SKULL MORPHOLOGY AND PHYLOGENETIC RELATIONSHIPS OF A NEW MIDDLE TRIASSIC PLAGIOSAURID TEMNOSPONDYL FROM GERMANY, AND THE EVOLUTION OF PLAGIOSAURID EYES

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Abstract: A partial skull from the Lower Keuper (Middle Triassic) of Germany is recognized as belonging to a new genus and species of plagiosaurid temnospondyl. It is readily identified by the following autapomorphies: (1) extremely large orbits medially extended to give very thin interorbital region and cheek; (2) posterior skull table abbreviated, with splint-like supratemporals, postparietals and parietals; (3) supraorbital lateral line sulcus absent on frontal, with blind ending on parietal, and continued at the anterior margin of the postorbital; (4) occiput sloping posteriorly, with subtympanic fossa exposed in ventral view; (5) cultriform process and basicranial suture extremely narrow; (6) mandibular and maxillary teeth very long with crowns markedly curved inwards. The new taxon shares the following derived character states with *Plagiosternum*: (1) the pentagonal shape of orbits; (2) the slender interorbital region and cultriform process; (3) the small-scale, polygonal pit-and-ridge ornament on posterior skull table, with single prominent tubercles rising from ridges. Phylogenetic analysis finds plagiosaurids to be monophyletic within a broad range of temnospondyls, nesting within a clade of short-skulled stereospondyls. *Plagiosuchus* is the most basal plagiosaurid, and *Plagiosternum* forms the sister group to the new taxon. The biological significance of the large orbits of plagiosaurids and their relationships to the eyeballs is discussed. The only type of eyeball that would be feasible for all known plagiosaurids would be a small spherical structure possibly situated near the anterior edge of the orbit. For those plagiosaurs with extremely large shallow orbits like *Plagiosternum* and *Megalophthalma*, a possible adaptation would be a lens-less eye comprising a flat retinal plate across the entire orbit.

Key words: amphibians, eyeballs, Mesozoic, orbits, Stereospondyli, Temnospondyli.

PLAGIOSAURIDS were a small clade of bizarre Triassic temnospondyls that evolved an extremely flattened skull and body and heavy armour formed by numerous interdigitating bony plates (Nilsson 1946; Shishkin 1987; Hellrung 2003). Like few other early tetrapods, their anatomy leaves little doubt that they were exclusively aquatic. Their feeding mechanism, deduced from the structure of the skull, hyobranchial apparatus and mandible, was recently found to have been focused on suction feeding while resting on the bottom of water bodies (Jenkins *et al.* 2008; Damiani *et al.* 2009; Witzmann and Schoch 2013). Based on the anatomy of their branchial arches, evidence for their possession of internal gills has been reported (Schoch and Witzmann 2011). This small clade was not only highly distinct from all other temnospondyls, but in turn falls into three divergent groups which differ substantially in the anatomy of their skulls and postcrania: (1) *Plagiosu-*

chus, retaining a high skull and body, had a single row of osteoderms on its back but countless mineralized spherules in its skin (Witzmann and Soler-Gijón 2010) and a derived, elongated skull that lacked the postorbital, postfrontal and prefrontal bones (Damiani *et al.* 2009); (2) *Gerrothorax*, most heavily armoured, retained a full complement of bones within a wide-parabolic skull but had modified the pectoral and pelvic girdles correlating with the flattened trunk (Hellrung 2003; Schoch and Witzmann 2012; Witzmann and Schoch 2013); and (3) *Plagiosternum*, the largest genus whose skull was intermediate in height but had huge orbits framed by strut-like medial and cheek bones (Warren 1995). The three genera also differ substantially in the structure of the dermal ornament, which makes even small fragments readily identifiable.

Here, we report a fourth taxon from the Middle Triassic Lower Keuper of southern Germany. The find

preserves a fairly large portion of the skull and mandible, sufficient to diagnose it as a new species. More importantly, the overall anatomy is so divergent from the aforementioned genera that it adds essential data to our knowledge of the diversity of plagiosaurids. The present study has the following four objectives: (1) diagnose the new taxon; (2) describe its anatomy; (3) assess the bearing of the new find on plagiosaurid phylogeny as well as the origin of the group which is still in a state of controversy; and (4) discuss the relationship of the eyeballs to the huge orbits of plagiosaurids.

MATERIAL

The specimen under study is a partial skull preserving the orbits, posterior skull table and large parts of the palate, and the anterior portion of the left mandibular ramus. It is stored at the Muschelkalkmuseum Hagdorn, Ingelfingen, Germany, under inventory number MHI 2047. The skull measures 158 mm midline length as preserved and approximately 190 mm in total; the greatest skull width is unknown, because the cheek regions are broken off on both sides.

Anatomical abbreviations. cor-t, coronoid teeth; de-t, dentary teeth; ec, ectopterygoid; eo, exoccipital; f, frontal; fom, foramen magnum; frp, frontoparietal; ifp, interfrontoparietal; j, jugal; l, lacrimal; m, maxilla; n, nasal; or, orbit; p, parietal; pi, pineal foramen; pl, palatine; pm, premaxilla; po, postorbital; pof, postfrontal; pp, postparietal; prf, prefrontal; ps, parasphenoid; pt, pterygoid; qj, quadratojugal; ret, retina; sq, squamosal; st, supratemporal; sta, stapes; sta-fo, stapedial foramen; stf, subtympanic fossa; sym, symphysis; ta, tabular; v, vomer.

Institutional abbreviation. MHI, Muschelkalkmuseum Hagdorn, Ingelfingen, Germany.

SYSTEMATIC PALAEONTOLOGY

This published work and the nomenclatural acts it contains have been registered in Zoobank: http://zoobank.org/References/D0318B76-8359-4DD2-BA0F-38ED7A7B09D5

TEMNOSPONDYLI Zittel, 1888
STEREOSPONDYLI Zittel, 1888
PLAGIOSAURIDAE Jaekel, 1914
PLAGIOSTERNINAE Shishkin, 1986

MEGALOPHTHALMA gen. nov.

LSID. urn:lsid:zoobank.org:act:/8CF2372D-040F-41A9-9D38-8B0FC0FE229E

Type species. *Megalophthalma ockerti* sp. nov. from the Middle Triassic of Germany.

Megalophthalma ockerti sp. nov.
Figures 2A–D, 3A–G

LSID. urn:lsid:zoobank.org:act:C63B042E-5199-4DF2-961A-3435883010BE

Derivation of name. The genus name refers to the huge orbits (from the Greek *megale* meaning large and *ophthalmós* meaning eye), and the species name honours amateur palaeontologist and geologist Willi Ockert, who found and prepared the skull in 1985.

Holotype. MHI 2047, a partial skull with anterior portion of the left mandibular ramus.

Material. The holotype is the only known specimen.

Diagnosis. *Megalophthalma ockerti* has a range of readily identified, unique features. Autapomorphies: (1) orbits medially extended to give very thin interorbital region (only half the width compared to *Plagiosternum granulosum*) and cheek; (2) posterior skull table abbreviated (only two-thirds the length compared to *P. granulosum*), with splint-like supratemporals, postparietals and parietals; (3) supraorbital lateral line sulcus absent on frontal, with blind ending on parietal, and continued at the anterior margin of the postorbital; (4) occiput sloping posteriorly, with subtympanic fossa exposed in ventral view; (5) cultriform process and basicranial suture extremely narrow; (6) mandibular, palatine-ectopterygoid and maxillary teeth very long with crowns markedly curved inwards. *Megalophthalma ockerti* shares with *Plagiosternum* the following derived character states: (1) pentagonal shape of orbits; (2) slender interorbital region and cultriform process; (3) small-scale, polygonal pit-and-ridge ornament on posterior skull table, with single prominent tubercles rising from ridges.

Occurrence. Schumann limestone quarry, Vellberg, Baden-Württemberg, southern Germany.

Stratigraphical range. Hauptsandstein (main sandstone unit) of Lower Keuper (Erfurt Formation, ku1), Longobardian (Upper Ladinian), upper Middle Triassic, dating 240 Ma (Menning and Hendrich 2005; Fig. 1).

Description

General structure. The skull differs from that of all other plagiosaurids (and temnospondyls) in the enormous size of the orbits

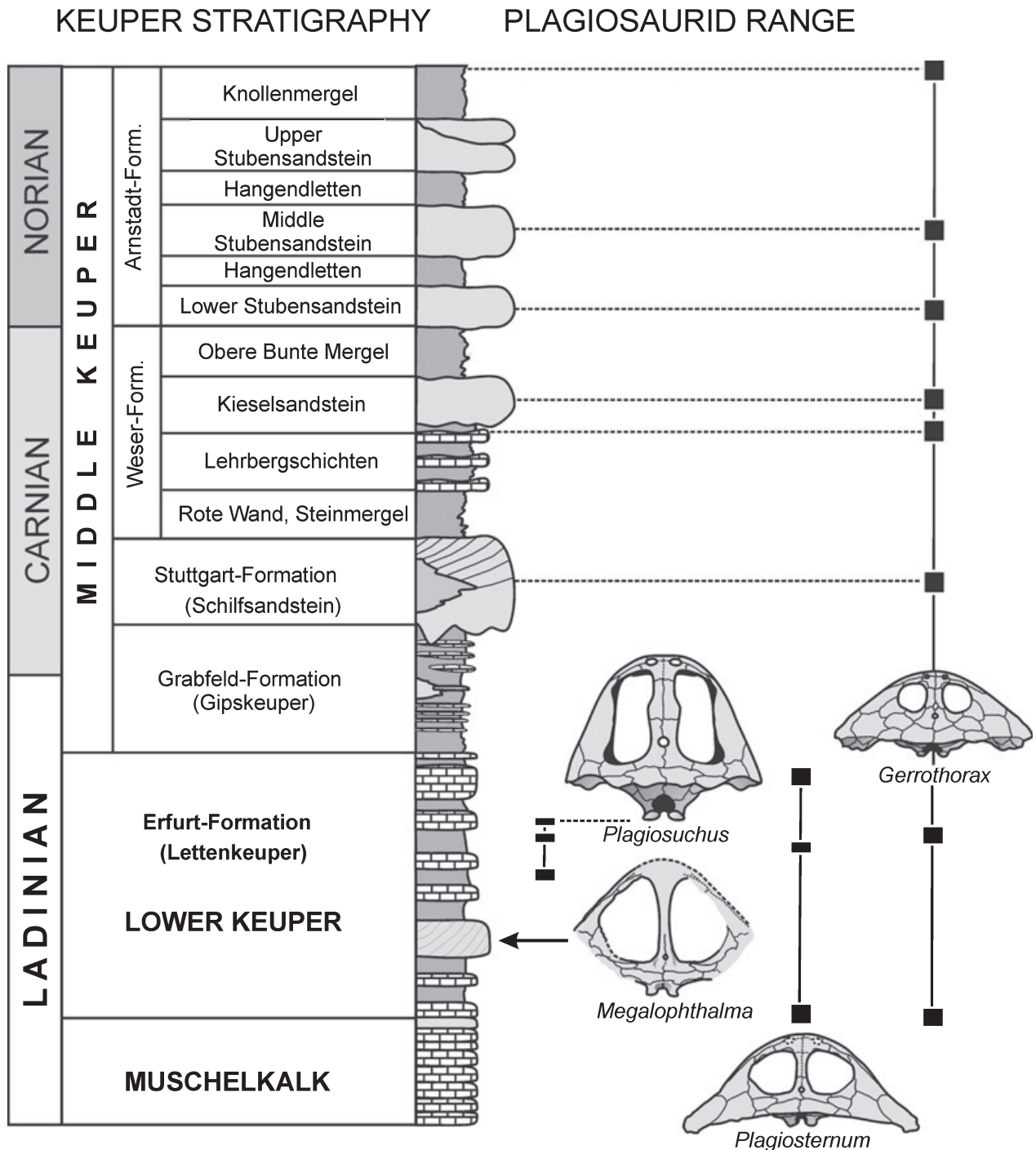## KEUPER STRATIGRAPHY   PLAGIOSAURID RANGE

FIG. 1. Stratigraphical range of plagiosaurids in the Middle and Upper Triassic of the Germanic Basin.

combined with an extreme reduction in interorbital region and posterior skull table (Fig. 2). The outline of the preserved skull portion is generally similar to that of *Plagiosternum granulosum*, giving a triangular overall shape. However, the unknown cheek region of *Megalophthalma* precludes further comparisons. In the following description, we shall refer to the other plagiosaurids by their generic names, represented by their most completely known species, with *Plagiosternum granulosum* as *Plagiosternum*,

Gerrothorax pulcherrimus as *Gerrothorax* and *Plagiosuchus pustuliferus* as *Plagiosuchus*.

Dermal ornament. Throughout the preserved regions of skull and mandible, the ornament (or sculpture) of dermal skull bones is similar to that of *Plagiosternum*. It consists of numerous small polygons framed by high ridges which bear tubercles at the junction points of the ridges (Fig. 2A). In general, the
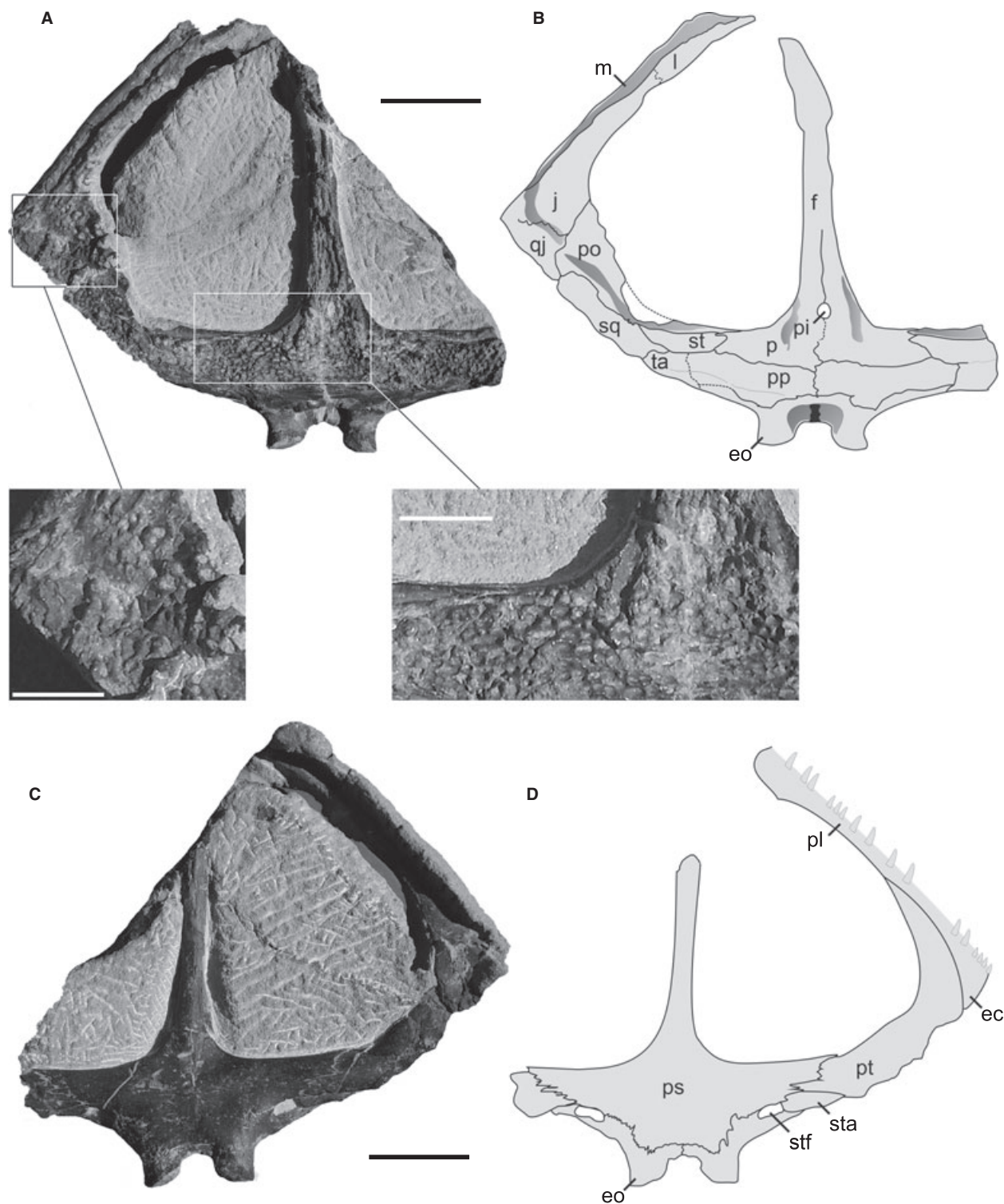
FIG. 2. Type and only specimen of *Megalophthalma ockerti* gen. et sp. nov. (MHI 2047) from the Middle Triassic of Germany. A–B, dorsal view with higher resolution photographs of dermal ornament; C–D, ventral view. All scale bars represent 50 mm, with the exception of the close-up photographs, in which they represent 10 mm.

ornament is not as uniform as in *Plagiosternum*, with substantial variation between jugal, parietal and frontal regions, whereas the parietal, supratemporal, postparietal and tabular regions share the typical plagiosternine, small polygons; the jugal and postorbital regions have fewer, larger and more irregularly placed polygons with more numerous tubercles; and

finally, the frontal region bears elongated ridges without any polygons.

Lateral lines. Sulci of the lateral line system are well expressed on the lateral margin of the parietal, the anterior margin of the postorbital and all along the jugal (Fig. 2A–B). Their course differs substantially from that in *Plagiosternum* in the following points: (1) the parietal sulcus ends just posterior to the posterior margin of the orbit (in *Plagiosternum* it continues onto the postorbital); (2) the postorbital sulcus runs at the anteriomedial margin of the element (in *Plagiosternum*, it is well offset from the margin); and (3) the frontal sulcus is present only in its anterior portion, confined to the lateral margin of the element.

Snout. Only the anterolateral margin of the orbit is preserved, exposing an elongated and slender lacrimal, but no naris (Fig. 2A–B). The preserved portion is similar to that of *Plagiosternum*, but the reconstruction suggests that the tip of the snout must have been narrower.

Orbit region. In *Plagiosternum* and *Plagiosuchus*, the prefrontal and postfrontal are absent. Consistent with this, the postfrontal is absent in *Megalophthalma*, but because of incomplete preservation, it cannot be ascertained if the prefrontal was present or not. In contrast to *Plagiosuchus*, the postorbital is present and generally similar to that of *Plagiosternum*. However, the postorbital is more slender in *Megalophthalma* and anterolaterally more extended, framing the larger orbit. The most typical orbital features shared between *Plagiosternum* and *Megalophthalma* are the markedly oblique posterolateral margin of the orbit. *Megalophthalma* is unique in having strut-like frontals with a longitudinal ridge ornament (Fig. 2A–B). The midline suture is difficult to trace but appears to be continuously present in the frontals. The small, round pineal foramen is located in a similar position as in *Plagiosternum*, slightly anterior to the posterior margin of the orbit.

Posterior skull table. This region is dominated by the parietals and postparietals which, in contrast to other plagiosaurids, are of similar length (Fig. 2A–B). The supratemporal is extremely short, forming a thin strut-like bone wedged in between the equally slender tabular and postorbital. The parietal and postparietal have a very regular ornament of small polygons, which are round on the parietal, but transversely oval on the postparietal, tabular and supratemporal. The medial margin of the parietal sulcus is framed by a sagittal series of tubercles, as is the frontal. The posterolateral corner of the postparietal bears a small area with raised pustules, as well.

Cheek. The anterior cheek region, as far as preserved, includes the jugal and anterior rim of the squamosal; the posterolateral regions are broken off (Fig. 2A–B). The postorbital is extremely elongated, extending from the posterior end of the orbit in an anterolateral direction to about its mid-level. Its anterolateral, broader portion is aligned at an angle of 120° towards the posteromedial rod-like part. The anterolateral part of the postorbital is covered by large tubercles. The squamosal forms a slender, pointed medial projection sutured to the supratemporal.

Palate. The palate elements parallel those of the skull roof in being extraordinarily slender (Fig. 2C–D). The cultriform process, palatine ramus and especially the basal plate of the parasphenoid form simple, strut-like bones, framing very large interpterygoid vacuities. The parasphenoid and pterygoid are edentulous, and their surface is smooth. The ventral side of the cultriform process is markedly rounded, whereas the central portion of the basal plate is gently concave. The basipterygoid region is unusually narrow for a stereospondyl, resembling the condition in dissorophids in shape and in the pronounced serrated suture line. Neither the choana nor the adductor chamber is preserved. However, the palatine and anterior part of the ectopterygoid are well preserved with a continuous row of teeth. Together with the mandible (see below) and the maxilla, both bones reveal an interesting dentition pattern: seen from inside the buccal cavity, the coronoid teeth are the smallest, followed by the row of much larger teeth on the palatine and ectopterygoid, then the very large dentary teeth and finally the substantially smaller but more numerous maxillary teeth. A further characteristic is the posteroventrally exposed subtympanic fossa (Figs 2C–D, 3A–B), which points exclusively posteriorly in other plagiosaurids (Shishkin 1987; Witzmann *et al.* 2012).

Stapes. The present find is exceptional in preserving both stapes in articulation. So far, the plagiosaurid stapes is only known from CT scans of *Gerrothorax* from Kupferzell (Witzmann *et al.* 2012). The stapes of *Megalophthalma* resembles that of *Gerrothorax* in being a robust element of roughly tetrahedral shape, with a dorsoventrally expanded footplate and a sheet-like, horizontally broadened distal process (Fig. 3C). A large stapedial foramen is present slightly medial to mid-length, pointing posteriorly. Details of articulation (both the footplate with the braincase and the distal end) are not exposed. The stapes of *Gerrothorax* and *Megalophthalma* further resembles the blade-like condition of the stapes in *Batrachosuchus* as figured by Watson (1956, text-fig. 7). Witzmann *et al.* (2012) suggested that the stapedial morphology of *Batrachosuchus* and plagiosaurids might be regarded as a paedomorphic trait, retaining the larval growth trajectory rather than transforming into a rod-like element as in most other temnospondyls.

Mandible. The anterior portion of the left mandibular ramus is preserved in the holotype (Fig. 3D–G). Two tooth rows, one on the dentary and one of the coronoids, are well visible, although the particular bones of the mandible cannot be distinguished by sutures. The dentary teeth range in length between 9 and 11 mm, being almost double the length of the teeth in a similar-sized *Plagiosternum*. The crowns are markedly bent inwards. The coronoid teeth are less than half the length of those in the dentary, but form a continuous arcade paralleling that of the dentary, very much like in *Plagiosternum*. This differs from the situation in *Gerrothorax* where the coronoid bones have smaller teeth well separated from each other (Hellrung 2003; Schoch and Witzmann 2012) and from *Plagiosuchus* which lacks coronoid teeth altogether (Damiani *et al.* 2009). In the symphysis, two tooth rows are present. Whereas the coronoid teeth are a similar size throughout, the dentary teeth become increasingly longer towards the symphysis. There is no trace of symphyseal fangs, which is a
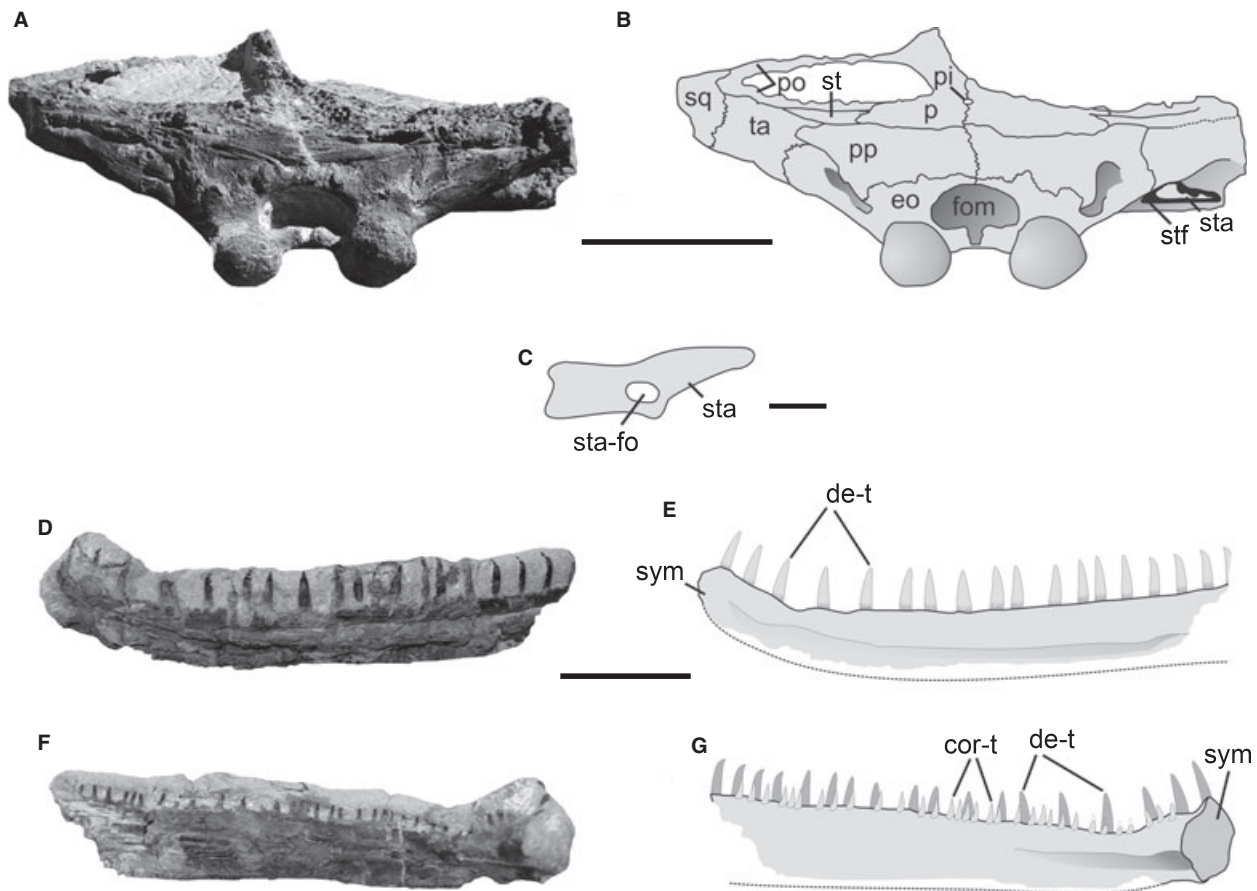
FIG. 3. Type and only specimen of *Megalophthalma ockerti* gen. et sp. nov. (MHI 2047) from the Middle Triassic of Germany. A–B, occipital view; C, reconstruction of stapes in posterior view; D–E, mandible in labial view; F–G, mandible in lingual view. Scale bars represent 50 mm in A–B, D–G and 10 mm in C.

consistent feature among plagiosaurids. The splenials are characterized by enlarged tubercles positioned along the ventral face of the mandible, again a feature shared with *Plagiosternum*.

The reconstructed skull roof and palate of *Megalophthalma* are shown in Figure 4.

PHYLOGENETIC ANALYSIS

Although plagiosaurid morphology varies substantially between genera, a set of highly derived characters suggests their monophyly (Shishkin 1987; Warren 2000; Hellrung 2003; Schoch 2008a, 2013). At the same time, their position within the higher-rank phylogenetic framework of temnospondyls remains controversial (Panchen 1959; Milner 1990, 1997; Yates and Warren 2000; Schoch 2008a). Studies of plagiosaurids should pursue two aims, the rigorous test of relationships both within the group and within temnospondyls by parsimony analysis. Here, we pursue the first aim, and prompted by the discovery of

Megalophthalma ockerti, the following phylogenetic questions will be addressed:

1. Which is the closest relative of *Megalophthalma*?
2. Is Plagiosauridae really a monophyletic taxon? This question will be addressed by including the four most completely known plagiosaurids: *Plagiosuchus pustuliferus*, *Gerrothorax pulcherrimus*, *Plagiosternum granulosum* and *Megalophthalma ockerti*.
3. Given their monophyly, what are the ingroup relationships of plagiosaurids? In particular, are the similarities in orbit size and skull bone reduction shared by *Plagiosternum*, *Megalophthalma* and *Plagiosuchus* synapomorphies or are these traits more likely to have evolved convergently?

In the present analysis, we are unable to focus on the broader question of where the plagiosaurids nest exactly among temnospondyls. As we adhere to different views regarding the systematic position of brachyopids and chigutisaurids, a much larger taxon sample would be required to answer that question. To take as broad an
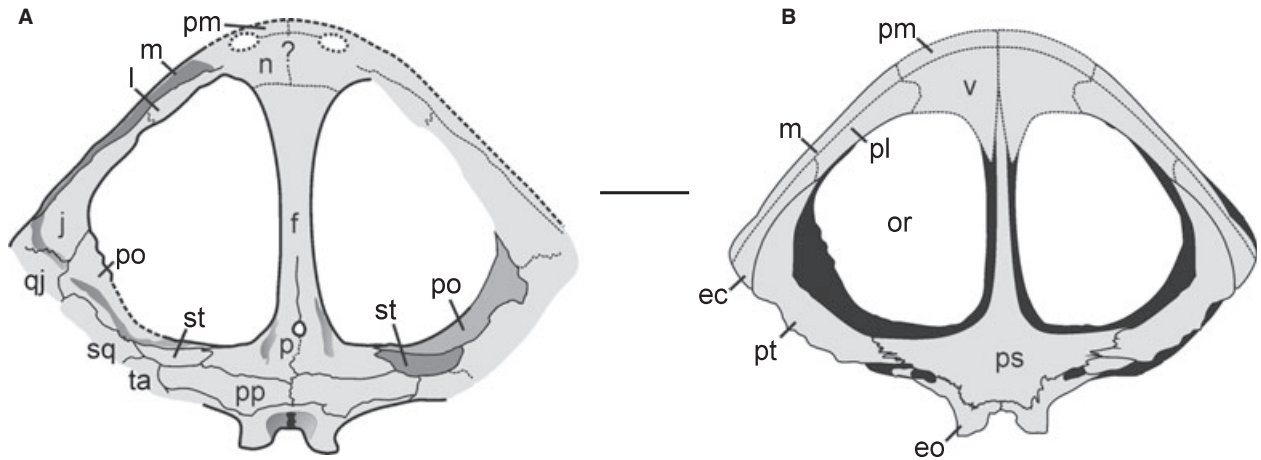
FIG. 4. Reconstructed skull of *Megalophthalma ockerti* gen. et sp. nov. from the Middle Triassic of Germany, based on MHI 2047. A, skull roof; B, palate. Scale bar represents 50 mm.

approach as possible, we have adopted the character-taxon matrix of Schoch (2008*a*) which includes representatives of all major stereospondyl clades and a set of successively more distant outgroups.

Taxa

Outgroups: (1) *Dendrerpeton acadianum* (Holmes *et al.* 1998); (2) *Trimerorhachis insignis* (Case 1935; Pawley 2007; Milner and Schoch 2013); (3) *Sclerocephalus haeuseri* (Boy 1988; Schoch and Witzmann 2009); ingroups: (4) *Uranocentrodon senekalensis* (Van Hoepen 1915); (5) *Lydekkerina huxleyi* (Pawley and Warren 2005; Jeannot *et al.* 2006; Hewison 2007); (6) the Rhytidosteidae as a terminal taxon, based on data in Warren and Black (1985) and *Rhytidosteus capensis* (Cosgriff 1965), *Deltasaurus kimberleyensis* (Cosgriff 1974), *Peltostega erici* (Säve-Söderbergh 1936; Janvier 1983) and *Trucheosaurus major* (Marsicano and Warren 1998); (7) *Siderops kehli* (Warren and Hutchinson 1983); (8) *Batrachosuchus watsoni* (Watson 1956; Warren and Marsicano 2000); (9) *Laidleria gracilis* (Kitching 1957; Warren 1999); (10) *Plagiosuchus pustuliferus* (Damiani *et al.* 2009); (11) *Gerrothorax pulcherrimus* (Hellrung 2003; Jenkins *et al.* 2008; Schoch and Witzmann 2012); (12) *Plagiosternum granulosum* (Damiani *et al.* 2009); (13) *Megalophthalma ockerti* (present work); (14) Capitosauria (Schoch 2000, 2008*b*; Damiani 2001); (15) *Trematolestes hagdorni* (Schoch 2006); (16) *Lyrocephaliscus euri* (Säve-Söderbergh 1937; Mazin and Janvier 1983); (17) *Almasaurus habbazi* (Dutuit 1972); (18) *Callistomordax kugleri* (Schoch 2008*a*); (19) the Metoposauridae as represented by *Metoposaurus diagnosticus* (Milner and Schoch 2004; Sulej 2007). Material of all taxa was examined by the authors.

Characters

Altogether, 108 characters from all parts of the skeleton were considered (see Schoch 2008*a*). Characters 1–100

were adopted from Schoch (2008*a*); the remaining characters are new and listed in the Appendix.

Analysis

The software package PAUP 3.1 (Swofford 1991) was employed. All characters were treated unordered. The analysis was run in the branch-and-bound mode, which was also used to calculate Bremer support values.

Results

The analysis gave two most parsimonious trees requiring 209 steps (CI: 0.56, RI: 0.744, RC: 0.416). In the following list, the supporting synapomorphies are given in brackets, followed by Bootstrap and Bremer support measures; for a list of characters 1–100, please see Schoch (2008*a*). Node 1: Stereospondyli (6, 42, 44, 51-1, 62, 64, 69, 83, 85, 97; Bootstrap: 98, Bremer: 5); Node 2: Postrhinesuchid stereospondyls (33, 34, 53; Bootstrap: 62, Bremer: 1); Node 3: Capitosauria + Trematosauria + rhytidostean group (45, 55, 59; Bootstrap: 98, Bremer: 4); Node 4: Trematosauria + rhytidostean group (18, 51-2; Bootstrap: 61, Bremer: 1); Node 5: Trematosauria (4, 48, 50; Bootstrap: 94, Bremer: 4); Node 6: *Trematolestes*, *Almasaurus*, *Callistomordax*, Metoposauridae (8, 23, 73, 95; Bootstrap: 68, Bremer: 2); Node 7: *Almasaurus*, *Callistomordax*, Metoposauridae (74, 75; Bootstrap: 96, Bremer: 4); Node 8: *Callistomordax*, Metoposauridae (29, 61, 65; Bootstrap: 80, Bremer: 4); Node 9: rhytidostean group (no unambiguous synapomorphies; Bootstrap: 72, Bremer: 4); Node 10: *Siderops*, *Batrachosuchus*, *Laidleria*, and Plagiosauridae (27, 108; Bootstrap: 73, Bremer: 2); Node 11: *Laidleria* and Plagiosauridae (30-2, 77, 99, 100; Bootstrap: 66, Bremer: 2); Node 12: Plagiosauridae (1, 21, 72-2, 82, 84, 104; Bootstrap: 100, Bremer: 4); Node 13: *Gerrothorax*, *Plagiosternum*, *Megalophthalma* (101, 102, 103; Bootstrap: 84, Bremer: 2); Node 14: *Plagiosternum* and *Megalophthalma* (105, 106; Bootstrap: 98, Bremer: 4).

DISCUSSION

Relationships of Megalophthalma *within the Plagiosauridae*

The monophyly of the four plagiosaurid genera found here is not surprising, as the four share six well-defined, unique character states some of which had been highlighted by previous authors (Shishkin 1987; Hellrung 2003; Damiani *et al.* 2009; Schoch 2013). Following the present topology (Fig. 5), the flattening of the skull and body occurred in two steps, with *Plagiosternum* and *Megalophthalma* assuming an intermediate condition between the plesiomorphic *Plagiosuchus* and the highly apomorphic *Gerrothorax*. Although the postcranium is unknown in *Megalophthalma* and largely unknown in *Plagiosternum*, attachment areas for dermal scales on the posteroventral margin of the interclavicle in *Plagiosternum* indicate that the plagiosternine clade possessed gastral (ventral) scales like *Plagiosuchus* and *Gerrothorax* (Witzmann 2011); the presence of a dorsal 'carapace' of osteoderms remains to be documented.

The occiput, posterior skull table and orbital region are highly modified in both *Plagiosternum* and *Megalophthalma*, indicating a sister taxon relationship. The same region is also uniquely derived in *Plagiosuchus*, where in addition to the pre- and postfrontal, the postorbital is also absent. There is little doubt that the full complement of cranial bones in *Gerrothorax* forms the primitive condition. However, despite the shared absence of the postfrontal (and possibly also of the prefrontal, whose presence or absence cannot be determined in *Megalophthalma*) between the three taxa, *Plagiosuchus* is here found to form the basalmost plagiosaurid, grounded on characters from different parts of the skeleton: the higher occiput and overall skull, the longer basicranial region and the much higher (longer) ascending process of the clavicle. Further features unknown in *Megalophthalma* but definitely more primitive in *Plagiosuchus* than all known plagiosaurids are the slender and high cleithrum and ilium. Finally, a squamosal embayment – absent in all other plagiosaurids – appears to be present in *Plagiosuchus* (*contra* Damiani *et al.* 2009).

The plagiosternine type of ornament has often been described as more typical temnospondyl than the pustular ornament of *Gerrothorax* and *Plagiosaurus*. However, in *Plagiosternum*, *Megalophthalma* and *Plagiosuchus*, tubercles and pustules are present in various forms, mostly rising at the junction points of ridges. Especially in the mandible, *Plagiosternum* and *Plagiosuchus* have essentially the same ornament. This suggests that the pustules of *Gerrothorax* may simply be a derived version of the ornament, in which the ridges are not continuous (Shishkin 1973, 1987; see also Witzmann *et al.* 2010).

The eyes of Megalophthalma *and other plagiosaurids*

The unprecedentedly large orbits of *Megalophthalma* stimulated us to consider the relationship of the eyes to the orbits, not only in the new genus but also in all plagiosaurids, specifically whether the eyeball occupied all or most of the orbit, or whether it no longer bore any relationship to the orbit. No sclerotic ring or isolated sclerotic plates have been identified in any plagiosaurid that might give a clue as to the size of the eyeball, so this discussion must have a significantly theoretical content. However, there are constraints on the shape and size of functional eyeballs, and *Megalophthalma* needs to be assessed in this context.

The first detailed life reconstruction of a plagiosaurid depicting the eyes was that of *Gerrothorax* by Nilsson (1946, text-fig. 13, and Fig. 7A here). *Gerrothorax* is one of the smaller plagiosaurids with a skull growing to 80 mm length and 240 mm width. The orbits in the largest skulls were relatively smaller than in other plagiosaurids but were nevertheless circular structures about 40 mm in diameter (Fig. 6A). Nilsson depicted the orbits as completely occupied by large circular lidless dorsally directed eyes. Nilsson's reconstruction was well drawn and detailed, and clearly caught the imagination of those who saw it. As a consequence, subsequent reconstructions of *Gerrothorax* over the last 65 years have almost all been based on Nilsson's figure and depicted *Gerrothorax* or its relatives with very large flattened eyes (Warren 2000, text-fig. 16b; Carroll 2009, pl. 10).

Other plagiosaurid genera all have relatively larger orbits but have not been the subject of life restorations. *Plagiosuchus*, as redescribed by Damiani *et al.* (2009), has a uniquely modified 200-mm-long skull resembling an elongate variant of *Gerrothorax* with huge orbitotemporal fenestrae (Fig. 6B). Each fenestra consists of a relatively rounded anterior lobe and a roughly rectangular posterior extension. These are separated by a slight constriction, and it is clear that only one of the two lobes could have held the eyeball. The rounded nature of the anterior lobes, combined with their proximity to the lacrimal bone, suggests that the eyeballs were situated in the anterior region of the orbitotemporal fenestrae. The eyeballs would thus have been much smaller than the orbitotemporal fenestrae, but if they fully occupied the anterior lobes, they would still have been circular structures about 60 mm in diameter and even larger than those of *Gerrothorax*. The skull of *Plagiosternum* (as reconstructed by Gastou in Damiani *et al.* 2009) is more similar to that of *Gerrothorax* in general shape but has even larger rounded orbits, each 90 mm diameter in a 150-mm-long skull (Fig. 6C). Finally, *Megalophthalma*, described here, has trapezoidal orbits with rounded corners, each orbit mea-
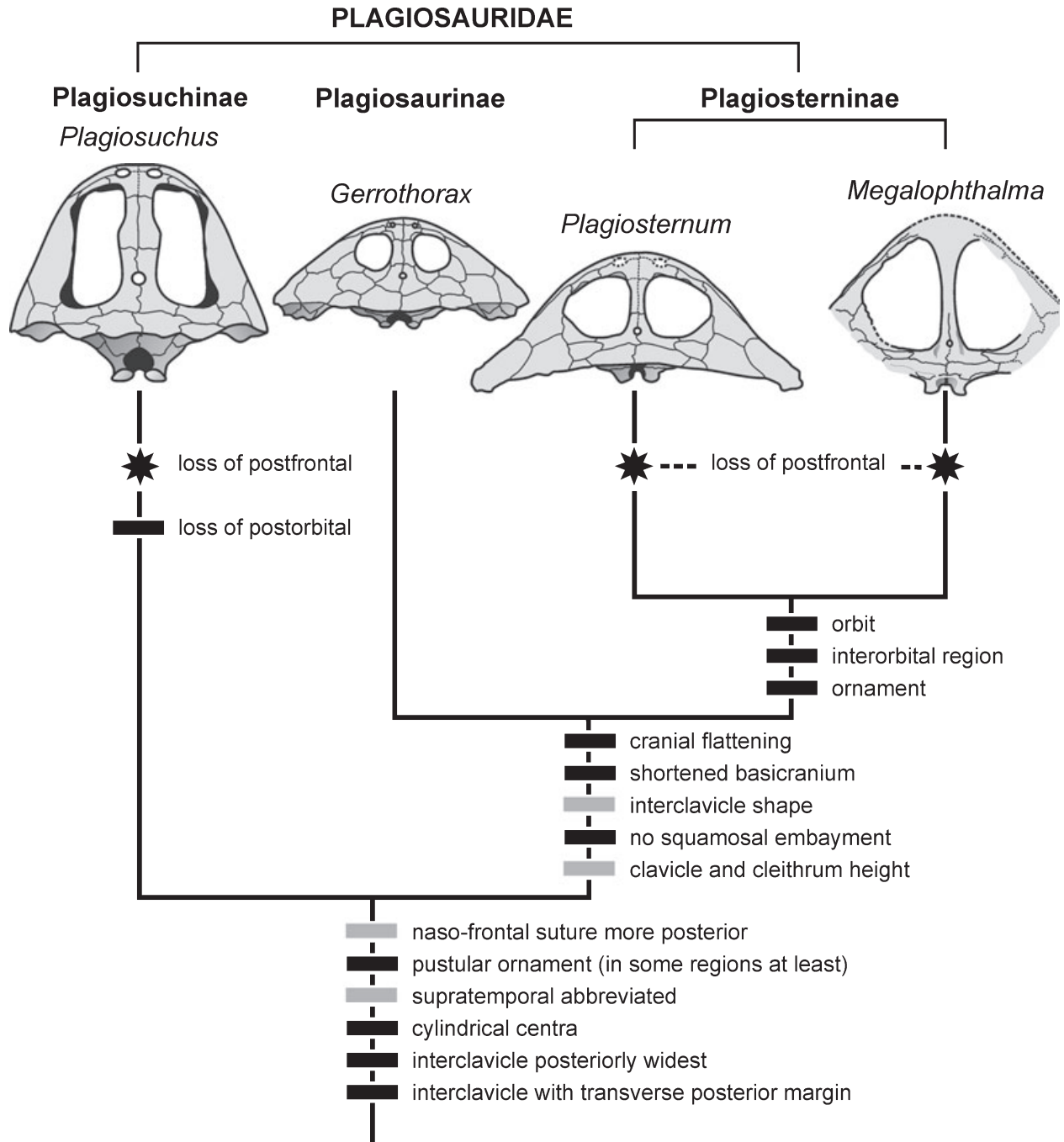
PLAGIOSAURIDAE

FIG. 5. Four-taxon statement of plagiosaurid intrarelationships as found in the present analysis. The six synapomorphies of the Plagiosauridae are listed at the basal node. The grey boxes indicate homoplasies, whereas the black boxes represent unambiguous synapomorphies.

suring about 150 mm long by 100 mm wide in a 200-mm-long skull (Fig. 6D). The skulls of these taxa were extremely shallow. In the case of *Gerrothorax*, *Plagiosternum* and *Megalophthalma*, the material is sufficiently uncrushed that we can be certain that the skulls were only 20–30 mm deep. In *Plagiosuchus*, the only substantial

skull is clearly very crushed, but the anterior region is unlikely to have been more than 50 mm deep.

Thus, within the Plagiosauridae, the length: width: depth of orbital region appears to be as follows. *Gerrothorax*: 40 mm × 40 mm × 30 mm; *Plagiosuchus* (anterior lobe): 60 mm × 60 mm × 50 mm; *Plagiosternum*: 90 mm ×
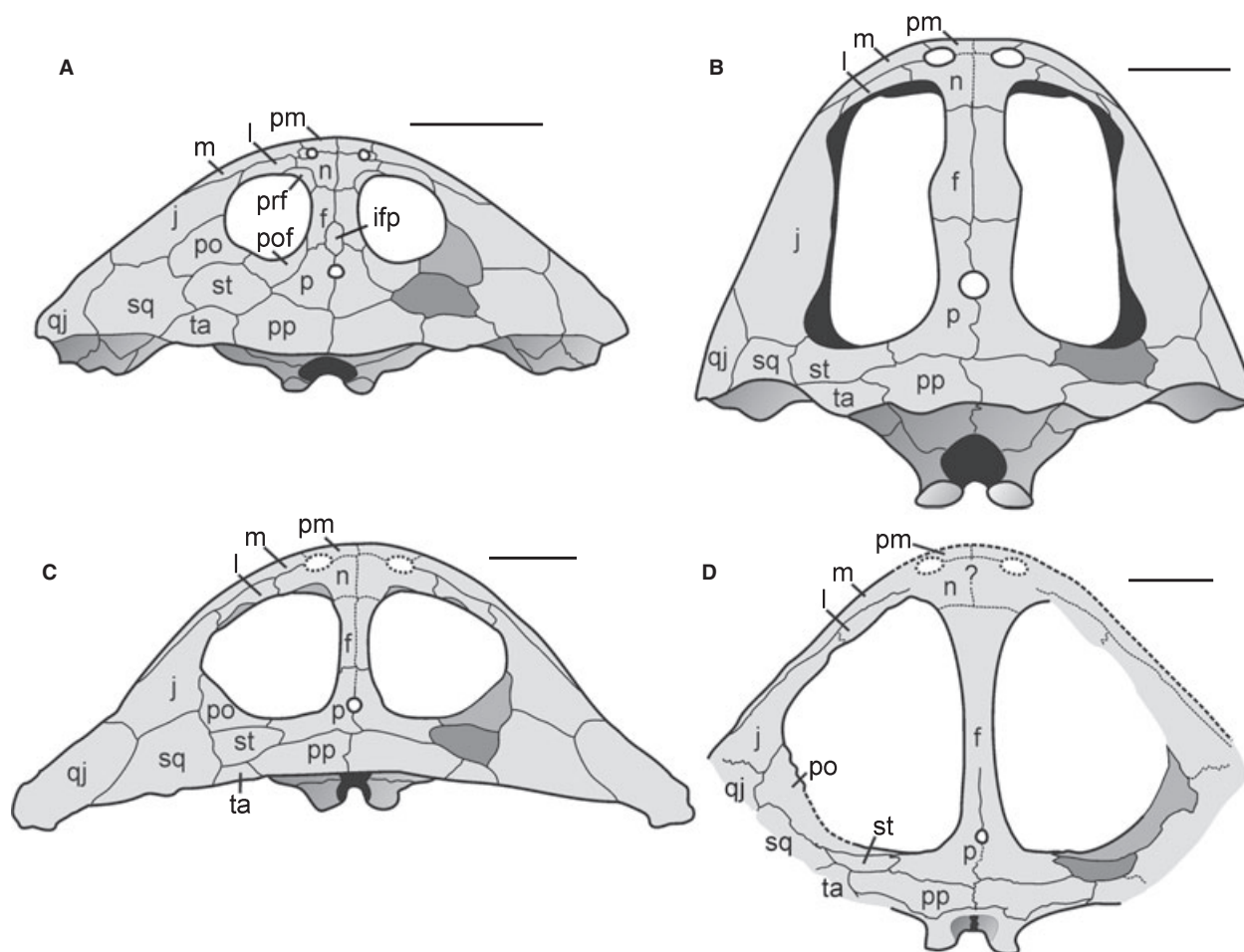
FIG. 6. Reconstruction of the skull roofs of the four best preserved plagiosaurid genera from Germany. Postorbital (when present) and supratemporal are highlighted for comparison. A, *Gerrothorax pulcherrimus* (redrawn from Schoch and Witzmann 2012); B, *Plagiosuchus pustuliferus* (redrawn from Damiani *et al.* 2009); C, *Plagiosternum granulosum* (redrawn from Damiani *et al.* 2009); D, *Megalophthalma ockerti*. Scale bars represent 50 mm.

90 mm × 20 mm; and *Megalophthalma*: 150 mm × 100 mm × 20 mm. From these figures, it can be deduced that if these genera had eyes similar to those depicted by Nilsson in *Gerrothorax*, those of *Gerrothorax* and *Plagiosuchus* would have been somewhat flattened spherical structures, whereas those of *Plagiosternum* and *Megalophthalma* must have been extremely flattened discus-like structures.

Most workers, including the authors, consider that temnospondyls form the stem group of the lissamphibians, in which case the eyes of frogs and salamanders should serve as the primary actualistic model for temnospondyl eyes. Apart from burrowing and troglobitic forms, all modern lissamphibians have nearly spherical eyeballs containing relatively large near-spherical lenses which accommodate by contraction and relaxation of the *protractor lentis* muscles which move the lens towards and away from the retina (Walls 1942). The lens does not change shape during accommodation. In terrestrial frogs and salamanders with relatively large eyeballs that

fill the orbit, the skull is sufficiently deep that the eyeball bulges only slightly into the palate, although it may temporarily be pushed down into the buccal region during swallowing. In the following discussion, four models for plagiosaur eyes are considered, two based on the lissamphibian construction, one based on the eye-shape as depicted by Nilsson and one based on an extant abyssal fish.

A first possibility is that plagiosaurs had large lissamphibian-type spherical eyeballs filling the orbital space. In *Gerrothorax* and *Plagiosuchus*, such an eyeball would be just possible, but in order for it not to protrude significantly into the palate, it would have to form a full hemisphere above the level of the dermal skull roof. In *Plagiosternum* and *Megalophthalma,* such eyeballs would either occupy the mouth completely and permanently, or would exist as two balloon-like structures above the level of the dermal skull roof. The skulls are simply too shallow for a spherical eyeball that fills the orbit.
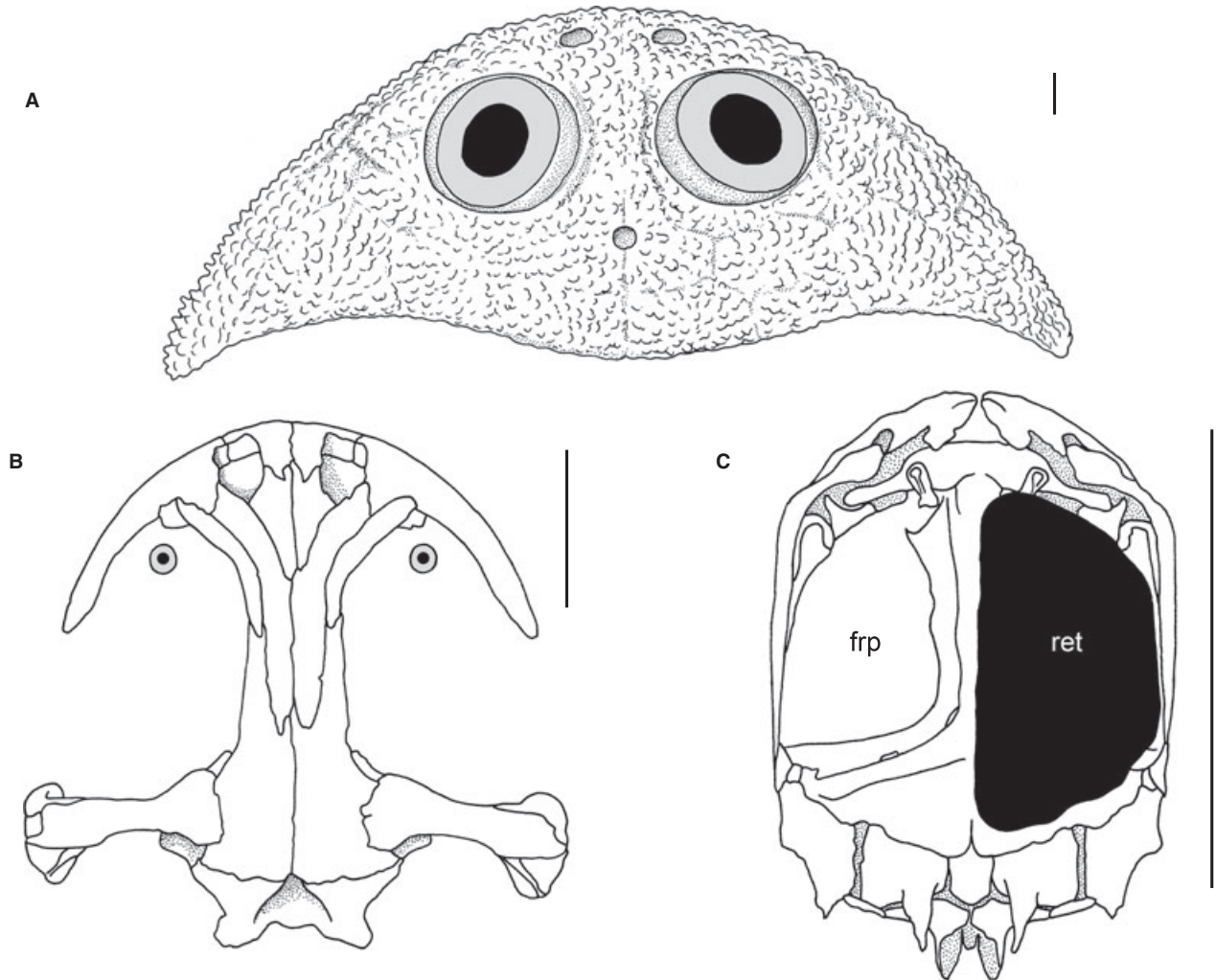
FIG. 7. A, restoration of the head of *Gerrothorax pulcherrimus*, with large flattened eyes filling the orbital region (redrawn from Nilsson 1946, fig. 13); B, dorsal view of skull of *Cryptobranchus allegheniensis* (redrawn from Carroll and Holmes 1980, fig 5, with palate omitted) with position and size of eyes indicated; C, dorsal view of skull of *Ipnops murrayi* (redrawn and simplified from Theisen 1965, fig. 1) showing the extent of the right retina indicated in black. Scale bars represent 10 mm.

The second possibility is that the eyeballs were of similar construction to those in lissamphibians but did not fill the orbits and were relatively small structures. The eyeball might be a spherical structure up to a centimetre in diameter and would then function optically in the same way as those of extant lissamphibians, while not protruding much above the head or into the buccal region. There are precedents for this among living aquatic lissamphibians. As examples, pipid frogs and cryptobranchid salamanders (Fig. 7B) all possess skulls with large orbits but have tiny eyeballs situated at the anterior edge of the orbit. This actualistic precedent could apply to all plagiosaurids although there is little prospect of the exact position of the eyeball being determined. If the eyeballs were tiny, there might be tiny sclerotic plates present which could have been overlooked, but in the absence of other evidence, it seems most plausible to assume that the eyeball was situated near the front of the orbit as in *Pipa* and *Andrias*. This seems to be the only realistic option that would be applicable to all the plagiosaurid taxa.

A third possibility might be that the eyeballs in plagiosaurids were large but had diverged in construction from the lissamphibian condition and had evolved flattened lenses that would permit the entire eyeball to be a flat structure that would fit in the orbit without bulging significantly dorsally or ventrally. This would result in the type of eye depicted by Nilsson (Fig. 7A). Apart from the lack of actualistic analogue in the lissamphibians, the problem here is that a large flattened lens would not be able to focus on a closely situated retina. Such a lens would be in close proximity to the retina below it and yet, because it was a flattened lens, would have a focal

point many centimetres beyond the retina for distant objects and a near infinite focal length for close objects. This seems an unlikely structure to be of use to any animal and even less so in a plagiosaurid with large orbits.

In the case of *Megalophthalma* and possibly *Plagiosternum*, there is a fourth, rather remote, possibility for which there is an actualistic analogue, though not in any way related to the amphibians. Among the abyssal aulopiform teleost fishes is the family Ipnopidae, the type genus of which, *Ipnops*, has lensless eyes. The skull is flattened dorsoventrally, and the two upwardly directed eyes comprise large flat retinas which cover about 80% of the dorsal surface of the head (Theisen 1965, text-fig. 1; and Fig. 7C here). The eyes are covered by a large thin transparent composite frontoparietal ossification which is presumed to give structural support and protection to the retina. This configuration is not only unique within the family but also within the entire Teleostei. The pelagic larvae have normal spherical eyeballs, and the change to the adult structure occurs during metamorphosis (Okiyama 1981). It appears that the eyes are reduced to structures that can detect moving objects, immediately above the fish, which create an unfocussed shadow on the eyes backlit by the light from the surface. As a proposal for a plagiosaur eye, this is admittedly a remote possibility but it would be consistent with the unprecedentedly huge orbital area associated with the flattened skull in *Megalophthalma* and consistent with a lifestyle involving resting on the substratum of a water body and seizing animals moving overhead.

In conclusion, we suggest that the large fish-like eyes that have become associated with plagiosaur restorations since Nilsson's work may not characterize the group. The only type of eyeball that would be equally functionally viable for all known plagiosaurid genera would be a very small spherical structure resembling those found in modern pipid frogs and cryptobranchid salamanders and possibly situated near the anterior edge of the orbit. For those plagiosaurids with less large orbits, larger eyeballs might be possible but they would need to protrude above the head to an extent that would make them very vulnerable structures. For those plagiosaurs with extremely large shallow orbits, a possible adaptation would be a lens-less eye comprising a flat retinal plate across the entire orbit. This would presumably appear as a featureless matte-black surface to the head.

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APPENDIX: ADDITIONAL CHARACTERS

List of characters additional to those of Schoch (2008a)

Characters 1–100 were defined and their states were listed in Schoch (2008a). The following characters were added in the present analysis.

(101) Cranial flattening. Skull table markedly higher than pre-orbital region (0), or equally low from occiput to tip of snout (1).

(102) Basicranium shortened. Pterygoid–parasphenoid suture as long as basal plate is wide (0) or substantially shorter (1).

(103) Clavicle height. Dorsal process of clavicle elongated and pointed (0) or low bearing a concave facet for articulation with cleithrum (1).

(104) Naso-frontal suture. Frontal extending anterior to orbit, level with prefrontal (0) or set well behind anterior orbit margin (1).

(105) Ornament. Dermal bones covered with polygonal ridges (0) or ridges bearing tubercles at junction points (1).

(106) Postorbital. Postorbital forming posterior margin of orbit, with or without lateral process (0), or expanding anterolaterally along lateral orbit margin (1).

(107) Loss of postfrontal. Full complement of circumorbital bones (0) or postfrontal absent (1).

(108) Tabular horn. Tabular with posterior projection (horn), usually offset from main element (0) or without a horn (1).

Character–taxon matrix

	1 Den	2 Tri	3 Scc	4 Ura	5 Lyd	6 Sid	7 Bat	8 Lai	9 Rhy	10 Ger	11 Pls	12 Plm	13 Me	14 Cap	15 Tre	16 Lyr	17 Alm	18 Cal	19 Met
101	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0
102	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0
103	0	0	0	0	0	0	0	0	0	0	0	1	?	0	0	0	0	0	0
104	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0
105	0	0	0	0	0	0	0	0	0	–	0	1	1	0	0	0	0	0	0
106	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
107	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
108	0	0	0	0	0	0	1	1	0	1	1	1	?	0	0	0	0	0	0

Alm, Almasaurus habbazi; *Bat, Batrachosuchus watsoni*; *Cal, Callistomordax kugleri*; Cap, Capitosauria; *Den, Dendrerpeton acadianum*; *Ger, Gerrothorax pulcherrimus*; *Lai, Laidleria gracilis*; *Lyd, Lydekkerina huxleyi*; *Lyr, Lyrocephaliscus euri*; *Me, Megalophthalma ockerti*; *Met, Metoposaurus diagnosticus*; *Plm, Plagiosternum granulosum*; *Pls, Plagiosuchus pustuliferus*; *Rhy, Rhytidosteidae*; *Scc, Sclerocephalus haeuseri*; *Sid, Siderops kehli*; *Tre, Trematolestes hagdorni*; *Tri, Trimerorhachis insignis*; *Ura, Uranocentrodon senekalensis*.