

A POSSIBLE LATE CRETACEOUS “HARAMIYIDAN” FROM INDIA

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A new specimen from India represents the first mammal described from the Infratrappean beds (= Lameta Formation), the first record of “Haramiyida” from the subcontinent, and as much as a 90-million-year extension of the temporal range of this poorly known group. The specimen is part of a collection of mammalian fossils from the Infra- and Intertrappean beds of Andhra Pradesh, India (Maastrichtian) that includes more than 60 isolated teeth, dentulous jaws, and postcranial elements of several new eutherians and at least one gondwanatherian. Here we describe the isolated molariform from the collection and provisionally refer it to a new genus and species of ‘Haramiyida.’ The remainder of the collection will be described elsewhere.

The enigmatic ‘Haramiyida,’ which may be the paraphyletic stem group of multituberculates (e.g., Butler, 2000), are mostly known from isolated teeth from the Late Triassic to Middle Jurassic of western Europe (e.g., Butler, 2000), the Middle Jurassic of China (Maisch et al., 2005), the Late Jurassic of Tanzania (Heinrich, 1999, 2001), and possibly the Early Jurassic of North America (Jenkins et al., 1983) and the Early Cretaceous of Morocco (Butler and Hooker, 2005). A maxilla, dentaries, and some postcranial material are also known from the Late Triassic of Greenland (Jenkins et al., 1997).

Although the topic of higher-level phylogenetic relationships within Allotheria is controversial (see Kielan-Jaworowska et al., 2004), we currently favor the hypothesis of Butler (2000) and Butler and Hooker (2005) that the ‘Haramiyida’ are a paraphyletic stem group, consisting of all allotherians not belonging to Multituberculata, and adopt their classification of the group. Their hypothesis is based on shared, derived dental features, namely cheek teeth with multiple, mesiodistally oriented rows of cusps, and evolution of an inferred bilateral mesiodistal chewing movement in the Allotheria (Butler, 2000; Luo et al., 2002). Opponents cite the homoplasy of the triossicular middle ear and postcranial features required by this hypothesis (e.g., Luo et al., 2002). However, a recent study indicating multiple independent origins of the triossicular middle ear may remove some of the obstacles against this hypothesis (Rich et al., 2005). According to convention, we place the name of the paraphyletic taxon in quotations.

Specimen orientation and cusp nomenclature used here follow those for molariforms of haramiyids and eleutherodontids (families within the ‘Haramiyida’) proposed by Butler (2000). Haramiyid upper molariforms have two main mesiodistal rows of cusps labeled A and B (buccal and lingual) and on some an accessory distolingual cingulum, which can bear a series of cuspules or crenulations. Eleutherodontid upper molariforms have three main rows of cusps labeled A, B, and BB (buccal to lingual). The latter row, which is best developed mesially, might be homologous with the distolingual cingulum of haramiyids. Individual cusps of these rows are numbered from the distal to mesial end of the upper molariform crown. Cusps at the distal end of haramiyid upper molariforms tend to be larger and more constant than the smaller and more variable cusps at the mesial end. Eleutherodontid upper molariforms have a large distal cusp (B1) and distinct cusps at the ends of each of the three rows of cusps. As these taxa are known only from isolated teeth, tooth position and tooth row count are largely unclear. We use the morphology of haramiyid and particularly eleutherodontid upper molariforms as a framework for orientation of the Indian specimen. However, we stress that it would be naive to assume that the morphological traits used to orient much older haramiyid and eleutherodontid molariforms directly apply to the latest

Cretaceous specimen. The orientation adopted below should be considered a working hypothesis adopted for the convenience of description. Its testing awaits further discoveries.

Institutional Abbreviation—GSI/SR/PAL, Geological Survey of India, Southern Region (Hyderabad), Palaeontology Division, which is the repository of the specimen.

SYSTEMATIC PALEONTOLOGY

ALLOTHERIA Marsh, 1880

‘HARAMIYIDA’ Hahn, Sigogneau-Russell, and Wouters, 1989

?HARAMIYIDAE Simpson, 1947

AVASHISHTA, gen. nov.

Etymology—*avashisht*, (Sanskrit) that which survives, referring to the survival of the ‘Haramiyida’ into the latest Cretaceous.

Type Species—*Avashishta bacharamensis*, sp. nov.

Diagnosis—As for the type and only species.

AVASHISHTA BACHARAMENSIS, sp. nov.

(Fig. 1A–D)

Etymology—*bacharamensis*, from near the village of Bacharam, Andhra Pradesh, India.

Holotype—GSI/SR/PAL-B215, a nearly complete right upper molariform.

Type Locality and Horizon—Maastrichtian, Infratrappean beds near Bacharam, Andhra Pradesh, India (17° 20' N, 79° 50' E). The sediments are made up of sandstones, which are conglomeratic in places, grayish clays, and marls of varying thickness (2.5–3.0 m). Additional data are available from the GSI.

Diagnosis—Upper molariform differs from those of (1) other ‘haramiyidans’ in that the main longitudinal groove is restricted to the distal end of the crown; (2) haramiyids in that it has five cusps in the A and B rows, a large BB cusp, and low, well-separated cusps (except the Late Jurassic *Allostaffia*); and (3) eleutherodontids in its ovoid occlusal outline and lack of a distinct row of BB cusps.

Description—Our working hypothesis is that GSI/SR/PAL-B215 is a right upper molariform. The specimen has suffered some breakage at the mesial end of the crown; some enamel is missing from the distal end and lateral sides of the crown; and the roots are not preserved. In lateral view (Fig. 1A, B), the crown is saddle-shaped with its occlusal surface rising toward both its mesial and distal ends. In occlusal view (Fig. 1C, D), the crown narrows toward one end, which is presumed to be the distal end. The large, damaged cusp on the lingual side of the distal end of the crown is cusp B1. The A row consists of five cusps, of which four are subequal in height and a fifth (A1) is damaged but evident in buccal view (Fig. 1A). These cusps are buccolingually compressed and steeply sloped on their lingual sides, especially cusps A2–A4. The grooves separating the cusps (particularly the mesial cusps) slope mesially from the base of the crown toward the occlusal surface similar to the mesial inclination of the cusps of multituberculate upper molars. From B1, a low, rounded ridge, which consists of two cusps (B2, B3), extends mesially to two prominent cusps (B4, B5). Cusp B4 is lower than cusps in the A row and has a rounded pyramidal shape with a transversely expanded base. Cusp B5,

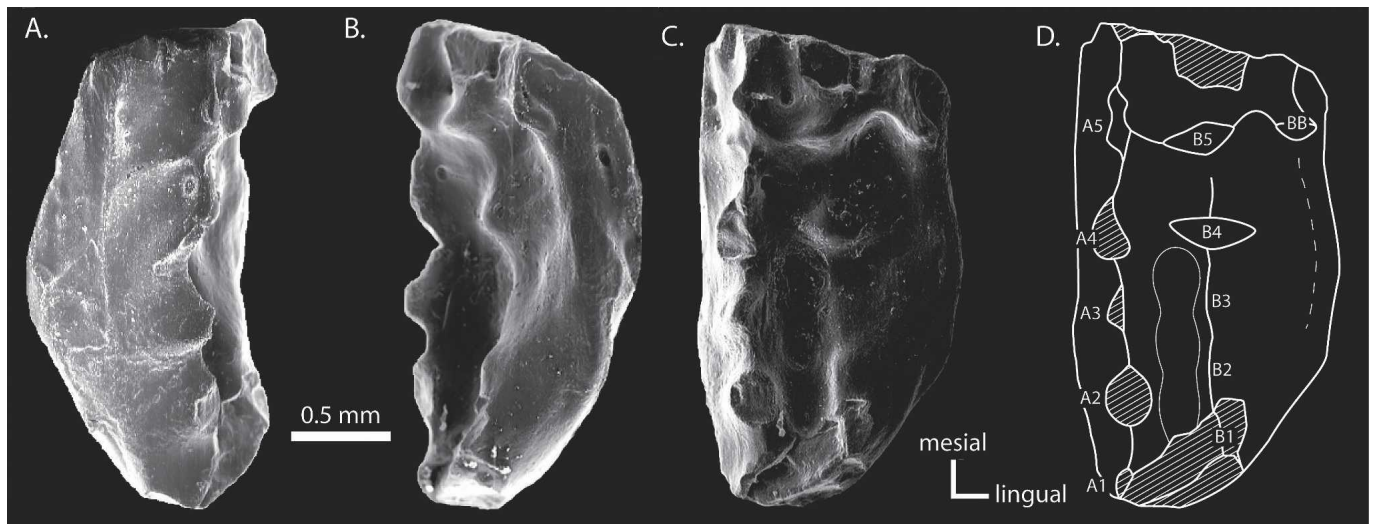


FIGURE 1. Scanning electron microscope images of the right upper molariform, GSI/SR/PAL-B215, of *Avashishta bacharamensis* in (A) buccal, (B) lingual, and (C) occlusal views. D, schematic drawing of specimen in occlusal view with proposed cusp identifications. Hatched areas indicate breakage.

which has suffered some damage, is nearly equal in height to cusps in the A row and its base is expanded transversely to connect with A5 buccally and with a relatively large cusp lingually, interpreted as the BB cusp. The transverse connection at the mesial end of the crown may be comparable to the U-shaped ridge found in the upper molariforms of *Thomasia* (Late Triassic–Early Jurassic), or, if the mesiodistal orientation is reversed, the transverse connection may be comparable to the connection that joins cusps A1 and B1 in *Thomasia*. We favor the former interpretation. The lingual margin of the crown from cusp B1 to cusp BB is relatively smooth but may have contained a low cingulum that was lost to wear. The area between the B row and the lingual margin is a very shallow basin. The area between the A and B rows forms, at the distal end of the crown, a distinct but shallow longitudinal groove, which may be comparable to the main longitudinal groove of *Thomasia* molariforms. Two concavities along this groove may have received cusps of the opposing lower molariform. The minimum length of the crown is 2.43 mm and the maximum width is 1.33 mm.

Comparisons—The latest Cretaceous age for *Avashishta* and the mesiodistal rows of cusps on its upper molariform prompt comparisons with multituberculates. However, the detailed morphology of the new specimen (e.g., incomplete longitudinal groove, concavities along the groove) suggests that *Avashishta* had an orthal chewing motion characteristic of ‘haramiyidans’ rather than a palinal chewing motion characteristic of multituberculates (Butler and Hooker, 2005). Among ‘haramiyidans,’ *Avashishta* is morphologically most comparable to haramiyids and eleutherodontids. GSI/SR/PAL-B215 possesses what may be a lingual cingulum, like some upper molariforms of haramiyids, and a mesiolingual BB cusp, like upper molariforms of eleutherodontids. In other regards, the morphology of the new specimen is distinguishable from the upper molariforms of those haramiyoid families.

Thomasia is a haramiyid from the Late Triassic to Early Jurassic of western Europe (e.g., Kielan-Jaworowska et al., 2004). Its upper molariforms differ from GSI/SR/PAL-B215 in that (1) the A row has only three cusps; (2) the main longitudinal groove extends most of the mesiodistal length of the crown; and (3) although a distolingual cingulum might be present, they lack a large mesiolingual cusp (BB cusp).

Eleutherodon, the only eleutherodontid genus, is known from the Middle Jurassic of England and Wales (Kermack et al., 1998; Butler and Hooker, 2005) and the ?late Middle Jurassic of China (Maisch et al., 2005). Upper molariforms of *Eleutherodon* are similar to GSI/SR/PAL-B215 in possession of an A row with more than three cusps and a large mesiolingual BB cusp. They differ from GSI/SR/PAL-B215 in that (1) the main longitudinal groove is broad and deep and extends most of the mesiodistal length of the crown; (2) the occlusal outline is rhomboidal rather than long and ovoid; (3) the BB row is distinct and contains numerous cusps; and (4) like *Thomasia*, their cusps tend to be tightly packed mesiodistally.

Another haramiyid, *Allostaffia* (formerly *Staffia*, but see Heinrich 2004), is known from the Late Jurassic of Tanzania by two lower molariforms and an upper molariform (Heinrich, 1999, 2001). We differ from Heinrich (2001) in the orientation of the isolated upper molariform, suggesting that what he has identified as buccal and lingual sides should be reversed. His A row would be the B row, and his short mesiobuccal cingulum (AA row) would be a mesiolingual cingulum (BB row). This upper molariform is similar to GSI/SR/PAL-B215 in possession of (1) a crown that is saddle-like in lateral view; (2) low and well-separated cusps with blunt apices (although this may reflect similar states of preservation); (3) a main longitudinal groove that is deepest at the distal end of the crown; (4) a buccal wall of the main longitudinal groove that is steeper than the lingual wall; and (5) BB cusps at the mesial end of the crown. It differs from GSI/SR/PAL-B215 in that (1) the main longitudinal groove is broader, deeper, and longer; (2) mesial and distal transverse ridges linking the A and B rows are not prominent; and (3) it lacks a broad, shallow valley between the B row and the lingual margin of the crown.

In sum, *Avashishta bacharamensis* has morphological similarities to ‘haramiyidans’ and particularly, *Allostaffia*, but it may represent a previously unknown mammalian group. Pending the discovery of additional material, we provisionally refer *Avashishta bacharamensis* to the most morphologically comparable group of Mesozoic mammals currently known, the ‘Haramiyida.’

DISCUSSION AND CONCLUSIONS

A recent surge of paleontological fieldwork in Mesozoic sediments of the southern continents is yielding important fossil discoveries that are reshaping previous phylogenetic and biogeographic interpretations. The first mammals described from the Late Cretaceous of India were the eutherians *Deccanolestes hislopi* and *D. robustus*, which appeared to have phylogenetic ties with Laurasian taxa (Prasad and Sahni, 1988; Prasad et al., 1994). These fossil occurrences were consistent with an aspect of prevailing paleocoastline reconstructions suggesting that the Indian subcontinent was geographically isolated from most other southern landmasses by the Early Cretaceous (~148 Ma; Williams, 1986). Indeed, the phylogenetic affinities of the Indian eutherians hinted at an earlier than expected collision with Asia and an immigration of eutherians of Laurasian origin. However, as geophysical evidence accumulated, it began to appear likely that the Indian subcontinent’s geographic connections with other southern landmasses persisted well into the Late Cretaceous (~88–82 Ma) via land bridges such as the Gunnerus Ridge or the Kerguelen Plateau (see Rana and Wilson, 2003 and references therein). Discovery in India of an as-yet-unnamed sudamericid gondwanatherian (Das Sarma et al., 1995; Krause et al., 1997) supported this hypothesis, providing biogeographic links between India and other

southern landmasses during the Late Cretaceous (Krause et al., 1997). When a third eutherian species from the Late Cretaceous of India, *Sahnitherium rangapurensis*, was published (Rana and Wilson, 2003), Gondwanan occurrences of eutherians were no longer considered 'biogeographic anomalies' (Patterson and Owen, 1991). By then, boreosphenidans, including eutherians, had been described from the Cretaceous of South America, Africa, and Madagascar (Gayet et al., 2001; Sigogneau-Russell, 1995; Krause, 2001).

Avashishta appears to represent another paleobiogeographic link among southern continents and supports the hypothesis that the Indian Late Cretaceous mammalian fauna included lineages of both Laurasian and Gondwanan origins. Although 'haramiyidans' are documented from northern continents, their temporal range on those continents extends from the Late Triassic to Middle Jurassic. Whereas, on the southern continents, *Allostaffia* is known from the Late Jurassic of Tanzania (Heinrich, 1999, 2001), *Hahnodon* and *Denisodon*, which Butler and Hooker (2005) have reinterpreted as 'haramiyidans,' are known from the Early Cretaceous of Morocco (Sigogneau-Russell, 1991; Hahn and Hahn, 2003); and now, *Avashishta* is known from the Late Cretaceous of India. The emerging biogeographic pattern suggests that 'haramiyidans' were present on Laurasian continents from the Late Triassic until at least their last record in the Middle Jurassic, but survived on Gondwanan continents well into the Cretaceous. While we grant that this working hypothesis should be approached with caution, as mammalian fossils from the Mesozoic are sparse, the absence of 'haramiyidans' from well-sampled Late Jurassic and Early Cretaceous localities from the northern continents supports this hypothesis (Kielan-Jaworowska et al., 2004). Further, if the morphological similarity of *Avashishta bacharamensis* and *Allostaffia aenigmatica* reflects the phylogenetic relationship between these taxa, these data would support the hypothesis of a southern stock of 'haramiyidans.' In sum, the currently available data suggest that the origins of the Indian Late Cretaceous mammalian faunas were biogeographically complex and involved components of both Laurasian and Gondwanan origins.

Acknowledgments—We gratefully acknowledge the Director General, Geological Survey of India, for his kind permission and providing necessary facilities; Drs. K. Ayyasami, J. Hooker, A. Sahni, C. A. E. Strömberg, J. A. Wilson, and the Berkeley Natural History Museums for assistance with logistics and manuscript preparation; Dr. Z. Kielan-Jaworowska, one anonymous reviewer, and a panel of editors for critical reviews; and the Welles Fund (SA, GPW), UCMP, and NSF (GPW) for financial support. We especially thank Jane Mason for her skillful preparation of the specimen casts and Mullick Mohini for help with the Sanskrit translation of the generic name.

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Submitted 18 August 2005; accepted 3 October 2005.