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The temnospondyl *Parotosuchus nasutus* (v. Meyer, 1858) from the Early Triassic Middle Buntsandstein of Germany

Rainer R. Schoch

Abstract

The capitosaur *Parotosuchus nasutus*, exclusively known by historical finds from Merkel's Quarry at Bernburg (Saale), forms one of the most frequent tetrapods of the continental Triassic. A revision of the surviving material reveals a remarkable size range (14–44 cm skull length) of this large temnospondyl. *P. nasutus* is characterized by (1) quadrate condyles well posterior to occipital ones, (2) supratemporal in adults anteriorly twice as wide as posteriorly, (3) palatine very slender, distance between choana and interpterygoid vacuity much shorter than choana, and (4) interpterygoid vacuity twice the length of vomer plus premaxilla. Ontogenetic changes include broadening of the nasal, frontal, parietal, postfrontal, supratemporal, and tabular horn, whereas the proportions of snout and skull table are isometrically correlated. Phylogenetic analysis finds *P. nasutus* to nest with *P. haughtoni*, *P. orenburgensis* and *P. helgolandicus* within a monophyletic Parotosuchidae, which in turn is confirmed as basalmost clade of Capitosauroidea.

Keywords: Buntsandstein, Capitosauria, Parotosuchidae, phylogeny, Triassic

1. Introduction

Many continental Triassic palaeoecosystems were dominated by putative stem-group amphibians, the temnospondyls, which reached sizes far beyond those of modern lissamphibians (Warren et al. 1997; Schoch & Milner 2000). The largest of these were the capitosauroids, which measured up to 5 or 6 m body length, and whose appearance was in between a giant salamander and a caiman (Damiani 2001a; Schoch 2008). Temnospondyls were first discovered in Germany, and one of the first capitosauroids, indeed Triassic tetrapods to be described was the 2–3 m long *Parotosuchus nasutus* from the Middle Buntsandstein of Bernburg an der Saale, east-central Germany (v. Meyer 1858). This long-snouted form, which is often referred to as a stereotypic Early Triassic temnospondyl, has a characteristic parabolic skull, profound lateral line grooves, and a polygonal ornament of ridges on the dermal bones of the skull and pectoral girdle. These giant temnospondyls were largely aquatic even as adults, as is indicated by their possession of a lateralis organ, feeble limbs, and long swimming tails (Watson 1958; Schoch & Milner 2000).

P. nasutus was first named and described by Meyer (1858), who referred it to *Capitosaurus* Münster, 1836 a taxon reported from the stratigraphically much younger Ladinian Benk Sandstone Member of the Gipskeuper. As discussed by Jaekel (1922), Kamphausen (1990) and Schoch (2008), *Capitosaurus arenaceus* is more likely to form a close relative of the Late Triassic genus *Cylotosaurus*, but this identification is rendered difficult by the fragmentary state of the type specimen. For several decades, a wide range of similar Early and Middle Triassic taxa was referred to *Capitosaurus*, until Jaekel (1922) coined the name *Parotosaurus* for the Bernburg taxon. However, as this name had already been given to a lizard, it was renamed into *Parotosuchus* by Ochev & Shishkin (1968).

P. nasutus has remained one of the few long-known temnospondyls that have never been revised. A better knowledge of temnospondyls, particularly from the Late Triassic, is not just an end in itself: they are one of few tetrapod groups that are abundant in Early and Middle Triassic red-bed deposits and have been used for biochronological correlation (Shishkin 1995; Lucas & Schoch 2002). Restorations of the skull roof and palate of *P. nasutus*, based on new material collected after v. Meyer's (1858) description, were figured by Schroeder (1913) as comparison in his report on *P. helgolandicus*, but he provided no further description. Roepke (1923) added only few morphological data, instead focusing on architectural aspects of temnospondyl skulls. In their revision of the capitosauroids, Welles & Cosgriff (1965) gave a detailed account of all the material of *P. nasutus* cited or figured in the literature, but added little on the morphology of this taxon. The aims of the present study are fourfold: (1) clarify the systematic palaeontology of *P. nasutus*, (2) provide a morphological description of all identified skeletal elements, (3) assess ontogenetic changes in the relatively large sample, and (4) analyze the impact of the new data on our understanding of capitosauroid phylogeny and evolution.

2. Geological setting and stratigraphy of Bernburg Fossillagerstaette

All the material referred to *Parotosuchus nasutus* was collected at Merkel's Quarry, located at the western

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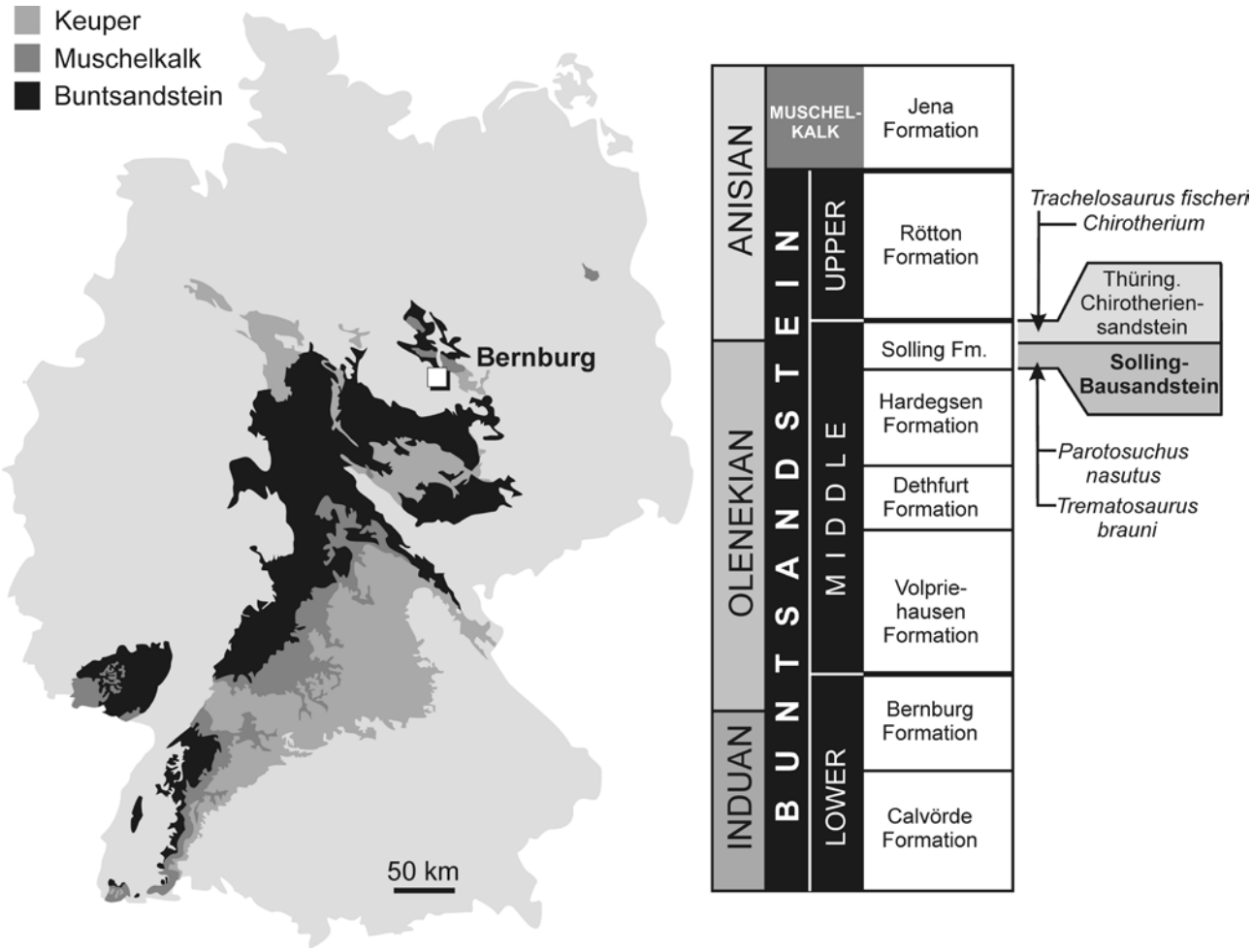


Fig. 1. Locality and stratigraphy of Merkel's Quarry, the type locality of *Parotosuchus nasutus*.

periphery of Bernburg an der Saale (Saxony-Anhalt, Germany; Fig. 1). The first specimens were reported by Braun in Strombeck & Mansfeld (1841) and then described by Burmeister (1849) and v. Meyer (1858). This sandstone pit, the exposed area of which measures some 90 m in length, was active from at least the 1830's through the 1920's (Keilhack & Dammer 1913). Throughout this time, it continued to produce temnospondyl specimens until it was closed and filled (Wagner 1935).

By the sheer number of specimens, Merkel's Quarry forms the richest tetrapod Fossillagerstaette in the Buntsandstein and coeval sequences across Europe. It produced several hundred skull remains of *Trematosaurus brauni*, a long-skulled temnospondyl described by Burmeister (1849) and v. Meyer (1858). The wide size range of *Trematosaurus* indicates that these aquatic predators lived at or very near the site of their burial. Unlike the majority of vertebrate deposits in the Buntsandstein, Merkel's Quarry yielded a second taxon, the capitosauroid *Parotosuchus nasutus*. Although less common than *Trematosaurus*, *Parotosuchus* is well documented with skulls, mandibles, and dermal elements of the pectoral girdle, whereas limbs and vertebrae are absent (v. Meyer 1858; Wagner 1935).

Aside from the temnospondyls, the only other tetrapod remains from Merkel's Quarry are the disarticulated skeleton of *Trachelosaurus fischeri* Broili & Fischer, 1917 and the (still undescribed) end of a limb element that stems from an unidentified archosauriform, both held at the collection of the Geological Institute at Halle (MLU). The quarry also forms the type locality of *Pleuromeia sternbergi* (Münster 1839), which was regularly found in life position in various horizons.

Merkel's Quarry ranges in the Solling Formation, which forms the top of the Middle Buntsandstein. Traditionally, this formation was considered to be of Early Triassic (late Olenekian) age. However, in recent time, the upper part of the Solling Fm. (e.g., Thüringischer Chirotheriensandstein) has been dated as earliest Anisian

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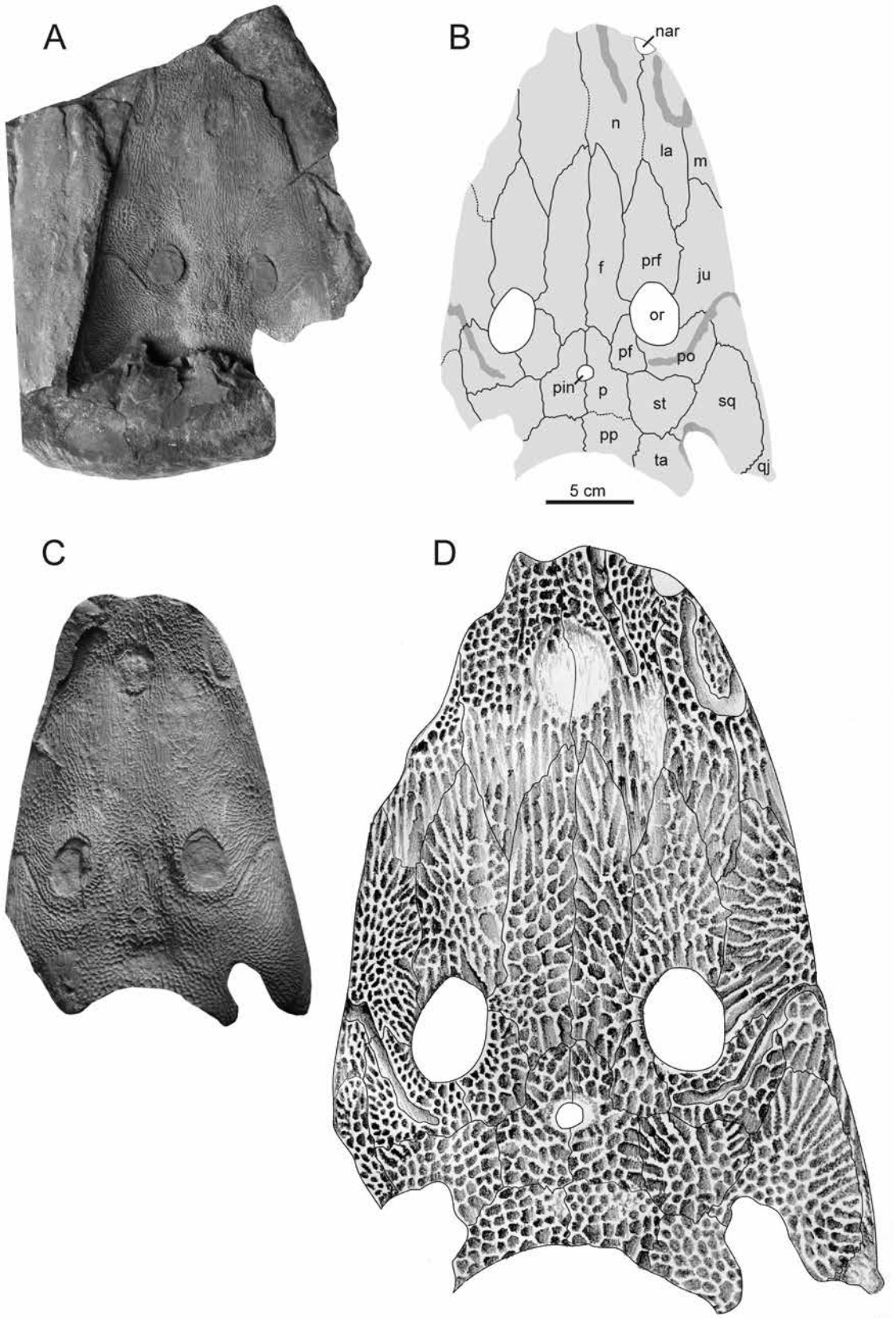


Fig. 2. Type material of *Parotosuchus nasutus*. A–D, neotype as designated in the present study (MB.Am448).

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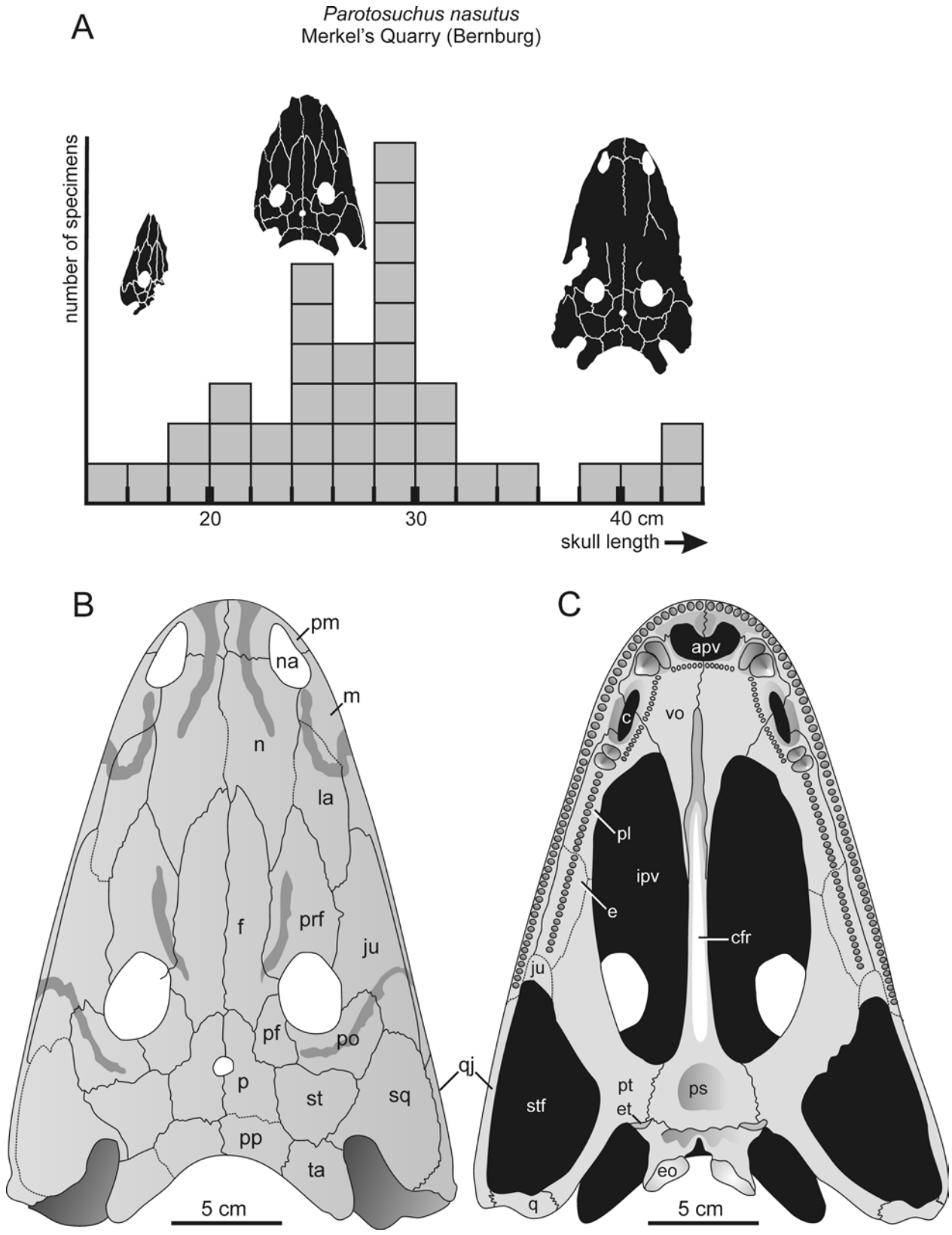


Fig. 3. A, Size range of studied material of *Parotosuchus nasutus* (see Material section for institutional numbers and further data). **B, C**, Cranial restoration of adult *P. nasutus*, based primarily on the type specimen (B, dorsal view, C, ventral view).

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(KOZUR & BACHMANN 2005; SZURLIES 2005). The crucial question then arises from which horizon within the Solling Formation the temnospondyl finds stem. HAACK (1923) discussed the available evidence on the stratigraphic position and range of the different taxa found in Merkel's Quarry, concluding that *Trematosaurus* and *Parotosuchus* came from a massive, clast-bearing sandstone ("Bausandstein", probably Niedersächsischer Bausandstein, after PUFF & RADZINSKI 2014) below the now-exposed sandstone sequence, which is formed by the Thüringischer Chirotheriensandstein, and from which it is separated by the Tonige Zwischenschichten (Fig. 1). This is important because the age of the Thüringischer Chirotheriensandstein has been discussed to be either latest Olenekian or earliest Anisian (KOZUR & BACHMANN 2005) in age, whereas the lower part of the Solling Formation has an undisputed Olenekian age (LEPPER et al. 2014, and references therein).

Magnetostratigraphically, the Solling Formation and the lower part of the Röt Formation fall into the Olenekian (MENNING & KÄDING 2014). Palynologically, the entire Solling Formation marks a change from lycophytes to conifers, indicating the return of forests in the Buntsandstein basin; in this respect at least the Solling Formation shares many features of the Röt Formation (BACKHAUS et al. 2014).

In contrast to the temnospondyls, *Trachelosaurus* was found in the Thüringischer Chirotheriensandstein, whereas *Pleuromeia* had a wider range across the different sandstone horizons. This is consistent with WAGNER (1935), who reported that by the 1930s, the quarry had already been filled with debris, and that the horizon which yielded the temnospondyl skulls was several metres below the then-existing base of the quarry. The very interesting sedimentological update of HAUSCHKE et al. (2005) on Merkel's Quarry therefore covered only the uppermost part of the sandstone sequence. Their conclusion that the Thüringischer Chirotheriensandstein was deposited in a deltaic setting influenced by a transgrading sea (or rather a large lake, see PUFF & RADZINSKI 2014) is therefore not to be applied to the temnospondyl-bearing "Bausandstein" horizon, which, according to the available evidence probably formed in reworked lake deposits that formed in channel sands (WAGNER 1935).

3. Material

The examined material forms only a part of the original sample, which was spread over a wide range of private collections. As is the case with v. MEYER's (1858) original material, many of these privately held specimens appear to be lost. In the following list, skull midline length (premaxilla–postparietal) of specimens is given in brackets.

- GG (Geologisches Institut Greifswald): GG 22.163 (tiny skull, 14 cm), 22.186 (large palate, ~44 cm).
- GIH (Geologisches Institut Universität Heidelberg): GIH BS1 (complete skull, only dorsal side exposed, 30.5 cm, type specimen of *Mastodonsaurus weigelti*, Fig. 4C–D), GIH BS2 (nearly complete skull, 29 cm), GIH BS3 (palate, 31 cm), GIH BS4 (partial skull, type of *Capitosaurus fronto*, Fig. 4A, B).
- GPS.MLU (Geologisches Institut, Universität Halle an der Saale): 2016.01 (skull with mandibles, Fig. 6B), 2016.07 (mandible, Fig. 8G), 2016.10 (thoracal rib, Fig. 9C), 2016.16 (skull), 2016.18 (anterior palate), 2016.23 (left skull portion, Fig. 6C), 2016.28 (anterior palate), 2016.30 (skull fragment), 2016.31 (skull fragment), 2016.35 (right clavicle, Fig. 9A), 2016.36 (good palate, Fig. 8B), 2016.40 (small skull, 16 cm, Fig. 5A, B), 2018.01 (skull with good palate and occiput, Fig. 7A–D, 8A), 2018.02 (large skull, Fig. 5C, D), 2018.03 (large anterior palate, Fig. 8E), 2018.04 (posterior skull portion), 2018.05 (right part of palate and left part of roof, Fig. 8C),
- MB (Museum für Naturkunde, Berlin): Am 445 (cast, partial skull roof), Am 448 (skull roof, 26 cm, neotype), Am 447 (partial snout), Am 451 (anterior palate).
- MNVD (Museum für Natur- und Vorgeschichte Dessau): 11153 (anterior palate), 11166 (skull, Fig. 6E), 11172 (palate), 11173 (orbital portion of skull), 18434 (anterior palate), 18435 (occipital portion).
- MSB (Museum Schloss Bernburg): G395 (skull roof in internal view, 18.3 cm), G403 (snout), G424 (preorbital region).
- SMNS (Staatliches Museum für Naturkunde Stuttgart): 5776 (nearly complete skull, 25.5 cm), 5957 (skull, 28 cm), SMNS 12799 (small dentary with well-preserved symphysis), 81697 (cast, left half of skull roof, 16.8 cm).

Anatomical abbreviations: 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.

4. Systematic palaeontology

Temnospondyli ZITTEL, 1888

Stereospondyli ZITTEL, 1888

Capitosauroidea (SÄVE-SÖDERBERGH, 1935)

Parotosuchidae SCHOCH & WERNEBURG, 1998

Parotosuchus OCHEV & SHISHKIN, 1968

Capitosaurus MÜNSTER, 1836 partim
Parotosaurus JAEKEL, 1922
Archotosaurus PATON, 1976

Type species: *Parotosuchus nasutus* (v. MEYER, 1858).

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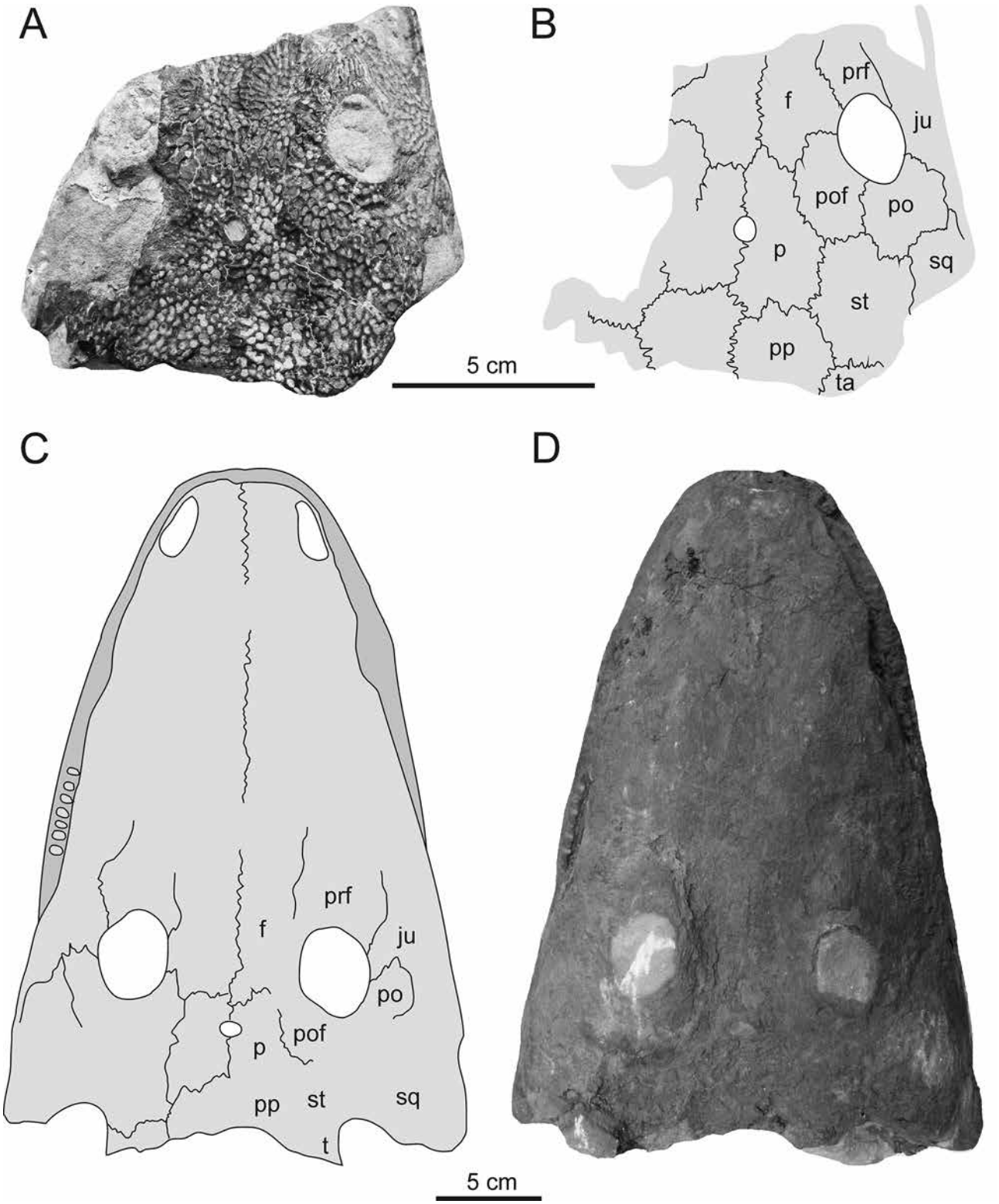


Fig. 4. Type material of taxa referred to *Parotosuchus nasutus*. **A, B**, type of *Capitosaurus fronto* V. MEYER, 1858 (GIH BS4). **C, D**, type of *Mastodonsaurus weigelti* WAGNER, 1935 (GIH BS1).

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Parotosuchus nasutus (v. Meyer, 1858)
Figs. 2–9

Capitosaurus nasutus v. Meyer, 1858
Capitosaurus fronto v. Meyer, 1858
Parotosaurus nasutus (v. Meyer 1858) Jaekel, 1922
Mastodonsaurus weigelti Wagner, 1935

Lectotype: Welles & Cosgriff (1965) designated the first skull figured by v. Meyer (1858: pl. 24) as lectotype, which was presumed by Schoch & Milner (2000) to have been located in the Senckenberg Museum at Frankfurt am Main. In fact, v. Meyer (1858) received his material from a private collector, the mining officer Bischof from Mägdesprung near Harzgerode, and unfortunately this sample has not survived in a public collection. The loss of the type material prompts the designation of a neotype (ICZN 1999).

Neotype: MB.Am448, a nearly complete skull roof (26.1 cm) preserved as natural mould (Fig. 2). This is by far the best-preserved skull and forms a highly diagnostic specimen.

Type locality: Merkel's Quarry, at Teichweg near Fuhne creek, SE of Bernburg an der Saale, Saxony-Anhalt, Germany (Fig. 1).

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

Referred specimens: Altogether, 37 skulls and two postcranial remains from the type locality and horizon have been identified as stemming from *P. nasutus* (Fig. 3). The complete list is given in the Material section.

Diagnosis: A parotosuchid growing to 44 cm skull length. Autapomorphies: (1) quadrate condyles well posterior to occipital ones, (2) supratemporal in adults anteriorly twice as wide as posteriorly, (3) palatine very slender, distance between choana and interpterygoid vacuity much shorter than choana, (4) interpterygoid vacuity twice the length of vomer plus premaxilla. Shared derived characters with *P. orenburgensis*: (1) tabular horn thickened (in large specimens) with rounded end, (2) orbits and nares have nearly equal distance.

Status of *Capitosaurus fronto*: This species, considered congeneric with *P.* (*Capitosaurus*) *nasutus* by V. Meyer (1858), was based on a single specimen still preserved in the Heidelberg collection (GIH BS4, Fig. 4A). V. Meyer (1858) characterized *C. fronto* as differing from *P. nasutus* by its smaller size and especially the wider interorbital region, to which the species name refers. The much larger sample available now indicates that GIH BS4 falls within the range of individual variation of the studied sample (see Section 5.7). However, this specimen does have more clearly serrated sutures, the cheek is somewhat steeper, and the postorbital not as wide as in other specimens. Although there is little ground fo upholding a separate species, only a range of better preserved new specimens could clarify this case.

Status of *Mastodonsaurus weigelti*: This taxon was based on a nearly complete skull and partial cranium, to which two skull fragments and one isolated interclavicle and clavicle were referred (Wagner 1935). This author reported the snout of the skull to be narrower than in *P. nasutus* and the anterior palate to have medially separate palatal openings (apertura praemaxillaris). Re-examination revealed that the anterior palatal opening is not exposed in the cited specimen (Fig. 4B, C), but it is conceivable that two larger tooth sockets were misidentified by Wagner as paired openings. The specimens described by Wagner (1935) fall within the variation range of *P. nasutus* as examined here, and they lack synapomorphies of *Mastodonsaurus* (cf. Schoch 1999).

5. Description

5.1. Skull

The skull of *P. nasutus* is elongate, 1.3 times longer than wide, and the snout has a parabolic outline (Figs. 2–5). The skull tapers gently towards the nares, contrasting the more triangular-shaped skulls of the other four *Parotosuchus* species (Schroeder 1913; Konzhukova 1955; Damiani 2002; Sulej & Niedźwiedzki 2013). In contrast to these, the quadrate condyles are substantially more posterior than the occipital ones, a feature that is more consistent with basal capitosaurs and rhinesuchids (Eltink et al. 2016a, b).

The oval orbits are relatively small (ratio orbit length: skull length is 0.12), especially compared with *Eryosuchus* (0.17) or *Mastodonsaurus* (0.2). The preorbital skull is more than three times longer than the postorbital skull table (3.2), a feature to which the species name *nasutus* referred. The distance between the orbits is only slightly wider than that between the nares, giving a rather wide tip of the snout (Fig. 5C, D). The nares are nearly as long as the orbits, but only half as broad.

The 3D structure of the skull, which is well preserved in most specimens, is intermediate in height between Late Palaeozoic eryopiform temnospondyls (e.g., *Eryops*: Sawin 1941; *Sclerocephalus*: Schoch & Witzmann 2009) and other capitosauroids, which have much more flattened skulls (e.g., *Cyclotosaurus*, see Sulej & Majer 2009; *Mastodonsaurus*, see Schoch 1999). The orbits form the most exposed region of the skull roof, facing dorsolaterally. Their rim is not as elevated as in the more heavily ossified *P. orenburgensis*, but the general surface structure of the interorbital region is very similar in *P. nasutus*. In contrast to the taxon from Russia, the pineal foramen was not located on a raised area.

The sutures of the dermal skull bones are consistent with those of many capitosauroids, among which the separation of prefrontal and postfrontal is the most significant. In contrast to some specimens of *Cyclotosaurus*, the separation of the two elements is always established in *P. nasutus*, although the extent to which the frontal contributes to the orbit margin varies within and between individuals. Characteristic features of *P. nasutus* are the prefrobtals and frontals having pointed anterior ends at same level, supratemporals being as wide as postorbitals and substantially wider than parietals, and the parietals are much longer than the postparietals. Contributing to the different skull outline, the cheek is slenderer than in other *Parotosuchus* species, with a narrower squamosal. The

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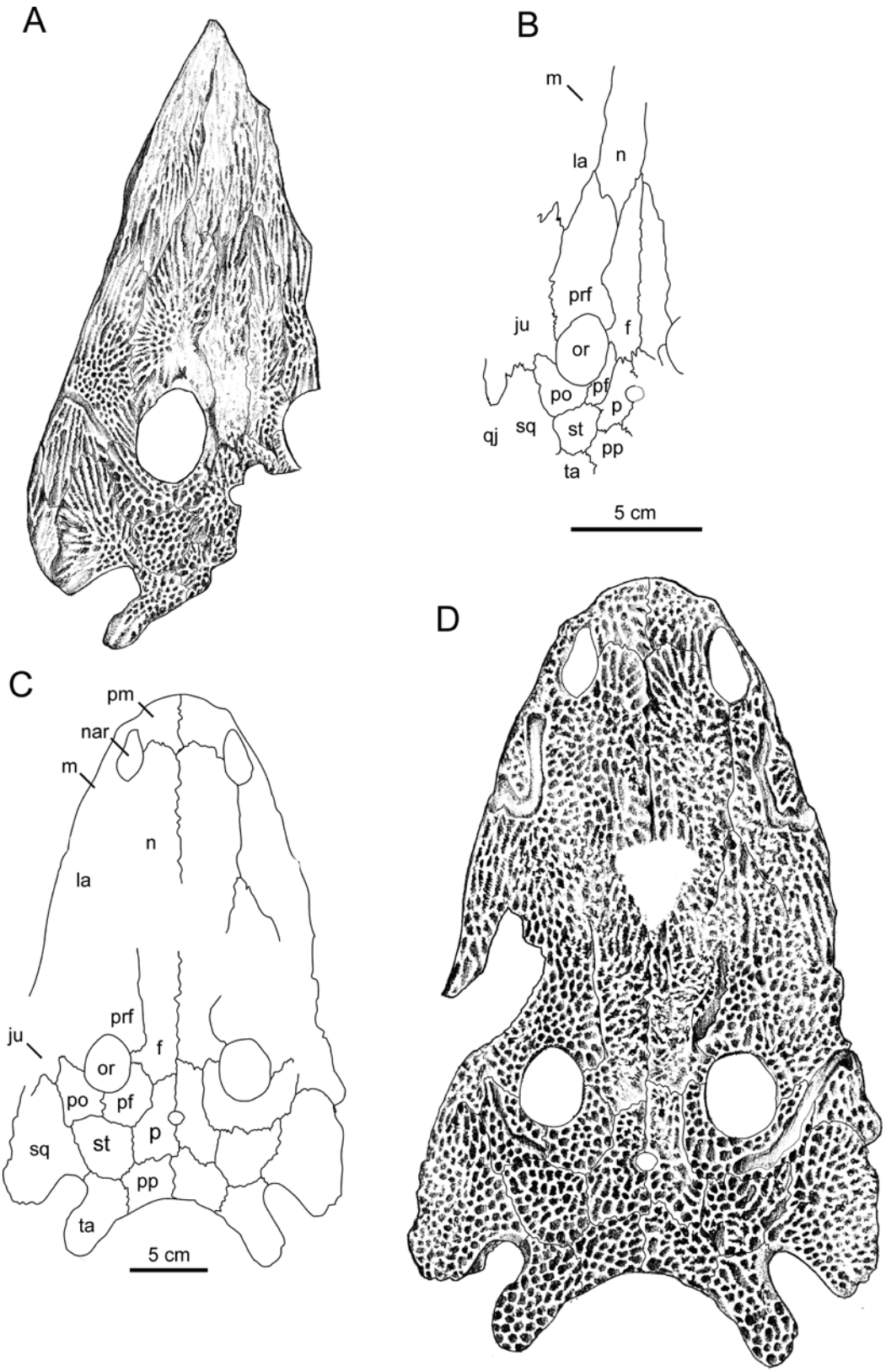


Fig. 5. Skull material referred to *Parotosuchus nasutus*, skull roof in dorsal view, **B**. small skull (16 cm long, GPS.MLU.2016.40), **C, D** large skull (34.7 cm long, GPS.MLU.2018.02).

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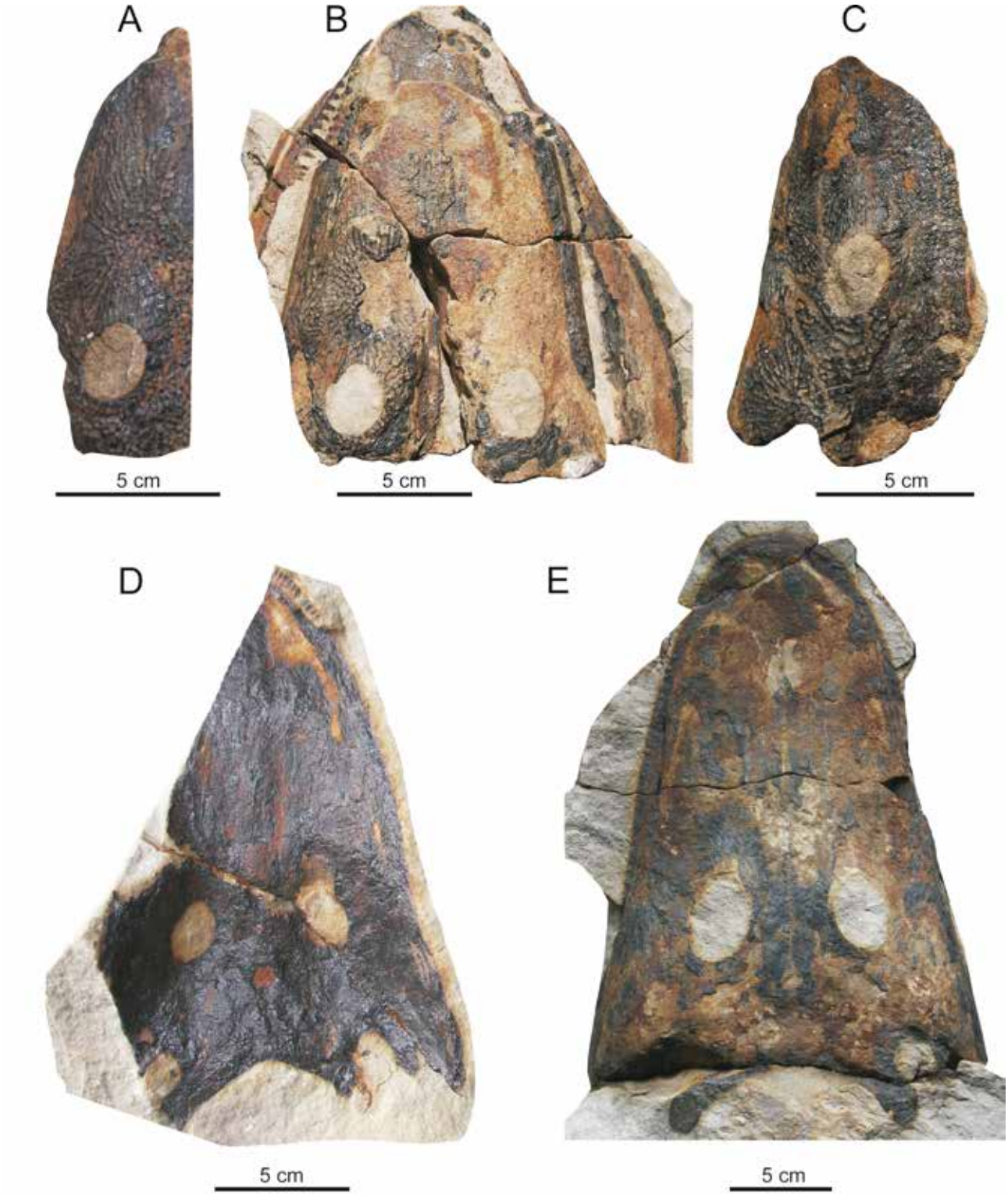


Fig. 6. Skull material referred to *Parotosuchus nasutus*, skull roof in dorsal view. **A**, left portion of small skull (GPS.MLU.2018.06), **B**, anterior part of skull with associated mandibles (GPS.MLU.2016.01), **C**, left-central portion of skull (GPS.MLU.2016.23), **D**, fairly complete skull, only internal bone surface preserved (GPS.MLU.2018.07). **E**, skull roof (MNVD 11166).

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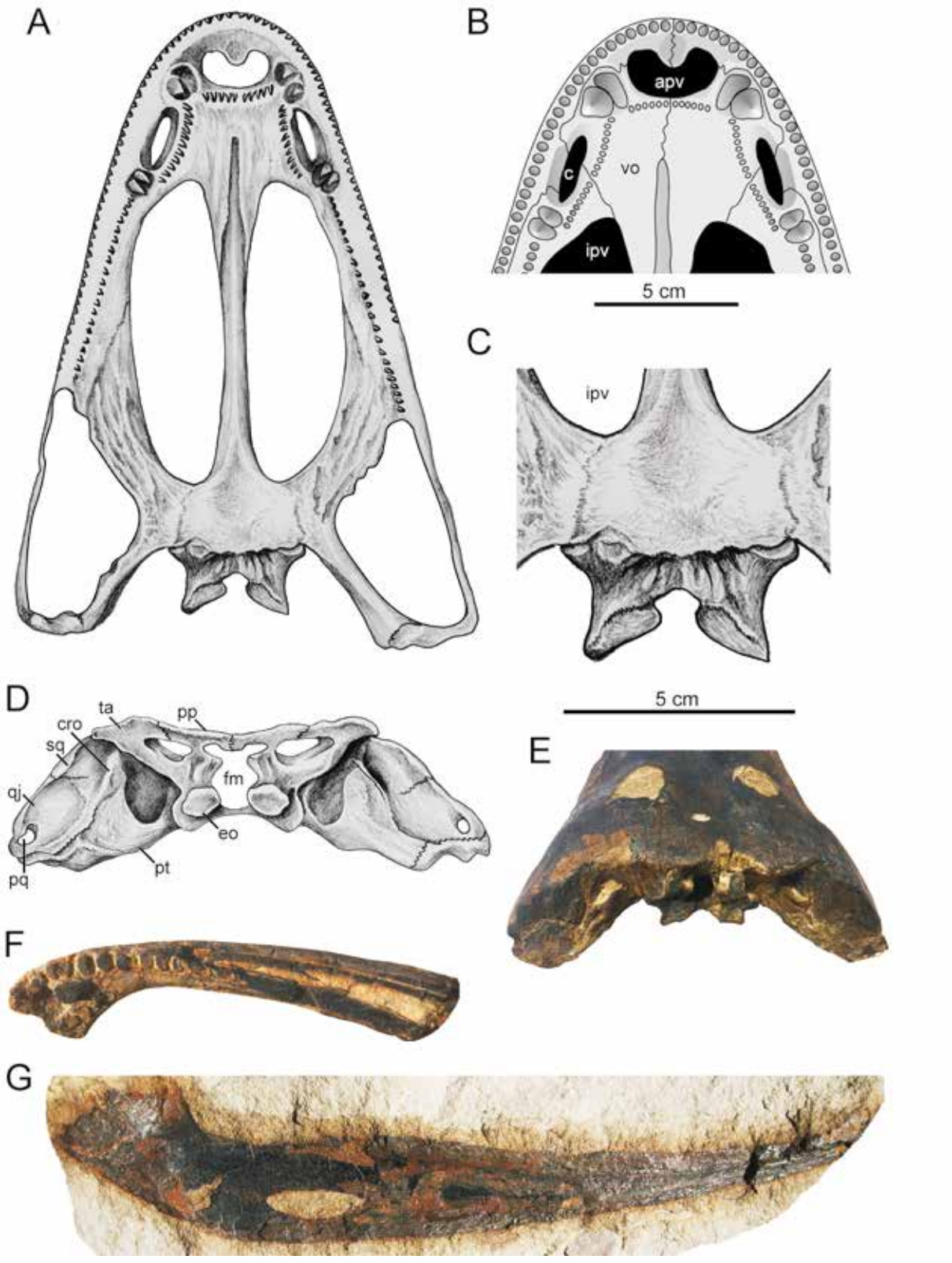


Fig. 7. Skull material referred to *Parotosuchus nasutus*, palate and occiput. A, C, E, GPS.MLU.2018.01. **A**, good palate, **B**, anterior palate (restored), **C**, close-up of basicranial region, **D**, occiput, **E**, oblique posterodorsal view on occiput (SMNS 5957), **F**, symphyseal region (SMNS 12799), **G**, mandible (GPS.MLU.2016.07).

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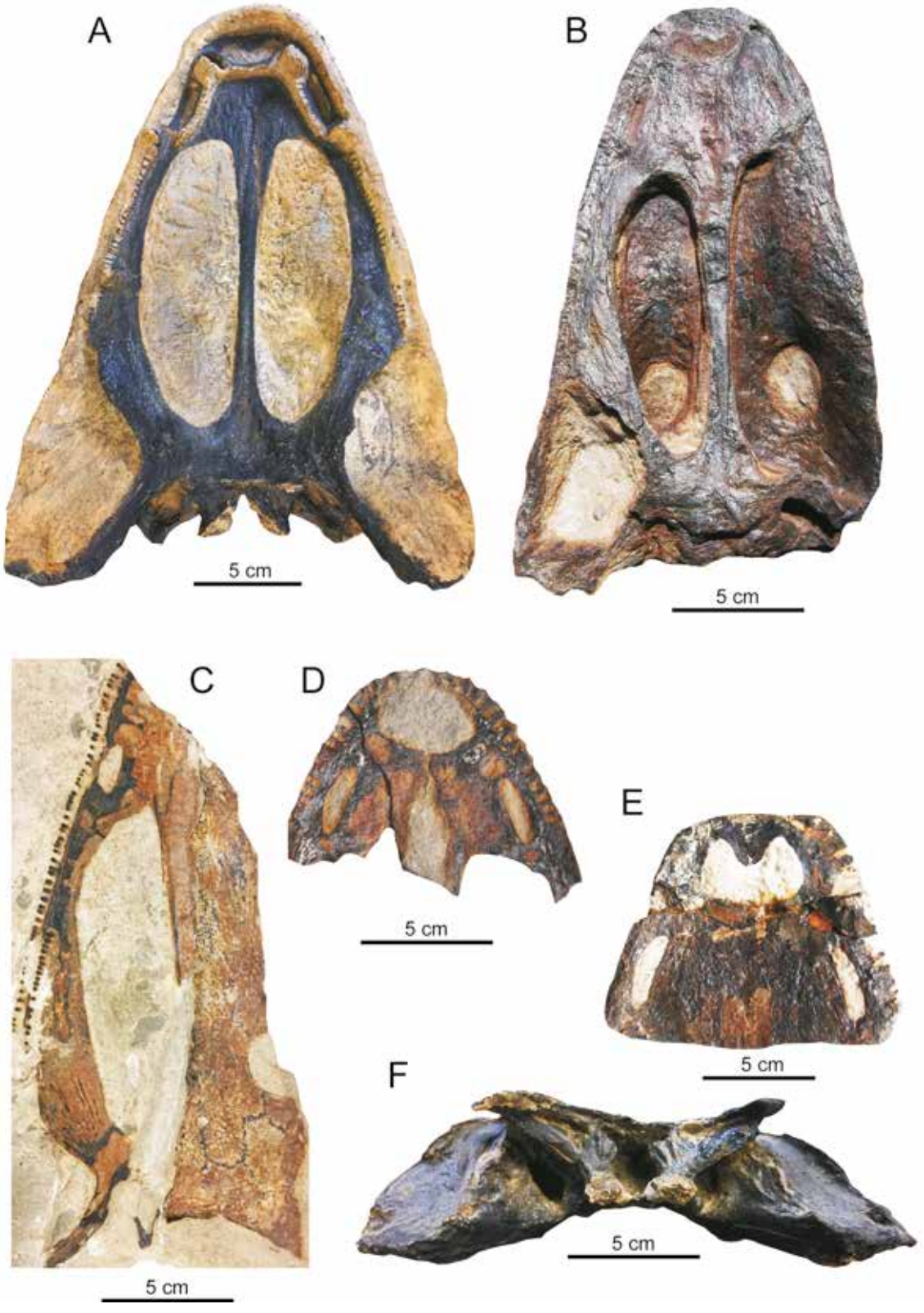


Fig. 8. Skull material referred to *Parotosuchus nasutus*, palate and occiput. **A**, good palate (GPS.MLU.2018.01), **B**, medium-sized palate (GPS.MLU.2018.36), **C**, palate and skull roof (GPS.MLU.2018.05), **D**, anterior palate (MSB G403), **E**, large anterior palate (GPS.MLU.2018.03), **F**, occiput (GPS.MLU.2018.01).

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postorbital is slightly more pointed than in *P. orenburgensis*, and laterally deeply wedged into the jugal. The postorbital portion lateral to the orbit is as wide as that posterior to the eye opening.

Unlike in "higher" capitosauroids, which have more laterally directed tabular horns, the tabular is always posterolaterally aligned and has a well-rounded end. Typically, the tabular is larger by area than the postparietal, a feature consistent throughout the genus *Parotosuchus*. In contrast to other *Parotosuchus* species, especially *P. haughtoni*, the squamosal embayment is proportionally larger and more open posterolaterally. Similar to other *Parotosuchus* species, the posterior margin of the skull table is semilunar.

5.2. Palate

The palate bones are thinner than in closely related species, notably *P. orenburgensis* and *P. helgolandicus*. This results from the proportionally much larger interpterygoid vacuities, as well as the more slender and thin pterygoids, palatines, and ectopterygoids (Figs. 7, 8). The tooth patches known from many Palaeozoic temnospondyls are entirely absent, so that the dentition is confined to the two tooth rows on the maxilla and the vomer-palatine-ectopterygoid arcade. Only two pairs of fangs are present: one large on the vomer, a smaller one on the palatine, whereas the ectopterygoid bears only a row of uniform, small teeth.

The vomer is flat with a smooth surface, except for the narrow countersunk region in the sagittal midline, where the cultriform process is exposed. This region (fodina vomeralis) is narrower than in *P. orenburgensis* and anteriorly not expanded. There is a continuous row of small teeth medial to the choana and posterior to the premaxilla, which is aligned medial to the vomerine fang pair. The crowns of these teeth are aligned posteromedially. The fangs themselves also have posteromedially oriented crowns.

The premaxilla and vomer are sutured anterior to the vomerine fangs, leaving a wide unpaired opening that occupies more than two-thirds of the width of the snout, as measured at the transverse premaxillo-vomerine suture. The anterior palatal opening is crescent-shaped, with a gently rounded posterior margin, markedly rounded lateral margins, and a large anteromedial constriction by a rounded posteromedial process of the premaxillae. The suture between the premaxillae is strongly serrated within this process. The premaxilla, which is more rounded than in *P. orenburgensis* and *P. helgolandicus*, houses 10 to 12 medium-sized teeth, which are longer than the vomerine and palatine teeth, but markedly smaller than the anterior maxilla teeth. Like the vomerine teeth, but less strongly so, their crowns are curved inwards, towards the buccal cavity.

The choana is characteristically elongate but very narrow, more slender than in most other capitosaurs. It is still wider and proportionally larger than in the other three *Parotosuchus* species, but in adults of *P. nasutus* it is clearly narrower than in juveniles.

The pterygoid is elongated and the slender palatine ramus is about twice as long as the stout quadrate ramus. The basipterygoid ramus is very short and sutured with the basal plate of the parasphenoid. The length of this suture measures only half the width of the basal plate, in contrast to mastodonsaurids and cyclotosaurids, where it is posteriorly much extended. The entire basipterygoid and palatine rami are covered by polygonal ridges, as well as the anteriormost portion of the quadrate ramus. The ornament is more extensive than in *P. orenburgensis* and *P. helgolandicus*.

The parasphenoid is slender with a differentiated cultriform process measuring four times the length of the rectangular basal plate. There is a medial ventral ridge that rises on the anteriormost portion of the basal plate, close to the merger with the cultriform process. This ridge extends only along the posterior half of the process, which is anteriorly flattened. The basal plate is markedly wider posteriorly, and its anteromedial portion forms a bowl-shaped depression. It is edentulous but covered by numerous radially arranged grooves converging in a point close to the centre of the basal plate, and additional tiny tubercles on top of the ridge and along its flanks. The posterior margin of the parasphenoid houses paired muscular pockets, partially subdivided by a medial process. Only the anterior margin of the pockets is formed by the parasphenoid, the bulk of these paired depressions extends broadly onto the ventral surface of the exoccipitals. Lateral to the pockets, the exoccipitals and parasphenoid form a ventrally bulging suture that probably housed an opening of the eustachian tube.

5.3. Braincase and occiput

The occiput is exposed in a range of skulls, while in SMNS 5957, the exocciptals have been dorsally freed from their dermal bone cover (Fig. 7E). The occipital condyles are smaller and more widely separated than in the other three *Parotosuchus* species of which complete skulls are known, giving a substantially larger foramen magnum than in these. As the thickness of dermal bones is not as excessive as in the other *Parotosuchus* species, the postparietals and tabulars form only a thin dorsal margin of the occiput. There is a well offset lamina ascendens of the pterygoid, well preserved in SMNS 5957, forming an almost vertically aligned lamella with a sigmoidal curvature in dorsal view (Fig. 8B). The paraquadrate foramen is rounded and located close to the ventrodistal margin of the quadratojugal, at the margin of a large oval depression that covers

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most of the occipital area of the quadratojugal. The crista obliqua of the pterygoid is present, but not as pronounced as in trematosauroids (Bystrow & Efremov 1940). The exoccipitals are massive, with transversely oval and paired occipital condyles well separated by a wide gap left by the unossified basioccipital. The vertical columns are robust but only narrowly sutured to the tabulars, with broad dorsomedial portions bearing two deep grooves and framed by three marked crests on their occipital surface (Fig. 8B). The exoccipitals are sutured to the parasphenoid but fail to meet the pterygoids. Laterally, the exoccipital and parasphenoid leave a slit-like opening bordered by a bulge, probably the opening of the eustachian tube (Schoch 2000a, 2002a). Ventrally, the exoccipitals have a markedly roughened surface probably as attachment area for hypaxial musculature. The otic and epipterygoid regions are not exposed in any specimen. In *P. orenburgensis*, the epipterygoid is well-preserved, forming a flat, curved sheet of bone similar to the central portion of the palatoquadrate in *Mastodonsaurus giganteus* (Schoch 2002b), albeit less extended and lacking the additional processes.

5.4. Mandible

Only few diagnostic remains of mandibles are preserved (Fig. 7F, G). In *P. nasutus*, the lower jaw is markedly deeper and has a more convex ventral margin than in co-occurring *Trematosaurus*. It is consistent with the mandible of *P. orenburgensis* in general proportions, although the Meckelian fenestra is substantially longer and lower. The mandible is also less deep than in the Russian taxon, more similar to other medium-sized capitosauroids, such as *Kupferzellia* (Schoch 1997). The post-glenoid region (sensu Jupp & Warren 1985) is short and rounded, with the hamate process present but much lower than in mastodonsaurids or cyclotosaurids, consistent with that of *P. orenburgensis* (Konzhukova 1965).

The symphysis (SMNS 12799; Fig. 7F) bears: a continuous row of marginal teeth, similar in size to those further posterior but with narrower bases; a pair of tusks (of which in the studied specimen the medial one is much larger); and a posterior row of five teeth, which are slightly smaller than the marginal teeth and whose bases are rounded. The anterior coronoid and presplenial are well preserved and their sutures are consistent with those in *Mastodonsaurus* (Schoch 1999).

5.5. Visceral skeleton

The only two preserved visceral elements are the stapes and basibranchial, which form the usual ossification of this part of the skeleton. The stapes is elongate and anteroposteriorly compressed. It is preserved in articulation on both sides of GPS.MLU.2018.01, which permits only its posteroventral side to be examined. The distal end points into the squamosal embayment, close to the suture between tabular and squamosal. The proximal portion is bifurcate, with a ventral process apparently articulating with the parasphenoid. There is a large stapedial foramen in the proximal half of the element, and a second foramen at about mid-level of the stapes. The basibranchial is only preserved in one specimen, where it is exposed due to an oblique break between skull roof and palate. It forms a slender and small, poorly differentiated element, much less pronounced than in stereospondylomorphs (Witzmann 2006; Schoch & Witzmann 2009), rhinesuchids (van Hoepen 1915), or plagiosaurids (Witzmann & Schoch 2013).

5.6. Referred postcranial material

Only few postcranial elements are known of *P. nasutus*, because the material consists of isolated bones or skulls rather than articulated skeletons. Comparison with close relatives is further rendered difficult, because among the Parotosuchidae, there is not a single species known by an articulated skeleton.

The bulk of the available 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. Two elements, a clavicle and a partial interclavicle at GIH, differ from the mentioned bones in their broader and shorter proportions (Fig. 9A, B). These are generally consistent with elements in other capitosauroids and are here referred to *P. nasutus*. Several rib fragments are consistent in shape, especially the outline and position of uncinate process, with capitosaurs, such as *Mastodonsaurus giganteus* (Fig. 9C, D; Schoch 1999). The bodily proportions, structure of the vertebrae, relative size of limbs, trunk and tail, remain unknown.

5.7. Ontogeny and variation

Diagnostic skulls of *P. nasutus* cover a wide size range (Fig. 3), with the smallest (GG 22.163, 14 cm long) less than half as long as the largest complete specimen (GIH-BP1, 34.7 cm). The bulk of the material falls in the 25–30 cm size range.

In general, stereospondyl skulls grew at a remarkably isometric rate. In particular, the elongate preorbital region was established early (Warren & Hutchinson 1988; Warren & Schroeder 1995). In *P. nasutus*, the most conspicuous changes in the skull roof were identified in the

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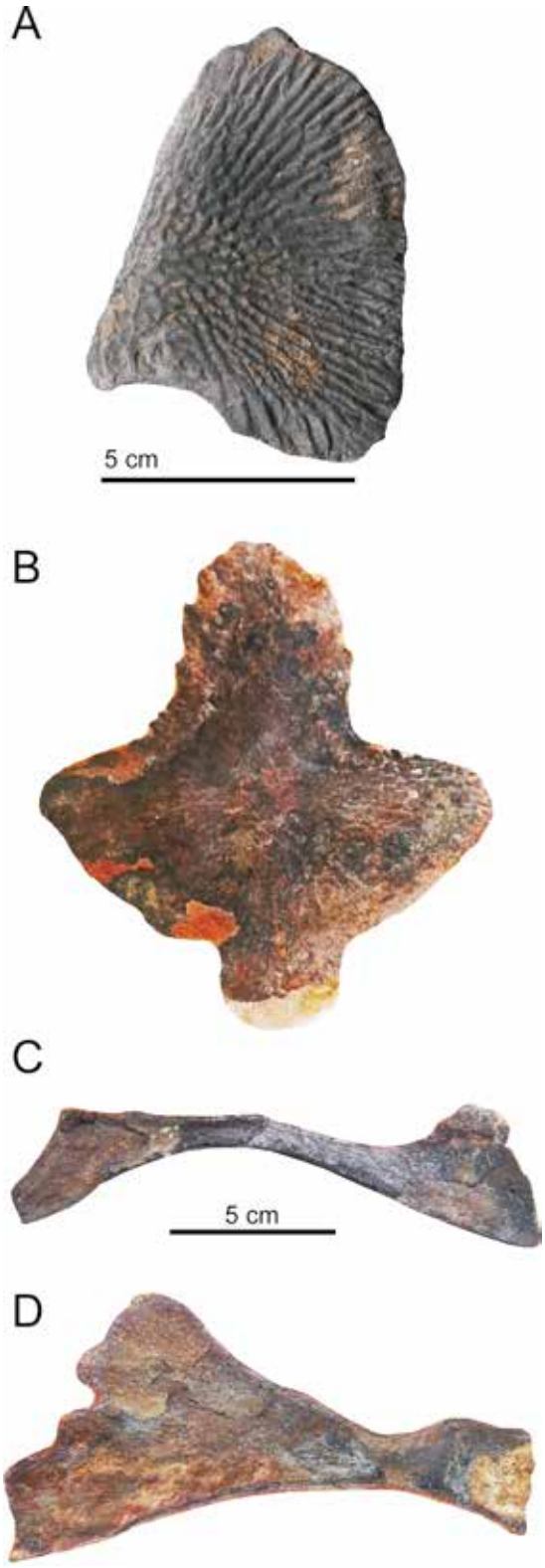


Fig. 9. Postcranial material referred to *Parotosuchus nasutus*. **A**, right clavicle (GPS.MLU.2016.35). **B**, interclavicle (GPS.MLU.2018.09). **C**, posterior thoracal rib (GPS.MLU.2016.10). **D**, anterior thoracal rib (GPS.MLU.2018.08).

posterior skull table. The strongest allometry is the broadening of the interorbital and internarial region, driven by widening of frontal and nasal elements.

As mentioned in the taxonomical section, individual variation in the interorbital distance is considerable. Ontogenetically, the ratio interorbital distance to skull length ranges from 0.13 in juveniles to 0.21 in adults. Individually, large specimens vary between slender-skulled (0.17, Fig. 5C) and wide-skulled versions (0.21, Fig. 4B, C), with the type holding an intermediate position (0.19, Fig. 2). Although the fragmentary nature of most skulls precludes exact measuring and statistical tests, it is more likely that there is a continuous range rather than two clusters.

The frontals are narrower than the prefrontals in the juveniles, whereas in adults they have nearly equal width. The postfrontals at least double their width proportionally, both expanding medially as well as accommodating the negative allometry of the orbits. The parietals and supratemporals are each extended along their lateral margins, whereas the tabular horn becomes wider both along the occipital margin and the rim of the otic notch. The squamosal develops a large falciform crest along its otic margin.

In contrast, there are no significant changes in dermal ornament or the proportional width of the lateral line sulci. Even the ornamented ventral side of the pterygoid was established in small specimens. The orbit margins are slightly raised in juveniles, getting much more pronounced in adults. Both the raised orbit margins and the thickened tabular horns are features of *P. orenburgensis*, which appears to extend the ontogenetic series of *P. nasutus* rather than forming a distinct morphology.

Dermal ornament also underwent some changes. Small specimens (Fig. 5A) have a more finely pitted skull roof and more densely set elongated ridges on the squamosal, jugal, prefrontal, and lacrimal. Larger specimens such as the type (Fig. 2D) have polygonal rather than rounded pits. In the largest specimens, the pitted ornament is extended at the expense of areas with elongated grooves and ridges (Fig. 5D).

In the palate, the interpterygoid vacuity is slightly wider and posteriorly more rounded in large specimens, whereas the choana is narrower and proportionally longer in adults. The ornament on the ventral side of the pterygoid is present already in the smallest specimens.

6. Phylogeny of parotosuchids

6.1. State of the art

Capitosaurs form a speciose clade spanning the entire Triassic with almost worldwide distribution, and new taxa are discovered on a regular basis. The relationships of capitosaurs were studied by Watson (1919, 1951, 1958, 1962),

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SÄVE-SÖDERBERGH (1935), ROMER (1947, 1966), WELLES & COSGRIFF (1965), and KAMPHAUSEN (1989). First cladistic analyses in which some capitosaurs were considered were conducted by YATES & WARREN (2000), SCHOCH (2000b) and DAMIANI (2001a). All subsequent papers made use of variants of the DAMIANI's (2001a) matrix, such as SCHOCH (2008), MAGANUCO et al. (2009), FORTUNY et al. (2011a), SIDOR et al. (2014), LIU (2016), WITZMANN et al. (2016), and MARZOLA et al. (2017).

As for the position of *Parotosuchus*, DAMIANI (2001a), STEYER (2003), SCHOCH (2008), MAGANUCO et al. (2009), and LIU (2016) all found this genus to nest in (or form) the basalmost clade of capitosauroids, consistent with the traditional hypothesis (WATSON 1962; SCHOCH 2000b). However, FORTUNY et al. (2011) and SIDOR et al. (2014) retained *Parotosuchus* higher within their Capitosauria clade, more closely related to *Mastodonsaurus* and *Cyclotosaurus* than to *Paracyclotosaurus* and *Edingerella*.

6.2. Phylogenetic analysis

In the present study, the four best-known species of *Parotosuchus* were included in the matrix of SCHOCH (2008), in addition to the two more recently described capitosauroids *Calmasuchus* (FORTUNY et al. 2011a) and *Antarctosuchus* (SIDOR et al. 2014). In a phylogenetic analysis supported by the TNT 1.0 package, a total of 24 taxa and 69 morphological characters was analyzed under the New Technology Search option (1000 replicates). The analysis gave five most parsimonious trees (140 steps), with a consistency index of 0.56 and a retention index of 0.78 (Fig. 10).

Here, the basal position of *Parotosuchus* within the Capitosauria is essentially corroborated, with *Parotosuchus* nesting above the basal capitosaurians *Edingerella* and *Watsonisuchus* (Fig. 10) and below *Cherninia*, *Xenotosuchus*, *Eryosuchus*, *Kupferzellia*, and the "higher" capitosauroids (*Stanocephalosaurus*, *Yuanansuchus*, *Antarctosuchus*, *Calmasuchus*, *Mastodonsaurus*, *Eocyclotosaurus*, *Quasicyclotosaurus*, and *Cyclotosaurus*). This is in line with many previous findings in which capitosauroids were monophyletic, contrasting the more recently proposed alternative (FORTUNY et al. 2011a; SIDOR et al. 2014) of a diphyletic Capitosauroidea, in which *Edingerella* and *Watsonisuchus* nest at the base of a large "Paracyclotosauria" clade. The closure of the otic notch (squamosal embayment) had long been rated highly as a phylogenetic signal, but biomechanical analyses indicate that this pattern probably emerged convergently as a response to changes in modes of prey capture and biting (FORTUNY et al. 2011b, 2012).

When included, the position of the incompletely known genus *Odenwaldia* is ambiguous, depending on the inclusion of *Cherninia*. When both taxa are considered, they form sister taxa, supported by their shared possession of a medially divided anterior palatal vacuity, which is a rather rare charcater-state in capitosaurs. When *Odenwaldia* is omitted, *Cherninia* nests at the base of post-parotosuchid capitosauroids. Finally, without *Cherninia*, *Odenwaldia* forms an unresolved polytomy with (1) *Wetlugasaurus* and *Watsonisuchus*, (2) Parotosuchidae, and (3) all higher capitosauroids. Arguments for a higher, post-parotosuchid position of *Cherninia* are the laterally directed tabular horn and the elongated basicranial suture (DAMIANI 2001b). *Odenwaldia*, in turn, is still more plesiomorphic than parotosuchids in retaining the prefrontal-postfrontal contact, more consistent with *Wetlugasaurus*, trematosauroids, and more basal stereospondyls. This indicates conflicting evidence with *Edingerella* and *Watsonisuchus*, as highlighted by the results of some recent analyses, where both these two taxa nested higher within capitosauroids (FORTUNY et al. 2011a; SIDOR et al. 2014).

6.3. Parotosuchidae and capitosaur evolution

The consistent morphology (otic notch, basicranial region, posterior skull table, choana) of the four *Parotosuchus* species agrees with the existence of a clade Parotosuchidae, and *P. nasutus* is here confirmed as the basalmost species of the clade, as found already by SCHOCH (2008). There may be a size-related effect contributing to this phylogenetic interpretation, because most specimens of *P. nasutus* are smaller than the types of the three other species, and many differences between *P. nasutus* and the other three are related to the relatively lower level of ossification in the former. Conceivably, the specimens from Bernburg represent a time-averaged population, as they were all found in the same horizon. This suggests that adult specimens should be present in that sample, which indicates that the poorer ossification of *P. nasutus* is not a result of immaturity of available specimens, but that the differences to other *Parotosuchus* species were indeed established in adults.

The geological age of the four taxa does not match their phylogeny, but stratigraphical resolution is poor, highlighted by the still open question of the exact age of the Bernburg Fossillagerstaette. In the Germanic Basin, diagnostic remains of *Parotosuchus* are confined to only two localities, Bernburg (*P. nasutus*) and Heligoland (*P. helgolandicus*). The only roughly similar find, a fragmentary anterior palate from the Middle Buntsandstein of the Black Forest in southwestern Germany, was shown to be more consistent with *Wetlugsaurus* than *Parotosuchus* proper (SCHOCH 2011).

A range of potential parotosuchids has been described in the literature, which WELLES & COSGRIFF (1965) and

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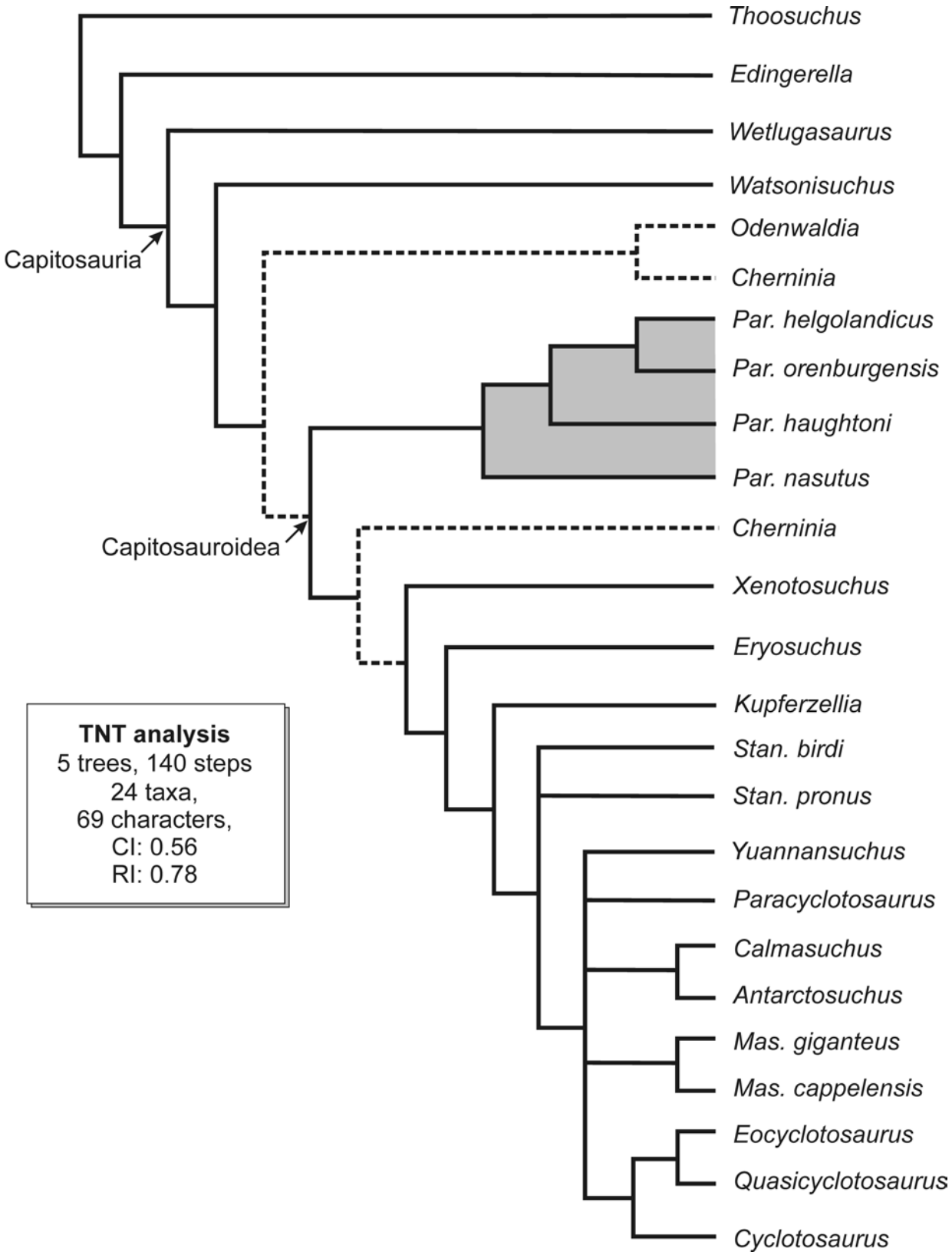


Fig. 10. Phylogeny of capitosauroids with special emphasis on the position of *Parotosuchus nasutus* and the Parotosuchidae. The position of *Cherninia megarhina* critically depends on the inclusion of *Odenwaldia*.

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SCHOCH & MILNER (2000) had already discussed in some detail. In most cases, more diagnostic material is required from these taxa to permit their placement in a phylogeny and to assess their affinities to *Parotosuchus*. The Parotosuchidae may well have been more speciose and widely distributed across Pangaea, as suggested by SIDOR et al. (2007), who reported *Parotosuchus* sp. from Antarctica, based on a palate fragment with a slit-like choana; as discussed in SIDOR et al. (2014), this find differs from *Antarctosuchus* and may stem from a parotosuchid. In 2009, SHISHKIN & SULEJ named and described *P. spelaeus*, based on exquisite but isolated elements from Czatkowice in Poland. They reported numerous isolated bones from that fissure-fill deposit, which also yielded important reptile material (DZIK 2009). The Polish specimen bears some resemblance to parotosuchids, but as shown in their restoration, the skull material stems from juvenile capitosaurs or small forms such as *Edingerella*, and apomorphies of *Parotosuchus* are either not apparent (choana) or not preserved (basicranium). A referral of this taxon to the Parotosuchidae is therefore impossible without more complete material. The case is more clear-cut for *Parotosuchus ptaszynskii*, based on a posterior palate and mandible from Olenekian deposits at Wióry at the foothills of the Holy Cross Mountains, southeastern Poland (SULEJ & NIEDŹWIEDZKI 2013). The preserved parts are quite consistent especially with *P. orenburgensis* and *P. helgolandicus*, thus bridging the gap between the Germanic Basin and the Southern Urals. Finally, the material of *P. orientalis* (OCHEV 1966) is very fragmentary, but generally consistent with that of *P. orenburgensis*, so that this taxon probably forms part of the Parotosuchidae.

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Appendix – Character-taxon matrix

Antarctosuchus
0 1 0 1 0 0 1 2 0 0 1 ? 1 1 0 1 1 0 0 1 1 1 0 0 0 1 1 1 1 1 1 1 ? 0 ? ? ? ? 1 1 ? ? ? ? ? ? ? 0 0 1 1 0 ? ? 0 0 0 ? 1 ? 1 ? 0 ? ? 0 0 0 0
Benthosuchus
1 1 0 0 1 0 1 1 ? 1 0 1 0 1 1 1 0 0 1 1 0 1 1 1 1 1 0 0 0 1 1 0 0 0 1 1 1 1 1 1 0 0 0 0 1 1 1 0 1 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0
Calmasuchus
1 1 0 1 0 0 1 2 0 0 1 1 0 1 0 1 1 0 0 2 0 1 0 0 0 1 1 1 1 1 1 1 1 1 0 ? 1 ? ? 1 1 ? 2 0 0 ? ? ? 0 0 0 0 0 0 1 0 0 0 1 0 0 1 ? 0 ? ? 0 1 0 0
Cherninia
0 1 0 1 1 0 0 2 0 0 2 1 1 1 0 1 0 0 0 2 0 1 0 0 1 1 1 1 0 1 1 1 1 0 1 1 1 1 1 1 ? ? ? ? ? ? ? 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 ? 0 0 0 0 1
Cyclotosaurus
0 1 0 1 0 0 0 2 0 ? 1 1 1 1 0 0 1 2 0 ? 1 1 0 1 1 1 1 1 1 1 1 1 1 1 0 1 1 1 1 1 1 2 2 1 0 ? ? ? 0 1 1 1 1 0 2 0 0 0 0 1 1 1 1 0 0 1 1 0 0 0
Edingerella
0 1 1 0 0 0 1 1 0 2 1 ? 0 1 0 0 0 0 1 1 0 1 0 0 1 0 0 1 0 1 0 0 0 0 0 1 1 0 1 1 0 1 0 0 1 ? 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 ? 0 0 0 0 0
Eocycloto
1 1 0 1 0 0 1 2 0 2 0 1 1 1 1 1 1 0 0 2 1 1 0 1 1 1 1 1 1 1 1 1 1 0 1 1 1 1 1 1 2 2 1 ? ? ? ? 0 1 1 1 0 1 2 0 0 0 2 0 1 1 1 0 0 1 0 0 0 0
Eryosuchus
0 1 0 1 0 0 0 2 0 ? 2 1 1 1 0 1 0 0 0 ? 0 1 0 0 1 1 1 1 0 1 1 1 1 0 1 1 1 1 1 1 2 2 1 0 1 1 0 0 0 1 0 0 0 0 0 0 0 0 0 1 1 0 0 1 0 0 0 0 0
Kupferzellia
0 1 0 1 ? 0 0 2 0 0 2 1 1 1 0 0 0 2 0 0 0 1 0 0 1 1 1 1 0 1 1 1 1 0 1 1 1 1 1 1 1 1 1 1 0 1 1 0 0 1 1 1 1 0 1 0 0 0 0 1 1 1 1 0 0 0 1 0 0 0
Mastodonsaurus cappelensis
0 1 0 1 0 0 1 2 0 2 2 1 0 0 0 1 1 0 0 2 1 1 0 1 1 1 1 1 1 1 1 1 1 1 0 1 1 1 1 1 1 2 2 1 0 1 1 0 1 0 1 0 1 1 0 0 0 1 0 1 0 1 1 1 1 0 1 0 0 0 0 0
Mastodonsaurus giganteus
0 1 0 1 0 0 1 2 0 2 2 1 0 0 0 1 1 0 0 2 1 1 0 1 1 1 1 1 1 1 1 1 1 1 0 1 1 1 1 1 1 2 2 1 0 1 1 0 1 0 1 0 1 1 0 0 0 1 0 1 0 1 1 1 1 0 1 0 0 0 0 0
Odenwaldia
1 1 0 0 1 0 0 2 0 ? ? 1 1 1 0 ? 0 ? ? 2 ? ? ? ? ? ? ? ? ? 1 ? ? ? 0 1 1 1 ? 1 1 ? ? ? ? ? ? ? ? ? ? ? 0 0 0 0 0 0 0 ? 0 ? 1 0 ? 0 0 0 0 0
Parotosuchus haughtoni
0 1 0 0 2 0 0 2 0 0 2 1 1 1 0 1 0 0 0 0 0 1 0 0 1 1 1 1 0 1 1 1 1 0 1 1 1 1 0 1 1 1 1 1 1 ? ? 0 0 1 1 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 ? 0 0 1 0 0
Parotosuchus nasutus
0 1 0 0 1 0 0 2 0 0 2 1 1 1 0 1 0 0 0 0 0 1 0 0 1 1 1 1 0 1 1 1 1 0 1 1 1 1 0 1 1 1 1 1 1 1 1 0 0 1 1 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 ? 0 0 1 1 0
Parotosuchus orenburgensis
0 1 0 0 2 0 1 2 0 0 2 1 1 1 0 1 0 0 0 0 0 1 0 1 1 1 1 1 0 1 1 1 1 0 1 1 1 1 0 1 1 1 1 1 1 1 1 0 0 1 1 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 1 1 1
Parotosuchus helgolandicus
0 1 0 0 2 0 1 2 0 0 2 1 1 1 0 1 0 0 0 0 0 1 0 1 1 1 1 1 0 1 1 1 1 0 1 1 1 1 0 1 1 1 1 1 1 1 1 0 0 1 1 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 1 0 1
Paracyclotosaurus crookshanki
0 1 0 1 0 0 1 2 0 1 2 1 1 1 0 1 1 0 0 2 1 1 0 0 1 1 1 1 1 1 1 1 1 1 0 1 1 1 1 1 1 ? ? 0 0 ? 1 0 0 0 1 1 0 1 1 0 0 0 1 1 1 1 1 1 ? 0 0 0 0 0
Quasicyclotosaurus
0 1 0 1 0 0 1 2 0 1 0 1 1 1 0 1 1 0 0 2 1 1 0 1 1 1 1 1 1 1 1 1 1 1 0 1 1 1 1 1 1 1 1 1 0 ? ? ? 0 1 1 1 0 1 2 0 0 0 2 1 1 1 1 0 ? 1 0 0 0 0
Sclerothorax
0 1 0 0 1 0 0 ? 0 0 1 1 1 1 0 ? 1 ? ? ? 0 ? ? ? ? 0 1 1 0 1 ? 1 1 0 1 1 1 1 1 1 1 1 1 0 0 ? 1 0 0 1 0 0 0 0 0 0 0 0 0 0 0 ? 0 0 ? 0 1 0 0 0
Stanocephalosaurus birdi
0 1 0 1 0 0 0 2 0 0 2 1 1 1 0 1 1 0 0 1 0 1 0 0 1 1 1 1 1 1 1 1 1 1 0 1 1 1 1 1 1 1 1 1 0 0 1 1 0 0 0 1 1 0 1 1 0 0 0 1 1 0 1 0 0 0 1 0 0 0 0
Stanocephalosaurus pronus
0 1 0 1 0 0 0 2 0 0 2 1 1 1 0 1 1 0 0 0 0 1 0 0 1 1 1 1 1 1 1 1 1 1 1 0 1 1 ? 1 1 1 ? 1 1 0 ? 1 0 0 0 1 1 0 1 1 0 0 0 1 1 1 1 0 0 0 0 0 0 0 0
Thoosuchus
1 1 1 0 0 1 1 1 1 1 0 1 0 0 1 1 0 0 1 2 0 1 1 2 0 1 0 0 0 0 0 0 0 0 1 0 0 1 1 0 0 0 0 1 1 1 1 0 1 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0
Watsonisuchus
0 1 0 0 1 0 0 2 0 0 2 1 1 1 0 1 0 0 1 0 0 1 0 0 1 1 1 1 0 1 1 1 0 0 1 1 1 1 1 1 1 1 1 0 0 1 1 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 ? 0 0 0 0 0
Wetlugasaurus
0 1 0 0 1 0 0 2 0 0 0 1 1 1 1 1 0 0 1 0 0 1 1 0 1 1 1 1 0 1 1 0 1 0 1 1 1 1 1 1 1 1 1 0 0 1 1 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 ? 0 0 0 0 0 0 0 0
Xenotosuchus
0 1 0 1 0 0 0 2 0 ? 1 1 1 1 0 1 1 0 0 0 0 1 0 0 1 1 1 1 0 1 1 1 1 0 1 1 1 1 1 1 1 1 1 0 0 1 1 0 0 1 0 ? 0 0 0 0 0 0 0 1 1 1 0 0 ? 0 0 0 0 0
Yuanansuchus
0 1 0 1 0 0 1 2 0 2 0 1 1 1 0 0 1 0 0 ? 0 1 0 0 1 1 1 1 1 1 1 1 1 1 0 1 1 1 1 1 1 ? ? ? ? ? ? ? 0 0 ? 1 ? 1 0 0 0 0 0 1 0 1 1 0 ? 0 0 0 0 0

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