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Osteology of the temnospondyl *Trematosaurus brauni* BURMEISTER, 1849 from the Middle Buntsandstein of Bernburg, Germany

RAINER R. SCHOCH

Abstract

The slender-skulled temnospondyl *Trematosaurus brauni* forms the most common tetrapod in the Early Triassic of Germany, and is documented by numerous finds from Merkel's Quarry at Bernburg (Saale). The revision of the available material includes 75 skulls with a size range between 10.9 and 41 cm skull length, and a small suite of postcranial elements. *T. brauni* is characterized by a temporal sulcus of lateral line with two portions, a well-established occipital sulcus, a preorbital region slightly shorter than half skull length, and a wide interorbital distance with very small rounded orbits. Individual variation was substantial, ranging from wide-triangular-skulled morphs to ones with slightly elongate preorbital region. Despite the size range, few ontogenetic changes have been identified: (1) the length of orbit decreased gently proportionally with size, and (2) the width of postorbital skull table relative decreased proportionally with size. Phylogenetic analysis finds *T. brauni* to nest with the very similar *Trematosuchus* well within a clade of slender-skulled trematosauroids. Together, the two genera form the sister taxon of *Tertrema* and the rostrum-bearing lonchorhynchines, whereas *Trematolestes* and *Tertremoides* assume a more basal position within a monophyletic Trematosauridae, which forms the sister taxon of the short-snouted metoposaurid relatives.

Keywords: Olenekian, phylogeny, Stereospondyli, Trematosauridae, Triassic.

1. Introduction

The Early Triassic red-beds of Central Europe, referred to as Buntsandstein ('coloured sandstone') in Germany, have long been known to occasionally yield bones of large and long-extinct amphibian relatives, the temnospondyls (BURMEISTER 1849; V. MEYER 1858; SCHROEDER 1913; SEIDLITZ 1920; V. HUENE 1932; WERNEBURG 1993; SCHOCH 2011a). This rock sequence yields representatives of two major temnospondyl clades, the capitosauroids and trematosauroids, both of which reached sizes well beyond 2 m body length (WARREN 2000; SCHOCH & MILNER 2000; SCHOCH et al. 2002). Among the first of these Triassic taxa to be discovered was the long-snouted *Trematosaurus brauni* BURMEISTER, 1849 from a sandstone quarry at Bernburg an der Saale, north of Halle, in east-central Germany (BRAUN 1842). In this so-called Merkel's Quarry, numerous skulls were collected from the 1840s through 1920s (WAGNER 1935; SCHOCH 2018), which are deposited in numerous collections in Germany and beyond (SCHOCH & MILNER 2000). As outlined by BURMEISTER (1849), the president of the court at Bernburg, CARL VON BRAUN, was an engaged collector of fossils and amounted a large collection of temnospondyl material from Merkel's Quarry. In 1842, BRAUN reported these finds, there coining the name *Trematosaurus* (referring to the pineal foramen as *trema*, the Greek word for "hole"), but delivered no formal description.

The first author to attempt a comprehensive treatment of the taxon was BURMEISTER (1849), who also provided comprehensive figures, although mostly restorations without reference to particular specimens of the large sample. Comparing *Trematosaurus* with other taxa, MEYER (1855) discussed the "labyrinthodont" features of then-known Triassic temnospondyls. In a further study, MEYER (1858) provided more accurate illustrations, preferring specimens as preserved over restorations. He studied the material on which BURMEISTER had based his description (BISCHOFF collection), along with additional specimens from two other private collections. BURMEISTER's original sample remains unkown even though some (or all) specimens studied by him may still exist.

FRAAS (1913) and DREVERMANN (1913, 1920) added some further observations on *T. brauni*, based on material housed at the collections in Stuttgart (SMNS) and Frankfurt am Main (NMS), highlighting similarities with other Triassic temnospondyls. JAEKEL (1903), WATSON (1919) and HUENEHuene (1921) further commented on the taxon based on their first-hand examination of material at Greifswald, Cambridge, and Tübingen. Based at Halle University, which always helds the largest collection of Bernburg material, WAGNER (1935) then studied ontogenetic changes in the skull of *T. brauni*. However, despite a thorough survey of the existing material and some interesting findings on allometry, this author provided only few and rather general illustrations that do not match the quality of former authors. Hence, *T. brauni* has remained one of the few long-known temnospondyls that have never been thoroughly revised. Even more so than had been the case for *Parotosuchus nasutus*, the still larger sample of *Tremato-*

saurus specimens from the type locality has never been studied as a whole, probably because of its wide distribution in various museum collections.

The objectives of the present study are as follows: (1) to clarify the systematic palaeontology of *T. brauni*, (2) to describe all identified skeletal elements in detail, (3) to trace ontogenetic changes, and (4) to analyze the phylogeny of trematosauroids with particular emphasis on the position of *T. brauni* and the status and composition of the Trematosauridae.

2. Material

The studied material preserves a large part of the original sample, which was spread over a wide range of collections (Wagner 1935). Most common are partial skulls, often preserved as internal mould (steinkern), with fragmentary bones (suggesting crude preparation), and abundant are natural moulds without any bone left, probably because the positive counterpart was not collected (e.g., GPS.MLU 2016.20, Fig. 2). Postcranial remains are con-

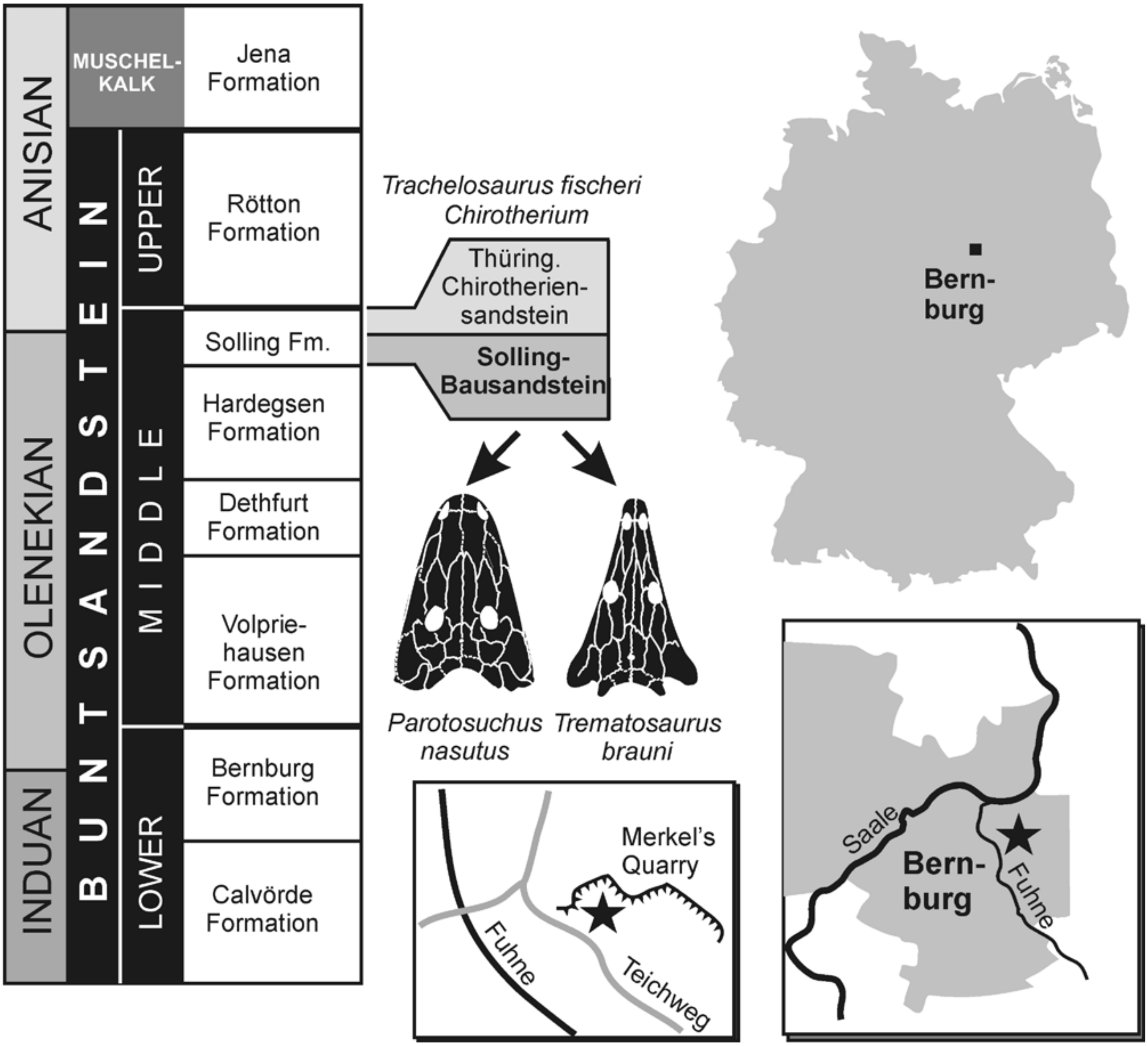

Fig. 1. Locality and stratigraphic context of Merkel's Quarry, the type locality of *Trematosaurus brauni* Burmeister, 1849 (modified from Schoch 2008).

fined to dermal elements of the shoulder girdle (clavicle, interclavicle), whereas no other bones could be unequivocally identified as belonging to *Trematosaurus brauni*. This may reflect either a collecting bias (emphasis on large finds such as skulls or dermal bones), or a taphonomic bias such as current sorting.

Most of the specimens are embedded in a white-yellowish sandstone with a black bone colour (sometimes with brown halo), but a few specimens were found in a grey sandstone in which bone has a more bluish-grey colour. As these differences in lithology were not mentioned by authors, who knew the locality when it was still accessible, it is impossible to decide whether these differences reflect separate beds or local variation of the same horizon.

In the following list, skull midline length (premaxilla–postparietal) of specimens is given in brackets.

1. GG (Geologisches Institut Greifswald): GG 22.159 (posterior portion of skull, ~24 cm), GG 22.159 (skull,21.9 cm), GG 22.162 (partial skull,~31.2 cm), GG 22.164 (steinkern of skull,19.6 cm), GG 22.165 (posterior skull portion, 19 cm), GG 22.166 (two-thirds of skull,16.9 cm), GG 22.187 (skull roof,19 cm), GG 22.188 (complete palate,21.6 cm),
2. GIH (Geologisches Institut Heidelberg): BS5 (complete skull, natural mould, 25 cm), BS6 (partial steinkern, 21.3 cm), BS7 (palate, 10.9 cm), BS8 (partial skull roof, 23.5 cm).
3. GIJ (Geologisches Institut Jena, uncatalogued): 1 (skull, 16.2 cm), 2 (partial skull, ~32.1 cm), 3 (skull, 34 cm).
4. GMG (Geowissenschaftliches Museum Göttingen): uncatalogued 1: posterior two-thirds of of skull (~20 cm); 2: posterior skull portion (~13 cm); posterior skull portion (~16 cm); two-thirds of skull (~28 cm).
5. GPS.MLU (Geologisches Institut, Universität Halle an der Saale): 2016.02 (steinkern of skull, 18.2 cm), 2016.03 (cheek portion, ~16 cm), 2016.04 (skull roof, 18.3 cm), 2016.05 (complete skull, 25.7 cm), 2016.06 (skull, ~22 cm), 2016.11 (palate, 14 cm), 2016.20 (excellent skull roof with ornament, ~25.5 cm), 2016.33 (clavicle), 2016.37 (partial interclavicle), 2019.01 (skull roof, 15.6 cm): 2019.02 (skull roof, 40 cm), 2019.03 (palate, 13.2 cm), 2019.04 (palate, 37 cm), 2019.05 (skull), 2019.06 (posterior palate with stapes, ~19 cm), 2019.07 (complete mandible), 2019.08 (interclavicle).
6. MB (Museum für Naturkunde, Berlin): Am.585 (snout fragment), Am.596 (steinkern of skull, ~23 cm), Am.600 (two-thirds of skull, 16 cm), Am.602 (skull fragment, ~20.3 cm), Am.603 (palate fragment), Am.614 (palate, 18.3 cm), Am.616 (steinkern of skull, 18.5 cm), Am.936 (skull roof in internal view, 19.6 cm), Am.938 (posterior part of palate, ~17.2 cm), Am.959 (palate, 24.7 cm).
7. MNM (Museum für Naturkunde Magdeburg): 2661 (palate, 18.1 cm), 4852 (complete palate, 14 cm), 6587 (palate, 19.6 cm), 6588 (skull roof with medial portion lacking with parasphenoid exposed in dorsal view), 13304 (posterior palate, 21 cm).
8. MNVD (Museum für Natur- und Vorgeschichte Dessau): 11154 (complete palate, 15.4 cm), 11156 (two-thirds of a skull roof, 18.5 cm), 11164 (fragment of preorbital region, ~26 cm), 11165 (steinkern of a skull, 16.5 cm), 11167 (skull margin and mandible in lateral view, 41 cm), and five interclavicles (G 367, G 368, G 383, G 427, G 428).
9. MSB (Museum Schloss Bernburg): G 366 (medial part of skull, 23 cm), G 370 (palate, 19.7 cm), G 366 (skull roof, 18.5 cm), G 407 (mandible in labial view, 14 cm), G 423 (skull roof, 21.5 cm), G 366 (posterior skull fragment), G 447 (medial part of skull, 21 cm).
10. NHMS (Naturhistorisches Museum Schleusingen): VT 21 (posterior half of palate, ~27.5 cm).
11. NMS (Naturmuseum Senckenberg, Frankfurt am Main): WS 4484 (good palate, described by Drevermann 1920; 14.6 cm).
12. SMNS (Staatliches Museum für Naturkunde Stuttgart): 4484a (quite complete skull, internal view of roof, 14.5 cm), 4484b (posterior skull portion, ~14 cm), 4484c (fragmentary skull, ~25 cm), 4485 (dentary with teeth), 4526 (posterior palate, ~19 cm), 6207a (nearly complete skull, 17.9 cm), 6207b (excellent mould of cheek, ~22 cm), 6207c (posterior half of left mandible), 59412 (posterior half of skull, ~18 cm), 59423 (right half of skull, 23 cm), and two interclavicles (4486, 7958).
13. UMZC (University of Cambridge Museum of Zoology): T.126 (Watson 1951).

Anatomical abbreviations: aa, area aspera (dentigerous region), cfr, ridge on cultriform process, cro, crista obliqua, e, ectopterygoid, eo, exoccipital, et, eustachian tube, f, frontal, fm, foramen magnum, ipv, interpterygoid vacuity, ju, jugal, la, lacrimal, m, maxilla, n, nasal, na, naris, p, parietal, pf, postfrontal, pin, pineal foramen, pl, palatine, pm, premaxilla, po, postorbital, pp, postparietal, pq, paraquadrate foramen, prf, prefrontal, ps, parasphenoid, pt, pterygoid, q, quadrate, qj, quadratojugal, sq, squamosal, st, supratemporal, sta, stapes, ta, tabular, vo, vomer.

3. Systematic palaeontology

Temnospondyli Zittel, 1888

Stereospondyli Zittel, 1888

Trematosauroidea (Säve-Söderbergh, 1935)

Trematosauridae Watson, 1919

Trematosaurus Burmeister, 1849

Trematosaurus Braun, 1842 (nomen nudum)

Type species: *Trematosaurus brauni* Burmeister, 1849.

Trematosaurus brauni Burmeister, 1849
Figs. 2, 4–9

Labyrinthodon ocella Meyer, 1855
Labyrinthodon brauni (Burmeister, 1849) Owen, 1861
Trematosaurus fuchsi Seidlitz, 1917

Syntypes: Specimens of currently unknown whereabouts (former Bischoff collection as mentioned by v. Meyer in 1858), on which Burmeister's paper was based, and parts of which were figured by Meyer (1858: pls. 27–28).

Type locality: Merkel's Quarry, at Teichweg near Fuhne creek, SE of Bernburg an der Saale, Saxony Anhalt, Germany (Fig. 1). See Wagner (1935), Hauschke et al.

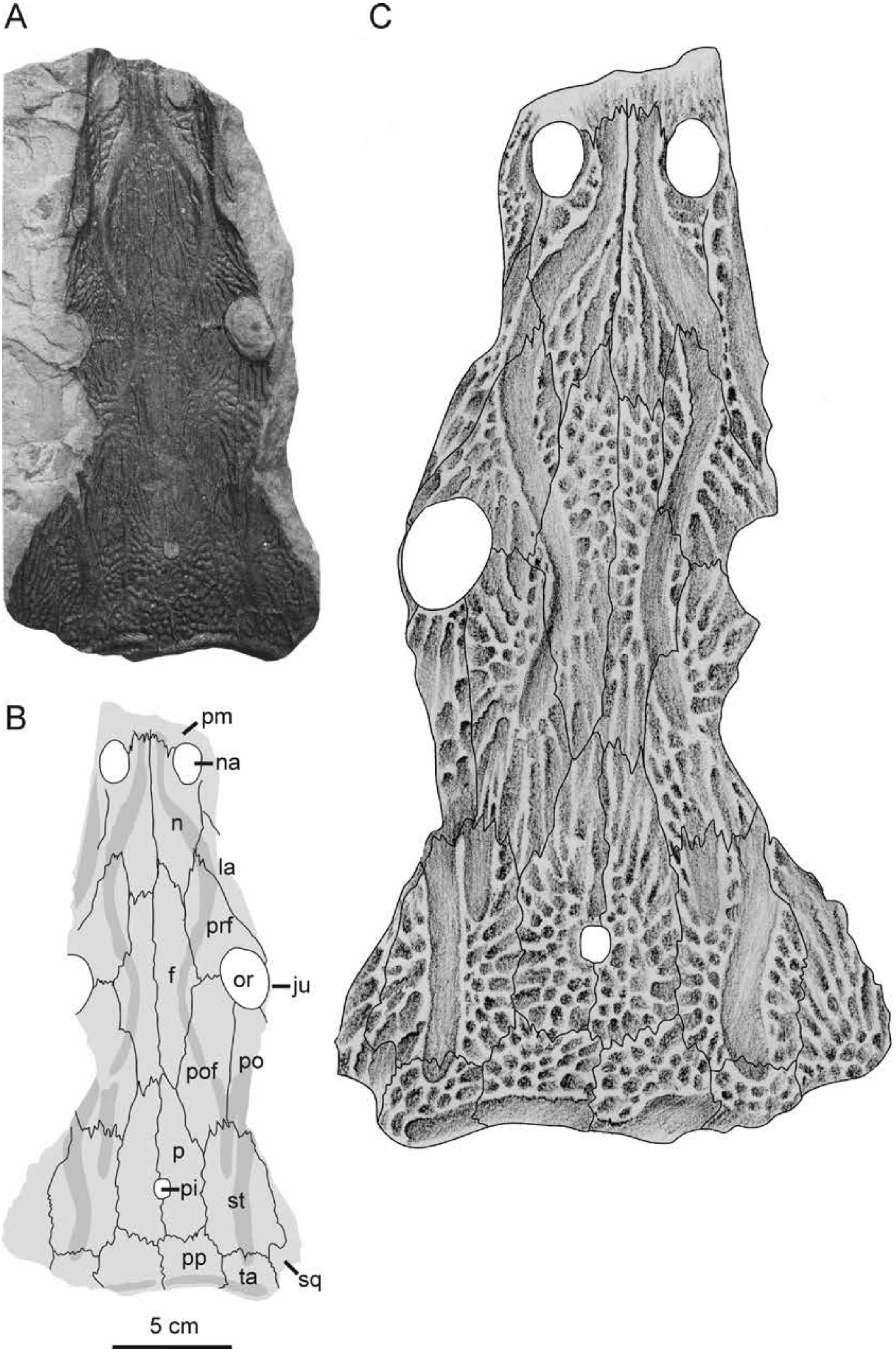

Fig. 2. *Trematosaurus brauni* Burmeister, 1849. Skull roof (GPS.MLU 2016.20). A: Original (natural mould); B: interpretation; C: drawing based on cast of original.

(2005), Hauschke & Szurlies (2016), and Schoch (2018) for details on the locality.

Type horizon: Bausandstein, white to grey sandstone unit below Thüringer Chirotheriensandstein, ? lower Solling Formation, ? late Olenekian (Fig. 1).

Referred specimens: Altogether, 75 skulls, four mandibles, and around ten postcranial remains from the type locality and horizon have been identified as stemming from *T. brauni* (Fig. 3). This sample does not include the syntypes (see above). The complete list is given in the Material section.

Diagnosis: A trematosaurid growing to 41 cm skull length. Autapomorphies: (1) temporal sulcus of lateral line with two portions, (2) occipital sulcus continuous, (3) preorbital region slightly shorter than half skull length (0.43–0.49), (4) interorbital distance wide (interorbital distance/ skull length: 0.15–0.2). Derived characters shared with other trematosauroids: (5) quadratojugal with posterolateral projection, (6) parasphenoid with sharp ventral keel. Shared derived characters with *T. sobeyi*: (1) postfrontal and postorbital longer than parietal and supratemporal, (2) prefrontal-postfrontal nearly as wide as frontal. Plesiomorphic features: naris located near the lateral margin (in contrast to Schoch & Milner 2000: fig. 77), skull rather high in the occipital region (in contrast to capitosaurs).

Comment: Neither Burmeister (1849) nor v. Meyer (1858) selected a type, which is why Schoch & Milner (2000) considered Burmeister's original sample (Bischoff collection of v. Meyer's terminology) as syntypes. Meyer's (1858) figured specimens could not be identified in any of the samples studied here. Because Burmeister did not describe or figure original material (except for a few postcranial elements), it is impossible to know which specimens were available to him, and to match these with the existing samples in the current collections. Because further material is likely to persist in some private collections, the syntypes cannot be considered as lost, and therefore designation of a neotype is not an option.

4. Description

4.1. Skull

The skull is elongate triangular, with the lateral margins straight or very gently concave. In well-preserved skulls (Figs. 2, 4), the quadratojugal has a pronounced lateral and posterior projection. The orbits are small and positioned slightly anterior to the midlevel, and their distance varies but is always wide compared with many other temnospondyls. In the posterior skull table, the dominating elements are the postfrontal and postorbital, which exceed the length of the parietal and supratemporal. A squamosal embayment (otic notch) is well established, widening posterolaterally. The posterior margin of the skull table is markedly concave.

The tip of the snout is blunt, having an extended portion anterior to the naris much like in other trematosauroids. This portion has a rectangular outline, with marked polygonal ornament, and well-established lateral line sulci that continue posteriorly onto the nasal. The naris has a highly variable outline and general length, ranging from relatively elongate oval (GPS.MLU 2016.20) to elongate oval, about twice as long as wide (GIH.BS 5) – with a continuous range of shapes in between (Fig. 5). The opening is bordered by about equally long portions of premaxilla and nasal/maxilla. Consistent across the sample, however, is the lateral position of the opening, a feature contrasting former restorations in which the naris was depicted as having a more medial position (e. g., Schoch & Milner 2000, Fig. 77).

The nasal varies considerably within and between specimens in relative length, especially with respect to the frontal. Even in the largest specimen (2019.02, Fig. 6B), it is slightly shorter than the frontal, whereas in GIH BS5 (Fig. 5A) the nasal forms the longest element in the skull by far. It is always elongate and usually has a pointed anterior end, with straight or stepped lateral margins, bordered posteriorly by the prefrontaland frontal, laterally by the very slender lacrimal, and anteriorly by the maxilla and premaxilla. The lacrimal is poorly preserved in most specimens, and its sutures are difficult to trace even in excellently preserved skulls (Figs. 2, 4) because the lateral line sulci are so dominant. It appears to form an elongate and very slender, sometimes splint-like bone, wedged between the prefrontal and maxilla. The maxilla is the longest bone in the skull by far, having an elongate but low alary process that merges continuously into the very thin posterior ramus, which terminates in a point level with the posterior fourth of the skull, where the maxilla forms a posterolaterally aligned suture with the quadratojugal. Most of the dorsal surface of the maxilla is smooth or finely striated.

The width of the orbital region is about two-thirds that of the posterior margin of the skull, with its largest section formed by the wide interorbital region. This falls into similarly broad portions, namely the prefrontal-postfrontal suture and the frontal, respectively. The orbits are located at the margin of the skull, framed by a narrow jugal and maxilla laterally. Their outline varies broadly between specimens, ranging from nearly round to elongate oval. As analyzed in the section on ontogeny, orbit length has negative allometry with respect to skull length, but variation also occurs between skulls of the same size. The prefrontal is markedly shorter than the frontal and has a triangular outline with the long axis pointing anteromedially. The postfrontal, one of the longest elements of the skull roof, is aligned posteromedially and contricts the frontal somewhat in its posterior third. The postorbital is about as long as the postfrontal, with which it shares an elongate and straight suture. It has a pointed end wedging in between the supratemporal and squamosal. Laterally, it has a straight posterolaterally aligned suture with the jugal. The latter, also one of the longest element of the skull roof, is very slender and forms the entire lateral margin of the orbit.

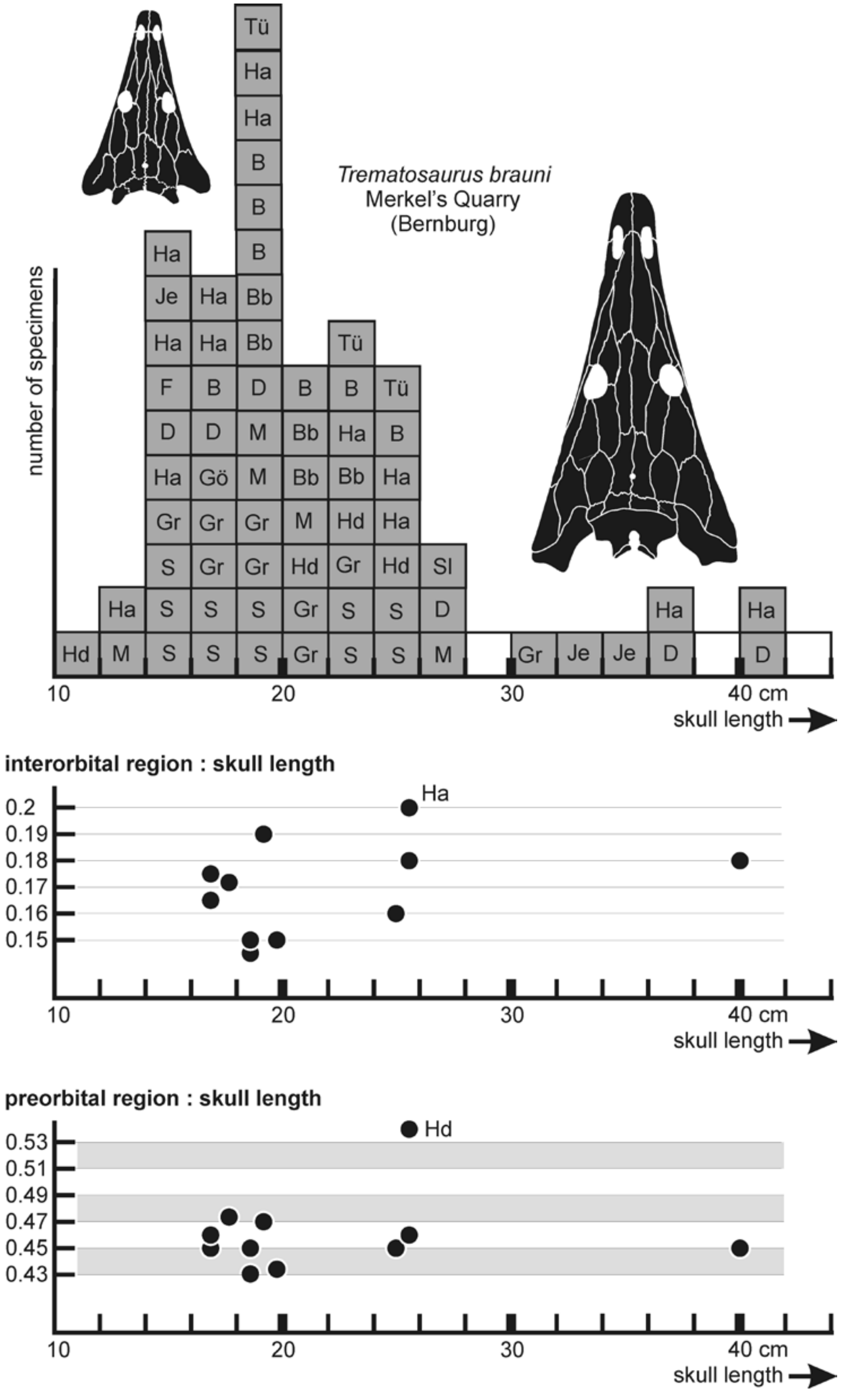

Fig. 3. A, Size range of studied material of *Trematosaurus brauni* Burmeister, 1849 (see Material section for institutional numbers and further data). Institutional abbreviations: B = Berlin (MB), Bb = Bernburg (Saale) (MSB), D = Dessau (MNVD), F = Frankfurt am Main (NMS), Gr = Greifswald (GG), Gö = Göttingen (GMG); Ha = Halle an der Saale (GPSMLU), Hd = Heidelberg (GIH), J = Jena (GMJ), M = Magdeburg (MNM), S = Stuttgart (SMNS), Sl = Schleusingen (NHMS).

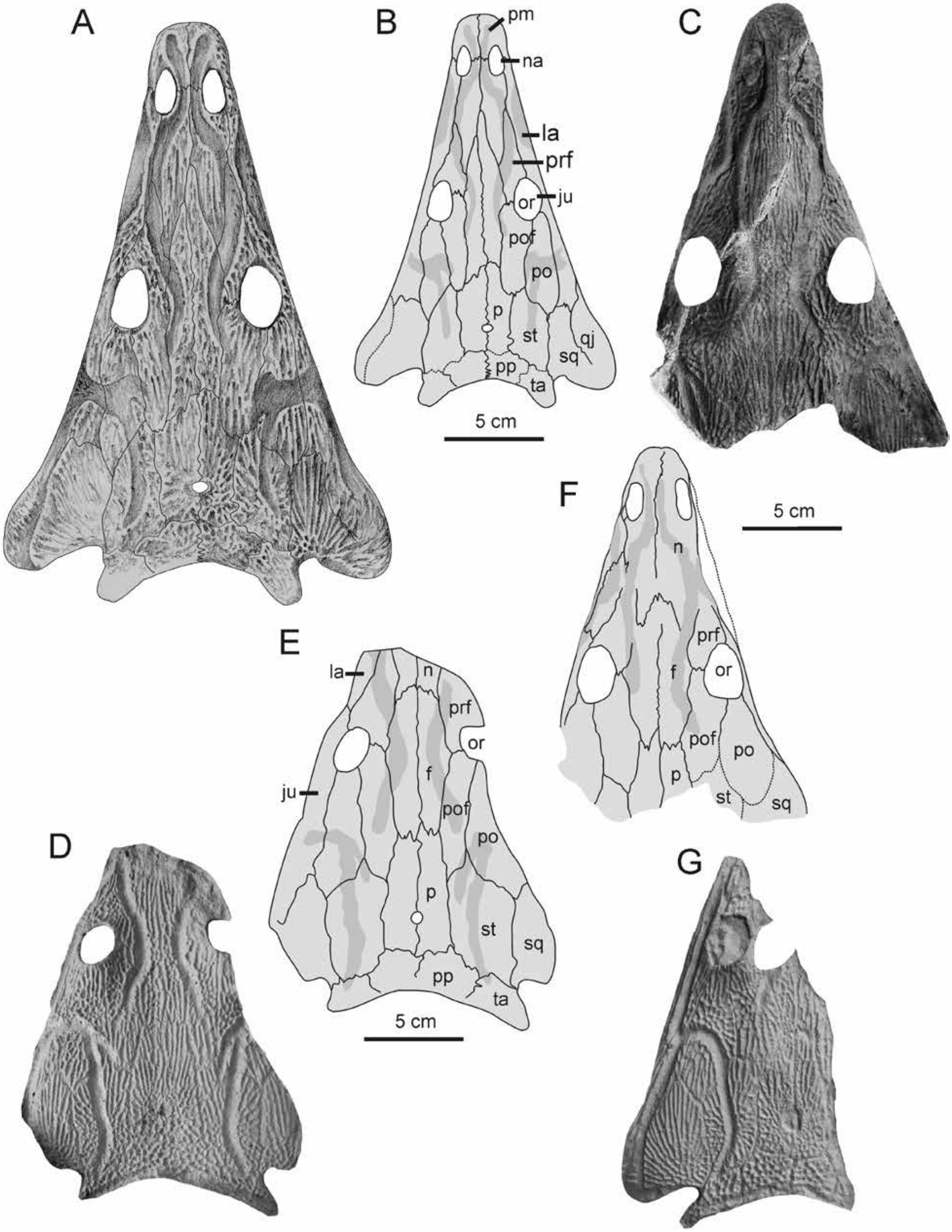

Fig. 4. Cranial morphology of *Trematosaurus brauni* Burmeister, 1849. A, B: GPS.MLU 2019.01; C: GG 22.187; D, E: MNVD 11156; F, GG 22.187; G, GPS.MLU 2016.03.

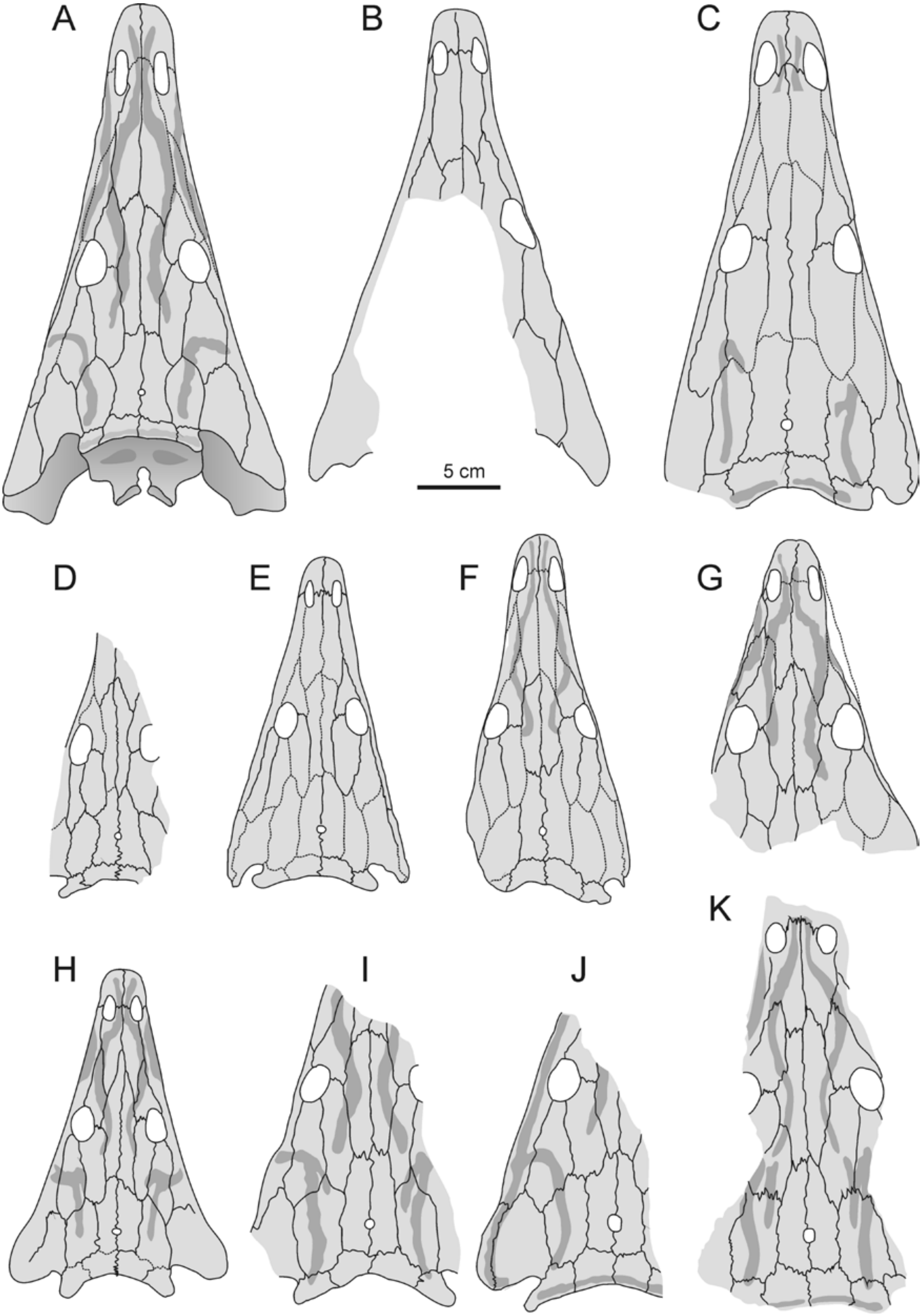

Fig. 5. Skull roofs of *Trematosaurus brauni* Burmeister, 1849. A: GIH BS 5; B: MNM 6588; C: GPS.MLU 2016.05; D: GG 22.166; E: GPS.MLU 2016.04; F: SMNS 6207; G: GG 22.187; H: GPS.MLU 2019.01; I: MNVD 11156; J, GPS.MLU 2016.03; K: GPS.MLU 2016.20.

The parietal forms a long rectangle about three times as long as wide. In most specimens, it has an almost straight lateral margin, as the postfrontal and supratemporal sutures form a continuous sagittal line rather than a step. The parietal is slightly longer and much narrower than the supratemporal, and slightly more slender than the frontal. It has straight or gently curved lateral margins, but markedly serrated sutures with the postparietal and frontal. The pineal foramen is located in the posterior third of the bone. It forms a small oval opening, ranging from sagittally elongated to transversely broadened. The supratemporal is rectangular in outline, having a straight sagittal medial and a posterolaterally aligned lateral margin, whereas its anterior suture is serrated and often stepped where the postorbital and postfrontal are sutured.

The squamosal sutures with the tabular, separating the supratemporal from the margin of the squamosal embayment. Compared with the postorbital and postfrontal, it is a rather short element, of roughly triangular outline with a pointed anterior end. Laterally, it is bordered by a slender quadratojugal that forms the bulk of the laterally convex, downturned cheek margin. This gives the skull a curved lateral margin, which turns into the horizontal plane near the quadratojugal-maxilla suture. The tabular forms the posteriormost portion of the skull roof, well posterior to the squamosal and postparietal. It has a distinct horn projecting posterolaterally, somewhat narrower near the tip than at its base. In contrast, the postparietal forms a transversely rectangular element that is only slightly wider than the tabular. In dorsal view, the occipital margin of the skull table is concave to a variable degree, with the suture between the postparietals forming the apex of the concavity.

The lateral line system is very well established, consisting of distinct continuous grooves on the skull roof, consistent with those in *Benthosuchus sushkini* (Bystrow & Efremov 1940) and *Thoosuchus yakovlevi* (Getmanov 1989), but substantially broader than these. In *T. brauni*, the sulci are as follow: (1) the supraorbital sulcus is more complete (continuous) than in most other temnospondyls, reaching from the region anterior to the naris to the midlevel of the postfrontal. It is markedly curved, crossing the nasal, a small portion of the lacrimal, the medial part of the prefrontal, the midlevel of the frontal, and ends in the central portion of the postfrontal. (2) In close proximity to the latter, the infraorbital sulcus runs from a position near the anterior end of the maxilla along the jaw margin towards the cheek, where it forms a small step to merge onto the quadratojugal (Fig. 5J); near that step, a medial branch runs across the posterior portion of the postorbital to curve posteriorly and split into two branches. The medial of these branches, present in *T. brauni* and a few other taxa (*Aphaneramma rostratum* and *Lyrocephaliscus euri*: Säve-Söderbergh 1936; *Trematosaurus galae*: Novikov 2010), is short and slender and varies in its morphology across the sample. The lateral branch crosses the supratemporal entirely, terminating in the anterior part of the tabular. (3) The infraorbital sulcus continues posterior to the step where the temporal sulcus branches off, running across the jugal and squamosal, where it curves posteromedially. (4) Finally, the occipital sulcus, only present in trematosauroids, forms a transverse and continuous commissure joining the centres of the tabulars and running on both postparietals. This sulcus is narrower than the temporal sulcus, but varies in its course relative to the occipital margin of the bones.

The dermal ornament of the skull roof consists of well-established polygonal ridges. The pits and grooves bordered by these ridges are much thinner than the lateral line sulci, which are 2–3 times wider and substantially deeper than the grooves in most regions. The ridges are most clearly expressed and elongated on the squamosal, anterior supratemporal and parietal, and the posterior part of the nasal. In the anterior region of the frontal and posterior part of the postfrontal and postorbital, elongate ridges are present in some, but not all specimens.

4.2. Palate

The palate bones are delicate and their ventral surface is often poorly preserved. The premaxilla is posteromedially sutured to the vomer, bordering sagittally oval, broadly separate anterior palatal openings. These accommodated the rather small and laterally placed symphyseal tusks of the dentary. Unlike in other stereospondyls, the medial bony bar, formed by tightly sutured premaxilla and vomer, does not form a depressed region, but is aligned at the same level as the dentigerous parts of the palate.

The vomer is four times longer than wide, with the posterior fourth formed by an elongate and thin posteromedial process underplating the anteriormost portion of the parasphenoid, meeting the process of the countersided element in a long suture. Contrasting the situation in capitosaurs, the cultriform process is entirely concealed by the vomer for about one third of its length. Posterior to the vomerine processes, the very slender cultriform process emerges, bearing a sharp ventral keel. Dorsally, the parasphenoid has a V-shaped outline, where it was attached to the floor of the unossified sphenethmoid.

The interpterygoid vacuities reach about half the length of the palate (tip of premaxilla – posterior margin of exoccipital) and are three times longer than wide. Their anterior end is narrower than the posterior one, but both are rounded. However, the posterolateral margin is formed by the palatine ramus of the pterygoid, which has a straight rather than rounded margin as in *Thoosuchus* or *Benthosuchus* (Bystrow & Efremov 1940; Getmanov 1989).

The choana is more than twice as long as wide and has an symmetrical oval shape. It is bordered by a row of

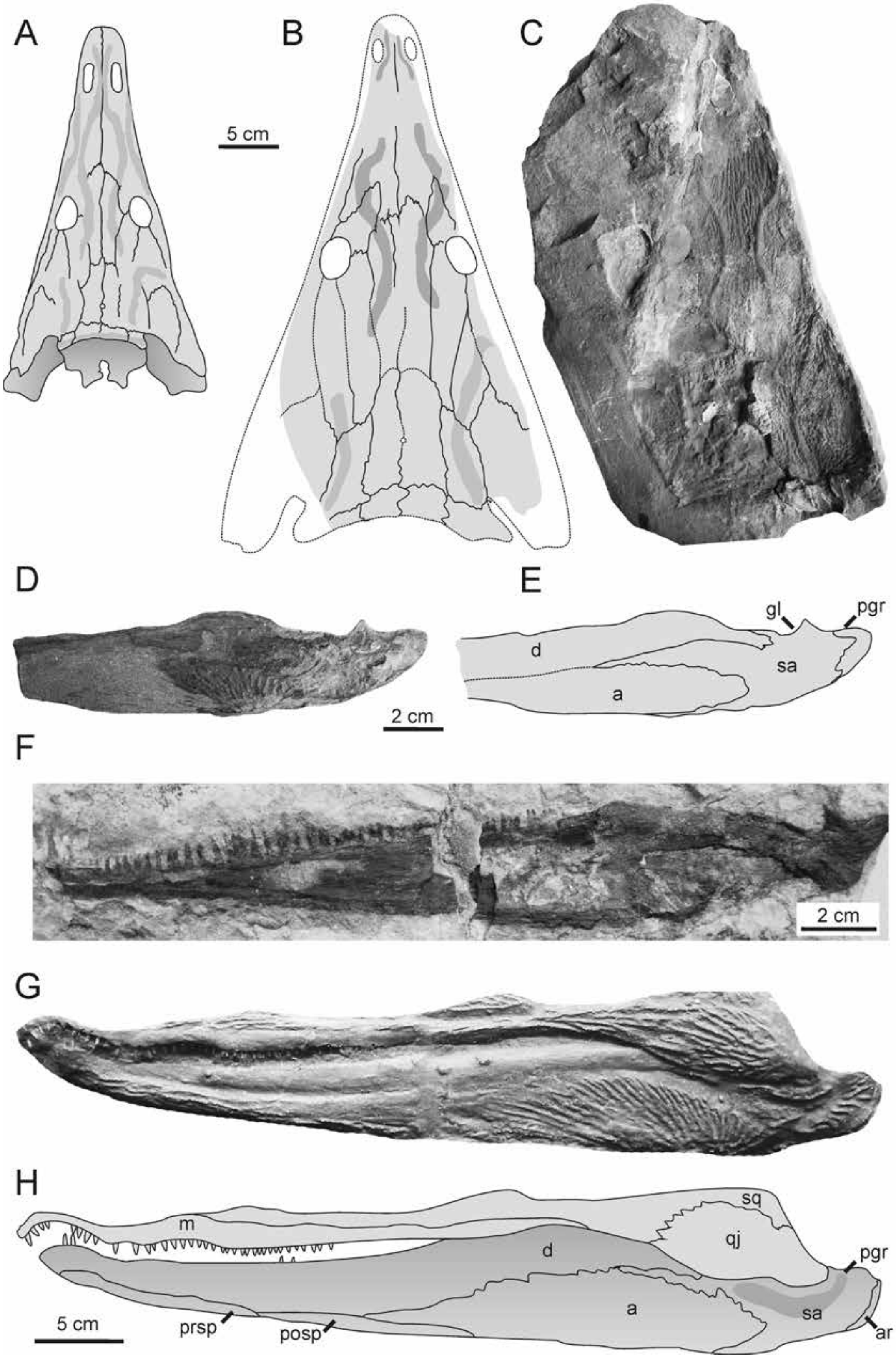

Fig. 6. Skull and mandible of *Trematosaurus brauni* Burmeister, 1849. A: GIH BS 5; B, C: GPS.MLU 2019.02; D, E: SMNS 6207c; F: GPS.MLU 2019.07; G, H: MNVD 11167.

teeth both laterally (maxilla) and medially (vomer). The maxilla and premaxilla meet along the anterolateral margin of the choana. The parachoanal vomerine tooth row is aligned straight parasagittally and does not follow the curvature of the choanal margin. There is a small patch of additional teeth in the midline, level with the anterior part of the choana; this is somewhat smaller and contains less teeth than in *Thoosuchus* and is more similar to the condition in *Angusaurus* (Getmanov 1989). The suture between palatine and vomer runs almost in parallel to the midline suture, and bordered by the much wider palatine, the vomer forms a very slender, long-rectangular element.

The pterygoid is relatively short, with a slender palatine ramus that is slightly shorter than the ectopterygoid and only about as long as the palatine. The quadrate and basipterygoid rami are form a continuous, narrow plate sutured along most of its length to the basal plate of the parasphenoid. The central region of the basal plate (parasphenoid) and the pterygoid (basipterygoid and palatine rami) are covered by slightly raised areas that are very finely pitted. These areas are usually poorly preserved due to damage caused by crude preparation. They correspond to similar-sized regions in other stereospondyls (Getmanov 1989; Maganuco et al. 2009; Marsicano et al. 2017) which are dentigerous and were termed "area aspera" by Bystrow & Erfremov (1940). The dorsal face of the basal plate has a smooth and flat central area and two ridges on each side, an anterior transversely aligned crista parafenestralis and a posterior, posterolaterally curved crista parapterygoidea (Shishkin 1973; Schoch 2000). The latter is more distinctly raised and formed the area of articulation for the stapes (see Visceral skeleton). Dorsally, the centre of the basal plate is dominated by elongate grooves for the internal carotid artery, which entered the parasphenoid somewhere along its posterolateral margin and left the bone in paired openings slightly anterior to mid-length of the basal plate, running in separate elongate grooves towards the base of the cultriform process (Fig. 8D).

The exoccipitals are ventrally underplated by a posterior extension of the basal plate, much like in *Benthosuchus*, *Thoosuchus*, and *Angusaurus*. The extreme elongation of the basal plate also results in an extended suture between parasphenoid and pterygoid, although the latter also sutures the exoccipital, contrasting the situation in the aforementioned taxa. An opening for the eustachian tube is present (Fig. 7B). As in *Thoosuchus yakovlevi*, the exoccipitals are entirely fused in the midline.

4.3. Dentition

Teeth are rarely well-preserved in the Bernburg material because of the crude preparation of most skulls. However, tooth sockets or broken bases are present and sometimes well-preserved, and in a few specimens, imprints of the tooth crowns are present (Fig. 7C, D). Both tusks and other teeth are labyrinthodont (except for the smallest teeth on the vomer); usually with a few rather faint grooves along the base. The tips may be slightly curved lingually. Keeled tusks or regular teeth have not been observed in any specimen, which might either have distinguished *T. brauni* from *Tertrema acuta*, *Trematolestes hagdorni*, and other trematosauroids (Säve-Söderbergh 1936; Schoch 2006), or are simply not preserved in the available sample.

Tusks are only present on the symphysis, vomer and palatine, and a suite of enlarged teeth is also present in the anterior part of the ectopterygoid. The vomerine and palatine tusks are arranged in pairs, with the anterior tooth usually somewhat more compressed at the base but projecting somewhat more medially. The bases of the vomerine tusks are slightly larger than those of the palatine, whereas the symphyseal tusks are not preserved in any specimen in which their size could be compared to that of the palatal tusks.

The premaxilla teeth are largest near the midline suture, decreasing in size (= area of tooth sockets, length of crown) towards the posterior end of the element. The dentition of the maxilla consists of 5–8 larger teeth in the anteriormost portion, followed by rather uniform and very small teeth further posterior, a consistent feature of *Trematolestes hagdorni* and lonchorhynchines as well. The teeth of the palatine and ectopterygoid are larger than those of the maxilla and less numerous, but as these are closely set and aligned in a straight row. As is typical of stereospondyls, the marginal and palatal tooth rows have tooth bases that are not round, but transversely elongated and usually are tightly attached to the bases of neighbouring teeth, without leaving any free space.

In the dentary, the teeth are substantially larger than in the maxilla, matching those of the palatine-ectopterygoid tooth row (Fig. 6F). They appear to have been longest in the anterior third of the dentary. In SMNS 4485, an isolated dentary in lateral view, the symphyseal tusk is large (longer than the dentary is deep), having 3–4 times the length of the other dentary teeth.

4.4. Braincase and occiput

Only two regions of the skull contain substantial amounts of endochondral bone, namely the quadrate and exoccipital. The braincase (sphenethmoid, basisphenoid), otic capsules (prootic, opisthotic), and the ventral and dorsal portions of the occiput (supraoccipital, basioccipital) remained largely or fully cartilaginous. There is no trace of an epipterygoid which is usually ossified in other temnospondyls, including trematosauroids (Säve-Söderbergh 1936; Getmanov 1989). Its absence in *T. brauni*

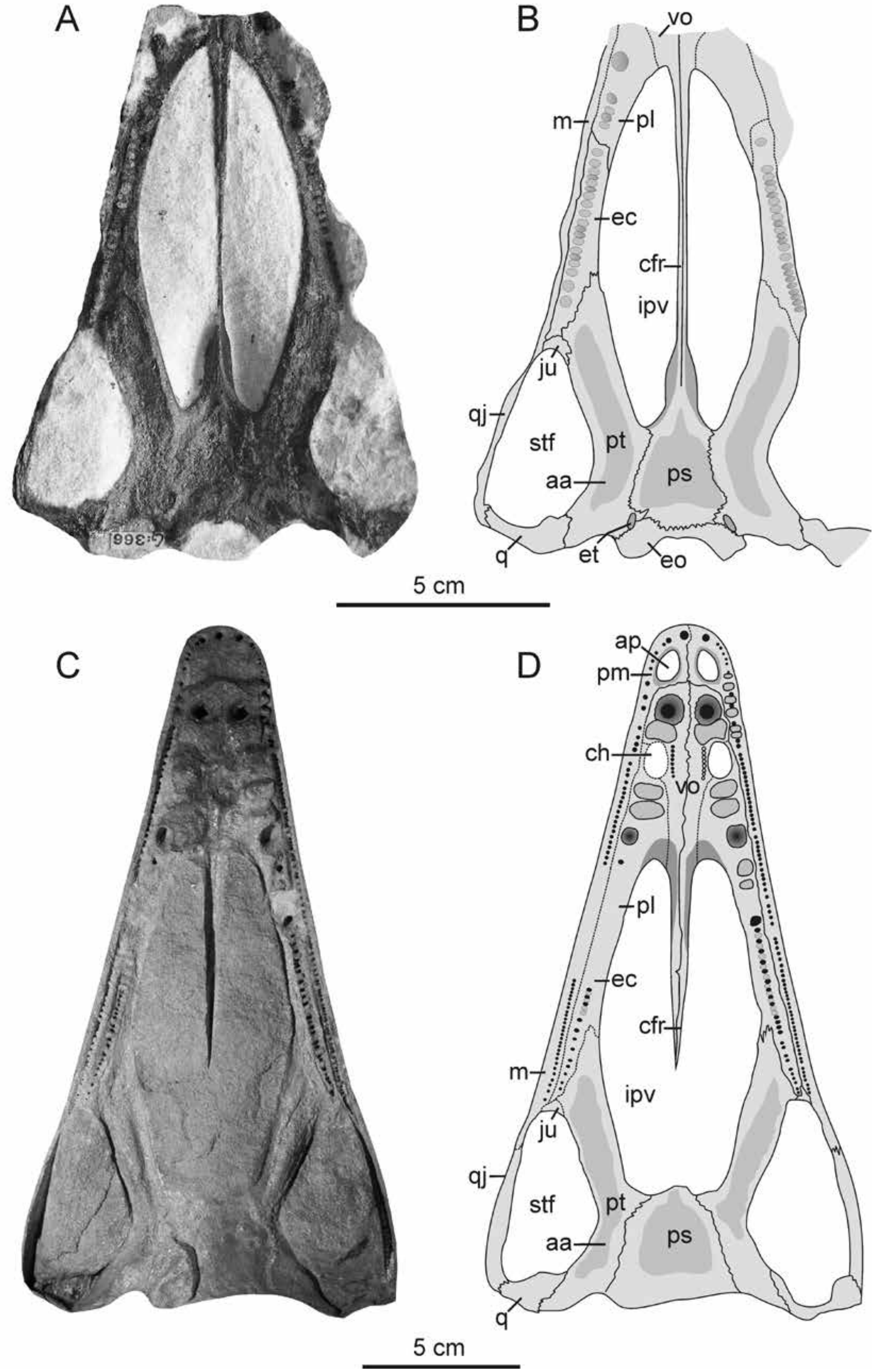

Fig. 7. Palate of *Trematosaurus brauni* BURMEISTER, 1849. A, B: MSB G 366; A, C: GG 22.188.

may be due to the lack of material permitting insight into this region. The generally poor ossification of the braincase is consistent with the condition in other trematosaurids (Säve-Söderbergh 1936), but contrasts the more heavily ossified endocrania of capitosaurs (Schoch & Milner 2000).

The dorsal side of the parasphenoid is remarkably smooth, with only a faint trace of coarse bony structure probably forming an incipient ossification of the basioccipital; it is not as well-developed as in *Aphaneramma rostratum* (Säve-Söderbergh 1936: pls. 18–19) or *Thoosuchus yakovlevi* (Getmanov 1989). In *T. brauni*, the basisphenoid region remained cartilaginous, and its floor is entirely smooth. As in *Thoosuchus yakovlevi* and *Angusaurus dentatus*, the exoccipitals are widely separate and relatively small, with relatively high vertical column and a paroccipital ramus that is wider than in the Russian genera. The basioccipital does not contribute the occipital facet, which therefore consists of fully separate exoccipital facets.

The occiput is well-preserved in MNM 6588, revealing a fairly high posterior skull portion and a steep-angled cheek (quadratojugal and most of squamosal nearly vertically aligned). The lateral flank of the cheek is more vertical than in *Thoosuchus yakovlevi*, *Benthosuchus sushkini*, and capitosaurs. The occipital face of the quadratojugal forms a high triangular trough, demarcated by the more medial parts by a thin, nearly vertical ridge.

4.5. Cranial morphs

Divergent cranial morphs in the same sample have been reported in a range of temnospondyls (e.g., Boy 1990, 1985). The studied sample of *T. brauni* includes several peculiar specimens that stand out of the bulk of material, but a consistent bimodal pattern (e.g., like in a sexual dimorphism) is not apparent. Rather, these specimens may form end points on a range of variation in different directions. GIH BS5, a complete skull preserved as natural mould (41 cm, Fig. 6A), has an exceptionally long preorbital region (with the nasal substantially longer than the frontal) and a posteriorly sloping occiput. This specimen is very similar to *Tertrema acuta* in the proportions of the preorbital region and occiput (Wiman 1914), but lacks the diagnostic features in the palate and dentition (Schoch & Milner 2000). Conversely, GG 22.187 (~19 cm, Fig. 4C) forms an unusually broad skull with a proportionally short, wide triangular snout; the postorbital region is incomplete. Despite their divergent morphologies, these specimens fall well within the range of *T. brauni* in all other aspects (Figs. 3, 5), which is why they are referred to the same taxon.

4.6. Mandible

Mandibles of *T. brauni* are rare in the sample and poorly preserved, rendering the medial (lingual) side particularly poorly known. The best specimen is the large, laterally exposed skull margin and attached mandible (MNVD 11167, 41 cm skull length, Fig. 6G), which preserves the entire left mandible in lateral (labial) view. The lower jaw is overall of similar depth (as measured from the level of the glenoid facet ventrally), but the region anterior to the glenoid is raised to give a substantial coronoid process. This is lower than in *Trematolestes hagdorni* or *Metoposaurus diagnosticus*, but higher than in capitosaurs. The ventral margin of the angular is almost straight, and the surangular tapers continuously towards the posterior end, which is rounded and lingually formed by the articular. The dentary and angular are separated by a long, anteriorly tapering process of the surangular (Fig. 6E). The postsplenial and presplenial are of similar length, exposed well only on the labial side shape. Lingually, an elongate Meckelian fenestra is visible, but the only specimen preserving this region is rather damaged (Fig. 6F). The surangular bears a deep and wide lateral line sulcus. The coronoids are not preserved well enough in any specimen as to expose the sutures.

4.7. Visceral skeleton

The visceral skeleton of trematosaurids is known from only few specimens, foremost the type of *Trematolestes hagdorni*, which preserves ossified ceratobranchials and an elongate basibranchial (Schoch 2006). Hyobranchial elements have not identified in *T. brauni*, but the lack of articulated skeletons at Bernburg precludes the preservation of such delicate elements; the same is true for the dentigerous ossicles that covered the interpterygoid vacuities in many temnospondyls, and which have also been found in *Trematolestes*, but which are not preserved in *T. brauni*. Hence, the only visceral element present in the latter taxon is the stapes, probably because it was firmly attached to the dorsal side of the parasphenoid (Fig. 8D). Besides its presence, there are no further details preserved, because only its proximal head region is present and the ventral process is not exposed because of the close attachment to the parasphenoid. The presence of a thin, compressed stapedial shaft is indicated by cross-sections of such an element in the otic region of various skulls.

4.8. Referred postcranial material

Only isolated postcranial elements are known from Merkel's Quarry, and they are much rarer than skulls. The

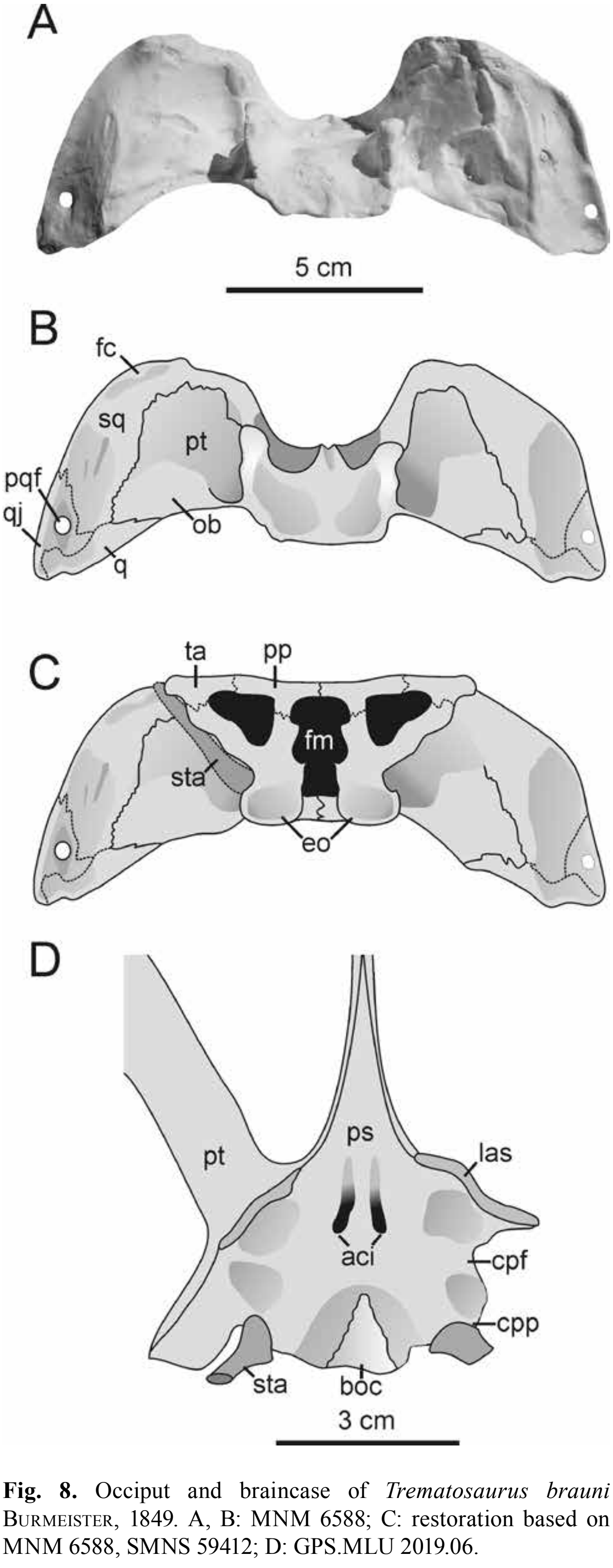

Fig. 8. Occiput and braincase of *Trematosaurus brauni* Burmeister, 1849. A, B: MNM 6588; C: restoration based on MNM 6588, SMNS 59412; D: GPS.MLU 2019.06.

bulk of the postcranial elements from Merkel's Quarry may be referred to *Trematosaurus brauni*, which is readily identified because of its elongated and slender clavicle and interclavicle, both of which are distinct from *Parotosuchus nasutus* (Schoch 2018).

The interclavicle has a huge anterior process, comprising more than half the length of the element (Fig. 9B, C). In contrast, the posterior process is much abbreviated, more so than in *Aphaneramma rostratum* (Säve-Söderbergh 1936), *Wantzosaurus elongatus* (Steyer 2002) or *Trematolestes hagdorni* (Schoch 2006). The posterior portion, as well as the outline of the ornamented area, is most similar to that in *Lyrocephaliscus euri* and also consistent with *Platystega depressa* (Nilsson 1943). The dermal ornament consists of radially arranged ridges merging in a central point at about the posterior fourth of the element. The clavicle is elongate with the portion posterior to the ascending process measuring only one sixth that of the anterior blade, and the medial margin of the ventral blade is markedly curved anteromedially(Fig. 9A). The ornament of the clavicle is consistent with that of the interclavicle in the morphology of the ridges and their convergence in a single point, which lies near the base of the ascending process.

Vertebrae or limb elements are not present in the examined collections and were either not collected or primarily absent because of taphonomic filtering. Burmeister (1849) figured a single scapulocoracoid, whose current provenance is unknown and whose referral to *T. brauni* remains hypothetical, as the scapulocoracoid of *Parotosuchus nasutus* is also unknown (Schoch 2018).

4.9. Ontogeny and variation

Diagnostic skulls of *T. brauni* cover a wide size range, with the smallest (10.9 cm) about a quarter the length of the largest (41 cm). The bulk of the material falls in the 16–20 cm size range (Fig. 3). Despite this considerable range, allometries or other ontogenetic changes are rather few. The smallest specimens already had all apomorphic features well established, and the quadrate and exoccipital are invariably present and well ossified. Growth series in *Trematolestes hagdorni* indicates that the dermal skull must have been formed at an early stage, and was probably quickly followed by the ossification of the quadrate, exoccipital, and vertebral centra (Schoch 2006). The allometric changes found in *T. brauni* are as follows:

1. Length of orbit gently decreased proportionally with size (orbit length:skull length ranging from 0.12 in small skulls to 0.08 in the largest skull).
2. Width of postorbital skull table (between squamosal embayments) relative to length of postorbital skull (posterior margin of orbits to midline margin of postparietals) decreased proportionally with size.

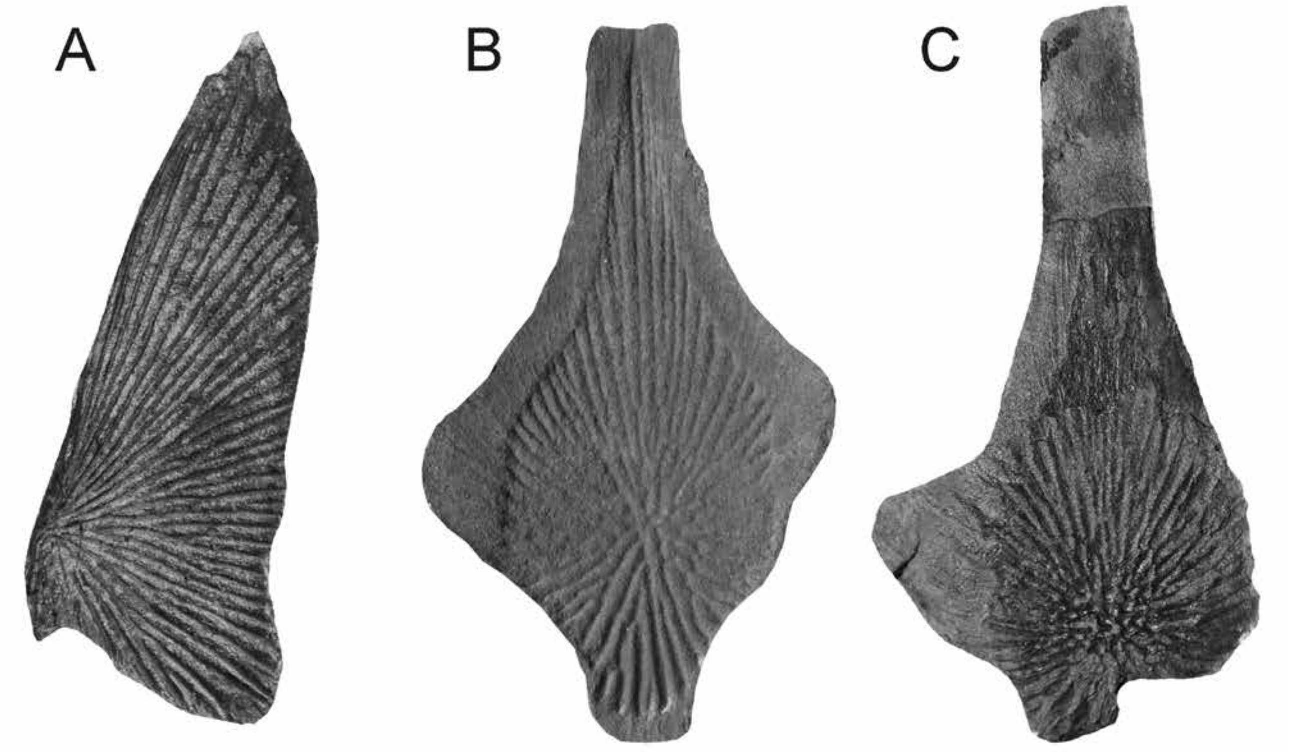

Fig. 9. Postcranial material referred to *Trematosaurus brauni* BURMEISTER, 1849. A: Right clavicle (GPS.MLU.2016.33); B: interclavicle (GPS.MLU.2019.08); C: fragmentary interclavicle (GPS.MLU.2016.37).

Two of the most frequent allometric changes (BOY 1974; STEYER 2000) in temnospondyls, affecting the interorbital distance (relative to skull length) and length of the preorbital region (relative to skull length), vary broadly in *T. brauni* and show no allometric variation (Fig. 3). The same applies for the pineal foramen, which often decreases in size in temnospondyls, but not in *T. brauni*.

In sum, the individual variation found in the present analysis, confirming earlier observations by WAGNER (1935), is extraordinarily broad even compared to close relatives of *T. brauni* (e.g., *Benthosuchus, Thoosuchus, Trematolestes*).

5. *Trematosaurus* and the phylogeny of the Trematosauroidea

5.1. History of research

As one of the major stereospondyl groups, the Trematosauroidea were considered in various phylogenetic studies. Early hypotheses were proposed by WATSON (1919), SÄVE-SÖDERBERGH (1935), ROMER (1947), SHISHKIN (1964, 1973, 1987), HAMMER (1987), and WARREN & BLACK (1985) which are summarized in SCHOCH (2013). Trematosauroids also came increasingly into focus after the thorough anatomical studies of SÄVE-SÖDERBERGH (1936), BYSTROW & EFREMOV (1940), and GETMANOV (1986, 1989) had established the descriptive platform for later phylogenetic analyses; these monographs also included the analysis of variation and ontogeny in some forms (*Benthosuchus*, *Thoosuchus*, *Aphaneramma*), which provided a broader basis for phylogenetic character recognition. More recently, especially the thorough monograph of SULEJ (2009) on *Metoposaurus* has extended this platform further. Despite the rather unusual extent of anatomical information (and inference), trematosauroids remain a problematic group until the present day, because the majority of taxa is based on very fragmentary material (SCHOCH & MILNER 2000; SCHOCH et al. 2002; NIELD et al. 2006; NOVIKOV 2007, 2010, 2012a).

MILNER (1990) included trematosauroids in his first larger phylogenetic study of temnospondyls, and SCHOCH & MILNER (2000) largely followed that topology. These analyses suggest rhinesuchids are basalmost true stereospondyls, followed by a large clade (Rhytidostea) of short-faced taxa (lydekkerinids, rhytidosteids, and chigutisaurids), and the two speciose sister groups Trematosauroidea and Capitosauroidea.

The first computer-based cladistic analyses of stereospondyls that included trematosauroids were published

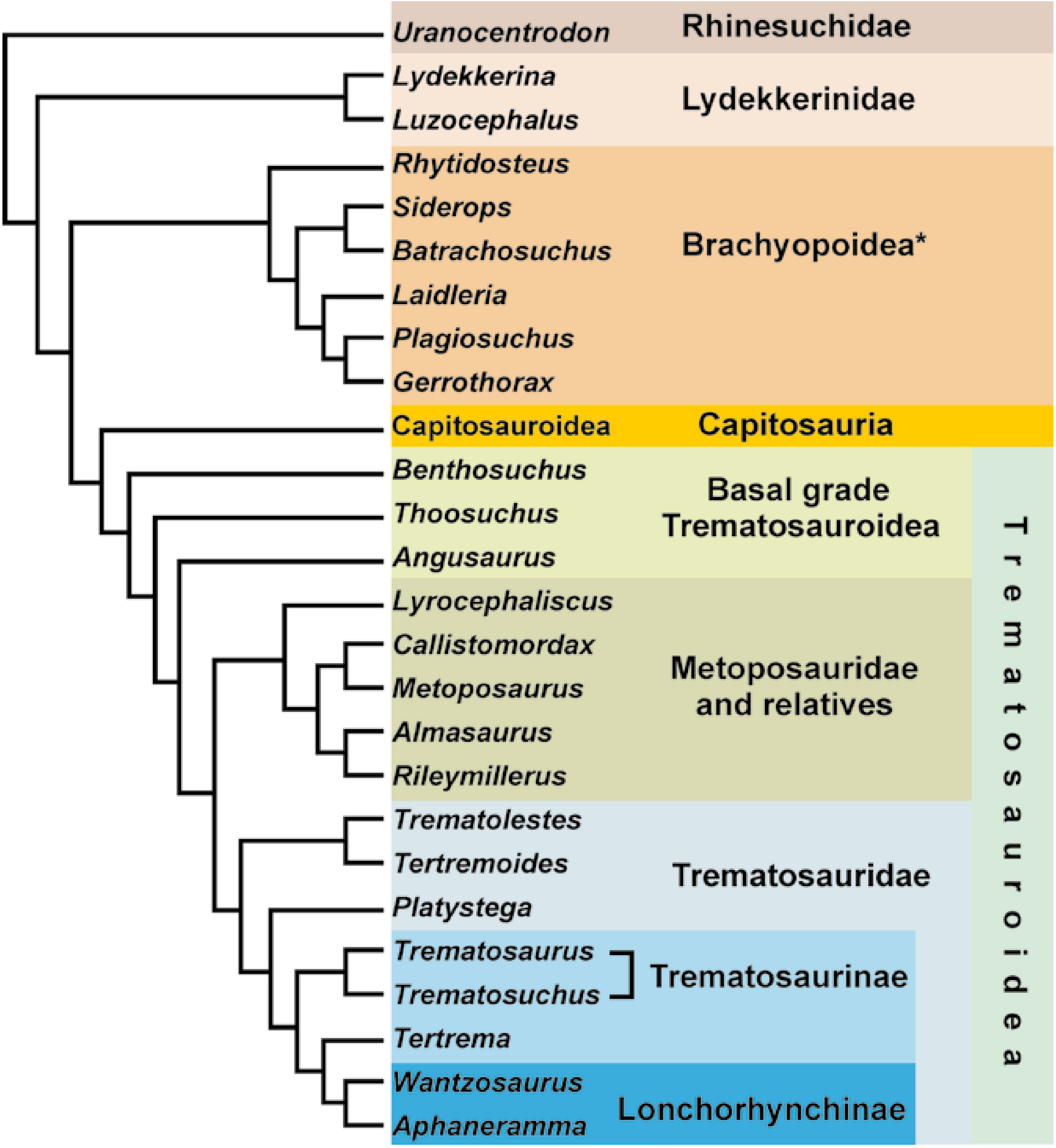

Fig. 10. Phylogeny of trematosaurs with special emphasis on the position of *Trematosaurus brauni* within the Trematosauroidea.

by Yates & Warren (2000), Steyer (2002, 2003), and Damiani & Yates (2003), followed by Schoch (2006, 2008a, 2011b), Maganuco & Pasini (2009), and Fortuny et al. (2017). Among these, Steyer (2002) presented the first analysis of trematosaurid intrarelationships. All aforementioned authors agreed that Rhytidostea did not form a clade, Yates & Warren (2000) found lydekkerinids to nest with capitosaurs, a possibility that had already been mentioned by Shishkin (1980). An early hypothesis according to which metoposaurids were derived from dvinosaurs (Säve-Söderbergh 1935; Shishkin 1973) has not gained support from cladistic analyses (Schoch 2013).

All recent authors agreed that Lydekkerinidae represent a more basal clade, nesting between rhinesuchids and all higher taxa. Another consistent finding of recent studies is that rhytidosteids, brachyopids, chigutisaurids, and plagiosaurids are probably monophyletic (in the following sections referred to as Brachyopoidea*), differing from Milner's (1990) concept of a brachyopid relationship to the dvinosaurians that had also formed the basis of classification in Schoch & Milner (2000).

A major problem that remains unsettled is the interrelationship of the three large clades Brachyopoidea*, Trematosauroidea, and Capitosauroidea (Fig. 10). Schoch (2008a) highlighted two alternatives, which were found as variants in his analysis. In the more extended analysis of Schoch (2013), trematosauroids were found to nest with brachyopoids*, a clade referred to as Trematosauria as introduced by Yates & Warren (2000). A variant of this was reported by Maganuco et al. (2009) who found metoposaurids to form a clade with brachyopoids*, with long-snouted trematosauroids forming the sister group of this short-snouted assemblage.

Both Damiani & Yates (2003) and Schoch (2008a) found cladistic support for an earlier hypothesis of Milner (1990) in which the Late Triassic metoposaurids originated from within a larger trematosauroid clade, after the split with brachyopoids* and capitosauroids. In that topology, the short-snouted *Lyrocephaliscus* formed the basalmost taxon of a grade with the Moroccan *Almasaurus* leading to the Metoposauridae. The discovery of *Callistomordax* in the German Middle Triassic essentially corroborated this hypothesis, as this taxon was found to nest between *Almasaurus* and metoposaurids, at the same time retaining various trematosauroid character-states (Schoch 2008a). In contrast to Maganuco et al.'s (2009) finding, this metoposaurid clade was found to nest *within* the slender-skulled trematosauroids (Damiani & Yates 2003; Schoch 2008a). A further generally accepted hypothesis was that the Russian genera *Benthosuchus*, *Thoosuchus*, and *Angusaurus* formed a grade towards the higher trematosauroids, with many of the trematosauroid synapomorphies evolving in a stepwise fashion (Getmanov 1986, 1989).

Fortuny et al. (2017) employed the data set of Steyer (2002) in which they examined the relationship of the trematosaurids including the lonchorhynchines. They found lonchorhynchines to form a very derived clade within trematosauroids, being sister-taxa of the trematosaurines within the Trematosauridae. However, as their analysis dealing mostly with trematosaurids, did not include metoposaurids, *Almasaurus*, and *Callistomordax*, the topology cannot be fully compared with the aforementioned studies. They also found no basal grade of Russian genera (*Benthosuchus-Thoosuchus-Angusaurus*), instead finding Lonchorhynchinae between *Benthosuchus* and *Trematolestes*, and *Thoosuchus* and *Angusaurus* to nest still higher as a grade towards *Trematosaurus*, *Trematosuchus*, *Lyrocephaliscus*, *Platystega*, and *Tertrema*.

5.2. Phylogenetic analysis

In a phylogenetic analysis based largely on the data sets of Schoch (2006, 2008a), supported by the TNT 1.0 package, 29 taxa and 114 characters (see Appendix) were analyzed under the Traditional Search and New Technology Search options, the latter carried out in the Ratchet mode with 1000 replicates. Both variant analyses gave one identical, most parsimonious tree (247 steps), with a consistency index of 0.49 and a retention index of 0.72 (Fig. 10).

The single tree reveals a topology of stereospondyls consistent with that of the more recent studies, notably in the basalmost position of Rhinesuchidae (*Uranocentrodon*), the nesting of Lydekkerinidae (*Lydekkerina* + *Luzocephalus*) above the rhinesuchids, and the Brachyopoidea, Trematosauroidea, and Capitosauroidea forming the three "advanced" clades of Stereospondyli, which is consistent with all studies after Yates & Warren (2000). *Luzocephalus*, which was emphasized by Shishkin (1980) to have lydekkerinid affinities, was included here, because Steyer (2002) found it to be related to trematosauroids. However, as already found by Damiani & Yates (2003), *Luzocephalus* is probably a relative of *Lydekkerina*. The Brachyopoidea* is found as a monophyletic group, composed of *Rhytidosteus* as basal sister taxon of all others, which fall into (1) a clade formed by Brachyopidae (*Batrachosuchus*) and Chigutisauridae (*Siderops*) and (2) the Plagiosauridae with their sister taxon *Laidleria* (Yates & Warren 2000). Further consistent with the findings of Schoch (2008a), the Capitosauroidea and Trematosauroidea form sister taxa, with the latter including two major branches: (1) a clade of short-faced taxa (*Lyrocephaliscus*, *Almasaurus*, *Rileymillerus*, *Callistomordax*, and Metoposauridae) and a clade of slender-skulled forms (Trematosauridae). The latter group falls into the following successive sister taxa: (a) a basal clade formed by *Trematolestes* + *Tertremoides*, (2) the fragmentarily known taxon *Platystega*, (3) *Trematosaurus* + *Trematosuchus*, (4) *Tertrema*, and (5) *Wantzosaurus* + *Aphaneramma*.

This topology differs from that of former analyses (Steyer 2002; Schoch 2006, 2008a; Fortuny et al. 2017), especially in the high placement of *Trematosaurus* + *Trematosuchus* and the basal nesting of *Trematolestes* + *Tertremoides*. The basal split between lonchorhynchines and all other trematosauroids, found by Fortuny et al. (2017), was not corroborated by the present data set.

In a slightly extended analysis, the South African genus *Microposaurus casei* (Damiani 2004) was included, which gave a poorly resolved consensus of 28 most parsimonious trees, in which the three Russian taxa were still retained as a basal grade, the lonchorhynchines and metoposaurid relatives as two clades, but all other taxa nested in a polytomy. Notably, *Microposaurus* did not fall within the Brachyopoidea* despite the inclusion of *Rhytidosteus*, with which it had earlier been associated (Shishkin 1964).

5.3. Aspects of trematosauroid evolution

Trematosauroids had largely diversified by the earliest Triassic, which is revealed by the presence of lonchorhynchines and trematosaurines in many localities around the globe (v. Huene 1920; Säve-Söderbergh 1936; Welles 1993; Nield et al. 2006; Novikov 2010, 2012a; Fortuny et al. 2017). In the topology found by Fortuny et al. (2017), the trematosauroid ghost lineage would have to date back well into the Lopingian; in the tree obtained by the present analysis, this is(see Schoch 2008a for discussion). The present data cannot help resolving this issue, but provide some insight into the branching pattern of trematosauroids. Contrasting Fortuny et al.'s 2017 findings, *Benthosuchus*, *Thoosuchus*, and *Angusaurus* are still likely to form a grade towards all other taxa. The divergent placement of *Trematolestes* results in part from its possession of a small naris close to the anterior margin, which may be interpreted as derived rather than plesiomorphic. In addition, the region medial to the choana is poorly known, leaving the presence and arrangement of teeth unknown. A more detailed study of this taxon will form the subject of a future project, once new material has been fully prepared.

Trematosaurus brauni is very similar to *Trematosuchus sobeyi* in the proportions of the skull, the size and position of the orbits, and the structure of the palate (Haughton 1915; Shishkin & Welman 1994). *T. brauni* is more consistent with both *Tertrema* and the Lonchorhynchinae than formerly thought, which is especially obvious in the similarity of the lateral line sulci and the dentition.

The placement of *Platystega* is tentative, because this taxon is based on poor material; conflicting evidence indicates that *Platystega* might be related to *Lyrocephaliscus* and the stem of the metoposaurids (Schoch 2006), or alternatively with the incompletely known genera *Inflectosaurus* and *Microposaurus* (Fortuny et al. 2017).

Finally, the knowledge of ontogeny might be crucial for a more profound understanding of trematosauroid phylogeny. Although *Trematosaurus brauni* reveals few clear-cut ontogenetic changes, major changes have been reported in *Aphaneramma rostratum* (Säve-Söderbergh 1935) and *Wantzosaurus elongatus* (Steyer 2002) are known to exist in *Trematolestes hagdorni* (Schoch 2006 and unpublished data). Future phylogenetic analyses will have to take this into account, a necessity that was most thoroughly examined by Steyer (2000).

6. Fossillagerstätten and palaeoecology

In stark contrast to younger Triassic deposits in Central Europe, the Buntsandstein has yielded only occasional finds of tetrapods, and among these the stereospondyls rank first in both frequency and distribution. Apart from the bulk of material, which was collected as isolated finds, a few localities have produced mass accumulations of bones or even complete skulls. The richest deposits, measured by the number of collected specimens, are Bernburg/Saale and Kappel in the Black Forest. Whereas Kappel forms a mass accumulation of all kinds of bones from one particular taxon, *Mastodonsaurus cappelensis* (Wepfer 1923), Bernburg produced apparently sorted elements and skulls from two highly distinct taxa, the capitosaur *Parotosuchus nasutus* and the trematosaurid *Trematosaurus brauni* (Braun 1842; Meyer 1858). More exceptional fossillagerstätten appear to be those that yielded the probably semi-terrestrial *Sclerothorax hypselonotus* (v. Huene 1932; Schoch et al. 2007), which is known from several almost fully articulated skeletons.

The Bernburg deposits fall into two different horizons, a lower, massive fluvial sandstone sequence (Bausandstein) containing the temnospondyls, and an upper deltaic-coastal marine, more even bedded sandstone (Thüringischer Chirotheriensandstein), in which tetrapod tracks dominate and that has produced the single disarticulated skeleton of the protorosaur *Trachelosaurus fischeri* (Broili & Fischer 1917; Hauschke et al. 2005; Schoch 2018). The entire sequence is dominated by the fossil plant *Pleuromeia goldfussi*, which is believed to have flourished at or near coastal settings, suggesting that the fluvial sandstones containing the temnospondyls were deposited in channels not far from the ingrading sea. This is consistent with evidence that both trematosaurids and capitosauroids also occurred in marine deposits (Lindemann 1991; Schoch & Milner 2000).

Both temnospondyl taxa present at Bernburg were evidently aquatic dwellers, as indicated by the presence of lateral line sulci, and their morphology suggests that *Parotosuchus* was a caiman-like top-predator, probably of small tetrapods and large fish, whereas *Trematosaurus* was probably a lateral strike-hunter, focused on smaller vertebrates and invertebrates. In their finite element analysis, Fortuny et al. (2011) found that *Trematosaurus* (along with *Benthosuchus* and *Thoosuchus*) shares patterns with amphibious predators, suggesting that *Trematosaurus* might have been able to forage on land as well as in the water, which would match the fluvial-deltaic setting in which the material is preserved. As both taxa are present in Merkel's Quarry with small juveniles, it is likely that both lived in the preserved habitat rather than were their carcasses washed in from elsewhere. The frequency of specimens across the size range is consistent with the distribution of other aquatic temnospondyls (Boy 1995; Witzmann & Schoch 2006) and quite distinct from that of metamorphosing taxa (Boy 1990; Werneburg 1991). The presence of two large predators indicates that the habitat was rich enough to permit two such taxa, but unfortunately, no other components of that palaeoecosystem are preserved. Trematosaurids appear to have been excellent swimmers, as their bodily proportions with a long and high, laterally compressed tail are consistent with those of small crocodiles (Schoch 2006).

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Appendix

The characters 1–100 were taken from Schoch (2008a), originally composed from a range of sources (see citation therein). Additional characters employed in the present analysis are as follows:

(101) Width of lateral line sulci (0, thin grooves; 1, wide and shallow grooves).
(102) Occipital sulcus on postparietal and tabular (0, absent; 1, present).
(103) Temporal sulcus entering tabular (0, no; 1, yes).
(104) Temporal sulcus with two branches (0, no; 1, yes).
(105) Orbit size (0, small to large; 1, minute, less than 10% skull length).
(106) Transverse tooth row on vomer (0, straight; 1, V-shaped; 2, parallel).
(107) Premaxilla greatly elongated (0, no; 1, yes).
(108) Anterior palatal vacuities closed (0, no; 1, yes).
(109) Anterodorsal dentary foramen (0, absent; 1, present).
(110) Rostrum with splint-like nasal and lacrimal (0, absent; 1, present).
(111) Massive palatine-pterygoid contact (0, absent; 1, present).
(112) Palatal tusks only slighty larger than teeth in palatal row (0, absent; 1, present).
(113) Minute maxillary teeth (0, no; 1, yes).
(114) Frontal much narrower than postfrontal (0, no; 1, yes).
Capitosauroidea has been coded on the basis of the basalmost taxon, Parotosuchidae (Schoch 2008a).

Character-taxon matrix

Dendrysekos helogenes
000000000010?00000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000
000000000000
Trimerorhachis insignis
000000000000000000000000010010011000101001110000000000000000000000010001000000000000000000001001000000000000000000
000000000
Sclerocephalus haeuseri
000000000000001001100000100000001000000000000000001000000000000000000000000000000000000110000000001000000000000000
0000000000
Uranocentrodon senekalensis
000001000000001001100010101000000101000100000010010001100000000001010101000000000000001010011100000110000000000000
000000
Lydekkerina huxleyi
0000010000?0?10011000101110100111101010010010110001?110000000101010110000000000000001010001100000110000000000000000
0000
Luzocephalus blomi
00000100000000000011000101110100111101000?10010110001?1?000?00010?????????????????????????????????????00000000000000
Siderops kehli
0000111011000110101111011101012111111111111011010?0201011111101010100100000000010001010110100110010000000000000000
Batrachosuchus watsoni
0000111011000110101111011111012111011111111011111102011111111101010???1???????????????????????????????00000000000000
Laidleria gracilis
000011100000011010011101111110221110111011101101110201111111001010??2100100001?000??????1110??????01100000000000000
Rhytidosteus capensis
01001110000001101000010111010011110111101101101010201011001001010?????????????????????????0???????0000000000000000
Gerrothorax pulcherrimus
10000100100000100100111011111102211101111110101101010201011111001010002100200011?00010110000000110110110000000000000000
Plagiosuchus pustuliferus
10000100100000101100111011111102211101111110101101010201011111001010002100200001?00011110000000000001011000000000000000
Capitosauria
010000000000101011100010111010011110101011101101100201010001001010201110100000111001010000000000000110000000000000
000
Aphaneramma rostratum
0011110000000010010100101110100111101000011111111012010100110010102??10001000001000201110011?00?0?10000111211111111
Trematolestes hagdorni
00111101000000100101001111101001111110000111111110120111001100101120010101000001010201211011100101100001000000000011
Lyrocephaliscus euri
0011110000000111010100101110100111101100011111111012011110110010?????????????????????????????????????11010000000000

Rileymillerus cosgriffi
00011101001??11000100111101100211111101111111111111201010?110011100??????????????01?????????????????00001000000000
Almasaurus habbazi
0011110?0000111000100111110100211111101111111111101201010111001110 2??10001100001000101200010?00?0110000000000000000
Metoposaurus diagnosticus
001111011100111000100111110111211111101111111111110201110111011111211110111110110001012000100001011001000000000000000
Callistomordax kugleri
0011110111001110001001111101112111111010111111111012011101110111112111011111000101010120101010010110000000000000000
Benthosuchus sushkini
001001000001110010000101110100111101000011111111012011000010010101 0?1000100000???01011??????????????0000000000000
Thoosuchus yakovlevi
0010110000011100100001011101001111010000111111110120110001100101????1000100000???01011??????????????0000000000000
Angusaurus dentatus
0010110000000110010000101110100111101000011111111012011000110010 1???????????????????????????????????00001000000000
Trematosaurus brauni
0011110000000110010100101110?00?1110100001111111101201010011001011 2??????????????02011??????????????11111000000000
Trematosuchus sobeyi
00111100000001100101001011100000111010000111111110120101001100 10????0?????????????????????????????1???1000000000
Tertrema acuta
00111100000001?0101001011100000111110 0?0111111110120101001100 10???100000001
Platystega depressa
001111000000?10010100101110100 1111?100?0111111110120101001100 10???000000000
Tertremoides ambilobensis
00101101000001101010011111010011 11?100?01111111101201??00110010?????????????????????????????????????00100000000000
Wantzosaurus elongatus
0011111000000010010?101011110000111?1000?111111110 1201??001100101??????????????000010????????????????01100211111111