Discovery of *Fallomus ladakhensis* Nanda & Sahni, 1998 (Mammalia, Rodentia, Diatomyidae) in the lignites of Nong Ya Plong (Phetchaburi Province, Thailand): systematic, biochronological and paleoenvironmental implications

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ABSTRACT

The paleontological surveys in the lignites of the Tertiary basin of Nong Ya Plong in Central Thailand have led to the discovery of a new fossiliferous locality. This locality, located in the Cha Prong pit, has yielded relatively well preserved fossils (two mandibles and isolated teeth) of a diatomyid rodent, *Fallomus ladakhensis* Nanda & Sahni, 1998, which was first described only from two isolated lower molars from the Oligo-Miocene Kargil Formation in Ladakh (India). This additional material allows better characterization of the Diatomyidae and discussion about the possibility of phylogenetic relationships with the Pedetidae. The occurrence in Nong Ya Plong of *F. ladakhensis* in association with a typically late Oligocene rhinocerotid (of western

KEY WORDS
Mammalia,
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European affinities) testifies to the existence of Oligocene deposits in Thailand – a period still scantily documented in South Asia. The Paleogene/Neogene transition is particularly significant in South Asia in terms of climatic changes, which are related to the important paleogeographic and paleogeomorphological events consequent to the India-Eurasia collision. The fauna from Nong Ya Plong, coupled with those of the Oligocene of Pakistan and India, provides a glimpse into the evolutionary history of mammal communities in South Asia and into the paleoenvironmental conditions (inferred) during this critical time interval.

RÉSUMÉ

Découverte de Fallomus ladakhensis *Nanda & Sahni, 1998 (Mammalia, Rodentia, Diatomyidae) dans les lignites de Nong Ya Plong (Phetchaburi Province, Thaïlande) : implications d'ordre systématique, biochronologique et paléoenvironnemental.*

Les prospections paléontologiques dans les lignites du bassin tertiaire de Nong Ya Plong en Thaïlande ont abouti à la découverte d'une nouvelle localité fossilifère. Cette localité, située dans le puits de Cha Prong, a livré un matériel relativement bien préservé (deux mandibules et des dents isolées) d'un rongeur diatomyidé, *Fallomus ladakhensis* Nanda & Sahni, 1998, initialement décrit par seulement deux molaires inférieures provenant de la formation oligo-miocène de Kargil au Ladakh (Inde). Ce matériel supplémentaire permet de mieux définir la famille des Diatomyidae et de discuter leurs éventuelles relations avec les Pedetidae. La présence à Nong Ya Plong de *F. ladakhensis* en association avec un rhinocérotidé typique de l'Oligocène supérieur (d'Europe occidentale) démontre l'existence de dépôts oligocènes en Thaïlande – une période peu documentée en Asie du Sud. La transition Paléogène/Néogène est particulièrement significative en Asie du Sud en termes de changements climatiques. Ces changements sont liés à d'importants bouleversements paléogéographiques et paléogéomorphologiques résultant de la collision Inde-Eurasie. La faune de Nong Ya Plong ainsi que celles de l'Oligocène du Pakistan et d'Inde constituent les seules documentations fossiles en ce qui concerne l'histoire évolutive des communautés de mammifères en Asie du Sud et les conditions paléoenvironnementales associées durant cet intervalle de temps.

MOTS CLÉS
Mammalia,
Rodentia,
Diatomyidae,
Fallomus,
Oligocène supérieur,
Thaïlande,
Pakistan,
biochronologie,
paléoenvironnement,
paléobiogéographie.

INTRODUCTION

The coal mines of Thailand, notably those of the Peninsular Thailand, are well known for having yielded the famous Tertiary fossiliferous localities of the Krabi Basin (i.e. Ban Pu Dam, Bang Mark and Wai Lek; e.g., Ducrocq *et al.* 1992, 1995a). The paleontological study of the mammalian fossils has led to the description of numerous new taxa belonging to several orders (e.g., Ducrocq *et al.* 1992, 1993, 1995a, b, 1998; Ducrocq 1999a, b; Chaimanee *et al.* 1997, 2000; Marivaux *et al.* 2000; Peigné *et al.* 2000; Métais *et al.* 2001). Considering its exceptional mammalian diversity, the Krabi assemblage is generally considered as a reference fauna in South Asia, with a late Eocene age formally established on the basis of faunal (e.g., Ducrocq *et al.* 1995a) and paleomagnetic data (Benammi *et al.* 2001). The Neogene of Thailand is also well documented in the northernmost part of the country by numerous localities ranging from the middle Miocene (Li, Pong, Lampang, Mae Moh, Mae Teep, Phitsanulok basins; e.g., Ducrocq *et al.* 1994) to the late middle-late Miocene (Chiang Muan and Khorat basins, respectively; e.g., Chaimanee *et al.* 2003), with faunas quite similar to those recorded from the well known Siwalik Group of Pakistan. In August 2001, the joint Thai-French team (Department of Mineral Resources, Bangkok-Institut des Sciences de l'Évolution, Montpellier) surveyed the coal mines of the Nong Ya Plong Basin in the Phetchaburi Province (Central Thailand; Fig. 1). The sedimentary deposits of the mines consist mainly of mudstones and sandstones intercalated with lignite beds. The preliminary survey made on the main coal seam of the Cha Prong pit has led to the discovery of several fossil remains, notably micro- and medium sized mammals (rodents, dermopterans, chiropterans, carnivores, artiodactyls, and perissodactyls). In this paper, we describe relatively well preserved material (two mandibles and isolated teeth) of a diatomyid rodent, *Fallomus ladakhensis* Nanda & Sahni, 1998, which was first described from only two isolated lower molars from the Oligo-Miocene Kargil Formation in Ladakh (India). This new material will be discussed with special emphasis on systematic, biochronological, and paleoenvironmental implications.

ABBREVIATIONS

SHM-CP	Srisuk House Museum, Cha Prong, Thailand;
TF	Thai fossil (Department of Mineral Resources, Bangkok);
DBC	Dera Bugti locus C (Paali Nala, Balochistan, Pakistan).

The dental terminology (Fig. 2) used for describing the new material is adapted from Wood & Wilson (1936) and Flynn *et al.* (1986).

SYSTEMATICS

Order RODENTIA Bowdich, 1821
Family DIATOMYIDAE Mein & Ginsburg, 1997
Genus *Fallomus* Flynn, Jacobs & Cheema, 1986

Fallomus ladakhensis Nanda & Sahni, 1998

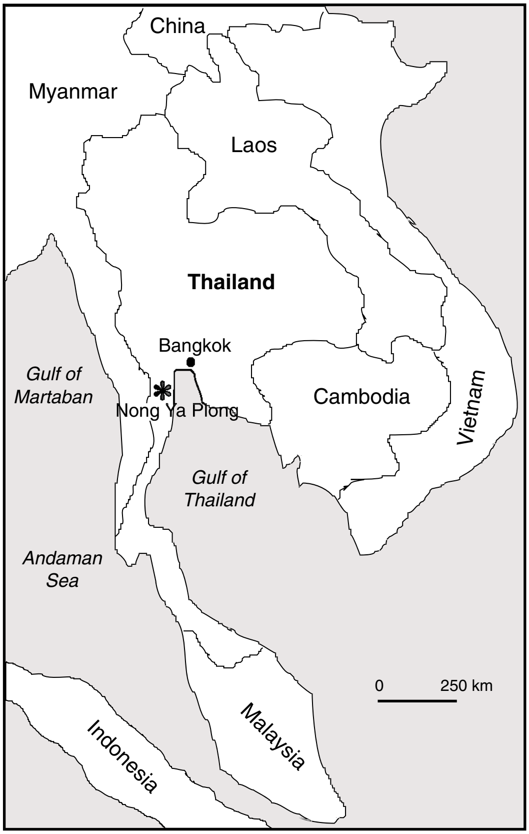

FIG. 1. — Location map of the fossiliferous locality of Nong Ya Plong in Central Thailand (✱).

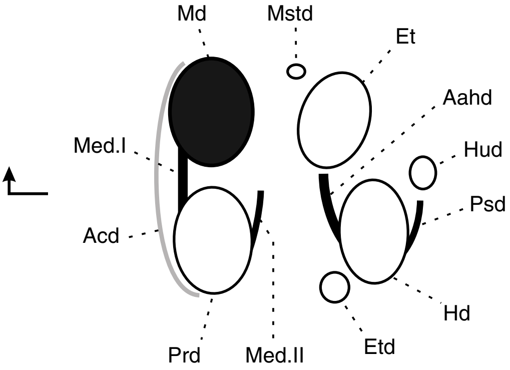

FIG. 2. — Dental terminology used for the lower teeth (after Wood & Wilson 1936; Flynn *et al.* 1986): **Aahd**, anterior arm of hypoconid; **Acd**, anterocingulid (anterolophid); **Et**, entoconid; **Etd**, ectostylid; **Hd**, hypoconid; **Hud**, hypoconulid; **Md**, metaconid; **Med.I**, metalophulid I (ancestral paralophid); **Med.II**, metalophulid II (= protolophid or posterior arm of protoconid); **Mstd**, mesostylid; **Prd**, protoconid; **Psd**, posterolophid.

TABLE 1. — Dental measurements (in mm) of *Fallomus ladakhensis* Nanda & Sahni, 1998 from the lignite of Nong Ya Plong (Phetchaburi Province, Thailand).

		Length	Width	Height
SHM-CP 353	p4	2.11	1.70	1.13
	m1	2.05	2.10	1.47
	m2	2.21	2.46	1.75
	m3	-	-	2.15
SHM-CP 250	p4	1.96	2.10	1.22
	m1	1.86	2.41	1.46
	m2	2.29	2.51	1.80
	m3	2.92	2.70	1.93
TF 6181	m1	2.00	2.04	1.72
TF 6182	m1	1.99	1.94	1.17

REFERRED MATERIAL. — 2 left mandibles with p4-m3 (SHM-CP 250, 353), 2 left m1s (TF 6181, 6182). The specimens are stored in the paleontological collections of the Department of Mineral Resources in Bangkok, Thailand.

LOCALITY. — Cha Prong pit of Nong Ya Plong coal mine, Phetchaburi Province, Thailand (Fig. 1).

PALEOGEOGRAPHIC DISTRIBUTION. — Ladakh, northwestern Himalaya of India, Phetchaburi Province of Thailand.

AGE. — Late Oligocene.

EMENDED DIAGNOSIS. — Species slightly larger and significantly more hypsodont than *Fallomus quraishyi* Marivaux & Welcomme, 2003. It differs from *F. razae* Flynn, Jacobs & Cheema, 1986, *F. ginsburgi* Marivaux & Welcomme, 2003 and *F. quraishyi* in lacking the anterocingulid on molars, and in having more protruding labial and lingual cuspids that merge in generating a fully transverse bilophodont dental pattern. It differs from the previous species plus *Diatomys* Li, 1974 in showing the entoconid of both premolars and molars anteriorly displaced with respect to the hypoconid, cuspids less anteriorly inclined, and in having an enlarged hypoconulid twinned with the hypoconid, thus forming a small third posterior loph.

DESCRIPTION

Dental material

Lower premolar. The p4 is rectangular in outline and it is characterized by a strong anteroconid situated anteriorly between the protoconid and metaconid. This tooth is more labiolingually compressed on SHM-CP 250 (Fig. 3C) than on SHM-CP 353 (Fig. 3A). The hypoconid is the smallest cuspid of the tooth and connects both the inflated entoconid and the strong hypoconulid in a moderate stage of wear. The ectostylid is more salient on SHM-CP 353 than on SHM-CP 250.

First and second lower molars. m1 and m2 are similar in shape (oval-shaped) and in overall morphology, except that m2 is slightly larger (Table 1) than m1, and shows an entoconid more anteriorly displaced with respect to the hypoconid. Both teeth have protruding labial (protoconid and hypoconid) and lingual (metaconid and entoconid) cuspids that merge labiolingually in generating a transverse bilophodont pattern from the first stages of wear. On the moderately worn and isolated specimen TF 6181 (Fig. 3B), the size of the cuspids can be better appreciated, thus showing that the hypoconid is smaller than the protoconid, metaconid, entoconid, and hypoconulid. There is no posterolophid linking the hypoconid to the hypoconulid. A "false" posterolophid appears artificially after wear by contact between the sides of the inflated hypoconid and hypoconulid, generating a small third posterior loph. On SHM-CP 353 (Fig. 3C), the hypoconulid of m1 and m2 is as large as the protoconid or the entoconid (as on the holotype WINF/A 1706 described by Nanda & Sahni [1998]; Fig. 4B), whereas it is reduced on the m1 of SHM-CP 250 (Fig. 3A). The trigonid and the talonid do not show a significant difference of elevation, and they remain separated by the deeply incised transverse sinusid, which is labiolingually open due to the lack of an ectolophid. The protoconid and the metaconid are linked anteriorly by a metalophulid I that forms the anterior margin of the teeth. The protoconid does not show a development of its posterior arm (metalophulid II absent). The ectostylid, located anterolabially to the hypoconid, is nearly indistinct on the m2 of SHM-CP 250 (Fig. 3A), whereas it is very prominent on its m1, and on both teeth of SHM-CP 353 (Fig. 3C).

Third lower molar. The m3 of SHM-CP 250 (Fig. 3A) is the largest tooth of the toothrow (Table 1). This tooth is morphologically similar to m2, but differs in showing a larger hypoconu-

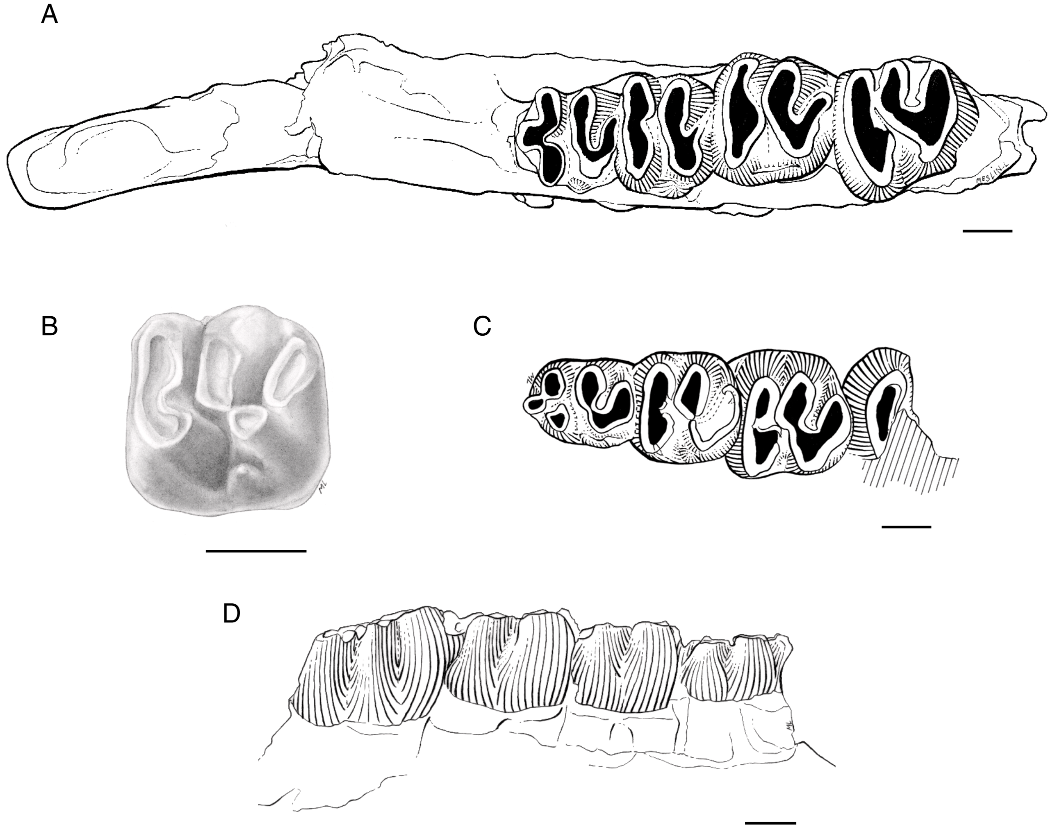

FIG. 3. — *Fallomus ladakhensis* Nanda & Sahni, 1998 from Nong Ya Plong, Thailand; **A**, SHM-CP 250, left mandible with p4-m3; **B**, TF 6181, left m1; **C**, SHM-CP 353, left mandible with p4-m2 (m3 broken); **D**, labial view of SHM-CP 250. Scale bars: 1 mm. Drawings by Laurence Meslin (ISEM).

lid that forms, in association with the hypoconid, a posterior lobe on the talonid (as on WINF/A 1707 described by Nanda & Sahni [1998]; Fig. 4A). Compared with m2, the entoconid is more anteriorly located with respect to the hypoconid and it is nearly twinned with the metaconid but separated from it by a shallow groove corresponding to the labiolingually opened sinusid.

Incisor enamel microstructure

A fragment of incisor was removed from the mandible SHM-CP 353 (Fig. 5A) and embedded in artificial resin. The fragment was subsequently polished longitudinally, then etched for 30 sec with H_3PO_4 (37%) to make microstructural details visible. The specimen was examined under the scanning electron microscope at different resolutions (Fig. 5B-D).

In longitudinal section, the total enamel thickness is about 205 mm with 86% representing the portio interna (PI, inner region). The portio externa (PE, outer region), with radial enamel, is indeed very thin (Fig. 5B). The PI consists of decussating layers of prisms appearing as Hunter-Schreger bands (HSB), 3-4 prisms wide per band (Fig. 5C). The straight HSB are inclined at 50° to the enamel-dentine junction (EDJ). There is no well marked transition zone between adjacent decussating HSB. The interprismatic matrix (IPM) in the PI is thin and never surrounds the

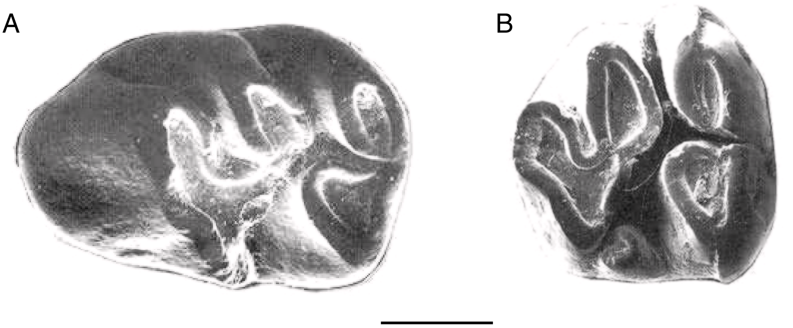

Fig. 4. — *Fallomus ladakhensis* Nanda & Sahni, 1998 from the Wakka Chu section, Ladakh, India; **A**, WINF/A 1707, right m3; **B**, WINF/A 1706, right m2 (holotype). Scale bar: 1 mm.

prisms but appears as interrow sheets running at a high angle (> 80°, nearly rectangular) to the prism direction and anastomozing only rarely between the prisms (Fig. 5C, D). Such a crystallite arrangement in PI determines typical multiserial enamel (Korvenkontio 1934). The pattern of the IPM arrangement further typifies a derived multiserial condition designated as multiserial subtype III (see Martin 1994).

COMPARISONS

The dental morphology of both upper and lower teeth of the Oligo-Miocene Diatomyidae is primary characterized by the absence of transverse and longitudinal crests, the occurrence of an enterostyle and an ectostylid at the posterior lingual and labial margins of the internal sinus and external sinusid, respectively, and by the development of inflated cusps and cuspids that usually merge labiolingually in generating a transverse bilophodont occlusal pattern. *Fallomus ladakhensis* differs substantially from the other species of the genus (*F. razae*; *F. ginsburgi*; *F. quraishyi*; early Oligocene) and *Diatomys* (early middle Miocene; Li 1974; Mein & Ginsburg 1985, 1997) in showing a tendency to the acquisition of a trilophodont pattern on lower teeth as a result of the prominent development of the hypoconulid (Figs 3; 4; 6B). Although lacking in *Diatomys* (Fig. 6A), the hypoconulid occurs, however, in *F. razae*, *F. ginsburgi* and *F. quraishyi*, but it is moderately developed (as high as the ectostylid), or strongly reduced to nearly indistinct on some specimens (Fig. 6C-E). Such a strong and unequivocal development of the hypoconulid in *F. ladakhensis* is associated with the anterior displacement of the entoconid, notably on m3, which is very close to the metaconid (Figs 3A; 6B). The entoconid is labiolingually opposed to the hypoconid in *Diatomys* and only slightly anteriorly displaced in the other species of *Fallomus* whatever the degree of development of the hypoconulid. *F. ladakhensis* differs significantly from the other early Oligocene species of the genus in having teeth clearly hypsodont (Fig. 3D). For instance, the ratio (R) of height to length of the moderately worn m1 (TF 6181) of *F. ladakhensis* is about 0.9, almost twice as hypsodont as *F. razae*, *F. ginsburgi* and *F. quraishyi*, which were actually relatively low crowned (R # 0.5). *Diatomys liensis* Mein & Ginsburg, 1985 appears also clearly high crowned with respect to the early Oligocene *Fallomus* forms, but compared with *F. ladakhensis*, it remains relatively less hypsodont (R # 0.7). *F. ladakhensis* also differs from the early Oligocene forms in the crystallite arrangement of the incisor enamel microstructure. In *F. ladakhensis*, the IPM organizes in interrow sheets running at a high angle (> 80°, nearly perpendicular) to the prism direction and anastomozes only rarely between the prisms (multiserial subtype III). Such an organization is substantially different from that observed for example in *F. ginsburgi* (Fig. 7A, B), where the IPM runs at an acute

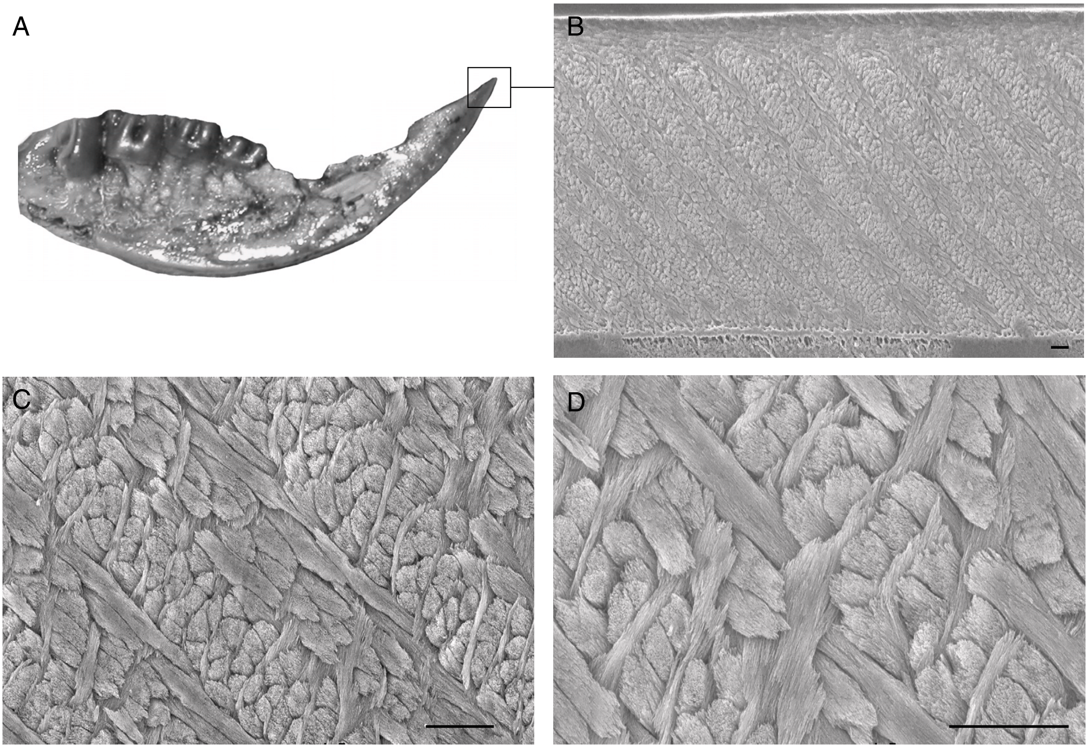

FIG. 5. — Scanning electron photomicrographs of the incisor enamel microstructure of SHM-CP 353, showing multiserial Hunter-Schreger bands (HSB); **A**, area of analysis on the lower incisor of SHM-CP 353; **B**, total enamel width showing the reduced portio externa; **C**, portio interna showing decussating HSB with 3-4 prism layer wide per band; **D**, detail of C showing the thin interprismatic matrix that runs at a high angle (> 80°) to the prism direction and anastomozes only rarely. Scale bars: 10 µm.

angle to the prism direction and anastomozes regularly between the prisms (multiserial subtype II). In terms of biomechanics, the crystallite arrangement typifying the subtype III is more efficient for strengthening the enamel in the third dimension. As a result, the subtype III is generally considered as the most derived state of multiserial HSB (Martin 1994). In that respect, regarding the incisor enamel microstructure, *F. ladakhensis* is more advanced evolutionarily than *F. ginsburgi.* In contrast, the enamel microstructure of *F. ladakhensis* is very close to that observed in the incisors attributed to *Diatomys liensis* from the early middle Miocene (Fig. 7C, D), in having the same number of prisms per HSB, and in showing the same degree of complexity of the IPM (i.e. organization and orientation). *F. ladakhensis* lacks, however, the transition zones between HSB, which are clearly visible in *Diatomys* (Fig. 7C). In *Diatomys*, the prisms are more steeply inclined than the bands and they bend apically from one HSB to the next, thus generating transition zones.

DISCUSSION

SYSTEMATIC AND BIOCHRONOLOGICAL IMPLICATIONS

The genus *Fallomus* was originally described by Flynn *et al.* (1986) from isolated teeth discovered in detrital deposits of the lower Chitarwata Formation in the Bugti Hills (Sulaiman geological Province of eastern Balochistan, Pakistan) – deposits erroneously established as early Miocene by Raza & Meyer (1984). The systematic status of *Fallomus*, initially considered as Chapattimyidae *incertae sedis* (*Fallomus razae*), has been widely questioned (Mein & Ginsburg 1997; Flynn 2000; Marivaux *et al.* 2002a; Marivaux & Welcomme 2003). As a matter of fact, the recent discovery of a richly fossiliferous locality in the Bugti Hills (Paali DBC2), having yielded numerous and additional specimens of *Fallomus*, notably teeth of two new species (*F. ginsburgi* and *F. quraishyi*, Marivaux & Welcomme 2003), has allowed to clarify the systematic status of the genus. *Fallomus* is now formally included among the Diatomyidae (Marivaux *et al.* 2002a; Marivaux & Welcomme 2003), as it had been previously suspected by Flynn *et al.* (1986) and hypothesized by Mein & Ginsburg (1997). The well diversified mammal assemblage of the Paali locality in the Bugti Hills has allowed revision of the age attributed to the classic rodent fauna, which is in fact early Oligocene instead of early Miocene (Marivaux *et al.* 1999, 2000; Welcomme *et al.* 2001). The reinterpretation of the Bugti biostratigraphy, notably the lowermost part of the Chitarwata Formation, providing an accurate age for *F. razae*, *F. quraishyi*, and *F. ginsburgi*, is particularly significant in extending back to the early Oligocene the stratigraphic range of the Diatomyidae, which were artificially limited to the early Miocene. *F. ladakhensis* was first described from few dental specimens found in the purple red mudstone of the Wakker Chu section of the Kargil Formation in Ladakh (north-western Himalaya of India; Nanda & Sahni 1998). The precise age of these deposits is still discussed but generally considered to be late Oligocene to early Miocene (i.e. pre-Siwalik) on the basis of plants, charophytes, molluscs, spores and pollen evidence, and faunal comparisons (for details see Nanda & Sahni 1990; Kumar *et al.* 1996; Nanda & Sahni 1998). As previously mentioned by Kumar *et al.* (1996) and Nanda & Sahni (1998), *F. ladakhensis* from Kargil is noticeably more advanced morphologically with respect to its relatives from Pakistan (lower Chitarwata Formation of the Bugti Hills) in having a larger size, a significantly higher-crowned nature of its molars, and, as we have shown with the new specimens described here, in showing a more derived incisor enamel microstructure. These morphological characteristics clearly indicate that the Kargil rodents are appreciably younger in age than those from the Bugti Hills. Concerning the age of the new Thai fossiliferous locality from the lignite deposits of Nong Ya Plong, the occurrence of *F. ladakhensis* constrains an Oligo-Miocene age for these deposits. However, a late Oligocene age could be advanced given that *F. ladakhensis* occurs in association with a second upper premolar of a rhinocerotid, which is referable to *Diaceratherium* cf. *lamilloquense* (Antoine pers. comm. 2003). This latter taxon was so far restricted to the late Oligocene of western Europe (Brunet *et al.* 1987). In that respect, *F. ladakhensis* is critical for better understanding the evolutionary history of the Diatomyidae since it occupies an intermediary temporal position between the early Oligocene Bugti species of *Fallomus* and the early-middle Miocene species of *Diatomys*. Nevertheless, even though *F. ladakhensis* appears more primitive than *Diatomys* in some characters such as the enlarged hypoconulid (lost in *Diatomys*) forming a small third posterior loph of both premolars and molars, the entoconid more anteriorly displaced with respect to the hypoconid, the cuspids more inflated and less anteriorly inclined, and the large m1 (reduced in *Diatomys*), considering the molar crown height alone, *F. ladakhensis* could be viewed as more advanced evolutionarily than *Diatomys* in showing teeth slightly more hypsodont. A trilophodont dental pattern (bilophodont in *Diatomys*) associated with a greater molar crown height in *F. ladakhensis* may reflect adaptation to a particular diet distinct from that of *Diatomys*. However, the incisor enamel microstructure of both *F. ladakhensis* and *Diatomys* is not significantly different, and both taxa exhibit the most derived subtype of multiserial HSB (subtype III), which is efficient for strengthening the enamel in the third dimension.

DIATOMYIDAE AND PEDETOIDEA: A PLAUSIBLE RELATIONSHIP?

The family Diatomyidae (initially monogeneric) was erected in 1997 by Mein & Ginsburg for the

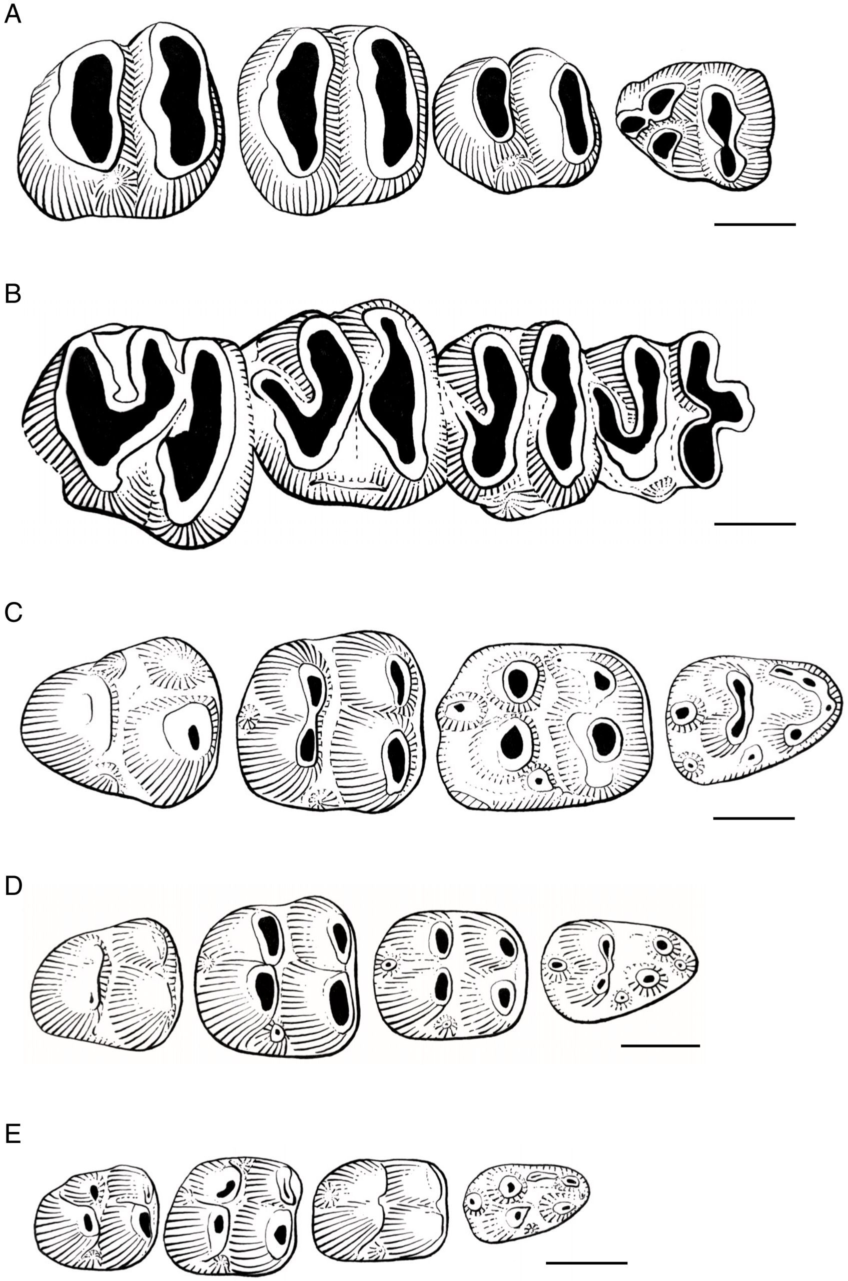

FIG. 6. — Schematic drawings comparing the lower dentition of different species of Diatomyidae; **A**, right m3-m1 and left p4, *Diatomys liensis* Mein & Ginsburg, 1985 from Li, Thailand (Mein & Ginsburg 1985); **B**, left p4-m3, *Fallomus ladakhensis* Nanda & Sahni, 1998 (SHM-CP 250 reversed) from Nong Ya Plong, Thailand; **C**, *Fallomus quraishyi* Marivaux & Welcomme, 2003 (right m3 DBC 452, right m2 DBC 455, right m1 DBC 457, dp4 right DBC 458) from the early Oligocene of the Bugti Hills, Pakistan (Marivaux & Welcomme 2003); **D**, *Fallomus ginsburgi* Marivaux & Welcomme, 2003 (right m3 DBC 508, right m2 DBC 528, right m1 DBC 550, right dp4 DBC 568) from the early Oligocene of the Bugti Hills, Pakistan (Marivaux & Welcomme 2003); **E**, *Fallomus razae* Flynn, Jacobs & Cheema, 1986 (left m3 DBC 1181 [reversed], left m2 DBC 1162 [reversed], left m1, left dp4 DBC 1174 [reversed]) from the early Oligocene of the Bugti Hills, Pakistan (Marivaux & Welcomme 2003). Scale bars: 1 mm. Drawings by Laurence Meslin (ISEM).

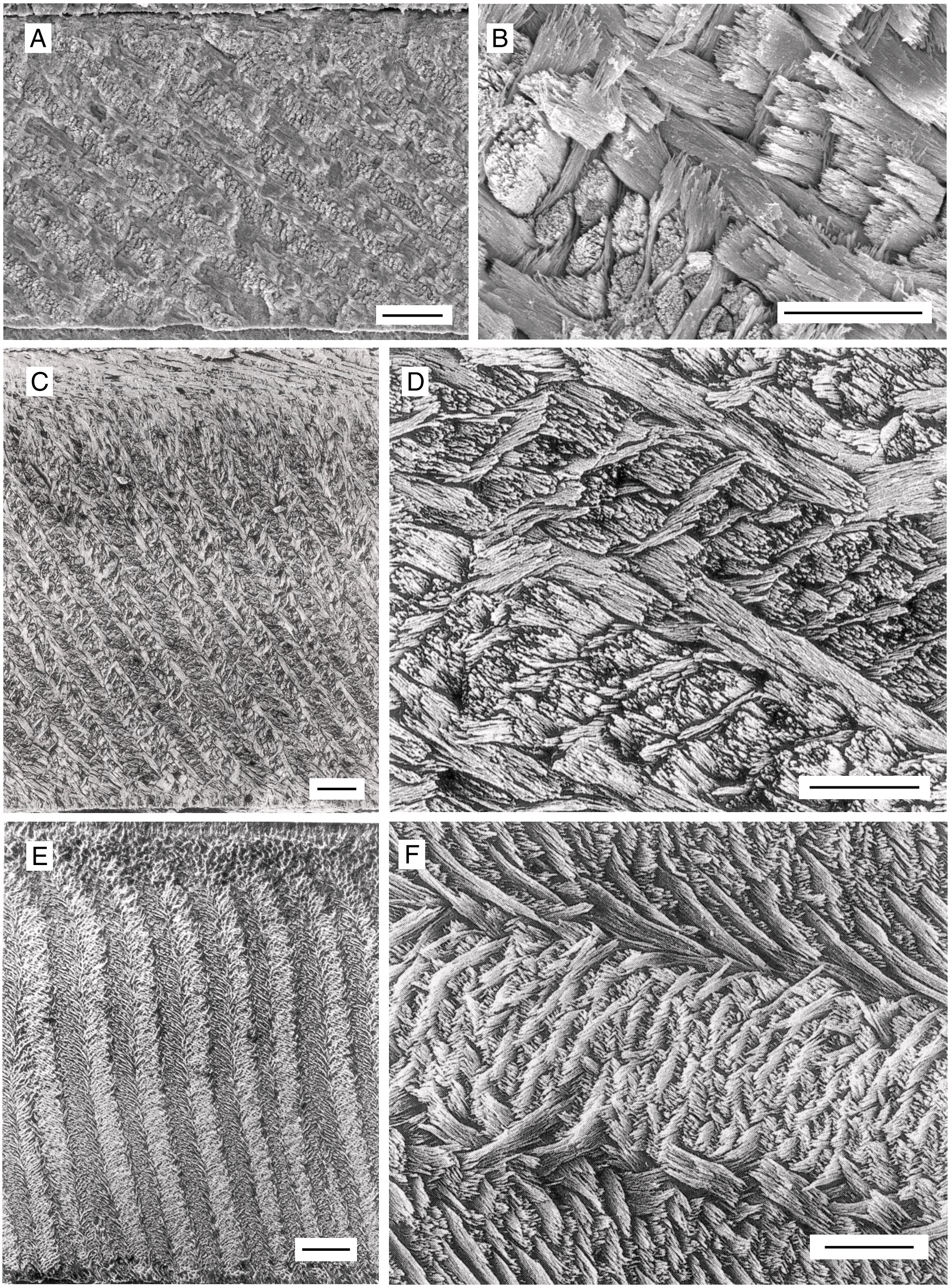

FIG. 7. — Scanning electron photomicrographs of the incisor enamel microstructure; **A**, **B**, cf. *Fallomus* Flynn, Jacobs & Cheema, 1986 from the early Oligocene of the Bugti Hills, Pakistan (Marivaux 2000); **C**, **D**, cf. *Diatomys liensis* Mein & Ginsburg, 1985 from the early middle Miocene of Mae Long, Thailand (Martin 1995); **E**, **F**, *Megapedetes pentadactylus* MacInnes, 1957 from the early Miocene of Rusinga, Kenya (Martin 1995). Scale bars: A, C, E, 30 µm; B, D, F, 10 µm.

different species of the genus *Diatomys* (*D. shantungensis* Li, 1974; *D. liensis*; *Diatomys* sp. [Jaeger *et al.* 1985]) from the early to middle Miocene of South Asia (Pakistan, Thailand, China, Japan), and possibly *Fallomus*. On the basis of its simplified bilophodont dental pattern, *Diatomys* was originally described as a "probable geomyoid" (Li 1974), then later placed in or considered closely related to the Pedetoidea (*sensu* McKenna & Bell 1997; including *Megapedetes* MacInnes, 1957, *Parapedetes* MacInnes, 1957, and *Pedetes* Illiger, 1811) owing to the apparently similar tooth morphology (Mein & Ginsburg 1985; Flynn *et al.* 1986), the development of multiserial incisor enamel (Martin 1997; Fig. 7E, F), and a sciurognathous mandible. Such a relationship is still questioned since the Pedetoidea (*Megapedetes*, *Parapedetes*) were already well established in the Miocene of Africa (e.g., MacInnes 1957; Walker *et al.* 1969), and *Diatomys* did not have the saltatorial adaptations observed on extant pedetids (Mein & Ginsburg 1997). In that respect, could the Pedetoidea share a common Paleogene ancestor with the Diatomyidae? There is actually no paleontological evidence for strongly substantiating such a phylogenetic hypothesis. From dental evidence, the Diatomyidae could be closely related to the Ctenodactylidae, Chapattimyidae, Yuomyidae, and the Hystricognathiformes (e.g., Mein & Ginsburg 1997; Marivaux *et al.* 2002a, in press a and b), which are Paleogene groups of rodents descended from the earliest "ctenodactyloid rodent" radiation in Asia. However, the precise phylogenetic position of the Diatomyidae with respect to these Asian groups is unclear since there is no pre-Oligocene fossil record of diatomyids. There is, indeed, an important morphological hiatus between the dental pattern of the early Oligocene species of *Fallomus* and that of the known middle or late Eocene related rodent groups of Asia. The evolutionary history of the Pedetoidea is poorly documented as well. They have a limited fossil record extending back to the early middle Miocene of Africa (e.g., MacInnes 1957; Walker *et al.* 1969). Both fossil (limited to *Megapedetes* and *Parapedetes*) and living species (*Pedetes*) exhibit a highly derived dental pattern (bilobed), which is autapomorphic and therefore particularly difficult to compare with other rodent groups (Luckett & Hartenberger 1985). As a matter of fact, the higher phylogenetic relationships of the Pedetoidea among Rodentia have been assessed primarily by considering molecular and morpho-anatomical aspects of the single modern form (*Pedetes*, Pedetidae). Their phylogenetic position is still widely disputed. Although some morpho-anatomical features (George 1985; Luckett 1985) and the enamel incisor microstructure (Martin 1995) tend to support a sister group relationship between the Pedetidae and the Ctenodactylidae (and by extension the Diatomyidae), molecular data (Montgelard *et al.* 2000, 2002; Huchon *et al.* 2002) and some characters of the middle-ear (Lavocat & Parent 1985) or the carotid arterial pattern (Bugge 1985), instead consistently support a sister group relationship between the Pedetidae and the Anomaluridae (Anomaluroidea + Pedetoidea: Anomaluromorpha *sensu* McKenna & Bell 1997). This latter phylogenetic viewpoint conflicts with Diatomyidae-Pedetoidea relationship inasmuch as Diatomyidae-Anomaluridae association is highly unparsimonious (Marivaux *et al.* 2002a, in press a and b). The Diatomyidae would be therefore an independent group, which probably extinguishes in Asia by the end of the middle Miocene (see Flynn *et al.* 1995; Flynn 2000).

PALEOENVIRONMENTAL IMPLICATIONS

The development of lophodont and moderately hypsodont teeth in both *F. ladakhensis* and *Diatomys* probably provided more efficiency in grinding abrasive foods (e.g., Butler 1985), which is more likely to be expected in fairly arid environments. However, the degree of hypsodonty exhibited by these taxa is not as important as that developed in certain Late Paleogene rodent lineages, such as the theridomyids from western Europe (e.g., Vianey-Liaud & Ringeade 1993). For these European rodents, a parallel is clearly established between the degree of hypsodonty (increasing) and the environmental changes related to the major climatic deteriorations that have been primarily recorded during the late Eocene-early Oligocene interval (e.g., Vianey-Liaud 1991). The contrast in crown height observed between the early Oligocene and late Oligocene species of *Fallomus*, but also with the early-middle Miocene species of *Diatomys*, is significant, and it may reflect exploitation of limited open habitat or a change in the environmental conditions during that time interval. In representing the single early Oligocene locality of South Asia, the well diversified faunal assemblage from Pakistan (Paali DBC2), in which the low-crowned species of *Fallomus* are reported (Marivaux & Welcomme 2003), is particularly informative in terms of paleoenvironment, because it suggests warm and humid environmental conditions at this period. Indeed, this locality contains mainly micro- and medium-sized mammals, such as small prosimian and anthropoid primates (Marivaux *et al.* 2001, 2002b), lophiomerycid and tragulid artiodactyls (Métais pers. comm. 2003), dermopterans, petauristine sciurid and anomaluroid rodents (Marivaux 2000, unpublished data), for which their closest living relatives are mostly related to dense forested habitats, notably tropical and subtropical forests. These particular environmental conditions are certainly related to the fact that the paleolatitude of the Bugti Hills *c.* 31 Ma was *c.* 14° farther south than in recent times (i.e. 15°N) due to the northward drift of the Indian Plate (e.g., Mattauer *et al.* 1999). However, the strong faunal similarity during the late Eocene/early Oligocene interval among Pakistan, southern China and peninsular Thailand mammal localities (e.g., Ducrocq *et al.* 1995a; Qi & Beard 1998; Marivaux *et al.* 2000, 2002a, b) suggests the existence of a wide South Asian faunal province (Antoine *et al.* 2003), which was probably under quite similar climatic conditions at this period. By contrast, the mammal compositions reported from the late Oligocene deposits of the Bugti Hills, mainly represented by macromammals thus far (perissodactyls, Antoine *et al.* 2003; artiodactyls, Métais *et al.* 2003), are locally indicative of drier and more open environments at this period, whereas those from Kargil (primarily composed of traguloid artiodactyls and *F. ladakhensis*) would be rather still indicative of forested habitats. In that context, *F. ladakhensis* probably lived in such paleoenvironmental conditions but in area, however, characterized by limited open habitat. The evidence of a dominant forested habitat is supported by the mammal fauna associated with *F. ladakhensis* in Nong Ya Plong (unpublished data). The occurrence in this locality of dermopterans (flying lemurs), which nowadays live in equatorial, tropical and subtropical rain forests of Southeast Asia (Thailand, Indonesia, etc.), but also of a browser rhinocerotid (Antoine pers. comm. 2003), and megachiropterans, clearly indicates that the late Oligocene paleoenvironment in Nong Ya Plong was certainly forested, at least locally, with a climate probably still warm and relatively humid. The paleoenvironment inferred for the early-middle Miocene localities of Thailand (Mae Long, Li Basin) in which *Diatomys* occurred, seems to have been in contrast more open, and small areas of forests were probably intermixed with grassland under a tropical climate (see Ducrocq *et al.* 1994) – conditions that were seemingly identical to those estimated in northern Pakistan from the roughly coeval fauna of the lower Siwalik (Ducrocq *et al.* 1994). The fossiliferous localities in South Asia remain still scarce for the end of the Paleogene period. However, the few paleontological evidences from Thailand, China, Myanmar and Pakistan, although incomplete, provide the only glimpse into the evolutionary history of several mammal groups. The composition of the mammalian communities across time is closely related to the evolution of paleoenvironmental conditions, which clearly changed in some parts of South Asia between the early Oligocene and the early Miocene. The Paleogene/Neogene transition is indeed particularly significant in South Asia in terms of climatic changes. It is well established that the important paleogeographic and geomorphological changes in this area, mostly related to the India-Eurasia collision (i.e. retreat of the Paratethys Sea and accentuation of the Himalayan orogeny), have reformed the atmospheric circulation in involving climatic deterioration (Ramstein *et al.*

1997; Fluteau *et al.* 1999). Paleontological investigations in the Oligocene of South Asia have therefore great potential to enlighten both mammal and climate evolution during this critical period.

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