CRANIAL MORPHOLOGY OF A NEW PHYTOSAUR (DIAPSIDA, ARCHOSAURIA) FROM THE UPPER TRIASSIC OF INDIA: IMPLICATIONS FOR PHYTOSAUR PHYLOGENY AND BIOSTRATIGRAPHY

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Abstract: Detailed description and phylogenetic assessment of a phytosaur skull collected from the Tiki Formation of the Rewa Gondwana Basin of India and earlier diagnosed as Parasuchus hislopi, show that it pertains to a new genus and species, Volcanosuchus statisticae. The new taxon is characterized by marginal overlapping of the nostrils by the antorbital fenestrae, external nares situated on a bulbous and raised dome, the lateral surface of the jugal ornamented by a prominent ridge defined by multiple tubercles and radiating thread-like structures, and distinct ornamentation patterns on the rostrum and skull table. Phylogenetic analysis nests Volcanosuchus within Mystriosuchinae, where it forms a sister taxon to (Rutiodon + Leptosuchomorpha) and marks the transition between the basal Parasuchidae and more derived Mystriosuchinae phytosaurs. Evolution of the phytosaur skulls resulted in changes from non-overlapping nostril and antorbital fenestra to an overlapping state, anteroposterior elongation of the exoccipital-supraoccipital shelf, appearance of a median ridge on the basioccipital, and reduction of the supratemporal fenestra. Considerable faunal overlap of the Tiki Formation is evident with the lower Maleri Formation, which is late Carnian based on the occurrence of Hyperodapedon, Parasuchus and Exaeretodon. The Tiki Formation correlates with the Ischigualasto Formation of Argentina, the upper part of the Santa Maria Formation, and the overlying lower Caturrita Formation of Brazil, the Isalo II Beds of Madagascar, Losiessmouth Sandstone of Scotland, and the lower Tecovas Formation of the Chinle Group of North America, and ranges from late Carnian to early/middle Norian.

Key words: archosaur, Gondwana, India, Late Triassic, phytosaur, phylogeny.

Phytosaurs represent an extinct group of archosaurs that existed from the Middle to the Late Triassic (Stocker & Butler 2013; Ezcurra 2016; Stocker et al. 2017). These are important biostratigraphical marker fossils and are used for global correlation of the Late Triassic deposits (Lucas 1998, 2010, 2018; Stocker & Butler 2013; Martz & Parker 2017). These archosaurs were essentially medium-to large-sized (2–12 m in length), quadrupedal and bore superficial similarities to the crocodilians (Chatterjee 1978; Stocker & Butler 2013). Although the earliest known phytosaur is from the Middle Triassic of China (Stocker et al. 2017), these forms are known otherwise exclusively from Upper Triassic horizons (Stocker & Butler 2013), and are especially abundant in North America (Stocker 2010, 2012a; Stocker & Butler 2013). Phytosaurs are reported from Germany, Greenland, Italy, Portugal, Lithuania, Turkey, Austria, Poland (Buffetaut et al. 1988; Jenkins et al. 1994; Renesto & Paganoni 1998; Dzik 2001; Hungerbühler 2002; Brusatte et al. 2013; Stocker & Butler 2013; Butler et al. 2014, 2019), China (Stocker et al. 2017) and Thailand (Buffetaut & Ingavat 1982). From the Gondwanan region, phytosaurs are known from Morocco (Fara & Hungerbühler 2000), Brazil (Kischlat & Lucas 2003), Zimbabwe (Barrett et al. 2017) and India (Chatterjee 1978; Hungerbühler et al. 2002; Novas et al. 2011).

Phytosaurs are known from several Upper Triassic horizons of the Pranhita-Godavari Basin, one of the major Gondwana basins of India (Fig. 1A, B). These include Parasuchus hislopi and an undescribed Rutiodon/Angistorhinus-like form from the lower part of the Maleri Formation (Chatterjee 1978; Kutty et al. 2007; Bandyopadhyay 2011; Kammerer et al. 2016), two new taxa similar to Leptosuchus and Angistorhinus from the upper part of the Maleri Formation (Hungerbühler et al. 2002, Fig. 1C) and an undescribed Nicrosaurus-like form from the lower Dharmaram Formation (Bandyopadhyay 2011;
Novas et al. (2011). None of these phytosaurs was studied in detail except for Parasuchus hislopi.

Lydekker (1885) described Parasuchus hislopi based on multiple skeletal elements. Although the species name was considered invalid (von Huene 1940), Chatterjee (1978) reinstated the species Parasuchus hislopi by describing two nearly complete and associated skeletons from the lower part of the Maleri Formation. Additionally, Chatterjee (1978) assigned a partial skull, ISIR 44, collected from another Upper Triassic horizon, the Tiki Formation of the Rewa Gondwana Basin, to Parasuchus hislopi. Subsequent revision by Kammerer et al. (2016) of Parasuchus hislopi also suggested that the Tiki specimen belonged to Parasuchus hislopi, although there is no formal description of this specimen. In the current work, we comprehensively describe the Tiki phytosaur specimen, discuss its taxonomic identification, and ascertain its phylogenetic position and interrelationships. The work also evaluates the biostratigraphical significance of the Tiki phytosaur with respect to other global occurrences.

Institutional abbreviations. BSPG, Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany; FMNH UC, Field Museum, University of Chicago Collections, Chicago, USA; ISI, Indian Statistical Institute, Kolkata, India; GPIT, Paläontologische Sammlung der Universität Tübingen, Tübingen, Germany; TMM, Vertebrate Paleontology Laboratory, Texas Natural Science Center, Austin, TX, USA; TTUP, Texas Tech University, Lubbock, USA; UCMP, University of California Museum of Paleontology, Berkeley, CA, USA; UMMP, University of Michigan Museum of Paleontology, Ann Arbor, MI, USA; USNM, United States National Museum, Washington, DC, USA; ZMNH, Zhejiang Museum of Natural History, Hangzhou, China.

Anatomical abbreviations. afn, antorbital fenestra; afo, antorbital fossa; al.r, alveolar ridge; asc, ascending process of maxilla; bpt, basipterygoid process; ch, choana; d, dentary; ec, ectopterygoid; en, external naris; f, frontal; ins, internarial septum; ift, infratemporal fenestra; j, jugal; l, lacrimal; mg, Meckelian groove; mfs, median mandibular shaft; mx, maxilla; n, nasal; pa, palatine; pmx, premaxilla; pmxf, premaxillary fossa; prf, prefrontal; pt, pterygoid; pt.fl, flange of pterygoid; q, quadrate; qf, quadrate foramen; qj, quadratojugal; q.r.pt, quadrate ramus of pterygoid; sm, septomaxilla; sof, suborbital fenestra; spl, splenial; sym.pl, symphyseal plate; subtf, subtemporal fenestra; v, vomer.

Abbreviations used for measured parameters. When added to the anatomical abbreviations, the suffix L indicates length, and W and H indicate width and height, respectively. \( \alpha \), angle of the ascending maxillary process with vertical plane; \( \beta \), angle of the descending maxillary process with vertical plane; \( \theta \), symphyseal angle of the mandible; afnL, length of antorbital fenestra; afnW, width of antorbital fenestra; afoL, length of antorbital fossa measured along the dorsal margin of the antorbital fenestra; afoW, width of antorbital fossa measured along the posterior margin of the antorbital fenestra; chL, length of choana; chW, width of choana; enH, height of external naris measured along the posterior margin; enL, length of external naris; en-o, distance between external naris and orbit measured along dorsal midline;
Holotype. ISIR 44, a partial skull with the anterior part of the rostrum and occipital region missing.

Referred specimen. IITKGPR803, a partial right mandibular ramus.

Type locality and horizon. Upper Triassic Tiki Formation of the Rewa Gondwana Basin, India; near Tihki village (23°56′N; 81°22′E), Shahdol District, Madhya Pradesh, India (Chatterjee 1978).

Differential diagnosis. The taxon differs from all other phytosaurs by a unique combination of the following features: external nares elevated on a bulbous and raised dome; marginal overlapping of external nares by antorbital fenestrae; thread-like ornamentation on premaxilla and maxilla; prominent ridge and radiating thread-like patterns on jugal; teardrop-shaped ornamentation on nasal, lacrimal, prefrontal and frontal. Autapomorphic characters of Volcanosuchus in relation to Mystriosuchinae include marginal overlapping (<50%) of the nares by antorbital fenestrae; thread-like ornamentation on premaxilla and maxilla; teardrop-shaped ornamentation on the nasal, lacrimal, prefrontal and frontal; prominent ridge and radiating thread-like patterns on jugal.

Remarks. The Tiki skull (ISIR 44) originally assigned to the genus Parasuchus hislopi shows significant morphological variations from the Maleri neotype specimens. These variations were attributed to ontogeny and sexual dimorphism (Chatterjee 1978, p. 92, text-fig. 4c). Subsequently, Kammerer et al. (2016) reviewed Parasuchus hislopi and corroborated Chatterjee (1978) thereby referring ISIR 44 to the same taxon based on several small circular nodes on the jugal, absence of a depression on the nasal and presence of a rugose posterior margin and low circum-narial morphology. The current study shows that ISIR 44 is characterized by a high dome-like narial prominence, skull table ornamented with anteroposteriorly arranged teardrop-like structures, and the jugal bearing a ridge and thread-like radiating patterns. These features are not seen in ISIR 42–ISIR 43. Moreover, several other features not present in the non-Mystriosuchinae phytosaurs characterize ISIR 44. These include partial overlapping of the antorbital fenestra and nostril, and a reduced antorbital fossa, which are diagnostics of the more derived clade, the subfamily Mystriosuchinae. Hence, ISIR 44 is more derived than Parasuchis hislopi and is assigned to the subfamily Mystriosuchinae (sensu Stocker 2010; Butler et al. 2014; Kammerer et al. 2016) as a new taxon.

State of fossil preservation. The skull (ISIR 44, Figs 3–8) is partially preserved with the anterior portion of the rostrum, part of the right skull table posterior to the orbits and the entire occiput missing. The entire right lateral surface posterior to the anteroventral corner of the infratemporal fenestra and the posterior portion of the

**SYSTEMATIC PALAEONTOLOGY**

**ARCHOSAURIA** Cope, 1869–1870 (*sensu* Ezcurra 2016)

Order PHYTOSAURIA Jaeger, 1828

Family PARASUCHIDAE Lydekker, 1885 (*sensu* Kammerer et al. 2016)

Subfamily MYSTRIOSUCHINAE von Huene, 1915 (*sensu* Kammerer et al. 2016)

Genus VOLCANOSUCHUS nov.

Figures 3–10

**LSID.** urn:lsid:zoobank.org:act:D92C31D8-554D-4233-8D3F-FF6054C98787

Derivation of name. Generic name, derived from the Latin word ‘volcanus’ referring to the raised dome-like narial prominence, which resembles a high volcanic crater in lateral view, and ‘suchus’ meaning crocodile-like.

Diagnosis. As for the type and only species.

**Volcanosuchus statisticae** sp. nov.

Figures 3–10

**LSID.** urn:lsid:zoobank.org:act:D876C0E9-53B1-471F-8691-8DDFB7A5A2CA

Derivation of name. Specific name is after the Indian Statistical Institute, Kolkata, one of the first institutes in India to promote and establish a school of vertebrate palaeontology.

Holotype. ISIR 44, a partial skull with the anterior part of the rostrum and occipital region missing.
right palate is also missing. The premaxillary rostrum contains two prongs held together by a metal rod placed between the latter (Fig. 3). The skull table is tilted ventrolaterally towards the right and, consequently, the right-hand side of the skull table bears a dorsoventral compression. A portion of the internarial septum, the anterior half of the right antorbital fossa, the posterior extension of the left squamosal and a part of the quadratojugal ramus of the pterygoid have been reconstructed with plaster of Paris (calcium sulphate hemihydrates). In general, the specimen is well-preserved and bears c. 28 tooth alveoli on each side of the preserved upper jaw, all of which are devoid of teeth and matrix covered. The specimen is brownish in colour and recovered from a ‘boulder of calcareous sandstone’ of the Tiki Formation (Chatterjee 1978, p. 85), the latter being subsequently identified as a lenticular peloidal calcirudite unit. This fossil locality has also yielded a partial right mandibular ramus (ITKKGPR803) containing a well-preserved and undistorted symphyseal plate.

**DESCRIPTION**

**Skull**

*Snout and skull roof.* The skull, ISIR 44 (Figs 3–8), is medium sized (estimated SL = 555 mm), robust, transversely expanded posteriorly (SW = 224 mm) and has a high skull table (SH/SL = 0.22; Datta *et al.* 2019*a*, appendix S1). The dorsal surface (Figs 3, 4), along with parts of the lateral surface (Fig. 5A–D) of the skull, bears ornamentation. The premaxillary rostrum (Fig. 3) is moderately thick (pmxW = 42 mm) with a convex dorsal surface, which bears thin thread-like, interconnecting ornamentation (Fig. 4A, B). The premaxilla extends posteriorly and has sutural contact with the septomaxilla–nasal complex (Fig. 3). A long and deep, anteriorly extending furrow separates the two V-shaped prongs of the septomaxilla. Posteriorly the septomaxilla forms a major portion of the internarial septum with the septomaxilla–nasal suture located close to the posterior margin of the nostril. The septomaxilla forms the medial half of the anterior margin of the naris, the lateral half of which is formed by the nasal (Fig. 3). The dorsal surface of the septomaxilla bears rugosity (Fig. 3).

The external nares (enL/enW = 3.1; Datta *et al.* 2019*a*, appendix S1) occur as a pair of anterodorsally oriented (in lateral view) teardrop-shaped/elliptical, non-emarginated openings separated by a prominent and robust internarial septum (Fig. 3), and posteriorly bear rugosity (Fig. 4C, D). The posterior margins of the nares do not converge at the mid-line, thereby forming a V-shaped furrow. Posterior to the nares, the nasal extends up to the frontal, forming a wide and horizontal platform in dorsal view, and borders the nares laterally (Fig. 4C, D). Coarse, teardrop-like ornamentation characterizes the nasal (Fig. 4C, D). Just anterior to the nasofrontal suture, the nasal tapers and is bounded on either side by the prefrontals (Fig. 4C, D). The nasofrontal suture is wavy and is located at a level just anterior to the posterior margin of the antorbital fenestra (Fig. 4C, D).

Above the posterodorsal margin of the antorbital fossa rests a small, triangular prefrontal (Fig. 4C, D). As on the nasal, the prefrontal bears teardrop-shaped ornamentation on its dorsal surface (Fig. 4C, D). The prefrontal extends posteriorly along the lateral margin of the frontal and forms the anterodorsal margin of the orbit. Only a small portion of the frontal is preserved and it shares a straight anteroposteriorly oriented suture with the prefrontal. Similar to the nasal and the prefrontal, the frontal bears teardrop-shaped ornamentation (Figs 3, 4C, D).

**Lateral elements of the skull.** The most prominent feature in lateral view is a swollen, elevated dome on which rest the external nares (enH = 73 mm; Datta *et al.* 2019*a*, appendix S1). The external nares are relatively large in this specimen, each being about 73 mm in height (enH), and are laterally bordered by the antorbital fossa; the anterior margin of the naris therefore projects anteriorly. The external nares (Figs 3, 4C, D) are located at a slightly elevated level on the external surface of the skull, and the naris opens very close to the lateral margin of the orbit (enL = 31 mm). The external nares are bordered laterally by the maxillary process of the premaxilla (Figs 3, 4C, D). The maxillary process of the premaxilla is long and extends anteriorly along the lateral margin of the orbit (enL = 31 mm). The external nares are separated from the anterior margin of the orbit by a shallow furrow (Fig. 4C, D). The external nares are surrounded by a prominent ridge, which extends anteriorly and laterally from the external nares (enL = 31 mm) and terminates posteriorly at the level of the lateral margin of the orbit (enL = 31 mm). The external nares are bordered posteriorly by the maxillary process of the premaxilla (Figs 3, 4C, D). The premaxilla extends posteriorly along the lateral margin of the orbit (enL = 31 mm) and terminates posteriorly at the level of the lateral margin of the orbit (enL = 31 mm). The external nares are bordered anteriorly by the maxillary process of the premaxilla (Figs 3, 4C, D). The maxillary process of the premaxilla is long and extends anteriorly along the lateral margin of the orbit (enL = 31 mm). The external nares are separated from the anterior margin of the orbit by a shallow furrow (Fig. 4C, D). The external nares are bordered posteriorly by the maxillary process of the premaxilla (Figs 3, 4C, D). The maxillary process of the premaxilla is long and extends anteriorly along the lateral margin of the orbit (enL = 31 mm). The external nares are bordered anteriorly by the maxillary process of the premaxilla (Figs 3, 4C, D). The maxillary process of the premaxilla is long and extends anteriorly along the lateral margin of the orbit (enL = 31 mm).
The nasal prominence is similar to that of *Angistorhinus grandis* (Mehl 1915, p. 134, fig. 3), although it is below the level of the skull table (Fig. 5). The internarial septum lies at the level of the lateral margins of the external nares for most of its length (Fig. 5A, B). Only the anterior part of the internarial septum rests above the lateral margins of the nares, given that the latter are oriented anteroventrally. The zigzag premaxilla–maxilla suture occurs just anterior to the external naris (Figs 5, 6A, B), as seen in all other phytosaurs (Kammerer et al. 2016). A sliver of the maxilla slides beneath the premaxilla in this region. The lateral surface of the maxilla, anterior to the antorbital fenestra, bears small, interconnecting thread-like ornamentation (Fig. 6A–D). Anterior to the antorbital fenestra, the maxilla bifurcates into two processes. These are: (1) the ascending maxillary process (sensu Butler et al. 2014), which partly forms the dorsal margin of the antorbital fenestra and is bordered by the nasal anterodorsally and the lacrimal posterodorsally (Fig. 5); and (2) the main body of the maxilla, which is bordered by the jugal posteriorly, and forms the ventral margin of the antorbital fenestra (Fig. 5A, B). At the anterior end of the antorbital fenestra, the main maxillary body is not perpendicular to the vertical plane but makes an angle to it, and is termed here as the descending maxillary process (Fig. 2C). The ascending maxillary process is inclined at an acute angle to the vertical plane ($\alpha = 73^\circ$) whereas the descending process makes an angle ($\beta$) of $101^\circ$ (Datta et al. 2019a, appendix S1).

In lateral view, the ventral margin of the orbit rests above the dorsal margin of the antorbital fenestra (Fig. 5). The circumorbital ridge is thin, weakly elevated, rugose (Fig. 5A, B), and most prominent along the anterodorsal orbital margin. The antorbital fenestra (afnl/afnW = 3.1; Datta et al. 2019a, appendix S1) is large, oval and partially surrounded by a deep antorbital fossa (Figs 5, 6E–H). The fossa is present only along the posterior and dorsal fenestral margins. The dorsal margin is formed by the ascending maxillary process and the lacrimal; the latter continuing as the posterior margin of the fossa (Fig. 6E–H). A sliver of the lacrimal borders the prefrontal laterally as a thin, anteriorly convex element. Teardrop-shaped ornamentation is found only on the dorsal surface of the lacrimal (Fig. 4C, D). The jugal forms the posteroventral margin of the antorbital fossa (Fig. 5). Laterally, the antorbital fenestra is depressed into the skull and the nasal forms a prominent overhanging shelf above it. The ventral margin of the antorbital fenestra is formed by the maxilla anteriorly and jugal posteriorly (Figs 5, 6E, F). The maxilla–jugal suture is located at the mid-length of the ventral margin of the antorbital fenestra (Fig. 6E, F).

Another diagnostic feature is the marginal overlap of the anterior end of the antorbital fenestra and the posterior end of the external naris (Figs 5, 6A–D). The lacrimal–jugal suture is located beneath the ventral margin of the orbit along the posteroventral margin of the antorbital fenestra (Fig. 6E–H). The lacrimal–jugal suture beneath the orbit has a dorsally directed concave flexure, which is most prominent on the left lateral surface of the skull (Fig. 5A, B). The jugal is elongate ($\text{JL}/\text{JH} = 1.2$) and bears thread-like, radiating ornamentation just posterior to the antorbital fossa in left lateral view (Fig. 6E, F). However, the right jugal does not exhibit such thread-like ridges because of poor preservation, although a weakly raised, anteroposteriorly oriented ridge ornamented with small tubercles is evident (Fig. 6G, H). The left jugal has a faint impression of such a ridge, given that most of that area is missing and reconstructed with plaster of Paris.

The jugal–quadratejugal suture is zigzag in nature and located posterior to the infratemporal fenestra (Fig. 5A, B). The jugal extends posteriorly beneath the ventral margin of the quadratejugal and forms a short protuberance (Fig. 5A, B). The partially preserved posteroventral process of the jugal is more prominent on the right side. It extends dorsally to the posteroventral corner of the infratemporal fenestra (Figs 5C, D, 6G, H). Only the left infratemporal fenestra (itfL/itfW = 1.1) is preserved, which is trapezoid in shape and extends beneath the orbit posteriorly, covering almost half of its length (Fig. 5A, B). On the anteroventral margin of the left infratemporal fenestra, the fossa is poorly developed (Fig. 5A, B). The jugal forms the anteroventral and the entire ventral margin of the infratemporal fenestra, whereas the posterior margin is formed largely by the squamosal (Fig. 5A, B). The latter ventrally borders the quadratejugal at the posteroventral corner of the infratemporal fenestra in lateral view. Beneath the ventral margin of the infratemporal fenestra, the subtemporal fenestra is partially visible (Fig. 5A, B). The quadratejugal is bordered posteriorly by the quadrate (Fig. 5A, B).

**Quadrate–quadratejugal complex.** The quadrate–quadratejugal complex bears two well-developed condyles, with a broader lateral condyle and a smaller medial condyle (Fig. 7). The quadrate–quadratejugal suture extends dorso-medially from the lateral half of the lateral condyle past the quadrate foramen. The quadrate foramen is large, crescent shaped and posterolaterally oriented (Fig. 7). The quadratejugal and quadrate form its anterior margin, whereas the ventral margin is largely formed by the quadrate, with a small part formed by the quadratejugal. The lateral and medial margins of the quadrate foramen are formed by the quadratejugal and quadrate, respectively.

**Palate.** Ventrally, the premaxillary rostrum bears a series of elliptical and/or circular alveoli, which increase in size posteriorly (Fig. 8A, B). These alveoli are closely packed; inter-alveolar septa are poorly developed, and bound medially by pairs of thin and sharp alveolar ridges. These
**FIG. 3.** *Volcanosuchus* *statisticae* gen. et sp. nov. Holotype, ISIR 44, a partial skull in dorsal view. A, photograph. B, line drawing. The inserted metal rod, matrix-covered and reconstructed areas are marked by cross-hatching. *Abbreviations:* afn, antorbital fenestra; afo, antorbital fossa; en, external naris; f, frontal; ins, internarial septum; j, jugal; l, lacrimal; mx, maxilla; n, nasal; pmx, premaxilla; prf, prefrontal; qj, quadratojugal; sm, septomaxilla. Scale bar represents 50 mm.
are most prominent near the rostral mid-length (alveoli 11–15), and tend to be flush with the surface posteriorly (Fig. 8A, B). The alveolar ridges are separated by a well-developed, concave premaxillary fossa (pmxfW = 37.9 mm; Datta et al. 2019a, appendix S1; Fig. 8A, B). The alveoli on the maxilla are larger than the premaxillary alveoli (Fig. 8). The premaxilla–maxilla suture is located at the rostral mid-length, near alveolus 14 (Fig. 8C, D). Posteriorly the premaxilla extends up to the anterior border of the choana, where it meets the palatine laterally and the vomer posteriorly (Fig. 8C, D). The maxillary alveoli increase in size posteriorly, with the largest one lateral to the choana (Fig. 8C, D). The alveolar rim lateral to the choana is swollen.
The choana is elliptical \((\text{chL/chW} = c.7; \text{Datta et al.}, 2019a, \text{appendix S1})\), and separated by the vomers, which occur as a thick median ridge. The premaxilla forms the anterior choanal margin, whereas the palatine forms the anterolateral and lateral margins (Fig. 8). The posterior margin of the choana is formed by the pterygoid and vomer (Fig. 8). Posterior to the premaxilla, the maxilla constitutes the lateral margin of the palate, which extends beyond the posterior margin of the choana (Fig. 8).

Medial to the maxilla, the lenticular palatine \((\text{paL/paW} = 4.7)\) is large, elongate and slightly convex with its medial margin dipping dorsally into the choanae (Fig. 8C, D). Anteriorly the palatine meets the premaxilla (Fig. 8), while posteriorly it wedges between the pterygoid and the
ectopterygoid (Fig. 8A, B). The suborbital fenestra (softL/softW = c.3) occurs as a short boomerang-shaped vacuity, which is bordered by the palatine anteriorly and medially, whereas the lateral and posterolateral margins are formed by the maxilla and ectopterygoid, respectively (Fig. 8A, B). The suborbital fenestra is located posterior to the choana, near the lateral margins of the palate.

Only the left subtemporal fenestra is preserved, which occurs as a large, sub-rectangular opening (subtfL/subtfW = c.2; Fig. 8A, B) posterior to the suborbital fenestra. The anterior margin of the subtemporal fenestra is formed by the pterygoid and the ectopterygoid while the posteromedial margin is formed by the quadrate (Fig. 8A, B). A weakly developed pterygoid flange extends laterally into the subtemporal fenestra (Fig. 8A, B). Laterally, the subtemporal fenestra is bordered by the jugal, whereas the quadratojugal–quadrate complex forms the posterolateral and posterior margins (Fig. 8A, B). The left pterygoid is partially preserved, and its anterior half is bordered laterally and medially by the palatine and vomer, respectively. Posteriorly, it bears a weakly developed pterygoid flange, medial to which is a deep concavity for the basipterygoid process of the basisphenoid (Fig. 8A, B). The quadrate ramus of the pterygoid is robust but the position of the pterygoid–quadrate suture along this ramus cannot be determined. The rest of the palate and braincase is not preserved.

**Mandible**

The partial right mandibular ramus (IITKGPR803, Figs 9, 10) is mediolaterally compressed, robust and high (symH/symW = 1.4). In dorsal view, the mandibular width increases posteriorly across the symphyseal region coupled with a progressive decrease in the width of the median shaft. The latter is raised with respect to the alveoli and borders them medially (Fig. 9A, B). Posterior to the symphysis the ramus diverges away from the horizontal at an angle of 18°. A total of 21 alveoli are preserved, all of which are devoid of teeth. The alveoli progressively increase in size posteriorly and are circular in outline. The posterior-most alveoli (19–21) are elongate with their long axes nearly parallel to that of the mandibular ramus (Fig. 9A, B). The alveoli are restricted to the dentary, with the latter forming the entire dorsal surface of the preserved length of the mandibular ramus and the anterior portion of the ramus in ventral view (Fig. 9C, D).
The dentary–splenial zigzag suture rests posterior to the symphyseal region and continues posteriorly and ventro-laterally (Fig. 10A, B).

The dorsolateral surface of the preserved mandibular ramus is formed mainly by the dentary (Fig. 10A, B), whereas the splenial forming the preserved median shaft continues posteriorly to border the alveoli medially as a raised rounded ridge (Fig. 10C, D). Medially, the elongate symphyseal plate is rippled with numerous oblique-to-horizontal ridges and grooves (Fig. 10C, D), and is

**FIG. 8.** *Volcanosuchus statistiae* gen. et sp. nov. IITKGP803, partial right mandibular ramus. A–B, dorsal view: A, photograph; B, line drawing; C–D, ventral view: C, photograph; D, line drawing. *Abbreviations*: d, dentary; msf, median shaft; spl, splenial; sym.pl, symphyseal plate. Scale bar represents 50 mm.

**FIG. 9.** *Volcanosuchus statistiae* gen. et sp. nov. IITKGP803, partial right mandibular ramus. A–B, dorsal view: A, photograph; B, line drawing; C–D, ventral view: C, photograph; D, line drawing. *Abbreviations*: d, dentary; msf, median shaft; spl, splenial; sym.pl, symphyseal plate. Scale bar represents 50 mm.
identified as a class III symphysis (*sensu* Holliday & Nesbitt 2013). The dorsal half of the symphyseal plate is tear-drop shaped and bears a small, medially directed projection. A shallow, but prominent Meckelian groove divides the symphyseal plate into a dorsal and a ventral half (Fig. 10C, D). The Meckelian groove terminates

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**FIG. 10.** *Volcanosuchus statisticae* gen. et sp. nov. IITKGPR803, partial right mandibular ramus. A–B, lateral view: A, photograph; B, line drawing. C–D, medial view: C, photograph; D, line drawing. *Abbreviations:* d, dentary; msf, median shaft; mg, Meckelian groove; spl, splenial; sym.pl, symphyseal plate. Scale bars represent 50 mm.

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**FIG. 11.** *Volcanosuchus statisticae* gen. et sp. nov. A–C, holotype, ISIR 44, restored skull: A, dorsal; B, ventral; C, lateral views; long thread-like and small teardrop-like ornamentations are indicated by arrowhead and arrows, respectively. D, IITKGPR803, restored partial mandible in dorsal view. *Abbreviations:* afn, antorbital fenestra; afo, antorbital fossa; bpt, basipterygoid process; d, dentary; ec, ectopterygoid; en, external naris; f, frontal; ift, infratemporal fenestra; j, jugal; l, lacrimal; msf, median mandibular shaft; mx, maxilla; n, nasal; pmx, premaxilla; prf, prefrontal; q, quadratojugal; sm, septomaxilla; sof, suborbital fenestra; spl, splenial; subtf, subtemporal fenestra; v, symphyseal angle. Scale bars represent 50 mm.
shortly after entering the symphyseal plate in the form of a Meckelian fossa.

Reconstruction of the skull and mandible

The missing elements of the snout, including the extent of the premaxilla, and skull roof have been reconstructed based on other Mystriosuchinae genera such as Brachysuchus (Case 1929, fig. 3), Angistorhinus grandis (Mehl 1915, p. 134, fig. 3) and Rutiodon (Colbert 1947, p. 83, fig. 7). Volcanosuchus (ISIR 44) is phylogenetically bracketed by these forms and shows overall similarity, including overlapping of the nostrils by the antorbital fenestra, elevated circumnarial morphology and robusticity of the skull table. The width of the premaxillary rostrum of ISIR 44 appears wider due to the insertion of a metal rod between its two halves (Fig. 3A) because of which, only the widths of the two rostral halves were considered during reconstruction (Fig. 11A). The orbital region bears a slight dorsolateral inclination towards the right. Consequently, the right side of the skull shows dorsoventral compression with the ventral margin of the orbit descending below the dorsal margin of the antorbital fenestra, unlike the left side. For restoration, both sides of the skull were brought to the same level, and the ventral margin of the right orbit was raised above the dorsal margin of the antorbital fenestra. The rest of the reconstruction involved making mirror images of the preserved portions of the cranium and juxtaposing them with the latter. The occiput was not restored because most of it was not preserved.

The reconstructed skull of Volcanosuchus is robust and comprises a posteriorly expanding triangular skull with a long premaxillary rostrum (SL/SW = 2.5). The nostrils are teardrop shaped (L/W = c. 3), orbits are small and oval (oL/oW = 1.1), weakly emarginated and dorsolaterally oriented, whereas the supratemporal fenestrae were equally small and elliptical (Fig. 11A). In comparison, the antorbital fenestra is large, elongated and broadly triangular (afnL/afnW = c. 3) in dorsal view. The anterior end of the maxilla and most of the skull roof including the nasals, frontals, prefrontals and lacrimals is characterized by a dense pattern of small, teardrop-shaped ornamentation whereas the rostrum, composed essentially of the premaxillae, contains long, thread-like ornamentation (Fig. 11A, C).

In ventral view (Fig. 11B), the choanae are large, elliptical (chl/chW = c.7), bifurcated by a robust vomer, and bordered anterolaterally and posteriorly by the palatines and pterygoid, respectively. The suborbital fenestra is distinct and boomerang shaped. Numerous alveoli border the premaxilla and maxilla; the alveoli are closely spaced and increase in size posteriorly. In lateral view, several features such as the nares placed on a dome-shaped prominence (enH/SL = 0.13), marginal overlapping of the nares and antorbital fenestra, high skull roof (SH/SL = 0.22), laterodorsally placed orbits, an elliptical antorbital fenestra bordered by a distinct fossa, jugal ornamented by a ridge and radiating fine thread-like patterns, and a trapezoid infratemporal fenestra (Fig. 11C), characterize Volcanosuchus.

Given that the partial right mandibular ramus (IITKGPR803) is without any distortion, the symphyseal region of the mandible was reconstructed by simply mirror imaging the left portion. The restored mandible is robust and wide posterior to the symphysis, with a symphyseal angle (θ) of 36° (Fig. 11D). The median shaft narrows at the posterior symphyseal end and occupies 40% of the mandibular width (Fig. 11D).

COMPARISON WITH OTHER PHYTOSAUR GENERA

ISIR 44 shows similarity in overall skull morphology with the Late Triassic phytosaurs based on an elongated rostrum, at the posterior end of which are the dorsally facing external nares. This is in marked contrast to the Middle Triassic short-snouted phytosaur Diandongosuchus from the Falang Formation of China (Stocker et al. 2017, p. 2, fig. 1). Traditionally, earlier workers (Chatterjee 1978; Kammerer et al. 2016) have assigned the specimen ISIR 44 to Parasuchus hislopi, a non-Mystriosuchinae member of Parasuchidae. However, the non-Mystriosuchinae phytosaurs, including the genera Wannia (Fig. 12A), Parasuchus (P. bransoni, P. hislopi and P. angustifrons; Fig. 12B–D) and Ebrachosuchus (Fig. 12E), are characterized by non-overlapping of the nostrils by the antorbital fenestrae (Stocker & Butler 2013), which is in contrast to that seen in ISIR 44 (Fig. 11A–C). Hence, comparison with several non-Mystriosuchinae and Mystriosuchinae phytosaurs based on skull proportions and various other cranial features indicates that ISIR 44 is a new taxon within the subfamily Mystriosuchinae. However, characteristic features of the leptosuchomorphs such as the rostral crest, dorsoventrally taller than wide premaxilla, depression of the parieto-squamosal bars below the level of the skull roof, and a long posterior process of the squamosal (Stocker & Butler 2013) are either absent or not preserved in ISIR 44.

Skull proportions

There are distinct differences in the skull proportions of the phytosaur taxa examined. Although complete skulls of Wannia (Fig. 12A) and P. angustifrons (Fig. 12C) are not preserved, all other available non-Mystriosuchinae
phytosaurs, such as *P. bransoni* (Fig. 12B, SL/SW = 3.2), *P. hislopi* (Fig. 12D, SL/SW = 3.25) and *Ebrachosuchus* (Fig. 12E, SL/SW = 3.52), have much longer and more slender skulls with long rostra (SL/SW ≥ 3). In contrast, robust skulls with relatively short rostral length (SL/SW < 3) are seen in the Mystriosuchinae taxa such as...
Angistorhinus grandis (Fig. 12F, SL/SW = 2.6), Brachysuchus (Fig. 12G, SL/SW = 2), and Rutiodon (Colbert 1947, pl. 8; SL/SW = 2.5). Given that Volcanosuchus is closely related to these genera (current study), a short rostral length is suggested for this new taxon (Fig. 12H, SL/SW = 2.5). Similar rostral length is also seen in the leposuchomorph Smilosuchus (Long & Murry 1995, p. 44, fig. 27D; p. 46, fig. 29A), with SL/SW = 2.01. The more derived forms such as Machaeroprosopus lottorum (Hungerbühler et al. 2013, p. 276, fig. 5; p. 278, fig. 7; SL/SW = 3.1) and Mystriosuchus westphali (Hungerbühler 2002, p. 384, fig. 2A, B; SL/SW = 3) have relatively more elongation compared to Volcanosuchus.

However, Volcanosuchus shows a similar lateral skull profile (Fig. 12H, SH/SL = 0.22) to the non-Mystriosuchinae and Mystriosuchiane taxa. These include Diandongosuchus (ZMNH M8770, SH/SL = 0.19), P. hislopi (ISIR 42, SH/SL = 0.17), Ebrachosuchus (BSPG1931 X 501, SH/SL = 0.17), Brachysuchus (UMMP 10336, SH/SL = 0.18), Angistorhinus grandis (FMNH UC631, SH/SL = 0.18), Rutiodon (USNM214513, SH/SL = 0.17), Smilosuchus (UCMP 27200, SH/SL = 0.2, Machaeroprosopus lottorum (TTU-P10076, SH/SL = 0.18) and Mystriosuchus westphali (GPIT 261/001, SH/SL = 0.19). Compared to P. bransoni (TMM 31100-101, SH/SL = 0.14), it is distinctly high.

**Premaxilla**

Similar to that of other Late Triassic phytosaurs, Volcanosuchus is characterized by a long premaxilla with respect to the maxilla (pmlx/mxl = c. 2, Datta et al. 2019a, appendix S1), which is in marked contrast to Diandongosuchus, in which the premaxilla is shorter than the maxilla (Stocker et al. 2017). Furthermore, Volcanosuchus has thread-like interconnecting ornamentations on the dorsal and lateral surfaces of the premaxilla (Figs 3, 4A, B), which contrasts with the unornamented premaxillae of Diandongosuchus, Wannia (Stocker 2012b; Stocker et al. 2017), and P. hislopi (ISIR 42–ISIR 43). It also differs from P. bransoni (Lees 1907), in which the premaxillary ornamentation includes irregular pits and rugosities. Faint longitudinal ridges and a couple of longitudinal grooves and ridges on the premaxilla distinguish P. angustifrons and Ebrachosuchus, respectively (Butler et al. 2014) from Volcanosuchus. Angistorhinus grandis and Rutiodon have unornamented premaxillae (Mehl 1915; Colbert 1947) whereas in Brachysuchus the premaxilla is rugose (Case 1929). Both Volcanosuchus and Rutiodon (Stock潜水年份2b) bear an uncrusted premaxillary rostrum. However, unlike Volcanosuchus, the premaxillary rostrum of Rutiodon is unornamented, although a few small foramina are seen in dorsal view (Stock潜水年份2a).

**Maxilla**

The lateral maxillary surface of Volcanosuchus bears thread-like interconnecting patterns (Fig. 6C, D), whereas in Wannia it is occupied by numerous small, randomly distributed foramina (Stocker 2012b, p. 254, fig. 3A, B), and is featureless in Diandongosuchus (Stocker et al. 2017, p. 2, fig. 1), P. angustifrons (Butler et al. 2014, p. 163, fig. 3D) and P. hislopi. In Diandongosuchus, in contrast to Volcanosuchus, the maxilla extends posteriorly onto the jugal ridge (Stocker et al. 2017). The lateral surface of the maxilla beneath the nares of Ebrachosuchus is featureless (Butler et al. 2014, p. 181, fig. 9C). Angistorhinus grandis (Mehl 1915, p. 134, fig. 3), Brachysuchus (Case 1929, plate 3), Rutiodon (Colbert 1947, p. 83, fig. 7) and Protome (Stocker 2012a, p. 575, fig. 3) have unornamented maxilla.

The angle of inclination of the ascending process of the maxilla (sensu Butler et al. 2014) is similar in Volcanosuchus (ISIR 44, α = 73°), P. angustifrons (BSPG 1931X502, α = 74°) and Brachysuchus (UMMP 10336, α = 76°) but smaller in the basal forms such as Diandongosuchus (ZMNH M8770, α = 40°), Wannia (TTUP00539, α = 63°), P. hislopi (ISIR 42, α = 64°) and Ebrachosuchus (BSPG 1931X501, α = 60°). In contrast, the Mystriosuchinae taxa show variable angles of the ascending maxillary process, as is evident from Angistorhinus grandis (FMNH UC631, α = 40°) and Rutiodon (USNM214513, α = 67°). In Volcanosuchus the angle of the descending maxillary process with the vertical plane (β) is 101°, which is smaller than that of Diandongosuchus (ZMNH M8770, β = 107°) and P. hislopi (ISIR 42, β = 110°), and similar to that of P. angustifrons (BSPG 1931X502, β = 105°) and Rutiodon (USNM214513, β = 104°). In contrast, the descending maxillary process of the other derived phytosaurs has a much smaller angle of inclination. This includes Angistorhinus grandis (FMNH UC631, β = 85°) and Brachysuchus (UMMP 10336, β = 79°) as well as the non-mystriosuchid Ebrachosuchus (BSPG 1931X501, β = 95°).

**Septomaxilla**

In Volcanosuchus, the septomaxilla forms the internarial septum and the anteromedial narial margins. In Diandongosuchus the septomaxilla is absent, whereas in Wannia the septomaxilla forms the entire anterior margin of the nares but is excluded from the internarial septum (Stocker 2012b; Stocker et al. 2017). The septomaxilla of Volcanosuchus bears distinct rugosity, whereas in P. angustifrons, Ebrachosuchus (Butler et al. 2014) and Angistorhinus grandis (Mehl 1915) the septomaxilla is unornamented. The septomaxillae in Angistorhinus grandis
(Mehl 1915) and Protome (Stocker 2012a) form the entire anterior margin of the nostril, thereby excluding the nasal. This condition is in contrast to Volcanosuchus, where the anterior margin of the nostril is shared by the septomaxilla and the nasal.

**External nares**

Volcanosuchus may be distinguished from other genera examined based on the shape of the external nares, which are elongate, teardrop shaped (ISIR 44, enL/enW = 3.1) with rounded posterior margins, and separated along the midline. These external nares are similar to P. angustifrons (BSPG 1931X502, enL/enW = 4; Butler et al. 2014), although in Diandongosuchus (ZMNH M8770, enL/enW = 8) the nares are elongated and lensoidal, and bordered by a fossa along the anteroventral corner (Stocker et al. 2017). Furthermore, the nostrils of Diandongosuchus are along the anterior end of the rostrum, whereas in Volcanosuchus these are at the posterior rostral end, as in other Late Triassic phytosaurs. In Wannia (TTUP00539; enL/enW = 2.1) the external nares are roughly oval in outline, and tend to diverge away posteriorly (Stocke 2012b). In contrast, the external nares are slender and roughly elliptical in outline in P. hislopi (ISIR 42, enL/enW = 3.7), whereas those of Ebrachosuchus are dorsolaterally oriented and subtriangular, with the posterior margins meeting along the midline (Butler et al. 2014).

The nares of Volcanosuchus are elevated on a bulbous dome-like structure, and the nasals surrounding the nostrils laterally are swollen (Fig. 11C). This dome-like structure is relatively much higher than the dorsal prominence of Wannia. The latter flares posteriorly in dorsal view and is further enhanced by a mediolateral constriction of the skull ventral to the nares (Stocke 2012b). Such a lateral constriction is not seen in Volcanosuchus. In P. hislopi and P. angustifrons, the nares are weakly elevated and well emarginated with a rugose posterior margin (Butler et al. 2014; Kammerer et al. 2016). The posterior and posterolateral margins of the nares are raised and thickened in P. angustifrons (Butler et al. 2014), which is not seen in Volcanosuchus. In the former, the lateral narial margins are stepped in lateral view, with a distinct concavity anteriorly and a raised knob-like convexity posteriorly (Butler et al. 2014). The raised posterior edge of the narial region approximates the shape of a triangle in lateral view in P. bransoni (Kammerer et al. 2016). In Ebrachosuchus the nares are non-elevated and emarginated (Butler et al. 2014). Ebrachosuchus differs from Volcanosuchus in having the posterior margin of the nares weakly raised, while the lateral margins are pendulous over the anterior part of the maxillae along its entire length (Butler et al. 2014). The lateral flaring of the posterolateral margins of the nares are observed in Ebrachosuchus (Butler et al. 2014), but such flaring is not observed in Volcanosuchus, although both the taxa bear rugosity along the posterior margin of the nares.

Although the narial morphology of Angistorhinus grandis (Mehl 1915) and Rutiodon (Colbert 1947) is similar to that of Volcanosuchus, with the nares elevated on a dorsal prominence, there are distinct differences between the taxa. In Angistorhinus grandis the external nares are situated above the level of the skull roof and the dorsal prominence is restricted only to the posterior narial ends (Mehl 1915). As in Volcanosuchus, the nares of Rutiodon remain at the level of the skull roof (Colbert 1947). The ornamentation on the narial prominence also differs from Volcanosuchus, given that irregular pits and rugosity are present in Angistorhinus grandis and Brachysuchus, respectively (Mehl 1915; Case 1929). In contrast, the external nares of Protome differ from Volcanosuchus in being elliptical and elevated on a crest, which is slightly elevated above the skull roof (Stocke 2012a).

**Internarial septum**

The internarial septum is level with the lateral narial margins in Volcanosuchus, whereas in Wannia the lateral narial margins are high and dorsal to the internarial septum (Stocke 2012b, p. 254, fig. 3). The internarial septum rests above the level of the external nares in P. hislopi, P. angustifrons and Ebrachosuchus, with the septum well arched in P. hislopi (Butler et al. 2014; Kammerer et al. 2016). The nares of Angistorhinus grandis consist of a slender internarial septum, with the latter remaining below the level of the lateral and posterior border of the nares, giving the appearance of a single narial opening (Mehl 1915), which contrasts with the two distinct nostrils of other phytosaur genera examined, including Volcanosuchus.

**Nasal**

Volcanosuchus is characterized by prominent, teardrop-shaped ornamentation on the nasals, whereas in Diandongosuchus and Wannia, the nasals bear dorsoventrally oriented faint grooves and ridges (Stocke 2012b; Stocke et al. 2017). Coarse ridges and furrows characterize the surface of the nasals in P. hislopi (ISIR 43), whereas in P. bransoni small tubercles and irregular pits and elevations are present (Lees 1907). In P. angustifrons, in contrast, the nasals are devoid of any ornamentation except for the rugose lateral margins above the antorbital fossa (Butler et al. 2014). Moreover, P. angustifrons differs from Volcanosuchus in having a pair of depressions on the nasals posterior to the narial margins (Butler et al. 2014). In Ebrachosuchus, rugosity is restricted laterally and the
circumnarial region is not inflated (Butler et al. 2014). The nasal of Protome is non-inflated, unornamented and bears a fossa along the posteromedial margin of the nostril (Stocker 2012a). The portion of the nasals surrounding the circumnarial region in Angistorhinus grandis and Brachysuchus is characterized by irregular pits and rugosity, respectively (Mehl 1915; Case 1929).

**Lacrimal, prefrontal and frontal**

The lacrimal of Volcanosuchus bears teardrop-shaped ornamentation (Figs 4D, 11A), in contrast to the unornamented lacrimal of P. hislopi and P. angustifrons and the rugose lacrimal in Diandongosuchus and Ebrachosuchus (Butler et al. 2014; Stocker et al. 2017). In Ebrachosuchus, unlike in Volcanosuchus, the surface of the lacrimal forming the posterior margin of the antorbital fossa is not separated by a prominent rim from the adjoining lateral surface of the lacrimal, which lies adjacent to the orbit. In Angistorhinus grandis, the lacrimal extends anteriorly, forming the majority of the dorsal border of the antorbital fenestra (Mehl 1915). Moreover, the dorsal surface of the lacrimal bears irregular pitting (Mehl 1915), unlike those in Volcanosuchus. The shape of the prefrontal in Volcanosuchus is similar to that of Diandongosuchus (Stocker et al. 2017), P. angustifrons (Butler et al. 2014), P. hislopi and P. bransoni (Lees 1907) in being triangular in outline. Volcanosuchus differs from Diandongosuchus, P. angustifrons, P. hislopi, P. bransoni and Ebrachosuchus in bearing teardrop-shaped ornamentation on the prefrontal and lacking a pre-orbital depression. Contrary to Volcanosuchus, the prefrontal in Ebrachosuchus bears coarse rugosity along with deep pits (Butler et al. 2014).

Similar to the nasals, prefrontals and lacrimals, the frontal in Volcanosuchus bears teardrop-shaped ornamentation, in contrast to the rugose and pitted frontal in Diandongosuchus, P. bransoni, P. angustifrons and Ebrachosuchus (Butler et al. 2014; Stocker et al. 2017). Multiple coarse ridges and furrows characterize the frontal of P. hislopi. Furthermore, unlike Volcanosuchus, a pair of depressions characterizes the frontals in Diandongosuchus, P. bransoni, P. angustifrons, P. hislopi and Ebrachosuchus (Butler et al. 2014; Kammerer et al. 2016; Stocker et al. 2017).

The ornamentation pattern on the prefrontal and frontal in Angistorhinus grandis differs from those in Volcanosuchus, given that the former contains irregular pitting (Mehl 1915). The prefrontal in Angistorhinus grandis is quadrangular in (Mehl 1915). When the dorsal view of the skulls of these two taxa is brought to the same length, the frontal in Angistorhinus grandis extends much closer to the external nares (Mehl 1915) compared with Volcanosuchus. The nasofrontal suture in Angistorhinus grandis is concave, whereas that in Volcanosuchus is wavy.

Protome differs from Volcanosuchus in having multiple ridges ornamenting the prefrontal and frontal (Stocker 2012a). The prefrontal is irregular in outline in Protome (Stocker 2012a).

**Orbit**

Contrary to the ‘Parasuchus-grade’ phytosaurs (Butler et al. 2014; Kammerer et al. 2016), the orbit of Volcanosuchus is weakly emarginated, with its ventral margin placed dorsal to the dorsal margin of the antorbital fenestra. These features are also not seen in Ebrachosuchus, in which the orbital ridges are strongly thickened and anteriorly have a preorbital depression (Butler et al. 2014). Similar to Volcanosuchus, Diandongosuchus has a weakly developed orbital ridge, but the ventral margin of the orbit in the latter rests ventral to the dorsal margin of the antorbital fenestra. A well-developed orbital ridge is seen in Protome (Stocker 2012b), which continues on to the prefrontal. However, the orbit of Protome is similar to that of Volcanosuchus in being dorsolaterally oriented with the ventral margin remaining dorsal to the dorsal margin of the antorbital fenestra.

**Jugal**

As mentioned earlier, a distinct ridge is present along the lateral surface of the jugal in Volcanosuchus, similar to Diandongosuchus, Wannia and P. angustifrons. A similar ridge is also present in Ebrachosuchus. However, this ridge is unornamented and posterodorsal in orientation in Wannia (Stocker 2012b) and Ebrachosuchus (Butler et al. 2014), which contrasts with that of Volcanosuchus, in which it is characterized by multiple tubercles. P. bransoni and P. angustifrons exhibit a row of nodes or tubercles (Kammerer et al. 2016). In P. angustifrons and Diandongosuchus, the ridge is unornamented and extends onto the maxilla (Butler et al. 2014; Stocker et al. 2017). According to Kammerer et al. (2016), the surface of the right jugal ventral to the orbit in P. hislopi (neotype ISIR 42) consists of a series of poorly preserved nodes while on the left jugal no nodes are discernible. The referred specimen, ISIR 43 also lacks jugal nodes because of poor preservation (Kammerer et al. 2016). Re-examination of both of these specimens shows that the lateral surface of the jugal beneath the orbit does not preserve any nodes. Rather, the surface of the right jugal in ISIR 42 bears multiple fractures, which, when restored by plaster of Paris, gave rise to the appearance of a series of small weakly elevated regions (Datta et al. 2019a, appendix S2).

The jugal forms the posteroventral and a part of the ventral margin of the antorbital fenestra in Volcanosuchus,
and the maxillojugal suture is anterior to the posterior margin of the fenestra. *Wannia* does not exhibit this condition, given that the jugal does not border the antorbital fenestra and the maxillojugal suture rests posteriorly (Stocker 2012b). In *P. angustifrons*, *P. bransoni* and *Ebrachosuchus*, the maxillojugal suture is located posterior to the antorbital fenestra (Lees 1907; Butler et al. 2014). However, in *P. hislopi* and *Volcanosuchus*, the maxillojugal suture is placed anteriorly and shows similarity with that of *Angistorhinus grandis* and *Brachysuchus*. In these taxa, the jugal forms the posterior half of the ventral margin and a part of the posterior margin of the antorbital fenestra. Unlike *Angistorhinus grandis*, however, *Volcanosuchus* contains a ridge on the jugal, the latter forming the entire ventral margin of the infratemporal fenestra.

**Antorbital fossa and fenestra**

*Volcanosuchus* has a large, elongate oval (ISIR 44; afnL/afnW = 3.1) antorbital fenestra, which is similar in proportion to that of *Diandongosuchus* (ZMNH M8770; afnL/afnW = 3.1). However, it is slender in the nonmystriosuchid phytosaurs such as *Wannia* (TTUP00539, afnL/afnW = 4.5), *P. hislopi* (ISIR 42, afnL/afnW = 3.5) and *P. angustifrons* (BSPG 1931X502, afnL/afnW = 4.5). The antorbital fenestra in *P. bransoni* (TMM 31100-101, afnL/afnW = 1.9) and *Ebrachosuchus* (BSPG 1931X501; afnL/afnW = 2.02) is comparatively broader. The antorbital fenestra of *Angistorhinus grandis* differs from *Volcanosuchus* in being slenderer (afnL/afnW = 4.2) and completely overlapping the nares (Mehl 1915). Complete overlap of the nares by the antorbital fenestra is observed in *Brachysuchus* and *Rutiodon* (Case 1929; Colbert 1947), which contrasts with the non-overlapping of the external nares and antorbital fenestra in the nonmystriosuchinae phytosaur genera and the marginal overlapping of *Volcanosuchus*.

The antorbital fossa is reduced in *Volcanosuchus*, and present only along the dorsal and posterior margins of the antorbital fenestra. This contrasts with that of *Diandongosuchus* and *Wannia*, in which the fenestra is nearly surrounded by the fossa (Stocker 2012b; Stocker et al. 2017). The antorbital fossa is well developed in *P. hislopi*, *P. bransoni* and *P. angustifrons* (Butler et al. 2014; Kammerer et al. 2016), compared with *Volcanosuchus*, but in *Ebrachosuchus* the fossa is immensely reduced, present only along the anteroventral and posterior margins of the fenestra (Butler et al. 2014). In *Volcanosuchus* the dorsal surface of the antorbital fossa is formed by the maxilla and lacrimal, similar to *Diandongosuchus*, *Wannia* and the ‘Para-suchus-grade’ phytosaurs (Stocker 2012b; Butler et al. 2014; Kammerer et al. 2016; Stocker et al. 2017). However, unlike *Volcanosuchus* in which the jugal forms part of the antorbital fossa, the latter is formed exclusively by the maxilla and lacrimal in the non-mystriosuchid phytosaurs such as *Diandongosuchus*, *Wannia*, *P. hislopi*, *P. bransoni*, *P. angustifrons* and *Ebrachosuchus* (Stocker 2012b; Butler et al. 2014; Kammerer et al. 2016; Stocker et al. 2017). Furthermore, unlike in *Volcanosuchus*, the maxilla forms only a small part of the dorsal antorbital fossa in *Angistorhinus grandis* (Mehl 1915).

**Infratemporal fenestra**

The infratemporal fenestra in *Volcanosuchus* extends anteriorly almost up to the mid-length of the orbit, and its ventral margin is formed by the jugal. In *P. bransoni* the jugal also forms the entire ventral margin of the infratemporal fenestra (Lees 1907). The infratemporal fenestra in *P. hislopi* is in line with the posterior margin of the orbit, while in *P. angustifrons* and *P. bransoni* it rests just anterior to the posterior margin of the orbit (Kammerer et al. 2016). Moreover, in *P. hislopi* the ventral margin is shared by the jugal and quadratojugal and in *P. angustifrons* only the anterior-most part is formed by the jugal (Butler et al. 2014; Kammerer et al. 2016). *Volcanosuchus* is similar to *P. bransoni*, in that the posterior margin of the infratemporal fenestra is formed largely by the squamosal, with the quadratojugal restricted to the posteroventral end (Lees 1907). In *P. hislopi* and *P. angustifrons*, however, the squamosal and the quadratojugal form the posterior margin of the fenestra (Butler et al. 2014; Kammerer et al. 2016).

The anterior extent of the infratemporal fenestra in *Ebrachosuchus* is greater than in *Volcanosuchus* and extends beyond the mid-point of the orbit (Butler et al. 2014). Unlike *Volcanosuchus*, the ventral margin of the infratemporal fenestra in *Ebrachosuchus* is shared by the jugal and the quadratojugal (Butler et al. 2014), and in both forms the posterior infratemporal fenestral margin is formed by the squamosal, with the quadratojugal forming only the posteroventral margin.

The infratemporal fenestra extends anteriorly well beyond the mid-point of the orbit in *Angistorhinus grandis*, *Brachysuchus* and *Rutiodon* (Mehl 1915; Case 1929; Colbert 1947). Similar to *Volcanosuchus*, the jugal forms the entire ventral margin of the infratemporal fenestra in *Brachysuchus*, and the squamosal forms the majority of the posterior margin of the infratemporal fenestra in both *Angistorhinus grandis* and *Brachysuchus* (Mehl 1915; Case 1929). *Angistorhinus grandis* differs from *Volcanosuchus*, in that the jugal–quadratojugal suture is located at the mid-length of the ventral margin of the infratemporal fenestra.
Premaxillary–maxillary alveoli

The alveoli of *Volcanosuchus* show a progressive increase in size from the premaxilla to the maxilla. The maxillary alveoli are closely spaced, mostly circular in outline, and those lateral to the choanae have thick swollen margins. In contrast, the anterior maxillary alveoli of *Wannia* are smaller than the posterior maxillary alveoli as well as the premaxillary alveoli (Stocker 2012b). Although the maxillary alveoli are closely spaced as in *Volcanosuchus*, those lateral to the choanae do not bear swollen margins. The alveoli in *Ebrachosuchus* are subcircular and widely spaced, separated by well-developed interalveolar septa (BSPG 1931X501; sofL/sofW = 9.2). The alveoli of *Ebrachosuchus* and those lateral to the choanae show a progressive increase in size posteriorly. In contrast, the anterior maxillary alveoli of *Volcanosuchus*, the estimated number of alveoli on either side is c. 28, and the alveoli show a progressive increase in size posteriorly. In contrast, the premaxillary–maxillary alveoli of *Angistorhinus* are of equal size, bordered by rounded alveolar ridges and separated by well-developed interalveolar septa in *Angistorhinus grandis* (Mehl 1915). In *Brachysuchus* the premaxillary alveoli are similar sized, succeeded by smaller anterior maxillary alveoli (Case 1929). The maxillary alveoli progressively increase in size posteriorly (Case 1929).

Alveolar ridge

In *Volcanosuchus* the alveolar ridges are thin, sharp and widely spaced, which contrasts with the rounded and thick alveolar ridges observed in all *Parasuchus* species. Similar to *Volcanosuchus*, the alveolar ridges are widely spaced in *P. angustifrons* (Butler et al. 2014), whereas in *P. hislopi* these ridges are closely spaced. In *Ebrachosuchus*, however, the alveolar ridges are weakly developed and present only on some areas of the premaxilla (Butler et al. 2014).

Choanae

The choanae of *Volcanosuchus* are elliptical in outline and bordered by the premaxilla anteriorly and palatine laterally, and by the pterygoid posteriorly. The maxilla is excluded from bordering the choana, a feature shared by *P. bransoni* (Stocker 2012b). In contrast, the maxilla forms the anterolateral border of the choana in *Wannia, P. hislopi, P. angustifrons* and *Ebrachosuchus*, thereby excluding the premaxilla from the choana (Stocker 2012b; Butler et al. 2014; Kammerer et al. 2016).

The shape of the choana in *P. hislopi, P. bransoni* and *Ebrachosuchus* (Lees 1907; Butler et al. 2014; Kammerer et al. 2016) is elliptical, whereas in *P. angustifrons* it is slit-like (Butler et al. 2014). The choana is roughly triangular in *Angistorhinus grandis*, which is similar to that of *Volcanosuchus*. It differs from the latter in having the premaxilla excluded from the choana (Mehl 1915). The choana of *Volcanosuchus* (ISIR 44; chL/chW = c.7) is slender and more elongated than that of *Angistorhinus grandis* (FMNH UC631; chL/chW = 3.4), whereas that of *Brachysuchus* (UMMP 10336; chL/chW = 8.7) is slit-like and more elongated than that of *Volcanosuchus*.

Suborbital fenestra

The suborbital fenestra differs considerably in shape and proportions among the phytosaurs. In *Volcanosuchus*, the suborbital fenestra is small and boomerang shaped (ISIR 44; sofL/sofW = 3.2) while in *Wannia* it is elongate, and comparatively larger (TTUP00539, sofL/sofW = 6). In *Wannia* a small fenestra is placed anterior to the suborbital fenestra (Stocker 2012a), which is absent in *Volcanosuchus*. The shape of the suborbital fenestra differs in two different species of *Parasuchus*. It is lensoid in *P. bransoni* and boomerang shaped in *P. angustifrons* (Lees 1907; Butler et al. 2014). Both *Ebrachosuchus* (BSPG 1931X501; sofL/sofW = 8.4) and *Angistorhinus grandis* (FMNH UC631; sofL/sofW = 9.2) exhibit extremely elongated and slit-like suborbital fenestra (Butler et al. 2014; Mehl 1915). The suborbital fenestra of *Brachysuchus*, however, is short and elliptical (Case 1929) but similar in proportions (UMMP 10336, sofL/sofW = 3.1) to that of *Volcanosuchus*.

Pterygoid, quadrato–quadratojugal complex

A striking difference between *Volcanosuchus* and *Wannia* is the presence of a dorsoventrally deep pterygoid–quadratojugal complex in the latter, with the posteroventral margin of the pterygoid bearing a sharp shelf (Stocker 2012b). In *Volcanosuchus* the pterygoid–quadratojugal complex is relatively slender, dorsoventrally compressed and devoid of a shelf. In *Volcanosuchus*, the quadratojugal complex is crescentic and posterolaterally oriented. *P. bransoni* has a similar orientation of the quadratojugal complex (Lees 1907). In all other *Parasuchus*-grade phytosaurs and *Ebrachosuchus*, the quadratojugal complex faces posteriorly. The quadratojugal complex is oval in *P. hislopi* and *Ebrachosuchus* whereas in *P. angustifrons* it is elliptical (Butler et al. 2014). Both *Angistorhinus grandis* and *Brachysuchus* differ from *Volcanosuchus* in having small and circular quadratojugal complex facing posteriorly (Mehl 1915).
Mandible

The mandible of Volcanosuchus (Fig. 11D, IITKGPR803, $\text{symH}/\text{symW} = 1.4; \theta = 36^\circ$) is dorsoventrally slender but wider at the symphysis than that of P. hislopi (ISIR 42, $\text{symH}/\text{symW} = c. 2; \theta = 25^\circ$). The median mandibular shaft of the former ($\text{msfW} = 40\%$ of $\text{symW}$) is, however, narrower than that of P. hislopi (ISIR 42, $\text{msfW} = 56\%$ of $\text{symW}$). In contrast to that of P. hislopi (ISIR 42; Chatterjee 1978, p. 91, fig. 3b), in which the splenial is barely visible laterally, the ventrolateral surface of the mandible in Volcanosuchus is formed by the splenial with the dentary–splenial suture distinctly visible laterally (Fig. 10A, B).

The mandible of Mystriosuchinae phytosaurs, such as Angistorhinus (TMM 31098-2, $\text{msfW} = 67\%$ of $\text{symW}; \theta = 47^\circ$) and Brachysuchus (UMMP 10336, $\text{msfW} = 64\%$ of $\text{symW}; \theta = 42^\circ$) has a significantly broader median shaft and is markedly wider at the posterior terminus of the symphysis in comparison with Volcanosuchus. The mandible of Volcanosuchus (IIITKGPR803, $\text{symH}/\text{symW} = 1.4$), however, is comparatively dorsoventrally higher than the mandible of Brachysuchus (UMMP 10336, $\text{symH}/\text{symW} = 0.9$). In contrast to Volcanosuchus, the dentary–splenial suture in Brachysuchus is not visible laterally, with only a sliver of the splenial visible laterally (Case 1930, pl. 2).

From the foregoing discussion, it is evident that marginal overlapping of the nostril by the antorbital fenestra characterizes the Tiki specimen (ISIR 44), suggesting that it belongs to the more derived subfamily Mystriosuchinae and is not restricted to the basal family Parasuchidae as previously thought. In addition, ISIR 44 exhibits several characteristic features involving skull proportions, patterns of ornamentation on different bones, sutural patterns and fenestral morphology to suggest that it pertains to a new Mystriosuchinae taxon Volcanosuchus statisticae. Although the partial mandibular ramus (IITKGPR803) was not associated with ISIR 44, it may be assigned to Volcanosuchus because it was collected from the same fossil locality and markedly differs from that of Parasuchus hislopi based on symphyseal robustness and angle, and dentary–splenial arrangement.

**PHYLOGENETIC ANALYSIS**

**Taxa**

Twenty phytosaur taxa were used for the phylogenetic analysis. Euparkeria capensis (Ewer 1965; Kammerer et al. 2016) has been used as the outgroup taxon, whereas the phytosaur genera used, exemplify the higher-level phytosaur taxonomy (Stocker 2010; Kammerer et al. 2016; Jones & Butler 2018). Sources of information for these taxa are as follows: Parasuchus hislopi (ISIR 42–ISIR 43), Volcanosuchus statisticae (ISIR 44), Diadongosuchus fuyuanensis (Stocker et al. 2017), Wannia scurriensis (Stocker 2012b), Parasuchus bransoni (Lees 1907; Stocker 2012b; Kammerer et al. 2016), Parasuchus angustifrons (Butler et al. 2014), Ebrachosuchus (Butler et al. 2014), Angistorhinus grandis (Mehl 1915; Kammerer et al. 2016; Jones & Butler 2018), Brachysuchus (Case 1929; Kammerer et al. 2016), Rutiodon (Colbert 1947); Protome (Stocke 2012a); Pravusuchus hortus (Stocke 2010), Leptosuchus crobiensis (Stocke 2010; Jones & Butler 2018), Smilosuchus adamanensis (Long & Murry 1995; Kammerer et al. 2016), Smilosuchus gregorii (Long & Murry 1995; Kammerer et al. 2016), Machaeroprosopus jablonskiae (Parker & Irmis 2006; Stocker 2010), Machaeroprosopus lotorum (Hungerbühler et al. 2013), Machaeroprosopus mccauleyi (Stocke 2010), Mystriosuchus westphali (Hungerbühler 2002) and Mystriosuchus planirostris (Hungerbühler 2002).

**Characters**

Eighty-six cranial characters have been used (Datta et al. 2016), appendix S3), of which 53 characters are after Hungerbühler (2002), Stocker (2010), Kammerer et al. (2016), and Jones & Butler (2018). Several of these characters were either modified or combined. Twenty-eight new characters have been added, which includes five narial characters, two characters describing antorbital fenestra, one orbital character, two characters based on the infratemporal fenestra, two characters describing the quadrate foramen, and the suborbital and subtemporal foramen each described by a single character. Six and three characters define the pre-narial and circumnarial regions, respectively. The new characters include those describing the skull roof and three characters describing lateral elements of the skull.

**Results**

The phylogenetic analysis was performed on a data matrix comprising 21 taxa and 86 characters (Datta et al. 2019a, appendix S4) in TNT version 1.1 (Goloboff et al. 2008), using New Technology Search with default settings for sectorial searching, ratchet, tree drift and tree fusing. The constraint for the number of times the minimum tree length is to be found was set at 50. Symmetric resampling was carried out with 10,000 replicates and a change probability of 33 for obtaining group present/contradicted (GC) values (Goloboff et al. 2003) to assess the support for each node (Kammerer et al. 2016; Xu et al. 2018). The Traditional search option was used in Symmetric resampling (Xu et al. 2018).
The analysis recovered nine most parsimonious trees with a tree length of 277, consistency index (CI) of 0.491 and retention index (RI) of 0.587. The results of the analysis comply with that of Stocker (2012b), Kammerer et al. (2016), Stocker et al. (2017) and Jones & Butler (2018), although there are a few major differences. The strict consensus tree (Fig. 13A) is poorly resolved although there is a clear distinction between the basal non-Mystriosuchinae and the more derived Mystriosuchinae phytosaurs (sensu Kammerer et al. 2016). Parasuchus hislop and Parasuchus angustifrons are recovered as sister taxa. Ebrachosuchus neukami is the most derived non-Mystriosuchinae taxon. Within the clade Mystriosuchinae, Angistorhinus grandis and Brachysuchus are resolved as sister taxa, whereas Volcanosuchus forms a polytomy with Rutiodon and the more derived leptosuchomorph forms. The Mystriosuchini taxa, Machaeroprosopus mccauleyi, and Machaeroprosopus lottorum, and Mystriosuchus planirostris and Mystriosuchus westphali are recovered as sister taxa, respectively.

The 50% majority-rule tree shows a comparatively higher resolution (Fig. 13B). Diandongosuchus and Wannia are the least derived and form a polytomy at the base of Phytosauria. Similar to the results of the strict consensus, Parasuchus hislop and Parasuchus angustifrons are resolved as sister taxa and Ebrachosuchus is the most derived among non-Mystriosuchinae forms. Angistorhinus grandis and Brachysuchus are resolved as sister taxa, whereas Volcanosuchus forms a polytomy with the derived forms such as Rutiodon, Protome, and Machaeroprosopus jablonskiae, and is more derived in comparison to Angistorhinus grandis and Brachysuchus.

The resolution of the resampled tree (Fig. 13C) is perceptibly greater compared with the former two. Diandongosuchus is the least derived taxon, at the base of Phytosauria, which is conformable with that of Jones & Butler (2018). Nine unambiguous synapomorphies (Table 1) support clade A (Phytosauria). These are: moderately elongated snout (1); trapezoidal skull with width across squamosals less than width across the quadrate (2); transverse rostral width between the antorbital fenestrae ≥1.5-fold the interorbital width in dorsal view (3); non-terminal nares placed anterior to antorbital fenestra (11); presence of orbital ridges (18); foramina or sculptures present on the lateral surface of the maxilla (41); ornamentation in the form of ridges, grooves and pits present on the nasals (52); ornamentation in the form of rugosity and pits present on the dorsal surface of the frontals (54); and quadratojugal subtriangular in outline (77).

Clade B (Parasuchidae) is well resolved by five synapomorphies such as dorsally oriented nares (4); non-terminal nostrils placed posteriorly on the snout (12); reduced antorbital fossa with maxilla and lacrimal/jugal fossa either in contact dorsally or not in contact (15); moderately reduced suborbital fenestra (29); and angle of ascending maxillary process (α) ≥ 55° (44). Within Parasuchidae, Parasuchus hislop + Parasuchus angustifrons (clade C) are recovered as sister taxa based on the angle of descending maxillary process (β) ranging between 115 and 100° (45). In clade D, Ebrachosuchus is the closest non-Mystriosuchinae taxa to the subfamily Mystriosuchinae, and is supported by the infratemporal fenestra extending beneath the middle or anterior half of the orbit (23).

Volcanosuchus is placed within Mystriosuchinae (clade E), as a sister taxon to (Rutiodon + Leptosuchomorpha). Clade E is well resolved and supported by four synapomorphies. These are: elevation of the nostrils on a dorsal prominence present along both the anterior and posterior margin of the nares (5); non-terminal nares with its posterior margin behind the anterior rim of the antorbital fenestrae (11); ≥ 50% of the external nares overlapped by the antorbital fenestrae (13); and palatine extending anteriorly beyond the anterior rim of the choana (86). Within Mystriosuchinae, Angistorhinus grandis and Brachysuchus are recovered as sister taxa in clade F. The latter is supported by the three synapomorphies: dorsoventral expansion of the posterior process of squamosal in lateral view (61); curved parietal–squamosal bar that is medially convex and wide (69); and approximately of the same mediolateral width as the postorbital–squamosal bar (70).

Within clade G Rutiodon is the most derived of the Mystriosuchinae taxa closest to Leptosuchomorpha based on: parietal process of the squamosal beneath the skull roof and a partially depressed supratemporal fenestra (21); greatly expanded posterior process of the squamosal, which are rounded posteriorly (61); and gently sloping dorsal edge of parieto-squamosal bar (67). Leptosuchomorpha (clade H) is poorly resolved, with Leptosuchus crosbiensis being the least derived taxon within this clade. The latter is supported by two synapomorphies: the long posterior squamosal process extending beyond the opisthotic process of the squamosal (60); and medially expanded dorsal edge of the squamosal (62).

The most derived Mystriosuchini (clade I) is well resolved, with Machaeroprosopus jablonskiae being the least derived taxon within this clade. The latter is supported by fully depressed supratemporal fenestra, with the posterior process of the parietal and the entire parietal–squamosal bar below the level of the skull roof (21). The most derived clade, clade I, comprises (Machaeroprosopus lottorum + Machaeroprosopus mccauleyi) and (Mystriosuchus westphali + Mystriosuchus planirostris), and is supported by characters such as: narrow slit-like intermaxillary fossa (37); approximately transverse sutural articulation between the postorbital and squamosal in dorsal view (56); and exoccipital–supraoccipital shelf broad and overhanging over the foramen magnum and occipital condyle (80).
Discussion

The phytosaur interrelationships obtained from the present phylogenetic analysis are largely comparable with that of previous studies (Stocker 2012b; Kammerer et al. 2016; Stocker et al. 2017; Jones & Butler 2018), although there are several distinct differences. In accordance with Stocker et al. (2017) and Jones & Butler (2018), Diadongosuchus is recovered as the least derived taxa within Phytosauria, whereas the family Parasuchidae is well-defined and supported by five synapomorphies. As suggested by Kammerer et al. (2016) and Jones & Butler (2018), Parasuchus hislop and Parasuchus angustifrons are recovered as sister taxa, whereas Ebrachosuchus is closer to Mystriosuchinae than Parasuchus.

The recovery of Volcanosuchus (ISIR 44) as a Mystriosuchinae taxon is based on the overlapping of the nostrils by the antorbital fenestrae (11), and extension of the pala- tine beyond the anterior margin of the choana (86). Hence, ISIR 44 was more derived than previously
suggested by Chatterjee (1978), and by Kammerer et al. (2016). The basal position of Volcanosuchus in the sub-family Mystriosuchinae can be explained by marginal overlapping (<50%) of the nares by the antorbital fenestrae (13) compared with other Mystriosuchinae taxa, which show a strong (≥50%) overlapping of the nares by the antorbital fenestrae. Volcanosuchus is defined by the autapomorphic characters such as thread-like ornamentation on the premaxilla and maxilla (36, 41), teardrop-shaped ornamentation on the nasal and frontal (52, 54) and lateral surface of the jugal ornamented by a ridge bearing tubercles, and radiating thread-like fine structures.

Contra Kammerer et al. (2016), Angistorhinus and Brachysuchus are resolved as sister taxa based on curved parieto-squamosal bars (69), dorsoventrally expanded posterior process of the squamosal (61) and parieto-squamosal bars having the same mediolateral width as the postorbital-squamosal bar (70). Moreover, Rutiodon was the most derived non-leptosuchomorph taxon in the current work, which contradicts Jones & Butler (2018). This is based on the character states such as the partially depressed supratemporal fenestra and the parietal process of the squamosal depressed beneath the skull roof (21), rounded posterior process of the squamosal, which is greatly expanded dorsoventrally (61), and gently sloping parieto-squamosal bar (67). However, the placement of Protome with other leptosuchomorph taxa is in accordance with Jones & Butler (2018). Machaeroprosopus jabolonskiae is the least derived taxon within Mystriosuchinae while Mystriosuchus westphali and Mystriosuchus planirostris are recovered as sister taxa (Jones & Butler 2018). Machaeroprosopus mccauleyi and Machaeroprosopus lottorum show a sister-taxa relationship based on the presence of slit-like supratemporal fenestra due to strongly developed medial lamella of the postorbital-squamosal bar (58).

Thirteen characters are not homoplasious (CI = 1, RI = 1, homoplasy index (HI) = 0; Skelton & Smith

| TABLE 1. Synapomorphistic characters at each node of the resampled tree. |
|-----------------------------------------------|
| Node A: Order Phytosauria (1, 2, 3, 11, 18, 41, 52, 54, 77) |
| Moderate snout length, trapezoidal occiput with width across squamosal less than width across the ventral edge of quadrato-, transverse rostral width between the antorbital fenestrae in dorsal view ≥1.5-fold the width of the interorbital area, non-terminal nares placed completely anterior to the antorbital fenestra and snout, presence of orbital ridges, ornamentation on the lateral surface of the maxilla in the form of sculpture or foramina; ridges, grooves and pits present on the nasals, ornamented dorsal surface of the frontal, subtriangular-shaped quadratojugal |
| Node B: Family Parasuchidae (4, 12, 15, 29, 44) |
| Dorsally directed nasal openings, non-terminal nares placed posteriorly on the snout, reduced antorbital fossa with lacrimal/jugal and maxillary fossae either in contact dorsally or not in contact with one another, suborbital fenestra moderately reduced, angle of ascending maxillary process with the vertical plane (α) ≥ 55˚ |
| Node C: Parasauchus angustifrons + Parasuchus hislopi (45) |
| Angle of descending maxillary process with the vertical plane range: 115˚ > β ≥ 100˚ |
| Node D: Ebrachosuchus + all taxa above (23) |
| Infratemporal fenestra extended anteriorly process between the middle or anterior half of the orbit |
| Node E: Mystriosuchinae (5, 11, 13, 86) |
| Nares elevated on a dorsal prominence present along both the anterior and posterior margin of the nares, non-terminal nares with its posterior margin behind anterior margin of antorbital fenestra, ≥50% of the external naris overlapped by the antorbital fenestra, palatine extends anteriorly beyond the anterior rim of choana |
| Node F: Angistorhinus + Brachysuchus (61, 69, 70) |
| Posterior process of squamosal is dorsoventrally expanded in lateral view, parietal–squamosal bar is curved and medially convex, parietal–squamosal bar is wide and approximately of the same mediolateral width as the postorbital-squamosal bar |
| Node G: Rutiodon + all taxa above (21, 61, 67) |
| Parietal process of squamosal depressed below the skull roof and partially depressed supratemporal fenestra, posterior process of squamosal rounded and greatly expanded, dorsal edge of parieto-squamosal bar is gently sloping |
| Node H: Leptosuchomorpha (60, 62) |
| Long posterior process of squamosal extending posteriorly far beyond the opisthotic process of the squamosal, medially expanded dorsal edge of the squamosal |
| Node I: Mystriosuchini (21) |
| Supratemporal fenestra fully depressed with the entire parietal–squamosal bar and the posterior process of parietal below level of skull roof |
| Node J: Mystriosuchus planirostris + all taxa above (37, 56, 80) |
| Inter-premaxillary fossa present as a narrow slit, approximately transverse sutural articulation of squamosal with postorbital in dorsal view, exoccipital–supraoccipital shelf broad and overhangs foramen magnum and occipital condyle |

The number of each character in the data matrix is given in parentheses.
2002) as shown by PAUP* 4.0b10 (Swofford 2000) and define the evolution of the phytosaur cranium. There are several ancestral phytosaurian conditions, which included the non-terminal nostrils, a slender parioto-squamosal bar that trends straight posteriorly to articulate with the squamosal, and a sloping or vertical medial edge of the palatine below the posterior part of the palatal vault. The non-Mystriosuchinae phytosaurs are characterized by the nostrils positioned anterior to the anterior border of the antorbital fenestrae. The quadrate foramen is roughly circular and the suborbital fenestra is moderately reduced. In the basal non-mystriosuchid forms such as Wannia, the maxilla–jugal suture is located posterior to the antorbital fenestrae. However, in more derived non-mystriosuchid taxa, such as Parasuchus hislopi and Ebrachosuchus, the maxilla–jugal suture rests ventral to the antorbital fenestra. A low and dorsovertically compressed cross-section of the posterior half of the postorbito-squamosal bar and a narrow medial lamella of the postorbito-squamosal bar is observed in the non-mystriosuchid phytosaurs. Non-Mystriosuchinae phytosaurs are typified by parietal–squamosal bars extending straight posteriorly, and narrower or of the same mediolateral width as the parieto-squamosal bar. In the basal forms, the exoccipital–supraoccipital shelf is anteroposteriorly short and the basioccipital between the tubera comprises a concave depression. Furthermore, within Parasuchidae (outside Mystriosuchinae) the lateral extent of the basitubera is equal to that of the basiptyerygod processes in basal forms such as Wannia scurriensis. However, in the more derived forms such as Parasuchus angustifrons and Ebrachosuchus, the lateral extent of the basitubera exceeds that of the basiptyerygod processes.

The more derived Mystriosuchinae phytosaurs (sensu Kammerer et al. 2016) are characterized by overlapping of the nostrils by the antorbital fenestrae. The degree of overlap increases from a partial overlap (<50%) in Volcanosuchus to a greater degree of overlap (>50%), as is observed in the Mystriosuchinae taxa Rutiodon and the leptosuchomorph phytosaurs. Volcanosuchus, therefore, marks the intermediate stage/transition from the non-Mystriosuchinae to the Mystriosuchinae phytosaurs. The quadrate foramen changes from circular in the basal forms to crescentic as seen in Volcanosuchus. Mystriosuchinae phytosaurs, however, exhibit several basal features such as a moderately reduced suborbital fenestra, maxilla–jugal suture ventral to the antorbital fenestra, a narrow medial lamella of the postorbito-squamosal bar, low and dorsovertically compressed cross-section of the posterior half of the postorbito-squamosal bar, short exoccipital–supraoccipital shelf, the basioccipital between the tubera comprising a concave depression and the lateral extent of the basitubera at par with the lateral extent of the basiptyerygod process.

In the subfamily Leptosuchomorpha (sensu Stocker 2010), the suborbital fenestra becomes greatly reduced and the morphology of the basioccipital between the tubera changes from being depressed to bearing an anteroposteriorly oriented ridge. Leptosuchomorph phytosaurs, however, retained some basal characters such as maxilla–jugal suture located ventral to the antorbital fenestra, a narrow medial lamella of the postorbito-squamosal bar, and lateral extent of the basitubera equal to that of the basiptyerygod process. In the most derived clade, Mystriosuchini (Kammerer et al. 2016), the medial lamella of the postorbito-squamosal bar is moderate to strongly developed. Consequently, in these forms, the supratemporal fenestra is either half of its original width or abridged to a slit. However, the medial lamella continues to be narrow in the genus Mystriosuchus. In this genus only, the cross-section of the posterior half of the postorbito-squamosal bar becomes high and triangular. The exoccipital–supraoccipital shelf expands from being anteroposteriorly short in basal forms to a broad shelf overhanging the foramen magnum and occipital condyle.

**BIOSTRATIGRAPHIC IMPLICATIONS**

Recent calibration of the geological time scale places the Carnian–Norian boundary at c. 228 Ma, and the Norian stage lasted c. 20 myr (Gradstein et al. 2012; Ogg et al. 2016). This is based on radioisotopic and magnetostatigraphic data from marine strata (Irmis et al. 2010, 2011; Olsen et al. 2011). Intense debate exists regarding the Late Triassic vertebrate biochronology, especially on the North American biostratigraphic correlations. One school proposed correspondence between the Adamanian/Revueltian and Carnian/Norian boundaries, and considered Otischalkian and Adamanian to be Carnian faunachrons (Lucas 1998, 2018). Others have argued for an entirely post-Carnian age for the Chinle Formation in Arizona and New Mexico (Irmis et al. 2010, 2011; Olsen et al. 2011; Martz et al. 2013), and the Otischalkian and Adamanian to be early Ladinian (early early Norian) and late Ladinian (late early Norian), respectively (Martz & Parker 2017). This has resulted in considerable confusion in terms of global correlation, especially for the Gondwana faunas of different stratigraphic horizons where radioisotopic data are absent (Abdala & Ribeiro 2010). The conventional method based on vertebrate faunal similarity correlated the major vertebrate-bearing Upper Triassic horizons around the world with those from India (Fig. 14), based on the lowest and highest occurrences of multiple index taxa. These included the multi-specific rhynchosaur Hyperodapedon (Mukherjee & Ray 2014; Schultz et al. 2016), the traversodontid Exaeretodon (Abdala & Ribeiro 2010; Ray 2015), the aetosaurs
Longosuchus, Desmatosuchus (Desojo et al. 2013; Martz & Parker 2017; Lucas 2018), the metoposaurids, Apachesaurus, Koskinonodon and Metoposaurus (Lydekker 1890; Branson & Mehl 1929; Hunt 1993), and the non-mystriosuchid phytosaur Parasuchus (Kammerer et al. 2016).

Of the three Upper Triassic vertebrate fossil-bearing horizons in India, the Maleri Formation of the Pranhita-Godavari Basin straddles the Carnian–Norian boundary (Fig. 1B). This is evident from the two distinct non-overlapping vertebrate faunas of this formation (Kutty & Sengupta 1989). The lower Maleri fauna has yielded two phytosaurs (Table 2), of which Parasuchus hislopi is well-examined (Chatterjee 1978; Kammerer et al. 2016) in comparison with another undescribed form, which is ambiguously identified as ‘Rutiodon/Angistorhinus’ by Kutty et al. (2007), Novas et al. (2011) and Bandyopadhyay (2011). Considerable uncertainty exists regarding the fossil locality of this specimen; as a result, we refrain from considering this specimen in the current study. Other important biostratigraphic markers consist of a rhynchosaur Hyperodapedon huxleyi, which shows high abundance in the fauna; a metoposaur Panthasaurus maleriensis; a Typothorax-like aetosaur; a traversodontid Exaeretodon statisciae and a cynodont Deccanodon maleriensis (Bandyopadhyay 2011; Nesbitt et al. 2017; Chakravorti & Sengupta 2019; Table 2). Based on these index taxa, the lower Maleri Formation was considered as early Carnian (Langer 2005; Ray 2015; Schultz et al. 2016; Ogg et al. 2016; Martz & Parker 2017; Lucas 2018).

Hyperodapedon-dominated beds of the lower Ischigualasto Formation, Argentina have been dated as 231.4 ± 0.3 Ma (Martínez et al. 2011), that is, late
TABLE 2. Late Triassic vertebrates from the lower Maleri and Tiki formations of India.

| Taxa                      | Lower Maleri                                                                 | Tiki                                      |
|---------------------------|------------------------------------------------------------------------------|-------------------------------------------|
| Ptychoceratodontidae      | Ptychoceratodus virupa                                                        | Ptychoceratodus oldhami, Ceratodus sp.    |
|                           |                                                                               | Gnathorhiza sp.                           |
| Gnathorhizidae            | –                                                                             | –                                         |
| Polyacrodontidae          | Polyacrodus? contrarius                                                      | –                                         |
| Xenacanthidae             | Mooreodontus indicus                                                          | Mooreodontus indicus, M. jaini, Tikiodontus asymmetrics |
|                           |                                                                               | L. incumbens                              |
|                           |                                                                               | Pristrisodus tikiensis                    |
| Lonchidae                 | –                                                                             | L. statisticae                            |
| Metoposauridae            | Panthasaurus maleriensis                                                      | –                                         |
| Phytosauria               | Parasuchus histopi, cf.                                                       | Volcanosuchus statisticae                 |
|                           |                                                                               | leptosuchomorph-grade                     |
| Rhynchosaurida            | Hyperodapedon huxleyi                                                        | Hyperodapedon tikiensis                   |
| Allokotosaurida           | Maleriasaurus robinsonae                                                      | –                                         |
|                           |                                                                               | –                                         |
| Rauisuchidae              | –                                                                             | Tikisuchus romeri                         |
| Aetosauria                | cf. Tytophorax                                                                | Undescribed                               |
| Archosauriformes          | –                                                                             | Galtonia sp., Protecovasaurus sp.,        |
|                           |                                                                               | indeterminate forms                       |
| Dinosauriformes           | Alwalkeria maleriensis                                                        | Undescribed                               |
|                           |                                                                               | saurischian, indeterminate theropod      |
| Cynodontia                | Exaeretodon statisticae                                                       | Ruberodon                                 |
|                           | Deccanodon maleriensis                                                        | Rewaconodon tikiensis                     |
| Mammaliformes             | –                                                                             | Tikitherium copei                         |
|                           |                                                                               | Gondwanodon tapani                        |

Sources: Chatterjee (1978), Kutty & Sengupta (1989), Datta (2004, 2005), Datta et al. (2004, 2019b), Bandyopadhyay (2011), Ray et al. (2016, 2019), Bhat et al. (2018a, b), Bhat & Ray (2018), Chakravorti & Sengupta (2019).

Carnian (Gradstein et al. 2012; Schultz et al. 2016), Langer et al. (2017) suggested a late Carnian – earliest Norian age for the horizons where Hyperodapedon is abundant. These included the Lossiemouth Sandstone Formation, Scotland (Benton & Walker 1985), Hyperodapedon Assemblage Zone of Santa Maria Formation, south Brazil (Langer et al. 2007), Middle Wolfville Formation, Nova Scotia and Popo Agie Formation, Wyoming of North America (Lucas et al. 2002), and the lower Maleri and Tiki formations of India (current study).

The late Carnian age of the lower Maleri Formation is corroborated by the presence of Exaeretodon (E. statisticae; Chatterjee 1982) given that the genus is also known from the late Carnian Hyperodapedon Assemblage Zone of Santa Maria Formation of Brazil (E. riograndonensis; Langer et al. 2007), and Ischigualasto Formation of Argentina (E. argentinus; Abdala & Ribeiro 2010). It may be noted that Exaeretodon is not known from the Tiki Formation but the latter has yielded a sister taxon, Ruberodon roychowdhurii (Ray 2015). Different aetosaurian taxa were reported from the Maleri and Tiki formations of India. These include a Tytophorax-like aetosaur and numerous aetosaur osteoderms from the lower Maleri and Tiki formations, respectively. Moreover, aetosaurans similar to Paratypothorax and Desmatosuchus (Kutty et al. 2007; Bandyopadhyay 2011) are known from the Rhaetian lower Dharmaram Formation. However, none of these was studied in detail and are not considered in the current study. In general, aetosaurs have been instrumental for correlating the Late Triassic strata of North America such as the Chinle Formation of Arizona and New Mexico, and Dockum Group of Texas (Martz & Parker 2017). This included the genus Desmatosuchus, the lowest and highest occurrences of which are from the Los Esteros Member, Santa Rosa Formation, Dockum Group (D. spurensis) and the Middle Member of the Cooper Canyon Formation, Dockum Group (D. smallii), respectively (Parker 2016; Lucas 2018), and which ranges from early to middle Norian. In the Gondwanan region, other than India, Desmatosuchus has been reported from the Isalo II Beds of Madagascar (Burmeister 2000).

An important faunal component of the Late Triassic is the metoposaurid temnospondyls, which are known from several localities of North America, Europe, Morocco, India and Madagascar (Dutuit 1976, 1978; Chakravorti & Sengupta 2019). The North American and the European forms are represented by the genera Koskinonodon and Apachesaurus; and Metoposaurus, respectively. The lowest and highest occurrences of these genera essentially range from middle/late Carnian (Stuttgart Formation, Germany) to middle Norian (Sonsela Member, Chine Formation, northern Arizona, and Tecoavas Formation, Dockum Group, northeast New Mexico; Long & Murry 1995; Chakravorti & Sengupta 2019; Parker & Martz 2011), with Apachesaurus being known from the higher Bull Canyon Formation, Dockum Group (late Norian – early Rhaetian). The metoposaurid taxa from Morocco belong to the endemic genera Dutuitosaurus and Arganasaurus, whereas Madagascar has yielded poorly preserved or fragmentary indeterminate metoposaurid remains (Buffa et al. 2019; Fortuny et al. 2019). In addition, the Indian metoposaurids are now assigned to a new endemic taxon, Panthasaurus maleriensis, which is distinguished from the erstwhile Metoposaurus based on several characteristic features (Chakravorti & Sengupta 2019). Hence, the taxon-specific global distribution of the metoposaurids and their
long range from middle/late Carnian to middle/late Norian show that these tetrapods are not robust index taxon for Late Triassic global correlation.

Another principal correlative of the Late Triassic is the phytosaurs, of which the basal parasuchid genus *Parasuchus* had a global distribution. This genus is known from the Camp Spring Conglomerate and Colorado City Formation of the Dockum Group of Texas and the Popo Agie Formation of Wyoming in North America (*P. bransoni*; Long & Murry 1995), which are early Norian in age (Martz & Parker 2017). *Parasuchus* is also known from the late Carnian Krasiejów, Poland (*Parasuchus* sp.; Dzik & Sulej 2007), and the Blasensandstein Formation of Germany (*P. angustifrons*; Butler et al. 2014), Timesgadiouine Formation, Morocco (*P. magnoculus*; Fara & Hungerbühler 2000), and is highly abundant in the lower Maleri Formation, India (*P. hislopi*; Chatterjee 1978). The lowest and highest occurrences of *Parasuchus* are from the late Carnian to early Norian. Furthermore, in many of these deposits, *Parasuchus* coexists with the later-derived Angisthorhinus-grade phytosaurs (Lucas 1998; Lucas et al. 2002) and the rhychoosaur genus *Hyperodapedon*.

Previous literature has correlated the Tiki Formation with the lower Maleri Formation (Lucas 1998; Datta 2004) and the Camp Springs Member of the Dockum Group of North America and suggested a Carnian (Tuvalian) age for the formation (Datta 2004; Datta et al. 2004). Recent findings of a large traversodontid (Ray 2015), along with abundant *Hyperodapedon* (*H. tikiensis*, Mukherjee & Ray 2014) show correlation with several Carnian horizons such as the Ischigualasto Formation of Argentina, the upper part of the Santa Maria Formation, and the overlying lower Caturrita Formation of Brazil, and the Isalo II Beds of Madagascar (Ray 2015; Ray et al. 2016). The current work shows that *Parasuchus hislopi* is not known from the Tiki Formation given that the only known phytosaur skull (ISIR 44) belonged to the new genus *Volcanosuchus*, a more derived Mystrosuchinae-grade phytosaur basal only to *Rutiodon*. In addition, numerous well-preserved isolated teeth points towards the presence of a leptosuchomorph-grade phytosaur in the Tiki fauna (Datta et al. 2019b). Moreover, the Tiki fauna encompasses a rich and varied range of vertebrate microfossils (Table 2) comprising undescribed rhychocephalians (Bhat 2018), and different types of archosauromorphs including *Galtoria*, and *Protocovasaurus* (Ray et al. 2019). This microvertebrate fauna shows similarity with that of the lower Tecovas Formation of the Chinle Group of North America (Bhat et al. 2018a; Ray et al. 2019), the latter being early-middle Norian in age (Martz & Parker 2017). Thus, the Tiki Formation ranges from late Carnian to early/middle Norian, in contrast to the late Carnian age of the lower Maleri Formation.

**CONCLUSIONS**

1. In the current work, an isolated and partial phytosaur skull, from the Late Triassic Tiki Formation of the Rewa Gondwana Basin of India and previously identified as *Parasuchus hislopi*, is described in detail, compared with other phytosaur genera and assigned to a new genus and species *Volcanosuchus statisticae*.

2. *Volcanosuchus* is characterized by marginal overlapping of the nostrils by the antorbital fenestrae, lateral surface of the jugal ornamented by a prominent ridge defined by multiple tubercles and radiating thread-like structures, external nare situated on a bulbous and raised dome, thread-like ornamentation on the premaxilla and maxilla, and teardrop-shaped ornamentation on the skull table.

3. Phylogenetic analysis places *Volcanosuchus* within the derived phytosaur subfamily Mystrosuchinae, where it is recovered as a sister taxon to (*Rutiodon* + Leptosuchomorph) based on overlapping of the nostrils by the antorbital fenestrae and extension of palatine beyond the anterior margin of the choana. The genus marked the transition from the basal non-Mystrosuchinae to the more derived Mystrosuchinae phytosaurs based on marginal overlapping (<50%) of the nare by the antorbital fenestrae. *Angisthorhinus* and *Brachysuchus* are resolved as sister taxa, whereas *Rutiodon* was the most derived non-leptosuchomorph taxon.

4. Characteristic phytosaurian conditions include non-terminal nostrils and a narrow parieto-squamosal bar extending straight posteriorly to articulate with the squamosal. The evolution from the basal non-Mystrosuchinae to the derived Mystrosuchinae phytosaurs was marked by changes from non-overlapping to overlapping nostril with respect to the antorbital fenestra, and circular to crescentic quadrate foramen. In the more derived leptosuchomorphs changes are related to the appearance of a median ridge on the basioccipital between the basitubera and highly reduced suborbital fenestra. In the most derived Mystrosuchini, cranial evolution included a reduced supratemporal fenestra due to broadening of the medial lamella of the postorbital-squamosal bar and overhanging of the exoccipital-supraoccipital shelf over the foramen magnum and occipital condyle.

5. Major vertebrate-bearing Upper Triassic horizons around the world are correlated with those from India based on vertebrate faunal similarity. The lowest and highest occurrences of several taxa such as the rhychoosaur *Hyperodapedon*, the traversodontid *Exaeretodon*, the metoposaurs, *Apachesaurs*, *Koskinodon*, *Metoposaurus* and *Panthusaurus* and the phytosaur *Parasuchus* are discussed. The Tiki
Formation correlates with the Ischigualasto Formation of Argentina, the upper part of the Santa Maria Formation, and the overlying lower Caturrita Formation of Brazil, the Isalo II Beds of Madagascar, Lossiemouth Sandstone of Scotland, and the lower Tecovas Formation of the Chinle Group of North America, and ranges from late Carnian to early/middle Norian.

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DATA ARCHIVING STATEMENT

This published work and the nomenclatural acts it contains, have been registered in ZooBank: http://zoobank.org/References/ADA359AC-C2BE-45C3-86DB-5CB66D30A6C6
Data for this study are available in the Dryad Digital Repository: https://doi.org/10.5061/dryad.dg25nt5.

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