Journal of Paleontology, 92(2), 2018, p. 221–239
Copyright © 2017, The Paleontological Society
0022-3360/18/0088-0906
doi: 10.1017/jpa.2017.63

JOURNAL OF PALEONTOLOGY
A PUBLICATION OF THE Paleontological SOCIETY

A new hybodont shark (Chondrichthyes, Elasmobranchii) from the Upper Triassic Tiki Formation of India with remarks on its dental histology and biostratigraphy

Mohd Shafi Bhat,[1]* Sanghamitra Ray,[1] and P. M. Datta[2]

[1]Department of Geology and Geophysics, Indian Institute of Technology, Kharagpur 721302, India ⟨shafialig@gmail.com⟩, ⟨sray@gg.iitkgp.ernet.in⟩
[2]Greenwood Housing Cooperative Society Limited, 315B Upen Banerjee Road, Kolkata 700060, India ⟨shiladutta59@yahoo.in⟩

Abstract.—A new lonchidiid genus, *Pristrisodus*, from the Upper Triassic Tiki Formation of India is described based on multiple, well-preserved, isolated teeth. Comparative analysis resulted in synonymizing *Parvodus tikiensis* and *Lissodus duffini,* which are known from the same horizon and resulted in a new taxon, *Pristrisodus tikiensis* n. comb. These teeth are elongated with mesiodistal length greater than or equal to twice the labiolingual width and have a high principal cusp, lateral cusplets, a distinct ridge near the crown-root junction labially and higher up on the crown lingually, weak ornamentation, and linear depression along the crown-root junction. Five morphotypes based on overall shape, robustness and crown height are determined. The teeth show a gradual monognathic heterodonty. The anterolateral teeth (morphotypes I – II) have high, pyramidal principal cusp with two or three small but pointed cusplets, and triangular labial and lingual protuberance. The posterolateral teeth (morphotypes III – IV) have four incipient cusplets, relatively low principal cusp, bilobed/rounded, hanging labial and incipient lingual protuberances. Morphotype V comprises anterior teeth that are broad, triangular and robust, and have rounded/blunt principal cusp, one cusplet, and low, hanging labial peg. Multivariate analyses corroborate the qualitative assessment of the Indian hybodonts. Dental histology of *Pristrisodus* n. gen., shows that it is distinctly different from other lonchidiid genera. The assemblage of freshwater sharks, along with other vertebrate microfossils of the Tiki Formation, shows similarity with that of the lower Tecovas Formation of the Chinle Group, USA. The euryhaline nature resulted in the adaptation of the hybodonts to freshwater systems in India during the Carnian.

Introduction

Hybodont sharks, one of the most successful chondrichthyan lineages, appeared in the Late Devonian (Ginter et al., 2002) and became extinct at the end of the Cretaceous (Becker et al., 2004). The hybodonts attained a high diversity during the Triassic, but their abundance started decreasing from the Jurassic onwards (Cuny et al., 2007). These were mostly euryhaline, capable of inhabiting rivers and lakes (Cuny, 2012). Freshwater hybodont sharks are reported from different horizons throughout the world (Heckert, 2004; Fischer, 2008; Klug et al., 2010; Cappetta, 2012; Johns et al., 2014; Manzanares et al., 2016), although complete preservation of these forms are rare, and mostly represented by various types of teeth, cephalic spines, and scales (Fischer et al., 2010; Klug et al., 2010). All hybodonts are characterized by a tooth enameloid containing single apatite crystallites (Reif, 1973) and anaulacorhize or sponge-like pattern of root vascularization (Maisey, 1987; Cappetta, 2012).

In India, several isolated and discrete Gondwana basins (Fig. 1.1, inset) are rich in varied vertebrate fossil assemblages (Bandyopadhyay, 1999, 2011), including vertebrate microfossils (e.g., Datta et al., 1978; Datta, 1981, 2005; Yadagiri, 1986; Prasad and Sahni, 1987; Prasad and Cappetta, 1993; Patnaik, 2003). Studies on fossil fish teeth collected from the Gondwana sediments of India are scarce and was initiated by Jain et al. (1964), who reported an undescribed dipnoan, subholostean, and pleuracanth fishes from the Upper Triassic Maleri Formation of the Pranhita-Godavari (PG) Basin. Later, Jain (1980) described *Xenacanthus indicus* from the same formation. The hybodont fishes, including *Lonchidion indicus*, were described from the Jurassic Kota Formation of the same basin by Yadagiri (1986). Subsequently, the formation yielded different hybodont taxa (Prasad et al., 2004). Prasad et al. (2008) described multiple hybodonts from the Upper Triassic sediments of India, whereas a diverse assemblage comprising actinopterygians, dipnoans, and indeterminate chondrichthyans was reported from the Lower Triassic Panchet Formation of the Damodar Basin by Gupta (2009).

The current study focuses on a new collection of isolated hybodont teeth collected from the Upper Triassic Tiki Formation of the Rewa Gondwana Basin, India, which are described based on gross dental morphology and histology. Comparison with other existing Late Triassic hybodont taxa shows that these

---

* Corresponding author

belong to a new genus. Multivariate analyses are performed on the hybodont teeth to determine the validity and robustness of the new taxon.

Geological setting

The Rewa Basin is relatively long in ENE–WSW direction (Fig. 1.1) with basin-fill strata gently dipping towards the North. The Upper Gondwana succession of the basin comprises a thick, conformable, and continuous Triassic succession composed of the basal Pali Formation, followed upwards successively by the sand-dominant Karki and Tiki formations, which are unconformably overlain by the Jurassic Parsora Formation (Mukherjee et al., 2012). Of these formations, the Upper Triassic Tiki Formation is essentially a mud-dominated fluvial succession with subordinate amounts of coarse- to fine-grained quartzo-feldspathic sandstone units. The mudstone units have yielded a diverse array of vertebrate fossils, unionid bivalves, and petrified wood (Sahni and Tewari, 1958; Datta, 2004; Mukherjee et al., 2012; Mukherjee and Ray, 2014; Ray, 2015). Based on the overall floral and faunal content, the Tiki Formation is correlated with the lower part of the Maleri Formation of the Pranhita-Godavari Basin, the Ischigualasto Formation of Argentina, and the *Hyperodapedon* Assemblage Zone of the upper part of the Santa Maria Formation of Brazil, which places the Tiki fauna within the Ischigualastian Land Vertebrate Faunachron (LVF) and a proposed early Carnian age for the formation (Ray, 2015). However, recent recovery of a mystriosuchine phytosaur from the Tiki Formation suggests that the horizon could be younger than that previously proposed (Datta et al., 2016).

A vertebrate microfossil locality or microsite (sensu Sankey, 2008; Fig. 1.2) has yielded the specimens described in the current work. The fossils were extracted from a mudrock-rich unit, which is ~1.5 m thick and lies above a thick unit of peloidal calcirudites (Fig. 1.3). The mudrock unit is located in an overbank deposit and shows pedogenic modifications in the form of slickensides, color mottling, and glaebules (Bhat, 2017). Along with the hybodonts, the mudstone unit has yielded numerous teeth of yet undescribed xenacanthids and actinopterygians, isolated teeth, skull fragments and postcrania of basal tetrapods, lepidosauromorphs, archosauriforms, and cynodonts (Bhat, 2015; Bhat et al., 2015; Ray et al., 2016). In addition, the mudstone hosts partial and complete skeletal elements of large metoposaurid temnospondyls, phytosaurs, and rhynchosaurs.

Materials and methods

Material.—Studied material includes 45 well-preserved, isolated hybodont teeth from the Upper Triassic Tiki Formation of India, the details of which are given in Supplemental Data 1. For comparative purpose, the Indian species of the genera *Parvodus* (*P. tikiensis*) and *Lissodus* (*L. duffini*), as described by Prasad et al. (2008), are studied (Supplemental Data 2). The quantitative analyses include several other valid taxa in which the morphometric variables could be measured. These include *Parvodus rugianus* and *Parvodus curvidens* (Ansorge, 1990; Duffin and Theis, 1997; Underwood and Rees, 2002), *Lissodus minimus* (Duffin, 1993), *Jiaodontus montaltissimus*, and *Jiaodontus vedenemus* (Klug et al., 2010). The details of these taxa are given in Supplemental Data 2. These hybodont teeth are quantitatively analyzed based on measured morphometric variables (Fig. 2) such as the apicobasal height (ABH), mesiodistal length (MDL), labiolingual width (LLW), and height of the principal cusp (PCH). Ratio variables such as crown profile (ABH/MDL) and crown-base proportion (BL/BW), although used for qualitative description, were not used in the statistical analyses because these overemphasize some variables and do not help in differentiating the teeth (Hendrickx et al., 2015).

Vertebrate microfossil extraction.—Initial assessment of the microsite for fossil-richness was carried out by spot sampling using coning and quartering method, where the exposed area of the microsite was subdivided into four quadrants. Scree material from the surfaces of these quadrants was removed after careful examination for microfossils, and small quantities of rock samples were collected from each quadrant and examined for vertebrate microfossils. Considerable yield of vertebrate microfossils resulted in prospecting of the microsites for bulk sampling (Bhat, 2017). Litholog was prepared to ascertain the microfossil-bearing stratum, bulk samples of nearly three tons of red mudstone were collected, screened by wet and dry sieving methods, and residues examined under a microscope for extraction of vertebrate microfossils following the procedures outlined by Hibbard (1949), Cifelli et al. (1996), Heckert (2004), and Bhat (2017). Terminology used in the present work to describe tooth morphology (Fig. 2) follows Duffin (1985), Rees and Underwood (2002), Shimada (2002), Whitenack and Gottfried (2010), and Cappetta (2012).

Quantitative analyses.—Statistical analyses were performed using PAST 2.07c (Hammer et al., 2001). The analyses included a principal component analysis (PCA) to evaluate the differentiation of the specimens based on variance of their variables and a discriminant analysis (or canonical variate analysis, CVA) to assess the consistency of identification between qualitative and quantitative methods (Hammer and Harper, 2006). These analyses for taxonomic positioning of isolated teeth follow Smith (2005), Smith et al. (2005), and Hendrickx et al. (2015). Teeth with missing measurements may blur the analyses, and hence were omitted from the analyses.

Thin-section preparation.—Thin-sections of the hybodont teeth were prepared by using cutting and grinding techniques as suggested by Donath (1995). Before sectioning, the teeth were embedded in epoxy resin (Chinsamy and Raath, 1992), and ground and polished in the required direction by carborundum (silicon carbide) powder of various grit sizes (600–1000 μm). The tooth surface was subsequently cleaned with 0.5 μm α-alumina (Al_2O_3), and the polished surface was mounted on glass slides, 1.5–1.75 mm in thickness, with the help of an epoxy solution. The glass slide along with the embedded specimen was then cooled for 12–16 hours and the specimen was cut down to a thickness of 45 μm with the help of a PetroThin™ (Thin Section System). The thin section obtained was again ground manually to a thickness of 30–35 μm by carborundum powder. Final polishing of the specimen was performed with a

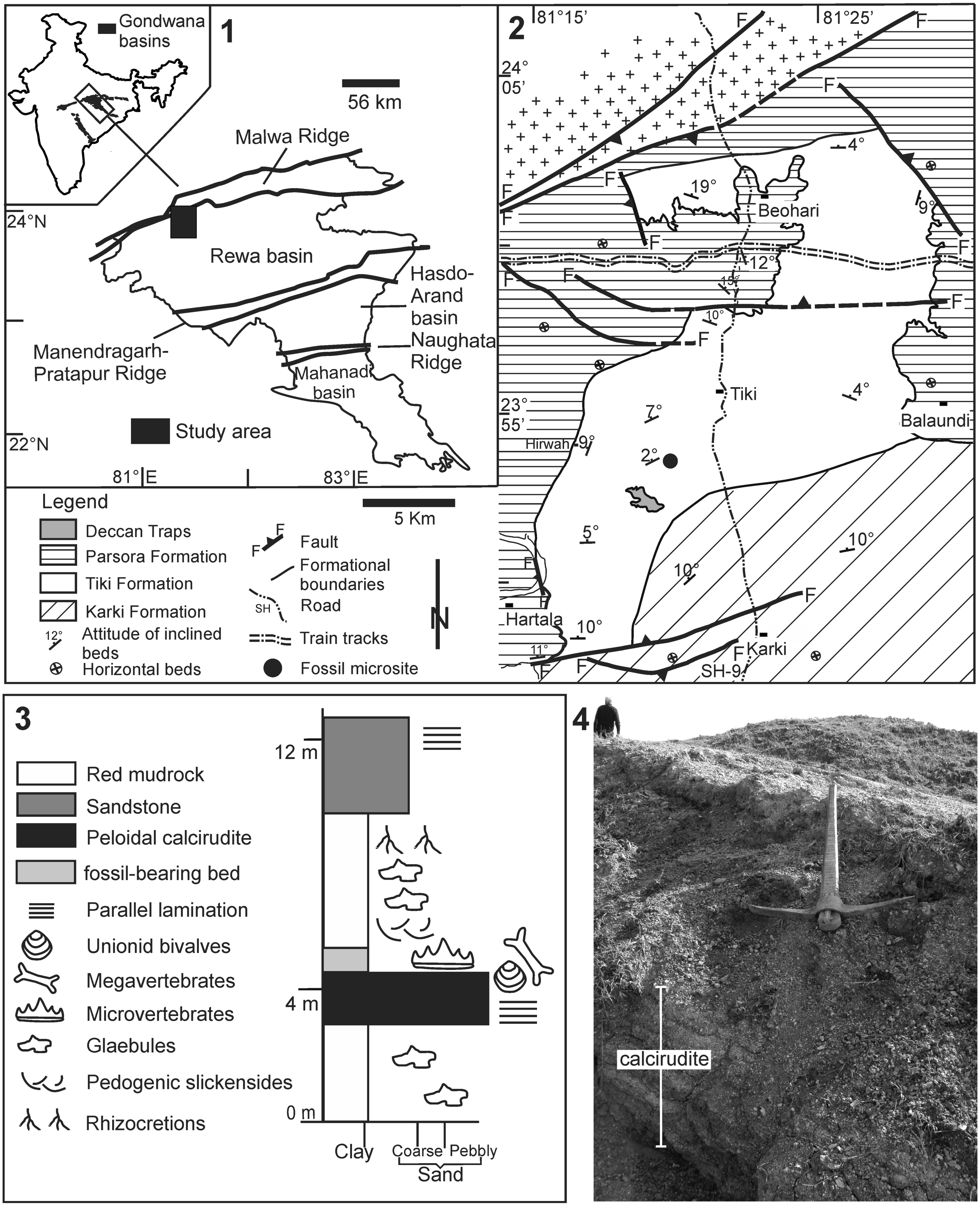

Figure 1. (**1, 2**), Geological maps of the (**1**) Rewa Gondwana Basin showing the study area. Inset: major Gondwana basins of peninsular India; (**2**) study area (after Mukherjee et al., 2012) showing the fossil microsite; (**3**) litholog showing the vertebrate microfossil-bearing mudstone horizon; (**4**) microvertebrate-bearing mudstone unit overlying the peloidal calcirudite (after Bhat, 2017).

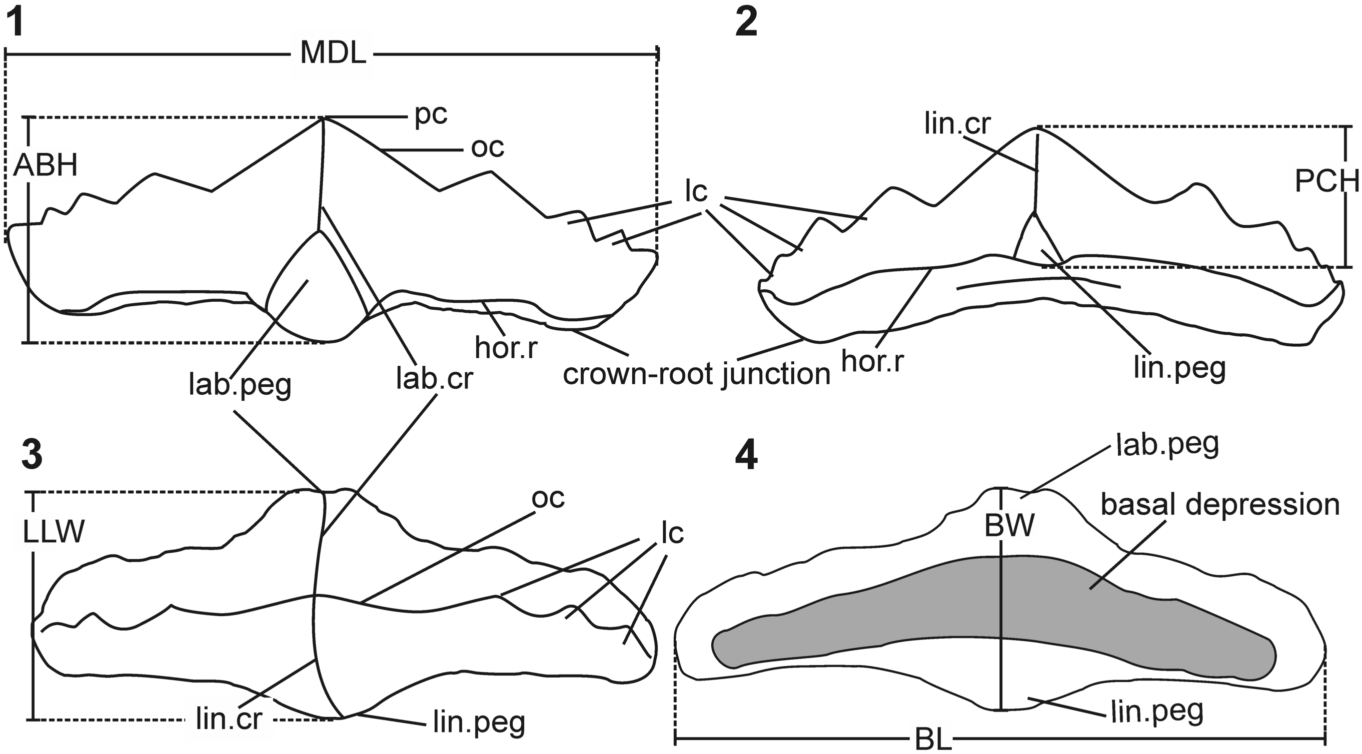

Figure 2. Schematic representation of major morphological features and indices to the measured parameters of a hybodont shark tooth in (**1**) labial, (**2**) lingual, (**3**) occlusal, and (**4**) basal views. Abbreviations: ABH = apicobasal height; BL = basal length; BW = basal width; hor.r = horizontal ridge; lab.cr = labial crest; lab.peg = labial peg; lc = lateral cusplet; lin.cr = lingual crest; lin.peg = lingual peg; LLW = labiolingual width; MDL = mesiodistal length; oc = occlusal crest; pc = principal cusp; PCH = height of principal cusp.

0.5 μm α-alumina liquid. The thin sections were examined under a polarizing petrographic microscope (Leica-DMEP) for detailed histological study and photographs were taken by a Leica DFC290 camera. Terminology for describing dental histology follows Francillon-Vieillot et al. (1990).

Scanning Electron Microscopy.—SEM of the specimens was carried out following the standard procedures outlined by Reed (2005). The specimens were first washed with distilled water followed by acetone immersion. All teeth were mounted on small aluminum metallic stubs with the help of carbon tape to reduce the charging effect. The investigation was carried out under Field Emission (FE)-SEM (ZEISS) SUPRA-^{TM} 55, at the Indian School of Mines, Dhanbad, India, and FE-SEM (ZEISS) AURIGA COMPACT, in the Central Research Facility at the Indian Institute of Technology, Kharagpur, India.

Repositories and institutional abbreviations.—The collected specimens are housed in the Vertebrate Palaeontology Laboratory of the Department of Geology and Geophysics, Indian Institute of Technology Kharagpur, India. IITKGP, Indian Institute of Technology, Kharagpur, India; VPL/JU, Vertebrate Palaeontology Laboratory, University of Jammu, India.

Tooth morphological and histological abbreviations.—ABH, apicobasal height; BL, basal length; BW, basal width; hor.r, horizontal ridge; lab.cr, labial crest; lab.peg, labial peg; lc, lateral cusplet; lin.cr, lingual crest; lin.peg, lingual peg; LLW, labiolingual width; MDL, mesiodistal length; oc, occlusal crest; pc, principal cusp; PCH, height of principal cusp; en, enameloid; ord, orthodentine; osd, osteodentine.

Systematic paleontology

Class Chondrichthyes Huxley, 1880
Subclass Elasmobranchii Bonaparte, 1838
Order Hybodontiformes Maisey, 1975
Superfamily Hybodontoidea Owen, 1846
Family Lonchidiidae Herman, 1977, sensu Rees, 2008

Genus *Pristrisodus* new genus

Type species.—*Parvodus tikiensis* (Prasad et al., 2008) collected from the Upper Triassic Tiki Formation of India.

Diagnosis.—As for the type and only species.

Etymology.—Generic name is derived from the Latin word '*pristris*' meaning shark and the Greek word '*odous*' meaning tooth.

Occurrence.—Tiki Formation of the Rewa Gondwana Basin (Otischalkian, Carnian); near the village of Tiki (23°56'N, 81°22'58"E), Shahdol District, Madhya Pradesh, India.

Pristrisodus tikiensis (Prasad et al., 2008)
Figures 3–7

2008 *Parvodus tikiensis* Prasad et al., p. 421, fig. 3A–U.
2008 *Lissodus duffini* Prasad et al., p. 425, fig. 4A–R.

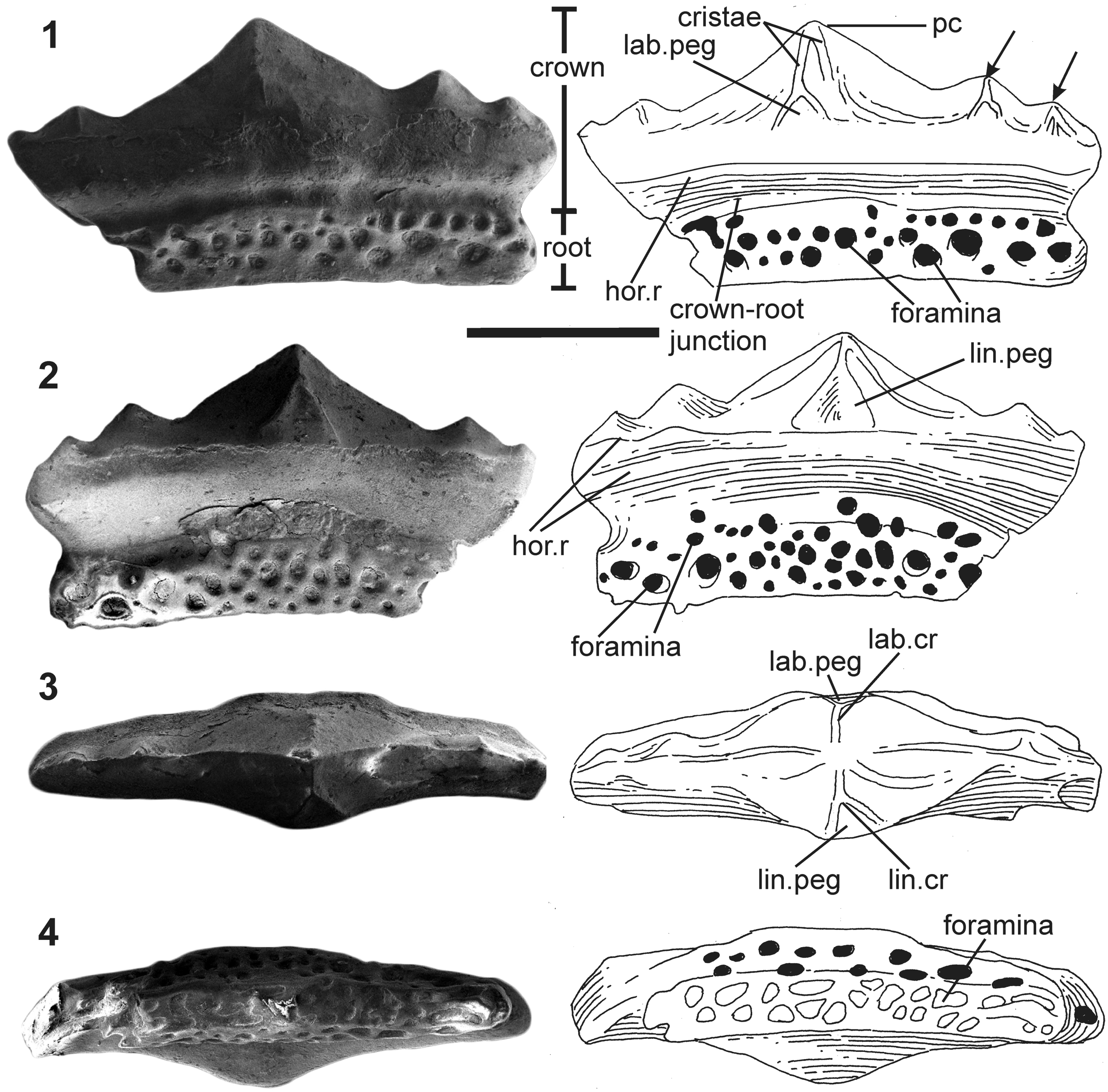

Figure 3. *Pristrisodus tikiensis* (Prasad et al., 2008). IITKGPP23, a complete anterolateral tooth (morphotype I) in (**1**) labial, (**2**) lingual, (**3**) occlusal, and (**4**) basal views. Arrows indicate lateral cusplets. Abbreviations: hor.r = horizontal ridge; lab.cr = labial crest; lab.peg = labial peg; lin.cr = lingual crest; lin. peg = lingual peg; pc = principal cusp. Scale bar represents 1 mm.

Holotype.—VPL/JU/TF/140, a lateral tooth recovered from the Upper Triassic Tiki Formation of the Rewa Gondwana Basin (Prasad et al., 2008).

Referred specimens.—IITKGPP01–IITKGPP29, IITKGPP43–IITKGPP58, 45 isolated teeth (current study), details of which are given in Supplemental Data 1; VPL/JU/TF/137–VPL/JU/TF/149, 13 isolated teeth (Prasad et al., 2008).

Revised diagnosis.—Lonchidiid hybodont characterized by elongated teeth with mesiodistal length greater than or equal to twice the apicobasal height, a high principal cusp, labial horizontal ridge situated near crown-root junction, lingual ridge high up on crown, linear depression or groove along the crown-root junction, small vertical cristae as crown ornamentation. Anterior teeth are broad, triangular and robust, have subdued and blunt principal cusp, a pair of incipient lateral cusplets, and low, hanging labial peg. Anterolateral teeth have high, pyramidal principal cusp with two or three small but pointed lateral cusplets, and triangular labial and lingual protuberances. Posterolateral teeth have four incipient lateral cusplets, prominent bilobed/rounded, hanging labial and small/incipient lingual protuberances.

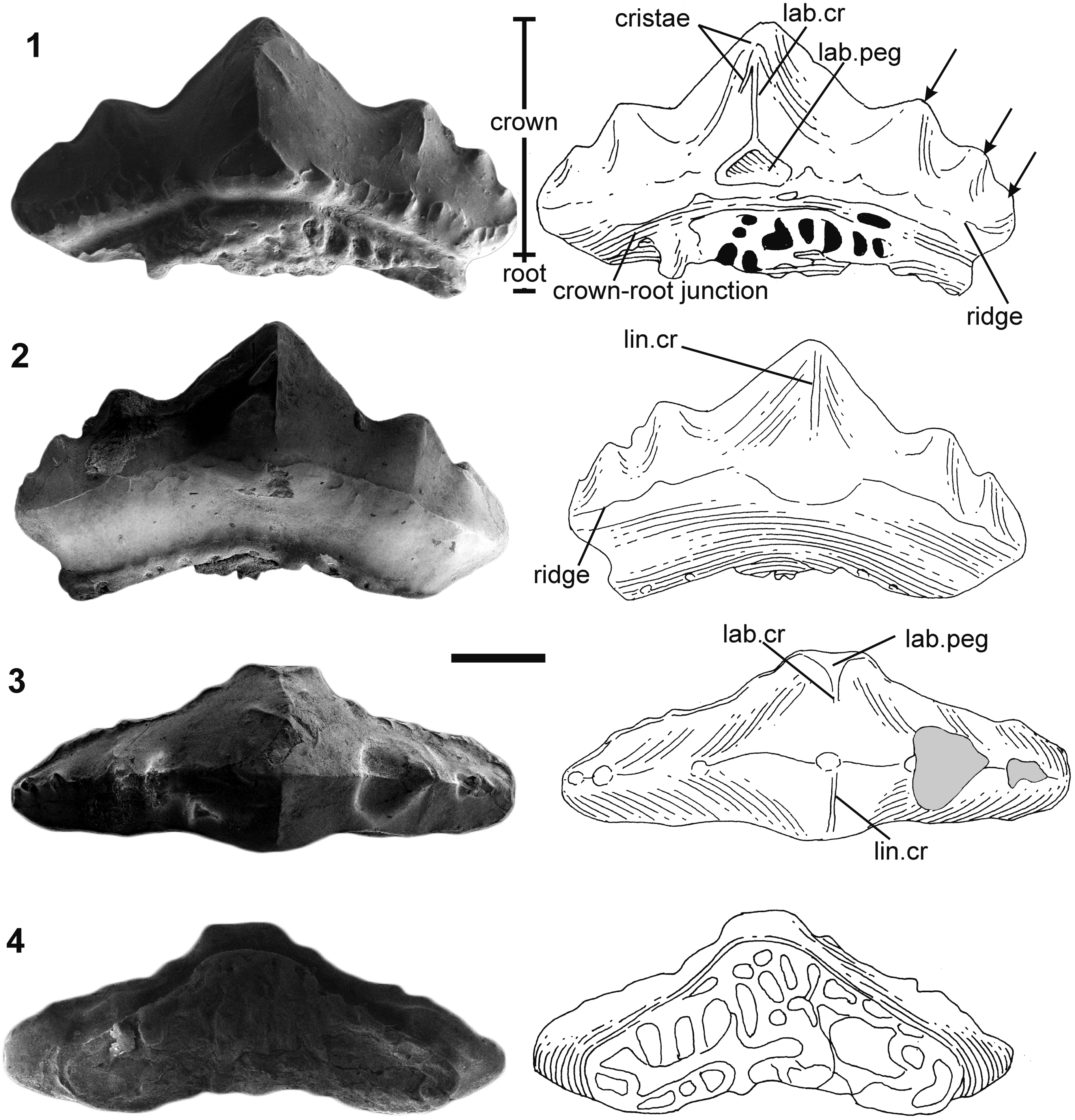

Figure 4. *Pristrisodus tikiensis* (Prasad et al., 2008). IITKGPP11, an anteriorly placed tooth with partially preserved root (morphotype II) in (**1**) labial, (**2**) lingual, (**3**) occlusal, and (**4**) basal views. Arrows indicate lateral cusplets. Gray shading indicates broken areas. Abbreviations: lab.cr = labial crest; lab. peg = labial peg; lin.cr = lingual crest. Scale bar represents 1 mm.

Remarks.—Prasad et al. (2008) reported three lonchidiid genera from the Tiki Formation, comprising *Lonchidion* (*L. estesi*, *L. incumbens*), *Parvodus* (*P. tikiensis*), and *Lissodus* (*L. duffini*). The Indian species of *Lonchidion* (Prasad et al., 2008, p. 419, fig. 2A–O) are different from *Pristrisodus tikiensis* in having a weakly developed principal cusp and indistinct or absence of lateral cusplets. However, the specimens assigned to *Parvodus tikiensis* (Prasad et al., 2008, p. 421, fig. 3A–U) and *Lissodus duffini* (Prasad et al., 2008, p. 425, fig. 4A–R) are remarkably similar to each other in terms of mesiodistal length (MDL), apicobasal height (ABH), and height of principal cusp (PCH; Table 1). These specimens (see Supplemental Data 2) are much smaller than the different morphotypes of *Pristrisodus* n. gen., in terms of MDL, although the coronal profile (MDL/ ABH = 2.43) of the measured specimens of *Parvodus tikiensis* and *Lissodus duffini* falls within the ranges of the newly

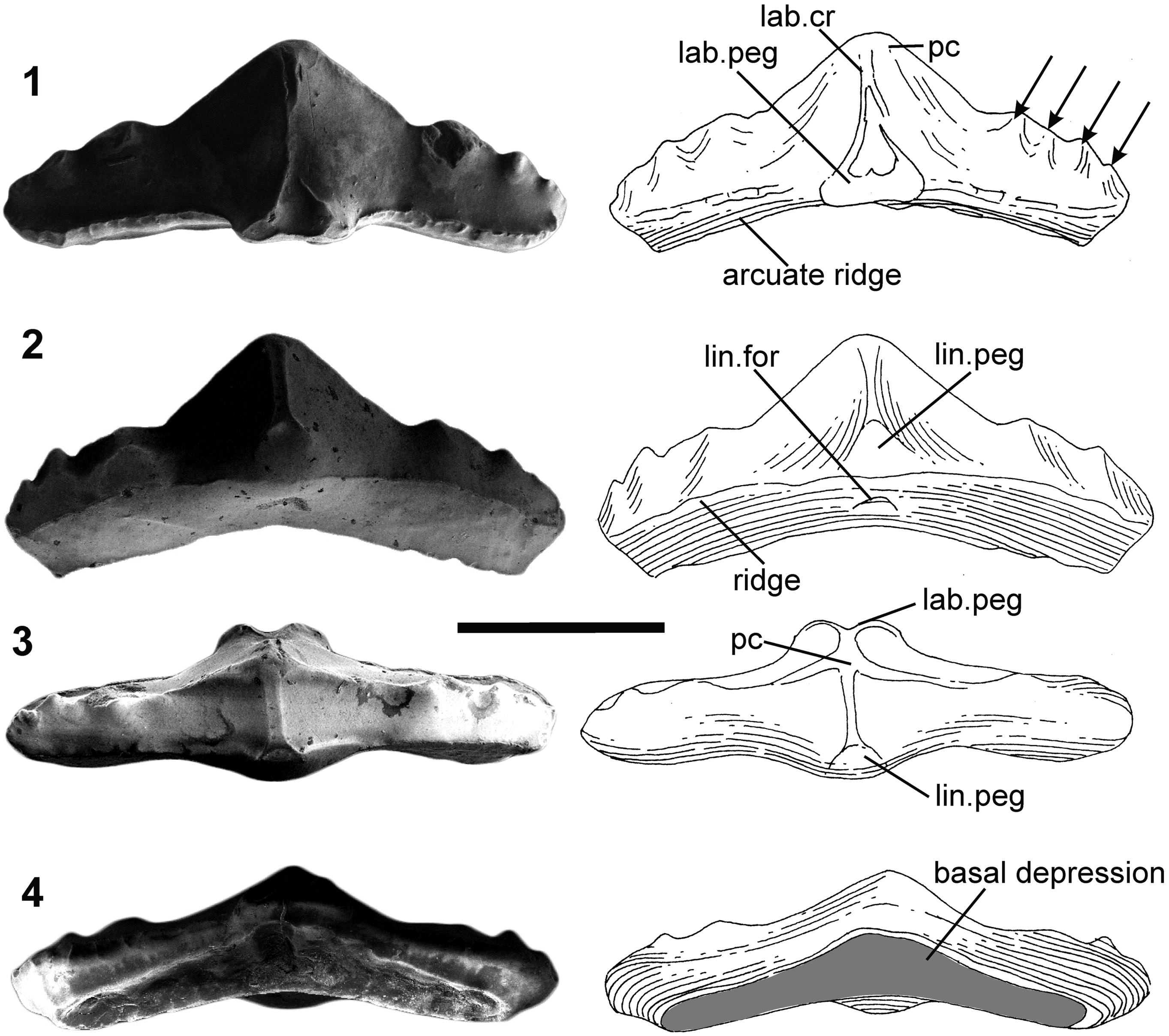

Figure 5. *Pristrisodus tikiensis* (Prasad et al., 2008). IITKGPP26, a posterolateral tooth with root not preserved (morphotype III) in (**1**) labial, (**2**) lingual, (**3**) occlusal, and (**4**) basal views. Arrows indicate four lateral cusplets. Gray shading indicates basal depression. Abbreviations: lab.cr = labial crest; lab. peg = labial peg; lin.for = lingual foramen; lin.peg = lingual peg; pc = principal cusp. Scale bar represents 1 mm.

examined teeth in the current work. Moreover, the specimens designated as *P. tikiensis* and *L. duffini* (Prasad et al., 2008) bear morphological similarity with the new specimens (Supplemental Data 1) based on their gracile appearance, absence of strong vertical folds or ornamentation (which contrasts with other species of *Parvodus* [Cappetta, 2012]), similar mesiodistal elongation, and well-developed lateral cusplets (in contrast to other species of *Lissodus* [Cappetta, 2012]). In the current work, the two taxa, *P. tikiensis,* and *L. duffini* are re-assigned to the new taxon, *Pristrisodus tikiensis*.

Description

Within the taxon *Pristrisodus tikiensis* (Prasad et al., 2008), five tooth morphotypes (I–V) can be distinguished based on crown proportions, number of cusplets, height of the principal cusps, forms of the labial and lingual pegs, and ornamentation (Table 2). Because the cusps are straight and upright, the different morphotypes of *P. tikiensis* represent teeth along different positions of the lower jaw, as suggested for the genus *Lissodus* (Rees and Underwood, 2002) and for hybodonts in general (Cappetta, 2012), and show a gradual monognathic heterodonty. Morphotypes I–II were positioned more anteriorly in comparison to the more posterior positioning of morphotypes III–IV, as is suggested by the sharper, high, and pointed principal cusps of the former in comparison to the relatively rounded principal cusps of the latter (sensu Cappetta, 2012). Morphotype V is considered to be anteriorly placed because of its broad and triangular shape, as suggested by Heckert et al. (2007) for *Lonchidion humblei*. In *Parvodus tikiensis* and *Lissodus*

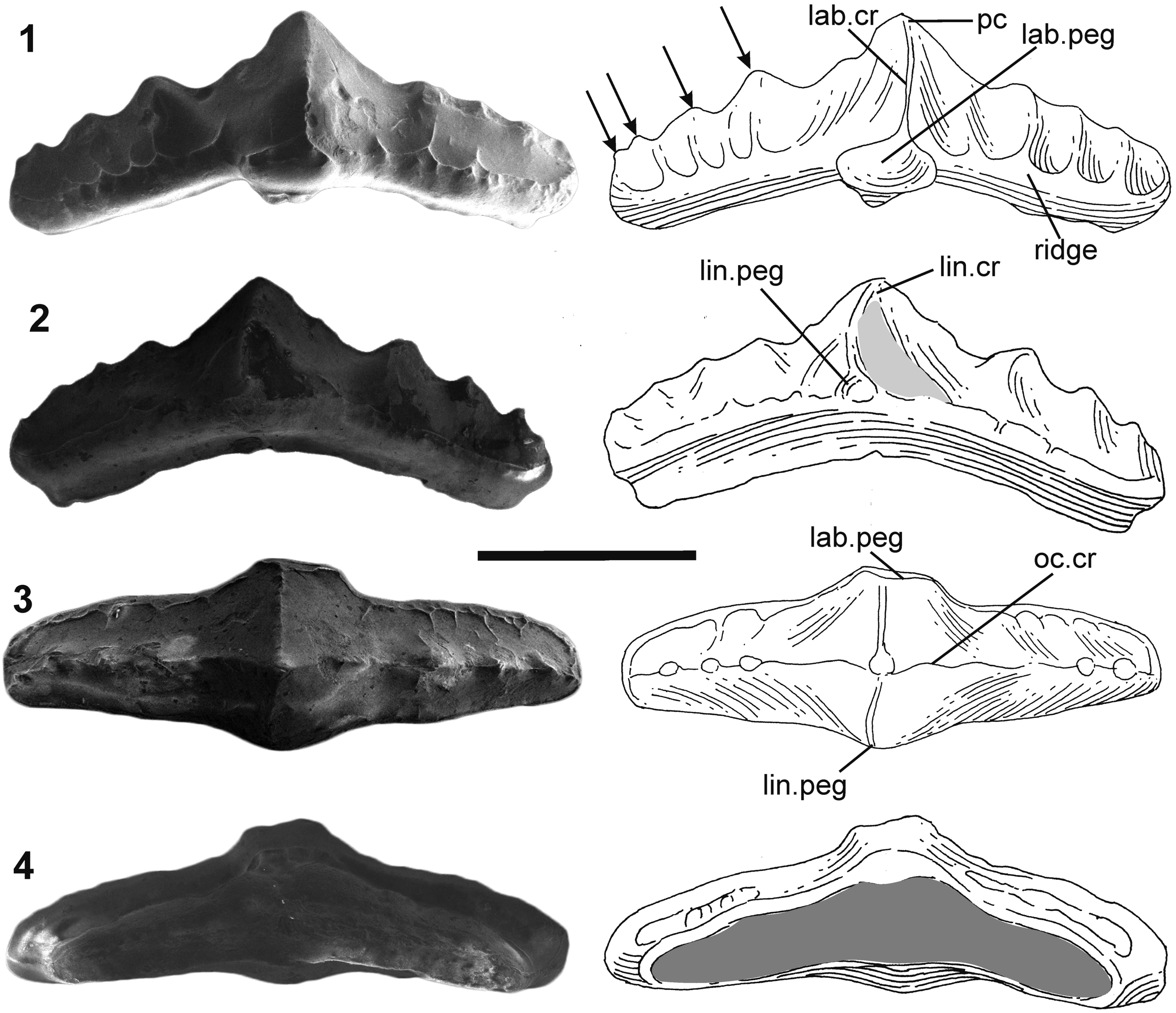

Figure 6. *Pristrisodus tikiensis* (Prasad et al., 2008). IITKGPP13, a posterolateral tooth (morphotype IV) in (**1**) labial, (**2**) lingual, (**3**) occlusal, and (**4**) basal views. Arrows indicate four lateral cusplets. Light- and dark-gray shadings indicate broken area and basal depression, respectively. Abbreviations: lab.cr = labial crest; lab.peg = labial peg; lin.cr = lingual crest; lin.peg = lingual peg; oc.cr = occlusal crest; pc = principal cusp. Scale bar represents 1 mm.

duffini, the crown proportions in longitudinal (MDL/ABH) and occlusal (MDL/LLW) views are equal (= 2.4) to each other, and nearly equal to that of morphotypes IV and V of *Pristrisodus* n. gen. In the current study, all the morphotypes of *Parvodus tikiensis* (Prasad et al., 2008, p. 421, fig. 3A–U) and *Lissodus duffini* (Prasad et al., 2008, p. 425, fig. 4A–R) are re-assigned as lateral and anterior teeth of morphotypes IV and V of *Pristrisodus* n. gen., respectively, based on their mesiodistal elongation, number of lateral cusplets, and triangular shape of the anterior teeth (Patterson, 1966; Maisey, 1983; Hodnett et al., 2013).

Morphotype I.—Morphotype I comprises three well-preserved anterolateral teeth. The anterolateral tooth IITKGPP23 (Fig. 3.1–3.4) shows a well-developed principal cusp and two pairs of cusplets. Average mesiodistal length (MDL) of morphotype I is 3.05 ± 0.6 mm (N = 3, Table 1) and average labiolingual width (LLW) is 0.8 ± 0.06 (N = 3, Table 1). The crown ratio (MDL/LLW = 3.8) in occlusal view is much greater than that in longitudinal (MDL/ABH = 2.65) view, suggesting that the teeth are robust. The principal cusp is pointed and strongly developed in all the specimens. The occlusal crest is sharp and blade-like (Fig. 3.1, 3.2). The labial and lingual crest regions show bulges, whereas the rest of the lateral region of the crown is compressed (Fig. 3.3). There are straight horizontal ridges on the labial and lingual faces of the crown, although the former is near the crown-root junction and the latter is situated higher up on the crown (Fig. 3.1, 3.2). Small vertical apical cristae are seen on the principal cusp and lateral cusplets. Both labial and lingual protuberances are triangular in shape, although the former is much smaller than the latter (IITKGPP23). There is a constricted, slightly concave groove at

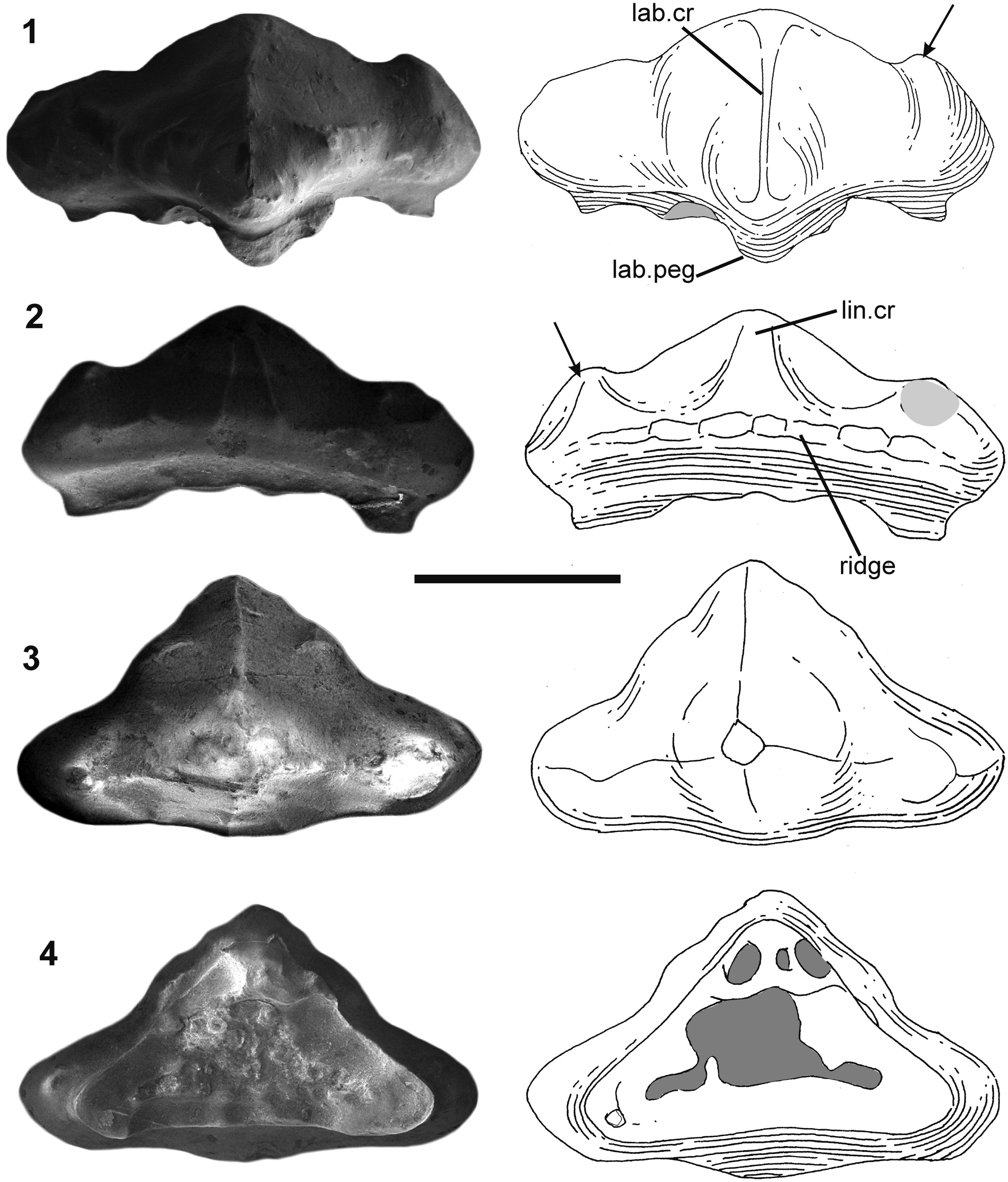

Figure 7. *Pristrisodus tikiensis* (Prasad et al., 2008). IITKGPP14, an anterior tooth (morphotype V) in (**1**) labial, (**2**) lingual, (**3**) occlusal, and (**4**) basal views. Arrow indicates a lateral cusplet. Light- and dark-gray shadings indicate broken area and basal depression, respectively. Abbreviations: lab.cr = labial crest; lab. peg = labial peg; lin.cr = lingual crest. Scale bar represents 1 mm.

the crown-root junction on all sides. The roots are either partially or completely preserved in all specimens of morphotype I, and display an anaulacorhize vascularization pattern (Fig. 3.1). A set of regular foramina is arranged linearly along the dorsal end of the labial face of the root, whereas ventrally, the foramina are randomly arranged. The crown-base is slightly curved in

Table 1. Average and standard deviation of the measured dimensions of the Indian hybodonts examined.

Taxa	N	MDL	LLW	ABH	PCH	BL	BW
Pristrisodus							
Morphotype I	3	3.05 ± 0.6	0.8 ± 0.06	1.32 ± 0.2	0.6 ± 0.1	2.7 ± 0.5	0.6 ± 0.1
Morphotype II	3	2.8 ± 0.4	1.1 ± 0.1	1.4 ± 0.25	0.8 ± 0.06	2.5 ± 0.15	0.7 ± 0.2
Morphotype III	6	2.4 ± 0.3	0.9 ± 0.1	0.9 ± 0.1	0.6 ± 0.1	1.9 ± 0.3	0.5 ± 0.1
Morphotype IV	16	2.8 ± 0.4	0.9 ± 0.1	0.9 ± 0.1	0.6 ± 0.1	2.3 ± 0.4	0.5 ± 0.1
Morphotype V	17	2.3 ± 0.4	1 ± 0.2	0.97 ± 0.1	0.5 ± 0.1	1.8 ± 0.4	0.6 ± 0.1
*P. tikiensis**	6	1.7 ± 0.6	0.7 ± 0.2	0.7 ± 0.3	0.4 ± 0.2	1.9 ± 0.8**	0.5 ± 0.1**
*L. duffini**	6	1.7 ± 0.4	0.7 ± 0.2	0.7 ± 0.14	0.4 ± 0.1	1.7 ± 0.7	0.6 ± 0.2

Index to measured parameters is given in Figure 2. Abbreviations: ABH, apicobasal height; BL, length in basal view; BW, maximum width in basal view; LLW, labiolingual width of hybodonts; MDL, mesiodistal length; N, number of specimens; PCH, height of principal cusp. Single (*) and double asterisks (**) indicate(s) after Prasad et al. (2008) and N = 3, respectively. All measurements are in mm.

Table 2. Characteristic features distinguishing the five morphotypes of *Pristrisodus tikiensis* (Prasad et al., 2008).

Morphotypes	I	II	III	IV	V
N	3	3	6	22*	23*
MDL / ABH	2.65	2.0	2.67	2.67	2.4
MDL / LLW	3.8	2.54	2.67	2.55	2.3
BL / BW	4.5	3.6	3.8	4.6	3.1
Principal cusp	———high, pointed——		———High, rounded———		Low, rounded
Lateral cusplets	two	two/three	three/four	four	One
Labial peg	triangular	triangular	bilobed	rounded	large, below crown-root junction
Lingual peg	triangular	absent	incipient	small	absent
Labial hor.r near crown-root junction	straight	————curved and crenulated————			absent
Lingual hor.r high on the crown	straight	—curved and smooth—		curved and crenulated	wide, crenulated
Other features	bifurcating cristae	cristae present	lingual foramen	small cristae	triangular in shape

Index to the abbreviations is given in Table 1.
Single (*) asterisk indicates that total number of specimens examined for the morphotypes IV and V incorporate specimens of *Parvodus tikiensis* and *Lissodus duffini*, respectively.

outline, concave towards the labial face and has multiple circular pits or foramina (Fig. 3.4).

Morphotype II.—There are three isolated teeth which show overall similarity with morphotype I in terms of a pointed, robust principal cusp, but have three lateral cusplets on one side of the principal cusp and two on the other (Fig. 4.1). These teeth have crown proportions similar to morphotype I, where MDL/LLW > MDL/ABH (Table 2). In most of the specimens, the height of the principal cusp is twice the height of the three lateral cusplets (e.g., IITKGPP11, Fig. 4.1, 4.2). A similar high principal cusp is also seen in IITKGPP20. Small vertical ridges (or cristae) extending along the crest are seen in the specimens (Fig. 4.1). The labial and lingual crests are sharp and prominent. The labial peg is large, triangular, and displaced towards the root, whereas on the lingual side, the peg is absent though the region has a prominent and large subcircular bulge (Fig. 4.1, 4.2). The ridge near the crown-root junction is curved and crenulated in labial view (Fig. 4.1), whereas it is smooth, curved, and situated midway on the crown in lingual view (Fig. 4.2). In occlusal view, the labial and lingual sides show a distinct difference in outline, especially at the labial and lingual pegs (Fig. 4.3). The root is partially preserved, showing an anaulacorhize vascularization pattern, and contains several large and irregular foramina. In basal view, the crown-base is distinctly sub-triangular in outline (Fig. 4.4).

Morphotype III.—Morphotype III is based on six well-preserved teeth (Supplemental Data 1), where the crown proportions in longitudinal (MDL/ABH) and occlusal (MDL/LLW) views are equal, unlike that in the morphotypes I and II (Table 2). All the specimens of morphotype III (Supplemental Data 1) are characterized by a bilobed labial peg, a slightly rounded principal cusp, and three or four pairs of lateral cusplets on either side of it (Fig. 5.1). Vertical ridges are present on the principal cusp and cusplets (Fig. 5.1). The curved ridges on the labial and lingual faces of the crown are similar to those seen in morphotype II. Although the lingual face is smooth, it contains an incipient lingual peg and a curved horizontal ridge. There is a foramen just below this lingual peg (Fig. 5.2). In occluso-lingual view, the crest is prominent (Fig. 5.3). The tooth has a centrally depressed base, which has a triangular outline that is slightly concave towards the lingual side (Fig. 5.4).

Morphotype IV.—Twenty-three isolated teeth were examined and comprise sixteen newly collected specimens (Supplemental Data 1) and the specimens originally assigned to *Parvodus tikiensis* (VPL/JU/TF/137–VPL/JU/TF/143, Supplemental Data 2). The labiolingual width (LLW) equals the apicobasal height (ABH) in morphotype IV (Table 1), whereas the crown proportions (MDL/ABH and MDL/LLW) are nearly equal to each other, as in morphotype III (Table 2). The principal cusp is broadly V-shaped with a rounded apex and has four pairs of cusplets on each side of the principal cusp (Fig. 6.1). The large triangular labial peg is positioned towards the base of the crown (Fig. 6.1), which contrasts with a small, subcircular lingual peg (Fig. 6.2). The latter is shifted towards the crown in comparison to the labial peg. The occlusal crest is sharp and slightly curved (Fig. 6.3). The ridges on the labial and lingual faces of the crown are curved and crenulated. There are small but distinct cristae along the lateral cusplets in labial and lingual views. The base of the crown is subtriangular but narrow and highly elongated (avg. BL/BW = 4.2 [N = 22]), centrally depressed and concave towards the lingual side (Fig. 6.4).

Morphotype V.—This morphotype is based on twenty-four isolated teeth comprising seventeen newly collected specimens (Supplemental Data 1) and the specimens originally assigned to *Lissodus duffini* (VPL/JU/TF/143–VPL/JU/TF/149, Supplemental Data 2). Morphotype V is characterized by robust teeth with a rounded principal cusp (Fig. 7.1, 7.2) and one incipient lateral cusplet on each side. The teeth have distinct triangular outlines in occlusal and basal views where MDL/LLW (= 2.3) and BL/BW (= 3.1) are low in comparison to the other morphotypes (Table 2). However, their crown proportions are similar to those seen in morphotypes III and IV (MDL/LLW = MDL/ABH, Table 2). The crown has an enlarged and robust labial peg that extends beyond the crown-root junction (Fig. 7.1), whereas the lingual peg is absent (Fig. 7.2). The horizontal ridge is not visible in labial view, but it is prominent, wide, and crenulated in lingual view. The occlusal crest is broad and almost flat (Fig. 7.3). The base of the crown is distinctly triangular and has a central depression (Fig. 7.4).

Discussion.—The low-crowned teeth and presence of anaulacorhize root vascularization suggest that *Pristrisodus* n. gen., conforms to the hybodontiform tooth morphology (Ginter et al., 2010). *Pristrisodus* n. gen., fits the familial diagnosis of the Lonchidiidae, which includes small teeth with mesiodistal expansion, well-developed labial protuberances, and presence of irregularly arranged foramina on the root (Rees and Underwood, 2002). The family Lonchidiidae, established for the genus *Lonchidion* (Herman, 1977), was synonymized with Polyacrodontidae (Cappetta, 1987), although recent works show that the former is valid (Rees and Underwood, 2002; Cappetta, 2012). The family comprises eleven genera characterized by the shape of the crown in labial and occlusal views, height of the principal cusp, number and nature of lateral cusplets, ornamentation, and nature of the root (Wang et al., 2009; Klug et al., 2010; Cappetta, 2012). Of these, *Dabasacanthus* and *Gansuselache* are essentially Paleozoic forms (Ginter et al., 2010). Both forms bear similarity with *Lissodus*, although these possess several distinguishing features. *Dabasacanthus* is represented by an articulated juvenile with very small teeth, which have prominent labial pegs but lack lateral cusplets and ornamentations (Ginter et al., 2010). On the other hand, teeth of *Gansuselache* have a high crown-root junction labially, widely separated lateral cusplets from the principal cusps, and a strongly developed, flared occlusal crest (Wang et al., 2009; Ginter et al., 2010). The tooth morphology of five Mesozoic lonchidiid genera is distinctly different from the teeth of *Pristrisodus* n. gen., and includes *Bahariyodon* (Fig. 8.1, 8.2), *Hylaeobatis* (Fig. 8.3–8.5), *Isanodus* (Fig. 8.6, 8.7), *Vectiselachos* (Fig. 8.8–8.10), and *Diplolonchidion* (Fig. 8.11, 8.12). In contrast to *Pristrisodus* n. gen., *Bahariyodon* is characterized by a high cusp with wide base, prominent cristae, and a lingual crown face that is produced into a distinct shelf (Cappetta, 2012). The shapes of teeth of *Hylaeobatis* are rectangular (Fig. 8.5), whereas *Isanodus* teeth are deeper than long and have a stout crown with rounded apex (Fig. 8.6, 8.7; Cuny et al., 2006). The teeth of *Vectiselachos*, conversely, are small, have a well-demarcated principal cusp, no lateral cusplets, and a root that is much thinner than the crown (Fig. 8.8–8.10). *Diplolonchidion* differs from other lonchidiid genera, including *Pristrisodus* n. gen., in possessing two distinct and robust labial pegs slightly offset mesiodistally from the central crown (Fig. 8.11, 8.12). *Diplolonchidion* was included in Polyacrodontidae by Heckert and Lucas (2006), and *Lissodus* was placed in an unknown family by Rees (2008), although Cappetta (2012) placed them in the family Lonchidiidae with a scope for future revision of the family.

The teeth of *Pristrisodus* n. gen., show superficial similarities to the genera *Lissodus* (Fig. 8.13–8.15), *Lonchidion* (Fig. 8.16–8.18), *Parvodus* (Fig. 8.19, 8.20), and *Jiaodontus* (Fig. 8.21–8.24) based on symmetry and shape and size of the principal cusp and lateral cusplets. However, the lateral teeth of *Pristrisodus* n. gen., (Figs. 3–7, 8.21) are mesiodistally at least three times more elongated than those of *Lissodus africanus* (Broom, 1909; Duffin, 1985), and the lateral cusplets are well developed in contrast to the weakly developed ones or their near absence in all species of *Lissodus* (Duffin, 1985; Rees and Underwood, 2002; Duncan, 2004; Fischer, 2008; Prasad et al., 2008), such as *L. cassangensis* (Teixeira, 1956). In addition, the crown of *Lissodus* possesses weakly developed folds (Underwood and Rees, 2002), in contrast to *Pristrisodus* n. gen., *Lonchidion* (Fig. 8.16–8.18) differs from *Pristrisodus* n. gen., (Fig. 8.25) in having a weakly developed principal cusp, multiple cusplets, a prominent and narrow labial peg, and a broad root. The root of *Pristrisodus* n. gen., has a single row of foramina proximal to the crown-root junction, and distally, the foramina are randomly oriented (Fig. 8.25). Such a pattern contrasts with that of *Hybodus parvidens* (Patterson, 1966), where the foramina are irregularly distributed throughout the root without any specialized pattern. The lateral teeth of *Parvodus* (Fig. 8.19, 8.20; Rees and Underwood, 2002) are different from those of *Pristrisodus* n. gen., in having a very high crown profile and strong vertical folds. The two known species of *Jiaodontus* (*J. montaltissimus*, [Fig. 8.21, 8.22] and *J. vedenemus* [Fig. 8.23, 8.24]) are distinctly different from *Pristrisodus tikiensis* in having teeth with a high coronal profile, protruding and bulging labial peg, strong ornamentation in the form of prominent ridges on their labial and lingual faces, and a strongly convex labial face (Klug et al., 2010). Hence, *Pristrisodus* constitutes a new genus belonging to the family Lonchidiidae, which is distinct from all other valid lonchidiid genera.

Quantitative assessments

Results.—To overcome discrepancy arising due to positional differences, only lateral teeth of the genera examined are considered (Supplemental Data 2). In the case of *Pristrisodus tikiensis*, the anterior and anteriorly placed teeth are omitted from the analyses, whereas those teeth that are definitely lateral in position are used in the analyses. This includes twenty-two lateral teeth, which are placed posteriorly (morphotypes III–IV) with respect to morphotypes I–II (Supplemental Data 1). The examined teeth of *Lissodus duffini* were identified as lateral in position by Prasad et al. (2008), although these are found to be morphologically similar to morphotype V (anterior) teeth of *Pristrisodus tikiensis*.

PCA was applied to the variance-covariance matrix of the four variables, ABH, MDL, LLW, and PCH, which characterize the crown elongation, width, thickness, and height of the

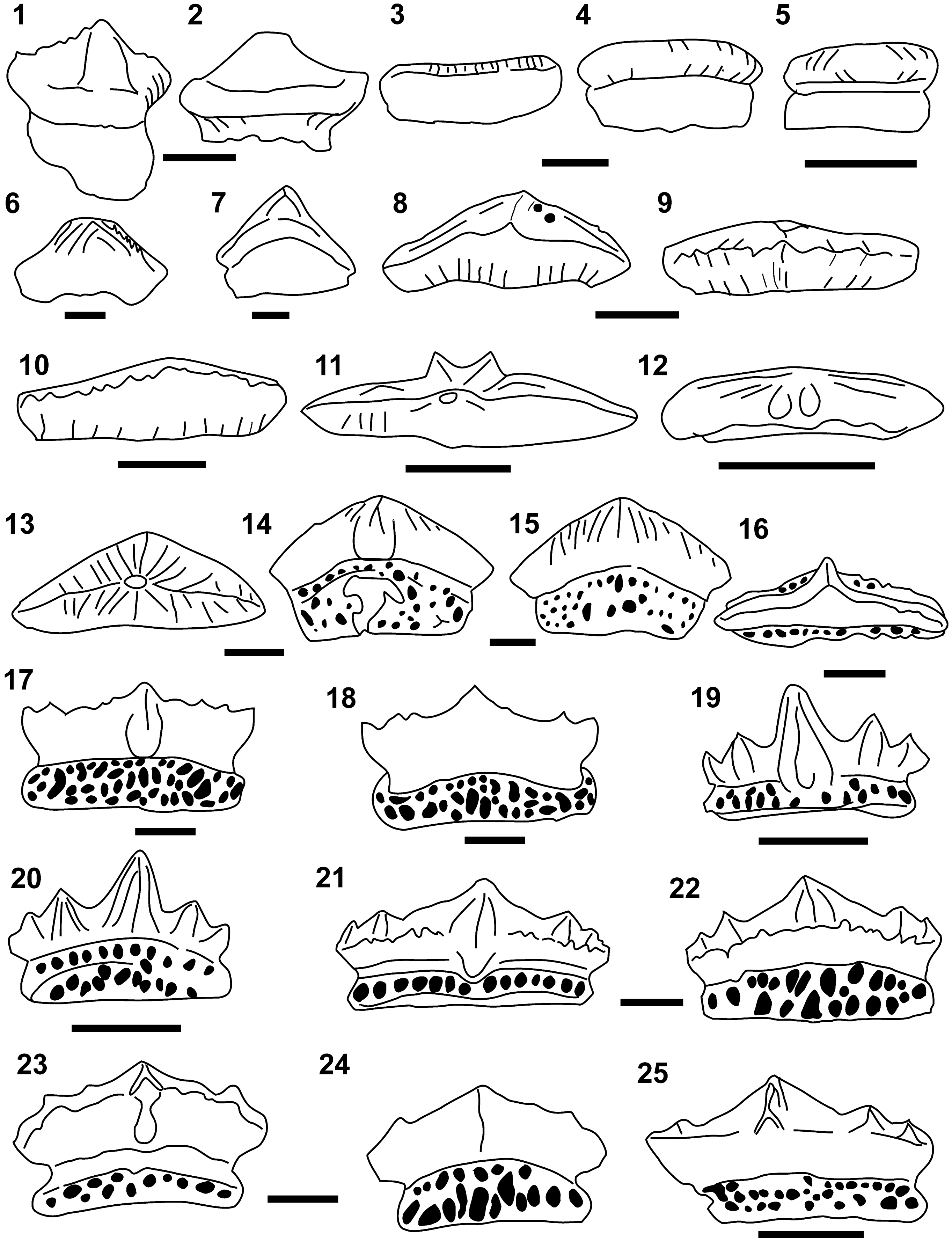
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25

Table 3. Principal component coefficient of the first four axes.

Variables	PC 1	PC 2	PC 3	PC 4
Mediodistal length (MDL)	0.817	–0.456	–0.251	–0.244
Labiolingual width (LLW)	0.275	–0.179	0.876	0.354
Apicobasal height (ABH)	0.439	0.848	0.141	–0.261
Height of principal cusp (PCH)	0.251	0.201	–0.387	0.864
Eigenvalue	1.582	0.086	0.029	0.012
% variance	92.565	5.025	1.696	0.713

principal cusp. Because all of the variables were measured in the same unit (mm), the variance-covariance matrix is used for analyses (Hammer et al., 2001). As the first three principal components account for 99.29% of the total variance (Table 3), PC 4 is discarded. PC 1 is mainly a size axis, as shown by the high and positive coefficients of the four variables. On PC 2 or the first shape axis, high positive value is seen for crown heights (ABH and PCH), which load opposite to the crown length and width (MDL and LLW). On the other hand, LLW shows high positive value and loads opposite to other crown-proportion variables on PC 3.

Principal component scores are plotted on PC 1 and PC 2 (Fig. 9.1), and PC 2 and PC 3 (Fig. 9.2) to show the scatter of the hybodont teeth examined. Although distinct clustering of the taxa is seen, *Lissodus duffini* and *Parvodus tikiensis* (Prasad et al., 2008) show close occupation of morphospaces with that of *Pristrisodus tikiensis* (Fig. 9.1). However, *Parvodus rugianus* shows considerable overlapping of convex hull polygon with that of *Parvodus tikiensis* and *Pristrisodus* n. gen., (Fig. 9.1), suggesting that all these taxa have similar size ranges. The other available lonchidiids examined (*Parvodus curvidens*, *Lissodus minimus*, and *Jiaodontus* [*J. montaltissimus* and *J. vedenemus*]) show distinctly separate occupation of zones in the morphospaces (Fig. 9.1, 9.2). Principal component scores plotted on PC 2 and PC 3 (Fig. 9.2) show that the Indian taxa have overlapping of morphospaces with each other and with that of *Lissodus mimimus*. Other taxa occupy separate and distinct morphospaces.

CVA shows that 78% of the total teeth analyzed (N = 45) have been correctly assigned (Table 4), whereas all the European forms show 100% correct assignment. The anterior teeth of *L. duffini* are 100% correctly assigned. Species of *Jiaodontus* show 67%–75% correct assignment of lateral teeth, whereas *Parvodus tikiensis*, as originally described by Prasad et al. (2008), show only 33% correctly assigned lateral teeth. Such a low percentage accounts for considerable overlap of the convex hull polygon of *Parvodus tikiensis* with that of *Pristrisodus tikiensis* (Fig. 10). On the other hand, the morphospace of *Lissodus duffini*, although distinct, is close to the morphospace of *Pristrisodus tikiensis*. Such close clustering of the morphospaces of the Indian genera (Fig. 10) contrasts with that of other genera examined, in which the latter are distributed in distinct and separate morphospaces.

Discussion.—Fossil chondrichthyans are mostly described based on tooth morphology (e.g., Duffin, 1985; Shimada, 2002; Fischer et al., 2011; Johns et al., 2014), which has inherent problems because most of the teeth are found isolated and exhibit various forms of heterodonty (Shimada, 2005; Whitenack and Gottfried, 2010; Cappetta, 2012). In the current work, application of PCA and CVA for hybodont teeth tests the validity of *Pristrisodus* n. gen., in comparison to other Indian, European, and Chinese taxa, and is represented graphically (Figs. 9, 10) by the occupation of different zones of morphospaces (convex hull polygons). Although the sample size is small, in both the analyses, the specimens of *Parvodus tikiensis* and *Lissodus duffini* (Prasad et al., 2008) show either overlapping of zones or close clustering with the morphospace of *Pristrisodus tikiensis* (Figs. 9, 10). These multivariate analyses thus corroborate the qualitative findings of the current study, where the specimens designated as *P. tikiensis* and *L. duffini* by Prasad et al. (2008) are found to be similar to the newly collected Tiki specimens, and are re-assigned to *Pristrisodus* n. gen. Moreover, loadings on different measured parameters in PCA (Table 3) show that crown height (ABH and PCH) loads opposite to crown length and width (MDL and LLW), and these crown proportions are key identification features for the different hybodont taxa analyzed.

Tooth histology

Description.—Two lateral teeth (morphotype IV, IITKGPP50 and morphotype III, IITKGPP29) were longitudinally and transversely sectioned, respectively, to reveal their tooth micro-morphology (Fig. 11). In both specimens, the crown has a thin (47 µm) outer enameloid layer overlying a thick dentine (Fig. 11.1). The latter is composed of an outer thick orthodentine (sensu Sire et al., 2009) and an inner narrow osteodentine (sensu Carlson, 1989). Although orthodentine usually comprises an outer dense pallial dentine surrounding an inner layer of circumpulpar (Carlson, 1989), in *Pristrisodus* n. gen., the pallial dentine is restricted to the enameloid-dentine boundary and is hard to differentiate as in other hybodonts (Johnson, 2003). Profuse dentine tubules of two distinct types are seen in longitudinal view. The first type is coarse and situated towards the crown base (Fig. 11.2), whereas the second type is slender, feather-like, and found in the apical region of the crown (Fig. 11.3). In occlusal view (Fig. 11.4–11.6), a thick zone of orthodentine (285 µm along the vertical axis) overlies a narrow osteodentine (89 µm along the same vertical axis). The latter surrounds a small, central pulp cavity, which has a circular outline (diameter = 113 µm). The osteodentine is characterized by multiple, elliptical, and circular denteons that form a radiating pattern surrounding the pulp cavity (Fig. 11.6).

←

Figure 8. Representative lonchidiid hybodonts, (**1–2**) *Bahariyodon*: (**1**) anterior tooth in lingual view, (**2**) lateral tooth in labial view; (**3–5**) *Hylaeobatis*: (**3–4**), symphyseal tooth in (**3**) occlusal, (**4**) lingual views, (**5**) lateral tooth in labial view; (**6–7**) *Isanodus*: (**6**) anterolateral tooth in lingual view, (**7**) posterior tooth in labial view; lateral tooth of (**8–10**) *Vectiselachos*: (**8**) occlusal, (**9**) labial, and (**10**) lingual views; (**11–12**), *Diplolonchidion* in (**11**) occlusal and (**12**, labial views; (**13–15**) *Lissodus* in (**13**) occlusal, (**14**) labial, and (**15**) lingual views; (**16–18**), *Lonchidion* in (**16**) occlusal, (**17**) labial, and (**18**) lingual views; (**19–20**), *Parvodus* in (**19**) labial and (**20**) lingual views; (**21–24**) *Jiaodontus*: (**21–22**) *J. montaltissimus* in (**21**) labial and (**22**) lingual views; (**23–24**) *J. vedenemus* in (**23**) labial and (**24**) lingual views; (**25**), *Pristrisodus* n. gen., (morphotype I) in labial view. Sources of information: Klug et al. (2010), Cappetta, (2012), and current study. Scale bars represent 1 mm, except for 5 mm (**3–5**), 500 µm (**21–24**).

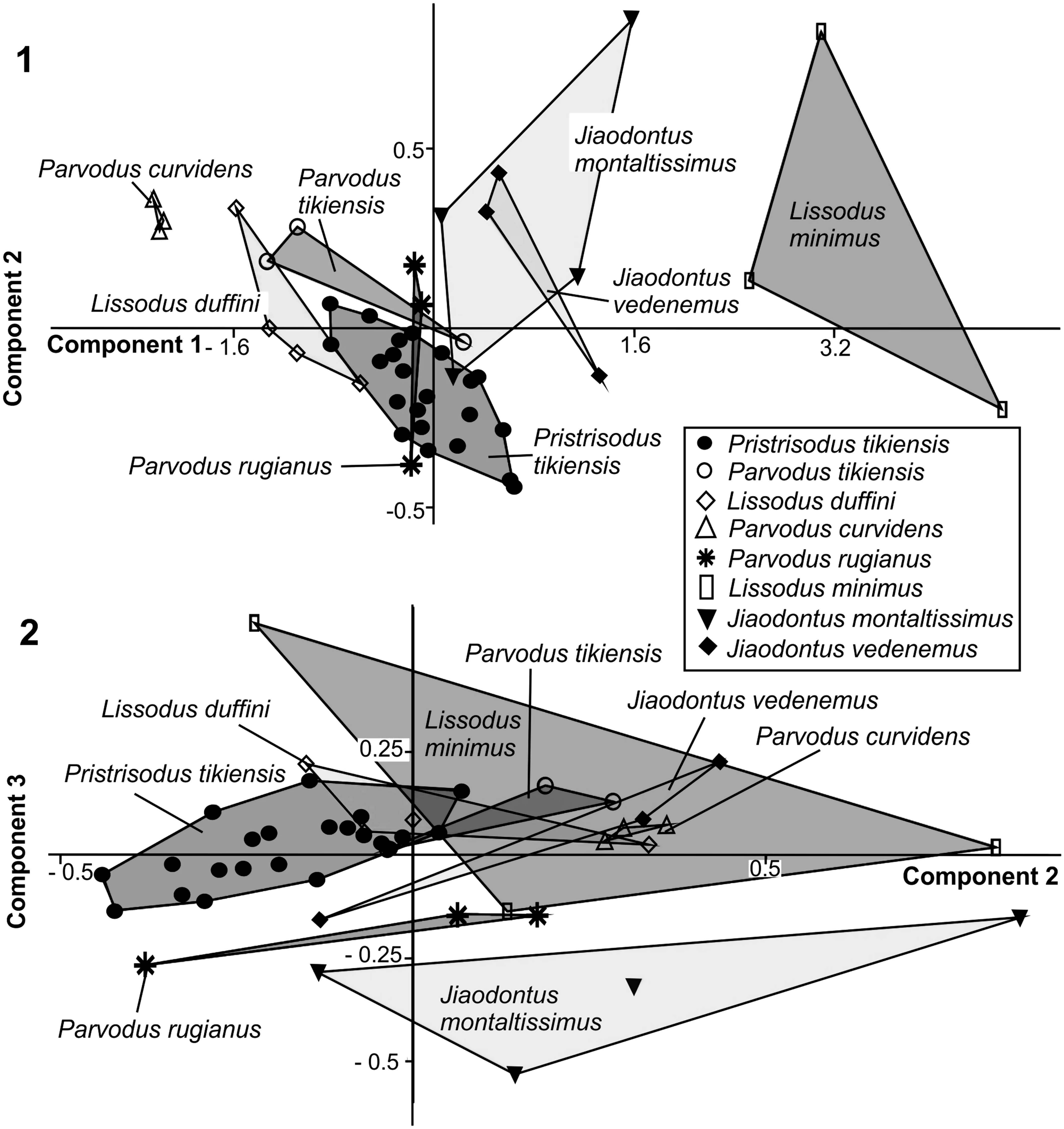

Figure 9. Graphical result of principal component scores of hybodont teeth plotted on (**1**) first two principal components, PC 1 and PC 2, and (**2**) second and third principal components, PC 2 and PC 3. Variable loadings and component eigenvalues are given in Table 3.

Discussion.—In comparison to the numerous valid hybodont genera known (Cappetta, 2012), histologies of only a few have been examined. Pioneering work on hybodont tooth histology was carried out by various workers, such as Stensiö (1921), Patterson (1966), Reif (1973), Johnson (1981), and Maisey (1987). Presence of orthodentine and absence of osteodentine is considered a basal/primitive feature of hybodonts (Maisey, 1987). In general, dental histology of the hybodonts may be subdivided into orthodont and osteodont types. In the first case, the whole crown beneath the enameloid is formed by the orthodentine with a pulp cavity present, whereas in the second type, a central thick osteodentine is present with the orthodentine occurring as a thin layer between the enameloid and the osteodentine. *Polyacrodus*, *Lonchidion*, and *Paleobatus* have teeth with an outer enameloid and pallial dentine overlying a thick orthodentine, thereby forming the orthodont taxa

(Maisey, 1987). In contrast, *Hybodus* and *Acrodus* have a central core of osteodentine underlying an outer enameloid and pallial dentine, and are known as the osteodont type. However, in *Lissodus* (*L. angulatus*), both types are found (Błażejowski, 2004). The osteodentine type is usually found in lateral and posterior teeth of *L. angulatus*, whereas its anterior teeth are orthodentine type. Subsequently, Rees and Underwood (2002) and Heckert et al. (2007) corroborated that *Lissodus* (*L. minimus*) and *Lonchidion* (*L. humblei*), respectively, are of orthodentine type and lack osteodentine in the crown.

Histology of the lateral teeth of *Pristrisodus* n. gen., is distinctly different from that of *Polyacrodus*, *Lonchidion*, *Paleobatus*, *Hybodus*, and *Acrodus*, which are either orthodont or osteodont (Maisey, 1987), but similar to the lateral tooth of *Lissodus* (*L. angulatus* Stensiö, 1921) in having a thin outer layer of enameloid overlying an outer orthodentine and an inner osteodentine. In contrast to *Lissodus*, the lateral teeth of *Pristrisodus* n. gen., are characterized by a thick orthodentine surrounding a thin osteodentine, which in turn surrounds the pulp cavity (Fig. 11.6). Hence, co-existence of the two types (orthodont and osteodont) within a single taxon is evident in *Pristrisodus* n. gen., as seen in *Lissodus*, which contrasts with that of other hybodont genera studied.

Table 4. Number of correctly assigned teeth as determined by canonical variate analysis (CVA); (Eigenvalue of Axis 1 = 8.086, which accounted for 74.46% of the variation; Eigenvalue of Axis 2 = 1.45, which accounted for 13.35% of the variation).

	Number of teeth correctly assigned	Total	% correctly assigned
Pristrisodus tikiensis	16	22	73
Parvodus tikiensis	1	3	33
Lissodus duffini	4	4	100
Parvodus rugianus	3	3	100
Parvodus curvidens	3	3	100
Lissodus minimus	3	3	100
Jiaodontus montaltissimus	3	4	75
Jiaodontus vedenemus	2	3	67
Total	35	45	78

Concluding remarks

The Late Triassic Tiki Formation of the Rewa Gondwana Basin, India has yielded a new lonchidiid shark, *Pristrisodus* n. gen., based on numerous well-preserved, isolated teeth. Five distinct morphotypes are identified within *Pristrisodus* n. gen., based on crown proportions, number of cusplets, height of the principal cusps, form of the labial and lingual pegs, and ornamentation, which suggest a gradual monognathic heterodonty. Based on their overall shape and robustness, morphotype V is considered an anterior tooth, morphotypes I–II are positioned relatively anteriorly with respect to morphotypes III–IV. *Parvodus tikiensis* and *Lissodus duffini* are synonymized and reassigned to *Pristrisodus* n. gen., as *Pristrisodus tikiensis*, which is corroborated by multivariate analyses. Dental histology of *Pristrisodus* n. gen., is extremely distinctive and does not pertain to either the orthodont or osteodont type, and is of a mixed type, where a thick covering of orthodentine surrounds a relatively thin osteodentine and a central pulp cavity.

The Tiki Formation has yielded a rich assemblage of freshwater hybodonts along with various yet undescribed ceratodontiform dipnoans, xenacanthids, and actinopterygians (Bhat, 2015). Such high abundance of Late Triassic freshwater fishes is similar to that found in the Chinle Group of USA (Heckert, 2004). Additionally, the Tiki dromatheriid *Rewaconodon* (Datta et al., 2004) and archosauriform teeth as found in the Tiki Formation are present in the lower Tecovas Formation of the Chinle Group, USA (Heckert, 2004; Bhat et al., 2017). Because the latter is Adamanian in age (Tanner et al., 2013), such similarity in the vertebrate assemblages

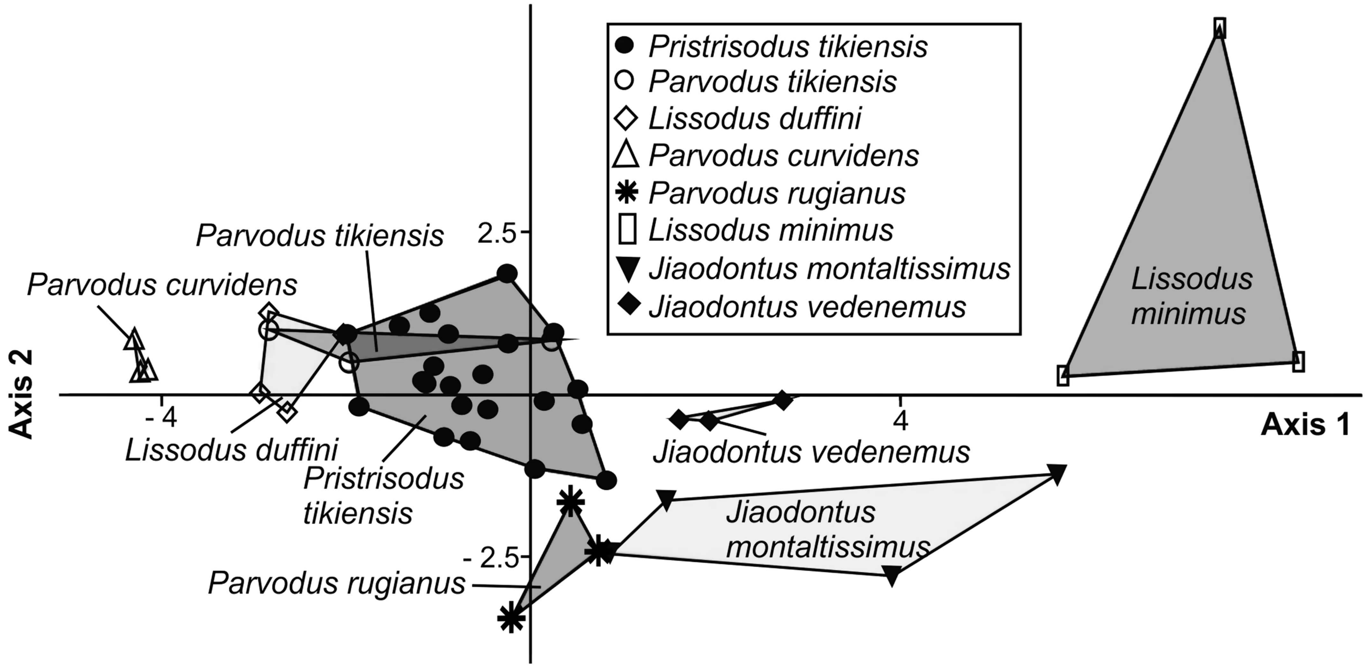

Figure 10. Graphical result of the canonical variate analysis of hybodont teeth along the first two canonical axes of maximum discrimination in the dataset (Eigenvalue of Axis 1 = 8.086, which accounted for 74.46% of the variation; Eigenvalue of Axis 2 = 1.45, which accounted for 13.35% of the variation).

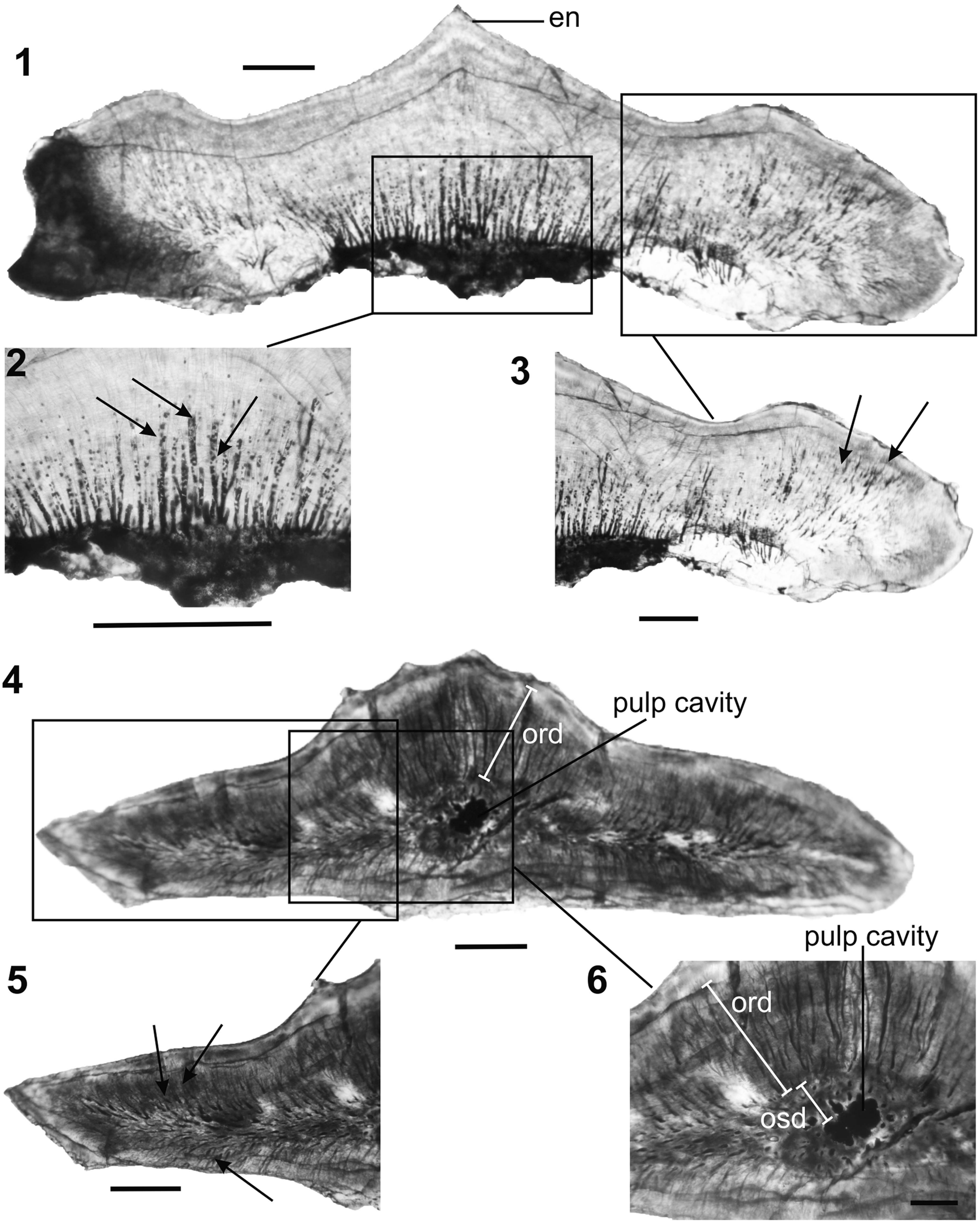

Figure 11. *Pristrisodus tikiensis* (Prasad et al., 2008). (**1–3**), Longitudinal section of a lateral tooth (IITKGPP50, morphotype IV) in lingual view showing (**1**) a thin capping of enameloid on the principal cusp, (**2**) vascular canals (arrows), and (**3**) dentinal tubules (arrows) at higher magnification; (**4–6**), transverse section of a lateral tooth (IITKGPP29, morphotype III) in occlusal view showing (**4**) a small, centrally located pulp cavity surrounded by a thick zone of orthodentine, (**5**) profuse dentinal tubules (arrows), and (**6**) a distinct pulp cavity surrounded by a narrow zone of osteodentine, which is overlain by a thick zone of orthodentine. Abbreviations: en = enameloid, ord = orthdentine, osd = osteodentine. Scale bars represent 0.2 mm (**1, 2, 4, 5**), 0.1 mm (**3, 6**).

corroborates the findings of Ray et al. (2016) and Datta et al. (2016) that the Tiki Formation may be younger than previously suggested.

India is one of the three widely separated regions, including Argentina (Johns et al., 2014) and Madagascar (Burmeister et al., 2006), from where Late Triassic freshwater hybodonts are reported. Three hybodont genera *Lonchidion*, *Polyacrodus* (Prasad et al., 2008), and *Pristrisodus* n. gen., (current study) are known from India, of which the latter genus is endemic. *Lonchidion* is known from North America (Murry, 1981; Cappetta, 2012), India (Prasad et al., 2008), and Spain (Manzaneras et al., 2016), whereas *Polyacrodus* is known from Germany and eastern France (Cappetta, 2012), although there are doubts regarding its validity (Rees, 2008; Cappetta, 2012). Hence, the Indian hybodont fauna shows resemblance to the European and North American forms that are known from coeval horizons. Most of these genera were euryhaline in nature (Maisey, 1989; Cuny et al., 2006), which may have resulted in their adaptation to freshwater systems in India during the Carnian. Further study is required to explain their migration along the coastlines prior to Pangaean rifting.

Acknowledgments

We thank D. Mukherjee of the Geological Studies Unit, Indian Statistical Institute, Kolkata, India for active participation during fieldwork, and critical comments on an earlier draft of the manuscript. We are grateful to C. Duffin of the Earth Science Department, Natural History Museum UK for valuable suggestions and insightful discussions during preparation of the revised draft of the manuscript. The constructive criticism and comments of two anonymous reviewers, D. J. Ward, and J. Kriwet are gratefully acknowledged. We are indebted to A. Bhaumik of the Department of Applied Geology, Indian School of Mines, Dhanbad, India, N. Bhowmik, and K. Datta for facilitating Scanning Electron Microscopy. C. Desarkar is acknowledged for thin-section preparations. Financial assistance and infrastructural facilities were provided by the Department of Science and Technology, India and the Indian Institute of Technology, Kharagpur, India, respectively.

Accessibility of supplemental data

Data available from the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.mq282

References

Ansorge, J., 1990, Fischreste (Selachii, Actinopterygii) aus der Wealdentonscholle von Lobber Ort (Mönchgut/Rügen/DDR): Paläontologische Zeitschrift, v. 64, p. 133–144.

Bandyopadhyay, S., 1999, Gondwana vertebrate faunas of India: Proceedings of the Indian National Science Academy, v. 65, p. 285–313.

Bandyopadhyay, S., 2011, Non-marine Triassic vertebrates of India, *in* Calvo, J.O., Porfiri, J., Gonzalez, B., and Santos, D.D., eds., Paleontología y Dinosaurios desde América Latina: EDIUNC, Editorial de la Universidad Nacional de Cuyo, Mendoza, Argentina, p. 33–46.

Becker, M.A., Chamberlain, J.A., and Terry, D.O., 2004, Chondrichthyans from the Fairpoint Member of the Fox Hills Formation (Maastrichtian), Meade County, South Dakota: Journal of Vertebrate Paleontology, v. 24, p. 780–793.

Bhat, M.S., 2015, A new and diverse late Triassic fish assemblage from India: International conference on current perspectives and emerging issues in Gondwana evolution, Lucknow, India, Abstract Volume, p. 22.

Bhat, M.S., 2017, Techniques for systematic collection and processing of vertebrate microfossils from their host mudrocks: a case study from the Upper Triassic Tiki Formation of India: Journal of the Geological Society of India, v. 89, p. 369–374.

Bhat, M.S., Ray, S., and Datta, P.M., 2015, Small archosauriform teeth from the Late Triassic of India: implications on early radiation of the dinosaurs: XXV Indian Colloquium on Micropaleontology and Stratigraphy, Aurangabad, India, Abstract Volume, p. 70–71.

Bhat, M.S., Ray, S., and Datta, P.M., 2017, Multivariate analyses reveal a new assemblage of diverse and small archosauriforms (Reptilia, Diapsida) from the Upper Triassic of India: Geophysical Research Abstracts Volume 19, EGU2017-18516, European Geosciences Union General Assembly 2017.

Błażejowski, B., 2004, Shark teeth from the Lower Triassic of Spitsbergen and their histology: Polish Polar Research, v. 25, p. 153–167.

Bonaparte, C.L.J., 1838, Selachorum tabula analytica: NuoviAnnali delle Scienze Naturali Bologna, v. 1, p. 195–214.

Broom, R., 1909, The fossil fishes of the Upper Karroo Beds of South Africa: Annals of South African Museum, v. 7, p. 251–269.

Burmeister, K.C., Flynn, J.J., Parrish, J.M., and Wyss, A.R., 2006, Paleogeographic and biostratigraphic implications of new Early Mesozoic terrestrial vertebrate fossils from Poamay, central Morondava Basin, Madagascar, *in* Harris, J.D., Lucas, S.G., Spielmann, J.A., Lockley, M.G., Milner, A.R. C., and Kirkland, J.I., eds., The Triassic-Jurassic terrestrial transition: Bulletin of the New Mexico Museum of Natural History, v. 37, p. 457–475.

Cappetta, H., 1987, Chondrichthyes II: Mesozoic and Cenozoic Elasmobranchii, *in* Schultze, H.-P., ed., Handbook of Paleoichthyology 3B: Stuttgart, Gustav Fischer Verlag, 193 p.

Cappetta, H., 2012, Chondrichthyes: Mesozoic and Cenozoic Elasmobranchii: Teeth, *in* Schultze, H.-P., ed., Handbook of Paleoichthyology 3E: Munich, Verlag Dr. Friedrich Pfeil, 512 p.

Carlson, S.J., 1989, Vertebrate dental structures, *in* Carter, J.G., ed., Skeletal Biomineralization: Patterns, Processes and Evolutionary Trends, Vol. 1: New York, Van Nostrand Reinhold, p. 531–556.

Chinsamy, A., and Raath, M.A., 1992, Preparation of fossil bone for histological study: Palaeontologia Africana, v. 29, p. 39–44.

Cifelli, R.L., Madsen, S.K., and Larson, M.E., 1996, Techniques for recovery and preparation of microvertebrate fossils: Oklahama Geological Survey Special Publication, v. 96, p. 1–24.

Cuny, G., 2012, Freshwater hybodont shark in Early Cretaceous ecosystems: a review, *in* Godefroit, P., ed., Bernissart Dinosaurs and Early Cretaceous Terrestrial Ecosystems: Bloomington, Indiana University Press, p. 519–529.

Cuny, G., Suteethorn, V., Kamha, S., Buffetaut, E., and Philippe, M., 2006, A new hybodont shark assemblage from the Lower Cretaceous of Thailand: Historical Biology, v. 18, p. 21–31.

Cuny, G., Suteethorn, V., Buffetaut, E., and Ouaja, M., 2007, Hybodont sharks from the Aptian–Albian of Tunisia and Thailand: Bulletin de la Société d'Etude des Sciences Naturelles d'Elbeuf, v. 1, p. 71–85.

Datta, D., Mukherjee, D., and Ray, S., 2016, A new phytosaur (Diapsida; Archosauria) bonebed from the Late Triassic Tiki Formation of India: taphonomic signatures: 76th Annual Meeting of the Society of Vertebrate Paleontology, Salt Lake City, Utah, Program and Abstracts, 2016, p. 123.

Datta, P.M., 1981, The first Jurassic mammal from India: Zoological Journal of the Linnean Society of London, v. 73, p. 307–312.

Datta, P.M., 2004, A suggestion for an early Tuvalian time segment for the Tiki Formation, South Rewa Gondwana Basin, India and other correlatable continental sequences: Albertina, v. 30, p. 6–7.

Datta, P.M., 2005, Earliest mammal with transversely expanded upper molar from the Late Triassic (Carnian) Tiki Formation, South Rewa Gondwana Basin, India: Journal of Vertebrate Paleontology, v. 25, p. 200–207.

Datta, P.M., Yadagiri, P., and Rao, B.R.J., 1978, Discovery of Early Jurassic micromammals from Upper Gondwana sequence of Pranhita-Godavari Valley, India: Journal of the Geological Society of India, v. 19, p. 64–68.

Datta, P.M., Das, D.P., and Luo, Z.X., 2004, A Late Triassic dromatheriid (Synapsida: Cynodontia) from India: Annals of the Carnegie Museum, v. 73, p. 72–84.

Donath, K., 1995, Preparation of Histologic Sections: Hamburg, EXAKT–Kulzer Publication, 16 p.

Duffin, C.J., 1985, Revision of the hybodont selachian genus *Lissodus* Brough (1935): Palaeontographica A, v. 188, p. 105–152.

Duffin, C.J., 1993, Mesozoic chondrichthyan faunas 1. Middle Norian (Upper Triassic) of Luxembourg: Palaeontographica A, v. 229, p. 15–36.

Duffin, C., and Theis, D., 1997, Hybodont shark teeth from the Kimmeridgian (Late Jurassic) of northwest Germany: Geologica Palaeontologica, v. 31, p. 235–256.

Duncan, M., 2004, Chondrichthyan genus *Lissodus* from the Lower Carboniferous of Ireland: Acta Palaeontologica Polonica, v. 49, p. 417–428.

Fischer, J., 2008, Brief synopsis of the hybodont form taxon *Lissodus* Brough, 1935, with remarks on the environment and associated fauna: Freiberger Forschungshefte, v. 528C, p. 1–23.

Fischer, J., Schneider, J.W., and Ronchi, A., 2010, New hybondontoid shark from the Permo-Carboniferous (Gzhelian–Asselian) of Guardia Pisano (Sardinia, Italy): Acta Palaeontologica Polonica, v. 55, p. 241–264.

Fischer, J., Voigt, S., Schneider, J.W., Buchwitz, M., and Voigt, S., 2011, A selachian freshwater fauna from the Triassic of Kyrgyzstan and its implication for Mesozoic shark nurseries: Journal of Vertebrate Paleontology, v. 31, p. 937–953.

Francillon-Vieillot, H., Buffrénil, V., de, Castanet, J., Géraudie, J., Meunier, F.J., Sire, J.Y., Zylberberg, L.L., and Ricqlès, A., de, 1990, Microstructure and mineralization of vertebrate skeletal tissues, *in* Carter, J.G., ed., Skeletal Biomineralization: Patterns, Process and Evolutionary Trends: New York, Van Nostrand Reinhold, v. 1, p. 471–530.

Ginter, M., Hairapetian, V., and Klug, C., 2002, Famennian chondrichthyans from the shelves of North Gondwana: Acta Geologica Polonica, v. 52, p. 169–215.

Ginter, M., Hampe, O., and Duffin, C., 2010, Chondrichthyes: Paleozoic Elasmobranchii: Teeth, *in* Schultze, H.-P., ed., Handbook of Paleoichthyology 3D: München, Verlag Dr. Friedrich Pfeil, 168 p.

Gupta, A., 2009, Ichthyofauna of the Lower Triassic Panchet Formation, Damodar Valley basin, West Bengal, and its implications: Indian Journal of Geosciences, v. 63, p. 275–286.

Hammer, Ø., and Harper, D., 2006, Palaeontological Data Analysis: Oxford, Blackwell Publishing, 351 p.

Hammer, Ø., Harper, D.A.T., and Ryan, P.D., 2001, PAST: palaeontological statistics software package for education and data analysis: Palaeontologia Electronica, v. 4, p. 1–9.

Heckert, A.B., 2004, Late Triassic microvertebrates from the Upper Triassic Chinle Group (Otischalkian–Adamanian: Carnian), southwestern U.S.A: Bulletin of the New Mexico Museum of Natural History and Science, v. 27, p. 1–170.

Heckert, A.B., and Lucas, S.G., 2006, Micro- and small vertebrate biostratigraphy and biochronology of the Upper Triassic Chinle Group, southwestern USA, *in* Harris, J.D., Lucas, S.G., Spielmann, J.A., Lockley, M.G., Milner, A.R.C., and Kirkland, J.I., eds., The Triassic–Jurassic terrestrial transition: New Mexico Museum of Natural History and Science, v. 37, p. 94–104.

Heckert, A.B., Ivanov, A., and Lucas, S.G., 2007, Dental morphology of the hybodontoid shark Lonchidion humblei Murry from the Upper Triassic Chinle Group, USA: New Mexico Museum of Natural History and Science Bulletin, v. 41, p. 45–48.

Hendrickx, C., Mateus, O., and Araújo, R., 2015, The dentition of megalosaurid theropods: Acta Palaeontologica Polonica, v. 60, p. 627–642.

Herman, J., 1977, Les Sélaciens des terrains néocrétacés et paléocènes de Belgique et des contrées limitrophes. Eléments d'une biostratigraphie intercontinentale: Mémoirs pour Servir à Explication des Cartes Géologiques et Minières de la Belgique, v. 15, p. 1–450.

Hibbard, C.W., 1949, Techniques of collecting microvertebrate fossils: Contributions from the Museum of Paleontology, University of Michigan, v. 8, p. 7–19.

Hodnett, J.-P., Elliot, D.K., Olson, T.J., and Wittke, J.H., 2013, Ctenacanthiform sharks from the Permian Kaibab Formation, Northern Arizona: Historical Biology, v. 24, p. 381–395.

Huxley, T.H., 1880, On the Application of the laws of evolution to the arrangement of the Vertebrata, and more particularly of the Mammalia: Proceedings of the Scientific Meetings of the Zoological Society of London, v. 43, p. 649–662.

Jain, S.L., 1980, Freshwater xenacanthid (= pleuracanth) shark fossils from the Upper Triassic, Maleri Formation, India: Journal of the Geological Society of India, v. 21, p. 39–47.

Jain, S.L., Robinson, P.L., and RoyChowdhury, T.K., 1964, A new vertebrate fauna from the Triassic of the Deccan: Quaternary Journal of the Geological Society of London, v. 120, p. 115–124.

Johns, M.J., Albanesi, G.L., and Voldman, G.G., 2014, Freshwater shark teeth (Family Lonchidiidae) from the Middle–Upper Triassic (Ladinian–Carnian) Paramillo Formation in the Mendoza, Precordillera, Argentina: Journal of Vertebrate Paleontology, v. 34, p. 512–523.

Johnson, G.D., 1981, Hybodontoidei (Chondrichthyes) from the Wichita-Albany Group (Early Permian) of Texas: Journal of Vertebrate Paleontology, v. 1, p. 1–41.

Johnson, G.D., 2003, Dentitions of *Barbclabornia* (new genus, Chondrichthyes: Xenacanthiformes) from the Upper Palaeozoic of North America: Mitteilungen aus dem Museum für Naturkunde in Berlin, Geowissenschaftliche Reihe, v. 6, p. 125–160.

Klug, S., Tütken, T., Wings, O., Pfretzschner, H., and Martin, T., 2010, A Late Jurassic freshwater shark assemblage (Chondrichthyes, Hybodontiformes) from the southern Junggar Basin, Xinjiang, Northwest China: Palaeodiversity and Palaeoenvironments, v. 90, p. 241–257.

Maisey, J.G., 1975, The interrelationships of phalacanthous selachians: Neues Jahrbuch für Geologie und Paläontologie Monatshefte, v. 9, p. 553–567.

Maisey, J.G., 1983, Cranial anatomy of *Hybodus basanus* Egerton from the Lower Cretaceous of England: American Museum Novitates, v. 2758, p. 1–64.

Maisey, J.G., 1987, Cranial anatomy of the Lower Jurassic shark *Hybodus reticulatus* (Chondrichthyes: Elasmobranchii), with comments on hybodontid systematics: American Museum Novitates, v. 2878, p. 1–39.

Maisey, J.G., 1989, *Hamiltonichthys mapesi*, g. & sp. nov. (Chondrichthyes; Elasmobranchii), from the Upper Pennsylvanian of Kansas: American Museum Novitates, v. 2931, p. 1–42.

Manzanares, E., Pla, C., Martínez-Pérez, C., Ferrón, H., and Botella, H., 2016, Lonchidion derenzii, sp. nov., a new lonchidiid shark (Chondrichthyes, Hybodontiforms) from the Upper Triassic of Spain, with remarks on lonchidiid enameloid: Journal of Vertebrate Paleontology, DOI: 10.1080/02724634.2017.1253585

Mukherjee, D., and Ray, S., 2014, A new Hyperodapedon (Archosauromorpha, Rhynchosauria) from the Upper Triassic of India: implications for rhynchosaur phylogeny: Palaeontology, v. 57, p. 1241–1276.

Mukherjee, D., Ray, S., Chandra, S., Pal, S., and Bandyopadhyay, S., 2012, Upper Gondwana succession of the Rewa basin, India: understanding the interrelationship of lithologic and stratigraphic variables: Journal of the Geological Society of India, v. 79, p. 563–575.

Murry, P.A., 1981, A New species of freshwater hybodont from the Dockum Group (Triassic) of Texas: Journal of Paleontology, v. 55, p. 603–607.

Owen, R., 1846, Lectures on the Comparative Anatomy and Physiology of the Vertebrate Animals. Delivered at the Royal College of Surgeons of England in 1844 and 1846. Part 1: Fishes: London, Longman, Brown, Green, and Longmans, 308 p.

Patnaik, R., 2003, Reconstruction of Upper Siwalik palaeoecology and palaeoclimatology using microfossil palaeocommunities: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 97, p. 133–150.

Patterson, C., 1966, British Wealden sharks: Bulletin of the British Museum (Natural History), v. 11, p. 283–350.

Prasad, G.V.R., and Cappetta, H., 1993, Late Cretaceous selachians from India and the age of the Deccan Traps: Palaeontology, v. 36, p. 231–248.

Prasad, G.V.R., and Sahni, A., 1987, Coastal-plain microvertebrate assemblage from the terminal Cretaceous of Asifabad, Andhra Pradesh: Journal of the Palaeontological Society of India, v. 32, p. 5–19.

Prasad, G.V.R., Manhas, B.K., and Arratia, G., 2004, Elasmobranch and actinopterygian remains from the Jurassic and Cretaceous of India, *in* Arratia, G., and Tintori, A., eds., Mesozoic Fishes 3: Systematics, Paleoenvironments and Biodiversity: München, Germany, Verlag Dr. Friedrich Pfeil, p. 625–638.

Prasad, G.V.R., Singh, K., Parmar, V., Goswami, A., and Sudan, C.S., 2008, Hybodont shark teeth from continental Upper Triassic deposits of India, *in* Arratia, G., Schultze, H.-P., and Wilson, M.V.H., eds., Mesozoic Fishes 4: Homology and Phylogeny: München, Germany, Verlag Dr. Friedrich Pfeil, p. 413–432.

Ray, S., 2015, A new Late Triassic traversodontid cynodont (Therapsida, Eucynodontia) from India: Journal of Vertebrate Paleontology, DOI: 10.1080/02724634.2014.930472.

Ray, S., Bhat, M.S., Mukherjee, D., and Datta, P.M., 2016, Vertebrate fauna from the Late Triassic Tiki Formation of India: new finds and their biostratigraphic implications: Palaeobotanist, v. 65, p. 47–59.

Reed, S.J.B., 2005, Electron Probe Analysis and Scanning Electron Microscopy in Geology: Cambridge, UK, Cambridge University Press, 189 p.

Rees, J., 2008, Interrelationships of Mesozoic hybodont sharks as indicated by dental morphology—preliminary results: Acta Geologica Polonica, v. 58, p. 217–221.

Rees, J., and Underwood, C.J., 2002, The status of the shark genus *Lissodus* Brough, 1935, and the position of nominal *Lissodus* species within the Hybodontoidea (Selachii): Journal of Vertebrate Paleontology, v. 22, p. 471–479.

Reif, W.E., 1973, Morphologie und Ultrastruktur des Hai – Schmelzes: Zoologica Scripta, v. 2, p 231–250.

Sahni, M.R., and Tewari, A.P., 1958, New unionids from the Triassic (Gondwana) rocks of Tihki, Vindhya Pradesh and Maleri, Hyderabad, Deccan: Records of the Geological Survey of India, v. 87, p. 406–417.

Sankey, J.T., 2008, Vertebrate Paleoecology from microsites, Talley Mountain, Upper Aguja Formation (Late Cretaceous), Big Bend National Park, Texas, *in* Sankey, J.T., and Baszio, S., eds., Vertebrate Microfossil Assemblages: Their Role in Paleoecology and Paleobiogeography: Bloomington, Indiana, Indiana University Press, p. 61–77.

Sire, J.Y., Donoghue, P.C.J., and Vickaryous, M.K., 2009, Origin and evolution of the integumentary skeleton in non-tetrapod vertebrates: Journal of Anatomy, v. 214, p. 409–440.

Shimada, K., 2002, Dental homologies in lamniform sharks (Chondrichthyes: Elasmobranchii): Journal of Morphology, v. 251, p. 38–72.

Shimada, K., 2005, Types of tooth sets in the fossil record of sharks, and comments on reconstructing dentitions of extinct sharks: Journal of Fossil Research, v. 38, p. 141–145.

Smith, J.B., 2005, Heterodonty in *Tyrannosaurus rex*: implications for the taxonomic and systematic utility of theropod dentitions: Journal of Vertebrate Paleontology, v. 25, p. 865–887.

Smith, J.B., Vann, D.R., and Dodson, P., 2005, Dental morphology and variations in theropod dinosaurs: implications for the taxonomic identification of isolated teeth: Anatomical Record, v. 285A, p. 699–736.

Stensiö, E.A., 1921, Triassic Fishes from Spitsbergen. Part IA: Vienna, 307 p.

Tanner, E.H., Spielmann, J.A., and Lucas, S.G., 2013, The Triassic System: new developments in Stratigraphy and Paleontology: Bulletin of the New Mexico Museum of Natural History and Science, v. 61, p. 1–612.

Teixeira, C., 1956, Sur un hybodontide du Karroo del'Angola: Revista da Faculdade de Ciencias, Lisboa, Series C, Ciencias Naturais, v. 5, p. 135–136.

Underwood, C.J., and Rees, J., 2002, Selachian faunas from the earliest Cretaceous Purbeck Group of Dorset, southern England: Special Papers in Palaeontology, v. 68, p. 107–119.

Wang, N.-Z., Zhang, X., Zhu, M., and Zhao, W.-J., 2009, A new articulated hybodontoid from Late Permian of northwestern China: Acta Zoologica (Stockholm), v. 90, p. 159–170.

Whitenack, L.B., and Gottfried, M.D., 2010, A morphometric approach for addressing tooth-based species delimitation in fossil mako sharks, Isurus (Elasmobranchii: Lamniformes): Journal of Vertebrate Paleontology, v. 30, p. 17–25.

Yadagiri, P., 1986, Lower Jurassic lower vertebrates from Jurassic Kota Formation, Pranhita-Godavari Valley of India: Journal of the Palaeontological Society of India, v. 31, p. 89–96.

Accepted 8 June 2017