High diversity of acrodontan lizards in the Early Eocene Vastan Lignite Mine of India

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ABSTRACT. The Ypresian Cambay Formation at Vastan Mine in Gujarat, western India, has yielded a rich herpetological fauna including snakes, lizards and amphibians, but strangely, lizards are only represented by Acrodonta. Here we describe the acrodontan assemblage based on numerous, diverse and well-preserved dentaries, premaxillae, and maxillae. Among the five taxa described one new genus and species characterised by a short splenial represents the youngest occurrence of the extinct family Priscagamidae. The other four taxa belong to the extant family Agamidae. Two of them previously known, *Vastanagama susanae* and *Tinosaurus indicus*, are here revised. The two other taxa are new. The first one, *Suratagama neeraae* gen. and sp. nov., is characterised by the presence of six small pleurodont teeth with a nearly cylindrical shaft and an obtusely pointed apex. The second one, *Indiagama gujarata* gen. and sp. nov., has rectangular teeth in lateral view, unicuspid crowns forming a nearly horizontal cutting edge, and wear facets on both the lingual and labial sides of the dentary. Our results confirm that Acrodonta is the only lizard group present in Vastan, whereas many other groups are already present from the beginning of the Early Eocene on the other continents. The diversity of the agamids in Vastan and the absence of non-acrodontan lizard in India tentatively support the Out-of-India hypothesis for agamids.

KEYWORDS: Squamata, Agamidae, Cambay Formation, Gujarat, Ypresian.

1. Introduction

The Cambay Shale Formation, exposed at the Vastan open cast lignite mine near the Vastan village about 40 km north east of Surat, Gujarat, western India (Fig. 1) is known for its well preserved diverse fauna of terrestrial mammals as well as other vertebrates (Rana et al., 2004, 2005; Bajpai et al, 2005, 2009; Bajpai & Kapur, 2008; Rose et al., 2006; Sahni et al., 2006). The mammalian fauna of the Cambay Formation is represented by the earliest modern mammals from the Indian subcontinent with the highest diversity of early bats (Smith et al., 2007), the earliest lagomorph (Rose et al., 2008), the first Asian ailuravine rodent (Rana et al., 2008), primitive adapoid and omomyid primates (Rose et al., 2009a), primitive artiodactyls (Kumar et al., 2010), and the first Indian tillodonts (Rose et al. 2009b, 2013). Other vertebrates include marine and non-marine fishes (Rana, et al., 2004; Nolf et al., 2006), oldest birds of the Indian subcontinent (Mayr et al. 2007, 2010), terrestrial and aquatic snakes (Rage et al., 2008), agamid lizards (Prasad and Bajpai, 2008) and the earliest ranid and bombinatorid frogs (Bajpai and Kapoor, 2008; Folie et al., 2013).

The present paper deals with the lizards from Vastan Lignite Mine, which represent only acrodontans. The Acrodonta is a large monophyletic clade of lizards belonging to the Iguania. It includes Chamaeleonidae, Agamidae and the extinct family Priscagamidae (Camp, 1923; Estes et al., 1988).

The family Agamidae is a large group with 52 extant genera and 420 species known from Asia, Australia, Africa and Europe (TIGR Reptile Database: Uetz et al., 2007). They are omnivorous, diurnal (Witten, 1993; Pianka and Vitt, 2003) and can reach 5 to 100 cm in snout-vent length (Witten, 1993). Most of them occupy terrestrial habitats but some are arboreal (e.g., *Calotes* and *Lyriocephalus*) or semi-aquatic (e.g., *Hydrosaurus*) (Pianka and Vitt, 2003).

Prasad and Bajpai (2008) previously reported two species of acrodontan agamids on the basis of fragmentary dentaries and maxillae from Vastan. The new collection of acrodontans here described, based on well-preserved dentaries and maxillae from the same horizon at Vastan, allows a revision of these two species and enable diagnoses and detailed descriptions of three new genera and species including a new priscagamid.

2. Material and methods

The fossil lizards from the Vastan lignite mine described in this paper are represented by four nearly complete dentaries, twelve fragmentary dentaries, one nearly complete maxilla, ten fragmentary maxillae, and one jaw fragment. All the material was recovered from the same horizon by subsurface picking as well as screen washing through meshes of 5mm, 2mm and 1mm. Large bones stopped by the mesh of 5mm have been sorted in the field. Small bones stopped by the meshes of 2mm and 1 mm were picked out and sorted in laboratory under a binocular microscope. Beside the dental specimens described here, postcranial bones have also been found. Among these latter were about 200 vertebrae. Half of them are not identified and the other half corresponds to 15 different morphotypes. These specimens are nevertheless not described here as it is very difficult to assign them to one or another taxon known from Vastan. All specimens are originally black or dark in colour. Specimens were coated (whitened) with ammonium chloride for digital imaging and the smallest specimens were photographed with a low environmental scanning electronic microscope FEI Quanta 200.

The present figured specimens are stored in the collections of the H.N.B. Garhwal University, Srinagar, Uttarakhand, India. Institutional Abbreviations.—GU/RSR/VAS, H.N.B., Garhwal University, Srinagar, Uttarakhand, India; IITR/SB/VLM, Vertebrate Paleontology Laboratory, Department of Earth Sciences, Indian Institute of Technology, Roorkee, India.

3. Geological setting

Vastan Mine is developed in exposures of the lower Eocene Cambay Shale. Most of the sequence at the mine consists of near-shore intertidal, estuarine, and lagoonal strata, rich in organic remains including mollusks, foraminiferans, and plants, as well as fossil vertebrates (Rana et al., 2005; Sahni et al., 2006). The fossil lizards, like most of the small terrestrial vertebrates

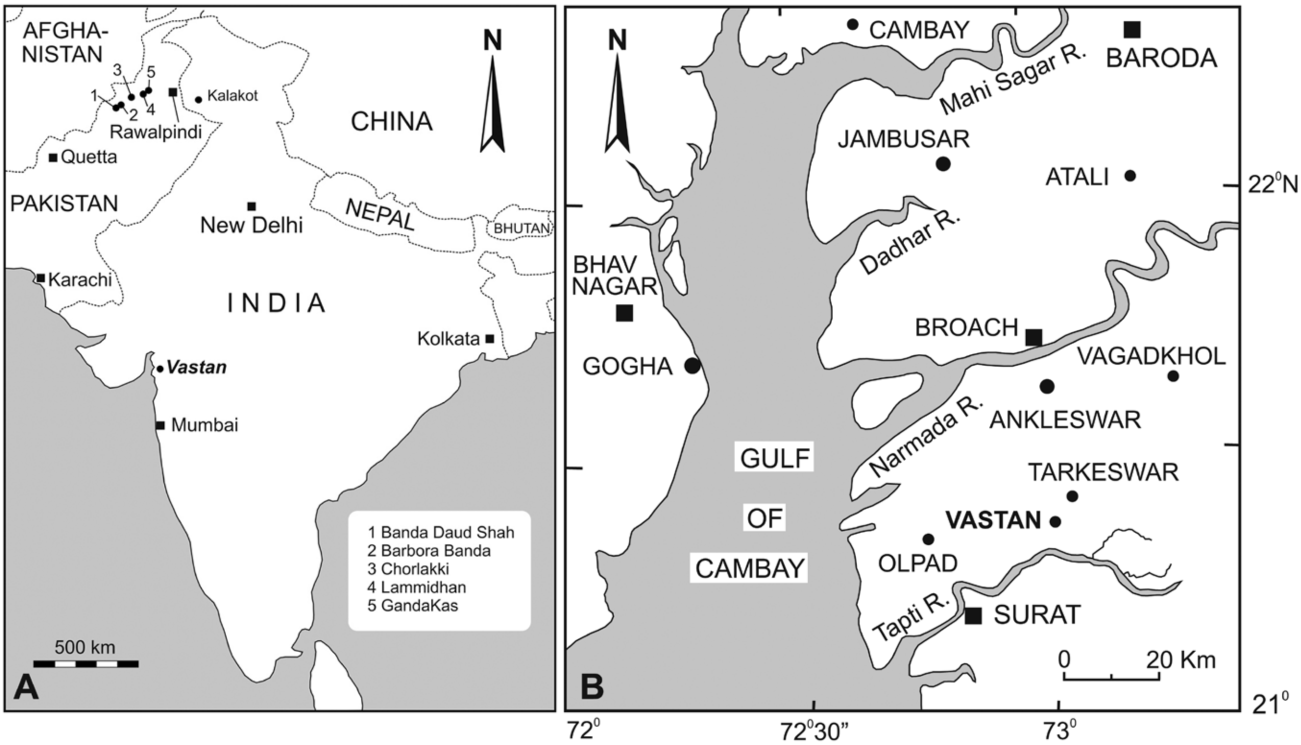

Figure 1. A. Map of Indian subcontinent showing the location of Early and Middle Eocene terrestrial vertebrate localities including Vastan Lignite Mine. Squares represent major cities and black dots vertebrate localities. B. Location map of the area around Vastan Lignite Mine, Surat District. Squares represent major cities and black dots lignite mines.

from Vastan Mine, come from thin lenses (<0.5 m thick and <5.0 m long) of dark, clayey silt and shale with abundant plant matter, about 1 m above the lower of two major lignite layers (Lignite 2) occurring in the mine (Fig. 2). Approximately 1–2 m higher is a dark clay zone that has produced larger terrestrial mammals (anthracobunids). Marine shell beds occur both below and above the mammal-bearing layers, indicating a near-shore environment. A stratigraphic section through this part of the mine (Fig. 2) contains the age-diagnostic foraminiferan *Nummulites burdigalensis burdigalensis* from about 14 m above the mammal layers (Sahni et al., 2006). This foraminiferan is indicative of Shallow Benthic Zone SBZ 10 (Schaub, 1981; Serra-Kiel et al., 1998), which indicates a middle Ypresian age, approximately 53 Ma (Berggren and Aubry, 1998; Luterbacher et al., 2004). However, dinoflagellate cysts reported from the section suggest that the deposits could be of early Ypresian age, ~54–55 Ma (Garg et al., 2008). Strontium isotope age estimates for Vastan Lignite deposit based on $^{87}Sr/^{86}Sr$ values for diverse taxa, cluster at an age value of 54.0 Ma (Clementz et al., 2011). The $\delta^{13}C$ chemostratigraphy further suggests that the vertebrate fossil bearing horizon, is at least ~1 Ma younger than the Paleocene Eocene Thermal Maximum (Samanta et al., 2013).

To summarise on the age constrain of the vertebrate bearing bed of Vastan mine all the data confirm that it does not correspond to the beginning of the Ypresian but suggest more an early to middle Ypresian age (around 54.0 Ma).

4. Systematic paleontology

Order Squamata Oppel 1811
Infraorder Iguania Cope 1864
Superfamily Acrodonta Cope 1964
Family Priscagamidae Borsuk-Bialynicka and Moody 1984

Heterodontagama gen. nov.

Etymology: In reference to the strong heterodont morphology of the tooth row and a*gama*, a suffix for priscagamid taxa

Type and only known species: *Heterodontagama borsukae* sp. nov.

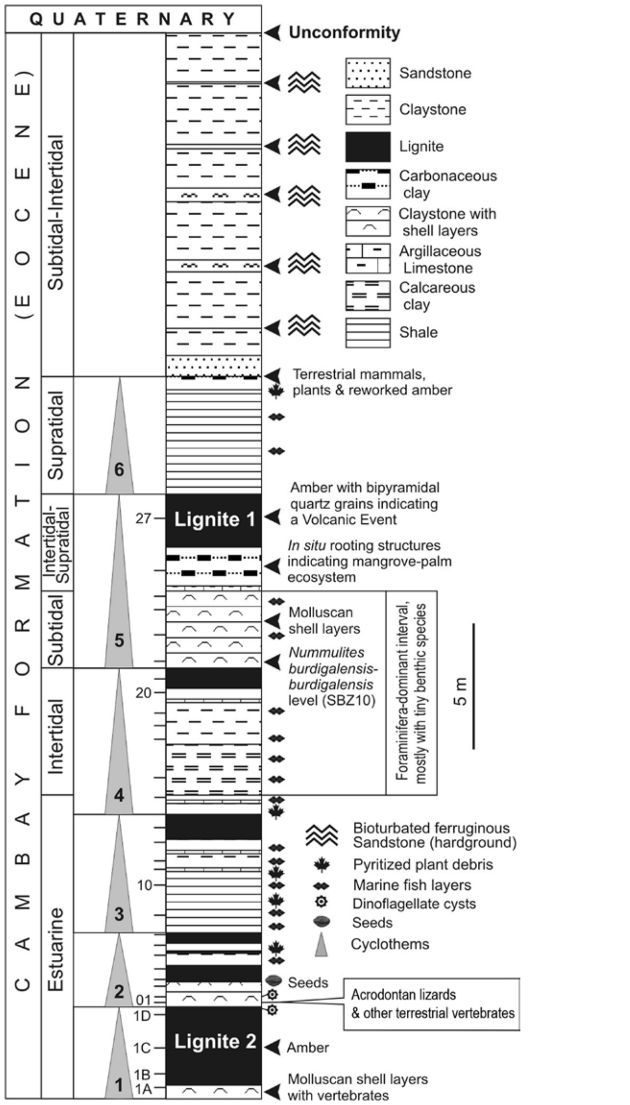

Figure 2. Stratigraphic section through the lower Eocene Cambay Formation in Vastan Mine. Section shows position of the vertebrate-producing layer in which the fossil lizards have been found relative to the two principal lignites in cycles 1 (lignite 2) and 5 (lignite 1). Note the presence of foraminiferan *Nummulites burdigalensis burdigalensis* from about 14 m above the fossiliferous layer.

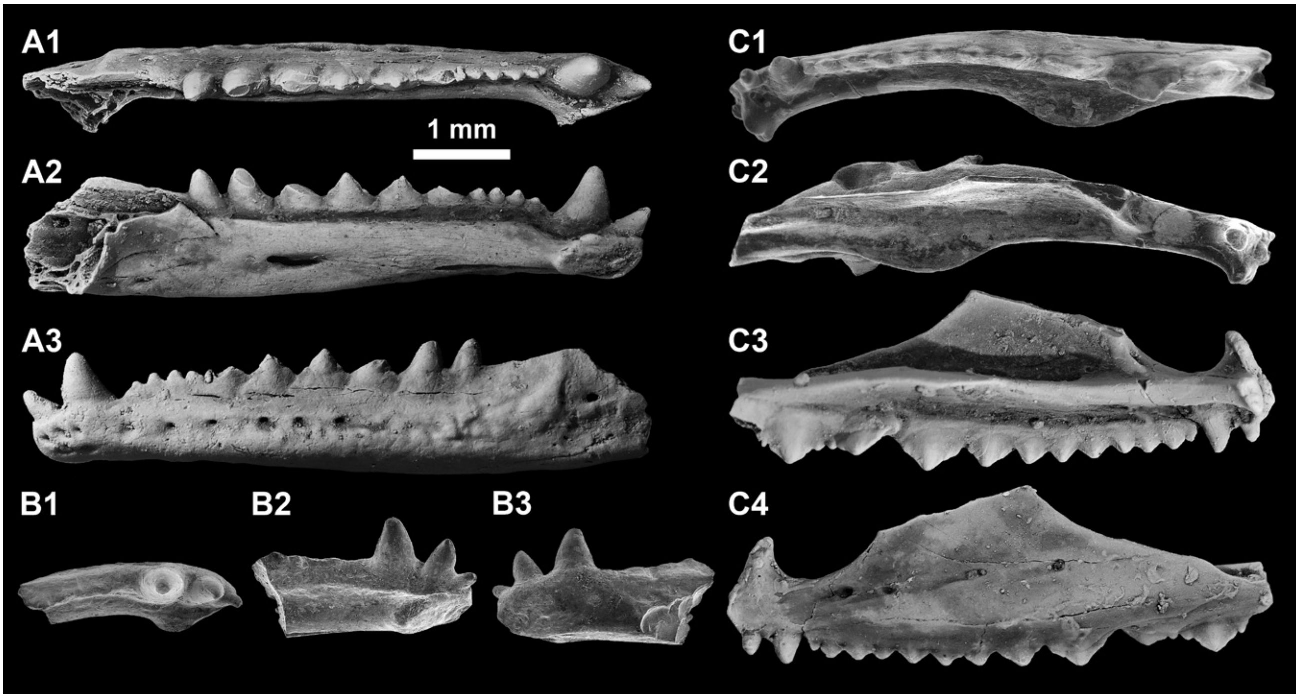

Figure 3. ***Heterodontagama borsukae* gen. et sp. nov.**, Early Eocene, Vastan Lignite Mine, Gujarat, India. A. GU/RSR/VAS-2035, holotype, nearly complete left dentary, in occlusal (A1), lingual (A2) and labial (A3) views; B. GU/RSR/VAS-2046, anteriormost part of a left dentary in occlusal (B1), lingual (B2) and labial (B3) views; C. GU/RSR/VAS-2036, nearly complete left maxilla in occlusal (C1), dorsal (C2), lingual (C3) and labial (C4) views. The arrow indicates the splenial and dashed line indicate the suture with the dentary.

Diagnosis: Differs from Chamaeleonidae by having anterior pleurodont teeth and from Agamidae by presenting a splenial on the lingual face of the dentary and by having an significant labial process of the coronoid on the dentary. Among Priscagamidae, it differs from all taxa by presenting a rather short splenial. It further differs from *Priscagama* by presenting a short labial overlap of the coronoid on the dentary; from *Pleurodontagama* by having acrodont teeth; from *Mimeosaurus* by having a long and slender dentary, an elongated and lightly built maxilla, and by bearing some anterior pleurodont teeth; from *Phrynosomimus* by presenting the anterior inferior alveolar foramen of the dentary that opens between the splenial dorsal margin and the ventral margin of the subdental shelf of the dentary; and from *Flaviagama* by having an anteromedial process of the coronoid well-extending to the posterior end of the tooth row, under the last dentary tooth.

Heterodontagama borsukae **sp. nov.**
(Fig. 3)

Etymology*:* In honor of Dr. Magdalena Borsuk-Bialynica, Institute of Paleobiology, Polish Academy of Sciences, Warsaw, for her contribution to the knowledge of the Priscagamidae.

Holotype: GU/RSR/VAS-2035, nearly complete left dentary, with parts of splenial, coronoid and angular.

Paratype: GU/RSR/VAS-2036, nearly complete left maxilla.

Referred material: GU/RSR/VAS-2046, anteriormost part of a left dentary, GU/RSR/VAS-2050, a jaw fragment.

Type horizon and locality: Cambay Shale Formation, early to middle Ypresian, Early Eocene, Vastan Lignite Mine, Surat District, Gujarat, India.

Diagnosis: The same as the genus.

Description: The dentary GU/RSR/VAS-2035 (Fig. 3A) is elongated, slightly built, narrows anteriorly and bears twelve loci for teeth. It only lacks the posteriormost part of the bone. In lingual view, the symphysial facet is subelliptical and horizontal, the Meckelian sulcus opens anteriorly up to the fifth acrodont tooth where it is covered by the splenial, and a shallow subdental shelf is present below the tooth row. In labial view, the bone presents shallow rugosities and ten mental foramina. Discrete interdental wear facets are present on the dental parapet. Posteriorly, a large triangular depression is clearly visible and marks the contact with the antero-labial process of the coronoid that therefore covers the dentary.

The dentition is heterodont (Fig. 3A). The first two teeth are pleurodont and caniniform. The anteriormost tooth is small and strongly inclined forwards, the second tooth is more than 1.5 times the size of the first tooth. On specimen GU/RSR/VAS-2046 (Fig. 3B), a third pleurodont tooth is observed anterior to these first two teeth and is less than half the size of the tooth just behind it. The pleurodont teeth are followed by four small acrodont sub-conical teeth forming the hatchling dentition (*sensu* Robinson, 1976) and by four labio-lingually compressed, triangular and large acrodont teeth, increasing in size posteriorly. The last two teeth are slightly recurved posteriorly and the last apex is slightly striate.

The splenial is narrow dorso-ventrally in lingual view. It occupies two thirds of the dentary length and and covers most of the Meckelian sulcus (Fig. 3A). The anterior inferior alveolar foramen opens between the splenial dorsal margin and the ventral margin of the subdental shelf of the dentary. Two small mylohyoid foramina also open in the posterior portion of the splenial.

A small part of the angular bone is preserved on the posteroventral margin of the dentary (Fig. 3A).

The anterior process of the coronoid is partially preserved and visible on the lingual face of the dentary (Fig. 3A2). It fits into a slot in the dentary, extending up to the level of the last tooth.

The only maxilla definitively attributable to this taxon (GU/RSR/VAS-2036, Fig. 3C) preserved thirteen teeth and lacks its posteriormost part and the dorsal part of the facial process. In labial view, four labial foramina are open at the base of the facial process. The posterior margin of the facial process (suborbital margin of the maxilla) is convex and slopes smoothly to the posterior tip. It does not show any posterior reentrant for the jugal. The anterior margin of the facial process tapers ventrally, is curved inwards, and presents an important dorso-labial expansion anteriorly that contacted the premaxilla. In lingual view, the supradental shelf is shallow and the symphysial surface (maxillary lappet, *sensu* Evans, 2008) likely brings this maxilla into contact with the opposite maxilla behind the premaxilla.

The maxilla (Fig. 3C) is characterized by a strongly heterodont dentition corresponding to the same pattern as on the dentary GU/RSR/VAS-2035 (Fig. 3A). From front to back are present: two pleurodont teeth, five acrodont hatchling teeth and six additional acrodont teeth. The two last preserved teeth are tricuspid with two lateral accessory cusps located near the base of the main cusp.

Discussion: The maxilla and dentaries can be attributed with confidence to this taxon, because their sizes, and tooth morphologies closely match together.

Acrodont dentition occurs in families Priscagamidae, Agamidae, and Chamaeleonidae, which constitute the Acrodonta, and also in trogonophid Amphisbaenia and in Sphenodontida (Estes et al., 1988; Gans, 1960). The bones from Vastan are too large and teeth are too numerous to match with amphisbaenians. They resemble Sphenodontia by having a heterodont dentition, additional posterior teeth (Harrison, 1901; Cooper et al., 1970) and a reduced splenial (see Evans et al., 2002). However, the following characters are sufficient to assign the Indian dentaries and maxilla to Acrodonta (as recognized by Evans et al., 2002): anterior pleurodont teeth enlarged and caniniform; pleuroacrodont additional teeth; posterior teeth with blade like edge and additional lateral cusps; and absence of wear facets on the lingual side of the dentary (Fig. 3). Moreover, the deflection observed at the level of the premaxillary process and joining the symphysial surface of the maxilla behind the premaxilla is considered as an apomorphy of Acrodonta (Cope, 1864; Rieppel, 1984; Estes et al., 1988; Gauthier et al., 2012).

Among Acrodonta, the Vastan taxon differs from Chamaeleonidae by having pleurodont teeth and by presenting fully acrodont additional teeth (for a discussion of the differences between agamids and chamaeleonids see Moody & Rocek, 1980; Bailon, 1991; Blain, 2005; Delfino et al., 2008). The Vastan maxilla resembles that of many agamid lizards by having a distinct reentrant for the jugal. However, agamids do not present a well-developed splenial with posterior mylohyoid foramina and do not have a labial process of the coronoid on the dentary (restricted to a dorsal facet on the labial side of the lower jaw in extant agamids). Therefore, the Vastan taxon cannot be attributed to Chamaeleonidae or Agamidae. However these two characters are diagnostic of priscagamid lizards, an extinct group restricted to the Late Cretaceous of the Gobi Basin and considered as the sister group of living agamids or as the sister group to crown Acrodonta (Smith, 2009; Gauthier et al., 2012; for a contrary opinion, see Alifanov, 2000). The somewhat rugged lateral surface of the dentary (Fig. 3A3), the presence of a splenial bone and variations in tooth implantation (Fig. 3A2) are indeed reminiscent of some priscagamid lizards (Borsuk-Bialynicka and Moody, 1984).

Compared to the family Priscagamidae, the Vastan taxon differs from the species so far described by the presence of a rather short splenial, whereas priscagamids have a long splenial (Borsuk-Bialynicka and Moody, 1984). It resembles *Priscagama* by the presence of few semi-pleurodont posteriormost teeth and closely spaced teeth (their bases are fused together). It further resembles *Priscagama gobiensis* by having the anteromedial process of the coronoid fitting into a slot beneath the tooth-bearing border of the dentary, up to the level of the last tooth (Smith, 2009). However, this overlap of the coronoid is long in *Priscagama*, whereas it is short on the Vastan taxon. This latter presents anterior pleurodont teeth on a long and slender dentary and an elongated and lightly built maxilla. These characters also preclude attribution of the new species to *Pleurodontagama* which has a completely pleurodont dentition, or to *Mimeosaurus*, which has a completely acrodont dentition (Borsuk-Bialynicka and Moody, 1984; Borsuk-Bialynicka, 1996). Moreover, *Mimeosaurus* presents short and robust bones (notably a short and deep maxilla; Gao & Hou, 1996). *Phrynosomimus* presents an anterior inferior alveolar foramen of the dentary opening ventral to the anteroventral process of the coronoid at splenial-dentary suture (see Alifanov, 1996; Gao & Norell, 2000), whereas this foramen opens between the dorsal margin of the splenial and the ventral margin of the subdental shelf of the dentary in the new species. *Flaviagama* presents an anteromedial process of the coronoid that does not extend to the posterior end of the tooth row, whereas this process extends well under the last dentary tooth on the Vastan taxon (Fig. 3A2). Moreover, the teeth of *Flaviagama* (see Alifanov, 1989: fig. 1f) seem more pleurodont than acrodont. All these characters allow us to attribute the above described material to a new genus and species, *Heterodontagama borsukae*.

Family Agamidae Spix 1825

Genus *Suratagama* gen. nov.

Etymology: In reference to the *Surat* District in Gujarat, India and a*gama*, a suffix for agamid taxa.

Type and only known species: *Suratagama neeraae* sp. nov.

Diagnosis: Differs from extant and most fossil agamids by having six small, cylindrical and pointed pleurodont teeth; differs from Uromastycinae by presenting teeth with pointed apexes; differs from most of the Eurasian Paleogene agamids by lacking anterior and posterior carinae on dentary and maxillary teeth.

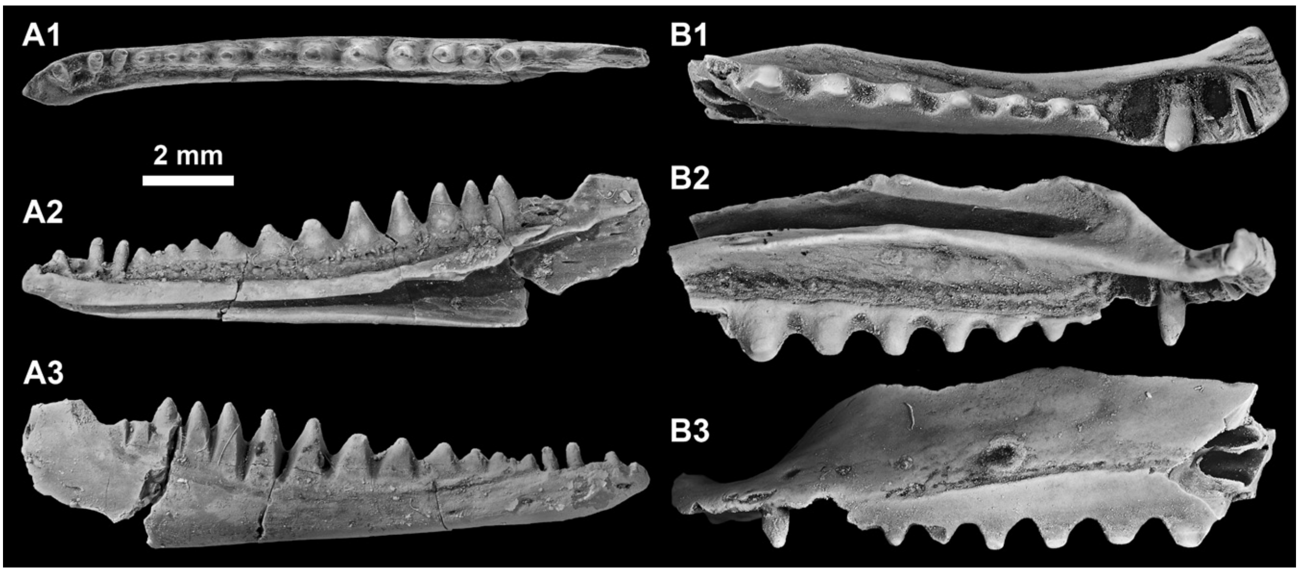

Figure 4. *Suratagama neeraae* gen. et sp. nov., Early Eocene, Vastan Lignite Mine, Gujarat, India. A. GU/RSR/VAS-2030, holotype, nearly complete right dentary, in occlusal (A1), lingual (A2) and labial (A3) views; B. GU/RSR/VAS-2033, nearly complete left maxilla in ventral (B1), lingual (B2) and labial (B3) views.

***Suratagama neeraae* sp. nov.**
(Fig. 4)

Etymology: In honor of Prof. Neera Sahni, Panjab University, Chandigarh.

Holotype: GU/RSR/VAS-2030, a nearly complete right dentary.

Referred material: GU/RSR/VAS-2033, a partial left maxilla and GU/RSR/VAS-2040, middle to anterior part of a right dentary.

Type horizon and locality: Cambay Shale Formation, early to middle Ypresian, Early Eocene, Vastan Lignite Mine, Surat District, Gujarat, India.

Diagnosis: The same as the genus.

Description: GU/RSR/VAS-2030 is a right, elongated and lightly built dentary presenting eighteen loci for teeth and lacking only its postero-ventral tip. In lingual view, the posterior part of the Meckelian sulcus opens rather widely and narrows anteriorly and extends up to the base of the first pleurodont tooth. The symphysial surface is small, subelliptical and located beneath the anterior tip of the subdental shelf. Under the level of the last posterior tooth, a triangular surface (or intramandibular lamella *sensu* Smith, 2009) marks the contact between the anteromedial process of the coronoid and the dentary. In labial view, the dentary is evenly smooth with five small, elliptical mental foramina. The first is below the posterior side of the first pleurodont tooth whereas the posteriormost one is located under the sixth acrodont tooth. There is a faint labial ridge extending all along the base of the acrodont teeth. Posteriorly, the coronoid process is broken above the level of the tooth row but clearly projects dorsally. Interdental wear facets are well-developed on the dental parapet.

The dentition is heterodont. All the teeth are unicuspid and lack anterior and posterior carinae. GU/RSR/VAS-2030 presents six anterior loci for small, cylindrical and pointed pleurodont teeth, but only two of them are preserved. A very short diastema separates them from five acrodont, closely spaced, labio-lingually compressed, triangular hatchling teeth (the second tooth being extremely small and reduced to a tiny cusp) gradually increasing in size posteriorly. Eight pleuroacrodont teeth are present in the posterior part of the dentary. The first two teeth are triangular and labio-lingually compressed and resemble the hatchling dentition. The last five teeth are more conical, less labio-lingually compressed and their tip is more pointed. The last tooth is missing, only the locus has been preserved indicating the presence of this last tooth. A single replacement pit seems to open at the base of the fifth pleurodont tooth (counted from front to back).

GU/RSR/VAS-2033 is the anterior part of a left maxilla presenting ten loci for teeth. Seven of them are complete, three others are restricted to tooth bases. A rather deep supradental gutter extends lingually above the tooth row (as on the dentary). The facial process only preserved its base which is antero-posteriorly elongated. Anteriorly, the premaxillary process is poorly developed.

The dentition of the maxilla is very similar to that of the dentary teeth. Four anterior loci for pleurodont teeth are present. However, only one tooth is preserved which is elongated, cylindrical and presents a pointed apex. The acrodont teeth are unicuspid, labio-lingually compressed, triangular and lack anterior or posterior carina.

Discussion: The maxilla and dentaries are associated based on similarities in morphology and size, number and succession of the teeth. They also share the presence of a rather broad subdental and supradental gutter between the teeth bases and the dental shelf.

The presence of an intramandibular lamella marking the contact between the anteromedial process of the coronoid and the dentary is a synapomorphy of Iguania (Smith, 2009; Gauthier et al., 2012). Anterior pleurodont teeth enlarged and caniniform, triangular acrodont teeth, presence of posterior pleuroacrodont teeth, and absence of wear facets on the lingual side of the dentary are sufficient to assign this taxon to Acrodonta. Among this group, the absence of splenial is characteristic of agamid lizards.

Within this family, the Vastan taxon differs from extant agamids by bearing six anterior pleurodont teeth whereas extant species usually have between 1 and 5 pleurodont teeth, replacing the anterior part of the hatchling series (Cooper et al., 1970). This great number of anterior pleurodont teeth is nevertheless not necessarily a primitive or derived condition within Acrodonta (Smith & Schaal, 2011).

At Vastan, two Eocene agamid species have previously been described (Prasad and Bajpai, 2008). Both species *Vastanagama susanae* and *Tinosaurus indicus* differ respectively from the present species by having three to four pleurodont teeth. One further agamid lizard, *Bharatagama rebbanensis*, known from the Jurassic of India (Evans et al., 2002), presents five anterior pleurodont teeth. However, it is about half the size of the Vastan species, the diastema between the pleurodont teeth and the hatchling teeth and the junction between hatchling and posterior acrodont teeth is more pronounced, the dentary is higher dorso-ventrally, and labially only three wear facets are present at the tooth bases.

Other agamid species are known from the Paleogene of Eurasia. However, these taxa have fewer anterior pleurodont teeth than the Vastan taxon and present distinct anterior and posterior carinae on acrodont teeth. As an example, from the Oligocene of the Phosphorite du Quercy, France, *Uromastyx europaeus*, has no anterior pleurodont teeth and *Quercygama galliae* has only three pleurodont teeth (Augé & Smith, 1997). Among Paleogene fossil agamids, the Uromastycinae indet. described by Averianov & Danilov (1996) from the Early Eocene of Kyrgyzstan have pleuroacrodont teeth bearing blunt crowns without a pointed central cusp. This is an apomorphic character of Uromastycinae according to Alifanov (1991) and Averianov & Danilov (1996). Indeed, the crown of the pleuroacrodont teeth of *Uromastyx* is subhorizontal and bears an antero-posteriorly oriented cutting edge (see Averianov & Danilov, 1996: figs 1-6; Augé, 2005: fig. 46). These features likely result from the necessity of precise occlusion linked to the herbivorous condition of *Uromastyx* (Schwenk, 2000). Finally, the posterior additional teeth of the Vastan taxon presenting a pointed tip differ strongly from those of uromastycine lizards and from the posterior teeth of *Brevidensilacerta xichuanensis* from the Middle Eocene of China, which have a rounded apex and no pointed central cusp (Li, 1991).

The only fossil agamid with tooth morphology approaching that of the Indian taxon is an incomplete dentary (Acrodonta HD-1) from the Middle Eocene of China (Huadian Basin, Jilin Province; Smith & Schaal, 2011). This specimen presents six anterior pleurodont teeth on the dentary, and has tall and unicuspid acrodont teeth lacking anterior and posterior carinae. Acrodonta HD-1 possibly represents the same taxon as *Suratagama neeraae*.

Genus *Vastanagama* Prasad and Bajpai, 2008

***Vastanagama susanae* Prasad and Bajpai, 2008**
(Fig. 5A)

Holotype: IIT-1050, anterior part of left dentary (Prasad and Bajpai, 2008: fig. 2-3).

Referred material: GU/RSR/VAS-2001-2002, nearly complete right dentaries, GU/RSR/VAS-2003, anterior part of a left dentary, GU/RSR/VAS-2007, anteriormost part of a left maxilla, and GU/RSR/VAS-2031, anteriormost part of a right maxilla.

Type horizon and locality: Cambay Shale Formation, early to middle Ypresian, Early Eocene, Vastan Lignite Mine, Surat District, Gujarat, India.

Remark: This species was originally described under the name *Vastanagama susani* (Prasad and Bajpai, 2008). We modify the species name in *V. susanae* to agree with the gender of the person honored, Dr. Susan E. Evans.

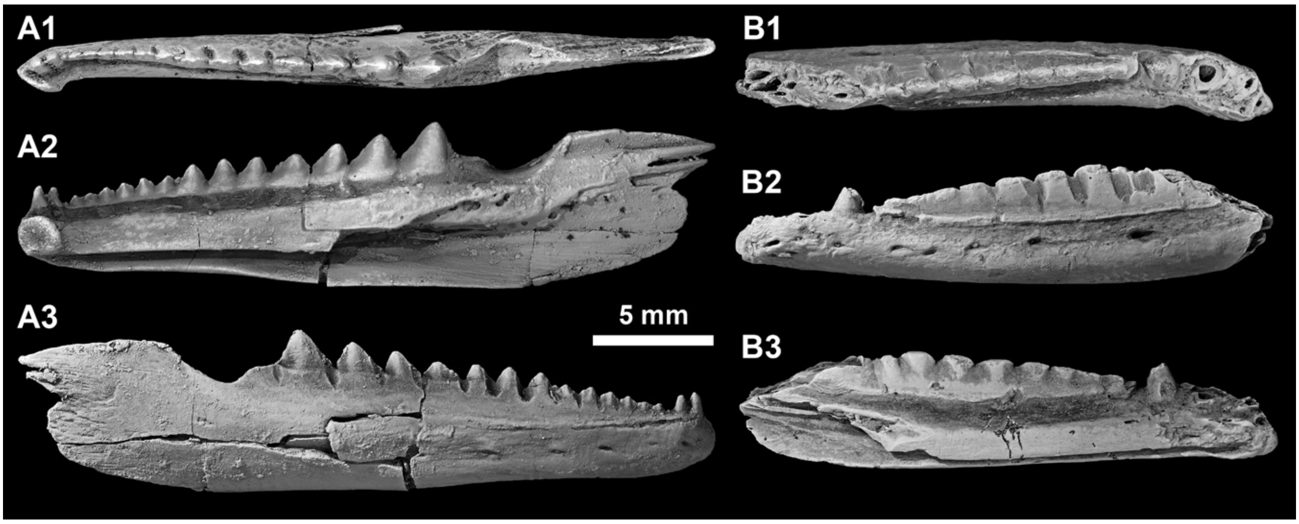

Figure 5. A. ***Vastanagama susanae***, Early Eocene, Vastan Lignite Mine, Gujarat, India; GU/RSR/VAS-2001, nearly complete right dentary, in occlusal (A1), lingual (A2) and labial (A3) views. B. ***Indiagama gujarata* gen. and sp. nov.**, Early Eocene, Vastan Lignite Mine, Gujarat, India; GU/RSR/VAS-2009, nearly complete left dentary, in occlusal (B1), labial (B2) and lingual (B3) views.

Emended diagnosis: Differs from all known taxa of agamid lizards by the following combination of characters: sub-circular symphysis surrounded by a weak raised ridge and dorso-lingually located above the anterior end of the Meckelian sulcus; Meckelian sulcus with a narrow anterior part and widely open posteriorly; subdental shelf rather deep anteriorly that tapers steadily after the level of the 12th tooth; closely spaced heterodont dentition with three anterior pleurodont teeth, followed by 5-6 small, acrodont hatchling teeth and seven pleuroacrodont additional teeth; triangular and labio-lingually compressed hatchling and additional teeth with some bearing minute lateral cups.

Description: GU/RSR/VAS-2001 (Fig. 5A) is a nearly complete, elongated right dentary (33 mm long) which evenly tapers anteriorly (2.0 mm depth anteriorly; 7.0 mm depth posteriorly). In lingual view, the symphysis is subcircular. The Meckelian sulcus opens widely posteriorly and is reduced to a narrow labiolingually-oriented furrow anteriorly. The subdental shelf is rather high dorso-ventrally and a subdental gutter is present at the base of the teeth. Behind the last tooth, the dorsal margin presents an important depression that could represent the imprint of a broken tooth. However, it is doubtful because the same depression is also present on dentary GU/RSR/VAS-2002. The posterodorsal end of the dentary bears a moderately elevated coronoid process projecting posteriorly and presenting a bifurcated posterior end.The coronoid process also shows a distinct facet extending beneath the subdental shelf to receive the anteromedial process of the coronoid bone. In labial view, the dentary is smooth, moderately convex labially and presents a row of 6 foramina, situated in the anterior half of the bone (the first opens below the second pleurodont tooth, the last below the twelfth tooth; Fig. 5A3). The posterior area shows no contact trace with the coronoid. The dental parapet shows deep, V-shaped interdental wear facets. These latter are absent on the lingual surface of the dentary.

The dentition is heterodont and begins with two pleurodont teeth (an incipient third pleurodont tooth is present on dentary GU/RSR/VAS-2002). The first tooth is larger than the second one. Both teeth are slightly curved lingually, their base is enlarged and their tip is moderately pointed. They are followed by 6 small, hatchling acrodont teeth. These teeth are triangular, labio-lingually compressed and bear a blunt tip. They are closely spaced and fused at their bases. Incipient lateral cusps are present on some of these teeth. The posterior acrodont teeth are triangular, labio-lingually compressed, pleuroacrodont, markedly larger than the hatchling teeth and steadily increase in size posteriorly. All the posterior teeth show two sharp, anterior and posterior carinae and some small additional cusps appear on those carinae. However, their number and implantation on each tooth is particularly irregular. Indeed, on specimen GU/RSR/VAS-2001, the fourth additional tooth shows two anterior and one posterior cusp, whereas the fifth additional tooth bears no cusp.

Discussion: Except for minor variations, the dentaries described here are very similar in morphology and size to the dentaries assigned to *Vastanagama susanae* by Prasad & Bajpai (2008). The new material from Vastan allows additional observations and emendation of the original diagnosis, in particular the irregular pattern of cusp implantation on additional subacrodont teeth. As far as we know, this pattern is unique among agamid lizards.

Prasad & Bajpai (2008) used a combination of characters that allows reference of *Vastanagama* to agamid lizards. The absence of an anterolabial process of the coronoid confirms this attribution. However, a character described in the specimens of *Vastanagama* by Prasad & Bajpai (2008), the presence of long, narrow facet for the angular on the ventral margin of the dentary seems absent from our specimens. The angular certainly became fused to the dentary along its ventral margin with increasing size and this may be related to the ontogenetic stage. According to Frost & Etheridge (1989), among acrodont iguanians, the angular can be fused to neighboring bones.

In particular, *Vastanagama susanae* differs from *Tinosaurus* by its small cups and its deep anterior subdental shelf. It also differs from three Eocene agamids from Mongolia, *Zephyrosaurus*, *Talosaurus* and *Mergenagama* (Gao & Dashzeveg, 1999) in having a narrow Meckelian sulcus anteriorly and a long and rather flat coronoid process. *Vastanagama* differs also from Acrodonta HD-1 and HD-2 from the Middle Eocene of China (see Smith & Schaal, 2011) respectively by having two pleurodont teeth (6 on HD-1) and by its well-developed accessory cusps (no accessory cusps on HD-2).

Genus *Indiagama* gen. nov.

Etymology: In reference to India and a*gama*, a suffix for the agamid taxa.

Type and only known species: *Indiagama gujarata* sp. nov.

Diagnosis: Differs from chamaeleonid lizards in having anterior pleurodont teeth and posterior pleuroacrodont teeth and resembles Agamidae in having a heterodont dentition and an open Meckelian groove. It differs further from all known fossil and recent agamid lizards in having rectangular teeth in lingual and labial view, unicuspid crowns forming a nearly horizontal cutting edge, and the presence of rectangular wear facets on both the lingual and labial side of the dentary.

***Indiagama gujarata* sp. nov.**
(Fig. 5B)

Etymology: In reference to the Gujarat State of India.

Holotype: GU/RSR/VAS-2009, an incomplete left dentary.

Type horizon and locality: Cambay Shale Formation, early to middle Ypresian, Early Eocene, Vastan Lignite Mine, Surat District, Gujarat, India.

Diagnosis: The same as the genus.

Description: The holotype, GU/RSR/VAS-2009, is a partial left dentary lacking an unknown portion of the posterior end and presenting 12 loci for teeth (Fig. 5B). It is the only specimen of this morphology known from the Vastan locality. This dentary is robustly built and its preserved section measures 23 mm long. In lingual view, its ventral border is evenly curved and it steadily narrows anteriorly. A well-developed and deep dental gutter is present along much of the tooth row and overcomes a deep subdental shelf which is of equal dorso-ventral height along most of the dentary. Beneath the subdental shelf, the Meckelian sulcus is reduced to a very narrow furrow extending up to the poorly preserved symphysis. Posteriorly, the Meckelian sulcus becomes widely open after the level of the 6th acrodont tooth. In labial view, the surface is slightly convex labially with a row of seven foramina. The first foramen is located beneath the base of the first pleurodont tooth whereas the posterior-most one is under the last preserved posterior tooth. Well-developed wear facets are mainly present on the labial side of the dentary but some shallow marks could be also observed on the lingual side of the bone. A faint labial ridge extends all along the base of the acrodont teeth.

The dentition is heterodont. The first four teeth are pleurodont and widely spaced. However, none of them is fully preserved. The fourth tooth preserved its base which is large stoutly built, and circular in cross-section. Although broken, this tooth is much higher than the nine adjacent hatchling teeth. These latter are closely spaced and increase progressively in size. Their tooth shafts become progressively labio-lingually compressed towards the apex. The first four acrodont teeth are heavily worn and closely spaced with their shafts nearly fused. The last five additional teeth are also acrodont, rectangular and their bases are closely spaced but the lateral sides of their shaft are separated lingually and labially by large and rectangular wear facets. These teeth show no trace of accessory or main cusps. Finally, in dorsal view, the teeth apexes are so well-aligned that they form a long and distinct cutting edge.

Discussion: The presence of heterodont dentition and an open Meckelian groove suggest affinities with the family Agamidae. The presence of unicuspid rectangular acrodont teeth presenting rectangular wear facets in lingual and labial view and forming a nearly horizontal cutting edge in occlusal view distinguishes this Vastan taxon from all known extinct and living agamid lizards. Moreover, the other agamid genera described at Vastan differ from this taxon in having triangular, pluricuspid additional teeth and not fused hatchling teeth.

The hatchling dentition of the extant agamid genus *Uromastyx* tends to become fused during ontogeny and the additional pleuroacrodont teeth appear somewhat rectangular in profile. Moreover, *Uromastyx* usually presents lost or reduced anterior pleurodont teeth although according to Cooper & Poole (1973) or Robinson (1976) some specimens can present caniniform pleurodont teeth. Three Paleogene agamid taxa with unicuspid teeth have been referred to *Uromastyx*: Uromastycinae indet. from the Early Eocene of Kyrgyzstan (Averianov & Danilov, 1996), *Uromastyx europaeus* from the Early Oligocene of France (Augé, 1988) and an indeterminate Uromastycinae from the lower Oligocene of Egypt (Holmes et al., 2010). However, the dentary of the Vastan taxon differs strongly from *Uromastyx* in having a Meckelian sulcus reduced to a narrow furrow anteriorly and limited by parallel dorsal and ventral rims, whereas the Meckelian sulcus of *Uromastyx* steadily tapers anteriorly.

The dentary of the Vastan taxon is also similar to the dentary of *Brevidensilacerta xichuanensis* from the Middle Eocene of Xichuan, Henan Province, China, (Li, 1991). However, this latter species has smaller teeth, curved pleurodont teeth, the dental gutter is closed beneath the sixth pleuroacrodont tooth, and the Meckelian sulcus tapers steadily anteriorly. In particular, several features of the specimens figured by Li (1991: fig 1) require considering the possibility of referring *Brevidensilacerta* to uromastycine lizards.

Genus *Tinosaurus* Marsh, 1872

Type species *Tinosaurus stenodon* Marsh, 1872

***Tinosaurus indicus* Prasad and Bajpai, 2008**
(Fig. 6)

Holotype: IITR/SB/VLM/ 904, left dentary (Prasad and Bajpai, 2008: fig. 5-6).

Referred material: GU/RSR/VAS-2008, 2015, 2037-2039, 2051-2052, seven dentary fragments; GU/RSR/VAS-2016-18, 2022-2023, 2025-2026, seven maxillary fragments.

Type horizon and locality: Cambay Shale Formation, early to middle Ypresian, Early Eocene, Vastan Lignite Mine, Surat District, Gujarat, India.

Diagnosis: see Prasad & Bajpai (2008).

Description: The best preserved dentary, GU/RSR/VAS-2008 (Fig. 6A) is an elongated, slender and rather delicate incomplete left dentary of 20 mm long. It only lacks the posterior end. The dental row is incomplete and only nine loci are preserved. In lingual view, the symphysis is a nearly horizontal elliptical, narrow, anteroposteriorly elongated facet. The Meckelian sulcus is broken posteriorly. However, it is steadily narrows anteriorly, ending beneath the symphysis where it very shallow and ventrally oriented. A deep, slightly concave dental gutter extends along the tooth bases and a convex subdental shelf overhangs the Meckelian sulcus. In labial view, the dentary presents five elliptical small mental foramina and the dental parapet shows deep, V-shaped interdental wear facets. These facets are absent on the lingual surface of the dentary. In dorsal view, the bone is convex, tapers anteriorly and ends with a weak mandibular symphysis.

The dentition is heterodont. The teeth are well-individualised and gradually increase in size posteriorly. GU/RSR/VAS-2008 presents three rather closely spaced anterior pleurodont teeth. However, these teeth are broken. The morphology of the pleurodont teeth can be seen on GU/RSR/VAS-2015, an anterior fragment of a left dentary that preserved the third complete pleurodont tooth and the bases of the two others. The third tooth is conical, unicuspid, high, slightly posteriorly recurved and bears a rather pointed apex. On GU/RSR/VAS-2008, the pleurodont teeth are followed by three small, acrodont, hatchling teeth. These latter are poorly preserved and however present a similar morphology to the adjacent pleuroacrodont teeth, except for their size. These last four teeth are triangular, widely spaced and much larger than the hatchling teeth. They are tricuspid, the main central cusp being slightly directed posteriorly and bordered by two smaller lateral cusps. As the posterior part of the dentary is missing, the number and the morphology of the posteriormost teeth are unknown. It also appears that the base and the lateral margins of the posteriormost additional teeth are somewhat squared off in labial view.

GU/RSR/VAS-2037 is a relatively well-preserved left dentary lacking its anterior tip. Its posterior extremity is preserved and confirms that the posterior part of the Meckelian sulcus opens widely. Medially, beneath the level of the two last teeth, a subtriangular surface marks the contact between the anteromedial process of the coronoid and the dentary in the posterodorsal area. The coronoid process slightly projects dorsally, posteriorly to the level of the tooth row. The posterior additional teeth resemble those described above. However, they are less widely spaced, the lateral sides of the posterior additional teeth seem squared off (particularly in labial view) and their lateral cusps are more developed. This observation is nevertheless here considered as being intraspecific or ontogenic variation as it is also observed in extant agamid lizards.

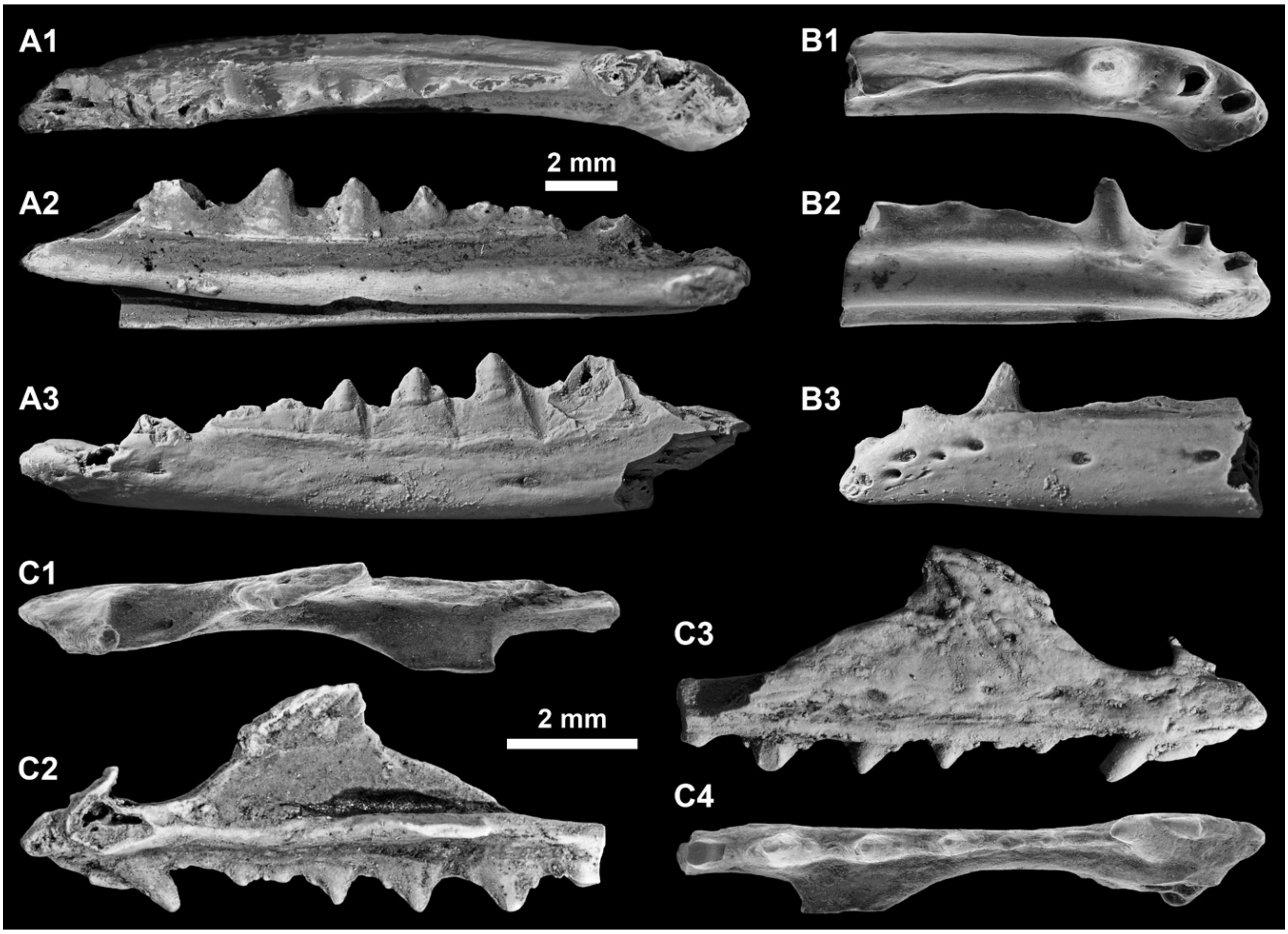

Figure 6. ***Tinosaurus indicus***, Early Eocene, Vastan Lignite Mine, Gujarat, India. **A**. GU/RSR/VAS-2008, nearly complete left dentary, in occlusal (A1), lingual (A2) and labial (A3) views; B. GU/RSR/VAS-2015, anteriormost part of a left dentary in occlusal (B1), lingual (B2) and labial (B3) views; **C**. GU/RSR/VAS-2018, nearly complete right maxilla in dorsal (C1), lingual (C2), labial (C3) and occlusal (C4) views.

The right maxilla GU/RSR/VAS-2018 (Fig. 6C) is incomplete and lacks its anteriormost and posteriormost extremities. Eight loci for teeth are preserved. A triangular facial process is nearly complete. Its top is located above the level of the first additional, pleuroacrodont tooth and no important medial deflection is observed. Posteriorly, the facial process descends sharply (it is nearly vertical) and at the level of the second additional tooth, it drops gradually towards the posterior end of the tooth row, beyond the level of the palatine process, and does not reach the posterior end of the maxilla. The posterodorsal margin of the facial process (suborbital margin of the maxilla) has no reentrant for the jugal, and no lacrimal indentation or trace of contact with the lacrimal or the prefrontal is visible on the medial surface of the facial process. In lingual view, the supradental shelf is shallow along the entire length of the maxilla except above the first pleuroacrodont tooth, where it is expanded medially, forming a well-developed palatine process. In labial view, the facial process presents a rugged surface and a row of five-six labial foramina. In dorsal view, the premaxillary process is dorsally and medially deflected, forming a well-developed dorsal expansion that certainly contacted the nasal process of the premaxilla. The medial expansion of this process is unknown as the medial end of the maxilla is damaged. However, the supradental shelf was likely in contact with the opposite maxilla behind the premaxilla.

The dentition is similar to that of the dentary GU/RSR/VAS-2008. The first two anterior teeth are conical, pleurodont, and the second tooth is likely much larger than the first one. This caniniform tooth is very inclined posteriorly. A diastema separates the pleurodont teeth from the hatchling, acrodont series presenting two small, triangular tricuspid teeth. Immediately adjacent to these teeth, four additional teeth, increasing in size posteriorly, are very similar to those of the additional series of the dentary. In labial view, interdental, triangular wear facets are present on the surface of the maxilla. These wear facets are absent lingually.

Discussion: Maxillae and dentaries have been associated based on their similar tooth morphology and distribution. However, the best-preserved maxilla GU/RSR/VAS-2018 (Figure 6C) is smaller than the dentaries. It is therefore interpreted as belonging to a young individual. The presence of heterodont dentition, an open Meckelian groove and a medial contact of the maxillae behind the premaxilla are characteristic of Agamidae. Within agamid lizards, *Leiolepis* and Draconinae and *Tinosaurus* present tricuspid teeth. However, the peculiar morphology of the tricuspid pleuroacrodont teeth and similar shape and size allow to identify this last Vastan taxon as *Tinosaurus indicus* described by Prasad & Bajpai (2008). This attribution can be confirmed by the following characters: the dentary is long (GU/RSR/VAS-2008 is 20 mm) ; teeth present a high central cusp surrounded by lateral smaller cusps ; the presence of a narrow, cylindrical subdental ridge between the Meckelian fossa and the alveolar border ; the presence of a nearly horizontal, elliptical, narrow, anteroposteriorly elongated symphysial facet ; and closely spaced hatchling teeth versus widely spaced pleuracrodont teeth.

Smith & Schaal (2011) proposed a thorough revision of the genus *Tinosaurus*. In this revision, the author suggest that *Tinosaurus* is monophyletic and may be easily distinguished from most extant and fossil agamids. It also appears that a close relationship exists between *Tinosaurus*, *Uromastyx* and *Leiolepis*. *Uromastyx* and *Leiolepis* may be sister-taxa and are basal agamid lizards. The new Vastan specimens indicate that: 1) In *T. indicus*, the hatchling acrodont teeth are much smaller than the posterior additional teeth. A similar size difference is seen in *Leiolepis belliana* and in other species attributed to *Tinosaurus* such as *T. domuensis* (Hou, 1974). 2) The symphysial facet of *T. indicus* is horizontally oriented, as in *T. europeocaenus*, *Draco* (Agaminae) and *Hydrosaurus* (Evans et al., 2002: fig. 10) whereas in many agamid lizards, the symphysis enlarges and becomes subvertical. 3) The lack of lacrimal indentation on the posterodorsal side of the facial process also occurs in *Uromastyx* and *Leiolepis*, as well as in Iguanidae, thus it may be a primitive feature. In addition, *T. indicus* has no reentrant for the jugal on the posterodorsal margin of the facial process. Among agamids, *Tinosaurus* is uniquely similar to *Leiolepis* in this respect. These characters indeed support the observations of Smith & Schaal (2011).

5. Discussion and conclusion

5.1. Diversity of the lizard fauna

The assemblage of lizards from Vastan is only composed of acrodontan lizards including one priscagamid and four agamids represented by five genera and five species. This pattern of low lacertilian diversity suggests that, before its isolation, India has been successfully colonized by relatively few lizard lineages (i. e., stem agamid lizards) and that subsequently, agamids certainly radiated to unusually high abundance and species richness in India when this continent was isolated (Fritz & Rahbek, 2012). Other closely related cases are known including the diversity of agamid lizards in Australia (more than 60 recognized species in 13 genera, Cogger, 2000; Melville et al., 2001) or the marked radiation of Chamaeleonidae in Madagascar (Raxworthy et al., 2002; Townsend & Larson, 2002). The presence and diversity of agamids identified in the Early Eocene of the Vastan Lignite Mine in India likely confirm this hypothesis. Similarly, the assemblage of amphibians is only composed of frogs which are relatively diverse, with at least four families. Salamanders are absent at Vastan (Folie et al., 2013).

The long presence of Acrodonta in India is attested by the lizard assemblage reported from the Early-Middle Jurassic of the Kota Formation of peninsular India (Evans et al., 2002). Before this, the occurrence of acrodont fossil priscagamids in Asia during the Late Cretaceous and records of pleurodont and acrodont lizards in the Campanian and Maastrichtian of Mongolia, China, Canada and Europe (e.g., *Xianglong* from the Early Cretaceous of China; Li et al., 2007) led several authors to suggest a Laurasian (Central Asian) origin of Acrodonta (Alifanov, 1993; Gao & Hou, 1995). The discovery of Acrodonta in India during the Jurassic supports their Gondwanian origin. This hypothesis was originally proposed by Estes (1983) and is still followed by several authors (e.g., Macey et al., 2000; Pianka & Vitt, 2003; Okajima & Kumazawa, 2010) including Melville et al. (2009). The molecular analysis made by these authors predicted that basal acrodont lizards existed in Gondwana prior to its fragmentation (see Melville et al., 2009 and literature therein) and estimated an Eocene origin of the Agaminae in Asia due to the India-Asia collision. Moreover, the Gondwanan origin of Acrodonta is consistent with the view that Agamidae vicariantly diverged from Chamaeleonidae on the India/Madagascar landmass (divergence time 100 – 85 MYA, Hedges et al., 2009).

5.2. Out-of-India hypothesis

Three of the four taxa identified in Vastan are endemic. They therefore do not bring information about dispersal of agamids In or Out of India.

The Out-of-India hypothesis was originally expressed by Krause & Maas (1990) who suggested that several faunal and floral groups in the modern Asian biota originated in the isolated Indian subcontinent, subsequently disembarking and spreading to the northern landmasses (Eurasia and North America, see Karanth, 2006). To be fair, fossil evidence relevant to the Out-of-India hypothesis is currently scarce (Bajpai & Kapur, 2008). For examples, among frogs, ranoids and maybe bombinatorids support a Gondwanan origin, with dispersal to Eurasia via India, as suggested by both paleontological (Folie et al., 2013) and molecular studies (Bossuyt & Milinkovitch, 2001; Bossuyt et al., 2006). Fossil evidence also includes the agamid lizards from the Early Eocene of Vastan (Prasad & Bajpai, 2008). The endemic agamid lizards from Vastan confirm this support for an Out of India dispersal. The lizard assemblage from Vastan is by far the richest and most diverse agamid fauna reported in the Cenozoic of Eurasia.

However, the presence of *Tinosaurus* and of a priscagamid lizard in Vastan contradicts the Out-of-India Hypothesis. Indeed, Prasad & Bajpai (2008) suggest that *Tinosaurus* is a descendent of *Tikiguania* from the Late Triassic of India involving dispersal "Out of India" to Asia when the initial land connection was established, or possibly even earlier by trans-Tethyan dispersals. However, the Early Triassic record of agamids in India is now questioned (Datta & Ray, 2006; Hutchinson et al., 2012). Moreover, the Paleocene record of continental Asia (i. e., excluding Indian subcontinent) includes *Qianshanosaurus huangpuensis, Anhuisaurus huainanensis*, and *Tinosaurus doumuensis* from the Paleocene of China (Hou, 1974), *Tinosaurus postremus* from the Paleocene of Central Asia (Averianov, 2001), and two undescribed species belonging to the subfamily Isodontosaurinae, erected by Alifanov (1993: table 1). *Tinosaurus doumuensis* has agamid relationships, as recognized by Hou (1974). In addition, the proportions of the dentary and the tricuspid teeth are clearly reminiscent of the agamid genus *Tinosaurus*, which is also the case of the dentary of *Tinosaurus postremus* Averianov 2001, from the Paleocene of Kazakhstan. The genus *Tinosaurus* was therefore already present in Asia before the India-Asia collision. Afterwards, fossil lizards of Early Eocene age in continental Asia are rare. Among them there are undescribed lizard remains from Mongolia (Dashzeveg et al., 1987; Alifanov, 1993), and from the Early Eocene (late Ypresian) of Kyrgyzstan (Averianov & Udovichenko 1993; Averianov & Danilov, 1996). These authors convincingly demonstrated that several lizard remains of Central Asia (Kyrgyzstan) are related to the extant agamid *Uromastyx*. In addition, a jaw fragment from the Early-Middle Eocene of Pakistan is referred to *Tinosaurus* sp. (Rage, 1987). *Tinosaurus* then dispersed from Asia in the Early Eocene (Smith, 2009). However, the route followed by these taxa is not clear. A route from Asia to North America is a first possibility. A second possibility could be a dispersal from Asia to Europe and then to North America. The presence of *Tinosaurus* in Europe (Earliest Eocene MP7 of Dormaal, Belgium; Augé, 2005) indeed likely precedes the occurrence of the genus in North America (Early Eocene Wa4 or younger, Wasatch Formation of the Washakie Basin, Wyoming, USA; Smith, 2006).

To sum up, the Asian acrodont record may be divided into three periods. 1) Late Cretaceous: only stem agamids (Priscagamidae) are attested in continental Asia; 2) Paleocene: it seems that both stem agamids (*Qianshanosaurus)* and more derived forms like *Tinosaurus* are present. 3) Eocene: Only crown agamids are present (e. g. *Uromastyx*; *Tinosaurus*). However, restudy of the Cenozoic agamid assemblages from Asia must precede further speculations on agamid dispersal between Asia and India. In addition, for several groups, the direction of faunal migration remains highly equivocal. For example, mammals from Vastan are close to European forms (Rana et al., 2008; Rose et al., 2009; Kumar et al., 2010) and according to Bajpai et al. (2009) the available data suggest that faunal dispersals between India and Asia were bidirectional (Chatterjee & Scotese, 2010). The presence of a group of Laurasian origin, anguid lizard, in the Maastrichtian of India at Naskal (Prasad & Rage, 1995) suggests an early terrestrial connexion between Eurasia and India implying dispersal into India rather than Out of India and Buffetaut (1987) points out an increase in Laurasian taxa on the Indian subcontinent early in the Tertiary. In the same vein, the presence of *Heterodontagama borsukae* at Vastan is surprising as the oldest members of this acrodont group are from the Upper Cretaceous of the Gobi Basin (Borsuk-Bialynicka & Moody, 1984). It therefore could result from dispersal of Asian Priscagaminae into India and represents a relictual species in the Early Eocene.

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