# The role of Asia in the origin and diversification of hystricognathous rodents

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Marivaux, L., Vianey-Liaud, M., Welcomme, J.-L. & Jaeger, J.-J. (2001). The role of Asia in the origin and diversification of hystricognathous rodents. — *Zoologica Scripta*, *31*, 225–239.
In the absence of a comprehensive pre-Oligocene fossil record, the origin and early evolution of hystricognathous rodents have long been the subject of much uncertainty. Baluchimyinae (Rodentia) were initially interpreted as a subfamily of the ctenodactyloid Chappatimyidae (sciurognathous), a group considered to be endemic to the Indian subcontinent and to be closely related to hystricognathous rodents. A newly discovered early Oligocene hystricognathous rodent, *Bugtimys zafarullahi* gen. n. et sp. n., described herein, from the Bugti Hills (Balochistan, Pakistan) sheds new light on the higher level taxonomy of the previously described Baluchimyinae. As a contribution to the phylogenetic debates regarding the origin of Hystricognathi, we present a cladistic assessment of the dental evidence for the Palaeogene hystricognathous rodent cladogenesis. Our phylogenetic results consistently support the monophyly of the Hystricognathiformes clade (including Tsaganomyidae plus Hystricognathi) of which baluchimyine rodents are clearly members. There is, however, no support for the monophyly of a baluchimyine clade. Nonetheless, 'baluchimyines' are for the moment reinterpreted as Hystricognathi *incertae sedis*. Hystricognathous rodents appear to be well diversified at least since the early Oligocene, both in Africa and South America (phiomorphs and caviomorphs, respectively), and also now in south Asia. Furthermore, our phylogenetic results support close relationships between early hystricognathous and Asian 'ctenodactyloid' rodents, which clearly points to an Asian origin for Hystricognathi. In this phylogenetic framework, 'baluchimyines' and tsaganomyids are representatives of an initial phase of diversification of hystricognathous rodents in Asia. Oligocene phiomorphs and caviomorphs (sister groups) seem therefore to share a common 'Asian' hystricognathous ancestor. This reinforces the possibility that the early dispersal of hystricognathous rodents to South America was not from Africa but from Asia.
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## Introduction

Tullberg's (1899) long-standing classification of Rodentia comprises the two suborders Sciurognathi and Hystricognathi, identified using the angle of the jaw relative to the plane of the incisors. Although the monophyly of extant Hystricognathi (e.g. porcupines, chinchillas, guinea-pigs, ... ) is now accepted and well defined by morpho-anatomical (e.g. Luckett & Hartenberger 1993) and molecular (Nedbal *et al.* 1996; Huchon *et al.* 2000; Mouchaty *et al.* 2001; Murphy *et al.* 2001) characters, and also supported by endoparasite studies (Hugot 1999), questions about their phylogenetic and palaeobiogeographical origins still exist. Hystricognathous rodents exhibit a widespread Old and New World distribution at least since the early Oligocene, represented by the two

biogeographically circumscribed taxa, the African Phiomorpha (*sensu* Lavocat 1962, 1973) and the South American Caviomorpha (*sensu* Wood 1955). However, in the absence of a comprehensive pre-Oligocene fossil record for hystricognathous rodents, such an Oligocene distribution on two widely separated land masses is still debatable regarding palaeogeography and dispersal models. Palaeobiogeographical affinities of this group first focused on their putative origin from the primitive European Paramyidae (Wood 1968), the North American 'Franimorpha' (e.g. Wood 1972; for which an 'incipient hystricognathy' was reported on some taxa, but unrecognized by Dawson 1977 and Korth 1984) or the Palaeogene European 'Theridomorpha' (Lavocat 1969, 1980). Wood (1974) suggested that South American and African

hystricognathous rodents presented disjunctive patterns of evolution from an ancestral North American stock (the Eocene franimorphs), which independently dispersed into South America and into Africa via Asia. In contrast, Lavocat (1973, 1974, 1976) assumed that Phiomorpha and Caviomorpha originated from a common African ancestor and proposed Africa as the most likely source of hystricognathous rodent colonizers to South America, via a trans-Atlantic sweepstake route. Subsequent discoveries in Asia of Eocene Ctenodactyloidea rodents, particularly the Chapattimyidae from the Indian subcontinent, have led some authors (Hussain *et al.* 1978; Jaeger *et al.* 1985; de Bruijn 1986; Flynn *et al.* 1986; Jaeger 1988) to propose close relationships of ctenodactyloid Chapattimyidae to hystricognathous rodents. As a working hypothesis, Hussain *et al.* (1978) suggested that Chapattimyidae were the ancestral group for Phiomorpha and for Caviomorpha. These Asian ctenodactyloid rodents reached north Africa during the late Eocene (as supported by Jaeger *et al.* 1985), but also presumably South America via North America by way of the Bering Strait route — in agreement with Wood's hypothesis for a North American origin of caviomorphs. However, the fossil record has so far failed to provide palaeontological evidence of the occurrence of chapattimyid-like ctenodactyloid rodents in North America. In fact, the sister group hypothesis of Ctenodactyloidea with Hystricognathi has not been strongly supported by fossils (Hartenberger 1985; Wood 1985; Wang 1997). There is actually only limited dental palaeontological evidence, and the unfortunate lack of mandibule material means that there is no test for such a presumptive phylogenetic hypothesis. However, the Ctenodactyloidea–Hystricognathi affinities have been substantiated by a set of morpho-anatomical (Bugge 1985; George 1985; Luckett 1985; Meng 1990; Martin 1993, 1994, 1997; Bryant & McKenna 1995) and molecular (e.g. Huchon *et al.* 2000) studies, which strongly support the sister group relationship between extant Ctenodactylidae (ctenodactyloids) and Hystricognathi (the Ctenohystrica, *sensu* Huchon *et al.* 2000).

Rodents from the Bugti Hills and the Zinda Pir Dome in Pakistan (Flynn *et al.* 1986; Flynn & Cheema 1994) were originally considered to represent a distinctive group of early Miocene rodents, the Baluchimyinae, that radiated on the Indian subcontinent during the mid-Cainozoic from 'autochthonous evolution' of the Eocene ctenodactyloid Chapattimyidae. In spite of the initial uncertainty about their age (now considered to be early Oligocene rather than early Miocene; Welcomme & Ginsburg 1997; Marivaux *et al.* 1999, 2000; Welcomme *et al.* 2001), baluchimyines have consistently been regarded as a group possibly closely related to the hystricognathous rodents. From several advanced dental features, these Pakistani rodents have been suspected to represent a potential near outgroup of hystricognathous rodents,

more specifically related to the primitive African thryonomyoids (Flynn *et al.* 1986; Jaeger 1988; Flynn & Cheema 1994). Furthermore, Bryant & McKenna (1995) have subsequently suggested that baluchimyines might be a member of Hystricognathiformes, a taxon including extant Hystricognathi and Tsaganomyidae (an extinct family considered as the 'nearest outgroup of hystricognathous rodents' mainly on the basis of the middle ear structure and the lower jaw condition). However, the critical lower jaw character (hystricognathy) has not been previously evaluated for available baluchimyine material.

Recent field expeditions in the early Oligocene deposits of the Bugti Hills (Balochistan, Pakistan) have led to the discovery of a diverse assemblage of fossil vertebrates (Paali locality), including terrestrial micromammals (carnivores, chiropteres, insectivores, primates and rodents, plus marsupials) and medium-sized macromammals (artiodactyls and perissodactyls). These terrestrial fossils are associated with aquatic, marine and deltaic vertebrates (fishes, selachians, reptiles, chelonians, … ). We report here the discovery of a new early Oligocene hystricognathous rodent, *Bugtimys zafarullahi* gen. et sp. n. This specimen has profound implications for the phylogenetic and systematic status of Baluchimyinae (Flynn *et al.* 1986), and consequently for the evolutionary history of early hystricognathous rodents. As a contribution to the phylogenetic and palaeogeographical debates for the origin of hystricognathous rodents, we present here a cladistic assessment of the dental evidence for the Palaeogene hystricognathous rodent cladogenesis in a higher systematic context. Our results are discussed with special emphasis on palaeobiogeographical implications.

## Systematic palaeontology

Order RODENTIA Bowdich, 1821
Infraorder Hystricognathi Tullberg, 1899

### Genus *Bugtimys* gen. n.

*Type species.* B. zafarullahi sp. n.
*Type locality.* Paali Nala C2 (Bugti Hills, Balochistan, Pakistan).
*Formation and age.* Bugti Member, Lower Chitarwata Formation, early Oligocene.
*Etymology.* The name derives from the Bugti tribes.

*Diagnosis.* Large hystricognathous rodent characterized by a pronounced pentalophodont pattern with cusps still differentiated, by the development of a metalophular spur on the upper molars, a reduced metaconule, a strong and oblique protocone, a well-developed posterior arm of the paracone which joins a labial mesostyle connected to the long median mesolophule, a deep and shallow sinus labially and partially closed by an incipient mure, a complete metalophulid II
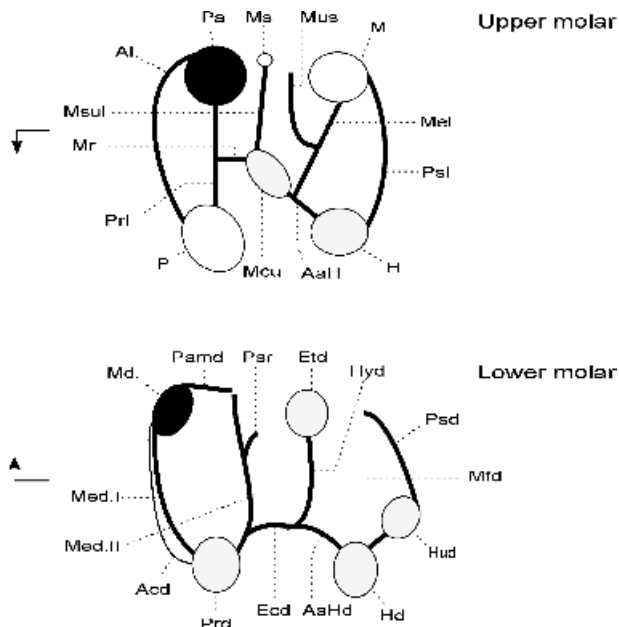
**Fig. 1** Terminology used for hystricognathous rodent molars (after Wood & Wilson 1936). *Upper molars*: P, protocone; Prl, protoloph; Mr, mure; Msul, mesolophule; Al, anteroloph; Pa, paracone; Ms, mesostyle; Mus, metalophular spur; M, metacone; Mel, metaloph; Psl, posteroloph; H, hypocone; AaH, anterior arm of the hypocone; Mcu, metaconule. *Lower molars*: Prd, protoconid; Acd, anterocingulid; Med.II, metalophulid II; Med.I, metalophulid I; Md, metaconid; Pamd, posterior arm of the metaconid; Psr, protospur; Etd, entoconid; Psd, posterolophid; Mfd, metafossettid; Hud, hypoconulid; Hd, hypoconid; AaHd, anterior arm of the hypoconid; Ecd, ectolophid.

which develops a protospur from its median part, a protoconid backwardly positioned with respect to the metaconid and by a low and labially widened anterocingulid on the lower molars (see Fig. 1 for terminology).

### *Bugtimys zafarullahi* sp. n. (Fig. 2A–N)

*Holotype.* DBC 1261, right lower jaw with m2–3 and the incisor (Palaeontology Department, ISEM, University of Montpellier, France; Fig. 2L–N).

*Other material.* 19 dP3 or P3 (1458–1476); 11 left P4 (DBC 404–414); 16 right P4 (DBC 388–403); 3 left dP4 (DBC 385–387); 1 right dP4 (DBC 384); 11 left M1 (DBC 1281–1291); 6 right M1 (DBC 415–417, 1278–1280); 21 left M2 (DBC 1292–1312); 5 right M2 (DBC 1313–1317); 7 left M3 (DBC 1333–1339); 17 right M3 (DBC 1318–1332); 6 left dp4 (DBC 374–379); 4 right dp4 (DBC 380–383); 8 left p4 (DBC 1352–1359); 12 right p4 (DBC 1340–1351); 16 left m1 (DBC 1360–1375); 12 right m1 (DBC 1376–1387); 12 left m2 (DBC 1388–1399); 12 right m2 (DBC 1400–1411); 10 left m3 (DBC 1426–1435); 14 right m3 (DBC 1412–1425); 1 right

P4 (GSP 21548; fig. 20D; Flynn *et al.* 1986); 1 right m3 (GSP 21541; fig. 21D; Flynn *et al.* 1986).

*Etymology.* Named in honour of Zafarullah Khan Baloch, in recognition of his help during the fieldwork in the Bugti Hills.

*Diagnosis.* As for the genus.

### *Description*

Jaw dorsoventrally slender with a short, shallow diastema; masseteric fossa with a strong ventral masseteric ridge extending forwards below the posterior half of the premolar; masseteric ridge ventrolaterally curved into a pronounced but incomplete angular process arising lateral to the plane of the incisor, showing a typical hystricognathous condition; single large mental foramen situated in front of the anterior root of the premolar; ascending ramus and coronoid process not preserved.

Single-cusped and single-rooted dP3 or P3, strongly reduced and developing a circular outline.

dP4 pentalophodont with large protocone and hypocone linked by the remains of a low, longitudinal endoloph; low and normally curved anteroloph, connected anterolabially to the anterior arm of the paracone but unlinked anterolingually to the protocone; inflated metaconule connected to the strong anterior arm of the hypocone; well-developed mesolophule from the metaconule; minute labial mesostyle connected both to the anterior arm of the metacone and to the posterior arm of the paracone to form a low labial wall.

P4 heart-shaped, displaying a peculiar morphology characterized by a reduced to indistinct hypocone, the occurrence of an endoloph, and a double connection of the metaconule to the protocone and the hypocone; mesiodistally compressed metacone and paracone, with the metacone occupying a more labial position; mesolophule never reaching the labial side of the tooth, and often extending backwards towards the lingual side of the metacone; relatively high anteroloph, connected both to the protocone and the paracone; metalophular spur present but often weakly developed.

Similar morphological pattern for M1 and M2, but the hypocone is more labial on M1; oblique protocone representing the largest cusp of teeth; high and curved anteroloph linked to the protocone and the paracone; reduced metaconule connected to the strong, straight anterior arm of the hypocone; high mesolophule reaching a minute labial mesostyle; deep and shallow sinus, labially closed by an incipient longitudinal mure linking the anterolabial side of the metaconule to the median part of the protoloph; metaloph developing in its median part a labially directed metalophular spur which never reaches the labial side of the tooth, but occasionally intercepts the mesolophule in its median part; metalophular spur constituting an incipient sixth transverse crest;
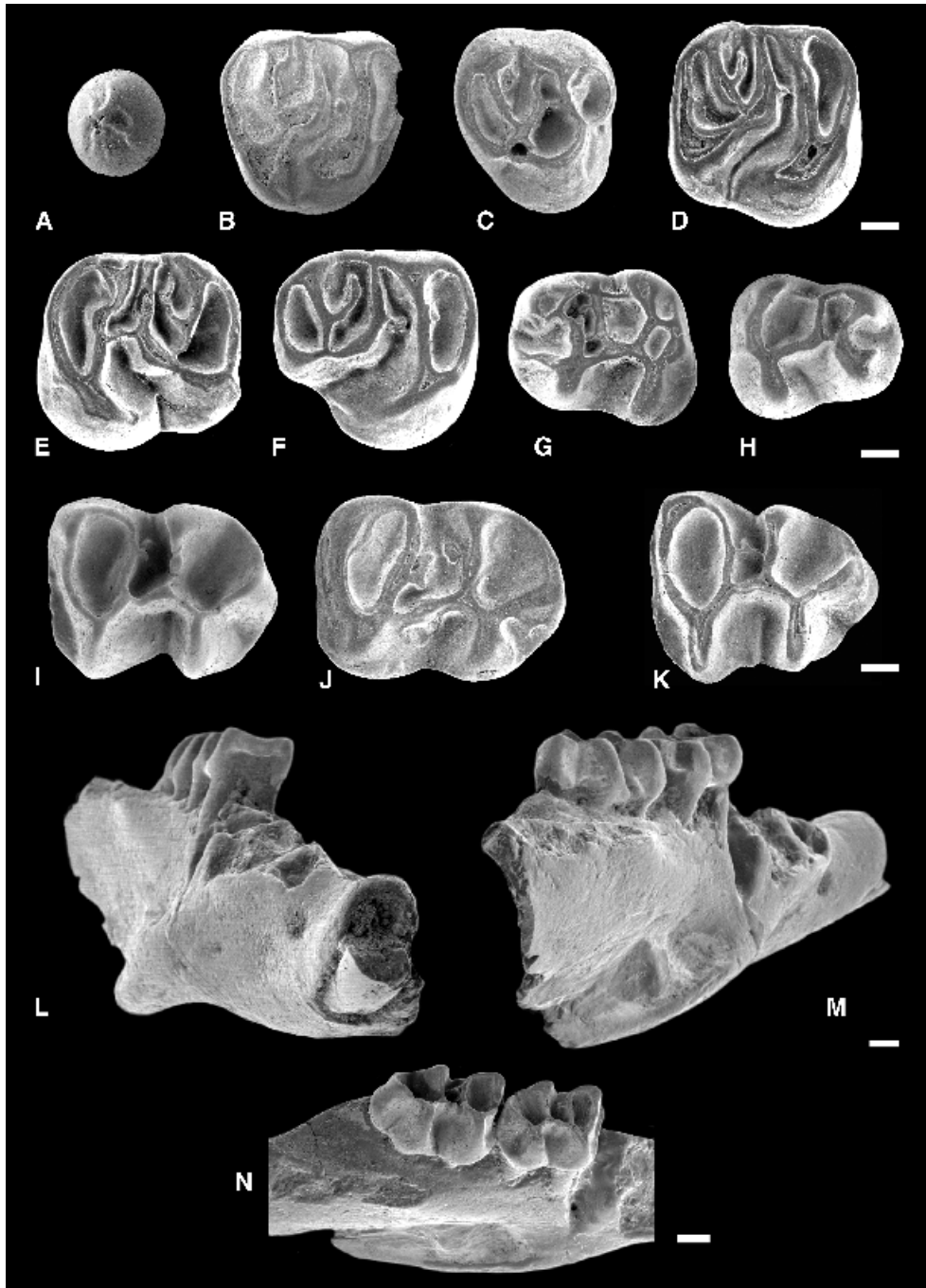
**Fig. 2** A–N. *Bugtimys zafarullahi* gen. n. et sp. n. —A. DBC 1458, dP3 or P3 (1.52 × 1.528). —B. DBC 385, right dP4 (3.099 × 3.132). —C. DBC 402, right P4 (2.59 × 3.039). —D. DBC 415, right M1 (3.148 × 2.959). —E. DBC 1292, left M2 (3.094 × 3.002). —F. DBC 1330, right M3 (3.293 × 3.065). —G. DBC 375, right dp4 (2.916 × 2.31). —H. DBC 1345, left p4 (2.523 × 1.974). —I. DBC 1360, left m1 (3.117 × 2.235). —J. DBC 1388, left m2 (3.931 × 2.752). —K. DBC 1429, left m3 (3.584 × 2.768). —L. DBC 1261, right lower jaw, anterolabial view. —M. DBC 1261, right lower jaw, posterolabial view. —N. DBC 1261, right lower jaw, occlusal view. Scale = 1 mm. Length × width (mm).

strong posterior arm of the paracone usually reaching the labial extremity of the mesolophule; oblique and straight metaloph, always connected to the posterolingual side of the metaconule; high posteroloph linking the hypocone to the metacone; accessory enamel crestules and wrinkles occurring in some cases.

M3 basically similar to M1–2, but differing by a reduced and labially positioned hypocone; longitudinally orientated anterior arm of the hypocone perpendicular to the protoloph; metaconule indistinct; anteroloph, protoloph, mesolophule, metaloph, metalophular spur and posteroloph are all parallel.

dp4 characterized by a trigonid narrower than the talonid; protoconid and entoconid, respectively, opposed to metaconid and hypoconid; large and labiolingually developed hypoconulid; posterolophid unconnected to the entoconid; weak development of the anterocingulid displaying a minute anteroconid; metalophulid I absent; long posterior arm of the protoconid constituting a metalophulid II; complete ectolophid showing a large mesoconid in central position; transverse mesolophid reaching the posterolingually elongated metastylar fold; mesolophid always connected to the metalophulid II by a short protospur stemming from the posterior arm of the protoconid, and isolating (with the ectolophid) a small rounded fovea; mesolophid displaying in its median part, a minute spur extending backwards towards the entoconid; strong, forwardly directed hypolophid, connected to the anterior arm of the hypoconid.

p4 less complex than dp4; indistinct hypoconulid; posterolophid twinned with the entoconid; highly variable hypolophid structure either interrupted labially or absent; longitudinal ectolophid bearing a minute mesoconid; transverse mesolophid reaching the lingual side of the teeth, or medially interrupted; short and low anterocingulid; metalophulid I absent; complete metalophulid II.

m1 and m2 rectangular in outline, but differing in more labial entoconid on m2; well-developed lophodont pattern, with main cuspids still recognizable and subequal in height; low and labially enlarged anterocingulid; protoconid occupying a distal position with regard to the metaconid; posterior arm of the protoconid extending lingually and reaching the metastylar fold to form a complete metalophulid II; metalophulid I and II isolating a vast, oval anterofossettid; protospur always developed on the median part of the metalophulid II, sometimes displaying a bifid posterior extremity, never connected to the hypolophid; entoconid more anteriorly positioned than the hypoconid; straight and transverse hypolophid fusing with the strong anterior arm of the hypoconid; reduced hypoconulid; narrow posterolophid never connected with the entoconid; wide sinusid; mesoconid absent on the ectolophid.

m3 slightly larger than m2, but with a talonid narrower than the trigonid; anterocingulid occupying the entire width of the tooth.

**Table 1** Cheek tooth dimensions for *Bugtimys zafarullahi* gen. n. et sp. n.

| | Length (mm) | | Width (mm) | |
|---|---|---|---|---|
| | Range | $x \pm s$ | Range | $x \pm s$ |
| Right dP4 | 2.71–3.1 | 2.91 ± 0.28 | 3–3.13 | 3.08 ± 0.08 |
| Left P4 | 2.15–2.91 | 2.54 ± 0.22 | 2.71–3.52 | 3.01 ± 0.24 |
| Right P4 | 2.33–2.87 | 2.67 ± 0.30 | 2.74–3.32 | 3.11 ± 0.22 |
| Left M1 | 2.67–3.17 | 2.92 ± 0.17 | 2.6–3.38 | 3.02 ± 0.23 |
| Right M1 | 2.84–3.17 | 3.06 ± 0.12 | 3.08–3.26 | 3.19 ± 0.08 |
| Left M2 | 2.68–3.92 | 3.11 ± 0.32 | 2.78–3.41 | 3.06 ± 0.18 |
| Right M2 | 2.8–3.04 | 2.90 ± 0.17 | 2.92–3.14 | 3.02 ± 0.10 |
| Left M3 | 3.05–3.9 | 3.35 ± 0.32 | 3–3.41 | 3.24 ± 0.14 |
| Right M3 | 2.84–3.33 | 3.17 ± 0.14 | 2.86–3.42 | 3.23 ± 0.15 |
| Left dp4 | 2.63–3.12 | 2.87 ± 0.19 | 2.18–2.54 | 2.36 ± 0.13 |
| Right dp4 | 2.77–2.95 | 2.88 ± 0.10 | 2.12–2.4 | 2.31 ± 0.16 |
| Left p4 | 2.62–3.1 | 2.81 ± 0.18 | 2.13–2.52 | 2.36 ± 0.13 |
| Right p4 | 2.6–3.13 | 2.81 ± 0.17 | 2.15–2.67 | 2.33 ± 0.16 |
| Left m1 | 2.83–3.4 | 3.16 ± 0.20 | 2.32–2.61 | 2.46 ± 0.09 |
| Right m1 | 3–3.4 | 3.19 ± 0.13 | 2.32–2.55 | 2.45 ± 0.09 |
| Left m2 | 3.33–3.95 | 3.56 ± 0.21 | 2.65–2.89 | 2.74 ± 0.08 |
| Right m2 | 3.24–3.62 | 3.42 ± 0.10 | 2.41–2.73 | 2.59 ± 0.10 |
| Left m3 | 3.47–3.95 | 3.69 ± 0.15 | 2.5–2.98 | 2.76 ± 0.17 |
| Right m3 | 3.33–3.98 | 3.61 ± 0.18 | 2.52–3.02 | 2.75 ± 0.13 |

### Comparison

The dental structure of *Bugtimys* (Table 1) (displaying lophodont, moderately high crowned and slightly unilaterally hypsodont cheek teeth, with a mesolophule labially extended from a distinct metaconule joining the hypocone on upper molars, a hypolophid connected to the anterior arm of the hypoconid and a well-developed metalophulid II on lower molars) is consistent with the diagnosis of Baluchimyinae proposed by Flynn *et al.* (1986). *Bugtimys* is characterized by its peculiar dental complexity related to the addition of enamel crestules, such as the metalophular spur, the mure, the protospur and the metastylar fold, which confer on *Bugtimys* a derived baluchimyine pattern. The overall dental organization of *Bugtimys* is close to that of *Hodsahibia azrae* (Flynn *et al.* 1986), but differs in the development of enamel crestules, a slender metaconule (in oblique position), a strong posterior arm of the paracone usually connected to the mesolophule on the upper molars, a smaller hypoconulid and the absence of a mesolophid on the lower molars. *Bugtimys* is clearly distinguished from *Hodsahibia* by the lower deciduous premolar structures which are stockier and anteriorly wider on *Bugtimys*, displaying a narrower metafossettid, a minute anteroconid, plus reduced hypoconulid and mesoconid. The dental morphology of *Bugtimys* is reminiscent of that of *Asterattus* (Flynn & Cheema 1994) in the development of

enamel crestules. However, *Bugtimys* differs from *Asterattus* in the constant development of the metalophular spur, a more reduced metaconule, the loss of the endoloph, a strong hypocone, a well-pronounced hypocone–metaconule connection, the lack of anterostyle and an uncompressed paracone–metacone on the upper molars. The morphology of the few lower molars, identified by Flynn & Cheema (1994) as m1 (Z 886; fig. 4D) and m2 (Z 887; fig. 4E) of *Asterattus*, is reminiscent of the morphology of what we identify as p4 and dp4 of *Bugtimys*. On the basis of our sample, we suspect an initial erroneous dental definition for these lower teeth. Despite these possible controversies, *Bugtimys* is different in the constant development of the mesoconid, the well-developed hypoconulid and the protospur of the metalophulid II, which reaches the mesolophid posteriorly on dp4. The p4 of *Bugtimys* is less mesiodistally elongated, develops a mesoconid and presents a different organization of the ectostylid.

*Bugtimys* differs from *Lophibaluchia* (Flynn *et al.* 1986) in the development of the mure, the reduced but nonetheless distinct metaconule and the metaloph structure which is more advanced on the upper molars of *Lophibaluchia* (unconnected to the anterior arm of the hypocone but backwardly directed and connected to the posteroloph). *Bugtimys* can also be distinguished from other baluchimyines, *Baluchimys* (Flynn *et al.* 1986; Marivaux *et al.* 2000) and *Lindsaya* (Flynn *et al.* 1986), in having a larger size, a well-established lophodont pattern, the lack of an endoloph, the development of the mure, the reduced metaconule, the strong mesolophule extending towards the labial margin of the tooth, the metalophular spur on the upper molars, the development of a strong metalophulid II (with its protospur) and the lingual opening of the talonid basin on the lower molars. Except for *Lophibaluchia*, which displays a derived organization on some dental traits, these characters are derived in *Bugtimys* with respect to the other described baluchimyines.

The general dental organization of *Bugtimys* is reminiscent of that of the African hystricognathous thryonomyoids (phiomorphs) from the Oligocene Fayum deposits (Wood 1968) in having a lophodont dental pattern, an incipient mure, the lack of an endoloph and a protospur on the lower molars. In contrast, the constant development of the posterior arm of the protoconid into metalophulid II, a more pronounced hypoconulid, the mesolophule constituting a well-differentiated transverse crest, the development of a metalophular spur, the metaconule–metaloph connection and a still well-pronounced and labiolingually elongated metaconule, which is indistinct on Egyptian Oligocene forms such as *Phiomys* and *Metaphiomys* (Wood 1968), set *Bugtimys* apart from the African forms. In addition, early phiomorphs appear to be more derived than *Bugtimys* by their enlarged and constant mure, and by their advanced metaloph topology, which extends backwards towards the median part of the posteroloph as in *Lophibaluchia*

(Flynn *et al.* 1986). The same is true for the South American forms (caviomorphs), where some taxa display an advanced dental pattern with a strong reduction of the metaloph (backwardly directed or even lost), a strong mesolophule, an indistinct metaconule, a complete and large mure, the development of a taeniodont pattern (on both the upper and lower molars) and the loss of the hypoconulid on the lower molars.

## Phylogeny
### Fossil sampling
The possibility of close phylogenetic relationships between Bugti taxa and early Palaeogene hystricognathous rodents is explored in this analysis. Ingroup taxa include the new material of Paali and other putative 'chapattimyid' material (*Baluchimys*, *Lindsaya*, *Lophibaluchia*, *Hodsahibia*, *Fallomus*), previously described by Flynn *et al.* (1986), the Indo-Pakistani Eocene Chapattimyidae (*Birbalomys*, *Chapattimys*), the Palaeogene Ctenodactyloidea from Asia, such as Yuomyidae (*Advenimus*, *Petrokoslovia*), Tamquammyidae (*Tamquammys*, *Tsinlingomys*) and Ctenodactylidae (*Protataromys*, *Tataromys*, *Yindirtemys*), and Miocene Diatomyidae (*Diatomys*). Among hystricognathous rodents, we have selected the early African phiomorphs, Thryonomyoidea (*Phiomys*, *Metaphiomys*, *Protophiomys*), Miocene Thryonomyidae (*Paraphiomys*, *Paraulacodus*) and Diamantomyidae (*Diamantomys*), and Oligocene (Deseadan) South American caviomorphs (*Platypittamys*, *Incamys*, *Branisamys*, *Sallamys*). Anomaluridae (*Nementchamys*), Zegdoumyidae (*Glibia*), Cricetidae (*Pappocricetodon*), Sciuravidae (*Knightomys*, *Prolapsus*), Cylindrodontidae (*Mysops*), Ischyromyoidea (*Ailuravus*, *Reithroparamys*, *Franimys*, *Corbarimys*, *Hartenbergeromys*), Theridomyidae (*Theridomys*, *Elfomys*, *Remys*, *Suevosciurus*, *Protadelomys*), Gliridae (*Eogliravus*) and the primitive families Cocomyidae (*Cocomys*) and Alagomyidae (*Tribosphenomys*, *Alagomys*) have been implemented in the analysis to assess the phylogenetic relationships of hystricognathous rodents within a phylogenetic framework comprising the main representatives (families) of early Tertiary Rodentia. Mimotonida (*Mimotona*) and 'Mixodontia' (*Eurymylus*, *Rhombomylus*, *Heomys*) have been selected for an outgroup comparison. The Hystricognathiformes concept (Tsaganomyidae plus Hystricognathi) introduced by Bryant & McKenna (1995), which assumes 'that Baluchimyinae may be a member' of that group, is tested by the addition of the hystricognathous *Tsaganomys altaicus* (Tsaganomyidae).

### Phylogenetic reconstruction
As our samples comprise mainly isolated teeth (incisors, premolars and molars), our phylogenetic analysis is based primarily on dental traits. A total of 105 dental characters (99 related to the complexity of the dental morphology, and six corresponding to the schmelzmuster associated with the incisor enamel microstructure) have been compiled from our

direct observations (from original and cast specimens) and from the available literature. Only two cranial characters have been implemented in the analysis (the lower jaw condition and the shape/size of the foramen infraorbitaire of the maxilla). A list of the 107 selected characters with their character states and the data matrix may be inspected on the journal's World Wide Web site.

The data matrix was managed by MacClade 3.04 (Maddison & Maddison 1992). Heuristic searches using stepwise addition and a randomized input order of taxa (100 replications) were performed by PAUP 3.1.1 (Swofford & Begle 1993). The degree of support for particular nodes was evaluated with the Decay Index (Bremer 1988) by AutoDeacay 2.9.2 (Eriksson 1996), using heuristic searches that retained suboptimal trees.

## Results and discussion
### Phylogenetic trees
The analysis yielded two equally most parsimonious trees. Each tree has a total length of 902 steps, a consistency index (CI) = 0.314 and a retention index (RI) = 0.632. A strict consensus tree, transposed onto a chronostratigraphical context, is shown in Fig. 3. As a measure of homoplasy (Goloboff 1991), the CI associated with the most parsimonious trees generated here reveals a high degree of homoplasy in the distribution of dental character states. However, the low value of the CI may be partially explained by the high taxon/character ratio. This ratio involves some non-exclusive autapomorphies on terminal taxa. Nonetheless, overall, this homoplasy seems relatively well structured (adapted from the RI).

The differences between the two trees involve the rearrangement of *Knightomys* and *Prolapsus* (sciuravids) which make, alternatively, Sciuravidae monophyletic or paraphyletic. In spite of these minor irresolutions, the phylogenetic pattern provides significant information on hystricognathous rodent relationships.
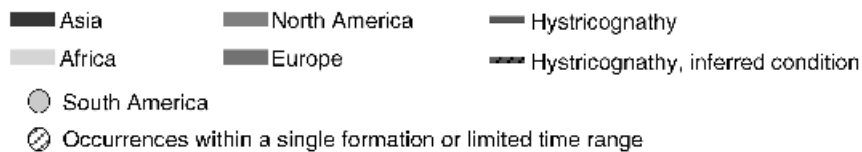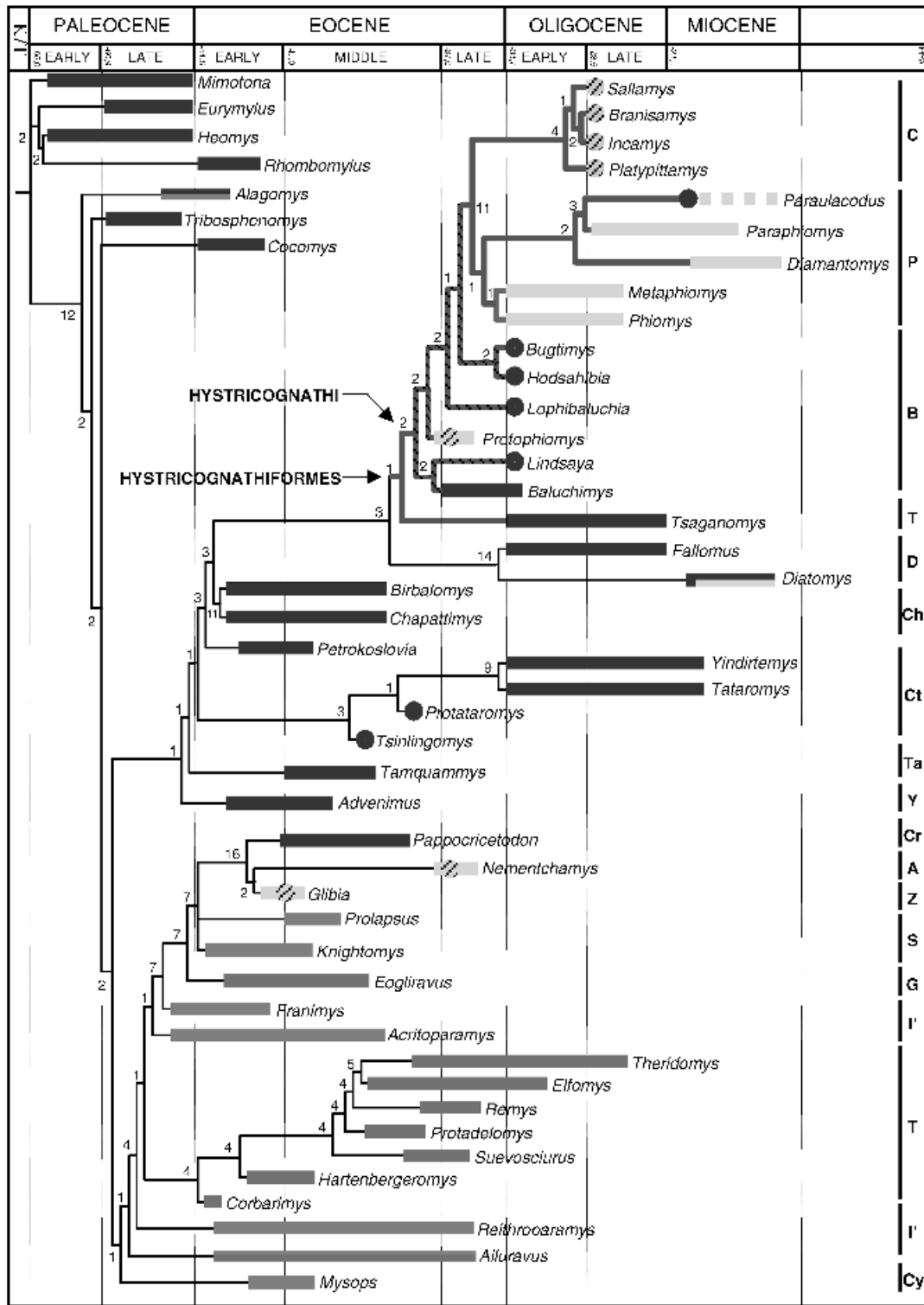
### The monophyly of hystricognathous rodents: the concept of Hystricognathiformes
As pertinently shown by Bryant & McKenna (1995), although *Tsaganomys* secondarily develops a protrogomorphous condition of the infraorbital foramen (autapomorphic character), it displays an undoubtedly hystricognathous condition of the lower jaw, a multiserial enamel, a reduced lacrimal and lacks an internal carotid artery, derived characters shared with other hystricognathous rodents. Nonetheless, *Tsaganomys* retains some plesiomorphic characters of the middle ear structure, such as an unfused malleus and incus, unexpanded malleus head, enlarged alisphenoid and imperforate pterygoid fossa, thus showing that *Tsaganomys* lacks some important derived characters upon which Hystricognathi are diagnosed. The dental structure of *Tsaganomys* also fails to include some of the most diagnostic characters for

Hystricognathi, such as the well-developed hypocone and mesolophule, and the metaloph unconnected to the protocone but usually to the anterior arm of the hypocone or to the posteroloph on upper molars. These cranial and dental characters set *Tsaganomys* apart from other hystricognathous rodents. Taking into consideration all of these morphological characters, Bryant & McKenna (1995) defined Hystricognathiformes as 'the clade consisting of *Tsaganomys* and Hystricognathi, plus all rodents more closely related to them than to Ctenodactylidae', where *Tsaganomys* represents 'the nearest outgroup of living hystricognathous rodents'. From the results of our phylogenetic analysis (Fig. 3), we identify a monophyletic clade in which *Tsaganomys* is the sister group of a clade including the previously described baluchimyine taxa, *Protophiomys*, *Bugtimys* and the early phiomorphs and caviomorphs (depicted as sister groups). Bryant & McKenna (1995) further suggested that 'Hystricognathiformes may include, in addition to *Tsaganomys* and Hystricognathi, taxa often more closely allied with them than with any other crown group, such as *Phiomys*, *Metaphiomys*, ... , possibly the "Chapattimyidae" (Baluchimyinae, *sensu* Flynn *et al.* 1986), and *Platypittamys*, as well as *Branisamys*, *Incamys*, and *Sallamys*'. Our phylogenetic results are consistent with these phylogenetic presumptions. Except for *Bugtimys*, where the hystricognathous condition of the lower jaw may be investigated, we have no knowledge of the diagnostic cranial characters for *Baluchimys*, *Lindsaya*, *Protophiomys*, *Lophibaluchia* and *Hodsahibia*. However, it is clear from our results based mainly on dental characters that these taxa are more closely related to hystricognathous rodents than to sciurognathous Chapattimyidae. They differ from primitive Eocene chapattimyids (e.g. *Birbalomys*, *Chapattimys*) in several more advanced dental characters shared with Hystricognathi, such as the strong development of the anterior arm of the hypocone which is connected to the metaconule (sometimes strongly reduced), the loss of the protoconule and the mesoconid, the incipient or well-developed mesolophule, the lack of a metaloph–protocone connection and the development of a multiserial schmelzmuster associated with incisor enamel microstructure. The morphological pattern of cheek teeth is also more lophate than in chapattimyids, but less than in phiomorphs or in caviomorphs. In contrast, a metaconule still well distinct, a metaloph–metaconule connection, an endoloph and a well-marked hypoconulid on *Baluchimys*, *Lindsaya* and *Protophiomys* are plesiomorphic character states. The endoloph is, however, lost in *Bugtimys*, *Hodsahibia* and *Lophibaluchia* and the sinus remains linguolabially opened, except for *Bugtimys* where a thin mure is developed.

### Systematic implications
The phylogenetic systematics adapted from the dichotomous tree topology presented here (Fig. 3) seem to be difficult to

conceive as they imply the paraphyly of some higher systematic rodent groups. Within this phylogenetic framework, if we consider Baluchimyinae as a subfamily of Chapattimyidae (*sensu* Flynn *et al*. 1986) and hystricognathous rodents as their sister group, Chapattimyidae and Ctenodactyloidea are paraphyletic groups. Our analysis consistently supports the monophyly of Hystricognathiformes, a clade comprising here Tsaganomyidae, baluchimyines, *Protophiomys*, phiomorphs and caviomorphs. From dental evidence, it seems therefore likely that *Baluchimys*, *Lindsaya*, *Lophibaluchia* and *Hodsahibia* display, as for *Bugtimys*, the hystricognathous condition of the lower jaw (optimized character, adapted from our cladistic analysis). The same is true for *Protophiomys*, initially referred to the Phiomyidae (Jaeger *et al*. 1985) and subsequently considered as a chapattimyid of baluchimyine affinity (Flynn *et al*. 1986; McKenna & Bell 1997). *Protophiomys* is here regarded as more closely related to baluchimyines than to phiomorphs. Baluchimyine taxa are henceforth members of Hystricognathiformes. Our results consequently necessitate a reconsideration of 'Chapattimyidae', from which baluchimyines are now excluded. The systematic status of *Fallomus*, initially considered as Chapattimyidae *incertae sedis* (Flynn *et al*. 1986), is also questionable. Following the results of our analysis, *Fallomus* is more closely related to Diatomyidae (*Diatomys*) than to Chapattimyidae. We therefore endorse the systematics recently suggested by Mein & Ginsburg (1997), which refer *Fallomus* to the Diatomyidae. In this way, Chapattimyidae are limited to early and middle Eocene taxa, as originally defined by Hussain *et al*. (1978). Although the phylogenetic position of 'baluchimyine' taxa is now clearly established, there is, however, no support for the monophyly of this group adapted from the inferred pattern of branching points within the phylogenetic tree (Fig. 3). 'Baluchimyine' taxa are nested within Hystricognathiformes and represent the earliest offshoots of Hystricognathi. Baluchimyines are interpreted here as Hystricognathi *incertae sedis* (as their dental morphology is more comparable to that of Hystricognathi than to that of Tsaganomyidae).

### Sister group of Hystricognathiformes

As previously argued by Meng (1990) and further supported by this analysis, no shared derived cranial or dental characters demonstrate a close phylogenetic relationship between hystricognathous rodents and 'Franimorpha' (*sensu* Wood 1955, 1980, 1985; Patterson & Wood 1982; including Eocene sciuravids, reithroparamyids and cylindrodontids rodents).

Furthermore, the alternative hypotheses involving paramyids (Wood 1968) or theridomorphs (Lavocat 1969, 1980) as putative stem groups for hystricognathous rodents are also ruled out here. Even if sciuravids and theridomorphs develop some similar (but convergent) derived characters with Hystricognathi on upper molars, such as the loss of the endoloph, the strong anterior arm of the hypocone connected to the metaconule, the loss of the lingual metaloph (metaconule–protocone connection) and, for theridomorphs only, the development of a mure and of a third loph (at the same location as the mesolophule), they present divergent lower molar patterns. Early members of Hystricognathi retain a primitive lower molar pattern characterized by a well-developed metalophulid I, a weak anterocingulid, a lingually directed posterior arm of the protoconid (metalophulid II) and a distinct hypoconulid. They develop, however, some derived characters, such as the complete ectolophid and hypolophid, the loss of the mesoconid and the strong development of the anterior arm of the hypoconid. In contrast, sciuravids are characterized by the labiolingual development of the mesoconid, the incomplete hypolophid, the loss of the metalophulid I and the strong anterocingulid (anterolophid) which secondarily occupies the position of the ancestral metalophulid I. Theridomorphs also differ in the labial position of the posterior arm of the protoconid distally orientated, occupying the position of the ectolophid of Hystricognathi, the strong mesolophid, the weak anterior arm of the hypoconid and a complex metalophulid I.

Ctenodactyloidea has been previously considered as a stem group of rodents originating from an Eocene Asian radiation, which comprises Ctenodactylidae, Chappatimyidae, Yuomyidae and Cocomyidae (Dawson *et al*. 1984). Cocomyidae in this usage includes *Cocomys*, *Tsinlingomys* and *Tamquammys*. *Cocomys* displays a primitive protrogomorphous condition of the maxilla and lacks a hypolophid on the lower molars, and was subsequently excluded from Ctenodactyloidea by Flynn *et al*. (1986), whereas *Tsinlingomys* and *Tamquammys* were referred to Ctenodactylidae (as originally viewed by Wood 1977) owing to the morphology of their premolars, and to the fact that *Tamquammys* presented a hystricomorphous condition. We agree with Flynn *et al*. (1986) in excluding *Cocomys* from Ctenodactyloidea as it represents (as for Alagomyidae) an earliest offshoot of the radiation of Rodentia, and thus a sister group to the clade of other rodents. Concerning *Tamquammys*, we follow Shevyreva (1983) and Tong (1997) in referring this taxon to the Tamquammyidae. In our analysis,

**Fig. 3** Strict consensus of two equally most parsimonious trees transposed onto a chronostratigraphical context with palaeobiogeographical references. Each tree has a total length of 902 steps, a consistency index (CI) = 0.314 and a retention index (RI) = 0.632. Decay index values are labelled on each node. *Symxbols*: C, caviomorphs; P, phiomorphs; B, 'Baluchimyinae'; T, Tsaganomyidae; D, Diatomyidae; Ch, Chapattimyidae; Ct, Ctenodactylidae; Ta, Tamquammyidae; Y, Yuomyidae; Cr, Cricetidae; A, Anomaluridae; Z, Zegdoumyidae; S, Sciuravidae; G, Gliridae; I', Ischyromyidae ('paraphyletic'); T, Theridomorphs; Cy, Cylindrodontidae.

Ctenodactylidae can be identified as a monophyletic group if *Tsinlingomys*, *Protataromys*, *Yindirtemys* and *Tataromys* (plus all other Oligocene and Miocene taxa) are considered to be members. As recognized by Wang (1997) and Dashzeveg & Meng (1998), it is clear that Ctenodactylidae, but also Chapattimyidae, can be viewed as 'core' taxa of Asian ctenodactyloids with respect to Yuomyidae (here *Advenimus* and *Petrokozlovia*) or Tamquammyidae, which involve contentious connotations.

The aim of our analysis is not to shed light on the complex relationships among ctenodactyloids (which has recently been carried out by Dashzeveg & Meng 1998). However, our phylogenetic results clearly demonstrate the existence of close phylogenetic relationships between early hystricognathous and ctenodactyloid rodents (here Yuomyidae, Tamquammyidae, Ctenodactylidae, Chapattimyidae (excluding 'Baluchimyinae' and *Fallomus*) and Diatomyidae). Nonetheless, Hystricognathiformes are not the sister group of Ctenodactyloidea, but a group nested within the ctenodactyloid rodents, and more precisely related to Chapattimyidae and Diatomyidae. The broad concept of Ctenodactyloidea cannot be applied in this phylogenetic framework as it represents a paraphyletic group (in agreement with Bryant & McKenna 1995). It is traditionally assumed that extant Ctenodactylidae are living remnants of this Palaeogene 'ctenodactyloid' radiation. In fact, the same is true for extant Hystricognathi which also descend from the ancestral 'ctenodactyloid' stock. Our results are therefore consistent with the hypothesis of a sister group relationship between extant Ctenodactylidae and Hystricognathi, which is widely substantiated by a set of biological studies (Bugge 1985; George 1985; Luckett 1985; Meng 1990; Bryant & McKenna 1995; Huchon *et al.* 2000).

### Multiserial schmelzmuster associated with the incisor enamel microstructure

The study of the incisor enamel microstructure has provided a reliable tool for phylogeny and systematics at the familial or higher levels in rodents (e.g. Martin 1993, 1994). It is widely accepted that the pauciserial schmelzmuster is primitive for Rodentia, and that a multiserial condition represents a derived stage of the pauciserial condition. In that context, the multiserial schmelzmuster characterizing both extant Ctenodactylidae and Hystricognathi has been interpreted as a derived character inherited from a common ancestor (Martin 1993, 1994, 1997). However, although Ctenodactylidae developed a fully multiserial condition in the Eocene (Martin 1993), Eocene Chapattimyidae retain a typical pauciserial condition. In our analysis, chapattimyid rodents are considered as the nearest sister group of Diatomyidae plus Hystricognathiformes. In fact, the acquisition of the multiserial enamel within the clade comprising 'ctenodactyloids' plus Hystricognathiformes occurred at least twice: first in

Ctenodactylidae and Tamquammyidae, then subsequently in Diatomyidae and Hystricognathiformes, where it represents a synapomorphy for the two later taxa. As a result, this derived condition, apparently shared in extant Ctenodactylidae and Hystricognathi, would represent a morphological tendency (grade) developed within these two closely related crown clades. The same is true in several lineages of rodents derived from the 'Ischyromyoidea', where a uniserial schmelzmuster associated with the incisor enamel microstructure (second derived condition from the primitive pauciserial enamel) proves to be acquired independently more than once (e.g. Martin 1997).

### Evolution of the upper molar pattern within Hystricognathi (Fig. 4)

One of the key dental characters exhibited by 'baluchimyine' rodents is the development of the third crest (from the anterior
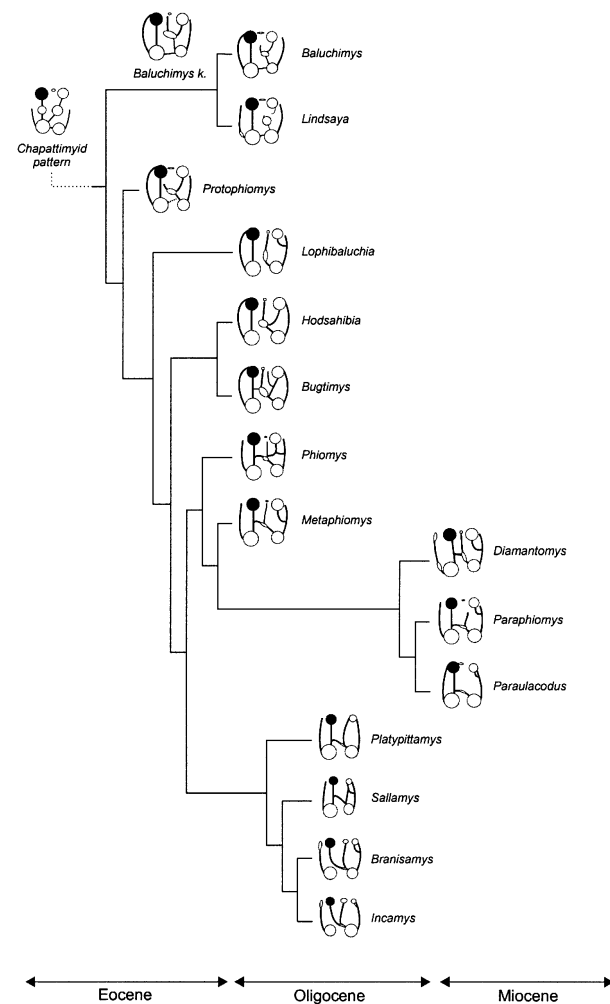


**Fig. 4** Evolution of the upper molar pattern within Hystricognathi (*Baluchimys k*. = *B. krabiense*; Marivaux *et al.* 2000).

margin) on the upper molars. This incipient or well-developed crest, named the 'mesolophule' (Flynn *et al.* 1986), extending labially from the metaconule (and not from a mesocone), demonstrates how a pentalophodont pattern may be acquired by derivation of a tetralophodont pattern. The tetralophodont pattern (comprising four transverse crests: anteroloph, protoloph, metaloph connected to the metaconule and posteroloph) is the primitive condition observed among early rodents (although the lophodonty is still not well developed in these rodents). The development of a pentalophodont pattern (comprising anteroloph, protoloph, mesolophule, metaloph connected to the metaconule and posteroloph) represents a derived condition for 'baluchimyines'. Oligocene phiomorphs (*Phiomys* and *Metaphiomys*) exhibit a pentalophodont pattern with a well-developed third loph (here homologous to the mesolophule). However, this pattern differs in the structure of the metaloph, which displays a derived state (unconnected to the strongly reduced to indistinct metaconule, but backwardly directed and connected to the posteroloph for *Metaphiomys*; connected both to the reduced metaconule and the posteroloph for *Phiomys*). Miocene diamantomyid phiomorphs (*Diamantomys*) retain the typical pentalophodont pattern (as *Metaphiomys*), whereas Oligocene and Miocene thryonomyids acquire a derived penta-tetralophodont pattern by the secondarily strong reduction of the metaloph (*Paraphiomys*), and even a trilophodont pattern by the loss of both the metaloph and the mesolophule (*Paraulacodus*, *Gaudeamus*, *Neosciuromys*, extant *Thryonomys*). On the other hand, South American caviomorphs have a well-developed third loph (the mesolophule), but generally display an advanced reduction or even loss of the metaloph (reduced and labially connected to the posteroloph for *Sallamys* and *Branisamys*; lost for *Platypittamys* and *Incamys*). The tetralophodont pattern (anteroloph, protoloph, mesolophule and posteroloph) of caviomorphs is therefore secondarily acquired from a pentalophodont structure. Finally, on the basis of the current Oligocene fossil record, if pentalophodonty corresponds to a derived molar condition for 'baluchimyines' with respect to 'ctenodactyloids', it represents a plesiomorphic molar condition for phiomorphs and caviomorphs (in agreement with Hoffstetter & Lavocat 1970; Lavocat 1973, 1974, 1976; Bryant & McKenna 1995).

### Palaeobiogeographical implications for 'baluchimyines'

Chapattimyidae, Ctenodactylidae and Yuomyidae have been interpreted as distinct ancestral Asian rodents originating from an early Palaeogene widespread 'ctenodactyloid' radiation in Asia (Hussain *et al.* 1978; Hartenberger 1982a,b). Ctenodactylidae and Yuomyidae occurred exclusively in central Asia during the Palaeogene, whereas Chapattimyidae were restricted on the Indian subcontinent, considered as vicariants of Ctenodactylidae and Yuomyidae (Jaeger *et al.*

1985; Flynn *et al.* 1986). The chapattimyid distribution has been tentatively explained by the geographical isolation of the Indian plate during some part of the lower Eocene, due in part to a shallow Eocene Tethys Sea (Blondeau *et al.* 1986) separating mainland Asia from the Indian subcontinent (Jaeger *et al.* 1985; Flynn *et al.* 1986; Jaeger & Rage 1995). From this palaeogeographical scenario, Flynn *et al.* (1986) have interpreted Baluchimyinae and *Fallomus* as representatives of a subsequent and endemic radiation of Chapattimyidae, isolated on the Indian subcontinent throughout the middle–late Eocene, the entire Oligocene and the early Miocene, a view supported by Kumar *et al.* (1997). However, the occurrence at the Paali locality of rodents, such as Cricetidae (Marivaux *et al.* 1999), Sciuridae, Zapodidae and Anomaluridae (L. Marivaux, in preparation), associated with 'baluchimyines' and *Fallomus* precludes the isolation hypothesis of the Indian subcontinent during some part of the Palaeogene. The widespread palaeogeographical distribution of taxa collected in Paali demonstrates the existence of communications between the Indian subcontinent, Eurasia and Africa during the Palaeogene. In addition, the recent discovery of *Baluchimys krabiense*, a new 'baluchimyine' species, from the late Eocene of Southeast Asia (Krabi Basin of Thailand; Marivaux *et al.* 2000) proves that these rodents were not exclusively restricted on the Indian subcontinent, but had a widespread south Asian distribution at least since the late Eocene. In addition, we have emphasized the dental affinities between *Baluchimys* and the late Eocene African *Protophiomys* (Marivaux *et al.* 2000). As mentioned above, *Protophiomys* is clearly nested within 'baluchimyines' (Fig. 3). *Protophiomys* may be therefore interpreted as an African representative of the south Asian group. As a result, 'baluchimyine' rodents presumably exhibited a widespread south Asian–north African distribution from the late Eocene. Thus, the endemism hypothesis of the rodent fauna on the Indian subcontinent (Flynn *et al.* 1986) is ruled out too. This late Eocene 'baluchimyine' distribution thus reflects Palaeogene faunal exchanges between south Asia and the Arabo-African continent (long before the well-known Miocene collision between Africa and Eurasia), which have been substantiated by other mammalian groups, such as anthracotheres (Ducrocq 1995, 1997) and primates (Thomas *et al.* 1988; Chaimanee *et al.* 1997; Jaeger *et al.* 1998, 1999; Tong *et al.* 1999).

### Hystricognathous rodents: an Asian origin

Although weakly represented, the fossil record of hystricognathous rodents shows that this group displayed a widespread Old and New World distribution from early Oligocene time. Tsaganomyidae were widely distributed in central Asia throughout the Oligocene (e.g. Bryant & McKenna 1995), whereas 'baluchimyine' taxa occupied a widespread south Asian–north African distribution at least since the late

Eocene. Phiomorphs are well represented from African and Omani Oligocene deposits of the Fayum (Osborn 1908; Wood 1968) and Taqah (Thomas *et al.* 1989) localities, respectively. In South America, caviomorphs have a well-documented record in the late Oligocene (Deseadean) of Bolivia and Patagonia, but have also been identified from the Eocene–Oligocene 'Tinguiririca' age of the central Chilean Andes (Wyss *et al.* 1993). The occurrence of hystricognathous rodents in three distinct palaeogeographical provinces (Africa, South America and Asia) from the earliest Oligocene indicates that the origin and early diversification of this group long preceded that period. There is obviously a considerable amount of unknown diversity in the early evolutionary history of Hystricognathi and Hystricognathiformes. Nonetheless, the fact that late Eocene and Oligocene Hystricognathiformes (comprising the Asian Tsaganomyidae and 'baluchimyine' taxa, the African phiomorphs and the South American caviomorphs) represent a clade rooted within the Asian 'ctenodactyloid' rodents (Fig. 3) clearly points to an Asian origin and initial diversification of hystricognathous rodents (in agreement with Bryant & McKenna 1995). Being descendants of a common but virtually unknown 'Asian' Eocene hystricognathous ancestor, Tsaganomyidae and 'baluchimyine' taxa are representatives of the initial diversification phase in Asia (judging from their basal position on the phylogenetic tree; Fig. 3). Oligocene phiomorphs and caviomorphs are deep rooted within this early Asian radiation (Fig. 3), and therefore seem to share a common Asian hystricognathous ancestor. These two taxa, circumscribed in Africa and in South America, respectively, reflect a subsequent palaeogeographical disjunction of hystricognathous rodents, which corresponds to a second diversification phase of the group.

### An Asian origin for caviomorphs and platyrrhines?

The presence of hystricognathous rodents in South America remains one of the most perplexing problems in the evolutionary history of the group. South America was an island continent during most of the Tertiary and there is no geophysical support testifying to the existence of a corridor dispersal route with North America or Africa during Eocene or Oligocene time, except with Antarctica (e.g. Barker *et al.* 1991). Moreover, no fossil rodent has been found in the diverse South American faunas from Palaeocene to mid-Eocene times (Wyss *et al.* 1993; Vucetich *et al.* 1999). The appearance of caviomorphs in Oligocene deposits from Patagonia, Bolivia and Chile *a fortiori* requires a colonization of South America by hystricognathous rodents. The fact that South America was isolated raises the possibility that a trans-oceanic sweepstakes dispersal route from other land masses may have taken place during the Eocene — as previously speculated in the context of an African origin for caviomorphs

(Lavocat 1973, 1974, 1976). The same is true for the platyrrhine anthropoid primates (New World monkeys), for which a parallel is established. Indeed, these primates suddenly appeared in the Oligocene fossil record of South America, presumably from Africa (Hoffstetter 1969, 1972; Ciochon & Chiarelli 1980; Holroyd & Maas 1994; Fleagle & Kay 1997).

An alternative point of view is provided by molecular studies which assume a Mesozoic divergence age between sciurognathous and hystricognathous rodents (Kumar & Hedges 1998), and generally a Late Cretaceous divergence between South American caviomorphs and African phiomorphs (e.g. Mouchaty *et al.* 2001). These inferred ages of divergence are used to propose hypotheses of vicariance divergence related to the Mesozoic continental break-up, and more precisely here to the opening of the southern Atlantic (e.g. Croizat 1979; Mouchaty *et al.* 2001), that ideally explain the palaeodistribution (but a Late Cretaceous distribution) of hystricognathous rodents on both distinct land masses. However, in the absence of any fossil record of Cretaceous rodents (much less hystricognathous rodents), such a scenario remains utopian and questionable. Furthermore, the earliest fossil record of 'primitive rodents' (so far non-hystricognathous) is not older than the latest Palaeocene, suggesting a Tertiary radiation.

Recent discoveries of Asian Eocene primates have stimulated the hypothesis that Asia was an important theatre of early anthropoid evolution (Chaimanee *et al.* 1997; Jaeger *et al.* 1998, 1999; Ducrocq 1999, 2001). In fact, there is ongoing debate as to whether anthropoids arose in Africa or in Asia, and as to whether South American platyrrhines originated from an Asian group of anthropoids. In the same way, if we take into account the fact that African phiomorphs and South American caviomorphs might share an Asian common hystricognathous ancestor, the possibility exists that the dispersal of hystricognathous rodents to South America was not from Africa. These alternative points of view (regarding the origin of anthropoid primates and hystricognathous rodents) cast doubt on the currently favoured dispersal model, a westward trans-Atlantic dispersal route from Africa to South America. The possibility that New World monkeys (proto-platyrrhines) reached South America from Asia via North America [1] or via Australia–Antarctic [2] (Gondwanan palaeogeographical model) has been recently evaluated by Houle (1999). The scenario involving a terrestrial dispersal in the northern hemisphere [1] via North America (by way of the Bering Strait) seems unlikely as there is no palaeontological evidence (anthropoid primates or hystricognathous rodents) from the well-known North American Palaeogene faunas. On the other hand, although South America was connected to the Antarctic Peninsula until the late Eocene (opening of the Drake Passage occurring approximately 37 Ma; Barker *et al.* 1991), the Gondwanan palaeogeographical

scenario [2] also seems highly improbable because of a major water barrier separating Antarctica and Australia during the Eocene (at least from 50 Ma; Woodburne & Case 1996) and the occurrence of unfavourable palaeowinds (Barron & Peterson 1991) for rafting dispersal. Besides, despite the possibility of Eocene temperate conditions in the Antarctic Peninsula (Francis 1986; Truswell 1991; Vizcaino *et al.* 1997), allowing land mammal habitations, no primate or rodent remains have ever been reported from Antarctica or Australia.

## Conclusions

The discovery of a new hystricognathous rodent from Pakistan (Bugti Hills) has improved our knowledge of the early diversification of Hystricognathi. Our cladistic assessment of dental evidence for the Palaeogene hystricognathous rodent cladogenesis substantiates the close relationships between hystricognathous and Asian 'ctenodactyloid' rodents, and thus an Asian origin for Hystricognathi. The fact that 'baluchimyine' taxa are considered as members of Hystricognathiformes (Hystricognathi *incertae sedis*) highlights the role of south Asia in the early evolutionary history of hystricognathous rodents. These rodents have been well diversified in Africa, South America and south Asia since the Oligocene. However, the fossil record of hystricognathous rodents (virtually unknown before the late Eocene) is still inadequate for proposing a realistic palaeobiogeographical model to explain their subsequent arrival in South America. Nonetheless, the phylogenetic relationships between South American caviomorphs and Afro-Asian hystricognathous rodents are now firmly settled. Caviomorphs and phiomorphs seem to share a common 'Asian' hystricognathous ancestor. This raises the possibility that South American hystricognathous rodents, and perhaps anthropoid primates, might be directly descended from Asia rather than from Africa. These alternative hypotheses cannot be rejected without further Palaeogene palaeontological evidence from these three continents.

## Acknowledgements

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