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ADDITIONAL INFORMATION ON THE ARCHOSAURIFORMS FROM THE LOWERMOST TRIASSIC PANCHET FORMATION OF INDIA AND THE AFFINITIES OF "*TERATOSAURUS*(?) *BENGALENSIS*"

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Abstract. The Panchet Formation of northeastern India preserves an Induan (earliest Triassic) vertebrate assemblage with only one valid archosauromorph species, the proterosuchid *Samsarasuchus pamelae*. Two other archosauromorph species have been named for this unit: "*Ankistrodon indicus*" and "*Teratosaurus*(?) *bengalensis*". "*Ankistrodon indicus*", based on a fragment of maxilla with two partial teeth, is indistinguishable from other proterosuchid species and is considered a *nomen dubium*. "*Teratosaurus*(?) *bengalensis*" is represented by an isolated, almost complete tooth that was distinguished from "*Ankistrodon indicus*" in the presence of mesial denticles. "*Teratosaurus*(?) *bengalensis*" is also indistinguishable from other valid proterosuchid species and considered likely a *nomen dubium*. However, it remains unresolved if "*Teratosaurus*(?) *bengalensis*" represents a second Panchet archosauromorph species different from *Samsarasuchus pamelae* and "*Ankistrodon indicus*" because the presence of mesial denticles cannot be determined in these species due to their incompleteness. Here we describe two new Panchet Proterosuchidae specimens collected from the same locality as the holotypes of the three above-mentioned species. These new specimens are maxillary fragments and one of them has almost complete teeth with mesial denticles on the apical portion of the crowns, as in "*Teratosaurus*(?) *bengalensis*." The rest of their morphology is congruent with that of *Samsarasuchus pamelae* and "*Ankistrodon indicus*." As a result, the specimens reported here expand our anatomical knowledge of the Panchet archosauriform assemblage and indicate that there is no current evidence for the presence of more than one valid archosauromorph species in the Panchet Formation.

Key words. Archosauriformes. Proterosuchidae. Induan. Taxonomy.

Resumen. INFORMACIÓN ADICIONAL SOBRE LOS ARCOSAURIFORMES DE LA FORMACIÓN PANCHET DEL TRIÁSICO MÁS BAJO DE LA INDIA Y LAS AFINIDADES DE "*TERATOSAURUS*(?) *BENGALENSIS*". La Formación Panchet del noreste de la India preserva una asociación de vertebrados induanos (Triásico Temprano) con una sola especie de arcosauromorfo válida, el proterosúquido *Samsarasuchus pamelae*. Dos otras especies de arcosauromorfos han sido nombradas para esta unidad: "*Ankistrodon indicus*" y "*Teratosaurus*(?) *bengalensis*". "*Ankistrodon indicus*", basado en un fragmento de maxilar con dos dientes parciales, es indistinguible de otras especies de proterosúquidos y es considerado un *nomen dubium*. "*Teratosaurus*(?) *bengalensis*" está representado por un diente aislado casi completo que fue diferenciado de "*Ankistrodon indicus*" por la presencia de dentículos mesiales. "*Teratosaurus*(?) *bengalensis*" es también indistinguible de otras especies válidas de proterosúquidos y considerado probablemente como un *nomen dubium*. Sin embargo, permanece sin resolverse si "*Teratosaurus*(?) *bengalensis*" representa una segunda especie de arcosauromorfo de Panchet diferente de *Samsarasuchus pamelae* y "*Ankistrodon indicus*" porque la presencia de dentículos mesiales no puede ser determinada en estas especies debido a su incompletitud. Aquí describimos dos nuevos especímenes de Proterosuchidae de Panchet colectados en la misma localidad que los holotipos de las tres especies mencionadas anteriormente. Estos nuevos especímenes son fragmentos de maxilar y uno de ellos tiene dientes casi completos con dentículos mesiales en la porción apical de las coronas, como en "*Teratosaurus*(?) *bengalensis*". El resto de su morfología es congruente con aquella de *Samsarasuchus pamelae* y "*Ankistrodon indicus*". Los especímenes comunicados aquí expanden nuestro conocimiento anatómico de la asociación de arcosauriformes de Panchet e indican que no hay actualmente evidencia de la presencia de más de una especie válida de arcosauromorfo en la Formación Panchet.

Palabras clave. Archosauriformes. Proterosuchidae. Induano. Taxonomía.

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The earliest Triassic fossil record informs about the aftermath of the deadliest mass extinction documented in the Phanerozoic and the dawn of the Mesozoic faunal and floral assemblages (Bakker, 1977; Raup, 1979; Erwin, 1994; Benton *et al.*, 2004; Chen & Benton, 2012; Romano *et al.*, 2020). In particular, the most informative continental vertebrate assemblages that date back to the aftermath of the end-Permian mass extinction are those in current-day South Africa, western Russia, and China (*e.g.*, Gower & Sennikov, 2000; Benton *et al.*, 2004; Smith & Botha, 2005; Smith & Botha-Brink, 2014; Gastaldo *et al.*, 2020; Romano *et al.*, 2020; Viglietti *et al.*, 2022). Nevertheless, discoveries of the last decades have improved our knowledge of the earliest Triassic continental vertebrate assemblages of other regions of the globe, such as those in current-day Brazil, Australia, and India (*e.g.*, Gupta, 2009; Kear, 2009; Das & Gupta, 2012; Pinheiro *et al.*, 2016; McLoughlin *et al.*, 2020; De-Oliveira *et al.*, 2020, 2022; Hamley *et al.*, 2021; Pal, 2021; Ezcurra *et al.*, 2022, 2023). This new information leads to a more holistic knowledge of the tempo and mode of the biotic recovery in the Early Triassic world.

The archosauromorph diapsids are one of the main vertebrate groups that diversified in the aftermath of the end-Permian mass extinction (Ezcurra & Butler, 2018). The archosauromorphs are reptiles that include extant crocodiles and birds, as well as a huge diversity of completely extinct forms (*e.g.*, tanystropheids, allokotosaurs, pterosaurs, sauropods, non-avian theropods) that explored novel and disparate ecological spaces since the Triassic (see Ezcurra *et al.*, 2021 for a brief summary). A recent revision of the archosauriform specimens—Archosauriformes is a more taxonomically restricted clade within Archosauromorpha—from the Lower Triassic Panchet Formation of north-eastern India has shed light on this post-extinction continental assemblage, as well as the taxonomic composition and interrelationships of the worldwide distributed clade Proterosuchidae (Ezcurra *et al.*, 2023). Proterosuchids are particularly relevant in the context of the end-Permian mass extinction because they are the only archosauromorphs with body fossils occurring on both sides of the vertebrate fossil-defined Permo/Triassic boundary (Tatarinov, 1960; Charig & Sues, 1976; Ezcurra *et al.*, 2013, 2014).

The archosauromorph assemblage of the lowermost Triassic upper portion of the Panchet Formation (*sensu* Tripathi, 1962) is composed of the remains of the recently described proterosuchid *Samsarasuchus pamelae*, other specimens that could also belong to this species but cannot be identified unambiguously beyond cf. Proterosuchidae or Proterosuchidae genus and species indeterminate (one of the specimens currently identified as cf. Proterosuchidae is the holotype of "*Ankistrodon indicus*", which is based on a non-diagnostic fragment of maxilla with two partial teeth; Ezcurra *et al.*, 2023), and the holotype of "*Teratosaurus*(?) *bengalensis*" Dasgupta, 1928. Dasgupta (1928) erected this latter species based on an isolated tooth and considered that it differed from "*Ankistrodon indicus*" because of the presence of mesial denticles in the crown. Ezcurra *et al.* (2023) concluded that the morphology of "*Teratosaurus*(?) *bengalensis*" cannot be distinguished from that of South African and Chinese proterosuchids (*i.e.*, *Proterosuchus fergusi*, "*Chasmatosaurus*" *yuani*), which also preserve mesial denticles close to the tip of the crown. Thus, "*Teratosaurus*(?) *bengalensis*" is a non-taxonomically valid species. The tooth crowns of cf. Proterosuchidae of the Panchet Formation (including the holotype of "*Ankistrodon indicus*") lack their apical ends and it cannot be determined if mesial denticles were present in this unpreserved region of the teeth (Ezcurra *et al.*, 2023). As a result, Ezcurra *et al.* (2023) stated that it remained inconclusive if "*Teratosaurus*(?) *bengalensis*" could represent a second archosauromorph taxon in the Panchet Formation, distinct from those tooth-bearing bones that they referred to cf. Proterosuchidae.

New archosauromorph bones with teeth implanted in them were recently collected in the upper portion of the Panchet Formation by two of us (YPS and NAS). These specimens preserve almost complete tooth crowns and allow comparing the preserved regions of bone with those of Panchet specimens previously referred to cf. Proterosuchidae. Here, we describe these new archosauromorph specimens from the Panchet Formation and discuss their implications in the taxonomic richness of the vertebrate assemblage of this Indian unit.

GEOLOGICAL SETTING

The intracratonic Raniganj Basin lies within the

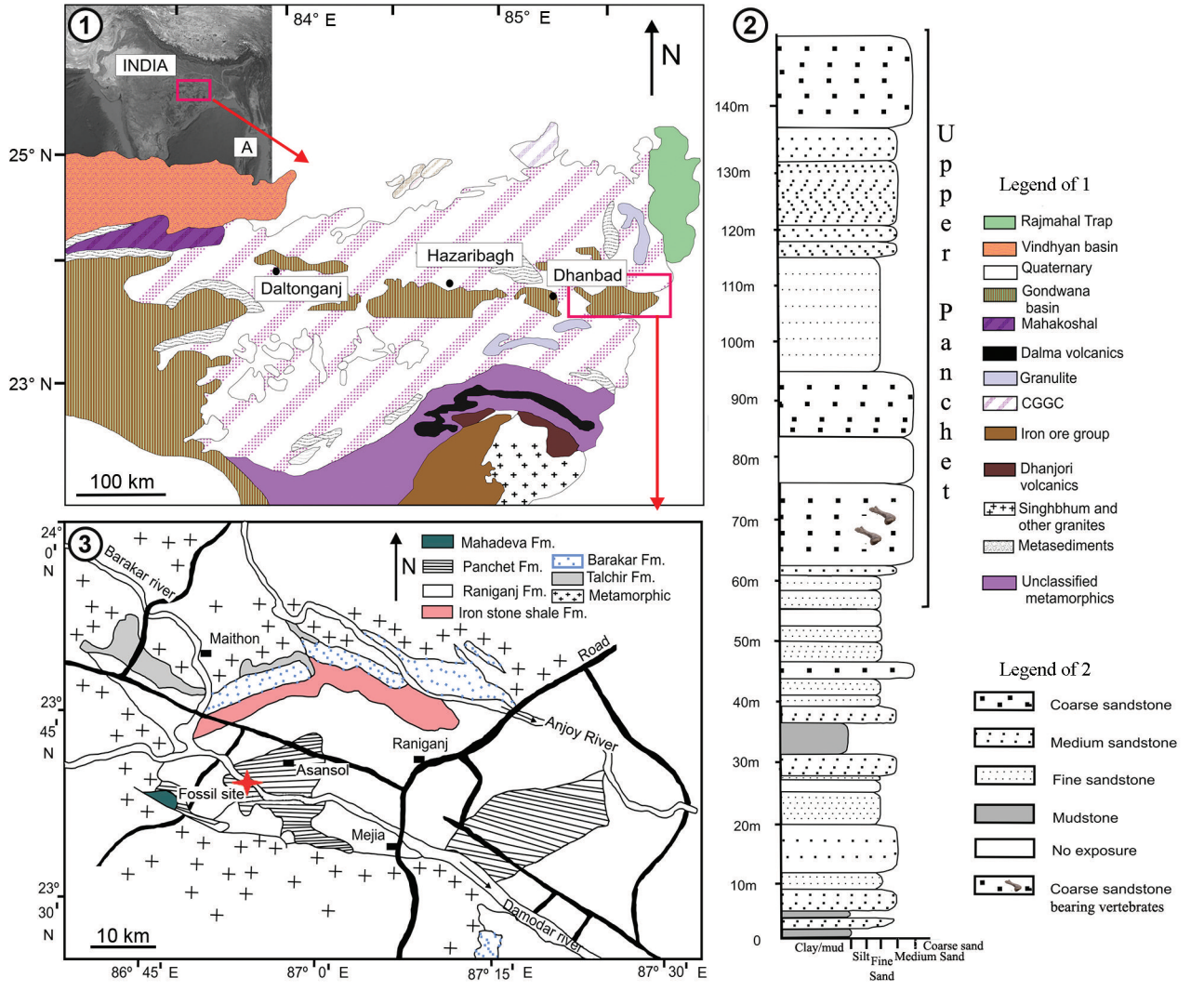

Figure 1. **1,** Map of India showing the location of the basement Chotanagpur Granite Gneissic Complex along with the Raniganj Basin (modified from Acharyya, 2003). **2,** General lithosection of the Panchet Formation (modified after Gupta, 2009) that indicates the occurrence of the new proterosuchid specimens reported here. **3,** Geological map of the Raniganj Basin depicting different formations, with the fossil site and lithosection log indicated with a red star (modified from Murthy *et al.*, 2010). Abbreviations: **Fm.,** Formation.

Son-Damodar lineament in eastern India. This basin is composed of ~2,000 m thick sedimentary deposits comprising formations of both the Lower and the Upper Gondwana Supergroup, ranging from the late Carboniferous to Early Cretaceous (see Ghosh *et al.*, 1996). The Precambrian basement, Chotanagpur Granite Gneissic Complex (CGGC), fed the sediments of the Raniganj Basin (Pascoe, 1956; Patel *et al.*, 2014). The Raniganj Basin is positioned between 23° 03′ N to 23° 51′ N; 86° 42′ E to 87° 28′ E within the CGGC (Fig. 1.1) and it comprises six formations: the Talchir, Barakar, Barren Measure, Raniganj, Panchet, and Supra-Panchet formations (Ghosh *et al.*, 1996) (Fig. 1.2).

The Panchet Formation is well-exposed in the Bardaman District of West Bengal, eastern India, and it has a thickness of about 150 m near the Dumdumi and Doeli villages (Gupta, 2009; Ezcurra *et al.*, 2023). This formation is underlain by the Raniganj Formation and overlain by the Supra-Panchet Formation. Based on lithology, earlier workers divided the Panchet Formation into Lower and Upper parts (Dasgupta, 1922, 1926; Robinson, 1958; Tripathi & Satsangi, 1963). The lithologies of the lower Panchet deposit comprise thick argillaceous red mudstone

and siltstone and thin arenaceous sandstone beds of pale yellow, khaki green, and greyish to greenish colours alternating with the argillaceous beds. The sandstones are mainly arkosic with subordinate quartz arenite (Gupta, 2005). The upper Panchet is characterised by coarse, sometimes pebbly to medium-grained, yellowish brown, massive to planar and trough cross-bedded sandstone units with subordinate siltstone and argillaceous rocks. The sandstones are mainly matrix-supported sub-lithic arenite with subordinate arkoses (Gupta, 2005). The Panchet Formation was deposited during the Induan stage of the Early Triassic (Cosgriff, 1984; Ray, 2005; Ezcurra *et al.*, 2023). The fossil content of the Panchet Formation includes fish scales, teeth, and tooth plates of an unknown number of species of actinopterygians, dipnoans, and chondrichthyans, several temnospondyls (*i.e.*, the trematosaurids *Indolyrocephalus* and *Gonioglyptus*, the rhytidosteid *Indobrachyops*, the lydekkerinid *Lydekkerina*, the lapillopsid *Manubrantlia*, the plagiosaurid *Capulomala*, the brachyopid *Pachygonia*, a probable tupilakosaurid, and an indeterminate benthosuchid), the dicynodonts *Lystrosaurus murrayi*, *Lystrosaurus* cf. *L. curvatus* and *Lystrosaurus* cf. *L. declivis*, the cynodonts *Thrinaxodon bengalensis* and *Panchetocynodon damodarensis*, an indeterminate non-archosauromorph neodiapsid, the proterosuchid *Samsarasuchus pamelae*, and indeterminate cf. Proterosuchidae, Proterosuchidae, and Chasmatosuchinae specimens (Ezcurra *et al.*, 2023 and references therein).

MATERIAL AND METHODS

The new archosauromorph specimens reported here were collected in yellow-brownish pebbly sandstones of the upper Panchet Formation at the Deoli locality (23° 39′ 02″ N; 86° 52′ 53″ E) in 2019 by YPS and NAS (Fig. 1). The Deoli locality has also yielded the holotypes of the archosauriforms "*Ankistrodon indicus*", "*Teratosaurus*(?) *bengalensis*", and *Samsarasuchus pamelae* (Huxley, 1865; Dasgupta, 1928; Ezcurra *et al.*, 2023). In particular, the new specimens reported here were found 300 m to the west of the holotype of *Samsarasuchus pamelae* (see Ezcurra *et al.*, 2023). The specimens were collected in small blocks of matrix containing the bones following excavation using hammers and chisels. Wherever necessary, broken bones were adhered with cyanoacrylate adhesives. All the archosauromorph specimens from the Panchet Formation used for comparative purposes (see Ezcurra *et al.*, 2023) were studied at firsthand by one of us (MDE) to the exclusion of those reported by Pal (2021).

Institutional abbreviations. BIOPS/PT-P, Biostratigraphy, Palaeontology and Sedimentology Lab of Central University of Punjab, Bathinda/Panchet/Palaontology, Chandigarh, India; **CGS GHG,** Council for Geoscience (Gideon H. Groenewald collection), Pretoria, South Africa; **GSI,** Geological Survey of India, Kolkata, India; **ISIR,** Indian Statistical Institute, Reptiles, Kolkata, India; **IVPP,** Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; **NMQR,** National Museum, Bloemfontein, South Africa; **PIN,** Borissiak Paleontological Institute of the Russian Academy of Sciences, Moscow, Russia; **QMF,** Queensland Museum, Brisbane, Australia; **RC,** Rubidge Collection, Wellwood, Graaff-Reinet, South Africa; **SAM-PK,** Iziko South African Museum, Cape Town, South Africa; **UFRGS-PV,** Universidade Federal do Rio Grande do Sul, Paleontologia de Vertebrados, Porto Alegre, Brazil; **UNIPAMPA,** Universidade Federal do Pampa, São Gabriel, Brazil.

SYSTEMATIC PALAEONTOLOGY

DIAPSIDA Osborn, 1903 [Gauthier & de Queiroz (2020)]
ARCHOSAUROMORPHA von Huene, 1946
[Gauthier (2020a)]
ARCHOSAURIFORMES Gauthier *et al.*, 1988
[Gauthier (2020b)]
PROTEROSUCHIDAE von Huene, 1908
sensu Ezcurra *et al.*, 2013

Genus and species indeterminate
Figures 2, 3

Material. BIOPS/PT-P01, anterior portion of left maxilla with five, at least partially preserved, alveoli and two almost complete tooth crowns (Figs. 2.1, 2.4. 3.1–3.2); BIOPS/PT-P02, fragment of mid- or posterior alveolar region of left maxilla with six, at least partially preserved, alveoli and two teeth broken at the base of the crown (Fig. 2.2, 2.3, 2.5).

Stratigraphic and geographic occurrence. Yellow-brownish

pebbly sandstones of the upper Panchet Formation (Early Triassic: middle–late Induan; see Ezcurra *et al.*, 2023), Raniganj Basin (in other papers referred to the Damodar Basin) at the Damodar River bed locality, near Deoli village (23° 39′ 02″ N; 86° 52′ 53″ E), West Bengal, east India (Fig. 1).

Description. The two specimens reported here include regions of the maxilla already described or morphologically congruent with those of the cf. Proterosuchidae of the Panchet Formation (see Ezcurra *et al.*, 2023, figs. 18, 19). BIOPS/PT-P01 is the anterior end of a left maxilla that preserves teeth in the second and fourth tooth positions of a total of five preserved alveoli (Fig. 2.1, 2.4). The tooth crowns only lack their apicalmost tips. BIOPS/PT-P02 represents a portion of the horizontal process of a left maxilla that preserves six tooth positions, with two teeth *in situ* that are broken slightly apical to the base of the crown (Fig. 2.2, 2.3, 2.5). Anatomical comparisons are mainly focused on other partial maxillae of the Panchet Formation referred to cf. Proterosuchidae (ISIR 1075, 1076, GSI 2190, 2259). The novel morphological features of BIOPS/PT-P01 and BIOPS/PT-P02 with respect to these previously described specimens are related to a more dorsally preserved anterior end of the maxilla and the more complete tooth crowns.

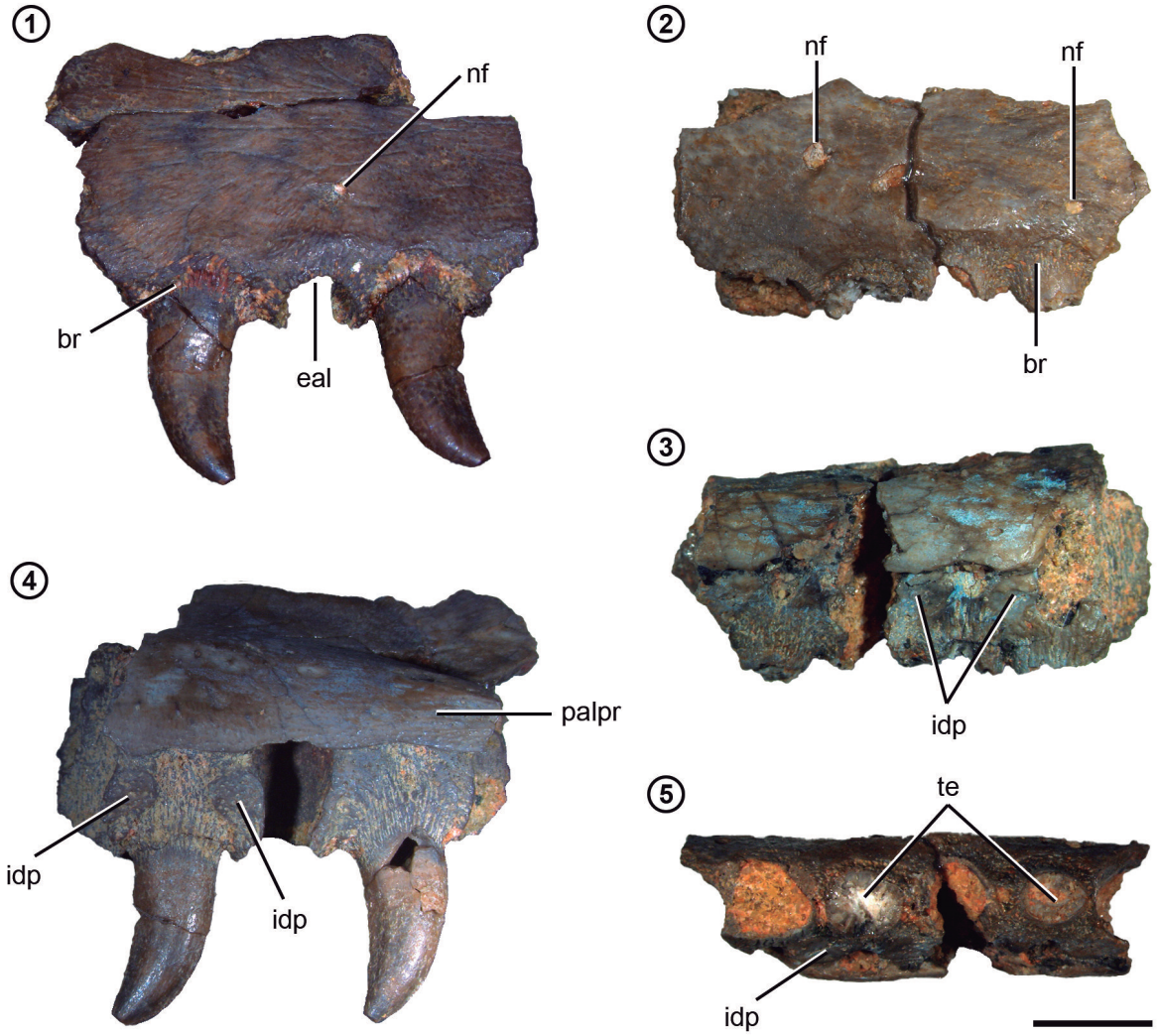

Figure 2. Panchet Proterosuchidae maxillae. **1, 4,** Anterior end (**BIOPS/PT-P01**); and **2, 3, 5,** partial horizontal process (**BIOPS/PT-P02**) of left maxillae in **1, 2,** lateral, **3, 4,** medial, and **5,** ventral views. Abbreviations: **br,** bony ridges; **eal,** empty alveolus; **idp,** interdental plate; **nf,** neurovascular foramen; **palpr,** palatal process; **te,** teeth. Scale bar= 5 mm.

The lateral surface of the preserved region of the anterior process of the maxilla of BIOPS/PT-P01 is mostly flat and lacks ornamentation. However, there are some shallow, but distinct, grooves that are generally anteroposteriorly oriented. The series of primarily anteroventrally oriented striations on the lateral surface of the anterior tip of the maxilla of the cf. Proterosuchidae Panchet specimen ISIR 1076 is absent or occurred more anteriorly than it is preserved in BIOPS/PT-P01. There is only one preserved small, circular neurovascular foramen positioned approximately 4 mm dorsal to the third tooth position (Fig. 2.1: nf). This foramen is positioned dorsal to an alveolus that lacks an erupted tooth, contrasting with the cf. Proterosuchidae Panchet specimens ISIR 1075 and ISIR 1076, in which their neurovascular foramina are positioned dorsal to the alveoli bearing an erupted tooth. The anterior end of the maxilla of BIOPS/PT-P01 is dorsoventrally taller than the height of the mesial maxillary tooth crowns. This condition could not be assessed in the cf. Proterosuchidae Panchet specimens ISIR 1075 and ISIR 1075 because of the lack of preservation (Ezcurra *et al.*, 2023), but it resembles the morphology present in South African (*e.g.*, *Proterosuchus fergusi*: RC 846, SAM-PK-11208) and Chinese (*e.g.*, "*Chasmatosaurus*" *yuani*: IVPP V36315, V4067) proterosuchids. Thus, BIOPS/PT-P01 bolsters the interpretation of the absence of an anterior maxillary foramen in ISIR 1075 and ISIR 1076. By contrast, a large anterior maxillary foramen is commonly present in other Permo–Triassic non-archosauriform saurians (*e.g.*, *Planocephalosaurus robinsonae*: Fraser, 1982; *Protorosaurus speneri*: Gottmann-Quesada & Sander, 2009; *Macrocnemus bassanii*: Miedema *et al.*, 2020; *Azendohsaurus madagaskarensis*: Flynn *et al.*, 2010; *Mesosuchus browni*: Dilkes, 1998; *Prolacerta broomi*: Modesto & Sues, 2004) and some early archosauriforms (*e.g.*, *Proterosuchus fergusi*: RC 846; *Osmolskina czatkoviensis*: Borsuk-Białynicka & Evans, 2009). The two foramina preserved in the horizontal process of BIOPS/PT-P02 are also small and open laterally (Fig. 2.2: nf). The posterior foramen is positioned considerably closer to the alveolar margin than the anterior one. None of the neurovascular foramina extends ventrally as a groove, contrasting with the condition in erythrosuchids (*e.g.*, *Erythrosuchus africanus*, *Garjainia prima*; Ezcurra, 2016). The grooves preserved in BIOPS/PT-P01 neither converge with the neurovascular foramen (Fig. 2.1). In BIOPS/PT-P02, both lateral and medial surfaces of the horizontal process are convex dorsoventrally, but the latter has a more pronounced curvature. This results in a progressively narrower process towards its dorsal margin. There is no facet for articulation with a palatal bone on the preserved medial surface of the horizontal process.

On the medial surface of the anterior process of BIOPS/PT-P01, the base of the palatal process is placed immediately dorsal to the alveolar margin of the bone (Fig. 2.4: palpr), as occurs in cf. Proterosuchidae Panchet specimens (Ezcurra *et al.*, 2023), *Proterosuchus goweri* (NMQR 880), *Proterosuchus fergusi* (RC 846), "*Chasmatosaurus*" *yuani* (IVPP V36315), *Kalisuchus rewanensis* (QMF8998), *Guchengosuchus shiguaiensis* (Butler *et al.*, 2019a), *Garjainia* spp. (Gower *et al.*, 2014; Ezcurra *et al.*, 2019; Butler *et al.*, 2019b), *Chalishevia cothurnata* (Butler *et al.*, 2019c), *Euparkeria capensis* (SAM-PK-6048, SAM-PK-13666; Sookias *et al.*, 2020), and *Osmolskina czatkoviensis* (Borsuk-Białynicka & Evans, 2009). The base of this process projects only very weakly medially and possesses a horizontally oriented main axis. The alveolar margin of the anterior process of the maxilla is mainly straight in lateral view, as in cf. Proterosuchidae Panchet specimens (Ezcurra *et al.*, 2023) and most other early archosauriforms (Ezcurra, 2016), but contrasting with the concave margin present in *Proterosuchus goweri* (Ezcurra & Butler, 2015) and the upturned anterior end present in erythrosuchids (*e.g.*, *Erythrosuchus africanus*, *Garjainia prima*; Gower, 2003; Ezcurra, 2016; Butler *et al.*, 2019b).

Tooth implantation is ankylothecodont in both BIOPS/PT-P01 and BIOPS/PT-P02, with bony ridges connecting the bone to the base of the crown (Fig. 2.1, 2.2: br), as in the maxillae of the cf. Proterosuchidae Panchet specimens (Ezcurra *et al.*, 2023), *Proterosuchus* spp. (Ezcurra, 2016), *Prolacerta broomi* (Modesto & Sues, 2004), *Teyujagua paradoxa* (Pinheiro *et al.*, 2020), *Tasmaniosaurus triassicus* (Ezcurra, 2014), some early erythrosuchids (*e.g.*, *Fugusuchus hejiapanensis*, *Guchengosuchus shiguaiensis*, some specimens of *Garjainia*; Ezcurra *et al.*, 2019; Butler *et al.*, 2019a, 2019b), and *Kalisuchus rewanensis* (Ezcurra, 2016). There are vertical and pentagon-shaped, dorsoventrally taller than anteroposteriorly broad, interdental plates between the

alveoli in BIOPS/PT-P01 and BIOPS/PT-P02 (Fig. 2.3–2.5: idp). The anteroposteriorly short interdental plates are well separated from each other and partially expose the root of the teeth, but there is no visible reabsorption pit in these specimens. The presence of interdental plates is an apomorphy of Archosauriformes, but convergently acquired within Tanystropheidae and Allokotosauria (Nesbitt, 2011; Ezcurra, 2016; Pinheiro *et al.*, 2016). BIOPS/PT-P01 and BIOPS/PT-P02 share with cf. Proterosuchidae Panchet specimens and other proterosuchids the presence of interdental plates well separated from each other, whereas they closely approach or contact each other in the maxillae of *Kalisuchus rewanensis*, erythrosuchids, and eucrocopods (Ezcurra *et al.*, 2023). The interdental plates extend dorsally to the same level as the lateral wall of the alveolar margin and possess multiple, densely distributed pits on their medial surface.

The teeth have long roots that are deeply implanted in their alveoli and the pattern of empty alveoli suggests an alternate tooth replacement in both BIOPS/PT-P01 and BIOPS/PT-P02. The ventrally concave lateral margins of the empty alveoli indicate that the replacement of the teeth involved the loss of part of the bony margin of the socket that was subsequently regenerated by bone growth (Fig. 2.1: eal). Subsequently, the bone fused again to the base of the crown, as occurs in other archosauromorphs with ankylothecodont tooth implantation (*e.g.*, *Proterosuchus fergusi*: RC 846). The interdental plates are fused to the lingual surface of the tooth in at least the second tooth position of BIOPS/PT-P01.

Two almost complete teeth are preserved in BIOPS/PT-P01 and two teeth broken around the boundary between root and crown are preserved in BIOPS/PT-P02. The bases of the crowns are labiolingually compressed (Fig. 2.5: te), as in *Prolacerta broomi*, *Teyujagua paradoxa*, *Tasmaniosaurus triassicus*, and early-diverging archosauriforms (Nesbitt, 2011; Ezcurra, 2014, 2016; Pinheiro *et al.*, 2016). The labiolingual compression of the crowns increases toward their apices. The mesial margin is strongly convex and the distal one concave, but with a lower curvature, in labial/lingual views in both crowns of BIOPS/PT-P01. This results in recurved crowns with their apex positioned distally to the base of the crown (Fig. 2.1, 2.4), resembling the condition in other proterosuchids (Ezcurra & Butler, 2015). The mesial margin has a distinct carina and denticles restricted to its apical third (Fig. 3.1–3.3), as occurs in "*Teratosaurus*(?) *bengalensis*", *Proterosuchus* (*e.g.*, *Proterosuchus fergusi*: SAM-PK-11208; Fig. 3.4), "*Chasmatosaurus*" *yuani* (IVPP V36315), and a dentary referred to *Chasmatosuchus rossicus* (PIN 2354/26; Sennikov, 1995). By contrast, the distal margin has a serrated carina through most of the apicobasal height of the crowns to the exclusion of its base. The basal-most mesial denticles are similar in size to the distal ones, but more apically they become considerably less mesiodistally

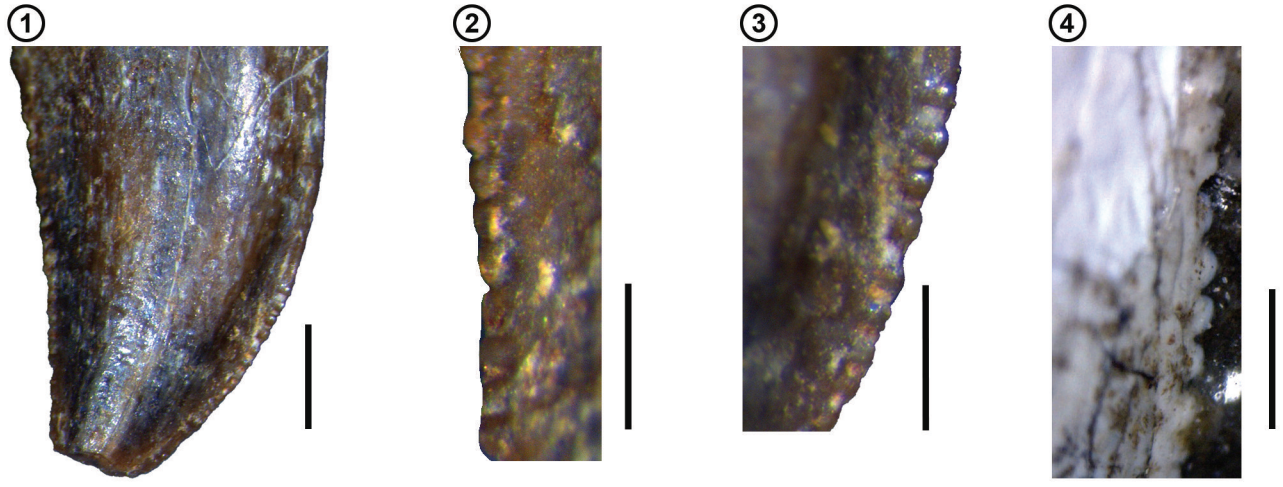

Figure 3. Panchet Proterosuchidae tooth (**BIOPS/PT-P01**) and comparison with ***Proterosuchus fergusi*** (**CGS GHG 231**). **1,** Apical third; **2,** distal denticles; **3,** mesial denticles of fourth maxillary tooth of Panchet proterosuchid; **4,** mesial denticles of second maxillary tooth of ***Proterosuchus fergusi***; in **1–3,** lingual and **4,** labial views. Scale bars= 1 mm in (1) and 0.5 mm in (2–4).

developed than the distal ones (Fig. 3.1–3.3). *Teyujagua paradoxa* lacks denticles on the mesial margin of the crowns (Pinheiro *et al.*, 2016, 2020) and an isolated tooth crown referred to *Archosaurus rossicus* (PIN 1100/85a) has small, poorly mesiodistally developed denticles that extend through at least more than the apical half of both mesial and distal margins. The best-preserved tooth crown of the dentary of *Sarmatosuchus otschevi* has sub-equally developed mesial and distal denticles, but it cannot be determined how far they extended basally (PIN 2865/68-11). Similarly, an erupting tooth in the maxilla of *Kalisuchus rewanensis* has mesial denticles but it cannot be determined how far they extended basally on the crown (QMF8998). In most erythrosuchids (*e.g.*, *Guchengosuchus shiguaiensis*: Butler *et al.*, 2019b; *Garjainia prima*: Ezcurra *et al.*, 2019; Butler *et al.*, 2019b; *Erythrosuchus africanus*: Gower, 2003; *Chalishevia cothurnata*: Butler *et al.*, 2019c) and early eucrocopods (*e.g.*, *Euparkeria capensis*: Sookias *et al.*, 2020; *Rhadinosuchus gracilis*: Ezcurra *et al.*, 2015) the mesial denticles extend basally to the apical third of the crown and are similarly or slightly less mesiodistally developed than the distal denticles. The denticles of BIOPS/PT-P01 have a rounded margin and short interdenticular sulci that do not extend onto the rest of the crown (Fig. 3.1–3.3). The denticles are relatively small, with seven serrations per millimetre on both mesial and distal margins, resembling the count of eight and seven serrations per millimetre in the maxillae and dentaries, respectively, of the cf. Proterosuchidae Panchet specimens (Ezcurra *et al.*, 2023). The tooth crowns lack ornamentation or wear facets, contrasting with the presence of enamel wrinkles in the erythrosuchid *Chalishevia cothurnata* (Butler *et al.*, 2019c). There is no mesiodistal or labiolingual expansion at the base of the crowns.

DISCUSSION

The new specimens described here are assigned to Proterosuchidae because of the presence of the following combination of character states that distinguishes the clade from other archosauromorphs: an ankylothecodont tooth implantation, anteroposteriorly narrow interdental plates that are well separated from each other, and mesial denticles restricted to the apical third of the tooth crown (Ezcurra, 2016; Ezcurra *et al.*, 2023). The new specimens reported here provide novel anatomical information about the archosauriform tooth-bearing bones of the Panchet Formation, such as the presence of a dorsoventrally tall anterior process of the maxilla and mesial denticles on the tooth crowns. The latter feature is particularly relevant because of its taxonomic implications and discussion of the taxonomic richness of the vertebrate assemblage of the upper Panchet Formation. Ezcurra *et al.* (2023) described the new proterosuchid species *Samsarasuchus pamelae* from the upper Panchet Formation, but these authors could not refer these tooth-bearing bones unambiguously to this species because of the lack of overlapping morphology with the type specimens. As a result, Ezcurra *et al.* (2023) assigned these tooth-bearing bones to cf. Proterosuchidae, although they could potentially belong to *Samsarasuchus pamelae*, because it could not be determined the presence of mesial denticles on the apical third of the crown. Similarly, the lack of overlapping characters with the hypodigm of *Samsarasuchus pamelae* prevents the referral of BIOPS/PT-P01 and BIOPS/PT-P02 to this species. Only new, more complete specimens would allow assigning these cf. Proterosuchidae and Proterosuchidae tooth-bearing bones of the upper Panchet Formation to a species-level taxon.

Huxley (1865) erected the new reptile genus and species "*Ankistrodon indicus*" from the upper portion of the Panchet Formation. However, this genus and species was subsequently considered *nomina dubia* because the holotype cannot be distinguished from the more complete proterosuchid specimens that were collected in South Africa and China in the first half of the 20th century (Charig & Reig, 1970). Von Huene (1942) assigned "*Ankistrodon indicus*" to the genus "*Chasmatosaurus*", whose type species is the South African "*Chasmatosaurus vanhoepeni*." Subsequently, Welman (1998) interpreted the holotype of the South African species *Proterosuchus fergusi* as diagnostic, and considered "*Chasmatosaurus*" and "*Chasmatosaurus vanhoepeni*" as subjective junior synonyms of the former species. Thus, the proterosuchid specimens from the Panchet Formation, including the holotype of "*Ankistrodon indicus*", have been referred to the genus *Proterosuchus* since then (Bandyopadhyay, 1999, 2011; Das & Gupta, 2012; Bandyopadhyay & Ray, 2020; Pal, 2021).

Ezcurra *et al.* (2023) included the holotype of "*Ankistrodon indicus*" among the cf. Proterosuchidae specimens of the Panchet Formation.

The taxonomic history of "*Teratosaurus*(?) *bengalensis*", another archosauromorph species from the upper Panchet Formation (Dasgupta, 1928), is more obscured. Ezcurra *et al.* (2023) considered that it was likely that "*Teratosaurus*(?) *bengalensis*" was not a valid species, but its revision went beyond the scope of their work. Although the holotype of "*Teratosaurus*(?) *bengalensis*" could not be located in its repository to be studied firsthand as part of our study, here we consider that this species cannot be distinguished from those of the more complete South African and Chinese proterosuchid species based on the morphological description provided by Dasgupta (1928). In addition, the new Proterosuchidae specimens reported here bolster this interpretation because their dental morphology is identical to that of "*Teratosaurus*(?) *bengalensis*" and their tooth-bearing bone anatomy is completely congruent with that of the cf. Proterosuchidae specimens from the Panchet Formation and proterosuchids from other regions of the world (*e.g.*, the presence of anteroposteriorly short, pentagon-shaped interdental plates). Thus, "*Teratosaurus*(?) *bengalensis*" is here considered a *nomen dubium* and a cf. Proterosuchidae specimen because of the presence of small mesial denticles restricted to the apical third of the crown. It should be noted that the genus *Teratosaurus* is a valid taxon of pseudosuchian archosaur (Brusatte *et al.*, 2009).

In conclusion, there is no current evidence for the presence of more than one archosauromorph species in the upper Panchet Formation of India. This very low taxonomic richness differs from that in several other Induan–early Olenekian archosauromorph-bearing geological units worldwide (*e.g.*, Jiucaiyuan Formation of China: two species [*Prolacertoides jimusarensis* and "*Chasmatosaurus*" *yuani*]; upper levels of the Balfour and Katberg formations of South Africa: five–six species [*Noteosuchus coletti*, *Prolacerta broomi*, *Proterosuchus fergusi*, *Proterosuchus goweri*, *Proterosuchus alexanderi*, and Archosauriformes indet. NMQR 3570]; Sanga do Cabral Formation of Brazil: four species [Tanystropheidae indet. UFRGS-PV-492-T, *Elessaurus gondwanoccidens*, *Teyujagua paradoxa*, Chasmatosuchinae indet. UNIPAMPA 750]; Rybinskian Gorizont of Russia: two species [*Chasmatosuchus rossicus*, *Tsylmosuchus samariensis*]; Young, 1973; Gower & Sennikov, 2000; Ezcurra & Butler, 2015; Pinheiro *et al.*, 2016; De-Oliveira *et al.*, 2018, 2020, 2022; Ezcurra *et al.*, 2023). As a result, the apparent low archosauromorph richness of the upper Panchet Formation is very likely a sampling artefact. Thus, more work is necessary to reach a more comprehensive understanding of the vertebrate assemblage of the Panchet Formation and enrich our knowledge about the aftermath of the mass extinction event at a more global level.

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