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NEW INSECTIVOROUS PLACENTALS FROM THE EOCENE OF PAKISTAN

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ABSTRACT

We report the discovery of two lower molars of small placental mammals from the late early/middle Eocene Kuldana Formation of the Kala Chitta Hills, Punjab, Pakistan. The first of these is tribosphenic, but lacks an entoconid. We name it *Perizalambdodon punjabiensis* and suggest that it may be related to the tenrecoid radiation of Africa. A second partial lower molar of a small tribosphenic placental is too incomplete to be identified to the family level. However, it does not pertain to any described taxon from Indo-Pakistan. Together with recent finds in the early Eocene of India, these teeth suggest that the diversity of the small insectivorous placentals from Indo-Pakistan was significant, and that much of this fauna remains to be discovered.

Key words: Eocene, Indo-Pakistan, Insectivores, Tenrecoids

INTRODUCTION

The fossil record of Palaeogene small insectivorous mammals from South Asia is very small. Placental mammal teeth and postcranials were reported from latest Cretaceous sediments associated with the Deccan Traps in Andhra Pradesh (Prasad *et al.*, 1994; Godinot and Prasad, 1994). Only a few samples of tribosphenic therians are known from the Palaeogene of the Indian subcontinent. Russell and Gingerich (1981) found small insectivorous teeth in the Eocene Mami Khel Formation (then called Kuldana Formation) of North-West Frontier Province (Pakistan). They identified two upper molars as the erinaceomorph *Seia shahi*, three lower cheek teeth as the proteuthere *Pakilestes lathrius*, and an upper and lower molar as two unnamed species of bats. Thewissen *et al.* (2001) found the first metatherian from Indo-Pakistan: a jaw with one complete lower molar of a didelphid marsupial from the Eocene Kuldana Formation of Punjab, Pakistan (Fig. 1). Gingerich *et al.* (2001) mentioned, but did not describe or figure insectivorous placentals from Gandhera Quarry in southern Pakistan. Bajpai *et al.* (2005a and b) discovered placental insectivores of several families as well as primitive marsupials in the Vastan Lignite Mine in Eastern Gujarat. Placental tribosphenic mammals from Vastan include the palaeoryctid *Anthraryctes vastanensis*, the cimolestid *Suratilestes gingerichi*, the apatemyid *Frugivastodon cristatus*, and the insectivorans *Vastania sahnia* and *Cambaya complexus* (Bajpai *et al.*, 2005a). Rana *et al.* (2005) recovered a cimolestid?, also at the Vastan Lignite Mine.

The present description only adds one and a half teeth to the sample of small tribosphenic mammals from pre-Oligocene deposits of Indo-Pakistan. Although small, these teeth are important because they may have implications for the origin of modern tenrecoids. Either way, the new fossils add taxa to the diversity of small mammals with primitive dentitions from northern Pakistan.

The specimens are part of the Howard University, Geological Survey of Pakistan project (H-GSP). They will be housed at the headquarters of the Geological Survey of Pakistan in Quetta.

SYSTEMATIC PALEONTOLOGY

Order **Lipotyphla** Haeckel, **1866**
Family unclear, probably new
Genus ***Perizalambdodon*** n. gen.

Type and only species: *P. punjabiensis* n. sp.

Derivation of name: *Peri* is Greek for around, *zalambdodon*, refers to zalambdodont tooth morphology. Together these suggest a relation between the new genus and post-Eocene placentals with zalambdodont teeth.

Diagnosis: Trigonid with three cusps, from large to small, protoconid, metaconid, and paraconid. Talonid lacking talonid basin and lacking entoconid.

Age and Distribution: late early Eocene/middle Eocene of northern Pakistan.

Perizalambdodon punjabiensis n. sp.
(Fig. 2A-B; Pl. I, Fig. 3A)

Derivation of name: *punjabiensis* is Latin and means "coming from Punjab." It refers to the province of Pakistan where the specimen was found.

Diagnosis: Generic and specific diagnosis cannot be distinguished at present.

Holotype and Only Specimen: H-GSP 92168, right lower molar (m1 or m2, fig. 1A and B) from H-GSP Locality 9610 (early

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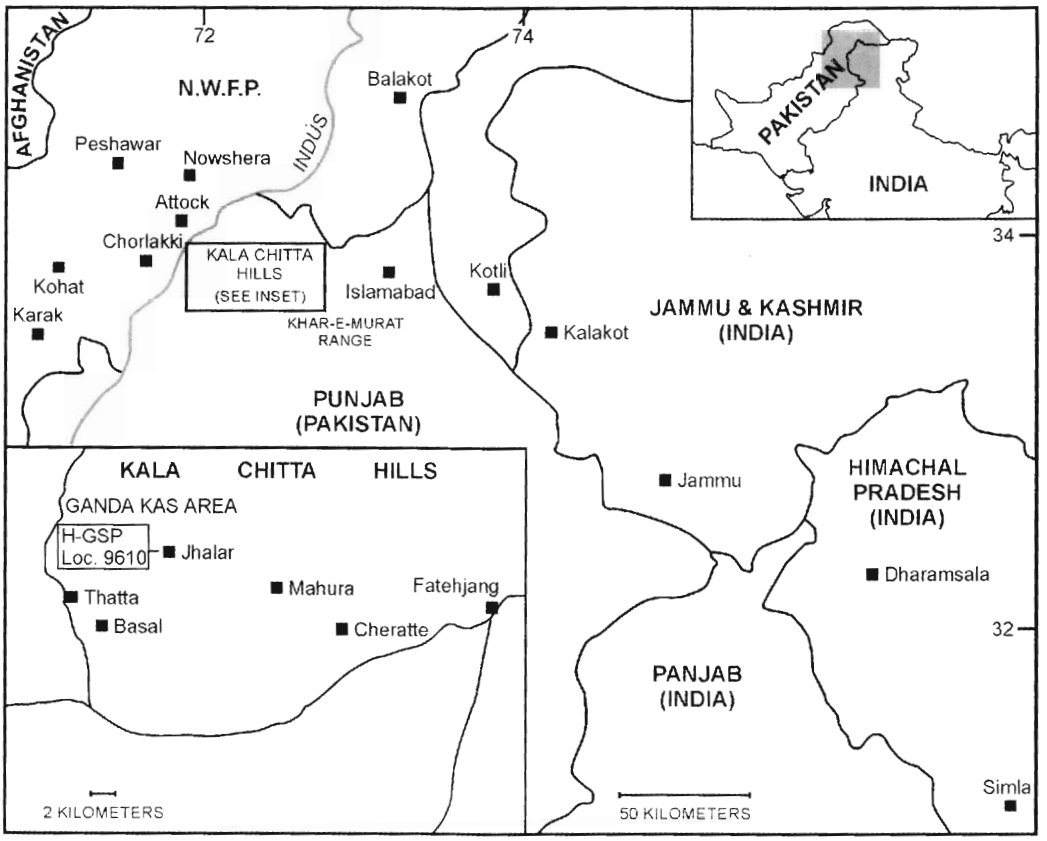

Fig. 1. Location map of the fossil-yielding locality. The inset shows position of the Kala Chitta Hills in Punjab, Pakistan.

Eocene), Jhalar Area of the Kala Chitta Hills (Punjab, Pakistan, see Thewissen *et al.*, 1998, for locality description). The metaconid is broken at its base, and much of the enamel on the lingual side of the tooth is damaged. A small interdental facet on the posterior side of the tooth indicates that it is not m3.

Description: H-GSP 92168 is a small lower molar (length: 0.93 mm; trigonid width: 0.63 mm; talonid width: 0.54 mm). On the trigonid, the protoconid is the largest cusp, followed by the metaconid. The paraconid is much smaller than either other trigonid cusp, and placed on the antero-lingual corner of the tooth. The paraconid is oval in cross-section. The metacristid is stronger than the paracristid, but these crests are more similar in size than in H-GSP 92167 (described below). There is no crest connecting paracristid and metacristid. Anteriorly, there is a small cingulum, mostly developed as a small cusp. This is the only cingulum present.

The talonid is much lower than the trigonid. There are only two cusps on the talonid, a large hypoconid, and a smaller hypoconulid. The hypoconulid is labial to the axis of the tooth, but is not twinned with the hypoconid. The lingual side of the talonid slopes smoothly to the posterior side of the trigonid, and therefore, there is no talonid basin. The cristid obliqua is low and touches the base of the trigonid below the notch in the metacristid.

Comparisons: H-GSP 92168 resembles a tribosphenic tooth with a trigonid basin that is not widely open labially, a protoconid that is distinctly higher than the metaconid and no twinning between hypoconulid and hypoconid. These three features are unlike marsupials. The only pre-Oligocene placental insectivores from Indo-Pakistan are *Deccanolestes*, *Pakilestes*, *Seia*, *Anthraryctes*, *Suratilestes, Frugivastodon*, *Vastania*, and *Cambaya*. *Perizalambdodon* is not closely related to *Deccanolestes* and *Frugivastodon*, which have a well-basined talonid with a large entoconid. The new specimen is too small to pertain to *Seia shahi*, and lacks the very high trigonid characteristic of palaeoryctids. However, the new species cannot be compared in detail because *Seia* or *Anthraryctes* are only known from upper teeth. *Pakilestes* and *Suratilestes* have a large projecting paraconid, widely open trigonid and well-developed trigonid basin, unlike *Perizalambdodon*. *Vastania* has an entoconid, unlike *Perizalambdodon*. There are also differences with H-GSP 92167 (see below), and we believe that *Perizalambdodon* is not closely related to any of the known insectivores from the pre-Oligocene of Indo-Pakistan.

Absence of the entoconid occurs in several unrelated insectivore families. Some apatemyids lack the entoconid, but they retain a talonid basin and their long, square trigonid is unlike that of *Perizalambdodon* and *Pakilestes*. The entoconid is also absent in certain palaeoryctids, but these differ from *Perizalambdodon* in the very high trigonid.

The absence of the basined talonid is unusual among

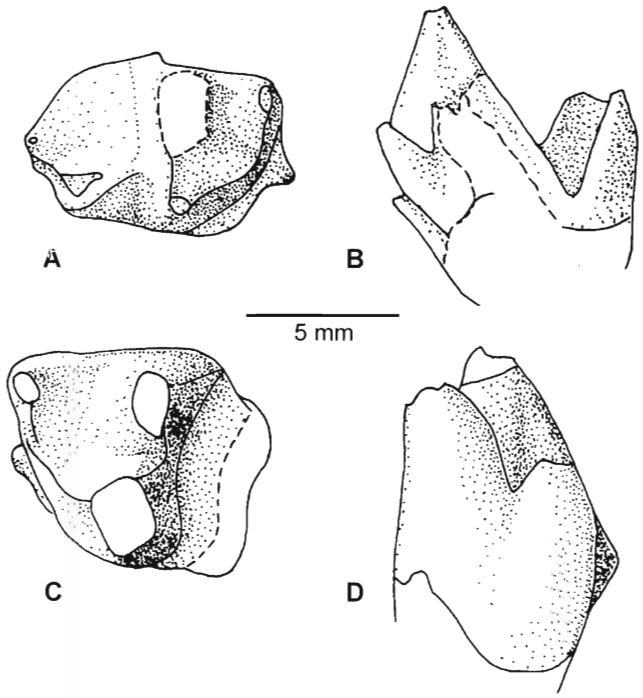

Fig. 2. Tribosphenic lower molars from the early Eocene Kuldana Formation of the Kala Chitta Hills, Pakistan. Holotype lower molar (H-GSP 92168) of *Perizalambdodon punjabiensis* in occlusal (A) and lingual (B) view. Unidentified trigonid (H-GSP 92167) of small insectivorous placental in occlusal (C) and lingual (D) view.

primitive mammals. Absence of this basin implies that one of the essential functions of tribosphenic teeth, crushing between protocone and talonid basin, was reduced. Reduction of this function suggests that the protocone of *Perizalambdodon* was small or absent (and thus implies a morphological difference with *Seia* and *Anthraryctes*).

Absence of the entoconid and lack of the talonid basin occurs in apternodontids. *Perizalambdodon* is similar to the North American apternodontid *Parapternodus antiquus* Bown and Schankler (1982) in the main features of the talonid, especially the lack of the entoconid and the long, lingually sloping talonid. These two taxa differ in that *Parapternodus* has a higher trigonid with higher cusps, a larger paraconid that is more anteriorly placed, and retains only a single cusp on the talonid (hypoconid). Apternodonids are only described from North American, but Russell and Zhai (1987) reported an undescribed apternodontid from the middle Eocene of Mongolia. Apternodontids are sometimes thought to be related to tenrecoids (Butler, 1988; Asher, 1999; but see McDowell, 1958).

The entoconid and the talonid basin are absent in a number of modern lipotyphlan insectivores, such as tenrecoids and chrysochlorids. This talonid morphology is commonly associated with zalambdodonty in these forms. The evolutionary history of tenrecids is poorly documented, but they are generally held to be closely related to potamogalids (Butler and Hopwood, 1957; Asher, 2000). The two families are commonly classified as Tenrecoidea. Miocene Kenyan tenrecoids have a well-developed talonid, but lack a talonid basin with a single talonid cusp (Butler and Hopwood, 1957; Butler, 1985). In two derived features (absence of talonid basin, absence of entoconid) they are similar to *Perizalambdodon*. The trigonid of these African forms is primitive, not unlike that of *Perizalambdodon*.

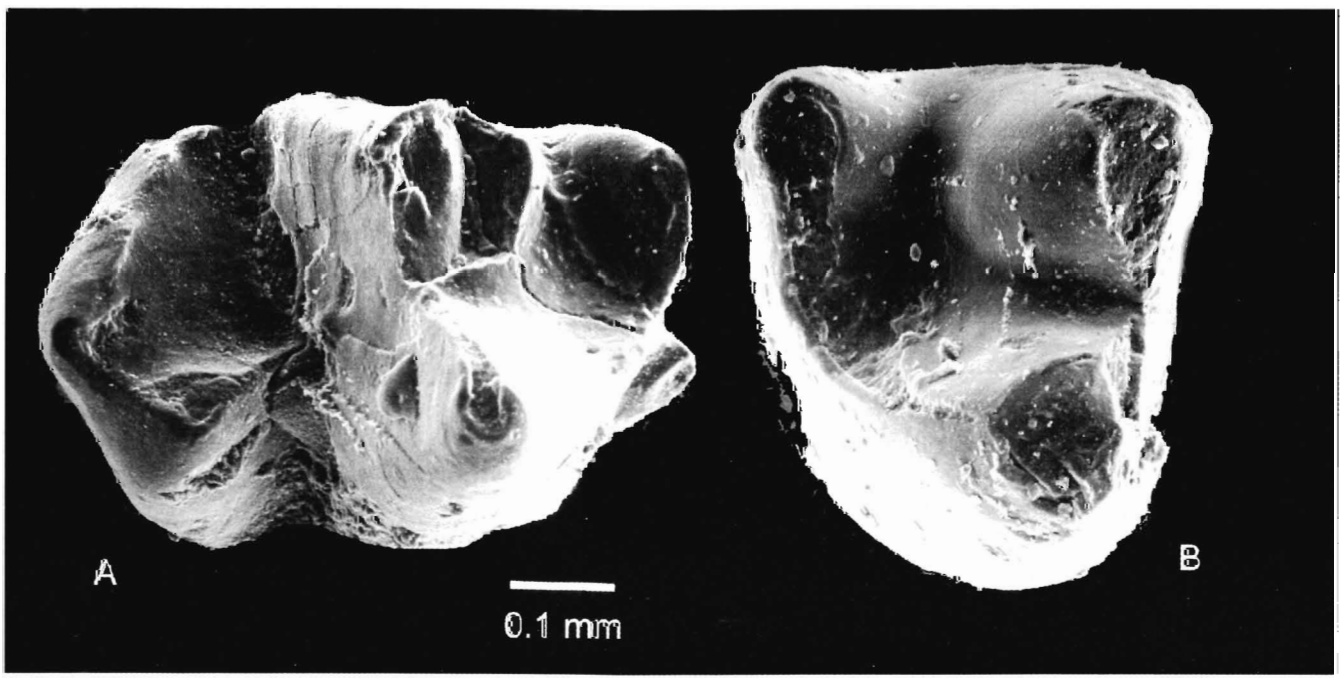

Fig. 3. Eocene insectivores from Pakistan in occlusal view. Right lower molar, holotype of *Perizalambdodon punjabiensis* (A, H-GSP 92168) and left trigonid of indeterminate placental insectivore (B, H-GSP 92167).

Widanelfaresia from late Eocene of Egypt has been suggested as a tribosphenic relative of tenrecoids (Seiffert and Simons, 2000). The talonid of *Widanelfarasia* is primitive, retaining entoconid and talonid basin. Tenrecoids are thus more similar to *Perizalambdodon* than to *Widanelfarasia*, and the derived shape of the talonid may predate *Widanelfaresia* and extend into the Eocene.

Given the limited material and the unusual morphology, we cannot assess the affinities of *Perizalambdodon* with any degree of certainty. However, the talonid similarities to tenrecoids are intriguing, especially since this is an endemic African group. If these are supported by further evidence, then there are interesting implications that go beyond mammalian phylogeny.

It appears that the reduction of the talonid basin and possibly zalambdodonty is ancient, and was well underway at the time of *Perizalambdodon*, the late early or middle Eocene. This argues for an ancient origin of the families of tenrecoids (and possibly chrysochlorids if these are closely related: Asher, 2000). This is consistent with a Cretaceous divergence date of the lipotyphlan families as proposed by molecular data (e.g., Stanhope *et al.*, 1998). It is also consistent with an early divergence of lipotyphlan families as implied by the identification of derived lipotyphlans in the early Cretaceous of Australia as proposed by Rich *et al.* (1997, 1999).

The biogeographic implications of *Perizalambdodon* are ambiguous. Indo-Pakistan, with Seychelles-Madagascar adjacent to its western margin, separated from Africa about 160-150 Ma ago, and Madagascar broke away from Indo-Pakistan in the late Cretaceous (Krause *et al.*, 1997a). If *Perizalambdodon* is related to tenrecoids, it is possible that the origin of tenrecoids predates the divergence of Madagascar and Indo-Pakistan.

Order **Proteutheria** Romer, 1966,
or
Order **Lipotyphla** Haeckel, 1866
Gen. et sp. indet.
(Fig. 2C-D; Fig. 3B)

Referred Specimen: H-GSP 92167, trigonid of left lower molar (fig. 1C and D) from H-GSP Locality 9610, near Jhalar in the Kala Chitta Hills, Pakistan (for locality information see Thewissen *et al.*, 1998).

Description: H-GSP 92167 is the trigonid of a small lower molar (width: 0.88 mm). The largest cusp on the trigonid is the protoconid, followed by a slightly smaller metaconid, and a much smaller paraconid which is circular in cross section. The metacristid is strong and high, in contrast to the low paracristid. There is no crest connecting para- and metaconid. The posterior side of the trigonid is preserved, and it is clear that the trigonid was much higher than the talonid and that the cristid obliqua had a low contact with the trigonid. Oblique striations indicate extensive microwear on the posterior side of the trigonid. A cingulum is only present on a part of the anterior aspect of the tooth, where it develops into a slight cusp lingually.

Comparisons: The protoconid is higher than the metaconid, and the trigonid basin is not open widely on its lingual side in H-GSP 92167. These features indicate that the tooth probably pertains to a placental mammal. It is unlike *Deccanolestes* in having a metacristid much higher than the paracristid. H-GSP 92167 is smaller than *Seia*, but cannot be directly compared, and the new specimen is larger than *Suratilestes* and *Vastania*. *Pakilestes* has a stronger, more anteriorly placed paraconid, and the trigonid of *Frugivastodon* and *Cambaya* is more open and flat. H-GSP 92167 also differs from *Perizalambdodon*. The paraconid of H-GSP 92167 is more or less circular in cross-section, whereas in *Perizalambdodon* it is oval. In H-GSP 92167 the paracristid is lower on the trigonid than in *Perizalambdodon*. At present, insufficient material is known for the taxon to allow identification beyond placental mammal, although it establishes the presence of another insectivorous mammal in the Eocene of Indo-Pakistan.

CONCLUDING REMARKS

Insectivorous mammals from southern continents are rare. The main significance of *Perizalambdodon* is that it may represent a relative of the tenrecoids, as indicated by the morphology of its talonid. More complete fossils are required to test this hypothesis, but it would point at an ancient divergence of the families of lipotyphlan insectivores.

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