

## Cladistic analysis of the dormouse genus *Graphiurus* Smuts, 1832 (Rodentia: Gliridae), with comments on evolution of its zygomaseteric construction and subgeneric taxonomy

Igor Ya. Pavlinov & Elena G. Potapova

**ABSTRACT.** Cladistic analysis of relationships among 10 *Graphiurus* species based on 30 cranial characters allowed us to recognize three clades. Accordingly, *Aethoglis* (includes *G. nagtglasi*) and *Claviglis* (includes *G. crassicaudatus*) are to be treated as subgenera. Monophyly of *Graphiurus* s.str. (supposedly including all other species) is formally proved by our analyses but requires future investigation pending on inclusion of more taxa and characters. Diagnoses of *Aethoglis* and *Claviglis* are provided. A possible scenario for the evolution of zygomaseteric construction in *Graphiurus* is discussed. It is supposed that primitive hystricomorphy is initial, whereas myomorphy is a derived zygomaseteric feature of this genus.

**KEY WORDS:** Gliridae, *Graphiurus*, *Aethoglis*, *Claviglis*, taxonomy, zygomaseteric construction.

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## Кладистический анализ сонь рода *Graphiurus* Smuts, 1832 (Rodentia: Gliridae), с заметками по эволюции зигомассетерной конструкции и подродовой систематике

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**РЕЗЮМЕ.** Кладистический анализ родственных связей между 10 видами *Graphiurus* по 30 краниологическим признакам позволяет различать три клады. На этом основании таксоны *Aethoglis* (включая *G. nagtglasi*) и *Claviglis* (включая *G. crassicaudatus*) следует рассматривать как подроды. Монофилия подрода *Graphiurus* s.str. (предположительно включающего все прочие виды) предварительно подтверждена нашим анализом, но необходимо исследование большего числа признаков и видов. Даны диагнозы подродов *Aethoglis* и *Claviglis*. Обсуждаются возможные пути эволюции зигомассетерной структуры в роде *Graphiurus*. Предполагается, что для этого рода исходным состоянием была примитивная гистрикоморфия, а производным — миоморфия.

**КЛЮЧЕВЫЕ СЛОВА:** Gliridae, *Graphiurus*, *Aethoglis*, *Claviglis*, систематика, зигомассетерная конструкция.

### Introduction

The above-species taxonomy of the native African dormice still remains largely controversial. Formerly, four genus-group taxa have been erected by different authors. The first was *Graphiurus* Smuts, 1832 with the type species *G. capensis* Smuts, 1832 (now synonymized with *G. ocularis* Smith, 1829). Genus *Claviglis* Jentink, 1888 (type species *C. crassicaudatus* Jentink, 1888) has been offered to separate all other African dormice species from *Graphiurus* s.str. Subsequently, the genus *Gliriscus* Thomas et Hinton, 1925 has been established for *G. platyops* Thomas, 1897, and the genus *Aethoglis* Allen, 1936 has been offered for *G. nagtglasi* Jentink, 1888. Thus, four genera in total have been recognized for the African dormice by the middle of XX century, of which two (*Graphiurus* s.str. and *Aetho-*

*glis*) appeared to be monotypical, while *Claviglis* was treated as including most of the species (Allen, 1939).

Later on, lumping tendency predominated in mammalian taxonomy; all native African dormice were included in the single genus *Graphiurus* in which only two subgenera were recognized, nominotypical *Graphiurus* s.str. with one species and *Claviglis* with the remainders (Ellerman *et al.*, 1953; Misonne, 1974). Meanwhile, Rosevear (1969) suggested that *G. crassicaudatus* and *G. nagtglasi* (formerly *G. hueti*, see Grubb & Ansell, 1996; Holden, in press) be kept as members of a separate subgenus (or even genus) *Claviglis* (which synonymizes *Aethoglis* with the latter); and to unite all other species (possibly save *G. ocularis*) to be united in the subgenus *Gliriscus* (see also Holden, 1993, 1996). Contrary to this, it was shown by the second author (Potapova, 2001) that *Claviglis* proper

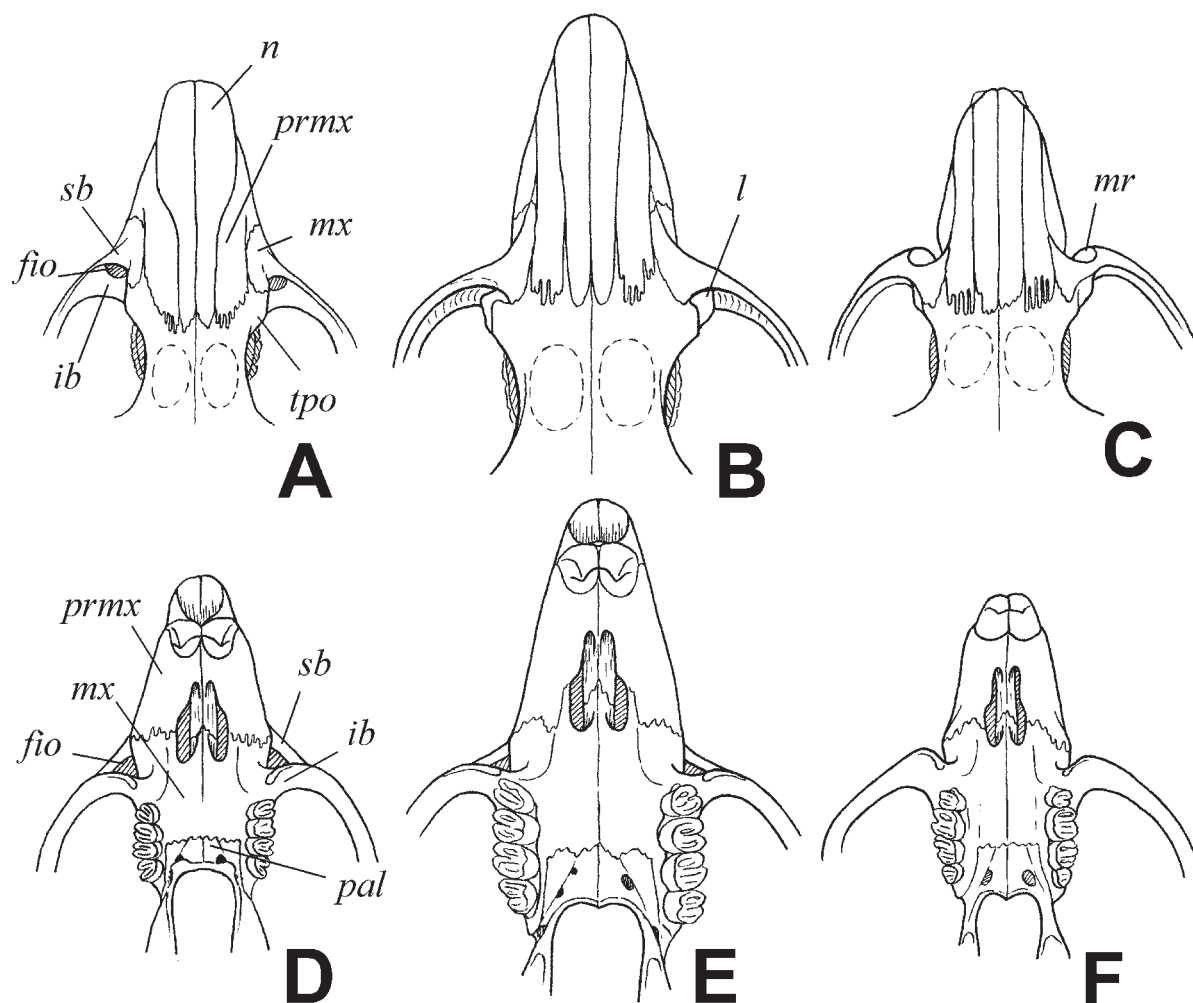


Figure 1. Rostral region and palate in *Graphiurus murinus* (A, D), *G. nagtglasi* (B, E) and *G. crassicaudatus* (C, F) in dorsal (A–C) and ventral (D–F) views (after Potapova, in press, with emendations).

Abbreviations: *fio* — infraorbital foramen, *mr* — masseteric ridge, *mx* — maxillare, *n* — nasale, *pal* — palatinum, *prm* — praemaxillare, *sb*, *ib* — superior (*sb*) and inferior (*ib*) branches of the anterior zygomatic root, *tpo* — praeorbital tubercle.

and *Aethoglis* differ both from each other and from the remainder of graphiurines by auditory bullar morphology, a conclusion later supported in part by study of zygomasseteric morphology (Rossolimo *et al.*, 2001). Respectively, it was suggested to recognize them as different monotypical subgenera, all other species being included in the nominotypical subgenus *Graphiurus* s.str. (Rossolimo *et al.*, 2001).

Nearly all the above concepts of graphiurine taxonomy were based on combinatorial (that is, basically typological) analysis of few skull traits. For instance, monotypy of *Graphiurus* s.str. was substantiated by reduction of upper premolar in *G. ocularis*, subgeneric status of *Gliriscus* — by flatness of the skull in *G. platyops*, separateness of *Aethoglis* and *Claviglis*, as well as their unity, was based originally on several quantitative skull characters of respective type species. More comprehensive analysis of skull morphology, including zygomasseteric construction and mastoid

was undertaken by the present authors (Potapova, 2001, in press; Rossolimo *et al.*, 2001), but without explicit phylogenetic argumentation.

In this paper, we intend to provide phylogenetic bases for subgeneric classification of the genus *Graphiurus* using formal cladistic analysis. Special attention will be paid to evolution of zygomasseteric construction which is one of the key characters in glirid phylogeny and classification. As the morphological background of the present analysis has been published elsewhere (Potapova, 2001, in press; Rossolimo *et al.*, 2001), we do not give any detailed descriptions here. The results provided herein are to be considered preliminary, as not all the *Graphiurus* species was studied by us.

## Materials and methods

The following ten species of *Graphiurus* were studied: *G. angolensis* de Winton, 1897, *G. christyi* Dollman, 1914,

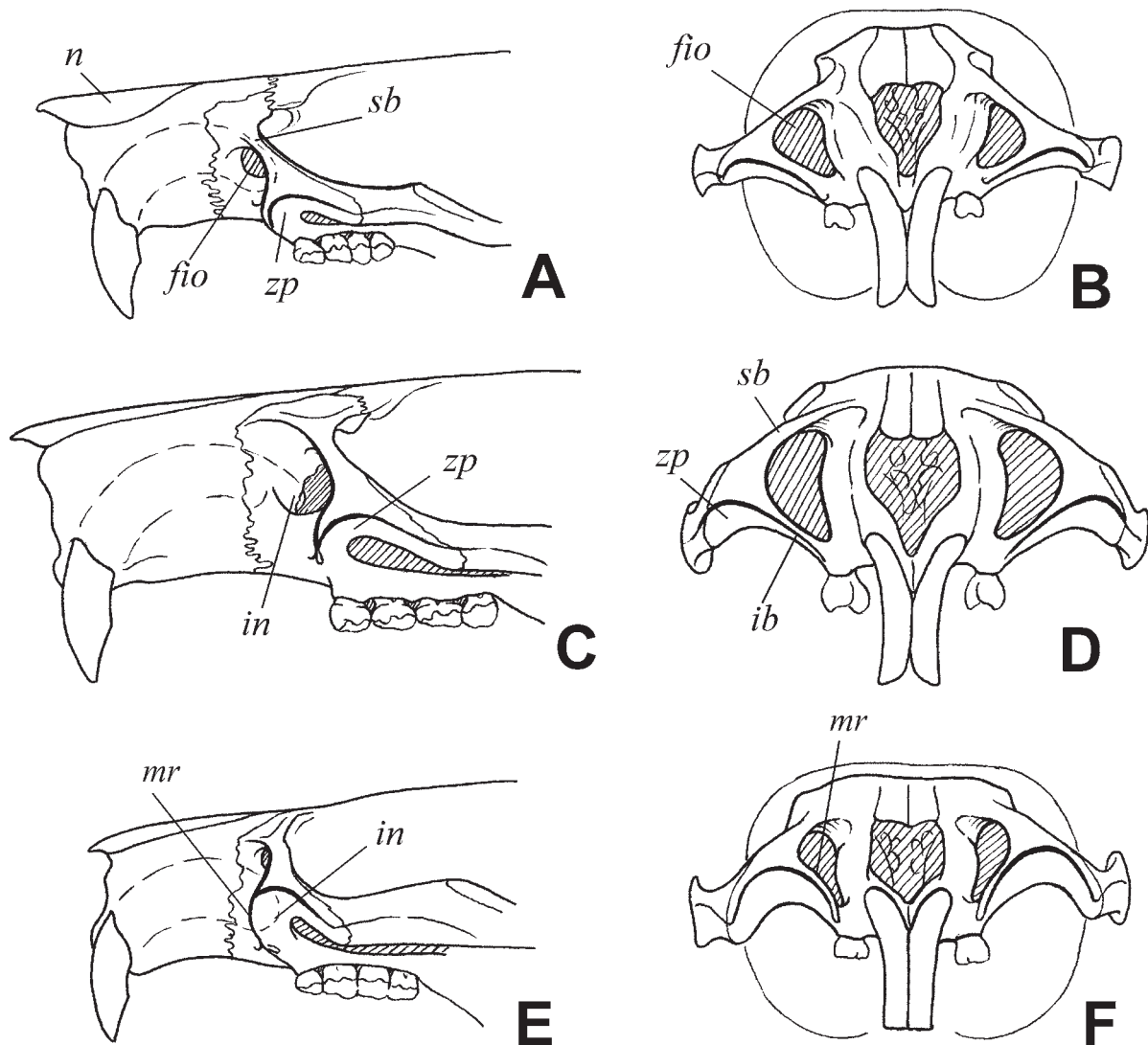


Figure 2. Rostral region in *Graphiurus murinus* (A, B), *G. nagtglasi* (C, D), *G. crassicaudatus* (E, F) in lateral (A, C, E) and frontal (B, D, F) views (after Potapova, in press, with emendations).

Abbreviations: *fio* — infraorbital foramen, *in* — posterior edge of incisor, *mr* — masseteric ridge, *n* — nasale, *sb*, *ib* — superior (*sb*) and inferior (*ib*) branches of the anterior zygomatic root, *tpo* — praeorbital tubercle, *za* — zygomatic arch, *zp* — zygomatic plate.

*G. crassicaudatus* Jentink, 1888, *G. kelleni* Reuvsen, 1890, *G. lorraineus* Dollman, 1910, *G. murinus* Desmarest, 1822, *G. parvus* True, 1839, *G. nagtglasi* Jentink, 1988, *G. ocularis* Smith, 1829, *G. surdus* Dollman, 1912. Additionally, the following rodent species were included in the sample studied to make the similarity relations among graphiurines by some morphological structures more evident: *Spermophilus* sp., *Glis glis* Linnaeus, 1766 and *Dryomys laniger* Felten & Storch, 1968. The specimens examined (see Appendix 1) belong to collections of the American Museum of Natural History (AMNH), Muséum National d'Histoire Naturelle (MNHN), and Zoological Museum of Moscow University (ZMMU).

Thirty morphological traits used in cladistic analysis to represent the following skull portions: rostrum, zygomatic construction (Figs. 1 and 2), braincase, palate, dentition, mandible, auditory bulla (Fig. 3). Quantitative charac-

ters were estimated by visual examination of the specimens, while quantitative measurements have been taken by caliper and categorized afterward. Character descriptions are given in Appendix 2; the data matrix is given in Tab. 1.

Parsimony cladistic analysis was conducted with PAUP 3.1.1 (Swofford, 1993). The characters in different runs were included in either unordered or irreversible (some of them, see Results and discussion section) modes, all equally weighted. Branch-and-bound algorithm was employed for searching initial minimum-length trees and 50% majority-rule consensus tree was calculated for each branch-and-bound run. Additionally, bootstrapping (with 100 replicates) was used to assess support of tree topologies. In all runs, the trees were rooted by an artificial outgroup in which character states were defined by one of us (EP), taking into consideration most probable evolutionary scenarios for respective characters in sciurognath rodents.

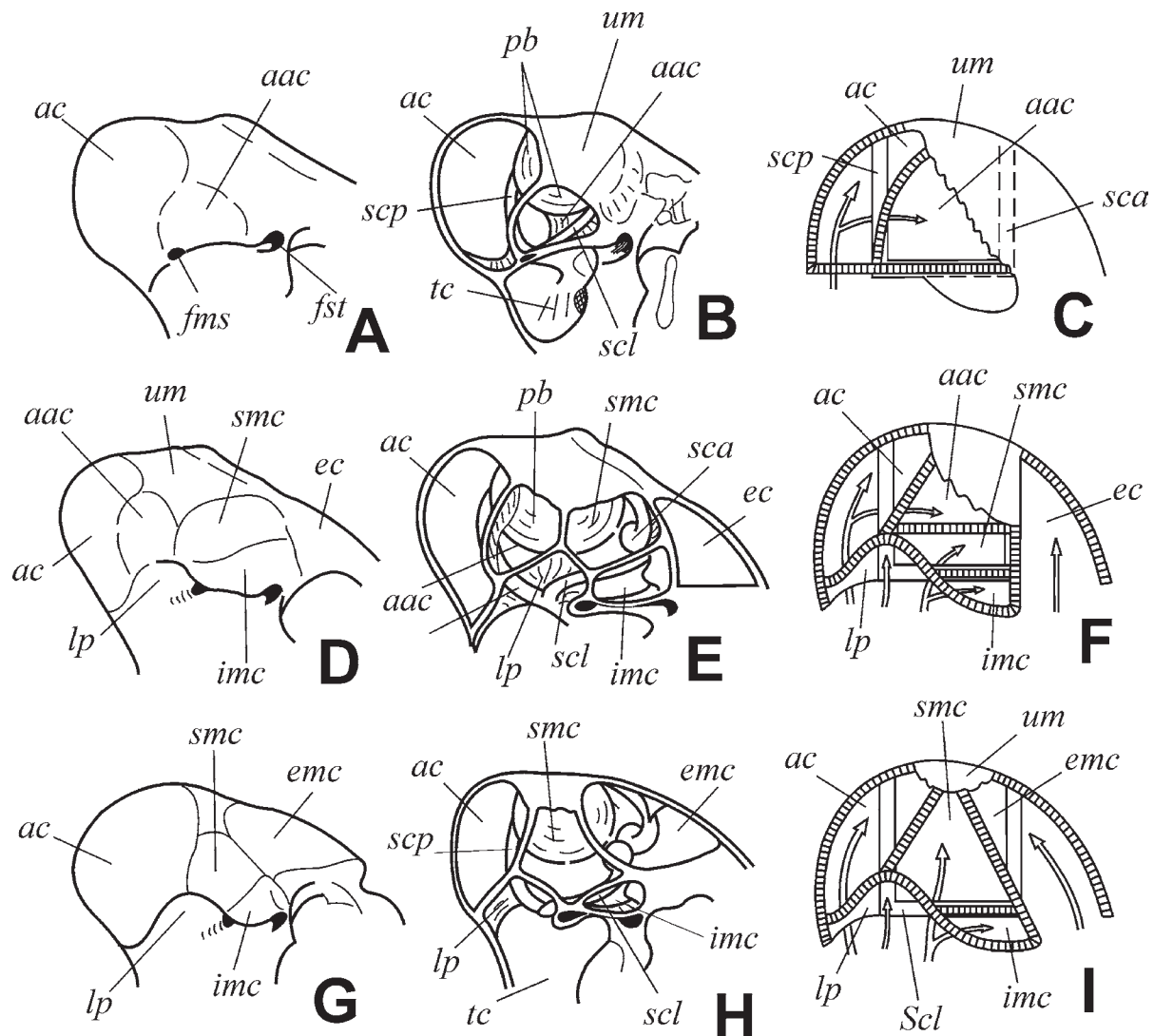


Figure 3. External (A, D, G) and internal (B, E, H) mastoid morphology and scheme of the tympanic cavity expansion into mastoid (C, F, I) in *Graphiurus nagtglasi* (A–C), *G. crassicaudatus* (D–F), *G. lorrainus* (G), *G. murinus* (H, I) in lateral and slightly dorsal view. The lateral outer wall removed in B, E, and H. Arrows in C, I, and F indicate direction of the tympanic cavity expansion. The septae between the chambers as well as the anterior, dorsal and posterior outer walls of the mastoid are shaded. After Rossolimo *et al.* (2001), with emendations.

Abbreviations: *ac* — antral chamber, *aac* — additional antral chamber, *ec* — epitympanic chamber, *emc* — epitympano-mastoid chamber, *fms* — foramen for stapedius muscle, *fst* — stylomastoid foramen, *imc* — inferior mastoid chamber, *lp* — lateral pocket, *pb* — parafoveolar bulge, *sc* — semicircular canals: anterior (*sca*), lateral (*scl*), posterior (*scp*), *smc* — superior mastoid chamber, *tc* — tympanic cavity, *um* — uninflated parts of the mastoid.

## Results and discussion

**Analyses of all species.** In these analyses, all taxa are considered together and all characters are unordered. In respect to graphiurines, the consensus cladogram (Fig. 4A) indicates that *G. nagtglasi* and *G. crassicaudatus* belong to basal divergence of African dormice. Among the remaining graphiurine species, *G. ocularis* takes the most isolated position. Bootstrapping gives a quite similar tree topology (Fig. 4B), but bootstrap estimates are noteworthy. As a matter of fact,

only few clades are strongly supported; the clade which includes all *Graphiurus* species but *G. nagtglasi* and *G. crassicaudatus* is most heavily supported. Looking at the latter cladogram, it could be concluded that the graphiurine species studied here form the following three clades: 1) *G. nagtglasi*; 2) *G. crassicaudatus*; 3) *G. ocularis*, *G. lorrainus*, *G. parvus*, *G. angolensis*, *G. murinus*, *G. kelleni*, *G. surdus*, and *G. christyi*. Within the latter clade, two subclades could be recognized as defined most strongly by this run: *G. ocularis* and *G. surdus* + *G. christyi*.

Table 1. Character state matrix used in cladistic analyses (for characters see Appendix 2).

Characters Taxa	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
Outgroup	1	1	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
<i>Spermophilus</i>	2	1	0	0	0	4	1	1	0	1	0	0	0	1	0	?	0	0	0	0	1	0	0	1	1	0	0	0	0	0
<i>Glis glis</i>	1	0	0	0	1	3	1	1	1	0	0	0	0	0	0	2	0	0	1	0	1	0	1	1	1	1	0	0	0	0
<i>Dryomys laniger</i>	1	0	0	0	0	3	1	1	1	0	1	1	0	0	0	2	0	0	0	0	1	2	1	1	1	1	1	1	1	0
<i>G. angolensis</i>	0	1	0	1	?	1	0	0	0	?	1	2	0	0	1	0	0	1	0	0	0	2	1	1	1	1	1	1	1	0
<i>G. christyi</i>	2	1	0	1	?	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	2	1	1	1	1	1	1	1	0
<i>G. crassicaudatus</i>	1	0	1	1	1	2	0	1	2	1	2	0	0	1	0	1	0	0	1	1	1	1	1	1	0	1	1	1	1	1
<i>G. kelleni</i>	1	1	0	1	?	1	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	2	1	1	1	1	1	1	1	0
<i>G. lorrainensis</i>	1	1	0	2	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	2	1	1	1	1	1	1	1	0
<i>G. murinus</i>	1	1	0	1	0	1	0	0	0	1	1	1	0	0	0	0	0	1	0	0	0	2	1	1	1	1	1	1	1	0
<i>G. nagtglasi</i>	2	0	0	0	1	1	1	1	1	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1
<i>G. ocularis</i>	?	1	0	2	0	1	1	0	0	0	1	1	0	1	0	0	1	1	0	0	0	2	1	1	1	1	1	1	1	0
<i>G. parvidens</i>	1	1	0	2	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	2	1	1	1	1	1	1	1	0
<i>G. surdus</i>	2	1	0	1	0	1	0	0	0	0	1	1	0	0	0	0	0	1	1	0	0	1	1	1	1	1	1	1	1	0

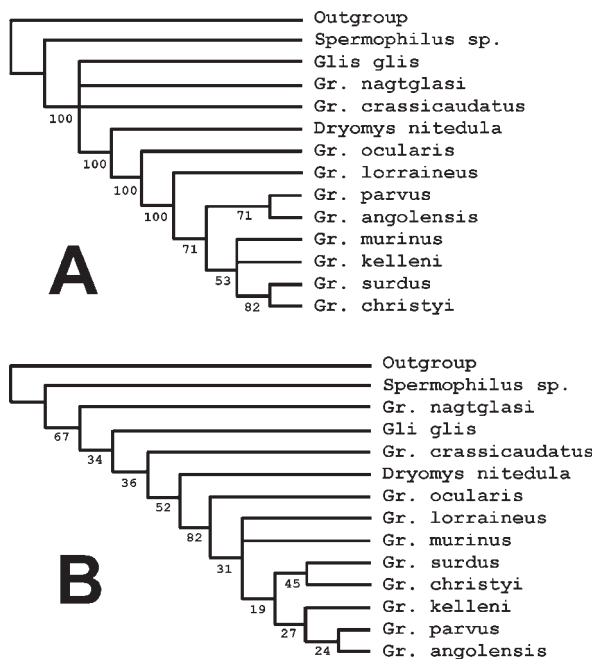


Figure 4. Consensus (A) and bootstrap (B) cladograms for all taxa studied. Numerals at the nodes indicate percentage of respective clades in the set of all calculated trees (A) and bootstrap support values (B).

The fact that both *Glis* and *Dryomys* appear among graphiurine species is by no means to be taken as demonstration of paraphyletic status of the native African dormice. Instead, such a branching pattern stresses the scale of differences in skull characters among the above three clades. Besides, this pattern is significant in understanding some important trends within graphiuri-

rines themselves (see section of zygomatic evolution below).

**Analyses of graphiurine species.** In these analyses, only graphiurines are being studied, so non-graphiurines have no effect on optimization of respective tree topologies. In the present case, the characters are included in different runs either all unordered or some irreversible (characters 6, 8, 15, 17, 20, 22, and 24–30).

The run with unordered characters produces the consensus cladogram (Fig. 5A) with branching pattern quite similar to already discussed. Again, *G. nagtglasi* takes the most basal position and next to it *G. crassicaudatus* branches out. However, unlike preceding analyses, the present one places *G. surdus* in the basal position of clade (3) of remaining species while *G. ocularis* is clustered with *G. lorrainensis*, *G. parvus* and *G. angolensis*. The consensus cladogram for partly irreversible characters (Fig. 5B) differs from the previous one only by basal (for the clade 3) position of *G. murinus*, position of *G. ocularis* remaining the same.

Bootstrapping of both unordered and partly irreversible characters (Fig. 5C, D) produces a cladogram which agrees in general with the branching topology just discussed, with support of the above clade (3) remaining the highest. It is noteworthy that *surdus* branches out first in this clade in both bootstrap runs.

Clade (3), accordingly to results of cladistic analysis, is formally defined by a set of characters: 2(1), 5(0), 8(0), 16(0), 18(1), 22(2), 25(1), and 30(0) (see Appendix 1 for their interpretation). Of these, however, 8(0) probably and 30(0) certainly are plesiomorphic and have to be excluded from the synapomorphy list of this clade; 22(2) reflects overall pneumatization of the tympanic bulla, so homoplasies are highly probable;



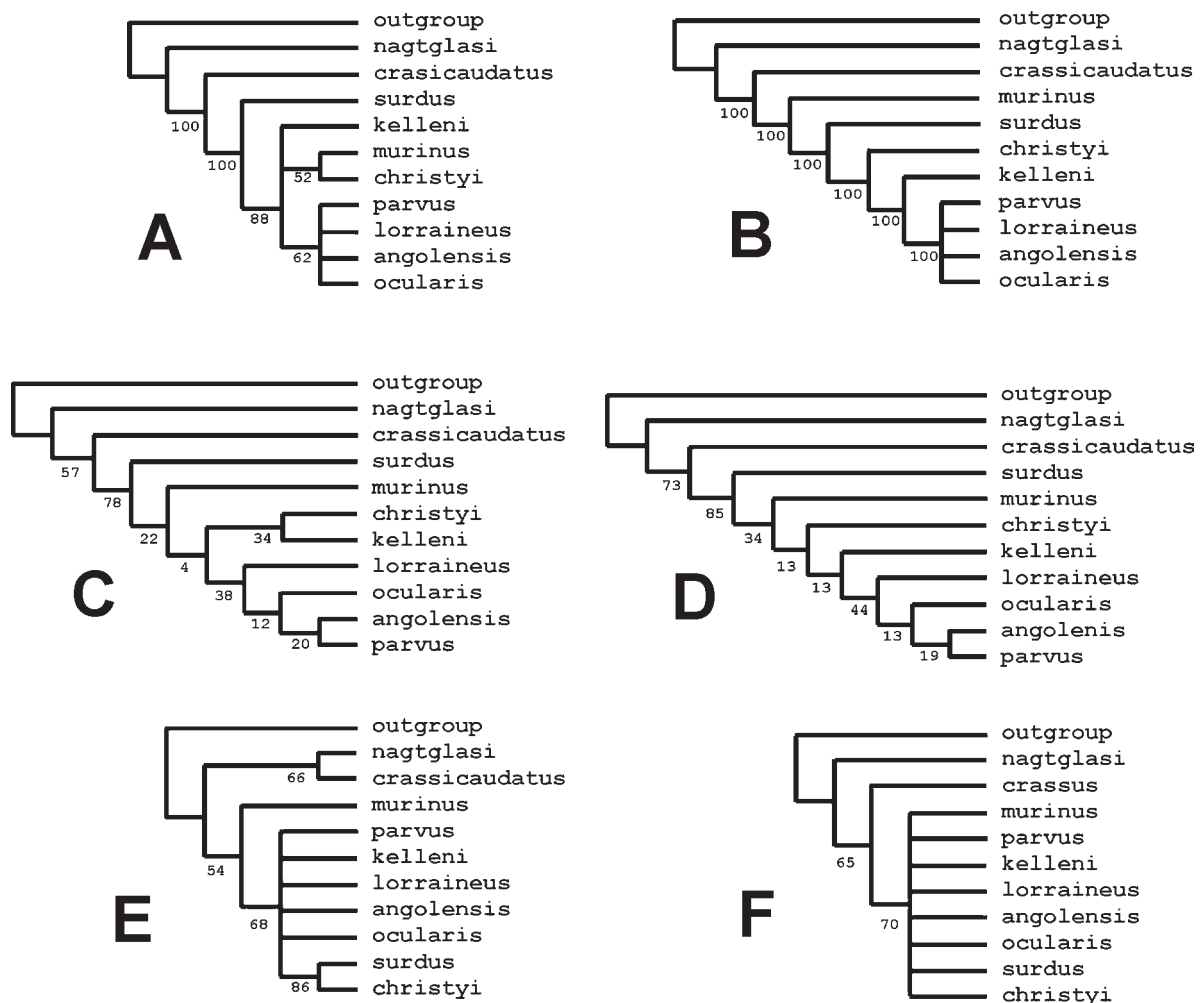


Figure 5. Cladograms for graphiurines only: consensus trees based on unordered (A) and partly irreversible (B) characters (tree length 55); C and D — the same based on bootstrapping; E — consensus tree calculated with constrain (tree length 56); F — consensus tree calculated with minimal tree length predefined as 56. Numerals at the nodes are the same as on Fig. 4. See text for explanations of cladograms (E) and (F).

others being of uncertain polarity and thus of uncertain phylogenetic value. Thus, the hypothesis of monophyly of this clade is actually not very strongly supported. However, the fact that use of irreversible characters also leads to the same tree topology, with but greater tree length due to more homoplasies (in characters 8, 18, 22, and 30), seems to leave no room for other possibilities.

Of particular interest might be the question of the relationship between the two species belonging to the basal radiation of graphiurines. As pointed out by Rosevear (1969), *G. nagtglasii* and *G. crassicaudatus*, despite their great size differences, share a lot of similarities in skull traits among at least West African graphiurines. To see if any cladistic support exists for these similarities, we ran PAUP with a constraint prohibiting paraphyly of *G. nagtglasii* + *G. crassicaudatus* group. The resulting consensus tree (Fig. 5E) appeared to be only one step longer (tree length 46) than the original one for unordered characters (tree length 45). As a matter of fact, this new topology appears to be

the only next shortest tree, trees with any other possible topologies being several more steps longer.

Character analysis revealed that the *G. nagtglasii* + *G. crassicaudatus* group is defined on the constrained tree by the following character states: 2(0), 5(1), 8(1), 16(1), and 30(1) (see Appendix 2 for their interpretation). Of this set, the shared synapomorphies of characters 8 and 30 are undoubtedly significant, others being quite vague in respect to their polarity and hence for cladistic reliability.

In order to study this grouping more exhaustively, another run of PAUP was conducted in which the minimal length of unconstrained trees to be searched by branch-and-bound algorithm was predefined as 46. The topology of consensus tree for cladograms calculated under this condition does not contain the *G. nagtglasii* + *G. crassicaudatus* clade (Fig. 5F), which means that the latter clade occurs less frequently than alternative (paraphyletic) branching pattern. Thus, the specific character set of the *G. nagtglasii* + *G. crassicaudatus*

group revealed by the previous analysis does not unambiguously support its monophyly.

To sum up, all the results displayed above indicate that, given the species and the characters studied here, recognition of the three species groups within graphiurines seems to be most cladistically consistent. However, when considering results of our cladistic analyses, one ought to take into consideration incompleteness of our data set with respect to species representation. In particular, it lacks *G. platyops*, the type species of *Gliriscus*. Other missing species, as they are listed by Holden (2003) — *G. microtis* Noack, 1887, *G. monardi* St. Leger, 1936, *G. rupicola* Thomas et Hinton, 1925, may change the branching pattern of graphiurine cladogram that resulted from our data matrix.

**Evolution of zygomaseteric construction.** The genus *Graphiurus* is unique among glirids in having two types of zygomaseteric construction. It is primitively hystricomorphous in *G. nagtglasi* and in all the species belonging to clade (3), and it is primitively myomorphous in *G. crassicaudatus*; in other glirids included in our analysis it is typified as pseudosciuromorph (see Rossolimo *et al.*, 2001).

It is generally adopted that in rodent zygomaseteric evolution, sciurormorph and hystricomorph types are independent direct derivatives of protrogomorphy while myomorphy originated from primitive (non-advanced) hystricomorphy. However, as far as genus *Graphiurus* is concerned, two mutually exclusive hypotheses have been suggested to explain the observed morphology of recent species (no good fossils are available for these dormice lineage). According to one of them, graphiurine non-advanced hystricomorphy is secondary derived, and originated from non-advanced myomorphy (Daams & Bruijn, 1995), or pseudomyomorphy (see Vianey-Liaud, 1989, for its definition). Another concept treats non-advanced hystricomorphy in *Graphiurus* as primitive condition for this genus (Wahlert, 1985; Vianey-Liaud, 1989; Wahlert *et al.*, 1993; Landry, 1999; Rossolimo *et al.*, 2001; Potapova, in press).

To assess validity of either of these hypotheses, we analyzed distribution of character 6 states over the cladogram based on unordered characters (Fig. 6). For the nodes of the cladogram, the most probable character states were attributed by the PAUP subroutine following certain formal rules (see Swofford, 1993). The most parsimonious hypothesis following from such branching and distribution patterns presumes evidently that primitive hystricomorphy appeared first in the history of the genus *Graphiurus* while myomorphy is secondary relative to it. Indeed, in the cladogram under consideration, transition from protrogomorphy (postulated for the artificial outgroup) to hystricomorphy first and then to myomorphy presumes only three steps, while transition from protrogomorphy to myomorphy and then to hystricomorphy requires two more steps.

It is evident from this argumentation scheme that the immediate ancestor of the genus *Graphiurus* was most probably hystricomorphous. This condition was inherited by *G. nagtglasi* and by the clade (3). As to the

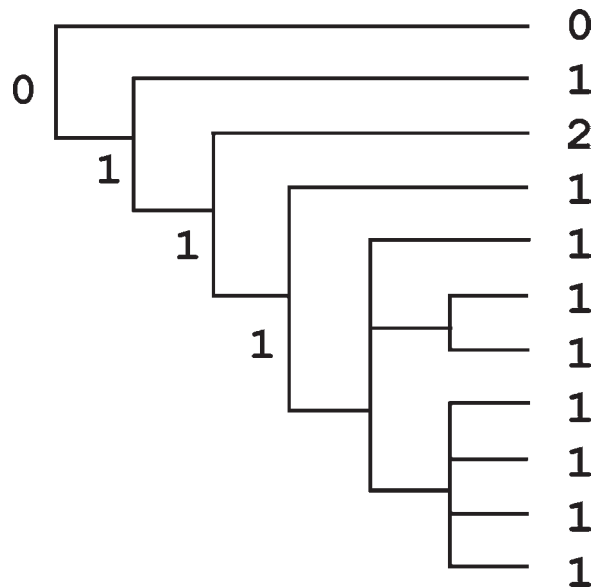


Figure 6. Distribution of the character 6 (zygomaseteric construction) states over cladogram for all taxa studied (the same as in Fig. 4a). Numerals at the branch tips indicate character states in each species, numerals at the nodes indicate supposed ancestral states for respective clades (see Appendix 2 for character description).

myomorphy (exhibited by clade 2), according to our cladistic hypothesis, it originated only once in the history of the genus. However, some signs of beginning of transition from hystricomorphy to myomorphy can be observed in *G. nagtglasi* and *G. surdus* (Fig. 2C, D). This may indicate that evolutionary trend toward primitive myomorphy may be characteristic to graphiurines in general and discriminates them from other glirids whose zygomaseteric construction tends to become pseudosciuromorphous. The latter differs from the typical sciurormorphy by rather large infraorbital foramen and from myomorphy by masticatory muscle not penetrating into this foramen (Rossolimo *et al.*, 2001; Potapova, in press). So, other species not included in our analysis should be studied to resolve the question.

**Taxonomic implications.** The above cladistic analysis implies that at least two subgenera, in addition to the nomynotypical one, can be recognized in the genus *Graphiurus*, namely *Aethoglis* and *Claviglis*. Short description of their skull morphology is provided below.

Subgenus *Aethoglis* includes *G. nagtglasi* only. In it, the skull is elongated, with zygomatic arch originating posterior to the caudal end of the incisor alveoli and with the anterior margin of the auditory bulla positioned posterior to the zygoma. Nasals are narrow and projected anteriorly beyond the incisors. Zygomaseteric construction is basically hystricomorph but demonstrates initial stage of forming the myomorphy (Fig. 2C, D): infraorbital foramen is rather large, superior anterior zygomatic root is shifted dorsally and is situated at the same level as inferior one, zygomatic plate is just little expanded on the lateral side of zygoma (not so

much as in *Claviglis*). Palate is wide and ends at the same level as the upper toothrow. The upper premolar is situated directly under inferior branch of anterior zygomatic root. The tympanic bulla is not large, its mastoid portion is inflated and contains only two chambers — antral and accessory antral. The mandible is elongated, its body is narrow, masseteric ridges originate at the level of anterior edge of the first lower molar, and the ventral border of angular process is situated lower than the symphyseal edge.

Subgenus *Claviglis* includes probably only *G. crassicaudatus*. Its skull is short, with wide braincase. The zygomatic arch originates at the level of the caudal end of incisor alveoli; the auditory bulla originates ventrally relative to the posterior zygomatic root. Rostrum is short. Nasals are narrow with practically parallel sides, not projected anteriorly beyond the incisors. Zygomas-seteric construction tends to be myomorphous: infraorbital foramen is narrow beneath, superior anterior zygomatic root is placed higher dorsally than in *Aethoglis* and is situated posterior to the level of inferior branch, zygomatic plate is conspicuously expanded on the lateral side of zygoma and eventually forms a small ridge directed forward. Palate is narrow and ends posterior to the upper toothrow. The latter is long and begins at the same level as the anterior zygomatic root. The tympanic bulla is of average size; the main contribution to its pneumatization belongs to tympanic portion while mastoid portion is the least in the genus. The epitympanic cell does not expand into mastoid, the mastoid contains five chambers: antral and accessory antral, lateral pocket, superior and inferior mastoid chambers. Mandible is massive, its corpus is wide, masseteric ridges originate anterior to edge of the first lower molar; angular process rises upward at the same level as the symphyseal corner.

The remaining species studied here presumably constitute a monophyletic clade which is a sister group to the above two subgenera. On this basis, this clade could formally be treated taxonomically as a subgenus, as well. However, as we already stated above, we were unable to study *G. platyops*, the type species for *Gliriscus*. As far as *G. ocularis* is concerned, one can not exclude a possibility for its reduced upper molar to be quite significant as taxonomic character, although it is not appropriate for accessing the common ancestry relationships, because it is an autapomorphy. If *G. ocularis* is retained with other species of the clade in question, the respective subgenus should be named *Graphiurus*; if it is kept in its own subgenus, and if *G. platyops* is proved to be member of our clade (3), the remaining species would constitute subgenus *Gliriscus*.

Skull morphology within the clade (3), as it is understood here, is rather diverse. Its most significant features are the shape of nasals and morphology of the zygomas-seteric construction. The nasals are club-shaped and widened anteriorly. They project anteriorly beyond the incisors. Zygomas-seteric construction is primitively hystericomorphous: the infraorbital foramen is large, superior branch of the anterior zygomatic root is situat-

ed more or less ventrally and anterior to level of its inferior branch, zygomatic plate does not expand, or occasionally minimally expand in some species, on the lateral side of zygoma. The upper toothrow is short and begins posterior to inferior branch of zygomatic root. Tympanic bulla is large, mastoid portion with five chambers, of which antral one is the largest. Accessory antral cell is absent. Mandible body is narrow, masseteric ridges originate anterior to the first lower molar.

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## Appendix 1. List of *Graphiurus* specimens examined

- G. angolensis*: AMNH # 88175, 88176 (Angola).  
*G. christyi*: AMNH 49916, 49905 (Congo).  
*G. crassicaudatus*: MNHN 80/1980 (Cote d'Ivoire).  
*G. kelleni*: ZMMU S-145815 (Namibia).  
*G. lorraineus*: MNHN 1208/1998, 1209/1998, 1174/1998 (Cote d'Ivoire).  
*G. murinus*: MNHN 85/1980, 92/1980 (Cote d'Ivoire), MNHN 368/1964 (Chad), MNHN 102/1970 (Zambia), MNHN 431/1981 (King N'ma Town), MNHN 105/1970, ZMMU S-150932, S-150937 (Ethiopia).  
*G. nagtglasi*: MNHN # 2905/1995 (Agiologowme), MNHN 136/1963 (Boukoko), ZMMU S-145589, S-145590 (Ghana), MNHN 1209/1998 (Cote d'Ivoire).  
*G. ocularis*: AMNH 168333 (South Africa, Namaqualand).  
*G. parvus*: ZMMU S-167674 (Nigeria), MNHN 508/1973 (Cote d'Ivoire).  
*G. surdus*: MNHN 543/1970 (Republique de Guinee).

## Appendix 2. Cranial characters used for the phylogenetic analysis

### Rostral part

1. Rostrum is short (0), of average length (1), or long (2).
2. Nasals are narrow with practically parallel sides (0) (Fig. 1B, C) or club-shaped and widened anteriorly (1) (Fig. 1A).
3. Nasals are projected anteriorly (0) (Fig. 1A, E; Fig. 2A, C), or ended posterior relative to incisors (1) (Fig. 1C; Fig. 2E).
4. Nasals are ended at the level of the superior anterior zygomatic root (0) (Fig. 1B), posterior to the root or eventually just posterior to the preorbital tubercle (1) (Fig. 1A), or extend far backwards into the orbit (2).
5. Maxillary is ended anteriorly relative to caudal edge of praemaxillare (0) (Fig. 1A), or at the level of caudal edge of praemaxillare or a little bit posteriorly (1) (Fig. 1B, C).

### Zygomasseteric construction

6. Zygomatic plate is protrogomorph (0), primitively hystricomorph (1) (Fig. 2A, B), primitively myomorph if zygomatic plate is slightly expanded onto lateral side of anterior zygomatic root and eventually forms a small ridge directed forward (2) (Fig. 2C), pseudosciuromorph as in *Glis* and *Myoxus* (3), or typically sciuromorph as in *Spermophilus* (5).
7. Superior anterior zygomatic root is situated at the level of caudal end of incisor (0) (Fig. 2A, E) or posterior to it (1) (Fig. 2C).
8. Superior anterior zygomatic root is situated more ventrally (0) (Fig. 2A) or more dorsally (1) (Fig. 2C, E) relative to the roof of the skull.
9. Superior anterior zygomatic root is situated anterior to (0) (Fig. 2A), at the same level as (1) (Fig. 2C), or posterior to (2) (Fig. 2E) the inferior anterior zygomatic root.
10. The zygomatic arch is narrow (0) (Fig. 2A), or wide (1) (Fig. 2E).

### Braincase

11. Braincase narrow (0), average in width (1), or wide (2).

### Palate

12. Palate is short (0) (Fig. 1D), or long (1) (Fig. 1F).
13. Palate is wide (0), or narrow (1).
14. Palate is ended anterior to or eventually at the level of the third upper molar (0) (Fig. 1D, E), or it is ended posterior to the third upper molar (1) (Fig. 1F).

### Upper tooththrow

15. Upper tooththrows are parallel (0), or converge posteriorly (1).
16. Upper tooththrow is relatively short (0), average in length (1), or long (2).
17. Upper premolar is large (0), or small (1).
18. Upper premolar is situated at the level of inferior anterior zygomatic root (0) (Fig. 1E, F) or posterior to it (1) (Fig. 1D).

### Mandible

19. Mandible body is narrow (0), or wide (1).
20. Angular process is situated below to (0), or at the same level as (1) symphyseal corner.
21. Masseteric ridges originate anterior to or at the level of edge of the first lower molar (0), or posterior to it (1).

### Auditory bulla (Fig. 3)

22. Bulla is small (0), of average size (2), or enlarged (2).
23. The anterior edge of bulla is situated caudally (0), or ventrally (1) relative to the posterior zygomatic root.
24. Epitympanic portion of bulla is slightly (0), or more significantly (1) inflated.
25. Epitympanic chamber does not extend (0) (Fig. 3E, F), or extends (1) (Fig. 3H, I) into mastoid.
26. Superior mastoid chamber is absent (0) (Fig. 3B, C), or present (1) (Fig. 3E, F, H, I).
27. Inferior mastoid chamber is absent (0) (Fig. 3B, C), or present (1).
28. Lateral invagination of the mastoid is absent (0) (Fig. 3B, C), or present (1) (Fig. 3E, F, H, I).
29. Antral chamber of the mastoid is absent (0), or present (1) (Fig. 3).
30. Accessory antral chamber of the mastoid is absent (0) (Fig. 3H, I), or present (1) (Fig. 3B, C, E, F).