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FOSSIL LIZARDS FROM THE JURASSIC KOTA FORMATION OF INDIA

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ABSTRACT—The Mesozoic lizard fauna of Gondwana is virtually unknown. We report here on a lizard assemblage from the Upper Member of the Kota Formation of peninsular India, usually considered to be of Early–Middle Jurassic age. The dominant form, *Bharatagama rebbanensis*, gen. et sp. nov., has a predominantly acrodont dentition. Comparison with living and extinct taxa suggests that this new genus is a primitive acrodont iguanian distinct from the Cretaceous priscagamids. It predates known records of iguanian lizards by some 80 Ma, and provides evidence that iguanians had begun to diversify before the break-up of Pangea. A second fully pleurodont taxon is known from the same deposit. It is tentatively attributed to the Squamata but is too fragmentary for further determination.

INTRODUCTION

Living squamates fall into two major clades—Iguania (pleurodont 'iguanids' and acrodont 'agamids' and chameleons) and Scleroglossa (all other lizards, snakes and amphisbaenians) (Estes et al., 1988). Their fossil history is extremely patchy, especially with respect to two crucial components. Firstly, there is no record prior to the Jurassic; no Triassic or Permo–Triassic 'lizard' described to date has been verified as such (e.g., Evans, 1980, 1984, 1988, 1998a, b). Secondly, there is little information on the early history of the Lepidosauria as a whole in southern continents (Gondwana). Fragmentary lizard remains have been described from the Upper Jurassic of Tanzania (Zils et al., 1995), and from the basal Cretaceous of both Morocco (Richter, 1994; Broschinski and Sigogneau-Russell, 1996) and South Africa (Ross et al., 1999). Where identifiable, these lizards represent families also known from contemporaneous deposits in Laurasia (e.g., paramacellodid scincomorphs; Evans and Chure, 1998). New lizard material has recently been recovered from the Aptian/Albian Crato Limestone Formation of Brazil, but is still largely undescribed (Evans and Yabumoto, 1998). Even the Late Cretaceous lizard fauna of Gondwana is poorly known, limited to a single skull of *Pristiguana* from Brazil (Estes and Price, 1973) and some fragmentary remains.

India remained part of Gondwana until well into the Early Cretaceous. Yadagiri (1986) described fragmentary lepidosaurian remains from the Kota Formation of peninsular India, attributing two lizard specimens to a varanoid and fragments of acrodont dentition to a sphenodontian. As a result of more extensive recent collecting, a larger and more diverse microvertebrate assemblage is now known from these beds. The lepidosaurian remains include two crown-group sphenodontians (Evans et al., 2001), fragments of fully pleurodont maxillae, and more than one hundred jaw fragments of a primarily acrodont taxon which is strikingly different from any known rhynchocephalian. The pleurodont and undescribed acrodont specimens form the subject matter of the present paper.

Institutional Abbreviations—**BMNH**, The Natural History Museum, London; **UCL**, University College London; **VPL/JU/KR**, Vertebrate Palaeontology Collections, University of Jammu (Kota Reptiles).

GEOLOGY

The fossiliferous beds of the Kota Formation occur in the Pranhita-Godavari Valley of Andhra Pradesh, peninsular India. The formation derives its name from the village of Kota located on the left bank of the Pranhita, a tributary of Godavari River, where the type section is located. Other important sections are exposed near the villages Manganpalli, Metpalli, Kunchevalli, Darogapalli, Paikasigudem, Akkalapalli, and Kadamba. The Kota Formation is divisible into Lower and Upper Members (Rudra, 1982). The latter is characterized by a sequence which includes: (1) light cream coloured, bedded limestone bands intercalated with clays and mudstones (these beds directly overlie the red clays of Lower Member), (2) red clays with ferruginous mudstones overlying the limestone zone, and (3) siltstones and fine grained sandstones overlying the ferruginous mudstones. The fossils described here were collected from the intercalated clays and mudstones in the lower horizons of the Upper Member.

The Kota Formation was assigned a Jurassic age by King (1881) and, more specifically, a Liassic age by Krishnan (1968). A Liassic (Early Jurassic) age for the Upper Member is supported primarily by fish fossils (Jain, 1973, 1974, 1983; Yadagiri and Prasad, 1977), with independent evidence from paleobotany (Prabhakar, 1986). However, Govindan (1975), and later Misra and Satsangi (1979), dated the Upper Member as Middle Jurassic based on an ostracode fauna extracted from the limestones and intercalated clays. In recent reviews, Bandyopadhyay and Roy Chowdhury (1996) proposed a Toarcian age (c. 190 Ma, Gradstein et al., 1995) for these beds, while Datta et al. (2000) simply date them as Early Jurassic. New micropaleontological analyses are ongoing, and clarification of the dating must await these results.

MATERIAL

The microvertebrate material from the Upper Member of the Kota Formation comprises fragmentary and disarticulated bones of fish, lepidosaurs (rhynchocephalians and lizards), archosaurs (crocodiles, ornithischian and theropod dinosaurs) and, more rarely, mammals (Datta, 1981; Yadagiri, 1984, 1985, 1986; Prasad, 1986; Yadagiri and Rao, 1988; Bandyopadhyay and Roy Chowdhury, 1996; Prasad and Manhas, 1997). Most of the tet-

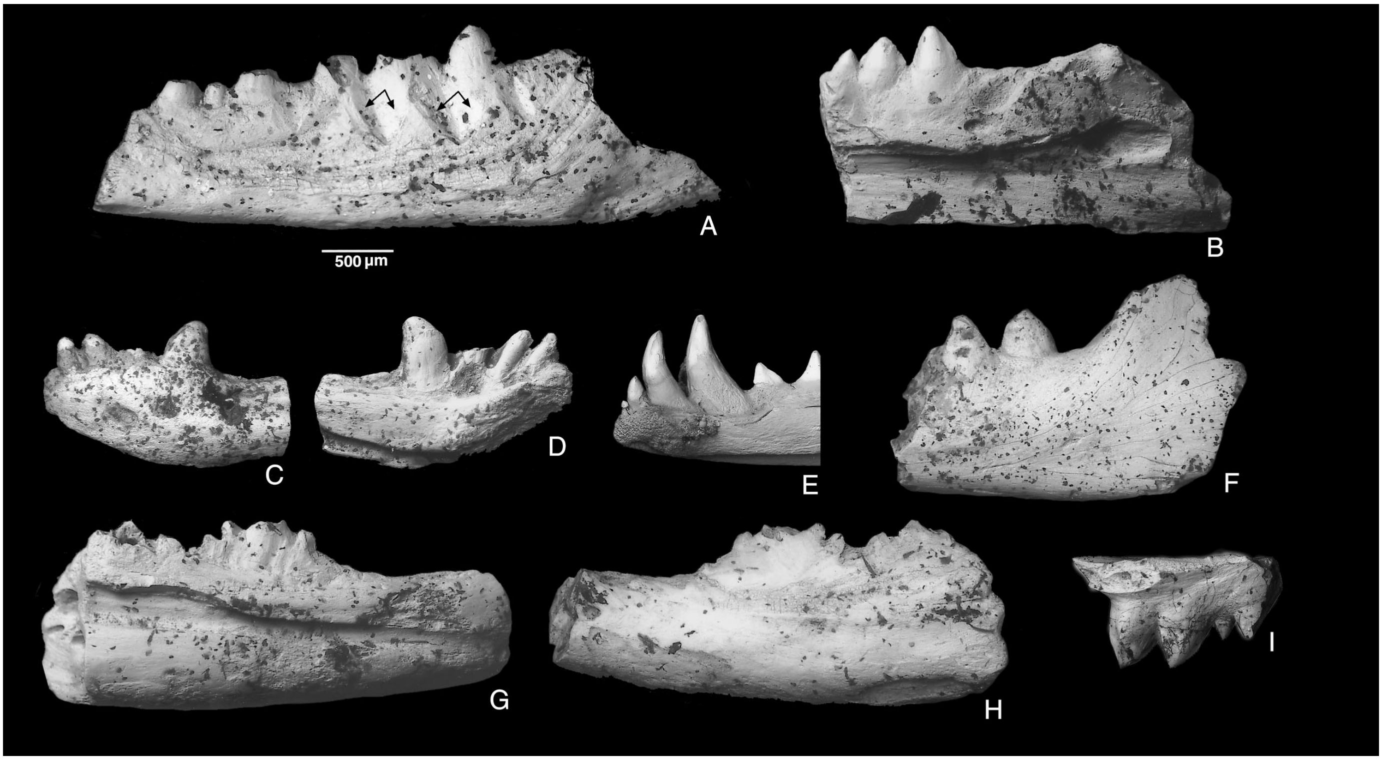

FIGURE 1. *Bharatagama rebbanensis*. **A**, VPL/JU/KR 66, holotype partial left dentary in lateral view, arrows mark wear facets; **B**, VPL/JU/KR 97, posterior region of right dentary, medial view; **C–D**, VPL/JU/KR 67, symphysial region of left dentary, in **C**, lateral and **D**, medial views. **E**, symphysial region, medial view, of right dentary of the extant *Draco* sp. (UCL collection). **F**, VPL/JU/KR 76, posterior region of left dentary, lateral view; **G–H**, VPL/JU/KR 83, mid-region of a left dentary in **G**, medial and **H**, lateral views; **I**, VPL/JU/KR 92, posterior fragment of a right maxilla, lateral view. All specimens to the same scale.

rapod taxa are represented by fragments of dentition, with rare postcranial remains.

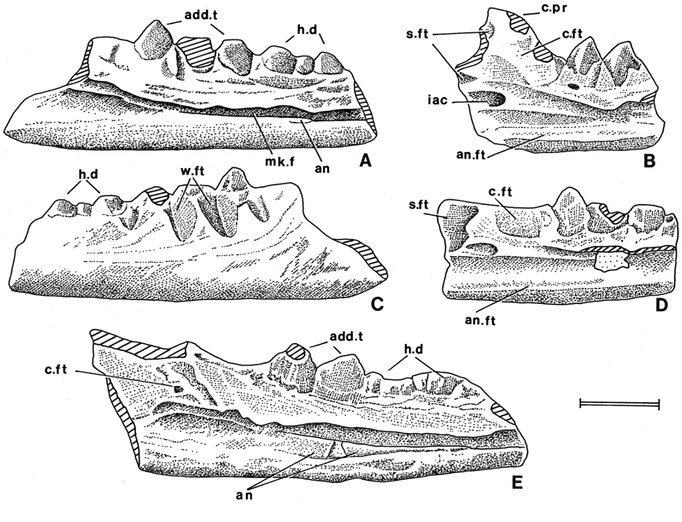

FIGURE 2. *Bharatagama rebbanensis*. Dentary. **A**, **C**, VPL/JU/KR 66, holotype left dentary in **A**, medial and **C**, lateral views; **B**, VPL/JU/KR 76, posterior left dentary, immature, in medial view; **D**, VPL/JU/KR 78, posterior left dentary, immature, in medial view, coronoid process broken; **E**, VPL/JU/KR 70, partial left dentary with associated and partially fused angular, medial view. Scale bar equals 1mm. **Abbreviations**: **add.t**, additional teeth; **an**, angular; **an.ft**, angular facet; **c.ft**, coronoid facet; **c.pr**, coronoid process; **h.d.**, hatchling dentition; **iac**, opening of inferior alveolar canal; **mk.f**, Meckelian fossa; **s.ft**, surangular facet; **w.ft**, wear facet.

SYSTEMATIC PALAEONTOLOGY

LEPIDOSAURIA
SQUAMATA
IGUANIA
ACRODONTA Cope 1864 (=CHAMAELEONIDAE sensu Frost and Etheridge, 1989) *BHARATAGAMA REBBANENSIS*, gen. et sp. nov.

(Figs. 1–8)

Etymology—Bharat (Sanskrit): India; and agama, in reference to the acrodont ‘agamids’; Rebbana, a small town close to the type locality.

Holotype—University of Jammu, Geology Department collections VPL/JU/KR 66. Posterior part of a right dentary (Figs. 1A, 2A, C).

Horizon and Locality—Paikasigudem, near Rebbana, Pranhita-Godavari Valley, Andhra Pradesh, India. Kota Formation, Paikasigudem Section, from clays and mudstones intercalated with the limestone beds in the lower horizons of the Upper Member.

Referred Specimens—These form an important part of the hypodigm. VPL/JU/KR 88, anterior region of a left maxilla (Fig. 7A, B); VPL/JU/KR 90, 92, posterior ends of right maxillae (Figs. 1I, 8G); VPL/JU/KR 91, left maxilla; anterior symphysial region of left (VPL/JU/KR 67, 80, 103) and right (VPL/JU/KR 79, 98, 100) dentaries (Figs. 1C, D, 3A–F); mid-region of dentary with hatchling dentition from left (VPL/JU/KR 69, 81–84, 87) and right (VPL/JU/KR 68, 85–86) sides (Figs. 1G,

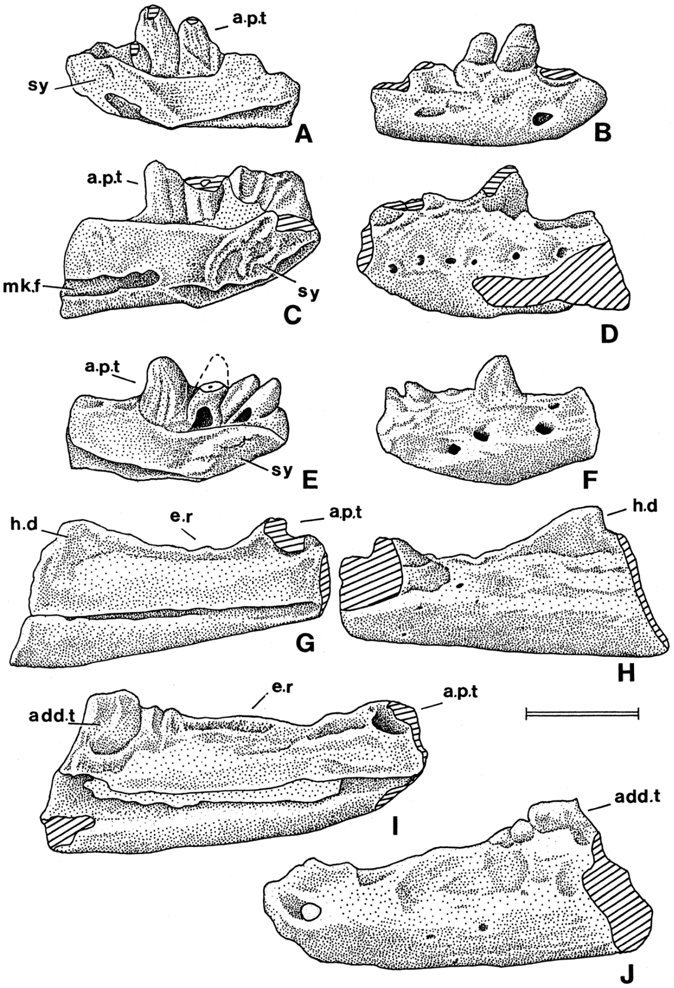

FIGURE 3. *Bharatagama rebbanensis*. Anterior dentary. **A–B**, VPL/JU/KR 79, symphysial region, right dentary, in **A**, medial and **B**, lateral views; **C–D**, VPL/JU/KR 80, more mature specimen of left symphysial region, in **C**, medial and **D**, lateral views; **E–F**, VPL/JU/KR 67, left symphysial region with full dentition in **E**, medial and **F**, lateral views; **G–H**, VPL/JU/KR 81, mid-section of left dentary immediately behind symphysial region showing ridge of eroded hatchling teeth and fused posterior hatchling teeth, **G**, medial and **H**, lateral; **I–J**, VPL/JU/KR 82, as above, with beginning of additional series. Scale bar equals 1mm. **Abbreviations**: as Figure 2, with **a.p.t.**, anterior pleurodont teeth; **e.r.**, ridge of eroded hatchling teeth; **sy**, symphysial surface.

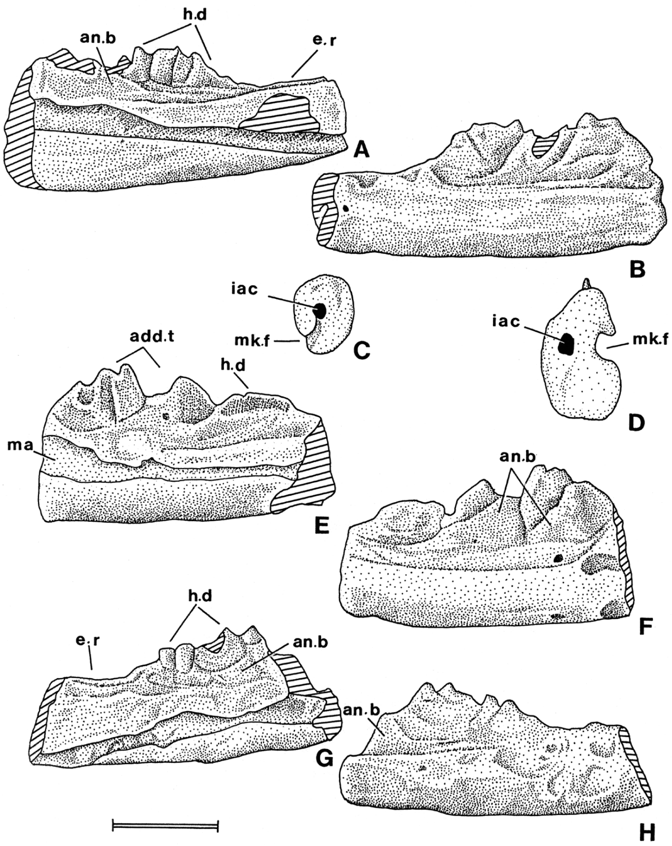

FIGURE 4. *Bharatagama rebbanensis*. Middle section of dentary. **A–D**, VPL/JU/KR 83, left dentary, **A**, medial, **B**, lateral, **C**, cross-section at anterior end, **D**, cross-section at posterior end; **E–F**, VPL/JU/KR 84, partial left bone showing fused hatchling teeth and early additional tooth, with deposits of ankylosing bone, **E**, medial and **F**, lateral views; **G–H**, VPL/JU/KR 85, right dentary, with ridge of eroded teeth and fused hatchling teeth, **G**, medial and **H**, lateral views. Scale bar equals 1mm. **Abbreviations**: as Figures 2–3, with **an.b**, ankylosing bone.

H, 3G–J, 4A–H, 8A, B); posterior dentition of left (VPL/JU/KR 72–73) and right (VPL/JU/KR 71, 97) dentaries (Fig. 5A–D); posterior region of left dentary (VPL/JU/KR 70, 76, 78, 93–94, 104–105) and right dentary (VPL/JU/KR 74–75, 77, 95–96) (Figs. 1B, 2B, D, 5E–H, 8C, D, F); around fifty additional uncatalogued dentary specimens. All specimens come from the type locality and horizon.

Diagnosis—Small (head length c.15 mm) reptile with a predominantly acrodont shearing dentition characterized by the following combination of character states: dentary with five anterior pleurodont teeth that are striated and increase in size from front to back; jaw underlying hatchling dentition tubular, with Meckelian fossa in this region closed or nearly closed by expansion of subdental shelf; posterior additional dentition of 2–4 blade-like, mediolaterally flattened teeth with sharp margins and deep labial wear facets; splenial small or absent; angular slender and elongate, extending forward to level of hatchling dentition, fused (sometimes without visible suture) to lower margin of Meckelian fossa in adults; maxilla with three or four anterior pleurodont teeth that decrease sharply in size from front to back; no tapering anterior premaxillary process, narrow premaxillary facet along anterodorsal margin of maxilla and extending onto small anteromedial shelf.

Remarks—The above suite of derived characters diagnoses the species. The combination of a relatively short robust jaw and a pleurodont/acrodont/pleuroacrodont dentition supports the interpretation of *Bharatagama* as an advanced lepidosaur (more basal taxa have elongated jaws with small teeth). The combination of a long fused angular; a short row of pleurodont anterior teeth in a shallow symphysial region; an elongate anteromedial symphysial surface restricted to the dorsal margin of the Meckelian fossa in adults; an acrodont dentition in which the teeth are broad but unflanged, and lack interstices; a pleuroacrodont additional series which follows a fully acrodont hatchling series; a strong pattern of precise dorsoventral (orthal) shear on the labial, but not lingual, surfaces of the dentary teeth; and an abutting premaxillary-maxillary contact in which a medial maxillary shelf extends behind an, apparently, narrow premaxilla, are all characters shared with acrodont iguanians. *Bharatagama* resembles Cretaceous priscagamids like *Priscagama* (Borsuk-Bialynicka and Moody, 1984) in tooth number, tooth shape, and implantation, but differs in the loss/reduction of the splenial, in lacking any trace of an extensive labial flange

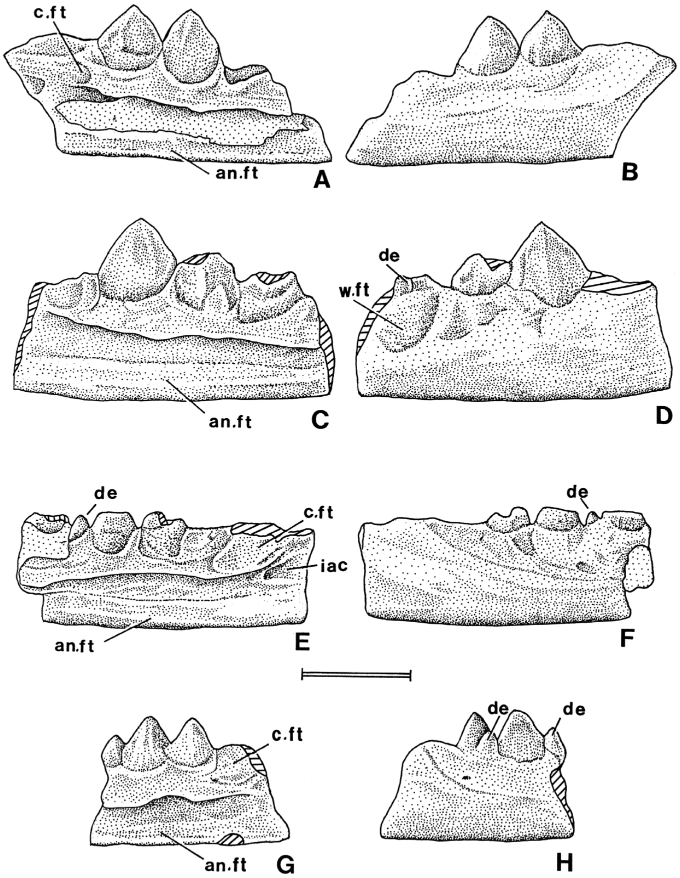

FIGURE 5. *Bharatagama rebbanensis*. Posterior additional teeth of dentary. **A–B**, VPL/JU/KR 72, immature left bone with facet for angular, **A**, medial and **B**, lateral views; **C–D**, VPL/JU/KR 73, immature left bone, **C**, medial and **D**, lateral views; **E–F**, VPL/JU/KR 74, immature right bone, showing coronoid facet and entry of inferior alveolar canal, **E**, medial and **F**, lateral views; **G–H**, VPL/JU/KR 75, immature right bone, **G**, medial and **H**, lateral views. Scale bar equals 1mm. **Abbreviations**: as Figures 2–3, with **de**, denticle.

on the coronoid, and in having an angular which extends much further forward along the ventral margin of the Meckelian fossa (Gao and Hou, 1996).

DESCRIPTION

Bharatagama is currently represented only by dentary and rare maxillary specimens.

Dentary

No complete dentary of *Bharatagama* is available, but the bone is represented by around 100 specimens from both adult and immature individuals. Four distinctive regions can be recognized—symphysial, hatchling/juvenile dentition, posterior dentition, and postdental, with sufficient intermediate specimens to confirm the association and permit reconstruction (Fig. 6A, B).

The shallow symphysial region is represented by six specimens (Figs. 1C, D, 3A–F). The alveolar border bears five weakly pleurodont teeth that increase in size posteriorly. In any one specimen, one or more teeth typically bear medial replacement pits. The subdental ridge restricts the Meckelian fossa to the ventral border of the bone. Anteromedially, the ridge bears a large, ovoid symphysial surface with its long axis positioned roughly horizontally. The tip of the Meckelian fossa may extend into the back of this surface (smaller specimens; Fig. 3A, B, E, F) or close briefly before reaching it (larger specimens; Fig. 3C, D), but the symphysial surface lies on the dorsal rim of the fossa. The lateral surface of the bone is convex and bears a varying number of small nutrient foramina.

Several specimens (e.g., VPL/JU/KR 68–69, 81–87) show the transition between the anterior pleurodont dentition and the more posterior acrodont series (Figs. 1G, H, 3G–J). Immediately behind the largest of the pleurodont teeth, there appears to be a short diastema (e.g., VPL/JU/KR 70, 81–82). Closer examination, however, reveals the eroded bases of small acrodont hatchling teeth (or a ridge representing all that is left of these structures, e.g., Figs. 3G, I, 4A). In specimen VPL/JU/KR 68, a very young individual, the anterior hatchling teeth are triangular and acrodont. In other specimens, only the more posterior hatchling teeth are preserved, often as a serrated blade of fused or partially fused denticles (e.g., VPL/JU/KR 83–85, Fig. 8A, B). The jaw below this hatchling tooth series remains shallow and forms a potential zone of weakness between the firm symphysis and the thicker deeper posterior part of the jaw. However, the jaw in this region is strengthened by the closure or near closure of the Meckelian fossa and the bowing of the lateral surface so that the bone is nearly cylindrical (Fig. 4A–C).

Specimens VPL/JU/KR 84 and VPL/JU/KR 92 (Figs. 3I, 4E) are amongst those which preserve parts of the hatchling dentition and the adult permanent dentition. The teeth of the adult permanent dentition are large and distinctive (e.g., VPL/JU/KR 66, 71–73). On the lateral surface, this region of the jaw is characterized by deep regular scoring of the teeth and bone, providing evidence of precise vertical occlusion between the upper and lower jaw dentitions (e.g., VPL/JU/KR 66, 94, Figs. 1A, 2C, 8F). Medially, the subdental ridge is of moderate depth, and the Meckelian fossa opens out slightly. In smaller specimens, the lower margin of the dentary is shallow and bears a long narrow facet for the angular (e.g., VPL/JU/KR 73, Fig. 5C). This extends forward to the level of the hatchling dentition. By contrast, many of the larger specimens seem to show a quite different structure, with the ventral margin of the Meckelian fossa deeper and thickened (e.g., VPL/JU/KR 82, Fig. 3I; VPL/JU/KR 83, Fig. 1G). Crucially, these specimens show no trace of an angular facet. This difference is explained by a small number of specimens (e.g., VPL/JU/KR 66, 70, 96, Fig. 2A, E) in which the angular is preserved in association, separated or partially separated from the dentary by the remains of a suture. From specimens such as VPL/JU/KR 66 and 70, it is clear that, in the adult, the angular became fused to the dentary along the ventral margin of the Meckelian fossa. Furthermore, with increasing size, this region of the jaw frequently shows rugosities resulting from additional bone deposition. This may correspond to the attachment of a large pterygoideus muscle mass, as in some living agamids. No specimen shows any trace of a splenial facet, either dorsally or ventrally, and this element had probably been lost or greatly reduced.

The postdental region is preserved in a relatively small number of specimens and is never complete posteriorly (e.g., VPL/JU/KR 76, 77). Dorsally, the bone extends into a small rounded coronoid process (frequently broken) that supported the labial face of the coronoid bone (e.g., VPL/JU/KR 76, Figs. 1F, 2B). The lateral surface of this process lacks any trace of a facet and it is unlikely that the associated coronoid bone bore a labial flange. Medially, the post-dental region carries an anterior facet for the coronoid (e.g., Figs. 2B, D, 5A, E, G), and a posterior one for the surangular (e.g., VPL/JU/KR 76, Fig. 2B). The foramen for entry into the inferior alveolar canal lies below the coronoid facet rather than forward within the Meckelian fossa

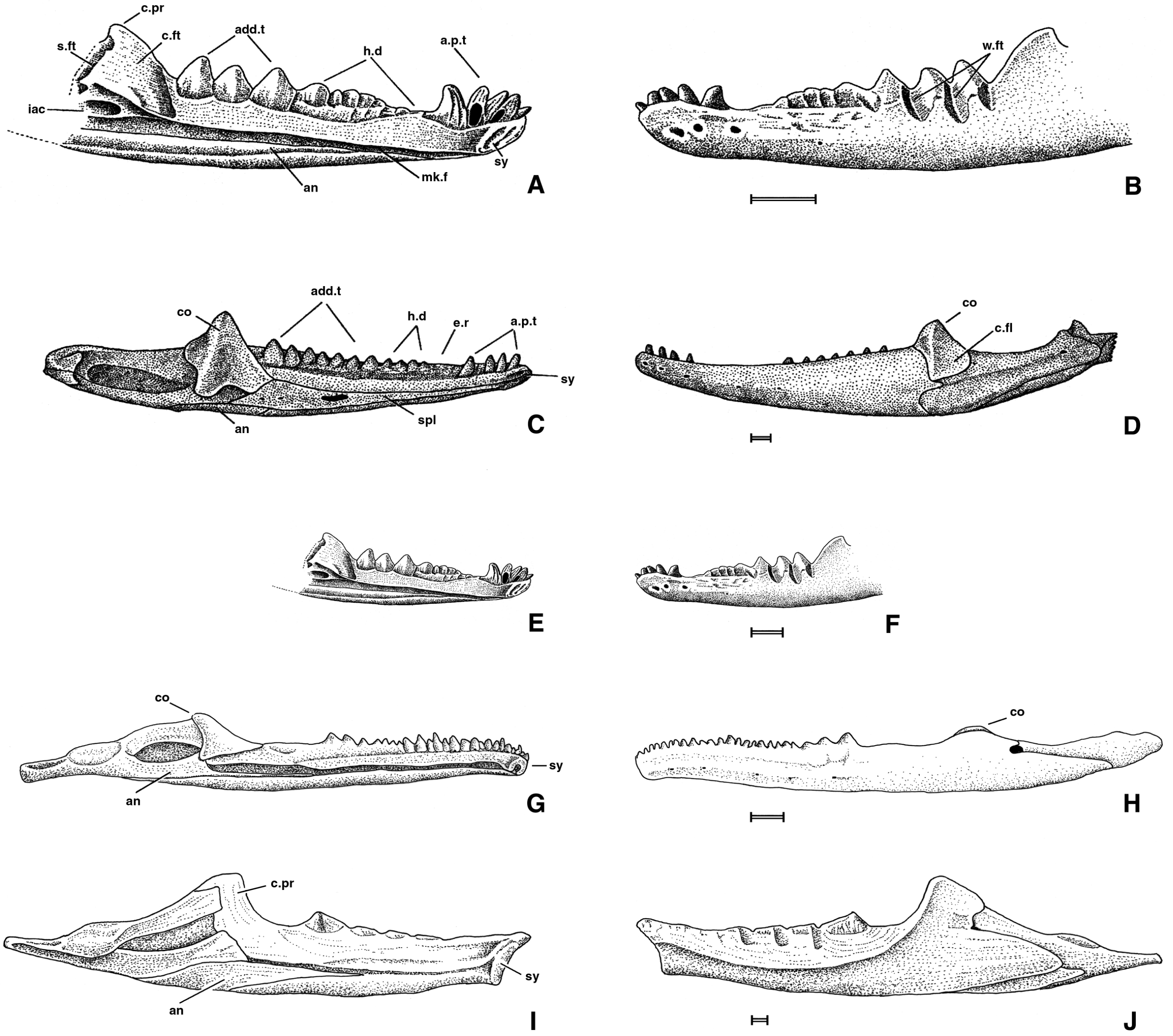

FIGURE 6. *Bharatagama rebbanensis*. Reconstruction of left dentary in **A**, medial and **B**, lateral views. **C–D**, reconstruction of left jaw ramus of the priscagamid *Priscagama gobiensis*, Late Cretaceous, Mongolia, in **C**, medial and **D**, lateral views (redrawn from Borsuk-Bialynicka and Moody, 1984:fig. 4). **E–F**, as for **A–B**, but reduced for comparison. **G–H**, reconstruction of the lower jaw ramus of *Diphydontosaurus avonis* (redrawn from Whiteside, 1986:fig. 4, reversed for comparison). **I–J**, reconstruction of the lower jaw ramus of *Clevosaurus hudsoni* (redrawn from Fraser, 1988:fig. 19b, c). Scale bars equals 1mm. **Abbreviations**: as Figures 2–5, with **c.fl**, coronoid labial flange; **co**, coronoid; **spl**, splenial.

as in most lizards. It is unclear how far the posteroventral margin of the dentary extended.

Maxilla

Maxillae are rarer than dentaries in microvertebrate accumulations, probably because they break up more easily. The maxilla of *Bharatagama* is represented by at most four specimens. One of these (VPL/JU/KR 88), an anterior left maxillary fragment (Fig. 7A, B), can be attributed with confidence since the shape, size and implantation of the teeth closely match those of the corresponding symphysial region of the dentary. The shallow alveolar margin bears four weakly pleurodont teeth. The anterodorsal region of the maxilla is distinctive in lacking a tapering anterior premaxillary process. Instead, a narrow premaxillary facet runs down the narrow steeply angled anteromedial margin of the bone and onto a small ventromedial shelf (Fig. 7A, B). Thus the tip of the maxilla must have abutted against the lateral edge of the premaxilla, with the medial shelf extending behind the premaxilla. The premaxilla has not been recovered but, assuming that the upper pleurodont teeth correspond roughly in size and arrangement to those of the dentary (as suggested by VPL/JU/KR 88), there is relatively little space for the premaxillary dentition. With a total of 5 pleurodont teeth on each dentary, and four on each maxilla, the premaxilla may have been narrow, with perhaps no more than three small teeth. A similar condition is seen in a specimen of the extant agamid *Hydrosaurus amboinensis* (UCL collection) which has six pleurodont teeth on each dentary, five on each maxilla, and three on the median premaxilla.

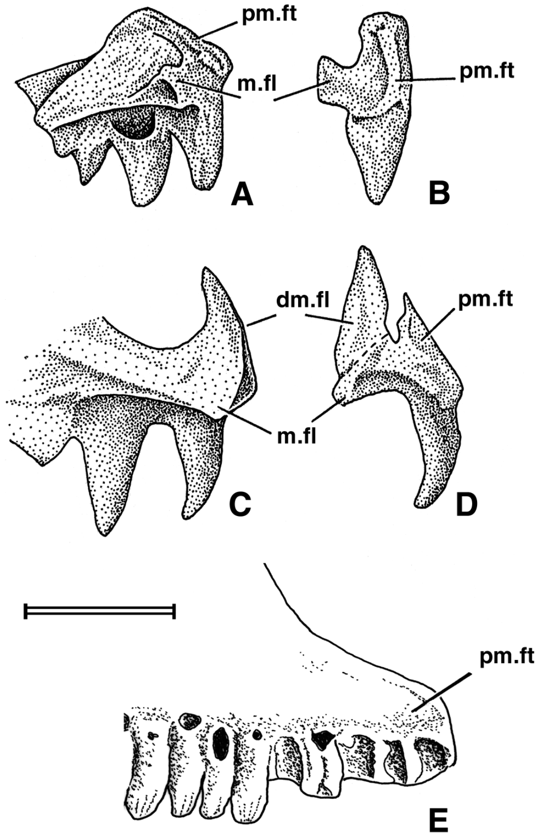

FIGURE 7. **A–B**, *Bharatagama rebbanensis*. VPL/JU/KR 88, anterior region of a left maxilla, showing premaxillary facet (**pm.ft**) and medial flange (**m.fl**). **C–D**, *Draco* sp. (UCL collection), anterior region of a left maxilla, showing extended medial flange and extra dorso-medial flange (**dm.fl**), dotted line marks ventral limit of the latter. **E**, *Diphydontosaurus avonis*, premaxillary process (redrawn from Whiteside, 1986:fig. 7b, reversed for comparison). Scale bar equals 1mm.

Three specimens from the posterior end of the maxilla of *Bharatagama* are tentatively associated (VPL/JU/KR 90–92, Figs. 1I, 8G). Each preserves part of a short narrow jugal process with compressed conical acrodont teeth of similar shape to those at the back of the dentary (Fig. 8).

Dentition

Bharatagama is characterized by a strongly heterodont dentition in which the first four (maxilla) or five (dentary) teeth are pleurodont, cylindrical and recurved, with lingually striated and slightly compressed tips. In the maxilla, the first two teeth are substantially larger than the teeth following; tooth three is less than half the size of the tooth anterior to it while tooth four is little more than a denticle at the base of tooth three (Fig. 7A). In the dentary, the pattern is reversed, with the largest pleurodont tooth at the rear. Behind these symphysial teeth, the dentary bears a series of 13–15 teeth, including around 11 small teeth from the hatchling dentition, and two to four additional teeth. The hatchling teeth, where preserved, are mediolaterally flattened cones fused to the apex of the jaw. Their bases tend to merge and become surrounded by ankylosing bone, while the most anterior teeth are eroded into an irregular ridge (e.g., VPL/JU/KR 83, 85, Fig. 8A, B). They are fully acrodont. The additional teeth are triangular and blade-like, with sharp edges and a pointed tip (Figs. 1B, 5A–D, 8C, D). They are fused to the jaw, but their bases extend onto the lingual surface (Figs. 1B, 5A, C, 8C, D) so that they are really pleuroacrodont. The long axis of each tooth base is aligned with that of the jaw and the tooth bases are in contact without interstices. A variably developed deposit of ankylosing bone surrounds the base of each tooth (e.g., VPL/JU/KR 84, 85, Fig. 4F).

The anterior pleurodont teeth show medial replacement pits. The acrodont dentition was apparently not replaced, but additional teeth were added from the back of the tooth series. However, in some immature specimens, small denticles are occasionally found between, and labial to, the larger additionals (e.g., VPL/JU/KR 74, 75, Fig. 5E–H). These may simply be aberrant, or perhaps represent the posterior part of the hatchling dentition onto which the first additionals have encroached.

Labial wear facets on the dentary (e.g., Figs. 1A, 2C, 8F) show that *Bharatagama* employed precise vertical shear to deal with its prey, probably in combination with a strong muscular tongue as in living taxa (Schwenk, 1988, 2000). We would expect the corresponding teeth of the maxilla to be highly polished on their medial surfaces, and this is the case in attributed specimens. By contrast, the medial surfaces of most dentary teeth are smooth and unworn, although posterior teeth occasionally show a narrow central ridge (Fig. 8D).

LEPIDOSAURIA
SQUAMATA
Family Indet.

A second Kota reptile is represented by a fragmentary right maxilla (VPL/JU/KR 62) (Fig. 9A). A second partial maxilla (VPL/JU/KR 61, Fig. 9B, C), may belong to the same taxon, but this is not certain. VPL/JU/KR 62 represents the central part of the bone, including the base of the facial process and the beginning of the jugal process. Despite the very fragmentary nature of the specimen, it presents some interesting features. The tooth implantation is fully pleurodont with long conical tooth bases and, at least in VPL/JU/KR 61, conical striated tips (Fig. 9C). The more posterior teeth of VPL/JU/KR 62 are compressed but appear to have been somewhat wider. They bear medial replacement pits. Above them, the supradental shelf is narrow. The jugal facet lies on the medial face of the postorbital process, so that the anterior process of the jugal would have been hidden in lateral view and the maxilla would have entered the orbital margin. Just above the jugal facet, the orbital rim contains a narrow groove. This may have been the base of the lacrimal foramen, or a shallow facet for a reduced lacrimal bone. From the preservation, it is not clear which. The labial surface of the bone bears eroded nutrient foramina, but is unusual in being sharply angled so that the facial process is almost horizontal rather than vertical. It suggests the animal had a depressed skull. The strongly pleurodont tooth implantation suggests this small reptile was an early crown-group squamate, but without additional material, more detailed attribution is impossible.

LEPIDOSAURIA
SQUAMATA
Family Indet.
Paikasisaurus indicus Yadagiri 1986

Yadagiri (1986) gave a preliminary account of Kota Formation microvertebrates, also based on material recovered from the Paikasigudem section. Amongst these specimens, he recorded rhynchocephalian remains (although some of these appear to pertain to *Bharatagama*) and two fragments of apparently pleurodont dentition. On the basis of these pleurodont fragments, he erected a new genus of varanoid lizard, *Paikasisaurus*. This attribution relied on the presence of weak basal striae in one specimen, but these striae bear no resemblance to the characteristic infolded plicidentine of varanoid lizards. The holotype (Geological Survey of India, Training Institute, Hyderabad, GSI.TI.14) is a frag-

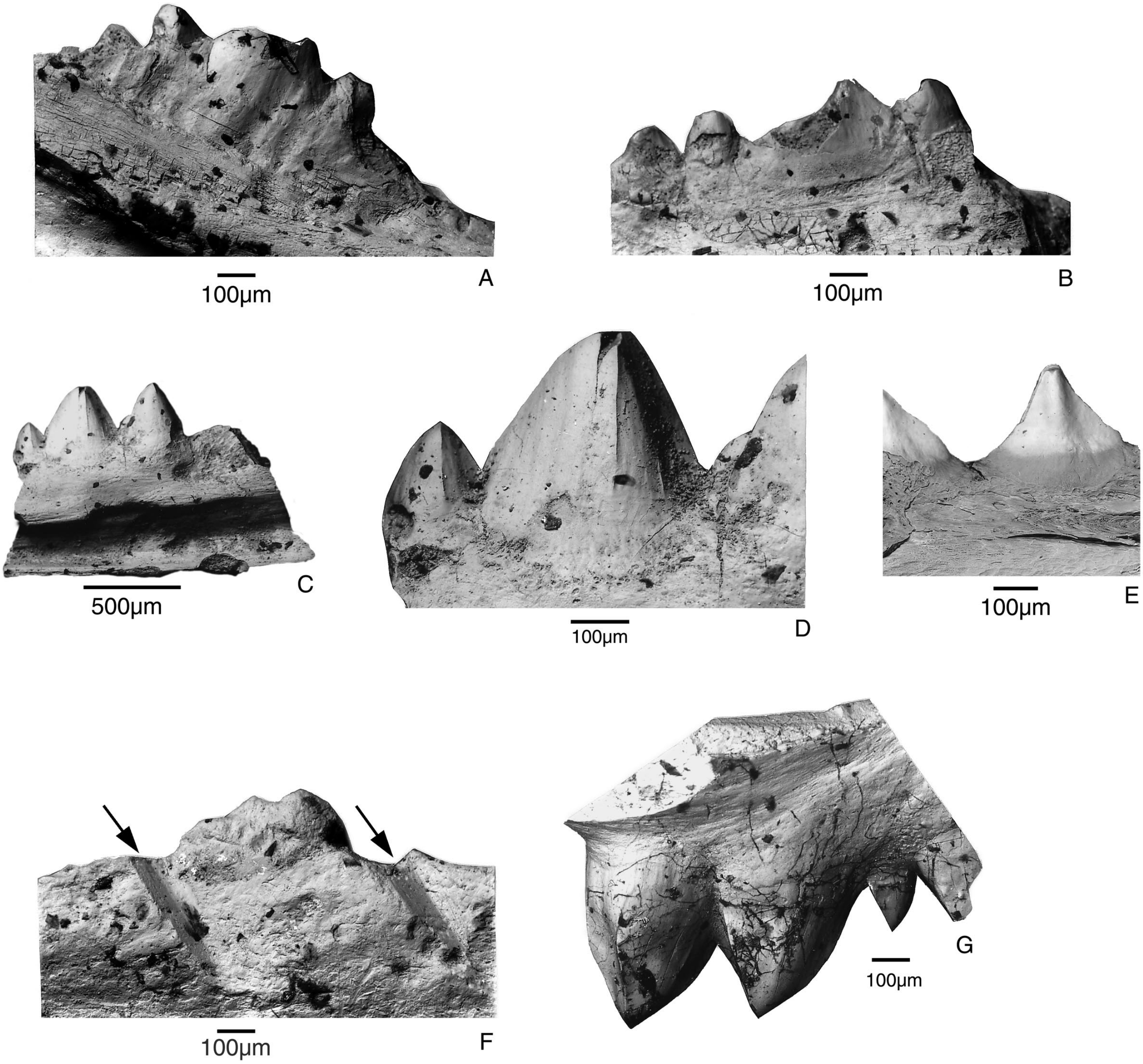

FIGURE 8. *Bharatagama rebbanensis*. Features of the dentition. **A**, VPL/JU/KR 83, fused posterior hatchling dentition, left dentary, medial view; **B**, VPL/JU/KR 85, fused hatchling dentition, right dentary, medial view; **C–D**, VPL/JU/KR 75, additional teeth of right immature dentary, medial view, **C**, complete specimen, **D**, enlargement of teeth. **E**, the extant agamid *Draco* sp. (UCL collection), additional dentary teeth, right dentary, medial view. **F**, VPL/JU/KR 94, posterior fragment of left dentary, lateral view, showing deep regular wear facets (arrowed); **G**, VPL/JU/KR 92, posterior fragment of right maxilla, at base of jugal process, lateral view. Scale bars as indicated.

ment of jaw with two teeth. It was interpreted as the tip of a left dentary but, as illustrated, could equally be the tip of a right maxilla. The teeth are small and recurved, with thick conical bases and some apical striation. The second referred specimen (GSI.TI.15) bears a single deeply pleurodont tooth from either the maxilla or dentary. There is no evidence to support the attribution of the two specimens to a single genus. Both are undiagnostic, and no derived characters were given in the description or diagnosis that would either characterise the taxon (or taxa) or differentiate it from any existing taxon. *Paikasisaurus* should therefore be regarded as a nomen dubium. GSI.TI.15 could belong to the same taxon as the pleurodont lizard described above. GSI.TI.14 might also be part of this, but could equally belong to *Bharatagama*, or to a third taxon.

THE RELATIONSHIPS OF *BHARATAGAMA*

Conspecificity of the *Bharatagama* Material

The first important consideration is whether *Bharatagama*, as described here, might be a chimera, constructed from parts of sphenodontian and pleurodont lizard jaws. This is unlikely for several reasons. The Kota sphenodontians (Evans et al., 2001) are fully acrodont and are represented by symphysial, hatchling and additional tooth series of typical form. In its turn, *Bharatagama* is represented by sufficient overlapping specimens of the dentary to be certain that the symphysial regions bearing pleurodont teeth belong with the attributed acrodont jaw fragments. Any comparison with the lower jaws of other taxa must therefore take this combination of characters into account. In

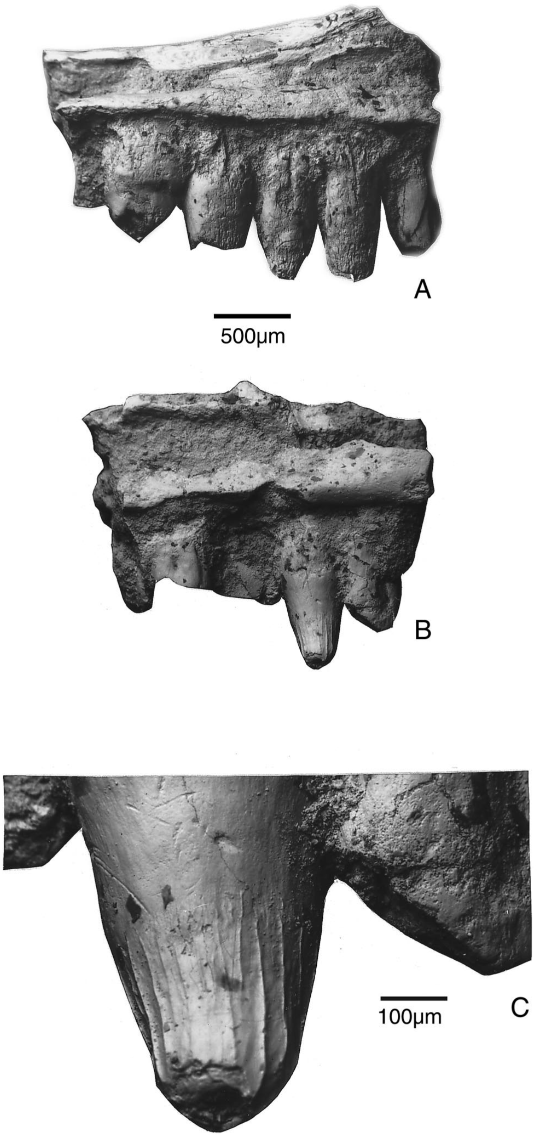

FIGURE 9. Kota Formation, pleurodont maxillary fragments. **A**, VPL/JU/KR 62, posterior orbital process of left maxilla, medial view; **B–C**, VPL/JU/KR 61, central part of ?left maxilla, **B**, medial view, **C**, enlargement of tooth tip showing striae. Scale bars as indicated.

addition, the anterior pleurodont teeth of the dentary match those of the referred maxilla (VPL/JU/KR 88) in size, shape and ultrastructure. The association is further strengthened by the fact that the dramatic reduction in tooth size through the first four positions in the maxilla VPL/JU/KR 88 mirrors the increase in tooth size in the lower dentition, and (allowing for a premaxilla) the pleurodont series appear to end abruptly at the same point in both jaws.

Acrodonty

Acrodonty has arisen three times within Lepidosauria: in Rhynchocephalia (with the pleurodont *Gephyrosaurus* as the most primitive taxon, Evans, 1988; Gauthier et al., 1988; Wu, 1994; Reynoso, 1996; Wilkinson and Benton, 1996), in Amphisbaenia (with only the trogonophids showing the condition), and within Iguania (chameleons and 'agamids', the Acrodonta of Cope, 1864, Estes et al., 1988). Most amphisbaenians, including the earliest known fossil taxa (Estes, 1983a), have pleurodont teeth and very short jaws, and this was clearly the basal condition from which trogonophids arose. The jaws of *Bharatagama* are therefore incompatible.

Rhynchocephalia (sensu Gauthier et al., 1988) comprises the pleurodont Lower Jurassic *Gephyrosaurus* (Evans, 1980) and Sphenodontia (the pleuroacrodont *Diphydontosaurus*, Whiteside 1986, the living *Sphenodon*, and all fully acrodont rhynchocephalians). Sphenodontians had a global distribution in the Late Triassic and Early Jurassic (see Evans et al., 2001, for a review), and there are two genera of crown-group sphenodontians (sensu e.g., Wu, 1994; Reynoso, 1996; Wilkinson and Benton, 1996) in the Kota deposits (Evans et al., 2001). By contrast, acrodont iguanians are first recorded from the Aptian–Albian of Asia (Nessov, 1988; Alifanov, 1993b). Traditional classifications (e.g., Romer, 1956) recognize two groups—Agamidae and Chamaeleontidae, but most recent authors (e.g., Estes et al., 1988; Schwenk, 1988; Frost and Etheridge, 1989; Macey et al., 1997) have found no support for a monophyletic Agamidae (but see Joger, 1991). The informal term agamid therefore simply denotes an acrodont iguanian that lacks the specializations of chameleons.

Although many characters of the skull and postcranial skeleton separate Sphenodontia and Acrodonta, their jaws and dentition show convergence (Robinson, 1976). Both groups are predominantly acrodont (but with demonstrably pleurodont ancestors); both have a hatchling dentition that is variably replaced anteriorly and to which mature teeth (additionals) are added posteriorly (Harrison, 1901; Cooper and Poole, 1970); both show loss or reduction of kinesis in relation to the development of precise shear; and, with the exception of the Cretaceous priscagamids (Borsuk-Bialynicka and Moody, 1984; Frost and Etheridge, 1989), both show loss or reduction of the splenial, an anteroventral extension of the angular, and a posterolateral extension of the dentary. All of these features are also found in *Bharatagama*.

The nature of the Kota microvertebrate material clearly makes a rigorous cladistic analysis impossible, but several distinctive features of the lower jaw and the anterior region of the maxilla in *Bharatagama* permit more detailed comparison.

Character Analysis

On the basis of recent studies, the Middle Jurassic lepidosauromorph *Marmoretta* (Britain; Evans, 1991) is the sister taxon of Lepidosauria and provides an outgroup for character discussion. The basal rhynchocephalian condition is best represented by *Gephyrosaurus* and the Triassic *Diphydontosaurus*, while the structure of early lepidosaurs can be extrapolated from *Gephyrosaurus*. Basal squamates remain poorly known, but the Upper Jurassic *Bavarisaurus* from Germany has emerged as a basal form in recent analyses (e.g., Evans and Barbadillo, 1998). The pleurodont iguanian sister group of Acrodonta has yet to be recognized (Frost and Etheridge, 1989). Within Acrodonta, the Cretaceous priscagamids (*Priscagama* and *Pleurodontagama*, Borsuk-Bialynicka and Moody, 1984; Borsuk-Bialynicka, 1996; *Mimeosaurus*, Gilmore, 1943; Gao and Hou, 1996; *Flaviagama*, Alifanov, 1989) are considered the sister group of all living taxa (Frost and Etheridge, 1989), while *Uromastyx* and *Leiolepis* emerge as basal members of the extant clade (Moody, 1980; Frost and Etheridge, 1989). The position of *Tinosaurus* from the early Tertiary of North America, Asia and Europe (Gilmore, 1928; Estes, 1983a; Augé and Smith, 1997) is unclear.

Tooth Implantation—The subpleurodont implantation of basal lepidosauromorphs was replaced by a shallow pleurodonty in *Marmoretta* (Evans, 1991). Basal rhynchocephalians were either pleurodont (*Gephyrosaurus*) or heterodont, with first

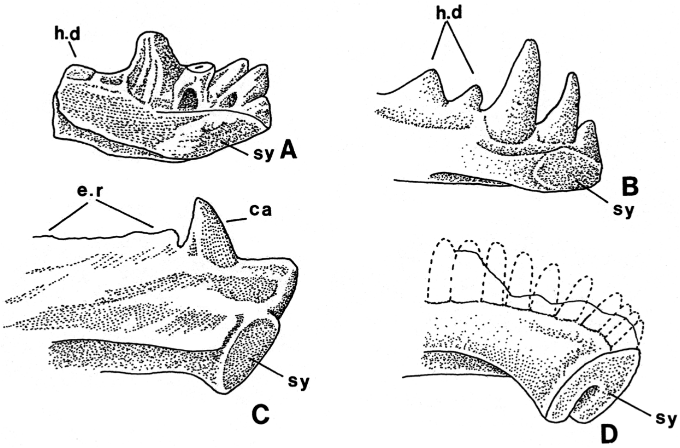

FIGURE 10. Symphysial region of lepidosaurian left dentary, medial view. **A**, *Bharatagama*, VPL/JU/KR 67. **B**, *Draco* (UCL collection). **C**, *Sphenodon*, juvenile (UCL X.809). **D**, *Gephyrosaurus* (BMNH R/UCL T.860). Not to scale.

pleurodont and then pleuroacrodont teeth (*Diphydontosaurus*, Fig. 6G, H). All remaining rhynchocephalians have a fully acrodont dentition (Fig. 6I, J). Basal squamates show a deeper pleurodont attachment, and this is particularly marked in pleurodont iguanians. Amongst acrodonts, the teeth of chameleons are usually attached to the crest of the jaw, as in sphenodontians, but in agamids, the tooth bases of mature additional teeth extend lingually to a variable degree (Augé, 1988, 1997; SEE, pers. obs.). In *Priscagama* (Fig. 6C, D), this medial extension is obvious and the posterior three to six teeth, while fully ankylosed, are essentially pleuroacrodont in implantation (Borsuk-Bialynicka and Moody, 1984). Thus priscagamids and many living agamids differ from sphenodontians in having a tooth series in which pleurodont anterior teeth are followed by small fully acrodont teeth along the jaw crest, and then by pleuroacrodont additionals. By contrast, *Diphydontosaurus* shows a smooth transition from pleurodont anteriorly to pleuroacrodont posteriorly; juvenile teeth are fully pleurodont and the most acrodont teeth are those at the back of the tooth row (Fig. 6G). *Bharatagama* shows the agamid pattern: pleurodont, acrodont, and then pleuroacrodont.

Anterior Dentary Teeth—In both *Gephyrosaurus* and *Diphydontosaurus* (Figs. 6G, 10D), more than half of the tooth row consists of small, conical pleurodont teeth. These have been lost in more crownward taxa, where at most one or two anterior hatchling teeth may be replaced by a larger successional. In contrast, living agamids usually have between 1–6 recurved pleurodont teeth that replace the anterior part of the hatchling series (Cooper and Poole, 1970). These teeth continue to be replaced well into ontogeny and one or more may be enlarged into caniniforms (Gao and Hou, 1996). Small prey is normally taken by tongue, while larger or stronger prey is seized by anterior teeth, and then shifted to the back of the tooth row (Cooper and Poole, 1970). In predominantly herbivorous taxa (e.g., *Uromastyx*), or where the tongue is specialized for capture (e.g., chameleons), the anterior pleurodont teeth are lost or reduced (Augé, 1988). In *Priscagama* (Borsuk-Bialynicka, 1996; Borsuk-Bialynicka and Moody, 1984; Fig. 6C, D), there were 3–5 anterior pleurodont teeth on the dentary, but only two in the related *Flaviagama*. The anterior symphysial series in *Bharatagama* (Fig. 10A) thus most closes resembles that of insectivorous living agamids such as *Draco* (Fig. 10B) or the priscagamids *Priscagama* and *Pleurodontagama* (Borsuk-Bialynicka, 1996).

Shape of the Posterior Additional Teeth—Although both crown-group sphenodontians and acrodont iguanians have acrodont teeth, there are differences in the shape of the additional teeth (Cooper and Poole, 1970; Robinson, 1976). In sphenodontians, the upper teeth are typically flanged while the lowers are offset or flanged, with the long axis of the tooth running from anterolateral to posteromedial, so that the anterior part of the tooth tends to cover the posterior border of the tooth in front. In 'agamids', the additional teeth are typically labiolingually compressed (Cooper and Poole, 1970). They may also be offset (Robinson, 1976), but in this case the long axis of the tooth is positioned so that it runs anteromedial to posterolateral, and the posterior edge of one tooth covers the anterior edge of the tooth behind. This difference is clear in derived agamids like *Calotes*; it is less clear in many others where the teeth are blade-like rather than offset (e.g., priscagamids).

Amongst crown-group sphenodontians, the flanges are small in basal taxa (Evans et al., 2001), becoming extensive in some more apical ones (Fraser, 1988; Fig. 6J). Where the flanges are small, they are associated with conical rather than blade-like teeth, and Reynoso (1996:215) describes sphenodontian teeth generally as triangular with a ''rounded shape in cross-section''. By contrast, the teeth of agamids are typically laterally compressed (Cooper and Poole, 1970) and either blade-like or tricuspid. They typically lack interstices in agamids (Cooper and Poole, 1970), but not chameleons. Priscagamid additionals (Fig. 6C, D) are labio-lingually compressed blades lacking any trace of either offsetting or flanges. This morphology most closely matches the additional teeth of *Bharatagama*.

Length of the Dentary and Tooth Row—As in primitive lepidosauromorphs generally, both *Gephyrosaurus* and *Diphydontosaurus* have shallow elongate jaws with many small teeth (Fig. 6G, H). Crown-group sphenodontians and squamates independently evolved a shorter, deeper jaw (Fig. 6I, J). The short tooth row of *Bharatagama* is therefore derived. Borsuk-Bialynicka (1996:fig. 5) figures a specimen of *Priscagama* with only only two large blade-like additional teeth, although further teeth are figured in the reconstruction (Fig. 6C, D). *Flaviagama* has 3–4 large additionals (Alifanov, 1989).

Tooth Replacement Patterns—The teeth of primitive lepidosauromorphs were replaced continually throughout life. *Gephryosaurus* and *Diphydontosaurus* inherited the same pattern, although there is reduced replacement in the additional series (Evans, 1985; Whiteside, 1986). In acrodont sphenodontians, only a few anterior teeth show replacement, with one or two cycles of successional teeth gradually replacing the first of the hatchling series. In acrodont iguanians, replacement generally continues in the anterior pleurodont series, presumably important if these teeth are used in seizing prey (e.g., Schwenk, 2000). The anterior replacement pattern of *Bharatagama* therefore resembles that of living acrodonts as well as the most basal rhynchocephalians, although it differs from the latter in having fewer teeth involved.

Wear Patterns—In *Marmoretta*, the conical teeth of the upper and lower jaws apparently employed a simple puncture-crush mechanism to incapacitate prey. Wear is random. Rhynchocephalians are characterized by the possession of an enlarged palatine tooth row which runs parallel, or nearly parallel, to that of the maxilla, with the dentary teeth biting upwards into the channel between the upper rows. The mechanism can be further improved by incorporating an element of anteroposterior (propalinal) shear. In *Gephyrosaurus*, this is permitted by an elongated articular surface. Thus an animal with continuous replacement, and without precise occlusion, could use its jaws more efficiently. The situation in *Diphydontosaurus* is less clear cut. It shares the long jaw, anterior pleurodont teeth, and elongated articular surface of *Gephyrosaurus* (Fig. 6G, H), but appears to have had an orthal component to the bite. Whiteside

(1986) described and figured discrete posterior wear facets, but notching the bone of the jaw rather than the teeth. Effective dorsoventral (orthal) shear requires a permanent dentition to allow wear surfaces to develop between upper and lower teeth. Within living squamates, precise dorsoventral shear occurs only in acrodonts. The lower teeth occlude inside the uppers, their lateral surfaces fitting closely against the lingual aspect of the maxillary teeth, with the gradual development of precise complementary wear surfaces (Cooper and Poole, 1970; Augé, 1997). Crown-group sphenodontians show greater variation. *Sphenodon*, *Opisthias*, and *Cynosphenodon*, among others (Reynoso, 1996) retained (or regained) propalinal shear despite the permanency of the dentition, and this is marked by horizontal wear facets on the bone of the jaw (medially and laterally). Many other crown-group sphenodontians (e.g., the Triassic *Clevosaurus*, Fraser, 1988, Fig. 6I, J), developed precise dorsoventral shear, but in association with extensive accessory flanges and a strong overlap between successive additional teeth. Strong wear facets are most obvious on the labial surface of the dentary, but wear also occurs medially because of the enlarged palatal row.

The well-defined dorsoventral wear facets preserved in *Bharatagama* (Fig. 6B) thus match those of acrodont iguanians and some derived rhynchocephalians. However, the absence of lingual wear on the dentary teeth renders it unlikely that a large palatine tooth row was present in the Kota genus.

The Symphysial Region of the Dentary—In both *Marmoretta* and *Gephyrosaurus*, the dentary symphysis is a large oval terminal disc split into two parts by the tip of the Meckelian fossa. A similar condition occurs in *Diphydontosaurus* (Fig. 6G), but most sphenodontians reduce the surface to a more vertically oriented, but still terminal, surface (Figs. 6I, 10C). The Mexican *Cynosphenodon* (Lower Cretaceous; Reynoso, 1996) is unusual in having the symphysial surface divided by the apex of the Meckelian sulcus, but the bulk of the facet lies ventral to the sulcus. Reynoso (1996) lists a broad mandibular symphysis as characteristic of crown-group sphenodontians. In basal squamates, the symphysial surface is reduced to a small anteromedial surface above the level of the Meckelian fossa. This arrangement permits compensatory movements and spreading of the jaw rami. In acrodont iguanians, however, probably in conjunction with reduced kinesis, the symphysis enlarges to give a firmer midline contact. Nonetheless, the symphysial surface remains essentially medial and is restricted to the upper margin of the Meckelian fossa. The dentary symphysis of *Bharatagama* is strong, but in its orientation (largely horizontal) and position (medial and restricted to the dorsal margin of the Meckelian fossa in mature animals), it more closely matches that of priscagamids and living acrodont lizards such as *Draco* (Fig. 10B) and *Hydrosaurus*.

Anterior Jaw Shape—A second feature of the symphysial region is its overall shape. In basal taxa (Fig. 6G, H), the dorsal and ventral margins of the dentary are almost parallel, converging gradually towards the symphysis. In acrodont sphenodontians, the distal end of the dentary typically remains deep with a nearly vertical anterior border and a deep blade of bone below the teeth on the alveolar margin (Fig. 6I). Squamates generally have a more tapering anterior dentary. In acrodonts (including priscagamids, Borsuk-Bialynicka, 1996) this region is shallow—the bases of the teeth being close to the ventral margin of the jaw (Figs. 6C, 10B). This is similar to the condition in *Bharatagama* (Fig. 10A).

The Opening of the Inferior Alveolar Canal—The inferior alveolar canal carries the mandibular nerve and blood vessels into the dentary. Primitively, the entry foramen lies within the Meckelian fossa a short way anterior to the level of the last tooth position. This location is maintained in most squamates, including the small sample of acrodonts examined (the foramen is frequently hidden by accessory jaw bones), but in sphenodontians, the entry foramen often lies further back. In this respect, *Bharatagama* resembles sphenodontians.

The Coronoid Process of the Dentary—The coronoid region provides an insertion point for the bulk of the external adductor musculature. In *Marmoretta*, *Gephyrosaurus*, and *Diphydontosaurus* (Fig. 6G, H), the coronoid bone is shallow and sits against a slight expansion of the posterodorsal margin of the dentary. Dorsal extension of the coronoid bone occured independently in sphenodontians and squamates, presumably in association with other factors such as jaw shortening. In derived sphenodontians, the coronoid bone is buttressed labially by an expansion of the dentary (the coronoid process of the dentary, Fig. 6J). In squamates, dentary expansion rarely occurs, but acrodont iguanians are an exception. Acrodonta show a tendency for the dentary to extend onto the labial surface of the coronoid (Frost and Etheridge, 1989), forming a distinct coronoid process in some taxa (e.g., *Uromastyx*, *Hydrosaurus*, *Amphibolurus*, SEE, pers. obs.; the Eocene *Pseudotinosaurus*, Alifanov, 1993c; and the Oligocene *Quercygama*, Augé and Smith, 1997). Thus although the coronoid process of *Bharatagama* most closely resembles that of a sphenodontian, the character is equivocal.

Presence or Absence of a Splenial—In primitive reptiles, the splenial is a thin lamina of bone that covers the medial side of the mandible from the symphysis to the coronoid. It was lost early in rhynchocephalian history (already absent in *Gephyrosaurus*), but was retained in the ancestors of squamates, although it rarely extends to the tip of the jaw. The splenial has been lost or strongly reduced in living acrodonts and in some pleurodont iguanians (polychrotines, some tropidurines, Etheridge and De Queiroz, 1988). The elongated splenial of priscagamids may therefore represent a primitive retention or a secondary expansion (Fig. 6C, D). The reduction/absence of a splenial in *Bharatagama* is equivocal. It would be consistent with either a rhynchocephalian or a non-priscagamid acrodont.

The Structure of the Angular—The angular of primitive lepidosauromorphs makes a significant contribution to the posterolateral margin of the mandible and then runs forward along the ventromedial border of the Meckelian fossa. The rhynchocephalian angular is generally somewhat shallower posteriorly but also runs forward below the Meckelian fossa to a point roughly half way along the tooth row (Fig. 6G). Acrodont iguanians, like *Bharatagama*, show a similar morphology, but the angular tends to be longer (Frost and Etheridge, 1989), and can be fused to neighbouring bones. In *Uromastyx*, for example, it extends forward towards the anterior end of the jaw forming almost the entire ventral margin of the Meckelian fossa; in the adults of both *Uromastyx* and *Bharatagama*, it is fused to the dentary.

Premaxillary–maxillary Junction—In *Marmoretta*, the tapering anterior process of the maxilla fits into a deep socket on the lateral face of a relatively broad, paired, premaxilla. In lepidosaurs, the maxilla usually has a shorter tapering anterior process that either abuts the lateral margin of the premaxilla (all known rhynchocephalians, Fig. 7E) or clasps its palatal shelf between small medial and lateral processes (most squamates). In iguanians generally, the premaxilla is braced posteriorly by a medial or dorsomedial maxillary shelf. In acrodonts, this is further modified. A dorsally extended premaxillary process abuts the lateral face of the premaxilla, while the medial shelf extends to meet the opposite maxilla in the posterior midline. In derived taxa, this medial shelf has a further dorsal expansion (dorsomedial flange; Fig. 7C, D) bracing the nasal process of the premaxilla from behind. This arrangement is considered diagnostic of acrodont iguanians (e.g., Frost and Etheridge, 1989; Gao and Hou, 1996). In association with the strong maxillary shelves, the acrodont premaxilla is a narrow median bone with a reduced tooth count (1–5; Cooper and Poole, 1970). Chameleons show an exaggerated condition in which the maxillae have a particularly strong median contact and the premaxilla is little more than a narrow median splint.

The anterior maxillary region of *Bharatagama* matches that of acrodonts in bearing a narrow premaxillary facet along the dorsomedial margin of the premaxillary process and in the possession of a medial shelf that extended behind the premaxilla. The main difference between *Bharatagama* and extant agamids is that the medial shelf is smaller and lacks the dorsal extension (Fig. 7A, B). If our interpretation of anterior tooth numbers is correct, then, as in 'agamids', the premaxillary tooth count (and thus the bone itself) was also reduced.

Conclusion—The jaws of *Bharatagama* show a mosaic of character states. The enlarged coronoid process of the dentary is predominantly (but not exclusively) a sphenodontian character, as is the posterior position of the inferior alveolar foramen. However, these traits are in conflict with a larger character set, most notably: the shape and morphology of the symphysial region of the dentary and its pleurodont teeth; the shape and pleuroacrodont implantation of the additional teeth (following a fully acrodont juvenile series); the absence of wear on the lingual surfaces of the dentary teeth; the length and fusion of the angular; and the morphology of the anterior maxilla and its relationship to the premaxilla. No rhynchocephalian shows this combination of character states. Allowing for independent development of the coronoid process of the dentary in *Bharatagama* (as in several living and fossil agamids), there are no character conflicts between *Bharatagama* and acrodont iguanians. *Bharatagama* meets the diagnosis of Acrodonta given by Frost and Etheridge (1989) and Gao and Hou (1996) (acrodont teeth, a medial maxillary shelf), and shares details of the dental sequence, the symphysial region, and precise occlusion. While it remains possible that *Bharatagama* represents an unknown reptilian lineage convergent on acrodont iguanians, attribution to Acrodonta is more parsimonious on current evidence.

Priscagamids form a monophyletic group (Borsuk-Bialynicka and Moody, 1984; Frost and Etheridge, 1989; Gao and Hou, 1996) characterized by a large coronoid labial flange that covers the posterolateral surface of the dentary. However, the presence of a labial flange in many pleurodont iguanians (Etheridge and De Queiroz, 1988) raises the possibility that the priscagamid condition is primitive. Priscagamids form the sister group of living acrodonts (Frost and Etheridge, 1989) which form a second monophyletic group characterized by loss or reduction of the splenial (large in priscagamids), extension of the dentary up the labial side of the coronoid (absent in priscagamids), and the tendency towards anterior elongation of the angular (short in priscagamids). The splenial character is discussed above and its polarity is problematic. Nonetheless, *Bharatagama* shares these characters of living acrodonts and lacks the priscagamid labial coronoid flange. It cannot therefore represent a lineage ancestral to priscagamids. Consequently, the low number, blade-like shape, and pleuroacrodont implantation of the additional teeth in both *Bharatagama* and priscagamids (Borsuk-Bialynicka and Moody, 1984; Borsuk-Bialynicka, 1996) are probably plesiomorphic within Acrodonta.

FIGURE 11. Map of Middle Jurassic continental positions based on Golonka et al. (1996) and Smith et al. (1994), and showing localities yielding early acrodont iguanians. ***1**, Kota Formation, Andhra Pradesh, India, ?Toarcian; ***2**, Kazakhstan, Coniacian (Nessov, 1988); ***3**, Khobur, Mongolia, Aptian–Albian (Alifanov, 1993b). Aptian–Albian localities in Central Asia (Uzbekistan) have also yielded indeterminate iguanian remains (Gao and Nessov, 1998).

IGUANIAN ORIGINS AND BIOGEOGRAPHY

Since rhynchocephalians and squamates are sister groups, the presence of crown-group sphenodontians in deposits of Late Triassic (Carnian) age (e.g., Fraser and Benton, 1989; Sues and Olsen, 1990), provides evidence for the Triassic origin and diversification of squamates. However, with the exception of the new Kota material, the earliest currently known lizards are from the Middle Jurassic of Britain (Bathonian, c. 165 Ma: Evans, 1993, 1994a, 1998a). Since these assemblages contain both scincomorph and derived anguimorph lizards (Evans 1994a, 1998a), they support an early scleroglossan diversification and push the estimated timing of the iguanian-scleroglossan dichotomy back into the Early Jurassic or even Late Triassic. Nonetheless, while scleroglossan lizards have been recorded from a range of Jurassic localities in Laurasia (North America, Britain, France, Germany, Kazakhstan, China, Evans, 1998b), iguanians have never been found. The French Jurassic *Euposaurus*, sometimes cited as an acrodont iguanian (e.g., Estes, 1983a), is actually an indeterminate pleurodont lizard to which two juvenile sphenodontian skeletons were attributed (Evans, 1994b), while the supposed iguanian *Fulengia* (Lower Jurassic, China: Carroll and Galton, 1977), is a juvenile prosauropod dinosaur (Evans and Milner, 1989). Since current phylogenetic hypotheses predict the occurrence of iguanians in the Jurassic, their absence from known localities suggests an ecological or biogeographic bias.

Twenty years ago, the apparent absence of pleurodont iguanians in the Mesozoic of Laurasia led Estes (1983a, b) to suggest that pleurodont iguanians (and thus Iguania as a whole) had a Gondwanan origin. The hypothesis was supported by the predominantly Gondwanan distribution of living taxa, and a single Mesozoic record from the Upper Cretaceous of Brazil (*Pristiguana*, Estes and Price, 1973). Estes proposed that the basal squamate stock had been split into a northern scleroglossan clade and a southern iguanian one by the break-up of Pangea. Part of the ancestral iguanian stock subsequently became separated by some ecological or physical barrier in northern or northeastern Gondwana, developed acrodonty, and entered northern continents during the later Mesozoic (to give rise to the Asian priscagamids). Pleurodont iguanians followed later in the Tertiary.

More recent discoveries have compromised parts of Estes' hypothesis. The discovery of scincomorph lizards in the Upper Jurassic of Africa (Zils et al., 1995) provides evidence that iguanians and scleroglossans diverged prior to the break-up of Pangea, not as a result of vicariance. In addition, the Mesozoic iguanian record of Laurasia has improved. Aptian–Albian deposits in Central Asia and Mongolia have yielded indeterminate iguanians (Gao and Nessov, 1998) and priscagamids (Nessov, 1988; Alifanov, 1993b), while a diversity of both pleurodont and acrodont iguanian taxa have been recovered from the Campanian and Maastrichtian of Mongolia (Borsuk-Bialynicka and Moody, 1984; Alifanov, 1989; Borsuk-Bialynicka and Alifanov, 1991), China (Gao and Hou, 1996), Canada (Gao and Fox, 1996) and Europe (Astibia et al., 1991). These finds have led to the conclusion that iguanians originated in Laurasia, with Asia as the most likely source (e.g., Greer, 1989; Alifanov, 1993a; Gao and Hou, 1996).

However, just as Estes' (1983a, b) biogeographic hypothesis rested heavily on the absence of a Mesozoic Laurasian record for pleurodont iguanians, so recent theories are underpinned by the paucity of the Gondwanan record. If correctly interpreted, the Kota lizard material begins to fill this gap. India was part of Gondwana until the Early Cretaceous (Fig. 11), breaking away from the Antarctica-Australia block some 120 Ma ago (Early Aptian; Powell, 1979). On current age estimates, the Kota lizards are amongst the earliest known anywhere in the world, and predate the earliest previously recorded iguanian by some 80 Ma. The presence of acrodont iguanians in India at this time is consistent with a recent molecular study (Macey et al., 2000) which predicted that basal acrodonts existed in Gondwana prior to its fragmentation. Nonetheless, this does not preclude the possibility that iguanians generally, or acrodonts specifically, originated elsewhere in Pangea, with subsequent dispersal into southern regions during the Late Triassic or Early Jurassic. A comprehensive squamate record is needed from all continents before this issue can be resolved.

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