Brief report

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A herpetotheriid marsupial from the Oligocene of Bugti Hills, Balochistan, Pakistan

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Didelphimorph marsupials were widely distributed in Asia during the Cenozoic, but their occurrence in the Indian subcontinent has not so far been demonstrated. Here, we describe a new herpetotheriid marsupial *Asiadidelphis akbarbugtii* sp. nov. from the early Oligocene Bugti Member of the Chitarwata Formation, Bugti Hills, Pakistan. The discovery of the herpetotheriids in the Oligocene of Pakistan represents the most southern occurrence of the family, which was thought to have occurred only to the north of the Alpine-Himalayan Suture. Our data suggest that episodic faunal exchanges occurred between the Asian mainland and the Indian subcontinent during the late Paleogene, and that the southern Asian faunas were not as completely isolated by the Himalayan chain as formerly believed.

Introduction

Fossil vertebrates from the Tertiary of the Bugti Hills have been known since the late nineteenth century (Lydekker 1884), and intensive collections were made early in the twentieth century (Pilgrim 1912; Forster-Cooper 1924). First envisaged as possibly Oligocene in age by Pilgrim (1908), the lowermost strata of the Chitarwata Formation, which yielded part of the classic "Bugti fauna" were subsequently re-interpreted as early Miocene in age (Raza and Meyer 1984). This "early Miocene" age was primarily based on the reassessment of ancient collections and inappropriate correlation with the alleged coeval Miocene deposits of the Zinda Pir Area, about 300 km north of Dera Bugti. Within the last decade, intensive biostratigraphical frameworks and meticulous collections of vertebrates in the Bugti Hills demonstrated the presence of a dozen successive fossiliferous levels ranging from the Early Oligocene to the Late Miocene (Welcomme and Ginsburg 1997; Welcomme et al. 2001). The Oligocene age of the base of the Chitarwata Formation is now admitted for the entire Sulaiman Range (including the Zinda Pir Dome Area) although some disagreements still persist about whether the lowermost strata of the Chitarwata Formation are of early or late Oligocene age (Lindsay et al. 2005).

The fossiliferous locality Paali Nala-DBC2 (Dera Bugti, level C, locus 2) is located about 30 km southwest of Dera Bugti (Fig. 1). It consists of deltaic sands that yielded the first early Oligocene mammalian fauna from the Indian Subcontinent. The early Oligocene age of Paali Nala-DBC2 is inferred by biochronology, on the basis of rodents (Marivaux et al. 1999; Marivaux and Welcomme 2003), rhinocerotids (Antoine et al. 2003, 2004), and foraminifers (Welcomme et al. 2001). About fifty mammalian species belonging to nine different orders have been identified in Paali Nala-DBC2, making this locality a critical window into the late Paleogene diversity of mammals in the Indian Subcontinent.

Among the dental material collected so far, three upper molars exhibit a didelphidian dilambdodonty (*sensu* Crochet 1980a: 28, figs. 2, 3, 4) and five strong and aligned stylar cusps, which exclude close affinities with Placental adapisoriculid Lipotyphla (Gheerbrant 1991). The fossil record of Cenozoic marsupials is particularly poor in Asia (Fig. 4). It consists of a dozen of isolated teeth reported from the Eocene of China (Qi et al. 1996), India (Thewissen et al. 2001; Bajpai et al. 2005), Kazakhstan (Gabunia et al. 1984, 1990; Emry et al. 1995), Turkey (Kappelman et al. 1996; Maas et al. 1998), and from the Miocene of China (Storch and Qiu 2002), and Thailand (Mein and Ginsburg 1997; Ducrocq et al. 1992).

Material and methods

The higher systematics of marsupials follows the classification proposed by Marshall et al. (1990) rather than that of McKenna and Bell (1997), and the dental terminology is that proposed by Clemens (1966). Measurements are in millimeters (mm), and were taken by following protocol proposed by Crochet (1980a). The dental material described below was obtained by screen washing, and it is temporarily stored in the collections of the Institut des Sciences de l'Évolution of Montpellier (ISEM), France, where silicone casts are permanently available. The original specimens belong to the Pakistan Museum of Natural History (PMNH) in Islamabad, Pakistan (permanent repository).

Systematic paleontology

Super-cohort Marsupialia Illiger, 1811

Order Didelphimorphia Gill, 1872

Family Herpetotheriidae Trouessart, 1879

Genus *Asiadidelphis* Gabunia, Shevyreva, and Gabunia, 1990

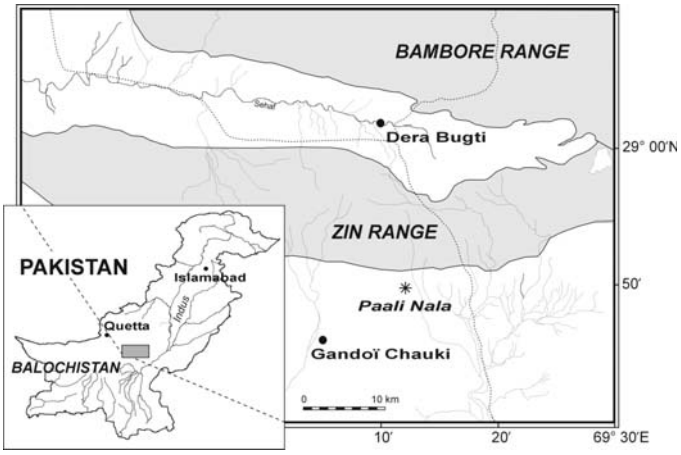

Fig. 1. Geographic location of the marsupial-bearing locality of Paali Nala-DBC2 (denoted by an asterisk), the lowermost part of the Chitarwata Formation (Bugti Member, Oligocene), in the Bugti Hills (Central Pakistan, eastern Balochistan) .

Asiadidelphis akbarbugtii sp. nov.

Figs. 2, 3.

Holotype: PMNH-DBC2-2180, a left M2 (Figs. 2A, 3B).

Referred material: PMNH-DBC2-2179 (Figs. 2B, 3A), a left M2; PMNH-DBC2-2223 (Fig. 2C), a right M4.

Type locality: Paali Nala-DBC2, Bugti Hills, Balochistan, Pakistan (Welcomme et al. 2001).

Formation and age: Chitarwata Formation; Bugti Member, Early Oligocene (Welcomme et al. 2001).

Etymology: The name is dedicaced to Nawab Akbar Shahbaz Khan Bugti, tribal chief of the Bugti People, leader of the Jamhoori Watan Party, recently deceased; in recognition of his great interest in our paleontological investigations and his kind hospitality during all the French field expeditions in the Bugti territory.

Differential diagnosis.—*Asiadidelphis akbarbugtii* differs from *A. zaissanense* and *A. tjutkovae* in its larger size, and in having the lingual border of upper molars more rounded, more massive cusps, more developed conules, larger stylar cusp C on M2, and from *A. zaissanense* in showing a distinct anterior cingulum. Moreover, the upper molars of *A. akbarbugtii* are also characterized by a lesser development of the didelphidian dilambdodonty.

Description.—PMNH-DBC2-2179 (length = 2.84 mm, width = 3.85) and PMNH-DBC2-1980 (length = 2.84 mm, width = 3.68) are two left M2; the first one appears slightly weathered, but the wearing surfaces are still clearly visible (Fig. 3). The labial border is weakly concave. Stylar cusps A and B are strongly worn, so that a single wearing surface is preserved (Fig. 3A, B). The cusp C is strong and high in regard to its limited wearing surface. The cusp D is not visible, but such an absence is frequent in the Herpetotheriidae (Crochet 1980a). The cusp E is the lowest cusp, and it is located on the labial end of the metacrista. The preprotocrista joins the stylar cusp A. The paracone is slightly shifted labially with respect to the metacone. The centrocrista does not reach the stylar line, which corresponds to strict didelphidian dilambdodonty as defined by Crochet (1980: 28). The large development of the conules can be deduced from the large size of the corresponding wear surfaces. The lingual margin of the crown surrounding the protocone is noticeably rounded, suggesting that these teeth are both M2.

UMC-DBC2-2223 (Fig. 3C) is a right M4 (length = 1.84 mm; width = 3.12 mm). The anterior styles and the stylar cusp A are freshly broken. According to the size of its partly preserved labial base, the stylar cusp B was probably high. The small cusp located just posterior to the cusp B can be identified as either the cusp D or a duplication of the cusp C, as observed in *Amphiperatherium* (Crochet 1980). The cusp C is high and it displays a distinct horizontal wearing surface. Because of the labial position of the paracone, the reduced metacentrocrista is not linked to the cusp C. Conules are well developed. The paracingulum extends labially along the preserved part of the paracone.

Discussion

Despite slight variations in morphology and size, all the specimens from Paali described here are referred to *Asiadidelphis akbarbugtii* sp. nov. The relative size of stylar cusps, their position on the labial margin of the molar (especially on PMNH-DBC2-2179 and PMNH-DBC2-2180), the didelphidian dilambdodonty, the lingual position of the paracone, and the lack of hypocone are all suggestive of close affinities with didelphimorph marsupials (order Didelphimorphia Gill, 1872). More-

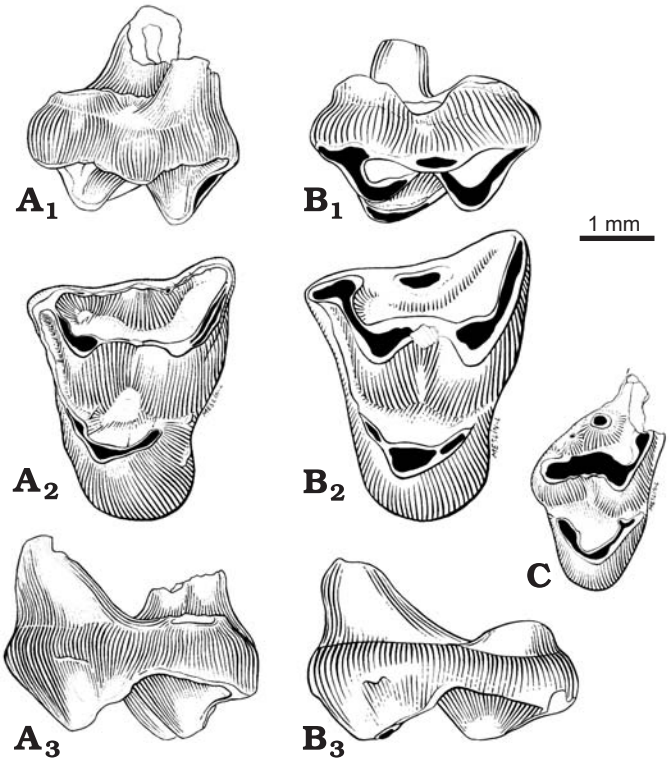

Fig. 2. *Asiadidelphis akbarbugtii* sp. nov. from Paali Nala-DBC2 (Bugti Hills, Balochistan, Pakistan). **A**. Holotype PMNH-DBC2-2180, left M2 in labial (A_1), occlusal (A_2), and mesial (A_3) views. **B**. PMNH-DBC2-2179, left M2 in labial (B_1), occlusal (B_2), and mesial (B_3) views. **C**. PMNH-DBC2-2223, right M4 in occlusal view. Original drawings by Laurence Meslin, copyright CNRS-Meslin.

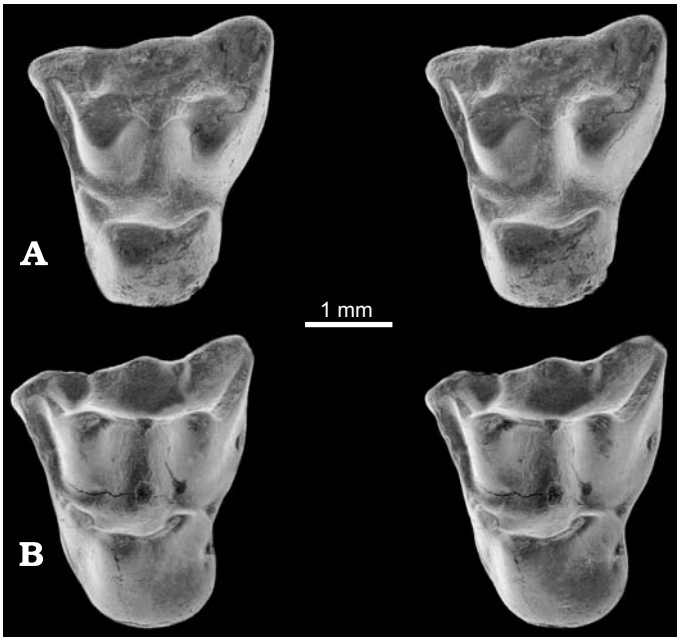

Fig. 3. *Asiadidelphis akbarbugtii* sp. nov. from Paali Nala-DBC2 (Bugti Hills, Balochistan, Pakistan). **A**. PMNH-DBC2-2179, left M2 in occlusal view. **B**. PMNH-DBC2-2180 (holotype), left M2 in occlusal view. Stereo pairs.

over, within Didelphimorphia, characters like the slenderness of the principal cusps, and the absence of a lingual cingulum undoubtedly indicate that these teeth belong to a member of the Herpetotheriidae Trouessart, 1879. The attrition surfaces extending along the lingual sides of the paracone and metacone are not interpretable in term of microwear pattern as teeth seemingly underwent post-mortem polishing resulting from a probable phase of fluvial transport. However, microwear, located on the apices of the cusps suggests the prominence of abrasion chewing processes during occlusion (Crochet 1980b).

The current picture yielded by the poor fossil record of Cenozoic marsupials suggests that the peradectids were widely distributed in the Old World, since they are reported from the early Eocene of Tunisia (Chambi) with *Kasserinotherium tunisiense* (Crochet 1986; Hartenberger et al. 2001), and from both the early Oligocene of Egypt (Gebel El Qatrani, Fayum) and the Arabic peninsula (Taqah, Sultanate of Oman) with *Qatranitherium africanum* (Simons and Bown 1984; Crochet et al. 1992). The peradectids are also known in the early Miocene of China (Songlinzhuang) with *Sinoperadectes clandestinus* (Storch and Qiu 2002) and from the middle Miocene of Thailand (Mae Long and Li Basins) with *Siamoperadectes minutus* (Ducrocq et al. 1992; Mein and Ginsburg 1997). The few specimens of marsupials reported from the Eocene of Turkey and referred to the Herpetotheriinae (Kappelman et al. 1996), and to "? Marsupialia, gen. and sp. indet." (Maas et al. 1998) display an unusual and highly specialized dental morphology within the Marsupialia, and their affinities remain unresolved so far.

In contrast, the herpetotheriids (order Didelphimorphia) seem to have been geographically restricted to the north side of the Tethys Sea. *Asiadidelphis zaissanense* is known from the late Eocene (Gabunia et al. 1990) and *Asiadidelphis tjutkovae* from the early Oligocene (Emry et al. 1995) of the Zaysan Basin, Eastern Kazakhstan. Qi et al. (1996) reported the occurrence in China of an "*Asiadidelphis*-like opossum (Didelphidae)" from the middle Eocene fissure fillings of Shanghuang (Jiangsu Province), but the specimen are yet to be described in detail. Recently, Bajpai et al. (2005) reported two new genera from the early Eocene of India, both based on lower molars (*Indodelphis* and *Jaegeria*). According to the oblique orientation of the wear surfaces in *Indodelphis*, it is unlikely referable to the Peradectidae, in which these surfaces are invariably horizontal (Crochet 1980a). *Indodelphis* is probably rather referable to the Herpetotheriidae like *Asiadidelphis*, but further comparisons with the later genus are precluded as all the species of *Asiadidelphis* are based only on upper molars. At this point however, we cannot exclude that *Indodelphis* is actually a junior synonym of *Asiadidelphis*. The genus *Jaegeria* was reported by Bajpai et al. (2005) from the same locality and tentatively referred to "Didelphidae Herpetotheriinae". Again, the lower molars of *Jaegeria* prevent extensive comparisons with other Asian taxa, but both their morphology and size are reminiscent of the "Didelphidae Herpetotheriinae gen. et sp. indet." from the Ganda Kas area (Kuldana Formation) of northern Pakistan (Thewissen et al. 2001). However, we express some doubt on the real marsupial affinities of *Jaegeria* and "Didelphidae Herpetotheriinae gen. et sp. indet." because of several dental features including the pinched trigonid, the height of the prefossid in lingual view, and the somewhat medial position of the hypoconulid on the lower molars. Further material is necessary to test the systematic affinities of these enigmatic Asian taxa.

It clearly appears from this short overview of the Cenozoic fossil record of Asian marsupials that the upper teeth from Kazakhstan referred to *Asiadidelphis* (Gabunia et al. 1984, 1990; Emry et al. 1995) provide the most relevant comparisons for the new specimens from Paali. The genus *Asiadidelphis* is based on the species *A. zaissanense,* which is only documented by upper molars (Gabunia et al. 1990). However, because of the scarcity of the available material, we think that the diagnoses based on dental characters are not consistent enough to differentiate *Asiadidelphis* from the other genera belonging to the Herpetotheriidae. *A. tjutkovae* reported by Emry et al. (1995) does not provide additional morphological data for the genus since this species is mainly based on its size (25 to 30% larger than *A. zaissanense*). The well-preserved and complete upper molars from Paali possess most of the characters mentioned by Gabunia et al. (1990), including the connection between the preprotocrista and the stylar cusp A (Fig. $2A_2$). It is worth noting that this dental feature and the prominence of the stylar cusp C are also observable in *Amphiperatherium minutum*, a didelphimorph marsupial from the Paleogene of Europe (Crochet 1980a: 84).

Conclusion

The specimens from the Paali locality in Bugti Hills exhibit diagnostic characters of the genus *Asiadidelphis*, but their autapomorphies and larger size justify the recognition of a new species.

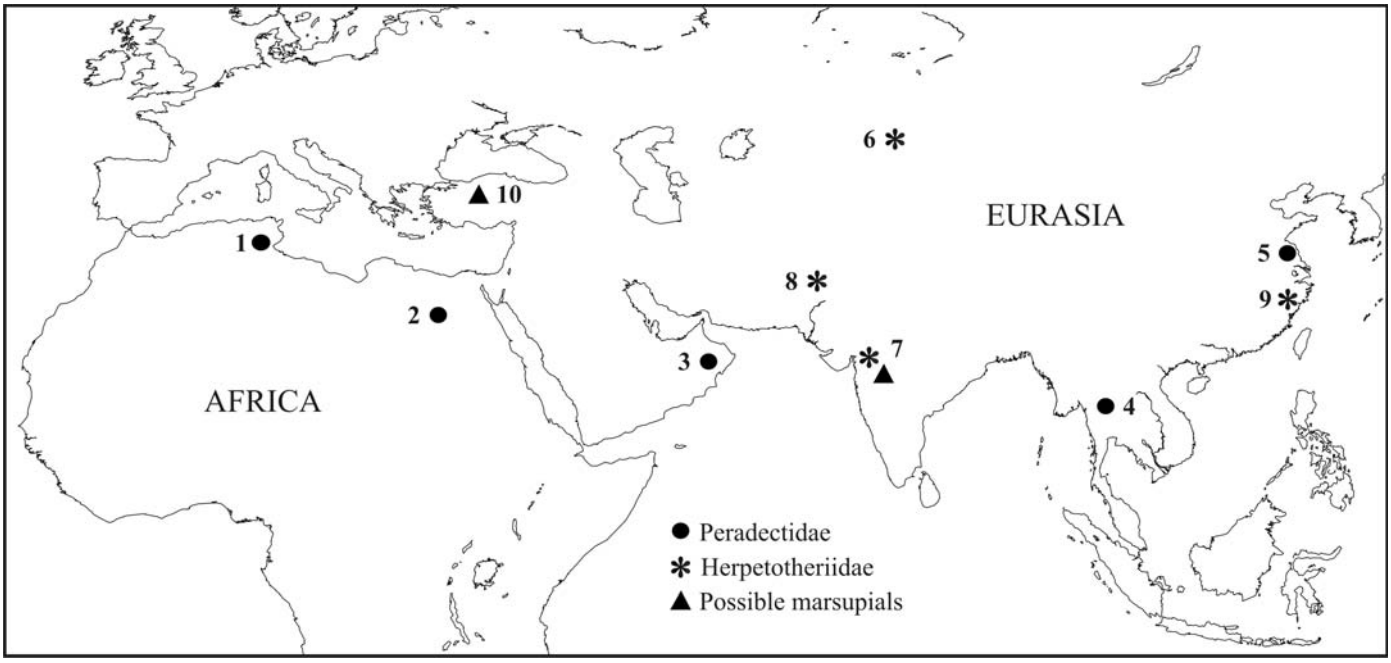

Fig. 4. Distribution of Cenozoic marsupials in North-Africa and Eurasia. Peradectidae: 1, Chambi, Tunisia (early Eocene); 2, Fayum, Egypt (early Oligocene); 3, Taqah, Oman (early Oligocene); 4, Li Basin, Thailand (middle Miocene); 5, Sonlinzhuang, China (early Miocene). Herpetotheriidae: 6, Zaissan Basin, Kazakhstan (late Eocene – early Oligocene); 7, Vastan lignite mine, India (early Eocene); 8, Bugti Hills, Pakistan (early Oligocene); 9, Shanghuang fissure fillings B and C, Jiangsu, China (middle Eocene). Localities that yielded remains of disputable marsupial affinity (see text): 7, Vastan lignite mine, India (early Eocene); 10, Kartal Formation, Turkey (Eocene).

The occurrence of *A. akbarbugtii* in Central Pakistan confirms the wide distribution of marsupials in Asia during the Paleogene. Although the fossil record of Paleogene marsupials in Asia remains poorly documented, the data have so far suggested that the herpetotheriids were mainly distributed north of the Alpine-Himalayan complex. In contrast, the peradectids may have been restricted to southern Asia with the exception of *Sinoperadectes* from the early Miocene of the Jiangsu Province, eastern China. The rise of the Himalayan Chain certainly constituted a physical barrier and it probably induced climatic changes that favored faunal provincialism in Asian during the middle and late Cenozoic. However, the presence of an undisputable Oligocene herpetotheriid in the southern Himalaya indicates that faunal exchanges also occurred between the Asian mainland and the Indian subcontinent as suggested by other groups of mammals (Clyde et al. 2003).

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