



## Diagnoses and contents of new African and Eurasian Murinae (Rodentia, Muridae) tribes

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### Abstract

We provide here diagnoses for new tribes of *MURINAE* in order to make their nomina nomenclaturally available for the community of rodentologists and zoologists. We provide here diagnostic morphological characters for five new well supported monophyletic molecular clades and summarise their modern and fossil contents by updating results of recent systematic studies.

### Key words

**RODENTIA**; *MURINAE*; electronic publication; nomenclatural availability.

### Introduction

The *MURIDAE* represent the largest family of rodents, including at least 730 species recorded by Wilson & Reeder (2005) in the last classification of mammals. Until recently, the taxonomy and composition of this group was unstable due to a high degree of homoplasy and morphological convergence. The development of molecular techniques has finally allowed clarification of the subfamilial relationships within the *MURIDAE* and confirmed the validity of five subfamilies (*DEOMYINAE*, *GERBILLINAE*, *LEIMACOMYINAE*, *LOPHIOMYINAE* and *MURINAE*) (Fabre *et al.* 2012; Schenk *et al.* 2013). Within the *MURINAE*, which represent the bulk of the diversity of the family, relationships have not been fully clarified despite some attempts by various authors (Misonne 1969; Carleton & Musser 2005).

Focusing on the phylogeny of African *MURINAE*, we recently published (Lecompte *et al.* 2008) the description, diagnosis and nomina (scientific names) of five new tribes of rodents among which four are African and one Eurasian. Unfortunately, these new nomina are nomenclaturally unavailable because they were published only online before 1<sup>st</sup> January 2012, and all online publications are unavailable before that date according to Article 8.5.1 of the 2012 Amendment to the *Code* (Anonymous 2012).

We therefore here publish a formal correction to our original work. The present paper, being published in a periodical printed on paper and distributed simultaneously to all subscribers, and accessible online after this paper distribution, is available under the traditional rules of zoological nomenclature for paper publications.

We refer to the original work (Lecompte *et al.* 2008) for the details of the phylogenetic information concerning the new taxa. The new tribes had there been defined only molecularly, based upon their position as monophyletic clades. Because these tribes have been confirmed on molecular criteria by a broader phylogenetic analysis and reemployed by Schenk *et al.* (2013), Fabre *et al.* (2015) and Denys & Winkler (2015) without having been correctly defined and named, we provide below their diagnoses in order to make their nomina nomenclaturally available.

To define morphologically the new tribes, we used the original morphological characters defining the type-species of genera, completed by skull and dental characters resulting from morphological phylogenies figured in Lecompte *et al.* (2002), Taylor (2004), Taylor *et al.* (2004), Denys & Winkler (2015) and Missoupe *et al.* (2016). We add also the fossil genera that may be attributed to some of these tribes following Denys & Winkler (2015).

## **Definitions and compositions of new tribes**

*APODEMINI* trib. nov.

### ***Name-bearing type (onomatophore)***

Type genus: *Apodemus* Kaup, 1829.

### ***Original type genus diagnosis***

Medium-sized mice, with hairy and short tail, naked ears. Resembling *Mus* Linnaeus, 1758 and living in NE Europe (Kaup 1829).

### ***Emended diagnosis of tribe***

*Mus*-like rodents, small size (head and body length (HB): 70–120 mm). Relatively long tail (100–120 % of HB), narrow hind feet, skull with broad braincase, opisthodont incisors without notch, long incisor foramina, absence of supraorbital ridges. Complex molars with t3 of M1/ well developed, lower m1 with four well developed and longitudinally linked cusps.

### ***Included genera***

Modern genera: *Apodemus* Kaup, 1829 (Eurasia) and *Tokudaia* Kuroda, 1943 (Japan).

Fossil genera: *Parapodemus*, Schaub, 1938; *Progonomys* Schaub, 1938; *Rhagamys*, Major, 1905; *Rhagapodemus Kretzoi*, 1959; and *Stephanomys* Schaub, 1938.

### ***Distribution***

Eurasian and peri-mediterranean.

### ***Comments***

Denys (2013) provided a diagnosis of the genus *Apodemus* through characters that we use here and allow the differentiation of *Apodemus* from *Mus*. Denys & Winkler (2015) incorrectly used the spelling *APODEMYINI* whereas Fabre *et al.* (2015) used *APODEMURINI*. In fact, Kaup (1929) had precised the etymology of *Apodemus* as being derived from the classical Greek ἀπόδημος (*apodemos*), meaning ‘abroad, travelling’, which implies that *APODEMINI* is the correct spelling for the nomen of the new tribe. Misonne (1969) listed *Tokudaia* as a member of the *Lenothrix* group and *Apodemus* in the *Parapodemus* group, both taxa belonging to the so-called *Lenothrix-Parapodemus* division of the *MURIDAE*. Musser & Carleton (2005) proposed an *Apodemus* division of the *MURIDAE* including *Tokudaia*.

### ***ARVICANTHINI* trib. nov.**

#### ***Name-bearing type (onomatophore)***

Type genus: *Arvicanthis* Lesson, 1842.

#### ***Original type genus diagnosis***

Lesson (1842) did not provide any diagnostic character to accompany his new generic nomen.

#### ***Diagnosis of tribe***

Medium to large sized rats (HB: 100–200 mm) with harsh or shaggy pelage, tail length equal to head and body or longer and ended by a discrete tuft of hairs, low number of mammae (1 or 2 pectoral mammal plus two inguinal ones). Plantar pads on the sole of the hind feet: 5 small, never 6. There is a trend to broadening of the molars with an exaggeration of the central cusps (t2, t5, t8) and a laminated pattern when teeth are worn. A middle anterior cusplet (named Sm) is often present in M/1; the posterior cingulum is small and larger in M/2 than in M/1. The upper M1/ has more than three roots and the M3/is large. The muzzle is short.

### **Included genera**

Modern genera: *Aethomys* Thomas, 1915; *Arvicanthis* Lesson, 1842; *Dasymys* Peters, 1875; *Dephomys* Thomas, 1926; *Desmomys* Thomas, 1910; *Golunda* Gray, 1837; *Grammomys* Thomas, 1915; *Hybomys* Thomas, 1910; *Lamottemys* F. Petter, 1986; *Lemniscomys* Trouessart, 1881; *Micaelamys* Ellerman, 1941; *Mylomys* Thomas, 1906; *Oenomys* Thomas, 1904; *Pelomys* Peters, 1852; *Rhabdomys* Thomas, 1916; *Stochomys* Thomas, 1926; *Thallomys* Thomas, 1920; and *Thamnomys* Thomas, 1907.

Fossil genera: *Parapelomys* Jacobs, 1978, *Saharamys* Mein & Pickford, 2010; *Saidomys* Slaughter & James, 1979.

### **Distribution**

Except *Golunda* which lives in India today, all the modern genera are endemic to Africa. Among the fossils, *Parapelomys* was described from Arabia, Pakistan and Ethiopia. *Saharamys* and *Saidomys* come from Egypt and East Africa.

### **Comments**

Lesson (1842) did not provide any diagnostic character to accompany his new generic nomen. Misonne (1969) created the *Arvicanthis* division inside the *MURIDAE* including 14 African and Asiatic genera: *Golunda*, *Aethomys*, *Arvicanthis*, *Dasymys*, *Dephomys*, *Hybomys*, *Lemniscomys*, *Mylomys*, *Pelomys*, *Thallomys* and *Stochomys*. That author also indicated some dental trends that we used above to characterize the tribe *ARVICANTHINI*, but he did not include in this division the stephanodont species of the tribe, such as *Grammomys*, *Thallomys*, *Thamnomys* and *Oenomys*, which he placed into a broad *Lenothrix-Parapodemus* division. Ducroz *et al.* (2001) proposed the nomen *ARVICANTHINI* without providing any diagnosis, so the tribe nomen was considered a *nomen nudum* by Musser & Carleton (2005). The latter authors proposed to group the different genera proposed in the *ARVICANTHINI* by Ducroz into six divisions. The *Arvicanthis* division included *Arvicanthis*, *Desmomys*, *Lemniscomys*, *Mylomys*, *Pelomys* and *Rhabdomys*. The *Aethomys* division was composed of *Aethomys* and *Micaelamys*. The *Dasymys* and *Golunda* divisions were monotypic. The *Hybomys* division comprised *Stochomys* and *Dephomys* plus *Hybomys*, and the *Oenomys* division comprised *Grammomys*, *Lamottemys*, *Oenomys*, *Thallomys* and *Thamnomys*. Denys & Winkler (2015) figured some dental characters and incorporated some Miocene fossils in the *ARVICANTHINI*. Schenk *et al.* (2013) and Fabre *et al.* (2015) confirmed molecularly the content of the *ARVICANTHINI*, and Missoupe *et al.* (2016) confirmed morphologically and molecularly the inclusion of the endemic *Lamottemys* and of *Thallomys* in this tribe. Fabre *et al.* (2015) incorrectly spelled the tribe nomen as *ARVIVANTHINI*. Bryja *et al.* (2017) in their revision of the *Grammomys-Thamnomys* complex also confirmed these genera as belonging to the new tribe *ARVICANTHINI*.

**MALACOMYINI** trib. nov.***Name-bearing type (onomatophore)***

Type genus: *Malacomys* Milne-Edwards, 1876.

Note: The publication year of the original description of the type species of the genus (*Malacomys longipes*) by Milne-Edwards (1876) has been incorrectly stated in the literature as 1877. A bibliographical search showed that in fact the text was presented at the meeting of the Philomathic Society of Paris on 12<sup>th</sup> February 1876 and inserted for publication in the 1875 volume which was published in 1876 (Callou pers. comm.). We here take the opportunity to correct this mistake.

***Original type genus diagnosis***

Long and narrow hind feet, long naked tail, soft dark dorsal pelage.

***Emended diagnosis of tribe***

Medium to large rats (HB: 120–170 mm) with long vibrissae, elongated muzzle, long naked tail (larger than head and body) and soft dark pelage. Five plantar pads on the sole of the narrow hind feet. Narrow and long rostrum, very short incisor foramen ending before the upper M1/, narrow molars with strong and isolated lingual cusps t1 and t4, no t9 on the upper M1/, t3 on M2/ absent.

***Included genus and distribution***

A single genus *Malacomys* Milne-Edwards, 1876, endemic to African rainforest, is known. There are as yet no fossils attributable to this tribe.

***Comments***

Misonne (1969) found this genus different from all other *MURINAE* and could not place it in the *Praomys* or *Arvicanthis* groups. He concluded that *Malacomys* could be a very advanced offshoot of the fossil *Parapodemus* group. It was placed in its own division by Musser & Carleton (2005) and Fabre *et al.* (2015). Denys & Winkler (2015) described and figured some dental characters.

**MILLIARDIINI** trib. nov.**Name-bearing type (onomatophore)**

Type genus: *Millardia* Thomas, 1911.

Note: The spelling *MILLARDINI* used for this tribe nomen in Lecompte *et al.* (2008) was incorrect, because the spelling of the nomen of the type genus is *Millardia* (see Dubois *et al.* 2013: 76). We hereby correct this mistake.

**Original type genus diagnosis**

Sole pads 4 or 5 but never 6. Fifth hind toe short, not reaching the base of fourth. Tail of medium length. Four pairs of mammae. Skull resembles that of *Rattus*, *Arvicanthis*, *Aethomys*, *Praomys* and *Mastomys*, all designated in the past by the genus nomen *Epimys* Trouessart, 1881, which was later placed in synonymy with *Rattus* Fischer, 1803. Palatal foramina very long. Posterior nasal opening of average breadth, close behind m3. Molars brachyodont, broad (Thomas 1911).

**Emended diagnosis of tribe**

Sole pads 4 or 5 but never 6. Fifth hind toe short not reaching the base of fourth. Tail of medium length. Four pairs of mammae. Small skull with very long incisor foramina, narrow mesopterygoid fossae. Molars brachyodont, broad, mesial t9.

**Included genera and distribution**

This tribe comprises the two modern genera *Cremnomys* Wroughton, 1912 and *Millardia* Thomas, 1911, both endemic to India. Among the fossils known from India, no genera can yet be attributed to this tribe.

**Comments**

*Millardia* and *Cremnomys* were included in a wide *Rattus* division of *MURIDAE* by Misonne (1970). This author mentioned some dental differences from *Praomys*, which we use here. But he considered both genera to be very closely related and placed them in a so-called *Praomys* subgroup. Musser & Carleton (2005) kept the two genera in a single *Millardia* division among *MURIDAE* and added to it two supplementary Indian genera, *Madromys* Sody, 1941 and *Diomys* Thomas, 1917. Fabre *et al.* (2015) indicated also that *Diomys* and *Madromys* may potentially be incorporated to this tribe but there is no taxonomic revision (either morphological or molecular) to confirm this hypothesis.

**PRAOMYINI trib. nov.****Name-bearing type (onomatophore)**

Type genus: *Praomys* Thomas, 1915.

**Original type genus diagnosis**

Inguinal mammae 2 pairs, size small, mouse-like form (Thomas 1915).

**Emended diagnosis of tribe**

Soft-furred rats of medium-size (HB: 100–130 mm) with naked tail equal to or longer than head and body length (HB), females bearing from 6 to 22 mammae (either continuous or separated). Six large plantar pads on the sole of the hind feet. On the skull, presence of a large squamoso-mastoid foramen, a wide auditory meatus on the tympanic bullae, mesopterygoid fossa larger than the parapterygoid one, incisor foramen long and stopping just before the root of the upper M1 or of the M2/. Cheek teeth rather small and narrow. The upper first molars have less than three roots. The t1 and t4 cusps of the upper M1/ are never aligned with the t2-t3 and the t5-t6 giving a very convex aspect to the prelobe of these molars. There is a t3 on the upper M2/ but not on the upper M3, and t9 is closely connected with t8.

**Included genera**

Modern genera: *Colomys* Thomas & Wroughton, 1907; *Heimyscus* Misonne, 1969; *Hylomyscus* Thomas, 1926; *Mastomys* Thomas, 1915; *Myomyscus* Shortridge, 1942; *Praomys* Thomas, 1915; *Stenocephalemys* Frick, 1914; *Zelotomys* Osgood, 1910.

Fossil genus : *Karnimata* (*pro parte*) Jacobs, 1978.

**Distribution**

Today the tribe is endemic to tropical Africa. Only one genus (*Myomyscus*) presents a species (*M. yemeni* Sanborn & Hoogstraal, 1953) found in Yemen and Arabia, and another (*Mastomys*) includes a species *M. erythroleucus* Temminck, 1853) in North Africa (Morocco). *Karnimata* is found both in India and Pakistan around 8.5 Myr and in Kenya at around 6.5 Myr.

**Comments**

Thomas (1915) established the subgenus *Praomys* to differentiate it morphologically from *Rattus* Fischer, 1803 and *Mastomys* Thomas, 1915. Morphological and molecular studies by Lecompte *et al.* (2001, 2002) allow clarification of the content of the genus *Praomys* and the integration of other taxa into a well supported monophyletic group. Moreover, the morphological phylogeny of the *Praomys* complex allowed the discovery

of some informative autapomorphic characters of the tribe (Lecompte *et al.* 2002). The morphological and molecular phylogeny of all representatives of this clade allowed clarification of the relationships within this taxon (Lecompte *et al.* 2002, 2005) and the addition of *Zelotomys*, *Stenocephalemys* and *Colomys*. According to Musser & Carleton (2005), this group is composed of two different divisions: the *Colomys* division (*Colomys*, *Nilopegamys* and *Zelotomys*) and the *Stenocephalemys* division (*Heimyscus*, *Hylomyscus*, *Mastomys*, *Myomyscus*, *Praomys* and *Stenocephalemys*). The very rare *Nilopegamys* Osgood, 1928 shares some morphological characters with this taxon and has also been suggested as a possible member of this group by Fabre *et al.* (2015). Denys & Winkler (2015) figured some dental characters and attributed the Neogene *Karnimata* to this group with a reservation concerning the monophyletic content of the genus which could include different genera.

## Conclusion

Despite important progress made recently in the classification of murid rodents, there is still much work remaining for the establishment of a correct taxonomy and the accurate ascertainment of the composition of tribes and genera. Molecular studies provide an important framework for this, but in all circumstances inclusion of anatomical characters remains an absolute necessity for improving our knowledge of biodiversity.

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## References

- Anonymous [International Commission on Zoological Nomenclature] (1999) *International code of zoological nomenclature*. Fourth edition. London (International Trust for zoological Nomenclature): i–xxix + 1–306.
- Anonymous [International Commission on Zoological Nomenclature] (2012) Amendment of Articles 8, 9, 10, 21 and 78 of the International Code of Zoological nomenclature to expand and refine methods of publication. *Bulletin of zoological Nomenclature*, **69** (3): 161–169.
- Bryja, J., Šumbera, R., Kerbis Peterhans, J. C., Aghová, T., Bryjová, A., Mikula, O., Nicolas, V., Denys, C. & Verheyen, E. (2017) Evolutionary history of the thicket rats (genus *Grammomys*) mirrors the evolution of African forests since late Miocene. *Journal of Biogeography*, **44**: 182–194.
- Denys, C. (2013) Genus *Apodemus*, Field mouse. In: D. C. D. Happold (ed.), *Mammals of Africa*, Vol. 3, *Rodents, hares and rabbits*, Bloomsbury Publishing, London: 377–378.
- Denys, C. & Winkler, A. (2015) Chapter 7. Advances in integrative taxonomy and evolution of African murid rodents: how morphological trees hide the molecular forest. In: P. Cox & L. Hautier (ed.), *Evolution of the rodents: advances in phylogeny, palaeontology and functional morphology*, Cambridge (Cambridge University Press): 186–220.



- Dubois, A., Crochet, P.-A., Dickinson, E. C., Nemésio, A., Aescht, E., Bauer, A. M., Blagoderov, V., Bour, R., de Carvalho, M. R., Desutter-Grandcolas, L., Frétey, T., Jäger, P., Koyamba, V., Lavilla, E. O., Löbl, I., Louchart, A., Malécot, V., Schatz, H. & Ohler, A. (2013) Nomenclatural and taxonomic problems related to the electronic publication of new nomina and nomenclatural acts in zoology, with brief comments on optical discs and on the situation in botany. *Zootaxa*, **3735** (1): 1–94.
- Ducroz, J.-F., Volobouev, V. & Granjon, L. (2001) An assessment of the systematics of arvicanthine rodents using mitochondrial DNA sequences: evolutionary and biogeographical implications. *Journal of mammalian Evolution*, **8**: 173–206.
- Fabre, P.-H., Hautier, L., Dimitrov, D. & Douzery, E. J. P. (2012) A glimpse on the pattern of rodent diversification: a phylogenetic approach. *BMC evolutionary Biology*, **12** (88). Online document <doi: 10.1186/1471-2148-12-88>.
- Fabre, P.-H., Hautier, L. & Douzery, E. (2015) A synopsis of rodent molecular phylogenetics, systematics and biogeography. In : P. G. Cox & L. Hautier (ed.), *Evolution of the rodents: advances in phylogeny, palaeontology and functional morphology*, Cambridge (Cambridge University Press): 19–69.
- Kaup J. J. (1829) *Skizzirte Entwicklungs-Geschichte und natürliches System der europäischen Thierwelt. Erster Theil welcher die Vogelsäugethiere und Vögel nebst Andeutung der Entstehung der letzteren aus Amphibien enthält*. Darmstadt (In commission bei Carl Wilhelm Leske), **18** (9): 154.
- Lecompte, E., Aplin, K., Denys, C., Catzeflis, F., Chades, M. & Chevret, P. (2008) Phylogeny and biogeography of African Murinae based on mitochondrial and nuclear gene sequences, with a new tribal classification of the subfamily. *BMC evolutionary Biology*, **8** (199): 1–21 + 4 additional online files. <doi:10.1186/1471-2148-8-199>. Online document <<http://www.biomedcentral.com/content/pdf/1471-2148-8-199.pdf>>.
- Milne Edwards, A. (1876) Sur quelques Mammifères et Crustacés nouveaux. *Bulletin de la Société philomatique de Paris*, (6), **11** : 8–10.
- Misonne, X. (1969) African and Indo-Australian Muridae. Evolutionary trends. *Zoologie* (Muséum royal de l’Afrique centrale, Tervuren), **172**: 1–219.
- Missoup, A. D., Nicolas, V., Eiseb, S., Chung, E. K. & Denys, C. (2016) Phylogenetic position of the endemic Mount Oku rat, *Lamottemys okuensis* (Rodentia: Muridae), based on molecular and morphological data. *Zoological Journal of the Linnean Society*, **177** (1): 209–226. <doi: 10.1111/zoj.12361>.
- Musser, G. G. & Carleton, M. D. (2005) Superfamily Muroidea. In: D. E. Wilson & D. M. Reeder (eds.), *Mammal species of the world, a taxonomic and geographic reference*, Third edition, Baltimore (The John Hopkins University Press): 894–1531.
- Schenk, J. J., Rowe, K. C. & Steppan, S. J. (2013) Ecological opportunity and incumbency in the diversification of repeated continental colonizations by muroid rodents. *Systematic Biology*, **62** (6): 837–864.
- Taylor, P. J. (2004) Geometric morphometric analysis of adaptive cranial evolution in southern African laminate-toothed rats (family: Muridae, tribe: Otomyini). *Durban Museum Novitates*, **29**: 110–122.
- Taylor, P. J., Denys, C. & Mukerjee, M. (2004) Phylogeny of the African murid tribe Otomyini (Rodentia), based on morphological and allozyme evidence. *Zoologica scripta*, **33**: 389–402.
- Thomas, O. (1911) A new murine genus and species from Sind, with diagnoses of three other new genera based on previously known species of “*Mus*”. *Journal of the Bombay natural History Society*, **20**: 996–999.
- Thomas, O. (1915) List of mammals (exclusive of Ungulata) collected on the Upper Congo by Dr. Christy for the Congo Museum, Tervueren. *Annals & Magazine of natural History*, (8), **16**: 465–481.
- Wilson, D. E. & Reeder, D. M. (2005) *Mammals species of the world. A taxonomic and geographic reference*. Third Edition. Baltimore (The John Hopkins University Press), **1 & 2**: 1–2142.

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