Palaeontologia Electronica
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AGAMID LIZARDS FROM THE EARLY EOCENE OF WESTERN INDIA: OLDEST CENOZOIC LIZARDS FROM SOUTH ASIA

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ABSTRACT

The discovery of agamid lizards from the Lower Eocene (ca. 53 Ma) deposits of Vastan Lignite Mine, western India, is reported, based on a number of dentaries and one maxilla. There are at least two distinct sets of dentary bones with varying morphologies, indicating the presence of two different taxa, *Vastanagama susani* gen. et sp. nov. and *Tinosaurus indicus* sp. nov. The new finds represent the oldest known occurrence of agamid lizards in the Cenozoic of South Asia. Though tricuspid, the teeth on the dentaries and maxilla of *V. susani* gen. et sp. nov. and *T. indicus* sp. nov. appear more closely related to *Tikiguania estesi*, a Late Triassic taxon from India, than to the various species of *Tinosaurus* known from the Paleogene of North America, Europe and Asia. Differences include the development of lateral cuspules on the posterior teeth and the presence of a broad, flat or convex platform-like subdental ridge on the dentaries of *V. susani* gen. et sp. nov. The significance of these fossils in the context of 'Out-of-India' and 'In-to-India' paleobiogeographic hypotheses is discussed.

KEY WORDS: Agamid, lizard, Cambay shale, Early Eocene, new species, biogeography

INTRODUCTION

In the Indian subcontinent, early Tertiary continental vertebrates have long been known from the upper part of the Subathu Formation (early Middle Eocene, ca. 47 Ma) of the Kalakot area in the state of Jammu and Kashmir, and from its type section near Subathu, Himachal Pradesh (Kumar 2000 and references therein); from the early Middle Eocene Kuldana Formation of northern Pakistan (Thewissen et al. 2001), and from the Lower Eocene coal-bearing Ghazij Formation of Baluchistan, western Pakistan (Gingerich et al. 1997, 1998, 2001). More recently, continental vertebrate-yielding horizons have been discovered in Lower Eocene deposits (Cambay Shale) in the lignite

PE Article Number: 11.1.4A

Submission: 6 July 2007. Acceptance: 29 January 2008

Prasad, Guntupalli V.R. and Bajpai, Sunil, 2008. Agamid Lizards from the Early Eocene of Western India: Oldest Cenozoic Lizards from South Asia. *Palaeontologia Electronica* Vol. 11, Issue 1; 4A:19p;
http://palaeo-electronica.org/2008_1/134/index.html

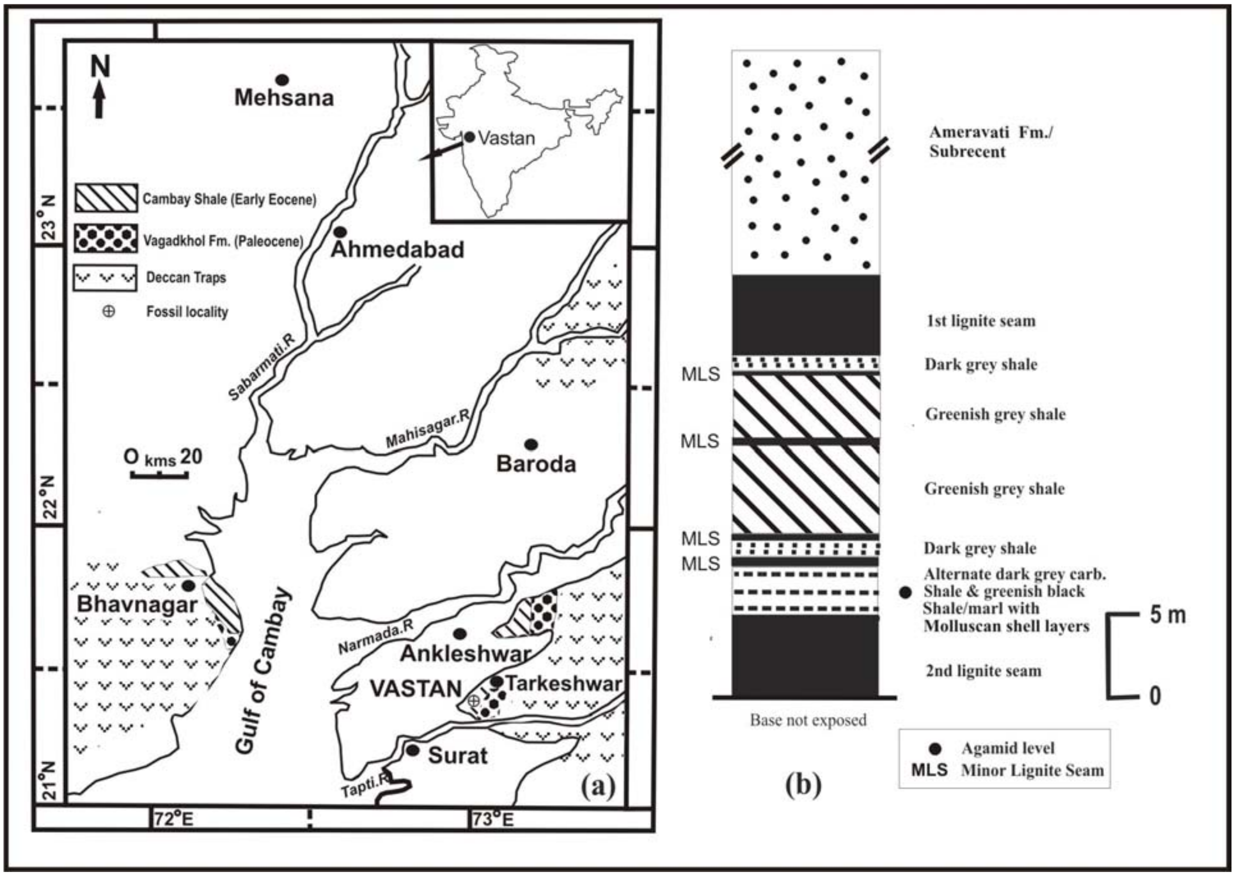

Figure 1. Location map of the fossil-bearing Vastan Lignite Mine, Surat District, Gujarat.

mines of District Surat, Gujarat state, western India (Figure 1). Initially known from fish remains (Samant and Bajpai 2001, Bajpai and Kapur 2004, Rana et al. 2004), the vertebrate fauna recovered from these mines, particularly that from Vastan, is diverse and now represented by amphibians, lizards, snakes, crocodiles, turtles, birds and mammals (Bajpai et al. 2005a, b, c, Rana et al. 2005, Bajpai et al. 2006a, Kapur 2006, Rose et al. 2006, Das, 2007, Mayr et al. 2007, Smith et al. 2007, collections under study at IIT, Roorkee). Until now, only the mammalian fauna of the Vastan Lignite Mine has been described in detail (Bajpai et al. 2005a, b, c, Rana et al. 2005, Bajpai et al. 2006a, Rose et al. 2006, Smith et al. 2007). The placental mammal fauna of this site includes cambaythere perissodactyls (*Cambaytherium bidens*, *C. thewissi*, *C. minor*, *Cambaytherium* sp. *A, Kalitherium marinus*), dichobunid artiodactyls (*Gujaratia indica*), palaeoryctids (*Anthraryctes vastanensis*), cimolestids (*Suratalestes gingerichi*), apatemyids (*Frugivastodon cristatus*), insectivores (*Vastania sahnia*), adapiform and omomyid primates (*Marcgodinotius indicus* and *Vastanomys gracilis*) and chiropterans (*Icaronycteris, Protonycteris*, *Archaeonycteris*?, *Hassianycteris*, *Cambaya*). Additional mammalian faunas, comprising hyaenodontids, tapiromorphs, primates, rodents, condylarths and insectivores, have been described by Kapur (2006) and Das (2007).

The terrestrial vertebrate-bearing strata from Vastan have been dated as Lower Eocene (Middle Ypresian, ca. 52 Ma), based on the presence of the benthic foraminifer *Nummulites burdigalensis* (Bajpai and Kapur 2004, Rana et al. 2005). *N. burdigalensis* forms part of the Shallow Benthic Zone 10, corresponding to the planktic foraminiferal zone P6 (in part) and P7 of Serra-Kiel et al. (1998). However, recent work on Vastan foraminifers (Saravanan 2007; see also Bajpai et al. 2007) suggests that the species previously identified as *N. burdigalensis* may actually pertain to *N. globulus*. More importantly, dinoflagellate cysts, though rare in the Vastan samples, include two temporally significant taxa: *Muratodinium fimbriatum* and *Hystrichosphaeridium tubiferum* (V. Prasad and R. Garg, personal commun., Birbal Sahni Institute of Palaeobotany, Lucknow, India; see Bajpai et al. 2006b). Considered together, the benthic foraminifer and dinoflagellate data suggest a somewhat older age (Early Ypresian, ca. 53.5 Ma) for the Vastan vertebrates, making it the oldest known continental vertebrate fauna in the Cenozoic of Southern Asia (see Bajpai et al. 2007). This is the best age estimate possible at present, but confirmation is required from additional data.

Cenozoic squamates of South Asia are extremely poorly known. Rage (1987) reported two fragmentary teeth of Middle Eocene agamid lizards from Pakistan. The presence of lizards in the Vastan fauna was recently mentioned (Bajpai et al. 2005b, Rose et al. 2006), but the material has not yet been described or illustrated. Here we describe two new species of agamid lizards, one representing a new genus *Vastanagama*, and the second belonging to *Tinosaurus.* The identifications are based on a number of dentaries and a maxillary fragment found in association with the mammal fauna. These fossils represent the oldest known lizards from the Cenozoic of South Asia. Older, pre-Cenozoic records from India include those from the Jurassic Kota Formation (Evans et al. 2002) and a recently described Late Triassic form from the Tiki Formation (Datta and Ray 2006).

The material described in this paper is housed in the Vertebrate Paleontology Laboratory, Department of Earth Sciences, Indian Institute of Technology, Roorkee, under the acronym IITR/SB/VLM.

SYSTEMATIC PALEONTOLOGY

Order SQUAMATA Oppel, 1811
Superfamily ACRODONTA Cope, 1864
Family AGAMIDAE Gray, 1827
Genus VASTANAGAMA gen. nov.

Generic Diagnosis. Dentary small (preserved length 9.20 – 9.60 mm); three pleurodont teeth, recurved third pleurodont tooth followed by tricuspid, acrodont and pleuroacrodont teeth with incipient development of lateral cuspules that are smaller in size than the central cusp as compared to those of *Tinosaurus*; relatively deep anterior part of the dentary; differs from all known taxa of agamid lizards in having a subspherical, vertically oriented, ventrally sloping symphyseal facet covering almost the entire anterolingual face of the dentary bone; broad and slightly convex to flat, platform-like subdental ridge between the alveolar margin and the dorsal margin of the Meckelian fossa; and close spacing of teeth.

Etymology. The genus is named after the Vastan Lignite Mine from where the specimens were recovered.

Type Species. *Vastanagama susani* sp. nov.

Holotype. IITR/ SB/ VLM 1050, left dentary.

Referred Specimens. IITR/SB/VLM/793, left dentary, IITR//SB/VLM/ 886 right dentary.

Horizon & Locality. Lower Eocene Cambay Shale of Vastan Lignite Mine, District Surat, Gujarat state, India.

Vastanagama susani sp. nov.

Specific Diagnosis. Same as for the genus.

Etymology. The species is named in honor of Dr. Susan E. Evans.

Description. IITR/SB/VLM/1050 (Figures 2.3-4, Figures 3.1-4, Figures 4.1-4) is a reasonably well-preserved left dentary representing the anterior and middle regions. The ventral margin of the dentary is more or less straight. The alveolar margin rises regularly from anterior to posterior. The lateral face of the dentary is convex and bears two shallow depressions possibly representing the nutrient foramina (Figure 2.4). The smaller of the two depressions lies ventral to the first acrodont tooth, whereas the larger posterior depression is positioned ventral to the third pleuroacrodont tooth. In dorsal view, the anterior end of the dentary is slightly curved medially. In medial view, a broad and slightly convex to flat, platform-like sub-dental ridge occurs between the alveolar margin and the Meckelian fossa (Figure 2.3). Anteromedially this ridge bears a vertically oriented and ventrally sloping, raised, subspherical symphyseal facet (Figure 2.3, Figures 3.2-4). The Meckelian fossa is broad posteriorly and tapers anteriorly. The tip of the Meckelian fossa closes before terminating posterior to the posteroventral border of the symphyseal surface (Figure 2.3). The lower margin of the dentary bears a long, narrow facet for the angular. This facet extends anteriorly to the level of the second pleuroacrodont tooth. No splenial bone is discernible.

The tooth-bearing surface consists of three conical, pleurodont teeth anteriorly that increase in size posteriorly. The tips of the first and second pleurodont teeth are broken. The third pleurodont tooth is slightly recurved and possibly represents a caniniform tooth. The pleurodont teeth are immediately followed by three triangular, labiolingually compressed acrodont teeth and five pleuroacrodont teeth. A very short diastema is present between the pleurodont and acrodont teeth (Figures 2.3-4). The bases of the acrodont teeth are in close contact with each other and their long axes

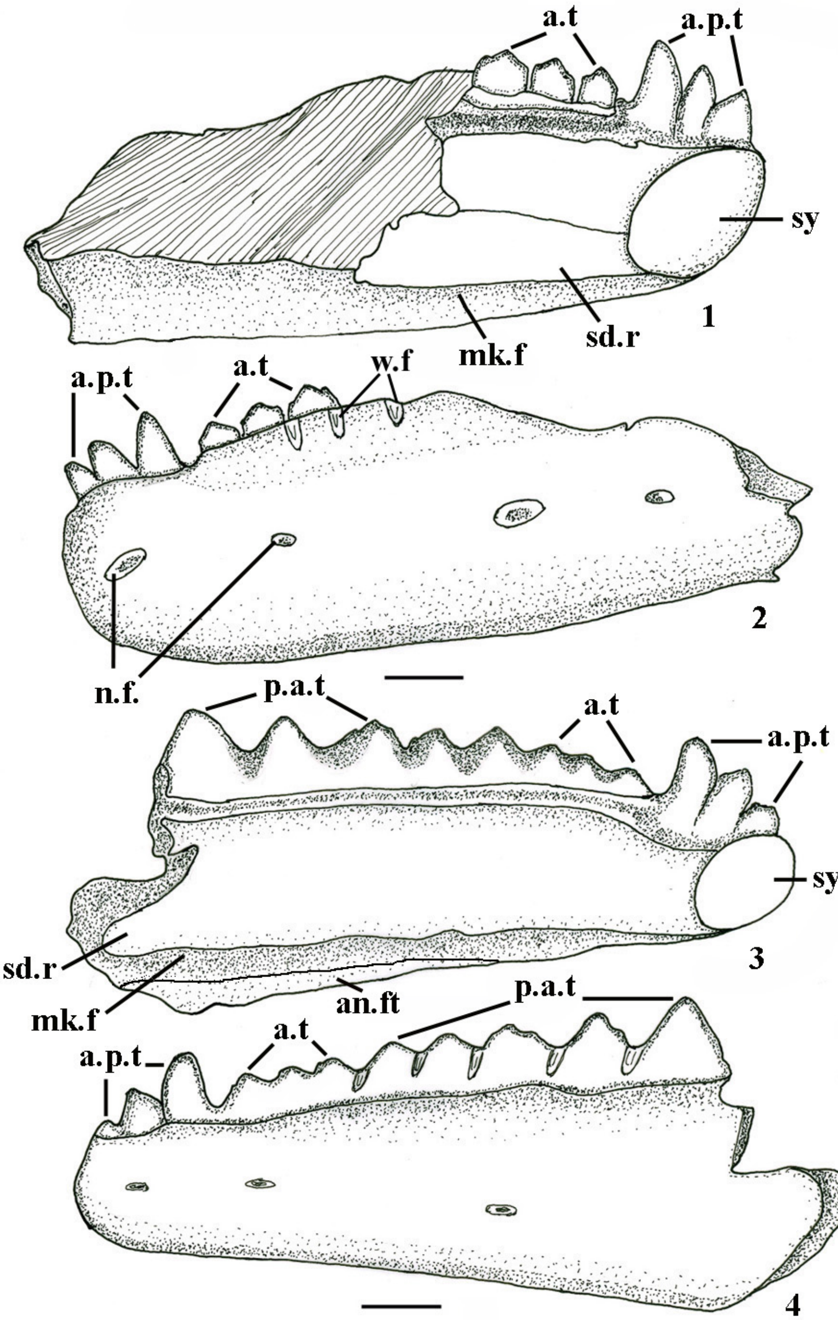

Figure 2. Line drawings of *Vastangama susani* gen.et sp.nov. IITR/SB/VLM/793, left dentary, 1. medial view, 2. lateral view. IITR/SB/VLM/1050, left dentary, 3. medial view, 4. lateral view. Hatched area marks broken areas on the bone. Scale bar equals 1 mm. Abbreviations: an.ft. - angular facet, a.p.t. - anterior pleurodont teeth, a.t. - acrodont teeth, e.r. - eroded ridge of hatchling teeth, mk.f. - Meckelian fossa, n.f. - nutrient foramina, p.a.t. - pleuroacrodont teeth, sd.r. - subdental ridge, sy. - symphysial surface, w.f.-wear facets.

are in line with that of the dentary. The crown surface of these teeth is obscured by matrix. Because of the fragile nature of the specimen, no attempt has been made to remove the matrix. Wherever the crown surface is exposed, minute lateral cuspules become exposed, showing the tricuspid nature of these teeth. The pleuroacrodont teeth are more strongly developed medially, overhanging the broad, platform-like subdental ridge (Figure 2.3, Figure 3.3). These teeth gradually increase in size posteriorly. Vertical grooves are formed between the pleuroacrodont teeth on the lateral face of the

Figure 3. *Vastanagama susani* gen. et sp. nov. IITR/SB/VLM/1050, left dentary, 1. lateral view, 2. medial view, 3. enlarged medial view of middle part of the dentary showing pleuroacrodont teeth, 4. enlarged medial view of anterior part of the dentary showing pleurodont teeth and symphyseal facet. IITR/SB/VLM/886, 5. lateral view, 6. medial view, 7. enlarged lateral view of posterior part of the dentary showing wear facets, 8. enlarged medial view of anterior part of the dentary showing pleurodont teeth and symphyseal facet. Scale bar equals 1 mm.

Figure 4. *Vastanagama susani* gen. et sp. nov. IITR/SB/VLM/793, left dentary, 1. medial view, 2. lateral view, 3. enlarged medial view of anterior part of the dentary showing symphyseal facet, pleurodont and acrodont teeth, 4. enlarged lateral view of anterior part of the dentary showing pleurodont and acrodont teeth. Scale bar equals 1 mm.

dentary, due to occlusion with the maxilla (Figure 2.4). The dentary bone is not preserved behind the fifth pleuroacrodont tooth.

Except for some minor variations, the dentaries IITR/SB/VLM 793 (Figures 2.1-2, Figures 4.1-4) and IITR/SB/VLM 886 (Figures 3.5-8) are very similar in morphology to IITR/SB/VLM 1050. IITR/SB/VLM/793 is nearly of the same size as IITR/SB/VLM/1050. Although this dentary increases in depth from anterior to posterior, the anterior region is not as shallow as that of IITR/SB/VLM/1050. The dentary has three conical, pleurodont teeth anteriorly in the symphyseal region and three acrodont teeth immediately posterior to the pleurodont teeth. Posterior to the preserved acrodont teeth, the tooth-bearing surface is chipped off, whereas its ventral surface is intact (Figure 2.1, Figure 4.1). The lateral face of the dentary has a rounded, convex ventral part, above which, at the mid-height of the dentary, occur four well-developed foramina (Figure 2.2). The anteriormost foramen occurs ventral to the second pleurodont tooth from anterior and the second foramen is positioned ventral to the second acrodont tooth. The third and fourth of the foramina lie on the posterior part of the lateral dentary face and are widely separated from the anterior two foramina. Weakly developed vertical grooves are present on the lateral face, anterior and posterior to the second and third acrodont teeth (Figure 2.2). These vertical grooves terminate ventrally above a shallow longitudinal depression, which is bounded ventrally by the foramina. Anteriorly, the dentary has a nearly vertical border (Figure 2.2). The two anteriormost pleurodont teeth are nearly vertical. The third acrodont tooth is larger than these two and slightly recurved posteriorly, and possibly represents a caniniform tooth. The three posterior acrodont teeth are tricuspid with indentations on the anterior and posterior cutting edges, well below the apex (Figure 2.1, Figure 4.1). These indentations represent incipient lateral cuspules. The acrodont teeth are closely spaced with their bases in contact with each other and are separated from the anterior pleurodont teeth by a very short diastema (Figures 2.1-2).

IITR/SB/VLM/886 (Figures 3.5-8) is very similar to IITR/SB/VLM/793 and 1050 in the morphology of the dentary, except for the presence of a strong vertical groove separating the symphyseal facet from the anterior border and a ridge of eroded teeth posterior to the pleurodont teeth. Only three highly eroded pleuroacrodont teeth are distinguished posteriorly. Vertical grooves are present between the three posteriormost teeth. The posterior part of the jaw is not preserved (see Table 1).

Table 1. Measurements (in mm) of dentary bones (as preserved)

IITR/SB/VLM 793	Length	9.60
	Anterior height	1.70
IITR/SB/VLM 886	Length	9.20
	Posterior height	3.43
	Anterior height	1.80
IITR/SB/VLM 1050	Length	9.33
	Posterior height	4.00
	Anterior height	1.66

Comparisons. The dentaries described here are referred to the family Agamidae because they exhibit a distinctive combination of characters, such as a subdental ridge, an acrodont dentition with some pleuroacrodont teeth posterior in the jaws, pleurodont teeth in the symphyseal region (Moody and Rocek 1980), and the absence of wear facets on the lingual surfaces of the dentary teeth (Evans et al. 2002). Augé and Smith (1997) also considered the presence of a subdental ridge and acrodont teeth followed by pleuroacrodont teeth posterior to the anterior pleurodont series to be primitive characters for agamids. Teeth with such an implantation were designated as “subacrodont”(pleuroacrodont), a condition intermediate in morphology between the large majority of lizards and typical agamids.

Fossil lizards with acrodont teeth are known in the form of *Tikiguania* (Datta and Ray, 2006), *Bharatagama* (Evans et al. 2002), *Priscagama*, *Pleurodontagama* (Borsuk-Bialynicka and Moody 1984, Borsuk-Bialynicka 1996), *Mimeosaurus* (Gilmore 1943, Gao and Hou 1995) and *Flaviagama* (Alifanov 1989) (Priscagaminae), *Tinosaurus* (Marsh 1872) and *Quercyagama* (Augé and Smith 1997). The dentaries referred here to *Vastanagama* have three anterior pleurodont teeth as in *Tikiguania* and *Quercyagama*, but unlike in *Bharatagama* (five), *Priscagama* (three to five), *Flaviagama* (two) and *Tinosaurus* (four). The posterior pleuroacrodont teeth are labiolingually compressed and tricuspid in *Vastanagama,* as in *Tikiguania* and *Tinosaurus*. In contrast, the posterior pleuroacrodont teeth are labiolingually compressed, blade-like and not tricuspid in *Bharatagama* and all priscagamids. However, the tricuspid teeth of *Vastanagama* and *Tikiguania* differ from those of *Tinosaurus* in having a relatively high central cusp and weakly defined lateral cuspules. *Vastanagama* has a comparatively short tooth row, as in *Bharatagama* and priscagamids. *Tikiguania* and *Tinosaurus europeocaenus* (Augé and Smith 1997), on the other hand, have a long tooth row. (Augé and Smith 1997). Dorsoventral wear facets are characteristic of *Tikiguania*, *Bharatagama*, priscagamids, *Tinosaurus, Quercyagama,* and living acrodonts, and they are also present in the dentaries of *Vastanagama*.

In acrodont iguanians, the dentary symphyseal facet lies medial in position, restricted to the dorsal margin of the Meckelian fossa. A strong, largely horizontally oriented symphyseal facet restricted to the dorsal margin of the Meckelian fossa is characteristic of *Bharatagama*, priscagamids, *Tinosaurus* and living acrodonts. In *Tikiguania*, this facet is comparatively small and slightly obliquely oriented to the long axis of the dentary. *Vastanagama* differs from all these taxa in possessing a large, subcircular, vertically oriented, ventrally sloping symphyseal facet. In *Tikiguania*, *Bharatagama*, priscagamids, *Tinosaurus*, and *Quercyagama*, the dentaries taper anteriorly and have shallow anterior regions with the bases of the teeth closer to the ventral dentary margin. In *Vastanagama*, the anterior part of the dentary is relatively deep, does not taper and the bases of the teeth are more distant to the ventral dentary margin. As in *Bharatagama, Tinosaurus* and *Tikiguania*, no splenial is present in *Vastanagama*, however, this bone is known to occur in the dentaries of priscagamids. Although *Vastanagama* compares well with *Tinosaurus* sp. in its short jaws and tricuspid posterior pleuroacrodont teeth (Augé 1990), the lateral cuspules of the teeth are well separated from the central cusp by deep vertical grooves, and the height difference between the central cusp and lateral cusps is much lower in *Tinosaurus* sp. On the whole, the three characters: subspherical, vertically oriented, large symphyseal facet; deep anterior part of the dentary; and broad, flat to convex, platform-like subdental ridge, are absent in any other known acrodont iguanian and strongly favor placement of the dentaries in the new genus *Vastanagama*. Among all known acrodont agamids, the *Vastanagama* dentaries are morphologically closer to *Tikiguania* in the development of a broad, convex or flat, platform-like subdental ridge, incipient lateral cuspules and a high median cusp on the teeth.

Genus TINOSAURUS Marsh, 1872

Emended Generic Diagnosis. Dentary generally elongated; several pleurodont teeth in the symphyseal region, one of which could be caniniform; acrodont teeth behind the anterior pleurodont teeth; posterior teeth pleuroacrodont; acrodont and pleuroacrodont teeth tricuspid; size of teeth reduced regularly anteroposteriorly; presence of a subdental ridge between the tooth row and the dorsal margin of Meckelian fossa; Meckelian fossa at times open anteriorly and ventrally at least to the front of the dentary. Differs from *Tikiguania* and *Vastanagama* in having a horizontal symphyseal facet; anterior part of premaxillary process of maxilla not raised; and well-developed palatine process of maxilla.

Type Species. *Tinosaurus stenodon* Marsh, 1872

Tinosaurus indicus sp. nov.

Holotype. IITR/SB/VLM/ 904, left dentary.

Referred Specimens. IITR/SB/VLM 1051, maxilla, IITR/SB/VLM 748, right dentary; IITR/SB/VLM 820, right dentary; IITR/SB/VLM 1040, right dentary.

Horizon & Locality. Lower Eocene Cambay Shale of Vastan Lignite Mine, District, Surat, Gujarat state, India.

Specific Diagnosis. Maxilla and dentary large in size (maximum preserved length 23 mm), anteroposteriorly elongated jaws with shallow anterior regions, teeth with high median cusp and poorly differentiated lateral cuspules; narrow, cylindrical subdental ridge between Meckelian fossa and alveolar border; symphyseal facet elliptical in outline, anteroposteriorly elongated and obliquely or horizontally oriented with respect to the long axis of the dentary; anteriorly closely spaced acrodont and posteriorly widely spaced pleuroacrodont teeth.

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

Description. IITR/SB/VLM 904 is a left dentary possessing five complete and two partially preserved teeth (Figures 5.3-4, Figures 6.3-6). The dentary is long anteroposteriorly, slender, and its ventral border is rounded, convex and straight. The alveolar border of the dentary rises gradually posteriorly so that the dentary becomes deeper posteriorly. The anterior symphyseal region is not preserved, and the posterior part of the dentary that comes into contact with the post-dentary bones is also broken. The lateral face of the dentary is convex and rounded ventrally, and flat or slightly convex dorsally (Figure 5.3). There are four foramina at the mid-height of the lateral face of the dentary that gradually increase in size posteriorly. The anteriormost foramen lies ventral to the second preserved acrodont tooth, the second one ventral to the gap between third acrodont and first pleuroacrodont tooth, the third one ventral to the area anterior to the second pleuroacrodont tooth, and the fourth is situated ventral to the third pleuroacrodont tooth (Figure 5.3). The anterior three foramina are in the form of slight depressions, whereas the posteriormost foramen is relatively large and deep. A very shallow and posteriorly widening depression extends over the lateral dentary surface from the anteriormost to the back of posteriormost tooth, lying dorsal to the foramina-bearing level and ventral to the vertical grooves between the teeth,

In lingual view, the teeth are implanted above a well-developed, subcylindrical, narrow, convex, subdental ridge, which extends just to the back of the posteriormost tooth. The subdental ridge overhangs the Meckelian fossa and extends to the anterior tip of the dentary, restricting the Meckelian fossa to the ventral border of the dentary (Figure 5.4). Posteriorly, the subdental ridge is broken. The Meckelian fossa is wide posteriorly and gradually becomes narrow anteriorly where it passes onto the ventral part of the dentary bone. Because the dentary is not preserved anteriorly and posteriorly, the original number of teeth is unknown. There are, however, five well-preserved teeth and two anteriormost teeth with broken crowns (Figures 5.3-4, Figures 6.3-4). The anterior symphyseal region consisting of pleurodont teeth is not preserved. The three anterior teeth are labiolingually compressed, and their bases are embedded into the dentary, representing an acrodont tooth implantation. These closely spaced acrodont teeth are triangular in outline with acutely pointed apices. Behind the acrodont teeth, there are four pleuroacrodont teeth with lingually more pronounced bases (Figure 5.4, Figures 6.4-5). These teeth are triangular in shape and widely separated from each other. All of the preserved teeth are tricuspid with small indentations along the mesial and distal margins resulting in minute lateral cuspules (Figures 5.3-4, 6.3-6). In the first, second and third pleuroacrodont tooth, the lateral cuspules are well-developed mesially, and these cuspules are worn distally because wear from the maxillary teeth is directed across the distal face of these teeth. Verti-

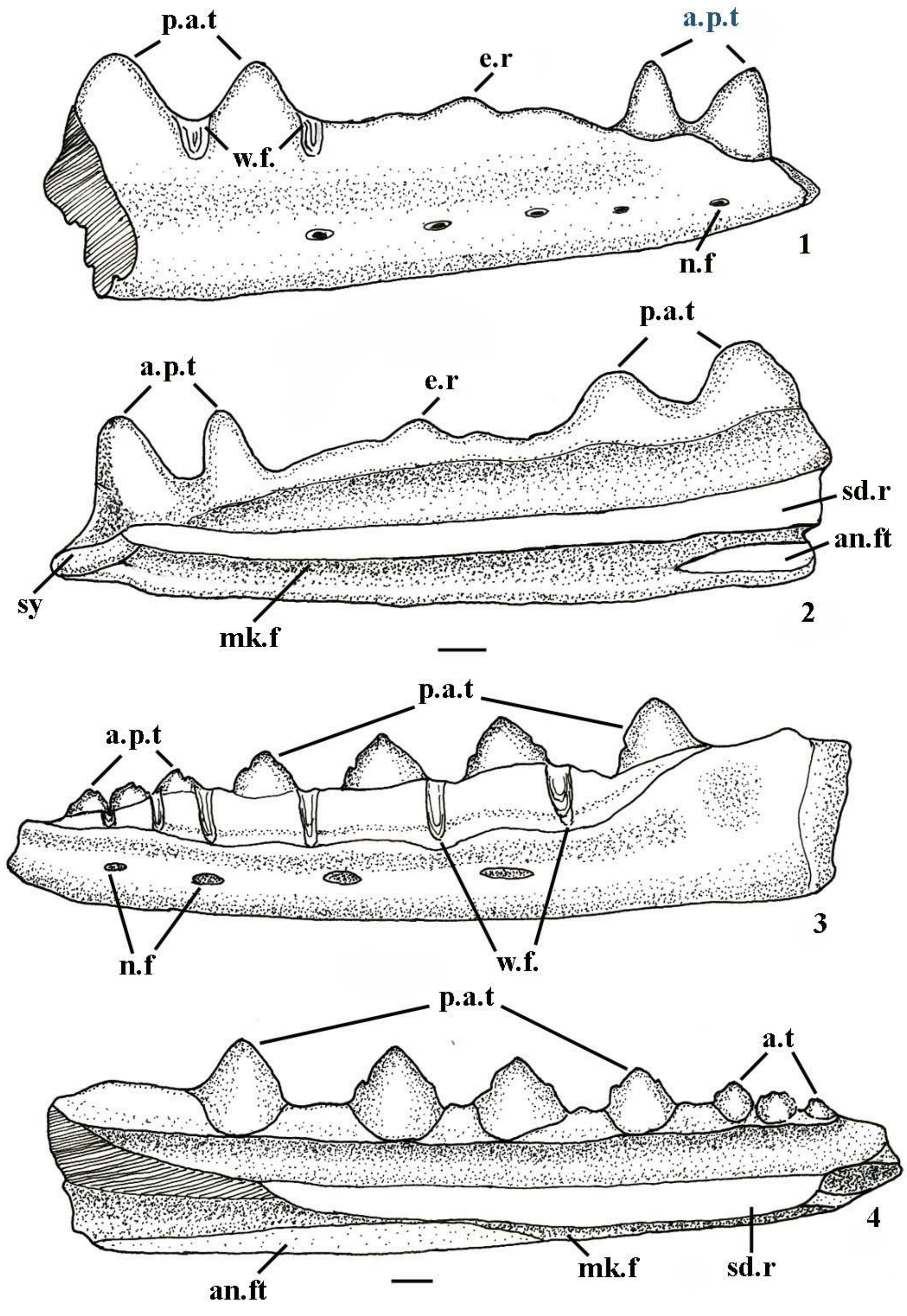

Figure 5. *Tinosaurus indicus* sp. nov., IITR/SB/VLM/820, right dentary, 1. lateral view, 2. medial view; IITR/SB/VLM/904, left dentary, 3. lateral view, 4. medial view. Hatched area marks broken area of bone. Scale bar equals 1 mm. Abbreviations: as Figure 2.

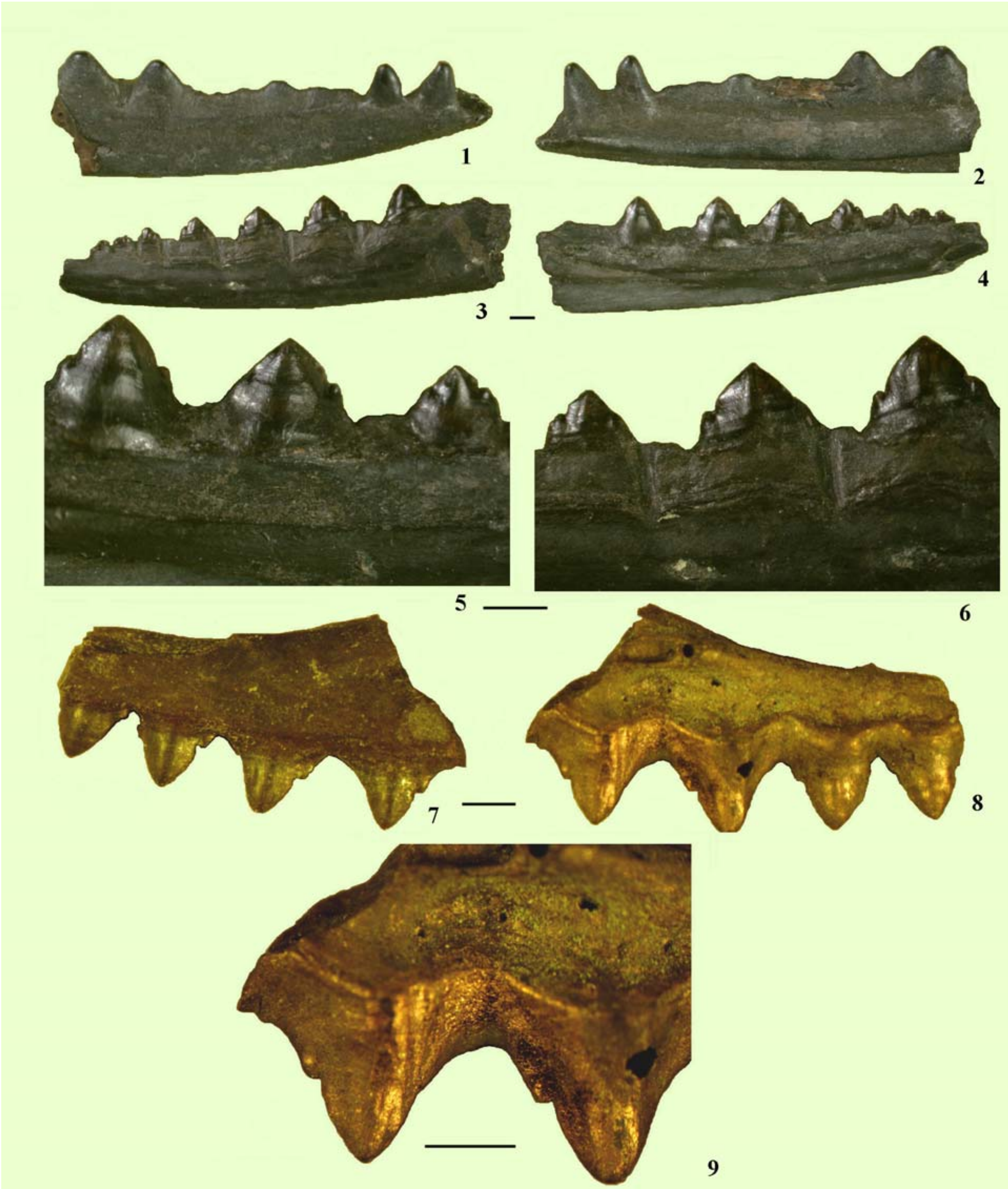

Figure 6. *Tinosaurus indicus* sp. nov., IITR/SB/VLM/820, right dentary, 1. lateral view, 2. medial view; IITR/SB/VLM/904, left dentary, 3. lateral view, 4. medial view, 5. enlarged medial view of pleuroacrodont teeth, 6. enlarged lateral view of pleurodont teeth showing wear facets; IITR/SB/VLM/1051, left maxilla, 7. lateral view, 8. medial view, 9. enlarged medial view showing wear facets. Scale bar equals 1 mm.

cal grooves or wear facets due to occlusion with maxillary teeth are present on the lateral surface of the dentary in the gap between the teeth (Figure 5.3, Figure 6.3, Figure 6.6). These grooves are less prominent between the anterior acrodont teeth. The vertical grooves lie just posteriorly to the distal part of each tooth. These wear facets develop in adult permanent dentition. No such wear facets are present posterior to the fourth pleuracrodont and posterior most tooth. This tooth is followed by a wide gap, and therefore it might represent the posteriormost tooth of the dentary. If this tooth represents the posteriormost position, then the straight dorsal margin of the posterior dentary would indicate that there was possibly no coronoid process. In medial view, a narrow angular facet borders the Meckelian fossa ventrally and occupies nearly the whole posterior half of the dentary.

IITR/SB/VLM 820 (Figures 5.1-2, Figures 6.1-2) is a right dentary in which the anterior and middle parts are preserved. This specimen is heavily eroded with rounded ends. It has a straight and rounded ventral border and several small, shallow depressions on its lateral face, which may represent nutrient foramina. On the medial surface of the dentary, the subdental ridge is a rounded convex horizontal bar that extends anteroposteriorly (Figure 5.2, Figure 6.2). This bar overhangs the Meckelian fossa, which is restricted to the ventral border and widens posteriorly. It has two pleurodont teeth anteriorly and there is a socket in front of the first preserved tooth, possibly for the first pleurodont tooth. The two preserved pleurodont teeth are not closely spaced but are rather separated by a broad U- shaped groove. The preserved first pleurodont tooth is larger than the second one and mesially inclined, whereas the second one is slightly recurved distally. The symphyseal facet of the dentary is elongated anteroposteriorly, but slightly obliquely oriented to the long axis of the dentary and subventral in position (Figure 5.2). Posterior to the pleurodont teeth, the dental series is highly eroded in the middle part and only two large, triangular teeth are present at the posterior portion of the dentary (Figures 5.1-2, Figures 6.1-2). These teeth can be regarded as pleuroacrodont as their bases are more strongly developed lingually. A short diastema is present between the pleurodont anterior teeth and the hatchling teeth of the eroded ridge (Figures 6.1-2). The lateral cuspules are not discernible. At the posterior end of the dentary, a narrow angular facet is present medially (Figure 5.2).

IITR/SB/VLM 748 appears to be similar to IITR/SB/VLM 904 and IITR/SB/VLM/820 in morphology and size, but it is heavily eroded. As in IITR/SB/VLM 904, a shallow longitudinal depression occurs between the rounded ventral margin and the area ventral to the vertical grooves between the teeth.

In comparison to the other dentaries described above, IITR/SB/VLM 1040 (Figure 7.1-3) is slender and has posterior pleuroacrodont teeth bearing fine striations below the apex of principal cusp and rugose ornamentation on the labial face. The ventral margin of this dentary is rounded and convex, and there is no angular facet. IITR/SB/VLM/1040 has an elliptical symphyseal facet, which is oriented anteroposteriorly and horizontally (Figure 7.1, Figure 7.3). Two pleurodont teeth are preserved anteriorly, and there is one possible socket for another tooth at the anterior tip of the dentary. The first preserved pleurodont tooth is inclined mesially. The second pleurodont tooth is much larger than any of the known pleurodont teeth in all of the specimens described, and its tip is broken and recurved. Laterally, the dentary bears seven foramina of which three are located anterior to the third pleurodont tooth. The pleurodont teeth of the symphyseal region are separated from the posterior pleuroacrodont teeth by a transitional eroded ridge with acrodont tooth implantation (Figures 7.1-3). A short diastema exists between the pleurodont teeth and the eroded ridge of the acrodont teeth. The pleuroacrodont teeth of this dentary have relatively longer (anteroposterior) bases and the lateral cuspules are more prominent. In IITR/SB/VLM/1040, the Meckelian fossa extends ventrally below the anterior two-thirds of the symphyseal facet.

IITR/SB/VLM 1051 (Figures 6.7-9) is a left maxillary fragment broken on both its anterior and posterior ends. The size of this maxilla matches the dentaries described above, and hence it is described as belonging to the same taxon. In lateral view, the dorsal margin of the maxilla is broken anteriorly above the first and second preserved teeth. The margin is intact posteriorly and dorsal to the remaining two teeth. The lateral face of the maxilla is generally flat, but slightly convex dorsal to the anteriormost three teeth. Dorsal to the fourth tooth, there is a slightly depressed area between the tooth-bearing surface and the dorsal margin of the maxilla. In lateral view, the four teeth have an acrodont implantation, and in medial view the teeth have a pleuroacrodont implantation. In medial view, the teeth overhang a rounded horizontal bar,

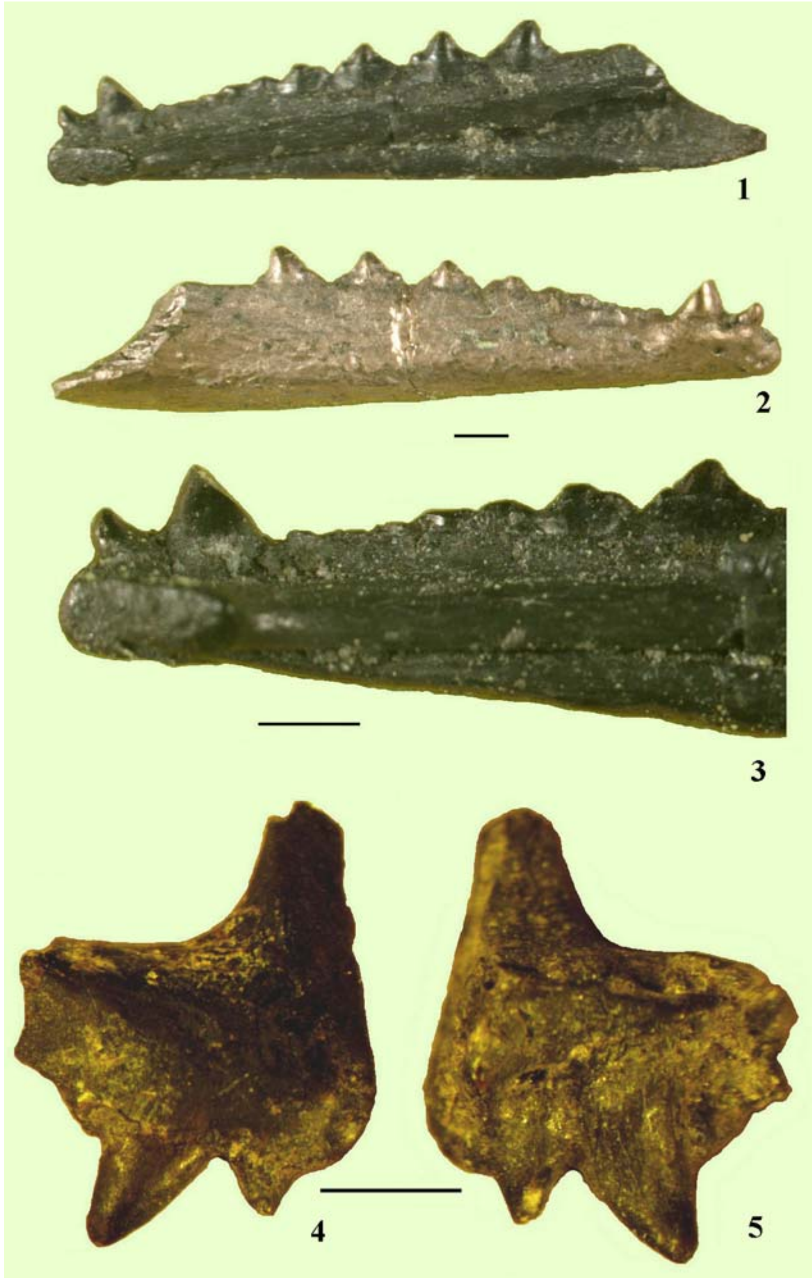

Figure 7. *Tinosaurus indicus* sp. nov. IITR/SB/VLM/1040, right dentary, 1. medial view, 2. lateral view, 3. enlarged medial view of anterior part of the dentary showing the symphyseal facet (on the left). IITR/SB/VLM/1052, right premaxilla, 4. lateral view, 5. medial view. Scale bar equals 1 mm.

which rises regularly from anterior to posterior. The teeth appear to be tricuspid with minute lateral cuspules at their mid-height on the posterior face. The central cusp of these teeth is very high, and the lateral cuspules are located at mid-height or close to the base. The absence of anterior lateral cuspules can be explained by lingual wear facets, which are located in this position. The presence of wear facets on the lingual face of the teeth suggests that this bone is a maxilla. The teeth increase in size gradually from anterior to posterior. The horizontal bar is expanded posteriorly dorsal to the third and fourth teeth and this expansion is possibly for the palatine process, which is broken in the present specimen.

IITR/SB/VLM 1052 (Figures 7.4-5) is a right premaxillary bone bearing a broad alveolar margin with two teeth. The premaxilla is broken both anteriorly and posteriorly. The nasal process is relatively thin, and its anterior face and tip are broken. The lateral face of the bone is convex. Posterior to the nasal process, the dorsal margin of this bone is straight. The nasal process is almost vertically orientated. See Table 2.

Table 2. Measurements (in mm), as preserved

IITR/SB/VLM 748	Length of dentary	23.00
	Posterior height	4.00
	Anterior height	2.30
IITR/SB/VLM 820	Length of dentary	18.20
	Posterior height	4.00
	Anterior height	2.20
IITR/SB/VLM 904	Length of dentary	18.50
	Posterior height	3.60
	Anterior height	2.60
IITR/SB/VLM 1040	Length of dentary	13.66
	Posterior height	2.33
	Anterior height	1.33
IITR/SB/VLM 1051	Length of maxilla	8.00
IITR/SB/VLM 1052	Length of premaxilla	2.50

Comparisons. The dentary bones represented by IITR/SB/VLM/904 possess three pleurodont teeth anteriorly, but they are comparatively larger than those referred to *Vastanagama*. Furthermore, these dentaries differ from those of *Vastanagama* in having an elliptical and anteroposteriorly elongated symphyseal facet oriented obliquely or horizontally to the long axis of the dentary, and in a narrow and subcylindrical subdental ridge. Within the family Agamidae, the morphology of IITR/SB/VLM/904 and other Vastan specimens described here is reminiscent of the Late Triassic genus *Tikiguania* and the Paleocene-Eocene genus *Tinosaurus*. Although in most of the specimens the dentary is broken posterior to the posterior teeth, in IITR/SB/VLM/904 an unworn additional tooth occurs posterior to the adult permanent teeth. This is considered as the posteriormost tooth of the dentary because it is followed by a wide gap. It is interpreted from the straight dental margin of the posterior region that the coronoid process did not exist. In this respect, IITR/SB/VLM/904, referred to *T. indicus* sp.nov. is similar to *Tikiguania*. As in *Tikiguania*, the dentaries of *T. indicus* are also elongated with a tapering anterior part bearing three pleurodont teeth, anteroposteriorly elongated symphyseal facet and tricuspid acrodont and pleuroacrodont teeth. However, the teeth of *Tikiguania* are closely spaced all along the jaw, contrasting with the widely spaced posterior pleuroacrodont teeth of Vastan dentaries. *Tikiguania* also has a dentary with a broad, flat, or convex subdental ridge, as compared to the narrow, subcylindrical subdental ridge on the Vastan specimens.

Tinosaurus is defined by the presence of caniniform teeth in the anterior part of the jaws and tricuspid acrodont/pleuroacrodont teeth posteriorly(Estes 1983, Augé 1990, Augé and Smith 1997, Augé 2005). Alternatively, it has also been defined by the tricuspid nature of the acrodont teeth alone (Hecht and Hoffstetter 1962). The genus *Tinosaurus* is at present represented by eight species: *T. stenodon* Marsh, 1872, *T. pristinus* (Leidy 1872) (Middle Eocene of North America, Gilmore 1928, Hecht 1959), *T. lushihensis* Dong 1965 (early Late Eocene of Honan, China), *T. asiaticus* (?early Upper Eocene Ulan Shireh Formation of Inner Mongolia, Gilmore 1943), *T. doumuensis* (Palaeocene Doum Formation of Anhui, China, Hou 1974), *T. yuanquensis* (Upper Eocene Zhaili Member, Hedi Formation, Yuanqu, Shanxi Province, China, Li 1991a), *Tinosaurus* cf. *T. lushihensis* (Middle Eocene Hetaoyuan Formation Xichuan Province, Henan Province, China, Li 1991b), *T. postremus* (Palaeocene of Kazakhstan, Averianov 2000) and *T. europeocaenus* (Palaeocene of Europe, Augé and Smith 1997, Augé 2005). Unidentified species of *Tinosaurus* have also been reported from the Early Eocene of Belgium (Hecht and Hoffstetter 1962; Godinot et al. 1978), the Early Eocene of France (Russell et al. 1982, Augé 1990), the early Middle Eocene Kuldana Formation, Kohat, Pakistan (Rage 1987) and the Upper Eocene Chadron Formation of North Dakota, USA (Smith 2006).

Because of the presence of characters diagnostic of *Tinosaurus* (a narrow, cylindrical subdental ridge, and anteriorly tapering dentaries) IITR/SB/VLM/904 and other dentaries and maxilla described here are assigned to this genus. Despite the fact that the posterior pleuroacrodont teeth of *T. indicus* sp. nov. are tricuspid as in various species of *Tinosaurus*, the development of lateral cuspules in *T. indicus* sp. nov. is different from the North American and Eurasian species of *Tinosaurus*. In most of the latter species, there are four anterior pleurodont teeth, the lateral cuspules are well separated from the central cusp by deep vertical grooves, and the height difference between the central cusp and the lateral cuspules is far less on the acrodont and pleuroacrodont teeth. In comparison, the lateral cuspules of *T. indicus* sp. nov. are incipient, hardly differentiated from the high central cusp and are located at mid-height of the tooth. In this respect, the tricuspid teeth of *T. indicus* sp. nov. are very similar to the posterior teeth of *Tikiguania*. *T. indicus* sp. nov. further differs from *Tinosaurus* cf. *T. lushihensis* and *T. asiaticus* in possessing non-overlapping posterior acrodont teeth and closely spaced teeth anteriorly, and widely spaced posterior subacrodont teeth. *T. indicus* sp. nov. is also distinguished from *T. yuanquensis* and all other known species of *Tinosaurus* from China in the presence of well-developed vertical grooves between the teeth on the labial face of the dentary. This indicates that shearing occlusion was less important in the Chinese species (Li 1991b) as compared to species from North America and Europe, and *T. indicus* sp. nov. The Vastan specimens also differ from *T. stenodon* and *T. pristinus* in possessing a shallower posterior portion of the dentary.

Two fragmentary teeth (GSP-UM 552-553) from the early Middle Eocene Kuldana Formation, Kohat, Pakistan, were referred to *Tinosaurus* sp. (Rage 1987). These teeth are comparable to those of Vastan Lignite Mine in their greater development of lateral cuspules on one side and less on the other. However, the groove between the median and lateral cuspules is developed more in GSP-UM 553 when compared to the Indian specimens. One of the teeth (GSP-UM 553) appears similar to the anterior acrodont teeth of *Vastanagama susani* gen. et sp. nov.

A fragmentary maxilla from the late Lower Eocene beds at Prémontré (Paris basin), France was referred to *Tinosaurus* sp. (Augé et al. 1997). The maxilla described here differs from the Prémontré specimen in having a very high median cusp on the tricuspid subacrodont teeth and minute lateral cuspules.

Because of the differences in the morphology identified between the Vastan dentaries and various other species of *Tinosaurus*, the new fossil material from India is referred to a new species of *Tinosaurus*, *T. indicus* sp. nov.

DISCUSSION

The India-Asia collision event is the best example of continent-continent collision and has attracted wide attention in recent years with respect to the biota present before and during the collision (Jaeger et al. 1989, Sahni and Bajpai 1991, Rage 1996, Prasad and Sahni 1999, Briggs 2003, Sahni 2006, Whatley and Bajpai 2006). In this context, the Late Cretaceous - Early Eocene terrestrial vertebrate assemblages have an important bearing on our understanding of the degree of isolation of the Indian subcontinent and the resulting endemism and possible dispersal routes, if any, during this time. Investigations of the Upper Cretaceous Deccan intertrappean biota have long shown the presence of a mixture of Laurasiatic (Sahni 1984, Jaeger et al. 1989, Sahni and Bajpai 1991, Prasad and Rage 1991, Prasad and Sahni 1999) and Gondwanic (Krause et al. 1997, Prasad and Sahni 1999) affinities. In recent years, however, a considerable degree of endemism has been demonstrated for the Maastrichtian continental biota of India based on freshwater ostracods, with about 100 new species having been recorded (e.g., Whatley and Bajpai 2000, 2005, 2006). Biotic endemism during the northward journey of India was also demonstrated by the extant *Nasikabatrachus sahyadrensis* (family Nasikabatrachidae), the sister group of the family Sooglossidae, the extant frog family of the Seychelles (Bossuyt and Milinkovitch, 2001, Dutta et al. 2004, Karanth 2006).

The continental vertebrate fauna of the Vastan Lignite Mine, which comprises the southeastern extension of the Ghazij Formation of Baluchistan (Pakistan), is highly significant from a paleobiogeographic point of view because it comes from a point in time during which the Indian plate was docking with Asia. During the Early Eocene, and possibly prior to the firm suturing between India and Asia, changes in ecological niches may have led to the origin and endemic evolution of certain groups of mammals such as quettacyonid condylarths (Gingerich et al. 1997), cetaceans (Bajpai and Gingerich 1998), cambaythere perissodactyls (Bajpai et al. 2005b, 2006a), and possibly anthracobunid tethytheres (Ginsburg et al. 1999). Krause and Maas (1990), in a seminal paper, hypothesized that certain mammalian groups such as artiodactyls, perissodactyls, and primates, which appeared at the Paleocene-Oligocene boundary (ca. 55 Ma) in the northern hemisphere, dispersed out of India when it made subaerial contact with Asia. More recently, this ‘Out-of-India’ dispersal hypothesis has been proposed on the basis of molecular data collected from many of the modern faunal and floral groups, such as ranid frogs (Bossuyt and Milinkovitch 2001), acrodont lizards (Macey et al. 2000), ratite birds (Cooper et al. 2001), and Crypterioniaceae plants (Conti et al. 2002). These studies suggest that the origin of these and many other animal and plant lineages occurred in the Indian subcontinent or other Gondwanan landmasses, and that they were rafted northwards on the drifting Indian plate, eventually spreading to the northern landmasses (Asia, Europe and North America) as a consequence of the contact between India and Asia. At present, there is limited fossil evidence for the 'Out-of-India' dispersal hypothesis: which includes ranoid frogs (Prasad and Rage 2004), freshwater ostracods (Whatley and Bajpai 2006) and *Lagerstroemia* (Lythraceae, Liu et al. 2007) from the Deccan intertrappean beds of India. However, the 'Out-of-India' hypothesis has been contested by Clyde et al. (2003) who, based on their study of the Early Eocene Ghazij mammal fauna of Pakistan, suggested that this fauna dispersed 'Into-India' rather than out of it. This idea is based on their interpretation that the mammal faunas of the lower and middle parts of the Ghazij Formation are relatively endemic, while in its upper part the fauna becomes dominantly holarctic.

The new dental material described here from the Lower Eocene Vastan Lignite deposits resembles the dental morphology of *Tikiguania* and *Tinosaurus* in having long jaws with an anteroposteriorly elongated, elliptical symphyseal face and three pleurodont teeth. Before the present discovery, *Tinosaurus* was reported only from the holarctic landmasses (North America, Europe, Kazakhstan, and China). Only two fragmentary teeth of *Tinosaurus* sp. were documented from the early Middle Eocene Kuldana Formation, Kohat, Pakistan (Rage 1987). The specimens described here are the oldest well-preserved jaws of agamid lizards from the Cenozoic rocks of South Asia. The fact that *Tinosaurus* occurs in the fossil record as early as in the Paleocene might suggest that *Tinosaurus* had originated somewhere in the Northern Hemisphere and dispersed in to India during the earliest Eocene or even Late Paleocene. Although the timing of the initiation of the India-Asia collision is controversial, most estimates vary between 65 Ma to approximately 50 Ma. Thus, the Vastan agamids, if they were immigrants from the north, document a dispersal event that occurred either after the establishment of well-developed dispersal corridors following a firm suturing between India and Asia, or via a series of intermittently emergent crustal blocks in the Neotethys sea (including island arcs), that provided a continuous terrestrial connection required for faunal interchanges before the two plates collided.

However, the oldest agamid lizard, *Tikiguania,* comes from the Late Triassic of India (Datta and Ray 2006). The close similarity in the development of central and lateral cuspules on the posterior teeth of *Tikiguania*, *Vastanagma susani* gen.et sp.nov. and *T. indicus* sp. nov., the presence of a broad, flat or convex, platform-like subdental ridge in *Tikiguania* and *Vastangama*, and the antiquity of *Tikiguania* suggest that the agamid lizards from Vastan may have been derived from a *Tikiguania*-like animal. The resemblance between *T. indicus* sp. nov. and *Tikiguania* in possessing caniniform teeth anteriorly and tricuspid pleuroacrodont teeth posteriorly, may offer an alternative explanation that the incipient development of labial cuspules in *Tikiguania* and *T. indicus* sp. nov. is the plesiomorphic state and that the well separated labial cuspules with deep vertical grooves and with reduced height difference between these cuspules and central cusp represents the derived state seen in North American and Eurasian species of *Tinosaurus*. This interpretation leads to the conclusion that *Tinosaurus* descended from the Late Triassic *Tikiguania* of India and dispersed out of India into Eurasia and North America when the initial land connection was established between India and Asia, or possibly even earlier by trans-Tethyan dispersals.

The assignment of some of the Vastan specimens to *Tinosaurus* is primarily based on the presence of tricuspid acrodont and pleuroacrodont teeth, and a narrow and cylindrical subdental ridge between the alveolar margin and the Meckelian fossa. However, as mentioned before, the holarctic species of *Tinosaurus* differ from the Vastan species *T. indicus* sp. nov. in the development of central and labial cuspules. In contrast to the North American and Eurasian species, *T. indicus* sp. nov. has incipiently developed labial cuspules lacking marked vertical grooves separating them from the central cusp, and greater height difference between the central and labial cuspules. Because this character is variably present in different species of *Tinosaurus* and extant agamids, it cannot be used as an apomorphy. Moreover, *Tinosaurus* is a poorly defined taxon and the monophyly of its component species is not established with apomorphies. For the convenience of description, however, the Vastan specimens (*T. indicus*) are tentatively assigned to *Tinosaurus* until better preserved material is available.

Estes (1983) proposed that the stem group squamates had a Pangaean distribution and that the split between southern iguanians and northern scleroglossans took place as a result of the separation of Laurasia and Gondwana during the Jurassic and subsequent land connections permitted north to south migration of these groups. However, some later discoveries of agamid lizards from the Late Cretaceous of Asia (Alifanov 1989, 1993, Borsuk-Bialynicka and Alifanov 1991, Gao and Hou 1995, Gao and Nessov 1998) have questioned the Gondwanan ancestry for Iguania, favoring a Laurasian center of origin for the iguanians. In their detailed study of the phylogenetics of modern acrodont lizards by molecular data, Macey et al. (2000) identified a number of modern agamid clades and suggested a Gondwanan origin for them. According to these authors, all of these agamid clades were introduced into Asia by the accretion of the Gondwanan plates at different times. The molecular studies were subsequently supported by new fossil discoveries (*Bharatagama*, Evans et al. 2002) from the Middle to Upper Jurassic Kota Formation and from the Upper Triassic Tiki Formation (*Tikiguania*, Datta and Ray 2006). The new fossil data from Vastan does not unequivocally support the 'Out-of–India' hypothesis, but we cannot rule out the possibility that some lineages of acrodont lizards, such as the new agamid lizard material described here, were introduced into Laurasia from India during one of the several trans-Tethyan dispersal phases (Macey et al. 2000, Gheerbrant and Rage 2006). Because the fossil record from the Gondwanan landmasses is scanty and incomparable to that from Laurasia, a clearer paleobiogeographic picture will only emerge when the fossil record from these landmasses becomes better represented.

ACKNOWLEDGMENTS

The authors are grateful to three anonymous reviewers for their critical comments and suggestions on the manuscript. Financial support for this study was provided to S.B. by the Department of Science & Technology (DST), New Delhi, Government of India. G.V.R.P acknowledges the grants for the Department of Geology, University of Jammu, under the FIST program of DST. We thank V.V. Kapur, D.P. Das and N. Saravanan for their considerable help, both in the field and laboratory. Thanks also to officers of the Vastan mine for facilitating field investigations and to O. Verma for processing the photographic images of agamid lizard specimens and making the figures.

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