First docodont mammals of Laurasian affinity from India

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Our present understanding of Mesozoic mammalian evolution is primarily based on fossil remains from the Laurasian continents. In stark contrast to its well-documented nature in the northern hemisphere, the fossil record is incomplete and poorly understood in the southern hemisphere. This is particularly true for the order Docodonta. Until now, docodont mammals have been recorded from the Middle and Upper Jurassic deposits of North America and Europe only. The presence of docodont mammals of Laurasian affinity (*Haldanodon* grade) in the Lower/Middle Jurassic Kota Formation of peninsular India is reported here. The new finds, represented by an isolated upper premolar and a lower molar, are the first documented evidences of typical Euramerican docodont mammals from the former Gondwanaland. Contrary to the long-held view of Laurasian origin and distribution, the new finds from India suggest Pangaean distribution for docodont mammals.

THE Kota Formation of Pranhita–Godavari valley, peninsular India, has long been known for its vertebrate fauna which includes fishes, sphenodontian reptiles, lizards, crocodiles, flying reptiles (pterosaurs) and dinosaurs (see Prasad and Manhas[1] for references). This formation also provides significant insights into the mammalian faunas of Early/Middle Jurassic time. The Kota mammalian fauna is represented by symmetrodonts (*Kotatherium haldanei*)[2], *Trishulotherium kotaensis*[3] (Tinodontidae), *Nakunodon paikasiensis* (Amphidontidae)[4], triconodonts (*Dyskritodon indicus* n. sp. (uncertain family)), *Indotherium pranhitai*, *Paikasigudodon yadagiri* n. comb. (Morganucodontidae)[1,3,5] and appears to be more diverse than that of other mammal-bearing Jurassic sites of the southern hemisphere. The Kota Formation has been assigned an Early Jurassic (Upper Lias) age based on fishes[6], pterosaurs[7] and Middle Jurassic age on the basis of ostracods[8]. In the present paper, two new mammalian teeth recovered from the Kota Formation at a site located west of Paikasigudem village (Figure 1), Rebbana Mandalam, Adilabad District, Andhra Pradesh (India) are described and their biogeographic significance is discussed. Besides the presently-described teeth, the mammalian collection from the Kota Formation also includes a number of isolated incisors, canines and a few molars, mandibular fragments and postcranial bones. These specimens come from the mudstones associated with the limestone bands of the Kota Formation (Figure 2). The cusp nomenclature followed in this paper is that of Krusat[9]. The specimens are housed in the vertebrate palaeontological collections of Jammu University (VPL/JU/KM/number).

Of the two new specimens recovered from the Kota Formation, one is left upper premolar (VPL/JU/KM/12) and the other is an incomplete right lower molar (VPL/JU/KM/14). VPL/JU/KM/12 has an asymmetrical outline with medianly-indented transverse posterior and obliquely straight anterior faces (Figures 3 *a* and 4 *a*). There are three principal cusps on the crown, two on the labial margin and one on the lingual side. Cusp 'A' is the highest cusp and is connected posteriorly to the postero-labial cusp 'C' by an angulated crest (Figures 3 *a* and 4 *a*). A deep notch separates the two labial cusps from each other (Figures 3 *b* and 4 *b*). Anteriorly, a crest connects cusp 'A' to a small anterolabial cingular cusp 'E'. A small worn cuspule as large as cusp 'E' and designated here as 'E′' occurs at the anterolabial margin of the crown slightly lingual to the former (Figures 3 *b* and 4 *a*, *b*). The two labial cusps, 'A' and 'C', have nearly flat labial faces. There is no ectoflexus. From the broken labial base of the tooth it appears that there might have existed a very narrow cingulum. The lingually extended talon bears an anteroposteriorly wide lingual cusp 'X', which is lower than 'A' but higher than 'C' (Figure 3 *c*). A worn crest descends lingually from the tip of cusp 'A' to its lingual base and might have extended to the lingual cusp in unworn condition as indicated by a weak trace of this crest lingual to the base of 'A' (Figure 4 *a*, *b*). A deep talon basin, separating the labial cusps from the lingual cusp, is present posterior to this crest. The posterior face of the lingual cusp is slightly chipped off (Figure 4 *a*).

The asymmetrical triangular outline of the crown with a transverse posterior face bearing a median indentation and a deep talon basin posterior to the crest from 'A' to the lingual cusp recall the crown morphology of docodont premolars[9,10]. Among all the known docodonts, VPL/JU/KM/12 approaches the upper premolar morphology of *Haldanodon exspectatus*[9] in having a doubly-pinched asymmetrical crown, anteroposteriorly wide lingual cusp, labially placed cusps 'A' and 'C', narrow ectocingulum, small cusp 'E' connected to 'A' by a crest, a small cuspule 'E′' at the anterolabial margin and slightly lingual to 'E', and the lingual part of the crown pushed towards the posterior end of the crown. The typical docodont upper molar features, such as a continuous crest extending from the lingual tip of 'A' to the lingual cusp 'X' and additional lingual cusp 'Y' (doubling of), which are not clearly discernible in the present state of preservation, might be cited against its inclusion in the family Docodontidae Simpson[11]. From the presence of a weak trace of the crest from 'A' to 'X', it appears that

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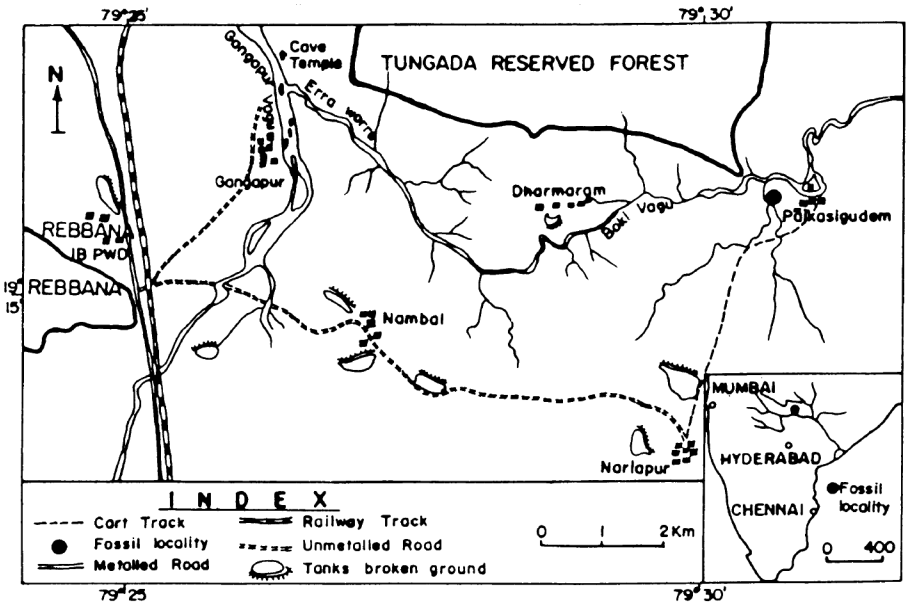

Figure 1. Map showing the mammal locality.

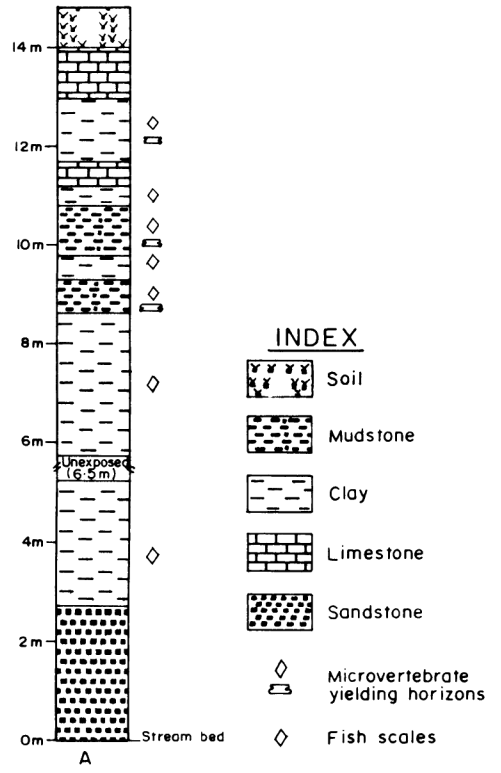

Figure 2. Stratigraphic column of the mammal-yielding section.

originally this crest might have been present and was possibly made indistinct during the course of wear. Secondly, posterior to cusp 'X' the lingual crown is chipped off (Figure 4 *a*), thereby making it very difficult to say whether cusp 'Y' was originally present or not. Since doubly-pinched asymmetrical crown with a posteriorly placed talon basin and unusually anteroposteriorly wide lingual cusp are unknown in any other group of Jurassic mammals and because of the close resemblance to the upper premolar morphology of *Haldanodon*, the new specimen from India is referred to the family Docodontidae.

VPL/JU/KM/14 is a fragmentary right lower molar (Figures 3 *d*, *e* and 4 *c*, *d*). The partly preserved cusp 'a' is the largest and highest cusp occupying the middle part of labial margin (Figure 3 *d*). The posterolingual cusp 'g' is the next largest cusp positioned on the lingual margin slightly posterior to the labial base of cusp 'a' (Figures 3 *d*, *e* and 4 *c*, *d*). A crest descends from the posterior tip of 'g' and connects this cusp to a small cusp 'd' situated at the posterolabial corner of the tooth (Figures 3 *d* and 4 *c*). Cusp 'd' is joined to a small posterolingual cuspule 'f' by an indistinct crest (Figure 4 *d*). A faint crest issued from the mid-height of the posterolabial face of 'a' terminates before reaching the crest linking 'g' with 'd'. Sharp crests extend from the lingual and labial tips of 'a' and 'g', respectively, and terminate at the respective bases of the two cusps, thereby leaving a notch between the two cusps (Figures 3 *d* and 4 *c*). The anterolingual cusp 'h' occurs as a lingual cingular swelling (Figures 3 *e* and 4 *c*, *d*). Another cuspule 'e', slightly larger than 'h', occurs anterolabial to the latter as a cingular cuspule (Figures 3 *e* and 4 *c*, *d*). An indistinct crest extends from the labial base of 'h' to the anterolabial base of 'a'. The crown is broken labial to 'e' (in the supposed locus of cusp 'b') and the part bearing the labial face of cusp 'a'. The anterior base of cusp 'a' is more anterior to that of 'g' (Figures 3 *d*, *e* and 4 *c*, *d*). Cusp 'a' has a flat broad face

posteriorly, whereas cusp 'g' is hollowed labially. The lingual cingulum encircles cusp 'g' and gently climbs up anteriorly (Figure 4 *c*, *d*).

VPL/JU/KM/14 is considered as a docodont because of the arrangement of cusps in nearly parallel rows (labial and lingual), presence of a high labial cusp 'a' and cusp 'g' posterolingual to it, transverse crest connecting these two cusps, fluted cusp 'g', crests joining 'g' with 'd' and 'd' with 'f', and the anterolingual cusp 'h'. VPL/JU/KM/14 resembles the lower molar morphology of *H. exspectatus*[9], in having cusp 'g' connected to 'd' by a straight anterolingually and posterolabially oriented crest and an indistinct crest joining 'd' with 'f'. But *Haldanodon* has deep talon basin, hollowed cusp 'a', and a distinct crest linking 'h' with 'b', which bifurcates the anterior crown into two steeply, lingually sloping shelves. The last character is also observed in *Simpsonodon*[12] and *Docodon*[11]. In contrast to the deep anterior basin of *Haldanodon*, *Docodon*, and *Simpsonodon*, in VPL/JU/KM/14, it is nearly flat. Therefore, VPL/JU/KM/14 has a crown which is at a primitive stage of development in comparison to *Haldanodon*, *Simpsonodon*, and *Docodon*, especially the latter two, which show a strong accentuation of crests and complexity of anterior and posterior basins with ridges and grooves, and enlargement of cusp 'b' and antero-lingual and postero-lingual cusps. On the other hand, it is slightly more advanced than *Delsatia rhupotopi* documented from the Late Triassic of France and representing a primitive stage of docodonty[13] in having an incipiently developed posterior basin.

The discovery of docodont mammals from the Jurassic of India assumes great significance because of two reasons. Firstly, it extends the geographic distribution of docodonts to the Gondwanaland, thereby negating a typical Laurasian distribution for this group. The order Docodonta is represented in the fossil record essentially by isolated teeth, incomplete jaws and rare cranial and postcranial bones. Until the present finds, members of the order Docodonta have been known from the upper Middle Jurassic (Middle/Upper Bathonian) strata of Isle of Skye, Scotland (*Borealestes serendipitus*), Upper Bathonian (Middle Jurassic) Kirlington Mammal beds, Oxfordshire,

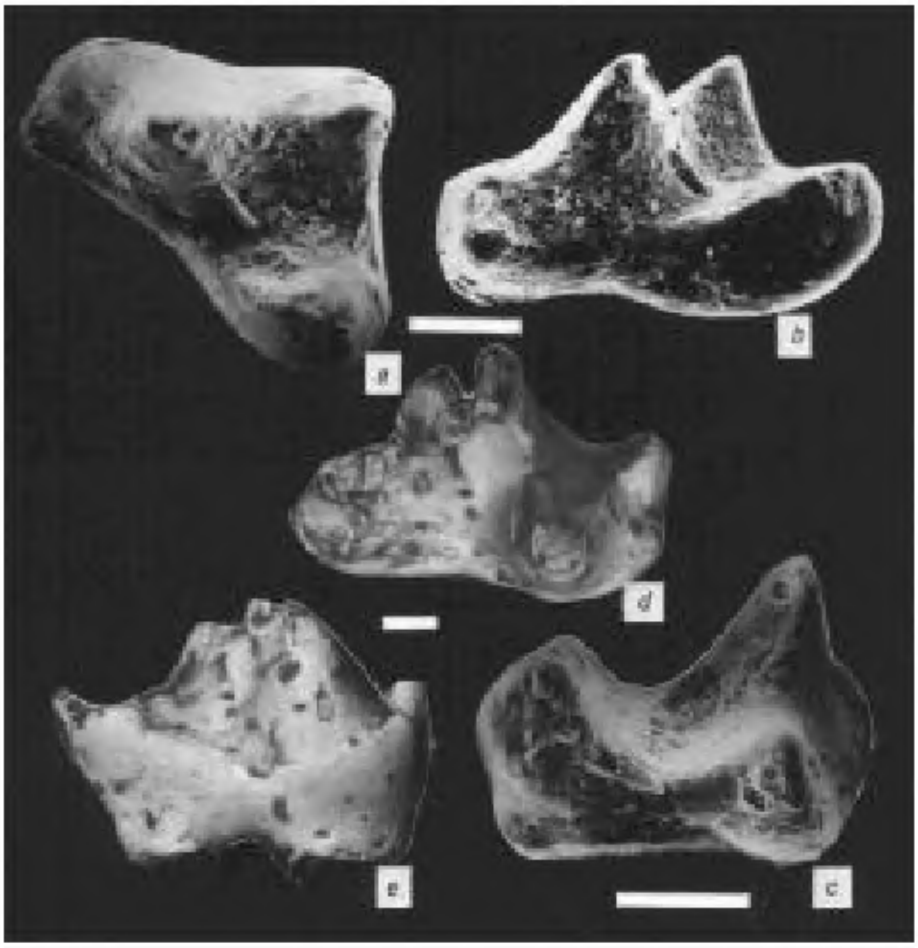

Figure 3. Scanning electron micrographs of docodont left upper premolar (VPL/JU/KM/12): ***a***, occlusal view; ***b***, anterior view; ***c***, posterior view, scale bar equals 500 μm; and docodont right lower molar (VPL/JU/KM/14): ***d***, occlusal view; ***e***, lingual view, scale bar equals 100 μm.

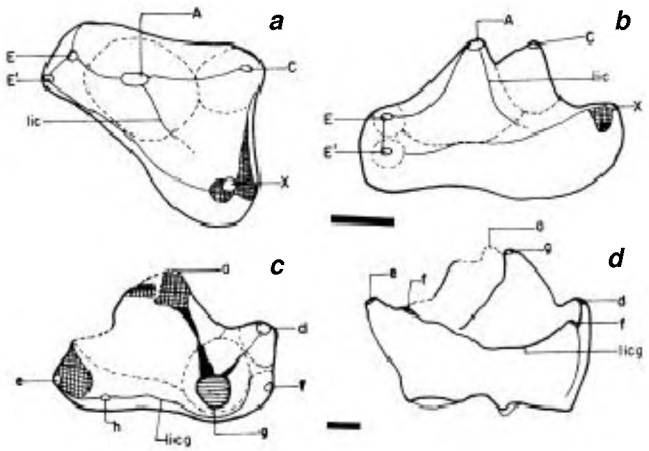

Figure 4. Line drawings of docodont left upper premolar (VPL/JU/KM/12): ***a***, occlusal view; ***b***, anterior view, scale bar equals 500 μm; and docodont right lower molar (VPL/JU/KM/14): ***c***, occlusal view; ***d***, lingual view, scale bar equals 100 μm. Cross-hatched areas mark enamel flaking or breakage.

England (*Simpsonodon oxfordensis*[12]), uppermost Jurassic Lulworth Beds of Durlston Bay, England (*Peraiocynodon inexpectatus*), Kimmeridgian Guimarota Coal, Portugal (*H. exspectatus*) and from the Upper Jurassic Morrison Formation, Como Bluff, USA. (*Docodon victori*, *D. striatus*, *D. affinis*, *D. crassus*, *D. superus*; see Kron[14] for references). Thus the published accounts show a typical Laurasian distribution for this group of mammals[14]. Pascual *et al.*[15] have indicated the presence of docodonts in the Late Cretaceous of South America. They consider *Reigitherium bunodontum*, known from the Campanian–Maastrichtian La Colonia Formation of Argentina, as a highly derived form representing a distinct family Reigitheridae, a sister group of Docodontidae. The present specimens from India on the other hand, are closer to the crown morphology of *Haldanodon* than to the South American genus *Reigitherium*. Therefore, the new finds are the first evidence of docodonts of *Haldanodon* grade outside the northern hemisphere. This suggests that early docodonts were widely distributed in both Gondwanan and Laurasian continents, at least up to the end of Jurassic or Early Cretaceous. One cannot exclude the possibility that after the separation of South America from Africa in the Early Cretaceous, endemic evolution of pre-existing docodont stock might have given rise to the highly evolved Late Cretaceous *Reigitherium* of South America. The absence of placentals and primitive docodonts in South America might be construed as an expression of incomplete fossil record. Yet it is important to emphasize that a clear picture will emerge only when the terrestrial vertebrate faunas of southern continents become better documented.

Secondly, if the Early Jurassic age of the Kota Formation is confirmed, this would become the oldest record of docodonts and invoke the Indian subcontinent as the centre of origin for this group. However, the chronostratigraphic position of Kota Formation within the Jurassic period (Early or Middle or Late) needs to be securely fixed before arriving at such a conclusion. Moreover, the mammalian record from Gondwanan land masses is still incomplete. The new finds also furnish evidence for greater diversity of early mammals in the southern continents.

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