Dental morphology and wear pattern of bamboo rats, genus *Rhizomys* (Rodentia: Spalacidae)

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Dental morphology and wear pattern of the bamboo rats

Rhizomys Gray, 1831 (Rodentia: Spalacidae)

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Abstract

Rhizomys, one of the most derived genera within the tribe Rhizomyini (Rhizomyinae, Spalacidae, Rodentia), comprises three species: *Rhizomys sinensis* Gray, 1831, *R. pruinus* Blyth, 1851 and *R. sumatrensis* (Raffles, 1821). A detailed description of the morphology and wear pattern of the cheek teeth of this taxon is provided based on the study of 41 skulls. The variability tracked is due primarily to wear, control of which facilitates comparison of different individuals, fossil or not, at different wear stages. For the first lower and upper molars, six stages of wear (0–5) are recognized. The second lower and upper molars show five stages of wear (0–4), whereas the third ones have four (0–3). The dental wear pattern in *Rhizomys* is comparable to that of the Pliocene *Brachyrhizomys shansius* Teilhard de Chardin, 1942.

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1. Introduction

Rhizomyini is a tribe of spalacid rodents within the subfamily Rhizomyinae (see Flynn, 2009; López-Antoñanzas et al., 2013). The name was created by Winge (1887), who regarded this taxon as within the Muridae. McKenna and Bell (1997) considered the rhizomyines a subfamily within the Muridae, **subdivided into** two tribes: the Rhizomyini and the Tachyoryctini. According to them, the Rhizomyini includes 5 genera (*Brachyrhizomys* Teilhard de Chardin, 1942, *Anepsirhizomys* Flynn, 1982, *Pararhizomys* Teilhard de Chardin and Young, 1931, *Rhizomys* Gray, 1831 and *Cannomys* Thomas, 1915). However, the genus *Pararhizomys* has a different and more simplified molar pattern so that it was excluded from the group (Flynn, 1982a, 2009; Wei et al., 2004; Zhang et al., 2005), even though it was considered a rhizomyid by some authors (Kowalski, 1968). For Flynn (2009), the extinct and extant genera *Miorhizomys* Flynn, 2009 (formerly attributed to *Brachyrhizomys* and before that, to *Rhizomyoides* Bohlin, 1946; see Flynn, 1982, 1990), *Cannomys* and *Rhizomys* are members of the Rhizomyini, whereas the genus *Anepsirhizomys* is of unclear affinities. The results of a recent cladistic analysis involving fossil and living species of the whole subfamily (López-Antoñanzas et al., 2013) has revealed that the tribe Rhizomyini is constituted by the extinct *Miorhizomys pilgrimi* (Hinton, 1933) and *Brachyrhizomys shansius* (Teilhard de Chardin, 1942) and the extant *Cannomys badius* (Hodgson, 1841), *Rhizomys sinensis* Gray, 1831, *R. pruinosus* Blyth, 1851 and *R. sumatrensis* (Raffles, 1821). The origin of the Rhizomyini is to be found at the beginning of the Late Miocene in a *Miorhizomys*-like form (López-Antoñanzas et al., 2013). Some of its most derived members belong to the genus *Rhizomys* Gray, 1831. Musser & Carleton (1993: 685, 2005: 913–915) provided a census of the extant species of *Rhizomys* recognized as valid (see also Ellerman and Morrison-Scott

1951: 550–553, 1966: 521–522). They concluded that 3 species of *Rhizomys* are well defined at present: *Rhizomys sinensis*, *R. pruinus* and *R. sumatrensis*. These species live in China, northern and northeastern India, Nepal, Bhutan, southeastern Bangladesh, Myanmar, Laos, Thailand, Cambodia, Vietnam, Malaysia and Sumatra, where they are known from a wide variety of habitats, from bamboo forest to cultivated land, and up to 4000 m in elevation (IUCN, 2010).

The dental morphology of fossil Rhizomyini has been described in detail (Black, 1972; Flynn, 1982a, 1982b, 2009; Flynn et al., 1990) and that of the extant *Cannomys* as well (López-Antoñanzas, 2012). However, it has not been adequately described in any modern representative of *Rhizomys*. Thus, the aim of the present paper is to provide an in-depth description of the dental morphology and dental wear pattern in *Rhizomys*, a genus whose species endure a high rate of dental abrasion.

Examining the dental wear patterns in extant animals and comparing them with those of their fossil relatives is useful in more than one respect. First, it helps preventing the assignment of fossil teeth from conspecific individuals at different stages of wear (and therefore appearance) to different species. Because the study of dental wear patterns allows determining the relative age of fossil individuals, it permits inferring the age-class structure of the fossil sample to which they belong. A good knowledge of the dental wear pattern makes it also possible to compare the hypsodonty in teeth of individuals belonging to different species. Finally, tooth-wear classes come in handy in cranial morphometric analyses so as to compare individuals of the same ontogenetic age (see e.g., Nicolas et al., 2010).

2. Material and Methods

The study presented below is based on the examination of original specimens, casts, and data from the literature. We examined the following: skulls of extant *Rhizomys sinensis* (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* (MNHN DH. 280, MNHN C.G. 1929-259, MNHN C.G. 1929-261, MNHN C.G.1892-1360, MNHN C.G. 1929-263, MNHN C.G.1958-724, MNHN C.G.1962-2297, MNHN C.G.1962-2295, MNHN C.G. 1929-266, MNHN C.G. 1929-272, MNHN C.G. 1929-260, MNHN C.G. 1929-267, MNHN C.G. 1993-48, MNHN C.G. 1929-264, MNHN C.G. 1937-1251, MNHN C.G. 1929-265, MNHN C.G. 1929-270, MNHN C.G. 1929-340, MNHN 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, MNHN C.G. 1962-2294, MNHN C.G. 2007-162, MNHN C.G. 1980-235, MNHN A 7.216, MNHN A7.215 in the MNHN), and isolated teeth, maxillary fragments and mandible fragments of the following extinct species: *Miorhizomys pilgrimi* (lower incisor AMNH 39327 and cast of D-278 in the BSP) and *Brachyrhizomys shansius* (cranium and mandible AMNH 117337).

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. The terminology used in the tooth descriptions follows the rodent dental terminology of Flynn (1982a) with some adjustments (see Fig. 1).

Abbreviations: AMNH: American Museum of Natural History, New York, USA; BMNH: Natural History Museum, London, United Kingdom; C.G.: Catalogue général du Laboratoire des Mammifères et Oiseaux, MNHN, Paris, France; GSI: Geological Survey of India, Kolkata, India; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; MNHN: Muséum national d'Histoire naturelle, Paris, France; Y-GSP: Yale-

Geological Survey of Pakistan, Quetta, Pakistan; ZMB: Zoologische Sammlung, Museum für
Naturkunde der Humboldt-Universität, Berlin, Germany.

3. Systematics

Genus *Rhizomys* Gray, 1831

Type species. *Rhizomys sinensis* Gray, 1831

Referred species. *Rhizomys pruinus*, *Rhizomys sumatrensis*

Rhizomys sinensis Gray, 1831

Gray, on the basis of a skull and skin brought from China by Mr. Reeves, recognized the new genus and new species of rodent *Rhizomys sinensis* in 1831. 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 in which the first molars are well worn by the time the third molars erupt (Fig. 3A-B). No individuals of *R. sinensis* were observed with 2nd molars still in crypts and third molars below the bone; first molars would be in wear stage 0 or 1 in these cases. The orange upper incisors are recurved and ventrally directed and lack major ornamentation.

Upper dentition

M1. Its occlusal outline is nearly square. This tooth is four rooted with the anterolingual root the most developed. The dental pattern of M1 is tetralophodont with anteroloph, protoloph, mesoloph and metaloph+posteroloph.

In early wear, M3 is just erupting (e.g., C.G.1912-851, ZMB 16768, Figs. 1A and 2A). The anteroloph of M1 connects lingually to the protoloph through the protocone and labially to the protoloph, isolating an anterior enamel lake. At this point, the mesoloph, which is a long continuation of the hypocone, joins labially the metaloph-posteroloph, isolating a posterior enamel lake, which is larger than the anterior one. The protoloph connects labially to the mesoloph and to the anteroloph. Thus, the tooth has two enamel lakes and a narrow and elongated central reentrant that divides the tooth into two parts. This lingual reentrant extends nearly to the base of the crown and it is transverse in occlusal view. In some specimens (e.g., ZMB 16768) this reentrant is divided into two parts due to the lingual junction between the mesoloph and the protoloph. In this case, a small central enamel lake is isolated. This morphology corresponds to wear stage 2.

After moderate wear, the morphology of M1 (e.g., ZMB 16760, Fig. 1C) is quite similar to that in the preceding stage. However, M1 is significantly reduced in size and the anteroloph and the protoloph combine, although a remnant of the anterior enamel lake persists (ZMB 16770). At this state, the specimens have the lingual reentrant divided and they show a lingual sinus and two major labial enamel lakes that correspond with the former anterosinus and mesosinus. The lingual sinus is still open and directed towards the central enamel lake. This morphology corresponds to wear stage 3.

In later wear (stage 4), the posterior enamel lake is reduced (ZMB 43373b, Fig. 2G). The sinus is still lingually open. With more wear, the occlusal surface is completely flat and the

enamel has disappeared from the labial and posterior borders of the tooth, although it persists on the anterior and lingual sides. The enamel lakes are reduced to small circular labial structures (ZMB 17411) and the lingual reentrant is closed off. This morphology corresponds to wear stage 5.

M2. It is four rooted with the anterolingual root the most developed. The dental pattern of *M2* is tetralophodont: anteroloph, protoloph, mesoloph and metaloph+posteroloph. In early wear (e.g., C.G.1912-851, ZMB 16768, Figs. 1A, 2A), the anteroloph is a long continuation of the protocone and joins labially the protoloph, which does not connect to the protocone. The mesoloph joins the metaloph-posteroloph through the hypocone. The lingual reentrant is confluent with the anterior and middle labial reentrants. The anterior part of the tooth is separated from the posterior one, the mure is lacking. In some specimens, the protoloph connects labially to the anteroloph and the mesoloph (ZMB 16768). This morphology corresponds to wear stage 1. When *M2* is at this point, *M1* is at wear stage 2. After moderate wear (e.g., ZMB 16770, Fig. 2C), the protoloph connects to the protocone and two elongated enamel lakes (anterior and posterior) are isolated. The lingual reentrant joins the middle reentrant and extends transversely across the occlusal surface. This morphology is wear stage 2 (wear stage 3 in *M1*). With more wear, the anterior enamel lake is reduced (e.g., ZMB 43373a and ZMB 43373b, Figs. 2E-G). In some specimens (ZMB 43373b), the protocone connects to the hypocone and divides the long central reentrant into two parts: the lingual sinus and an isolated and elongated central enamel lake. In this case, the tooth has three labial enamel lakes and a lingual reentrant still open. This morphology corresponds to wear stage 3 (wear stage 4 in *M1*). In later wear (e.g., ZMB 17411, Fig. 2I), the occlusal surface is completely flat and only a small anterolabial enamel lake persists labially. The enamel has

nearly disappeared from the labial border of the tooth. This is wear stage 4 (wear stage 5 in M1).

M3. This tooth has three roots; the posterior one is the most developed. When unworn (e.g., C.G. 1912-851, ZMB 16768; Figs. 1A, 2A), all the cusps of the tooth are recognizable. This tooth shows a tetralophodont dental pattern with anteroloph, protoloph, mesoloph and a short metaloph+posteroloph. The anteroloph is a long continuation of the protocone, the protoloph and posteroloph are isolated and the mesoloph is divided, with a labial cusp that could be called a mesostyle or hypoloph. The mure is lacking and the lingual re-entrant is confluent with both the anterior and middle labial reentrants. This morphology corresponds to wear stage 0. When *M3* is at this point, *M1* and *M2* are at wear stage 2 and 1, respectively. After moderate wear (e.g., ZMB 16770), the protoloph connects to the anteroloph and nearly connects to the protocone, isolating an elongated anterior enamel lake. The lingual reentrant is confluent with the anterior and middle reentrants. At this wear stage, the mesoloph joins labially both the posteroloph and the mesostyle. Therefore, on the posterior side of the tooth, there is an elongate posterior enamel-lake and a posterolabial re-entrant. This morphology corresponds to wear stage 1 (wear stage 3 in *M1* and 2 in *M2*). In later wear (e.g., ZMB 43373a, ZMB 43373b; Figs. 2E-G), the morphology of *M3* is quite similar to that at the previous wear stage. However, the posteroloph is combined with the mesoloph, isolating an elongated posterior enamel lake, and the posterolabial re-entrant has disappeared. This is wear stage 2, which corresponds to wear stage 4 in *M1* and 3 in *M2*. Later, the tooth is completely worn and only a flat surface (devoid of any enamel lake) shows up (e.g., ZMB 17411, see Fig. 2I). This morphology corresponds to wear stage 3 (wear stage 5 and 4 in *M1* and *M2*, respectively).

Lower dentition

m1. This tooth is **three** rooted. It shows a pentalophodont dental pattern with anterolophid, metalophid, mesolophid, hypolophid and posterolophid.

In early wear (e.g., C.G.1912-851, ZMB 16768, ZBM 17417, Figs. 1B, 2B), all labial re-entrants but the posterior **one are** already closed off. The anterolophid is combined with the metalophid, isolating a small anterior circular enamel-lake. The mesolophid connects labially and lingually to the metalophid and hypoconid, respectively. This results in the isolation of a second and elongate enamel-lake. In some specimens (e.g., ZBM 17417), there is an additional connection between the mesolophid and the metalophid at about the midpoint of the tooth. In this case, the second enamel-lake is divided into a small and circular labial enamel-lake and an elongate lingual one. In addition, the mesolophid joins the hypolophid isolating a third enamel-lake, which is confluent with the lingual re-entrant. Thus, the third enamel-lake is very elongate and extends transversely across the occlusal surface of the tooth. The posterolophid joins the hypolophid through the hypoconid, isolating an **elongate posterolabial** enamel-lake. With **slightly** more wear (Fig. 2B), the lingual re-entrant is closed off and the enamel disappears from the anterior border of the tooth. This morphology corresponds to wear stage 2. With further wear (stage 3; e.g., ZMB 16770, Fig. 2D), the second enamel-lake is divided and forms a small additional enamel-lake. The posterior reentrant is closed off. At stage 4 (e.g. ZMB 43373b, Fig.2G), the posterolophid and the hypolophid are combined. The posterior enamel-lake has disappeared or is reduced into a small and circular enamel-lake. The only specimen I have seen with further wear (ZMB 17411) is broken but seems to have a flat occlusal surface, nearly completely devoid of enamel.

m2. This tooth is square in occlusal outline. It has four roots, the posterolingual one being the most developed. It has four major lophs: anterolophid-metalophid, short mesolophid, hypolophid and long posterolophid. The mure is lacking and the posterior part of the tooth is isolated from the anterior one. In early wear (e.g., C.G.1912-851, ZMB 16768, ZMB 17417, see Figs. 1B and 2B), the anterolophid fuses with the metalophid, isolating a small and elongate anterior enamel-lake that disappears quickly with wear. The mesolophid joins labially this first lophid through the protoconid, and the hypolophid and posterolophid are isolated. All re-entrants are open and the labial one is confluent with both the middle and the posterior ones. This morphology corresponds to wear stage 1 (stage 2 in *m1*). After further wear (e.g. ZMB 16770), the morphology of the tooth is similar to that of the preceding stage, but the hypolophid connects to the posterolophid through the hypoconid, isolating a posterior and elongate enamel-lake, and to the anterolophid-metalophid. All lingual re-entrants are closed off. The labial re-entrant joins the middle enamel-lake. This morphology corresponds to wear stage 2 (wear stage 3 in *m1*). With further wear (e.g., ZMB 43373a, ZMB 43373b, Fig. 2F-H), the mesolophid connects to the hypolophid, isolating an elongate anterior enamel-lake. The sinusid is closed off and a labial enamel-lake is formed. This is wear stage 3 (wear stage 4 in *m1*). In later wear (ZMB 17411, Fig. 2J), the tooth is worn flat with some remnant of enamel lakes. This morphology corresponds to wear stage 4, which is coincident with wear stage 5 in *m1*.

m3. When unworn (e.g., C.G.1912-851, ZMB 17417), the metalophid is distinct from the anterolophid and connects lingually to it. Both structures will quickly fuse through wear (ZMB 16768; Fig. 2B), isolating a tiny and circular anterolingual enamel lake. The mesolophid, which is cusp-like, is a short continuation of the protoconid. The cusp-like hypolophid and the short posterolophid are isolated. The mure is lacking as the posterior part

of the tooth is isolated from the anterior one. This morphology corresponds to wear stage 0 (wear stages 2 and 1 in m1 and m2, respectively). In early wear (e.g., ZMB 16770), the morphology of the tooth is similar to that at the preceding stage, but the mesolophid and the hypolophid are fused, forming a central lophid. The third lophid is an arcuate structure that is isolated from the rest of the crown by a long re-entrant (the sinusid). This is wear stage 1 (wear stage 3 and 2 in m1 and m2, respectively). In advanced wear (e.g., ZMB 43373a, ZMB 43373b; Fig. 2F-H), the m3 significantly increases in size. The first lingual re-entrant is closed off, isolating an elongate middle enamel-lake. The small circular anterolingual enamel lake persists. This morphology corresponds to wear stage 2 (wear stage 4 and 3 in m1 and m2, respectively). In later wear (ZMB 17411, Fig. 2J), the occlusal surface of the tooth is flat. However, it still shows three small enamel lakes: labial and lingual elongate ones and a tiny, circular central one that has persisted through wear. All labial and lingual reentrants are closed off. This morphology corresponds to wear stage 3, which corresponds to wear stage 5 in m1 and wear stage 4 in m2.

Rhizomys sumatrensis (Raffles, 1821)

Raffles (1821: 258) named this species as *Mus sumatrensis* on the basis of a drawing and a specimen forwarded from Malacca (Malaysia) by W. Farquhar. The reason he chose *sumatrensis* as a species name when it had not been found in Sumatra remains unknown. Later on, Gray (1831: 95) included *M. sumatrensis* in the new genus *Rhizomys*. The type specimen was possibly lost in transit (P. Jenkins, pers. comm. 2012).

The teeth of *Rhizomys sumatrensis* and *R. sinensis* are quite similar, but some differences can be discerned. The molars of *R. sumatrensis* are high crowned, although not as much as

those of *R. sinensis*, and they have longer roots and much smaller M3 than *R. sinensis*.

Furthermore, M1 of *R. sumatrensis* is the largest tooth, whereas it is M2 in *R. sinensis*.

The dental wear pattern of *Rhizomys sumatrensis* is comparable to that in *R. sinensis*. New-born and infant individuals of *R. sumatrensis* (Fig. 3 A-D) were available in the collections of the MNHN (whereas such specimens were lacking for *R. sinensis*). The examination of these specimens allows describing wear stage 0 and 1 in the genus *Rhizomys*. In addition, due to the different morphology of M3 in *R. sumatrensis* with respect to the remaining congeneric species, the wear pattern of this tooth is also described in detail.

Upper dentition

M1. It is the only visible tooth in a new born skull of *Rhizomys sumatrensis* (A 7. 216, Fig. 3B). It shows a basic pentalophodont dental pattern with anteroloph, protoloph, mesoloph, metaloph and posteroloph. When unworn, the protoloph is isolated, the mesoloph is a long continuation of the hypocone and the metaloph does not join with the hypocone but with the posteroloph labially. All re-entrants, but the posterior one, are open. This morphology corresponds to wear stage 0. In specimens in which M3 are still in their crypts (e.g., A 7.215; Fig. 1D), the metaloph is fused with the posteroloph and only four crests are recognizable: anteroloph, protoloph, mesoloph and metaloph-posteroloph. At this state of wear, the anteroloph is a long continuation of the protocone, the protoloph is still secluded, the posterior part of the tooth is isolated from the rest of the crown by a long and continuous sinus (the mure is lacking), the mesoloph is a long continuation of the hypocone and the posteroloph connects to the hypocone. All labial and lingual re-entrants are still open. This morphology corresponds to wear stage 1.

1 M2. The morphology of M2 in specimen A 7.215 (Fig. 1D) is quite similar than that of M1.
 2
 3 However, the anterior part of M2 is antero-posteriorly compressed. As in M1, M2 has four
 4 major crests (anteroloph, protoloph, mesoloph and metaloph-posteroloph). The anteroloph
 5 and the protoloph unite with the protocone and the mesoloph and the metaloph-posteroloph
 6 join with the hypocone. The mesoloph is a long continuation of the hypocone. The anterior
 7 part of the tooth is isolated from the posterior one by a long, transversal sinus dividing the
 8 tooth into two parts (the mure is absent). This morphology corresponds to wear stage 0. When
 9 M2 is at this point, M1 is at wear stage 1.

20 M3. This tooth is three rooted, the anterolingual one being the most developed. When
 21 unworn (e.g., MNHN C.G. 2007-162, Fig. 3E), M3 shows a tetralophodont dental pattern
 22 with anteroloph, protoloph, mesoloph and short posteroloph. At this state, the anteroloph joins
 23 the protocone, the mesoloph is divided with a distinct mesostyle and the mure is lacking. This
 24 morphology corresponds to wear stage 0. When M3 is at this point, M1 and M2 are at wear
 25 stage 2 and 1, respectively. After moderate wear (ZMB 38840, Fig. 3G), the lingual re-entrant
 26 is closed off; it is confluent with the labial reentrant that is still open. At this point, the
 27 anteroloph joins the protoloph and protocone and the mesoloph connects to the posteroloph,
 28 isolating a small and circular posterior enamel-lake. This is wear stage 1. In later wear (ZMB
 29 21249; Fig. 3I), all re-entrants are closed off. The fusion of the anteroloph with the protoloph
 30 isolates an anterior enamel lake and that of the mesoloph with the posteroloph, a posterior
 31 enamel lake. In addition, the anteroloph-protoloph joins the mesoloph-posteroloph, isolating a
 32 third elongate lingual enamel-lake (ZMB 21249). The anterior and lingual enamel-lakes can
 33 also combine into a single one (ZMB 1847). This morphology corresponds to wear stage 2
 34 (wear stage 4 and 3 in M1 and M2, respectively).

1 *Lower molars.* The molars of this species are high crowned, although not as much as in
 2
 3
 4 *Rhizomys sinensis*, and with longer roots than in the latter.
 5
 6
 7

8 *m1.* This tooth is three rooted with the anterior root the most developed. When unworn
 9
 10 (e.g., A. 7.216; Fig. 3A), the m1 shows a basic pentalophodont dental pattern: anterolophid,
 11 metalophid, mesolophid, hypolophid and posterolophid. The anterolophid is connected
 12
 13 lingually to the metalophid. This anterior loph is isolated from the rest of the tooth by a long
 14 sinusid. The mesolophid is a long continuation of the protoconid; it is isolated. The
 15
 16 hypolophid loosely connects to the hypoconid. The posterolophid is an arcuate continuation
 17
 18 of the hypoconid. At this wear stage, all re-entrants, except for the most anterolingual one,
 19
 20 remain open. This morphology corresponds to wear stage 0.
 21
 22
 23
 24
 25
 26
 27

28 In early wear (stage 1; e.g., A. 7.215, Fig. 3C), the morphology of m1 is quite similar to
 29
 30 that at the preceding wear stage. However, the metalophid joins the anterolophid labially. In
 31
 32 addition, the mesolophid slightly connects to the hypolophid, which otherwise would be
 33
 34 completely isolated. The former is divided with a distinct mesostylid.
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 36
 37
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 39
 40

41 *m2.* This tooth is four rooted; the posterolingual one being the most developed. In
 42
 43 specimen A-7.215 (with unerupted m3), m2 is unworn (Fig. 3C). It has five lophs:
 44
 45 anterolophid, metalophid, short mesolophid, hypolophid and posterolophid. Both lingual and
 46
 47 labial anterolophid are distinct. The lingual anterolophid joins the metalophid, isolating a
 48
 49 small enamel-lake in the anterolingual corner of the tooth, which is quickly lost through wear.
 50
 51 The short mesolophid connects to the labial anterolophid. The hypolophid as well as the
 52
 53 arcuate posterolophid are isolated. All labial and lingual sinusids remain open. This
 54
 55 morphology is wear stage 0. When m2 is at this wear stage, m1 is at its first stage of wear. In
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 57 early wear (e.g., MNHN C.G. 2007-162; Fig. 3F), metalophid and anterolophid are fused in
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one major anterior loph that joins the mesolophid through the protoconid. Hypolophid and posterolophid are still isolated and the labial sinusid is confluent with both the anterior and posterior lingual re-entrants. This is wear stage 1, and at this point m1 is at stage 2.

m3. This tooth is three rooted with the posterior root the most developed. When unworn (e.g., MNHN C.G. 2007-162; Fig. 3F), it shows anterolophid, metalophid, very short mesolophid, hypolophid and posterolophid. At this wear stage, the anteroconid and the labial and lingual anterolophids are distinct. The lingual anterolophid joins the metalophid, isolating a small enamel-lake on the anterolingual corner of the tooth. The mure is absent and all labial and lingual sinusids remain open. This is wear stage 0. When m3 is at this stage of wear, m1 and m2 are at their second and first ones, respectively. In early wear (ZMB 38840; Fig. 3H), metalophid and anterolophid fuse, isolating a small anterolingual enamel-lake. This first loph joins labially the second loph, which is formed by the junction of the mesolophid with the hypolophid. The arcuate posterolophid is isolated. The mure is lacking. All labial and lingual reentrants are still open. This morphology corresponds to wear stage 1 (wear stage 3 and 2 in m1 and m2, respectively). After moderate wear (e.g., ZMB 1847, ZMB 21249; Fig. 3J), the morphology of the tooth remains quite similar to that at the previous wear stage. However, the lingual and labial re-entrants are closed off. This morphology is wear stage 2 (wear stage 4 and 3 in m1 and m2, respectively).

Rhizomys pruinus Blyth, 1851

This species was named by Blyth (1851: 519) after the examination of a few specimens from the Khásia Hills (Chérá Punji, Bangladesh). 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. A thorough examination of the teeth of this taxon has revealed a few differences with respect to *Rhizomys sinensis* and *R. sumatrensis*. M1 of *R. pruinus* is longer than wide, whereas the occlusal outline in *R. sumatrensis* and *R. sinensis* is square. M3 of *R. pruinus* is not as small as that of *R. sumatrensis*. In addition, M1 in *R. pruinus* is much more reduced through wear than in *R. sumatrensis* but somewhat less than in *R. sinensis*. The dental wear pattern of *R. pruinus* (Fig. 4A-N) is comparable to that in *R. sinensis* (see above).

4. Discussion and conclusion

The study of 41 skulls of extant *Rhizomys* has allowed me to determine the changes in dental wear pattern throughout life in this taxon. For the first lower and upper molars, six stages of wear (0–5) are recognized. The second lower and upper molars show five stages of wear (0–4), whereas the third ones have four (0–3). Wear stage 0 of the first lower and upper molars, in which the second molars are still in their crypts, is that of new-born individuals. Wear stage 0 of the second lower and upper molars (wear stage 1 of the first ones) corresponds to infants, in which the third molars have not erupted from the jaw bone yet. Wear stage 0 of the third lower and upper molars (wear stages 2 and 1 of the first and second ones, respectively), is that of juvenile individuals. Finally, wear stages 3–5 of the first molars (2–4 of the second molars and 1–3 of the third ones) are found in adult individuals.

The tribe Rhizomyini comprises the extant species belonging to the genera *Rhizomys* and *Cannomys* but also the extinct *Miorhizomys pilgrimi* and *Brachyrhizomys shansius* (see López-Antoñanzas et al., 2013). *M. pilgrimi* is a basal member of the tribe. Remains of this

taxon have been found in Late Miocene lower alternations in Haritalyangar, India (Hinton, 1933), in the Dhok Pathan Formation in the Potwar Plateau, Pakistan (Flynn, 1982a) and at the coeval Chinese locality of Lufeng (Flynn & Qi, 1982). All of them correspond to adult individuals. The morphology of the teeth of the specimens GSI HT6 (a hemimandible with m1-m3, Fig.5A), GSI D270 (Fig.5B) and YGSP 8366 (mandible fragments with m2-m3, Fig.5C) correspond to wear stages 3, 2, 1 for the m1, m2 and m3, respectively. YGSP 182 (a mandible fragment with m2-m3) is more worn (Fig. 5D); m2 of YGSP 182 is at wear stage 3 and the morphology of the m3 corresponds to wear stage 2.

Brachyrhizomys shansius, the sister species of the crown-group, has been recorded from several Pliocene localities of the Yushe Basin, Shanxi, China (Teilhard de Chardin, 1942; Flynn, 1993; Flynn, 2009). This species was regarded as a primitive type of *Rhizomys* and included in it as a subgenus by Flynn (2009). However, a cladistic analysis of the whole subfamily Rhizomyinae supports the reestablishment of the genus *Brachyrhizomys* (López-Antoñanzas et al., 2013). The dental wear pattern of *B. shansius* (Fig. 5) is comparable to that of the extant *Rhizomys* (Fig. 4). The dental wear morphology of the juvenile *B. shansius* (AMNH 117337; Fig. 5E-F), in which the third molars are just erupting, corresponds to wear stages 2, 1 and 0 for the first, second and third molars, respectively. Its wear pattern is similar to that of juvenile individuals of *R. pruiosus* (e.g., ZMB 17417; Fig. 4E-F).

Nevertheless, *B. shansius* has more marked upper molar wear than *R. pruiosus*. Thus, M1 and M2 of *B. shansius* are more worn than those of *R. pruiosus* at the same wear stage (Figs. 4A and 5A). The figured (Teilhard de Chardin, 1942; Flynn, 1993) individuals of *B. shansius* (specimens 31095 and 31096; Fig. 5G-I and specimen 14183; Fig. 5H) are adult. The morphology of 31095 (Fig. 5G) corresponds to the wear stage 3 for the first molars, 2 for the second and 1 for the third. Specimens 31096 and 14183 are at wear stages 2, 3 and 4 for their m3, m2 and m1, respectively (Fig. 5H-I).

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Fig. 1. Rhizomyini dental terminology used in this paper. *Rhizomys sinensis* (MNHN C.G. 1912-851). A. Right maxilla with M1-M3. B. Left mandible with m1-m3. Scale bar equals 2 mm.

Fig. 2. Dental wear pattern in *Rhizomys sinensis*. A-B. Stage of wear 2, 1 and 0 for the first, second and third upper and lower molars, respectively, juvenile individual (ZMB 16768). A. Right maxilla with M1-M3. B. Right hemimandible with m1-m3. C-D. Stage of wear 3, 2 and 1 for the first, second and third upper and lower molars respectively, adult individual (ZMB 16770). C. Right maxilla with M1-M3. D. Right hemimandible with m1-m3. E-H. Stage of wear 4, 3 and 2 for the first, second and third upper and lower molars, respectively, adult specimens (ZMB 43373a and ZMB 43373b). E. Right maxilla with M2-M3. F. Right hemimandible with m1-m3. G. Right maxilla with M1-M2. H. Right hemimandible with m1-m3. I-J. Stage of wear 5, 4 and 3 for the first, second and third upper and lower molars, respectively, adult individual (ZMB 17411). I. Right maxilla with M1-M3. J. Right hemimandible with m2-m3. Scale bar equals 5 mm.

Fig. 3. Dental wear pattern in *Rhizomys sumatrensis*. A-B. Stage of wear 0, new-born individual (A. 7. 216). A. Left m1 in occlusal view. B. Right M1 in occlusal view. C-D. Stage of wear 1 and 0 for the first and second upper and lower molars, respectively, infant (A. 7. 215). C. Left hemimandible with m1-m2. D. Right maxilla with M1-M2. E-F. Stage of wear 2, 1 and 0 for the first, second and third upper and lower molars, respectively, juvenile individual (MNHN C.G. 2007-162). E. Right maxilla with M1-M3. F. Left hemimandible with m1-m3. G-H. Stage of wear 3, 2 and 1 for the first, second and third upper and lower molars, respectively, adult individual (ZMB 38840); G. Right maxilla with M1-M3. H. Left hemimandible with m1-m3. I-J. Stage of wear 4, 3 and 2 for the first, second and third upper

and lower molars, respectively, adult individual (ZMB 21249). I. Left Maxilla with M1-M3.
J. Left hemimandible with m1-m3. Scale bar equals 5 mm.

Fig. 4. Dental wear pattern in *Rhizomys pruinosus*. A-C. Stage of wear 0, new-born individual (MNHN DH 280). A. Right m1 in occlusal view. B. Left m1 in occlusal view. C. Left M1 in occlusal view. D. Right M1 in occlusal view. E-F. Stage of wear 2, 1 and 0 for the first, second and third upper and lower molars, respectively, juvenile individual (ZMB 17417). E. Right maxilla with M1-M3. F. Right hemimandible with m1-m3. G-H. Stage of wear 3, 2 and 1 for the first, second and third upper and lower molars, respectively, adult individual (MNHN C.G. 1962-2295). G. Left maxilla with M1-M3. H. Right hemimandible with m1-m3. I-J. Stage of wear 3, 2 and 1 for the first, second and third upper and lower molars, respectively, adult individual (MNHN C.G. 1962-2297). I. Left maxilla with M1-M3. J. Left hemimandible with m1-m3. K-L. Stage of wear 4, 3 and 2 for the first, second and third upper and lower molars, respectively, adult individual (MNHN C.G. 1962-2294). K. Right maxilla with M1-M3. L. Right hemimandible with m1-m3. M-N. Stage of wear 5, 4 and 3 for the first, second and third upper and lower molars, respectively, adult individual (MNHN C.G. 1892-1360). M. Right maxilla with M1-M3. N. Right hemimandible with m1-m3. Scale bar equals 5 mm.

Fig. 5. Fossil Rhizomyini. A. *Miorhizomys pilgrimi* (GSI HT6), left mandible with m1-m3. B. *Miorhizomys pilgrimi* (GSI D270), right mandible fragment with m2-m3. C. *Miorhizomys* cf. *M. pilgrimi* (YGSP 8366), fragment of left m1 and m2-m3. D. *Miorhizomys* cf. *M. pilgrimi* (YGSP 182), left m2-m3. E. *Brachyrhizomys shansius* (AMNH 117337), right maxilla with M1-M3. F. *Brachyrhizomys shansius* (AMNH 117337), left mandible with m1-m3. G. *Brachyrhizomys shansius* (IVPP 31.095), right mandible with m1-m3. H. *Brachyrhizomys*

1 *shansius* (14183), fragment of right hemimandible with m2-m3. I. *Brachyrhizomys shansius*
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4 (IVPP 31.096), right mandible with m1-m3. Scale bar equals 4 mm. C and D are redrawn
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6 after Flynn (1982a), G and I after Teilhard de Chardin (1942) and H after Flynn (1993).
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