



Rhynchocephalians (Diapsida: Lepidosauria) from the Jurassic Kota Formation of India

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Despite their rarity today, rhynchocephalians formed a diverse Early Mesozoic clade with a comparatively good fossil record. They had a Pangaeian distribution in the Late Triassic and Early Jurassic, although the Gondwanan record remains more limited than the Laurasian one. We report here on new sphenodontian material from the Jurassic Kota Formation of peninsular India. Two taxa are represented, and both are attributed to new genera. One is a relatively derived sphenodontian with a premaxillary morphology similar to that of the Late Triassic/Early Jurassic genus *Clevosaurus*. The other is somewhat more primitive in its morphology, although clearly a crown-group sphenodontian. In addition, three dentary fragments and a partial maxilla signal the presence of a primitive pleurodont lepidosauromorph similar to the basal rhynchocephalians *Gephyrosaurus* and *Diphydontosaurus* from Britain.

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ADDITIONAL KEY WORDS: Reptilia – palaeontology – morphology – biogeography – Gondwana – Sphenodontia.

INTRODUCTION

The lepidosaurian clade Rhynchocephalia is represented today by a single genus, *Sphenodon*, with two species – *S. punctatus* and *S. guntheri* (Daugherty *et al.*, 1990) – surviving on small islands off the coast of New Zealand. This is in marked contrast to the situation in the Mesozoic, when rhynchocephalians were a diverse and widely distributed group. The earliest known rhynchocephalians are from the Late Triassic (Carnian) of North America (Sues & Olsen, 1990) and then Europe (Fraser & Benton, 1989), but the group was widespread over Pangaea in the Late Triassic and Early Jurassic (Tables 1, 2). Most early rhynchocephalians were probably small insectivores although one, *Pelecymala* (Fraser, 1986), may have been herbivorous. The group remained diverse in the Jurassic and Early Cretaceous – at least in Euramerica (Table 2), with the emergence of fast-running long-legged terrestrial forms (e.g. *Homoeosaurus*, Cocude-Michel, 1963), short-limbed long-bodied swimmers (pleurosaurs, Fabre, 1981; Carroll, 1985), and specialized

herbivores (*Eilenodon*, Rasmussen & Callison, 1981; *Toxolophosaurus*, Throckmorton, Hopson & Parks, 1981). One of the last known genera, the Mexican *Pamizinsaurus* (Aptian/Albian, Reynoso, 1997), was unique in having a covering of tiny bead-like osteoderms.

Rhynchocephalians disappeared from the Asian record in the Early Jurassic (the Late Jurassic/Early Cretaceous *Monjurosuchus* from China is not a rhynchocephalian, Evans, pers. obs. *contra* Sun *et al.*, 1992) and from the Euramerican record at the end of the Early Cretaceous (the last known taxa being from the Aptian/Albian of Mexico, Reynoso, 1996a, 1997, 1998; North America, Throckmorton *et al.*, 1981; Italy, Barbera & Macuglia, 1988). The reasons for these apparent extinctions are not understood. However, rhynchocephalians must have survived in parts of Gondwana (since they exist today in New Zealand) but we know very little about their post-Triassic southern history. Currently the Gondwanan record is limited to fragmentary remains from the Early Jurassic (Gow & Raath, 1977; Sues & Reisz, 1995) and Early Cretaceous (Rich, Molnar & Rich, 1983; Ross, Sues & De Klerk, 1999) of southern Africa and from the basal Cretaceous of Morocco (Evans & Sigogneau-Russell, 1997).

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Table 1. Rhynchocephalian distribution in the Late Triassic. Based on the following references: Fraser (1982, 1986, 1988), Fraser & Benton (1989), Whiteside (1986), Duffin (1995) and Renesto (1995) (Europe); Sues & Olsen (1990) and Chatterjee (1999) (North America); Ferigolo (1999) (Brazil); Flynn *et al.* (1997, 1999) (Madagascar); Wu (1994) (China). Age data taken from Gradstein *et al.* (1995)

| | North America | Europe | Asia | Gondwana |
|-----------------------|------------------------------|----------------------------|--------------------|-------------|
| | USA | Germany | China | Madagascar |
| | Indet. taxa | <i>Polysphenodon</i> | <i>Clevosaurus</i> | Undescribed |
| | <i>Clevosaurus</i> | England | | Brazil |
| Late Triassic 227 Mya | <i>cf Planocephalosaurus</i> | <i>Diphydontosaurus</i> | | Undescribed |
| | | <i>Planocephalosaurus</i> | | |
| | | <i>Clevosaurus</i> | | |
| | | <i>Sigmala</i> | | |
| | | <i>Pelecymala</i> | | |
| | | Wales | | |
| | | Indet. taxon | | |
| | | Scotland | | |
| | | <i>Brachyrhinodon</i> | | |
| | | Italy | | |
| | | <i>Diphydontosaurus</i> | | |
| | | Belgium | | |
| | | <i>cf Diphydontosaurus</i> | | |
| | | <i>Clevosaurus</i> | | |
| | | France | | |
| | | Indet. taxon | | |

Here we describe a new sphenodontian assemblage from the Jurassic Kota Formation of Andhra Pradesh in peninsular India.

GEOLOGY

The Pranhita–Godavari valley of peninsular India embodies a thick sequence of sedimentary rocks spanning the period of the early Middle Triassic to Early Cretaceous. This sedimentary succession has been referred to the Upper Gondwana Group. Hughes (1876) designated the term Kota-Maleri Beds for the Triassic and Jurassic vertebrate fossil bearing rocks of this basin. Following this, King (1881) made a detailed geological map of the basin. He separated the Kota-Maleri Beds into Triassic Maleri and Jurassic Kota Formations on the basis of field relationships, lithology and fossil characteristics. Subsequent detailed geological mapping and palaeontological investigations led Kutty (1969) to further subdivide the Triassic rocks of this belt into the lower Middle Triassic Yerrapalli Formation, upper Middle Triassic Bhimaram Sandstone, Upper Triassic (Carnian) Maleri Formation and Upper Triassic (Norian-Rhaetian) Dharmaram Formation.

The Kota Formation, which is the focus of the present study, derives its name from the village of Kota located on the left bank of the Pranhita, a tributary of the Godavari River. Other important sections of the Kota

Formation are exposed near the villages of Mangapalli, Metpalli, Kunchevalli, Darogapalli, Paikasigudem, Akkalapalli and Kadamba. According to the lithostratigraphic classification of Rudra (1982), the Kota Formation is divisible into Lower and Upper Members. The Lower Member comprises (1) a basal coarse, poorly sorted, pebbly sandstone which grades vertically into white fine grained sandstone with few pebbles followed upwards by (2) red, purple/violet, yellow to green clays and mudstones. The Upper Member is characterized by (1) light cream coloured, bedded limestone bands intercalated with clays and mudstones (these beds directly overlie the red clays of the Lower Member), (2) red clays with ferruginous mudstones overlying the limestone zone and (3) siltstones and fine-grained sandstones overlying the ferruginous mudstones. The majority of the fossils described here come from the clays and mudstones intercalated with the limestone beds of the Upper Member, exposed southwest of Paikaisigudem village (Fig.1). A few specimens were recovered from clays exposed east of the village of Gorlapalli. The clays have been bulk collected, screen washed and sorted to yield an assemblage of disarticulated, fragmentary bones from a variety of taxa including mammals, dinosaurs, fish, lizards, and the sphenodontians described here (Datta, 1981; Yadagiri, 1984, 1985, 1986; Prasad, 1986; Prasad & Manhas, 1997).

Table 2. Rhynchocephalian distribution in the Jurassic and Early Cretaceous. Based on the following references: Cocude-Michel (1963), Robinson (1973), Evans (1980, 1988, 1992, 1994, 1998), Evans & Fraser (1982), Fabre (1981), Carroll (1985) and Barbera & Macuglia (1988) (Europe); Wu (1994) (China); Gow & Raath (1977), Rich *et al.* (1983), Sues & Reisz (1995), Evans & Sigogneau-Russell (1997) and Ross *et al.* (1999) (Africa); Gilmore (1909), Simpson (1926), Rasmussen & Callison (1981), Throckmorton *et al.* (1981), Sues & Baird (1993), Sues, Shubin & Olsen (1994), Kirkland *et al.* (1997) and Fraser & Wu (1998) (North America); Reynoso (1993, 1996a,b, 1997, 1998) (Mexico). Age data taken from Gradstein *et al.* (1995)

| | North America | Europe | Asia | Gondwana |
|-------------------------|--|---|---|--|
| Albian 112 Mya | Mexico <i>Pamizinsaurus</i> <i>?Sapheosaur</i> | Italy <i>Chometokadmon</i> | | |
| Aptian 121 Mya | USA <i>Toxolophosaurus</i> | | | |
| Barriemian 127 Mya | USA <i>cf Toxolophosaurus</i> | | | |
| Hauterivian 132 Mya | | | | |
| Valanginian 137 Mya | | | South Africa Indet. taxon <i>cf Opisthias</i> | |
| Berriasian 144 Mya | | England <i>Opisthias</i> <i>Homoeosaurus</i> France <i>Pleurosaurus</i> | Morocco <i>Tingitana</i> Indet. taxon | |
| Tithonian 151 Mya | | Germany <i>Homoeosaurus</i> <i>Kallimodon</i> <i>'Piocormus'</i> <i>Pleurosaurus</i> | | |
| Kimmeridgian 154 Mya | Morrison Fm <i>Opisthias</i> <i>?Theretaurus</i> <i>Eilenodon</i> | France <i>Sapheosaurus</i> <i>'Piocormus'</i> <i>'Leptosaurus'</i> <i>Kallimodon</i> <i>Pleurosaurus</i> | | |
| Oxfordian 159 Mya | | | | |
| Middle Jurassic 177 Mya | Mexico <i>Cynosphonodon</i> <i>cf Opisthias</i> <i>cf Clevosaurus</i> | England Indet. sphenodontian | | |
| Early Jurassic 206 Mya | Canada <i>Clevosaurus</i> USA Undescribed taxa | Wales <i>Gephyrosaurus</i> Germany <i>Palaeopleurosaurus</i> | China <i>Clevosaurus</i> | Zimbabwe Indet. taxon South Africa <i>Clevosaurus</i> India <i>Godavarisaurus</i> <i>Rebbanasaurus</i> |

The Kota Formation was assigned a Jurassic age by King (1881). Krishnan (1968) was more specific, favouring an Early Jurassic (Liassic) age for the Upper

Member based on the fish fauna, and this interpretation has received support from several other sources. Jain (1973) identified species of *Tetragonolepis*

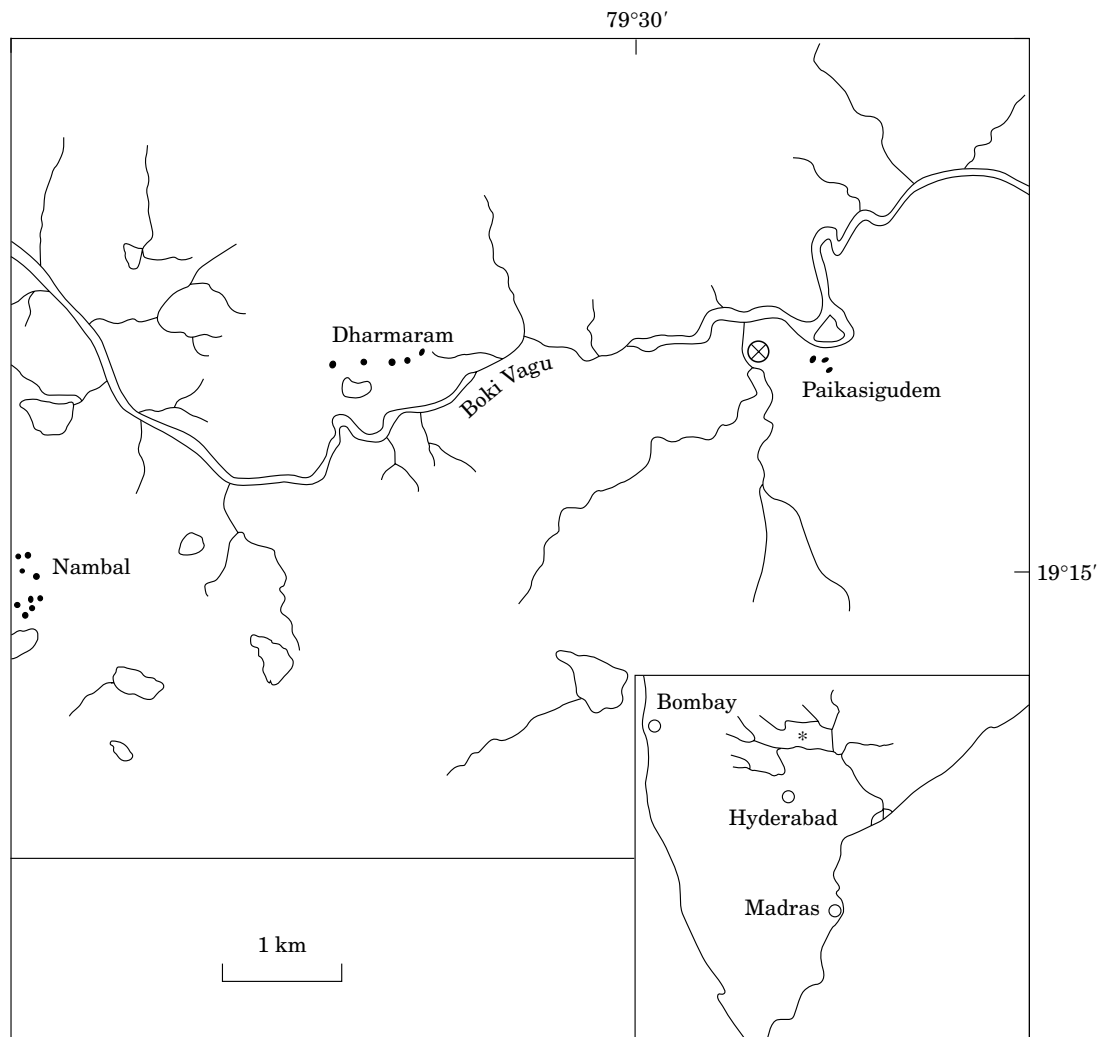


Figure 1. Map of the region close to the fossil locality with the Paikasigudem fossil locality marked. The inset map shows southern India and the Pranhita–Godavari river system. The asterisk shows the position of the Pranhita–Godavari valley where Paikasigudem is located.

and *Paradapedium* in the Kota fish fauna. He considered *Paradapedium* to be an Asian ecological substitute of *Dapedium* (Lower to Upper Liassic, Europe) while *Tetragonolepis* is otherwise known only from the Upper Liassic marine deposits of Europe. *Lepidotes deccanensis* from the same horizons shares some similarities with the European *L. elevensis* (Upper Liassic, Jain, 1983). A Liassic age was also favoured by Yadagiri & Prasad (1977) based on two new species of the fish *Pholidophorus*.

Independent support for a Liassic age for the Kota Formation has come from palaeobotanical studies of both charophytes (Bhattacharya *et al.*, 1994) and palynomorphs (Prabhakar, 1986), although many of the latter are long-ranging species. However, based on the recovery of the ostracodes *Darwinula* cf. *D.*

sarytirmenensis and *Timiriasevia* from the limestones and intercalated clays, Govindan (1975) suggested a Middle Jurassic age for the Kota Formation, since *D. sarytirmenensis* is known from the Middle Jurassic of Mangishlaka Peninsula in Russia and *Timiriasevia* ranges from the Middle Jurassic to the Palaeocene. The ostracode analysis has been extended by Misra & Satsangi (1979), but without revision of the age estimate.

Current evidence therefore supports an Early–Middle Jurassic age for the beds of the Upper Member of the Kota Formation and their included fossil assemblage, although further micropalaeontological work needs to be done and age estimates may be revised as further vertebrate taxa are analysed and described.

Anatomical abbreviations

| | |
|-------|--|
| A.f. | angular facet |
| ca | cavity |
| d.r | dental ridge |
| Ec.f. | ectopterygoid facet |
| f.5 | foramen for maxillary branch of fifth cranial nerve (trigeminal) |
| fl | tooth flange |
| h.tt | hatchling teeth |
| iac | inferior alveolar canal |
| J. f | jugal facet |
| J. pr | jugal process |
| ltr | lateral tooth row |
| mk.f | meckelian fossa |
| Mx.f | maxillary facet |
| Mx.pr | maxillary process |
| n | notch |
| N. pr | nasal process |
| or,b | orbital border |
| Pal.f | palatine facet |
| Pf.pr | prefrontal process |
| Pt.f | pterygoid facet |
| sds | subdental shelf |
| s.tt | successional teeth |
| sy | symphysis |
| wf | wear facet |

Institutional abbreviations

BMNH, Natural History Museum, London; UCM, University of Cambridge, Museum of Zoology; VPL/JU/KR, Vertebrate Palaeontology, University of Jammu, India, Kota Reptile Collection.

MATERIAL

All microvertebrate material extracted from the Kota horizons is broken and disarticulated. For the sphenodontians, dentaries are the most commonly preserved elements, although none is complete. The dentaries typically break into three sections – anterior symphyseal, hatchling dentition and mature dentition. In each case, there are two distinct types. There are also two types of premaxillae, the teeth of which broadly match those of the anterior dentary dentition. Maxillae are more fragmentary, but again there appear to be two principal types. For each, the preserved anterior region has a medial facet matching that of one or other of the premaxillae. Finally, there are two kinds of palatine, each with a dentition matching that of one or other dentary/maxilla type. We are therefore reasonably confident that two kinds of sphenodontian are present and that each can be characterized. The rhynchocephalian collection also includes a number of amphicoelous vertebrae and humeri that probably pertain to one or other of the sphenodontians, but they provide

little useful information and have not been included here.

Yadagiri (1986) and Prasad (1986) both mentioned, but did not name, fragmentary sphenodontian remains from the same locality. From Yadagiri's photographs, at least some of these fragments appear to pertain to an acrodont lizard which forms the dominant component of the Kota lepidosaurian assemblage. It is described elsewhere.

SYSTEMATIC PALAEOLOGY

LEPIDOSAURIA HAECKEL 1866

RHYNCHOCEPHALIA GUNTHER 1867

SPHENODONTIA WILLISTON 1925

REBBANASAURUS GEN. NOV.*Etymology*

From the small town of Rebbana, close to the type locality, and *saurus* (Greek), lizard or reptile.

Diagnosis

As for species.

REBBANASAURUS JAINI SP. NOV.*Etymology*

For Dr S. L. Jain, who made a major contribution to the early work on the Kota Formation.

Type specimen

VPL/JU/KR12, posterior region of a left dentary showing the morphology of the additional teeth (Figs 2A, B, 7I, 18B, D).

Type locality and horizon

Paikasigudem, about 6 km east of the town of Rebbana, Pranhita–Godavari Valley, Andhra Pradesh, India. Kota Formation, Paikasigudem village section, from clays and mudstones intercalated with the limestone beds of the Upper Member.

Referred specimens

About 50 catalogued and uncatalogued specimens in the collections of the University of Jammu, India, including one right (VPL/JU/KR20) and three left (VPL/JU/KR17–19) premaxillae, right (VPL/JU/KR30, 33) and left (VPL/JU/KR24–29, 31, 32, 34–35) maxillary fragments, right (VPL/JU/KR5, 8, 9, 14, 15) and left (VPL/JU/KR1–4, 7, 10, 11, 13, 16) dentary fragments and a left palatine (VPL/JU/KR21).

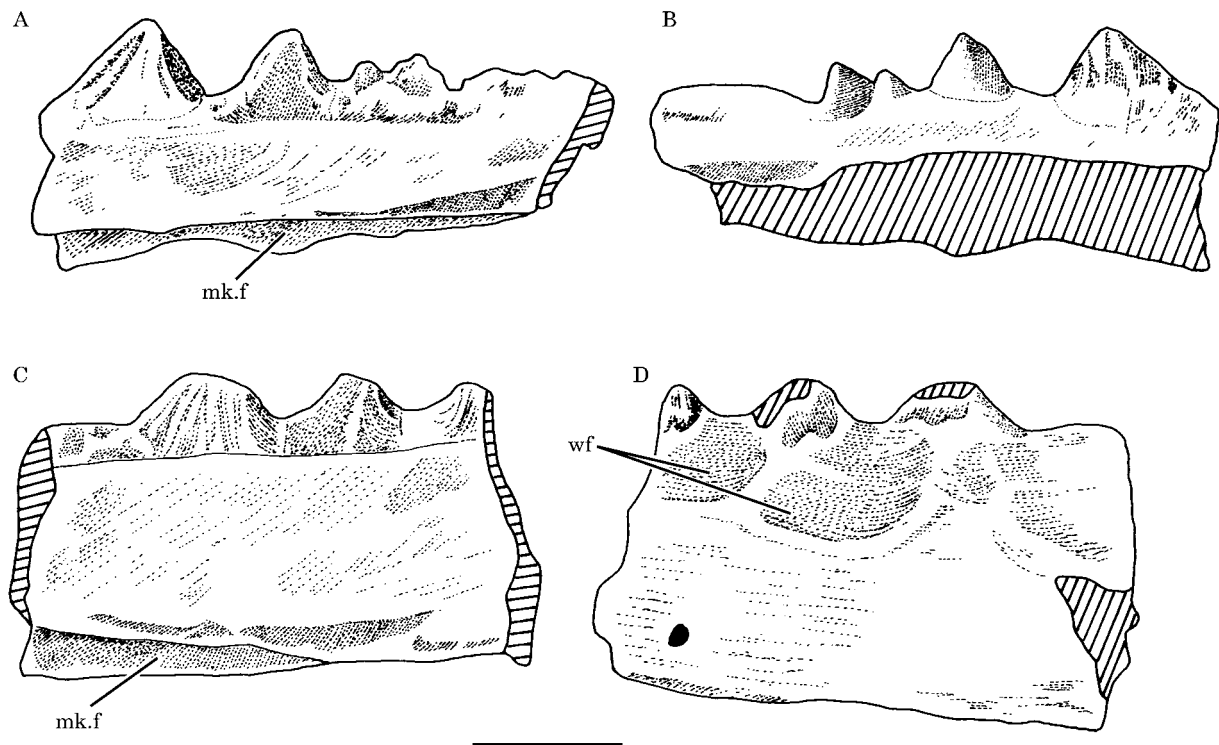


Figure 2. *Rebbanasaurus jaini* gen. et sp. nov. Dentary. A, B, holotype left posterior dentary VPL/JU/KR12 in A, medial, and B, lateral views. C, D, VPL/JU/KR13, a left posterior dentary, in C, medial, and D, lateral views. Scale bar = 1 mm.

Diagnosis

A small (estimated skull length 15–25 mm) primitive sphenodontian characterized by the following combination of characters: paired premaxillae each with three broad acrodont teeth, slender nasal process, narrow maxillary facet; maxillae with strong vertical posterior jugal process; anterior maxillary teeth slightly curved, posterior maxillary teeth broad based and striated, with small posterior flanges which are aligned with the long axis of the jaw rather than offset; dentary symphysis relatively short and anteroventral in orientation, separated from alveolar margin by a strong notch; premaxillary teeth, and anterior dentary and maxillary teeth with closely spaced vertical striae; dentary with five anterior successional teeth of which the most posterior is largest, but no caniniform; hatching teeth apparently conical without flanges or striae, but eroded by the upper dentition; posterior additional teeth robust with anterior facetting and posterior striae but at most incipient anterolateral flanges; additional teeth set very deeply into bone of attachment; subdental shelf unusually deep and robust with a very shallow Meckelian groove.

Remarks

Rebbanasaurus differs from the primitive rhy-

chocephalians *Gephyrosaurus* and *Diphydontosaurus* in having fully acrodont teeth and from most crown-group sphenodontians (e.g. *Clevosaurus*, *Pleurosaurus*, *Homoosaurus*, *Opisthias*, *Kallimodon*, pleurosaurs, *Tingitana*) in lacking strong overlapping flanges on the posterior maxillary additional teeth and in having more than one palatine tooth row. *Rebbanasaurus* lacks the unusual shape of the mandibular symphysis seen in the Mexican genera *Cynosphenodon* (Middle Jurassic, Reynoso, 1996b) and *Pamizinsaurus* (Lower Cretaceous, Reynoso, 1997), and the specialized herbivorous dentitions of *Toxolophosaurus* (Throckmorton *et al.*, 1981) and *Eilenodon* (Rasmussen & Callison, 1981). The Late Triassic *Brachyrhinodon* (Scotland) and *Polysphenodon* (Germany) are poorly known (Fraser & Benton, 1989), but, as described, both differ from *Rebbanasaurus* in having a more robust premaxilla and, less certainly, a single palatine tooth row with very enlarged anterior teeth. *Rebbanasaurus* resembles the primitive Late Triassic *Planocephalosaurus* (Fraser, 1982) in having strongly striated anterior teeth and in retaining more than one palatine tooth row but differs in several features: a shorter lateral palatine tooth row; a short medial palatine row with three teeth (up to 12 teeth in the second row in *Planocephalosaurus*); a longer nasal process of the premaxilla; a relatively narrow terminal dentary symphysis

(broader and ovoid in *Planocephalosaurus*); spatulate anterior dentary teeth (short and conical in *Planocephalosaurus*); no enlarged posterior dentary teeth; faceted dentary teeth and small flanges on the maxillary teeth. Separate generic status for *Rebbanasaurus* is therefore justified.

DESCRIPTION

Rebbanasaurus is the commonest of the Kota sphenodontians and is represented by premaxillae, maxillae, dentaries and a palatine.

Premaxilla (Figs 3H, I, 4A–C).

There are four premaxillae, three left (VPL/JU/KR17–19) and one right (VPL/JU/KR20). The bone is similar to that of generalized lepidosaurians, except that the lateral articular process for the maxilla is more expanded. The premaxillae are paired, each with a broad but shallow dental ramus and a long narrow nasal process. The three teeth increase in size from medial to lateral. In the smallest specimens, the posterior surface of the premaxilla shows no evidence of wear but in the larger VPL/JU/KR18, a facet has been worn at the base of the largest, most lateral, tooth.

Maxilla (Figs 3A–G, J, K, 4D, E, 18A, B)

Maxillae are generally more delicately built than dentaries and tend to fragment. For *Rebbanasaurus*, parts of the anterior, central and posterior regions of the maxilla are preserved, but no specimen carries more than a few teeth. The anteromedial surface of the bone bears a facet for the premaxilla. The central section of the bone is well represented by VPL/JU/KR30, a juvenile specimen, which preserves the posterior part of the facial process and the beginning of the orbital process (Fig. 3F). The medial surface bears a deep concave facet for the maxillary process of the palatine (VPL/JU/KR31, Fig. 3E), above which is the entry foramen for the maxillary nerve and blood vessels. There is no medial supra-alveolar shelf and no trace of a lacrimal facet. Several specimens preserve parts of the posterior process. The most complete is VPL/JU/24 (Figs 3J, 4D, E) which comprises the end of the orbital ramus and the tapering jugal process. This process is long, extending well beyond the end of the tooth row. Medially, the jugal facet is large, but L-shaped in cross-section, its principal part being vertical. The anterior part of the jugal was clearly deep but did not extend far along the maxilla, the tip of the facet reaching only the level of the penultimate tooth. Posterodorsal to the last tooth position, the edge of the jugal facet develops a slight lip that probably contributed to the ectopterygoid facet (Fig. 4D).

Dentary (Figs 2, 5, 6, 7)

The dentary is represented by parts of the symphyseal and central regions, but the posterior part of the bone has not been identified. Several specimens preserve the anterior symphyseal region, but the most complete are VPL/JU/KR1, 2 and 7. These range from juvenile (KR1) to adult (KR7: based on the heavy level of ossification) and have a distinctive morphology (Fig. 5). The alveolar border bears five relatively small, labiolingually compressed successional teeth, of which the first three are smaller than the last two, but there is no caniniform. These successional teeth are followed by the eroded hatchling dentition. The symphyseal surface is separated from the alveolar margin by a deep notch. As a result, the surface is shortened dorsoventrally and deflected downwards so that its orientation is anteroventral (Fig. 5). *Rebbanasaurus* is characterized by a subdental shelf which is deep throughout its length, limiting the Meckelian fossa to the ventral border (Figs 6, 7D, F). In mature animals, additional bone deposition within the fossa can leave little more than a medial groove (Fig. 6A–C). Similarly, some of the depth of the subdental ridge appears to be the result of extra deposition of ankylosing bone around the bases of the teeth. Additional bone deposition also occurs internally. In immature animals, the posterior part of the dentary contains a cavity, distinct from the alveolar canal, but this cavity is filled in mature animals to leave a very dense internal structure (e.g. VPL/JU/KR9, Fig. 6C). Labially the bone surface is perforated by sensory foramina.

Only a minority of specimens (e.g. VPL/JU/KR12–14) preserve parts of the posterior dentary region and additional tooth series.

Palatine (Figs 7J, K, 8)

A single left palatine is preserved (VPL/JU/KR21), although two fragmentary specimens (VPL/JU/KR22, 23) bear teeth which match those of the palatal and marginal series, and clearly also belong to the palatal region. VPL/JU/KR21 is attributed to *Rebbanasaurus* on the basis of the tooth structure. The teeth are pyramidal (faceted anteriorly like the dentary additionals) and have coarse striae (Fig. 7J). The outer row preserves six teeth of roughly equal size. The row is slightly curved so that it would have run posteromedially at an angle to the maxillary tooth row. A second, shorter, tooth row lies medial to the first. It carries only three teeth set onto a narrow but prominent ridge (Figs 7K, 8B). This ridge ends posterior to the last preserved tooth so it is unlikely that the row continued further backwards. However, the bone is broken anteromedially, and it is not possible to determine whether further medial rows might have been present.

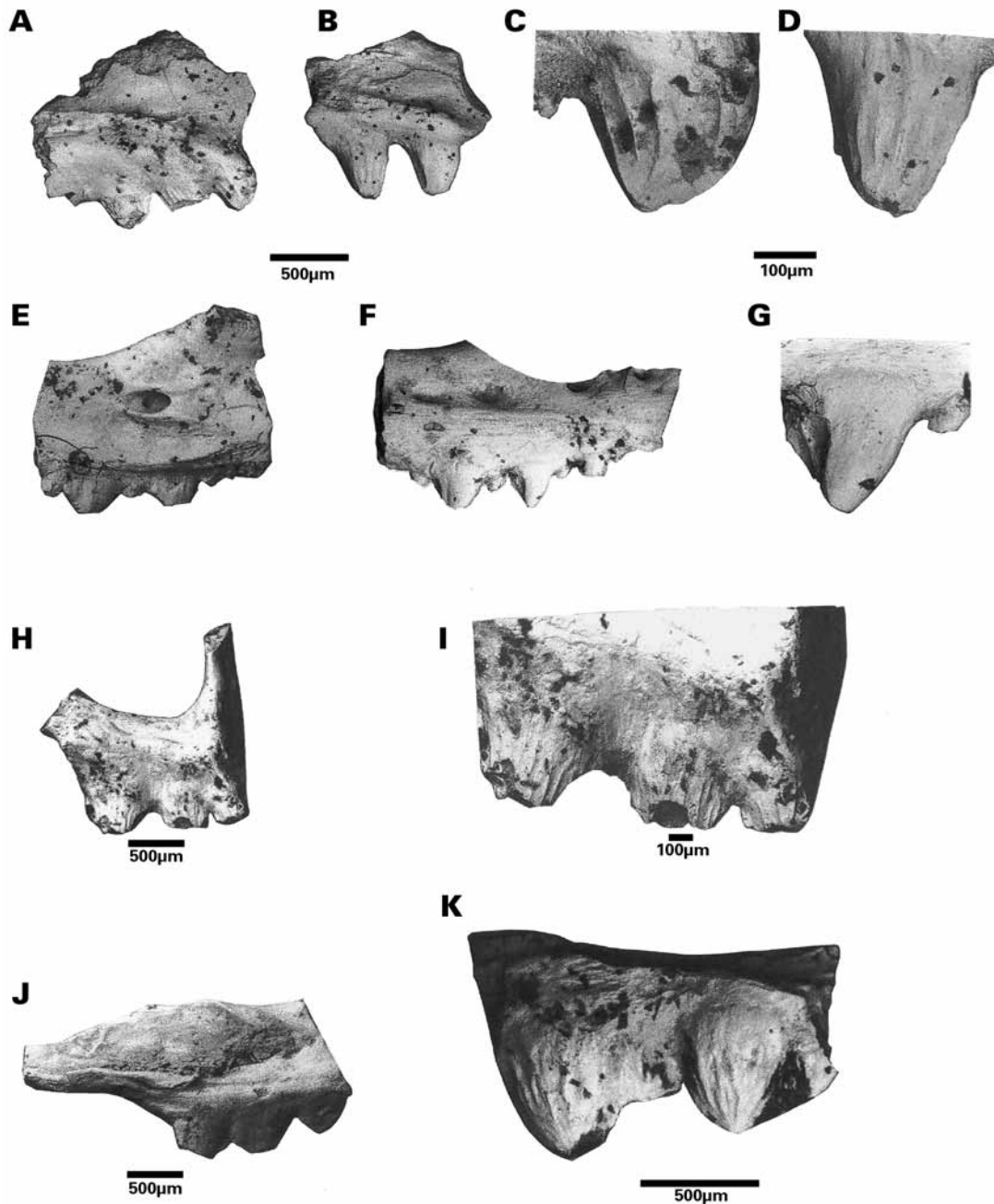


Figure 3. *Rebbanasaurus jaini* gen. et sp. nov. Dentition. A–G, J, K, maxilla; H, I, premaxilla. A, C, VPL/JU/KR35, anterior maxilla, in A, lingual view, C, enlargement of anterior tooth; B, D, VPL/JU/KR34, anterior maxilla, in B, lingual view, D, enlargement of second tooth; E, VPL/JU/KR31, central part of a left maxilla, lingual view, showing palatine facet; F, G, VPL/JU/KR30, central part of a right maxilla, labial view, showing F, beginning of orbital border, G, enlargement of tooth; H, I, VPL/JU/KR17, left premaxilla, in H, lingual view, with I, enlargement of dentition; J, VPL/JU/KR24, posterior process of a left maxilla, lingual view, showing jugal facet; K, VPL/JU/KR27, fragment of the posterior dentition, left maxilla, labial view. Scale bars as indicated.

The maxillary process is damaged anteriorly but was clearly deep; in shape, it matches the facet on the maxilla. The maxillary process is not perforated by a canal for the maxillary nerve and blood vessels, as

occurs in some rhynchocephalian taxa (e.g. *Gephyrosaurus*), nor is there a dorsal groove for these structures. However, the anterior tip of the bone is developed into a dorsal prominence which would have

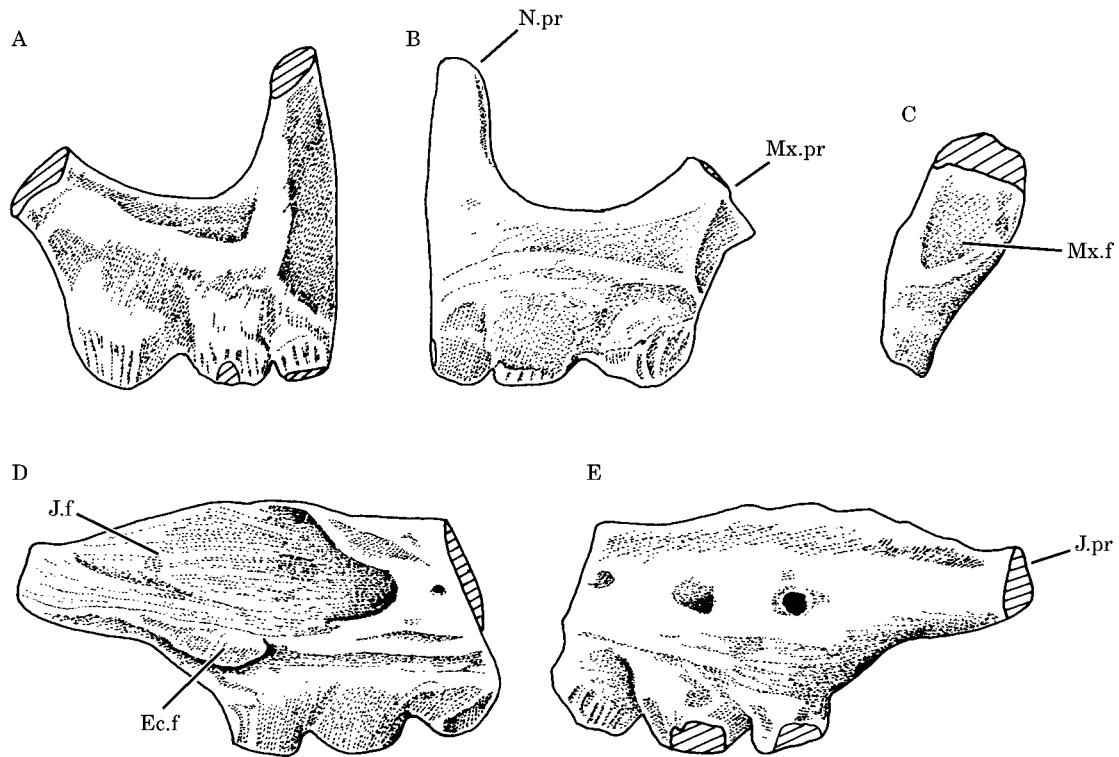


Figure 4. *Rebbanasaurus jaini* gen. et sp. nov. Upper dentition. A–C, VPL/JU/KR17, left premaxilla, in A, lingual, B, labial, and C, lateral, view showing facet for maxilla; D, E, VPL/JU/KR24, posterior region of left maxilla, in D, lingual, and E, labial, views. Scale bar = 1 mm.

met the prefrontal, providing a brace to the antorbital region of the skull. The posterodorsal region of the bone bears a deep medial facet for the pterygoid.

Dentition (Figs 2, 3, 7G–J, 17A, B, 18B–D)

All teeth have an acrodont implantation and most are striated, although the striations are coarsest on anterior teeth. Each premaxillary tooth is antero-posteriorly compressed with closely spaced vertical striations. The anterior dentary teeth of mature animals are very similar (e.g. VPL/JU/KR7, Fig. 5A). In contrast, the four anterior maxillary teeth are more rounded in cross-section and have tips which are compressed and slightly recurved (Fig. 3A–D). The maxillary hatchling dentition is not known. The teeth of the dentary hatchling dentition are small relative to the depth of jaw beneath them and appear to lack striae. Very few are preserved intact and some specimens (e.g. VPL/JU/KR4, Figs 7F, H) suggest that the upper and lower teeth bit into one another in this region, since the wear extends down the margins of the teeth and into the ankylosing bone at the base. The posterior additional teeth of the dentary are known only in a few specimens (e.g. the holotype, VPL/JU/

KR12, Figs 2A, 7I, 18B–D) and are broad based and conical with posterior striae and anterior facetting. As a result, the anterior face of the tooth is concave both labiolingually and dorsoventrally. It also has a slight asymmetry so as to create an incipient anterolateral flange (Fig. 18D).

The maxillary teeth are somewhat better preserved than those of the dentary. The teeth of the hatchling dentition characteristically alternate in size and are compressed cones with, at most, a small posterior recess and flange. In slightly older individuals, the teeth are still labiolingually compressed, but there is a more marked division of each tooth into a conical anterior region and a small recessed posteromedial blade (e.g. VPL/JU/KR26). The most distinctive teeth are at the posterior end of the mature maxilla (e.g. VPL/JU/KR27, Figs 3K, 17A, B). These teeth bear well-defined, closely spaced, vertical striae. The division between anterior and posterior parts of the tooth is still visible in labial view, but the posteromedial flange is thicker. In lingual view, the surface is either slightly grooved (younger individuals) or planar, and it may be polished down to the dentine in older individuals (e.g. VPL/JU/KR55). This polishing is evidence of tooth-to-tooth or tooth-to-jaw shear.

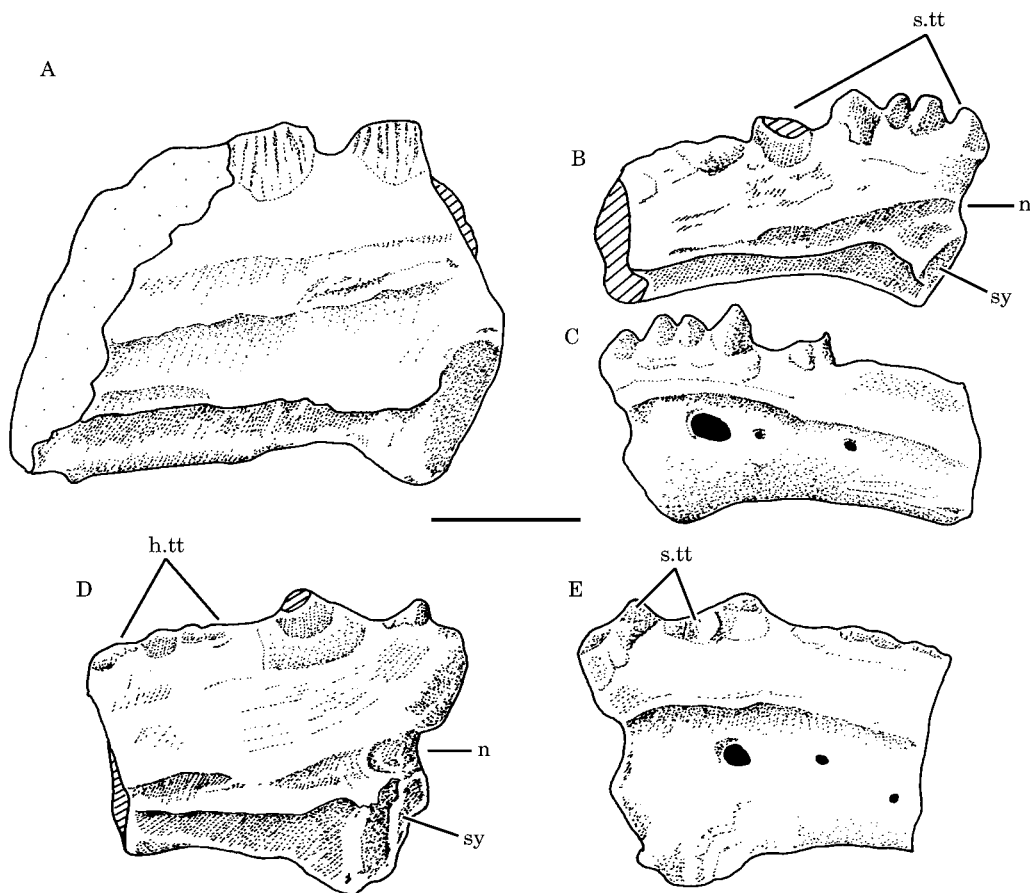


Figure 5. *Rebbanasaurus jaini* gen. et sp. nov. Symphyseal region of the dentary. A, VPL/JU/KR7, left adult dentary; B, C, VPL/JU/KR1, left juvenile dentary, in B, lingual, and C, labial, views; D, E, VPL/JU/KR2, left immature dentary, in D, lingual, and E, labial, views. Scale bar = 1 mm.

The holotype dentary shows no trace of lateral wear from the maxillary dentition, but wear surfaces are seen in a fragmentary specimen from a somewhat larger individual (VPL/JU/KR13, Figs 2D, 7G). The wear surfaces are shallow, lie between tooth positions and have a wide U-shaped ventral edge, with each facet discrete from the next. This separation of the wear surfaces precludes a long propalinal shear component (as in *Sphenodon*), but the facets also differ from the deep precise scoring seen in taxa with well-developed dorsoventral shear (e.g. *Clevosaurus*). It therefore seems likely that the jaw action was essentially dorsoventral, but with a small anteroposterior translatory movement of the lower jaw as the teeth occluded.

LEPIDOSAURIA HAECKEL 1866
 RHYNCHOCEPHALIA GUNTHER 1867 *SENSU*
 GAUTHIER ET AL., 1988
 SPHENODONTIA WILLISTON 1925
GODAVARISAURUS GEN. ET SP. NOV.

Etymology

From the river Godavari which runs near the type locality, and *saurus* (Greek), reptile or lizard.

Diagnosis

As for type and only species.

G. LATEEFI SP. NOV.

Etymology

For Mr Syed Lateef, the keeper of the R & B Guest-house, Rebbana, India, for his conscientious preparation and organization of fieldwork arrangements over several seasons.

Type specimen

VPL/JU/KR47, a partial right dentary (Fig. 9A, B).

Type locality and horizon

Paikasigudem, about 6 km east of the town of Rebbana, Pranhita-Godavari Valley, Andhra Pradesh, India. Kota Formation, Paikasigudem village section, from clays and mudstones intercalated with the limestone beds of the Upper Member.

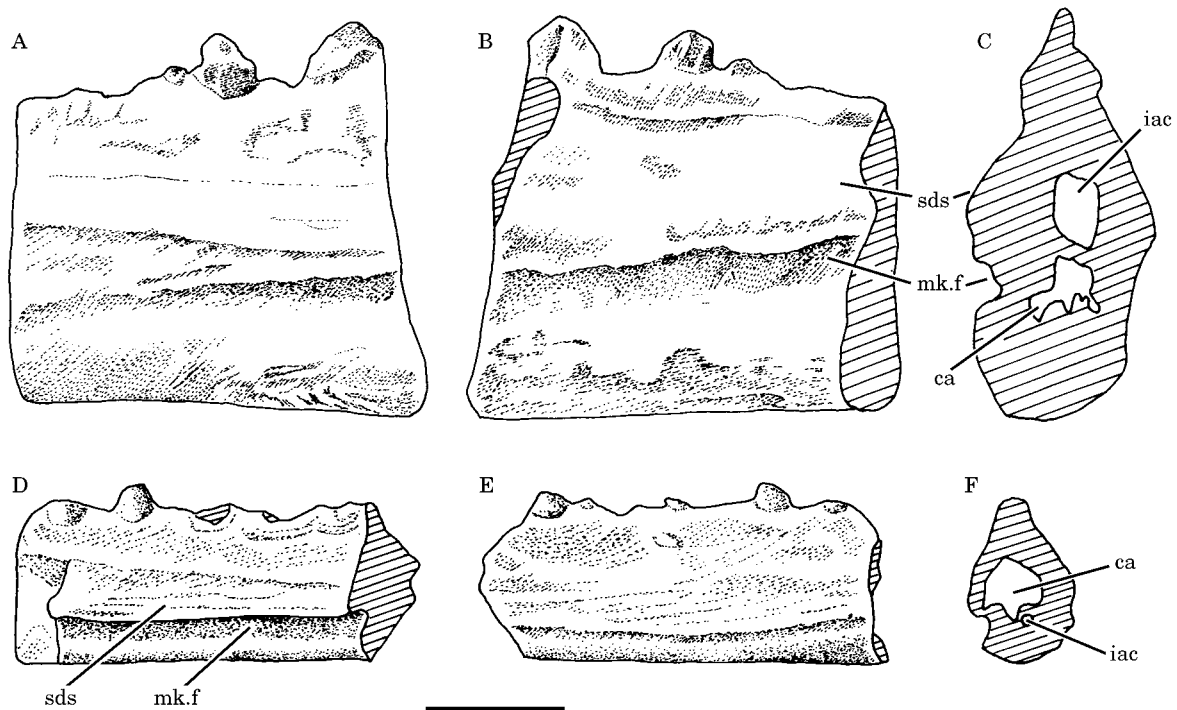


Figure 6. *Rebbanasaurus jaini* gen. et sp. nov. Dentary. A–C, VPL/JU/KR9, right mature adult bone, in A, labial, and B, lingual, views, C, cross-section showing thickened internal structure, alveolar canal lies above reduced internal cavity; D–F, VPL/JU/KR5, juvenile left bone, in D, lingual, and E, labial, views, F, cross-section showing internal cavity above alveolar canal. Scale bar = 1 mm.

Referred specimens

A right premaxilla (VPL/JU/KR45), fragments of right (VPL/JU/KR42, 44, 51, 52) and left (VPL/JU/KR40, 41, 43, 49, 50) maxillae, the symphyseal regions of right (VPL/JU/KR37, 48, 65) and left (VPL/JU/KR38) dentaries, and a more posterior fragment of a right dentary (VPL/JU/KR39). One specimen, a partial left palatine (VPL/JU/KR46), comes from equivalent beds at a second locality near the village of Gorlapalli.

Diagnosis

A small sphenodontian (estimated skull length less than 20 mm) showing the following combination of characters: premaxillae paired, broad and deep with four small teeth; strong lateral facet for the maxilla showing firm overlap; nasal process much shorter than lateral process, without obvious nasal facets; maxillary teeth conical and slightly recurved anteriorly with a small posteromedial flange; no palatal shelf, large planar facet for the palatine; maxilla broadly enters orbital margin, jugal facet small and narrow; dentary symphysis deep, terminal, although surface broader in juveniles, small notch separates symphyseal surface and alveolar margin; adult successional teeth broad based, spatulate and coarsely striated lingually but polished labially, juvenile teeth more pointed and

slightly recurved; subdental shelf shallow anteriorly, deepening posteriorly; hatchling teeth triangular; additional teeth pyramidal with strong anteromedial facet and incipient anterolateral flanges; posterior carinae but no striations; single palatine tooth row, teeth weakly flanged and similar in shape to those of the maxilla, broad shallow maxillary process.

Remarks

The premaxilla of the second Kota sphenodontian differs from that of most described sphenodontians in being deep and strongly U-shaped, with a small nasal process and a larger lateral process which may have excluded or nearly excluded the maxilla from the narial margin (Figs 10, 12A). Among known taxa, this type of premaxilla has been considered unique to *Clevosaurus* and therefore diagnostic of the genus (e.g. Wu, 1994; Sues & Reisz, 1995), although a similar premaxilla may have been present in the Albian *Pamizinsaurus* from Mexico (Reynoso, 1997). Other elements attributed to the Kota form differ from those of described species of *Clevosaurus* – most notably the shape of the palatine teeth (medio-laterally compressed and weakly flanged, rather than conical), the pyramidal, faceted, but only incipiently flanged, additional teeth of the dentary (broad based and strongly flanged in known

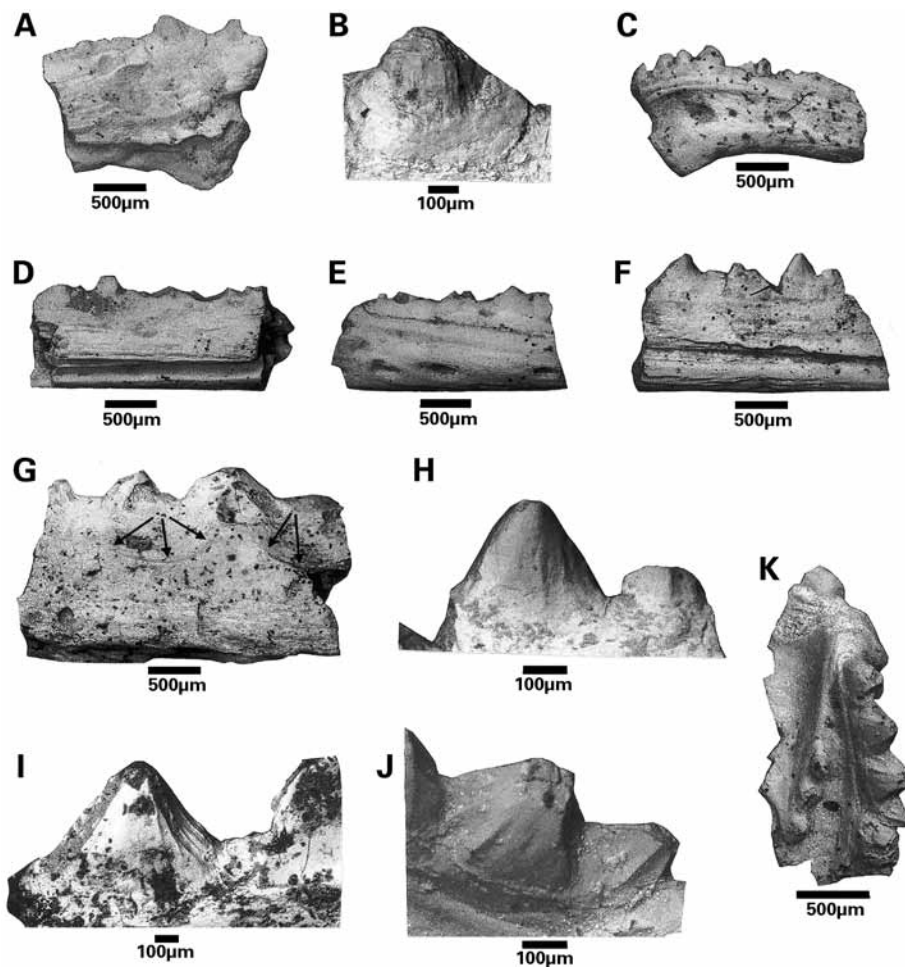


Figure 7. *Rebbanasaurus jaini* gen. et sp. nov. Dentary and palatine. A, B, VPL/JU/KR2, left dentary symphysis, lingual view, B, enlargement of successional tooth; C, VPL/JU/KR1, left anterior dentary, juvenile, labial view; D, VPL/JU/KR5, left dentary, juvenile, lingual view; E, VPL/JU/KR3, left juvenile dentary, labial view; F, H, VPL/JU/KR4, left dentary, immature, lingual view; G, VPL/JU/KR13, posterior region, mature dentary, labial view, arrows mark wear facets; H, as F, enlargement of anterior tooth showing wear cutting onto posterior margin; I, additional tooth of holotype dentary, VPL/JU/KR12, lingual view; J, K, VPL/JU/KR21, left palatine, J, tooth detail for comparison with I, K, palatal view. Scale bars as indicated.

Clevosaurus) and the weaker flanges on the maxillary teeth (strong in *Clevosaurus*). These differences argue against inclusion of the Kota material into *Clevosaurus*. Separate generic status for *Godavarisaurus* is therefore justified.

DESCRIPTION

Godavarisaurus is represented by a premaxilla, a palatine and parts of the maxilla and dentary.

Premaxilla (Figs 10, 12A)

The premaxilla is represented by a single right specimen (VPL/JU/KR45). It is U-shaped with a broad alveolar margin bearing four small teeth of similar size. The nasal process is narrow but relatively short and appears to bear no facets for the nasal bones.

Although the tip of the process is broken, it cannot have extended very much further dorsally since it is already tapered. Either the nares were confluent dorsally or the nasals extended anteriorly and abutted the premaxilla. The lateral margin of the bone, by contrast, is developed into a long maxillary process that probably excluded the maxilla from most, or all, of the margin of the external nares. The process bears a large band-shaped facet for the maxilla on its lateral surface (Fig. 10C), but no horizontal lateral flange (contra *Clevosaurus hudsoni* Fraser, 1988).

Maxilla (Figs 11, 12B–F, 17C–E)

The maxilla is known from fragments of the central and orbital regions and from a single specimen that appears to preserve the anterior tip. This last

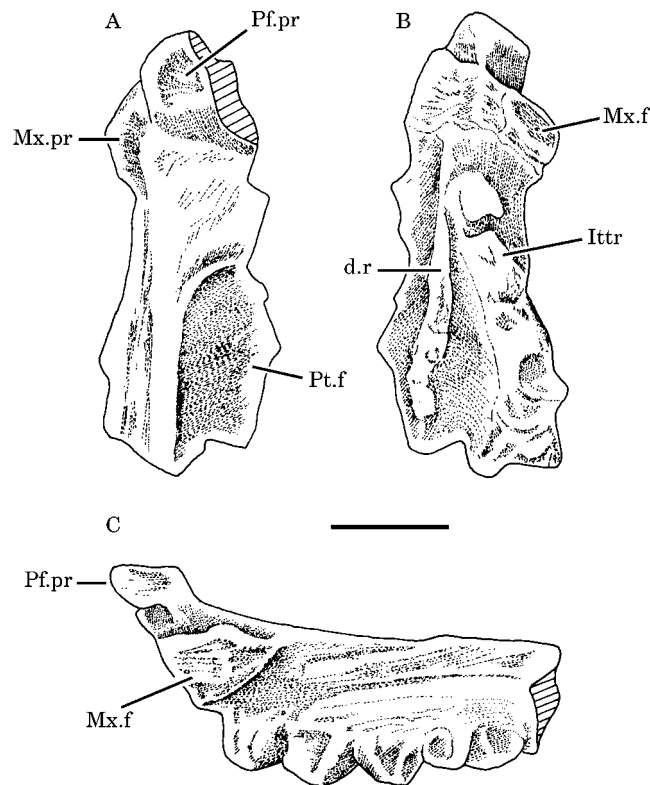


Figure 8. *Rebbanasaurus jaini* gen. et sp. nov. VPL/JU/KR21, left palatine, in A, dorsal, B, palatal, and C, left lateral, views. Scale bar = 1 mm.

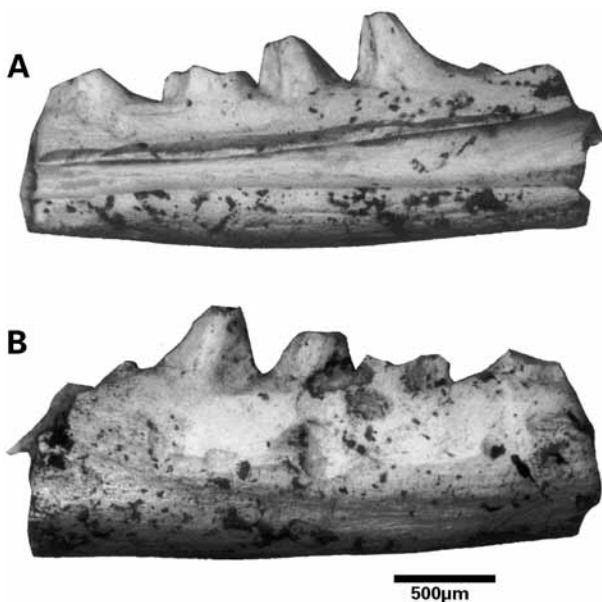


Figure 9. *Godavarisaurus lateefi* gen. et sp. nov. Holotype right dentary, VPL/JU/KR47, in A, lingual, and B, labial, views. Scale bar as indicated.

specimen, VPL/JU/KR49, is very small and bears several compressed anterior acrodont teeth. The anterior margin has a complete edge that is very thin and

nearly vertical. A large premaxillary facet covers the medial surface. The best specimens of the central maxilla are VPL/JU/KR44 and VPL/JU/KR40, although the latter is juvenile. The facial process has not been preserved in any specimen, but the orbital process is deep and vertical with perforating nutrient foramina. There is a large elongated surface for the palatine. Above it is the foramen for entry of the maxillary nerve and blood vessels. The maxilla clearly entered the orbital margin with the jugal contact limited to the posterior region of the bone.

Dentary (Figs 9, 13, 14, 18E)

Specimens VPL/JU/KR37 and VPL/JU/KR38 preserve the anterior symphyseal part of the bone, representing right and left sides respectively. The former is from an adult individual (Fig. 13A, B), the latter from a juvenile (Fig. 13C, D). They differ in the shape of the symphyseal surface (slightly broader in the juvenile) and the shape of the teeth (broad based and spatulate in the adult; narrower, conical and somewhat recurved in the juvenile). Both specimens preserve the bases of four fully acrodont teeth. Unlike *Rebbanasaurus*, only a small notch separates the symphyseal surface from the alveolar margin and, in the adult at least, the surface itself is longer and nearly vertical. The teeth are

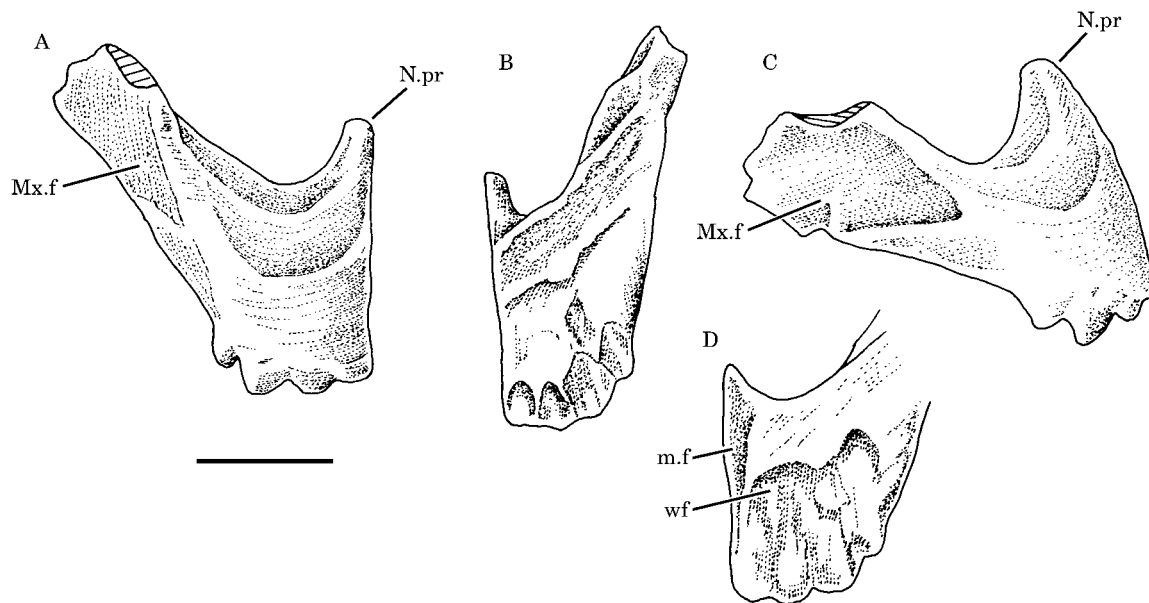


Figure 10. *Godavarisaurus lateefi* gen. et sp. nov. Right premaxilla, VPL/JU/KR45, in A, labial, B, lingual, and C, oblique right lateral, views, D, angled lingual view showing wear facets above teeth. Scale bar = 1 mm.

supported labially and lingually by a subdental shelf. This is shallow laterally and limited by a low ventral ridge which separates the alveolar region from the rest of the bone. Nutrient foramina lie below the ridge.

VPL/JU/KR39 is the central part of a juvenile jaw carrying six small triangular teeth of the hatchling dentition (Fig. 14E, F). Behind these, and separated from them by a small diastemma, there is a slightly larger pyramidal tooth with a faceted anterior margin. This matches teeth on more adult specimens and is presumably the first of the additional series. VPL/JU/KR39 also shows the form of the subdental shelf – deep anteriorly towards the symphyseal end, but becoming narrower under the posterior additional tooth series. The Meckelian fossa is thus very narrow anteriorly, but widens posteriorly – a shape in contrast to that of *Rebbanasaurus* (see above). The holotype dentary comes from a larger animal (although probably still immature) and preserves part of the additional dentition. The teeth are like those of the posterior tooth on VPL/JU/KR39. The ventral margin of the open Meckelian fossa is thickened and carries a facet for the angular (Fig. 13E).

Palatine (Figs 12C, 15)

VPL/JU/KR46 is the posteromedial part of a left palatine. It is attributed to *G. lateefi* on the basis of the general similarity of its dentition to that of the maxilla and the shape of the maxillary facet. It differs from the palatine of *Rebbanasaurus* in having a single lateral tooth row (four preserved teeth) which, allowing for the angle of the maxillary facet, would have run

parallel or nearly parallel to the marginal dentition. The maxillary process is long but quite shallow and fitted flush against the side of the maxilla. It is not perforated by the maxillary nerve and vessels that entered the maxilla above it. Dorsally, the bone lacks the prominent prefrontal boss seen in *Rebbanasaurus* and preserves no trace of the pterygoid facet.

Dentition (Figs 9, 11, 12, 14, 17C–E, 18E)

Like *Rebbanasaurus*, the teeth of the upper and lower jaws are rather different, and the association is made primarily on the similarities in shape between anterior dentary and premaxillary dentitions, with the premaxillary–maxillary association relying on their fit anteriorly. The premaxillary teeth are antero-posteriorly flattened and unstriated, with blunt crowns. The anterior teeth of the mature dentary are similar in shape, but coarsely striated lingually. There is no evidence of a caniniform. The additional teeth are anteromedially faceted with a small extension of the anterolateral edge to form a slight flange (larger than that of *Rebbanasaurus*, Figs 18D, E). There is also a small posterior carina, but no striae. The mature maxillary teeth are divided into a strong somewhat recurved conical anterior portion and a smaller posteromedial flange (Figs 11C, D, 17E). They are more delicately built than those of *Rebbanasaurus*. The juvenile teeth are of similar shape overall, but more planar (Figs 11A, B, 12, 17C). The palatine teeth resemble those of the maxilla in being weakly flanged, unstriated and recurved (Fig. 15D).

The only evidence of wear is found anteriorly. The

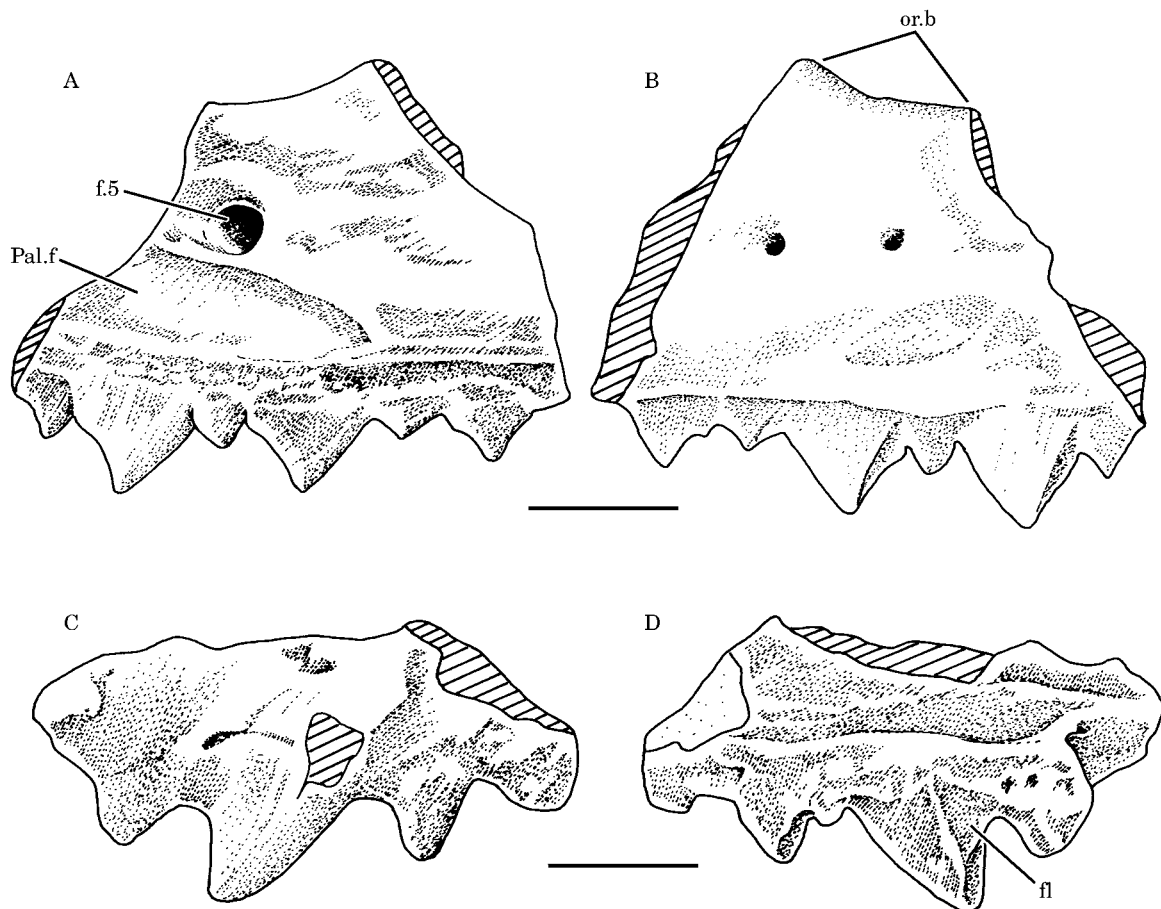


Figure 11. *Godavarisaurus lateefi* gen. et sp. nov. Maxilla. A, B, VPL/JU/KR40, juvenile left mid-region, in A, lingual, and B, labial, views; C, D, VPL/JU/KR44, fragment of mature right dentition, in C, labial, and D, lingual, views. Scale bars = 1 mm.

premaxilla bears two discrete wear facets on the posterior surface of the bone above the level of the tooth row, the medial facet being wider but slightly shorter than the more lateral facet (Fig. 10D). Clearly, the lower symphyseal dentition bit against the inner surface of the premaxilla in close occlusion. This is confirmed by the corresponding teeth of the dentary, particularly the two most anterior successionals, which have highly polished labial surfaces.

LEPIDOSAURMORPHA
INDET.

Four fragmentary specimens in the Kota collection (three dentary fragments and a partial maxilla) differ from those of any of the sphenodontians described here, but also from lizards. The largest specimen (VPL/JU/KR57) is part of a left dentary from just behind the symphyseal region (Figs 16A, B). The broad subdental ridge is ventromedial in orientation and lies above a narrow but deep ventral Meckelian fossa. The teeth have a weakly pleurodont implantation (the labial wall being slightly higher than the

lingual one), and are very small and closely packed (with around 11 tooth bases in the small section preserved). The crowns are eroded but empty positions between the bases indicate rapid replacement. Laterally, the bone is perforated by small nutrient foramina. There are two other dentary specimens (VPL/JU/KR58, 59), but they come from roughly the same region of the jaw and add little to the description given above. VPL/JU/KR60 is a fragment of a right maxilla showing a similar tooth implantation and the broken bases of small close-packed teeth (Figs 16C, D). The specimen preserves the lower part of the facial process that is notched posteriorly (possibly by a lacrimal foramen). There is no supra-alveolar shelf and therefore the choana must have been large and undivided.

These specimens are very fragmentary and therefore any attribution must be tentative, but the dentary in particular most closely resembles that of the basal rhynchocephalians *Gephyrosaurus* (Evans, 1980) from the Lower Jurassic (?Hettangian) of Wales and the Late Triassic *Diphydontosaurus* (Whiteside, 1986). Its

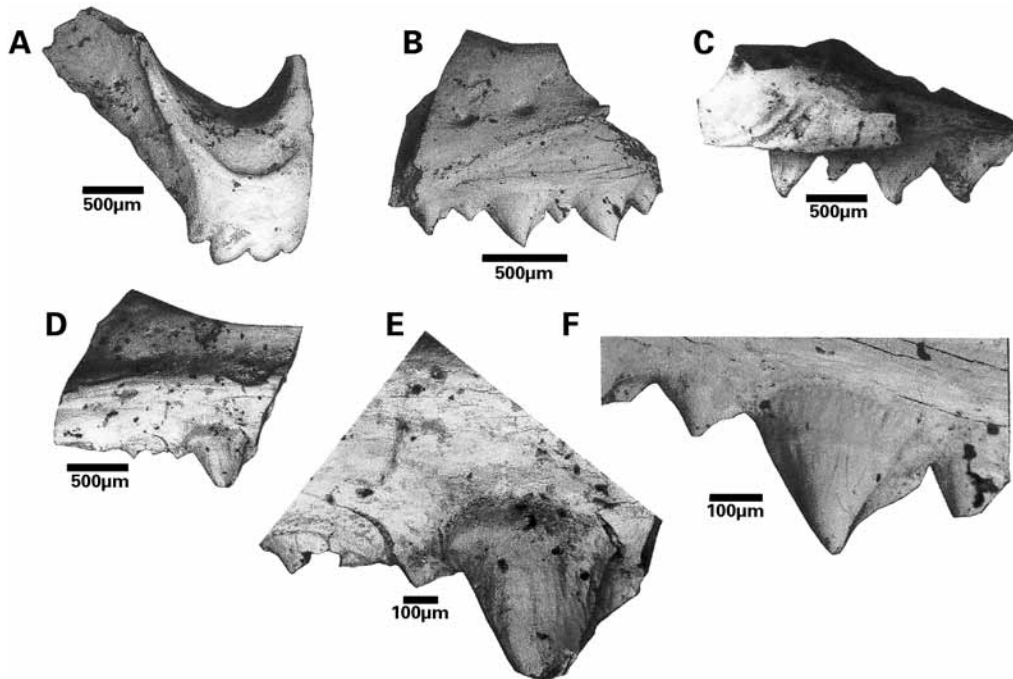


Figure 12. *Godavarisaurus lateefi* gen. et sp. nov. Maxilla and premaxilla. A, VPL/JU/KR45, right premaxilla, oblique labial view; B, VPL/JU/KR40, juvenile left maxilla, labial view; C, VPL/JU/KR46, left palatine, left lateral view to show recurved tooth profile; D, E, immature maxillary fragment, left, D, labial view, E, enlargement of tooth showing small posterior flange; F, as B, enlargement of tooth for comparison with E. Scale bars as indicated.

dentary morphology (Fig. 16E) appears to be primitive for lepidosaurs generally, although the large heavily buttressed symphysis is probably functional. Further Kota material is needed to determine whether the Indian specimens represent a taxon related to *Gephyrosaurus* or another primitive lepidosauromorph lineage.

DISCUSSION

THE SYSTEMATIC POSITION OF THE KOTA RHYNCHOCEPHALIANS

Rhynchocephalian phylogeny

Our knowledge of rhynchocephalian diversity has grown considerably over the last two decades, although there are still significant gaps in the record. Most recent analyses of rhynchocephalian relationships (e.g. Evans, 1988; Fraser & Benton, 1989; Wu, 1994; Reynoso, 1996a,b, 1997; Wilkinson & Benton, 1996) show broad areas of agreement (Fig. 19):

(1) The Lower Jurassic *Gephyrosaurus* (Evans, 1980) is the morphologically most primitive genus and forms the sister taxon to all other rhynchocephalians (Sphenodontia), although the Late Triassic *Diphydontosaurus* (Whiteside, 1986) is only marginally more derived. *Gephyrosaurus* has a

pleurodont dentition, but the posterior teeth were not replaced and are firmly attached to the jaw by ankylosing bone. In *Diphydontosaurus*, the posterior teeth approach the acrodon condition.

- (2) The genus *Planocephalosaurus* (Fraser, 1982) is fully acrodon but forms the sister group to all remaining sphenodontian taxa.
- (3) Within the crown group, eilenodonts (*Eilenodon*, Rasmussen & Callison, 1981; *Toxolophosaurus*, Throckmorton *et al.*, 1981) are the sister group of the sphenodontines (the living *Sphenodon* and, perhaps, the Middle Jurassic *Cynosphenodon*, Reynoso, 1996b). Reynoso (1997) places the Cretaceous *Pamizinsaurus* as the sister group of eilenodonts + sphenodontines, but see below.

The interrelationships of the crown-group taxa have proved more difficult to resolve. Wu (1994) and Reynoso (1996a,b) have argued for a monophyletic clade of clevosaurus, including *Brachyrhinodon* (Late Triassic, Scotland), *Polysphenodon* (Late Triassic, Germany) and *Clevosaurus* (Late Triassic–Early Jurassic of Britain, Belgium, Canada, USA, China and South Africa). However, neither Fraser & Benton (1989) nor Wilkinson & Benton (1996) found support for this arrangement – consistently aligning *Polysphenodon* with *Homoeosaurus*, and *Brachyrhinodon* with the remaining crown-group genera, although the position

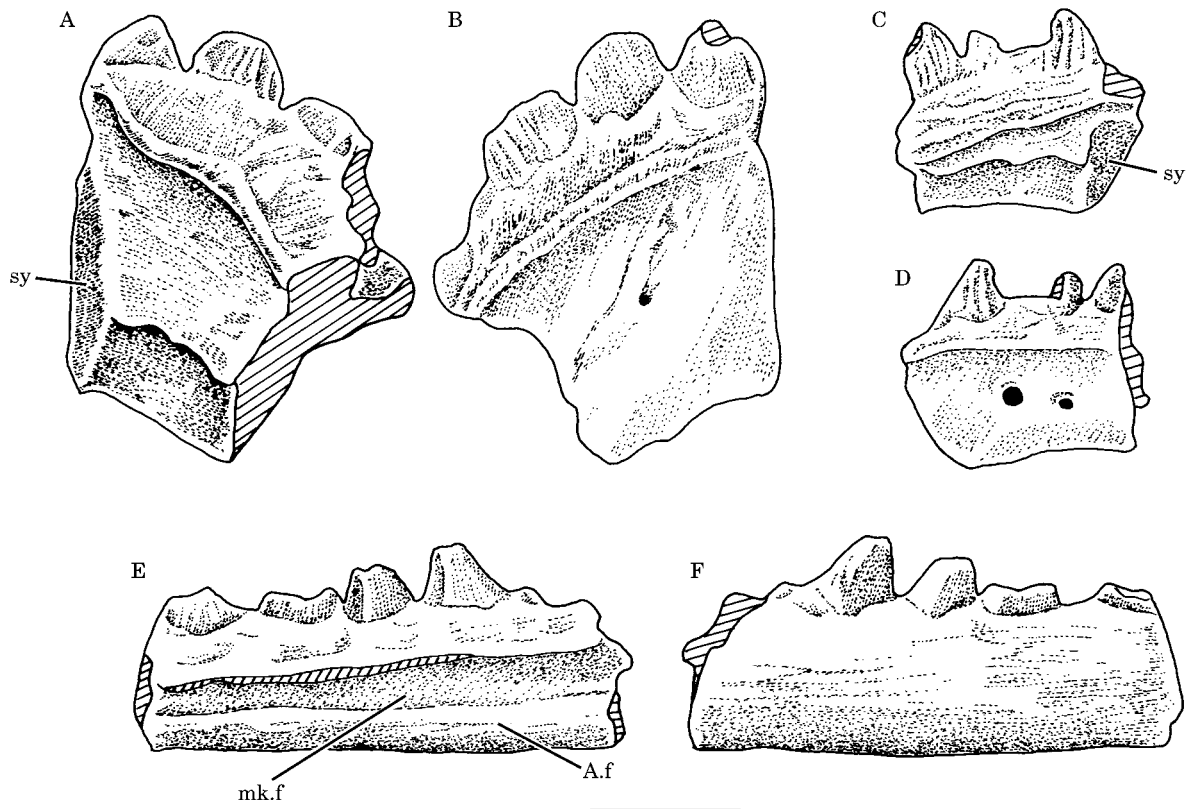


Figure 13. *Godavarisaurus lateefi* gen. et sp. nov. Dentary. A, B, VPL/JU/KR37, symphyseal region, mature right dentary, in A, lingual, and B, labial, views; C, D, VPL/JU/KR38, symphyseal region, juvenile left dentary, C, lingual, and D, labial, views; E, F, VPL/JU/KR47, holotype right dentary, in E, lingual, and F, labial, views. Scale bar = 1 mm.

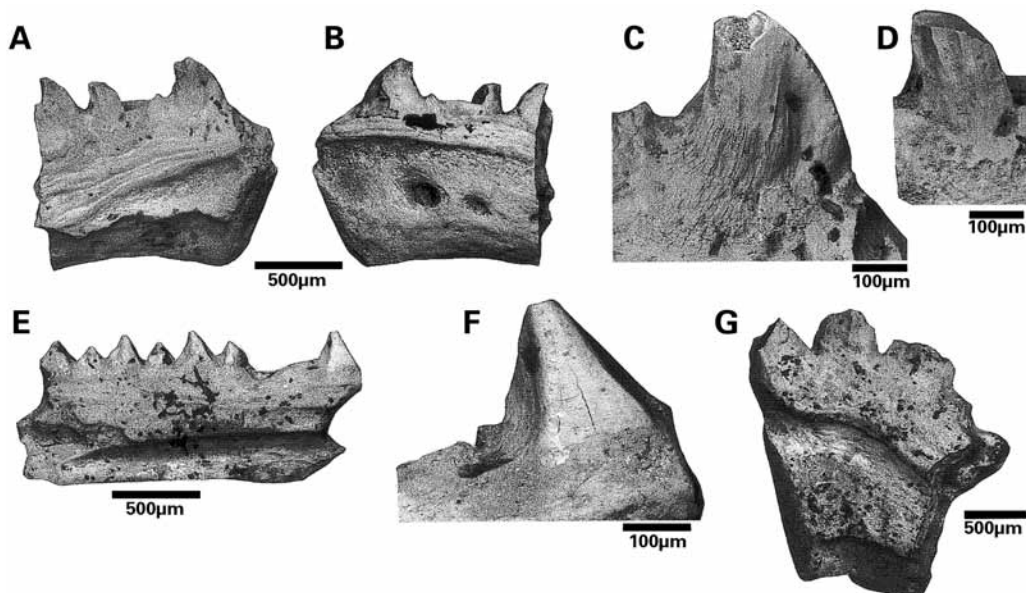


Figure 14. *Godavarisaurus lateefi* gen. et sp. nov. Dentary. A–D, VPL/JU/KR38, left symphyseal region, juvenile, in A, lingual, and B, labial, views, with enlargements of C, anterior, and D, third tooth positions; E, F, juvenile right dentary, VPL/JU/KR39, lingual view, showing E, hatchling dentition followed by first immature additional tooth, F, enlargement of additional tooth; G, VPL/JU/KR37, symphyseal region, mature right dentary, lingual view. Scale bars as indicated.

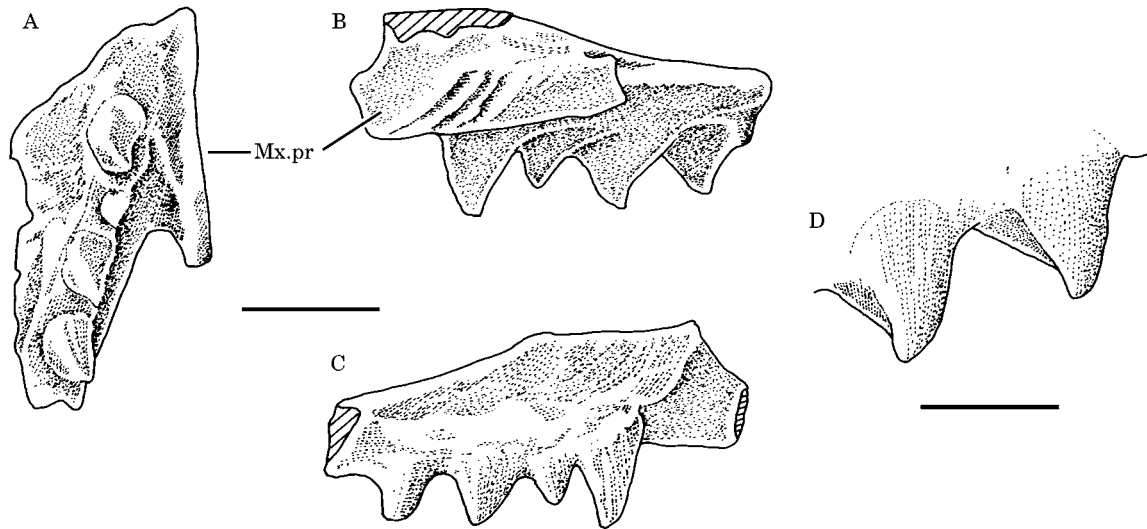


Figure 15. *Godavarisaurus latefi* gen. et sp. nov. Palatine. VPL/JU/KR46, left palatine, in A, palatal, B, left lateral, and C, right medial, views, D, posteromedial enlargement of teeth for comparison with those of the maxillary dentition. Main scale bar = 1 mm, scale bar for D, 0.5 mm.

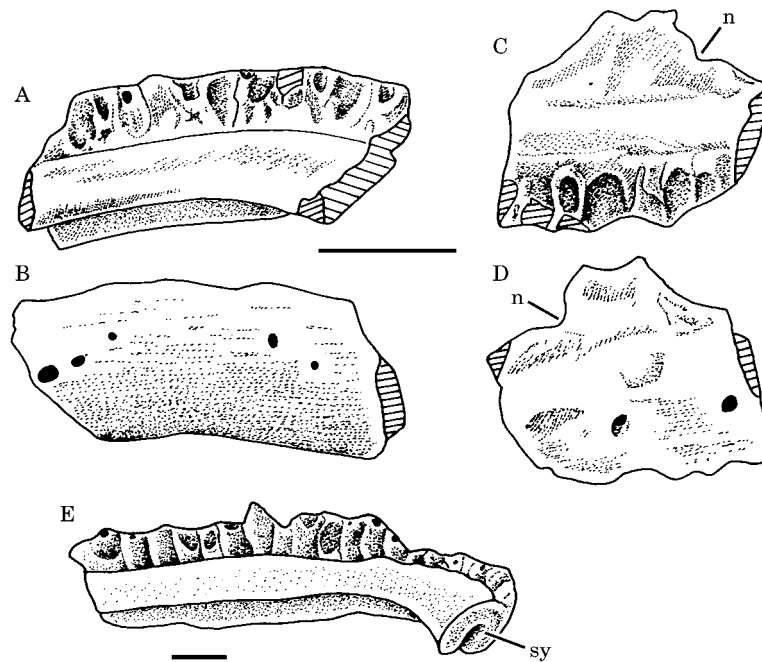


Figure 16. Lepidosauromorpha indet. A, B, VPL/JU/KR57, anterior region of a left dentary in A, lingual, and B, labial, views; C, D, VPL/JU/KR60, fragment of the mid-region of a right maxilla, in C, lingual, and D, labial, views. E, anterior dentary region of the basal rhynchocephalian *Gephyrosaurus* from the Liassic of South Wales (redrawn from Evans, 1980, fig. 42a, but reversed for comparison). Scale bars = 1 mm.

of *Clevosaurus* varies. Similarly, Reynoso (1996a,b) and Wu (1994) place pleurosaurs towards the base of the crown group, while Fraser & Benton (1989) and Wilkinson & Benton (1996) place them higher, as the sister group of *Kallimodon*. There are also problems

with the generic separation of *Opisthias* and *Homoosaurus* (Fraser & Wu, 1998) and of *Kallimodon*, *Sapheosaurus*, *Piocormus* and *Leptosaurus* (which may be growth stages of a single genus, Evans, 1994). These problems are reflected by the polytomies in Figure 19.

The position of the Aptian–Albian *Pamizinsaurus* from Mexico (Reynoso, 1997) is also equivocal. Figure 19 shows the position proposed by Reynoso (1997) on the basis of PAUP analysis. We re-ran Reynoso's data matrix (1996b, 1997). For a heuristic search (either simple or step-wise addition) we obtained a single tree (length 92) of the same topology as that of Reynoso (1997); a branch-and-bound re-run gave the same result. By permitting one additional step, we obtained eight trees, seven of which were essentially the same (for *Pamizinsaurus*) as the shorter tree; one placed *Pamizinsaurus* with *Clevosaurus*. However, a bootstrap analysis (heuristic search, simple addition, 100 replicates) produced a less resolved tree, with a polytomy for most taxa crown-ward of *Planocephalosaurus* (except the sphenodontine/eilenodontine clade which remained well supported). Thus although most analyses place *Pamizinsaurus* closer to the sphenodontine/eilenodontine clade (as shown in Fig. 19), a relationship to *Clevosaurus* cannot be ruled out on present evidence. This is relevant to later discussion.

Comparison

Godavarisaurus and *Rebbanasaurus*, like many other taxa from microsites (Fraser, 1986; Evans, 1992; Evans & Sigogneau-Russell, 1997), are too fragmentary to be included in a cladistic analysis, and we must rely on features of the tooth-bearing bones and dentition to try to place them within a phylogenetic framework.

Premaxilla. The primitive rhynchocephalian premaxilla, as seen in *Gephyrosaurus*, is similar to that of generalized lepidosaurs in being a shallow arch of bone with a long narrow nasal process and many small teeth. Reduction in tooth number occurs in sphenodontians – with three to four teeth on each side in adults of *Planocephalosaurus*, *Clevosaurus* and *Pamizinsaurus*, but only one or two in most other taxa. Typically, the lateral margin of the premaxilla abuts a short anterior maxillary process, but in *Clevosaurus* (Fraser, 1988), and perhaps also in *Pamizinsaurus* (Reynoso, 1997), a strong posterodorsal flange excludes or nearly excludes the maxilla from the narial margin.

The premaxillae of the Kota genera differ from one another. Those assigned to *Rebbanasaurus* have the generalized lepidosauromorph form with a long slender nasal process and a small lateral flange, but only three teeth. In these respects, the morphology is not unlike that of the premaxilla of *Planocephalosaurus*. The single premaxilla attributed to *Godavarisaurus* differs in being very deep, in having a short nasal process and in having a large lateral flange that extends posterodorsally and probably limited the entry of the maxilla into the narial margin. In these features, *Godavarisaurus* resembles *Clevosaurus*. This type of

premaxilla has been considered diagnostic for *Clevosaurus* (e.g. Sues & Reisz, 1995), but may have arisen more than once if its presence in the Mexican *Pamizinsaurus* is confirmed (Reynoso, 1997), and if *Pamizinsaurus* is unrelated to *Clevosaurus*.

Maxilla. In rhynchocephalians, maxillary shape varies with respect to the length and depth of the premaxillary and jugal processes, but one of the most significant features appears to be the degree of development, if any, of flanges on the maxillary teeth (Fig. 17). In *Gephyrosaurus* and *Diphydontosaurus* (Evans, 1980; Whiteside, 1986), the posterior maxillary teeth are more robust than those in the anterior part of the tooth row, but there is no major difference in shape. In *Planocephalosaurus* (Fraser, 1982; Evans, pers. obs.), the posterior maxillary teeth are enlarged but show no development of additional flanges. In the remaining taxa, however, the posterior maxillary teeth bear posteromedial flanges which vary in size from small (e.g. *Sphenodon*, *Palaeopleurosaurus*, *Pamizinsaurus*) or medium (e.g. *Brachyrhinodon*, *Poly-sphenodon*, *Tingitana*), to large (e.g. *Clevosaurus*, *Homoeosaurus*, *Kallimodon*). The function of these flanges and their mode of development are still poorly understood, but they form a consistent feature of the adult dentition. Both Kota taxa possess flanges on the posterior maxillary teeth. In *Rebbanasaurus*, the flanges are small but distinct in juvenile teeth, becoming broader and more robust in the adult where they contribute to the formation of a strong striated blade on posterior teeth (Fig. 17A, B). In *Godavarisaurus*, the maxillary teeth more closely resemble those of typical crown-group sphenodontians (Fig. 17C–I), with a conical anterior section and a small but distinct posterior flange which is offset medially. The maxillary teeth of both Kota genera thus show a more derived morphology than those of *Planocephalosaurus* but differ from those of *Clevosaurus*, *Homoeosaurus* and *Kallimodon*.

Palatine. The palatines of *Gephyrosaurus* and *Diphydontosaurus* match those of basal lepidosauromorphs in having several tooth rows, a condition that is retained in *Planocephalosaurus*. All other sphenodontians in which the palatine is known retain only a single enlarged lateral palatine row. The presence of a second, albeit reduced, palatine row in *Rebbanasaurus* is therefore a primitive feature, although the shape of the individual teeth is quite derived – being pyramidal with anterior and posterior facets rather than conical (as in many Late Triassic taxa).

The palate is poorly known in many Jurassic and Early Cretaceous taxa, but the palatine teeth of *Opisthias* and, to a lesser degree, those of *Sphenodon*

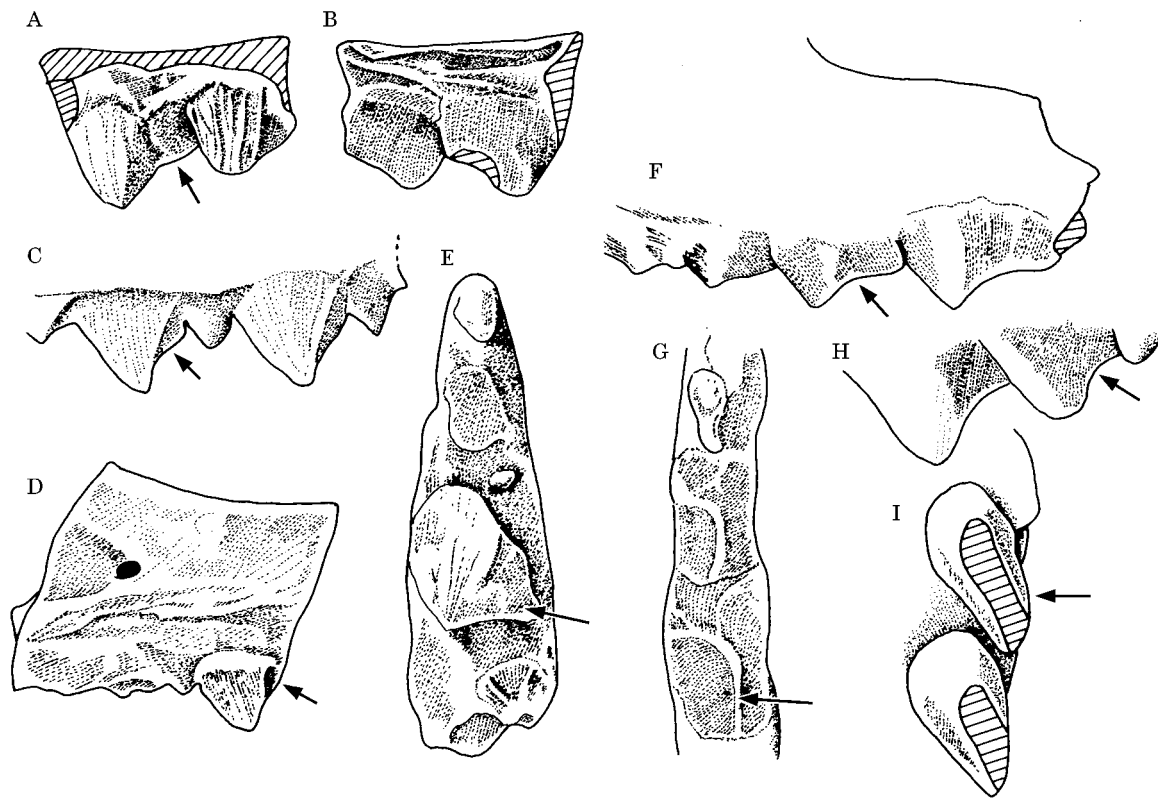


Figure 17. Comparison of maxillary dentitions in rhynchocephalians. A, B, *Rebbanasaurus*, VPL/JU/KR27, posterior dentition in A, labial, and B, lingual, views; C–E, *Godavarisaurus*, C, VPL/JU/KR40, left juvenile dentition, labial view, D, VPL/JU/KR 41, left immature dentition, labial view, VPL/JU/KR44, right mature dentition, occlusal view to show larger medial flanges; F, G, *Clevosaurus*, Cromhall, University Museum of Zoology, Cambridge (uncatalogued), posterior region of left maxilla in F, labial, and G, occlusal, views to show extensive medial flanges; H, I, *Sphenodon*, University College London, Zoology Museum, X.804, posterior region of juvenile maxilla, in H, labial, and I, occlusal, views. Not to scale.

and of an unnamed sphenodontian from the Middle Jurassic of England (Evans, 1992) differ from those of *Clevosaurus*, *Polysphenodon*, *Brachyrhinodon* and *Kallimodon* (Cocude-Michel, 1963) in bearing small posterolateral flanges. These small flanges are also present in *Godavarisaurus*.

Dentary. The dentaries of *Gephyrosaurus* and *Diphydontosaurus* differ from those of more derived taxa in being long and gracile, with a small ovoid terminal symphysis divided by a deep sulcus. The function of this sulcus is unclear but it may have provided attachment for ligaments. In crown-group sphenodontians, the jaw is deeper and shorter, with a more prominent coronoid process. It also has a characteristic symphyseal surface that is narrow, nearly vertical in orientation, and separated from the alveolar margin by a distinct notch. The symphyseal surface of *Planocephalosaurus* is intermediate in morphology, being somewhat broader and lacking the dorsal notch, although it differs from the symphysis of basal taxa in

having a more vertical orientation and in lacking the central sulcus. The only sphenodontian known to retain this central sulcus is the Middle Jurassic *Cynospheonodon* (Reynoso, 1996b). Both *Rebbanasaurus* and *Godavarisaurus* show the typically sphenodontian morphology of the symphyseal surface, although the surface is slightly wider in *Rebbanasaurus* – probably for added strength.

There are also conspicuous differences in the lower jaw dentition among different rhynchocephalian taxa. Three generalized patterns can be recognized. In basal taxa and in *Planocephalosaurus*, the posterior dentary teeth are simple cones (Fig. 18F). According to Cocude-Michel (1963), they also retain this structure in the Late Jurassic *Kallimodon*. In marked contrast, the dentary additional teeth of *Clevosaurus* (Fig. 18G), *Sigmala* (Upper Triassic, UK, Fraser, 1986) and the Early Cretaceous *Tingitana* bear enlarged antero-medial flanges which overlap the inner border of the tooth in front, forming a continuous cutting edge. These taxa are also unusual in having significantly fewer

individual teeth, although the relative overall length of the tooth row is similar. In the remaining taxa, where known, the dentition shows an intermediate state. *Opisthias* provides a good example (Figs 18H, I). The posterior additional teeth resemble half cones with a slightly concave faceted anteromedial surface. The labial and lingual edges of the facet are developed anteriorly (labial edge most prominent) so that they overlap both surfaces of the tooth in front, producing a nested sequence of teeth (Fig. 18I). Further anteriorly, the teeth change shape, becoming faceted on both the anteromedial and posteromedial borders, with a reduced overlap (Fig. 18H). This is similar to the condition in the living *Sphenodon* while the dentition of *Cynosphenodon* appears closer to that of *Opisthias*. The two Kota sphenodontians also have teeth of this type. In *Rebbanasaurus*, the anterior additional (more posterior teeth are not known) are robust cones with a quadrangular base. The teeth are faceted on the anterior surface with a slight asymmetry so that the labial margin of the facet is a little more pronounced than the lingual one, creating an incipient flange (Figs 18B, D), but there is no overlap of the tooth bases. The posterior surface of the tooth is not faceted but does bear striae (Figs 18B, C). The teeth of *Godavarisaurus* are more gracile and closer in general shape to those of *Opisthias* and *Sphenodon*. The anterior faceting differs from that of *Rebbanasaurus* in being deflected to the anteromedial surface, with a greater development of the labial margin (Fig. 18E).

Phylogenetic relationships

From the discussion above, and assuming we have associated elements correctly, it is clear that *Rebbanasaurus* and *Godavarisaurus* represent distinct taxa. Since both are fully acrodont, they lie crownward of *Gephyrosaurus* and *Diphydontosaurus*. In addition, on the basis of the maxillary tooth flanges and incipient flanges on the dentary teeth, both Kota taxa also lie crownward of *Planocephalosaurus*.

However, the retention in *Rebbanasaurus* of a number of primitive features (retention of a medial palatine tooth row, weak maxillary flanges, minimal flanges on the dentary teeth) suggests a position as the sister taxon of remaining taxa (Fig. 19). The robust dentition, deep build-up of ankylosing bone, strong symphysis, and heavily built dentary may reflect a durophagous diet.

Godavarisaurus is more problematic, although this is mainly a reflection of the current state of sphenodontian systematics. The premaxilla most closely resembles that of *Clevosaurus*, but the dentary and maxilla lack the extensively flanged teeth. In this respect, the dentition of *Godavarisaurus* more closely resembles that of *Opisthias*, *Sphenodon* and *Pamizinsaurus*, although the flanging is still more weakly

developed and the premaxilla is quite different. *Godavarisaurus* thus appears to be a primitive intermediate grade sphenodontian. The resemblances between its premaxilla and that of *Clevosaurus* may be convergent, or the two may have diverged from a common ancestor with a more generalized dental structure but a similar premaxilla. In the latter case, *Pamizinsaurus* might belong to the same clade. *Godavarisaurus* and *Pamizinsaurus* resemble each other in the degree of development of the maxillary tooth flanges but differ in the shape of the symphyseal region (strongly oblique in *Pamizinsaurus*), the length of the nasal process of the premaxilla (longer in *Pamizinsaurus*), the form of the anterior dentary teeth (triangular in *Pamizinsaurus*, small and spatulate in *Godavarisaurus*), the distribution of striae (on all teeth in *Pamizinsaurus*, but only the anterior dentary teeth in *Godavarisaurus*) and the development of flanges on the anterior dentary additional teeth (stronger in *Pamizinsaurus*).

BIOGEOGRAPHY AND EXTINCTION

The Gondwanan record of sphenodontians is still very limited, although recent finds in the Upper Triassic of Madagascar (Flynn *et al.*, 1997, 1999) and Brazil (Frigolo, 1999), and in the Lower Jurassic of Zimbabwe (Gow & Raath, 1977) and South Africa (Sues & Reisz, 1995), make it clear that the group was widely distributed through Gondwana in the Early Mesozoic (Table 1). Their presence in India at this time would therefore have been predicted since, prior to the break-up of Pangaea, the Indian–Madagascar–Seychellian plate was connected to Africa to the west and to Antarctica and Australia to the south. The Late Jurassic and Early Cretaceous record is much worse and is restricted to fragmentary remains from South Africa (Lower Cretaceous Kirkwood Formation, Rich *et al.*, 1983; Ross *et al.*, 1999) and Morocco (Lower Cretaceous, ‘Couches Rouges’, Evans & Sigogneau-Russell, 1997) (Table 2). This is unfortunate, since the Cretaceous appears to have been a critical period for the group.

The last surviving Euramerican sphenodontians occur in the Aptian–Albian of Mexico (Reynoso, 1996a, 1997), North America (Throckmorton *et al.*, 1981) and Italy (Barbera & Macuglia, 1988), and a mid-Cretaceous extinction of sphenodontians in northern continents seems likely. Their extinction in Asia apparently came earlier (currently the last known sphenodontian record is from the Early Jurassic Lufeng Formation of China, Wu, 1994). Among hundreds of well-preserved small reptile skulls from the Campanian and Maastrichtian of China and Mongolia, for example, there is not a single sphenodontian. Why they disappeared in Laurasia remains unknown, and the resolution of this question requires more information about the Jurassic and Cretaceous history

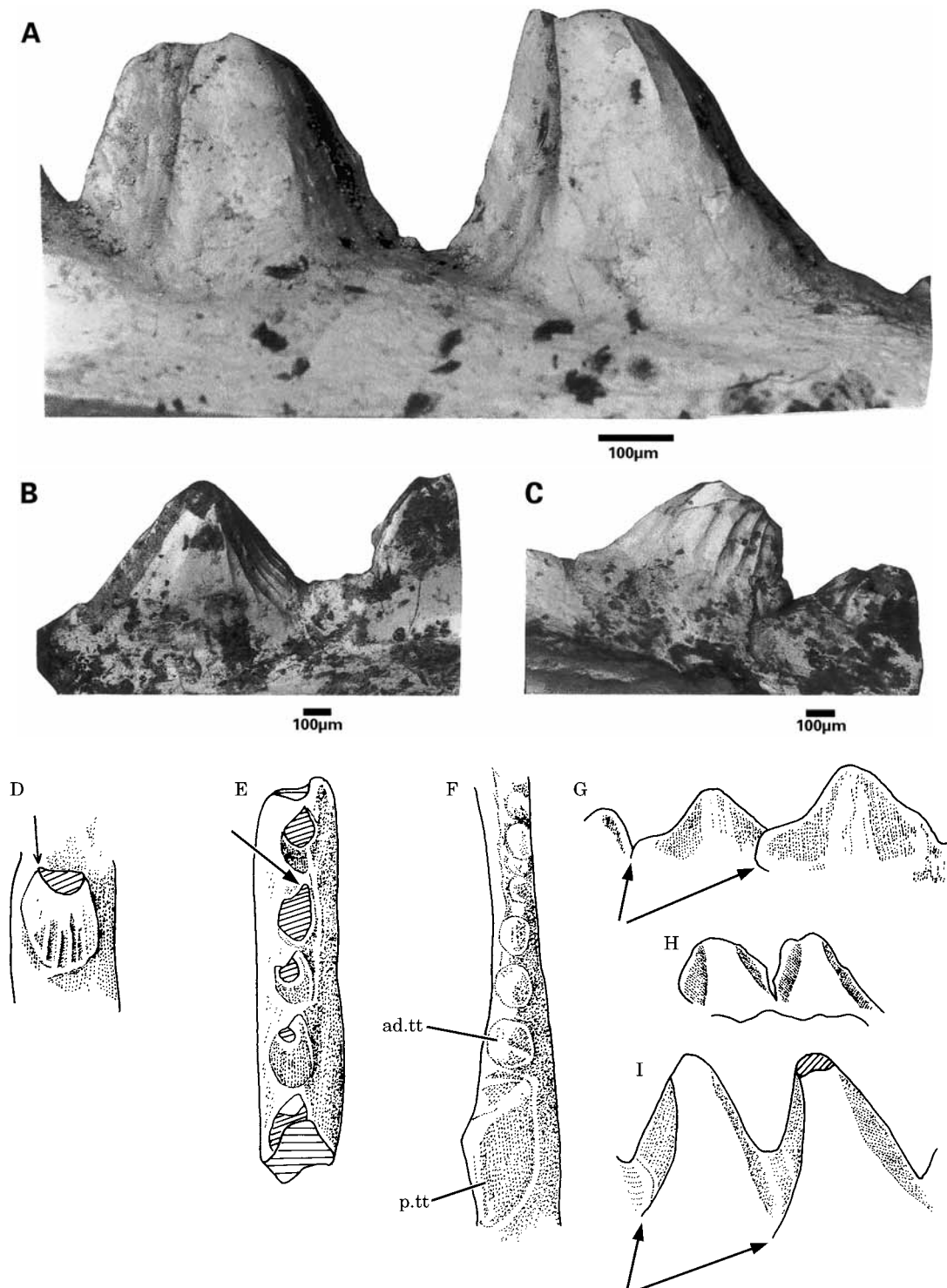


Figure 18. Comparison of dentary dentitions in rhynchocephalians. A, *Godavarisaurus*, teeth of holotype dentary, VPL/JU/KR47; B–D, *Rebbanasaurus*, teeth of B, holotype dentary VPL/JU/KR12 and C, VPL/JU/KR14, fragment of posterior dentition, D, as B, tooth in occlusal view showing slight labial flange; E, *Godavarisaurus*, as A, occlusal view, showing small labial flanges; F, *Planocephalosaurus*, BMNH R.5199, right posterior dentary in occlusal view to show absence of labial flanges and enlarged rear tooth; G, *Clevosaurus*, Cromhall, University Museum of Zoology, Cambridge (uncatalogued), posterior dentary teeth, labial view, showing extensive flanges; H, I, *Opisthias*, DORCM G10831, H, anterior additional, I, posterior additional, showing labial flanges and nested arrangement of flanges on posterior teeth. Not to scale.

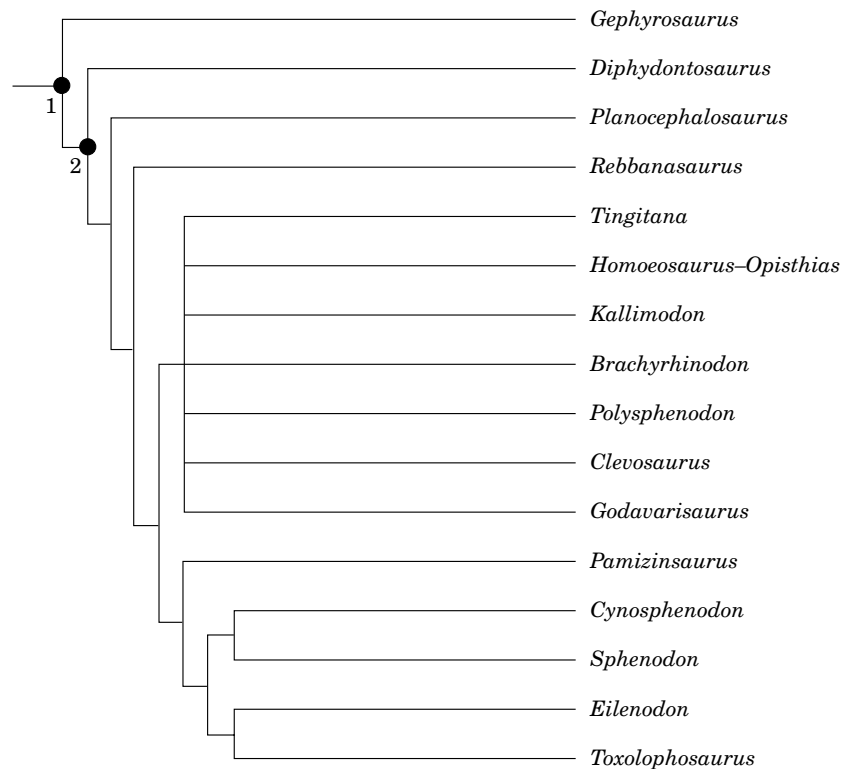


Figure 19. Summary cladogram showing suggested relationships of Kota sphenodontians amongst known rhychocephalian taxa, taken mostly from Wilkinson & Benton (1996) and from Reynoso (1996b, 1997). Node 1, Rhychocephalia; node 2, Sphenodontia.

of the group on both northern and southern continents. That they survived in Gondwana after the mid-Cretaceous is clear from their presence in New Zealand today, but we still know nothing of their history during this period. Sphenodontians have never been recorded from Australia, despite the relatively diverse Tertiary small vertebrate assemblages of Riversleigh, yet their distribution on neighbouring continents suggests that sphenodontians must also have been present in Australia in the Triassic or Early Jurassic.

Under current estimates, the Indian–Malagasy–Seychellian block began to break away from Africa around 165 Mya (Bathonian–Callovian) and from Australia–Antarctica block at about 120–130 Mya (Early Aptian) (Powell, 1979). The continent drifted north, with Madagascar separating at around 88 Mya (Coniacian/Santonian, Storey *et al.*, 1995) and the Seychelles at about 65 Mya (K–T boundary), synchronous with the initiation of Deccan volcanism. Since sphenodontians were present in India (and presumably Madagascar) in the Jurassic, they might be expected to have remained in these continents after they became isolated from the rest of Gondwana. Their pattern of survival in India during its journey northwards towards Asia is therefore of interest in the context of

their subsequent northern extinction. To date, the only Cretaceous horizons sampled in India have been those of the latest Maastrichtian Intertrappean beds (e.g. Naskal, Prasad, pers. obs.). These have yielded a diversity of frogs, mammals and lizards, but no sphenodontians, although further collection is needed. We hope that more extensive sampling of a variety of Intertrappean deposits, in conjunction with the exploration of Indian horizons of intermediate age, will shed new light on this question.

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