

# Current concepts of Gerbillid phylogeny and classification

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## Introduction

Gerbillids constitute a moderately small group of about 20 genera (PAVLINOV *et al.*, 1990; MUSSER and CARLETON, 1993). This group attracted close attention of taxonomists in the 70s and 80s, when several hypotheses about its relations with other muroids and principal phylogenetic divisions were elaborated (CHALINE *et al.*, 1977; PAVLINOV, 1982; TONG, 1989; PAVLINOV *et al.*, 1990). All these studies were morphological and considered a very limited data set, mainly dental and bullar morphology. One of the most surprising matters in this respect is that very few biochemical and cytogenetical works have been made with gerbillids, when compared with their "neighbors" in the classification (murids, arvicolids, etc.).

I do not mean that morphological data exhausted themselves and are now outdated. Instead, they still provide quite interesting information about gerbillid affinities and phylogeny. So, below I shall consider some focal points in the phylogeny and taxonomy of gerbillids, as they are seen by a morphologist.

## I The protoconulid story

On the basis of dental morphology, gerbillids have been continuously placed within the Palaearctic cricetids or considered as an independent family or subfamily. However, in the 70s, a hypothesis of their possible relation to Miocene myocricetodontines was proposed by paleontologists (JAEGER, 1977; CHALINE *et al.*, 1977). That was a really sudden idea, because the genus *Myocricetodon* with its closest allies possessing at least some accessory murid cusplets on lower molars was traditionally considered as a member of Murinae (JACOBS, 1978). Contrary to this, no recent gerbillid genus was known at that time to possess such a murid feature; only the Miocene *Protatera*, presumably related to taterillines, has been reported to possess a protoconulid on the first lower molar (JAEGER, 1977).

However, at the present moment, the protoconulid, one of the murid cusplets, was found in several recent gerbillid genera (fig. 1) as in *Ammodillus* (PAVLINOV, 1981) or in Asian *Tatera* and South African *Desmodillus* (PAVLINOV, 1985). In all these taxa, this small cusplet is clearly visible on the unworn first lower molar and disappears with tooth wear.

The presence of a protoconulid is clearly a primitive condition for gerbillids. The more advanced morphotypes of the anterior part of  $M_1$  are of two principal types, horseshoe and rhomboid ones (PAVLINOV, 1984). The first type is a characteristic feature of African taterillines, while the second is typical for *Gerbillus*, *Meriones* and their allies. In *Desmodillus*, it is possible to trace, in a set of teeth with various degrees of wear, the interrelations among these morphotypes. The protoconulid first becomes united with elements of the anteroconid to turn into the horseshoe type, and then the latter turns into the rhomboid type. If we take this ontogenetic transformation series as a kind of recapitulation, it could be supposed that the rhomboid type is a derivative of the horseshoe type, and the latter is a derivative of the type with an isolated protoconulid (PAVLINOV, 1984).

In this connection, one can note that the horseshoe type also occurs sometimes in *Gerbillus* (PETTER, 1956; PAVLINOV, 1984) for which the rhomboid type is typical. Following the above arguments, it is possible to consider such a condition as a kind of atavism. If this is

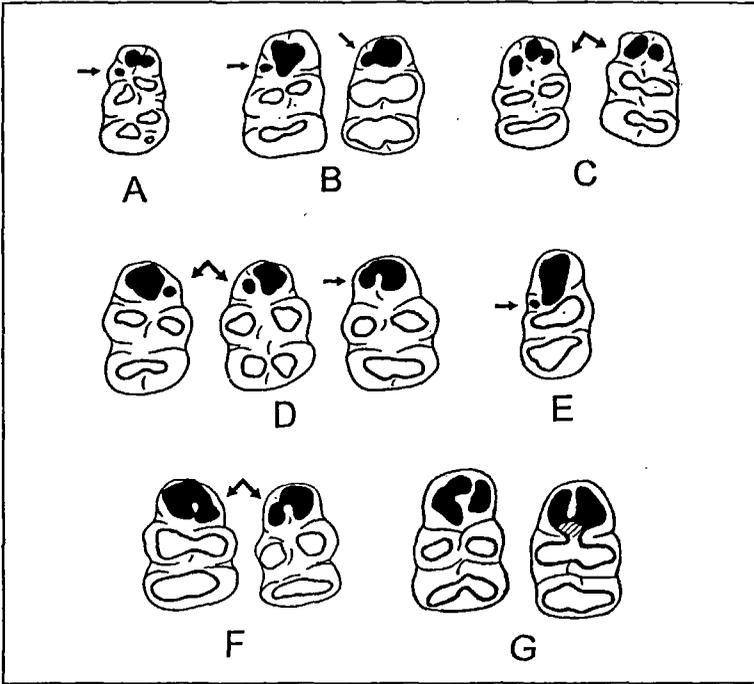


Figure 1

Dental crown pattern of minimally worn  $M_1$  in some gerbillids and their allies to show the presence of protoconulid and anteroconid (both shown in black). A) *Myocricetodon*, B) *Protatera*, C) *Tatera indica*, D) *Desmodillus*, E) *Ammodillus*, F) *Gerbillurus*, G) *Gerbillus*. Arrows indicate the position of the protoconulid. A and B are after JAEGER (1977); others are from PAVLINOV (1984).

correct, then it can be supposed that the horseshoe type of anteroconid was a characteristic feature of direct ancestors of *Gerbillus*. And this can be taken as an indirect evidence that the protoconulid occurred in the ancestors of many gerbillid genera, and not only of those still retaining it.

One may conclude that the most recent ancestors of gerbillids did have an accessory "murid" cusplet, namely a protoconulid, on the first lower molar. On the basis of this conclusion alone, it seems clear that cricetids cannot be ancestors of gerbillids. The hypothesis of gerbillid affinities to myocricetodontines looks more plausible in the light of the anteroconid morphology.

However, it seems premature to unite these taxa in the same family, as CHALINE *et al.*, (1977) suggested. On the one hand, the myocricetodontines show no evolutionary trends in dental morphology common to “real” gerbillids. On the other hand, they still possessed a fairly “murid” mandible (as it was drawn in JAEGER, 1977), which suggests their auditory bulla was murid-like as well, that is without significant pneumatization.

As to the gerbillids themselves, the anteroconid morphology may witness about the following. The Ethiopian *Ammodillus* occupies an isolated position, as it is the only recent representative of the family possessing a separate protoconulid that does not join with the anteroconid proper. The South African *Desmodillus* and *Gerbillurus* are very similar with respect to dental morphology. They both display a primitive horseshoe pattern of anteroconid and, by this, could be related phylogenetically to the taterilline lineage. Finally, the Asian *Tatera indica* displays a more primitive anteroconid morphology as compared to its African relatives.

## ■ Mastoid morphology

The next structure to be discussed is the morphology of the mastoid portion of the auditory bulla. LAY (1972), PAVLINOV (1980), and PAVLINOV *et al.* (1990) showed that gerbillid taxa differ from each others by both the degree and, more importantly, the type of mastoid pneumatization (fig. 2).

Omitting the details, pneumatization of a primitive solid mastoid can be considered as resulting from the penetration of tympanic cavity into the mastoid. Two principal pathways of this penetration are supposed to occur in the gerbillids, i.e. anterior and ventral. In the first case, the tympanic cavity penetrates into the mastoid through the dorsal part of the bulla, just above of the ossicles and before the mastoid. This process produces morphotypes B to E. The ventral penetration occurs through the posterior part of the bulla, just ventral to the mastoid. To it, morphotypes F to H belong.

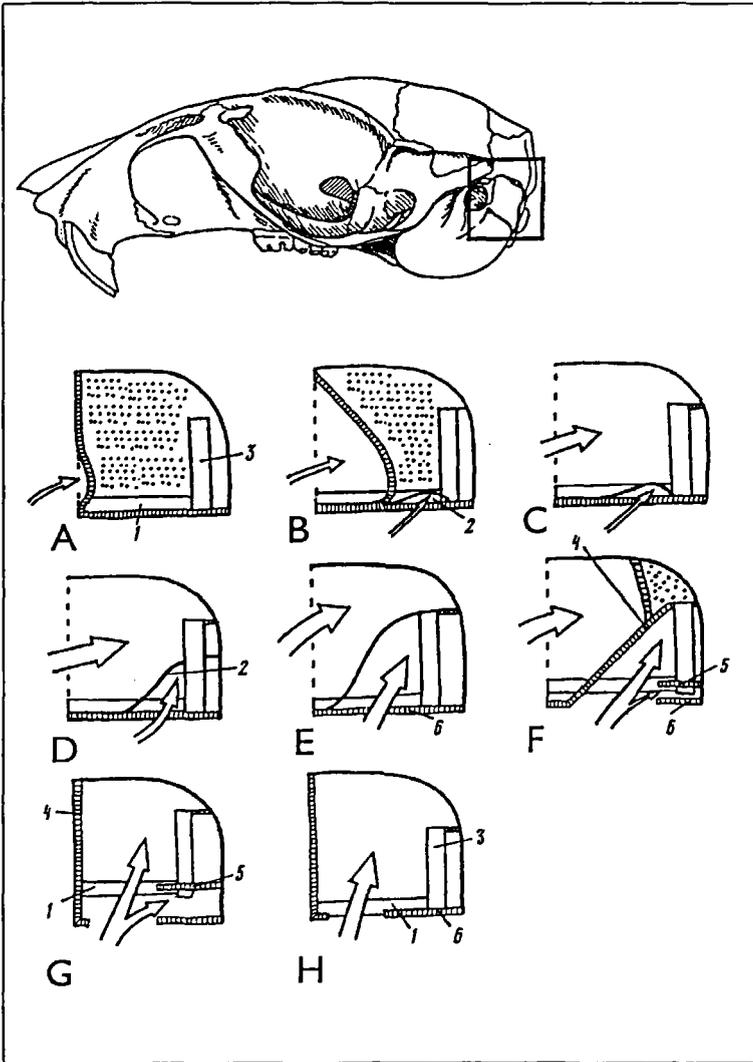


Figure 2

Principal morphotypes (A-H) of the mastoid in Gerbillidae (after PAVLINOV *et al.*, 1990). Schematic parasagittal section. Arrows indicate pathways of penetration of the tympanic cavity into the mastoid. Dashed line indicates an imaginary anterior border between tympanic and mastoid cavities (no bony septa separates them), dotted area indicates part of the lateral mastoid wall knitted with the parafloccular fossa. Figures designate respective bony elements: 1, 3) semicircular channels; 2) inner mastoid septa; 4) mastoid septa; 5) caudal septa; 6) tymano-mastoid septa.

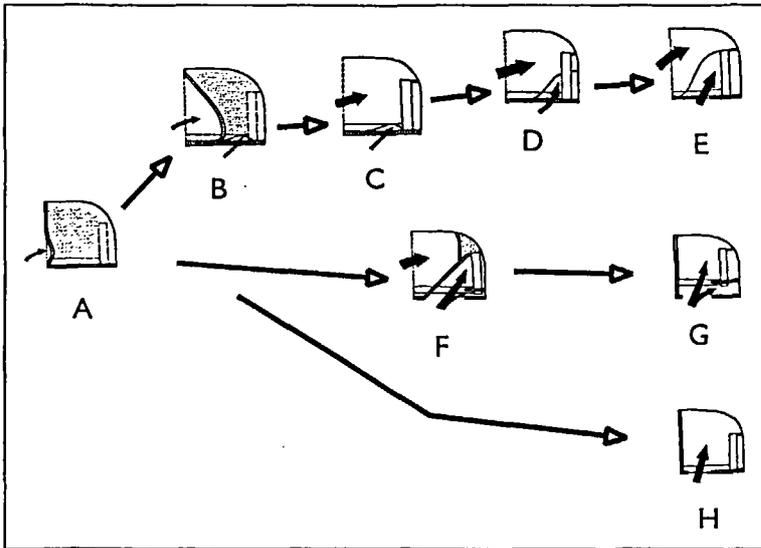


Figure 3  
Transformation series indicating supposed evolutionary relations between mastoid morphotypes in Gerbillidae. Morphotype designations are the same as on fig. 2.

There is also a secondary ventral penetration occurring within the so-called anterior type. The resulting pattern of mastoid chambers may be superficially very similar to those displayed by primary ventral penetration (compare morphotypes E and F). However, the bony elements separating the respective mastoid chambers are not really homologous: the diagonal septa includes the horizontal semicircular channel in morphotype E and does not include it in morphotype F.

Thus, one may suppose that each of these two pathways is quite constrained morphogenetically. As such it seems highly improbable for one of them to "switch" into the other. On this basis, it is possible to reconstruct transformation series of gerbillid mastoid morphotypes (fig. 3). It is then reasonable to hypothesize that the type of mastoid pneumatization can be taken as the evidence of phylogenetic affinities of respective gerbillid taxa. The most interesting points in this respect are the following.

Among the taterillines, *Taterillus* is the most primitive (morphotype A) and the Asian *Tatera* is the most advanced (morphotype C).

African *Taterona* and *Gerbilliscus* belong to different lineages, each displaying the initial stage of anterior and ventral penetrations (morphotypes B and F, respectively).

As with dental morphology, *Desmodillus* and *Gerbillurus sensu lato* are again very similar in mastoid structure (morphotypes B and C, respectively). They belong to the same lineage and differ only by the degree of pneumatization, the least being in the subgenus *Progerbillurus* (morphotype B).

*Desmodilliscus* (morphotype G) does not belong to the same lineage as *Desmodillus*, so they cannot be considered as close relatives. Instead, *Desmodilliscus* resembles in this respect to *Gerbillus* and *Meriones* and their allies (all possess morphotypes F or G).

Mastoid pattern in the genus *Pachyuromys* (morphotype H) is peculiar. It belongs to the ventral type of pneumatization but can be derived from a very primitive condition only.

## ■ The cladogram

The resulting cladogram (fig. 4) has been produced (PAVLINOV, 1982; PAVLINOV *et al.*, 1990) without using any computer program. It reflects relations among recent genera derived mainly from the data on dental and bullar morphology. The following peculiarities are to be stressed.

Taking Gerbillidae as a family, two subfamilies can be defined, Taterillinae and Gerbillinae *sensu stricto*. The former contains also *Desmodillus* and *Gerbillurus* as closest relatives, the latter – the remainder genera, except probably *Ammodillus*.

At the tribal level, two presumably monophyletic taxa are recognized in Taterillinae and four in Gerbillinae *sensu stricto*. Their contents are evident from the cladogram, so my additional comment might only be that *Desmodilliscus* and *Pachyuromys* both constitute monotypical tribes of their own. Notice also that both the middle ear and dental morphology place *Sekeetamys* with Rhombomyini rather than with Gerbillini *sensu stricto*. (PAVLINOV *et al.*, 1990).

At nearly the same time, a paleontologist, TONG (1989), published a phylogenetic tree of Gerbillidae which appeared to be very similar

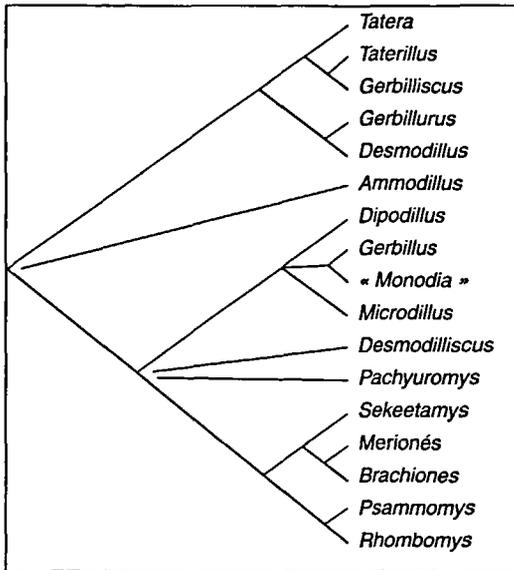


Figure 4  
Cladistic relations  
among recent  
genera of Gerbillidae  
(after PAVLINOV *et al.*,  
1990) derived  
mainly from  
dental and bullar  
morphology.

to that of mine (PAVLINOV, 1982; PAVLINOV *et al.*, 1990). The principal differences are the following.

The genera *Desmodillus*, *Ammodillus* and *Desmodilliscus* are placed by TONG (1989) together among the gerbillines proper. Based upon the morphological data described here, this suggestion seems to be incorrect. The patterns of bullar morphology in *Desmodillus* and *Desmodilliscus* belong to different types of pneumatization; these genera also have distinct dentitions. The position of *Ammodillus* remains unclear.

The genus *Pachyuromys* is placed by TONG (1989) close to *Brachiones*, which is improbable: the latter is just a specialized relative of *Meriones* (PAVLINOV *et al.*, 1990).

Among the questions regarding within-gerbillid affinities, of special interest are the relations among taterillines. Usually, *Tatera* proper, *Gerbilliscus* and *Taterona* are all considered congeneric, while *Taterillus* is given full generic rank. However, my data indicate that the Asian branch of this group represented by *Tatera sensu stricto* may be quite isolated from the African branch including the remaining taterillines. It is characterized by peculiar combination of a more

archaic dental pattern (initial stage of horseshoe anteroconid development) and a more advanced mastoid type. Contrary to this, *Gerbilliscus* and *Taterona* (together with *Taterillus*) possess the most advanced horseshoe anteroconid and a more primitive mastoid. The taxonomic conclusion might be that the genus *Tatera* is to be devoted to the Asian species only, while African taterans are to be included in a separate genus whose valid name should be *Gerbilliscus sensu lato*.

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