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硅藻鼠科(哺乳纲,啮齿目)与亚洲中始新世啮齿类的双脊齿

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摘要:亚洲特有的啮齿类硅藻鼠科自渐新世以来分布于东亚和南亚。现生硅藻鼠类的分布只限于老挝的喀斯特地区。就目前所知,这些具有豪猪型头骨-松鼠型下颌的啮齿类的颊齿都是不同程度的横向双脊齿。时代最早的硅藻鼠类产于巴基斯坦渐新世地层中,其颊齿的双脊齿构造上仍保留齿尖残迹,基本符合双脊齿型牙齿结构。至渐新世末期,硅藻鼠科的牙齿出现分化。中新世及以后硅藻鼠类的化石记录相对较少。分子生物学证据将硅藻鼠类归入Ctenohystrica,这种归属也从始新世梳趾鼠类的臼齿形态上得到一定的支持。除此之外,有关硅藻鼠类的起源问题几乎一无所知。亚洲中始新世的*Hydentomys*臼齿表现出轻微的双脊型,然而其他方面却与硅藻鼠类不同。另一个具双脊齿的啮齿类*Dolosimus*(新属)产于江苏中始新世,其具有更为发育的双脊齿,特别是臼齿型下牙。新属的不完整记录及其形态不能解决如下问题:它是否与后来出现的像硅藻鼠类和跃兔类这些具有明显双脊齿型颊齿的啮齿类有亲缘关系,或者只是这种形态发育中没有留下后继者的早期试验品。

关键词:亚洲,始新世,啮齿目,硅藻鼠科,双脊齿型颊齿

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THE DIATOMYIDAE (MAMMALIA, RODENTIA) AND BILOPHODONTY IN MIDDLE EOCENE ASIAN RODENTS

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Abstract The Asian endemic rodent family Diatomyidae is known to have inhabited eastern and southern Asia since the Oligocene. Its current distribution is limited to karstic regions of Laos. So far as known these hystricomorphous-sciurognathous rodents have some degree of transverse bilophodonty of the cheek teeth. The earliest recognized diatomyids, which are from the Oligocene of Pakistan, retain some traces of cusps on the cheek teeth, overlying the basically bilophodont tooth structure. By the end of the Oligocene there is some dental diversity within the family. Miocene and later diatomyids are relatively rare in the fossil record. Molecular evidence unites the diatomyids in the Ctenohystrica, an assignment that receives some support from the molar morphology of Eocene ctenodactyloids. Other than this connection, little is clear regarding the origin of the diatomyids. The middle Eocene Asian *Hydentomys* exhibits a slight degree of bilophodonty, but is otherwise unlike diatomyids. Another taxon of bilophodont

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rodent, *Dolosimus* n. gen. from the middle Eocene of Jiangsu Province, has still more precocious development of bilophodonty, especially in the lower molariform teeth. The incomplete record of this new taxon as well as its morphology cannot answer the question of whether this taxon is allied to such later appearing, strongly bilophodont rodents as diatomyids and pedetids, or is an early experiment of this striking morphological development that left no successors.

Key words Asia, Eocene, Rodentia, Diatomyidae, bilophodont cheek teeth

1 Introduction

The family Diatomyidae Mein & Ginsburg, 1997, encompasses Asian rodents that are characterized by their combination of an hystricomorphous/sciurognathous zygomasseteric structure; multiserial incisor enamel; dental formula 1/1, 0/0, 2-1/1, 3/3; transversely bilophodont cheek teeth lacking conules; premolars usually having 3 roots, molars 4 roots; relatively low temporomandibular joint; reduced coronoid process; and a relatively unspecialized postcranial skeleton. Their fossil record, comprehensively surveyed by Flynn (2006), extends into the Paleogene of the Indian subcontinent, with the genus *Fallomus* (Flynn et al., 1986; Marivaux and Welcomme, 2003). Three Oligocene species (28 or 25 Ma) of *Fallomus*, *F. razae*, *F. ginsburgi*, and *F. quraishyi*, have cheek teeth that are bilophodont but relatively more cuspate than in later diatomyids. *Fallomus ladakhensis* Nanda & Sahni, 1998, known by lower teeth and jaws from the late Oligocene of northern India and Thailand, is more hypsodont and more distinctly bilophodont than other species of *Fallomus* as well as having an enlarged hypoconulid forming a third, posterior loph on the lower cheek teeth (Marivaux et al., 2004). *Marymus* Flynn, 2007, known from isolated teeth from the later Oligocene (26 ~ 27 Ma) or early Miocene (23 ~ 24 Ma) of Pakistan (de Bruijn et al., 1981; Flynn 2007), is more strictly bilophodont in its upper and lower molar morphology but has large, cuspate premolars. The later Neogene record of diatomyids stems from southern and eastern Asia and includes the Miocene *Diatomys* Li, 1974 and *Willmus* Flynn & Morgan, 2005. The single Recent representative of the family, *Laonastes*, appears to be restricted to karstic areas of Laos (Dawson et al., 2006).

The Miocene *Diatomys* is currently the best known extinct member of its family, being represented by beautifully preserved, though compressed, fossils from the diatomaceous lacustrine shales of the Shanwang locality in Shandong Province, China, late early Miocene to early middle Miocene (14 ~ 17 Ma; Qiu et al., 1999). *Diatomys shantungensis* was originally based on two relatively complete skeletons (Li, 1974). The well preserved dentitions of these specimens show that the cheek teeth in each jaw quadrant include one premolar and three molars displaying a simple, transversely bilophodont occlusal pattern. Details of cranial and mandibular anatomy were difficult to interpret because of the lateral compression of the fossils. However, *Diatomys* was originally thought to have a non-enlarged infraorbital foramen (the sciuromorphous condition) and a sciurognathous lower jaw. Its postcranial skeleton lacks any obvious morphological adaptations for either leaping or burrowing.

In June 2005, a new and less compressed specimen of *D. shantungensis* was discovered from the type locality in Shandong Province. The new specimen, IVPP V 12692 (Fig. 1), complete with whiskers and traces of pelage, clarifies aspects of the cranial and mandibular anatomy of *Diatomys* that were either missing or obscured by postmortem deformation in previously described specimens of this species. V 12692 shows that the infraorbital foramen of *Diatomys* is very large; hence, *Diatomys* resembles *Laonastes* in having the hystricomorphous condition. V 12692 also shows that the mandible lacks a coronoid process and has a relatively low condyle; the masseteric fossa extends forward to a level below p4; an anteroposterior ridge, the linea obliqua, separates dorsal and ventral portions of the masseteric fossa; the angular process is in the same vertical plane as the incisor (the sciurognathous condition); the angular process extends posteriorly as far as the condylar process; the ventral side of the angular process is very

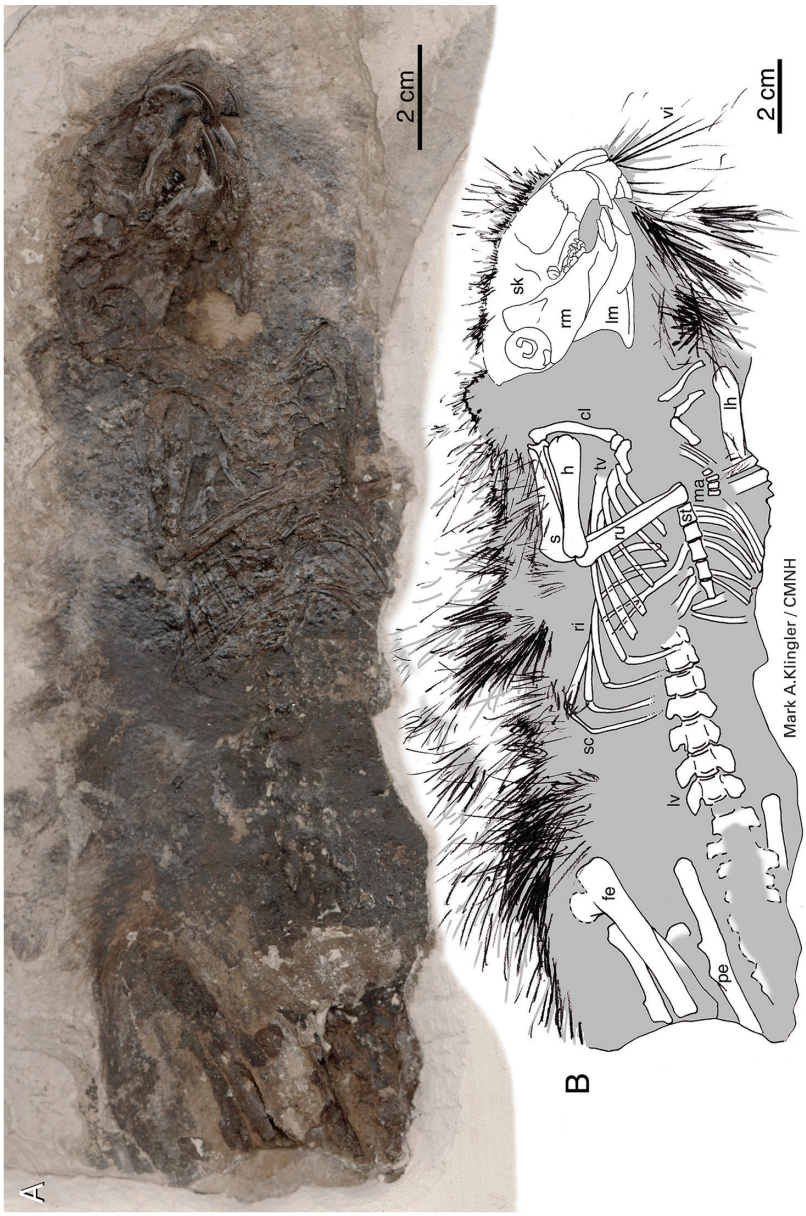

Fig. 1 *Diatomys shantungensis*, IVPP V 12692, complete with whiskers and traces of pelage, from the Shanwang locality, Shandong Province, China, late early Miocene to early middle Miocene
A. lateral view; B. outline drawing with some parts identified
Abbreviations: cl. clavicle; fe. femur; h. humerus; lh. left humerus; lm. left mandible; lv. lumbar vertebrae; ma. manubrium; pe. pelvis; ri. ribs; rm. right mandible; ru. radius + ulna; s. scapula; sc. sternal cartilage; sk. skull; st. sternum. tv. thoracic vertebrae; vi. vibrissa

slightly inflected; and the incisor root is short, extending posteriorly to a level below m2. Thus, the new specimen demonstrates that the mandibles of *Diatomys* and *Laonastes* are virtually identical in sharing the following derived characters: absence of a coronoid process, masseteric fossa extending forward to below p4, masseteric fossa subdivided into dorsal and ventral sections, condyle low but higher than tooth row, and shortened incisor.

In addition to the fossil vertebrates from the Shanwang locality, fossils of abundant grasses, dicotyledenous plants, and infrequent palms, suggest that the habitat in which *Diatomys* lived had a humid, warm temperate to sub-tropical climate, more humid and equable than present (Stromberg et al., 2007).

There is enough dental diversity within species of the Oligocene diatomyid *Fallomus* and between them and *Marymus* to suggest a considerably earlier origin for the family. So far, there has been little support for details of this origin other than the presence throughout much of Asia of a variety of ctenodactyloids (Fig. 2E, F), an old Asian clade having living representatives only in Africa (Flynn et al., 1986; Marivaux and Welcomme, 2003; Dawson et al., 2006). Such a relationship is favored by morphological evidence from fossil and living diatomyids as well as molecular evidence (Huchon et al., 2007) that lends support for the Ctenohystrica, a clade encompassing Diatomyidae, Ctenodactylidae, and the Hystricognathi.

2 Bilophodonty in Rodentia

In spite of their reasonable fossil record and moderately secure affinities based on morphological and molecular evidence, the origin of the Diatomyidae remains enigmatic. Bilophodont teeth similar to those of *Diatomys* have evolved a number of times within the Rodentia, as emphasized by Li (1974) in his original description of the genus, in which he mentioned this condition among geomyoids and pedetids. While bilophodonty is not restricted to these rodents, it is a frequently appearing characteristic in them. Perhaps the best documented series of changes among fossil rodents from a more cuspate occlusal pattern to a bilophodont one has been documented in the transition within the European geomyoid Eomyidae from *Eomys* to *Rhodanomys* to *Ritteneria* (Engesser, 1999). The relatively rapidly occurring transitional steps in this lineage involve both reduction of anteroposterior elements of the cheek tooth pattern and elimination of mesoloph and mesolophid.

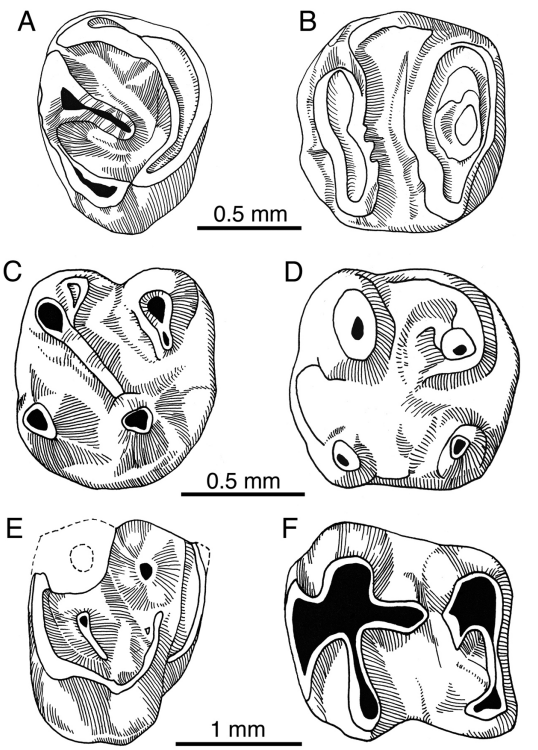

Fig. 2 Occlusal views of cheek teeth of ctenodactyloid and Rodentia indet.
Left, right upper molariform teeth; right, left lower molariform teeth, anterior ends to right; A, B. *Dolosimus dolus* gen. et sp. nov.; C, D. *Hydentomys crybelophus* (after Tong, 1997); E, F. *Tamquammys wilsoni* (after Dawson et al., 1984)

A recently described Asian rodent having a somewhat bilophodont cheek tooth pattern (Fig. 2C – D) is *Hydentomys* Tong, 1997, assigned initially to Geomyoidea, family incertae sedis. *Hydentomys crybelophus* Tong, 1997, and *H. major* Tong, 1997, are very small rodents, both from the Irdinmanhan (middle middle Eocene, approximately early Uintan) of the Hetaoyuan Formation, Henan Province. Only isolated teeth are known of these tiny rodents (teeth in the 0.6 to 0.9 mm size range). The cheek teeth are simple, low crowned, and cuspate; the 3-cusped p4 is reduced. The lower molars have four unconnected cusps and no ectolophid,

so there is some functional suggestion of a medial, transverse valley; cingula are very weak. The upper molars are wider than long, and are cuspate but with a metaloph extending between metacone and protocone. The combination in *Hydentomys* of cuspate cheek teeth with a suggestion of bilophodonty is somewhat reminiscent of the morphology shown by the diatomyid *Fallomus*. *Hydentomys* is still too incompletely known to make this more than a suggestion.

Unusual isolated mammal teeth from the middle Eocene Shanghuang fissure fillings in Jiangsu Province, China (Qi et al., 1996), document an early occurrence of a small mammal having a still more distinctly bilophodont lower molar pattern (Fig. 2A, B; Fig. 3). None of these teeth can currently be associated with jaws or adjacent teeth. Even their assignment to Rodentia is based mainly on elimination of all other mammalian taxa, and neither assignment of these teeth to loci nor association of upper and lower teeth is at all certain. Association of these teeth with diatomyids or other later rodents such as pedetids that have pronounced bilophodonty may be considered. On the other hand, the seemingly precocious development of this character in this rodent may indicate that no later relationships can be postulated. Although its place in rodent phylogeny is highly uncertain, it is here described as a new genus of Rodentia *incertae sedis*.

3 Systematic paleontology

Order Rodentia Bowdich, 1821
Family incertae sedis
Dolosimus gen. nov.

Type species *Dolosimus dolus* gen. et sp. nov. Only known species of genus.

Range Middle Eocene, Shanghuang fissure fillings, Jiangsu Province, China.

Diagnosis Rodent with brachydont cheek teeth having three roots on upper molariform teeth, two roots on p4 and lower molariforms. Little development of cusps, most elements of occlusal pattern subsumed into lophs(-ids). Upper molariform teeth have short metaloph between metacone and metaconule oriented toward protocone. Remaining raised occlusal pattern of upper molariform teeth formed by peripheral ridge. Trigonid of p4 elongate, narrower than talonid. Lower molars retain posterior arm of protoconid in early wear, become fully bilophate following wear; transverse valley wider buccally than lingually.

Etymology Latin, *dolosus*, deceitful; and *mus*, mouse, referring to uncertain relationships of this taxon.

Dolosimus dolus sp. nov.

Holotype IVPP V 16967. Right lower molariform tooth (anteroposterior 0.82 mm, transverse 0.88 mm).

Referred specimens Holotype and IVPP V 16968–16970, V 16978–16983, V 17011, lower m1 or 2; IVPP V 16971–16977, p4; IVPP V 17008–17010, ? m3; IVPP V 17012–17015, m3; IVPP V 16984–17007, upper molariform teeth.

Horizon and locality Middle Eocene (Irdinmanhan), Fissure D (IVPP loc. 93006.D), Shanghuang fissure fillings in the Triassic Shangqinglong limestone, Liyang County, Jiangsu Province, China.

Diagnosis As for genus.

Etymology Latin, *dolus*, deceit, in reference to the uncertain taxonomic and morphological assignments of these specimens.

Description Teeth that are presumed to be upper molars have three roots, the largest of which is below the lingual side of the tooth; the two smaller buccal roots are anteroposteriorly placed. Anterior and posterior wear facets preserved on some of the teeth confirm this orientation. The occlusal pattern is not deeply incised into the tooth, and whatever pattern exists is un-

usual enough to make determination of cusp homologies difficult. The sequence of wear in the upper molariform teeth seems to be as follows. In early wear (Fig. 3G, IVPP V 16984, anteroposterior, 1.0 mm, transverse, 1.1 mm; H, IVPP V 16985, anteroposterior 0.82 mm, transverse 1.1 mm) these teeth have an anterior shelf, interpreted to be paracone through protoloph to protocone, a distinct buccal valley between paracone and metacone; metacone at the posterobuccal side of the tooth; from this metacone a short loph extends toward the protocone; and a posterior ridge from the metacone to the area of a hypocone; a slight lingual groove separates protocone and hypocone. In several of the little worn teeth there is a small cuspule posterior to the hypocone. Following greater wear the anterior loph widens and the lingual valley closes (Fig. 3I, IVPP V 16986, anteroposterior 0.81 mm, transverse 1.0 mm). An upper molariform tooth becomes an oval bounded by a raised enamel and dentine ridge, widest buccally and having a very low ridge reaching obliquely from posterobuccal to anterolingual (Fig. 3J, IVPP V 16987, anteroposterior 0.88 mm, transverse 1.0 mm).

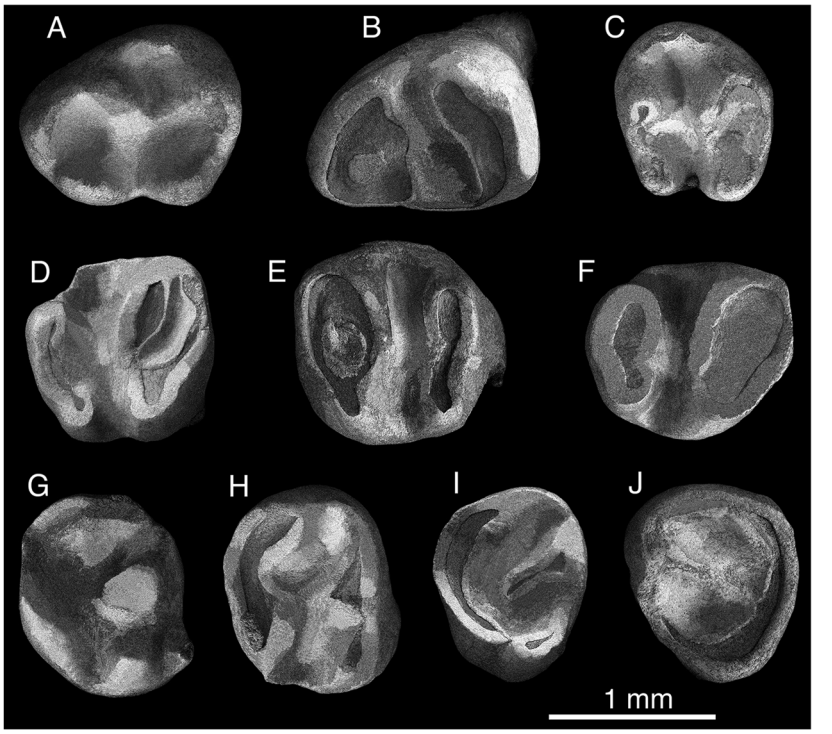

Fig. 3 *Dolosimus dolus* gen. et sp. nov., occlusal views of cheek teeth
A. IVPP V 16977, right p4; B. IVPP V 16972, right p4; C. IVPP V 16978, left m1/2; D. IVPP V 17011, left m1/2; E. holotype, IVPP V 16967, right m; F. IVPP V 17015, left m3; G. IVPP V 16984, left M; H. IVPP V 16985, left M; I. IVPP V 16986, left M; J. IVPP V 16987, right M

Teeth that are interpreted to be the lower molars associated with these upper teeth are more strictly bilophodont. They have two roots, consisting of a smaller anterior branch that swings anteriorly and larger posterior branch; the two branches unite close to the crown. In some specimens anterior and posterior wear facets are visible on the sides of the crown. The buccal end of the transverse valley is wider than the lingual. In less worn lower molars, there appears to be a posterior arm of the protoconid (Figs. 3C, D, IVPP V 17011 and V 16988, anteroposterior 0.88 mm, transverse 0.95 mm; E, IVPP V 16967, holotype). The trigonid of m3 (Fig. 3F, IVPP V 17015, anteroposterior 0.81, transverse 0.95) is similar to that of m1–2 but the talo-

nid is reduced in transverse width. There may be only one root below m3.

Association of several p4 with the bilophodont lower molariform teeth is based on the markedly lophate nature of moderately worn p4 (Fig. 3B). Relatively little worn p4 (Fig. 3A, IVPP V 16977, anteroposterior 0.95 mm, transverse 0.88 mm) has some development of small cusps connected by narrow ridges surrounding three valleys, one in the trigonid, one lingually between trigonid and talonid, and a third between protoconid and hypoconid; the latter two join following wear. The trigonid is elongated anteroposteriorly and decreases in width anteriorly. On the talonid the entoconid is set in only slightly from the lingual side, and there is a small hypoconulid. Following greater wear (Fig. 3B, IVPP V 16972, anteroposterior 1.0 mm, transverse 0.81 mm) p4 appears to be more clearly bilophodont. Two anteroposteriorly aligned roots support the p4 crown.

4 Discussion

The affinities of *Dolosimus* are very uncertain. Its most striking characteristic is the well developed bilophodonty of the lower molars. The middle Eocene *Hydentomys* has some similarity to *Dolosimus* in the morphology of the upper molariform teeth, but its affinities, originally considered to be with the Geomyoidea, are far from clear. Bilophodonty is a moderately frequently developed character in rodents but is otherwise known in Eocene rodents only in *Griphomys*, a North American Uintan-Duchesnean rodent of probable geomyoid affinities, and *Presbymys* of the North American Duchesnean and having very uncertain familial affinities (Wilson, 1940, 1949; Lillegraven, 1977). The Miocene *Diatomys shantungensis* is strongly bilophodont in both upper and lower molariform teeth, and is allied with a series of more or less bilophodont rodents from eastern and southern Asia. Among other Asian rodents that developed bilophodonty, the Neogene distylomyids (Bi et al., 2009) were noted for their strongly hypsodont cheek teeth in which the lophs of the upper molars are separate but those of the lower cheek teeth have a medial, connecting mure. *Megapedetes*, from the Miocene of eastern Africa, is nearly as distinctly bilophodont as its extant relative *Pedetes*. Among North American geomyoids, several, including the Oligocene *Meliakrouniomys* (Harris and Wood, 1969; Emry, 1972), and the Miocene *Jimomys* (Wahlert, 1976) and *Texomys* (Slaughter, 1981), have bilophodont cheek teeth, presumably developed convergently.

The diatomyids are the Asian rodents most characterized by this feature, but even the oldest known rodents currently assigned to the diaytomyids are Oligocene in age and are less completely lophodont, more cuspate, than *Dolosimus*. The closest rodent to this appears to be the approximately contemporary *Hydentomys*, but the similarity is mostly in the structure of upper molariform teeth for this rodent has less bilophodont lower molariform teeth and a reduced p4.

Based on the currently known record, *Dolosimus* must be regarded as a rodent that is precociously developed for bilophodonty. Whether it can be allied with later bilophodonts such as diatomyids, pedetids, or any of the geomyoids can only be a speculation at this time.

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