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Basalina, a Tillodont from the Eocene of Pakistan

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With Plate 15

Abstract

Basalina basalensis Dehm and Oettingen-Spielberg, 1958 from the middle Eocene of Ganda Kas, Pakistan originally was assigned to the Taeniodonta but here is reassigned to the Tillodontia. Basalina is a distinct genus of tillodonts diagnosable by its small size, rooted I2, loss of I3, relatively large C1, rudimentary P1, single-rooted P2, molariform P4 and mandibular symphysis extending beneath P4. The reassignment of Basalina extends the geographic range of the tillodonts into the subcontinent and supports previous suggestions of Asian affinities of the Eocene land mammals of India and Pakistan.

Kurzfassung

Basalina basalensis Dehm & Oettingen-Spielberg, 1958 aus dem Mitteleozän des Ganda Kas, Pakistan, war zuerst zu den Taeniodonta gestellt, wird jedoch hier zu den Tillodontia gerechnet. Basalina ist eine Gattung, die durch kleines Format, bewurzelten I2, fehlenden I3, relativ großen C1, rudimentären P1, einwurzeligen P2, molariformen P4 und dadurch gekennzeichnet ist, daß die Symphyse unter den P4 sich erstreckt. Die neue Zuweisung der Gattung Basalina dehnt die geografische Verbreitung der Tillodontia auf den Subkontinent aus, und bekräftigt die früher vertretene Ansicht über eine Verwandtschaft zwischen den eozänen Landtieren Asiens und Indien-Pakistans.

Introduction

Basalina basalensis was one of the most enigmatic forms described by Dehm and Oettingen-Spielberg (1958) in their classic monograph on the Eocene mammals from the Ganda Kas region, Pakistan. Known from a badly damaged and nearly edentulous left dentary fragment, Basalina was assigned to the Taeniodonta (Dehm & Oettingen-Spielberg, 1958, p. 7–10). Another edentulous left dentary fragment similar to the type speci-

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men of Basalina was identified by Dehm & Oettingen-Spielberg (1958, p. 10) as

"Taeniodontum gen. et. spec. indet."

Since its original description, Basalina has infrequently been mentioned in the literature. Romer (1966, p. 381) listed it as a taeniodont, but Patterson (in Butler et al., 1967) did not. Sahni & Khare (1973, p. 48), Flerov et al. (1974, p. 94, fig. 33) and Gingerich (1977, p. 192) also considered Basalina a taeniodont though later GINGERICH et al. (1979, p. 119) listed it as "Tillodontia(?)." GINGERICH & GUNNELL (1979, p. 150) recently stated that the morphology of Basalina "more closely resembles that of tillodonts [than taeniodonts]" and "on biogeographical evidence Basalina is also more likely to represent a tillodont than a taeniodont." Most recently WEST (1980, p. 510) listed Basalina as a tillodont.

Although it is evident that most recent authors consider Basalina to be a tillodont, no one has yet attempted to demonstrate this by restudying the type specimen in the light of new information on taeniodonts, tillodonts and other early Tertiary mammals that has appeared since Dehm & Oettingen-Spielberg (1958). We here reopen the discussion of the ordinal affinities of Basalina, redefine the genus as a tillodont and briefly discuss its implications for the Paleogene biogeography of the subcontinent.

Systematic Paleontology

Order Tillodontia MARSH, 1875 Family Esthonychidae COPE, 1883

Genus Basalina Dehm & Ofttingen-Spielberg, 1958

Type species: Basalina basalensis Dehm & Ofttingen-Spielberg, 1958, the only known species.

Distribution: Ganda Kas (DEHM & OETTINGEN-SPIELBERG, 1958) and Chorlakki

(WEST, 1980) localities, middle Eocene of Pakistan.

Revised diagnosis: Small tillodonts with rooted I2, I3 absent, relatively large C1, rudimentary P₁, single-rooted P₂, molariform P₄ and mandibular symphysis extending under the P4 trigonid.

Basalina basalensis Dehm & Oettingen-Spielberg, 1958

Holotype: Bayerische Staatssammlung für Paläontologie und historische Geologie München, Nr. 1956 II 2, a lest dentary fragment with I2 alveolus, C1 root, P1 alveolus, roots of P2-3, partial P4 and anterior roots of M1 (Pl. 15).

Horizon and locality of the type: Fundstelle 20 (DEHM & OETTINGEN-SPIEL. BERG, 1958) near Ganda Kas, north of Basal, western Punjab, Pakistan in the lower part of

the Kuldana Formation of middle Eocene age (WEST & LUKACS 1979, p. 13).

Referred specimens: West (1980) listed undescribed material from Chorlakki, Pakistan as B. basalensis. The edentulous jaw fragment identified by DEHM and OETTIN-GEN-Spielberg (1958) as "Taeniodontum gen. et spec. indet." here is identified as cf. B. basalensis (see later discussion).

Diagnosis: Same as for the genus.

Description: Dehm and Oettingen-Spielberg (1958, p. 8–10) provided a detailed description and measurements of the type specimen of *B. basalensis*. They also illustrated the specimen (Dehm & Oettingen-Spielberg, 1958, fig. 1; Pl. 2, fig. 1, a—e) and we illustrate it here (Pl. 15). There is little to add to Dehm and Oettingen-Spielberg's description except to note that our interpretation of the tooth formula of *B.* differs from theirs.

Discussion: Dehm and Oettingen-Spielberg (1958) identified the large, rooted anteriormost tooth preserved in the type specimen as the C_1 ; the alveolus anterior to it was identified as that of I_3 . The incomplete, but only preserved tooth near the posterior end of the jaw was deemed M_1 . Four single-rooted premolars intervened between the C_1 and M_1 , the first premolar only represented by a shallow alveolus. Behind M_1 were the roots of a larger M_2 .

Considering Basalina to be a tillodont, we suggest that the large anteriormost alveolus of the type specimen is that of I2, similar to 12 in Esthonyx (GINGERICH & GUNNELL, 1979). In all tillodonts 1₂ is enlarged and I₃ is greatly reduced or lost (GAZIN, 1953, p. 67). I₃ appears to have been lost in Basalina. The I₂ of Basalina is followed by a large C₁, as in Esthonyx (GINGERICH & GUNNELL, 1979, Pl. 1, fig. 4). The small, shallow alveolus behind C₁ could either be for a rudimentary P₁, or a double-rooted P₂ as in some specimens of Esthonyx (GINGERICH & GUNNELL, 1979, p. 132). In the type specimen of Basalina, the alveolus directly behind the C₁ is much smaller and shallower than the succeeding alveolus, and therefore we consider these alveoli to pertain to different teeth. Thus, the alveolus immediately following C₁ is for P₁. It is followed by a single, obliquely-oriented alveolus for P2; the P2 often is single-rooted and obliquely oriented in tillodonts (GAZIN, 1953, p. 67; GINGERICH & GUNNELL, 1979, text-fig. 2). P3 is double-rooted in all tillodonts and we consider the next two alveoli to be those of P3. That these two roots pertain to one tooth is suggested by the jaw fragment which is broken around them to form a depression, suggesting the breaking off of one piece. These two roots are broken off at different heights and the anterior root clearly is pitched forward whereas the posterior root is vertical, as in Esthonyx (GINGERICH & GUNNELL, 1979, text-fig. 2). The only partially preserved tooth in the type specimen of Basalina thus is a molariform, two-rooted P₄ as in all tillodonts (GAZIN, 1953). It is followed by an M₁ which, from the partial roots preserved, is slightly wider than P4, as in other tillodonts (GAZIN, 1953).

Our interpretation of the tooth formula of *Basalina* also is consistent with the deepening of its mandibular symphysis to under P_4 , a condition intermediate between that of *Esthonyx* and *Trogosus* (GAZIN, 1953). In addition, the mental foramina on the type specimen of *Basalina* are scattered under $P_{2\rightarrow4}$ according to our interpretation; this is the same position as in other tillodonts (GAZIN, 1953).

Accepting our interpretation of the tooth formula of Basalina, it resembles tillodonts in the following characters: deepening of the mandibular symphysis, under P_4 in Basalina (Pl. 15, fig. 4), intermediate between Esthonyx (usually under P_3 : Gazin, 1953, p. 61) and Trogosus (under M_1 : Gazin, 1953, p. 61); possession of four mental foramina scattered between P_{2-4} (cf. Gazin, 1953, p. 62); reduction of the number of roots of the anterior premolars, P_{1-2} : possession of a molariform, bunoselenodont P_4 ; and possession of a large tooth anterior to the canine, typically I_2 in tillodonts and so interpreted here for Basalina. The reduction of the anterior premolars (i. e., either their loss or reduction of the number of roots) is a synapomorphy of the Tillodontia separating them from the

closely related pantodonts (cf. GAZIN, 1953; CHOW & WANG, 1979) in which there typically are four, double-rooted lower premolars.

Basalina can be excluded from the Taeniodonta for the following reasons: 1. The lower cheek teeth of all taeniodonts are hypsodont, with enamel extending much further down the labial aspects of the teeth than the lingual aspects (PATTERSON, 1949). The enamel on the only preserved cheek tooth of Basalina is only slightly higher on the labial aspect than the lingual (Pl. 15, figs. 3, 4), as in Esthonyx (GINGERICH & GUNNELL, 1979).

2. The molariform cheek teeth of conoryctine taeniodonts (cf. WORTMAN, 1897; MATTHEW, 1937) possess trigonids with three distinct cusps (although in some forms the paraconid is much reduced) and talonids bearing subequal hypoconids, entoconids and hypoconulids. The trigonids and talonids are subcircular, of subequal height and no trace of a selenoid crest is present, as in Basalina. In the stylinodontine taeniodonts, to which Basalina originally was referred, the cheek teeth are either conoryctine-like in primitive forms, or are bilophodont in derived forms with the trigonids and talonids anteroposteriorly compressed and transversely broadened (PATTERSON, 1949). The cheek tooth preserved in the type specimen of Basalina thus bears little resemblance to the cheek teeth of any taeniodont.

cf. Basalina basalensis: The specimen referred by Dehm and Oettingen-Spielberg (1958) to "Taeniodontum gen. et. spec. indet." resembles the type specimen of Basalina in size and all discernible morphological details. It appears to be a left dentary fragment (Pl. 15, fig. 5–6) bearing the root of P_2 , the two alveoli for P_3 and part of the anterior root of P_4 . Two foramina are present below the posterior alveolus of P_3 and the leading edge of P_4 . Although we are reasonably confident the specimen pertains to Basalina it is so incomplete that we only identify it as cf. B. basalensis.

Paleobiogeographical Implications

Sahni and Kumar (1974) recently reviewed the Paleogene biogeography of the Indo-Pakistani subcontinent. They concluded (p. 223–224) that "migration of large terrestrial mammals from Central Asia to the Indian subcontinent was only possible at the beginning of the middle Eocene when the Indian Plate abutted against the Sino-Siberian Platform establishing a stable land route for dispersal." They qualified this conclusion by stating (p. 221) that the smaller mammals "may have crossed over from the Asiatic landmass in a sweepstake fashion by island hopping across the Tethys in advance of the larger mammals, by the late lower Eocene." The affinities of most of the Eocene land mammals of the subcontinent are with Asian forms (e. g., Dehm & Oettingen-Spielberg, 1958; Sahni & Khare, 1973; West, 1980), clearly supporting their conclusions.

The affinities of the marine and shoreline mammals (cetaceans, sirenians, moeritheres) of the Indo-Pakistani Eocene, as West (1980) has pointed out, are with those of the late Eocene-early Oligocene faunas of the Fayum, Egypt in the Tethyan region. West (1980, p. 531) thus suggested that "perhaps, during its northward drift, the South Asian subcontinent passed near enough to the eastern coast of Africa for a quasi-continental connection to have existed". West (1980, p. 531) justified this conclusion by claming that "the moeritheres, if they were terrestrial or amphibious, required continental connections for the African-South Asian distribution". We believe, however, that the moeritheres, generally

agreed to have been amphibious (COPPENS & BEDEN, 1978), may readily have swam across shallow marine barriers much as hippos evidently swam to Madagascar. We thus see little evidence to support West's suggestion. The fact that few land mammals other than moeritheres are shared between the Fayum and Eocene faunas of Indo-Pakistan suggests that no land connection existed between these areas prior to the middle Eocene.

Assignment of *Basalina* to the Tillodontia establishes the presence of this order in the subcontinent. Tillodonts are otherwise known from the latest Paleocene-middle Eocene of North America (Gazin, 1953; Gingerich & Gunnell, 1979), Paleocene and Eocene of China (e. g., Chow, 1963; Wang, 1975; Zhou et. al., 1977) and early (?) Eocene of Europe (Teilhard de Chardin, 1922; Gingerich & Gunnell, 1979); they are thus one of the most widely distributed orders of early Tertiary mammals. The three teeth of *Esthonyx* from Europe are of a form larger than *Basalina* (Gingerich & Gunnell, 1979). They might be used as slight evidence of European affinites of *Basalina* were it not for the fact that western Europe during the early Eocene and Paleocene was evidently separated from Asia by the north-south Turgai Straits, a barrier probably impervious to land mammal migration between the two continents (McKenna, 1975).

It is more likely that Basalina's closest relatives lie among the Chinese tillodont genera Lofochaius, Adapidium and Meiostylodon (Kuanchanius is a derived form close to Trogosus). However, our incomplete knowledge of Basalina and these Chinese forms (the lower dentitions of Lofochaius and Meiostylodon, for example, are virtually unknown) render assessment of close relationships speculative at best. Lofochaius is so primitive a tillodont that it would be easy to imagine it as the ancestor of all other tillodonts, including Basalina.

The fact that neither Basalina nor a tillodont very similar to Basalina in its degree of anterior dental reduction and molarization of P4 is known from Asia might be construed as evidence that Basalina reflects in situ evolution in the subcontinent of a more primitive tillodont that migrated there before the middle Eocene. This would support Sahni and Kumar's notion, cited earlier, that small mammals, like Basalina or its ancestor, may have reached the subcontinent before the middle Eocene. Such a conclusion, however, is based primarily on negative evidence and cannot be strongly defended. That no tillodonts are yet known from the Fayum or the rest of the Tethyan region is also negative evidence, but fits in well with the argument that the closest affinities of Basalina and the other land mammals of the Indo-Pakistani Eocene are with Asian land mammals.

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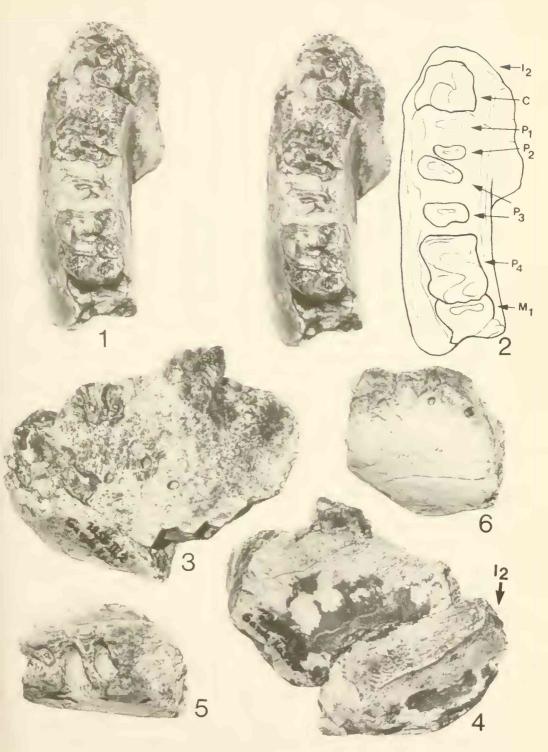
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Plate 15

- 1—4: Holotype of Basalina basalensis Dehm and Oettingen-Spielberg, 1958, a left dentary fragment with I₂ alveolus, C₁ root, P₁ alveolus, P₂₋₃ roots, partial P₄ and partial M₁ root; occlusal stereophotograph (1), interpretation of tooth formula (2), labial view (3) and lingual view (4); BSP 1956 II 2.
- 5-6: cf. Basalina basalensis, a left dentary fragment with P₂ root, P₃ alveoli and partial anterior P₄ root, occlusal (5) and labial (6) views; BSP 1956 II 3.
 All figures ×2.



LUCAS, S. G. & R. M. SCHOCH: Basalina.

Plate 15

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