

# The first multituberculate mammal from India

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Received: 20 February 2013 / Revised: 11 April 2013 / Accepted: 13 April 2013 / Published online: 5 May 2013  
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**Abstract** Mesozoic deposits of the former Gondwanaland are depauperate in early mammals, in general, and multituberculate mammals, in particular. Until now, the oldest multituberculate mammals known from the Gondwanan continents come from the Early Cretaceous of Morocco, NW Africa. Here, we report the presence of a new multituberculate mammal, *Indobaatar zofiae* gen. et sp. nov., from the Lower/Middle Jurassic Kota Formation, Pranhita-Godavari valley in peninsular India. This is the first record of a multituberculate from the Mesozoic rocks of India and possibly predates the oldest known multituberculates from Gondwanan continents. The new specimen, representing an upper premolar ( $P^4$ ), compares well with the upper premolar morphology of Eobaatarinae multituberculates known from the Early Cretaceous of Mongolia, China, England, and Spain. Together with the recent findings of cimolodontan multituberculates from the Early Cretaceous of Australia and Late Cretaceous of South America, the new discovery indicates a wide temporal and spatial distribution for multituberculate mammals in the former Gondwanaland.

**Keywords** Jurassic · Multituberculates · Mammals · India · Gondwanaland

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Communicated by: Robert Asher

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## Introduction

Multituberculates, an important group of mammals known predominantly from Mesozoic rocks, survived the Cretaceous–Palaeogene (K/Pg) boundary biotic crisis into the Palaeocene and Eocene. They are evolutionarily distinct from modern placentals, marsupials, and monotremes but converge on modern rodents in having chisel-like incisors separated by a diastema from broad molars with several rows of multiple tuberculated cusps. Multituberculates had a predominantly Northern Hemisphere distribution. Although *Mojo usuratus* from the Upper Triassic of Belgium was considered as the oldest multituberculate recorded so far (Hahn et al. 1987), the multituberculate affinity of this genus has been questioned (Kielan-Jaworowska et al. 2004; Butler and Hooker 2005). The oldest incontrovertible multituberculates are known from the Middle Jurassic (Late Bathonian) Forest Marble Formation at Kirtlington, Oxfordshire, England (Butler and Hooker 2005) and the youngest occurrence was reported from the Late Eocene of western North America (Kielan-Jaworowska et al. 2004). A large number of multituberculate taxa younger than those of Forest Marble Formation were recorded from the Upper Jurassic of Portugal and the USA, from the Early Cretaceous of Spain, Portugal, Mongolia, USA (Kielan-Jaworowska et al. 1987, 2004; Hahn and Hahn 2006; Badiola et al. 2008, 2011), China (Hu and Wang 2002; Kusuhashi et al. 2009, 2010), Japan (Kusuhashi 2008), Morocco (Sigogneau-Russell 1991; Hahn and Hahn 2003), and Australia (Rich et al. 2009), and from the Late Cretaceous of Mongolia, North America, Europe, and Argentina (Kielan-Jaworowska et al. 2004, 2007). Isolated teeth of multituberculates are also known from the Palaeocene and Eocene of North America and Europe (Kielan-Jaworowska et al. 2004).

Compared to their widespread occurrence in the Laurasian continents, multituberculate mammals are very

scarcely known from the former Gondwanaland with only two reports from the Early Cretaceous of Morocco (*Hahnodon* and *Denisodon*; Sigogneau-Russell 1991; Hahn and Hahn 2003), one from Australia (*Corriebaatar marywaltersae*; Rich et al. 2009) and two from the Late Cretaceous of Argentina (Multituberculata incertae sedis and *Argentodites coloniensis*; Kielan-Jaworowska et al. 2004, 2007). Butler and Hooker (2005) felt that the two Moroccan species might, in fact, represent haramiyidans. Besides these reports, an indeterminate tooth fragment from the Upper Cretaceous Maevarano Formation of Madagascar has been referred to Multituberculata incertae sedis (Krause and Grine 1996), but, so far, it has not been illustrated and sufficiently described.

Here, we document the first pre-Cretaceous multituberculate mammal from a Gondwanan continent. The new find is an upper left premolar ( $P^4$ ) of a plagiulacoid multituberculate and comes from the Kota Formation of Pranhita-Godavari valley, peninsular India. The Kota Formation is long known for its fish and dinosaur fauna. Following bulk screen washing of siltstones intercalated with the limestone beds of this formation exposed along a stream channel southwest of Paikasigudem village in Adilabad district, Andhra Pradesh state, India (Fig. 1), remains of many other vertebrate groups, such as hybodont sharks, sphenodontid reptiles, iguanian lizards, crocodiles, saurischian and ornithischian dinosaurs, and a variety of mammals have been recovered.

The age of the Kota Formation is not precisely known as it has not yielded any biostratigraphically significant index fossils. As no datable magmatic rocks occur above and below or intercalated with the Kota Formation, radiometric dates are also not available. It was assigned an Early Jurassic (Lias) age based on semionotid fish taxa *Tetragonolepis* and *Paradapedium* (considered as an Asian ecological substitute of Liassic *Dapedium* from Europe, Jain 1973). *Tetragonolepis* is known only from the Upper Liassic marine strata of Europe (Jain 1973). Similarly, *Lepidotes deccanensis* from the Kota Formation was considered to share some similarities with the Upper Liassic European *L. elevensis* (Jain 1983). Yadagiri and Prasad (1977) also preferred a Lower Jurassic age for the Kota Formation based on pholidophorid fishes. The Lower Jurassic age for the Kota Formation was further supported by palynomorphs (Prabhakar 1989) and charophytes (Bhattacharya et al. 1994). On the other hand, two works favored a slightly younger age for this formation. Govindan (1975), based on the ostracod *Darwinula* cf. *D. sarytirmensis* known from the Middle Jurassic Mangishlaka peninsula in Russia and *Timiriasevia* (Middle Jurassic to Palaeocene), suggested a Middle Jurassic age. A second palynological study of the Kota sediments indicated a slightly younger age of Middle to Upper Jurassic age. On the other hand, the sphenodontian taxa *Rebbanosaurus* and *Godavarisaurus* of the Kota Formation were considered primitive but lie

crownward of basal rhynchocephalians *Diphydontosaurus* of Late Triassic age, Early Jurassic *Gephyrosaurus*, Late Triassic *Planocephalosaurus* in their dental morphology (Evans et al. 2001). Similarly, *Bharatagama rebbanensis* from the Kota Formation was considered as a primitive acrodont iguanian lizard distinct from the Cretaceous priscagamids of Asia (Evans et al. 2002). Though the triconodont genus *Dyskritodon* is known from the Early Cretaceous of Morocco, the Indian species *D. indicus* (Prasad and Manhas 2002) is distinct from the Moroccan form at species level and very little is known about this enigmatic mammalian genus. Recently discovered ankylosaur dinosaur teeth also point to an Early Jurassic morphological grade. Therefore, the age assignments of Kota Formation seem to be based on tenuous grounds, and the balance of evidence at present is in favor of an Early Jurassic age. For the purpose of this paper, the Kota Formation is provisionally treated as Early/Middle Jurassic in age with the understanding that this age assignment is open to modification in future.

The new specimen (VPL/JU/KM/20) described below represents the first record of a multituberculate from Mesozoic rocks of India and presumably the oldest Gondwanan record. Prior to the present find, *Hahnodon* (Sigogneau-Russell 1991) and *Denisodon* (Hahn and Hahn 2003) from the Early Cretaceous of Morocco were the oldest known multituberculates from the former Gondwanaland. The cusp terminology of Kielan-Jaworowska et al. (2004) is adapted here. The phylogenetic scheme of Kielan-Jaworowska and Hurum (2001) is followed in this paper. The new multituberculate specimen is deposited in the Department of Geology, University of Jammu and carries the catalog number VPL/JU/KM/20. VPL/JU/KM stands for Vertebrate Palaeontology Laboratory, Jammu University, Kota Mammals.

#### Systematic Palaeontology

Class Mammalia Linnaeus 1758

Order Multituberculata Cope 1884

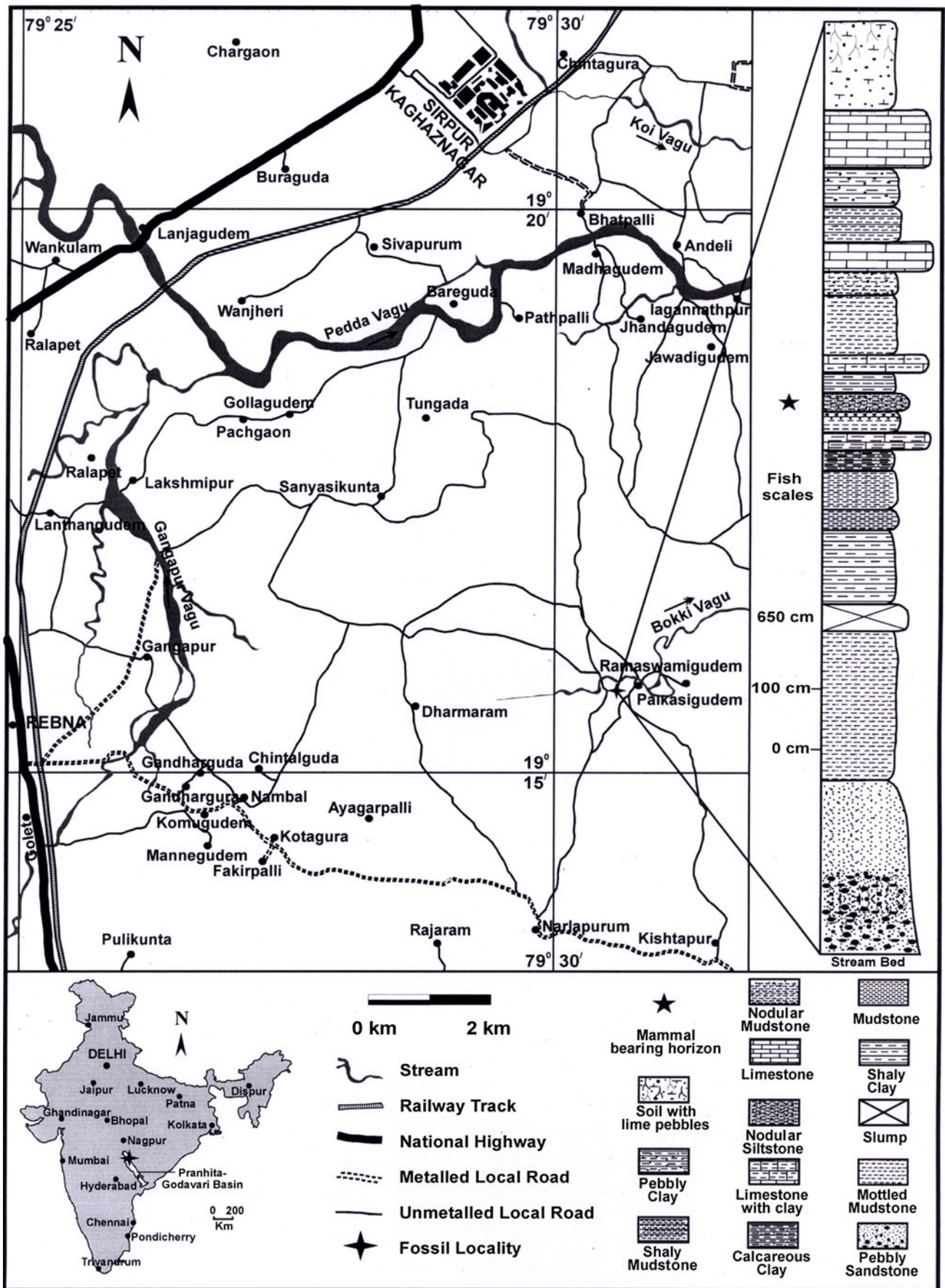
Family Eobaataridae Kielan-Jaworowska, Dashzeveg, and Trofimov 1987

*Indobaatar zofiae* gen. et sp. nov.

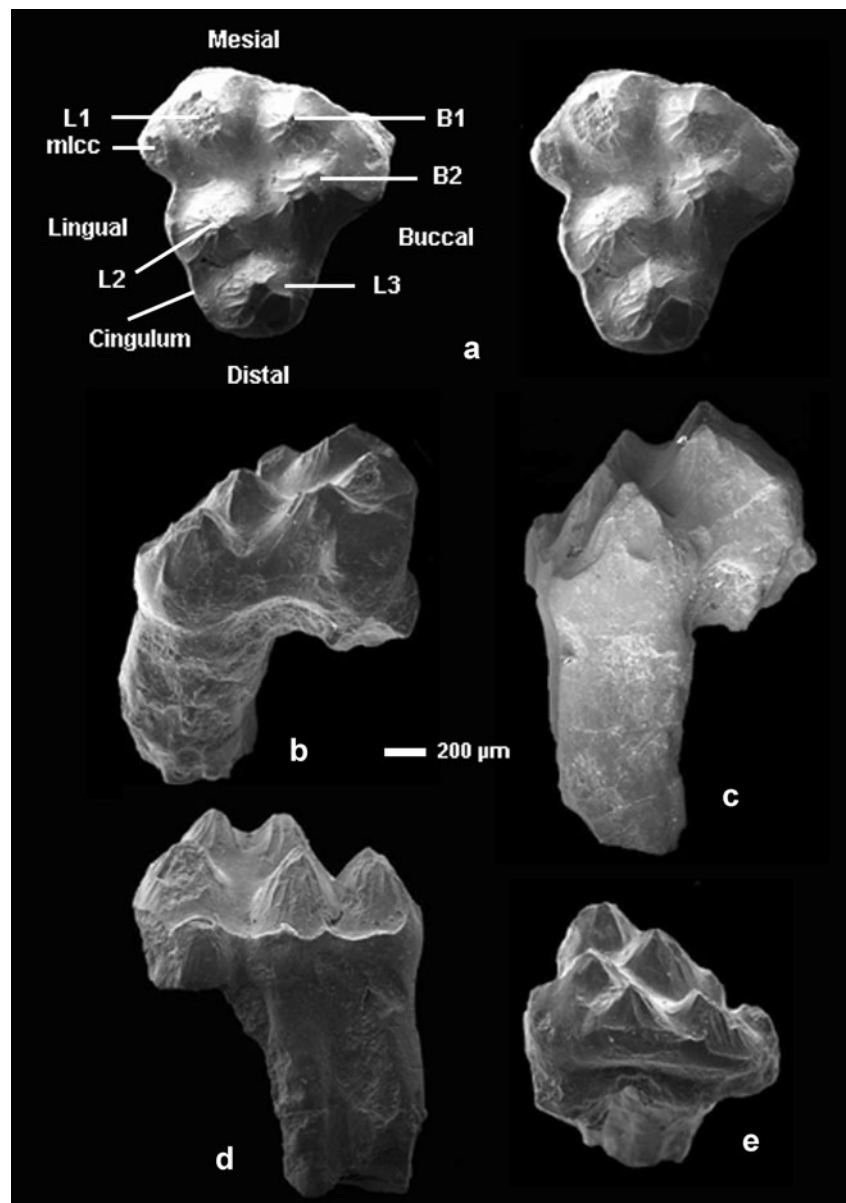
*Holotype* VPL/JU/KM/20, an isolated left upper premolar ( $P^4$ ) (Fig. 2).

*Etymology* Genus named for India, the country of origin; “baatar”—a Mongolian name meaning “hero,” commonly used for multituberculate genera. Species named in honor of Prof. Zofia Kielan-Jaworowska.

**Fig. 1** Location map and stratigraphic column of the fossil yielding section of the Kota Formation exposed southwest of Paikasigudem village, Adilabad District, Andhra Pradesh, India



**Fig. 2** *Indobaatar zofiae*, gen. et sp. nov. specimen VPL/JU/KM/20 (P<sup>4</sup>), holotype in **a** occlusal (stereo pair), **b** buccal, **c** distal, **d** lingual, and **e** mesial views, mlcc mesiolingual cingular cuspsule



**Stratigraphic horizon, age, and locality** Siltstones intercalated with the limestones of the Lower/Middle Jurassic Kota Formation exposed southwest of Paikasigudem village, Adilabad district, Andhra Pradesh state, India (Fig. 1).

**Diagnosis** P<sup>4</sup> characterized by two rows of cusps: three cusps in the lingual row and two in the buccal row; presence of a distinct lingual cingulum and a small cingular cuspsule lingual to mesial lingual cusp (L1); presence of a broad dorsolingually sloping groove separating L1 from the second lingual cusp (L2); three roots. VPL/JU/KM/20 shares a shelf buccal to the buccal row of cusps, narrowed distal part of the crown, slight oblique orientation of lingual cusp row to the mesiodistal axis of the crown, straight lingual, and

concave buccal margins with the upper distal premolars of eobaatarids. However, it differs from *Sinobaatar* (Hu and Wang 2002; Kusuhashi et al. 2009) and *Hakusanobaatar* (Kusuhashi 2008) in which P<sup>4</sup> or P<sup>5</sup> is characterized by more than three cusps in the lingual row that increase in height distally, and laterally protruding buccal and lingual wings in P<sup>5</sup>; P<sup>4</sup> of *E. magnus* (Kielan-Jaworowska et al. 1987), despite sharing a number of crown characters (two cusps in the buccal row, oblique orientation of lingual row to the mesiodistal axis of the crown, a buccal shelf, and wide spacing of cusps) with VPL/JU/KM/20, differs from the latter in having four cusps in the lingual row and an incipiently developed lingual shelf; differs from the P<sup>4</sup> of *E. hispanicus* (Hahn and Hahn 1992; Badiola et al. 2011)

in having a dental formula of two buccal:three lingual (2B:3L) cusps and in its small size; differs from  $P^5$  of *Eobaatar* sp. (Badiola et al. 2008; Canudo et al. 2010) in which the lingual row bears four cusps and the lingual margin has a wide laterally protruding shelf.

## Description

VPL/JU/KM/20 is a small (mesial width = 1.33 mm, lingual length = 1.46 mm), well-preserved left upper premolar ( $P^4$ ) consisting of two rows of cusps. There are two cusps in the buccal row (2B) and three in the lingual row (3L). All cusps have vertical faces buccally and steeply dorsolingually sloping faces lingually. In the buccal row, mesial buccal cusp (B1) is subequal or slightly smaller than distal buccal cusp (B2). The B1 is located opposite the mesial lingual cusp (L1), while B2 is situated mesiobuccal to the second lingual cusp (L2) and opposite the transverse groove separating L1 from L2 (Fig. 2a). The buccal cusps, though comparatively smaller than the lingual cusps in height, are slightly at a higher elevation than the latter. A broad longitudinal groove separating the buccal row from the lingual one lies at a higher level than the wide transverse groove separating L1 from L2. A broad, smooth, and dorsobuccally sloping shelf is present buccal to B1 and B2 (Fig. 2a–b, e). An indentation is present on the buccal face distal to B2 (Fig. 2a). The nearly equal lingual cusps are arranged slightly oblique to the long axis with a slight buccal shift of the distal cusp (Fig. 2a, c). A broad, dorsolingually sloping transverse groove separates L1 from L2. The lingual margin of the crown is notched at this groove. The second (L2) and third (L3) lingual cusps are connected by longitudinal crests issued from their tips (Fig. 2a, d). A distinctly developed cingulum is present on the lingual margin of the crown (Fig. 2a, d). A small cuspule is present on this cingulum at the lingual base of L1 (Fig. 2a, c–d). Skirting the base of lingual cusps, the cingulum becomes less prominent mesially and forms a narrow shelf between L1 and B1. A narrow cingulum is also present mesial to B1. The lingual cingulum terminates at the distolingual face of L3. Distal to the base of L3, a small swelling in the enamel may represent an incipient cuspule (Fig. 2c–d). The distal part of the tooth is narrower than the mesial one, which makes it subtriangular in outline (Fig. 2a, c). The tips of L2 and L3 are unworn, whereas the lingual face of L1 and distobuccal face of B1 are flaked off. The enamel on the distobuccal face of L3 is worn. The tip of the mesiolingual cuspule is also chipped. All the cusps are ornamented with radiating enamel ridges.

A well-preserved, relatively large root is present distally, dorsal to the lingual cusps L2 and L3. The lingual face of this root has a median longitudinal sulcus (Fig. 2d). The two distal cusps are supported by a partially preserved and

relatively small root (half the size of distolingual root) with a subspherical cross section. Another large root, broken at its base, transversely oriented, and with an elliptical cross section, supports L1 and the mesiolingual cuspule.

## Comparisons

The presence of multiple cusps in longitudinal rows, which is characteristic of allotherian cheek teeth, strongly favors the inclusion of VPL/JU/KM/20 in the subclass Allotheria. Within the allotherians, VPL/JU/KM/20 is assigned to the Order Multituberculata in view of the presence of low, conical cusps of subequal height occurring in longitudinal rows and ornamented with radiating enamel ridges. In comparison, haramiyidans have cusps of different heights that lack radiating enamel ridges. Though *Kirtlingtonia* (Butler and Hooker 2005), a haramiyidan from the Middle Jurassic of England, bears radiating enamel ridges on its premolar and molar cusps, the cusps are unequal in height.

The conical shape of the cusps with radiating enamel ridges is characteristic of multituberculate upper premolars. As compared to this, the lower premolars of multituberculates have an inner row of enlarged bladelike cusps and an outer row of reduced swellings (Hahn and Hahn 2000). VPL/JU/KM/20 with its conical cusps ornamented with radiating enamel ridges is, therefore, interpreted as a multituberculate upper premolar. The mesial upper premolars ( $P^{1-3}$ ) of most “plagiaulacidan” multituberculates have three or four cusps with or without additional cuspules and their longitudinal length is nearly equal to their transverse width (rounded with semicircular to semiquadrate occlusal outline). However, some mesiodistally elongated  $P^{1-3}$  (roughly rectangular in outline) with cusps not arranged in clear longitudinal rows have also been described for the plagiaulacid *Parabolodon elongatus* (Simpson 1928), the eobaatarid *Eobaatar? pajaronensis* (Hahn and Hahn 2001), and Plagiaulacidae or Eobaataridae gen. et sp. indet. (Canudo et al. 2010; Badiola et al. 2008, 2011). The distal upper premolars ( $P^4$  and  $P^5$ ) of “plagiaulacidan” multituberculates are generally mesiodistally elongated and bear more than four cusps in two longitudinal rows. VPL/JU/KM/20 with a mesiodistally elongated crown bearing five conical cusps in two longitudinal rows is, therefore, referable to the distal upper premolars ( $P^4/P^5$ ) of “plagiaulacidans.”

Kielan-Jaworowska and Hurum (2001) placed the “plagiaulacidan” families in three informal lineages, viz., the allodontid line (Allodontidae, Zofiabaataridae, “Plagiaulacida” incertae sedis), the paulchoffatiid line (Paulchoffatiidae, Hahnodontidae, Pinheirodontidae), and the plagiaulacid line (Plagiaulacidae, Albionbaataridae, Eobaataridae). Relatively elongated  $P^4/P^5$  having cusps with radiating enamel ridges argues against the inclusion of

VPL/JU/KM/20 in the allodontid line of multituberculates in which  $P^4$  and  $P^5$  are shorter mesiodistally, cusps are generally smooth, and the mesiobuccal shelf is absent.

The distal upper premolars with a shortened buccal row having two cusps and a lingual row with four cusps covering the entire longitudinal length of the crown are known to occur at least in four “plagiaulacidan” families, viz., Paulchoffatiidae, Pinheirodontidae, Plagiaulacidae, and Eobaataridae. In all these families, the buccal row of cusps is confined more or less to the mesial half of the crown (Hahn and Hahn 2003). In most of these families, the mesial face is slightly concave, while the distal part of the crown is either gently rounded or subrectangular in outline.

Within the paulchoffatiid line, mostly represented by the multituberculate genera from the Late Jurassic of Portugal,  $P^4$  mostly and  $P^5$  always have three rows of cusps as compared to two in VPL/JU/KM/20. Although the paulchoffatiid *Kuehneodon* (Hahn 1969) has two rows of cusps, it differs from VPL/JU/KM/20 in having a subrectangular crown with longitudinal rows of closely spaced cusps oriented parallel to each other and three cusps in the buccal row that decrease in height distally. *Hahnodon* and *Denisonodon*, of the family Hahnodontidae, are represented by lower second molars only (Hahn and Hahn 2003). A partially preserved specimen representing the distal part of the crown with a morphology distinctive from that of other “plagiaulacidan” families has been interpreted as a  $P^3$  or  $P^4$  of Hahnodontidae gen. et sp. indet. (Hahn and Hahn 2003: Fig. 4). The fragmentary nature of this tooth precludes its comparison with VPL/JU/KM/20.

The  $P^4$  and  $P^5$  of Pinheirodontidae possess two and three longitudinal rows of cusps, respectively (Kielan-Jaworowska et al. 2004). Among the known taxa of Pinheirodontidae, the distal upper premolars of *Sunnyodon* approach the crown morphology of VPL/JU/KM/20. The  $?P^5$  of *Sunnyodon notleyi* (Pinheirodontidae) from the Lower Cretaceous Purbeck Limestone Formation, England (Kielan-Jaworowska and Ensom 1992) is closely comparable to VPL/JU/KM/20 in the presence of two rows of cusps with two cusps in the buccal row and a prominent lingual cingulum. Likewise, the upper premolar ( $P^4/P^5$ ) of *Sunnyodon?* sp. described from the Lower Cretaceous (Berriasian-Valangian) Rabekke Formation of Scandinavia (Lindgren et al. 2004) has the same cusp formula of two buccal cusps and three lingual cusps (2B:3L) as that of VPL/JU/KM/20. However, *S. notleyi* and *Sunnyodon?* sp. are distinguished from VPL/JU/KM/20 in the symmetrical arrangement of cusps in the buccal row in the middle of the tooth length, the lingual cusps connected by a longitudinal crest, and transverse crests connecting the buccal and lingual cusps. Further, *S. notleyi* has an oval crown with four cusps in the lingual row and *Sunnyodon?* sp. has a subrectangular occlusal outline as compared to subtriangular outline of VPL/JU/KM/20. In both *S. notleyi* and *Sunnyodon?*

sp., there is no buccal shelf as in VPL/JU/KM/20, the two rows of cusps are oriented parallel to the mesiodistal axis of the crown, and in *Sunnyodon?* sp., the cusps in the lingual row increase in height distally.

The distal upper premolars of Albionbaataridae of the plagiaulacid line are distinguished from VPL/JU/KM/20 and all other multituberculates in having three longitudinal rows of numerous small cusps ( $P^5$  with a cusp formula of 5–7:7:7) and the lingual slope covered by prominent subparallel ridges, relatively flat occlusal surface, and in being very elongated (distinctly longer relative to their width). The distal upper premolars of Plagiaulacidae have an eroded lingual wall that slopes down deeply and all the cusps in the lingual row are partially or completely eroded (Kielan-Jaworowska and Ensom 1992). In marked contrast, the lingual wall of VPL/JU/KM/20 is not sloping deeply and the lingual cusps are not eroded. Within the family Plagiaulacidae, *Bolodon osborni* Simpson 1928 has well-preserved upper premolars  $P^4$  and  $P^5$ . The  $P^4$  of *B. osborni* has two longitudinal rows of cusps with radiating enamel ridges as in VPL/JU/KM/20 but differs from the latter in its large size, subrectangular occlusal outline, a cusp formula of three labial and four lingual (3B:4L) cusps, and in the presence of an additional row of small cusps on the buccal margin of the crown. In the  $P^5$  of *B. osborni*, though there are two cusps in the buccal row as in VPL/JU/KM/20, the lingual row has four cusps, the distal buccal cusp is larger than the mesial one, a strongly worn lingual row of cusps forms a steep slope lingually, and the cusps in the two longitudinal rows are closely spaced, making the longitudinal groove less prominent. The  $P^5$  of *B. minor* (Falconer 1857) has two buccal cusps and three lingual cusps as in VPL/JU/KM/20 but differs from the latter in its strongly worn lingual row of cusps and in having a cingulum anteriorly and buccally bearing small cusps.

VPL/JU/KM/20 in having two longitudinal rows of cusps, a shelf mesiobuccal to the buccal row of cusps, narrowed distal portion of the crown, slight oblique orientation of lingual row of cusps (mesiolingual–distolabial), nearly straight lingual margin, and curved (concave) buccal margin compares very well with the posterior upper premolars ( $P^4$  and  $P^5$ ) of Eobaataridae. The family Eobaataridae is currently represented by *Loxaulax valdensis* (Simpson 1928), *Monobaatar mimicus*, *E. magnus*, *E. minor* (Kielan-Jaworowska et al. 1987), *Sinobaatar lingyuanensis* (Hu and Wang 2002), *S. fuxinensis*, *S. xiei*, *Liaobaatar changi* (Kusuhashi et al. 2009) *Hakusanobatar matsuoii*, *Tedoribaatar reini* (Kusuhashi 2008), *Heishanobaatar triangulus* (Kusuhashi et al. 2010), and *Iberica hahni* (Badiola et al. 2011). *Parendotherium*, earlier regarded as an eobaatarid (Kielan-Jaworowska et al. 2004), has been transferred to *I. hahni* within the family Plagiaulacidae or Eobaataridae (Badiola et al. 2011). In addition to these, *Janumys erebos* (Eaton and

Cifelli 2001) from near the Early–Late Cretaceous boundary of UT, USA was referred to Eobaataridae by Hahn and Hahn (2006). *L. valdensis* (Woodward 1911; Simpson 1928) from the Lower Cretaceous (Valanginian) Waldhurst Formation, southeastern England is known by  $M_1$ ,  $M^2$ , and tentatively assigned anterior upper premolars and an  $I^2$  only. No distal upper premolars have been described for this taxon.

The  $P^4$  of *Monobaatar* known from the Early Cretaceous of Mongolia (Kielan-Jaworowska et al. 1987) is distinguished from VPL/JU/KM/20 by having a cusp formula of 3B:4L, very fine striae as ornamentation on the cusps (coarse ridges in VPL/JU/KM/20), narrowed mesial margin, the mesial cusp of the buccal row as the tallest cusp, the lingual cusps increasing in size distally, a ridge extending from the ultimate lingual cusp to the distal margin of the tooth, and obliquely and subvertically worn lingual row of cusps. Though both  $P^4$  and  $P^5$  have been reported for *E. magnus* from the Early Cretaceous of Mongolia based on isolated teeth (Kielan-Jaworowska et al. 1987), the  $P^5$  is now regarded as a variant of  $P^4$  in light of recent discoveries of more complete material from the Early Cretaceous of China (Kusuhashi et al. 2009). The  $P^4$  or  $P^5$  of *E. magnus* shares two longitudinal rows of cusps with two cusps in the buccal row, the oblique orientation of the lingual row of cusps with respect to the mesiodistal axis of the tooth, a buccal shelf, wide spacing of cusps, and a roughly subtriangular shape of the crown with VPL/JU/KM/20. However, there are four cusps in the lingual row in comparison to three in VPL/JU/KM/20 and an incipiently developed lingual shelf in *E. magnus*. *E. minor* Kielan-Jaworowska et al. 1987 is known by lower premolars only. No comparison is possible with *E. clemensi* described from the Lower Cretaceous (Barremian) Wessex Formation of Isle of Wight, southern England (Sweetman 2009), as it is based on  $M_1$  and tentatively referred  $M_2$  and  $I^3$ . The  $P^4$ s of *E. hispanicus* Hahn and Hahn 1992 from the Early Cretaceous of Spain (Badiola et al. 2011: Figs. 4.3–4.4) are partially preserved teeth that differ from VPL/JU/KM/20 in having a cusp formula of 3B:4L as compared to 2B:3L in the Indian specimen, relatively large size ( $L=1.92$  mm), lingual cusps increasing in size distally, and in the presence of tiny cuspules at the midlength of mesial margin and at the distal ends of buccal and lingual cusp rows. VPL/JU/KM/20 and the  $P^4$  of *E. hispanicus*, however, share a rounded mesiobuccal shelf and unworn lingual cusps. As *I. hahni* and *E. pajaronensis* (Hahn and Hahn 2001) from the Early Cretaceous of Spain are known by  $P^{1-3}$ , no comparison is possible with VPL/JU/KM/20. A  $P^5$  described from the Early Cretaceous of Spain under *Eobaatar* sp. (Canudo et al. 2010: Figs. 5.3–5.4; Badiola et al. 2008: Pl. 2) exhibits many morphological similarities to VPL/JU/KM/20, such as two

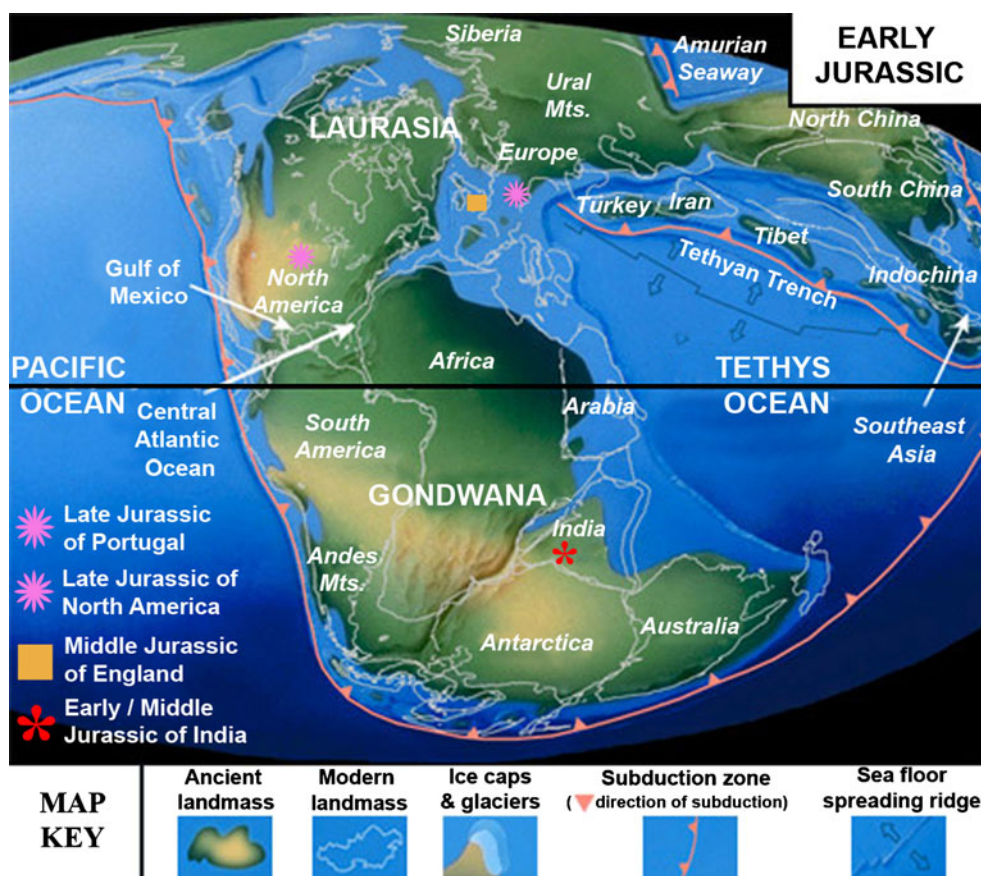
longitudinal rows of cusps, shortened buccal row of cusps with two cusps, considerably narrowed distal portion of the crown comprising only the lingual row of cusps, the presence of small shelf buccal to the buccal row of cusps and the lingual cusps not distinctly increasing in height distally, and a clearly developed triangular occlusal outline. However, *Eobaatar* sp. differs from VPL/JU/KM/20 in having four cusps in the lingual row and in the presence of a smooth and wide, strongly laterally protruding shelf covering the whole lingual margin longitudinally.

*Tedoribaatar*, *Liaobaatar*, and *Heishanobaatar* are known only by lower dentitions. In the upper premolars of *Sinobaatar* and *Hakusanobaatar*, the  $P^5$  is characterized by the extension of buccal and lingual walls of the crown below the cusps to form smooth and wide wings that strongly protrude laterally, three longitudinal rows of cusps, longitudinal ridges connecting the cusps of the main row, incipient distal basin, and rectangular occlusal shape. The  $P^5$  is also comparatively much larger than the  $P^4$ , being widened transversely and elongated longitudinally. This character is incipiently developed in the referred  $P^5$  of *E. magnus*. As the lingual shelflike structure is not present on VPL/JU/KM/20 and has only a less laterally protruding labial shelf as in  $P^4$  of *Sinobaatar* and *Hakusanobaatar*, and as the cusps of the main row are not connected by ridges, the Indian specimen is interpreted here as a  $P^4$ . The  $P^4$ s of *Sinobaatar* and *Hakusanobaatar* are distinguished from VPL/JU/KM/20 in having four and five lingual cusps, respectively, and the cusps increasing in height distally in the lingual row. In *Hakusanobaatar*, the labial row of  $P^4$  has also three cusps as compared to two in VPL/JU/KM/20 and *Sinobaatar*. In cf. *J. erebos* (Eaton and Cifelli 2001), the  $P^4$  is transversely narrower (laterally compressed) than in VPL/JU/KM/20, the longitudinal rows of cusps are parallel to each other with less distinctly separated cusps, and the cusps in the lingual row increase in size distally. It is evident from the above discussion that close similarities exist in the crown morphology between VPL/JU/KM/20 and the penultimate upper premolar of various taxa of Eobaataridae, which allows us to refer the Indian specimen to this family.

## Discussion

Multituberculates are scarcely known from the former Gondwanaland, in contrast to their widespread occurrence in rocks ranging in age from Middle Jurassic to Late Eocene of the Northern Hemisphere. The existing fossil record indicates that Laurasia was the center of origin for multituberculates and they may have dispersed to Gondwanan landmasses at a later time. The new discovery of a multituberculate from the Early/Middle Jurassic of India is very significant as these mammals are very

**Fig. 3** Early Jurassic palaeogeographic map showing the Jurassic occurrences of multituberculates (palaeomap based on Scotese (2001))



scarcely known from the former Gondwanaland. If the Early/Middle Jurassic age of the Kota Formation is confirmed, *Indobaatar* may even represent the oldest record of multituberculates in the southern continents. The occurrence of a multituberculate mammal with a broad morphological similarity to the eobaatarid taxa from the Early Cretaceous of Europe and Asia might be construed as evidence for a younger than Early/Middle Jurassic age for the Kota Formation. As the present specimen offers no phylogenetically significant dental characters that definitively align it with any of the known species of the family Eobaataridae, we consider the fossil material at hand insufficient to arrive at such a conclusion. The new find also suggests that multituberculates were more widely distributed in both Laurasian and Gondwanan continents. The close similarity in crown morphology of *Indobaatar* and eobaatarids from Europe and Asia points to the fact that closely related forms existed on both Laurasian and Gondwanan continents, albeit at different time intervals. This is not unexpected as palaeogeographic maps show contiguity of these landmasses in the Jurassic (Fig. 3) and Early Cretaceous. Since they were present in the Early/Middle Jurassic of India, and assuming that they had evolved into more derived forms of the Cretaceous period, one would expect to find multituberculates in the Upper Cretaceous rocks of India as well. The Upper Cretaceous Deccan

volcanosedimentary (intertrappean) sequences of India have been extensively studied in recent years for their fauna and flora. As a result, eutherian, gondwanatherian, and haramiyidan mammals in addition to other vertebrate groups have been documented from these strata (see Prasad 2012 for references). However, no Cretaceous multituberculate mammals have been reported so far from India. The lack of adequate fossils from different Mesozoic periods of Gondwanaland is possibly an artifact of sampling bias as this region is not well explored as far as Mesozoic mammals are concerned. The recent discovery of a cimolodontan multituberculate (*C. marywaltersae*) from the Early Cretaceous of Australia has been interpreted in terms of migration between Australia and Laurasian landmasses in the Valanginian to Albian (Rich et al. 2009). In light of the new find from India from older Jurassic rocks, we cannot rule out the possibility of derivation of *Corriebaatar* from a Gondwanan lineage of multituberculates. To test this, a more complete fossil record from different regions and time intervals of the former Gondwanaland needs to be documented.

**Acknowledgments** VP is thankful to the Department of Science and Technology (DST), New Delhi for funding a Fast Track project (SR/FTP/ES-46/2009) for this work. GVRP acknowledges the research grants from DST, New Delhi in the form of JC Bose National Fellowship. This work forms part of UGC SAP and DST FIST program of



Jammu University and UGC CAS II program of Delhi University (DU). Dr N. C. Mehra and R. K. Priyadarshini of the Department of Geology, DU are thanked for taking SEM photographs and for help during the making of figures, respectively.

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