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-sciurinmous 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 bilophodontal 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 Ctenohyrstrica, an assignment that receives some support from the molar morphology of Oocene ctenocephaloids. Other than this connection, little is clear regarding the origin of the diatomyids. The middle Eocene Asian Hydentomens exhibits a slight degree of bilophodonty, but is otherwise unlike diatomyids. Another taxon of bilophodonty
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 a hysticomorphous/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 Wellecomme, 2003). Three Oligocene species (28 or 25 Ma) of *Fallomus*, *F. razae*, *F. ginsburgi*, and *F. quraishi*, 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 hypoculid 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 Brujin 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 sciuramorphous 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 hysticomorphous 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
sightly 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 *Luonastes* 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 Fallosum 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 cuspatc 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.

A recently described Asian rodent having a somewhat bilophodont cheek tooth pattern (Fig. 2C - D) is Hydidentomys Tong, 1997, assigned initially to Geomyoidea, family incertae sedis. Hydidentomys crybelophus Tong, 1997, and H. major Tong, 1997, are very small rodents, both from the Irlinmanhan (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 cuspatc; 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 cuspidate but with a metaloph extending between metacone and protocone. The combination in *Hydentomys* of cuspidate 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**

*Doosimus gen. nov.*

**Type species** *Doosimus 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, *dolus*, deceitful; and *mus*, mouse, referring to uncertain relationships of this taxon.

*Doosimus 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 (Irundinan), 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, antero-posterior, 1.0 mm, transverse, 1.1 mm; H, IVPP V 16985, antero-posterior 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 postero-buccal 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, antero-posterior 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, antero-posterior 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, antero-posterior 0.88 mm, transverse 0.95 mm; E, IVPP V 16967, holotype). The trigonid of m3 (Fig. 3F, IVPP V 17015, antero-posterior 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 Grippomys, 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 distylomyids are the Asian rodents most characterized by this feature, but even the oldest known rodents currently assigned to the distylomyids are Oligocene in age and are less completely lophodont, more cuspatel, 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 distylomyids, pedetids, or any of the geomyoids can only be a speculation at this time.

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References
Bi S D, Meng J, Wu W Y et al., 2009. New distylomyid rodents (Mammalia; Rodentia) from the early Miocene Suoxoquan Formation of northern Xinjiang, China. Am Mus Novit, (3663): 1–18