**A comprehensive phylogeny of extinct and extant
Rhizomyinae (Rodentia): evidence for multiple
intercontinental dispersals**

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Abstract

The subfamily Rhizomyinae is known from the Late Oligocene up to the present. Today, this group comprises six species, which live in southern Asia and eastern Africa. Despite the current moderate diversity of the rhizomyines, they had a greater diversification and wider distribution in the past from Asia, their land of origin, to Africa where they entered during the Early Miocene. So far 33 fossil species can be referred to this group. A cladistic analysis involving fossil and living species has been carried out. *Prokanisamys* spp. turned out to be the most basal taxa of the ingroup. This analysis calls the monophyly of several genera into question and allows proposing a phylogenetic definition of the tribes Tachyoryctini and Rhizomyini. It also provides information about the origin of the African rhizomyines and allows inferring multiple dispersal phenomena from Asia to Africa in Early and Late Miocene times.

Keywords: Mammalia; Systematics; Cladistics; Cenozoic; Eurasia; Africa

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Rhizomyides

“Rhizomyides” mirzadi and “R”. punjabiensis

Miorhizomys

The crown group

Tribe Tachyoryctini.

Tribe Rhizomyini.

Conclusion

Acknowledgements

References

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intercontinental dispersals**

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Introduction

Living Rhizomyinae are fossorial muroid rodents from southern Asia and eastern Africa (Fig. 1) that belong to the family Spalacidae (Jansa and Weksler, 2004; Gogolevskaya et al., 2010). Despite their secretive way of life, they are important to the people who live in the same zones because, like other rodents (e.g., the cane rat *Thryonomys*; López-Antoñanzas et al., 2004), they are agricultural pests, but also can be a source of protein.

The living Asian forms (bamboo rats) include *Rhizomys* (a trispecific genus) and *Cannomys* (a monospecific genus). There is a single living African genus *Tachyoryctes*, the mole rat, which includes 2 extant species, although that diversity may be greatly underestimated (Musser and Carleton, 2005). No fossil of *Cannomys* has been found to date. However, the Asian *Rhizomys* (*Brachyrhizomys*) and the African *Tachyoryctes* are known since Late Miocene time. Although the rhizomyines are today moderately diversified, this subfamily, which is known from Late Oligocene times, has had a flourishing history as reflected by the finding-discovery of over 30 fossil species distributed in 11 genera (*Pronakalimys*, *Nakalimys*, *Prokanisamys*, *Kanisamys*, *Rhizomyides*, *Protachyoryctes*, *Tachyoryctes*, *Eicooryctes*, *Miorhizomys*, *Anepsirrhizomys* and *Rhizomys* (*Brachyrhizomys*)) in Africa, Thailand, Afghanistan, Pakistan, India, and China.

The systematic position of the rhizomyines is controversial. Some authors have placed them in a distinct Family Rhizomyidae (Miller and Gidley, 1918; Ellermann, 1940, 1941; Simpson, 1945; Ellerman and Morrison-Scott, 1951, 1966; Colbert and Hooijer, 1953; Flynn 1982a, 1982b, 1990, 1993; Flynn and Guo-qin Qi, 1982; Flynn and Sabatier, 1984; Flynn et al., 1983, 1995; Alemseged and Geraads, 2000; Wessels and de Bruijn, 2001), including the tachyoryctines with them. Other authors considered the rhizomyines as members (Lydekker, 1885; Palmer, 1897; Colbert, 1935) or a subfamily (Thomas, 1896; Tullberg, 1899; Musser and Carleton, 2005; Flynn, 2009) of the Spalacidae. As Winge (1887) originally did when he created the Tribe Rhizomyini, some other specialists considered the rhizomyines as a tribe within the Muridae. McKenna and Bell (1997) considered the rhizomyines a subfamily within the Muridae and subdivided it into two tribes: the Rhizomyini and the Tachyoryctini. The results of

~~recent analyses of mitochondrial and nuclear genes support a monophyletic Spalacinae plus Rhizomyinae, with Myospalacinae as sister group (Jansa and Weksler, 2004; Gogolevskaya et al., 2010) and leave little doubt about the inclusion of the rhizomyines in the Family Spalacidae. The results of recent analyses of nucleotide sequences support a monophyletic Spalacinae plus Rhizomyinae, with Myospalacinae as sister group (Norris et al., 2004; Gogolevskaya et al., 2010; see also Jansa and Weksler, 2004) and leave little doubt about the inclusion of the rhizomyines in the Family Spalacidae.~~

The similarity in many morphological traits among the three subfamilies probably stems from their common origin (Gogolevskaya et al., 2010) as well as convergence to a fully subterranean way of life through geological time.

However, the relationships within the rhizomyines (Asian bamboo rats and African mole rats) remain unclear. Some authors considered that the Asian rhizomyines are distantly related to the African representatives of the group (Endo et al., 2001; Musser and Carleton, 2005) and, therefore, they separate them into two different subfamilies: the Rhizomyinae (Asian) and the Tachyoryctinae (African). Other rodentologists considered that African fossil rhizomyines do not appear far from the Asian ones from a morphological viewpoint and they include them in a single subfamily, the Rhizomyinae (McKenna and Bell, 1997; Flynn, 2009; López-Antoñanzas, 2012; López-Antoñanzas and Wesselmann, in press). Furthermore, the origin of *Tachyoryctes* is controversial. Some authors advocated an independent African origin for this taxon (Ellerman, 1940, 1941; Lavocat, 1978; Endo et al., 2001), whereas others defended an Asian origin (Black, 1972; Jacobs, 1978; Sabatier, 1978; Munthe, 1980; De Bruijn et al., 1981; Flynn, 1982a, 1986, 1990, 2009; Flynn et al., 1990; Wessels and De Bruijn, 2001; Haile-Selassie et al., 2004; Wesselman et al., 2009). All these yet unresolved issues motivated us to provide a substantiated hypothesis of the mutual relationships within this subfamily based on cladistic methods.

Material and methods

The study presented herein is based on the examination of original specimens, casts, and data from the literature. We examined the following: skulls of extant *Rhizomys sinensis*

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(ZMB 16768, ZMB 17413, ZMB 45362, ZMB 43372, ZMB 43373, ZMB 17411, ZMB 16770, ZMB 17417, ZMB 16766 in the MB and C.G.1934-1237, C.G.1912-851 in the MNHN), *R. pruinus* (DH. 280, C.G. 1929-259, C.G. 1929-261, C.G.1892-1360, C.G. 1929-263, C.G.1958-724, C.G.1962-2297, C.G.1962-2295, C.G. 1929-266, C.G. 1929-272, C.G. 1929-260, C.G. 1929-267, C.G. 1993-48, C.G. 1929-264, C.G. 1937-1251, C.G. 1929-265, C.G. 1929-270, C.G. 1929-340, C.G. 1993-02 in the MNHN), *R. sumatrensis* (ZMB 1847, ZMB A1316, ZMB 38840, ZMB 48085, ZMB 21249 in the MB C.G.1993-49, C.G. 1962-2294, C.G. 2007-162, C.G. 1980-235, A 7.216, A7.215 in the MNHN), *Cannomys badius* (ZMB 3424, ZMB 44768, ZMB 44769 in the MB and CG-2000-761, CG-1860-382 in the MNHN), *Tachyoryctes macrocephalus* (ZMB 36656, ZMB 55165, ZMB 36649 in the MB and C.G. 1972-73, C.G. 1972-74, C.G. 1972-75, C.G. 1972-76, C.G. 1974-202 in the MNHN), *T. splendens* (ZMB 12, ZMB 78, ZMB 79, ZMB 80, ZMB 81, ZMB 83, ZMB 88, ZMB 114, ZMB 117, ZMB 3404, ZMB 3403, ZMB 9015, ZMB 16048, ZMB 28069, ZMB 36601-13, ZMB 36618, ZMB 36620-36621, ZMB 36624-36634, ZMB 36636-36637, ZMB 36640-36646, ZMB 36648, ZMB 36650-36655, ZMB 46257, ZMB 48300, ZMB 72559-72593, ZMB 7721 in the MB and C.G. 1993-217, C.G. 1993-231, C.G. 1993-220, C.G. 1993-238, C.G. 1933-2752, C.G. 2000-685, C.G. 1961-33, C.G. 1972-10, C.G. 1972-27, C.G. 1972-39, C.G. 1972-51, C.G. 1972-64, C.G. 1972-65, C.G. 1972-68, C.G. 1993-222, C.G. 1993-225, C.G. 1993-241, C.G. 1993-246, C.G. 1993-250, C.G. 1993-253, C.G. 1993-254, C.G. 1993-257, C.G. 1993-263, C.G. 1993-265, C.G. 1993-268, C.G. 1993-272, C.G. 1993-274, C.G. 1993-289, C.G. 1993-302, C.G. 1993-303, C.G. 1993-308, C.G. 1993-323, C.G. 1933-2746, C.G. 1933-2756, C.G. 1905-385, C.G. 1933-2745, C.G. 1933-2748, C.G. 1960-454, C.G. 1962-2292, C.G. 1970-210, C.G. 1972-16, C.G. 1972-19, C.G. 1972-44, C.G. 1972-46, C.G. 1972-50, C.G. 1972-54, C.G. 1972-58, C.G. 1993-221, C.G. 1993-223, C.G. 1993-232, C.G. 1993-238, C.G. 1993-245, C.G. 1993-281, C.G. 1993-288, C.G. 1993-294, C.G. 1993-304, C.G. 1993-307, C.G. 1993-318, C.G. 1993-322, C.G. 1960-453, C.G. 1962-2290, C.G. 1972-14, C.G. 1972-25, C.G. 1972-29, C.G. 1972-41, C.G. 1972-57, C.G. 1974-202, C.G. 1991-629, C.G. 1993-217, C.G. 1993-224, C.G. 1993-239, C.G. 1993-240, C.G. 1993-249, C.G. 1993-261, C.G. 1993-270, C.G. 1993-292b, C.G. 1993-295, C.G. 1993-296, C.G. 1993-316, C.G. 1961-921, C.G. 1972-11, C.G. 1972-15, C.G. 1972-17, C.G. 1972-24, C.G. 1972-33, C.G. 1972-

37, C.G. 1972-45, C.G. 1972-52, C.G. 1972-53, C.G. 1972-69, C.G. 1981-533, C.G. 1988-119, C.G. 1993-226, C.G. 1993-227, C.G. 1993-228, C.G. 1993-230, C.G. 1993-235, C.G. 1993-237, C.G. 1993-242, C.G. 1993-247, C.G. 1993-259, C.G. 1993-260, C.G. 1993-267, C.G. 1993-283, C.G. 1993-284, C.G. 1993-286, C.G. 1993-287, C.G. 1993-309, C.G. 1993-310, C.G. 1993-315, C.G. 1993-317, C.G. 1993-320, C.G. 1993-2747, C.G. 1972-06, C.G. 1972-21, C.G. 1972-26, C.G. 1972-30, C.G. 1972-34, C.G. 1972-43, C.G. 1972-59, C.G. 1972-62, C.G. 1972-66, C.G. 1972-67, C.G. 1993-231, C.G. 1993-234, C.G. 1993-236, C.G. 1993-256, C.G. 1993-275, C.G. 1993-278, C.G. 1993-285, C.G. 1993-290, C.G. 1993-291, C.G. 1993-300, C.G. 1993-305, C.G. 1993-314, C.G. 1962-2291, C.G. 1972-09, C.G. 1972-12, C.G. 1972-31, C.G. 1972-35, C.G. 1972-40, C.G. 1972-47, C.G. 1972-61, C.G. 1988-242, C.G. 1993-219, C.G. 1993-220, C.G. 1993-248, C.G. 1993-251, C.G. 1993-258, C.G. 1993-262, C.G. 1993-273, C.G. 1993-276, C.G. 1993-282, C.G. 1993-299, C.G. 1993-313, C.G. 1993-321, C.G. 1993-2749, C.G. 1972-18, C.G. 1972-20, C.G. 1972-23, C.G. 1972-42, C.G. 1972-48, C.G. 1972-55, C.G. 1972-56, C.G. 1972-71, C.G. 1993-218, C.G. 1993-229, C.G. 1993-243, C.G. 1993-264, C.G. 1993-269, C.G. 1993-271, C.G. 1993-277, C.G. 1993-279, C.G. 1993-292, C.G. 1993-297, C.G. 1993-298, C.G. 1993-306, C.G. 1993-311, C.G. 1993-319, C.G. 1993-324, C.G. 1972-07, C.G. 1972-08, C.G. 1972-13, C.G. 1972-22, C.G. 1972-28, C.G. 1972-32, C.G. 1972-36, C.G. 1972-38, C.G. 1972-49, C.G. 1972-60, C.G. 1972-63, C.G. 1972-70, C.G. 1993-233, C.G. 1993-244, C.G. 1993-252, C.G. 1993-255, C.G. 1993-266, C.G. 1993-280, C.G. 1993-293, C.G. 1993-301, C.G. 1993-312, C.G. 1933-2752, in the MNHN), isolated teeth, maxillary fragments and mandible fragments of the following extinct species: *Prokanisamys arifi* (casts of HGSP-116-22, HGSP-116-371, HGSP-116-83, HGSP-116-101, HGSP-116-123, HGSP-116-125, HGSP-116-14, HGSP-116-37, HGSP-116-42, HGSP-116-52, HGSP-116-61 in the BSP), *Kanisamys indicus* (casts of GSI-D271 in the BSP), *K. nagrii* (casts of AMNH 30.000 and AMNH 39323 in the BSP), *K. potwarensis* (AMNH 39321), *Rhizomyides punjabiensis* (AMNH 19762 and cast of GSI-D287 in the BSP), *R. sivalensis* (casts of D97, D275 and BM (NH) 15926 in the BSP) *Protachyoryctes tatroti* (cast of GSI-D272 in the BSP), *Anepsirhizomys pinjoricus* (casts of GSI-D278 and GSI-D280 in the BSP), *Miorhizomys nagrii* (casts of GSI-D273 and GSI-D285 in the BSP), *M. tetracharax* (upper incisor of AMNH 39326, cast of AMNH 39325 in the BSP), *M. pilgrimi* (lower

incisor of AMNH 39327 and cast of D-278 in the BSP). In addition, we reviewed unpublished original material of the following taxa recovered under the Harvard University-Geological Survey of Pakistan field program on the Potwar Plateau, Pakistan from 1994-2000: *Prokanisamys major*, *Kanisamys indicus*, *K. potwarensis*, *K. nagrii*, *K. sivalensis*, and *Rhizomyides punjabiensis*.

First, second, and third lower molars are designated as m1, m2, and m3, respectively, and first, second, and third upper molars as M1, M2, and M3, respectively. The terminology used in the tooth descriptions follows the rodent dental terminology of Mein and Freudenthal (1971), with some adjustments, and Flynn (1982a) (see Fig. 2).

The cladistic analysis treated as ingroup all extant and fossil species of this subfamily known to date. The taxonomic units chosen are the valid species of Rhizomyini and Tachyoryctini, namely *Rhizomys sumatrensis*, *R. sinensis*, *R. pruinosus*, *R. (Brachyrhizomys) shansius*, *R. (Brachyrhizomys) shajius*, *Cannomys badius*, *Miorhizomys nagrii*, *M. micrus*, *M. blacki*, *M. pilgrimi*, *M. harii*, *M. tetracharax*, *M. choristos*, *Protachyoryctes tatroti*, *Tachyoryctes makooka*, *T. konjiti*, *T. pliocaenicus*, *T. macrocephalus*, *T. splendens*, *Rhizomyides sivalensis*, *R. punjabiensis*, *R. carbonnelli*, *R. platytomeus*, *R. mirzadi*, *Kanisamys indicus*, *K. nagrii*, *K. sivalensis*, *K. potwarensis*, *Eicooryctes kaulialensis*, *Anepsirhizomys opdykei*, *A. pinjoricus*, *Pronakalimys andrewsi*, *Nakalimys lavocati*, *Prokanisamys kowalskii*, *P. arifi*, *P. benjavuni* and *P. major*, *P. sp.* (Jebel Zelten), (see [Supplementary File 1 "Systematics" below](#)). *Debruijnina arpati*, a basal Spalacinae according to the phylogenetic analysis of Flynn (2009), is selected as outgroup. A total of 44 phylogenetically informative characters (mainly of dental morphology) have been coded ([Supplementary File 1](#)). 24 characters are binary, whereas 20 are multistate. Owing to the lack of *a priori* information, all characters were unordered and equally weighted (Fitch optimality criterion). As some species are known so far from only a few specimens, the influence of intraspecific variation in the scoring of the characters could not be assessed.

1. *Hypsodonty*: Crown height on at least one side of the tooth greater than length or width of the tooth. This character has been scored as (0) absent; (1) moderate; (2) high.

2. *Size*: Length of the m2: (0) 1.5-2.5 mm; (1) 2.5-3.5 mm; (2) 3.5-4.5 mm; (3) 4.5-5.5 mm; (4) >5.5 mm

3. *Lophodonty*: (0) weak; (1) moderate; (2) high

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4. Masseteric crest: (0) with long anterior extension (1) with short anterior extension (2) without anterior extension
5. Lower masseteric crest: (0) inflated under m2; (1) not inflated
6. Dentary depth: (0) Shallow; (1) Moderate; (2) Deep
7. Infraorbital foramen: (0) with ventral slit; (1) with abbreviated ventral slit; (2) without ventral slit
8. Longitudinal ornamentation on the i: (0) double ridge; (1) single ridge; (2) absent
9. Anteroconid on the m1: (0) discernible; (1) absent (fused with the anterolophid)
10. Mure on the m1: (0) present; (1) constricted; (2) absent.
11. Labial anterolophid on the m1: (0) present; (1) absent
12. Mesolophid on the m1: (0) long and complete and separated from the hypolophid; (1) short and well-separated from the hypolophid; (2) short and migrated towards the hypolophid; (3) absent; (4) a long continuation of the protoconid
13. Posterior protoconid-metacomid connexion on the m1: (0) present; (1) absent
14. Anterosinusid on the m1: (0) present; (1) absent
15. Mure on the m2: (0) present; (1) constricted; (2) absent
16. Mesolophid on the m2: (0) long and complete and separated from the hypolophid; (1) short and well-separated from the hypolophid; (2) short and migrated towards the hypolophid; (3) absent; (4) a long continuation of the protoconid
17. Labial anterolophid on the m2: (0) present; (1) absent
18. Hypolophid on the m2: (0) not isolated; (1) isolated
19. Protosinusid on the m2: (0) present; (1) absent
20. Anterosinusid on the m2: (0) present; (1) absent
21. m3: (0) Reduced (shorter than the m2); (1) Enlarged (equal or larger than the m2)
22. Labial anterolophid on the m3: (0) present; (1) absent
23. Mure on the m3: (0) present; (1) absent
24. Mesolophid on the m3: (0) long and complete and separated from the hypolophid; (1) short and well-separated from the hypolophid; (2) short and migrated towards the hypolophid; (3) absent; (4) a long continuation of the protoconid

25. Posterosinusid on the m3: (0) large; (1) small; (2) absent (posterolophid fused with hypolophid)
26. Entoconid on the m3: (0) not isolated; (1) isolated
27. Protosinusid on the m3: (0) present; (1) absent
28. Anterosinusid on the m3: (0) present; (1) absent
29. Roots on the M1: (0) three; (1) four; (2) Hypselodont. The development of four roots on the M1 is a modern Rhizomyinae trait
30. Protosinus on the M1: (0) present; (1) absent
31. Mesoloph on the M1: (0) absent; (1) short; (2) long and complete; (3) long and complete but divided with a buccal cusp
32. Mesostyle on the M1: (0) may be present; (1) absent
33. Ectoloph on the M1: (0) present; (1) absent
34. Anterocone on the M1: (0) distinct; (1) fused with the anteroloph
35. Metaloph on the M1: (0) present and distinct from the posteroloph; (1) fused with the posteroloph
36. Posterosinus on the M1: (0) present; (1) absent
37. Mesoloph on the M2: (0) absent; (1) short; (2) long and complete; (3) long and complete but divided with a buccal cusp
38. Longitudinal crest on the M2: (0) present; (1) absent
39. Ectoloph on the M2: (0) present; (1) absent
40. Metaloph on the M2: (0) present and distinct from the posteroloph; (1) early fused with the posteroloph; (2) absent
41. Posterosinus on the M2: (0) present; (1) absent
42. Anterosinus on the M3: (0) open; (1) enclosed by anteroloph and paracone; (2) absent
43. Mesoloph on the M3: (0) absent; (1) short; (2) long and complete; (3) long and complete but divided with a buccal cusp
44. Posterior lake on the M3: (0) large; (1) small; (2) absent

The data matrix ([Table 1](#)) was built under Mesquite 2.6 (Maddison and Maddison, 2009) and processed with TNT (Goloboff et al., 2008) with the "traditional search" option (using TBR). Branch support was estimated through two complementary indices:

Bremer Support (Bremer, 1994) and Relative Bremer Support (Goloboff and Farris, 2001).

Abbreviations:

AMNH: American Museum of Natural History, New York; BAM: Bamian, Afghanistan; BMNH: The Natural History Museum, London, England; BSP: Bayerische Staatssammlung für Paläontologie und Historische Geologie, Munich, Germany; C.G: Catalogue général du Laboratoire des Mammifères et Oiseaux, MNHN, Paris, France; DMR: Department of Mineral Ressources, Bangkok, Thailand; FSL: Université Claude Bernard-Lyon 1, Villeurbanne, France; GSI, Geological Survey of India, Calcutta, India; H-GSP: Howard University-Geological Survey of Pakistan; IVAU: Department of Earth Sciences, Utrecht University, Utrecht, Netherlands. IVPP: Institute of Vertebrate Palaeontology and Palaeoanthropology, Beijing, China; KNM: Kenya National Museums, Nairobi, Kenya; MNHN: Muséum national d’Histoire naturelle, Paris, France; NME: National Museum of Ethiopia, Addis Ababa, Ethiopia; PMAE: Peabody Museum of Archaeology and Ethnology, Cambridge, USA; PMNH: Pakistan Museum of Natural History, Islamabad, Pakistan; PEC: Pul-e Charkhi, Kabul, Afgahnistan; SMF: Mammalogie-Sammlung, Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt am Main; UM2: Université des Sciences et Techniques du Languedoc-Montpellier 2, Montpellier, France; Y-GSP: Yale-Geological Survey of Pakistan, Quetta, Pakistan; YPM: Yale Peabody Museum of Natural History, New Haven, USA; Z: Zinda Pir area, Pakistan; ZMB: Zoologische Sammlung, Museum für Naturkunde der Humboldt-Universität, Berlin, Germany;

Systematics

Asian rhizomyines are widespread. They live in China, northern and northeastern India, Nepal, Bhutan, southeastern Bangladesh, Myanmar, Laos, Thailand, Cambodia, Vietnam, Malaysia and Sumatra (Fig. 1) where they are known from a wide variety of habitats (from bamboo forest to cultivated land, and up to 4000 m elevation) (IUCN,

2010). African rhizomyines are nowadays discontinuously distributed in the centre and, especially, the eastern part of the continent (Democratic Republic of the Congo, Uganda, Rwanda, Burundi, Tanzania, Kenya, Ethiopia, Somalia and possibly South Sudan and Eritrea) (Fig. 1) and they are also recorded from a wide variety of habitats (tropical moist forest and open woodland to savanna, grasslands and agricultural and pasture areas, sometimes above 4000 m) (IUCN, 2010).

Musser and Carleton (1993, pp. 685, 2005, pp. 913–915) have provided a census of the extant species of *Rhizomys* and *Cannomys* recognized as valid (see also Ellerman and Morrison-Scott, 1951, pp. 550–553, 1966, pp. 521–522). They concluded that 3 species of *Rhizomys* and a single species of *Cannomys* are well defined at present: *Rhizomys sinensis*, *R. pruinusosus*, *R. sumatrensis* and *Cannomys badius*. The taxonomy of *Tachyoryctes* is more controversial and the number of species included in this taxon ranges from 14 (Allen, 1939, pp. 361–363; Ellerman, 1941) to 2 (Misonne, 1971, p. 7; Rahm, 1980, pp. 23–27; Bucher, 1982, p. 478; Corbet and Hill, 1991). Musser and Carleton (1993, pp. 685–687; 2005, pp. 922–926) considered that the drastic reduction from 14 to 2 species deserves systematic attention, that has never been performed and therefore they cautiously recognized 11 (Musser and Carleton, 1993) and or 13 (Musser and Carleton, 2005) species. However, the recent morphometric approach given by Beolchini and Corti (2004) supports the hypothesis of Misonne (1971) of recognizing only 2 species in the genus *Tachyoryctes*: *T. macrocephalus* and *T. splendens*. Because our analysis is morphological, we evaluate these two species only, although we admit that *T. splendens* might actually be a cryptic species complex.

The morphology of the teeth of fossil rhizomyines has been described in detail (Colbert, 1933, 1935; Teilhard de Chardin, 1942; Bohlin, 1946; Colbert and Hooijer, 1953; Black, 1972; Jacobs, 1978; Sabatier, 1978, 1979, 1982; Brandy, 1979a, 1979b; Munthe, 1980; de Bruijn et al., 1981; Flynn, 1982a, 1982b, 1983, 1993, 2009; Flynn and Guo-qinQi, 1982; Wessels et al., 1982, 2003, 2008; Flynn et al., 1983, 1990; Sen, 1983; Flynn and Sabatier, 1984; Mein and Ginsburg, 1985, 1997; Tong and Jaeger, 1993; Lindsay, 1996; Wessels and de Bruijn, 2001; Wesselman et al., 2009; López-Antoñanzas and Wesselman, in press). Therefore, in this work, we only describe the teeth of the three modern genera and give a short historical background for the fossil ones as well as some pertinent additional details.

Genus *Rhizomys* Gray, 1831. Type species: *Rhizomys sinensis* Gray, 1831

Referred species: *Rhizomys pruinosus*, *R. sumatrensis*

On the basis of a skull and skin of a glirine quadruped brought from China by the amateur naturalist J. Reeves, Gray (1831, p. 95) described the new genus *Rhizomys* as follows: “*Dentes primores 2/2 maximi, elongati, triangulares, acutati: molares 3/3 3/3 radicati, subcylindrici, coronis transversim subparallelim porcatis; superiores internè lobati. Caput magnum. Oculi parvi aperti. Auriculæ nudæ conspicuæ. Corpus crassum subcylindricum. Pedes breves validi, digitis 5-5. Cauda mediocris, crassa, nuda*”. That is: Incisors 2/2 very large, elongate, triangular, pointed; molars 3/3 three rooted, subcylindrical, with crowns with transversal subparallel furrows; upper teeth lobated internally. Head large. Eyes small open. External ears naked visible. Body massive subcylindrical. Feet short robust, with 5-5 digits. Tail average, thick, naked.

Rhizomys sinensis Gray, 1831. Gray (1831) recognized the new genus and new species of rodent *Rhizomys sinensis*. The brief Latin diagnosis he gave (Gray, 1831: 95): “*Rhiz. pallidè cinerascens unicolor*” can be translated as follows: “*Rhiz. pale ash-grey single-colored*”. The type specimens are BMNH 49b (skin) and BMNH 1161a (skull) (P. Jenkins, pers. comm. 2012).

The molars of *Rhizomys sinensis* are short rooted and lack the mure. They show unilateral hypsodonty and a strong wear gradient with first molars well worn by the time the third molars erupt (Fig. 3A-B). The orange upper incisors are recurved and ventrally directed and lack major ornamentation. M2 and m2 are the largest teeth of the upper and lower tooth row, respectively. The dental pattern of the upper molars is tetralophodont with four lophs (anteroloph, protoloph, mesoloph, and metaloph+posteroloph). By wear, the labial reentrants are closed-off and three enamel lakes are isolated. The central one may be confluent with the lingual reentrant, forming a narrow and elongated central reentrant that may divide the tooth into two parts. The lower molars are lower crowned than the upper ones. M1 undergoes heavy wear earlier than posterior molars; the latter continue to erupt past its occlusal surface until, in old age, the molars are worn to the same level. The lower incisors lack major ornamentation

and their enamel is flat. The mandibular foramen is well posterior to the distal part of m3 (located a little above the m3 at the level of the tip of the coronoid process). The mental foramen is situated anteriorly to the anterior part of m1 at about the midline of the dentary. The pattern of m1 is pentalophodont (anterolophid, metaconid, mesolophid, hypolophid, and posterolophid) whereas m2 and m3 show four major lophs (anterolophid-metalophid, mesolophid, short hypolophid, and long posterolophid). With wear, the lingual and labial reentrants close off, isolating various enamel lakes, the number of which ~~depending depends~~ on the state of wear of the teeth.

Rhizomys sumatrensis (Raffles, 1821). Raffles (1821, p. 258) named this species as *Mus sumatrensis* on the basis of a drawing and a specimen forwarded from Malacca (Malasya) by W. Farquhar. The reason he chose *sumatrensis* as a species name when, by that time, it had not been found in Sumatra remains unknown. He gave the following diagnosis (Raffles, 1821, p.258): “The body is about seventeen inches in length, ten inches in circumference, and the height at the shoulder about five. The tail is six inches long, tapering, and blunt at the points, naked and scaly. The body is covered with rough greyish hair, brownish on the back. The head round and lighter coloured. Incisors large, two in each jaw. Eyes small. Ears naked. Fore-feet four-toed; hind-feet with a short fifth toe.” Later on, Gray (1831, p. 95) included *Mus sumatrensis* in the new genus *Rhizomys* and he gave the following brief Latin diagnosis: “*Pallidè fuscus, pilis raris albidis interspersis; corporis lateribus pedibusque saturatoribus; genis pallidioribus, occipite nigrescenti lineâ longitudinali albâ, pectore albido*”. This can be translated as: “Pale brown, with some hairs scattered whitish; with body broad and feet darker; with cheeks paler, back of the head blackish with a white longitudinal stripe, chest whitish”. The type specimen was possibly lost in transit (P. Jenkins, pers. comm. 2012).

The teeth of *Rhizomys sumatrensis* and *R. sinensis* are quite similar and only a few differences can be discerned. The molars of *R. sumatrensis* are high crowned, although not as high as those of *R. sinensis*, but they have longer roots and much smaller M3 than *R. sinensis*. Furthermore, M1 of *R. sumatrensis* is the largest tooth, whereas in *R. sinensis* it is M2.

Rhizomys pruinosus Blyth, 1851. This species was named by Blyth (1851, p. 519) after the examination of specimens collected by R. Frith in the Khasi hills (Cherrapunji, India). Blyth differentiated this species from *R. sumatrensis* in being “much less robust, having a much shorter tail, and a dense coat of fine soft fur instead of a thin coat of bristly fur”. However, he pointed out that their structural characters were essentially the same. The syntypes are supposed to be in the collection of the Indian Museum, Kolkata (P. Jenkins, pers. comm. 2012), but we were unable to obtain confirmation.

The dental pattern of the teeth of *R. pruinosus* is similar to that of the remaining species of the genus. There is only a minor difference concerning the smaller size of the molars.

Rhizomys (Brachyrhizomys) shansius (Teilhard de Chardin, 1942). Teilhard de Chardin (1942), on the basis of four lower mandibles from the Pliocene of Taoyang (Yushe Basin, Shanxi, China) named the new genus *Brachyrhizomys*, which was seen as a primitive type of *Rhizomys*, and the new species *B. shansius*. Later on, Flynn (2009) after a complete and detailed study of this species concluded that, even though it is distinct from all living species of *Rhizomys*, it is sufficiently closely related to them for *Brachyrhizomys* to be treated as a subgenus within *Rhizomys* (see Fig. 4F-G). The holotype of this species, IVPP 31.096, a right dentary with incisor, is housed in the IVPP. Additional material of this species has been found at other localities of the Yushe Basin (Flynn, 1993; Flynn, 2009).

Rhizomys (Brachyrhizomys) shajius Flynn, 1993. The holotype and only known specimen of this taxon (V8920), a right dentary fragment with m2-m3 comes from the Late Miocene YS 156 locality of the Tancun subbasin (south of Yushe) (Flynn, 1993). Smaller than *B. shansius*, it is housed in the IVPP.

Genus Cannomys Thomas, 1915. Type species: *Cannomys badius* (Hodgson, 1841)

Cannomys badius (Hodgson, 1841). This species was coined as *Rhizomys badius* by Hodgson (1841, p. 60) on the basis of a male specimen obtained from “some miles north of the great valley” of Nepal. He gave the following brief Latin

diagnosis: "Unicolor: pilis internē nigri cantibus schistaceis: longitudo Corporis 8 uncia, caudæ $2\frac{5}{8}$, capitis $2\frac{1}{4}$: Pedis antici (cum ungue) $1\frac{1}{16}$: pedis postici $1\frac{3}{8}$, auriculæ $\frac{1}{4}$ ". This can be translated as: "One-colored: with hairs internal blackish slate-colored: length of body 8 inches, tail $2\frac{5}{8}$, head $2\frac{1}{4}$: anterior foot (with claw) $1\frac{1}{16}$: posterior foot $1\frac{3}{8}$, external ear $\frac{1}{4}$ ". The type specimen is BMNH 1843.1.12.61 (skin and skull) (P. Jenkins, pers. comm. 2012).

Later on, Thomas (1915a) created the new genus *Cannomys* for which he took *Rhizomys badius* as type, but in which he also included two species now seen as junior synonyms. He gave the following diagnosis: "Size comparatively small. Palm and sole-pads normal, well defined, not granulated. Mammæ 2-2=8. Anteorbital foramina and posterior nares much as in *Rhizomys*. Incisors forming a segment of a large circle, their points thrown strongly forwards. Molars decreasing in size backwards, the first decidedly larger than the second, its grinding surface not worn lower than that of the latter". The species *Cannomys pater* coined by Thomas (1915b) is today also considered a junior synonym of *C. badius* (Musser and Carleton, 2005).

The upper molars of *Cannomys badius* show unilateral hypsodonty. The upper incisors are proodont and lack major ornamentation. The dental pattern of the M1 is tetralophodont (protocone-anteroloph, protocone-protoloph, hypocone-mesoloph and hypocone-metaloph-posteroloph), whereas the M2 and M3, much shorter than the M1, only have three transverse lophs (protocone-anteroloph-protoloph, hypocone-mesoloph and hypocone-metaloph-posteroloph) (Fig. 3D). Through wear, the lophs join at the margin of the tooth isolating two transversely elongated enamel lakes. The lower molars are lower crowned than the upper ones. The lower incisors lack major ornamentation and their enamel is flat. The mandibular foramen is well posterior to the distal side of the m3 (it is located a little higher than the m3 at the level of the extremity of the coronoid process). The mental foramen is situated anteriorly to the anterior side of the m1 at about the midline of the dentary. The dental pattern of the m1 is pentalophodont with five transverse lophids (anterolophid, protoconid-metalophid, protoconid-mesolophid, hypoconid-hypolophid and hypoconid-posterolophid), whereas that of the m2 and m3 has three lophids (anterolophid-metalophid, mesolophid and hypolophid-posterolophid) (Fig. 3C). By wear, all lingual reentrants are closed off forming lingual enamel lakes.

Genus *Tachyoryctes* (Rüppell, 1836). Type species: *Tachyoryctes splendens* (Rüppell, 1836)

Referred species: *Tachyoryctes macrocephalus*, *Tachyoryctes konjiti*, *Tachyoryctes pliocaenicus*, *Tachyoryctes makooka*.

Tachyoryctes splendens Rüppell, 1836. Rüppell (1836, p.36) named a new species of rodent that he discovered in Ethiopia (Fig. 5). In his work he pointed out that this rodent resembled very much *Bathyergus* from Cape of Good Hope in the skull, crown and size of the teeth, toes and claws. However, he also noticed some singularities in the Ethiopian animal like the small size of its pinna and its longer and more rounded tail. Since very few specimens of the genus *Bathyergus* were known at that time, he refrained from naming a new genus, even though unnamed eminent Londoner and Parisian experts thought otherwise. Nevertheless, in case someone wanted to transfer his species into a new genus, he added as a footnote the following thought: “Will man mit aller Gewalt diese Thier zu einer eigenen Gattung erheben, so dürfte man solche passender Weise *Tachyoryctes* benennen, von ταχύς, schnell, und όρύκτης, Gräber-²²; ~~which means~~ (“If one would by any means erect a new genus for this animal, he might name it appropriately *Tachyoryctes* from ταχύς, fast, and όρύκτης, burrower”). Rüppell (1842) reallocated this species to the genus *Rhizomys* including in it the new taxon *Rhizomys macrocephalus* (see below) as well. The genus *Tachyoryctes* was accepted in Heck (1851a, p.464) in a section written by C. Girard (Heck, 1851b, p. v). Heuglin and Fitzinger (1866, pp.32-33) and later authors also accepted *Tachyoryctes* as valid and included both *T. splendens* and *T. macrocephalus* in it. The lectotype of *T. splendens* is SMF 4317 (head and skin).

Tachyoryctes splendens has ever growing teeth showing unilateral hypsodonty. Upper and lower incisors are orange and flattened, and the lower incisor has a prominent ridge. The proodont upper incisors may also bear a fine longitudinal ridge. The upper molars lack the mure and the the anterior part of the teeth is isolated from the posterior one. When unworn, the M1 show a long anteroloph, a distinct and isolated protoloph, a long mesoloph that joins the hypocone and a metacone that connects

labially to a short posteroloph. The morphology of the M2 and M3 is similar to that of the M1 except for the anterior part of the teeth in which there is a single anterior crest (anteroloph-protoloph) (Fig. 3F). Rapidly during wear, the lophs join at the margin of the tooth isolating three (on the M1) or two (on the M2 and M3) enamel lakes, which will disappear with further attrition. When unworn, the m1 shows a cuspid-like isolated anterolophid, an isolated metaconid, the entoconid connected to the protoconid and an arcuate posterolophid, which is a long continuation of the hypoconid. The m2 and m3 have the anterolophid fused with the metaconid and the teeth show three oblique lophs (anterolophid-metaconid, entoconid-protocoid and hypoconid-posterolophid). The mure is lacking (Fig. 3G).

Tachyoryctes macrocephalus (Rüppell, 1842). Rüppell (1842) named the new species *Rhizomys macrocephalus* on the basis of a rodent from Shoah ~~province~~ Province (southern Ethiopia) that was sent to him. The lectotype is SMF 4318 (skull and skin). This species was soon reallocated to the genus *Tachyoryctes* (see above). The morphology of the cheek teeth of *T. macrocephalus* is similar to that seen in *T. splendens*. The difference between these taxa rests in the much greater size of the former.

Tachyoryctes pliocaenicus Sabatier, 1978. This species was named on the basis of eight mandibles (some of them incomplete) and a fragmentary skull with right and left M1-M2 from the Pliocene Hadar Formation, Ethiopia (Sabatier, 1978). The holotype, a right mandible with m1-m3 (AL.288.29), is housed in the NME.

Tachyoryctes konjiti Sabatier, 1982. This taxon was named by Sabatier (1982; see also Sabatier, 1979) on the basis of a hundred isolated molars from the Pleistocene locality of Garba VIII (Melka Kunturé, Ethiopia). Its holotype (Garba VIII B 16), an isolated M1, is housed in the NME. Additional material of *T. konjiti* has been found in other Pleistocene Ethiopian localities as Garba IV, Gombore Iy, Simbiro, Gombore II B/C, Garba III E, Garba X and Garba VIIIB (Sabatier, 1979; Galloti et al., 2010).

Tachyoryctes makooka Wesselman, Black et Asnake, 2009. This taxon was coined on the basis of various mandibles, maxillary fragments, isolated molars as well as some postcranial elements (Wesselman et al., 2009). Its holotype comes from the Late Miocene Digiba Dora Vertebrate Locality 1 (Middle Awash, Ethiopia) and is housed in the NME. This species has been also recovered from various Late Miocene-Pliocene localities of the Middle Awash (ALA-VP-2, AME-VP-1, AMW-VP-1, ASK-VP-3, GAW-VP-1, GAW-VP-3, KUS-VP-1, STD-VP-2, WKH-VP-1) (Wesselman et al., 2009). The morphology of the teeth of *T. makooka* has been described in detail by López-Antoñanzas and Wesselman (in press).

Genus Anepsirhizomys Flynn, 1982. Type species: *Anepsirhizomys opdykei* Flynn, 1982

Referred species: *Anepsirhizomys pinjoricus*

Anepsirhizomys opdykei Flynn, 1982. This taxon was named on the basis of a left dentary fragment with m1-m2 from the middle Pliocene locality DP70 (Bunha River area, Potwar Plateau, Pakistan) (Flynn, 1982a). Additional material of this species has not been found to date.

Anepsirhizomys pinjoricus (Hinton, 1933). Hinton (1933), in the course of the preparation of a monograph on Indian fossil rodents, which was never actually published, studied some rodent remains belonging to the GSI. This work led him to discover various new species of *Rhizomys*, one of which he named *Rhizomys pinjoricus*. Black (1972) reallocated this species to the genus *Rhizomyides* created by Bohlin (1946), which unfortunately he miswrote as “*Rhizomyoides*” (see below). It was not until 1990 that this taxon was suspected to be an *Anepsirhizomys* (Flynn et al., 1990). The holotype of this species (G.S.I. D278), a fragmentary mandible with m2-m3, is from the Late Pliocene of the Simla area, India. It is housed in the BMNH (paleontology collection). Additional material of this species has been recorded from the early Pleistocene near the base of the “Pinjor” strata (Nadah village, Simla Hills, India) (Flynn et al., 1990).

Genus *Miorhizomys* Flynn, 2009. Type species: *Miorhizomys nagrii* (Hinton, 1933)

Referred species: *Miorhizomys micrus*, *M. blacki*, *M. pilgrimi*, *M. harii*, *M. tetracharax*, *M. choristos*.

The detailed study of the oldest fossil skull and postcrania of *Rhizomys* (*Brachyrhizomys*) *shansius* from the Yushe Basin carried out by Flynn (2009) led him to realize that even if *Brachyrhizomys* from the Siwaliks of the Indian subcontinent share some synapomorphies with the former species (and extant *Rhizomys*), there are also noteworthy differences between them. Indeed, the Siwalik bamboo rats lack important synapomorphies of living rhizomyines and of *R. (Brachyrhizomys) shansius* ~~like such as~~ a high infraorbital foramen without open ventral slit (Flynn, 2009). Thus, he created the new genus *Miorhizomys* for large Siwalik bamboo rats and their Miocene relatives from southern China.

Miorhizomys nagrii (Hinton, 1933). Hinton (1933) on the basis of some remains he found among the material belonging to the GSI named four new species, which he considered as belonging to the genus *Rhizomys*. One of them was *Rhizomys nagrii*, which was based on a left dentary fragment with broken i and m2-m3 (GSI D273) from the Late Miocene lower alternations of Haritalyangar, Simla Hills, India. Black (1972) described in detail the material briefly diagnosed by Hinton (1933). In his revision, Black transferred this species to the genus *Rhizomyides* Bohlin, 1946, misspelling as *Rhizomyoides* (see below). Afterwards *R. nagrii* was reallocated to *Brachyrhizomys* (Flynn, 1982a). When Flynn (2009) named the new genus *Miorhizomys* he designated this as its genotypic species. The holotype of this taxon is housed in the BMNH (paleontology collection).

Additional material of this species has been recorded from the Late Miocene of Kaulial, Pakistan, as well as from localities Y270, Y260, Y182, Y330, Y261, Y317, Y464, Y262, Y892 of the lower Dhok Pathan Fm., Potwar Plateau, Pakistan (Flynn 1982a) and from the coeval vertebrate locality of Lufeng (about 9 km north of Lufeng city) in southern China (Flynn and Qi, 1982). ~~Furthermore, various~~ Several isolated molars of *Miorhizomys nagrii* ~~described by Jacobs (1978)~~ under the name *Rhizomyoides* cf. *R. nagrii* ~~had been~~ were collected ~~and described by Jacobs (1978) by him at from~~ the Late Miocene Dhok Pathan hominoid locality YGSP 182A, about 9.2 Myr.

Miorhizomys micrus (Flynn, 1982). The holotype and sole specimen recorded of this species (YGSP 5494) is a left dentary fragment with broken i1, m1-m3 from the Late Miocene (9.3 Myr) lower Dhok Pathan Formation in the Potwar Plateau, Pakistan (Flynn 1982a). The taxon was originally ascribed to *Brachyrhizomys*, but was reallocated to *Miorhizomys* by Flynn (2009). This material is currently housed at the PMAE and it should eventually be returned to Pakistan and be deposited at the PMNH.

Miorhizomys blacki (Flynn, 1982). *Brachyrhizomys blacki* was named by Flynn (1982a) on the basis of a single right dentary fragment with broken i1, m2-m3 recorded from the Late Miocene locality Y464 of the Dhok Pathan Formation in the Potwar Plateau, Pakistan. The taxon was originally ascribed to *Brachyrhizomys*, but was reallocated to *Miorhizomys* by Flynn (2009). This specimen is currently housed at the PMAE and it should eventually be deposited at the PMNH. Unfortunately no additional material of this species has been found to date.

Miorhizomys pilgrimi (Hinton, 1933). In 1933, Hinton named the new species *Rhizomys pilgrimi* for a partial right mandible with m2-m3 from the late Miocene lower alternations, Haritalyangar, India. This taxon has known the same taxonomic history as *Miorhizomys nagrii*. The holotype is housed in the BMNH (paleontology collection). *M. cf. pilgrimi* has been found at the Late Miocene (9.4-7.9 Myr) localities Y270, Y17, Y19, Y118, Y954, Y992, and Y1000 of the Dhok Pathan Formation in the Potwar Plateau, Pakistan (Flynn, 1982a), and at the coeval Chinese locality of Lufeng (Flynn and Qi, 1982).

Miorhizomys harii (Prasad, 1968). This taxon was named based on a single right dentary fragment with m1-m2 recovered from Haritalyangar, India. Its age is unknown, but Flynn (1982b) suggested an age close to 9 Myr (current time scale) on the basis of its stage of evolution. This species was originally considered as belonging to the genus *Rhizomys*. It was subsequently transferred to the genus *Brachyrhizomys* (Flynn, 1982b) and later to *Miorhizomys* (Flynn, 2009). No additional material of *M. harii* has been found to date.

Miorhizomys tetracharax (Flynn, 1982). This taxon was originally named as *Brachyrhizomys tetracharax* (Flynn, 1982a), but Flynn (2009) included it in *Miorhizomys*. The holotype of this species (YGSP 4810) consists of an associated palate with right and left I, M1-M3, right dentary fragment with i, m1-m3 and right half occiput with auditory region recorded from the Late Miocene (8.7 Myr) locality Y204 from the Dhok Pathan Formation in the Potwar Plateau, Pakistan (Flynn, 1982a). It is currently housed at the PMAE and it should be deposited eventually at the PMNH. More material of *Miorhizomys tetracharax* was found in the same formation at localities Y260 and Y388 (Flynn, 1982a), and more recently at Y631, Y952, and Y954. In India, Late Miocene remains of this species (Fig. 4E) were recorded from the Hari Scarp, Punjab (Flynn, 1982a), and from the “hominoid interval” of the Haritalyangar Scarp, Himachal Pradesh (Flynn et al., 1990). Finally, *M. tetracharax* was also found at the Late Miocene vertebrate locality of Lufeng in southern China (Flynn and Qi, 1982).

Miorhizomys choristos (Flynn, 1982). The holotype of this species (YGSP 4053), an associated snout with both I1, left and right dentary fragments with broken i1, m1-m3, a distal left humerus, a proximal left ulna, a right femur portion and cranial fragments is housed at the PMAE and it should be eventually deposited at the PMNH (Flynn, 1982a). It comes from the Late Miocene (8.3 Myr) locality Y172, Dhok Pathan Formation, Potwar Plateau, Pakistan. At that time, the holotype was the sole material found of this taxon. Later on, additional specimens were recovered from Y457, Y535, and in northern India from the “hominoid interval” of the Haritalyangar Scarp, Himachal Pradesh (Flynn et al., 1990).

Genus *Eicooryctes* Flynn, 1982. Type species: *Eicooryctes kaulialensis* Flynn, 1982

Eicooryctes kaulialensis Flynn, 1982. Flynn (1982a) named this taxon on the basis of some cranial and dentary fragments from the Late Miocene (8.0-7.2 Myr) localities Y434, Y437 and Y438 of the upper Dhok Pathan Formation, Kaulial Kas, Potwar Plateau, Pakistan. Its holotype, a palate and snout with broken incisors and left and right M1-M2 (YGSP 15320), is currently housed at the PMAE and it should eventually be

returned to Pakistan where it would be deposited at the PMNH. Recently additional material of this species was been found at locality Y898.

Genus *Protachyoryctes* Hinton, 1933. Type species: *Protachyoryctes tatroti* Hinton, 1933

Protachyoryctes tatroti Hinton, 1933. This species was named by Hinton (1933) on the basis of a partial right mandible with m1-m3 (GSI D272), which is housed in the BMNH (paleontology collection). Hinton (1933) indicated that this material comes from a Pliocene horizon near Tatrot village, Salt Range, Pakistan. However, its provenance has been thrown into doubt since, in particular, the discovery of new material belonging to this taxon at the Late Miocene (7.8-7.1 Myr) localities Y434, Y909, and Y369 in the Dhok Pathan Formation of the Potwar Plateau, Pakistan (Flynn, 1982a). Flynn (1982a) pointed out the presence directly beneath Tatrot of much older rocks (more than 6 Myr), which he suspected was the provenance of the holotype of *P. tatroti*. These doubts are supported by the great resemblance between this species and the Late Miocene *Tachyoryctes makooka*.

Genus *Rhizomyides* Bohlin, 1946. Type species: *Rhizomyides sivalensis* (Lydekker, 1884)

Synonymy: *Rhizomyoides* Black, 1972

Referred species: *Rhizomyides punjabiensis*, *R. carbonnelli*, *R. platytomeus*, *R. mirzadi*

This genus was created by Bohlin (1946) to include the two Siwalik rhizomyines known by him at that time (*R. sivalensis* (Lydekker, 1884) and *R. punjabiensis* (Colbert 1933)), which were considered, in those days as belonging to the genus *Rhizomys*. Hinton (1933) had named four new species of “*Rhizomys*” from the Siwaliks (*R. nagrii*, *R. pinjoricus*, *R. lydekkeri* and *R. pilgrimi*), but this was apparently unknown to Bohlin. According to Bohlin (1946), *R. sivalensis* and *R. punjabiensis* were congeneric and clearly distinct from *Rhizomys*. Thus, he proposed the genus *Rhizomyides* and chose *Rhizomyides sivalensis* as the type species. Black (1972) in his review of the fossil rodents from the Siwaliks mistook this genus name as *Rhizomyoides*. This spelling error

was repeated by subsequent authors (see e.g. Gupta et al., 1978; Vasishat et al., 1978; Brandy 1979a) until review by Flynn (1981).

Rhizomyides sivalensis (Lydekker, 1884). Lydekker (1878) briefly described two mandibular rami of a new rodent from Jabi, Punjab, Pakistan. Lydekker (1878) thought this material could probably represent a new species, but he cautiously proposed the name *R. sivalensis* and it turned out his thoughts were confirmed. As this new taxon was named with uncertainty it cannot be taken into account (~~article 67.2.5 of the International-International Commission on Zoological Nomenclature, code of zoological nomenclature, 2000~~1999: article 67.2.5) and it was Lydekker (1884) who made the name *Rhizomys sivalensis* available. Its holotype (GSI D97) is a left dentary fragment with i1, m2-m3 from Jabi. It is housed in the BMNH (paleontology collection). Additional material of this species has been recorded from the Potwar Plateau, Pakistan and from the Upper Siwaliks of the Siwalik Hills, India (Flynn, 1982a).

Rhizomyides carbonnelli (Brandy, 1979). Brandy (1979a) named this taxon *Rhizomyoides carbonnelli* repeating the spelling error made by Black in 1972 in the generic name *Rhizomyides* created by Bohlin in 1946 (see above). The holotype of this species (PEC 101) is a right mandible with i, m1-m3 from the Late Miocene-Early Pliocene of Pul-e Charkhi, Kabul, Afghanistan (Brandy, 1979a, 1979b, 1981). It is currently housed in the collections of the UM2 (B. Marandat, pers. comm. 2011).

Rhizomyides platytomeus Flynn, Heintz, Sen et Brunet, 1983. This species was named on the basis of a left dentary with i, m1-m3 (AFG 059) recorded from the middle Pliocene locality of Lataband, Sarobi Basin, Afghanistan (Flynn et al., 1983). It is currently housed in the paleontological collections of the MNHN (S. Sen, pers. comm. 2011). Unfortunately no additional material of this taxon has been found to date.

Rhizomyides mirzadi (Lang et Lavocat, 1968). Lang and Lavocat (1968) named the new species *Rhizomys mirzadi* on the basis of a right mandibular fragment with m2 (BAM 1) and *Kanisamys bamiani* based on an isolated m1 (BAM 2) from the Late Miocene Bamian Basin (Afghanistan). Brandy (1981) reallocated *Rhizomys mirzadi* to

the genus *Protachyoryctes*. The reexamination of these two specimens and an unpublished third one (BAM 3), led Flynn (1983) to gather all them in a sole species, which he transferred to the genus *Rhizomyides*. Thus, *Kanisamys bamiani* is a synonym of *Rhizomyides mirzadi*. The holotype (BAM 1) is currently housed in the collections of the MNHN (S. Sen, pers. comm. 2011).

Rhizomyides punjabiensis (Colbert, 1933). Colbert (1933) described a small rhizomyine that he named *Rhizomys punjabiensis*. Bohlin (1946) coined the new genus *Rhizomyides* and allocated this species to it. *R. punjabiensis* was later reassigned to the genus *Brachyrhizomys* (Flynn 1981, 1982a, 1982b, 1984, 1985). Flynn (1986, 1990) later recognized the appropriate attribution *Rhizomyides*, making it the oldest known species of this genus. The holotype (AMNH 19762), a right mandibular ramus with the m2 and m3 and the posterior portion of the incisor, and only record of this species in those days, comes from the Late Miocene (Flynn, 1982a) Lower Siwalik beds of Bilaspur, Punjab, India (Colbert, 1933). Additional material of this species has been recorded from the early Late Miocene of Pakistan, near Kaulial and at the localities Y797, Y259 and Y450 from the Nagri Formation, Potwar Plateau (Flynn, 1982a)

Rhizomyides lydekkeri (Hinton, 1933) and *Rhizomyides saketiensis* (Gupta, Verma et Tewari, 1978). *Rhizomyides lydekkeri* was named by Hinton (1933) as *Rhizomys lydekkeri*. Its holotype (BMNH 15925) is a partial mandible with m1-m3 that comes from the Pliocene Upper Siwaliks of Northern India. Colbert (1935) considered this specimen together with some others (BMNH 15926, 15927 and 15927a) as *Rhizomys* sp. and pointed out that they probably did not belong to *Rhizomys sivalensis* because of their larger size and more recent age. However, Black (1972) synonymized the two species, and Flynn (1982b) considered them to represent the genus *Rhizomyides*.

Gupta et al., (1978) named the new species *Rhizomyoides saketiensis* on the basis of two dentary fragments from the Pliocene/Pleistocene Tatrot beds at Saketi Park (Himachal Pradesh). The holotype (GSI 19549) is a partial right mandibular ramus with m2 and m3. Flynn (1983) reallocated this species to the genus *Rhizomyides*. It is unknown if *R. lydekkeri* and *R. saketiensis* represent the same species (Flynn, 1982b;

Flynn et al., 1983). Pending a re-examination of Hinton's (1933) original material, we have preferred not to ~~not~~ include these two taxa in our analysis.

Genus *Kanisamys* Wood, 1937. Type species: *Kanisamys indicus* Wood, 1937

Referred species: *Kanisamys nagrii*, *K. sivalensis*, *K. potwarensis*

In 1932, G. E. Lewis of Yale University collected some fossil rodents from the Siwalik deposits from the Chinji and Nagri zones of what was then North India, which he gave to A. E. Wood for study. Some of these specimens turned out to belong to a new genus that Wood (1937) named *Kanisamys*.

Kanisamys indicus Wood, 1937. The holotype of this species (YPM 13810), a right mandible with m1-m3, comes from the Chinji Zone, ~~South-south~~ of Chinji Village, now Pakistan (Wood, 1937). Additional material of this taxon has been found in Pakistan from Middle Miocene localities in the Chinji Formation (Flynn et al., 1995). Furthermore, a fragmentary mandible (specimen D 271) from near Chinji (Attock District) considered by Hinton (1933) as *Theridomys* was reallocated to *K. indicus* by Black (1972). *K. indicus* has also been recorded from the locality 18 in the Chinji Formation at Daud Khel (Munthe, 1980), from the locality H-GSP 107 in the Chinji Formation, Banda Daud Shah (Wessels et al., 1982) and at various localities in the Lower Manchar formation, Sind (Wessels and de Bruijn, ~~2003~~2001).

Kanisamys sivalensis Wood, 1937. The holotype of this species (YPM 13801), a left mandible with m1-m3, comes from Lower Alternations, East of Haritalyangar, India (Wood, 1937). Additional material of this taxon has been recorded from various Late Miocene localities in the Upper Nagri and lower Dhok Pathan formations, Potwar Plateau, Pakistan (Jacobs 1978; Flynn, 1982a; Flynn et al., 1995).

Kanisamys nagrii Prasad, 1968. This species was named on the basis of a single left dentary fragment (GSI 18086) with i1M2-3 (Prasad, 1968), which was refigured by Flynn (1982b). It comes from the Late Miocene Lower Alternations, East of Haritalyangar, India. Additional material of this taxon has been recorded in the same

area (Fig. 4A-C) as well as from the upper portion of the Chinji Formation, and the Late Miocene Nagri Formation, Potwar Plateau, Pakistan (Flynn, 1982a).

Kanisamys potwarensis Flynn, 1982. This species was named by Flynn (1982a) on the basis of various isolated molars (Fig. 4D). The holotype of this taxon (YGSP 8379), a left M3, comes from the Middle Miocene locality Y491 in the Chinji Formation, Potwar Plateau, Pakistan. Additional material of this taxon from the same area is now recognized at localities Y709, Y733, Y430, Y491, Y668, Y59, Y641, and Y651 and Y41 (14.3 to 13.4 Myr). *Kanisamys* cf. *potwarensis* has been mentioned from the Lower Siwalik Group of Ramnagar, Udhampur District, Jammu and Kashmir, India (Parmar and Prasad, 2006; Sehgal and Patnaik in press).

Genus *Nakalimys* Flynn et Sabatier, 1984. Type species. *Nakalimys lavocati* Flynn and Sabatier, 1984

Nakalimys lavocati Flynn et Sabatier, 1984. This taxon was named on the basis of a palate and mandible, two dentaries, an isolated lower incisor and some lower and upper molars from the early Late Miocene site of Nakali, Kenya (Flynn and Sabatier, 1984). The holotype (KNM-NA 7700) is a palate and mandible with left and right M1-M3 and i1 m1-m3. *Nakalimys* cf. *lavocati* has been found in the coeval site of Chorora, Ethiopia (Geraads, 1998).

Genus *Pronakalimys* Tong et Jaeger, 1993. Type species. *Pronakalimys andrewsi* Tong and Jaeger, 1993

Pronakalimys andrewsi Tong et Jaeger, 1993. This species was named on the basis of 13 partial lower jaws (7 with m1-m3, 5 with m1-m2 and 1 with m3) and a right maxilla with M1-M3 from the Middle Miocene site of Fort Ternan, Kenya (Tong and Jaeger 1993). The holotype (KNM-FT64-007) is a right maxilla. No additional material of this taxon has been found so far.

Genus *Prokanisamys* de Bruijn, Hussain et Leinders, 1981. Type species:

Prokanisamys arifi de Bruijn, Hussain et Leinders, 1981

Referred species: *Prokanisamys kowalskii*, *P. benjavuni*, *P. major*, *P. sp.* Libya

Except for a few remains of *Prokanisamys* sp. described by Wessels et al., (2003) from the Lower Miocene of Libya, all the specimens of this genus found to date come from the Asian continent (Pakistan and Thailand).

Prokanisamys arifi de Bruijn, Hussain et Leinders, 1981. This species was defined on the basis of some isolated molars (6 m1, 11 m2, 11 m3, 6 M1, 6 M2 and 16 M3) from the Lower Miocene H-GSP 116 locality of the Murree Formation, Banda Daud Shah, Kohät, Pakistan (de Bruijn et al., 1981). The holotype (specimen n°22) is a right m1 currently housed at the IVAU. Additional material of this species has been found at the localities Z126, Z122, Z120 and Z 124 of the Chitarwata and Vihowa Formations, Zinda Pir Dome, Pakistan, as well as at the localities H-GSP 81114a, H-GSP 8424, H-GSP 81114, H-GSP 8426 (Sehwan Section) and H-GSP 8107a, H-GSP 8209, H-GSP 8311 and H-GSP 8106 (Gaj River Section) of the Lower Manchar Formation, Sind, Pakistan (Wessels and de Bruijn ~~2003~~2001; Lindsay et al., 2005; Wessels 2009).

Prokanisamys kowalskii (Lindsay, 1996). Lindsay (1996) coined a new species of *Eumyarion* as *E. kowalskii* on the basis of various molars and some isolated incisors recorded from the latest Oligocene (Lindsay et al., 2005; Flynn, 2009) locality Z113, Zinda Pir Dome, Pakistan. Wessels and de Bruijn (2001) transferred *E. kowalskii* to the genus *Prokanisamys* because of the greater closeness to the latter genus than to *Eumyarion* from Europe and Western Asia. The holotype of this species (PMNH Z113/679) is a right isolated M1.

Prokanisamys benjavuni (Mein et Ginsburg, 1985). The preliminary results of a field campaign carried out in Li Mae Long, Lamphun district, Thailand by P. Mein and L. Ginsburg in 1984 in collaboration with the DMR and the University of Chiang Mai (Thailand) lead them to name a new species of rhizomyine: *Kanisamys benjavuni* (Mein and Ginsburg, 1985). Jacobs et al. (1989) reallocated this species to the genus *Prokanisamys*, a conclusion with which Mein and Ginsburg (1997) agreed after being

able to sample more specimens of this taxon. *Prokanisamys benjavuni* comes from Li, Lamphun district, Thailand. This locality was first considered as Early Miocene until the works of Chaimanee et al. (2007) proved it to be Middle Miocene in age. The holotype of this taxon (T Li 203), a left isolated m3 (the single complete m3 known at the time), is housed at the collections of the FSL under the number FSL 67035 (Mein, pers. comm. 2011). Additional material of this species has also been found in the MaeMoh Basin, northern Thailand (Chaimanee et al., 2007) as well as in some Pakistani late Early Miocene levels (5, 6 and 6 bis) of Dera Bugti (Welcomme and Ginsburg, 1997; Welcomme et al., 2001) and at H-GSP 8114a, H-GSP 8114, H-GSP 8424 and H-GSP 8426 localities in the Lower Manchar Formation, Sehwan Section (Wessels and de Bruijn, 2001).

Prokanisamys major Wessels et de Bruijn, 2001. The holotype of this species (specimen n° 4522) is an isolated left M1 from the Middle Miocene locality H-GSP 81.14 of the Lower Manchar Formation, Sind, Pakistan. It is currently housed at the IVAU. Additional material of this species has been found in the same area at late Early and Middle Miocene localities (H-GSP 8106, H-GSP 8227, H-GSP 8224, H-GSP 8424, H-GSP 8214, H-GSP 8425, H-GSP 8426, H-GSP 8427) as well as at some localities (Y-GSP 591, Y-GSP 592, Y-GSP 642, Y-GSP 501, Y-GSP 589, Y-GSP 491, Y-GSP 640, Y-GSP 641, Y-GSP 496, Y-GSP 634) of similar age on the Potwar Plateau, Pakistan (Flynn, 1986; Jacobs et al., 1990; Wessels and de Bruijn, 2001). The specimens from this latter area were first identified as *Prokanisamys benjavuni* (Flynn, 1986; Jacobs et al., 1990) until the discovery of the species *Prokanisamys major* (Wessels and de Bruijn, 2001).

Prokanisamys sp. Wessels, Fejfar, Peláez-Campomanes et de Bruijn, 2003. Two paleontological field campaigns carried out in 1983 and 1997 in various Miocene levels of the Marada Formation, Jebel Zelten, Libya, resulted in the discovery of some large and small mammals. Among the latter, five isolated teeth (3M1, 1m2, 1m3) of a species of *Prokanisamys* were found at the Early Miocene levels ATH4B, ATH5A1 and ATH7A2 (Wessels et al., 2003). This finding is of relevance not only as the only record

of *Prokanisamys* found to date in Africa, but also for being the oldest record of a rhizomyine found in this continent.

Phylogenetic analysis

Previous work

Flynn (1990). The first attempt at deciphering the relationships of the extinct and extant Rhizomyinae (Rhizomyidae *sensu* Flynn, 1982a) based on the synapomorphies of the different genera of rhizomyines (a group then at the family level) was carried out by Flynn (1990). According to the hand-generated cladogram (Fig. 6), the Asian *Prokanisamys* was the most basal genus of the ingroup, followed by the East African *Nakalimys*. The analysis supported the monophyly of (*Kanisamys*, *Protachyoryctes*, *Eicooryctes*, *Tachyoryctes*), which Flynn (1990) considered as the subfamily Tachyoryctinae. In addition, the clade (“*Brachyrhizomys*”, *Rhizomys*, *Cannomys*) would constitute the subfamily Rhizomyinae. Flynn (1990) inferred two plausible relationships for the sister genus of *Kanisamys*, *Rhizomyides*: either it belongs to the Tachyoryctinae or it is the sister taxon to the clade constituted by the Tachyoryctinae and Rhizomyinae.

New analysis

32 most parsimonious trees were generated with a length of 158 and a relatively high degree of homoplasy (CI = 0.456 and RI = 0.819). The strict and semi-strict consensus trees are identical and largely resolved (Fig. 7A) with five polytomies each. In the majority-rule consensus tree one of these polytomies disappears and one, although persisting, involves a reduced number of taxa (Fig. 7B). Bremer and relative Bremer support indices (Goloboff and Farris, 2001; Goloboff et al., 2003) for each node are indicated on the cladogram in the figure 7A.

The transformations supporting the topology of this tree (under the ACCTRAN and DELTRAN optimizations) are listed in Table 42. Each internal node is discussed below, beginning from the most basal (whenever both unambiguous and ambiguous synapomorphies support a given node, only the former are mentioned).

Node 62. *Prokanisamys* spp. + more derived taxa. This node is based on a single non-exclusive synapomorphy under ACCTRAN: mesolophid on the m2 short and well-separated from the hypolophid.

Node 61. *Prokanisamys* spp. This clade is sustained by two exclusive and unambiguous synapomorphies, i.e. weak lophodonty and mesolophid on the m3 short and well-separated from the hypolophid, and two non-exclusive and unambiguous synapomorphies, i.e. mesolophid on the m1 short and well-separated from the hypolophid (a convergence with *Nakalimys lavocati*, the node 53 and some individuals of *Miorhizomys nagrii* and *M. choristos*) and anterosinus on M3 enclosed by anteroloph and paracone (a convergence with node 58).

Node 60. *Pronakalimys andrewsi* + more derived taxa. This node is supported by one exclusive and unambiguous synapomorphy, i.e. ectoloph on M2 absent, and one non-exclusive and unambiguous synapomorphy, i.e. ectoloph on M1 absent (a convergence with *Prokanisamys kowalskii*).

Node 59. *Nakalimys lavocati* + more derived taxa. One exclusive and unambiguous synapomorphy supports this node, i.e. anteroconid on m1 absent, as well as one non-exclusive and unambiguous synapomorphy, i.e. m3 enlarged (a convergence with *Prokanisamys major*).

Node 58. (*Kanisamys potwarensis*, *K. indicus*) + more derived taxa. This node is supported by two exclusive and unambiguous synapomorphies, i.e. labial anterolophid on m1 absent and mesoloph on M2 long and complete. It is also sustained by three non-exclusive and unambiguous synapomorphies, i.e. moderate hypsodonty (a convergence with *Prokanisamys benjavuni*, *Tachyoryctes pliocaenicus* and *T. konjiti*), presence of mesostyle on M1 (a convergence with *Rhizomyides punjabiensis* and *Miorhizomys nagrii*) and anterosinus enclosed by anteroloph and paracone on M3 (convergence with node 61).

Node 57. *Kanisamys potwarensis* + *K. indicus*. One non-exclusive and unambiguous synapomorphy supports this clade, i.e. mesolophid long and complete and separated from the hypolophid on m2 (a reversal).

Node 56. *Kanisamys nagrii* + more derived taxa. This node is supported by five exclusive and unambiguous synapomorphies: high lophodonty, labial anterolophid absent on m2 and m3, protosinusid absent on the m2 and m3. Two additional non-

exclusive and unambiguous synapomorphies are present, i.e. posterior protoconid-metaconid connection absent on m1 (a convergence with some individuals of *Kanisamys indicus* and node 44) and mesolophid short and migrated toward the hypolophid on m3 (a convergence with *Pronakalimys andrewsi*).

Node 55. *Kanisamys sivalensis*+ more derived taxa. Two non-exclusive and unambiguous synapomorphies support this node, i.e. metaloph fused with posteroloph on M1 (a convergence with *Kanisamys potwarensis*) and posterosinus absent on the M1 (a convergence with *Kanisamys potwarensis*).

Node 54. *Miorhizomys micrus* + (*Rhizomyides mirzadi*, *R. punjabensis*) + (*Tachyoryctes makooka*, *Protachyoryctes tatroti*) + (*R. carbonnelli* (*R. platytomeus*, *R. sivalensis*)) + more derived taxa. This node is supported by five exclusive and unambiguous synapomorphies, i.e. dentary depth moderate, mesostyle on M1 absent, anterocone fused with anteroloph on M1, metaloph early fused with posteroloph on M2 and posterosinus absent on M2.

Node 53. *Rhizomyides mirzadi* + *R. punjabensis*. Two non-exclusive and unambiguous synapomorphies support this node, i.e. masseteric crest with short anterior extension (*Prokanisamys major* and maybe other species of this genus, *Miorhizomys micrus*, *M. nagrii*, *M. harii*, *Eicooryctes kaulialensis* and *Cannomys badius*) and mesolophid short and well-separated from the hypolophid on m1 (a convergence with node 61, *Nakalimys lavocati*, *Kanisamys potwarensis* and some specimens of *Miorhizomys nagrii* and *M. choristos*).

Node 52. *Rhizomyides carbonnelli* + (*R. platytomeus*, *R. sivalensis*). This node is supported by two non-exclusive and unambiguous synapomorphies, i.e. lower masseteric crest inflated under m2 (a convergence with *Protachyoryctes tatroti* and node 45) and presence of posterior protoconid-metaconid connection on m1 (a highly homoplastic character).

Node 51. *Rhizomyides platytomeus* + *R. sivalensis*. Two non-exclusive and unambiguous synapomorphies support this node, i.e. length of m2 between 4.5 and 5.5 mm (a convergence with some individuals of *Miorhizomys choristos*, *M. tetracharax*

and node 48) and mesolophid long and complete and separated from the hypolophid on m2 (a reversal).

Node 50. *Protachyoryctes tatroti* + *Tachyoryctes makooka*. This node is supported two non-exclusive and unambiguous synapomorphies, i.e. mesolophid short and migrated toward the hypolophid (a convergence with some specimens of *Kanisamys nagrii*, *K. sivalensis*, *Eicooryctes kaulialensis* and *Tachyoryctes pliocaenicus*) and mure on the m2 constricted (an homoplastic character that is also found in *Rhizomyides platytomeus*, *Miorhizomys harii*, *M. tetracharax*, *Rhizomys (Brachyrhizomys) shajius* and *Eicooryctes kaulialensis*).

Node 49. *Miorhizomys choristos* + *M. tetracharax* + *M. harii* + *M. blacki* + *M. nagrii* + *Rhizomys (Brachyrhizomys) shajius* + more derived taxa. This node is supported by no less than four exclusive and unambiguous synapomorphies, i.e. masseteric crest without anterior extension, M1 hypselodont and M2 and M3 absent, and six non-exclusive and unambiguous synapomorphies, i.e. longitudinal ornamentation on i absent (a convergence with *Miorhizomys micrus*), mure on m1 constricted (a convergence with *Tachyoryctes makooka*), mesolophid long and complete and separated from hypolophid on m2 (a reversal), posterosinusid small on m3 (a convergence with *Miorhizomys micrus*, some individuals of *M. pilgrimi* and *Tachyoryctes pliocaenicus*), anterosinusid absent on m3 (a convergence with some specimens of *Kanisamys nagrii* and either with the node 52 or, as a parallelism, with *Rhizomyides platytomeus* and *R. carbonnelli*) and protosinus absent on M1 (a convergence with *Prokanisamys benjavuni* and some individuals of *Rhizomyides punjabiensis*).

Node 48. *Rhizomys sinensis* + *Tachyoryctes splendens* + all the descendants of their common ancestor (crown group). This clade is sustained by only one exclusive and unambiguous synapomorphy, i.e. posterior lake absent on M3, but four non-exclusive and unambiguous synapomorphies, i.e. m2 length between 4.5 mm and 5.5 mm (a convergence with node 51 and some individuals of *Miorhizomys choristos* and *M. tetracharax*), mure on m3 absent (a convergence with *Miorhizomys choristos* and *M. tetracharax*), posterosinusid on m3 absent (a convergence with *Miorhizomys choristos* and *M. tetracharax*) and mesoloph long and complete on M3 (a reversal).

Node 47. *Anepsirhizomys opdykei* + more derived taxa. Two non-exclusive and unambiguous synapomorphies support this node, i.e. high hypsodonty (a convergence with node 41) and posterior protoconid-metaconid connection on m1 absent (a highly homoplastic character).

Node 46. *Anepsirhizomys pinjoricus* + more derived taxa. A single exclusive and unambiguous synapomorphy supports this node, i.e. masseteric crest with long anterior extension.

Node 45. *Eicooryctes kaulialensis* + more derived taxa. This node is supported by two exclusive and unambiguous synapomorphies, i.e. m2 length between 2.5 mm and 3.5 mm and mesolophid on m2 absent.

Node 44. *Tachyoryctes pliocaenicus* + *T. konjiti* + *T. macrocephalus* + *T. splendens*. Three non-exclusive and unambiguous synapomorphies support this node, i.e. mure on m1 absent (a convergence with node 42), posterior protoconid-metaconid connection on m1 absent (a highly homoplastic character) and anterosinusid on m1 present (a reversal).

Node 43. *Miorhizomys pilgrimi* + more derived taxa. This clade is sustained by only one non-exclusive and unambiguous synapomorphy, i.e. mesolophid on m2 that is a long continuation of the protoconid (a convergence with *Miorhizomys choristos*).

Node 42. *Rhizomys (Brachyrhizomys) shansius* + more derived taxa. This node is supported by three exclusive and unambiguous synapomorphies, i.e. deep dentary, infraorbital foramen without ventral slit and hypolophid on m2 isolated, and one non-exclusive and unambiguous synapomorphy, i.e. anterosinusid on m2 absent (a reversal).

Node 41. *Cannomys badius* + more derived taxa. This node is supported by one exclusive and unambiguous synapomorphy, i.e. mesolophid on m1 that is a long continuation of the protoconid, and two non-exclusive and unambiguous synapomorphies, high hypsodonty (a convergence with node 47) and entoconid on m3 isolated (a convergence with *Miorhizomys choristos* and *M. tetracharax*).

Node 40. *Rhizomys pruinosus* + *R. sinensis* + *R. sumatrensis*. This node is supported by two exclusive and unambiguous synapomorphies, i.e. mesoloph on M1 and M3 long and complete but divided, in early wear, with a buccal cusp, and one non-exclusive and unambiguous synapomorphy, i.e. mesoloph on M2 long and complete but divided, in early wear, with a buccal cusp (a convergence with *Miorhizomys choristos*).

Discussion

Prokanisamys

Prokanisamys is the oldest known genus of the rhizomyines. The results of this work support the monophyly of this taxon. They do not confirm ~~the position of that~~ the most ancient species of the genus, *P. kowalskii*, ~~is~~ as the most basal one within this clade. Even though this Late Oligocene species shows the first phase of the rhizomyine dentition, its lophodonty is incipient and its hypsodonty is hardly greater than that of typical muroids. We, therefore, hypothesize that further work will eventually resolve *P. kowalskii* as the most basal member of the genus.

The African *Pronakalimys* and *Nakalimys*

Pronakalimys and *Nakalimys* branch sequentially between *Prokanisamys* and *Kanisamys*. *Pronakalimys* and *Nakalimys* are indeed much closer morphologically to Early and Middle Miocene Asian fossil rhizomyines than to the African *Tachyoryctes*. The occurrence of *Prokanisamys* sp. from the Early Miocene of Jebel Zelten (Fejfar and Horáček 2006; Wessels et al., 2003, 2008) provides evidence of an Early Miocene migration of rhizomyines from Asia to Africa. However, the topology of our tree suggests that ~~the latter taxon~~ *Prokanisamys* sp. did not give rise directly to *Pronakalimys*, which would be the fruit of a second immigration of rhizomyines into Africa. As suggested by Flynn and Sabatier (1984), *Nakalimys lavocati* is more basal than *Kanisamys indicus* and not directly ancestral to *Tachyoryctes*.

Kanisamys

Wessels and de Bruijn (2001) pointed out that ancestor-descendent relationships within this genus were not clear. In fact, the genus *Kanisamys* is not monophyletic according to our results. However, *K. indicus* and *K. potwarensis* do form a clade and are, therefore, true *Kanisamys*. In contrast, “*K.*” *nagrii* and “*K.*” *sivalensis* insert sequentially on the stem leading to more derived rhizomyines. Flynn (1982a, 1984, 1986) was, therefore, correct in considering *K. potwarensis* most closely related to *K.*

indicus than to other species then considered as belonging to *Kanisamys*. His opinion that “*K*”. *nagrii* is more basal than “*K*”. *sivalensis* and that the former is closer to the latter than to either *K. indicus* or *K. potwarensis* is confirmed. Flynn (1982a, 1984, 1986) also suggested that “*K*”. *nagrii* and “*K*”. *sivalensis* are more derived than *K. indicus* and *K. potwarensis*, which is substantiated by our results. However, the suggestion that *K. indicus* would be a direct ancestor of “*K*”. *sivalensis* (Black, 1972; Flynn 1982a) is not supported.

Protachyoryctes

The sister species *Protachyoryctes tatroti* and “*Tachyoryctes*” *makooka* are both hypsodont, have reduced but distinct mesolophids and have retained the protosinus on the M1. This latter trait is distinctive of the most basal genera of the subfamily like *Prokanisamys*, *Kanisamys*, *Pronakalimys*, *Nakalimys* and *Rhizomyides* (see Flynn 1982a). It becomes less marked in *P. tatroti* and “*T.*” *makooka* (in which the protosinus is shallow). The topology of our cladogram implies that “*T.*” *makooka* should be reallocated to the genus *Protachyoryctes* (Fig. 7) as already hypothesized by López-Antoñanzas and Wesselmann (in press). From these results a unidirectional dispersal event from southern Asia to Africa at the origin of “*T.*” *makooka* can be inferred between 6 and 8 Myr (Figs. 8 and 9). Contrary to the suggestion of Black (1972), and what its name may suggest, *Protachyoryctes* is not closer to *Tachyoryctes* (*sensu stricto*) than to *Rhizomys*.

Rhizomyides

As currently understood, *Rhizomyides* is a paraphyletic taxon. True *Rhizomyides*, with *R. sivalensis* as type, constitute the sister group of *Protachyoryctes* according to the majority-rule consensus tree (Fig. 7B).

As Flynn (1982a, 1986, 1990) pointed out, *Rhizomyides* and *Kanisamys* share many traits (e.g., similar degree of hypsodonty, inclined masseteric crest, a strongly rounded I1, a large posterior enamel lake on M3). This fact led Flynn (1983, 1986) to think that the origin of *Rhizomyides* could have been earlier than reflected by its first occurrence in the fossil record and that it could have evolved from an early *Kanisamys*. This is not fully supported by our results. The fact that *Rhizomyides sivalensis* retained a strong

mesolophid on the M2 (usually reduced in *K. sivalensis*) led Flynn (1982a) to suggest that *R. sivalensis* may have evolved from *Kanisamys* outside Pakistan and later immigrated to the Potwar Plateau. This hypothesis is congruent with our results given that the species most closely related to *R. sivalensis* (*R. carbonnelli* and *R. platytomeus*) were both found in Afghanistan (Brandy, 1979a, 1979b, 1981; Flynn et al., 1983). In the Late Miocene a form close to *R. carbonnelli* would have evolved there to give rise to the lineages of *R. platytomeus* and *R. sivalensis* the latter taxon subsequently immigrating to the Potwar Plateau (Fig. 8). We agree with the suggestion of Flynn (1983) and Flynn et al. (1983) according to which there is probably neither direct relationship between *R. carbonnelli* and *R. sivalensis* nor between *R. platytomeus* and *Tachyoryctes*.

“*Rhizomyides*” *mirzadi* and “*R*”. *punjabiensis*

The generic attribution of “*Rhizomyides*” *mirzadi* and “*R*”. *punjabiensis* has been controversial. “*R*”. *mirzadi* has been considered as belonging to *Kanisamys* (Jacobs, 1978), *Protachyoryctes* (Brandy, 1981) and *Rhizomyides* (Flynn, 1983). “*R*”. *punjabiensis* was considered *Rhizomyides* by Bohlin, (1946), reassigned to *Brachyrhizomys* by Flynn (1982a) and returned to *Rhizomyides* by Flynn (1986, 1990). Our results suggest that a new genus name is required for these two taxa, which are sister species (Fig. 8).

Miorhizomys

Another interesting result of the present work is that the genus *Miorhizomys* does not appear monophyletic. Flynn (1982a) suggested that *M. micrus* is a conservative descendant of the “*Rhizomyides*” *punjabiensis* lineage. This hypothesis is not greatly different from the topology suggested by our tree, and *M. micrus* is the most basal species of *Miorhizomys* as currently understood. Interestingly enough, *Rhizomys* (*Brachyrhizomys*) *shajius* nests within the various species of *Miorhizomys*, and does not appear closely related to *R. (B.) shansius*. This is not very surprising because the former species is primitive in molar narrowness, low hypsodonty and retention of a mure, and short mesolophid on the m3), and is represented by only one jaw (Flynn 1993). Note

that *R. (B.) shajius*, while older (5.9 Myr vs 4–3.3 Myr, see Flynn, 2009), it occurs in the same basin as *R. (B.) shansius*.

The majority-rule consensus tree does not solve the interrelationships between *Miorhizomys blacki*, *M. nagrii* and *Rhizomys (Brachyrhizomys) shajius* (Fig. 7B). Nevertheless, it shows that *M. tetracharax*, *M. choristos* and *M. harii* form a monophyletic group of which *M. choristos* is the most basal species and in which *M. tetracharax* and *M. harii* are sister taxa. However, in the strict consensus tree (Fig. 7A), the interrelationships between *M. choristos*, *M. tetracharax*, *M. harii*, *M. blacki*, *M. nagrii* and *Rhizomys (Brachyrhizomys) shajius* remain unsolved. The number of true *Miorhizomys* species remains therefore unsettled. *M. micrus*, *M. blacki*, *M. nagrii* and *R. (B.) shajius* show some burrower adaptations. An increase of specialization toward a fossorial way of life is shown in the more derived *M. tetracharax*, *M. choristos* and *M. harii*, a trend continued by the most derived species of the subfamily.

The crown group

Another interesting result is the evidence of two important lineages originating from the basal node of the crown group (48). One corresponds to all taxa originating from node 47 (*Anepsirhizomys opdykei* + more derived taxa). This clade is characterized by the synapomorphies of having high hypsodonty and lacking posterior protoconid–metaconid connection on the m1. We understand this clade as the tribe Tachyoryctini and we provide it with the following phylogenetic definition: The most inclusive clade containing *Tachyoryctes splendens* (Rüppell 1836) but not *Rhizomys sinensis* Gray, 1831. The other lineage originates from node 43 (*Miorhizomys pilgrimi* + more derived taxa). It is characterized by the synapomorphy of having the mesolophid on the m2 as a long continuation of the protoconid. This clade is the tribe Rhizomyini, whose phylogenetic definition is: The most inclusive clade containing *Rhizomys sinensis* Gray, 1831 but not *Tachyoryctes splendens* (Rüppell 1836).

The divergence between the tribes Tachyoryctini and Rhizomyini can be estimated as having occurred about 10 Myr (Fig. 8), because the oldest record of *Miorhizomys pilgrimi* is near 9.5 Myr.

Tribe Tachyoryctini. This tribe is constituted by *Anepsirhizomys opdykei* and more derived taxa. Our work sheds light on the controversial taxonomic position of *Anepsirhizomys*. This genus of unclear affinity has been considered a rhizomyine as well as a tachyoryctine (Flynn et al., 1990). According to the results of our analysis, *Anepsirhizomys* is the most basal genus within the tribe Tachyoryctini. The reallocation of “*Rhizomys*” *pinjoricus* to *Anepsirhizomys* as suggested by Flynn et al. (1990) and Flynn (2009) is not supported by this work. *Anepsirhizomys pinjoricus* is actually more derived and should be reallocated into a genus of its own.

The African Tachyoryctini (*T. pliocaenicus* and more derived species) would come from an immigration of a species close to *Eicooryctes kaulialensis* in Africa. This is in agreement with the fact that *Eicooryctes* displays many derived characters shared by and even, for some of them, accentuated in the more modern species of *Tachyoryctes* (e.g., hypsodonty, absence of mesolophid on the m2 and m3, lack of protosinus on the M1).

Tribe Rhizomyini. This clade is constituted by *Miorhizomys pilgrimi* plus more derived taxa. The origin of the Rhizomyini is to be found at the beginning of the Late Miocene in a *Miorhizomy* -like form. According to our consensus trees, the most basal taxon of this clade is *Miorhizomys pilgrimi*.

After studying *Brachyrhizomys shansius*, Flynn (2009) concluded that this taxon should be treated as a subgenus of *Rhizomys* (see above). For this reallocation to be accepted, the genus *Cannomys* would have to be synonymized with *Rhizomys*. However, the former differs from the latter in its smaller size and in having proodont incisors and smooth sole pads (Nowak, 1999). Therefore, we favor the reestablishment of the genus *Brachyrhizomys*. *Cannomys* is the sister-group of *Rhizomys*.

Conclusion

The most basal representatives of the subfamily Rhizomyinae belongs to *Prokanisamys*. The oldest species of this genus is *P. kowalskii* from the Late Oligocene of Pakistan. This record is followed in age by *P. arifi* and *P. major* from Pakistan. These two species persisted into the Middle Miocene of Pakistan, where they were

sympatric with *Kanisamys indicus*. In Thailand, *P. benjavuni* is recorded in the Middle Miocene. During Late Miocene times, the rhizomyines experienced their greatest diversification with 14 species distributed across five genera (*Kanisamys*, *Rhizomyides*, *Protachyoryctes*, *Eicooryctes* and *Miorhizomys*) in Pakistan, India and China. Our results call the monophyly of several of these genera into question. The Asian Pliocene rhizomyine record suggests that the diversity of these animals dropped there at this time. In fact, they are only represented by four species belonging to four genera (*Rhizomyides*, *Brachyrhizomys*, *Anepsirhizomys* and a still unnamed genus for “A.” *pinjoricus*), which occurred in Afghanistan, Pakistan, India and China.

African fossil Rhizomyinae are scarce; the oldest and sole Early Miocene representative is *Prokanisamys* sp. from Jebel Zelten (Libya). This recent discovery provides evidence of an Early Miocene migration of members of this family between Asia and Africa through the “*Gomphotherium* landbridge”. In Africa, a single species of rhizomyine is known from the Middle Miocene (*Pronakalimys andrewsi* from Fort Ternan, Kenya), two from the Late Miocene (*Nakalimys lavocati* from Nakali, Kenya, and the recently discovered *Protachyoryctes makooka* from the Middle Awash, Ethiopia). From the Pliocene Hadar Formation (Afar, Ethiopia) a single species of *Tachyoryctes* is known (*T. pliocenicus*). The most recent fossil species of *Tachyoryctes* known to date is *T. konjiti*, which comes from the Pleistocene of Melka-Kunturé (Ethiopia).

Together with other rodents such as the Ctenodactylidae (López-Antoñanzas and Knoll, 2011), Diatomyidae (López-Antoñanzas, 2011), basal Muridae (López-Antoñanzas, 2009), Zapodidae (López-Antoñanzas and Sen, 2006) and Thryonomyidae (López-Antoñanzas et al., 2004), the rhizomyines provide a fine example of long distance dispersal of rodents consistent with geological evidence, indicating the establishment of an Early Miocene corridor between Afro-Arabia and Eurasia. Rhizomyines survive in Asia and Africa, and their phylogenetic relationships imply the ancestry to be found in Asia. This subfamily underwent a wide geographic expansion during Miocene times. From a morphological viewpoint African fossil rhizomyines appear close to the Asian ones, and the extant African rhizomyines share more synapomorphies with certain Pakistani Late Miocene species than with the older African taxa. The hypothesis that this subfamily dispersed more than once from Asia

into Africa could explain those facts and is supported by our results. ~~A first~~^{Initial} ~~geo~~dispersal of *Prokanisamys* from Pakistan to East Africa would have taken place at the beginning of the Early Miocene. From this first event *Prokanisamys* sp. from Jebel Zelten would have originated. The second and third dispersalist events may have taken place not earlier than 18 Myr and would have given rise to the Middle Miocene *Pronakalimys* and to the Late Miocene *Nakalimys* (Fig. 9). The hypothesis that African *Nakalimys* could have originated from the dispersal into Africa of an Asian *Kanisamys* by Middle Miocene times is not supported by our results.

With respect to the Late Miocene *Protachyoryctes makooka* and the African Tachyoryctini, two unidirectional dispersal events from southern Asia to Africa took place in Late Miocene times (not earlier than 8.2 Myr). The first one would have been at the origin of *Protachyoryctes makooka*, whereas the derivation of the African Tachyoryctini (*Tachyoryctes* spp.) would have come from an independent entry of this group into Africa (Fig. 9).

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For Peer Review

Fig. 1. Distribution of the extant Rhizomyines (after IUCN data) and fossil localities. 1, Taoyang, Yushe Basin, Shanxi, China; 2, Lufeng, Chuxiong Yi, Yunnan, China; 3, Mae Long and Mae Moh, Lamphang Province, Thailand; 4, 5, Haritalyangar, India; 6, Punjab, India; 7, Ramnagar, India; 8, Potwar Plateau (Dhok Pathan-Khaur, Chinji-Nagri, Tatrot-Hasnot regions), Pakistan; 9, Banda Daud Shah (Pakistan); 10, Zinda Pir Dome (Pakistan); 11, 12, Sind (Pakistan); 13, Lataband, Sarobi Basin, Afghanistan; 14, Pul-e Charkhi Kabul, Afghanistan; 15, Bamian Basin, Afghanistan; 16, Jebel Zelten (Libya); 17, Kada Hadar, Hadar Formation, Ethiopia; 18, Digiba Dora Vertebrate Locality 1 (Middle Awash, Ethiopia); 19, Melka Kunturé, Ethiopia; 20, Nakali, Kenya; 21, Fort Ternan, Kenya.

Fig. 2. Rhizomyidae dental terminology used in this paper. *Prokanisamys arifi*—A. Left M1, H-GSP 8311/4359. —B. Left M2, H-GSP 8311/4369. —C. Left M3, H-GSP 8311/4381. —D. Left m1, H-GSP 8311/4294. —E. Left m2, H-GSP 8311/4316. —F., Left m3, H-GSP 8311/4334. Scale bar equals 1 mm.

Fig. 3. Cheek teeth of *Rhizomys sinensis*, *Cannomys badius* and *Tachyoryctes splendens*. —A. Lower cheek teeth of *Rhizomys sinensis* (specimen C.G. 1912-851) with m1-m3. —B. Upper cheek teeth of the same specimen with M1-M3. —C. Lower cheek teeth of *Cannomys badius* (specimen C.G. 1860-382) with m1-m3. —D. Upper cheek teeth of the same specimen with M1-M3. —E. Lower cheek teeth of *Tachyoryctes splendens* (specimen C.G. 1993-217) with m1-m3. —F. Upper cheek teeth of the same specimen with M1-M3. Scale bar equals 2mm.

Fig. 4. Cheek teeth of *Kanisamys nagrii*, *Kanisamys potwarensis*, *Miorhizomys tetracharax*, *Rhizomys (Brachyrhizomys) sansius*.—A. Maxilla of *Kanisamys nagrii* (specimen AMNH 30000) with right M1-M3.—B. Maxilla of *Kanisamys nagrii* (specimen AMNH 30000) with left M1-M2. —C. Mandible of *Kanisamys nagrii* (specimen AMNH 39323) with m1-m3. —D. Maxilla of *Kanisamys potwarensis* (specimen AMNH 39321) with M1-M3. —E. Mandible of *Miorhizomys tetracharax*

(specimen AMNH 39325) with m1-m3). —F. Mandible of *Rhizomys* (*Brachyrhizomys*) *shansius* (specimen AMNH 117337) with m1-m3. —G. Maxilla of *Rhizomys* (*Brachyrhizomys*) *shansius* (specimen AMNH 117337).

Fig. 5. Reconstruction of *Bathyergus splendens* provided by Rüppell (1836).

Fig. 6. Relationships of extant and extinct Rhizomyines provided by Flynn (1990).

Fig. 7. Consensus trees generated by the cladistic analysis of the Rhizomyidae performed in this paper (matrix in Appendix 2). —A. strict and semi-strict consensus trees, nodes are designed in bold by numbers 40 to 62, Bremer and Relative Bremer Indices are showed at the appropriate nodes. —B, majority-rule consensus tree. The trees have a length of 158 steps, a consistency index (CI) of 0.456 and a retention index (RI) of 0.819.

Fig. 8. Calibrated phylogeny based on the cladistic relationships presented in Fig. 7 and the recorded temporal ranges (black). Grey bars represent missing ranges and missing ancestral lineages. Error bars indicate age uncertainty. Chronostratigraphical data from Sabatier (1979), de Bruijn et al. (1981), Flynn (1982a, 1983, 1986), Flynn et al. (1983, 1990, 1995, 2009), Sen (1983), Wessels et al. (2003), Chaimanee et al. (2007), Wesselman et al (2009) and Wessels (2009).

Fig. 9 Geographic distribution of rhizomyine rodents plotted onto the strict consensus of the most parsimonious trees of our analysis using Mesquite ver. 2.6 (Maddison and Maddison, 2009) as a two-state character.

Fig. 1. Distribution of the extant Rhizomyines (after IUCN data) and fossil localities. 1, Taoyang, Yushe Basin, Shanxi, China; 2, Lufeng, Chuxiong Yi, Yunnan, China; 3, Mae Long and Mae Moh, Lamphang Province, Thailand; 4, 5, Haritalyangar, India; 6, Punjab, India; 7, Ramnagar, India; 8, Potwar Plateau (Dhok Pathan-Khaur, Chinji-Nagri, Tatrot-Hasnot regions), Pakistan; 9, Banda Daud Shah (Pakistan); 10, Zinda Pir Dome (Pakistan); 11, 12, Sind (Pakistan); 13, Lataband, Sarobi Basin, Afghanistan; 14, Pul-e Charkhi Kabul, Afghanistan; 15, Bamian Basin, Afghanistan; 16, Jebel Zelten (Libya); 17, Kada Hadar, Hadar Formation, Ethiopia; 18, Digiba Dora Vertebrate Locality 1 (Middle Awash, Ethiopia); 19, Melka Kunturé, Ethiopia; 20, Nakali, Kenya; 21, Fort Ternan, Kenya.

96x52mm (300 x 300 DPI)

Fig. 2. Rhizomyidae dental terminology used in this paper. *Prokanisamys arifi*—A. Left M1, H-GSP 8311/4359. —B. Left M2, H-GSP 8311/4369. —C. Left M3, H-GSP 8311/4381. —D. Left m1, H-GSP 8311/4294. —E. Left m2, H-GSP 8311/4316. —F., Left m3, H-GSP 8311/4334. Scale bar equals 1 mm. 134x86mm (300 x 300 DPI)

Fig. 3. Fig. 3. Cheek teeth of *Rhizomys sinensis*, *Cannomys badius* and *Tachyoryctes splendens*. —A. Lower cheek teeth of *Rhizomys sinensis* (specimen C.G. 1912-851) with m1-m3. —B. Upper cheek teeth of the same specimen with M1-M3. —C. Lower cheek teeth of *Cannomys badius* (specimen C.G. 1860-382) with m1-m3. —D. Upper cheek teeth of the same specimen with M1-M3. —E. Lower cheek teeth of *Tachyoryctes splendens* (specimen C.G. 1993-217) with m1-m3. —F. Upper cheek teeth of the same specimen with M1-M3. Scale bar equals 2mm.
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Fig. 4. Cheek teeth of *Kanisamys nagrii*, *Kanisamys potwarensis*, *Miorhizomys tetracharax*, *Rhizomys* (*Brachyrhizomys*) *sansius*.—A. Maxilla of *Kanisamys nagrii* (specimen AMNH 30000) with right M1-M3.—B. Maxilla of *Kanisamys nagrii* (specimen AMNH 30000) with left M1-M2. —C. Mandible of *Kanisamys nagrii* (specimen AMNH 39323) with m1-m3. —D. Maxilla of *Kanisamys potwarensis* (specimen AMNH 39321) with M1-M3. —E. Mandible of *Miorhizomys tetracharax* (specimen AMNH 39325) with m1-m3). —F. Mandible of *Rhizomys* (*Brachyrhizomys*) *shansius* (specimen AMNH 117337) with m1-m3. —G. Maxilla of *Rhizomys* (*Brachyrhizomys*) *shansius* (specimen AMNH 117337).
250x350mm (300 x 300 DPI)

Fig.5 Reconstruction of Bathyergus splendens provided by Rüppell (1836)
35x14mm (300 x 300 DPI)

Fig. 6. Relationships of extant and extinct Rhizomyines provided by Flynn (1990).
55x36mm (300 x 300 DPI)

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Table 1

Character/taxon matrix used in the analysis of relationships of all extinct and extant species of Rhizomyinae. Characters are listed in material and methods. Character scoring: 0, 1 and 2, conditions of character: -, uncodable character; ?, character state uncertain.

Table 2

Synapomorphies common to the 32MPTs plotted on the strict consensus tree. Exclusive synapomorphies are indicated in bold. Italics indicate ambiguous synapomorphies. Node numbers are shown in Figure 7.

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<i>Debruijnina arpati</i>	0	0	1	?	?	?	?	?	0	0	0	0	0&1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	2	0	0	0	0	0	2	0	
<i>Rhizomys sumatrensis</i>	2	4	2	2	1	2	2	2	1	2	1	4	1	1	2	4	1	1	1	0	1	1	1	4	2	1	1	1	1	1	3	1	1	1	1	1	3	1	1	1	1	2	3	2	
<i>Rhizomys sinensis</i>	2	4	2	2	1	2	2	2	1	2	1	4	1	1	2	4	1	1	1	0	0	1	1	4	2	1	1	1	1	1	3	1	1	1	1	1	3	1	1	1	1	2	3	2	
<i>Rhizomys pruinosus</i>	2	4	2	2	1	2	2	2	1	2	1	4	1	1	2	4	1	1	1	0	1	1	1	4	2	1	1	1	1	1	3	1	1	1	1	1	3	1	1	1	1	2	3	2	
<i>R. (Brachyrrh.) shansius</i>	1	3	2	2	1	2	2	2	1	2	1	0	1	1	2	4	1	1	1	0	1	1	1	4	2	0	1	1	1	1	2	1	1	1	1	1	2	1	1	1	1	1	2	2	
<i>R. (Brachyrrh.) shajius</i>	1	2	2	2	?	1	?	?	?	?	?	?	?	?	1	2	1	0	1	1	1	1	0	2	1	0	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
<i>Cannomys badius</i>	2	0&1	2	1	1	2	2	2	1	2	1	4	1	1	2	4	1	1	1	?	1	1	1	4	2	1	1	1	1	1	2	1	1	1	1	1	2	1	1	1	1	2	2	2	
<i>Miorhizomys nagrii</i>	1	1&2	2	1	1	1	1	2	1	0	1	0&1	1	1	0	0	1	0	1	1	0	1	0	0&2	1	0	1	1	0	1	2&3	0	1	1	1	1	2	0	1	1	1	1	1&2	1	
<i>Miorhizomys micrus</i>	1	1	2	1	1	1	?	2	1	0	1	0	1	0	0	2	1	0	1	0	1	1	0	2	1	0	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
<i>Miorhizomys blacki</i>	1	2	2	2	1	1	1	2	?	?	?	?	?	?	0	0	1	0	1	1	1	1	0	2	1	0	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
<i>Miorhizomys pilgrimi</i>	1	3	2	2	1	1	1	2	?	?	?	?	?	?	2	4	1	0	1	1	1	1	1	4	1&2	0	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Miorhizomys harii</i>	1	2	2	1	1	?	?	?	2	1	1	1	0	1	0	1	1	0	0	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
<i>Miorhizomys tetracharax</i>	1	2&3	2	2	1	1	1	2	1	1	1	0	1	0	1	0	1	0	1	0	1	1	1	4	2	1	0	0	1	?	?	?	?	?	?	?	2	1	1	?	0	1	1	1	
<i>Miorhizomys choristos</i>	1	2&3	2	2	1	1	1	2	1	1	1	0&1	1	1	2	4	1	0	1	1	1	1	1	4	2	1	1	1	1	1	0	1	1	1	1	1	3	1	1	1	1	0	1	1	
<i>Protachyoryctes tatroti</i>	1	2	2	0	0	1	?	1	1	0	1	2	1	0	1	2	1	0	1	0	1	1	0	2	0	0	1	0	0	0	2	1	1	0	1	1	2	0	1	1	1	?	?	?	
<i>Tachyoryctes makooka</i>	1	1&2	2	?	?	?	?	1	?	1	1	1	2	1	0	1	2	1	0	1	0	1	1	0	2	0	0	1	0	0	0	2	1	1	1	1	1	2	0	1	1	1	1	2	2
<i>T. pliocaenicus</i>	1	0&1	2	0	0	1	1	1	1	2	1	2	1	0	2	2&3	1	0	1	0	1	1	1	3	1	0	1	0	2	1	2	1	1	1	1	1	2	1	1	1	1	2	2	2	
<i>T. macrocephalus</i>	2	2	2	0	0	1	1	1	1	2	1	3	1	0	2	3	1	0	1	1	1	1	1	3	2	0	1	1	2	1	2	1	1	1	1	1	2	1	1	1	1	2	2	2	
<i>Tachyoryctes splendens</i>	2	0&1	2	0	0	1	1	1	1	2	1	3	1	0	2	3	1	0	1	1	1	1	1	3	2	0	1	1	2	1	2	1	1	1	1	1	2	1	1	1	1	2	2	2	
<i>Rhizomyides sivalensis</i>	1	3	2	0	0	1	?	1	1	0	1	0	0	0	0	0	1	0	1	1	1	1	0	2	0	0	1	0	0	0	2	1	1	1	1	1	2	0	1	1	1	1	?	0	
<i>Miorh. punjabiensis</i>	1	1	1	1	1	1	?	?	1	1	0	0	1	0	0	1&2	1	0	1	1	1	0	0	2	0	0	1	0	0	0&1	1&2	0	1	1	1	1	2	0	1	1	1	1	2	0	
<i>Rhizomyides carbonnelli</i>	1	2	2	0	0	1	?	1	1	0	1	0	0	?	0	2	1	0	1	1	1	1	0	2	0	0	1	1	?	?	?	?	?	?	?	2	0	1	0	?	?	0	?		
<i>Rhizomyides playtomeus</i>	1	3	2	0	0	1	?	1	1	0	1	0	0	?	1	0	?	0	1	1	1	?	?	2	0	?	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
<i>Tachyoryctes konjiti</i>	1	1	2	?	?	?	?	?	1	1	2	1	3	1	0	2	3	1	0	1	1	1	1	3	2	0	1	1	2	1	2	1	1	1	1	1	2	1	1	1	1	2	2	2	
<i>Kanisamys indicus</i>	1	0	1	0	1	0	?	0	1	0	0&1	0	0&1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1&2	0	1	0	0	1	1	0	

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<i>Kanisamys nagrii</i>	1	0&1	2	0	1	0	1	1	1	0	0&1	0&2	1	0	0	2	1	0	1	0	1	0&1	0	2	0	0	1	0&1	0	0	1	0	1	0	0	0	2	0	1	0	0	1	1	0
<i>Kanisamys sivalensis</i>	1	1	2	0	1	0	1	1	1	0	0&1	0&2	1	0	0	2	1	0	1	0	1	1	0	2	0	0	1	0&1	0	0	1&2	0	1	0	1	1	2	0	1	0	0	1	1	0
<i>Kanisamys potwarensis</i>	1	0&1	1	0	1	0	?	1	1	0	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	1	1	2	0	1	1	0	1	1	0&1	
<i>Eicooryctes kaulialensis</i>	2	1	2	1	0	1	?	1	1	1	1	2	0	1	1	2&3	1	0	1	1	1	1	0	3	0	0	1	1	2	1	2	1	1	1	1	1	2	1	1	1	1	?	?	?
<i>Anepsirhizomys opdykei</i>	2	4	2	2	1	1	?	?	1	1	1	0	0	?	2	0	1	0	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Anepsirhizom. pinjoricus</i>	2	3	2	0	?	1	?	1	1	?	1	0	0	1	2	0	1	0	1	1	1	1	1	0	2	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
<i>Pronakalimys andrewsi</i>	0	0	1	0	0	1	?	?	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	2	0	0	0	0	0	0	1	1	1	0	0	0	1	0	1	0	0	0	1	2
<i>Nakalimys lavocati</i>	0	1&2	1	0	0	1	?	1	1	0	0	1	0	0	0	2	0	0	0	0	1	0	0	0&1	0	0	0	0	0	1	1	1	0	0	0	0&1	0	1	0	0	0	1	0	
<i>Prokanisamys kowalskii</i>	0	0	0	?	?	?	?	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	1	0	0	0	1	0	0	0	0	0	1	0	
<i>Prokanisamys arifi</i>	0	0	0	?	?	?	?	0	0	0	0	0&1	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0&1	0	0	0	0	1	1	0	
<i>Prokanisamys benjavuni</i>	1	0	1	?	?	?	?	?	0	0	0	1	0	0	0	1	0	0	0	0	0	0&1	0	1&3	0	0	0	0	0	1	0&1	1	0	0	0	0	1	0	0	0	0	1	0&1	0
<i>Prokanisamys major</i>	0	0	0	1	1	0	?	?	0	0	0	1	0	0	0	1	0	0	0	0	1	0&1	0	0&1	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0	1	1	0	
<i>Prokanisamys JebelZelten</i>	0	0	0	?	?	?	?	?	?	?	?	?	?	?	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0&1	1	0	0	0	0	?	?	?	?	?	?	?	?	
<i>Rhizomyides mirzadi</i>	1	1&2	2	1	1	?	?	?	1	0	1	1	0	0	0	2	1	0	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	2	0	1	1	?	?	?	?	

	Acctran	Deltran
<i>Rhizomys sumatrensis</i>		
<i>Rhizomys sinensis</i>	21(1→0)	21(1→0)
<i>Rhizomys pruinosus</i>		
<i>Rhizomys (Brachyrh.) shansius</i>	42(2→1)	
<i>Rhizomys (Brachyrh.) shajius</i>	16(0→2)	15(0→1); 16(0→2)
<i>Cannomys badius</i>	4(2→1)	2(3→0&1) ; 4(2→1)
<i>Miorhizomys nagrii</i>	4(2→1); 10(1→0) ; 15(1→0); 21(1→0); 29(1→0) ; 32(1→0); 38(1→0)	4(2→1); 10(1→0) ; 14(0→1); 21(1→0); 29(1→0) ; 32(1→0); 38(1→0)
<i>Miorhizomys micrus</i>	2(2→1); 4(0→1); 8(1→2); 20(1→0); 25(0→1)	2(2→1); 4(0→1); 8(1→2); 25(0→1)
<i>Miorhizomys blacki</i>	15(1→0)	
<i>Miorhizomys pilgrimi</i>		
<i>Miorhizomys harii</i>	4(2→1); 14(1→0); 16(0→1); 17(1→0)	4(2→1); 15(0→1); 16(0→1); 17(1→0)
<i>Miorhizomys tetracharax</i>	14(1→0); 20(1→0); 23(0→1); 24(2→4); 25(1→2); 26(0→1); 27(1→0) ; 28(1→0); 41(1→0)	15(0→1); 20(1→0); 23(0→1); 24(2→4); 25(1→2); 26(0→1); 27(1→0) ; 28(1→0); 41(1→0)
<i>Miorhizomys choristos</i>	15(1→2); 16(0→4); 23(0→1); 24(2→4); 25(1→2); 26(0→1); 31(2→0) ; 37(2→3); 42(1→0)	14(0→1); 15(0→2); 16(0→4); 23(0→1); 24(2→4); 25(1→2); 26(0→1); 31(2→0) ; 37(2→3); 42(1→0)
<i>Protachyoryctes tatroti</i>	34(1→0)	5(1→0); 34(1→0)
<i>Tachyoryctes makooka</i>	10(0→1)	10(0→1); 43(1→2); 44(0→2)
<i>T. pliocaenicus</i>	1(2→1); 12(3→2) ; 20(1→0); 25(2→1) ; 28(1→0)	1(2→1); 12(3→2) ; 20(1→0); 25(2→1) ; 28(1→0)
<i>T. macrocephalus</i>	2(1→2)	2(1→2)
<i>Tachyoryctes splendens</i>		
<i>Rhizomyides sivalensis</i>	28(1→0)	
<i>Rhizomyides punjabiensis</i>	3(2→1) ; 11(1→0)	2(2→1); 3(2→1) ; 11(1→0); 22(1→0); 32(1→0); 43(1→2)
<i>Rhizomyides carbonnelli</i>	40(1→0)	28(0→1); 40(1→0) ; 43(1→0)
<i>Rhizomyides playtomeus</i>	15(0→1)	15(0→1); 28(0→1)
<i>Tachyoryctes konjiti</i>	1(2→1)	1(2→1)
<i>Kanisamys indicus</i>	8(1→0)	8(1→0)
<i>Kanisamys nagrii</i>		
<i>Kanisamys sivalensis</i>		2(0→1)
<i>Kanisamys potwarensis</i>	12(0→1); 33(1→0) ; 35(0→1); 36(0→1); 40(0→1)	12(0→1); 33(1→0) ; 35(0→1); 36(0→1); 40(0→1)
<i>Eicooryctes kaulialensis</i>	4(0→1); 15(2→1) ; 23(1→0) ; 25(2→0)	4(0→1); 12(0→2); 15(2→1) ; 23(1→0) ; 25(2→0)
<i>Anepsirhizomys opdykei</i>	2(3→4); 20(1→0)	2(3→4); 20(1→0)
<i>Anepsirhizom. pinjoricus</i>		24(2→0)
<i>Pronakalimys andrewsi</i>	24(0→2); 44(0→2)	24(0→2); 44(0→2)
<i>Nakalimys lavocati</i>	12(0→1)	2(0→1&2) ; 12(0→1)
<i>Prokanisamys kowalskii</i>	33(0→1); 42(1→0)	33(0→1); 42(1→0)
<i>Prokanisamys arifi</i>		
<i>Prokanisamys benjavuni</i>	1(0→1); 3(0→1) ; 30(0→1)	1(0→1); 3(0→1) ; 30(0→1)
<i>Prokanisamys major</i>	21(0→1)	4(0→1); 21(0→1)
<i>Prokanisamys sp. (Libya)</i>		
<i>Rhizomyides mirzadi</i>	13(1→0)	13(1→0)
40	2(0→1) ; 31(2→3) ; 37(2→3); 43(2→3)	2(3→4); 31(2→3) ; 37(2→3); 43(2→3)
41	1(1→2); 2(3→0); 12(0→4) ; 26(0→1)	1(1→2); 12(0→4) ; 26(0→1); 42(1→2)
42	6(1→2) ; 7(1→2) ; 18(0→1) ; 20(1→0)	6(1→2) ; 7(1→2) ; 10(1→2); 18(0→1) ; 20(1→0)
43	10(1→2); 16(0→4); 24(0→4)	16(0→4); 24(2→4)
44	10(1→2); 12(2→3) ; 13(0→1); 14(1→0)	10(1→2); 12(0→3) ; 13(0→1); 14(1→0); 42(1→2)
45	2(3→1) ; 12(0→2); 16(0→3) ; 24(0→3)	2(3→1) ; 5(1→0); 16(0→3) ; 24(2→3) ; 29(1→2)
46	4(2→0) ; 5(1→0)	4(2→0) ; 8(2→1)
47	1(1→2); 8(2→1); 13(1→0); 29(1→2)	1(1→2); 13(1→0)
48	2(2→3); 15(1→2); 23(0→1); 24(2→0); 25(1→2); 42(1→2); 43(1→2); 44(1→2)	2(2→3); 14(0→1); 15(0→2); 23(0→1); 25(1→2); 43(1→2); 44(1→2)
49	4(0→2) ; 8(1→2); 10(0→1); 14(0→1); 15(0→1); 16(2→0); 25(0→1); 28(0→1); 29(0→1) ; 30(0→1); 38(0→1) ; 43(2→1) ; 44(0→1)	4(0→2) ; 8(1→2); 10(0→1); 16(2→0); 20(0→1); 25(0→1); 28(0→1); 29(0→1) ; 30(0→1); 38(0→1) ; 44(0→1)
50	5(1→0); 12(0→2); 15(0→1); 20(1→0); 44(0→2)	12(0→2); 15(0→1)
51	2(2→3); 16(2→0)	2(2→3); 16(2→0)
52	5(1→0); 13(1→0); 28(0→1); 43(2→0)	5(1→0); 13(1→0); 20(0→1)
53	2(2→1); 4(0→1); 12(0→1); 22(1→0); 32(1→0)	4(0→1); 12(0→1); 20(0→1)
54	2(1→2); 6(0→1) ; 20(0→1); 32(0→1) ; 34(0→1) ; 40(0→1) ; 41(0→1) ; 43(1→2)	2(0→2) ; 6(0→1) ; 31(1→2); 32(0→1) ; 34(0→1) ; 40(0→1) ; 41(0→1)
55	31(1→2); 35(0→1); 36(0→1)	35(0→1); 36(0→1)
56	3(1→2) ; 13(0→1); 17(0→1) ; 19(0→1) ; 22(0→1) ; 24(0→2); 27(0→1)	3(1→2) ; 13(0→1); 17(0→1) ; 19(0→1) ; 22(0→1) ; 24(0→2); 27(0→1)
57	2(1→0); 16(2→0)	16(2→0)
58	1(0→1); 11(0→1) ; 32(1→0); 37(1→2) ; 42(0→1)	1(0→1); 11(0→1) ; 32(1→0); 37(1→2) ; 42(0→1)
59	2(0→1); 9(0→1) ; 21(0→1)	8(0→1); 9(0→1) ; 21(0→1)
60	8(0→2); 16(1→2) ; 33(0→1); 39(0→1)	16(0→2); 33(0→1); 39(0→1)
61	3(1→0) ; 4(0→1); 12(0→1); 24(0→1) ; 42(0→1)	3(1→0) ; 12(0→1); 16(0→1); 24(0→1) ; 42(0→1)
62	16(0→1)	