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RESEARCH PAPER

Morphology and ontogeny of the plagiosaurid temnospondyl *Plagiosternum granulosum* from the Middle Triassic of Germany

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Abstract

Plagiosaurids form a small but highly disparate clade of Triassic temnospondyls that are characterized by extremely flattened and wide skulls, large orbits and a knobby to pustular ornamentation. The largest European taxon is *Plagiosternum granulosum* from the Middle Triassic of Germany. Originally known from fragmentary bonebed material only, recent finds add well-preserved specimens that reveal the structure of the skull, mandible and pectoral girdle in great detail. The humerus and atlas of *P. granulosum* are described for the first time, and a putative cleithrum is identified. Ontogenetic changes include a proportional extension of the orbit, a more convex occipital margin, elongation of the parietal, proportional increase of the occipital condyles and formation of pustular ornament at nodal points of reticulate ridges. The presence of gastral scales can be inferred from the structure of the interclavicle, but there is no evidence of osteoderms. *Plagiosternum granulosum* was the most salt-tolerant temnospondyl in the Ladinian palaeoenvironments, where it dwelled brackish lagoons and lakes and formed a community with nothosaurids and other euhaline taxa.

Keywords Plagiosauridae · Phylogeny · Stereospondyli · Temnospondyli · Triassic

Introduction

Temnospondyls form a vast clade of limbed vertebrates that is first recorded in the early Carboniferous and reached diversity peaks during the Triassic, before becoming extinct apparently at the end of the Early Cretaceous (Mehmood et al., 2025; Wagstaff et al., 2020). By Early Triassic time, the overwhelming majority of non-amniote tetrapods fell into only two major clades, the lissamphibians and stereospondyl temnospondyls. Whereas the former still constitute rare exceptions in the Triassic (Evans & Borsuk-Białynicka, 2009; Kligman et al., 2023; Schoch et al., 2020), the latter form abundant fossils in many lacustrine, fluvial, deltaic and shallow marine deposits across Pangaea (Moreno et al., 2024a; Mujal et al., 2025; Schoch, 2000; Steyer, 2012; Warren, 2000). Apart from the gracile, slender-skulled trematosaurs and the heavily built capitosauroid and metoposaurid apex predators, the short-faced brachyopoids form a third group of stereospondyls (Damiani & Steyer, 2005; Schoch & Milner, 2014; So & Mann, 2024; Warren & Hutchinson, 1983; Warren & Marsicano, 2000). Among these, the plagiosaurids form a small, highly distinctive clade of eleven genera with flattened bodies and extremely wide skulls. Some plagiosaurids evolved a carapace (Hellrung, 2003; Nilsson, 1946), many taxa had extremely enlarged orbits (Schoch et al., 2014) and certain dermal bones were repeatedly lost in separate clades (Witzmann & Schoch, 2024).

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Three clades can be distinguished within the Plagiosauridae, the Plagiosaurinae (*Plagiosaurus* and *Gerrothorax*), the Plagiosuchinae (*Plagioscutum* and *Plagiosuchus*) and the Plagiosterninae (*Plagiorophus, Melanopelta, Plagiosternum* and *Megalophthalma*) (Hellrung, 2003; Schoch & Milner, 2014; Shishkin, 1986). In the phylogenetic analysis of Witzmann and Schoch (2024), the Plagiosuchinae formed the sister group to the Plagiosaurinae plus Plagiosterninae, the latter being the largest group and composed of *Plagiorophus* forming the sister group of *Plagiosternum* plus *Megalophthalma*.

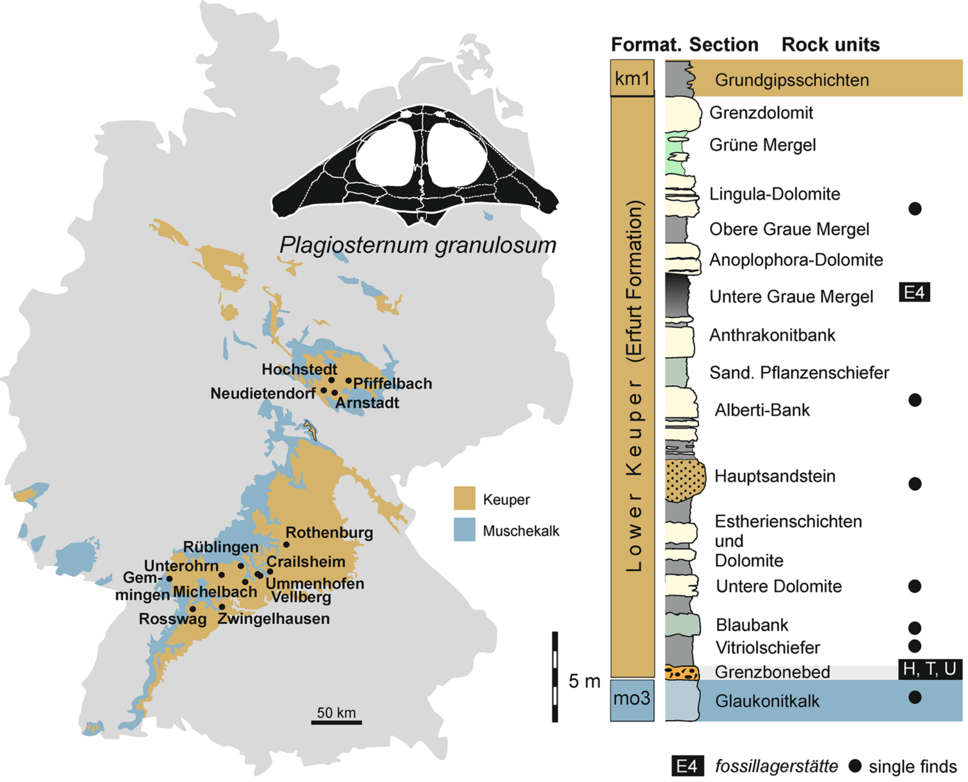
The largest plagiosaurid clade is the Plagiosterninae, known from the Lower Triassic of Brazil and the Middle–lower Upper Triassic of Russia, Germany and France (Brignon, 2021; Corroy, 1928; Dias-da-Silva & Milner, 2010; Moreno et al., 2024b; Shishkin, 1987). Here we reexamine the classic taxon *Plagiosternum granulosum*, which was historically the first species of the plagiosternine clade to be recognised (Fraas, 1889, 1896). After first reports by Meyer (1855) on material from Lunéville in Lorraine (France) and contradicting reconstructions of fragmentary material from Crailsheim by Fraas (1913) and Huene (1922), Warren (1995) reported a poorly preserved but relatively complete skull from Ummenhofen. Since that time, much new and better-preserved material has accumulated that adds to our knowledge of this large plagiosaurid (Schoch & Moreno, 2024). At the same time, the fossil deposits have come under focus which offers the opportunity to study the palaeoenvironments of this taxon. The objective of the present study is therefore to reexamine the existing material and palaeoenvironmental data of *Plagiosternum granulosum* and analyse its bearing on plagiosaurid phylogeny and palaeoecology.

Geological setting and collecting history

In vast areas between Lorraine and Thuringia, the Muschelkalk–Keuper boundary contains a 5–15 cm thick sandstone layer with abundant vertebrate remains, the Grenzbonebed (Hagdorn & Reif, 1988). It forms the base of the Lower Keuper sequence (Erfurt Formation) (Fig. 1) and overlies an unconformity that formed after deposition of the marine Muschelkalk sequence (Bachmann & Brunner, 1998). This bonebed is famous for its taxonomic diversity as well as the frequent occurrence of nothosaurids and pachypleurosaurid eosauropterygians, the enigmatic reptile *Blezingeria ichthyospondyla* and the temnospondyl *Plagiosternum granulosum* (Hagdorn & Reif, 1988).

Meyer (1855) first reported fragmentary material of temnospondyls from the Grenzbonebed of Lunéville in Lorraine (see Brignon, 2021). This included bones later identified as stemming from *Mastodonsaurus giganteus* (Schoch & Milner, 2000), and material referrable to the taxon now called

Fig. 1 Geographic and stratigraphic range of *Plagiosternum granulosum* (Fraas, 1889) in the German Triassic. *mo3* top of Upper Muschelkalk; *km1* basal Lower Keuper. *E4* Bed 4 at Vellberg-Eschenau, *H* Heldenmühle (type locality), *T* Tiefenbach, *U* Ummenhofen



Plagiosternum granulosum. During the second half of the nineteenth century, the Heldenmühle quarry at Crailsheim in Baden-Württemberg (Germany) yielded a wealth of bone material from the Grenzbonebed, which allowed Fraas (1889) to erect *Mastodonsaurus granulosus*. After he recognised the very distinct, broad triangular shape of the interclavicle, he also erected the genus *Plagiosternum* (Fraas, 1896). In another study, Fraas (1913) reported additional material including, for the first time, a partial skull that led him to a first tentative reconstruction. This reconstruction posed him difficulties because of its apparent aberrant wide and flat skull. Later, Huene (1922) updated this reconstruction and described other finds including mandible fragments and vertebral centra. Schmidt (1931) added plagiosaurid material from Hochstedt and Neudietendorf in Thuringia, which comprised a second partial skull from the Ockerdolomit, a regionally restricted dolostone horizon in the Lower Keuper. This confirmed the hypothesis of the former authors that the *Plagiosternum* skull was much shorter than that of capitosauroids and trematosauroids, the only known Triassic temnospondyls at that time.

From the late 1970s onward, private collectors intensified efforts in northern Württemberg, Bavaria and Thuringia, which was triggered by exposures during road construction, house building and quarry extensions. New material of *Plagiosternum granulosum* was collected at various places in these regions and donated to public collections at Ingelfingen (MHI), Stuttgart (SMNS) and Schleusingen (NHMS). This bulk of new material, in combination with the existing historic samples, provides a rich basis for a reexamination of *P. granulosum*.

Materials and methods

Material. The studied material includes numerous portions of the skull, mandible and pectoral girdle as well as a humerus and a small set of vertebral centra referred to this taxon. All specimens were collected in rocks of late Ladinian age (Meissner and Erfurt formations; Fig. 1). A complete list is given in the systematic section.

Abbreviations

Anatomical. adf, adductor fossa, an, angular, asp, ascending process of clavicle, bpp, basipterygoid process, ec, ectopterygoid, eo, exoccipital, eoc, occipital condyle, f, frontal, flp, finger-like projections of interclavicle, ios, infraorbital sulcus, ipv, interpterygoid vacuity, ju, jugal, la, lacrimal, ls, sulcus for lateral line, m, maxilla, mc, middle coronoid, n, nasal, nar, naris, ocf, occipital flange, p, parietal, pf, postfrontal, pi, pineal foramen, pl, palatine, plp, palatine process, pm, premaxilla, pms, premaxilla sulcus, po, postorbital, pp, postparietal, prf, prefrontal, ps, parasphenoid, psp, postsplenial, pt, pterygoid, q, quadrate, qj, quadratojugal, qp, quadrate process, sa, surangular, sp, splenial, sq, squamosal, st, supratemporal, stf, subtympanic fossa, stw, subtemporal window, syt, symphyseal teeth, ta, tabular, vo, vomer.

Institutional. FSUJ, Geologisches Institut, Friedrich-Schiller-Universität Jena, Germany. GPIT, Geologisch-Paläontologisches Institut Tübingen, Germany. MHI, Muschelkalkmuseum Hagdorn Ingelfingen, Germany. MB, Museum für Naturkunde Berlin, Germany. NHMS, Naturhistorisches Museum Schleusingen, Germany. NHMW, Naturhistorisches Museum Wien, Austria. SMNS, Staatliches Museum für Naturkunde Stuttgart, Germany.

Systematic palaeontology

Temnospondyli Zittel, 1888
Stereospondyli Zittel, 1888
Brachyopoidea Lydekker, 1885
Plagiosauridae Abel, 1919
Plagiosterninae Shishkin, 1986

Genus ***Plagiosternum*** Fraas, 1896

Type species. *Plagiosternum granulosum* (Fraas, 1889).

Plagiosternum granulosum (Fraas, 1889)
Figs. 2, 4a, b, 3, 4, 5a, b, 6–8

Xestorrhytias perrini Meyer, 1855, p. 78, pl. 62, fig. 5; *partim*
Mastodonsaurus granulosus Fraas, 1889, p. 94, pl. 6
Mastodonsaurus granulosum Fraas, 1896, p. 5, fig. 1
Plagiosternum perrini Corroy, 1928, p. 32, pl. 4, fig. 10

Holotype. SMNS 11824, a left clavicle (Fraas, 1889, pl. 6, fig. 1).

Type locality. Heldenmühle quarry, Crailsheim-Satteldorf, Baden-Württemberg, Germany (Fig. 1).

Type horizon and age. Grenzbonebed, basalmost Erfurt Formation (Ladinian: Longobardian, see Franz & Barnasch, 2021), Middle Triassic (Fig. 1).

Referred specimens. From a total of 31 localities in southern and central Germany.

1. Type locality: Crailsheim-Satteldorf, Heldenmühle quarry (Baden-Württemberg). Grenzbonebed (type horizon). GPIT-PV 44852 (partial interclavicle). GPIT-PV 44855 (interclavicle). GPIT-PV 44856 (partial mandible). GPIT-PV 44857 (right clavicle). SMNS 8675 (interclavicle; Fraas, 1913: 280). SMNS 8733

(interclavicle; Fraas, 1896: fig. 1). SMNS 11827 (left surangular). SMNS 11828 (partial dentary). SMNS 11830 (intercentrum Fraas, 1889: fig. 12; Huene, 1922: 418). SMNS 11831 (right ectopterygoid, Fraas, 1889: fig. 9; Huene, 1922: p. 418). SMNS 13168 (partial skull, Fraas, 1913: fig. 1). SMNS 13169 (posterior skull table, Fraas, 1913: 277). SMNS 13170 (partial clavicle, Fraas, 1913: 281). SMNS 84796 (left jugal). SMNS 84800 (right hemimandible). SMNS 84801 (left parietal). SMNS 84802 (left pterygoid). SMNS 84804 (left nasal). SMNS 84805 (left pterygoid). SMNS 97146 (right parietal). SMNS 97147 (left parietal). SMNS 97148 (right parietal). SMNS 97149 (left parietal). SMNS 97150 (right parietal portion). SMNS 97151 (left dentary, dorsally exposed).

2. Arnstadt-North, ICE construction site parallel to Autobahn BAB 71 (Thuringia). NHMS-WT 669 (23 cm wide interclavicle, Werneburg, 2004: fig. 21 above; portions of clavicle, jaws and skull).
3. Crailsheim-Satteldorf, Barenhalden quarry (Baden-Württemberg). Grenzbonebed. MHI 698 (intercentrum). MHI Ku 2001/4 (interclavicle portion).
4. Crailsheim-Sattelweiler (Baden-Württemberg). Grenzbonebed. MHI 173 (clavicle).
5. Crailsheim-Tiefenbach, Härer quarry (Baden-Württemberg). Grenzbonebed. MHI 730 (postparietals). MHI 891 (intercentrum). MHI 1027 (humerus). MHI 1347 (clavicula). MHI ON1 (pterygoid).
6. Crailsheim, Neidenfels quarry (Baden-Württemberg). Grenzbonebed. MHI 1113 batch (clavicle, atlas, intercentrum).
7. Crailsheim without specific locality data (Baden-Württemberg). Grenzbonebed. MB.Am.540 (? clavicle). MB.Am.541 (interclavicle). MB.Am.543 (unidentified dermal bone portions). MB.Am.682 (12 portions of dermal bone). NHMW uncatalgued (clavicle fragment).
8. Bibersfeld near Schwäbisch Hall (Baden-Württemberg). MB.Am.533 (clavicle).
9. Erkenbrechtshausen (Baden-Württemberg). Grenzbonebed. MHI 906 (interclavicle).
10. Gemmingen, Reimold quarry (Baden-Württemberg). MHI 1238 (interclavicle).
11. Gottwollshausen, Dölker quarry (Baden-Württemberg). Blaubank. MHI 204 (mandible portion).
12. Hilpertshof near Burgbernheim (Bavaria). Vitriolschiefer. MHI 1904 (left clavicle).
13. Hochstedt (Thuringia). FSUJ uncatalogued (clavicle fragments, type material of *P. nanum* Schmidt, 1931).
14. Kirchberg an der Jagst (Baden-Württemberg). Bonebed at base of Anthrakonitbank. MHI (left jugal).
15. Lösau (Bavaria). MB.Am.494 (clavicle).
16. Michelbach an der Bilz, Wilhelmsglück quarry (Baden-Württemberg). Lingula-Sandstein. MHI 1033 (parietals and postparietals).
17. Molsdorf, old locality (Thuringia). MB.Am.684 (possible cleithrum, Schmidt, 1931: fig. 9a, b); remark: the taxonomic assignment of this bone is uncertain, Schmidt (1931) assigned it to *Plagiosuchus pustuliferus*. MB.Am.685 (quadratojugal).
18. Molsdorf, ICE construction site near Autobahn junction BAB 4/71 (Thuringia). NHMS-WT 2835–2848 (numerous portions of scapular girdle and skull). NHMS-WT 2997 (juvenile clavicle).
19. Mundelsheim, Epple quarry (Baden-Württemberg). Glaukonitkalk (Fränkische Grenzschichten, Wimpfen Subformation, Meissner Formation). SMNS 82002 (right side of skull).
20. Neudietendorf (Thuringia). MB.Am.581 (clavicula). MB.Am.686 (anterior palate).
21. Obersontheim-Ummenhofen, Schneider quarry (Baden-Württemberg). Grenzbonebed. SMNS 56614 (complete large skull, Warren, 1995: figs. 1–5). Untere Dolomite. MHI (nasal).
22. Pfiffelbach (Thuringia). FSUJ uncatalogued (interclavicle).
23. Rosswag (Baden-Württemberg). Grenzbonebed. SMNS 82024 (clavicle).
24. Rothenburg ob der Tauber, quarry (Bavaria). Grenzbonebed. SMNS 90602 (right side of small skull).
25. Rüblingen, Kleinknecht quarry (Baden-Württemberg). Grenzbonebed. SMNS 81364 (left clavicle). SMNS 81365 (left clavicle; fig. 6b). Blaubank. MHI (clavicle).
26. Thuringia without further details. MB.Am.510 (interclavicle).
27. Unterohrn (Baden-Württemberg). Albertibank. MHI (interclavicle portion).
28. Vellberg-Eschenau, Schumann quarry (Baden-Württemberg). Hauptsandstein. MHI (both parietals). Untere Graue Mergel (E4). MHI 1805 (right clavicle). SMNS 90698 (left mandible, left clavicle, interclavicle; fig. 6h). SMNS 90720 (right mandible). SMNS 97153 (juvenile clavicle; fig. 6a). SMNS 97154 (juvenile left jugal). SMNS 97155 (posterior portion of mandible).
29. Zwingelhausen, Gläser quarry (Baden-Württemberg). Grenzbonebed. SMNS 97128 (large right quadratojugal. Blaubank. SMNS 91752 (posterior end of mandible). NHMS WT 3332 (frontal and parietal; fig. 3i, j).
30. Locality unknown (Thuringia). MB.Am.685 (left quadratojugal, Schmidt, 1931: fig. 24).
31. Bedheim, new quarry (South-Thuringia). NHMS-WT 3640 (right lateral region of dorsal skull roof with postorbital, jugal and squamosal).

Stratigraphic range. Present in ten successive horizons spanning some 30 m of rock section: Fränkische Grenzschichten (top of Meissner Formation, Upper Muschelkalk), Grenzbonebed, Vitriolschiefer, Blaubank, Untere Dolomite, Estherienschichten, Hauptsandstein, Albertibank, Untere Graue Mergel, and Lingula-Sandstein (all Erfurt Formation, Lower Keuper), late Ladinian, Middle Triassic.

Diagnosis, emended. A stereospondyl distinguished by the following combination of character states (autapomorphies among Plagiosauridae are marked with an asterisk*): (1) Prefrontal and postfrontal absent, (2) quadratojugal forming elongate lateral horn with ornament extending to ventral side, (3) postorbital triangular*, (4) orbit pentagonal*, (5) adult ornamentation consisting of reticulate ridges with small tubercles on some nodal points, juvenile ornamentation with parallel, curved long ridges*, (6) clavicle with low and spike-like ascending process broadly sutured with the cleithrum*, (7) interclavicle with finger-like posterolateral projections and grooves along posterior margin that probably accommodated spindle-shaped gastral scales*.

Comment. Panchen (1959) reported and figured a large articulated skeleton from Bjørnøya (Bear Island, Norway) as *Plagiosternum* sp.; this specimen, currently described by the senior author and colleagues, represents a distinct taxon. Shishkin (1986, 1987) and Shishkin et al. (2023) referred two Russian species to "*Plagiosternum*"; *P. paraboliceps* and *P. danilovi*. We follow Schoch and Milner (2014) in the generic distinction of the two Russian taxa, because they do not share the autapomorphies listed above. In particular, *Plagiorophus danilovi* has a transversely elongate postfrontal and a distally unexpanded quadratojugal. Moreno et al. (2024b) reported a fragmentary interclavicle (SMNS 59771) from Neustadt an der Aisch (Bavaria) collected in the Upper Estherienschichten (Upper Grabfeld, earliest Carnian) that is consistent with the Plagiosterninae in the mode pattern of ornamentation.

Description

By the number of specimens, *Plagiosternum granulosum* ranks third among the known plagiosaurids. It occurs in 29 localities and 10 horizons ranging from the top of the Muschelkalk to the Lingula-Sandstein in the upper part of the Erfurt Formation (Fig. 1). However, because of the selective nature of most deposits in which this taxon is preserved, the material is restricted to clavicles, interclavicles and skulls, whereas most of the postcranium remains unknown. The only other elements that are rarely preserved with diagnostic remains are vertebral centra, a putative cleithrum and a humerus. In the following description, we refer to the following authors when comparing *P. granulosum* to related plagiosaurids: *Gerrothorax pulcherrimus* (Hellrung, 2003; Jenkins et al., 2008; Schoch & Witzmann, 2012), *Megalophthalma ockerti* (Schoch et al., 2014), *Plagiorophus danilovi* (Shishkin, 1987), *Plagiosaurus depressus* (Witzmann & Schoch, 2024) and *Plagiosuchus pustuliferus* (Damiani et al., 2009).

General cranial proportions. The skull is most diagnostic by the large relative size of the orbits and the laterally expanded quadratojugals, by which it differs from plagiosaurines and plagiosuchines (Fig. 2). The skull is about 2.5–2.7 times wider than long. This ratio is consistent with *Gerrothorax pulcherrimus* (2.7), but differs from that of *Plagiosuchus pustuliferus* (1.6) and the taxon from Bear Island (2.2). This enormous cranial width is linked with the relative size of the orbit and the lateral extension of the squamosal, jugal and quadratojugal. The orbit measures about 0.58–0.62 times the length of the skull, as contrasted with *Gerrothorax pulcherrimus* (0.37). The posterior margin of the skull is nearly straight transverse without a squamosal embayment; in adults the postparietals have a markedly convex occipital margin.

Ornamentation. Even small fragments of dermal bone distinguish *Plagiosternum granulosum* from other taxa in the Ladinian deposits. In contrast to plagiosuchines and plagiosaurines, but consistent with other plagiosternines, the ornamentation of adults is composed of reticulate ridges that form small polygons in most places and elongated parallel ridges in zones of intensified growth (clavicle, interclavicle). In the posterior skull table, the nodal points of the polygons are taller and may have a pustular top in some places (Fig. 3). In some specimens, the long parallel ridges on the clavicle are connected by numerous successive, interconnecting ridges, together forming a honeycomb-like pattern (SMNS 13170, 90698). *Plagiosternum granulosum* shares this ornament only with its close relatives *Plagiorophus* spp. and *Megalophthalma ockerti.*

Lateral line organ. The lateral line sulci form continuous grooves surrounding the orbit and running up to the tip of the snout (Fig. 3). On the nasal, the supraorbital line parallels the orbit margin, then abruptly bends medially and finally curves anteriorly to continue on the premaxilla. This region is preserved in SMNS 90602. In posterior direction, the sulcus is narrow and deep, continuing onto the frontal where it again runs in parallel to the orbit margin. It continues on the parietal, where the sulcus widens again as it curves transversely posterior to the orbit posterior margin. The latter feature is subject to variation, with an extreme version lacking the transverse curvature (SMNS 97149, NHMS WT 3332). As preserved in SMNS 82002, the sulcus continues onto the

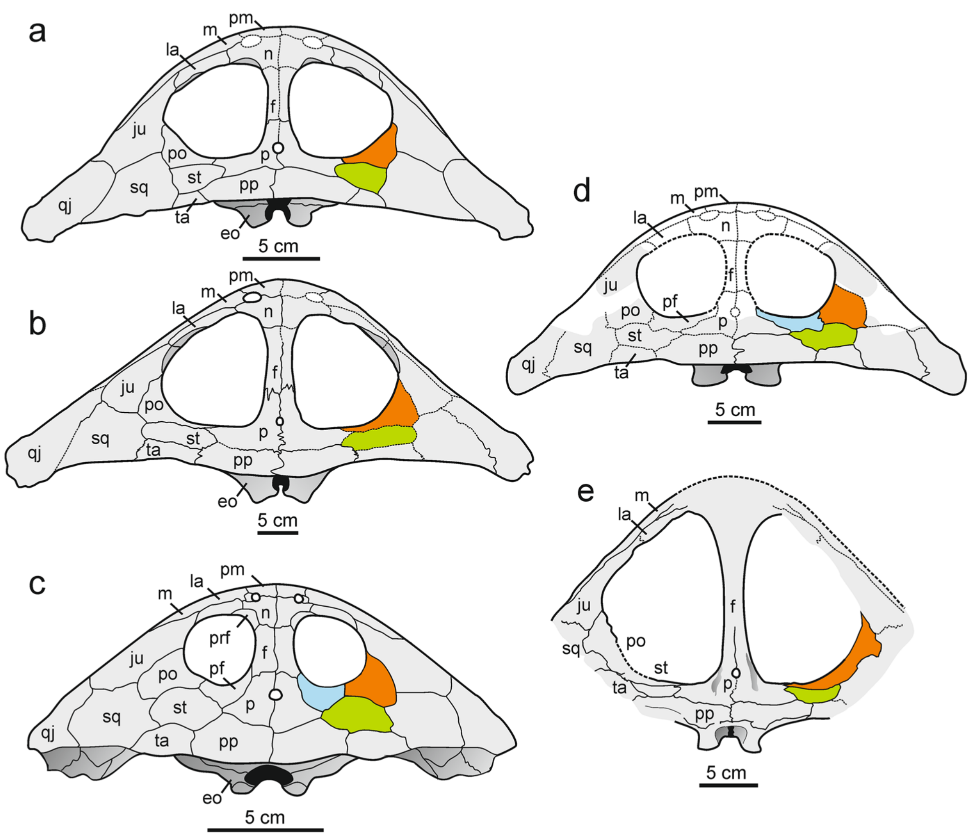


Fig. 2 Plagiosaurid skulls in dorsal view **a, b** *Plagiosternum granulosum* (Fraas, 1889). **a** juvenile (SMNS 82004); **b** adult (SMNS 13169, 56614); **c** *Gerrothorax pulcherrimus* (Fraas, 1913), modified from Schoch and Witzmann (2012); **d** *Plagiorophus danilovi* (Shishkin, 1986), modified after Shishkin (1987); **e** *Megalophthalma ockerti* (Schoch et al., 2014)

postorbital without touching the supratemporal and is again aligned in parallel to the orbit margin, finally merging into the jugal flexure at about midlevel of the jugal bone. A short temporal sulcus branches from the postorbital in posterior direction and crosses the centre of the supratemporal, much like in *Plagiorophus danilovi* (Shishkin, 1987).

Preorbital region. This is the most difficult region to reconstruct because it is heavily damaged in all specimens. The naris, well preserved on the left side of SMNS 56614, is small and transversely oval (Figs. 2, 4). The distance between the nares is 1.8 times wider than the interorbital distance. The nasal is nearly twice as wide anteriorly than posteriorly, with a strongly curved orbit margin, a gently curved narial margin, and a faintly serrated suture with the premaxilla.

Interorbital region. The orbits are larger than in most other temnospondyls except for *Megalophthalma ockerti* and *Plagiosuchus pustuliferus*. In the latter taxon, however, the skull has enormous orbitotemporal openings which are subdivided in anterior and posterior parts by a constriction of the frontals medially and the jugals laterally (Damiani et al., 2009). Only the anterior part might be homologous with the orbits proper. In *P. granulosum*, the orbits have a pentagonal outline, with their margin being straight sagittally, transverse posteriorly, oblique anterolaterally in the postorbital region, and further angled between the jugal and lacrimal bones. This outline varies individually between more rounded and more edged versions. The orbits become proportionately larger during ontogeny. The frontal and anterior parietal are very narrow, and because the prefrontal and postfrontal are absent, the frontal forms sagittally straight orbit margins (Figs. 3, 4). An interfrontal, known as a variant in *Gerrothorax pulcherrimus*, is absent here. The adult ornamentation of *P. granulosum* is consistent with that of the posterior skull table, involving irregular-sized polygons with tubercles on some nodal points (SMNS 13168, 13169, 97149).

Postorbital skull table. The skull table is relatively wide which correlates with the enormous orbits. This means that the postparietal, the lateral wing of the parietal and the supratemporal are laterally expanded with respect to other taxa (Fig. 3). Shared with *M. ockerti* is the absence of a postfrontal; *Plagiorophus danilovi* retains a substantial postfrontal and consequently the lateral wing of the parietal is much narrower. In *P. granulosum*, the pineal foramen varies in size and shape, but there is no clear correlation with ontogeny. It may be sagittally oval to rounded, and its length ranges

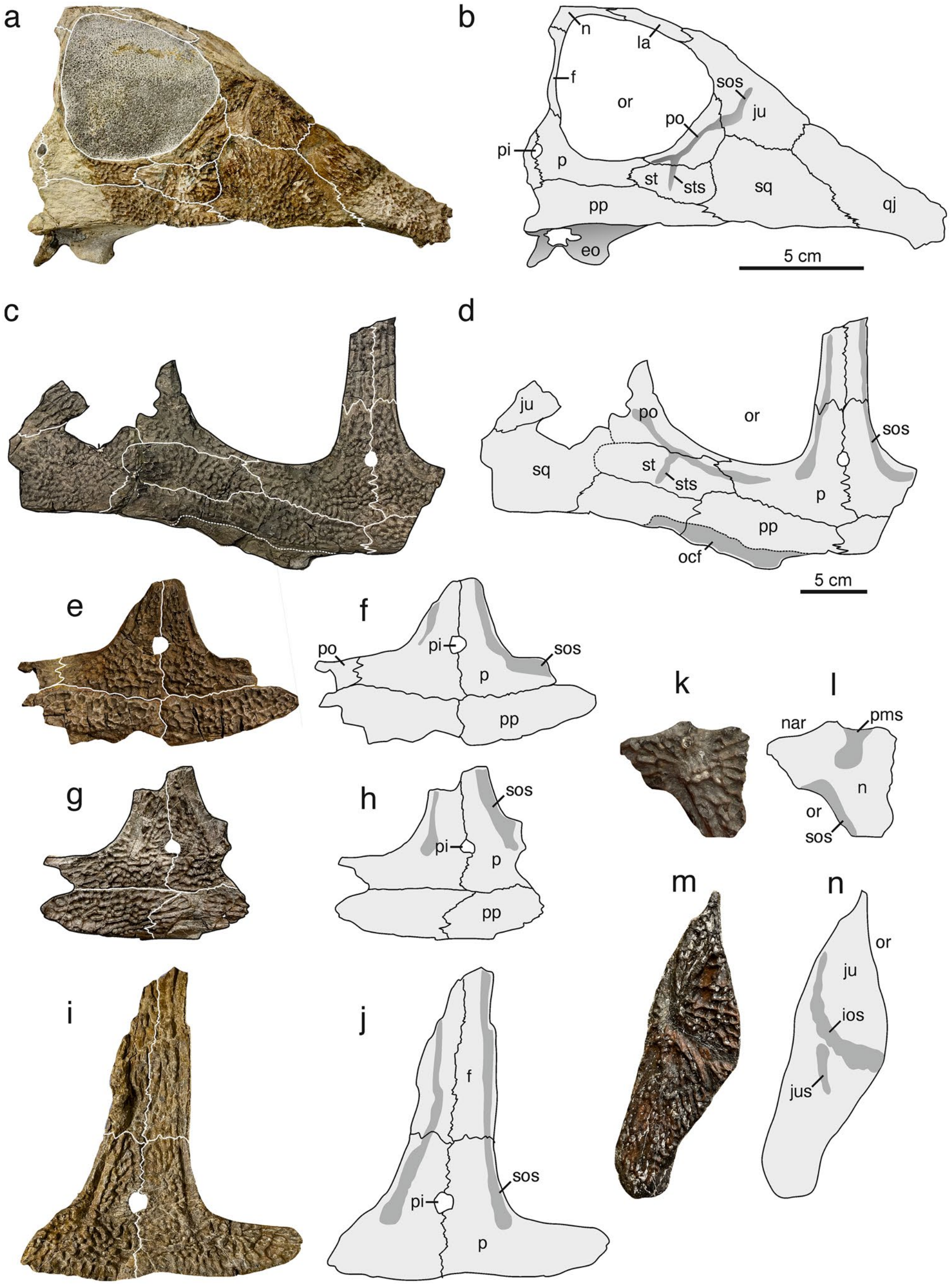


Fig. 3 Skull roof of *Plagiosternum granulosum* (Fraas, 1889). **a, b** right part of juvenile skull in dorsal view (SMNS 82002); **c, d** left part of adult skull (SMNS 13168); **e, f** posterior skull table (SMNS 13169); **g, h** posterior skull table (MHI 1033); **i, j** parietals and frontals (NHMS-WT 3332); **k, l** left nasal (SMNS 84004); **m, n** left jugal (MHI)

10–20% that of the parietal. In juveniles, the posparietal is longer and wider than the parietal and dominates the skull table, whereas in adults these bones have similar size. The tabular, supratemporal and the medial wing of the postorbital widen during ontogeny.

Cheek region. The postorbital is triangular with a thin medial wing and a main plate-like body similar in size to the supratemporal (Figs. 3, 4). The jugal is much longer with an extended and slender anterior (lacrimal) process and a triangular plate. A small early juvenile jugal from Vellberg-Eschenau (E4) shows a reticulate ornamentation consisting of elongate, shallow and very thin ridges (SMNS 97154). In larger specimens (SMNS 84796), these ridges are broader and small tubercles are present in some nodal points. The adult jugal is markedly curved laterally and has a thickened orbit margin. The trapezoidal squamosal comprises a smaller portion of the cheek than in most temnospondyls, because the quadratojugal is greatly expanded. The latter extends over almost half the width from the skull midline to the cheek margin. The quadratojugal has a substantial ventral flange that is ornamented on both the dorsal and ventral

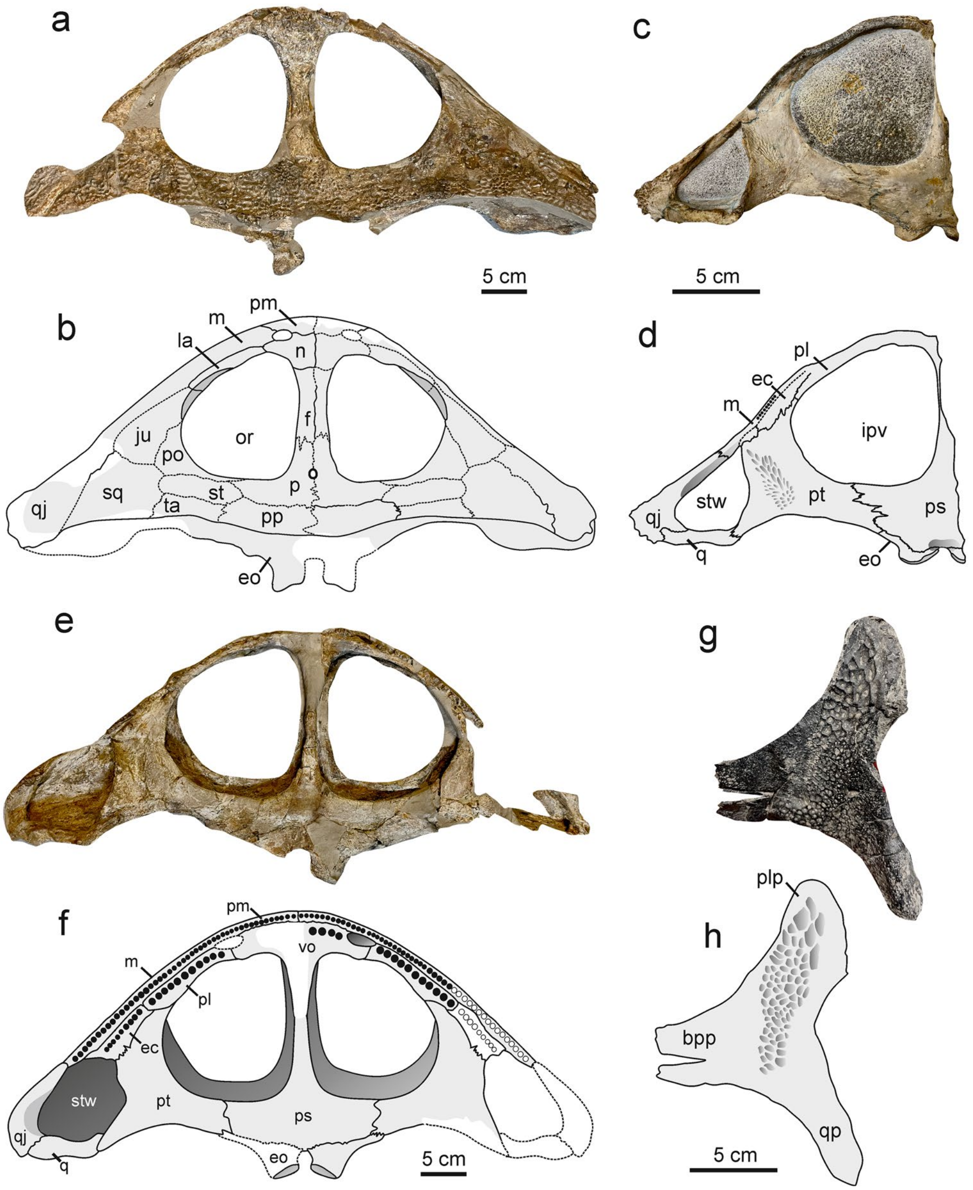


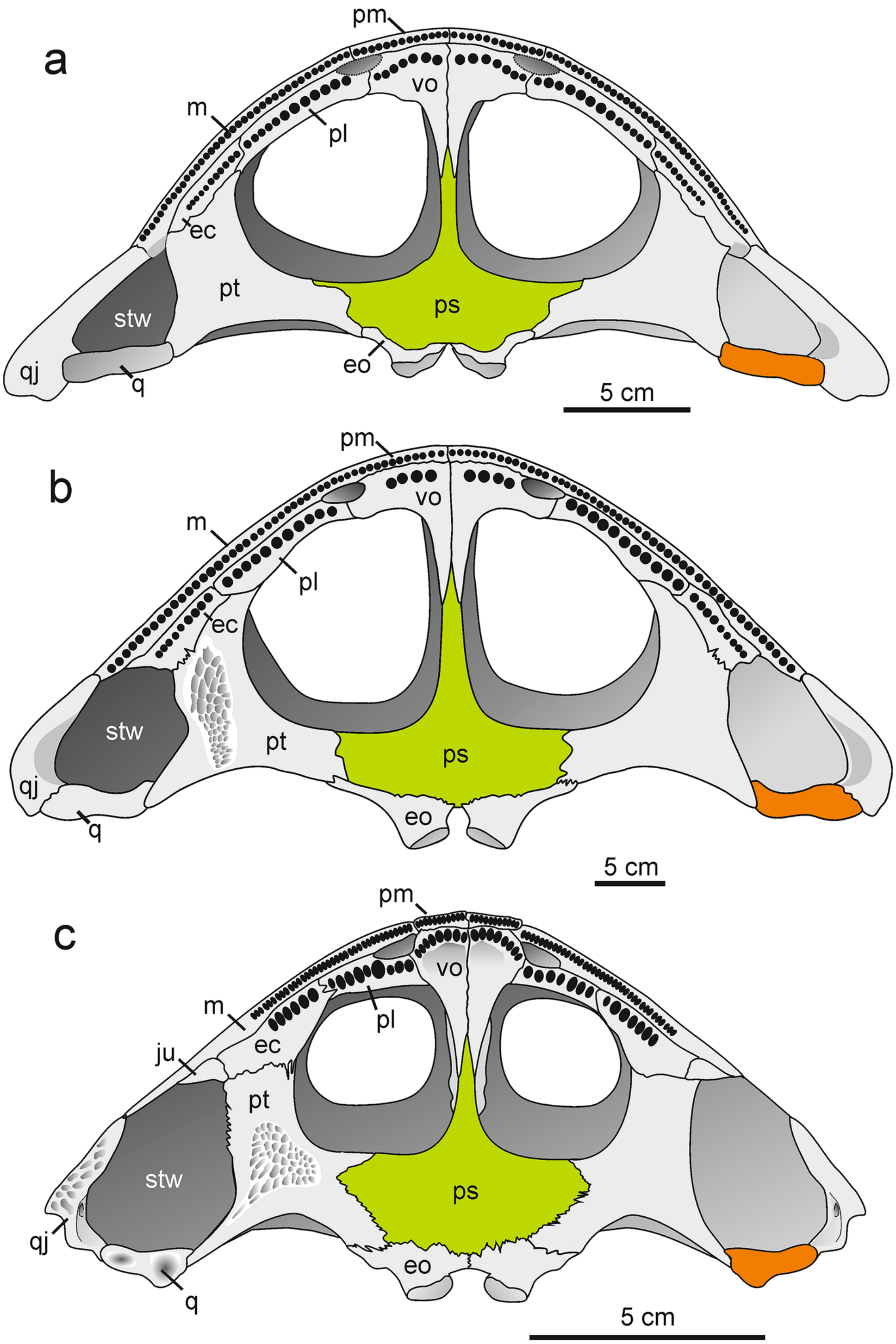
Fig. 4 Skull roof and palate of *Plagiosternum granulosum* (Fraas, 1889). **a, b** adult skull in dorsal view (SMNS 56614); **c, d** right part of juvenile palate in ventral view (SMNS 82002); **e, f** adult palate in ventral view (SMNS 56614); **g, h** left pterygoid in ventral view (SMNS 84805)

sides. This differs from most other plagiosaurids, including *Plagiorophus danilovi*, but is found to a much lesser degree than *in G. pulcherrimus*.

Dentition. The marginal and palatal teeth are elongate-conical and have labyrinthodontous bases. As far as preserved, they lack carinae. The tooth bases, mostly rounded, are less close each other than those of stereospondyls (Figs. 4, 5). As in other temnospondyls, the premaxilla and maxilla form a continuous marginal row of relatively small and close teeth, and the vomer, palatine and ectopterygoid house a continuous row of larger teeth. In contrast to *Plagiosuchus pustuliferus* and *G. pulcherrimus*, but consistent with *Megalophthalma ockerti*, both tooth rows reach further posteriorly, which is a primitive condition for stereospondyls (Yates & Warren, 2000). Plagiosternines thus had the largest gape among plagiosaurids.

Premaxilla and vomer. The tip of the snout is wide and framed by an elongate premaxilla housing 12–13 teeth. The marginal dentition of the premaxilla and maxilla, as well as that of the vomer is preserved in SMNS 90602 (Fig. 4). The vomer has a reverse L-shape, composed of an anterior, dentigerous plate and an elongated spike-like posteromedial process (Fig. 5). The vomerine plate is wider than in *Gerrothorax pulcherrimus* and the transversely elongate choanae are therefore much further apart. A curved transverse row of large vomerine teeth run along the anterior margin of the bone and continues onto the palatine. In contrast to *G. pulcherrimus*, the tooth bases are

Fig. 5 Plagiosaurid skulls in ventral view **a, b** *Plagiosternum granulosum* (Fraas, 1889). **a** juvenile (SMNS 82004); **b** adult (SMNS 56614); **c** *Gerrothorax pulcherrimus* (Fraas, 1913), modified from Schoch and Witzmann (2012)



rounded. The countersided posterior processes are sutured along the midline and form a triangular suture with the cultriform process of the parasphenoid.

Palatine and ectopterygoid. The palatine bears a minimum of 10–12 teeth (SMNS 56614). The ectopterygoid is much shorter than the palatine, which is the reverse condition of that in *G. pulcherrimus* (Fig. 5). The anteromedial end of the pterygoid has a faint contact with the palatine, excluding the ectopterygoid from the margin of the interpterygoid vacuity. The ectopterygoid bears at least nine teeth that increase slightly in size towards the anterior end. They are arranged in a single row near the lateral margin of the bone, and this row is continued on the palatine. The posterior half of the ectopterygoid bears a medial process that sutured the palatine ramus of the pterygoid. Contrasting

Gerrothorax and many stereospondyls, there is no ventral process of the jugal (insula jugalis).

Pterygoid. The pterygoid is consistent with that of *G. pulcherrimus* in general shape. However, in contrast to the large posteromedial process broadly suturing with the exoccipital in plagiosaurines, the pterygoid of *P. granulosum* contacts the exoccipital only in a narrow suture. The basipterygoid ramus is longer, but the quadrate ramus shorter than in *G. pulcherrimus*. Consistent with plagiosaurines, the ventral side of this ramus is ornamented along its lateral half, which reachs further ventrally than the basipterygoid region. There is not such a tall marginal crest as reported from *Plagiorophus danilovi*. The lateral part of the palatine ramus is gently ornamented in juveniles (SMNS 82002) and bears an extensive patch of reticulate ridges in larger specimens (SMNS 84802; Fig. 4g, h). The palatine ramus has a gently curved and tapering anterior end that sutures the narrow ectopterygoid along a weakly broadened facet. This contrasts with

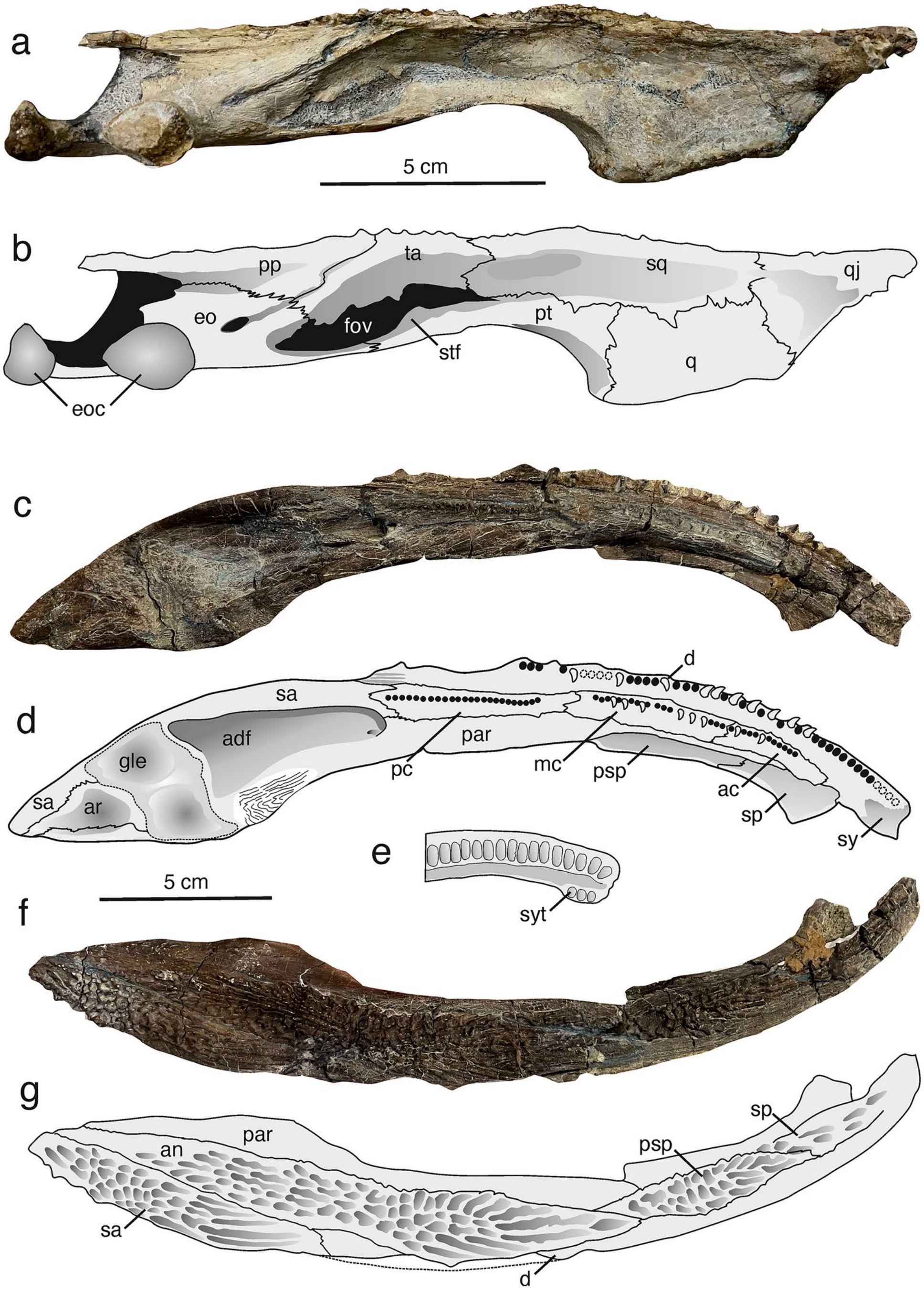


Fig. 6 Occiput and mandible of *Plagiosternum granulosum* (Fraas, 1889). **a, b** right part of juvenile occiput in posterior view (SMNS 82002); **c, d** left hemimandible in dorsal view (SMNS 90698); **e** symphyseal region of left dentary in dorsal view (SMNS 97151);q **f, g** left hemimandible in ventral view (SMNS 90698)

the shorter palatine ramus contacting a posteriorly extended ectopterygoid in *G. pulcherrimus*.

Parasphenoid. The parasphenoid has the shape of an inverse T, with a thin cultriform process underplated by the vomers at about midlevel (Fig. 5). The basal plate is about 30% shorter than in plagiosaurines and *Plagiorophus danilovi*, but still longer than in *M. ockerti*. It has an entirely smooth ventral surface, lacking both dermal ornament and dentigerous patches. In SMNS 82002, it underplates the anterior portion of the exoccipitals, leaving only a narrow and curved posteriormost part exposed in ventral view. Unlike in *G. pulcherrimus*, the exoccipitals do not meet posterior to the basal plate. The suture between the basal plate and pterygoid is serrated or strongly curved. The posteromedial portion of the basal plate is ventrally concave. The cultriform process has a flat ventral side and is narrower than in other plagiosaurids except *Megalophthalma ockerti*.

Occiput. The occiput is best preserved in the uncrushed juvenile skull SMNS 82002 (Fig. 6a, b). It is remarkably flat, with the cheek region only 1.5 times deeper than the distance between the skull table and condyles. This is most consistent with plagiosaurines but contrasts with *Plagiorophus danilovi*, in which the pterygoid and quadrate are substantially taller (Shishkin, 1987). The postparietal and tabular are sutured along their entire width to the exoccipital, without a posttemporal fenestra; this again differs from the condition in *M. ockerti* and *Plagiorophus danilovi*, which show a larger depression or a small roundish posttemporal opening. An oblique crest connecting the base of the condyle with the posterior margin of the tabular represents the paroccipital process. The ventral margin of the tabular is thin and serrated, apparently not fully ossified at the juvenile stage (SMNS 82002). The descending flange of the squamosal bears in its medial part a raised area of oval outline that was probably the insertion side of the depressor mandibulae muscle (Fig. 6A, B), as described in *Gerrothorax pulcherrimus* (Jenkins et al., 2008; Witzmann et al., 2012), *Plagiosaurus depressus* (Witzmann & Schoch, 2024) and *Plagioscutum ochevi* (Shishkin, 1986). The wide, transversely aligned gap between the pterygoid, exoccipital, squamosal and tabular forms the posterior entrance to the middle ear region and fenestra ovalis, the subtympanic fossa. The floor of this entrance is mostly formed by the pterygoid. Instead of a complicated groove-and-ridge structure like in *Plagiorophus danilovi*, the pterygoid of *P. granulosum* forms only a gentle boss-like structure in this region. The occipital condyles are well separated and protrude the occipital margin of the exoccipitals. The condyles are proportionately smaller than in *Plagiorophus danilovi*, and their shape is transverse oval like in *M. ockerti*. There is no trace of basioccipital or supraoccipital ossifications.

Visceral skeleton. The stapes or hyobranchium are not preserved in any specimen.

Mandible. The lower jaw is known from a range of well-preserved specimens (SMNS 11827, 84800, 90698, 90720). Huene (1922) attempted the first reconstruction of the mandible, based on a near-complete hemimandible from the type locality (SMNS 84800; Fig. 6c–g). The mandible is broad-parabolic in dorsal view, contrasting the more rounded lower jaws of plagiosaurines and the S-shaped mandible of plagiosuchines (Damiani et al., 2009; Hellrung, 2003). It is more consistent with the mandible of *Gerrothorax pulcherrimus* than that of plagiosuchines in the size of the adductor chamber, the triangular shape of the postglenoid area, and especially the length of the dentary tooth row. In addition, the anterior, middle and posterior coronoid elements bear a continuous row of small teeth, which are only half the size of the dentary teeth. This contrasts the situation in *G. pulcherrimus*, where the coronoid teeth are tiny and emplaced on widely separate patches, and *P. pustuliferus*, where the coronoids are endentulous. The symphysis of *P. granulosum* has a series of four larger teeth posterior to the dentary arcade; this is more consistent with plagiosaurines even though there the accessory teeth are small and usually only a pair is present. The symphyseal region of *P. granulosum* is not expanded in dorsal view. The postglenoid area is low and only very gently curved; the posterior end faces posterodorsally. This contrasts strongly with *Plagiorophus paraboliceps*, in which the postglenoid area is upturned with the long axis aligned at 45° to the dentary arcade. The labial side of the mandible is ornamented much like the skull roof, with radial ridges originating in the posteroventral part of the angular. The postplenial and splenial are covered by reticulate polygons, whereas the surangular bears a series of longitudinal, subparallel ridges. The teeth are conical and gently recurved and range in proportional size between the very long teeth of *Megalophthalma ockerti* and *G. pulcherrimus*.

Pectoral girdle. The clavicle and interclavicle are the only elements from the appendicular skeleton that can be safely referred to *P. granulosum*. These bones are highly distinct by their reticulate ornament (Fig. 7). Because of their massive structure and heavy ornamentation, fragments of the dermal pectoral girdle rank among the most common finds in the bonebeds of the Meissner and Erfurt Formation (Hagdorn & Reif, 1988; Hagdorn et al., 2015). We will further describe a peculiar bone from Molsdorf that may be a cleithrum of *P. granulosum*.

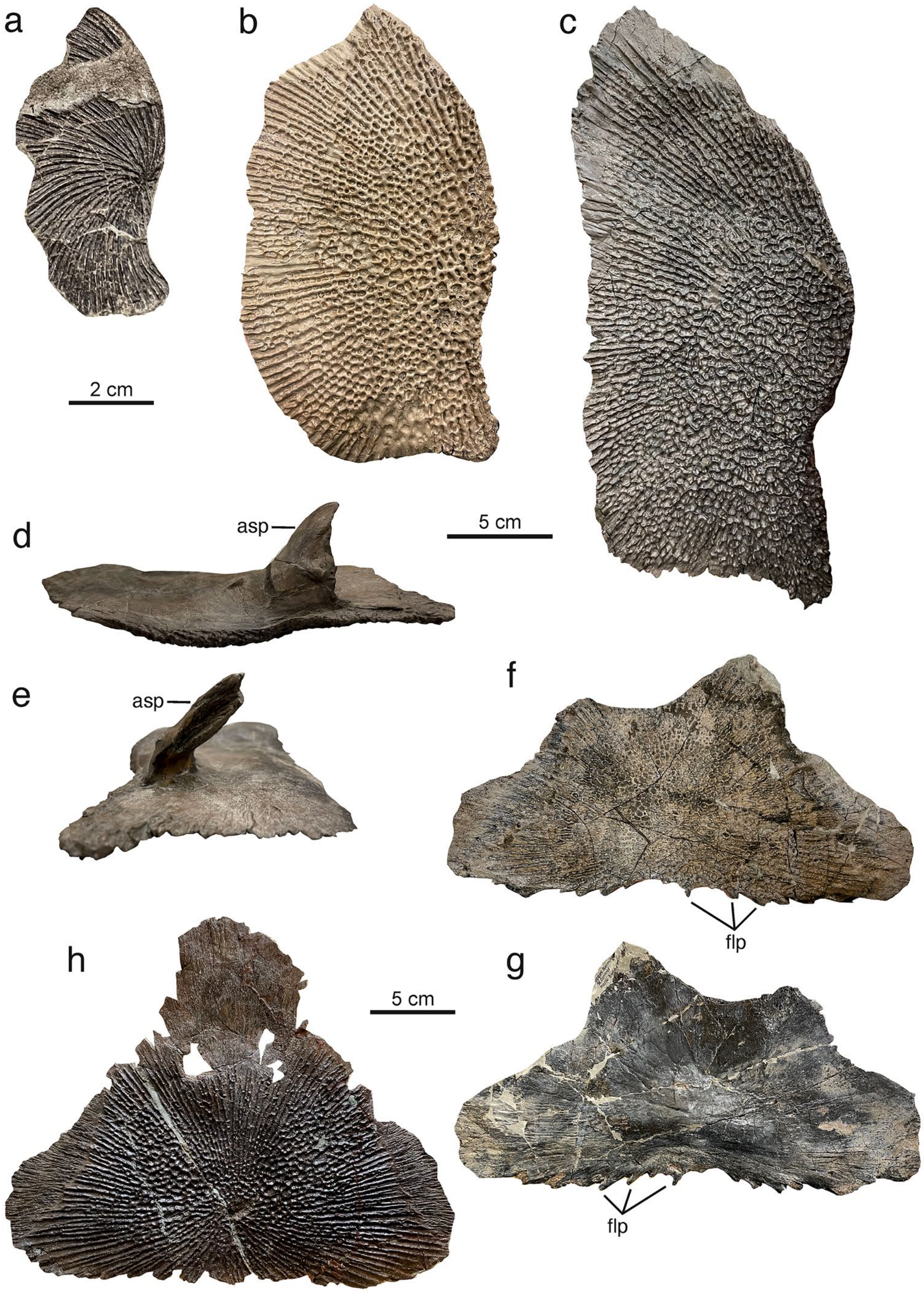


Fig. 7 Dermal pectoral girdle of *Plagiosternum granulosum* (Fraas, 1889). **a** small juvenile clavicle in ventral view (SMNS 97153); **b** adult clavicle in ventral view (SMNS 81365); **c–e** right adult clavicle (MHI 1805) in ventral (c), lateral (d), posterior (e) views; **f, g** partial interclavicle (MHI 1238) in ventral (f) and dorsal (g) views; **h** interclavicle in ventral view (SMNS 90698). Scale refers to all specimens

Clavicle. The clavicle forms an oval plate with a gently concave medial margin and an S-shaped lateral margin (Fig. 7a–c). The latter is most clearly expressed in juveniles. The posterolateral end of the clavicle forms a gently offset process. The clavicle is shorter than in plagiosuchines and plagiosaurines, and more massive than in *Gerrothorax pulcherrimus*. Although in adults the ridges are generally aligned radially, it is distinct from *Plagiorophus danilovi* in the more reticulate pattern, contrasted by the long radial ridges in the Russian taxon (Shishkin, 1987: tab. 8), and the posterior process in *Plagiosternum granulosum*. The medial margin of the clavicle is more similar to that of plagiosuchines than plagiosaurines, the latter being markedly kinked in its posterior portion. The dorsal side of the clavicle is smooth, posterolaterally giving rise to a triangular ascending process which has a long, serrated suture surface for the cleithrum. This indicates that the cleithrum must have been taller than in plagiosaurines and shorter than in plagiosuchines. The tight sutural connection between the clavicle and cleithrum is more consistent with plagiosaurines. In

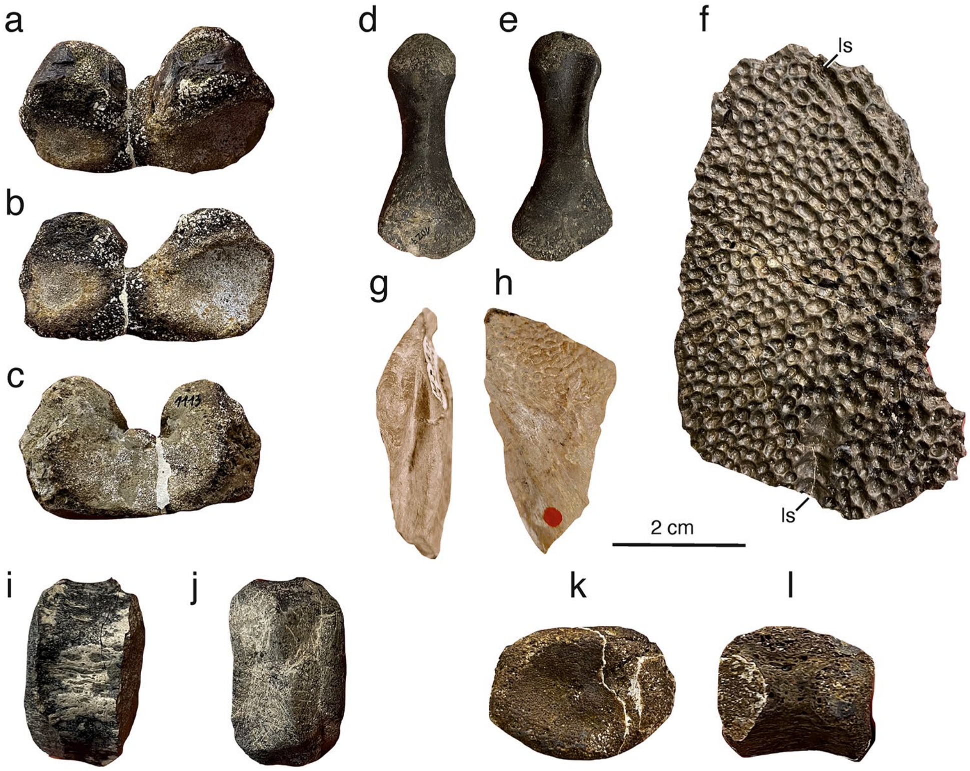


Fig. 8 Elements of the appendicular and axial skeleton of *Plagiosternum granulosum* (Fraas, 1889). **a–c** atlas (MHI 1113) in anterodorsal (a), anterior (b) and posterior views (c); **d–e** humerus (MHI 1027) in dorsal (d) and ventral views (e); **f** clavicle in ventral view with lateral line sulci (MHI); **g, h** cleithrum (MB.Am.684) in anterior (g) and lateral views (h); **i, j** intercentrum (SMNS) in ventral (i) and dorsal views (j); **k, l** intercentrum (MHI 698) in anterior (k) and lateral views (l). Scale refers to all specimens

at least one clavicle (MHI unnumbered from Crailsheim; Fig. 8f) we found traces of lateral line sulci on the external surface of the ventral blade, consisting of a short, broad sulcus in the posterior part of the bone and an oblique, narrower line in the anterior part. This appears to be a variable character. Lateral line sulci appear also on the ventral surface of some clavicles in *Trimerorhachis insignis* (Milner & Schoch, 2013: Fig. 8b, c). In contrast to plagiosaurines but similar to *Plagiosuchus pustuliferus*, the clavicle of *P. granulosum* bears a conspicuous groove on the dorsal surface lateral to the ascending process and in parallel to the lateral margin of the bone. The groove becomes narrower in an anterior direction.

Interclavicle. The interclavicle is delta-shaped with a broad triangular ornamented area (Fig. 7f–h). The lateral flanges overlapped by the clavicles are smaller than in plagiosuchines, and the posterolateral wing is not as distinctive as in *Gerrothorax pulcherrimus*. The ornament consists of radial ridges aligned in all directions, with the centre located in the posterior fourth of the element. Laterally and anteriorly, the ridges form continuous subparallel structures, merging into a reticulate pattern towards the centre. The dorsal side of the interclavicle is smooth and bears a broad transverse ridge in the posterior third of the bone, with unpaired anterior and posterior projections in the centre. The posterior margin of the interclavicle is well preserved in MHI 1238. The margin is transversely straight but markedly rugged, with 5–6 finger-like posterolateral projections on each side (Fig. 7g). These match in size and orientation the gastral scales of *Plagiosuchus pustuliferus*. Even though gastral scales are not preserved in *Plagiosternum granulosum*, the posterior margin of the interclavicle leaves little doubt that the finger-like projections were associated with such scales (see below). In plagiosaurines, there are broad unornamented flanges along the posterior margin of the interclavicle that were overplated by ventral osteoderms. These osteoderms are exclusive to plagiosaurines.

Putative cleithrum. Schmidt (1931: fig. 9a, b) illustrated a wedge-shaped bone fragment from Molsdorf (Thuringia) that he interpreted as a cleithrum of *Plagiosuchus pustuliferus* (MB.Am.684; Fig. 8g, h). This triangular bone fragment is flattened; its widened portion is sculptured on its external side, with the partially eroded sculpture being composed of low tubercles and vermicular ridges. The unsculptured part is tapering but its apex is broken. The narrower sides bear broad, deep grooves. At Molsdorf, remains of both *Plagiosuchus* and *Plagiosternum* were found. This bone fragment does not resemble any skull bone known in either taxon. The possibility that the bone represents an ascending process of a clavicle with the sculptured porton being a remnant of the clavicular blade can be ruled out since the clavicles of both *Plagiosuchus* and *Plagiosternum* bear a conspicuous groove between the lateral side of the ascending process and the clavicular blade. This groove is not present in MB.Am.684.

Therefore, we suggest that this bone fragment represents a part of a cleithrum, as already suspected by Schmidt (1931). MB.Am.684 resembles in some respect the cleithrum of the plagiosaurines *Gerrothorax* and *Plagiosaurus* (Nilsson, 1945; Witzmann & Schoch, 2024), although with significantly different proportions. If the cleithrum interpretation is correct, then the sculptured part of MB.Am.684 is the lateral surface of the cleithral head, which is lateroventrally inclined as in the plagiosaurine cleithrum. The unsculptured, pointed part would be the clavicular process, which articulated with the ascending process of the clavicle. The presence of a distinct anterior and posterior concavity would be unusual for a temnospondyl cleithrum. However, the anterior groove and shelf could be homologous to the area clavicularis and the posterior groove to the area scapularis of plagiosaurines. In contrast to MB.Am.684, these areas are larger and the processus clavicularis is much shorter in plagiosaurines (Nilsson, 1939, 1945; Shishkin, 1987; Witzmann & Schoch, 2024). Because of these differences and the fact that the cleithrum of *P. pustuliferus* has a different morphology, without a sculptured head (Schoch et al. in prep.), MB.Am.684 could belong to *Plagiosternum* whose cleithrum is still unknown. This interpretation, however, is contradicted by the fact that the sculpture of the cleithrum is tubercular and vermicular rather than reticulate, but it cannot be ruled out that the sculpture was variable in different parts of the body. This question can only be clarified by further finds of *Plagiosternum*.

Humerus. A single, relatively small humerus from the type horizon of Tiefenbach (MHI 1027) probably stems from *P. granulosum* (Fig. 8d, e). It differs substantially from both plagiosaurines and plagiosuchines, but the comparison is difficult because of the heavily worn condition of the bone. This humerus is tetrahedral with a well expanded distal end aligned at nearly a right angle to the proximal end. This distal end lacks any trace of a supinator and has no condyles. The only distinctive feature is a long deltopectoral crest extending from the proximal head to about midlevel of the element.

Axial skeleton. Altogether, some eight intercentra and one atlas from the type horizon were referred to *P. granulosum* (Fraas, 1913; Huene, 1922). Ribs and neural arches remain unknown.

A single fragmentary atlas from Neidenfels (MHI 1113; Fig. 8a–c) is low with clearly separated facets. The neural arch is broken. The element is much shorter than in plagiosuchines and plagiosaurines, and the facets are not as widely separated as in other plagiosaurids. Unlike in plagiosaurines, there is no medioventral projection between the facets, and the facets themselves are taller than in *G. pulcherrimus* and ovoid in shape (Fig. 8a–c).

Intercentra of the trunk region are generally much rarer than dermal bones, but have been found in several localities (MHI 1113, SMNS 8736, 11830). The intercentra are lower than in plagiosaurines and plagiosuchines, which might be caused by crushing. Some are remarkably short, similar to the atlas, but others are similar in length to those of other taxa. The ventral side is usually the best preserved one, gently concave with a smooth and locally pitted surface. The lateral side bears a pronounced parapophysis near the posterior margin and in some specimens the anterior margin is also slightly raised. This condition resembles that of *Plagiosuchus pustuliferus*, where the largest part of the parapophyseal facet is formed by the posterior side. This contrasts with plagiosaurines, where the facet is almost equally formed by the anterior and posterior sides, with the result that each intercentrum bears an anterior and a posterior half of a parapophysis. The dorsal side of the intercentra is mostly crushed or worn, but in SMNS 8736, raised paired facets for the neural arch are preserved in their posterior part: they are shorter and less clearly defined than in other plagiosaurids (SMNS 8736; Fig. 8i, j).

Osteoderms and gastral scales. The absence of flanges along the posterior margin for the articulation of ventral osteoderms (known from plagiosaurines) suggests that these were absent in *P. granulosum*. There is also no evidence of any dorsal osteoderms in this taxon. This agrees with the findings of Shishkin (1987) on *Plagiorophus danilovi*. However, the posterior projections along the margin of the interclavicle do suggest the presence of gastral scales with which they probably articulated. The size and shape of the projections agree with gastral scales of the slender elongated type known in *Plagiosuchus pustuliferus* and *Gerrothorax pulcherrimus* (Nilson, 1937; Witzmann, 2011). The plesiomorphic pattern of gastral scales in temnospondyls consists of posteromedially directed rows of scales running parallel to the posterolateral margins of the interclavicle, which meet anteromedially directed rows of scales posterior to the interclavicle in a so-called nodal point (Witzmann, 2007, 2011). The projections on the posterior interclavicular margin of *P. granulosum* indicates that the anteromedially directed rows of scales articulated directly with the interclavicle, and that neither posteromedial rows nor nodal point were present. A similar pattern of anteromedially directed scales without a nodal point is present in *Gerrothorax pulcherrimus* (Nilsson, 1937).

Ontogeny and size disparity. The preserved skulls range in length between 13.5 and 20.5 cm (Fig. 5). The partial skulls and skull elements from the type locality document a continuous range of sizes between these extremes. The preserved clavicles span a still wider range of sizes (Fig. 7a–c).

The smallest diagnostic specimens of *P. granulosum* are juvenile clavicles (SMNS 97153: 7 cm; MHI 1805: 9 cm)

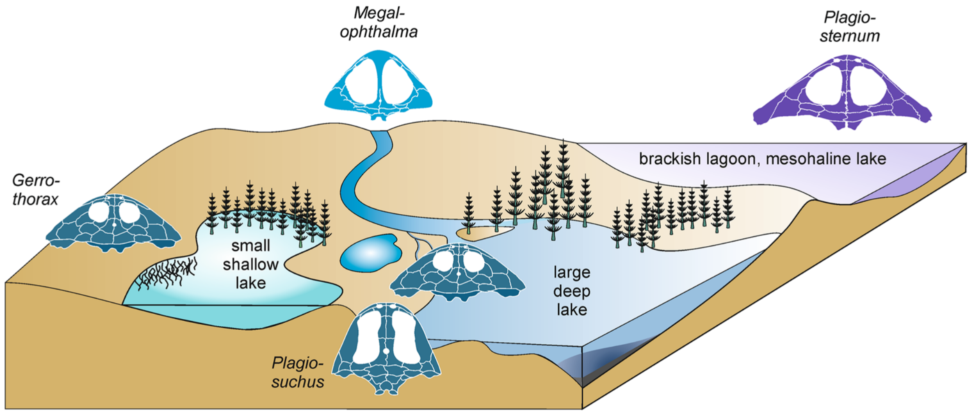


Fig. 9 Palaeoenvironments represented by the Lower Keuper (Erfurt Formation) in southern and central Germany and plagiosaurid taxa mapped onto their preferred habitats

from Vellberg-Eschenau, suggesting a skull length of 5.5 and 7.4 cm, respectively. This estimation is possible thanks to the preservation of both pectoral girdle and mandible on the same block from the E4 horizon at Vellberg-Eschenau (SMNS 90698). The juvenile clavicles bear a distinctive ornamentation that consists exclusively of thin, curved radial ridges. In some subadult specimens, this pattern is still preserved in traces, albeit overprinted by the adult reticulate pattern (Fig. 9).

In the preserved skulls, there is no substantial change in the ornamentation pattern, but the cranial morphology differs between the smallest and largest specimens. In the larger skulls (SMNS 13168, 56614), (1) the orbits are about 15–20% longer, (2) the posterior margin of the skull is medially convex but markedly concave between the tabular and quadratojugal, (3) the parietal has become proportionately longer at the expense of the postparietal, (4) the supratemporal is foreshortened and laterally not expanded, (5) the occipital condyles are substantially larger in proportion, (6) the subtemporal fenestra is larger and (7) the palatine is narrower than in juvenile specimens. Although the general outline of the skull did not substantially change, the lateral margin of juveniles is gently curved in S-shape fashion, whereas it is straight in adults.

Discussion

Ontogeny and evolution of the plagiosaurid ornamentation

The ontogeny of stereospondyls differs from that of other temnospondyls and lissamphibians in the early establishment of adult characters (Fröbisch et al., 2010). In stereospondyls, the dermal bones were already ornamented with densely placed pits and low ridges in small juveniles (Warren & Hutchinson, 1990). In plagiosaurids, the pustular ornament is a prominent feature, and its morphogenesis has been analyzed in depth by Shishkin (1987). Pustular ornament on dermal skull bones apparently evolved in parallel in the anuran *Pelobates fuscus* (Smirnov, 1995), the dissorophoid *Micropholis stowi* (Schoch and Rubidge, 2005) and the chroniosuchid *Madygenerpeton pustulatus* (Schoch et al., 2010).

In *Plagiosternum granulosum*, like in other plagiosaurids, the smallest bones are still largely consistent with those of adults in shape but differ in ornamentation, which is a common feature in temnospondyls (Boy, 1974). Shishkin (1987: fig. 32) described the divergent patterns of ornamentation in plagiosaurids in detail and proposed a morphogenetic model for their formation. He envisioned two separate ontogenetic pathways: (1) a successive partitioning of initially radial ridges into increasingly shorter ridges that end up in numerous single pustules or (2) a successive merging of radial ridges eventually creating a reticulate pattern.

Closer examination of the different patterns of ornamentation in plagiosaurids reveals a higher regional, individual and ontogenetic diversity than formerly described. We identified ornamental variety in the three major clades of plagiosaurids.

In *Plagiosuchus pustuliferus*, the ornamentation of the clavicle and interclavicle is composed of pustular structures much like in *Gerrothorax pulcherrimus*. In large specimens, these bones were extremely thick and massive in *P. pustuliferus*, and the pustules were larger and more closely set than in juveniles. The pustules are often arranged in radial rows on both elements. In the skull, the ornamentation consists of reticulate ridges, and the labial side of the mandible bears elongate radial or parallel ridges (Damiani et al., 2009). In the preorbital region (premaxilla, maxilla, nasal, lacrimal), the polygons are small. On the parietal and the posterior skull table, the ridges are reticulate or radial, but unusually tall and thickened, with tuberlces or pustules on the parietal, supratemporal, tabular and squamosal. On the frontal, parallel ridges are greatly thickened and house longs series of small round pits. Finally, a large area on the jugal lacks dermal ornamentation. Despite these differences in the ornamentation of *P. pustuliferus*, the reticulate pattern appears to form the underlying one and is likely plesiomorphic for this taxon.

In *Gerrothorax pulcherrimus* and *Plagiosaurus depressus*, both cranial and pectoral dermal bones are covered by pustules that are smaller and more widely spaced than in plagiosuchines. Reticulate or knobby patterns are not present on the skull, but small patches of reticulate patterns may form by amalgamation of pustules. On the clavicle, the pustules may be arranged in radial, subparallel elongated lines that resemble the thin radial ridges in other taxa, especially plagiosternines. This probably led Shishkin (1987) to propose his pathway 1, in which successive partitioning of ridges resulted in lines of pustules.

In plagiosternines and plagiosuchines, the knobby to pustular ornamentation pattern may originate from the excessive growth of reticulate ridges. This pattern diverged especially on the skull roof. It is highly regionalised in *Plagiosuchus pustuliferus*, whereas it remains uniform in *Plagiosternum granulosum*. The reticulate ridges thickened into knobby patterns in the posterior skull table of *P. pustuliferus*, and eventually developed pustules on single points. In *Plagiosternum granulosum*, the reticulate pattern remained small-scale throughout ontogeny, and pustules formed more regularly on the nodal points. This is most apparent in the posterior skull table, labial side of the mandible, and the centre of the dermal pectoral elements.

Even in *Gerrothorax pulcherrimus*, which usually has only low and uniform pustules, these grade into reticulate ridges on some osteoderms. At closer inspection, the pustules appear to have formed by locally intensified growth on an initially low ridge.

The ornamentation of the pectoral girdles varies through ontogeny in *Gerrothorax pulcherrimus* and *Plagiosternum granulosum*, as described by Shishkin (1987). In both taxa, the smallest scapular elements are covered by unusually fine, subparallel ridges. Then, in *Gerrothorax*, the ornamentation grows by a locally differentiated vertical accretion on the pre-existing low ridge, whereas in *Plagiosternum*, it grows by a successive addition of perpendicular ridges connecting parallel or radial ones. The pustular pattern therefore originates along different morphogenetic pathways and within different phases: (i) by local differentiation of juvenile ridges (*Gerrothorax* dermal bones), (ii) by excessive growth on nodal points in reticulate patterns (*Plagiosternum* skulls) and (iii) by a further, very localised modification of knobby ornament on a pre-existing reticulate pattern (plagiosuchine skull table).

Palaeoecology and habitats

The body proportions and anatomical features of plagiosaurids strongly suggest that they were permanently aquatic, bottom-dwelling predators (Hellrung, 2003; Jenkins et al., 2008; Schoch & Witzmann, 2011). However, the difference between plagiosaurid subclades are conspicuous, and they correlate with different environmental setting in which they occur. For instance, *Plagiosternum granulosum* does not only diverge from other plagiosaurids in morphology, but is also found in entirely separate deposits (Mujal et al., 2025). The new finds, along with focused collection at some sites, now permit a comparison of the different palaeoenvironments and their palaeoecological features.

Nitsch (2015) described the sedimentary succession of the Erfurt Formation as falling into three divergent settings: (1) fluvial and deltaic plains, (2) brackish water bodies and (3) shallow marine environments. The numerous fluvial channels have been mapped in many regions and are documented to have formed an extensive delta spanning the central part of the Central European Basin (Wurster, 1964). The fluvial system exceeded the present-day Indus and Mesopotamia systems by far in area, and in phases of raised sea level, the very flat plain was flooded over hundreds of kilometres (Nitsch, 2015: fig. 13.4). This resulted in the regionally consistent sequence of mudstones and dolostones that is so characteristic of the Lower Keuper (Brunner, 1973; Pöppelreiter, 1998; Wagner, 1913). Aigner et al. (1990) interpreted the whole sequence as based on repeated cycles of marine transgression, regression and fluvial progradation.

Many of the vast water bodies that resulted from such flooding events in the Erfurt Formation were oligo- to mesohaline, as suggested by ostracods and bivalves (Urlichs, 1982). These *fossillagerstätten* differ from those of freshwater lakes and swamps by their invertebrate faunas, but also very prominently by the composition of aquatic tetrapods (Hagdorn et al., 2015; Schoch & Seegis, 2016; Schoch et al., 2022). These brackish lagoons and lakes were at least as common and widespread as the numerous smaller freshwater lakes, and probably more common than the shallow marine environments that formed during sea level peaks in phases of marine ingression.

Plagiosternum granulosum is known from brackish lagoons (Vitriolschiefer, E4 within the Untere Graue Mergel) as well as shallow marine deposits (Glaukonitkalk, Blaubank, Untere Dolomite, Albertibank), but has not been found in deposits of freshwater lakes. Its occasional occurrence in river channel sandstones (Hauptsandstein) coincides with the presence of other euryhaline taxa in these channels which are interpreted as estuaries under occasional marine influence (Nitsch, 2015). Alternatively, the rivers might have reworked brackish sediments with their specific fauna.

The earliest evidence of *P. granulosum* is from the Glaukonitkalk in the uppermost Muschelkalk sequence. This shallow marine unit is rich in coquinas containing euryhaline bivalves (*Trigonodus*, *Myophoria*, *Costatoria*). The ostracods indicate brackish rather than fully marine conditions (Hagdorn & Simon, 2020). The top of the Muschelkalk

(Wimpfen Subformation) was eroded in northern Württemberg and its hard components were preserved in the disconformably deposited Grenzbonebed (Reif, 1971).

The slightly younger Grenzbonebed (basalmost Keuper) was interpreted as a tempestite formed by successive tropical storms (Reif, 1982). It covers some 50.000 km^2 and in southern Germany increases in magnitude from West to East, with peaks in the Crailsheim and Rothenburg regions where it reaches 15 cm thickness (Reif, 1971; Wagner, 1913). The fauna of this bonebed is very rich but clearly derived from different primary deposits that include marine, brackish and freshwater taxa (Hagdorn & Reif, 1988). Locally, *P. granulosum* may occur in higher frequency such as the Crailsheim region (Heldenmühle, Tiefenbach, Neidenfels). Occasionally, the last storm event led to the deposition of fresh bones such as the complete skull found at Ummenhofen or the partial skulls from Heldenmühle and Rothenburg (Hagdorn et al., 2015). Despite the wealth of material, the mixed faunas of the Grenzbonebed do not allow a more detailed reconstruction and distinction of the palaeoenvironments. However, the frequency of large intact bones or partial skulls of *P. granulosum* at the top of the bonebed might indicate that brackish conditions prevailed in the last phase or shortly after formation of the bonebed.

An assessment of the palaeoenvironment is easier for many horizons within the Erfurt Formation that also yielded *P. granulosum* in bonebeds and other layers composed of brackish taxa (Hagdorn & Reif, 1988). Nitsch (2015) reported, in the brackish lagoonal facies, dominant sheet sandstones and brackish mudstones and dolostones. In Württemberg, many deposits in the Vitriolschiefer, Estherienschichten, Albertibank, Untere Graue Mergel and Lingula-Sandstein fall into this category. In Thuringia, the Oberes Dunkles Band within the S2o sandstone unit may represent the lagoonal facies, yielding *P. granulosum* along with material of *Mastodonsaurus giganteus* and *Nothosaurus* sp. (Werneburg in Hagdorn et al., 2015).

The best-known *fossillagerstätte* of the brackish-lagoonal facies is the *Bakevellia*-bearing horizon E4, near the top of Untere Graue Mergel at Vellberg-Eschenau (Schoch & Seegis, 2016). This unit was found to range 19 km SE-NW (Vellberg–Bauersbach) and 15 km SW-NE (Vellberg–Neidenfels). At Vellberg-Eschenau, it encompasses a locally developed dolomitic coquina with an erosional surface followed by a sequence of greenish-grey, marly siltstones and claystones (Schoch, 2002; Schoch & Seegis, 2016). The claystones are locally fractured by desiccation cracks indicating intermittent subaerial exposure.

At Vellberg-Eschenau, the siltstones (E4) contain euryhaline taxa such as *Bakevellia goldfussi*, *Acrodus* sp., *Gyrolepis* sp., *Saurichthys* sp. and *Nothosaurus mirabilis*. These are known from many horizons in the Muschelkalk (Hagdorn & Simon, 2020). Remains of *P. granulosum* are common and include dermal bones of the skull and pectoral girdle as well as complete mandibles. Finds of a closely associated mandible and pectoral bones suggest the presence of disarticulated skeletons (SMNS 90698). Furthermore, *Nothosaurus mirabilis* and *P. granulosum* are present with specimens of different growth stages, suggesting that both taxa dwelled this habitat, which is consistent with the abundance of phosphatic coprolites.

The E3-E4 sequences formed in a shallow basin containing a brackish, meso- to brachyhaline water body (Schoch & Seegis, 2016). It probably started with the flooding of the preceding basin, during which the erosional surface was produced. The E3 coquina is consistent with other horizons that have been interpreted as marine ingression by Nitsch (2015). The influx of marine water also carried euryhaline taxa such as the sauropterygian *Nothosaurus mirabilis*. Its continued presence in the brackish E4 sequence indicates that salinity levels were tolerable for this apex predator. Its co-occurrence with the one metre long putative fish-eating *P. granulosum* suggests rich food supply in this shallow water body. Storms occurred regularly, as indicated by the numerous layers covered by *Bakevellia* shells. Consistent with other lagoonal deposits within the Lower Keuper, such as the Vitriolschiefer or Estherienschichten, these beds formed well above the storm wave base which did not exceed 5–10 m (Nitsch, 2015). Microerosional surfaces in some E4 layers are consistent with Pöppelreiter's (1998) reports for brackish mudstone sequences. The presence of mud-cracks in some areas, indicative of desiccation and subaerial exposure, further show the complexity of these settings in terms of environmental conditions.

Salinity tolerance. Our sedimentological data show that *P. granulosum* was restricted to brackish lagoons and large mesohaline lakes. All these environments share brackish conditions either with the typical impoverished brackish invertebrate faunas (*Lingula tenuissima*, *Anodonta gregaria*) or reduced shallow marine faunas (*Bakevellia goldfussi*, *Myophoria transversa*). In richer ecosystems, *P. granulosum* was accompanied by larger sauropterygian predators (Hagdorn et al., 2015).

Raised salinity tolerance has been repeatedly reported for some plagiosaurids (Sanchez & Schoch, 2013; Schoch et al., 2022; Witzmann & Soler-Gijón, 2010). This agrees with data on some other temnospondyls (Laurin & Soler-Gijón, 2001; Moreno et al., 2024a; Steyer, 2002), but in most cases not to the extent observed in *Plagiosternum granulosum*. A notable exception form the early Triassic marine deposits of Svalbard which yielded a diverse assemblage of trematosaurids (Lindemann, 1991). Steyer (2014) suggested that salinity tolerance may have been facilitated by salt or lacrimal glands in euhaline temnospondyls, and the enormous size of the orbits in *P. granulosum* might well have housed such an organ. This raises the question of what caused the convergent increase of orbit size in plagiosaurids.

In *Plagiosuchus pustuliferus*, the orbit assumed a highly irregular outline with emarginations in the region usually occupied by the postorbital in other temnospondyls (Damiani et al., 2009). The loss of circumorbital elements, which occurred convergently in up to three plagiosaurid clades (Witzmann & Schoch, 2024), might well have been triggered by different factors in divergent taxa. In *Plagiosuchus*, dorsal extension of the internal adductor muscle is a likely reason for the emragination and bone loss, paralleling the situation in extant batrachians (Schoch, 2014). Plagiosternines, in contrast, did not have enlarged adductor muscles, as evidenced by the normal size of the adductor fenestra in the mandible. In the particularly large-orbited *Megalophthalma ockerti*, Schoch et al. (2014) hypothesized that it might have housed a huge lenseless eye with a flat retinal plate across the entire orbit, a feature present in some ipnopid teleosts. Finally, *Plagiosternum granulosum* and the new Bear Island taxon are the only large-orbited plagiosaurids that inhabited environments with higher salinity.

Habitats. The body proportions of *P. granulosum* are still not entirely known, but the flattened skull with the low occiput and the vertically reduced pectoral girdle suggest that this plagiosaurid was most similar to the extremely flattened plagiosaurines. It is therefore likely that *P. granulosum* dwelled the floors of well-aerated areas in the above-described lagoons and brackish waters. Provided that this description was correct, the presence of this taxon would be an indicator of oxygenated lake floors. However, the presence of lateral line sulci on the ventral side of the clavicular blades suggests that *P. granulosum* also swam occasionally in the water column to catch prey. Its migration probably occurred during floods and might have been triggered by marine incursions. This would explain why its remains are also found in shallow marine horizons in the Glaukonitkalk, Blaubank, Untere Dolomite, Albertibank and Lingula-Dolomite. *P. granulosum* had a larger gape and longer tooth row than other plagiosaurids suggesting that it fed on larger prey. This might have included the full range of actinopterygians from 5 to 10 cm long polzbergiids (*Dipteronotus*, *Serrolepis*) over redfieldiids up to 30–50 cm long *Saurichthys* and *Gyrolepis*, all of which are known from the same deposits (Böttcher, 2015).

Finally, the find of a plagiosternine dermal bone fragment in the lower Carnian Grabfeld Formation testifies the continued presence of this clade in the Central European Basin (Moreno et al., 2024b). The reticulate ornamentation of this fragment, with raised nodal points, closely resembles that of *P. granulosum*. The deposit in which it was found, the Obere Estherienschichten, is consistent with the brackish lake facies of the Erfurt Formation in salinity levels and faunal composition.

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Declarations

Conflict of interest The authors declare that they have no competing interests.

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