Triconodont mammals from the Jurassic Kota Formation of India

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ABSTRACT
New mammalian teeth recovered from the Lower/Middle Jurassic Kota Formation, Pranhita-Godavari valley, peninsular India, are described. In its gross morphology, VPL/JU/KM/13 compares well with *Dyskritodon amazighi* Sigogneau-Russell, 1995, an Early Cretaceous triconodont from Morocco. Based on size and some morphological differences, this tooth is referred to a new species *Dyskritodon indicus* n. sp. Another fragmentary tooth (VPL/JU/KM/14) is assigned to Triconodonta indet. with possible affinities to morganucodontids. Re-examination and comparison of *Kotatherium yadagirii* Prasad & Manhas, 1997, previously documented from the same formation, with various Mesozoic mammalian groups reveal that *K. yadagirii* is not a symmetrodont, more likely a triconodont (family Morganucodontidae). Therefore, a new genus *Paikasigudodon* n. gen. is established for this taxon. *Indotherium pranhitai* Yadagiri, 1984 is retained in the family Morganucodontidae, but the type tooth as well as the attributed tooth (VPL/JU/KM/11) are now considered as upper molars.

KEY WORDS
Mammalia,
triconodonts,
Jurassic,
Kota Formation,
India,
new genus,
new species.

RÉSUMÉ
Mammifères triconodontes de la Formation Kota, Jurassique de l'Inde.
Cet article présente la description de nouvelles dents de mammifères découvertes dans la Formation Kota, du Jurassique inférieur/moyen, vallée de Pranhita-Godavari, Inde péninsulaire. VPL/JU/KM/13 montre de grandes ressemblances, dans sa morphologie générale, avec *Dyskritodon amazighi* Sigogneau-Russell, 1995, triconodonte du Crétacé inférieur du Marocain. La nouvelle espèce, *Dyskritodon indicus* n. sp., est définie par une différence de taille, d'âge et quelques particularités de structure. Un autre fragment de dent (VPL/JU/KM/14) est attribué à un Tricododonta indet., peut-être affine avec les morganucodontides. Par ailleurs, un nouvel examen de *Kotatherium yadagirii* Prasad & Manhas, 1997, décrit précédemment de la même formation, et sa comparaison avec divers groupes mammaliens du Mésozoïque, ont montré que *K. yadagirii* n'est pas un symmétrodonte, mais plus vraisemblablement un triconodonte (famille Morganucodontidae). Un nouveau genre, *Paikasigudodon* n. gen., est créé pour cette forme. Quant au taxon *Indotherium pranhitai* Yadagiri, 1984, il est maintenu dans la famille des Morganucodontidae, mais le spécimen type ainsi que la dent attribuée (VPL/JU/KM/11) sont ici considérés comme des molaires supérieures.

MOTS CLÉS
Mammalia,
triconodontes,
Jurassique,
Formation Kota,
Inde,
nouveau genre,
nouvelle espèce.

INTRODUCTION

In India, Mesozoic mammals have been documented from the Upper Triassic Tikhi Formation (Datta & Das 1996), the Lower/Middle Jurassic Kota Formation (Datta 1981; Yadagiri 1984, 1985; Prasad & Manhas 1997), and from the Upper Cretaceous Deccan intertrappean beds (Prasad & Sahni 1988; Prasad *et al.* 1994; Prasad & Godinot 1994; Godinot & Prasad 1994; Das Sarma *et al.* 1995; Krause *et al.* 1997). Among these micromammal-yielding stratigraphic levels, the Kota Formation of the Upper Gondwana Group, Pranhita-Godavari valley (peninsular India), assumes great significance because of the time frame during which it was deposited. This formation has traditionally been considered as Lower Jurassic in age based on semionotid (Jain 1973), coelacanth (Jain 1974a), and pholidophorid (Yadagiri & Prasad 1977) fishes, pterosaurs (Jain 1974b) and palynofossils (Prabhakar 1986), despite an alternative Middle Jurassic age favoured by other works based on ostracodes (Govindan 1975; Misra & Satsangi 1979). The present study of the micromammalian fauna from this formation puts into question the Early Jurassic age assignment. Age diagnostic palynofossils might prove useful in this respect. Even assuming an age slightly younger than the Lower/Middle Jurassic, the Kota Formation represents an important geological time period during which the early radiations of mammals were taking place.

The Kota Formation has been well known for its vertebrate fauna since the second half of 19th century. Despite the long history of vertebrate fossil collections including fishes, crocodiles, pterosaurs, and dinosaurs (Egerton 1851, 1854; Owen 1852; King 1881; Jain *et al.* 1962; Jain 1973, 1974a, b, 1983; Yadagiri & Prasad 1977; Yadagiri *et al.* 1979), mammals were discovered from this formation only at the beginning of the 1980s (Datta *et al.* 1978; Datta 1981). The first mammalian tooth recovered from the Kota Formation was referred to a then new genus and new species, *Kotatherium haldanei* Datta, 1981, of uncertain familial affinities within Symmetrodonta (Datta 1981). Yadagiri (1984) described two other supposed lower molars of symmetrodonts from this formation and placed each of them in a new

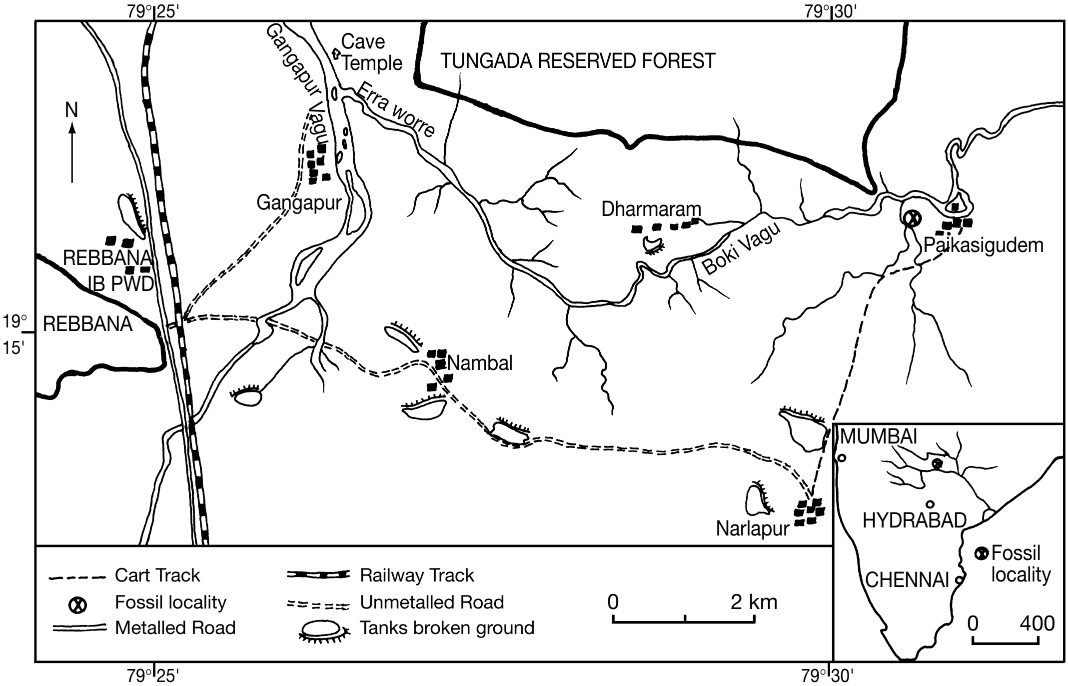

FIG. 1. — Location map of mammal-bearing section of the Kota Formation.

taxon: *Trishulotherium kotaensis* and *Indotherium pranhitai* (family *incertae sedis*). Subsequent to this, Yadagiri (1985) reported as new an amphidontid symmetrodont, *Nakunodon paikasiensis* Yagadiri, 1985, from this formation. Prasad & Manhas (1997) described an upper molar under a new species of *Kotatherium*, *K. yadagirii*, and included the two species of *Kotatherium* and *Trishulotherium kotaensis* in the symmetrodont family Tinodontidae. The type of *Trishulotherium kotaensis* Yadagiri, 1984, originally described as a lower molar, has recently been considered as an upper molar (Sigogneau-Russell & Ensom 1998). Prasad & Manhas (1997) discussed the taxonomic position of *Indotherium pranhitai* and tentatively referred it to the order Triconodonta, as closely allied to morganucodontids. Continued search for early mammals from the Kota Formation has led to the recovery of a few additional teeth referable to docodonts and triconodonts from a stream section exposed west of Paikasigudem village, Adilabad District, Andhra Pradesh State. The fossil yielding site is located about 10 km east of the nearest town, Rebbana (Fig. 1). Except for *K. haldanei* (Manganapalli dinosaur site), all the mammalian taxa reported until now from the Kota Formation come from this site. The Kota Formation is primarily composed of sandstones, limestones, clays, and mudstones, and is considered to have been deposited in a lacustrine environment (Yadagiri & Rao 1987). The microvertebrate assemblage recovered from the Paikasigudem site also includes two new taxa of sphenodontid reptiles (Evans *et al.* 2001) and one new taxon of agamid lizard (Evans *et al.* in press) as well as theropod and ornithischian dinosaur teeth. In the present paper, the newly discovered triconodont teeth are described, and the systematic position of VPL/JU/KM/10, originally assigned to *Kotatherium yadagirii* (family Tinodontidae) and of VPL/JU/KM/11 (*Indotherium pranhitai*) mistakenly thought to be a lower molar (Prasad & Manhas 1997), are re-examined. All the described specimens are deposited in the vertebrate palaeontological collections of Jammu University. Measurements of the specimens were taken with a Mitutoya TM measuring microscope.

ABBREVIATIONS

BMNH	The Natural History Museum, London;
MNHN	Muséum national d'Histoire naturelle, Paris;
VPL/JU/KM	Vertebrate Palaeontology Laboratory, Jammu University, Jammu, Kota Mammals;
GSI/SR/PAL	Regional Palaeontological Laboratory, Geological Survey of India, Southern Region, Hyderabad.

SYSTEMATICS

Order TRICONODONTA Osborn, 1888
Family *incertae sedis*

Genus *Dyskritodon* Sigogneau-Russell, 1995

TYPE SPECIES. — *Dyskritodon amazighi* Sigogneau-Russell, 1995.

EMENDED GENERIC DIAGNOSIS. — Lower molars with high and narrow crown and a cusp formula of *a* > *c* > *d* > *b*; cusps *a*, *c*, *d* decreasing regularly in height posteriorly; the posterior crests of *a* and *c* are slightly longer than the anterior ones; cusps *a* and *c* with swollen labial bases; *b* as a small cusp; differs from all known triconodonts in the cusp formula; differs from all triconodonts except *Gobiconodon* Trofimov, 1978 and *Dinnetherium* Jenkins, Crompton & Downs, 1983 in the presence of anterior notch between *e* and *f*; differs from all triconodonts with the exception of *Morganucodon* Kühne, 1949 in having a very small cusp *b*.

EMENDED SPECIFIC DIAGNOSIS. — Last lower molar with hardly visible cusp *e*; *b* very small, cingular, and lingual to *a* in position.

Dyskritodon indicus n. sp.
(Figs 2A-E; 3A-E)

HOLOTYPE. — VPL/JU/KM/13, a lower left molar.

ETYMOLOGY. — Species is named after India, the country of its origin.

HORIZON AND LOCALITY. — Mudstones associated with the limestone bands of Kota Formation, west of Paikasigudem village, Rebbana Mandalam, Adilabad District, Andhra Pradesh (State), India.

DIAGNOSIS. — *Dyskritodon indicus* n. sp. differs from the type species *D. amazighi* Sigogneau-Russell, 1995 in its smaller size (length of lower molar = 1.24 mm, maximum width = 0.46 mm), in having cusp *b* hardly lingual to *a-c* line; almost equally developed cusps *e* and *f* enclosing a relatively broader anterior notch.

DESCRIPTION

The tooth is well-preserved except for the breakage of the tips of cusps *a* and *c*. The crown is transversely narrow with three principal cusps in line anteroposteriorly. Cusp formula for this tooth is *a* > *c* > *d* > *b*. Cusp *a* is the largest cusp, anterior in position, and is connected to a small cusp *b* at its anterior base. Although the tips of *a* and *c* are broken, it seems that the posterior border of these cusps is slightly longer than the anterior one. Cusp *d* is much smaller than *c* and is placed perpendicular to the line of *a* and *c*, with a flat anterior face and a convex posterior face, both faces being separated by a crest ascending from the lingual cingulum. Cusps *a*, *c*, and *d* are separated from each other by V-shaped notches. Cusps *a* and *b* are closely appressed and separated from each other probably very close to the tip of *b* (Figs 2A; 3A). At the anterolingual base of cusp *b* is a small, vertical accessory cuspule *e* (Fig. 2B). The slightly crenulated cingulum is equally prominent all along the lingual margin of the tooth and terminates posteriorly as a vertical crest on cusp *d* (Fig. 3A); a narrow shelf is even present between the main cusps and the lingual cingulum. The lingual faces of cusps *a* and *c* are angulated. Their labial faces are strongly convex, *a* more so than *c*. These cusps are also swollen labially at their bases, but there is no labial cingulum. There is a small vertical, columnar cuspule *f* at the labial base of cusp *b* (Figs 2A; 3B). Cuspules *e* and *f* are nearly equal in size. In labial view, cuspule *f* is separated from cusp *a* by a shallow sulcus. Cuspules *e* and *f* enclose a well-developed sulcus anteriorly. Labially, *a*, *c* and *d* are separated from each other by broad, vertical sulci. Cusp *d* has a short labial face separated from the posterior face by a ridge. This ridge bears a very small cuspule at its mid-height (this could be an artefact of wear) (Figs 2D; 3C). The crown overhangs the roots on all sides. The anterior root is sub-spherical in cross section. The posterior root, which extends to the posterior base of *a*, is relatively longer anteroposteriorly. It is also labiolingually flattened and has a rounded posterior face. The roots taper ventrally. The tooth was least affected by wear except for narrow abraded facets on the posterolabial border of *a* and *c* (Figs 2B, D; 3B, C). In addition, a sub-spherically worn face is present on the postero-labial base of cusp *a* (Figs 2B; 3B).

Comparisons

VPL/JU/KM/13 presents the typical triconodont lower molar morphology with cusps *b*, *a*, *c*, and *d* arranged linearly in an anteroposterior direction, a well developed lingual cingulum and an anterior sulcus for receiving cusp *d* of the preceding tooth. At present, the order Triconodonta includes four named families: Morganucodontidae, Amphilestidae, Austrotriconodontidae, and Triconodontidae, and four unnamed families represented by *Jeholodens jenkinsi* Ji, Luo & Ji, 1999, *Tendagurodon janenschi* Heinrich, 1998, and *Dyskritodon amazighi* and *Ichthyoconodon jaworowskorum* Sigogneau-Russell, 1995, respectively. VPL/JU/KM/13 differs from morganucodontids, in which cusp *a* occupies a more substantial part of the crown; and a prominent central lingual cingular cusp *g* or kuehneocone is present. As in morganucodontids, the main cusp *a* is also much larger than the adjacent nearly equal cusps *b* and *c* in amphilestines, gobiconodontines, *Tendagurodon janenschi* ($a > c > b > d > e$), and *Austrotriconodon* Bonaparte, 1992 ($a > b > c > d$). Moreover, the long axes of accessory cusps *b* and *c* diverge away from the vertically oriented long axis of main cusp *a* in some amphilestines, in gobiconodontines, and *Jeholodens jenkinsi*. In *Gobiconodon*, the base of main cusp is constricted on both anterior and posterior faces (Jenkins & Schaff 1988: fig. 10A). Finally, triconodontids differ from VPL/JU/KM/13 in possessing subequal cusps *b*, *a*, and *c*. Although amphilestids, triconodontids, and *Jeholodens* also lack the cingular cusp *g* as does VPL/JU/KM/13, the lingual cingulum is medially arched in some amphilestids and discontinuous in *Jeholodens*. VPL/JU/KM/13 also differs from *Klamelia zhaopengi* Chow & Rich, 1984, an amphilestid known from the Middle or Late Jurassic of north-western China, in which the cingulum is not only continuous lingually, but also well-developed labially at the anterior and posterior ends of the crown. The crenulations mentioned here on the lingual cingulum are also known to occur in some amphilestids and triconodontids. There is no trace of a lingual cingulum in *Tendagurodon* Heinrich, 1998. *Ichthyoconodon jaworowskorum* Sigogneau-Russell, 1995 has a high, narrow, trenchant blade-like crown with sub-equal posteriorly inclined and deeply separated *b*, *a*, and *c* (*c* is being slightly more dominant) and only very faint cingulum.

In the molar interlocking mechanism also, VPL/JU/KM/13 differs from morganucodontids, *Jeholodens*, and *Triconolestes* Engelmann & Callison, 1998. In *Morganucodon* Kühne, 1949 and *Megazostrodon* Crompton & Jenkins, 1968, the broad posterior margin of the lower molar crown fits into a shallow embayment between *b* and *e*. In *Jeholodens*, the cingular cuspules *e* and *f* are absent. The crescent-shaped cusp *d* of the preceding tooth fits into the concave anteromedial margin of cusp *b* of the succeeding molar, thus lacking the molar interlocking mechanism of *Morganucodon* and *Megazostrodon* or for that matter that of VPL/JU/KM/13. In the amphilestine genus *Triconolestes*, known by fragmentary left lower molar from the Upper Jurassic of USA (Engelmann & Callison 1998), the interlocking mechanism is absent. But *Dinnetherium*, a triconodont of uncertain familial status known from the Lower Jurassic Kayenta Formation, Arizona, USA (Jenkins *et al.* 1983), shows interlocking by means of anterior cuspules *e* and *f* and overhanging of crown over roots as in VPL/JU/KM/13. *Dinnetherium* was placed in Amphilestidae by Stucky & McKenna (1993), but it has been considered closer to *Morganucodon* in occlusal pattern by others (Crompton & Luo 1993; Luo 1994; Kielan-Jaworowska & Dashzeveg 1998). A similar interlocking system is also seen in gobiconodontines. Cretaceous triconodontids developed tight

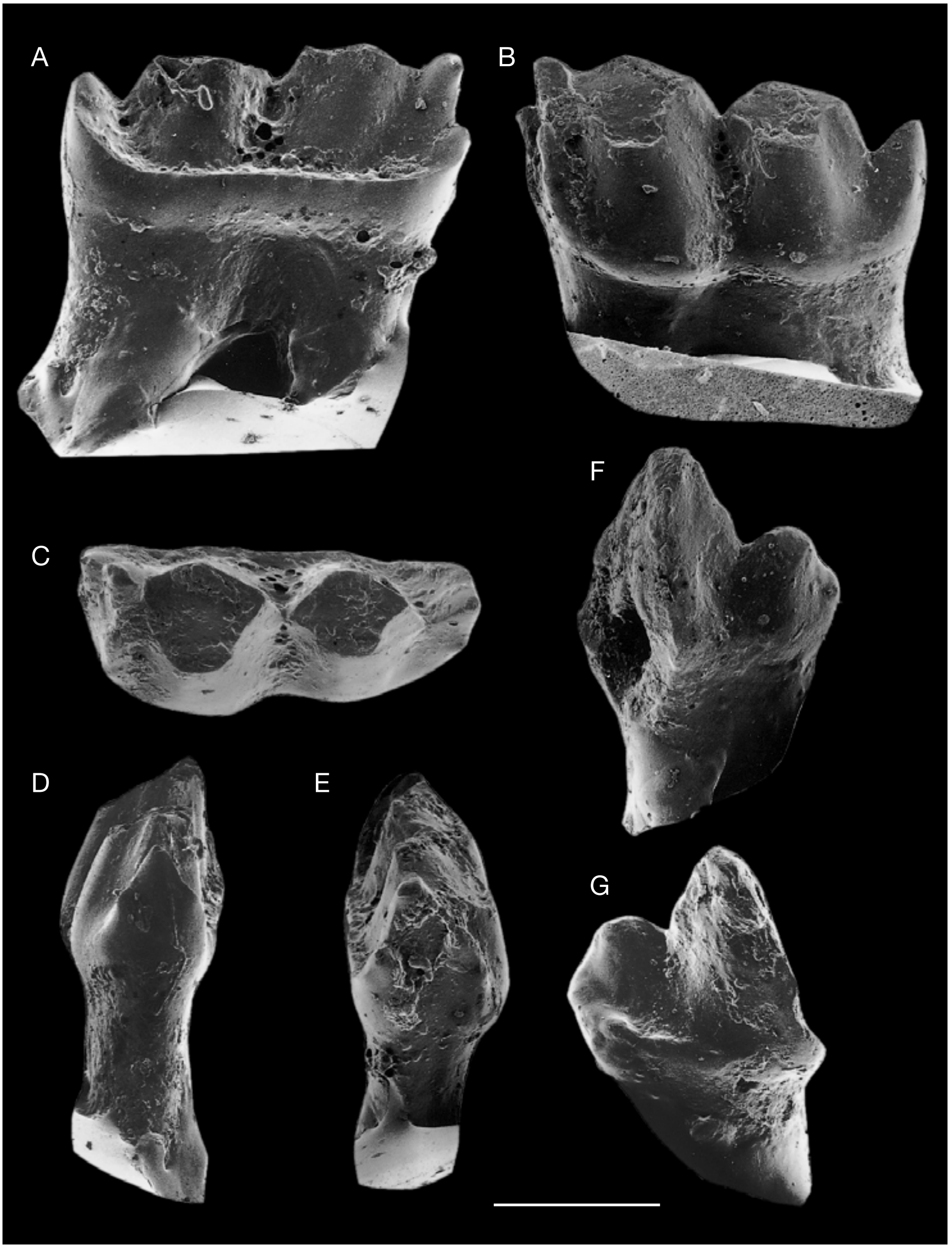

FIG. 2. — **A**-**E**, left lower molar, holotype (VPL/JU/KM/13); **A**, lingual view; **B**, labial view; **C**, occlusal view; **D**, posterior view; **E**, anterior view; **F**, **G**, Triconodonta indet., fragmentary left lower molar (VPL/JU/KM/15); **F**, labial view; **G**, lingual view. Scale bar: 0.5 mm.

interlocking between the adjacent teeth through a tongue and groove mechanism that extends well down the molar roots between *e* and *f*. In *Tendagurodon*, there is no *f* cuspule and no anterior indentation for the reception of cusp *d* of the preceding tooth. Similarly, *Ichthyoconodon* Sigogneau-Russell, 1995 also lacks the anterior interlocking mechanism of lower molars, so does

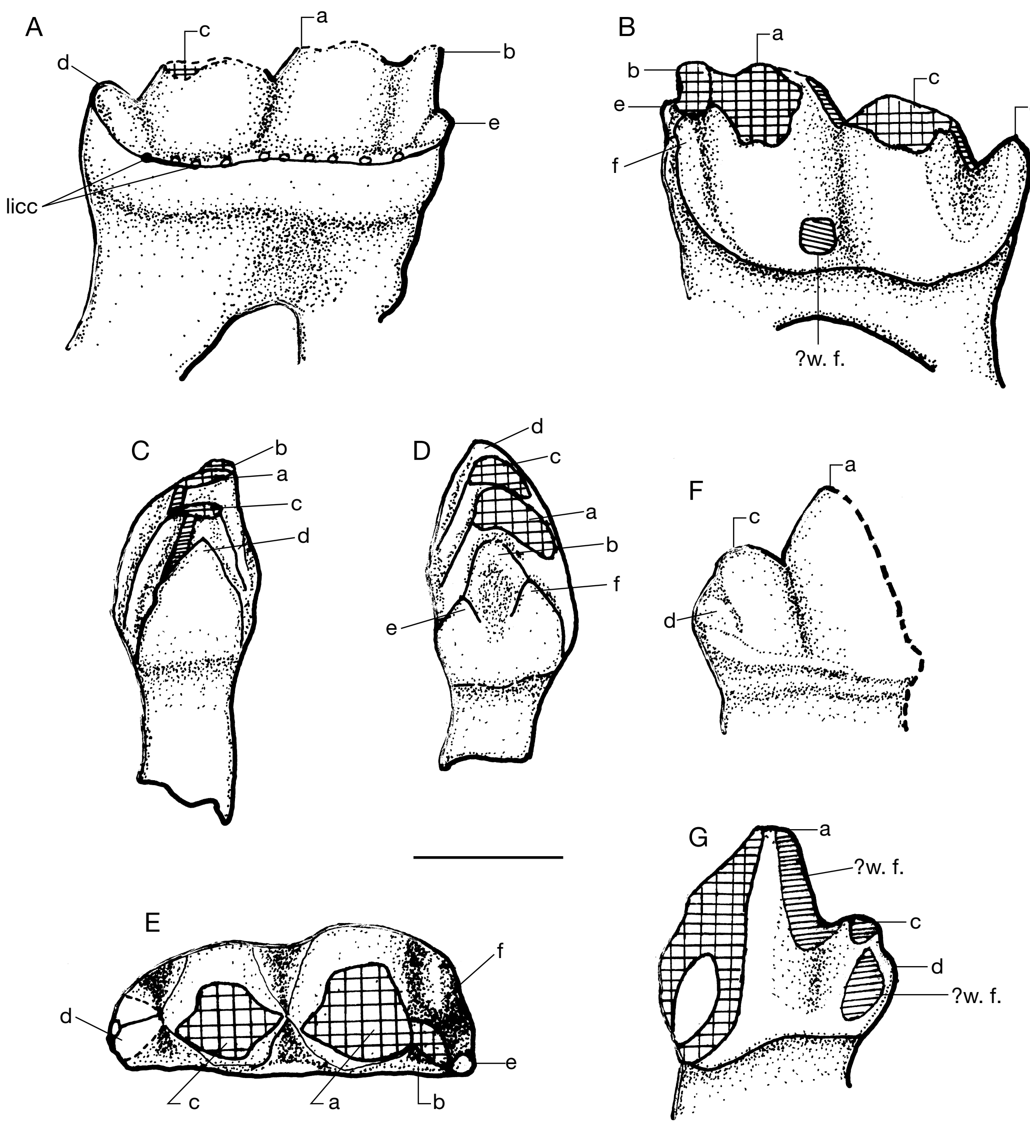

FIG. 3. — **A**-**E**, *Dyskritodon indicus* n. sp., left lower molar, holotype (VPL/JU/KM/13); **A**, lingual view; **B**, labial view; **C**, posterior view; **D**, anterior view; **E**, occlusal view; **F**, **G**, Triconodonta indet., fragmentary left lower molar (VPL/JU/KM/15); **F**, lingual view; **G**, labial view. Abbreviations: **a**-**f**, cusps *a*-*f*; **licc**, lingual cingular cuspule; **?w. f.**, ?wear facet. Hatched areas represent wear facets and crossed hatching demarcates broken areas in all figures. Scale bar: 0.5 mm.

Klamelia Chow & Rich, 1984. In the latter, the most anterior cusp *b* of one molar is medial to the most posterior cusp *d* of the preceding molar (Chow & Rich 1984). Moreover, VPL/JU/KM/13 can be further distinguished from *Klamelia* in the cusp formula (*a* > *c* > *b* > *d*) of the latter. Finally, in marked contrast to VPL/JU/KM/13, in *Klamelia* cusp *a* is considerably longer and taller than *b* and *c*.

Sigogneau-Russell (1995) described an unusual mammalian tooth and made the holotype of *Dyskritodon amazighi*, from the Early Cretaceous of Morocco. She discussed at length the molar morphology in different families of Triconodonta (Morganucodontidae, Amphilestidae, Austrotriconodontidae, Triconodontidae) and arrived at the conclusion that *Dyskritodon amazighi* possibly represents a new family of Triconodonta. The new tooth from the Kota Formation (VPL/JU/KM/13) recalls the crown morphology of *Dyskritodon amazighi* in a large number of characters. In both the Moroccan and Indian specimens, the crown is narrow labiolingually with cusps *a*, *c*, and *d* decreasing progressively in height posteriorly; cusps *a* and *c* dominate the crown and have slightly longer posterior crests than the anterior ones; cusp *d* is placed perpendicular to the *a-c* line and has a flat anterior face, a convex posterior face, and a short labial face separated from the posterior face by a ridge; cusps *a* and *c* have angulated lingual and labial faces and swollen labial bases separated by broad sulci; *e* and *f* cuspules are present anterior to cusp *b* (although Sigogneau-Russell [1995] reported the absence of cusp *e* in *D. amazighi*, re-examination of the holotype by GVRP and DSR revealed the presence of a very faint bump at the anterior base of cusp *b*, possibly a rudimentary *e* cuspule); in both, the anterior root is sub-spherical in cross section and the posterior root is anteroposteriorly longer, labiolingually flattened, and expands below cusp *a*; and the crown overhangs the roots on all sides. All these morphological similarities between *Dyskritodon amazighi* and VPL/JU/KM/13 favour inclusion of the latter in the genus *Dyskritodon*.

However, the two specimens exhibit the following morphological differences. VPL/JU/KM/13 (length = 1.24 mm) is smaller in size than *D. amazighi* (length = 1.85 mm). In VPL/JU/KM/13, cusp *b* is slightly lingual to *a-c* line (Fig. 3E), whereas it is a lingual cingular cusp in *D. amazighi*; it is relatively smaller than cusp *d*, but not as small as in *D. amazighi*. In VPL/JU/KM/13, two equally developed cuspules *e* and *f* occur at the anterolingual and anterolabial bases of cusp *b* enclosing a well-developed vertical sulcus between them, while cuspule *e* is hardly indicated in *D. amazighi* and is in the form of a very small bump at the anterior base of cusp *b*. Cuspule *f* of *D. amazighi* is situated at the anterolabial base of *a*, whereas it is at the anterolabial base of cusp *b* in VPL/JU/KM/13. It extends obliquely to the anterior part of *a* in *D. amazighi*, while it is more vertical on VPL/JU/KM/13. The lingual cingulum is also more developed in VPL/JU/JM/13 than in *D. amazighi* and thus a narrow and better-developed shelf occurs between the main cusps and the cingulum. The posterior root of VPL/JU/KM/13 is not as long anteroposteriorly as in *D. amazighi*. These morphological differences with *D. amazighi* justify its placement in a new species.

TRICONODONTA indet.
(Figs 2F, G; 3F, G)

REFERRED MATERIAL. — VPL/JU/KM/15, fragmentary lower left molar.

HORIZON AND LOCALITY. — Mudstones associated with the limestone bands of Kota Formation, west of Paikasigudem village, Rebbana Mandalam, Adilabad District, Andhra Pradesh (State), India.

DESCRIPTION

The specimen is a partial lower molar (length of preserved specimen = 0.814 mm, maximum preserved width = 0.465 mm). The anterior cusps and anterior root are broken off. The main cusp *a* is half preserved. It is the highest and largest cusp with a flat lingual face. It is connected to the small posterior cusp *c* (less than half the height of cusp *a*) by a posterior crest. The main cusp is vertical in the orientation of its long axis, whereas cusp *c* is slightly reclining posteriorly making an acute angle with that of cusp *a* (Figs 2G; 3F). It is separated from cusp *a* by a shallow V-shaped notch. The lingual face of cusp *c* is also flat. The posterior accessory cusp *d* is a very small, cingular cusp and is prolonged anterolingually by the lingual cingulum, which possibly bears two incipient cingular cuspules. Anterior to these cuspules, the cingulum becomes reduced and indistinct at the level of the middle of cusp *a*. The labial face of *a* is acutely angulated. A slight basal swelling is present between the cusps *a* and *d*. The labial face of cusp *c* is also convex, but less than that of cusp *a*. The posterior face of the crown is rounded. The enamel of the crown is poorly preserved. Hence it is difficult to say whether wear facets were present or not, though there appears to be a wear facet on the posterolabial face of *a* and an indistinct one on the labial face of cusps *c* and *d* (Fig. 3G). The labial tip of cusp *c* is also worn (Fig. 3G). The posterior root is anteroposteriorly long at the base of the cusps and supports the entire preserved part of the crown. This root tapers ventrally and is moderately flattened labiolingually. It has convex anterior and posterior faces. A very shallow sulcus extends from the base of the crown (below the junction of cusps *a* and *c*) to mid-length of the root.

COMPARISONS

Incompleteness of the tooth does not allow any definitive comments on its taxonomic position. Nevertheless, the presence of a high principal cusp with its long axis vertically oriented and an accessory cusp *c* with its long axis diverging away from that of *a* is seen in some amphilestines and gobiconodontines as well as *Jeholodens*. The latter and *Tendagurodon* differ from VPL/JU/KM/14 in the absence of a distinct lingual cingulum. If the wear facets observed for VPL/JU/KM/14 are correct, then the occlusion pattern for this tooth can be supposed to be similar to that of *Morganucodon*.

Family MORGANUCODONTIDAE Kühne, 1958

Genus *Paikasigudodon* n. gen.

TYPE SPECIES. — *Paikasigudodon yadagirii* (Prasad & Manhas, 1997) n. comb., by monotypy.

ETYMOLOGY. — Genus name derived from the village Paikasigudem where the mammal-bearing section is exposed.

DIAGNOSIS. — Upper molar crown bearing a high central cusp with a flat labial face and convex lingual face; cusp *B* higher than *C*; presence of a large anterolabial cusp connected to *B* by a sharp crest; presence of an anterior and a posterior small lingual cingular cuspule; rudimentary lingual cingulum between *A* and *B*. Differs from *Morganucodon* in the presence of a high central cusp *A* and large anterolabial cusp *F*; differs from *Morganucodon*, *Jeholodens*, *Austrotriconodon*, and all triconodontids in the non-linear arrangement of cusps; differs from *Morganucodon*, *Megazostrodon*, and *Gobiconodon* in the absence of a well-defined lingual cingulum and the presence of cusp *B* larger than cusp *C*; differs from *Gobiconodon* and *Megazostrodon* in the presence of asymmetrically placed *B* and *C*; differs from *Brachyzostrodon* Sigogneau-Russell, 1983 in the non-linear arrangement of cusps and non-wrinkled enamel on the crown.

Paikasigudodon yadagirii
(Prasad & Manhas, 1997) n. comb.
(Figs 4; 5)

Kotatherium yadagirii Prasad & Manhas, 1997: 565, 566.

HOLOTYPE. — VPL/JU/KM/10, left upper molar.

HORIZON AND LOCALITY. — Mudstones associated with the limestone bands of Kota Formation, west of Paikasigudem village, Adilabad District, Andhra Pradesh (state), India.

DIAGNOSIS. — Same as for genus.

DESCRIPTION

The tooth is a double rooted, bean-shaped, excellently preserved left upper molar (maximum length = 1.881 mm, anterior width = 1.063 mm, posterior width = 0.787 mm). The principal and accessory cusps form an obtuse angle in occlusal view. *A* is the largest and highest cusp with a vertically oriented long axis, a nearly flat or slightly convex labial face, and a more convex lingual face. Similarly, cusps *B* and *C* have convex lingual bases. Cusp *B* is the next largest cusp and is separated from cusp *A* at a slightly higher level than cusp *C* by a narrow, V-shaped notch (Fig. 5E). It is connected to *A* by a sharp crest and has a convex anterolingual face. Labially, it has a broad, flat face that is slightly obliquely oriented relative to the labial face of *A*. A sharp transverse crest joins cusp *B* with a relatively large anterolabial cusp *F* (less than half the size of cusp *B*). The tip of cusp *F* projects labially. It has a flat posterolingual face, which lies at a right angle with respect to the labial face of cusp *B*, and a rounded anterior face. A very small cuspule (possibly cusp *E*) also occurs at the anterolingual base of cusp *B*. Cusp *C* is slightly smaller than cusp *B*

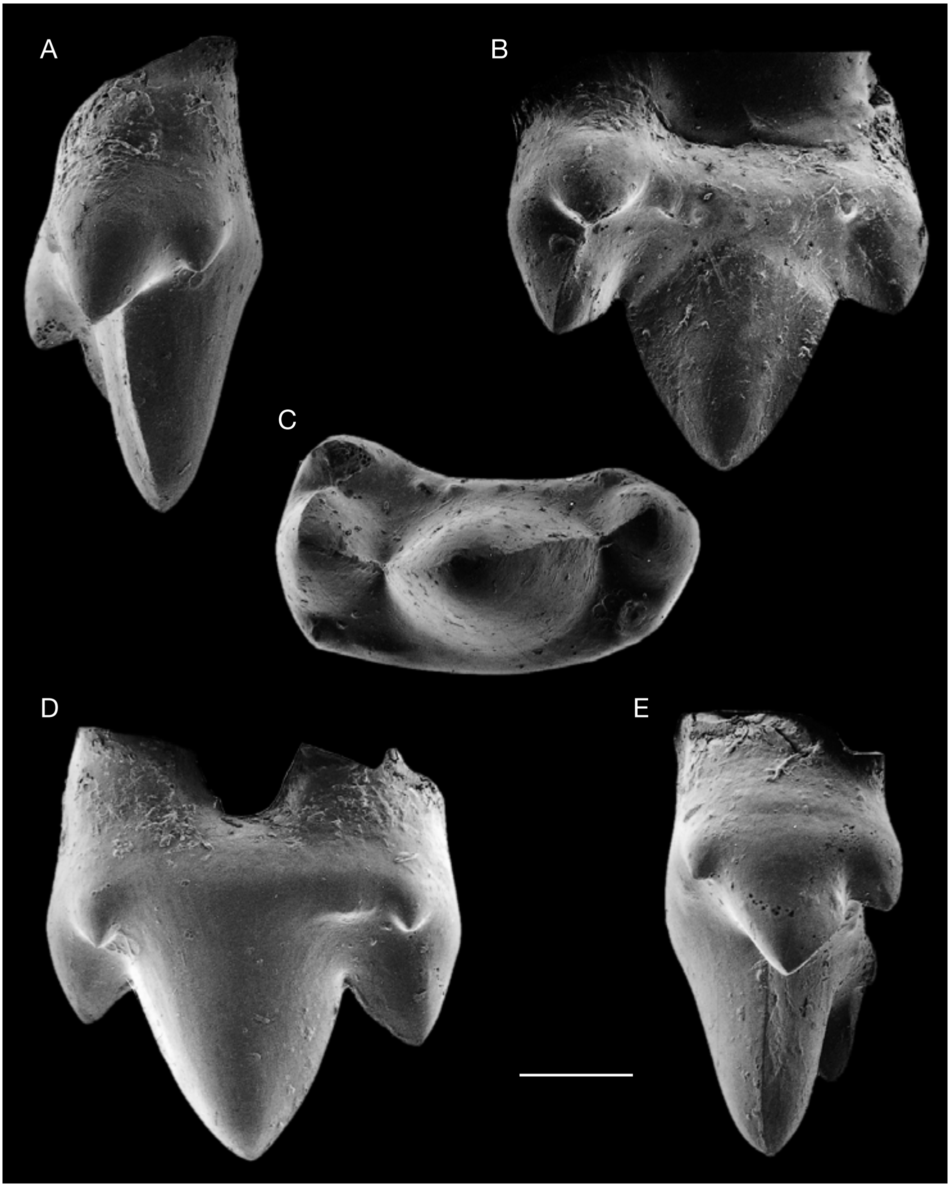

FIG. 4. — SEM photomicrographs of *Paikasigudodon yadagirii* (Prasad & Manhas, 1997) n. comb., left upper molar, holotype (VPL/JU/KM/10); **A**, posterior view; **B**, labial view; **C**, occlusal view; **D**, lingual view; **E**, anterior view. Scale bar: 0.5 mm.

but larger than the anterolabial cusp *F*. In occlusal view, it lies noticeably labial to the *A-B* line. It has a convex posterior face and moderately convex anterolabial and anterolingual faces that are separated by a crest. A small cingular cusp occurs at the anterolabial base of cusp *C*, and another slightly larger one at its anterolingual base (Fig. 5C, D). A weakly developed, narrow labial cingulum, beaded with minute cuspules, connects cusp *C* with cusp *F* (Figs 4B, C; 5C, E). These cingular cusps are minute and more or less of the same size. A narrow shelf is present anteri-

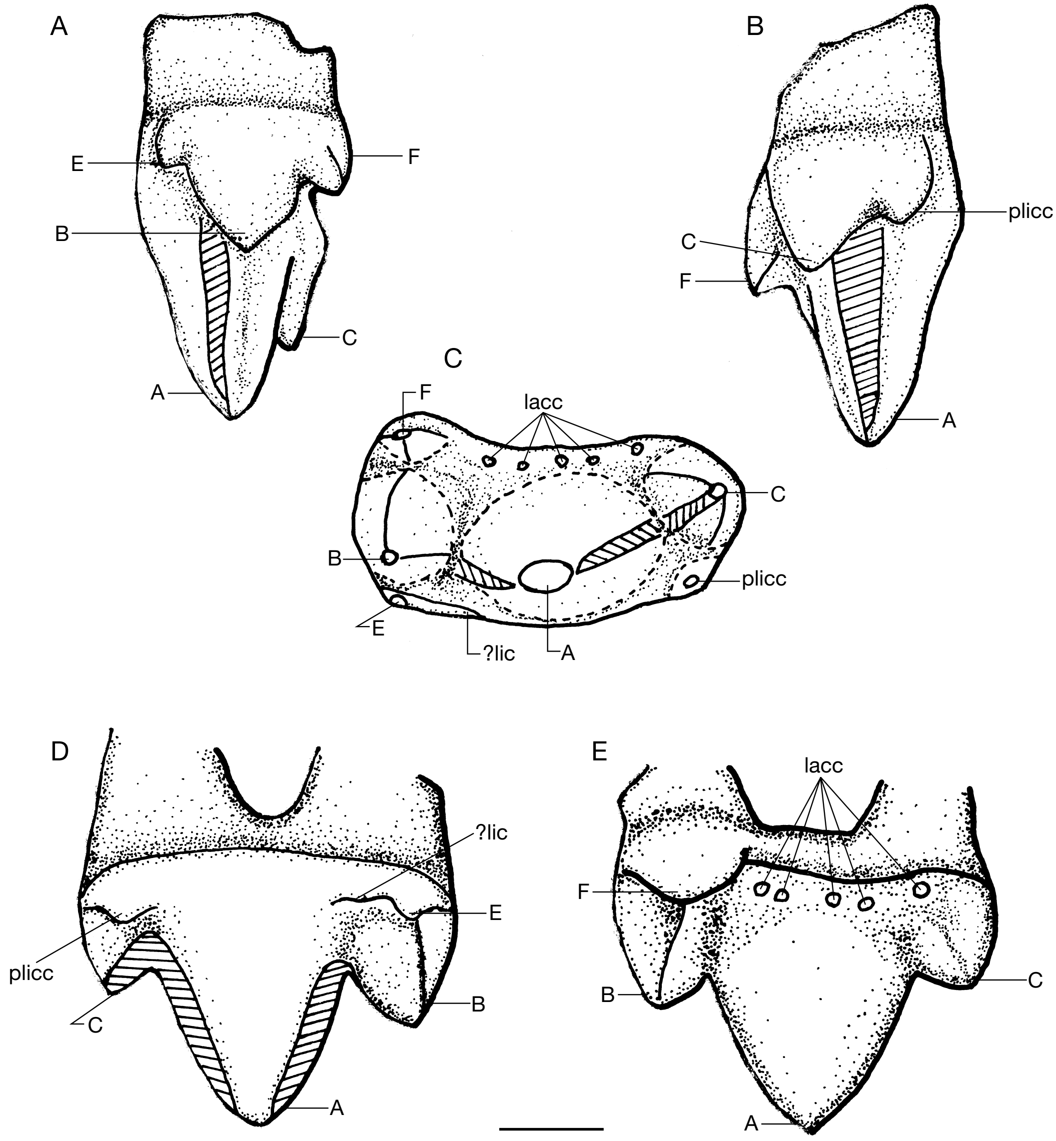

FIG. 5. — *Paikasigudodon yadagirii* (Prasad & Manhas, 1997) n. comb., left upper molar, holotype (VPL/JU/KM/10); **A**, anterior view; **B**, posterior view; **C**, occlusal view; **D**, lingual view; **E**, labial view. Abbreviations: **A**-**F**, cusps *A*-*F*; **lacc**, labial cingular cuspules; **?lic**, ?lingual cingulum; **plicc**, posterior lingual cingular cuspule. Scale bar: 0.5 mm.

orly. In occlusal view, the labial cingulum defines a slight ectoflexus because of the labial projection of cusps *C* and *F*. The lingual base of the crown is swollen, but no distinct cingulum is present except for a thickening of the lingual margin between *A* and *B* (Figs 4D; 5C, D), and the small cingular cusps posterolingually and anterolingually. In anterior view, the crown has a transverse aspect, only the posterior crest of *B* and anterior crest of *A* are in line. There are two subcylindrical roots.

The tooth is quite unworn. A weakly developed abrasion facet extends lingually from the posterior tip of cusp *A* to its base. This facet continues across the notch between *A* and *C* to just below the tip of *C* (Fig. 5C, D). Another very faint or indistinct abrasion facet can be seen on the anterolingual face of *A* extending from the notch between *B* and *A*. This facet is broad at the base of *A* and gradually narrows toward its tip to disappear before reaching it (Fig. 5C, D). The posterolingual face of *B* appears to be unworn. VPL/JU/KM/10 is considered to be an upper molar because of the presence of a rudimentary lingual cingulum between *A* and *B* with small anterolingual and posterolingual cingular cuspules in addition to the continuous labial cingulum. The non-linear arrangement of cusps as in the upper molars of certain triconodonts (*Gobiconodon* and *Megazostrodon*) and the absence of anterior interlocking mechanism also preclude its placement in lower molars.

COMPARISONS

Prasad & Manhas (1997) assigned VPL/JU/KM/10 to a new species of *Kotatherium*, *K. yadagirii* (family Tinodontidae), based on literature then available to them. Comparison of these specimens with originals and casts of Mesozoic mammals housed in BMNH and MNHN led the authors to the conclusion that VPL/JU/KM/10 is not a symmetrodont but a triconodont. VPL/JU/KM/10 differs from *Kotatherium haldanei*, a symmetrodont described from the Kota Formation (Datta 1981), in its bean-shaped crown (in occlusal view), vertically oriented symmetrical cusp *A* without any labial tilt, absence of an anterolingual shelf, presence of prominent cusp *B* slightly larger than *C*, posterolingual cuspule and a large anterolabial accessory cusp as large as the "metacone" of Datta (1981). In other early symmetrodonts (*Kuehneotherium* Kermack, Kermack & Mussett, 1968, *Eurylambda* Simpson, 1929, and *Woutersia* Sigogneau-Russell, 1983), the lateral cusps are separated from the main cusp close to their tips by shallow notches, whereas in VPL/JU/KM/10, *B* and *C* are broadly separated from *A* by deep notches. In symmetrodonts, the lateral cusps are symmetrically arranged on either side of the main cusp. In contrast to this, cusps are asymmetrically arranged and the crown is also asymmetrical in occlusal view on VPL/JU/KM/10. Although symmetrodonts have anterolingual cusp *E* (*Kuehneotherium*, *Woutersia*), they lack posterolingual cuspule and the large anterolabial cusp *F* of VPL/JU/KM/10. Furthermore, VPL/JU/KM/10 differs from primitive symmetrodonts (*Kuehneotherium*, *Woutersia*, and *Mictodon* Fox, 1984) in the absence of parastyle-metastyle interlock. These morphological differences are in favour of removing VPL/JU/KM10 from the order Symmetrodonta.

Among the various early mammalian groups, triconodonts exhibit a crown morphology nearest to that of VPL/JU/KM/10. The subfamily Amphilestinae is known only by lower molars and hence no comparison is possible with VPL/JU/KM/10. Among the different members of Triconodonta, gobiconodontines have molars with central cusp substantially taller and larger than the adjacent accessory cusps, which are nearly equal in size, as is the case in VPL/JU/KM/10. The upper molars of Gobiconodontinae (*Gobiconodon borissiaki* Trofimov, 1978, *G. hoburensis* [Trofimov, 1978], *G. ostromi* Jenkins & Schaff, 1988) show an incipient triangular arrangement of cusps and the degree of triangular arrangement increases posteriorly, reaching an angle of 145° to 158° on M3 and M4 (Kielan-Jaworowska & Dashzeveg 1998). In VPL/JU/KM/10, this angle is 145°. The upper molars of *Gobiconodon* change from oval to subrectangular anteriorly to rectangular crowns posteriorly. They show a labial indentation as in VPL/JU/KM/10. The labial cingulum of *Gobiconodon* is beaded as in VPL/JU/KM/10. The lingual cingulum is also well-developed in *Gobiconodon*, in which it is wider at the anterior and posterior ends than in the middle. In VPL/JU/KM/10, the lingual cingulum is incipient anteriorly and the tooth bears small cuspules anteriorly as well as posteriorly. Cusps *E* and *F* are known to occur in *Gobiconodon* (Kielan-Jaworowska & Dashzeveg 1998) as in VPL/JU/KM/10, but in the latter, cusp *F* is relatively very large in size. VPL/JU/KM/10 further differs from *Gobiconodon* in its bean-shaped crown, and in the presence of relatively high, anteroposteriorly long principal cusp *A* and asymmetrically placed *B* and *C*. In *Gobiconodon*, cusp *A*, though largest of the crown, is moderately higher than *B* and *C*. In VPL/JU/KM/10, wear facets are not present on the anterior and posterior parts of lingual cingulum as in *Gobiconodon*, rather they are restricted to the anterolingual and posterolingual faces of cusp *A* and the valley between *A* and *C*.

Another triconodont taxon in which the central cusp is high and the lateral cusps are smaller (nearly equal to each other) is *Jeholodens jenkinsi* described from the Late Jurassic/Early Cretaceous of Liaoning, China (Ji *et al.* 1999). But in *Jeholodens*, the cusps are aligned anteroposteriorly. There is no cingulum on the labial and lingual sides of M1, but a faint cingulum is present on the labial side of M2 and M3 of *Jeholodens*. No cingular cuspules are seen on the labial and lingual sides of cusp *B* on the exposed M1 of *Jeholodens*.

The triconodont which most closely approximates to VPL/JU/KM/10 in crown morphology seems to be *Megazostrodon rudnerae* Crompton & Jenkins, 1968, particularly M1 of this genus. As in VPL/JU/KM/10, the symmetrical main cusp dominates the bean-shaped crown, a labial median indentation is present, the anterior end of the crown is broader than the posterior one (this is also the case in *Gobiconodon*), a large cusp *F* is present labial to *B*, and the three main cusps form an obtuse-angled triangle. The lingual border of *Megazostrodon* upper molars is markedly convex as in VPL/JU/KM/10. In *M. rudnerae*, cusp *A* becomes less dominant on M2 and more posterior molars. By analogy, VPL/JU/KM/10 could be considered as M1. But in *M. rudnerae*, the main cusp is longer anteroposteriorly and extends to the labial margin in the middle. In addition, the height of the main cusp is greater than its anteroposterior length in VPL/JU/KM/10, whereas it is nearly equal in *M. rudnerae*. Cusp *B* is smaller than cusp *C* in *M. rudnerae*, while it is slightly larger than *C* in VPL/JU/KM/10. In this respect, the latter is more similar to *Austrotriconodon*, but in the latter genus cusp *B* is the largest of all cusps and the crown morphology is quite distinct from that of VPL/JU/KM/10. Cusp *D* is very small in *M. rudnerae*, whereas it is not present on VPL/JU/KM/10. Finally, unlike *M. rudnerae*, the labial cingulum of VPL/JU/KM/10 is uninterrupted in the middle and the tooth does not bear a distinct lingual cingulum although an incipient cingulum is present anterolingually between cusps *A* and *B*. In view of the above discussed morphological divergences from *Megazostrodon*, VPL/JU/KM/10 is placed under a new genus of the family Morganucodontidae closely allied to *Megazostrodon*.

Genus *Indotherium* Yadagiri, 1984

TYPE SPECIES. — *Indotherium pranhitai* Yadagiri, 1984.

EMENDED DIAGNOSIS. — Upper molars with oval crown with cusps *A* and *C* nearly equal in size and in line, *B* very small and developed as a cingular cusp; a deep groove separates *A* from *C*; steeply ventral sloping of labial faces of cusps *A* and *C*. Differs from *Morganucodon* in having a deep notch separating *A* and *C*; differs from *Megazostrodon* in the presence of equally developed *A* and *C*, main cusps arranged linearly rather than in a triangle, and in the absence of large cingular cuspules; differs from *Brachyzostrodon* in the presence of small, cingular cusp *B* and absence of wrinkles on the enamel.

Indotherium pranhitai Yadagiri, 1984
(Figs 6; 7)

HOLOTYPE. — GSI type No. SR/PAL/11, left upper molar.

REFERRED MATERIAL. — VPL/JU/KM/11, right upper molar.

HORIZON AND LOCALITY. — Mudstones associated with the limestone bands of Kota Formation, west of Paikasigudem village, Rebbana Mandalam, Adilabad District, Andhara Pradesh (state), India.

DIAGNOSIS. — Same as for the genus.

DESCRIPTION OF VPL/JU/KM/11

This is an eroded right upper molar (maximum length = 1.437 mm, anterior width = 0.77 mm, posterior width = 0.626 mm). The enamel on the labial surface of the crown is completely spalled off (Fig. 6A). The crests joining *A* with *B* and *C*

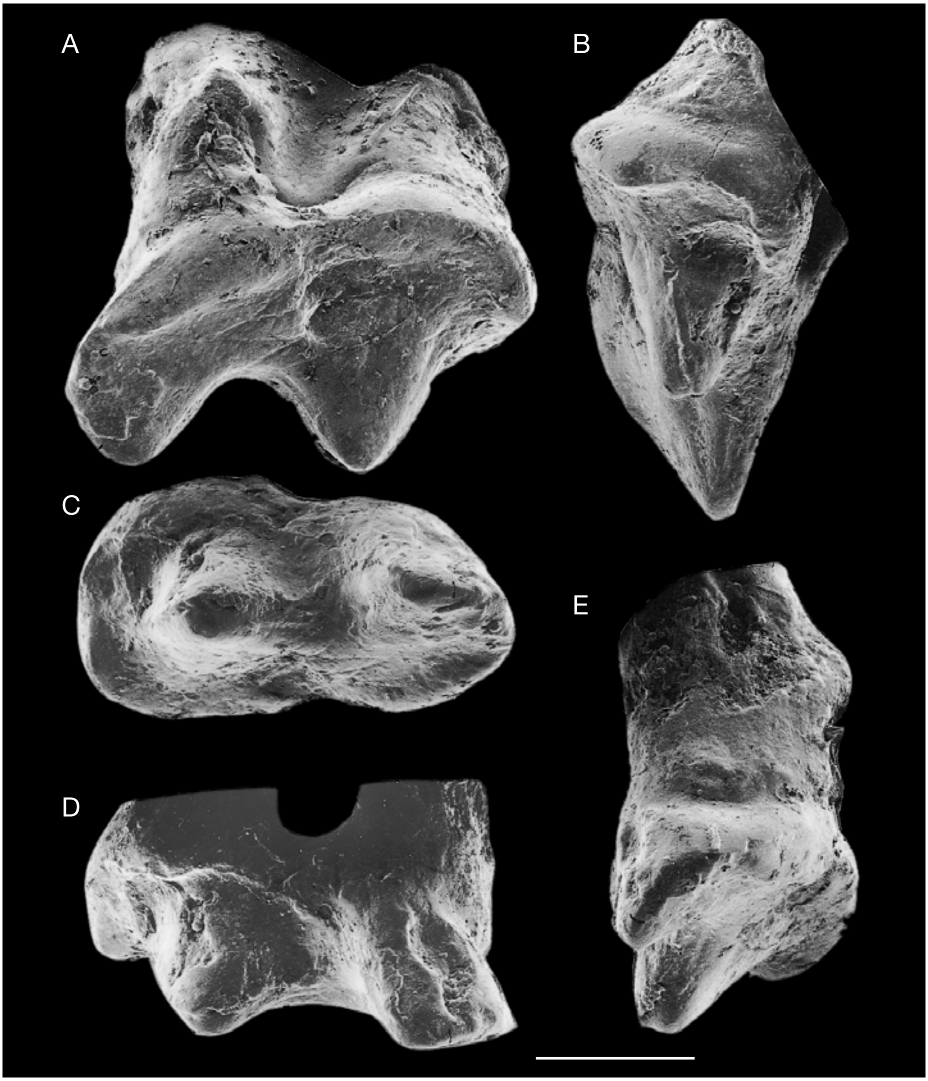

FIG. 6. — SEM photomicrographs of *Indotherium pranhitai* Yadagiri, 1984, right upper molar (VPL/JU/KM/11); **A**, labial view; **B**, anterior view; **C**, occlusal view; **D**, lingual view; **E**, posterolabial view. Scale bar: 0.5 mm.

are completely worn. The cusp formula for this tooth is *A* > *C* > *B*. In occlusal view, the tooth is roughly oval in outline, with slight indentations labially and lingually opposite the posterior limit of *A* (Figs 6C; 7B). The molar has two major cusps and one minor cusp (Figs 6A; 7C, D). The principal cusp *A* is located anterior to the mid-point of the tooth; cusp *C*, posterior to it, is about the same size. Cusp *C* is strongly reclined, cusp *A* is nearly vertical, and the two cusps are separated from each other by a broad, deep groove (Figs 6A; 7C, D). A small anterior cusp *B*, slightly offset from the line of *A* and *C*, arises from the anterior cingulum. A broad groove separates this cusp from *A*. The labial faces of cusps *A* and *C* are flat and slope steeply labioventrally. The labial cingulum arises from the mid-height of cusp *C* (Figs 6A; 7C), slopes down anteriorly

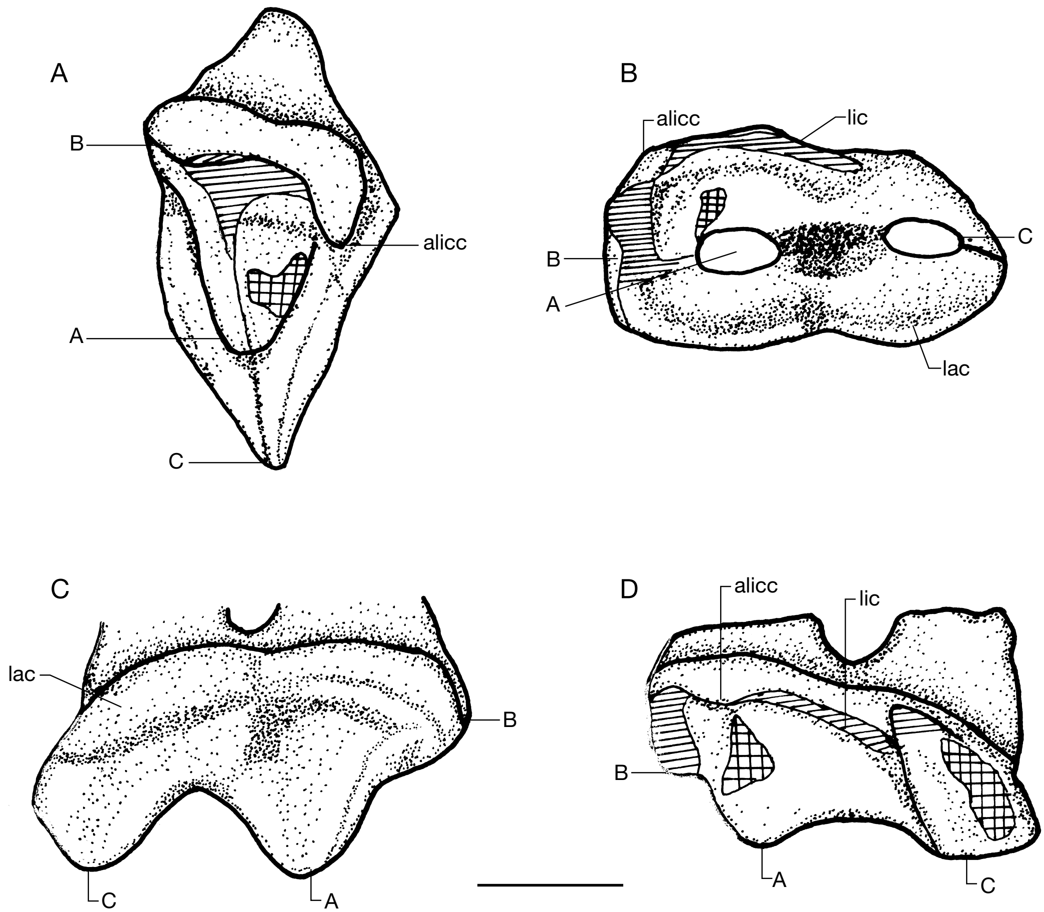

FIG. 7. — *Indotherium pranhitai* Yadagiri, 1984, right upper molar (VPL/JU/KM/11); **A**, anterior view; **B**, occlusal view; **C**, labial view; **D**, lingual view. Abbreviations: **A**-**C**, cusps *A*-*C*; **alicc**, anterior lingual cingular cuspule; **lac**, labial cingulum; **lic**, lingual cingulum. Scale bar: 0.5 mm.

and joins cusp *B* at a lower level. This cingulum appears to be narrow opposite cusp *A* and relatively wide and swollen opposite the groove separating cusp *A* from *C*. The highly eroded surface of this cingulum does not provide any evidence for cingular cuspules. Anterior to *A*, a wide shelf is present both labially and lingually. The labial cingulum is interrupted anteriorly by cusp *B*. It continues lingually and posteriorly as a narrow worn ridge to the anterior base of *C*. This cingulum bears a small cingular cuspule at the anterolingual base of *A* (Figs 6D; 7D).

The anterior root is only partly preserved, whereas the posterior root is relatively better preserved. The posterior root is dilated distally in labial view and its transverse width is greater than its length. Wear facets are visible on the lingual face of the crown. The lingual cingulum is quite worn (Fig. 7B, D). The lingual tip of *B*, anterolingual cingulum between *B* and anterolingual cingular cuspule, and the valley between *A* and *B* exhibit moderate wear (Figs 6C; 7B, D). The anterolingual cingular cuspule also exhibits some abrasion. The valley between the posterior base of *A* and anterior base of *C* is deeply grooved. The lingual face of *A* is chipped in its middle part. Therefore, it is difficult to say whether there was any wear facet in this region or not. The enamel on the lingual face of cusp *C* is chipped particularly near its ventral part, but its dorsal part shows a flat surface pointing to the presence of a possible wear facet here.

COMPARISONS

Yadagiri (1984) described GSI type No. SR/PAL/11 as a lower molar, placing it in the then new genus and species. He made it a type of *Indotherium pranhitai*, family *incertae sedis* (order Symmetrodonta). Prasad & Manhas (1997) described an additional molar (VPL/JU/KM/11) referring to *Indotherium pranhitai*. They transferred *I. pranhitai* from the order Symmetrodonta to the order Triconodonta because the principal cusps of the crown are arranged more or less in straight line. But they also mistook the new tooth for a lower molar, as Yadagiri (1984) did for the type. The two molars (GSI type No. SR/PAL/11 and VPL/JU/KM/11), appear to be very similar in their crown morphology. From the photographs and figures provided by Yadagiri (1984: pl. 2a-e, fig. 2a-f), the type specimen appears to be better preserved.

VPL/JU/KM/11 is considered to be an upper molar because of the presence of labial and lingual cingula and because of its similarity to maxillary teeth of morganucodontids. Within all known taxa of Triconodonta as discussed earlier in the section on *Dyskritodon*, *Austrotriconodon* and *Gobiconodon* differ from SR/PAL/11 and VPL/JU/KM/11 in the cusp formula and the arrangement of cusps on the crown. Any relationship with the family Triconodontidae can also be ruled out for VPL/JU/KM/11, because in all known taxa of this family, cusps *B*, *A*, and *C* of upper molars are sub-equal in size. The upper molars of *Jeholodens* are distinguished from VPL/JU/KM/11 in having a relatively large cusp *A*, cusp *B* excluded from cingulum, and the presence of cusp *D*.

It is only in *Morganucodon* Kühne, 1949 (Morganucodontidae) that cusp *B* is very small and occurs anterior to cusp *A* or slightly labial to the *A-C* line, and cusps *A* and *C* are equal or nearly equal in size. Some important morphological features common to *Morganucodon* and VPL/JU/KM/11 are: the presence of an anterior root that is circular or oval in cross section, with an anteroposterior long axis and transversely wide posterior root; balcony-like projection of crown over the posterior root (Figs 6A, D; 7C, D); *B* developed as a small cusp more or less in line with *A* and *C*; wide anterior shelf; posteriorly wide labial cingulum, lingual cingulum narrower than labial cingulum; tranversely wide and dilated posterior root. The occlusal pattern in *Morganucodon* was studied by Crompton & Jenkins (1968) and Mills (1971). According to these works, in the early stage of wear, a concave facet develops in the anterior part of lingual cingulum of *Morganucodon* upper molars. Subsequently, it extends from the cingulum to the bases of *A* and *B* and another facet develops on the lingual cingulum adjacent to cusps *A* and *C* because of the occlusion of cusp *c* of corresponding lower molar between cusps *A* and *C*. The wear facets observed on VPL/JU/KM/11 are more or less similar to those observed in *Morganucodon* in the early stages.

Of the known *Morganucodon* teeth, the morphology of Indian specimens approaches that of BMNH No. M26014 (Early Jurassic of Wales) the most. This specimen is a right maxillary fragment bearing two teeth possibly the antepenultimate and penultimate molars (because there is an alveolus behind the posterior most preserved tooth). Most of the morphological features observed in VPL/JU/KM/11 are also present in BMNH M26014. Cusp *C* is reclined in BMNH M26014 as well as in VPL/JU/KM/11 and GSI type No. SR/PAL/11. In the latter specimen, *C* is slightly smaller than cusp *A*, as it is in M26014. On the penultimate molar of M26014 and on VPL/JU/KM/11, the posterior crown overhangs the root like a balcony.

However, in *Morganucodon*, the groove between *A* and *C* is not as broad as in VPL/JU/KM/11. This character and the anterior crown morphology might be cited against the inclusion of the Indian specimens in the family Morganucodontidae. But in SR/PAL/11, this groove is nearly at the same level of development as in BMNH M26014 and uncatalogued specimens of *Morganucodon* from

Pant Quarry (Early Jurassic), Glamorganshire, England, housed in University College London. Therefore, the deep groove between *A* and *C* might be reflecting the highly eroded nature of VPL/JU/KM/11. On VPL/JU/KM/11, cusp *C* is stubby in appearance and cusp *D* is absent. The latter character is not very significant in distinguishing these taxa as cusp *D* is present on some specimens of *M. watsoni* (Crompton, 1974) and absent on others (Parrington 1971). The labial face of cusps *A* and *C* is steeply sloping labioventrally in VPL/JU/KM/11, whereas it is not so in *Morganucodon*. Another important distinction between the Indian specimens and the molars of *Morganucodon* lies in the anterior part of the crown. On the upper molars of *Morganucodon* with significant wear, there is a broad transverse notch separating cusps *A* and *B*. Because of this the lingual cingulum slopes dorsally from the anterolingual base of cusp *A*, whereas in VPL/JU/KM/11, this margin is horizontal and bears a small cingular cuspule at the anterolingual base of cusp *A*. However, it needs to be emphasised here that VPL/JU/KM/11 appears to be in the early stage of wear. The lingual cingulum of *Morganucodon*, unlike in VPL/JU/KM/11, bears a variable number of cuspules (Mills 1971). Moreover, *B* is not a cingular cusp in *Morganucodon* (see Mills 1971).

Ventrally sloping steep labial faces of *A* and *C*, absence of cuspules on the lingual cingulum except for the anterolingual cuspule, and presence of *B* as a cingular cusp are the morphological differences sufficient enough to distinguish the Indian specimens at generic level from *Morganucodon*.

DISCUSSION

The new finds from the Mesozoic deposits of India bring forth two important aspects. Although the Early Cretaceous Anoual fauna from Morocco was initially considered to be endemic to a large extent, subsequent discoveries have shown that certain taxa may be more widely distributed. For example, the symmetrodont *Thereuodon* (Sigogneau-Russell & Ensom 1998), an indeterminate talonid of a tribosphenic mammal (Sigogneau-Russell & Ensom 1994), and amphilestid triconodont (Sigogneau-Russell *et al.* 1998) are now known from the Early Cretaceous Purbeck Limestone Formation, England. The present report of the Moroccan genus *Dyskritodon* from the purported Lower/Middle Jurassic sediments of India further suggests a broad geographic distribution for some taxa.

Secondly the presence of an Early Cretaceous (?Berriasian) North African genus in the supposed Early/Middle Jurassic rocks of India raises an important question regarding the age of the Kota Formation. If the present age assignments are accepted, there is a gap of 45-50 m.y. between the Indian and Moroccan sites yielding *Dyskritodon*. At the known rates of mammalian evolution, no genus is expected to survive for such a long period. In the Mesozoic mammalian fossil record, the longest ranging genus is *Gobiconodon*. This triconodont genus is known to span over 20 m.y. extending from the ?Berriasian (Morocco, D. Sigogneau-Russell pers. comm.) to the ?Aptian/?Albian (Mongolia and USA). This implies that the dating of one of the two *Dyskritodon* yielding sites may be in error. Thus one can speculate on three alternative possibilities: 1) Anoual mammal-yielding site might be older than the presently accepted earliest Cretaceous age; 2) the Kota Formation might be younger than the long accepted Early Jurassic to Middle Jurassic age; and 3) attribution of VPL/JU/KM/13 to *Dyskritodon* is not valid. Since the Anoual mammal yielding level has been more precisely dated on the basis of nannofossils *Polycostella*, *Micrantholithus*, and *Nannoconus*, and sedimentological (mineralogical) data (Sigogneau-Russell *et al.* 1990) than the Kota Formation, it is more likely that the age of Kota Formation is younger than the widely accepted Early Jurassic. On the other hand, the presence of a morganucodontid, known elsewhere from the Upper Triassic-Early Jurassic deposits of South Africa, England, Switzerland, and China, and Middle Jurassic of England, in the same assemblage as *Dyskritodon* further compounds the age problem. This might point to either a long stratigraphic range (extending from Upper Lias to Berriasian) for *Dyskritodon* or late survival of morganucodontids into Late Jurassic or Early Cretaceous. As far as the third alternative is concerned, there is no basis for invalidating the attribution of VPL/JU/KM/13 to *Dyskritodon* as the Indian specimen is remarkably similar to the type species, *Dyskritodon amazighi* Sigogneau-Russell, 1995, in its crown morphology. In view of conflicting data at hand, it is felt that a thorough reassessment of the age of Kota Formation is urgently needed. A re-examination of the ostracode fauna and palynological analysis of the Kota samples might throw some light on this problem.

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