий подковообразный вариант у *Dipodillus*

The evolution of lophodont molar crown in gerbillines begins with equalization of size of both the main cusps and the flexuses/flexids between them. Separate cusps occur on minimally worn molars but transverse connections between cusps appear earlier and longitudinal connections appear later as compared to the typically bunodont teeth. This condition could be identified as the semi-lophodont type (Fig. 4b), it characterizes the genera *Gerbillurus*, *Desmodillus*, and *Pachyromys*. The next step is defined by far earlier development of transverse laminae and nearly complete disappearance of longitudinal bridgelets; this gives the advanced lophodont type, a condition most characteristic of the genus *Gerbilliscus*. Secondary asymmetry may appear in the evolved lophodont dentitions and involves skewness of the laminae on M1, especially on the lower one. It is most expressed in the genera *Ammodillus* and *Desmodilliscus* in which this skewness is opposite in direction (Fig. 4d,e).

Prismatic type begins with very early formation of both laminae and mures/murids. In one lineage of transformation of bunodont into prismatic tooth crown, elements of primary asymmetry

are preserved or eventually more expressed. This gives so called semi-prismatic dental crown type which could be observed in the nominative subgenus *Dipodillus* s.str. and in *Sekeetamys* (Fig. 4f,g). However, nearly all elements of primary asymmetry disappear and no secondary asymmetry is developed in the evolved prismatic type in which no signs of separate cusps could be observed at the earliest stage of the tooth wear. It is characteristic of the genus *Meriones* (Fig. 4h) and is most expressed in the genus *Rhombomys*. The latter acquired some noticeable traits of the prismatic molar specialization which includes differentiation of the enamel layers and appearance of the cementum in the flexuses/flexids (Fig. 4i). Another variant of specialization of the prismatic crown type can be observed in the genus *Brachiones* which differs by very wide dentine fields of interlaminal connections (Fig. 4j).

It is hard to suppose that most evolved versions of lophodont and prismatic types could transform into one another. However, such a transformation seems to be possible for more primitive variants. Thus, the Asian genus *Tatera* demonstrates moderately specialized molar crown which by its morphology is intermediate between these two advanced types.

Anteroconid of lower M1 earned special attention in recent studies of gerbilline phylogeny and taxonomy because it was shown to serve as an indicator of both ancestry and principal phylogenetic lineages of extant members of the subfamily (Pavlinov, 1981a, 1984a, 1985, 2001; Pavlinov et al., 1990). It included initially three separate elements, exteroanteroconid, interoanteroconid, and an accessory “murid” cusplet, the protoconulid. The first two isolated cusps could be observed on minimally worn molars in Asian *Tatera* (Fig. 5a) while the latter element usually occurs on minimally worn molars in the genera *Desmodillus* and *Ammodillus* (Fig. 5b-c). The more advanced anteroconid morphotypes are solid structures lacking these isolated elements, they are identified as horseshoe (Fig. 5d) and rhomboid (Fig. 5e) types. The first one is characteristic of the gerbils with the advanced lophodont molars (*Gerbilliscus*, *Taterillus*) and the second one is correlated with the bunodont and prismatic molars (*Gerbillus*, *Sekeetamys*, *Meriones*, etc.). Meanwhile, the horseshoe morphotype tends to transform into the rhomboid type in the gerbils with less advanced lophodont dentition (*Desmodillus*, *Tatera*). At last, evident traces of the horse-

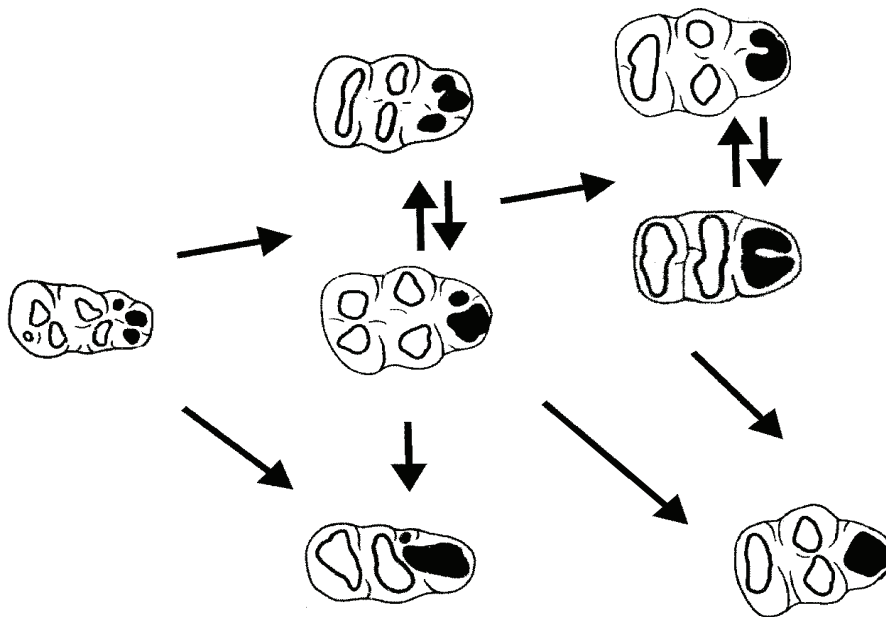


Fig. 6. Transformation series illustrating hypothesized evolution of anteroconid (shaded) of the 1st lower molar in Gerbillinae (after Pavlinov et al., 1990; Pavlinov, 2001)

Рис. 6. Трансформационная серия, показывающая предполагаемую эволюцию антероконоида (затемнен) нижнего М1 у Gerbillinae (по Pavlinov et al., 1990; Pavlinov, 2001)

shoe morphotype rarely occur in gerbils with bunodont and occasionally semi-prismatic molars for which the rhomboid type is more usual (*Gerbillus* and *Dipodillus*, Fig. 5f).

Judging by the above comparative data on the living gerbillines, including successions of the formation of definitive anteroconid with the tooth wear in the genera *Tatera* and *Desmodillus*, these advanced morphotypes could be interpreted as a result of integration of the above three initial elements. It means that predominating trend in the evolution of the anterior part of lower M1 in gerbillines included enlargement of its wear facet along with reduction of protoconulid to make the entire anteroconid lamina-like. An evolutionary scenario for the transformation series observed among living gerbillines, supported in part by the fossil evidence (see below), could be the following (Fig. 6; see also Pavlinov, 1985, 2001; Pavlinov et al., 1990).

Protoconulid known to occur in the extinct myocricetodontines (see below) was most probably preserved in the most archaic gerbillines. It became reduced with their advancement following the two principal pathways: it was either con-

served as a minute isolated cusplet (*Ammodillus*) or appeared to be included into the anteroconid proper. In the first case, the anteroconid became enlarged along with the molar crown laminization; such a condition could also be observed in the extinct genus *Protatera* as well in the extant *Ammodillus*. In the second case, there were two transformation pathways: exteroanteroconid was first fused either with interoanteroconid (as in *Desmodillus*) or with protoconulid (as in *Tatera* s.str.). These pathways “merged” subsequently to give the same primitive horseshoe morphotype. Characteristic of the latter is the posterior fossetid, while in more advanced variants of this morphotype the fossetid can also be anterior or occasionally a through one dissecting the anteroconid into two lateral parts.

All these variants are rarely observed in the living bunodont gerbils with predominating rhomboid anteroconid, so it is possible to treat them as atavisms indicating that the latter type originated from the horseshoe type. Rhomboid anteroconid became completely lamina-shaped in most gerbils with prismatic molars, though it deviates from this general trend in the genus *Bra-*

chiones in which anteroconid tends to be reduced in its size (see Fig. 4j).

MIDDLE EAR

The middle ear includes the transmitting system consisting of three auditory ossicles that transfer energy of the sound waves from the *tympanum* to the membrane of the oval window, and of the bony auditory bulla surrounding that system. Its peculiar transformations in desert rodents are well known and involve noticeable pneumatization of the bulla due to enlargement of its both tympanic and mastoid (ectotympanic and petromastoid, by their origin, respectively) portions. All changes of the first portion are described in terms of increase of its size and volume correlated with enlargement of the *tympanum* while the changes of the second one entail both its pneumatization and appearance of the new interior bony elements (septa), some of them subsequently changing their positions. Among auditory ossicles, most noticeable are changes in the *malleus* (Lay, 1972; Pavlinov et al., 1990).

All these modifications are thought to be adaptations to the physical properties of the sound waves dispersion under the arid air conditions (Alexander, 1968; Moore, 1981). It is of importance to call attention to the fact that the whole process of the middle ear morphological evolution is triggered by respective changes in shape and/or size of the *tympanum* and *malleus* while enlargement of the entire bullar size seems to be a secondary effect of those primary changes. Principal "aim" of this effect is to provide the evolved transmitting system with the proper ear volume. The bony elements emerging *de novo* in the tympanic and especially in the mastoid portions of the bulla were supposed sometimes to be adaptations to the sound perception participating in the "tuning" of the middle ear to the sound wave energy transfer (Simkin, 1965). However, an analysis of their diversity among specialized desert rodents made it more plausible to hypothesize that they fulfill just a mechanical function of reinforcement of the bullar walls and the semicircular canals (Pavlinov, 1988). The latter conclusion has certain concern to the discussion of possible transformations and homologies of the bony elements appeared in the pneumatized mastoid of the gerbillines.

In the present chapter, transformations of the middle ear morphology most concerning discus-

sion of phylogeny and taxonomy of Gerbillinae are considered in two sections. The first one contains evolutionary interpretation of comparative data on the mastoid. The second one is about transmitting system.

Mastoideum

Transformations and homologies of these mastoid bony elements in gerbillines constitute the foremost subject of the present section. I shall outline briefly my own approach to the analysis of the mastoid evolution without going into details published elsewhere (Pavlinov, 1980, 1988, 2001; Pavlinov et al., 1990). The homology suggested by D. Lay (1972) will be considered as well, as it presumes somewhat different evolution of the auditory bulla in Gerbillinae and hence their phylogeny.

Mastoid morphology starts its evolution with the condition observed in the most generalized (in this respect) rodents; among gerbillines, it is conserved in *Taterillus* and, with but some reservations, in *Gerbilliscus* (*Taterona*). It is characterized by complete concrescence of the bottom of the parafloccular recess with the mastoid lateral wall, so no mastoid cavity exists in such a primitive bulla.

The mastoid pneumatization can be interpreted (Webster, Webster, 1975; Pavlinov, 1988) as a result of penetration of the tympanic (ectotympanic) cavity into the mastoid (petromastoid). This process becomes evident as a gradual reduction of the parafloccular recess accompanied by appearance of a solid bony septum dividing the mastoid into two parts. Its initial position and subsequent transformations allow to specify both the hypothetical pathways of the mastoid pneumatization and homology of the resulted septa and air chambers delimited by them (Pavlinov, 1988; Pavlinov et al., 1990).

In gerbillines, the process of the mastoid pneumatization takes place by two principal pathways, anterior (or dorso-anterior) and ventral, by which the tympanic cavity penetrates into the mastoid (Fig. 7). The first one goes through the epitympanic recess into which two auditory ossicles, malleus and incus, are hanged; the second one goes through the arc of the lateral semicircular canal. These penetrations meet inside the mastoid and the mastoid septum appears at the zone of direct contact of the two pneumatization fronts.

Recent gerbillines differ from each other by position of that septum and by presence or ab-

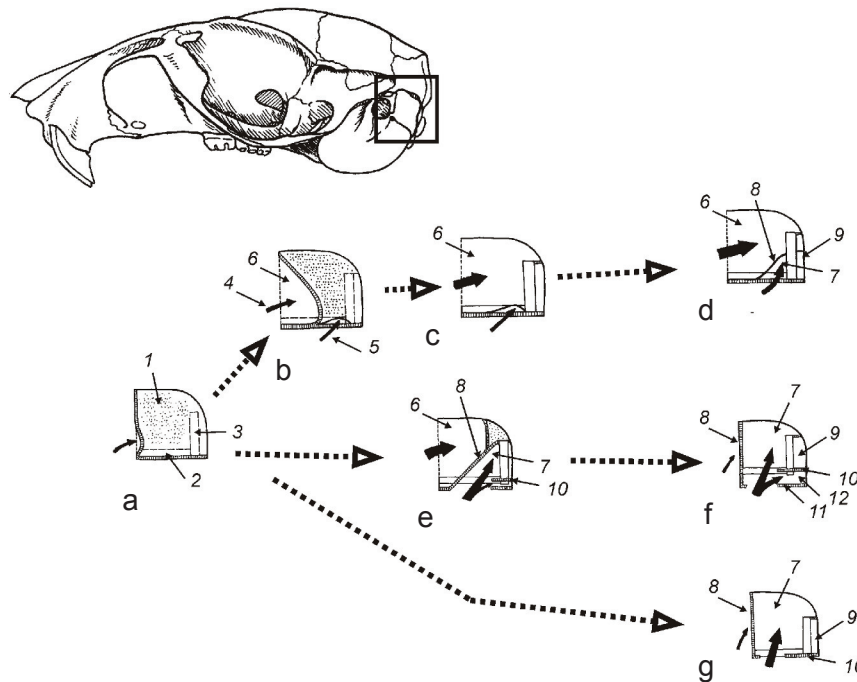


Fig 7. Transformation series illustrating hypothesized evolution of types of mastoid pneumatization in Gerbillinae (lateral view, very schematically). Solid arrows indicate pneumatization pathways, dashed arrows indicate transformation trends (after Pavlinov et al., 1990; Pavlinov, 2001).

Mastoid elements: 1 – parafloccular recess, 2 – lateral and 3 – posterior semicircular canal, 4 – anterior penetration, 5 – ventral penetration, 6 – epimastoid chamber, 7 – tympano-mastoid chamber, 8 – mastoid septum, 9 – posterior mastoid cell, 10 – tympano-mastoid septum, 11 – ventral mastoid septum, 12 – ventral mastoid chamber

Рис. 7. Трансформационная серия, показывающая предполагаемую эволюцию типов пневматизации мастоида у Gerbillinae (вид сбоку, очень схематично). Сплошные стрелки показывают способы пневматизации, точечные стрелки показывают направления эволюции (по Pavlinov et al., 1990; Pavlinov, 2001).

Элементы мастоида: 1 – парафлоккулярная ямка, 2 – боковой и 3 – задний полукружной канал, 4 – переднее влячивание, 5 – нижнее влячивание, 6 – эпимастоидная камера, 7 – тимпано – мастоидная камера, 8 – мастоидная септа, 9 – задняя мастоидная ячейка, 10 – тимпано – мастоидная септа, 11 – нижняя мастоидная септа, 12 – нижняя мастоидная камера

a – *Taterona* (*Gerbilliscus*), b – *Gerbillurus* (*Progerbillurus*), c – *Tatera*, d – *Desmodillus*, e – *Dipodillus*, f – *Meriones*, g – *Pachyuromys*.

sence of some accessory septa. These differences reflect not only various steps but also various types of the mastoid pneumatization differing from each other by predominance of one of the above two penetration pathways. The observed diversity can be arranged in a transformation series that illustrates two hypothesized principal strategies in the development of the entire mastoid cavity. One of them is characterized by prevailing of the anterior penetration while another is characterized by predominance of the ventral penetration. They

could be labeled, by names of their typical advanced representatives, as the *Desmodillus*-trend and the *Meriones*-trend of mastoid pneumatization, respectively.

The very first step of the mastoid pneumatization from the anterior (that is, by the *Desmodillus*-trend) is demonstrated by several species of *Gerbilliscus* (*Taterona*) in which the *fossa para-floccularis* still fills next the entire mastoid and just a minute penetration of the tympanic cavity via the epitympanic recess can be noticed (Fig.

7a). The *Gerbillurus* (*Progerbillurus*) shows the next step of the mastoid pneumatization of this type: the newly formed epimastoid chamber widely opened anteriorly into the tympanic cavity occupies about half of the mastoid while ventral penetration is very small (Fig. 7b). Subsequently, the epimastoid chamber fills up nearly the entire mastoid while ventral penetration still remains rudimentary, as in *Tatera* (Fig. 7c). And it is not until the entire auditory bulla becomes hypertrophied when ventral penetration becomes enlarged; it occupies first about one quarter of the entire mastoid cavity (*Gerbillurus* s.str.) and then about one third of it (*Desmodillus*). Due to this, the newly developed tympano-mastoid chamber appears ventrad to the epimastoid one and separated from it by the mastoid septum. So the entire mastoid cavity of most advanced variants of *Desmodillus*-type appeared to be two-chambered, with the epimastoid chamber predominating over the tympano-mastoid one (Fig. 7d).

It is of importance to stress that the lateral semicircular canal in *Desmodillus* goes along the tympano-mastoid suture, just as the mastoid septum does, the latter septum detaching from that suture and taking diagonal position in the posterior portion of the mastoid only. Caudally, this septum includes the posterior semicircular canal and connects it with the external wall of the mastoid. Because of diagonal position of the solid tympano-mastoid septum and of the lack of any other bony elements beneath the latter, the posterior mastoid cell appears opened ventrally into the tympanic cavity through the arc of the posterior semicircular canal.

Mastoid pneumatization by the *Meriones*-trend begins with simultaneous tympanic penetration by the both pathways, anterior and ventral, while parafloccular recess still occupies about half of the mastoid volume. Due to this, solid mastoid septum appears in the diagonal position to separate two chambers, epimastoid one above that septum and tympano-mastoid one beneath it. At this stage, an additional tympano-mastoid septum emerges along the tympano-mastoid suture to include lateral semicircular canal; it is perforated through the arc of the latter and delimits the tympano-mastoid chamber ventrally (Fig. 7e). This condition can be observed in *Gerbilliscus* s.str. and in *Dipodillus*, species of the latter demonstrating various stages of initial pneumatization of the mastoid by the *Meriones*-trend. Subsequent development of this type shown by *Meriones* (Fig.

7f) and its allies and by *Desmodilliscus* involves dorsal movement of the mastoid septum that takes vertical position along the boundary between the tympanic cavity and the epimastoid chamber thus completely isolating them from each other at the level of the epitympanic recess.

The succeeding pneumatization of the mastoid by *Meriones*-trend leads to the downward displacement of the tympano-mastoid suture while the tympano-mastoid septum including lateral semicircular canal stays at the same position and detaches entirely from that suture (it looks as dorsal displacement of the tympano-mastoid septum). A widely perforated accessory ventral mastoid septum appears at the tympano-mastoid suture to separate partially the tympanic and mastoid cavities (its germ could be noticed already in *Dipodillus*). Due to this, an accessory ventral tympano-mastoid chamber between tympano-mastoid and ventral mastoid septa appears, which seems to have no homologue in the variants of *Desmodillus*-trend. At last, one more independent accessory septum appears that connects posterior semicircular canal to the expanded mastoid wall; it delimits a posterior mastoid cell open into the tympano-mastoid chamber.

Comparison of mastoid variants in gerbillines indicates certain resemblance between *Dipodillus* and *Desmodillus* in diagonal position of the mastoid septum. This made D. Lay (1972) supposing, taking into account the differences in degree of their bullar pneumatization, that the first morphotype is a direct predecessor of the second. He suggested therefore that the septum taking vertical position in the mastoid of *Meriones* is a new one having no homologue in *Desmodillus* and eventually in *Dipodillus*. It seems to me that Lay's mistake was due to incompleteness of the data he had studied. He did not observe *Gerbillurus* (*Progerbillurus*) morphology; the latter is of importance by making it clear enough that mastoid in *Desmodillus* has *Progerbillurus*-like morphological predecessor. On the other hand, of importance is the similarity between mastoid morphology in *Dipodillus* and *Meriones* in presence of both tympano-mastoid and ventral mastoid septa, together with variation in position of the mastoid septum among *Dipodillus* species from diagonal to nearly vertical (not shown in the scheme). All these observations make it more parsimonious to accept the homology (based on the criteria discussed by Rieppel, 1994; Nelson, 1994) according to which the mastoid in *Meriones* originates from

that in *Dipodillus*. That is, that vertical septum in *Meriones* is the same mastoid septum taking diagonal position in *Dipodillus*. Whatever might be its exact homology to the similar septum in *Desmodillus*, it seems quite plausible to suppose that it is the genus *Meriones* that evolved directly from the *Dipodillus* mastoid condition, while *Desmodillus* seems to be a derivative of a condition observed in the subgenus *Gerbillurus* (*Progerbillurus*) and not in *Dipodillus*.

The mastoid of *Pachyuromys* is fully pneumatized and quite simple (Fig. 7g). It is similar to the one observed in *Meriones* and its allies by presence of the solid vertical septum separating mastoid cavity anteriorly from the tympanic one; thus, it is most probably homologous to the mastoid septum. However, there is only one septum delimiting mastoid cavity ventrally and attaching the mastoid wall along the tympano-mastoid suture. This condition does not correspond to the one observed in the advanced members of the *Meriones*-trend. However, this septum in *Pachyuromys* includes the lateral semicircular canal that allows to suppose its homology to the tympano-mastoid septum. If it is correct, then mastoid of *Pachyuromys* could be considered as a deviation from the *Meriones*-trend in which tympano-mastoid septum remains connected to the tympano-mastoid suture and so no ventral mastoid septum appears. With such a homology, the cavity that fills the entire mastoid in *Pachyuromys* is the tympano-mastoid chamber. Accessory posterior mastoid cell appears with the respective septum connecting the posterior semicircular canal to the mastoid wall.

Mastoid pneumatization in the genus *Ammodillus* is also peculiar. It is most similar to that observed in the gerbillines belonging to the *Desmodillus*-trend. The only difference involves presence of a small additional ventral penetration which leads to formation of a small ventral mastoid septum similar (homologous?) to that developed in the members of the *Meriones*-trend.

The final evolutionary interpretation of this pretty sophisticated transformation series is based on two premises. One of them, already declared above, is more than obvious: it asserts that the initial condition of the bullar evolution in Gerbillinae, as in all other mammal taxa, is non-pneumatized mastoid (petromastoid) and that its progressive pneumatization is more probable than a regressive. The second premise, less evident but no less important, is based on the concept of the epigenetic landscape of C.H.

Waddington and his followers; it presumes inertial nature of evolutionary changes of complex morphological structures. From this standpoint, it is rather improbable for the evolving mastoid morphology to “switch” freely among principal evolutionary trends outlined above. They can only “converge” in some instances by developing similar elements in the advanced morphotypes, as it is observed in *Ammodillus*.

Phylogenetic meaning of the entire transformation series of mastoid morphology interpreted on the basis of these two premises is as follows. Other things being equal, it is more probable for the gerbilline taxa sharing the same mastoid type, whatever being its pneumatization stage, to form a monophyletic clade, with the respective mastoid type being its synapomorphy. Contrary to this, if the taxa possess different mastoid types, it is more probable for them to belong to different monophyletic groups diverged at the very beginning of the mastoid evolution.

More particularly, it is more parsimonious to suppose that the less evolved mastoid morphologies in *Gerbillurus* (*Progerbillurus*) and *Dipodillus* are independent derivatives of the non-pneumatized mastoid in *Taterillus*. Respectively, the more advanced morphotype in *Desmodillus* unites the latter with *Gerbillurus* while the one in *Meriones* unites this genus with *Dipodillus*. This argumentation scheme seems to be most consistent with the demands of evolutionary cladistics and is of crucial importance for deducing correct phylogenetic hypothesis from the above morphological data for the subfamily Gerbillinae.

Transmitting system

Principal elements of the transmitting system of the middle ear to be considered here include the membranous *tympanum* and the bony *malleus*.

The *tympanum* may be simple or complicated, in the first case it consists of the main portion only, in the second case the latter is added with the *tympanum accessorium* (Fig. 8a–b). They are easy to recognize by presence or absence (respectively) of a bony septum filling or not the upper wall of the *meatus acusticus*. In the first case the septum covers the *capitulum mallei* (Fig. 8a), in the second case the latter is visible from the outside (Fig. 8b). Presence of *c. mallei* in Muroidea is a primitive condition, its absence is a derived condition; in some taxa it can secondarily appear (Lay, 1972; Webster, Webster, 1975; Pavlinov, 1980; and references there).

The *malleus* (Fig. 8c-e) consists of two just mentioned parts, the larger *caput malei* and smaller *manubrium*. The former can be lightly built with a straightened upper edge (Fig. 8c, e), or more massive and tear-shaped with a prominent upper edge (Fig. 8b); the latter takes horizontal or vertical position. A combination of lightly built *malleus* with horizontal *manubrium* is the initial condition for all Muroidea; its evolutionary transformations first involve shift of the *manubrium* from horizontal to vertical position and then weighting of the *caput malei*; the latter, however, can occasionally return from “massive” to the “light” condition. The most primitive variant is known to occur in generalized (in respect to bullar morphology) muroids and is never observed in Gerbillinae (Lay, 1972; Pavlinov, 1980).

Primitive lightly built *malleus* with horizontal *manubrium* is always correlated in rodents studied so far with the presence of *tympanum accessorium*. Gerbillines, in which such a condition does not occur, expose diversity in respect to combinations of basic morphotypes of the *caput malei* (“light” or “massive”) with either simple or complex *tympanum* (Lay, 1972; Pavlinov, 1979b, 1980; Pavlinov et al., 1990). It is this combinatoric that bears on reconstruction of phylogenetic relationships among certain gerbilline taxa. And recognition of primary and secondary nature of presence of the *tympanum accessorium* and lightly built *malleus* is the most important task. It could be fulfilled, with more or less decisiveness, using some rules for character polarity assessment, including the principle of “reciprocal illumination” (Hennig, 1966; Wiley, 1981; Pavlinov, 2005).

Taking into consideration the latter principle, similar and more detailed data on transformations of the auditory transmitting system in Arvicolinae (Pavlinov, 1984b) seem to be of certain importance. In particular, an additional morphological element was identified in the light *malleus* which makes it possible to recognize primary or secondary nature of such a bone. It is a kind of “rib” of the anterior portion of the *malleus* which goes either dorsally along upper edge of that portion (Fig. 8c) or medially along its midline (Fig. 8e). This rib always goes dorsally in the primitive *malleus* with horizontal *manubrium*, whereas it always takes medial position in the advanced massive *malleus*. Correspondingly, one may suppose that dorsal position of this rib in the light *malleus* in Gerbillinae indicates primary condition of the latter, while its medial position may indicate its secondary condition. The lat-

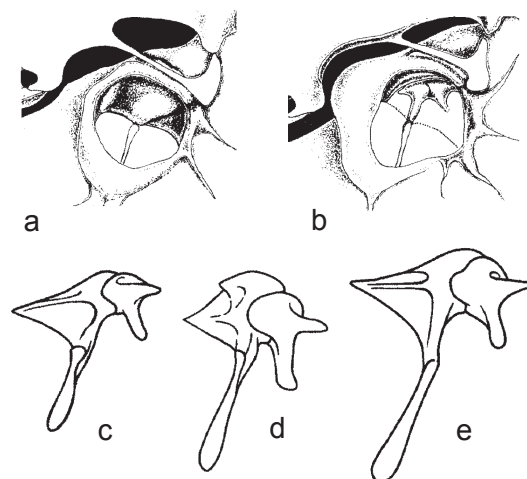


Fig. 8. Principal types of the *tympanum* and two auditory ossicles in Gerbillinae (buccal view, not to scale; a, b – after Harrison, 1972; c–e – after Pavlinov et al., 1990):

Рис. 8. Основные типы барабанной перепонки и двух слуховых косточек у Gerbillinae (вид снаружи, не в масштабе; а, б – по Harrison, 1972; с–е – по Pavlinov et al., 1990):

a – *Dipodillus dasyrurus*, b – *Gerbillus mesopotamiae*, c – *Gerbillus agag*, d – *Gerbilliscus kempi*, e – *Meriones meridianus*

ter seems to be true for several species of *Meriones* with the most inflated auditory bulla, in which *tympanum accessorium* is developed and *malleus* turns out to be lightly built bearing the midline rib (Pavlinov, 1979b).

There are at least two points in gerbilline phylogeny which resolutions may depend to a degree on the above analysis.

The first is the the subgeneric division of the genus *Dipodillus*. All its species are characterized by light *malleus* with dorsal rib (primary condition), some of them possessing *tympanum accessorium* (also primary condition) while others not. The latter is most probably a derived condition and may be considered as a synapomorphy allowing to recognize the subgenus *Petteromys*.

Another case is the transmitting system of the “higher gerbils” of subtribe Rhombomyina (genera *Meriones*, *Rhombomys* and allies). They *en masse* are characterized by simple *tympanum* and by massive *malleus*. This is a synapomorphy for Rhombomyina relative to the condition observed in most members of Gerbillina s.str. The latter conclusion makes it reasonable to suppose that the genus *Sekeetamys*, with its simple *tympanum* and massive *malleus*, belongs to the Rhombomyina rather than to the Gerbillina.

A REVIEW OF FOSSIL GENERA

Gerbilline paleontology is not especially rich, as compared with such Old World Muroidea as, say, cricetines, arvicolines, and murines (Tong, 1989; McKenna, Bell, 1997). Excluding the Pleistocene and subrecent findings that certainly belong to the extant genera or are very close to them (see most recent comprehensive references in Musser, Carleton, 2005), about a dozen of the extinct genera have been described from the Miocene and the Pliocene of Asia, Europe and Africa, which were thought to belong to gerbillines by some or other authors. They are known mainly by isolated teeth but few are represented by skull or even postcranial skeletal remains.

By the dental features (Fig. 9), those fossils could be classified roughly into groups with bunodont, lophodont and prismatic molars, according to the typification outlined in the morphological chapter above. “Bunodont fossils” to be considered here are myocricetodontines, before all the genus *Myocricetodon* as the most typical member of this group. Those with lophodont dentition are the genera *Protatera*, *Abudhabia*, *Debruijnimys*, and *Leakeymys*. At last, the fossils with prismatic molars are *Pseudomeriones*, *Epimeriones*, *Mascaromys*, *Parameriones* Chernov et Chetboun (not Heptner), and *Pliorhombomys*. All of them are briefly reviewed here.

Genus *Myocricetodon* Lavocat is known by isolated teeth and skull fragments from the middle Miocene–Pliocene of northern Africa, southwestern Europe, southern and central Asia (Jaeger, 1977; McKenna, Bell, 1997; Wessels, 1998; Qiu, 2001; Agusti, Casanovas-Vilar, 2003; Qiu et al., 2004).

The masseteric keel in *M. irhoudi* seems to be elongated nearly to the size observed in the extant *Gerbillus* but mandible in *M. parvus* possesses a large coronoid process and pretty shallow posterior curvature between its ascending and angular portions (Fig. 2f; see also Jaeger, 1977). By these features, myocricetodontine mandible differs from that of all living gerbillines and indicates indirectly that

auditory bulla in *Myocricetodon* was most probably not yet inflated and resembled that of typical Murinae (Pavlinov et al., 1990).

Molars in *Myocricetodon* are bunodont or sometimes semi-lophodont, with main cusps opposable or clearly alternating (Fig. 9a). The upper molars in some species generally resemble those in the Recent *Gerbillus*, but there is also an important difference. The latter involves presence of well developed “murid” accessory cusplets on lower teeth, namely proto- and mesoconulids on the 1st molar, and anterolophid and hypoconulid on the 2nd molar. Both upper and lower 3rd molars are always simplified with one root each.

The genus *Myocricetodon* and its closest allies were separated in the subfamily Myocricetodontinae (Lavocat, 1973) and were allocated to Gerbillidae/Gerbillinae as their least advanced members representing an ancestral or a sister group to all extant gerbillines (Chaline et al., 1977; Chaline, Mein, 1979; McKenna, Bell, 1997).

Myocricetodontines themselves are diverse morphologically, some of them having simple dental pattern while others displaying advanced dental features not known in the gerbillines. So at least some of the genera formerly allocated here (*Sindemys*, *Punjabemys*, *Mellalomys*, *Shamalina*, *Dakkamys*, etc.) were transferred to other murid taxa, megacricetodontines or dendromurines (McKenna, Bell, 1997), indicating paraphyletic status of the entire myocricetodontines (Bruijn, 1999). Heterogeneity of this group becomes even more obvious if to take into account that the extant genus *Calomyscus* belonging to basal radiation of Muroidea (Pavlinov, 2003; Musser, Carleton, 2005) was mentioned as a member of Myocricetodontinae by Agusti and Casanovas-Vilar (2003). At any rate, it is evident that the myocricetodontines had their own evolutionary history, and only typical members of this group could be placed close to the root of the tree for the Recent Gerbillinae (Jaeger, 1977; Chaline, Mein, 1979; Tong, 1989; McKenna, Bell, 1997).

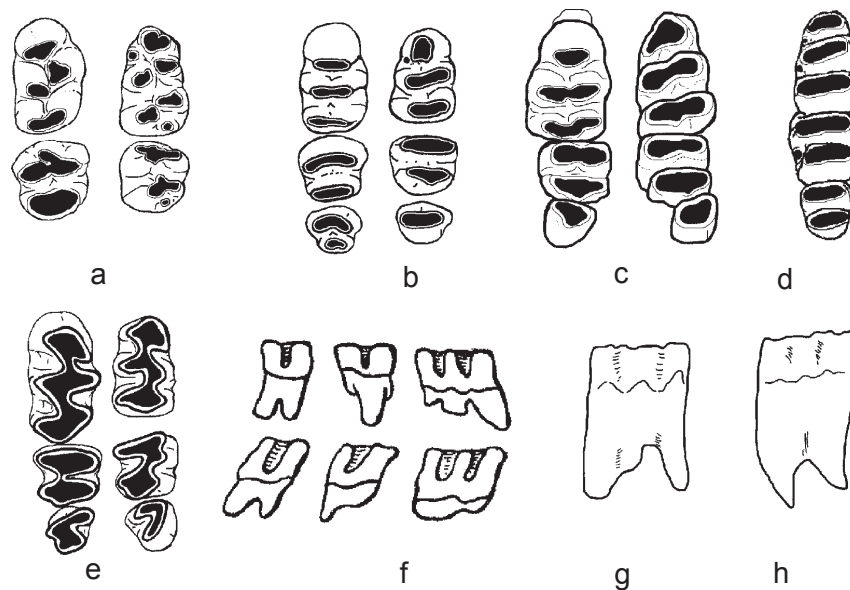


Fig. 9. Molars of some extinct and extant Gerbillinae and gerbilline-like rodents (after Pavlinov, 1982b, not to scale) (a–e – crown patterns, f–h – roots):

a – 1st and 2d upper and lower molars of *Myocricetodon ouedi* (after Jaeger, 1977), b – upper and lower molars of *Protatera algeriensis* (after Jaeger, 1977), c – upper and lower tooththrows of *Abudhabia radinskyi* (after Flynn et al., 2003), d – lower molars of *Leakeymys ternani* (after Lavocat, 1964), e – upper and lower molars of *Pseudomeriones* sp. (after Bruijn et al., 1970), f – upper and lower molars of *Epimeriones austriacus* (after Daxner-Hock, 1972), g – 1st lower molar of *Pliorhombomys*, h – 1st lower molar of a senile specimen of the extant Iranian *Rhombomys* (after Pavlinov, 1982b)

Рис. 9. Коренные некоторых вымерших Gerbillinae и песчанко-подобных грызунов (по Pavlinov, 1982b, без масштаба) (a–e – структура коронки, f–h – корни):

a – 1й и 2й верхние и нижние коренные *Myocricetodon ouedi* (по Jaeger, 1977), b – верхние и нижние коренные *Protatera algeriensis* (по Jaeger, 1977), c – верхние и нижние зубные ряды *Abudhabia radinskyi* (по Flynn et al., 2003), d – нижние коренные *Leakeymys ternani* (по Lavocat, 1964), e – верхние и нижние коренные *Pseudomeriones* sp. (по Bruijn et al., 1970), f – верхние и нижние коренные *Epimeriones austriacus* (по Daxner-Hock, 1972), g – 1й нижний коренной *Pliorhombomys*, h – 1й нижний коренной старой особи современной иранской формы *Rhombomys* (по Pavlinov, 1982b)

Genus *Protatera* Jaeger from late Miocene of northern Africa, south-western Europe and southern Asia is known by isolated teeth (Jaeger, 1977; Brandy, 1979; Geraads, 1998; Wessels, 1998; Agusti, Casanovas-Vilar, 2003). They are typically lophodont (Fig. 9b) with high transverse laminae deeply separated by valleys, the laminae being partially subdivided to show traces of the cones/conids very similar to those of living taterillines. Most peculiar for the *Protatera* is that it preserved isolated protoconulid on the lower M1 whereas its anteroconid is large and with no traces of separate intero- and anteroconids. This condition is most similar to the one observed in unworn teeth of the genus *Desmodillus* from southern Africa

(see respective account below). Moreover, a rudimentary protoconulid seems to be preserved in the lower M2, a feature not known in most of the Recent gerbillines (save the genus *Ammodillus*). Thus, the genus *Protatera* combines both pretty advanced and primitive dental structures which place it at the very base of taterilline radiation (Pavlinov, 1984a; Pavlinov et al., 1990).

Genus *Abudhabia* de Bruijn et Whybrow from the late Miocene–Pliocene of southern and central Asia is known by teeth and well preserved fragments of the skull and postcranial bones (Flynn et al., 2003; Qiu et al., 2004). It remarkably resembles the extant *Tatera* by elongated posterior palatal foramina and masseteric plate

while auditory bulla is smaller as compared to that of *Tatera* (see Flynn et al., 2003). Crowns of 1st and 2nd molars (Fig. 9c) are laminated, the laminae being clearly subdivided into main cones which are opposite on the upper molar and more skewed on the lower ones. There is a clear trace of hypoconule on the upper M1 fused with its posterior lamina. Upper anterocone resembles lamina by its shape, lower anteroconid is also wide and has tapered postero-labial part. This pattern much resembles configuration of the anteroconid at average stage of its wear in *Tatera* thus making it possible to suppose there was a small protoconulid on less worn lower M1 of *Abudhabia*, although Flynn et al. (2003) noticed that the horseshoe configuration is not apparent in their specimens. Third molars are reduced though not so much as in *Tatera*. The genus *Abudhabia* is certainly a taterilline, among extant taxa it is most similar and probably most close to the Asian genus *Tatera*.

Genus *Debruijnimys* Agusti from the late Miocene–early Pliocene of south-western Europe (Castillo, Agusti, 1996; Agusti et al., 2006) was reported to be similar to *Protatera* by Agusti and Casanovas-Vilar (2003). I did not see its description and thus have no comments on its morphology and phylogenetic relationships.

Genus *Leakeymys* Lavocat from late Miocene of eastern Africa is known by lower molars characterized by lophodont crown pattern and presence of complete set of additional “murid” cusplets in the lower dentition (Lavocat, 1964). The anteroconid is lamina-like in its shape and without any traces of the horseshoe pattern. The lower M3 is with two laminae. This genus was first interpreted as a relative to the African “*Tatera*” (Lavocat, 1964) and Kowalski (1974) agreed with this. But subsequently this hypothesis was abandoned: judging by bilophodont lower M3 and presence of murid cusplets combined with highly developed lophodonty, *Leakeymys* is most probably not gerbilline but may be close to cricetomyines (Pavlinov, 1984a; Tong, Jaeger, 1993).

Genus *Pseudomeriones* Schaub from late Miocene and Pliocene of Europe to southern and central Asia (Bruijn et al., 1970; Sen, 1977; Agusti, 1991; Patnaik, 1997; Wessels, 1998; Agusti, Casanovas-Vilar, 2003; Qui et al., 2004; Tesakov, Titiov, 2005) was the first extinct rodent referred to Gerbillinae. Its molar crowns are typically prismatic and superficially similar to those of the so called “higher gerbils” of the subtribe Rhombomy-

ina (Fig. 9e). It was this pattern that made this genus considered as a gerbilline by nearly all authors. However, the differences are also quite significant. Both lower and upper 1st molars of *Pseudomeriones* are with conspicuously alternating flexuses; in addition, the lower M2 is with rather large anterolophid fused with its first lamina, and the lower M3 is two-laminated. All these features are not characteristic of the Recent Rhombomyina at diagnostic level; what is more important, such a prismatic molar does not fit evolutionary trends in the rhombomyines with their strong tendency to tooth crown symmetrization. As to the anterolophid on lower M2 and second lamina on lower M3, they are absent even in most generalized members of the tribe Gerbillini. Therefore, allocation of the genus *Pseudomeriones* either to Rhombomyina or to Gerbillinae at all is more than questionable (Pavlinov, 1984a).

Genus *Epimeriones* Daxner-Hock from the Pliocene to the early Pleistocene of Europe has also prismatic molar crowns similar to those of *Meriones*. This feature was always considered as a decisive argument in favor of its belonging to Gerbillinae (Daxner-Hock, 1972; Kowalski, 1974; Terzea, 1976; Agusti, 1991; Wessels, 1998; Agusti, Casanovas-Vilar, 2003). However, the differences between this genus and the extant gerbillines with prismatic molars are no less drastic than in the case of the genus *Pseudomeriones* considered though involves other traits. The most principal difference is in root morphology: each of the 1st and 2nd molars in *Epimeriones* has the median root which is no less developed than posterior and anterior roots, and 3rd molars are with two roots each (Fig. 9f). Contrary to this, median roots are always much reduced and 3rd molars are always one-rooted in all living gerbillines, this condition being most expressed just in the above “higher gerbils” with prismatic molars. Therefore, just like in the case of *Pseudomeriones*, I do not think that the genus under consideration is close to any gerbilline lineage (Pavlinov, 1984a). Rather, both these genera with prismatic cheek teeth could be called “gerbillodont cricetines”, by analogy with microdontines widely distributed in Europe simultaneously with them (Gromov, Baranova, 1981).

Genus *Mascaromys* Tong known by several isolated molars from the Plio–Pleistocene of northern Africa was suggested to be a sister group for the extant rhombomyines (Tong, 1989). Its 1st and 2nd molars bear fully developed isolated laminae,

some are dumbbell-like due to partial strangulation, with no signs of longitudinal connection. This pattern much resembles that of minimally worn *Meriones* molars, save that the latter display nothing similar to strangulation. Thus, this genus might actually be an archaic representative of the “higher gerbils” lineage.

Genus *Parameriones* Tchernov et Chetboun was erected for the species *obeidiensis* Haas from the early Pleistocene of the Levant first described as a member of *Meriones* supposedly close to *M. persicus* (Tchernov, 1968). It is certainly a member of the subtribe Rhombomyina but its more precise allocation is not clear. Configuration of its enamel loops (see Tchernov, Chetboun, 1984) resembles that in *Psammomys* rather than in *Meriones*, so the species *obeidiensis* was included pro-

visionally in the genus *Psammomys* by Pavlinov et al. (1990).

It is to be noticed that the name *Parameriones* Tchernov et Chetboun, 1984 is preoccupied by *Parameriones* Heptner, 1937. It should be replaced by a new one if the generic status of this gerbil is supported by future investigations and a valid name is requested for it.

Genus *Pliorhombomys* Fokanov from early Pleistocene of Turkmenia is the closest predecessor of the recent *Rhombomys* differing from it by less advanced molar morphology (Fokanov, 1976; Gromov, Baranova, 1981; Pavlinov et al., 1990). In particular, it is characterized by rooted molars (Fig. 9g) and absence of cementum. Its relationship and status are discussed under *Rhombomys* below.

MODERN PHYLOGENETIC HYPOTHESES

The first attempts to study relationships of Gerbillinae to other rodents go back to the end of the 19th century (e.g. Tullberg, 1899). They were not strictly phylogenetic in the modern sense in reflecting rather grades of gerbilline evolution than monophyletic groups (see the taxonomic chapter below). As a matter of fact, first issues about phylogenetic relationships of Gerbillinae to other Muroidea and within themselves appeared in the late 1960s–70s only. Most recent studies, both morphological and molecular, are aimed at uncovering sister-group relationships both among gerbillines themselves and to their relatives.

The present chapter provides a brief review of principal ideas about the phylogeny of the subfamily Gerbillinae.

RELATIONSHIPS TO THE OTHER MUROIDEA

Relationships of Gerbillinae within Muroidea remained not quite certain until most recent times. This was due to advanced morphology of their living members sharply separating gerbillines from other muroids with a significant gap, on the one hand, and because of the lack of good paleontological records which would fill that gap, on the other hand.

If not to consider earlier schemes reflecting typological rather than phylogenetic relationships (they are reviewed in the introduction to the gerbilline classification below), very few hypotheses were forwarded in the modern literature. Most usually gerbillines were connected phylogenetically to Old World Cricetinae (e.g. Vorontsov, 1968), while R. Lavocat (1978) thought they were more close to African endemic lineages united by him under the name Nesomyidae Major. Occasionally, different gerbillines appeared to be “rooted” in different ancestors, Cricetinae and Cricetodontinae (Gromov et al., 1963; see account of Rhombomyina below).

A significant break in understanding of phylogenetic relationships of the gerbillines took place when a “myocricetodontine hypothesis” was put

forward presuming that the living Gerbillinae originated from the Miocene Myocricetodontinae or had most close common ancestor with them (Jaeger, 1977; Chaline et al., 1977; Pavlinov, 1982a, 1984a; Flynn et al., 1985; Tong, 1989; Pavlinov et al., 1990). This was based on great similarity of most generalized gerbillines and the genus *Myocricetodon* by the molar crown pattern (Jaeger, 1977; Brandy, 1979; see also review of the gerbilline paleontology above). The only embarrassing point was that most myocricetodontines possess more or less developed additional cusplets on lower molars then unknown in gerbillines. However, the subsequent uncovering of one of these cusplets in several extant gerbillines (Pavlinov, 1981a, 1984a, 1985, 2001; see also review of the gerbilline morphology above), as well as in the fossil *Protatera* most probably directly related to the taterillines (Jaeger, 1977; Pavlinov, 1984a), made that hypothesis more sound morphologically.

As it was observed in the above review of gerbilline paleontology, myocricetodontines themselves were pretty diverse in their dental crown pattern. So it looks more reasonable to consider them, at the best, a sister rather than an ancestral group of Recent gerbillines (Pavlinov, 1982a, 2001; Tong, 1989; Pavlinov et al., 1990). Anyway, the myocricetodontine hypothesis, when it was forwarded for the first time, appeared to be quite important by focusing on search for gerbilline closest relatives not among cricetines with their initially simple molars but among Afrotropical muroids with their complicated murid-like lower dentition (Lavocat, 1978; Pavlinov, 1982a, 1984a; Pavlinov et al., 1990).

Most interesting recent findings in muroid phylogeny based on molecular data seem to provide quite resolved picture of phylogenetic relationships of gerbillines with other major lineages of living Muroidea (Michaux et al., 2001; Jansa, Weksler, 2004; Stepan et al., 2004). According to them, the rodents relevant to the present discussion are clearly divided into three groups –

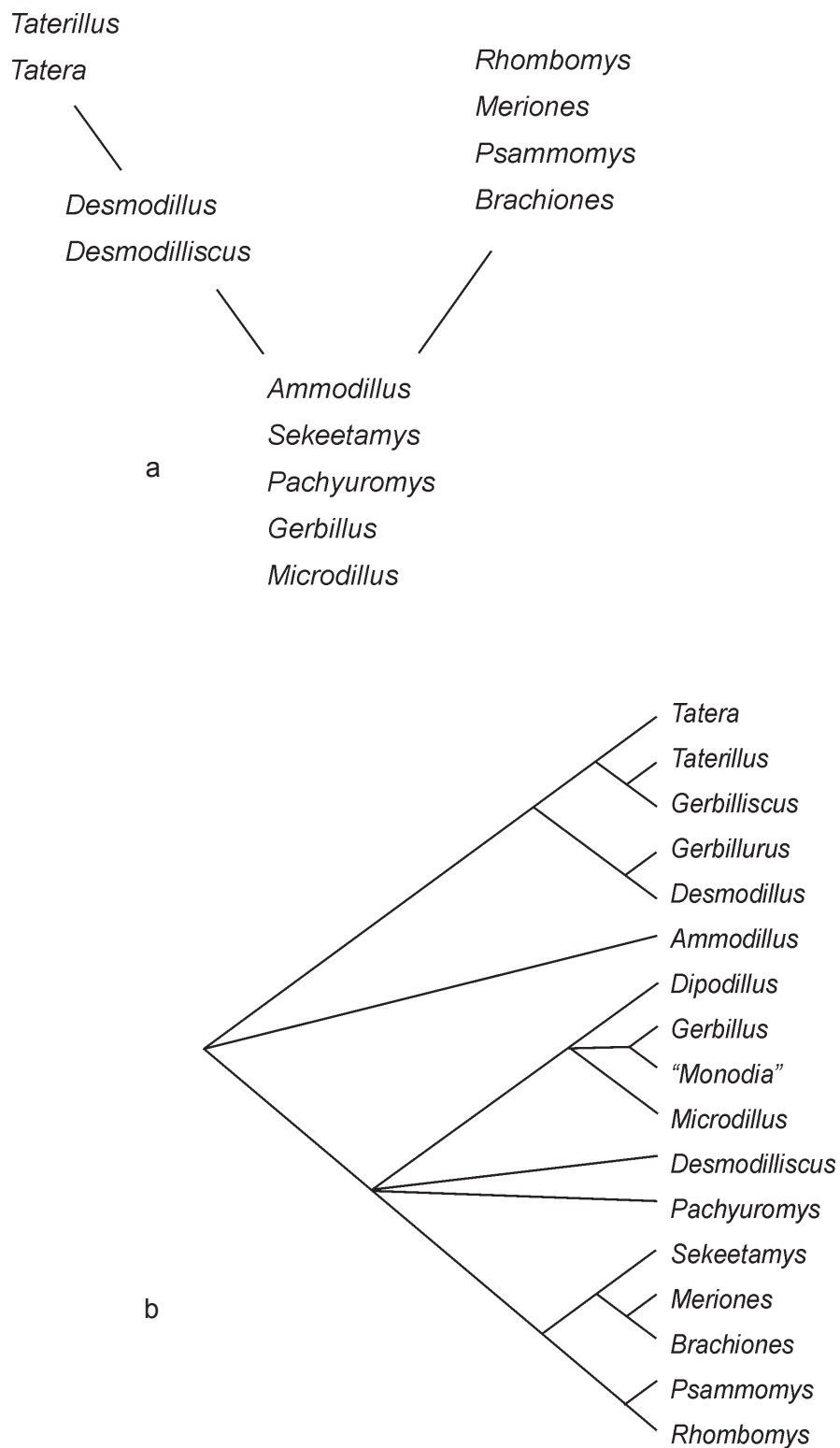
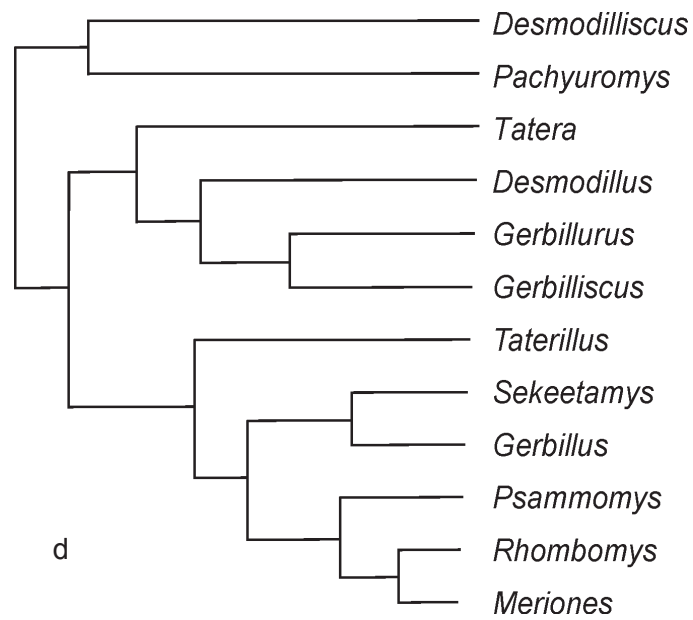
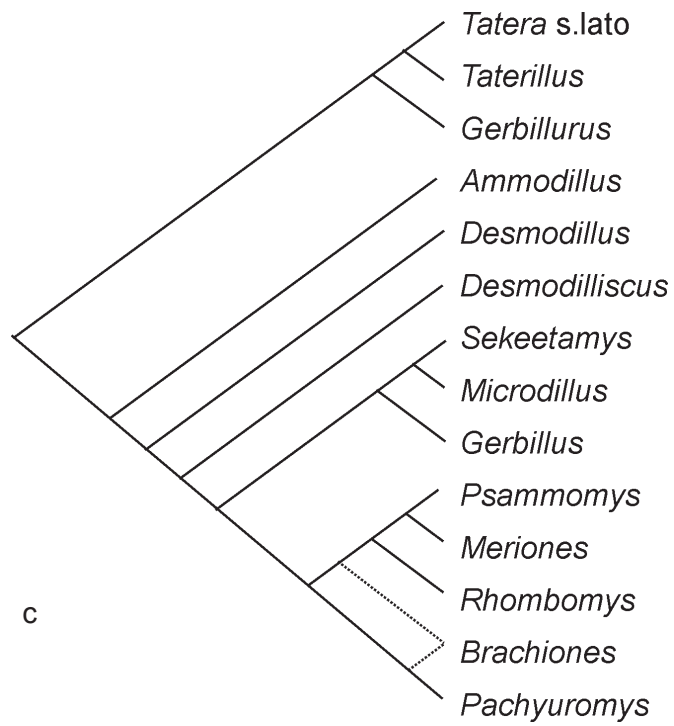


Fig. 10. Phylogenetic trees for the Recent Gerbillinae: a – after Petter (1975), modified, b – after Pavlinov et al. (1990), c – after Tong (1989) modified, d – after Chevret, Dobigny (2005), modified

Рис. 10. Филогенетические деревья для современных Gerbillinae: а – по Petter (1975), изменен, б – по Pavlinov et al. (1990), с – по Tong (1989), изменен, д – по Chevret, Dobigny (2005), изменен



Muridae, Nesomyidae, and Cricetidae, with the Recent gerbillines being a monophyletic clade evidently belonging to the first family. This molecular phylogenetic scheme is supported by several genes, both mitochondrial and nuclear, and so seems to be pretty well founded. In such a case, their most close living relatives are African endemics of the subfamily Deomyinae Lydekker (Musser, Carleton, 2005; Acomyinae of the authors, see Dubois et al., 1999; Michaux et al., 2001), and not members of the family Nesomyidae as it has been supposed by R. Lavocat (1978).

PHYLOGENETIC TREES FOR THE RECENT GERBILLINAE

The scheme of F. Petter (1975) was the first attempt to reflect phylogenetic and not pure taxonomic relationships among gerbilline genera (Fig. 10a). Although being “typological” in reflecting (not properly, to be true) transformations of the dental morphotypes, it was this scheme that separated lophodont taterillines (“*Tatera*” in its widest sense and *Taterillus*) from other members of Gerbillinae/Gerbillidae for the first time. Another branch in this scheme included the so called “higher gerbils” (genera *Brachiones*, *Psammomys*, *Meriones*, *Rhombomys*) with prismatic molar crown. Petter placed *Desmodilliscus* and *Desmodillus* at the base of the taterilline branch, while other genera with no special features peculiar to those two principal branches appeared to be piled into a kind of basal gerbilline “wastebasket”.

This scheme became much more detailed subsequently due to shoveling of that “basket”, as the genera sacked into it appeared to be quite different in respect to their morphology and genetics. The first of these efforts to be mentioned (by time precedence) appeared to be the phylogenetic tree based mostly on morphological traits of the mastoid part of auditory bulla and to less degree on dentition, with some addition from other morphological sources (e.g. zygo-masseteric construction) (Pavlinov, 1980, 1981a, 1982a; Pavlinov et al., 1990). In addition to taterilline clade, another major monophyletic group was recognized, which included *Gerbillus* with its allies (gerbillines proper) together with *Meriones* and its allies (Fig. 10b). Besides, several new branches in the tree were erected, each with one genus only (*Ammodillus*, *Desmodilliscus*, and *Pachyuromys*) while genera *Gerbillurus* and *Desmodillus* were suggested to joint taterilline branch as its basal outlet.

Another serious attempt to clarify phylogeny of Gerbillinae was undertaken by a paleontologist H. Tong (1989) whose tree (Fig. 12) resembled in general the one developed by me, especially in respect to basal dichotomy of taterillines and gerbillines. The differences involve the position of *Desmodillus*, *Pachyuromys* and, at a lower hierarchical level, also *Sekeetamys*. Tong placed *Desmodillus* close to basal radiation of the gerbilline fragment of the tree while *Pachyuromys* appeared within the clade of “higher gerbils”. This treatment is explained by different homology of mastoid elements borrowed by Tong from D. Lay (1972). The approaches to the mastoid homology developed by Lay and by myself are discussed briefly in the morphological chapter above; its details as applied to the particular genera listed in this paragraph are considered in respective taxonomic sections below.

Cytogenetic and allozyme analyses are to be mentioned as well. Though their taxonomic scopes were limited to fewer genera than studied morphologically, the results are remarkable in supporting taterilline clade, while relationships shown for other genera appear to be quite controversial. See summary of these results in the paper of Chevret and Dobigny (2005)

At last, several molecular phylogenetic trees were published based on both total DNA hybridization and mtDNA sequencing (Chevret, Dobigny, 2005). The latter is based on analyses of two genes, 12S rRNA and cytochrome *b*, and is quite complete in respect to the taxic representation and details of tree topology (Fig. 10d). The molecular tree differs most drastically from the above morphological schemes by transferring *Taterillus* from “*Tatera*” s.lato clade to *Gerbillus*–*Meriones* clade. This result appeared to be the most surprising outcome (to me at least) of Chevret and Dobigny’s investigation, as no good synapomorphy is known to support (*Taterillus* (*Gerbillus*, *Meriones*)) joint clade. Another strikingly new result of this analysis appeared to be a supposed monophyly of *Desmodilliscus*–*Pachyuromys* clade. The matter is that no “good” morphological synapomorphies (hypertrophied auditory bulla are not to be counted) are known at the present for this clade.

To sum up the results of all these investigations, both morphological and molecular, it can be concluded that three main branches in phylogenetic tree of the Gerbillinae are unanimously recognized by most recent authors: taterillines (maybe without genus *Taterillus*), gerbillines prop-

er, and rhombomyines. The two latter constitute a higher-level monophyletic clade, a point at which all the above trees come to a consensus. The “taterilline” (or maybe “gerbillurine”, see discussion of nomenclature in the account of subtribe Taterillina below) clade most certainly includes genera *Tatera* and *Gerbilliscus*, and the genus *Gerbillurus* is placed within or at a basal level of this fragment of the phylogenetic tree. The second group is very compact to include genus *Gerbillus* and its closest relatives (*Dipodillus*, *?Monodia*, *Microdillus*). At last, the rhombomyine branch includes genera *Meriones*, *Brachiones*, *Psammomys*, and *Rhombomys*. It is to be indicated also that both Pavlinov’s and Tong’s trees agree in placing the genus *Ammodillus* (unfortunately absent from the molecular tree) close to basal radiation of the entire subfamily Gerbillinae.

There four genera remain which position is less certain: *Desmodillus*, *Taterillus*, *Desmodilliscus*, and *Pachyuromys*. The genus *Desmodillus* is either considered as a member of taterilline clade (though in various positions), or placed close to basal radiation of the clade including gerbillines proper and rhombomyines; or occasionally it is placed within rhombomyines. However, it is noteworthy that morphological and DNA data on extant genera agree in treatment of this genus. The

genus *Taterillus* is placed together with *Tatera*–*Gerbilliscus* by morphological and cytogenetic data while allozyme and DNA data suppose it is closer to the gerbilline clade. Basal position to gerbillines is supposed also for *Desmodilliscus* by morphological and allozyme data while DNA analysis makes it forming quite separate clade with *Pachyuromys*. At last, the latter genus is also considered as a member of either its own clade (Pavlinov’s morphological data) or of rhombomyine group (supported by karyology and by Tong’s morphological interpretation). These versions are discussed in more detail in respective taxonomic sections below.

It is of importance to call attention on that all the differences just considered involve mainly those taxa which, according to one or another version, take (or are close to) a basal position in the phylogenetic tree of the subfamily Gerbillinae. At least to me, it is not surprising and should not bother much, as such kind of uncertainty is predetermined by modern principles of phylogenetic reconstructions (Pavlinov, 2005). Such a methodological standpoint makes it clear that higher resolution of basal radiation of the subfamily Gerbillinae could be achieved by its considering together with its close relatives within Muridae or occasionally with the members of other muroid families.

TAXONOMY OF RECENT GERBILLINAE

During decades of taxonomic studies in Gerbillinae, several classifications were forwarded which agree quite reasonably in some respects and differ in others. They are briefly reviewed here without going much into details, the reasons having been explained in the introductory chapter of the present contribution.

Nor shall I discuss taxonomic relationships of the fossil taxa allocated to the gerbillines (they are considered in the paleontological chapter above): a scope of this review is delimited by the contemporary fauna. The only point to be indicated is that exclusion of the extinct myocricetodontines from consideration does not seem (at least now) to have any effect on understanding of taxonomic relationships among the extant genera of subfamily Gerbillinae.

Thus, my primary goal here, as it was stated at the very beginning of the contribution, is to provide descriptions of the suprageneric taxa, the genera and subgenera recognized in the classification elaborated by me and published elsewhere (Pavlinov, 1982a; Pavlinov et al., 1990). It is not to say this classification is “the best”; however, it fits conditions of the evolutionary cladistics as a theoretical background of the present issue in being most supported by thorough analyses of some important morphological structures, including homology of auditory bulla and dental crown pattern (see morphological chapter above; also see Pavlinov, 2001).

In the subsequent sections, each taxon recognized in this classification is provided with the following information: principal morphological features and evolutionary trends; phylogenetic relations to other taxa and between its members including consideration of arguments *pro* and *contra* particular interpretations of memberships treated inconsistently by various authors; important paleontological data; and nomenclature upon a need. Some attention will be paid to subgenera while the species will be mentioned only in case of monotypy of respective inclusive taxa.

A REVIEW OF PRINCIPAL CLASSIFICATIONS

Gerbils constitute a taxonomically pretty well defined, not very large supergeneric group of the Old World rodents of the superfamily Muroidea ranking in taxonomic literature as a family or a subfamily. Their taxonomic distinctness is reflected, in particular, in that not any rodent genera evidently unrelated to the gerbils were ever allocated to this group. Alston's (1876) monograph on rodent classification seemed to be the only unlucky exception: he included all living gerbils in the same genus *Gerbillus* and included in his Gerbillinae also genera *Mystromys*, *Otomys*, and *Dasymys*, which are now allocated to different subfamilies of Muroidea.

Three principal versions of taxonomic rank and position of the group under consideration have been discussing in the taxonomic literature until most recent times. According to one of these conceptions, gerbils were treated as a separate family Gerbillidae along with Muridae, Cricetidae, etc. (Tullberg, 1899; Heptner, 1933; Chaline et al., 1977; Pavlinov et al., 1990; Pavlinov, 2003; etc.). Another treatment ascribes gerbils a subfamily rank Gerbillinae within the family Muridae in its widest sense, that is, including next to all muroid rodents (Thomas, 1896; Ellerman, 1941; Corbet, Hill, 1980; Carleton, Musser, 1984; McKenna, Bell, 1997; Musser, Carleton, 1993; etc.). These two classifications differ from each other mainly by formal ranking of the family-group taxa recognized, so they actually represent just two versions of largely the same taxonomic treatment. No less popular was placing Gerbillinae as a subfamily in the family Cricetidae Fischer together with the vole subfamily Arvicolinae Gray (= Microtinae Cope) (Miller, Guidley, 1918; Simpson, 1945; Arata, 1967; Sokolov, 1977). Finally, gerbillines were not so long ago suggested to be included in the family Nesomyidae Major (Lavocat, 1978), though not in the sense adopted by Musser and Carleton (2005; see below).

Recent findings in molecular phylogeny of the muroid rodents considered briefly above, supported by today predominating cladistic treatment of relation between phylogeny and classification, placed gerbils within the family Muridae as a taxon of the subfamily rank. In this classification, their closest neighbors are the members of the subfamily Deomyinae Lydekker (= Acomyinae Hanni et al., 1995). Accordingly, position of gerbillines in the classification of Muroidea can be represented as follows (after Musser, Carleton, 2005, with some modification):

Superfamily Muroidea s.lato
 Family Rhizomyidae Winge, 1887
 Family Spalacidae Gray, 1821
 Family Calomyscidae Vorontsov, Potapova, 1979
 Family Cricetidae Fischer, 1817
 Family Platacanthomyidae Alston, 1876
 Family Muridae Gray, 1821
 Subfamily Murinae s.str.
 Subfamily Otomyinae Thomas, 1897
 Subfamily Deomyinae Lydekker, 1889
 Subfamily Gerbillinae Gray, 1825
 Family Nesomyidae Major, 1897

As to the suprageneric classification of gerbils themselves, the first clearly articulated arrangement appeared to be the one suggested by W. Heptner (1933) who divided the family Gerbillidae into three subfamilies. One of them was Gerbillinae s.str. including genera of “lower gerbils” with bunodont and lophodont dentition. Another was Merioninae Heptner (non Brandt) with the genera possessing prismatic rooted molars. Subfamily Rhombomyinae Heptner included the sole genus *Rhombomys* with its hypsodont molars. The entire classification looks as follows:

Family Gerbillidae Gray, 1825
 Subfamily Gerbillinae s.str.
 Genera *Gebillus*, *Desmodillus*,
 Pachyuromys, *Tatera*, *Taterillus*
 Subfamily Merioninae Heptner, 1933
 Genera *Meriones*, *Brachiones*, *Psammomys*
 Subfamily Rhombomyinae Heptner, 1933
 Genus *Rhombomys*

This classification was gradistic in reflecting morphological progression of molar crown height in gerbils. Such an “odontological” aspect of the gerbil taxonomy was far more stressed later by I. Gromov who separated the genus *Rhombomys*

into monotypic tribe Rhombomyini and gathered all other genera in the nominative tribe Gerbillini s.str. (Gromov, Baranova, 1981).

Quite different classification was suggested by J. Chaline (Chaline et al., 1977; Chaline, Mein, 1979). He divided recent Gerbillidae in two subfamilies, Taterillinae Chaline et al. and Gerbillinae s.str., and added the extinct subfamily Myocricetodontinae Lavocat to reflect new findings in gerbilline phylogeny. This major taxonomic treatment was followed subsequently by some paleontologists (e.g. Agusti, Casanovas-Vilar, 2003; Qiu et al., 2004) including McKenna and Bell (1997) who lowered the ranks of respective taxa by one step (see below). Morphological basis of this taxonomic decision for the living taxa was drawn from bullar morphology: taterillines were defined as gerbils with non-inflated mastoid and gerbillines proper were characterized by pneumatized mastoid. Therefore, this classification, though it appeared to be in agreement with further developments (see below), seemed to be no less “gradistic” than that of Heptner, although on different morphological background. However, Chaline’s approach was not quite consistent with that background: for instance, one species of the genus *Gerbillurus* with least evolved auditory bulla (namely, *G. paeba*) was placed within Taterillinae while the species of *Gerbillus* s.lato with the likewise primitive mastoid pneumatization (allocated to *Dipodillus* by me) were left in Gerbillinae.

The next and the most detailed classification of Gerbillinae/Gerbillidae was suggested by me (Pavlinov, 1982a; Pavlinov et al., 1990) based on the phylogenetic tree discussed above (see Fig. 10b). It appeared to be more similar to that of Chaline et al. (1977) in recognizing the same two principal suprageneric taxa, taterillines and gerbillines proper, though they were defined by other morphological features (the types and not just a degree of mastoid pneumatization, before all) and so with the different taxonomic content. One more taxon of the same rank with those two main clades was erected for the genus *Ammodillus* based on its unique dental structure, and several other suprageneric taxa were recognized within both taterilline and gerbilline branches to reflect the hierarchy of phylogenetic pattern. The subfamily rank of the entire group under consideration being adopted, that classification looks as follows:

Subfamily Gerbillinae Gray, 1825
 Tribe Taterillini Chaline et al., 1977
 Subtribe Taterillina s.str.
 Genera *Tatera*, *Gerbilliscus*, *Taterillus*
 Subtribe Gerbillurina Pavlinov, 1982
 Genera *Gerbillurus*, *Desmodillus*
 Tribe Ammodillini Pavlinov, 1981
 Genus *Ammodillus*
 Tribe Gerbillini s.str.
 Subtribe Gerbillina s.str.
 Genera *Dipodillus*, *Gerbillus*, *Monodia*,
Microdillus
 Subtribe Desmodilliscina Pavlinov, 1982
 Genus *Desmodilliscus*
 Subtribe Pachyuromyina Pavlinov, 1982
 Genus *Pachyuromys*
 Subtribe Rhombomyina Heptner, 1933
 Genera *Sekeetamys*, *Meriones*,
Brachiones, *Psammomys*, *Rhombomys*

Phylogenetic analysis of H. Tong (1989) was not resulted in a formal classification. However, the respective tree (see Fig. 10c), as far as Recent members of the subfamily Gerbillinae are concerned, seems to be most consistent with the following possible classification:

Subfamily Gerbillinae Gray, 1825
 Tribe Taterillini Chaline, Mein, Petter, 1977
 Subtribe Taterillina s.str.
 Genera *Tatera* s.lato, *Taterillus*
 Subtribe Gerbillurina Pavlinov, 1982
 Genus *Gerbillurus*
 Tribe Ammodillini Pavlinov, 1981
 Genus *Ammodillus*
 Tribe Gerbillini s.str.
 Subtribe "Noname"
 Genus *Desmodillus*
 Subtribe Desmodilliscina Pavlinov, 1982
 Genus *Desmodilliscus*
 Subtribe Gerbillina s.str.
 Genera *Gerbillus*, *Microdillus*,
Sekeetamys
 Subtribe Rhombomyina Heptner, 1933
 Genera *Pachyuromys*, *Brachiones*,
Meriones, *Psammomys*, *Rhombomys*

Molecular phylogenetic tree of Chevret and Dobigny (2005) also was not represented in the form of any taxonomic system, although the authors discussed some important taxonomic outcomes of their findings. Following exactly the principles of the Hennigian cladistics requesting for equal taxonomic ranks of sister groups (e.g.

Wiley, 1981), the subfamily Gerbillinae, accordingly to Chevret and Dobigny's tree topology (see Fig. 10d), is to be divided into tribes Desmodilliscini (with genera *Pachyuromys*, *Desmodilliscus*) and Gerbillini s.str., the latter being further split into several subtribes (gerbillurines and gerbillines), each with respective "subsubtribes". However, if not to adopt principles of cladistic taxonomy so literally, the tree in question could be represented by the following system of monophyletic suprageneric taxa (note that the genera *Ammodillus* and *Brachiones* were absent from the sample studied genetically):

Subfamily Gerbillinae Gray, 1825
 Tribe Desmodilliscina Pavlinov, 1982
 Genera *Pachyuromys*, *Desmodilliscus*
 Tribe Gerbillurini Pavlinov, 1982
 Subtribe "Taterini" auct.
 Genus *Tatera*
 Subtribe "Noname"
 Genus *Desmodillus*
 Subtribe Gerbillurina s.str.
 Genera *Gerbillurus*, *Gerbilliscus*
 Tribe Taterillini Chaline, Mein, Petter, 1977
 Genus *Taterillus*
 Tribe Gerbillini s.str.
 Subtribe Gerbillina s.str.
 Genera *Gerbillus*, *Sekeetamys*
 Subtribe Rhombomyina Heptner, 1933
 Genera *Meriones*, *Psammomys*,
Rhombomys

At last, one more classification summarized by McKenna and Bell (1997) looks as follows (extinct taxa omitted):

Subfamily Gerbillinae Gray, 1825
 Tribe Gerbillini s.str.
 Subtribe Gerbillina s.str.
 Genera *Gerbillus*, *Microdillus*
 Subtribe Merionina Brandt, 1844 (*sic!*)
 Genera *Sekeetamys*, *Meriones*,
Brachiones, *Psammomys*, *Rhombomys*
 Subtribe Desmodilliscina Pavlinov, 1982
 Genus *Desmodilliscus*
 Subtribe Pachyuromyina Pavlinov, 1982
 Genus *Pachyuromys*
 Subtribe Taterillina Chaline, Mein, Petter, 1977
 Genera *Tatera*, *Taterillus*
 Subtribe Gerbillurina Pavlinov, 1982
 Genera *Gerbillurus*, *Desmodillus*
 Tribe Ammodillini Pavlinov, 1981
 Genus *Ammodillus*

The just above classification simplifies phylogenetic hierarchy of Gerbillinae acknowledged by most of the recent authorities. In particular, it does not reflect properly sister-group relationships between taterillines (in my sense) and gerbillines.

TRIBE TATERILLINI CHALINE, MEIN, PETTER, 1977

CONTENTS. This is one of the principal suprageneric groups in the subfamily Gerbillinae recognized by both morphologists (Petter, 1975; Pavlinov, 1982a, 2001; Tong 1989; Pavlinov et al., 1990) and, with some reservations, by molecular phylogeneticists (Chevret, Dobigny, 2005). According to the phylogeny and classification adopted here, it includes five Recent genera divided into two subtribes: the Taterillina s.str with the genera *Tatera*, *Gerbilliscus*, *Taterillus*; and the Gerbillurina with the genera *Gerbillurus*, *Desmodillus*. The genus *Taterillus* is excluded from here by Chevret, Dobigny (2005), with respective change of the tribal name.

MORPHOLOGICAL CHARACTERS. Taterillines are characterized by usually (save *Desmodillus*) enlarged masseteric plate with elongated keel and with wide orbital shield. This pattern is correlated with anterior displacement of the oral ending of the masseteric ridge on the mandible. All these peculiarities are caused by powerful development of both lateral and medial portions of the anterior branch of the masseteric muscle (Potapova, 1990; Pavlinov et al., 1990).

Auditory bulla is variable in size but with tympanic portion always significantly predominating. This portion is well inflated already in the species with no mastoid pneumatization and such a disproportion is retained even in the species with enlarged mastoid portion (e.g. in the subgenus *Gerbillurus* s.str.). The mastoid is not pneumatized in many members of Taterillina s.str. and with less or more developed cavity in others, being the largest in *Desmodillus* and in some species of *Gerbillurus*. Mastoid pneumatization usually follows the anterior pathway: the tympanic cavity penetrates into the mastoid first through the epitympanic recess (see morphological chapter above). The resulting epimastoid chamber remains dominating with the progress of mastoid pneumatization, while partial ventral penetration of tympanic cavity in the mastoid occurs at the final stage of the latter's development. So the cavity constituting the fully pneumatized mastoid, unlike the

one in Gerbillini, is strictly homologous to the epimastoid chamber (see Figs 7, 8). Mastoid septum bounding it from the beneath never takes vertical position in the taterilline genera. No additional tympano-mastoid septum appears, so it is the mastoid one that attaches the mastoid wall along the tympano-mastoid suture. The only exclusion from this general trend is the nominative subgenus *Gerbilliscus* s.str. in which the type of mastoid pneumatization is rather similar to that observed in the most primitive members of the tribe Gerbillini.

Molar crown is pretty high and laminated, it is semi-lophodont in less advanced or typically lophodont in most specialized members of the tribe. It is usually symmetrical, some traces of the primary asymmetry are noticeable in the subgenus *Gerbillurus* (*Progerbillurus*) only. Anterior part of lower M1 bears rudimentary isolated protoconulid on the least worn crown in at least one genus (*Desmodillus*) which becomes fused with the anteroconid proper with the tooth wear. Judging by ontogenetic sequences displayed by various stages of tooth wear in *Tatera* and *Desmodillus*, there are two ways of formation of definitive anteroconid in Taterillini. In *Tatera*, protoconulid and exteroanteroconid are fused first and then this structure is added with the interoanteroconid. In *Desmodillus*, elements of the anteroconid proper join first each other whereas the protoconulid remains isolated for some time (as in the extinct *Protatera*). The fully developed anteroconid in its most derived condition is usually of the horseshoe type, as it is common to the genus *Gerbilliscus*. This type is less expressed in other genera where the well worn anteroconid is not infrequently rhomboid in its shape.

PRINCIPAL FOSSILS. Fossil history of the tribe is represented by several genera with lophodont molars from Miocene and early Pliocene of northern Africa, southern Asia and south-western Europe. These are *Abudhabia*, *Debruijnimys*, and *Protatera* (see review of the paleontology above). The first two of them are typical taterillines proper by characters available from the remains while the last one displays a specific combination of advanced and primitive traits (the fully developed protoconulid on the lower M1) and is to be placed at basal radiation of the Taterillini. So, the known fossils give no possibility to trace more precisely both within- and intra-subtribal relationships in this clade.

COMMENTS. Monophyly of the tribe Taterillini (save the genus *Taterillus*) is supported by both

morphological and molecular data (Petter, 1975; Pavlinov, 1982a, 1987; Tong, 1989; Chevret, Dobigny, 2005). However, phylogenetic relationships among its genera are not clear enough. Generally speaking, this tribe could be considered as consisting of two “nuclei”, one with the genera *Tatera* and *Gerbilliscus* and another with the genus *Gerbillurus*. Molecular data are in favour of basal position of the genus *Tatera* relative to others while morphological data rather place the genus *Gerbillurus* at that position. It is the relationships of two other genera, *Taterillus* and *Desmodillus*, which allocation to and position within the tribe provides certain problems.

The genus *Taterillus* has been traditionally jointing to the first “nucleus”, this conception gaining good support from morphological data; they share synapomorphic traits in dental and zygo-masseteric morphology. But molecular data show this hypothesis might be incorrect and this genus should be excluded from the tribe under consideration at all (Chevret, Dobigny, 2005; Colangelo et al., 2007). This treatment is considered as well supported by genetists, but actually it is based on analysis of just two mtDNA genes.

The second “nucleus” serves as a kind of phylogenetic attractor for the genus *Desmodillus*: it is similar with *Gerbillurus* in dental and bullar morphology. But these similarities are not true synapomorphies: semi-lophodont crown pattern is rather plesiomorphic trait relative to typical lophodonty of the taterillines proper, while advanced bullar morphology might appear due to parallel evolution (see account of the subtribe Gerbillurina below). On another hand, not enlarged masseteric plate in *Desmodillus* indicates that closest ancestor of the subtribe Gerbillurina and eventually of the entire tribe Taterillini also possessed a similar plesiomorphic trait. This leaves this tribe without such an important synapomorphy.

Situation just outlined requests (as it is usually stated in such cases) further analyses and more characters. This conclusion is especially true for the genus *Taterillus* which is kept here following morphological evidence. As to the *Desmodillus*, it is also retained here as a member of Gerbillurina but it well might be that this genus is to be placed at basal radiation of the entire tribe. The arguments *pro* and *contra* for each of these treatments are considered at more length in the accounts of the respective genera below.

Shift of the genus *Taterillus* from this group to basal radiation of the Gerbillini suggested by mo-

lecular phylogenetic tree would request certain change in the nomenclature. If such a system is adopted, this genus becomes the only representative of the tribe Taterillini (by tautonymy). Respectively, all other members of the group under consideration are no longer “taterillines” formally, and another name is to be applied to it. A new name Taterini was proposed by genetists (Chevret, Dobigny, 2005) to reflect their taxonomic treatment, but it is anteceded by Gerbillurina Pavlinov, 1982, at the tribal level (see also comments to Taterillina s.str. below).

Subtribe Taterillina s.str.

CONTENTS. Three genera, *Tatera*, *Gerbilliscus* (including *Taterona*) and *Taterillus* are referred here to the nominative subtribe. The first two were usually treated as congeners until latest times; the third one was usually considered as most close to them though newest findings in molecular phylogeny suggest its sister-group relation to Gerbillini (see below).

MORPHOLOGICAL CHARACTERS. The skull is characterized by most robust zygo-masseteric construction for the subfamily, with a very long keel of the zydomatic plate and a well developed orbital shield (see Fig. 1b). This is synapomorphy for the subtribe, it also unites its members with the genus *Gerbillurus* (but not with *Desmodillus*).

The mastoid of auditory bulla is not pneumatized (most primitive for the subfamily) in *Taterillus* and *Gerbilliscus* (*Taterona*) or just slightly evolved in others, it is always smaller externally relative to the tympanic portion than in any other Recent Gerbillinae. Two different modes of mastoid pneumatization are observed; one (in *Tatera*) from the anterior only, similarly to Gerbillurina, another (in the subgenus *Gerbilliscus* s.str.) from both anterior and ventral pathways, as in Gerbillini. In the latter case, however, the mastoid retains very primitive condition.

Molar crown is of most advanced lophodont type, with laminae being formed very early and longitudinal bridgelets appearing much later. Laminae are usually with slightly curved axial lines, which makes the teeth secondarily asymmetrical. Anteroconid of the lower M1 is developed by the horseshoe type, it varies in the degree of specialization. Separate protoconulid is present on minimally worn tooth in *Tatera* while solid and fully developed anteroconid occurs in the two other genera. This advanced morphotype, as far as wear-

ing sequence in *Tatera* shows, is resulted from first fusion of protoconulid and exteroanteroconid, with interoanteroconid being added to this complex subsequently.

PRINCIPAL FOSSILS. It is very probable that the genus *Abudhabia* from the late Tertiary of southern (and probably central) Asia (Flynn et al., 2003; Qiu et al., 2004) belongs here. It possesses elongated keel of the masseteric plate and is very similar to the extant *Tatera* by less advanced lophodont molar crown (see paleontological review above, and Fig. 9c). Another fossil with probably close affinity to taterillines proper is *Debruijnimys* from the late Miocene of south-western Europe.

COMMENTS. Both monophyly of the tribe Taterillina and its close relationship to gerbillurines in the Recent fauna are supported by morphological data. Several hypotheses were forwarded about its phylogenetic status and taxonomic structure. According to the traditional treatment, the gerbils included here are divided into two genera, "*Tatera*" s.lato and *Taterillus* (e.g. Arata, 1967; Tong, 1989; Musser, Carleton, 1993). Cladistic analysis of morphological traits (Pavlinov, 1982a, 1984a, 1987, 2001; Pavlinov et al., 1990) supposes *Gerbilliscus* (including *Taterona* as a subgenus) and *Taterillus* are sister groups characterized by most advanced molar crown pattern relative to the Asian genus *Tatera* in which more advanced bullar morphology is observed. Molecular data (Chevret, Dobigny, 2005; Colangelo et al., 2007) are also in favour of generic separation of *Tatera* and *Gerbilliscus* and indicate close relationships between the latter and *Gerbillurus*, which means that they are to be united in the same subtribe not including the genus *Tatera*. Another striking novelty of molecular studies is that the genus *Taterillus* is to be excluded from this group. If this suggestion of molecular phylogeneticists is correct, the Gerbillirina Pavlinov would be its valid name (see also comments to the genus *Tatera* below).

All these molecular findings make the subtribe under consideration, as it is understood here, a paraphyletic assemblage. However, as it was already stated above, the latter treatment looks weakly supported from the morphological standpoint. So it seems premature to change the present classification until more genetic (and eventually morphological) evidence are available.

Genus *Tatera* Lataste, 1882

CONTENTS. This genus has long been considered as including, in addition to the Asian nomino-

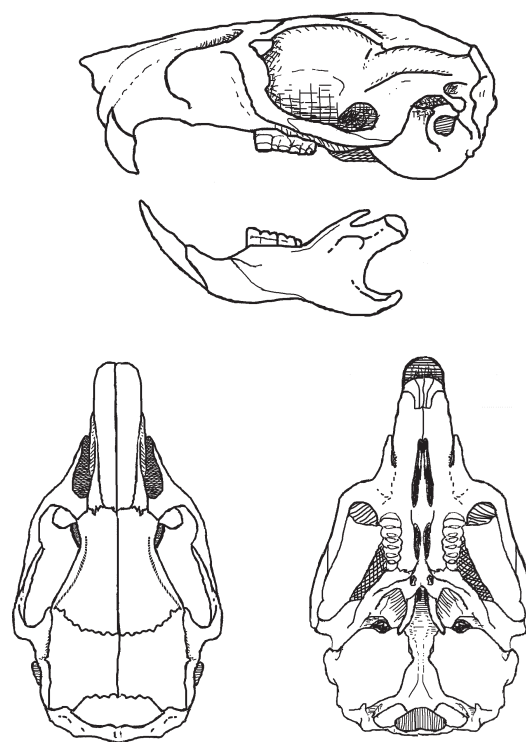


Fig. 11. Skull of *Tatera indica* (orig.)

Рис. 11. Череп *Tatera indica* (ориг.)

type species, about a dozen of African species here allocated to the genus *Gerbilliscus*. Moreover, *Tatera* and *Taterona* were sometimes united in the same nominative subgenus in such a traditional treatment (e.g. Davis, 1971). It was not until early 1980s when African and Asian members of "*Tatera*" s.lato were first recognized as different subgenera (Pavlinov, 1981b) and then as full genera (Pavlinov, 1982a, 1987, 2001, 2003; Carleton, Musser, 1984; Pavlinov et al., 1990; Musser, Carleton, 2005). The genus *Tatera* is here understood as containing *T. indica* Hardwicke only.

MORPHOLOGICAL CHARACTERS. The genus under consideration is characterized by skull morphology rather typical for the subtribe Taterillina (Fig. 11). It differs markedly from the other members of the latter by a peculiar combination of morphological features some of which are most advanced and others are primitive for this subtribe.

The advanced is the mastoid morphology in *Tatera*: it is fully pneumatized though not especially enlarged (see Fig. 7c) and with pretty thick walls. Therefore its pneumatization, unlike in other gerbils with similar type of mastoideum, is not visible from the outside. In this connection it is to be stressed that the mastoid pneumatization in this

genus is even more evolved than in *Gerbillurus* (*Progerbillurus*) and in *Dipodillus*. Its cavity is connected with the tympanic one anteriorly and is isolated from it ventrally by the solid mastoid septum. So, this type of pneumatization is similar to that observed in *Gerbillurina* and differs from the one known to occur in the nominative subgenus *Gerbilliscus* s.str.

Contrary to the mastoid, morphology of the anterior portion of lower M1 is quite archaic. It is frequently represented by two isolated elements on the minimally worn teeth (see Fig. 5a), of which the internal one is supposed to be homologous to interoanteroconid and the external one, judging by its shape, is homologous to the fused exteroanteroconid and protoconulid (Pavlinov, 1984a). This complicated structure turns with wear into horseshoe morphotype with posterior fossetid and then rather quickly turns into rhomboid type, unlike both *Gerbilliscus* and *Taterillus* in which it remains pretty long of the horseshoe shape.

COMMENTS. Such an archaic dental morphology seems to agree with the molecular phylogenetic tree of Chevret and Dobigny (2005) in which the genus under consideration takes a basal position within (my) *Taterillini*. Such a treatment stresses especially generic separation of *Tatera* and *Gerbilliscus*. If the anteroconid homology in *Tatera* is correct, then this pattern differs from that in Miocene *Protatera* (see paleontological account above) thus indicating not especially close relation between them.

The basal position of the genus *Tatera* in the tree for the tribe under consideration may make it reasonable to separate it in the monotypical subtribe of its own. A new name for the latter should be “*Taterini*” of Chevret and Dobigny (2005) but it seems to be a *nomen nudum* under provisions of Article 16.2 of the International Code of Zoological Nomenclature and so in need of a correct re-description.

Genus *Gerbilliscus* Thomas, 1897

CONTENTS. This was usually considered as a monotypic subgenus within Afro-Asian genus “*Tatera*” s.lato. Accordingly to the phylogenetic scheme developed on the basis of morphological data (Pavlinov, 1982a, 2001; Pavlinov et al., 1990) it is a full genus of entirely African distribution including all the species have been known previously as the “African taterans”. About 10 species are currently recognized most of which are referred now to the subgenus *Taterona* (Pavlinov et

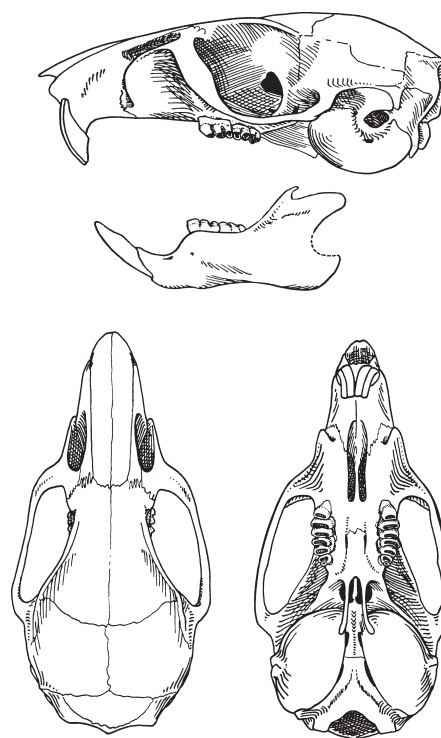


Fig. 12. Skull of *Gerbilliscus kempii* (after Rosevear, 1969)

Рис. 12. Череп *Gerbilliscus kempii* (по Rosevear, 1969)

al., 1990; Musser, Carleton, 2005); but their real number is most probably higher (Colangelo et al., 2005; Volobouev et al., 2007).

MORPHOLOGICAL CHARACTERS. This genus differs from the Asian *Tatera* cranially by conspicuously more inflated tympanic portion of the bulla (Fig. 12). However, the most significant are differences in mastoid morphology, which is at the very initial stage of pneumatization and filled in most part with *f. parafloccularis* (see Fig. 7a). It is of special interest that the ways of its pneumatization display both principal types known for the Gerbillinae. Its very small cavity appears as a penetration either from the anterior in the subgenus *Taterona* (like in the subgenus *Progerbillurus*) or from both anterior and ventral sides of the *mas-toideum* in the nominative subgenus (similar to *Dipodillus*; see Fig. 7e). This difference is evident from absence or presence (in diagonal position) of the mastoid septum.

Another principal difference between these two genera is the anterior part of lower M1. It is of most advanced horseshoe type in *Gerbilliscus*, without any trace of protoconulid (see Fig. 5d). Indeed, the “horseshoe” is formed in this genus at

the earliest stage of tooth wear, with the fossetid entering it from either forward or backward. Sometimes it goes from both directions to transect the anteroconid into two lateral portions, and frequently forming a closed hole at the later stages of tooth wear.

COMMENTS. As it is obvious from the morphological evidence and supported indirectly by molecular data, the genera *Gerbilliscus* and *Tatera*, as they are understood here, have diverged at that stage of their evolution when the mastoid bulla was not pneumatized, and the anterior portion of the lower M1 was represented by several separate cusplets. Subsequently, the former genus developed more advanced molars while the latter succeeded in the mastoid pneumatization.

Morphological differences between the genera *Gerbilliscus* and *Taterillus* are of less scale and involve few diagnostic characters (such as length of the posterior palatal foramina) with little phylogenetic significance. So, morphological data suggest their sister-group relationship (Pavlinov et al., 1990), while molecular data are against this treatment (Chevret, Dobigny, 2005).

Species groups within the genus are not clear. Its division into two subgenera, *Gerbilliscus* s.str. (containing *G. boehmi* only) and *Taterona* Wroughton (all the remainder species), is supported by the bullar and mandible morphology. However, cytogenetic and molecular data on *Taterona* (Qumsiyeh, Schlitter, 1991; Colangelo et al., 2005, 2007; Volobouev et al., 2007) indicate the latter is quite heterogenous and may represent a paraphyletic group (*G. boehmi* was not studied). Such a conclusion was especially stressed by Colangelo et al. (2005) who placed *Gerbillurus* within this genus, though with a weak support.

Genus *Taterillus* Thomas, 1910

CONTENTS. Includes about 10 species without any clear grouping (Pavlinov et al., 1990; Musser, Carleton, 2005).

MORPHOLOGICAL CHARACTERS. Here belong quite typical members of the nominative subtribe in respect to significantly enlarged anteriorly masseteric plate (Fig. 13), overall morphology of the auditory bulla and molar crown pattern. Tympanic portion is well inflated and predominates over mastoid one, the latter being without any trace of pneumatization, that is, most primitive in all the subfamily Gerbillinae. Molar crowns are typically lophodont, but there are some traces of ancestral bunodont condition: for instance, longitudi-

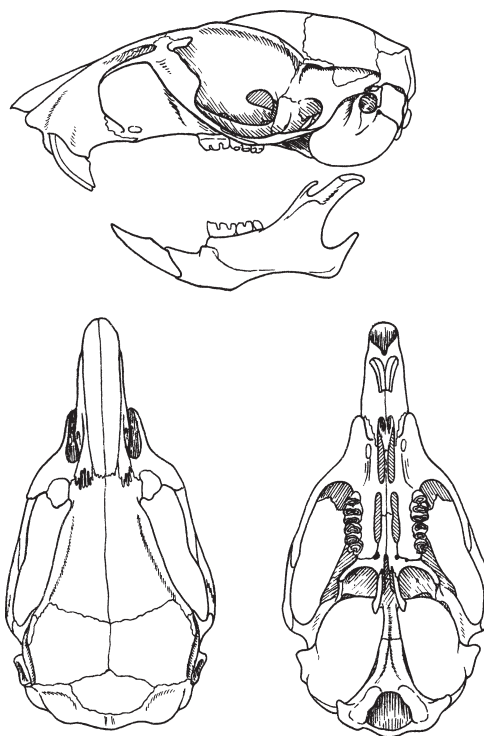


Fig. 13. Skull of *Taterillus gracilis* (after Pavlinov et al., 1990)

Рис. 13. Череп *Taterillus gracilis* (по Pavlinov et al., 1990)

nal bridgelets appear a little earlier than in *Gerbilliscus* and not infrequently in lateral position. Anteroconid of lower M1 is of the horseshoe type when it is little worn, but all phases of its wear are displaced at earlier ages as compared to *Gerbilliscus*, so it is used to be rhomboid-like on well worn tooth. This anteroconid is sometimes with tapered postero-labial angle which might be considered as a trace of the former protoconulid (such a peculiarity is also known for *Abudhabia*).

COMMENTS. This is another African representative of the subtribe Taterillina according to the classification exposed here. This genus was acknowledged, until most recent times, as closest relative of *Gerbilliscus* (Pavlinov, 1982a, 2001; Pavlinov et al., 1990) or, at any rate, of "*Tatera*" s.lato (Chaline et al. 1977; Tong, 1989). Similarity between *Taterillus* and *Gerbilliscus* s.lato is so striking that Pavlinov (1987) supposed they might be just subgenerically distinct. Morphological characters discriminating them are as follows: posterior palatal foramina are long and mandible is lightly built than in other taterillines.

However, molecular phylogeny based on two mtDNA genes (Chevret, Dobigny, 2005) suggests

Taterillus to be a basal member of the tribe Gerbillini; this is also supported by the allozyme data (Benazzou, 1984; cited after Chevret, Dobigny, 2005). But there are no specific morphological synapomorphies known so far to unite the genus under consideration with the genus *Gerbillus* and its allies; cytogenetic data are also against such a hypothesis (Qumsiyeh, 1986).

Subtribe Gerbillurina Pavlinov, 1982

CONTENTS. This group, as it is understood here (after Pavlinov et al., 1990), includes two genera endemic to southern Africa.

MORPHOLOGICAL CHARACTERS. Gerbillurines are characterized by more generalized dentition and, to some extent, zygo-masseteric construction, while bullar morphology is more advanced as compared to members of the nominative subtribe Taterillina.

As far as morphological traits diagnostic for the entire tribe Taterillini are concerned, it is to be stressed that elongated keel of masseteric plate occurs in the genus *Gerbillus* only, while in the genus *Desmodillus* it is not enlarged.

The auditory bulla varies from moderately to extremely pneumatized. Unlike in the members of Gerbillini, its tympanic portion predominates over mastoid one in the gerbillurines, even in those with hypertrophied mastoideum, which is typical for all the taterillines. The mastoid is just partially pneumatized in the least advanced subgenus *Gerbillus* (*Progerbillurus*) in which parafloccular recess filling its caudal part (see Fig. 7b). Such a morphology indicates that the mastoid pneumatization in gerbillurines begins with the anterior tympanic penetration while the slight ventral penetration occurs in the most enlarged bulla only (*Gerbillus* s.str. and especially *Desmodillus*). Due to this, the mastoid septum occupies diagonal position and never goes vertically. It divides mastoid cavity into two portions isolated from each other, the larger epimastoid chamber being widely opened into tympanic cavity anteriorly and the smaller tympanomastoid chamber communicating with the tympanic cavity ventrally through the arc of the lateral semicircular canal (see Fig. 7d).

As it was shown in the chapter on gerbilline morphology above, this kind of mastoid pneumatization differs from the one in the tribe Gerbillini; they correspond to two different developmental trajectories (see Fig. 7). This scheme of mas-

toid evolution presumes that it is rather improbable for the mastoid to “switch” from one trajectory to another. It is incorrect from this viewpoint to consider the mastoid type in advanced gerbillurines as a predecessor of that in gerbillines, as it is supposed by the homology of D. Lay (1972) or by the formal synapomorphy list on the phylogenetic tree of Tong (1989). Rather, our scheme makes it more plausible to suppose these trajectories reflecting independent branches of the phylogenetic tree of Gerbillinae.

Molar crown in Gerbillurina is less evolved than in Taterillina s.str. in being semi-lophodont (see Fig. 4b). That means that transverse laminae are developed at later stage than in the typical lophodont teeth (like in *Taterillus*) but earlier than in the typical bunodont ones (like in *Gerbillus*). This semi-lophodont crown pattern differs from the bunodont condition also in that its longitudinal elements are developed later and does not form asymmetrical S-shaped configuration on the 1st molars. This overall pattern is well developed in *Desmodillus* and more less so in *Gerbillus*.

The anterior part of lower M1 is pretty primitive, with isolated protoconulid in *Desmodillus* (see Fig. 5b). Unlike in *Tatera*, its transformation begins with fusion of extero- and interoanteroconids with subsequent joining of protoconulid to form the horseshoe or rhomboid anteroconid.

COMMENTS. Taxonomic fate of this group of gerbils has long been and still remains controversial. The genera it includes were and still are united not infrequently with various members of Gerbillini: *Gerbillus* was once thought to be a close relative of *Gerbillus*, while *Desmodillus* is combined sometimes with *Desmodilliscus*. At present, the position of gerbillurines as members of the tribe Taterillini (in its original sense) seems to be well supported both morphologically and genetically (Pavlinov, 1982a, 1984a, 1985; Pavlinov et al., 1990; Chevret, Dobigny, 2005). At the same time, the subtribe contents is not well founded.

According to the classification adopted here, this group is defined by semi-lophodont molar crown and specific mastoid pneumatization. However, its monophyly is not strongly supported if these features shared by *Gerbillus* and *Desmodillus* are treated cladistically. The matter is that each of these two genera possesses a specific combination of plesiomorphic and apomorphic traits and there is no unique “true” synapomorphy uniting all gerbillurines relative to other Taterillini. Indeed, the genus *Desmodillus* displays more

primitive zygo-masseteric construction and anteroconid than *Gerbillurus* (and any other African taterilline), while their interrelation in respect to the bullar and dental morphology is quite opposite.

Such a mosaic may indicate parallel evolution at least in some morphological traits which means gerbillurine synapomorphies might be not true in the strict (Hennigian) sense of this term but rather “underlying” (in the sense of Saether, 1983). This possibility was expressed by Pavlinov et al. (1990) and explicitly follows from both cytogenetic and molecular data (Qumsiyeh, 1986; Chevret, Dobigny, 2005; Colangelo et al., 2007). They indicate unambiguously a paraphyletic status of the subtribe under consideration, with the genus *Desmodillus* taking position next to the root of the taterilline phylogenetic tree and the genus *Gerbillurus* being a sister group to *Gerbilliscus*.

Genus *Gerbillurus* Shortridge, 1942.

CONTENTS. Belonging here are four species of the southern African pygmy gerbils divided into two or three subgenera (Pavlinov et al., 1990).

MORPHOLOGICAL CHARACTERS. Members of this genus are generally characterized by moderately elongated keel of zygo-masseteric plate (Fig. 14), which is less than in genera included in the subtribe Taterillina, and by semi-lophodont molar crown pattern. The latter is least advanced in the tribe in having certain characters in common with typical bunodont type (see Fig. 4b). In particular, the longitudinal bridgelets are frequently formed in lateral and not in axial position. Anterior part of the lower M1 is always solid, that is without separate protoconulid which is present inconspicuously only as a small outgrowth of postero-labial part of the anteroconid. The horseshoe pattern occurs at earlier stages of the tooth wear and disappears later, with the anteroconid becoming of the rhomboid type.

Pneumatization of the auditory bulla is variable in degree, especially of its mastoid portion, thus allowing to trace its transformation from least to more advanced variants within the type specific to the Gerbillurina. The mastoid is quite primitive, just partly pneumatized in *Gerbillurus* (*Progerbillurus*) (see Fig. 7b) and is most advanced in the members of nominative subgenus, as in the genus *Desmodillus* (see Fig. 7d).

COMMENTS. The species here included in *Gerbillurus* were once allocated to different genera (Roberts, 1951) or to different subgenera in the

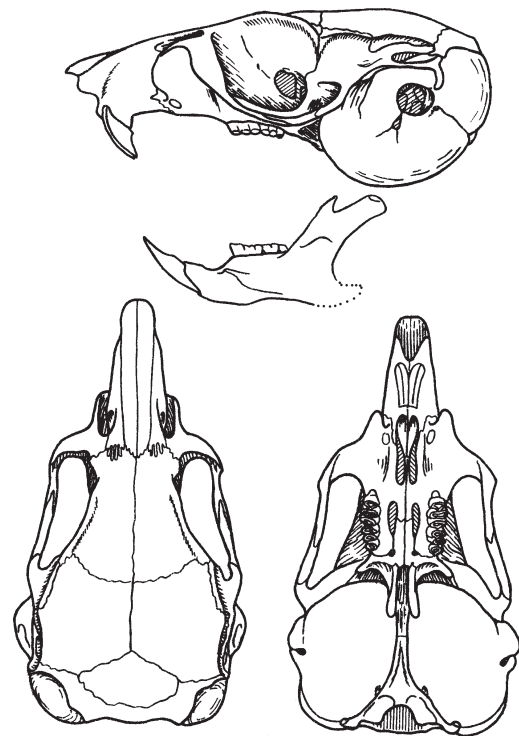


Fig. 14. Skull of *Gerbillurus setzeri* (after Pavlinov et al., 1990)

Рис. 14. Череп *Gerbillurus setzeri* (по Pavlinov et al., 1990)

genus *Gerbillus* (Ellerman et al., 1951). Subsequently, some morphological characters were revealed that appeared to discriminate them from the latter and, at the same time, made them close to taterillines (Lundholm, 1955; Herold, Niethammer, 1963). Both generic status and the current contents of *Gerbillurus* was finally acknowledged in the 1970s (Davis, 1971; Petter, 1975), and later the genus was transferred to Taterillinae/Taterillini (Chaline et al., 1977; Pavlinov, 1982a, 1987; Tong, 1989; Pavlinov et al., 1990; Chevret, Dobigny, 2005). Most recent molecular data (Colangelo et al., 2005) stress a close relation between *Gerbillurus* and *Gerbilliscus* by placing the former within the latter, though with a weak support.

There are three subgenera recognized within the genus, of which *Progerbillurus* Pavlinov, 1982 and *Paratatera* Petter, 1983 being monotypic and *Gerbillurus* s.str. containing two species (Pavlinov et al., 1990). Of these subgenera, *Progerbillurus* is the most primitive in having the least evolved zygo-masseteric structure and auditory bulla while *Paratatera* takes intermediate position between it and the nominative subgenus.

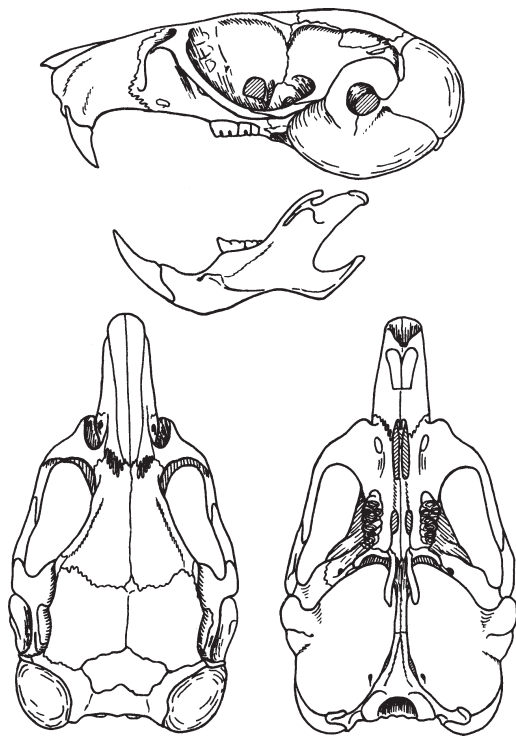


Fig. 15. Skull of *Desmodillus auricularis* (after Pavlinov et al., 1990)

Рис. 15. Череп *Desmodillus auricularis* (по Pavlinov et al., 1990)

Genus *Desmodillus* Thomas, Schwann, 1904

CONTENTS. Includes the sole species, *D. auricularis* A. Smith.

MORPHOLOGICAL CHARACTERS. This is the most advanced representative of the tribe Taterillini in respect to bullar morphology. The auditory bulla is hypertrophied, its mastoid part is fully pneumatized, with mastoid septum taking diagonal position and posterior mastoid chamber opened into the tympanic cavity (see Fig. 7d). Other cranial features of *Desmodillus* (Fig. 15) are more generalized than in *Gerbillurus* and in other taterillines. In particular, keel of the masseteric plate is not elongated, so the genus in question falls in this respect out from the formal morphological boundaries of the tribe Taterillini.

It is to be noticed in parentheses that this genus, due to its very large auditory bulla, is most similar by overall skull shape to *Pachyuromys* but not to *Desmodilliscus* (compare Fig. 15 with Figs 20 and 21 below), as it is usually but incorrectly stated by various authors.

Molar crown type is a little more advanced than in *Gerbillurus*. It is semi-lophodont with pretty

symmetrical configuration of main cusps, opposite elements of the crown tend to fuse quite early to form the transverse laminae.

The genus *Desmodillus* is very interesting in possessing a separate protoconulid on the lower M1 (Pavlinov, 1984a, 1985). However, unlike in the genus *Ammodillus* (considered below), it is clearly identifiable on minimally worn tooth only (see Fig. 5b) and fused quickly with the anteroconid to form with it a horseshoe shape typical to all taterillines. Thus, the genus under consideration is more primitive in this respect than the genus *Gerbillurus*. It is noteworthy that such an anteroconid pattern also occurs in the Miocene genus *Protatera* (see Fig. 9b) thus indicating a very ancient origin of *Desmodillus* (Pavlinov, 1985).

COMMENTS. This genus was sometimes put close to *Desmodilliscus*: some authors were probably misled by similarity of the names of these two genera (Simpson, 1945), while others followed wrong homology of their mastoid elements (e.g. Tong, 1989). However, belonging of *Desmodillus* to the tribe Taterillini, as it is understood here, seems quite clear from both morphological (Pavlinov et al., 1990) and molecular (Chevret, Dobigny, 2005) backgrounds.

From the standpoint of phylogenetically important dental and bullar morphology, the genus in question is most similar to *Gerbillurus* which in its turn shares some apomorphic features with typical taterillines. However, its membership in the subtribe Gerbillurina is not well supported, as it was indicated above in account of the latter. It might be that *Desmodillus* actually belongs to basal radiation of the entire tribe Taterillini; this point is supported by a very primitive anteroconid pattern and by quite generalized zygo-masseteric construction; molecular data also agree with this. This means that similarity between *Desmodillus* and *Gerbillurus* is explained by parallel evolution. In other words, one can not exclude that another subtribe is to be erected for the genus in question, with respective new family-group name.

TRIBE AMMODILLINI PAVLINOV, 1981

CONTENTS. Includes the only one genus, *Ammodillus*.

MORPHOLOGICAL CHARACTERS. This tribe is one of the most distinct taxa among living gerbillines by its cranial and dental morphology. It is characterized by unique combination of archaic protoconulid and hypoconulid and highly specialized

morphology of both masticatory apparatus and auditory bulla.

The skull (Fig. 16) is with elongated rostral part and with the braincase compressed laterally like in taterillines. Keel of the masseteric plate is not especially elongated and rather low (see Fig. 1d), the surface of *m. masster lateralis* attachment being enlarged mainly due to significant concavity of the masseteric plate, the orbital shield being widened. Morphology of *m. temporalis* attachments is the most advanced in gerbillines: the temporal plate of the braincase is very narrow and bounded above by strongly pronounced temporal ridge. Respective complete reduction of coronoid process of the mandible is unique among the Muroidea (see Fig. 2b).

The auditory bulla is completely pneumatized and large, its tympanic and mastoid portions are equally developed, like in Gerbillini s.str. and dissimilar to that in Taterillini. The pattern of mastoid pneumatization is pretty complicated. Judging by composition and position of the septa separating principal mastoid chambers, one may suppose that the mastoid was initially pneumatized anteriorly followed by the secondary ventral pneumatization. This resulted in diagonal position of the mastoid septa, like in advanced Gerbillurina, with which ammodillines are similar also in position of small posterior mastoid cell. However, there is a small additional ventral penetration which leads to formation of as small ventral mastoid septum similar (homologous?) to that in Gerbillini (see Pavlinov et al., 1990, for details).

Dentition is also one of the most specialized among Gerbillinae. The molar crown is pretty high, laminated, with developed teniodonty (*sensu* Shevyreva, 1976) on the 1st molars, especially on the lower one (see Fig. 4d). It is to be noticed that skewness of laminae on teniodont molars of *Ammodillus* is opposite to that in *Desmodilliscus* (see below): their inner angles are displaced caudally relative to the outer ones. But this secondary asymmetry of ammodilline molars is paradoxically “neutralized” by posterior convergence of the upper tooththrows: due to this, the upper laminae take perpendicular position relative to the longitudinal chewing movements of the lower tooththrows. Anteroconid of the lower M1 is large but, unlike in most other extant gerbillines (save *Desmodillus*), does not include small protoconulid, which remains separate even in rather worn teeth (see Fig. 5c). It is very small and may be absent occasionally due to individu-

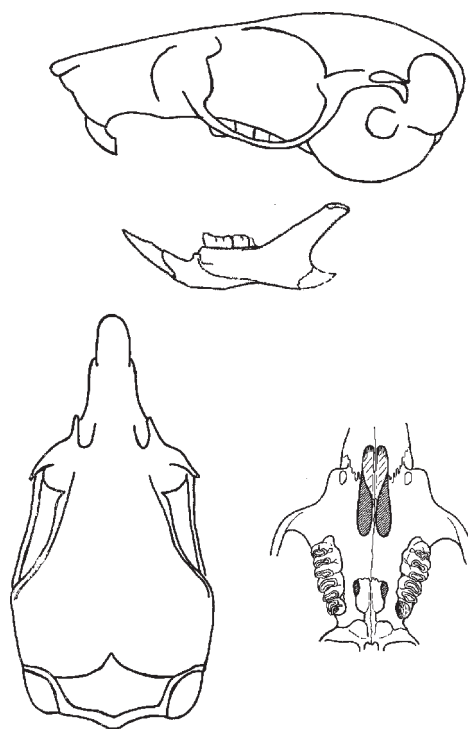


Fig. 16. Skull of *Ammodillus imbellis* (after Roche, Petter, 1968; Pavlinov et al., 1990)

Рис. 16. Череп *Ammodillus imbellis* (по Roche, Petter, 1968; Pavlinov et al., 1990)

al (or age) variation. A pretty well developed hypoconulid on the lower both M1 and M2 occurs which also distinguishes ammodillines from all other extant gerbillines.

COMMENTS. It is these additional isolated cusplets on the lower molars that indicate very ancient origin of the ammodillines. One may suppose that they branched out from the very root of the gerbilline phylogenetic tree allowing them to preserve such archaic dental murid features absent in other living members of Gerbillinae (Pavlinov, 1981a, 1982a, 1984a; Pavlinov et al., 1990). This could be taken as an argument of equating rank of ammodillines with other principal supergeneric groups of the subfamily Gerbillinae (see also McKenna, Bell, 1997). This conclusion is largely supported by H. Tong’s (1989) phylogenetic scheme (reproduced in Fig. 10c) where *Ammodillus* is placed basal to all the gerbillines.

Genus *Ammodillus* Thomas, 1904

CONTENTS. Includes the only species, *A. imbellis* Thomas, which distribution is confined to African Home (Roche, Petter, 1968; Pavlinov et al., 1990; Musser, Carleton, 2005).

TRIBE GERBILLINI S. STR.

CONTENTS. The nominative tribe, as it is treated here, contains no less than 10 Recent genera and about three quarters of species of the Recent Gerbillinae, so it is “typical” not only by its name but by its contents, as well. The genera included here are divided into four subtribes: Gerbillina s.str. (*Dipodillus*, *Gerbillus*, ?*Monodia*, *Microdillus*), monotypic *Desmodilliscina* and *Pachyuromyina*, and *Rhombomyina* (*Sekeetamys*, *Meriones*, *Brachiones*, *Psammomys*, *Rhombomys*).

MORPHOLOGICAL CHARACTERS. This tribe includes both most generalized and most advanced members of the subfamily Gerbillinae in respect to some important characters of cranial and dental morphology.

The bony elements of masticatory apparatus are not so highly specialized in most members of the tribe as compared to most taterillines and ammodillines. Keel of the masseteric plate is not much elongated; rather, in contrast to taterillines, it is its vertical expansion that enlarges surface of attachment of respective portion of the masseteric muscle in some *Rhombomyina* (see Fig. 1c). No orbital shield is especially developed.

The principal synapomorphy uniting this tribe, as it was just outlined, is a particular way of mastoid pneumatization in the auditory bulla. According to the scheme of morphological evolution discussed above (see morphological section), it is resulted from predominantly ventral penetration of tympanic cavity into the mastoid. This process begins with reduction of the parafloccular fossa due to both ventral and anterior tympanic penetrations, these pathways meeting at the middle of the mastoid to form diagonally situated mastoid septum, as it is seen in the genus *Dipodillus* (see Fig. 7e). Subsequent pneumatization, unlike the one in the advanced members of Taterillini, involves enlargement of just the tympano-mastoid chamber that moves mastoid septum to vertical position and thus fills nearly entire mastoideum. This process is usually (save *Pachyuromys*) accompanied by dorsal displacement of the tympano-mastoid septum relative to the tympano-mastoid suture (see Fig. 7f). An accessory ventral mastoid septum appears at this suture to define ventral boundary between tympanum and mastoid cavities and to delimit ventral mastoid chamber. At last, caudal expansion of the mastoid wall due to its further pneumatization leads to formation of a septal arc con-

necting posterior semicircular canal to the mastoid wall and delimiting accessory posterior mastoid cell open into the tympano-mastoid chamber. As a result, in most members of the tribe with fully developed pneumatization, the mastoid appears to be most complicated among members of the subfamily Gerbillinae; it includes tympano-mastoid and pretty large ventral mastoid chambers, and posterior mastoid cell. The only exclusion is the genus *Pachyuromys* in which neither ventral tympano-mastoid septum nor ventral mastoid chamber appear (see Fig. 7g).

Dental evolution of Gerbillini is generally ordered within the trend from primitive relatively lower-crowned bunodont type to advanced high-crowned prismatic type, the latter finally evolving into hypsodont (rootless) molars in the genus *Rhombomys* (a unique instance in Gerbillinae). No additional cusplets preserved except for small outgrowths of main cusps occurring as the cusplet rudiments in some Gerbillina s.str. with bunodont molars. Initial bunodont type (see Fig. 4a) is characterized by main cusps remaining clearly separated for pretty long time and by primary asymmetry that involves conspicuous difference in size of both the cusps (metacone is the smallest) and flexuses (paraflexus and hypoflexus on upper M1 are the widest). This primary asymmetry is inherited in semi-prismatic crown pattern (see Fig. 4f-g) that makes it different from the typical prismatic one of so called “higher gerbils”, the latter type appearing to be most simple, especially in the genus *Brachiones* (see Fig. 4h-j). A deviating variant of this general trend is secondarily asymmetric semi-lophodont molar in *Desmodilliscus* (see Fig. 4e). It is to be stressed that molar roots also got simplified along with the crown specialization, the medial root becoming much reduced.

Anteroconid of the lower M1 is of simple rhomboid type (see Fig. 5e). However, rare cases of a kind of horseshoe shape (see Fig. 5f) are revealed in some specimens of *Dipodillus* and *Gerbillus* (Petter, 1973; Pavlinov, 1984a). It could be interpreted as an atavistic morphotype indicating that the gerbilline rhomboid type evolved probably from the horseshoe one.

PRINCIPAL FOSSILS. There are several fossil genera (*Pseudomeriones*, *Epimeriones*, *Mascaromys*) that are considered as close relatives to the members of Gerbillini, specifically to the “higher gerbils” of the subtribe *Rhombomyina*. They are treated in both paleontological chapter above and in the account of the latter subtribe below.

COMMENTS. Typologically, this tribe seems to be a pretty artificial assemblage of quite heterogeneous forms. Phylogenetically, however, it is well supported by both morphological and molecular data, save few genera which position is not much clear and hence not stable. However, there are noticeable differences in opinions concerning the number and contents of the subtribes.

Two principal groups (subtribes of the present classification) are recognized by modern phylogeneticists, one with the genus *Gerbillus* and its closest allies (Gerbillina s.str.), another with the genus *Meriones* and its allies (Rhombomyina). The genus *Sekeetamys* takes uncertain position among them, here it is allocated to the tribe Rhombomyinae. The nominative subtribe is, strictly speaking, a symplesiomorphous assemblage, their significant overall similarity making it phylogenetically sound enough as a kind of “grade” of morphological evolution. The subtribe Rhombomyina is united by specialized features of dental crown and the auditory transmitting system. Two monotypic subtribes, Desmodilliscina and Pachyuromyina, are recognized on the basis of their highly derived autapomorphies (Pavlinov 1982a; Pavlinov et al., 1990).

A somewhat different phylogeny was suggested by H. Tong (1989) who included *Pachyuromys* in Rhombomyina (next to the genus *Brachiones*) and placed *Desmodillus* (here in Taterillini) at the base of the Gerbillini. The latter suggestion is caused by incorrect (from my standpoint) homology of the mastoid elements, while the former seems to be just a misunderstanding, as I see no specific synapomorphies of the genus *Pachyuromys* with rhombomyines and specifically with *Brachiones*.

Molecular data of Chevret and Dobigny (2005) agree with monophyly of both Gerbillina and Rhombomyina but give another treatment of position of the genera *Desmodilliscus* and *Pachyuromys*. These authors combine them in a separate clade that takes basal position relative to all other gerbillines. According to Chevret and Dobigny, its monophyly received strong bootstrap support (>90%), and genetic distance between these two genera (20.1 %) falls within the range of intergeneric distances revealed in other clades (8.6–21.5%). Each of these two genera is very specific morphologically with no synapomorphy (even “underlying”) known at the moment to unite them.

Another strange finding of Chevret and Dobigny is that the genus *Taterillus* (invariably placed by morphologists close in the *Tatera*–*Gerbillus*-

cus group) might be possibly a sister group to Gerbillini. This treatment was discussed above in the account of *Taterillus*.

The only recurrent comment of mine about these molecular ideas would be that they are based on just two mtDNA genes and more data are needed to discuss these serious contradictions between morphological and molecular phylogenetic hypotheses.

More comments on these suggestions are given in the accounts of respective subtribes.

Subtribe Gerbillina s.str.

CONTENTS. This subtribe includes three or four recognized genera of northern African–southern Asian pygmy gerbils: *Dipodillus*, *Gerbillus*, ?*Monodia*, *Microdillus* (Pavlinov et al., 1990; Musser, Carleton, 2005). All of them, however, are included in the same genus in most “lumping” classifications (e.g. Lay, 1983).

MORPHOLOGICAL CHARACTERS. This is one of the principal groups of the subfamily Gerbillinae displaying initial stages of evolution of most diagnostic features not only of its inclusive tribe but of the entire subfamily at all. Respectively, some of its least specialized members resemble to a certain degree some myocricetodontines, which are thought to be ancestral to the entire subfamily or at least to its nominative tribe (see paleontological account above).

The skull lacks any traces of specialization in zygo-masseteric construction (see Fig. 1a) developed by taterillines or rhombomyines. Mandible, however, is pretty advanced in its shape, with deep and wide posterior curvature separating its ascending and angular portions and with markedly diminished coronoid process (see Fig. 2a). Auditory bulla is small to medium in size, its mastoid portion is typical in the way of its pneumatization. It is partly filled with parafloccular fossa in few or fully pneumatized in most of the subtribe members, with mastoid septum being diagonal or vertical, respectively. Accessory tympanum occurs in nearly all members of the subtribe except for the subgenus *Dipodillus* (*Petteromys*).

Dental crown pattern is usually of bunodont type (see Fig. 4a), which is the most primitive condition for the subfamily. However, some of the members of the subtribe possess more evolved semi-prismatic pattern. In the first case, the cones usually remain independent from each other for a long time, consequence of their connections is not

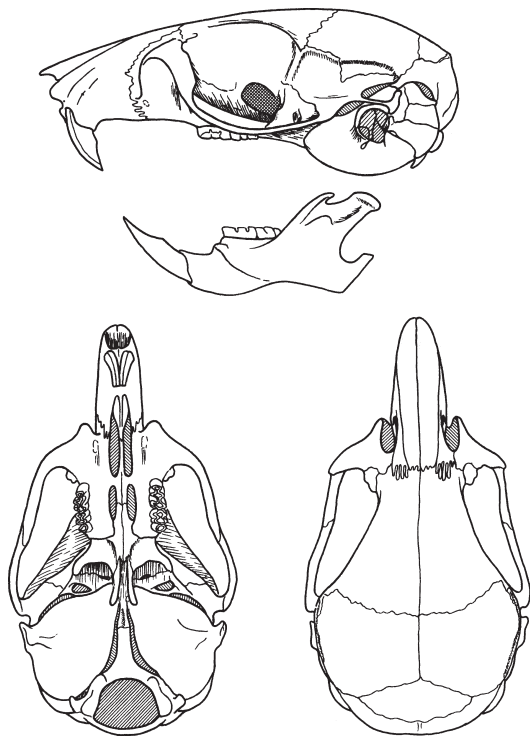


Fig. 17. Skull of *Dipodillus simonsi* (after Pavlinov et al., 1990)

Рис. 17. Череп *Dipodillus simonsi* (по Pavlinov et al., 1990)

strongly fixed, so the formation of isolated transverse laminae is not the common pattern of these “lower gerbils”. In semi-prismatic crown of *Dipodillus* s.str. (see Fig. 4f), however, the cusps appeared to be fused nearly as early as in the subtribe Rhombomyina. Primary asymmetry of dental crown is characteristic for all members of Gerbillina which becomes apparent in somewhat different sizes of both principal cusps and flexuses (see description of the tribe Gerbillini above). Secondary cusplets (such as anteroloph) may be present as small outgrowths of principal cones (e.g. in *Microdillus*).

COMMENTS. The genera included here are similar to each other and differ basically in degree and kind of specialization of dental crown which is most generalized in *Gerbillus*, *Monodia* and more advanced in *Dipodillus*, *Microdillus*. The supposed genus ?*Monodia* differs from others by the shape of mandible, while *Microdillus* is peculiar in having more evolved overall skull morphology combined with pretty complex (archaic) upper M3. All these differences seem to warrant generic separation of the taxa listed here.

However, such generic classification, at least as far as polytypic genera *Dipodillus* and *Gerbillus* are concerned, reflects mostly grades rather than clades of evolutionary relations. They are separated basically by degree of specialization of dental and bullar morphology and so are most probably paraphyletic assemblages. Therefore, comprehensive molecular phylogenetic analysis of the subtribe Gerbillina s.str is needed, as morphological characters are insufficient for recognition of monophyletic polytypic genera within it.

The southern African genus *Gerbillurus* was once considered together with *Gerbillus*, but at present this opinion is abandoned (see account of that genus above). Finally, the genus *Sekeetamys* is sometimes suggested to be a member of the subtribe under consideration by both morphological and molecular phylogeneticists (Tong, 1989; Chevret, Dobigny, 2005). It is allocated to Rhombomyina in the present study as the morphological characters in common to the genera *Gerbillus* and *Sekeetamys* seem to be of plesiomorphic nature. However, molecular phylogeny indicates that the latter genus may actually belong here as the most advanced member of this subtribe rather than being a most primitive representative of the subtribe Rhombomyina.

Genus *Dipodillus* Lataste, 1881

CONTENTS. Taxonomic boundary and species composition are unclear; in my classification (Pavlinov, 1982a; Pavlinov et al., 1990) it contains up to eight species divided into two subgenera, *Dipodillus* s.str. and *Petteromys*.

MORPHOLOGICAL CHARACTERS. This genus has skull typical for the subtribe (Fig. 17). It was originally defined as *Gerbillus*-like rodens with naked sole of the hind foot. The genus, as it is understood here, is characterized by bullar morphology most primitive for the tribe Gerbillini. The mastoid is just partially pneumatized, so the parafloccular fossa occupies its more or less significant part (see Fig. 7e). Respectively, the mastoid septum takes diagonal position thus demonstrating the very early step of mastoid evolution in the direction characteristic for the entire tribe. Accessory tympanum either absent (*Petteromys*) or present (*Dipodillus* s.str.). Contrary to the primitive bullar pattern, molar crown is of advanced semi-prismatic type (see Fig. 4f): molar cusps are slightly altering and longitudinal connections between them appear very early (see the chapter on gerbilline morphology above for details).

COMMENTS. The genus is most close to *Gerbillus* proper with which it is united by many authors. Its naked hind foot was given earlier as exclusive diagnostic feature for the genus (or subgenus) according to which the species of *Hendecapleura* (now in *Gerbillus*) were also included in *Dipodillus* (e.g. Osborn, Helmy, 1980). F. Petter (1959, 1971; also Cockrum et al., 1976) defined it as a genus of pygmy gerbils with semi-prismatic molar crown, and bullar morphology was subsequently added to its diagnosis (Pavlinov, 1982a; Pavlinov et al., 1990). However, there are opponents of such a treatment (e.g. Lay, 1983).

The subgenera recognized, *Petteromys* Pavlinov, 1982 and *Dipodillus* s.str., differ mutually by levels of specialization of dentition and auditory bulla (Pavlinov, 1982a; Pavlinov et al., 1990). Molar crown is with just slightly altering cusps in the subgenus *Petteromys* and with fully developed semi-prismatic pattern in the *Dipodillus* s.str. The former is peculiar by absence of the *tympanum accessorium* differing it from all other members of the inclusive subtribe (Pavlinov, 1980; Pavlinov et al., 1990). It is certainly a derived condition (see the morphological chapter above), but it is not now definitely clear if it could be considered as the true synapomorphy for *Petteromys*.

Genus *Gerbillus* Desmarest, 1804

CONTENTS. This is one of the most typical and certainly the most speciose genus of the subfamily Gerbillinae. In its widest sense (Lay, 1983), it is equal to the entire subtribe Gerbillina as the latter understood here. At present, it includes no less than 20–25 species divided into two subgenera, *Hendecapleura* and *Gerbillus* s.str.

MORPHOLOGICAL CHARACTERS. Members of this genus are characterized by generalized skull and dental morphology without specific combination of especially primitive and/or advanced morphological traits. The skull (Fig. 18) has moderately developed masseteric plate, not very long diastema and posterior palatal foramina, and pretty wide ascending ramus of the mandible (unlike those in *Microdillus*). Auditory bulla is moderately inflated, with mastoid fully pneumatized (*f. parafloccularis* is reduced) and mastoid septum taking vertical position (unlike that in *Dipodillus* s.lato). *Tympanum accessorium* is always present. Molar crown is most archaic in the subfamily, typically bunodont (see Fig. 4a). The main cones remain isolated long time from each others, more or less opposite (no tendency to alteration), their trans-

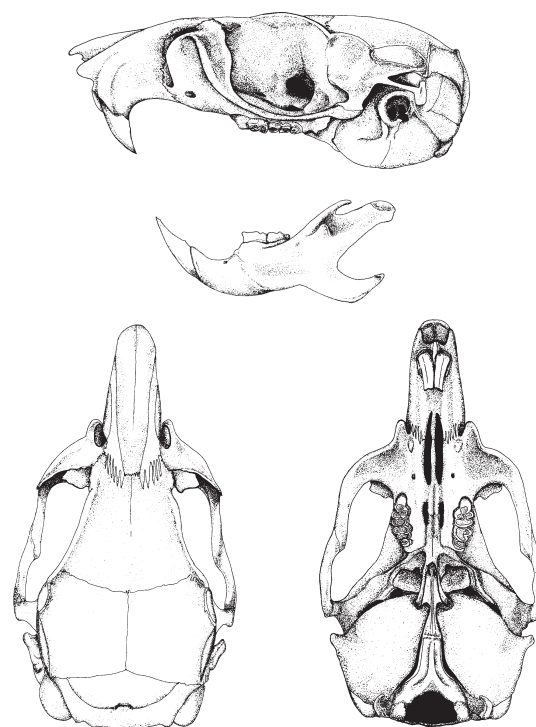


Fig. 18. Skull of *Gerbillus pyramidum* (after Osborn, Helmy, 1980)

Рис. 18. Череп *Gerbillus pyramidum* (по Osborn, Helmy, 1980)

verse junctions into laminae do not much precede formation of longitudinal connections with wear. Additional cusplets are not especially developed, and small anteroloph of the upper M2, if present, is always connected to paracone.

COMMENTS. As it was already stressed in the account of the subtribe Gerbillina, the boundaries between the genus *Gerbillus* and its closest relatives are quite fuzzy. The differences between *Petteromys*, *Hendecapleura* and *Gerbillus* s.str. reflect more grades rather than clades of evolution of this group, and the entire taxonomic situation needs a full revision based on molecular data. In some classifications (e.g. Osborn, Helmy, 1980), species of *Hendecapleura* are transferred to *Dipodillus*. One of *Gerbillus* species was also allocated here earlier (see account of these genera above).

Subgeneric classification of *Gerbillus* in the contents adopted here is also quite obscure. It is divided in two subgenera, *Hendecapleura* Latasté, 1882 and *Gerbillus* s.str. (e.g. Petter, 1971, 1975; Pavlinov et al., 1990). However, they differ only by hairiness pattern of the hind foot which is naked in the former and haired in the latter, such

a character seems evidently to be of just a minute phylogenetic significance.

Genus ?*Monodia* Heim de Balsac, 1943

CONTENTS. This is an enigmatic monotypic member of the nominative subtribe close to the *Gerbillus*.

MORPHOLOGICAL CHARACTERS. ?*Monodia* differs from *Gerbillus* by peculiar skull morphology. Ascending ramus of its mandible (see Fig. 2d) is with anterior margin standing closer to vertical but not covering M3, and with pretty large *pr. coronoides* separated by a wide curvature from *pr. articularis*. Besides, this mandible bears a large prominence (before the toothrow) to which *m. masseter laterals anterior* is attached. Its cranium is specific in having pretty narrow temporal plate of the braincase (nearly of the same size as in *Ammodillus*, see above), shortened upper diastema, and zygo-masseteric construction rather strong for such a fragile skull.

COMMENTS. The new genus and species *Monodia mauritaniae* was described very briefly by H. Heim de Balsac (1943) on the basis of the only one specimen from Mauritania. Subsequently, *G. juliani* was allocated without comment to this genus (Roche, Petter, 1968) but it was synonymized later with one of the species of *Hendecapleura* (Petter, 1975; Roche, 1975). I did not locate the original *Monodia* specimen during my visit to the Museum National d'Histoire Naturelle (Paris), and there is a suspicion that it was not preserved in the collection (F. Petter, pers. comm.). The only additional (and useful) information on this genus appeared to be available from the picture of the skull of the holotype of *Monodia mauritaniae* in the 1st edition of E.P. Walker's (1964) "Mammals of the World" (vol. 2, p. 849; omitted in subsequent editions) which seems to be typical *Gerbillus* in many respects (but see below).

However, when visiting the Mammal Division of the National Museum of Natural History in 1993, I have revealed in its collection two specimens of very small *Gerbillus*-like rodents from Mauritania which were of the same size but showed two markedly different kinds of skull morphology. One of them, no. 401520, appeared to be typical *Gerbillus* while another, no. 401002, differed from it and from other species of that genus seen by me in important traits of the skull indicated in the preceding section.

It is of interest that the specimen no. 401002 not just differs markedly by these features from

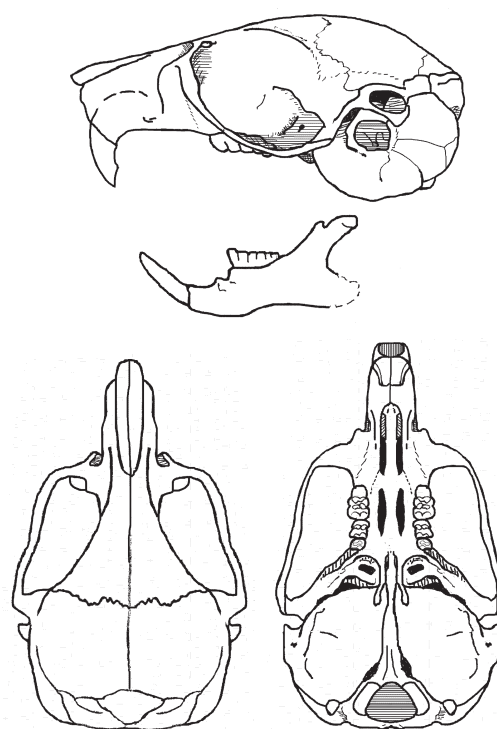


Fig. 19. Skull of *Microdillus peeli* (orig.)

Рис. 19. Череп *Microdillus peeli* (ориг.)

typical *Gerbillus* but shares certain similarity with *Desmodilliscus* in the mandible morphology. So it is quite probable that it actually represents a distinct genus (or a subgenus of unclear allocation) within the subtribe Gerbillina s.str. Unfortunately, it is impossible to identify unambiguously the skull of *Monodia* holotype pictured in Walker (1964) with the one just described. So my previous identification of this Mauritanian enigmatic taxon as *Monodia* still remains more than provisional and requests further clarification.

Genus *Microdillus* Thomas, 1910

CONTENTS. Includes the only species, *M. peeli* De Winton, from African Horne (Roche, Petter, 1968; Pavlinov et al., 1990; Musser, Carleton, 2005).

MORPHOLOGICAL CHARACTERS. Diagnostically differs from all other pygmy gerbils mainly by shortened tail (about 75% of the body length) and by some advanced cranial and dental traits (Pavlinov et al., 1990).

The skull (Fig. 19) is narrow in the interorbital constriction and in rostral part, with nasals relatively shorter than in *Gerbillus*. Keel of the masseteric plate is also shortened and more vertical than in any other Gerbillina. Upper diastema, how-

ever, is the longest for the Gerbillina which is also true for both anterior and posterior palatal foramina, the latter's length is nearly equal to that of the upper toothrow (similar to *Taterillus*). The bony bridge separating these foramina, unlike in *Gerbillus* and *Dipodillus*, is narrower than the width of either of them. Mandible is quite specialized in having rather narrow ascending branch and wide angular process. Auditory bulla is one of the largest among members of the subtribe Gerbillina, its mastoid part is fully pneumatized.

The molar crown is higher and more flattened than in *Gerbillus*. Upper M2 bears well developed anteroloph which is larger than in other Gerbillina and is connected to protocone, unlike that of *Gerbillus*. Upper M3 is complicated, usually with four cusplets forming two transverse laminae with wearing (probably an archaic condition).

COMMENTS. Close to *Gerbillus* s.lato and sometimes included in it when the latter is treated in the widest sense (Lay, 1983). However, its specialized features indicate that *Microdillus* evolved in somewhat different direction as compared to the typical *Gerbillus*. At least morphologically, the difference between the latter and *Microdillus* looks of the same scale as between *Gerbilliscus* and *Taterillus* thus supporting generic rank of the taxon under consideration. Advanced dentition of *Microdillus* made H. Tong (1989) supposing its sister-group relation to *Sekeetamys* here placed in Rhombomyina. However, they differ from each other by some important characters of the auditory transmitting system: in *Microdillus* it is the same as in *Gerbillus*, while *Sekeetamys* is similar in this respect to other rhombomyines (see account of the latter below).

Subtribe *Desmodilliscina* Pavlinov, 1982

CONTENTS. Very specialized, actually even unique in some respects monotypic genus *Desmodilliscus* belongs here.

MORPHOLOGICAL CHARACTERS. The desmodilliscine cranium is very peculiar in its shape (Fig. 20). The rostral part is short and widened, as is the anterior part of interorbital region, so the interorbital constriction is displaced caudally as compared to the other gerbillines. Posterior palatal foramina are the largest in the subfamily and protrude slightly forward in front of the upper toothrows. Auditory bulla is fully pneumatized and very large, with tympanic septum taking vertical

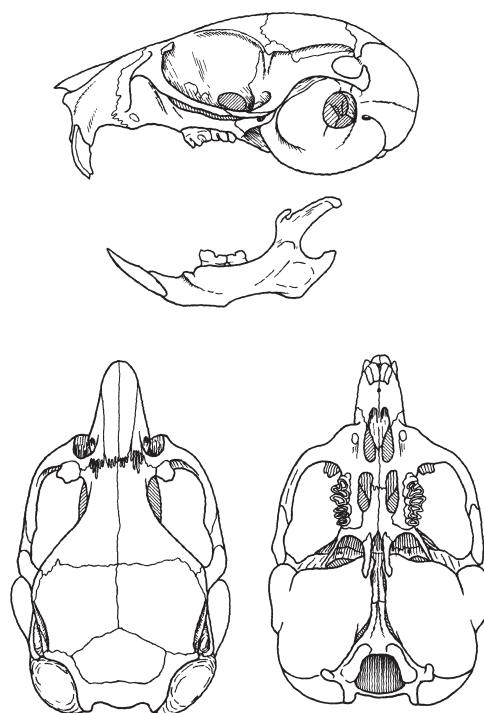


Fig. 20. Skull of *Desmodilliscus broweri* (after Pavlinov et al., 1990)

Рис. 20. Череп *Desmodilliscus broweri* (по Pavlinov et al., 1990)

position and tympanic-mastoid septum moved upward as in Rhombomyina and in advanced Gerbillina s.str. Posterior mastoid cell is distinct and opens into the mastoid cavity.

The masticatory apparatus is very specific. On the one hand, zygo-masseteric structure is among the least specialized in the subfamily Gerbillinae, with zygomatic arc going pretty high and masseteric plate being small and just slightly sloping (see Fig. 1a). On the other hand, the mandible is highly specialized, with sharp disproportion of ascending and angular parts (see Fig. 2c). The former is thin, with reduced *pr. coronoides*, the latter is very wide and significantly deflected from vertical position.

Dentition is unique in disappearing of the lower M3 while its upper homologue is typical in size and crown pattern. Such a combination does not allow to agree with F. Petter (1959) who explained such a reduction by forward expansion of the auditory bulla. Both upper and lower M1 are characterized by teniodonty (see Fig. 4e), with the laminae oriented in the direction opposite to that in the genus *Ammodillus* (see above). The lower M1 is characterized by a kind of "tripetalous" struc-

ture formed by elongated anteroconid and first lamina merged by a longitudinal bridgelet.

Specific morphology of desmodilliscine mandible and lower dentition might be causally related to the development of rather large cheek-pouches which are uniquely present in the group under consideration. They are similar to those known for Palaearctic cricetines (subfamily Cricetinae) in being outgrowths of the inner muscular walls of the oral cavity and do not go backward as far as level of the pinnae (Pavlinov et al., 1990).

In contrast to the above characters of high specialization, the desmodilliscines retain one feature very archaic for gerbillines. This are preputial glands so far revealed in these gerbils only (Pavlinov, 1986; Pavlinov et al., 1990).

COMMENTS. The genus *Desmodilliscus*, a sole member of the subtribe in question, was sometimes kept close to the southern African genus *Desmodillus* in some of the previous studies (Petter, 1959, 1975). However, bullar morphology clearly separates them indicating that *Desmodilliscus* belongs to Gerbillini s.str. whereas *Desmodillus* is a member of the tribe Taterillini (see account of the latter above).

Presence of preputial glands is usually considered as plesiomorphic trait for the muroid rodents (Carleton, 1980). This indicates desmodilliscines belonging to the basal radiation of the nominative tribe. The latter conclusion is supported not only by morphological but also by biochemical data (Benazzou, 1984; cited after Chevret, Dobigny, 2005).

Generally speaking, the results of DNA analysis (Chevret, Dobigny, 2005) agree with isolated position of desmodilliscines relative to other Gerbillini s.str., but treat that some particular way. DNA/DNA hybridization of Chevret (1994; cited after Chevret, Dobigny, 2005) placed them at basal level of the tree for the entire Gerbillinae. DNA sequencing study (Chevret, Dobigny, 2005) is also in favour of exclusion of desmodilliscines from the nominative tribe. Moreover, they indicate possible sister-group relation between *Desmodilliscus* and *Pachyuromys* which are included into one clade taking most basal position on the subfamily tree.

Unfortunately, there are no morphological feature known to me that might be considered as a unique synapomorphy for these two genera. Therefore I do not think that limited data on genetic similarity might overbalance taxonomic decision derived from a lot of morphological traits.

Genus *Desmodilliscus* Wettstein, 1916

CONTENTS. The species *D. broweri* Wettstein from African Sahel belt is the only known representative of this genus.

COMMENTS. Supposed relationships of *Desmodilliscus* to the genera *Desmodillus* and *Pachyuromys* are considered in the account of the subtribe Desmodilliscina.

Subtribe *Pachyuromyina* Pavlinov, 1982

CONTENTS. This is another monotypic subtribe within the nominative tribe Gerbillini including only the nominotypical genus, *Pachyuromys*.

MORPHOLOGICAL CHARACTERS. Pachyuromyines are probably among most morphologically specialized desert dwellers among gerbillines. These small rodents possess shortened ears and limbs, as well as the tail which is able to accumulate subcutaneous fat. The skull shape (Fig. 21) is mostly outlined by completely pneumatized auditory bulla, which is the largest in the subfamily, with just one mastoid cavity of unique inner structure. Molars are of advanced bunodont type with rather symmetrically situated cusps and with no additional cusplets.

According to homology of the bullar bony elements and chambers elaborated by the author (Pavlinov, 1988, 2001; Pavlinov et al., 1990), pachyuromyine mastoid contains only tympanomastoid chamber resulted from ventral penetration of the tympanic one through the arc of the lateral semicircular canal into the mastoid to fill it entirely (see Fig. 7g). Thus the vertical bony wall isolating mastoid and tympanic cavities anterior of the former is homologous with the mastoid septum of Rhombomyina, Desmodilliscina and advanced Gerbillina. Another septum demarcating the mastoid cavity ventrally is similar to and most probably homologous with the tympanomastoid septum of other members of Gerbillini differing in one but important respect. It is connected with lateral wall of the bulla along the tympanomastoid suture, and not dorsad to it, so neither ventral mastoid septum nor the chamber of the same name are formed in the pachyuromyine bulla. Posterior mastoid cell opens into the mastoid cavity, which is typical for all Gerbillini.

It is of interest to call attention to transformation of pachyuromyine mandible similar to certain degree to that characteristic for the most advanced grass-eating gerbillines (*Rhombomys*) and

arvicolines (*Microtus*). Its horizontal portion is shortened and bears well pointed lower angle, while the ascending portion is widened and with quite steep anterior edge. As pachyuromyines are generalized seed eaters with noticeable addition of invertebrates in the diet (Walker, 1964; Pavlinov et al., 1990), such a morphology cannot be attributed to the feeding adaptations. Another explanation might be that the caudal part of the mandible is “forced out” in forward (oral) direction due to hypertrophied auditory bulla (Pavlinov et al., 1990). However, this does not explain why the ascending ramus remains very wide whereas it becomes narrower under such condition in other gerbillines with enlarged auditory bulla.

COMMENTS. In one of the first phylogenetic schemes elaborated for Gerbillinae (Petter, 1959), the genus *Pachyuromys* was placed together with *Ammodillus* and with several other gerbillines with not advanced dentition at the base of this phylogenetic scheme (see Fig. 10a). This treatment is unwarranted by the nowadays knowledge of diversity of gerbilline morphology.

D. Lay (1972) supposed closeness of *Pachyuromys* to *Desmodillus* based on superficial similarity of their mastoid containing only one cavity in these two genera. Lay’s conclusion is not true for *Desmodillus* (see account of the subtribe Gerbillurina above) and presumes incorrect homology of mastoid elements (see details in the respective section on bullar evolution above). The homology adopted here indicates that these two genera, just like in case of the pair *Desmodillus* and *Desmodilliscus* (see above), belong to different tribes, as their mastoid pneumatization was initiated by different tympanic penetration pathways.

The type of mastoid pneumatization places the genus *Pachyuromys* among Gerbillini s.str., though with certain reservation. Its advanced mastoid morphology is clearly autapomorphic indicating its belonging to the basal radiation of that tribe (see Fig. 10b) and warranting subtribal status of Pachyuromyina.

H. Tong (1989) placed *Pachyuromys* in Rhombomyina making it a sister group of *Brachiones* (see Fig. 10c). This hypothesis is based on similarities in both bullar and dental crown morphology which, to me, are also more than superficial. As it is evident from transformation scheme developed for the mastoid on the basis of homology adopted here, pachyuromyines and rhombomyines differ in position of the tympano-mastoid septum. This scheme makes the former a sister group to

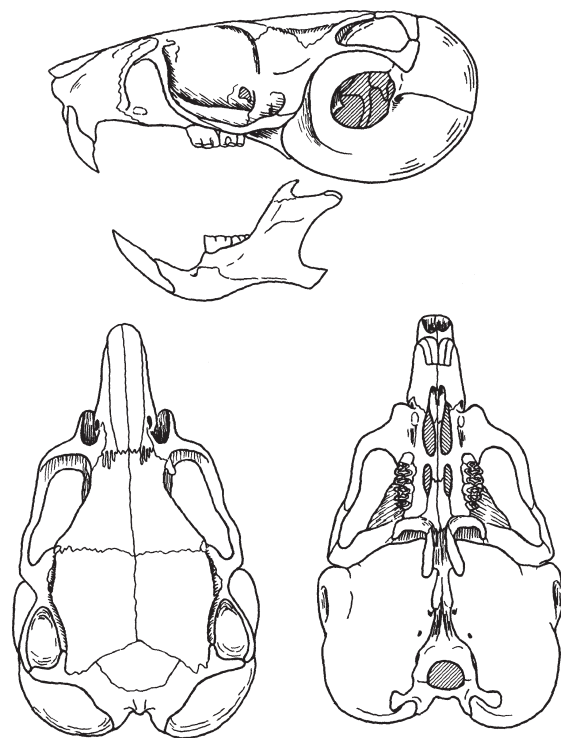


Fig. 21. Skull of *Pachyuromys duprasi* (after Pavlinov et al., 1990)

Рис. 21. Череп *Pachyuromys duprasi* (по Pavlinov et al., 1990)

the rhombomyine clade rather than places it within the latter. Contrary to this, Tong’s tree presumes transformation of the rhombomyine-like position of tympano-mastoid septum into the pachyuromyine-like which seems to be evidently less parsimonious hypothesis. As to the dental morphology, pachyuromyine pattern is clearly identifiable as an advanced bunodont type, while rhombomyine pattern is defined here as the prismatic one (see account of that subtribe below). So, again *Pachyuromys* can not be placed within rhombomyines by this feature, especially taking into consideration that dental morphology of *Brachiones* is one of the most specialized among Rhombomyina having nothing in common with *Pachyuromys*.

Molecular phylogenetic data (Chevret, Dobigny, 2005) join *Pachyuromys* to *Desmodilliscus* and place their clade at basal level of the subfamily tree. As I explained above (see accounts of the tribe Gerbillini and the subtribe Desmodilliscina above), this treatment contradicts morphological data and needs further clarification.

Genus *Pachyuromys* Lataste, 1880

CONTENTS. The species *P. duprasi* Lataste from

deserts of northern Africa is the only representative of this genus.

Subtribe Rhombomyina Heptner, 1933

CONTENTS. This clade includes four extant genera: *Meriones*, *Brachiones*, *Psammomys*, and *Rhombomys*. The term “higher gerbils” was coined by creators of gradistic classifications to reflect their advanced molar morphology (Heptner, 1933; Gromov et al., 1963). Besides, the genus *Sekeetamys* is also tentatively placed here.

MORPHOLOGICAL CHARACTERS. In rhombomyines, the initial bunodont tooth crown pattern is transformed into the prismatic type (see Fig. 4g-j). The crown is high, no separate cones could be identified even on the least worn molars, and laminae become connected by longitudinal bridgelets at a very early wear stage (Pavlinov, 1979a). There are only two major roots well developed in both M1 and M2, anterior and posterior ones, while the median roots are rudimentary. These features are least developed in *Sekeetamys* and most evolved in *Rhombomys* in which molars are mostly rootless. The general trend of molar “prismatization” leads to appearance of the cementum layers in the inner angles of molars in the genus *Rhombomys*, which is unique for the Gerbillinae.

Such an evolution of rhombomyine dentition parallel to that in the arvicolines triggered similar transformations in skull morphology. Within the rhombomyines, there is a strong trend of both the cranium and mandible to become higher, with shortened rostral part and more powerful zygomatic construction (Pavlinov, 2000). All of these features are most pronounced in the genus *Rhombomys*.

By bullar morphology, rhombomyines are typical members of the tribe Gerbillini. All of them possess fully pneumatized mastoid with the mastoid septum taking vertical position and isolating mastoid cavity anteriorly from the tympanic one (see Fig. f). There is also well developed tympano-mastoid septum perforated through the arc of lateral semicircular canal and displaced dorsally from the tympano-mastoid suture. Ventral mastoid septum is well developed and is connected to the bullar wall along tympano-mastoid suture thus delimiting pretty voluminous ventral mastoid chamber. Posterior mastoid cell also occurs.

Middle ear transmitting system in rhombomyines is to be mentioned separately (see morpho-

logical chapter above; see Fig. 8). The *malleus* is usually of massive type and *tympanum accessorium* is typically absent. Following the formal “rule of commonality” (Wiley, 1981), such a morphology is supposed to be a synapomorphy for the subtribe Rhombomyina relative to the condition observed in the subtribe Gerbillina s.str. However, *malleus* is lightly built and *tympanum accessorium* is present in some of the species of the genus *Meriones* having most enlarged auditory bulla. The latter surely indicates that such a combination corresponds to the derived condition in the subtribe under consideration.

PRINCIPAL FOSSILS. Besides five Recent genera listed above, the fossil genus *Mascaromys* Tong known by isolated teeth from the Plio–Pleistocene of northern Africa may belong here (Tong, 1989). By its characters, it is pretty archaic representative of the clade under consideration, which dentition is, however, more advanced than observed in the genus *Sekeetamys*. One more genus to be mentioned is *Pliorhombomys* from the early Pleistocene of Turkmenia (Fokanov, 1976) which is most close to the extant *Rhombomys* and could be included in it. At last, *Parameriones* Tchernov et Chetboun (not Heptner) was described from the Pleistocene of Levant as close to *Meriones* (Tchernov, Chetboun, 1984); it is included here in *Psammomys*.

Two other extinct genera, *Pseudomeriones* and *Epimeriones*, both with prismatic molars similar to those in living rhombomyines, are usually associated with this group (Daxner-Hock, 1972; Kowalski, 1974; Agusti, Casanovas-Vilar, 2003; etc.). But this similarity is superficial and more exhaustive analysis reveals very important differences putting these genera apart from morphological and phylogenetic limits of the subtribe. In particular, the genera just listed possessed pretty heavy medial roots on the upper M1 and M2 and two-rooted M3 in contrast to all extant Gerbillinae with reduced medial roots and one-rooted M3 (see also account of the gerbilline paleontology above for details; see Fig. 9e-f).

COMMENTS. In gradistic classifications, rhombomyines were sometimes divided into two groups, one for the genera with rooted molars and another for the genus *Rhombomys* (Heptner, 1933; Gromov, Baranova, 1981). It could be mentioned that I. Gromov (in Gromov et al., 1963) supposed genera *Meriones* and *Rhombomys* having originated from Cricetinae and Cricetodontinae, respectively; as no arguments were provided, this idea could be mentioned as just a curiosity.

At present, monophyly of all four genera of the “higher gerbils” is shown to be supported by both morphological and molecular data (Pavlinov, 1982a; Pavlinov et al., 1990; Chevret, Dobigny, 2005). There is a doubt only about *Sekeetamys* which is placed at basal radiation of the subtribe Rhombomyina but considered by many authors as a member of the subtribe Gerbillina s.str.; arguments pro and contra various treatments see in the account of that genus below. Besides, the genus *Pachyuromys* was included occasionally here by Tong (1989) but this concept seems to have no sound foundation (see above).

Unlike the above mentioned gradistic classifications, suggested cladogenetic relationships split the group of “higher gerbils” into two subgroups (presumably clades), one with genera *Meriones* and *Brachiones*, another with genera *Psammomys* and *Rhombomys* (Pavlinov et al., 1990). The characters discriminating them are the following: lacrimal bone is wide in the first group and narrow in the second; tympanic bulla is either inflated or rather flat beneath, respectively; upper toothrow is most wide at the level of first lamina of M2 or at first–second lamina of M1, respectively; enamel layer is thin and not differentiated in the genera *Meriones* and *Brachiones* whereas it is especially thick in the inner angles of M1 and M2 in the genera *Psammomys* and *Rhombomys*.

As to the inclusion of the genus *Sekeetamys* in this subtribe, it is based mainly on dental and bullar morphology, including construction of its auditory transmitting system (see account of this genus below).

Members of this subtribe are basically southern and central Asian in their distribution; northern African taxa are only specifically or subspecifically distinct from the Asian congeners. So the entire group seems to be most probably of southern Asian origin.

NOMENCLATURE. The valid name for this subtribe requires commenting (Pavlinov, Rossolimo, 1987). There are two family-group names based on the names of genera belonging here: one of them is derived from *Meriones*, the other from *Rhombomys*. Both were first introduced by J. Brandt (1844) and later, as new ones, by W. Heptner (1933). I used Heptner’s name Rhombomyinae elsewhere (Pavlinov, Rossolimo, 1987; Pavlinov et al., 1990; Pavlinov, 2003; also applied here) while Brandt’s name Merionina was used in McKenna and Bell (1997). Below follows an explanation of the position adopted by me.

The name Merionina Brandt, 1844 is based on the generic name *Meriones* Cuvier, 1823 not Illiger, 1811. The type of *Meriones* Cuvier is *Dipus labradorius* Kerr, 1792 (Palmer, 1904), now a junior synonym of *Zapus hudsonius*, the latter denoting the species belonging to North American dipodoid subfamily Zapodinae (Holden, Musser, 2005). Cuvier’s *Meriones* is available (Article 10.6 of the International Code . . . , 1999), and it is this treatment that was adopted by J. Brandt in his memoir on jerboas (Brandt, 1844). This conclusion follows unambiguously from Brandt’s listing his Merionina among family-group names of “Dipoda s. Macropoda Wagn.” and indicating distribution of “*Meriones* Fr. Cuv. (*Jaculus* Wagler)” as “America borealis” (Brandt, 1844: 71). It is evident that Brandt’s name Merionina is available but has nothing in common with gerbillines. Subsequently J. Brandt acknowledged priority of Illiger’s name over Cuvier’s in his review of gerbillines (Brandt, 1854, 1855), but without mentioning and altering original meaning of his Merionina. So, my conclusion is that the name Merionina Brandt cannot be used as the valid family-group name in any sense other than implied by *Meriones* Cuvier, and its listing in synonymy of Gerbillinae (Palmer, 1904) or its use as the valid tribal name in this subfamily (McKenna, Bell, 1997) is incorrect. However, original typification and availability of Merionina Brandt prevents use of either Merionidinae Schmidlein, 1893 (nom. nudum?) or Merioninae Heptner, 1933, as the valid family-group name because of their being junior homonyms of the available Merionina Brandt (Article 38 of the Code).

As to the Brandt’s *Rhombomys*-derived name, it appeared as “Gerbilli seu Rhombomyies” in Brandt (1855: 161) so it has a formal priority over Merionina by page. It was most probably based on *Rhombomys* Wagner by both tautonymy and context, as no other such name is known to exist in mammalian genus-group names synonymy. However, this name did not appear again in Brandt’s publications; in particular, the suprageneric group of “higher gerbillines” entered on the subsequent pages of the book just cited as “Mures merioniformes seu Arvicolini” (Brandt, 1855: 163, 305). Therefore, both spelling and context of this Brandt’s name “Rhombomyies” indicate it is just a not fully latinized name proposed as a synonym for “Gerbilli”, so it is unavailable and cannot be used as a valid family-group name (Articles 11.5 and 11.7 of the Code). It follows from nonavail-

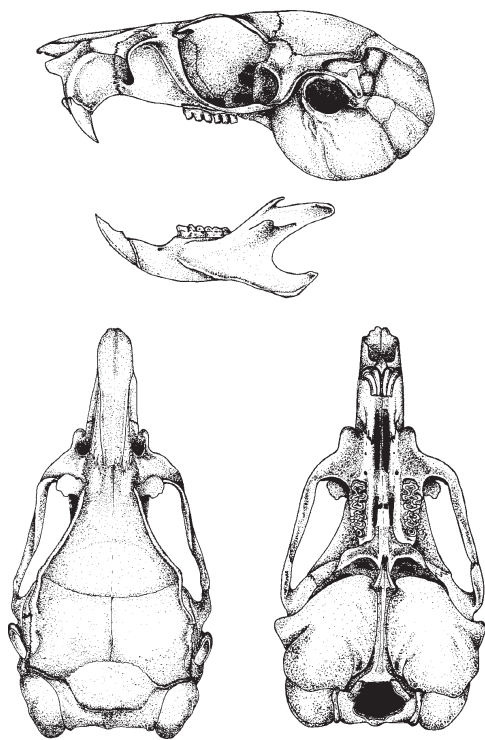


Fig. 22. Skull of *Sekeetamys calurus* (after Osborn, Helmy, 1980)

Рис. 22. Череп *Sekeetamys calurus* (по Osborn, Helmy, 1980)

ability of Rhombomyies Brandt that it does not enter in homonymy (Article 54.1 of the Code), so Rhombomyinae Heptner, 1933 should be used as the valid name for the least inclusive family-group taxon including *Rhombomys* Wagner.

Genus *Sekeetamys* Ellerman, 1947

CONTENTS. Includes one species, *S. calurus* Thomas, from the Near East.

MORPHOLOGICAL CHARACTERS. The skull is pretty lightly built, with enlarged bulla (Fig. 22). The molars are less prismatic than in *Meriones* but evidently more advanced than in any Gerbillina s.str. They bear clear characters of primary asymmetry of wearing facets, due to which dentin field on the upper M1 is S-shaped (see Fig. 4g).

Construction of the middle ear transmitting system in *Sekeetamys* is the same as in most other member of the subtribe Rhombomyina and differs from that observed in Gerbillina s.str. That is, *malleus* is of massive type and *tympanum acessorium* is absent.

COMMENTS. The genus takes intermediate position between advanced representatives of Gerbillina s.str. and generalized Rhombomyina in

many morphological characters. This is reflected in its “fluctuation” among these two clades in different classifications: some authors place it close to *Gerbillus* and its allies (Chevret, Dobigny, 2005), in particular to *Microdillus* (Tong, 1989), others place it with *Meriones*, up to including it in the latter genus (Ellerman, 1941, 1947, 1948; Charworth-Musters, Ellerman, 1947).

Morphological feature responsible for such an uncertainty is dental crown pattern found in *Sekeetamys*. It makes it equiprobable to consider the latter genus as either the most advanced member of Gerbillina s.str. or the most primitive member of Rhombomyina.

Middle ear morphology serves to me as a key indication of belonging of *Sekeetamys* to Rhombomyina. Of course, this synapomorphy taken alone is a rather weak support of hypothesis of a sister-group relations of *Sekeetamys* to other rhombomyines. But combined with semi-prismatic molar crown and larger size (extrinsic to the members of Gerbillina s.str.), it might witness for the phylogenetic scheme adopted here in which *Sekeetamys* is placed at the base of the phylogenetic tree for the subtribe Rhombomyina.

Controversy between morphological and molecular data is such that I would evaluate the entire situation with this genus as quite uncertain and requiring further investigations.

Genus *Meriones* Illiger, 1811

CONTENTS. This is one of the most typical members of the subfamily Gerbillinae, along with *Gerbillus* and *Gerbilliscus*. Belonging here are about 16 species from southern Asia and northern Africa. Four subgenera are usually recognized in this genus: *Meriones* s.str., *Parameriones*, *Pallasiomyis*, and *Cheliones*.

MORPHOLOGICAL CHARACTERS. Characters defining *Meriones* within Rhombomyina are as following. Interorbital constriction and brain case are not widened (Fig. 23), unlike in *Brachiones*. Lacrimal bone is nearly equal in length and width, upper incisors with one groove each, unlike in *Psammomys* and *Rhombomys*. Molar always with well developed roots, unlike in *Rhombomys*, with narrow longitudinal bridgelets connecting laminae, unlike in *Brachiones*, and these bridgelets are situated axially on upper M1, unlike in *Sekeetamys*.

COMMENTS. The genus *Meriones*, by its level of overall specialization, takes intermediate position between *Sekeetamys* and *Psammomys*. Its mono-

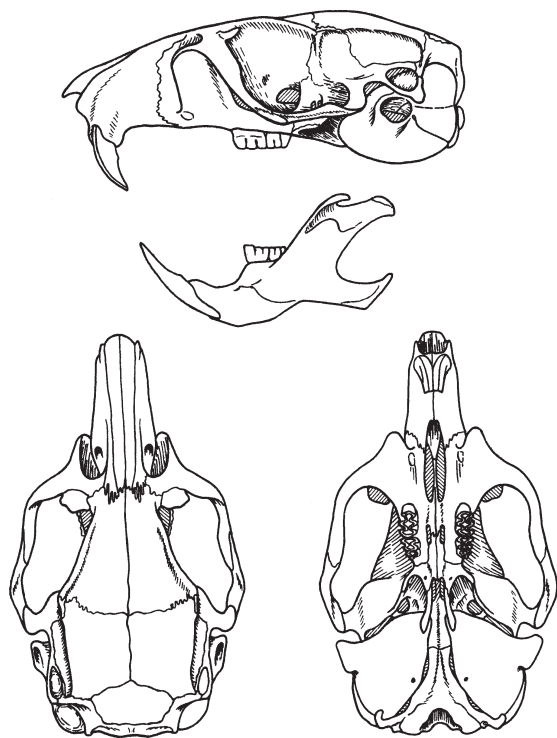


Fig. 23. Skull of *Meriones vinogradovi* (after Pavlinov et al., 1990)

Рис. 23. Череп *Meriones vinogradovi* (по Павлинов et al., 1990)

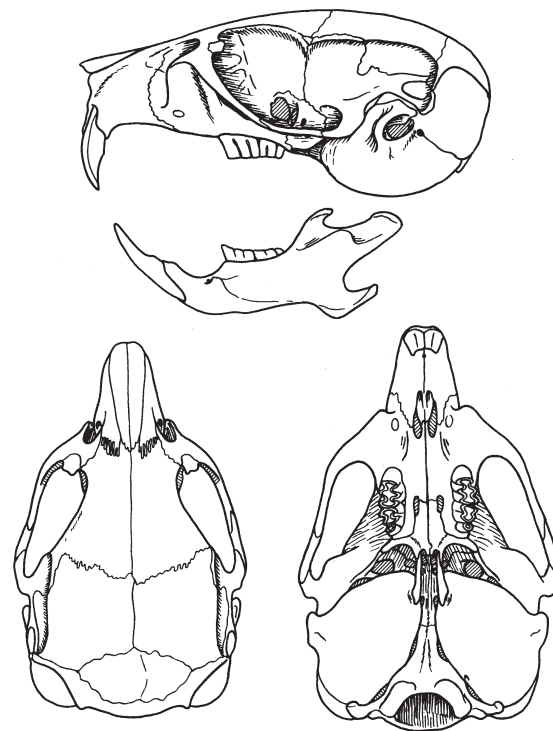


Fig. 24. Skull of *Brachiones przewalskii* (after Pavlinov et al., 1990)

Рис. 24. Череп *Brachiones przewalskii* (по Павлинов et al., 1990)

phyly and generic status was never seriously considered as disputable, though it was suggested that *Brachiones* might belong here (Sokolov, Orlov, 1980), and *Sekeetamys* was occasionally included in it (see the latter genus above).

Four subgenera are usually recognized in this genus: *Meriones* s.str., *Parameriones*, *Pallasiomys*, and *Cheliones*.

The nominative subgenus, in traditional classifications, includes nearly all species with not hypertrophied auditory bulla and with haired hindfoot. But cladistically its contents is to be restricted to its nominotypical species, *M. tamariscinus* Pallas, a position based on its very specific male genital morphology (Pavlinov, 1982a, 1986; Pavlinov et al., 1990).

The subgenus *Cheliones* Thomas, 1919 is one more monotypic subgenus which species, *M. hurrianae* Jerdon, evolved some characters in common with *Rhombomys* most probably due to similar ecology.

The subgenus *Parameriones* Heptner, 1937 seems to be well defined, as far as its nominotypical species, *M. persicus* Blanford, is concerned; but sometimes it is included in *Meriones* s.str.

(Gromov et al., 1963; Petter, 1975). Its diagnostic character defined originally is the naked hindfoot. It is shared by *M. persicus* with *M. rex* Yerbury et Thomas, which therefore is also included traditionally in this subgenus (Charworth-Musters, Ellerman, 1947; Harrison, 1972). But belonging of the latter species to *Parameriones* is not well found cladistically (Pavlinov et al., 1990).

The subgenus *Pallasiomys* Heptner, 1933 is rather heterogeneous morphologically and deserves a revision. According to my classification (Pavlinov et al., 1990), it includes all the species not allocated to the above mentioned subgenera, their uniting synapomorphy being specific genital morphology (Pavlinov, 1986). However, they differ significantly by morphology of transmitting system and by bullar size. In particular, the *tympanum* is simple in some species and complicated in others, the latter possessing lightly built *malleus*. The species with smaller bulla are included usually in the nominative subgenus (Gromov et al., 1963; Petter, 1971; Gromov, Baranova, 1981).

Genus *Brachiones* Thomas, 1925

CONTENTS. A monotypic genus which species,

B. przewalskii Buchner, is known from the Central Asia only.

MORPHOLOGICAL CHARACTERS. It is one of the most advanced members of Rhombomyina, though not of the type observed in the genus *Rhombomys*. Its skull (Fig. 24) is very peculiar in widened both interorbital constriction and braincase. It could also be distinguished from *Meriones* by very short both anterior and posterior palatal foramina and by just slightly developed auditory tube in spite of very large tympanic bulla.

Interlaminar junctions on M1 and M2 are very wide which could be noticed even at moderate stages of the tooth wear. Of special interest is significant reduction of anteroconid on the lower M1 (see Fig. 4j, Fig. 6); this character is unique for gerbillines among which a general tendency of widening anterocone predominates to make it of the same shape as the main laminae. The genus *Brachiones* deviates from this tendency and demonstrates initial stage of the secondary reduction of the laminated molar crown pattern.

COMMENTS. The genus *Brachiones* is well defined by several cranial and dental autapomorphies. It is most probably a deviating relative of the genus *Meriones* with which it forms a monophyletic group within Rhombomyina. There was a suggestion that *B. przewalskii* might be conspecific with *M. meridianus* (Sokolov, Orlov, 1980), but I see no serious grounds for such a view. H. Tong (1989) makes *Brachiones* close to *Pachyuromys*, but foundations of this hypothesis seem to be more than weak (see account of the latter genus above).

Genus *Psammomys* Cretzschmar, 1828

CONTENTS. The genus includes two species from northern Africa and south-east Asia. They are sometimes considered as conspecific, so *P. obessus* Cretzschmar might be its sole extant member; see Musser, Carleton (2005) for review of opinions.

MORPHOLOGICAL CHARACTERS. Morphologically, the genus in question seems to take an intermediate position between *Meriones* and *Rhombomys*. Its skull (Fig. 25) is with rather flat and wide braincase. Its molars are typically prismatic and always rooted, with no cementum. It could be identified by weakly developed or absent longitudinal groove on front surface of the upper incisor.

COMMENTS. W. Heptner (1933) placed *Psammomys* into his Merioninae, as his classification reflected grades defined by evolution of tooth crown height (see review of gerbilline classifi-

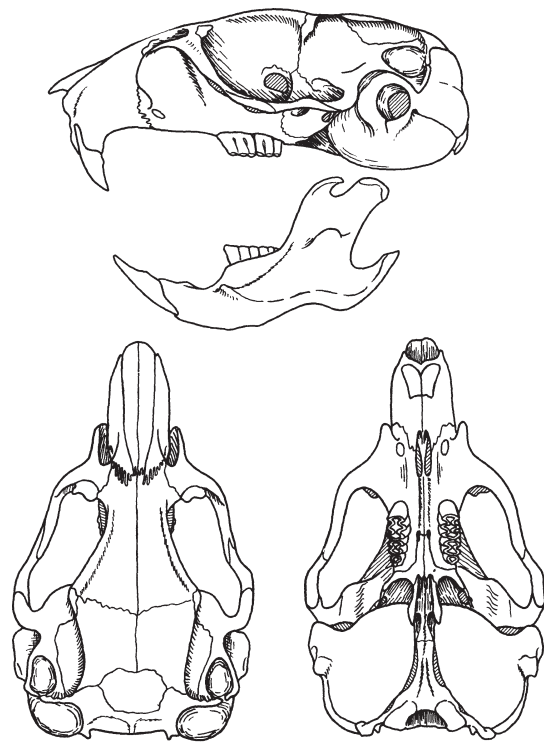


Fig. 25. Skull of *Psammomys obessus* (after Pavlinov et al., 1990)

Рис. 25. Череп *Psammomys obessus* (по Pavlinov et al., 1990)

cations above). F. Petter (1959) also placed it close to *Meriones* rather than to *Rhombomys*. In the molecular phylogenetic tree of Chevret and Dobigny (2005), *Psammomys* takes basal position in the group of “higher gerbils”. According to Pavlinov et al. (1990), there are some diagnostic cranio-dental characters not presumably bounded by specific adaptations that connect the genus in question not with *Meriones* but with *Rhombomys*. The characters in question are those that divide rhombomyines into two groups, *Meriones–Brachiones* and *Psammomys–Rhombomys*, they are listed in the account of the subtribe Rhombomyina above.

An extinct species *obeidiensis* Haas, 1966 from the Pleistocene of Near East, once allocated to *Meriones* and later separated by Tchernov and Chetboun (1984) into their genus *Parameriones* (not Heptner, 1937), was subsequently identified as a possible member of *Psammomys* by Pavlinov et al. (1990).

Genus *Rhombomys* Wagner, 1841

CONTENTS. Includes one extant Asian species, *R. opimus* Wagner.

MORPHOLOGICAL CHARACTERS. This is one of the most evolved gerbilline genera showing specialized characters of dentition not known in other members of the subfamily. These are rootless molars with cementum layers occurring in most advanced members of the genus and reflecting herbivorous specialization of this rodent. The latter explains also a specific structure of the skull of *Rhombomys* (Fig. 26). It bears noticeable feature in common with voles possessing rootless molars. Actually, the skull of *Rhombomys* resembles by its shape that of arvicolines in having powerfully developed zygo-masseteric structure with wide and high (but not especially long) keel of masseteric plate, shortened rostral part, shortened mandible with high horizontal portion, and very wide upper incisors. Each of the latter bears two slight longitudinal grooves on its front surface which is a diagnostic feature of the genus *Rhombomys*.

Molars in *Rhombomys* are with very high crown, rootless and constantly growing in most of its living populations. However, few senile specimens from Iran were revealed in the collections of the Zoological Institute (St. Petersburg) and the National Museum of Natural History (Washington, D.C.) in which roots are closed and conspicuously identifiable (Pavlinov, 1982b, 1996; Pavlinov et al., 1990; see also Fig. 9h). Besides, they differ from typical "rootless" races by having not so thick cementum layers.

PRINCIPAL FOSSILS. Genus *Pliorhombomys* with rooted high-crowned molars and no cementum was described from the Earlier Pleistocene of southern Turkmenia (Fokanov, 1976). It is certainly a phylogenetic predecessor of the Recent *Rhombomys* differing from it by less advanced dentition. Extant members of the latter genus with rooted molars take intermediate position between *Pliorhombomys* and typical rootless *Rhombomys* (see Fig. 9g-h). This fact reflects very rapid evolution in the lineage of *Pliorhombomys*–*Rhombomys* toward rootless condition due to herbivorous specialization. Because of this, they were suggested to be considered as congeners (Pavlinov, 1982b; Pavlinov et al., 1990).

COMMENTS. In gradistic classification paying most attention to tooth morphology, the genus *Rhombomys* takes quite isolated position as a sole

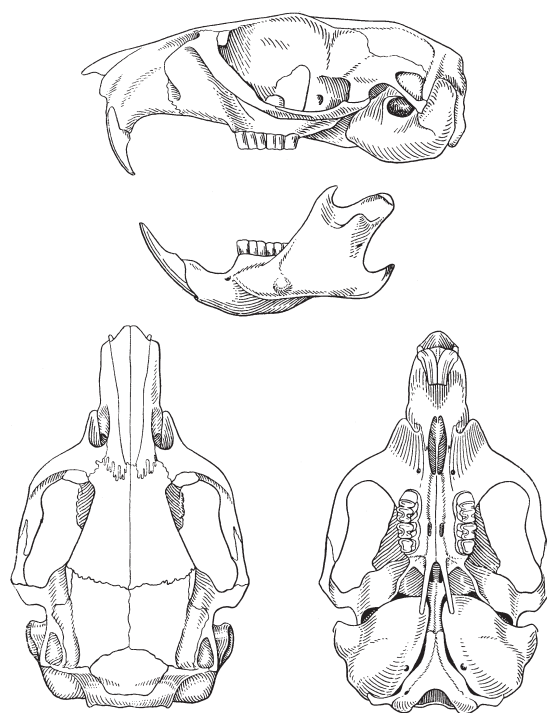


Fig. 26. Skull of *Rhombomys opimus* (after Gromov et al., 1963)

Рис. 26. Череп *Rhombomys opimus* (по Gromov et al., 1963)

member of the separate subfamily/tribe (Heptner, 1933; Gromov, Baranova, 1981). However, the rooted specimens of both extant and extinct *Rhombomys* s.lato fill that gap. Accordingly, the genus in question neighbours with *Meriones* and *Psammomys* in the phylogenetic classification adopted here. It is most close to the latter genus by the characters separating the groups *Meriones*–*Brachiones* and *Psammomys*–*Rhombomys* (see account of subtribe Rhombomyina above).

Taxonomic status of the extant rootless *Rhombomys* is not clear. The matter is that all younger Iranian specimens appeared to be with rootless molars, as were all the specimens seen by me from Turkmenia (several hundred skulls including the most adult ones). I was unable to find any differences in the skull morphology between them and the specimens with rooted molars other than those explained by age.

KEYS TO THE GENERA AND SUBGENERA

Below are the identification keys for the Gerbillinae provided for three main geographic regions separately, namely Asia, northern and eastern Africa, and southern Africa. They are addressed at the professional zoologists,

so they are based mainly on the skull and dental characters while the external features are indicated upon a need just to help with some difficult cases. The work with the keys requests at least a minimal level of knowledge of anatomical characters and terms discussed in the preceding chapters.

KEY TO THE ASIAN TAXA

1. Front surface of upper incisives nearly plain *Psammomys*
— Front surface of upper incisives with grooves 2
2. Front surface of each upper incisor with two slight grooves; molars with cementum, their roots usually absent or much lower than the crown (see Fig. 9h) *Rhombomys*
— Front surface of each upper incisor with one deep groove; molars without cementum, their roots well developed 3
3. Molar crown pattern lophodont, with laminae not skewed (see Fig. 4c); keel of masseteric plate long and covers the maxillo-premaxillar suture (see Fig. 11) *Tatera*
— Molar crown pattern of other types (bunodont, prismatic, or lophodont with skewed laminae); keel of masseteric plate shorter and does not cover the maxillo-premaxillar suture 4
4. Interorbital constriction wide (more than 20.5% of skull length, see Fig. 24); anterocon of lower M1 partly reduced (see Fig. 4g); lower surface of forefoot haired *Brachiones*
— Interorbital constriction not so wide (less than 20.5% of skull length); anterocon of lower M1 not reduced, lamina-like (see Fig. 4a,g); lower surface of forefoot naked 5
5. *Tympanum accessorium* absent, so only manubrium mallei is visible from the outside (see Fig. 8a) 6
— *Tympanum accessorium* present, so the auditory ossicles are visible from the outside (see Fig. 8b) 11
6. Lower surface of hindfoot naked 7
— Lower surface of hindfoot haired 9
7. Mastoid portion of auditory bulla just partly pneumatized, so the mastoid septum is diagonal (see Fig. 7e) *Petteromys*
— Mastoid portion of auditory bulla fully pneumatized, so the mastoid septum is vertical (see Fig. 7f) 8
8. Proximal pads of the hindfoot large *Sekeetamys*
— Proximal pads of the hindfoot small *Meriones (Parameriones)*
9. Lower surface of hindfoot completely haired *Meriones s.str.*
— Lower surface of hindfoot with small naked stripe 10

- 10. Posterior palatal foramina not exceed upper toothrow in length; cheek vibrissae present *Meriones (Cheliones)*
- Posterior palatal foramina not shorter than upper toothrow; cheek vibrissae absent *Meriones (Pallasiomys part.)*
- 11. Tooth crown prismatic (see Fig. 4h) *Meriones (Pallasiomys part.)*
- Tooth crown pattern bunodont (see Fig. 4a) 12
- 12. Lower surface of hindfoot naked *Gerbillus (Hendecapleura)*
- Lower surface of hindfoot haired *Gerbillus s.str.*

KEY TO THE NORTHERN AND EASTERN AFRICAN TAXA

- 1. Mandible without coronoid process (see Fig. 2b); lower M1–2 with hypoconid (see Fig. 4d) *Ammodillus*
- Mandible with coronoid process; no hypoconid on lower M1–2 2
- 2. Front surface of upper incisors plain *Psammomys*
- Front surface of upper incisors with grooves 3
- 3. No lower M3 (see Fig. 2c) *Desmodilliscus*
- Lower M3 present 4
- 4. Keel of masseteric plate long, covers maxillo-premaxillar suture (see Fig. 1b); molar crown pattern (nearly) symmetrically lophodont (see Fig. 4c); mastoid portion of auditory bulla not or minimally pneumatized 5
- Keel of masseteric plate shorter, does not cover maxillo-premaxillar suture; molar crown pattern of other types (asymmetrical if lophodont, see Fig. 4e); mastoid portion of auditory bulla partly or fully pneumatized 6
- 5. Posterior palatal foramina not enlarged (see Fig. 12) *Gerbilliscus*
- Posterior palatal foramina enlarged (see Fig. 13) *Taterillus*
- 6. Molar crown pattern prismatic (see Fig. 4h); tail longer than head and body *Meriones*
- Molar crown pattern not prismatic, usually with conspicuous cones (if the latter condition is not observed, tail shorter than head and body) 7
- 7. Auditory bulla hypertrophied (see Fig. 21), its mastoid portion without any septa (see Fig. 7g); tail twice shorter than head and body *Pachyuromys*
- Auditory bulla not especially hypertrophied, its mastoid portion with one or two septa (see Fig. 7e,f); tail longer than half of head and body 8
- 8. Mandible with large prominence before toothrow (see Fig. 2d) ?*Monodia*
- Mandible without such a prominence before toothrow 9
- 9. Posterior palatal foramina enlarged (see Fig. 19) *Microdillus*
- Posterior palatal foramina not so enlarged 10
- 10. Lower surface of hindfoot haired *Gerbillus s.str.*
- Lower surface of hindfoot not haired 11
- 11. *Tympanum accessorium* absent so only *manubrium mallei* is visible from the outside (see Fig. 8a) *Dipodillus (Petteromys)*
- *Tympanum accessorium* present, so the auditory ossicles are visible from the outside (see Fig. 8b) 12
- 12. Molar crown pattern semiprismatic (see Fig. 4f); mastoid portion of auditory bulla just partly pneumatized, so the mastoid septum is diagonal (see Fig. 7e) *Dipodillus s.str.*
- Molar crown pattern bunodont (see Fig. 4a); mastoid portion of auditory bulla fully pneumatized with the mastoid septum more or less vertical (see Fig. 7f) *Gerbillus (Hendecapleura)*

KEY TO THE SOUTHERN AFRICA TAXA

1. Keel of masseteric plate long and covers the maxillo-premaxillar suture (see Fig. 1b) **2**
— Keel of masseteric plate shorter and does not cover the maxillo-premaxillar suture **5**
2. *Tympanum accessorium* absent, so only *manubrium mallei* visible from the outside (see Fig. 8a); lower surface of hindfoot naked **3**
— *Tympanum accessorium* present, so the auditory ossicles visible from the outside (see Fig. 8b); lower surface of hindfoot not naked **4**
3. Front surface of each upper incisor with two slight grooves; mandible with partly reduced coronoid process ***Gerbilliscus s.str.***
— Front surface of each upper incisor with one deep groove; coronoid process of mandible not reduced ***Gerbilliscus (Taterona)***
4. Posterior palatal foramina short ***Gerbillurus (Paratatera)***
— Posterior palatal foramina long ***Gerbillurus s.str.***
5. Mastoid portion of auditory bulla hypertrophied and projects behind the occiput; tail shorter than head and body ***Desmodillus***
— Mastoid portion of auditory bulla small and does not project behind the occiput; tail longer than head and body ***Gerbillurus (Progerbillurus)***

CONCLUSIONS

There are several points of significant agreement between modern phylogenetic and classificatory schemes deduced from morphological and molecular data. One of them is monophyly of the group including genera *Tatera*, *Gerbilliscus*, *Gerbillurus*, and *Desmodillus*; another is the sister-group relationship of the subtribes Gerbillina s.str. and Rhombomyina, each usually considered as monophyletic.

It is of importance also that the both types of data coincide in recognizing generic separation of Asian *Tatera* and African *Gerbilliscus* formerly included in the same genus and even subgenus.

At the same time, there are also essential disagreements between phylogenetic hypotheses based on those two types of data. Skull and dental morphology supports placing genus *Taterillus* in the group including genera *Tatera* and *Gerbilliscus*, while mtDNA data indicate its sister-group relation to the tribe Gerbillini.

There is also a controversy about relationships between *Desmodillus* to *Pachyuromys*: they are placed in the nominative tribe by the morphological data or considered as constituting a separate clade basal to all other gerbillines by DNA data.

In both cases of the principal controversy, no morphological characters are known so far to be in favor of mtDNA-derived phylogenies. Therefore, it seems premature at the moment to insist upon priority of the molecular data over morphological ones, as genetists used to do. Further investigations are needed to incorporate more both morphological (for instance, postcranial skeleton) and molecular (nuclear DNA, before all) characters into a kind of consensus phylogenetic hypothesis.

There are several particular cases requesting further investigations. One of them is phylogenetic status of the subtribe Gerbillurina that might be paraphyletic; in this respect relationships between genera *Gerbillurus* and *Gerbilliscus* become of prime importance. Phylogenetic relationship of the genus *Sekeetamys* still remains unclear: it is placed either in Gerbillina s.str. or at basal

position in Rhombomyina. The whole nominative subtribe requests intensive study by molecular approach, as morphological data seem to be unable to recognize its monophyletic subgroups. This is especially true for the two of its polytypic genera, *Dipodillus* and *Gerbillus*, which are quite probably paraphyletic assemblages. The enigmatic genus ?*Monodia* also deserves special attention of taxonomists. At last, taxonomic status of extant *Rhombomys* populations with rooted and rootless molars is of interest.

Rhombomyina Heptner is shown to be a valid name for the subtribe including both *Rhombomys* and *Meriones*. Gerbillurini Pavlinov is shown to be a valid name for the tribe including *Tatera* and *Gerbillurus* if *Taterillus* is removed from it.

Although the present issue concerns primarily Recent taxa, two fossil genera, *Epimeriones* and *Pseudomeriones*, worth mentioning here. Their dental characters do not fit evolutionary trends of the extant gerbillines with prismatic tooth crown, so they do not probably belong to the subfamily Gerbillinae at all.

The above contradiction between morphological and molecular phylogenies has certain methodological interest. Adoption of the former means parallel evolution of mtDNA which might be caused by simple combinatorics of genes (Nei, Kumar, 2000, for details). Adoption of the latter means parallel evolution of morphological features which is not surprising by itself; the worse is impossibility to reveal any morphological synapomorphy for the groups recognized by molecular data. Such cases are known for the mammals, one of most famous is the concept of Afrotheria (Scally et al., 2002). Therefore, future studies on phylogeny and taxonomy of Gerbillinae based on more morphological and molecular data would be of utmost importance for clarifying one of the key problems of the modern phylogenetics: have the groups recognized by molecular data as presumably monophyletic clades any phylogenetic sense if they have no morphological synapomorphies.

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of the modern versions of gerbilline phylogeny. My special thanks are due to Mike Carleton for his critical comments on the earlier draft of the manuscript. I thank Drs Olga Voltzit and especially Alexander Sysoev (Zoological Museum of Moscow University) for their editorial work.

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REFERENCES

- Agusti J.* 1991. Gerbillides fossils d'Europe occidentale. In *Les Rongeurs et l'Espace* (Eds M. Le Berre, L. Le Guelte). Paris: R. Chabaud Ed. P. 177–182.
- Agusti J., Casanovas-Vilar I.* 2003. Neogene gerbils from Europe. In *Distribution and migration of Tertiary mammals in Eurasia. A volume in honour of Hans de Bruijn* (Eds J.W.F. Reumer, W. Wessels). *Deinsea*. V. 10. P. 13–21.
- Agusti J., Miguel G., Krijgsman W.* 2006. Evidence for African–Iberian exchanges during the Messinian in the Spanish mammalian record. *Palaeo*. V. 238. P. 5–14.
- Alexander R.M.* 1968. *Animal mechanics*. London: Sidgwick & Jackson. 364 p.
- Alston E.R.* 1876. On the classification of the order Glires. *Proc. Zool. Soc. London* (1876). P. 61–98.
- Arata A.* 1964. The anatomy and taxonomic significance of the male accessory reproductive glands of Muroid rodents. *Bull. Florida State Mus.* V. 9. № 1. P. 1–42.
- Arata A.A.* 1967. Muroid, gliroid, and dipodoid rodents. In *Recent mammals of the World: a synopsis of families* (Eds S. Anderson, J. Knox Jones). N.Y.: The Ronald Press Co. P. 226–253.
- Brandt J.F.* 1844. Remarques sur la classification des Gerboises eu egard surtout aux especes de Russie. *Bull. Acad. Imp. sci. St.-Petersb., classe phys.-math.* V. 2. № 14–15. P. 41–80.
- Brandt J.F.* 1854. Bemerkungen uber die Gattungen *Gerbillus*, *Meriones*, *Rhombomys* und *Psammodomys*. *Mel. biol.* V. 2. P. 300–304.
- Brandt J.F.* 1855. Untersuchungen uber die kraniologischen entwicklungsstudien und klassifikation der nager der jetwelt. *Mem. Acad. Sci. St.Petersburg*. Ser. 6. V. 9. Pt. 2. S. 1–365.
- Brandy D.* 1979. Rongeurs nouveaux du Neogene d'Afghanistan. *Compt. rend. Acad. sci.*, ser. D. T. 289 № 2. P. 81–83.
- Bruijn H. de.* 1999. A late Miocene insectivore and rodent fauna from the Baynunah Formation, Amirate of Abu Dhabi. In *Fossil vertebrates of Arabia* (Eds P.J. Whybrow, A. Hill). New Haven: Yale Univ. Press. P. 186–197.
- Bruijn H. de, Dawson M.R., Mein P.* 1970. Upper Pliocene Rodentia, Lagomorpha and Insectivora (Mammalia) from the Isle of Rhodes (Greece), I, II, III. *Proc. Kon. Nederl. Akad. Wetens.* B. 73. № 5. S. 535–595.
- Carleton M.D.* 1980. Phylogenetic relationships in neotomine–peromyscine rodents (Muroidea) and a reappraisal of the dichotomy within New World Cricetinae. *Misc. Publ. Mus. Zool. Univ. Michigan*. № 157. P. 1–146.
- Carleton M.D., Musser G.G.* 1984. Muroid rodents. In *Orders and families of Recent mammals of the World* (Eds S. Anderson, J. Knox Jones). N.Y.: Wiley-Intersci. P. 289–380.
- Castillo C., Agusti J.* 1996. Early Pliocene rodents (Mammalia) from Asta Regia (Jerez Basin, southwestern Spain). *Proc. Kon. Nederl. Akad. Wetens.* Ser. B. V. 99. № 1. S. 25–43.
- Chaline J., Mein P.* 1979. *Les rongeurs et l'évolution*. Paris: Doin. 235 p.
- Chaline J., Mein P., Petter F.* 1977. Les grandes lignes d'une classification evolutive des Muroidea. *Mammalia*. T. 41 № 3. P. 245–252.
- Charworth-Musters J.L., Ellerman J.R.* 1947. A revision of the genus *Meriones*. *Proc. Zool. Soc. London*. V. 117. pt. 2/3. P. 478–504.
- Chevret P., Dobigny G.* 2005. Systematics and evolution of the subfamily Gerbillinae (Mammalia, Rodentia, Muridae). *Mol. Phyl. Evol.* V. 35. № 2. P. 674–688.
- Cockrum E.L., Vaughan T.C., Vaughan P.J.* 1976. A review of North African short-tailed gerbils (*Dipodillus*) with description of a new taxon from Tunisia. *Mammalia*. T. 40. № 2. P. 313–326.
- Colangelo P., Corti M., Verheyen E., Annesi F., Oguge N., Makundi R.H., Verheyen W.* 2005. Mitochondrial phylogeny reveals different modes of chromosomal evolution in the genus *Tatera* (Rodentia: Gerbillinae) in Africa. *Mol. Phyl. Evol.* V. 35. № 3. P. 556–568.

- Colangelo P., Granjon L., Taylor P.J., Corti M.* 2007. Evolutionary systematics in African gerbilline rodents of the genus *Gerbilliscus*: Inference from mitochondrial genes. *Mol. Phyl. Evol.* V. 42. № 6. P. 797–806.
- Corbet G.B., Hill J.E.* 1980. A world list of mammalian species. London: Cornell Univ. Press. 226 p.
- Davis D.H.S.* 1971. Genera *Tatera* and *Gerbillurus*. In The mammals of Africa: An identification manual. Pt. 6.4 (Eds J. Meester, H.W. Setzer). Washington (D.C.): Smithsonian Inst. Press. P. 17–20.
- Daxner-Hock G.* 1972. Die wübeltierfauna aus dem Alt-Pliozän (Pont) vom Eichkogel bei Modling (Niederösterreich). IV. Gerbillinae (Rodentia, Mammalia). *Ann. Naturh. mus. Wienn.* B. 76. S. 143–160.
- Doyle J.J.* 1992. Gene trees and species trees: molecular systematics as one-character taxonomy. *Syst. Bot.* V. 17. № 1. P. 144–163.
- Dubois J.Y.F., Catzeflis F.M., Beintema J.J.* 1999. The phylogenetic position of “Acomyinae” (Rodentia, Mammalia) as sister group of a Murinae plus Gerbillinae clade: Evidence from the nuclear ribonuclease gene. *Mol. Phyl. Evol.* V. 13. № 1. P. 181–192.
- Ellerman J.R.* 1941. The families and genera of living rodents, vol. 2. London: British Museum (Natural History). 690 p.
- Ellerman J.R.* 1947. Notes on some Asiatic rodents in the British Museum. *Proc. Zool. Soc. London.* V. 117. pt. 2. P. 259–271.
- Ellerman J.R.* 1948. Key to the rodents of South-west Asia in the British Museum collection. *Proc. Zool. Soc. London.* V. 118. pt. 3. P. 765–816.
- Ellerman J.R., Morrison-Scott T.C.S., Hayman R.W.* 1951. Southern African Mammals, 1758 to 1951: A re-classification. London: Tr. Brit. Mus. (Nat. Hist.). 363 p.
- Felsenstein J.* 2003. Inferring phylogenies. Elsevier: Sinauer Assc. 664 p.
- Flynn L.J., Jacobs L.L., Lindsay E.H.* 1985. Problems in muroid phylogeny. In Evolutionary relationships among rodents: A multidisciplinary approach (Eds W.P. Lockett, J.L. Hartenberger). N.Y.: Plenum Press. P. 589–616.
- Flynn L.J., Winkler A.J., Jacobs L.L., Downs W.* 2003. Tedford’s gerbils from Afghanistan. *Bull. Amer. Mus. Nat. Hist.* V. 279. P. 603–624.
- Fokanov V.A.* 1976. [New genus and species of gerbil, *Pliorhombomys gromovi* Fokanov gen. et sp. nov. (Mammalia: Rodentia) from Late Pliocene of South Turkmenia]. *Proc. Zool. Inst. Acad. Sci. USSR.* V. 61. P. 122–124. [In Russian, with English summary]
- Geraads D.* 1998. Rongeurs du Mio-Pliocene de Lissasfa (Casablanca, Maroc). *Geobios.* V. 31. № 2. P. 229–245.
- Gromov I.M., Baranova G.I.* 1981. [Catalogue of mammals of USSR (Pliocene to Recent)]. Leningrad: Nauka. 465 p. [In Russian]
- Gromov I.M., Gureev A.A., Novikov G.A.* 1963. [Mammals of fauna of USSR, pt. 1]. Moscow–Leningrad: Nauka. 638 p. [In Russian]
- Harrison D.L.* 1972. The mammal of Arabia. V. 3 (Lagomorpha, Rodentia). London: Benn. 670 p.
- Hennig W.* 1966. Phylogenetic systematics. Urbana: Illinois Univ. Press. 263 p.
- Heim de Balsac H.* 1943. Genre nouvelle au de rongeur (Gerbillinae) de Mauritanie. *Bull. Mus. Natl. Hist. Nat.* (ser. 2). T. 15. № 5. P. 287–288.
- Heptner W.G.* 1933. Notizen über die Gerbillidae (Mammalia, Rodentia). V. Über die einteilung der Gerbillidae. *Zool. Anz.* Bd. 102. H. 3/4. S. 107–112.
- Herold W., Niethammer J.* 1963. Zur systematische Stellung der Sudafrikanischen *Gerbillus paeba* Smith, 1834 (Rodentia: Gerbillidae) auf Grund seines Alveolenmusters. *Saugeth. Mitt.* Bd. 11. № 2. S. 49–58.
- Hershkovitz P.* 1962. Evolution of neotropical cricetine rodents (Muridae) with special reference to the phyllotine group. *Field. Zool.* V. 46. P. 1–524.
- Hill C.R., Crane P.R.* 1982. Evolutionary aspects of phylogenetic approaches to taxonomic classification. In Problems in phylogenetic reconstructions (Eds K.A. Joysey, A.E. Friday). London: Acad. Press. P. 269–361.
- Holden M.E., Musser G.G.* 2005. Family Dipodidae. In Mammal species of the World, a taxonomic and geographic reference, 3rd ed. V. 2 (Eds D.E. Wilson, D. Reeder). Baltimore: John Hopkins Univ. Press. P. 871–893.
- International Code of Zoological Nomenclature, 4th Ed. 1999. London: Internat. Trust for Zool. Nomencl. 306 p.
- Jaeger J.-J.* 1977. Les rongeurs du Miocene moyen et superieur du Maghreb. *Paleovertebr.* V. 8. P. 3–166.
- Jansa S.A., Weksler M.* 2004. Phylogeny of muroid rodents: relationships within and among major lineages as determined by IRBP

- gene sequencing. *Mol. Phyl. Evol.* V. 31. № 2. P. 256–276.
- Kowalski K. 1974. Remains of Gerbillinae (Rodentia, Mammalia) from the Pliocene of Poland. *Bull. Polish Acad. Sci., ser. Biol.* T. 22. № 9. S. 595–598.
- Lavocat R. 1964. Fossil rodents from Fort Ter-nan, Kenya. *Nature.* V. 202. P. 1131
- Lavocat R. 1973. Les Rongeurs du Miocene d’Afrique oriental. 1. Miocene inferieur. *Mem. Trav. l’Ecole Pratiq. Hautes Etudes, Institute de Montpellier.* V. 1. P. 1–284.
- Lavocat R. 1978. Rodentia and Lagomorpha. In *Evolution of African mammals* (Eds V.J. Maglio, H.B.S. Cooke). Cambridge (Massachusetts): Harvard Univ. Press. P. 69–89.
- Lay D.L. 1972. The anatomy, physiology, functional significance and evolution of specialized hearing organs of gerbilline rodents. *J. Morphol.* V. 138. № 1. P. 41–120.
- Lay D.L. 1983. Taxonomy of the genus *Gerbillus* (Mammalia: Muridae: Gerbillinae) with comments on applications of generic and subgeneric names and an annotated list of species. *Z. Säugetierk.* Bd. 48. № 6. S. 329–354.
- Lundholm B.G. 1955. Description of new mammals. *Ann. Transvaal Mus.* V. 22. P. 279–303.
- Mares M. 1980. Convergent evolution among desert rodents: a global perspective. *Bull. Carnegie Mus. Nat. Hist.* V. 16. P. 1–51.
- McKenna M.C., Bell S.K. 1997. Classification of mammals above the species level. New York: Columbia Univ. Press. 631 p.
- Michaux J., Reyes A., Catzeflis F. 2001. Evolutionary history of the most speciose mammals: molecular phylogeny of muroid rodents. *Mol. Biol. Evol.* V. 18. № 11. P. 2017–2031.
- Miller G.S., Gidley J.W. 1918. Synopsis of the supergeneric groups of rodents. *J. Washington Acad. Sci.* V. 8. P. 431–448.
- Misonne X. 1969. African and Indo-Australian Muridae: evolutionary trends. *Ann. Mus. Roy. Afr. Cent., ser. in 8°. Sci. Zool.* № 172. P. 3–219.
- Moore W.J. 1981. The mammalian skull. London: Cambridge University Press. 369 p.
- Musser G.G., Carleton M.D. 1993. Family Muridae. In *Mammal species of the World: a taxonomic and geographic reference*, 2nd ed. (Eds D.E. Wilson, D. Reeder). Washington-London: Smithsonian Inst.. Press. P. 501–756.
- Musser G.G., Carleton M.D. 2005. Superfamily Muroidea. In *Mammal species of the World: a taxonomic and geographic reference*, 3rd ed. V. 2 (Eds D.E. Wilson, D. Reeder). Baltimore: Johns Hopkins Univ. Press. P. 894–1531.
- Nei M., Kumar S. 2000. Molecular evolution and phylogenetics. Oxford: Oxford Univ. Press. 333 p.
- Nelson G. 1994. Homology and systematics. In *Homology, the hierarchical basis of comparative biology* (Ed. B.K. Hall). London: Acad. Press. P. 102–149.
- Osborn D.J., Helmy I. 1980. The contemporary mammals of Egypt (including Sinai). *Field. Zool., nov. ser.* V. 5. P. 1–579.
- Palmer T.S. 1904. Index generum mammalium. *North Amer. Fauna.* № 23. P. 5–984.
- Patnaik R. 1997. New murids and gerbillids (Rodentia, Mammalia) from Pliocene Siwalik sediments of India. *Palaeovertebr.* V. 26. № 1. P. 129–165.
- Pavlinov I.Ya. 1979a. [On morphology of the tooth crown of higher gerbils (Mammalia, Gerbillinae)]. *Vestn. zool.* (Kiev). № 1. P. 33–36. [In Russian]
- Pavlinov I.Ya. 1979b. [Morphology and taxonomic significance of the auditory ossicles in the jirds of the genus *Meriones* (Rodentia: Cricetidae)]. *Zool. Zhurn.* (Moscow). V. 58. v. 11. P. 1703–1712. [In Russian, with English summary]
- Pavlinov I.Ya. 1980. [Evolution and taxonomic significance of the middle ear in the subfamily Gerbillinae (Rodentia: Cricetidae)]. *Bull. Mosc. Soc. Natur., Sect. Biol.* V. 85. v. 4. P. 20–33. [In Russian, with English summary]
- Pavlinov I.Ya. 1981a. [Systematic position of gerbils of the genus *Ammodillus* Thomas, 1904]. *Zool. Zhurn.* (Moscow). V. 60. v. 3. P. 472–474. [In Russian, with English summary]
- Pavlinov I.Ya. 1981b. [Subgeneric taxonomy of the genus *Tatera* Lataste, 1882 based on morphology of the osseous middle ear]. *Vestn. Zool.* № 3. P. 10–14. [In Russian, with English summary]
- Pavlinov I.Ya. 1982a. [Phylogeny and classification of the subfamily Gerbillinae]. *Bull. Mosc. Soc. Natur., Sect. Biol.* V. 87. v. 2. P. 19–31. [In Russian, with English summary]
- Pavlinov I.Ya. 1982b. [Molar morphology in the Iranian greater gerbil, *R. opimus*, with notes on taxonomy of the group *Rhombomys–Pliorhombomys* (Rodentia: Gerbillinae)]. *Vestn. Zool.* № 3. P. 53–57. [In Russian, with English summary]
- Pavlinov I.Ya. 1984a. [Evolution of the dental crown pattern in Gerbillidae]. *Arch. Zool. Mus.*

- Moscow Univ. V. 22. P. 93–134. [In Russian, with English summary]
- Pavlinov I.Ya. 1984b. [Evolution of the middle ear ossicles in the vole subfamily Microtinae]. *Arch. Zool. Mus. Moscow Univ.* V. 22. P. 191–212. [In Russian]
- Pavlinov I.Ya. 1985. [Contribution to molar morphology and phylogeny of gerbils (Rodentia: Gerbillinae)]. *Zool. Zhurn.* (Moscow). V.64. v.4. P. 574–582. [In Russian, with English summary]
- Pavlinov I.Ya. 1986. [Taxonomic significance of the male genital morphology in the subfamily Gerbillinae (Mammalia: Rodentia)]. *Bull. Mosc. Soc. Natur.*, Sect. Biol. V. 91. v. 1. P. 8–16. [In Russian, with English summary]
- Pavlinov I.Ya. 1987. [Cladistic analysis of gerbils of the tribe Taterillini (Rodentia, Gerbillinae), with notes on cladistic numerical methods]. *Zool. Zhurn.* (Moscow). V. 66. v. 6. P. 903–913. [In Russian, with English summary]
- Pavlinov I.Ya. 1988. [Evolution of the mastoid portion of auditory bulla of the specialized desert rodents]. *Zool. Zhurn.* (Moscow). V. 67. v. 5. P. 739–750. [In Russian, with English summary]
- Pavlinov I.Ya. 1990. [Cladistic analysis (theoretical aspects)]. Moscow: Moscow Univ. Publ. 160 p. [In Russian]
- Pavlinov I.Ya. 1996. New records of *Rhombomys opimus* (Mammalia, Gerbillidae) with rooted molars from Iran. *Vestn. Zool.* № 6. P. 18.
- Pavlinov I.Ya. 1998. [Toward axiomatic foundation of the evolutionary cladistics]. *Zhurn. Obschei Biol.* V. 59. № 6. P. 586–605. [In Russian, with English summary]
- Pavlinov I.Ya. 2000. [Geometric morphometrics of the skull of some muroid rodents (Mammalia, Rodentia): relation of the skull shape to trophic specialization]. *Zhurn. Obschei Biol.* V. 61. № 6. P. 583–600. [In Russian, with English summary]
- Pavlinov I.Ya. 2001. Current concepts of gerbillid phylogeny and classification. In African small mammals. Proc. 8th Internat. Symp. African small mammals. Paris: IRD Ed. P. 141–149.
- Pavlinov I.Ya. 2003. [Systematics of Recent mammals]. *Arch. Zool. Mus. Moscow Univ.* V. 47. P. 3–297. [In Russian]
- Pavlinov I.Ya. 2005. [Introduction to contemporary phylogenetics]. M.: KMK Science Press. 391p. [In Russian]
- Pavlinov I.Ya., Dubrovsky Yu.A., Rossolimo O.L., Potapova E.G. 1990. [Gerbillides of the World]. Moscow: Nauka Publ. 368 p. [In Russian]
- Pavlinov I.Ya., Rogovin K.A. 2000. [Correlation between sizes of pinna and auditory bulla in specialized desert rodents]. *Zhurn. Obschei Biol.* V. 61. № 1. P. 87–101. [In Russian, with English summary]
- Pavlinov I.Ya., Rossolimo O.L. 1987. [Systematics of mammals of USSR]. Moscow: Moscow Univ. Publ. 253 p. [In Russian]
- Pavlinov I.Ya., Shenbrot G.I. 1983. [Morphology of the male genital system and classification of the Dipodidae]. *Proc. Zool. Inst. Acad. Sci. USSR.* V. 119. P. 67–88. [In Russian, with English summary]
- Petter F. 1959. Evolution du dessin de la surface d'usure des molaires des Gerbillides. *Mammalia.* T. 23. № 2. P. 304–315.
- Petter F. 1971. Subfamily Gerbillinae. In The mammals of Africa: An identification manual. Pt. 6.3 (Eds J. Meester, H.W. Setzer). Washington (DC): Smithsonian Inst. Press. P. 1–13.
- Petter F. 1973. Tendances evolutive dans le genre *Gerbillus* (Rongeurs, Gerbillides). *Mammalia.* T. 37. № 4. P. 631–636.
- Petter F. 1975. La diversite des Gerbillides. *Monogr. Biol.* № 28. P. 177–183.
- Potapova E.G. 1990. Evolution of masticatory apparatus in Gerbillinae. In Evolutionary and genetic researches in mammals, pt. 2. Vladivostok. P. 159–163. In Russian
- Qiu Z.D. 2001. Glirid and gerbillid rodents from the middle Miocene fauna of Lanzhou, Gansu. *Vertebr. Palasiat.* V. 39. № 4. P. 297–305.
- Qiu Z.D., Zheng S.H., Zhang Z.Q. 2004. Gerbillids from the Late Miocene Bahe formation, Lantian, Shaanxi. *Vertebr. Palasiat.* V. 42. № 3. P. 193–204.
- Qumsiyeh M.B. 1986. Phylogenetic studies of the rodent family Gerbillidae. I. Chromosomal evolution in the Southern African complex. *J. Mammal.* V. 67. № 4. P. 680–692.
- Qumsiyeh M.B., Schlitter D.A. 1991. Cytogenetic data on the rodent family Gerbillidae. *Occas. Pap. Mus. Texas Tech. Univ.* № 144. P. 1–20.
- Rieppel O. 1994. Homology, topology, and typology: the history of modern debates. In Homology, the hierarchical basis of comparative biology (Ed. B.K. Hall. London: Acad. Press. P. 64–100).
- Robbins C.B. 1971. Dental nomenclature for *Taterillus* Thomas (Rodentia: Cricetidae). *Mammalia.* T. 35. № 4. P. 629–635.

- Roberts A. 1951. The mammals of South Africa. Johannesburg: Trust of "The mammals of South Africa" book fund. 700 p.
- Roche J. 1975. A propose de petites gerbilles a soles plantaires nues (sous-genre *Hendecapleura*) de l'est Africain. *Monit. zool. Ital. Suppl.* 6. № 13. P. 263–268.
- Roche J., Petter F. 1968. Faits nouveaux concernant trois gerbillides mal connus de Somalia: *Ammodillus imbellis* (De Winton), *Microdillus peeli* (De Winton), *Monodia juliani* (Saint Leger). *Monit. zool. Ital.*, nov. ser. Suppl. 2. P. 181–198.
- Rosevear D.R. 1969. The rodents of West Africa. London: Tr. Brit. Mus. (Nat. Hist.). 604 p.
- Saether O.A. 1983. The canalized evolutionary potential: inconsistencies in phylogenetic reasoning. *Syst. Zool.* V. 32. № 4. P. 343–359.
- Sally M., Madsen O., et al. 2002. Molecular evidence for the major clades of placental mammals // *J. Mammal. Evol.* V. № 8. P. 239–277.
- Sen S. 1977. La faune de rongeurs Pliocenes de Calta (Ankara, Turquie). *Bull. Mus. Natl. Hist. Nat. Sci. Terre.* V. 465. P. 1–171.
- Shenbrot G.I., Krasnov B.R., Rogovin K.A. 1999. Spatial ecology of desert rodents. Berlin: Springer Verlag. 200 p.
- Shevyreva N.S. 1976. [On parallel development of some types of dental crown in the rodents (Rodentia, Mammalia)]. *Proc. Zool. Inst. Acad. Sci. USSR.* V. 66. P. 4–47. [In Russian]
- Simkin G.N. 1965. [Types of bullar cavities in mammals in relation to their life habit]. *Zool. Zhurn.* (Moscow). V. 43. v. 10. P. 1538–1545. [In Russian]
- Simpson G.G. 1945. The principles of classification and a classification of mammals. *Bull. Amer. Mus. Nat. Hist.* V. 85. P. 1–350.
- Sokolov V.E. 1977. [Systematics of mammals. V. 2. Lagomorphs and rodents]. Moscow: Vys'shaya Shkola. 494 p. [In Russian]
- Sokolov V.E., Orlov V.N. 1980. [A guide to the mammals of Mongolian People Republic]. Moscow: Nauka. 350 p. [In Russian]
- Steppan S.J., Adkins R.M., Anderson J. 2004. Phylogeny and divergence-date estimates of rapid radiations in muroid rodents based on multiple nuclear genes. *Syst. Biol.* V. 53. № 4. P. 533–553.
- Tchernov E. 1968. Succession of rodent faunas during the upper Pleistocene of Israel. Yena: Paul Prey. 152 p.
- Tchernov E., Chetboun R. 1984. A new genus of gerbillid rodent from early Pleistocene of the Middle East. *J. Vertebr. Paleontol.* V. 4. № 4. P. 559–569.
- Terzea E. 1976. Presence des Gerbillides dans le Villafranchien superior de Roumanie. *Tr. Inst. Speologie "Emile Racovitza"*. T. 15. P. 191–199.
- Tesakov A.S., Titiov V.V. 2005. [Presence of a new late Miocene vertebrate fauna in Azove Region as a means of correlations]. In [Paleontological chronicle of regional and global events. Abstr. LI session Paleontol. Soc.] (Eds T.N. Bogdanov, N.G. Krymgholz). St.-Petersburg. P. 117–118. [In Russian]
- Thomas O. 1896. On the genera of rodents; an attempt to bring up to date the current arrangement of the order. *Proc. Zool. Soc. London.* pt. 4. P. 1012–1028.
- Tong H. 1989. Origine et evolution des Gerbillidae (Mammalia, Rodentia) en Afrique du Nord. *Mem. Soc. Geol. France*, nov. ser. 155. P. 1–120.
- Tong H., Jaeger J.-J. 1993. Muroid rodents from the Middle Miocene Fort Ternan Locality (Kenya) and their contribution to the phylogeny of muroids. *Palaeontographica.* Abt. A. T. 229. S. 51–73.
- Tullberg T. 1899. Uber das system der Nagethiere, eine phylogenetische studie. *Nova Acta Regiae Soc. Sci. Upsaliensis.* V. 3. P. 1–514.
- Volobuev V., Aniskin V.M., et al. 2007. Systematics and phylogeny of West African gerbils of the genus *Gerbilliscus* (Muridae: Gerbillinae) inferred from comparative G- and C-banding chromosomal analyses. *Cytog. Genome Res.* V. 116. № 2. P. 269–281.
- Vorontsov N.N. 1968. [Historical zoogeography of muroid rodents (Muroidea)]. In Problems in evolution. Novosibirsk: Nauka. P. 116–141. [In Russian]
- Walker E.P. 1964. Mammals of the World, 1st edition. V. 2. Baltimore: The John Hopkins Press. 644 p.
- Webster D.B., Webster M. 1975. Auditory systems of Heteromyidae: functional morphology and evolution of the middle ear. *J. Morphol.* V. 146. № 3. P. 343–376.
- Wessels W. 1998. Gerbillidae from the Miocene and Pliocene of Europe. *Mitt. Bayer. Staatssamm. Palaeontol. Hist. Geol.* Bd. 38. S. 187–207
- Wiley E.O. 1981. Phylogenetics: the theory and practice of phylogenetic systematics. N.Y.: Wiley & Sons. 439 p.

SUMMARY

Under consideration are modern ideas about phylogeny and taxonomy of the subfamily Gerbillinae. Most attention is paid to the classifications based on bullar and dental morphology, on the one hand, and on mtDNA data, on the other hand.

A kind of transformation series analyses are provided for diversity of the masticatory apparatus (primarily dental crown pattern) and the ossean middle ear (primarily bony elements reflecting types of mastoid pneumatization) in extant gerbillines. Phylogenetic hypotheses deduced from these analyses are discussed.

A brief review of the extinct genera usually allocated to Gerbillinae is given, with re-examination of their relation to the subfamily. The genera *Epimeriones* and *Pseudomeriones* are supposed to be not gerbillines.

A taxonomic system of the subfamily Gerbillinae above species level is provided. Diagnostic features of all recognized suprageneric taxa and genera of the Recent gerbillines are listed together with the discussion of their phylogenetic and taxonomic validity and relationships.

The existing phylogenetic schemes based on both morphological and molecular data agree in recognition of monophyly of two principal groups of the tribal rank. One of them includes *Tatera*, *Gerbilliscus*, *Gerbillurus*, and *Desmodillus*, the other includes all Gerbillina s.str. and Rhombomy-

ina. The latter two are acknowledged as monophyletic subtribes. It is shown that inclusion of *Desmodillus* in Gerbillini and of *Pachyuromys* in Rhombomyina suggested by Tong (1989) is based on incorrect mastoid homology and should be abandoned.

Some questions of nomenclature at the tribal/subtribal levels are discussed. One of them is caused by possible changing position of the genus *Taterillus*, and the other concerns a valid name for the group of "higher gerbils" (*Meriones*, *Rhombomys* and their allies).

Some problematic points for the future researches upon phylogeny and taxonomy of Gerbillinae are emphasized. Among them are: belonging of the genus *Taterillus* either to the group including genera *Tatera* and *Gerbilliscus* or to the basal radiation of Gerbillini s.str.; belonging of the genera *Desmodilliscus* and *Pachyuromys* to a monotypical subtribes of their own within Gerbillini s.str. or to a separate tribe; paraphyletic status of the subtribe Gerbillurina; position of *Sekeetamys* in either Gerbillini s.str. or in Rhombomyina. Unrecognized phylogenetic relations among members of the subtribe Gerbillina s.str., including uncertain status of *?Mnodia*, are also stressed.

Identification keys for the genera and subgenera of Gerbillinae are provided for three main geographic regions separately – Asia, northern and eastern Africa, and southern Africa.

РЕЗЮМЕ

Рассмотрены современные представления о филогении и классификации подсемейства песчанковых (*Gerbillinae*). Главное внимание уделено филогенетическим реконструкциям, основанным на морфологии черепа и зубной системы, а также на результатах анализа митохондриальной ДНК.

Сравнительные данные по жевательному аппарату (преимущественно структура зубной коронки) и костного среднего уха (главным образом костные элементы, связанные с типами пневматизации мастоида) представлены в форме трансформационных серий. На этой основе обсуждаются гипотезы о монофилии надродовых групп песчанковых.

Кратко рассмотрены ископаемые роды, относимые к *Gerbillinae*, обсуждены их родственные связи. Показано, что роды *Epimeriones* и *Pseudomeriones* не относятся к данному подсемейству.

Представлена надвидовая таксономическая система подсемейства *Gerbillinae*. Указаны морфологические признаки надродовых таксонов и родов современных песчанок, обсуждены трактовки их филогенетического статуса (состав, монофилия, родственные связи).

Существующие филогенетические схемы, основанные на морфологических и молекулярных данных, совпадают в признании монофилетического статуса двух основных групп ранга трибы. Одна из них включает роды *Tatera*, *Gerbilliscus*, *Gerbillurus* и *Desmodillus*, другая — представителей подтриб

Gerbillina s.str. и *Rhombomyina*; каждая из двух последних также признана монофилетичной. Показано, что включение *Desmodillus* в *Gerbillini* и *Pachyuromys* в *Rhombomyina* ошибочно, поскольку основано на некорректной гомологизации элементов мастоида.

Рассмотрены номенклатурные вопросы, связанные с названиями таксонов ранга трибы/подтрибы. Один из них связан с возможным изменением положения рода *Taterillus*, другой касается валидного названия для группы «высших песчанок» (*Meriones*, *Rhombomys* и близкие к ним).

Отмечены ключевые разногласия между схемами, основанными на морфологических и молекулярных данных. Главными из них являются следующие: включение рода *Taterillus* в монофилетическую группу, содержащую роды *Tatera* и *Gerbilliscus*, или его отнесение к базальной радиации *Gerbillini s.str.*; выделение родов *Desmodilliscus* и *Pachyuromys* в монотипические подтрибы в составе номинальной трибы или их включение в отдельную трибу; парафилетический статус подтрибы *Gerbillurina*; отнесение рода *Sekeetamys* к *Gerbillini s.str.* или к *Rhombomyina*. Подчеркнута неопределенность представлений о филогенетических связях между членами подтрибы *Gerbillina s.str.*, включая неясный статус рода ?*Monodia*.

Представлены определительные ключи для родов и подродов песчанок раздельно для трех регионов — Азии, Северной и Восточной Африки, Южной Африки.

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- Выпуск 2:** Морские лилии отряда Hyocrinida (Echinodermata, Crinoidea). *А.Н. Миронов, О.А. Сорокина*. 1998. М.: Зоомузей МГУ. 117 с. Ил.35 + 13 табл. Табл.1. Библ.83.
- Выпуск 3:** Планы строения конечностей и эволюция техники бега у тетрапод. *А.Н. Кузнецов*. 1999. М.: Зоомузей МГУ. 91 с. Ил.26. Табл.2. Библ.75.
- Выпуск 4:** Биологическое разнообразие иксодовых клещей и методы его изучения. *О.В. Волцит*. 1999. М.: Зоомузей МГУ. 98 с. Ил.38. Табл.4. Библ.98.
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- Выпуск 6:** Сравнительная морфология и эволюция женской репродуктивной системы и биология размножения гладконосых рукокрылых (Vespertilionidae, Chiroptera). *А.В. Борисенко*. 2000. М.: Зоомузей МГУ. 147 с. Ил. 35 + 28 фото. Табл. 12. Библ. 283.
- Выпуск 7:** Типы клещей – краснотелок (Trombiculidae) в Зоологическом музее Московского университета. *Н.И. Кудряшова*. 2004. М.: Зоомузей МГУ. 56 с. Библ. 84.
- Выпуск 8:** World catalogue of the family Sepsidae (Insecta: Diptera). *A.L. Ozerov*. 2005. М.: Зоомузей МГУ. 74 с. Библ. 218.

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- Том 32:** Млекопитающие Евразии. I. Rodentia (систематико-географический справочник). 1995. *О.Л. Россолимо* (ред.). М.: Изд-во МГУ. 240 с. Библ. 230.
- Том 33:** Млекопитающие Евразии. II. Non-Rodentia (систематико-географический справочник). 1995. *О.Л. Россолимо* (ред.). М.: Изд-во МГУ. 336 с. Библ. 450.
- Том 33** (дополнение): Млекопитающие Евразии. III. Cetacea, Sirenia (систематико-географический справочник). 1995. *О.Л. Россолимо* (ред.). М.: Изд-во МГУ. 32 с. Библ. 41.
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- Том 41:** Типы позвоночных в Зоологическом музее Московского университета. *И.Я. Павлинов, А.В. Борисенко* (ред.). 2001. М.: Изд – во МГУ. 250 с. Библ.562.
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- Том 47:** Систематика современных млекопитающих (2е изд.). *И.Я. Павлинов*, 2006. М.: Изд – во МГУ. 297 с. Библ. 105. Ил. 10.
- Том 48:** Линнеевский сборник. *И.Я. Павлинов* (ред.). 2007. М.: Изд – во МГУ. 454 с.

Другие издания

- Московские орнитологи. *В.Е. Флинт, О.Л. Россолимо* (ред.). 1999.
- Земноводные и пресмыкающиеся Подмосковья. *Е.А. Дунаев*. 1999.
- Муравьи Подмосковья: методы экологических исследований. *Е.А. Дунаев*. 1999.
- Разнообразие земноводных. *Е.А. Дунаев*. 1999.
- Птицы Москвы и Подмосковья – 1999. *М.В. Калякин* (составитель). 2000
- Млекопитающие Подмосковья. *С.В. Крускоп*. 2000
- Московские териологи. *О.Л. Россолимо* (ред.). 2001
- Разнообразие птиц. *Е.А. Коблик*. 2001
- Высшие чешуекрылые (Lepidoptera, Macrolepidoptera) северной части Мещеры... Вып. 2. *М.В. Усков* и др. 2001.
- Материалы зоолого-ботанических исследований в Национальном парке Ву Куанг. *А.П. Корзун, М.В. Калякин* (ред.). 2001.

- Краткий определитель наземных зверей России. *И.Я. Павлинов*. 2002.
- Наземные звери России: справочник – определитель. *И.Я. Павлинов, С.В. Крускоп, А.А. Варшавский, А.В. Борисенко*. 2002.
- Классификация современных млекопитающих (препринт). *И.Я. Павлинов*. 2002.
- Птицы Москвы и Подмосковья – 2000. *М.В. Калякин* (составитель). 2002.
- Птицы Москвы и Подмосковья – 2001. *М.В. Калякин* (составитель). 2003.
- Материалы зоолого-ботанических исследований в природном районе Ке Банг Национального парка Фон Ня (провинция Куанг Бинь, Вьетнам). *Л.П. Корзун, М.В. Калякин* (ред.). 2003.
- Исследования наземных экосистем Вьетнама. *Л.П. Корзун, В.В. Рожнов, М.В. Калякин* (ред.). 2003.
- Bats of Vietnam and adjacent territories. An identification manual. Biodiversity of Vietnam series. *A.V. Borissenko, S.V. Krusko*. 2003.
- Разнообразие змей. *Е.А. Дунаев, В.Ф. Орлова*. 2003.
- Птицы Москвы и Подмосковья – 2002. *М.В. Калякин* (составитель). 2004.
- Московские герпетологи. *О.Л. Россолимо, Е.А. Дунаев* (ред.). 2004.
- Новые виды пластинчатоусых жуков (Coleoptera, Scarabaeidae) палеарктической фауны. *А.А. Гусаков*. 2004.
- Разнообразие млекопитающих. *О.Л. Россолимо, И.Я. Павлинов, С.В. Крускоп, А.А. Лисовский, Н.Н. Спасская, А.В. Борисенко, А.А. Панютина*. 2004.
- Птицы Москвы и Подмосковья – 2003. *М.В. Калякин* (составитель). 2005.
- Введение в современную филогенетику. *И.Я. Павлинов*. 2003.
- Каталог моллюсков России и сопредельных территорий. *Ю.И. Кантор, А.В. Сысоев*. 2005.
- Зоологический Музей МГУ: коллекции и люди. *И.Я. Павлинов, Д.Л. Иванов*. 2005.
- Птицы Москвы и Подмосковья – 2004. *М.В. Калякин, О.В. Волцит* (составители). 2006.
- Атлас. Птицы Москвы и Подмосковья. *М.В. Калякин, О.В. Волцит*. 2006.
- Материалы зоолого-ботанических исследований в горных массивах Би Дуп и Хон Ба, Далатское плато, Южный Вьетнам. *Л.П. Корзун, В.В. Рожнов, М.В. Калякин* (ред.). 2006.
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