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Authors: DATTA, P. M., and RAY, SANGHAMITRA

Source: Journal of Vertebrate Paleontology, 26(4) : 795-800

Published By: The Society of Vertebrate Paleontology

URL: https://doi.org/10.1671/0272-4634(2006)26[795:ELFTLT]2.0.CO;2

Journal of Vertebrate Paleontology 26(4):795–800, December 2006

RAPID COMMUNICATION

EARLIEST LIZARD FROM THE LATE TRIASSIC (CARNIAN) OF INDIA

P. M. DATTA[1] and SANGHAMITRA RAY[2]
[1]Palaeontology Division, Geological Survey of India, Eastern Region, Kolkata 700091, India;
[2]Department of Geology & Geophysics, Indian Institute of Technology, Kharagpur 721302, India, sray@gg.iitkgp.ernet.in

Currently there are no confirmed reports of lizards before Jurassic (Evans, 2003). The earliest record of true lizards is from the Early-Middle Jurassic Kota Formation of the Pranhita-Godavai basin, India (Evans et al., 2002), although fossil records improved significantly from the Late Jurassic onward (Evans, 1993, 2003; Nessov, 1988). Here we report the discovery of a new lizard taxon from the Late Triassic Tiki Formation of the South Rewa basin, India (Fig. 1A). The material comprises a nearly complete mandibular ramus bearing pleurodont and acrodont dentition. Comparison with other extinct and living taxa suggests that this belongs to a new acrodont iguanian *Tikiguania estesi*, and strengthens the view that iguanians had begun to diversify before the break up of Pangaea.

The Tiki Formation, underlain and overlain by the Pali and Parsora Formations, respectively (Datta et al., 2004), is essentially a mud-dominated unit (Fig. 1B) and comprises subhorizontal and horizontal beds of red clay with palaeosol profiles, thinly laminated and/or cross-stratified sandstone, greenish grey siltstone, and sand-clay heterolithic units. The mud-dominated succession of the Tiki Formation has yielded megavertebrates such as a metoposaurid temnospondyl *Buettneria* (Sengupta, 2002), a phytosaurid *Parasuchus* (Chatterjee, 1978), a rauisuchid *Tikisuchus* (Chatterjee and Mazumdar, 1987), and a rhynchosaurid *Hyperodapedon* (Benton, 1983). In addition, microvertebrates, such as a dromatheriid nonmammalian cynodont, *Rewaconodon* (Datta et al., 2004), a morganucodontid mammal *Gondwanodon* (Datta and Das, 1996), and the earliest mammal with transversely expanded upper molar *Tikitherium* (Datta, 2005) were also known from the Tiki Formation. Based on its faunal content, the Tiki Formation has been correlated with the lower member of the Maleri Formation of the Pranhita-Godavari basin in southern India (Lucas, 1998; Datta, 2004) and the Camp Springs member of the Dockum Formation, USA (Datta et al., 2004), and was assigned a Late Triassic (Carnian) age (Benton, 1994; Datta, 2004; Datta et al., 2004).

The fossil material was collected from the calcareous, red mudstone unit in the lower part of the Tiki Formation, 4 km southwest of Tiki village in the South Rewa Gondwana basin, Madhya Pradesh, India (Fig. 1A, B). This material is not a lone occurrence but has occurred as part of the above mentioned microvertebrate assemblage. All the microvertebrate and macrovertebrate assemblages show calcite cementation and a thin coating of hematite. This is even prevalent as encrustations found at the bases of the teeth. The methodology for collection of these microfossils involved excavation of about 5 metric tons of rock material from a depth of approximately 1.5 m after removing the surface material. The excavated clay material was gradually removed by washing in water and the resulting residues were screened, dried, and manually sorted under a stereoscopic microscope.

SYSTEMATIC PALEONTOLOGY

LEPIDOSAURIA Haeckel, 1866
SQUAMATA Oppel, 1811
IGUANIA Romer, 1956
ACRODONTA Cope, 1864

TIKIGUANIA ESTESI, gen. et sp. nov.
(Fig. 2)

Holotype—GSI type Pal/CHQ-010, a nearly complete left mandibular ramus.

Etymology—The generic name refers to the Tiki Formation and the iguanian squamates; the specific epithet honours R. Estes, who contributed significantly towards understanding squamate phylogeny and biogeography.

Repository—Geological Survey of India Central Palaeontological Repository Unit, Kolkata, India.

Horizon and Locality—Late Triassic (Carnian) Tiki Formation of the South Rewa Gondwana basin (Fig. 1A); the locality is near the village of Tiki (23º 64.15’ N, 81° 22’ E), Shadol district, Madhya Pradesh, India.

Diagnosis—Small (lower jaw length *c*.17 mm) acrodont iguanian characterized by the following character states: long mandibular tooth row, three anterior pleurodont teeth that show elliptical wear facets and increase in size posteriorly, jaw underlying hatchling dentition slender, shallow indented Meckelian groove, acrodont and pleuroacrodont lateral dentition comprising 14 teeth that increase in size posteriorly, individual tooth labiolingually flattened, tricuspid-like, deep U-shaped labial wear facets, splenial absent, angular slender, long, and fused to the lower margin of the Meckelian groove, coronoid process absent.

Description—GSI type Pal/CHQ-010 is a nearly complete small (*c*. 17 mm) and slender left mandibular ramus (Fig. 2). The major bone, dentary bears a long tooth row and is composed of four distinct regions, namely an anterior symphyseal region followed by a hatchling/juvenile acrodont dentition, a lateral acrodont-pleuroacrodont dentition and a postdental region, which is partially broken posteriorly (Fig. 2A–E). The dentary is tapering anteriorly and bears a small, medial symphyseal region. The dentition is heterodont in which the first three anterior teeth near the symphyseal region are cylindroconical (Edmund, 1960), and pleurodont with the teeth ankylosed to the medial side of the high labial wall (Fig. 2F, G). These anterior teeth bears small elliptical wear facets and increase in size posteriorly (Fig. 2G). Behind these teeth, is a short diastema followed by four small acrodont hatchling teeth, which are triangular with broad bases and fused to the crest of the jaw (Fig. 2F). The ramus below the hatchling dentition remains shallow but rod-like and results in the near closure of the Meckelian groove. The rest of the dorsal surface of the dentary is composed of a long tooth row comprising three mature acrodont teeth followed by seven pleuroacrodont teeth (Fig. 2D). The former teeth are fully embedded on the dentary, whereas in the latter, the bases of the teeth are extended lingually to varying degrees. Individual tooth is triangular, tricuspid-like and labiolingually compressed. Deep U-shaped wear facets are present on the labial surface of the teeth (Fig. 2H) and also on the lateral dentary surface, suggesting that there was precise dental orthal occlusion between the lower and upper jaw teeth. In contrast, the lingual surfaces of all the teeth are smooth and unworn. Although the prominent labial wear facets suggest that the mandibular ramus under study is that of an adult animal, the presence of a pleurodont tooth at the posterior end (Fig. 2I) shows that GSI type Pal/CHQ-010 was possibly a sub-adult as most iguanians ontogenetically increase the number of teeth by adding new teeth at the posterior end of the tooth row (Edmund, 1960). These teeth are pleurodont, until they reach full size and are then ankylosed (Zaher and Rieppel, 1999). The long axis of each tooth base is aligned with that of the mandible, and the tooth bases are in contact without any interstices.

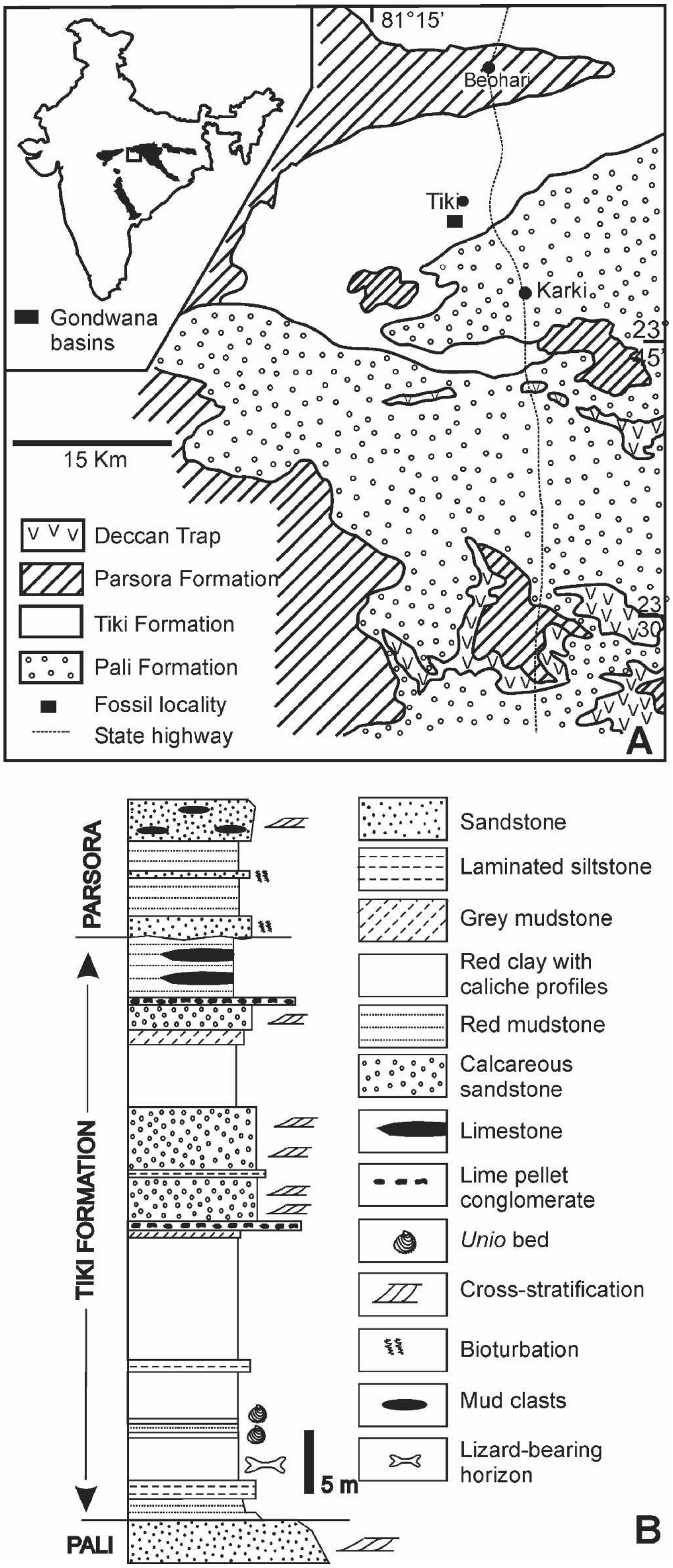

FIGURE 1. **A**, Geological map of the study area showing the fossil locality; **B**, generalized lithostratigraphic log showing the fossil horizon (modified from Datta et al., 2004).

Anteromedially the splenial is completely absent. The Meckelian groove, although open, is a shallow, narrow indentation bordered dorsally by the subdental ridge. Posteromedially the subdental ridge widens and the Meckelian fossa is visible. The latter is bordered ventrally by a narrow elongate angular. The coronoid process is absent in the postdental region. Posteriorly the mandibular ramus is broken and posterior extension of the postdental region is not ascertained.

DISCUSSION

All lepidosaurs (rhynchocephalians and squamates) show one of two kinds of tooth implantation (either pleurodonty and/or acrodonty) and not thecodonty (sensu Zaher and Rieppel, 1999), hence suggesting that *Tikiguania* is definitely a lepidosaur. Evans and colleagues (2002) have shown that acrodonty has arisen three times within Lepidosauria: in Rhynchocephalia (Sphenodontia), and in Squamata (in Amphisbaenia and in Iguania [Acrodonta]). Because most basal amphisbaenians have short jaws and pleurodont teeth (Estes, 1983a), this contrasts with findings in *Tikiguania*, which then cannot be considered as an amphisbaenian. However, *Tikiguania* shows certain features that are present in the jaws and dentition of both Rhynchocephalia and Acrodonta (Estes, 1983a; Evans et al., 2002), which necessitates a thorough comparison of *Tikiguania* with those taxa based on the characters noted by Evans and colleagues (2002). These are discussed subsequently.

Anterior Jaw Shape

In the basal rhynchocephalians such as the pleurodont *Gephyrosaurus* (Evans, 1980, 1985), and the pleuroacrodont *Diphydontosaurus* (Whiteside, 1986; Fig. 3A–D), the dorsal and ventral margins of the lower jaw are almost parallel and converge gradually toward the symphysis. In the more derived forms such as *Clevosaurus* (Fraser, 1988; Säilä, 2005; Fig. 3E, F) and *Sphenodon* (Robinson, 1976) the anterior end is deep and robust, and have a nearly vertical border (Evans et al., 2002). The squamates on the other hand generally have an anteriorly tapering anterior dentary. In the forms such as *Bharatagama* (Evans et al., 2002), *Priscagama* (Borsuk-Bialynicka and Moody, 1984), *Tinosaurus* (Estes, 1983a) and *Uromastyx* (Robinson, 1976), the anterior end of the dentary is shallow with the bases of the teeth close to the ventral margin (Fig. 3G–N). This latter type of jaw morphology is evident in *Tikiguania* (Fig. 3O–P).

Symphyseal Region

The symphyseal region of the dentary in the basal rhynchocephalians *Gephyrosaurus* (Fig. 3A, B) and *Diphydontosaurus* (Fig. 3C, D) is oval in shape and possess a median notch. In the squamates, especially in the acrodont iguanians such a notch is absent, and the symphyseal region is medially placed and restricted to the upper margin of the Meckelian fossa (Evans et al.,

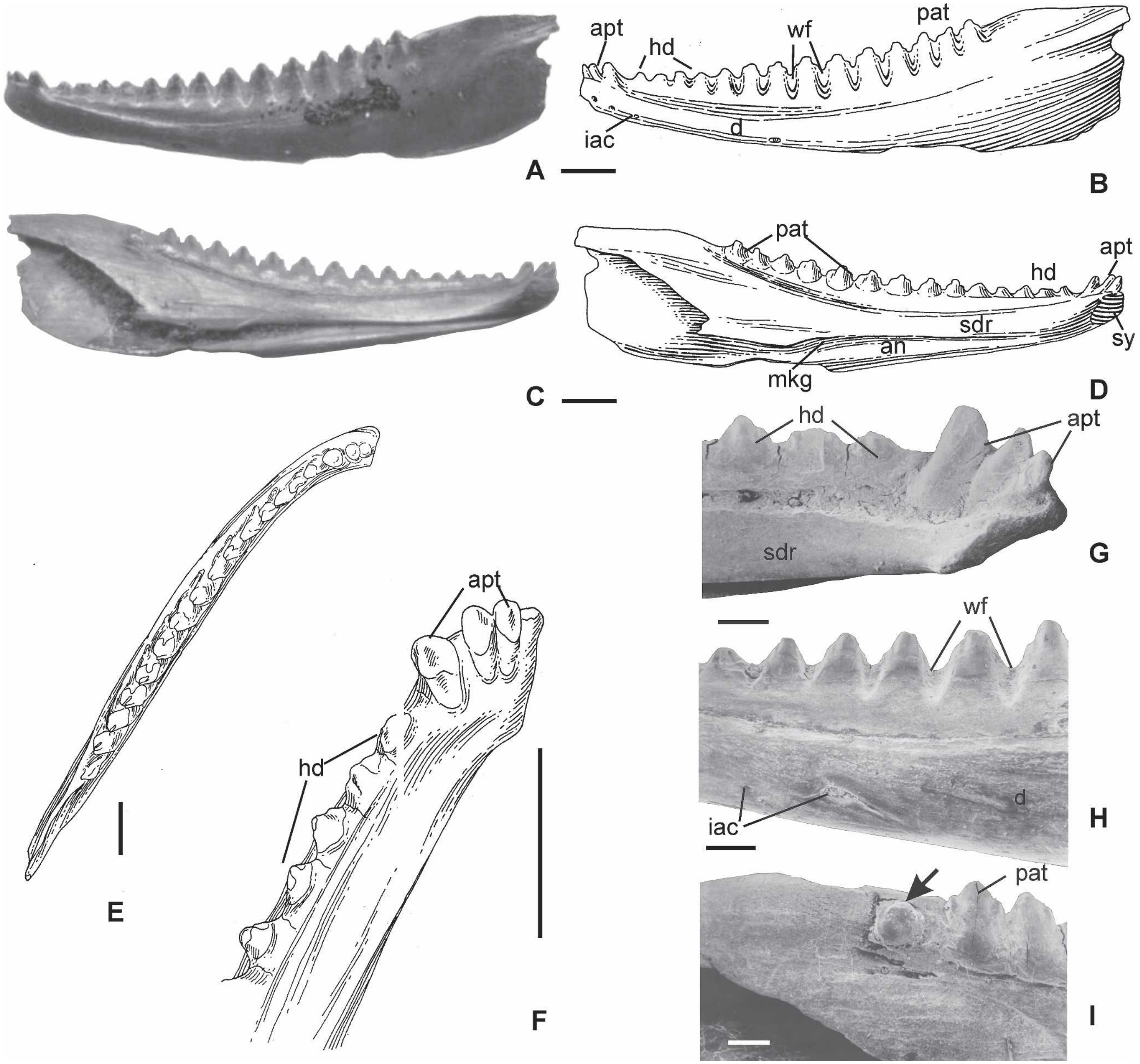

FIGURE 2. *Tikiguania estesi*, GSI type Pal/CHQ-010, holotype. Nearly complete left mandibular ramus in lateral (**A**, **B**), medial (**C**, **D**), and occlusal (**E**) views; anterior pleurodont teeth followed posteriorly by a gap and hatchling acrodont teeth at a higher magnification in occlusal (**F**) and medial (**G**) views; **H**, prominent wear facets on the labial surface of the teeth extending onto the lateral surface of the dentary; **I**, new pleurodont tooth (arrow) present distal to the mature pleuroacrodont teeth at the posterior end of tooth row. **Abbreviations**: **an**, angular; **apt**, anterior pleurodont teeth; **d**, dentary; **hd**, hatchling dentition; **iac**, inferior alveolar canal; **pat**, pleuroacrodont teeth; **mkg**, Meckelian groove; **sdr**, subdental ridge; **sy**, symphyseal region; **wf**, wear facet. Scale bars equal 2 mm (**A**–**F**) and 400 μm (**G**–**I**).

2002). *Tikiguania* has a small medial symphyseal region, which matches that of *Bharatagama* and extant acrodont lizards (Evans et al., 2002).

Tooth Implantation

Basal rhynchocephalians have pleurodont (Fig. 3A, B) and pleuroacrodont dentition, whereas the derived forms have fully acrodont dentition. Although squamates have relatively deeper pleurodont attachment, the acrodont dentition varies within this group. The chameleons have teeth attached to the crest of the jaw as in the sphenodontians. In agamids the tooth bases of mature additional teeth extend lingually to a varying degree and result in pleuroacrodont dentition (Evans et al., 2002). As such, cladistic analysis had questioned the monophyly of the Iguanidae and Agamidae but had recognized that of the Acrodonta as a whole (Frost and Etheridge, 1989; Evans, 2003), which encompasses Chameleonidae and Agamidae. The informal term 'agamid' therefore simply denotes an acrodont iguanian that lacks the specializations of chameleons (Evans et al., 2002). As in the 'agamids,' *Tikiguania* has an arrangement of pleurodont-acrodont-pleuroacrodont dentition where the anterior most

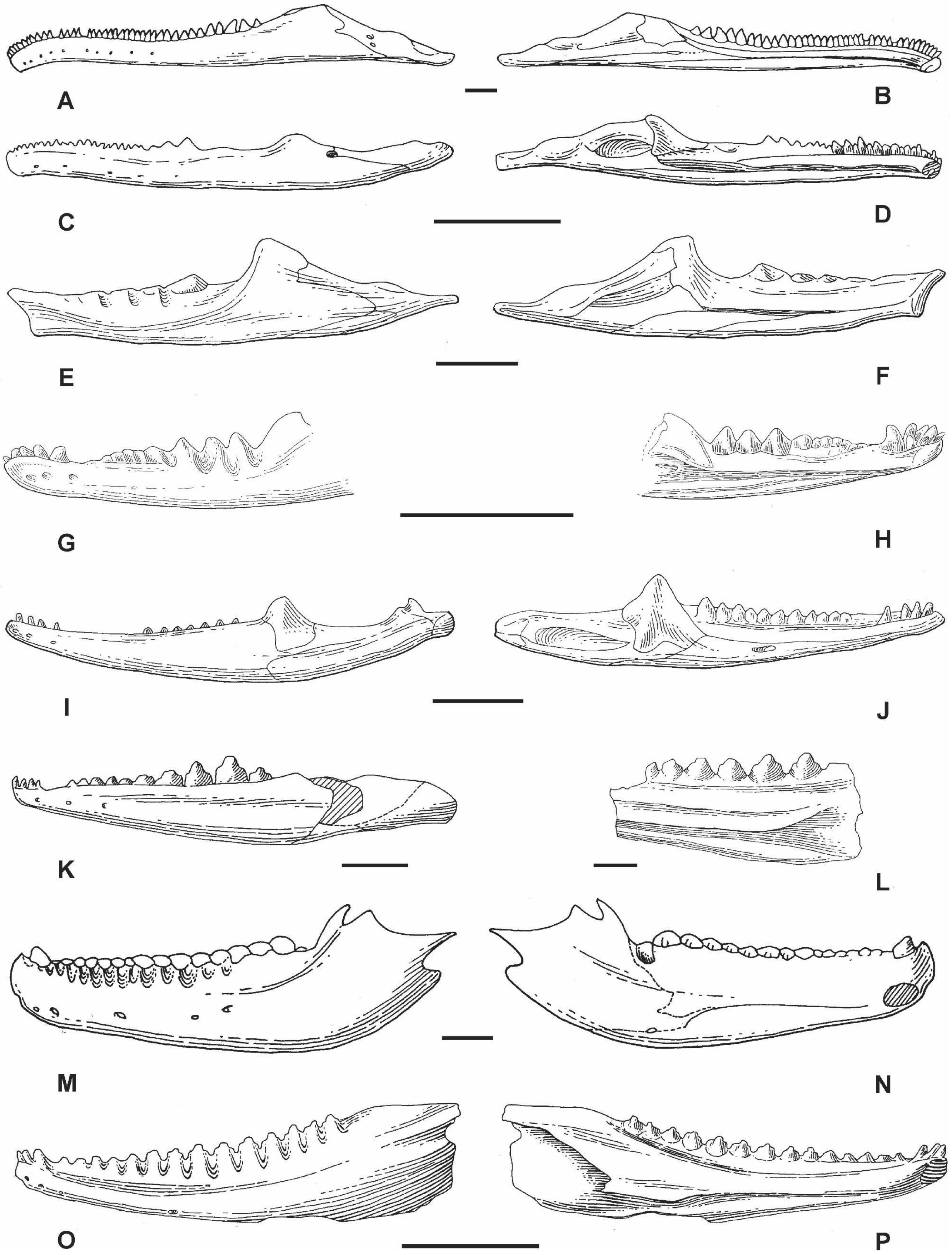

FIGURE 3. Lower jaws of several rhynchocephalians and acrodont iguanians brought to the same length for comparative purpose. **A**, **B**, *Gephyrosaurus* in lateral (**A**) and medial (**B**) views (after Evans, 1980); **C**, **D**, *Diphydontosaurus* in lateral (**C**) and medial (**D**) views (after Evans et al., 2002); **E**, **F**, *Clevosaurus* in lateral (**E**) and medial (**F**) views (after Fraser, 1988); **G**, **H**, *Bharatagama* in lateral (**G**) and medial (**H**) views (after Evans et al., 2002); **I**, **J**, *Priscagama* in lateral (**I**) and medial (**J**) views (after Evans et al., 2002); **K**, *Tinosaurus doumuensis* in lateral view; **L**, *Tinosaurus stenodon* in medial view (after Estes, 1983a); **M**, **N**, *Uromastyx* in lateral (**M**) and medial (**N**) views (after Robinson, 1976; reversed for comparison); **O**, **P**, *Tikiguania* in lateral (**O**) and medial (**P**) views. Scale bars equal 3 mm (**A**–**N**) and 0.5 mm (**O**, **P**).

teeth are pleurodont followed by hatchling acrodont teeth and posteriorly placed pleuroacrodont additional teeth.

Length of Tooth Row

In contrast to the basal rhynchocephalians, the more derived sphenodontians and squamates have a short and robust jaw (Evans, 2003) with a short tooth row (Fig. 3E–H). Thus the long tooth row with additional 10 lateral acrodont-pleuroacrodont teeth (lapt) of *Tikiguania* is a primitive character, and contrasts with the short tooth row of *Bharatagama* (lapt = 3, Evans et al., 2002) and *Priscagama* (lapt = 2–4, Evans, 2003), suggesting that *Tikiguania* is possibly more basal compared to the latter forms.

Anterior Dentary Teeth

In the basal rhynchocephalians the tooth row consists of numerous small, conical pleurodont teeth, which are lost in more crown-ward taxa such as *Clevosaurus* (Evans et al., 2002) and *Sphenodon*. In *Bharatagama* (Fig. 3G, H) and *Priscagama* (Fig. 3I, J), the number of anterior pleurodont teeth (apt) is five and three–five, respectively (Evans et al., 2002), whereas in living agamids it may vary between zero and six. In *Tikiguania*, this number is three and is well within the range of the agamids.

Shape of the Posterior Additional Teeth

The individual additional tooth of *Tikiguania* is labiolingually compressed, triangular, lack interstices and are tricuspid-like. These bear similarity with that of the Eocene agamid *Tinosaurus* (Fig. 3K, L) and contrasts with that of the sphenodontians. In these latter taxa, the lower jaw teeth are flanged and offset with the long axis of the tooth running from anterolateral to posteromedial (Evans et al., 2002).

Wear Patterns

Tikiguania has distinct U-shaped labial wear facets that extend into the lateral surface of the dentary, though there are no lingual wear facets (Fig. 3O, P). *Tikiguania* thus bears similarity with *Bharatagama* (Fig. 3G, H), which suggests that possibly a long palatine tooth row was not present (Evans et al., 2002) in these two genera. However, presence of distinct labial wear facets suggests a precise dorsoventral (orthal) occlusion and a permanent dentition that allowed wear facets to develop between the upper and lower jaw teeth. Within living squamates such precise dorsoventral shear occurs only in the acrodonts (Evans et al., 2002) that results in similar wear facets (Fig. 3M, N). In contrast, *Clevosaurus* (Fig. 3E, F) and other crown group sphenodontians bear strong wear facets both on the lateral and medial surface of the dentary. Hence, the wear facets of *Tikiguania* are more similar to those of the acrodont iguanians than the sphenodontians.

Coronoid Process

Tikiguania is distinctive from the spehnodontians (Fig. 3A–F) and acrodont iguanians such as *Bharatagama* (Fig. 3G, H), *Priscagama* (Fig. 3I, J), and *Uromastyx* (Fig. 3M, N) because it does not have a coronoid process. Evans and colleagues (2002) suggested that the dorsal extension of the coronoid process occurred independently in the sphenodontians and squamates, and is possibly related with shortening of the jaw.

Splenial

This bone usually present on the anteromedial surface of the lower jaw of the reptiles is absent in the rhynchocephalians, and is either reduced or absent in the living acrodonts, in some pleurodont iguanians, and in *Bharatagama* (Evans et al., 2002). However, an enlarged splenial is present in *Priscagama*. The absence of splenial in *Tikiguania* (Fig. 3O, P) is found to be similar to the rhynchocephalians and non-priscagamid acrodonts.

It may be concluded from the discussion that *Tikiguania* shares more characters with the acrodont iguanians than with the rhynchocephalians. These include a tapering anterior dentary, a medial symphyseal region, a strongly heterodont dentition in which the first three teeth are pleurodont, and are followed by acrodont and pleuroacrodont dentition, predominance of orthal occlusion as suggested by the labial wear facets, and absence of the splenial. In addition, *Tikiguania* is characterized by an open Meckelian groove, and a long, anteroventrally extended angular. Hence, *Tikiguania* pertains to the acrodont iguanians (Estes, 1983a; Evans et al., 2002), and was an agamid. However, *Tikiguania* is distinctive from other basal acrodont iguanians in having a long tooth row, reduced number of anterior pleurodont teeth, absence of a coronoid process and tricuspid-like lateral additional teeth. All these features hence justify the presence of a new genus and species, *Tikiguania estesi*.

Estes (1983b) suggested that there was an early Pangaean basal squamate assemblage that eventually evolved into scleroglossans of the northern continents and iguanians of the southern continents with the breakup of Pangaea during the Jurassic. Subsequent discovery of a series of Cretaceous iguanians from central Asia had led to an alternative hypothesis, which suggested a Laurasian ancestry for the iguanians (Alifanov, 1989; Gao and Nessov, 1998). Recent recovery of iguanians from the Early-Middle Jurassic sediments of India by Evans and colleagues (2002) has seriously questioned this alternative hypothesis and corroborated a molecular study that suggested that basal acrodonts were present in Gondwana before its fragmentation (Macey et al., 1997). This is accentuated by the current discovery of the Late Triassic (Carnian) iguanian assemblage from the Tiki Formation of India.

ACKNOWLEDGMENTS

We thank the Director-General, Geological Survey of India for giving permission to work on the material. The encouragement given by T. Lahiri, Director, Paleontology Division, Geological Survey of India, Kolkata is gratefully acknowledged. We thank S Evans, Dept. of Anatomy & Development Biology, University College London, London, for help with reprints, and discussions. We also thank the reviewers, M. Caldwell and S. Evans for constructive criticism. The Geological Survey of India and Indian Institute of Technology, Kharagpur are acknowledged for financial support and infrastructural facilities.

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Submitted 1 June 2005; accepted 24 June 2006.