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Growing giants: ontogeny and life history of the temnospondyl *Mastodonsaurus giganteus* (Stereospondyli) from the Middle Triassic of Germany

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Abstract

The Middle Triassic capitosaur *Mastodonsaurus giganteus* was the largest temnospondyl and the dominating aquatic predator in many European freshwater to brackish ecosystems. It is represented by numerous size classes, which are described and analysed for the first time. The documented size range encompasses specimens between 12–15 mm and 1200 mm in skull length. Early growth stages are restricted to dentaries and interclavicles, whereas juveniles are represented by partial skulls, mandibles, and girdles. The smallest specimens already possessed diagnostic features of the taxon, and small juveniles also shared the dermal ornament with larger specimens. The heavy, disc-shaped intercentra were established early in the juvenile phase. Cranial proportions were remarkably conservative throughout ontogeny, with the orbits proportionately decreasing in size only very moderately, the postorbital skull becoming slightly longer and the occipital margin more concave in the largest forms. Analysis of frequency distributions of *M. giganteus* in different Lower Keuper deposits in southern Germany reflects habitat preferences in specific phases of its life cycle. The coal-bearing deposit at Gaildorf yielded unusually large specimens with relatively well-ossified appendicular skeletons. In the more common lake shore facies, only adult specimens are present. In turn, juveniles might have dwelled in calmer environments. Smaller lakes were apparently less attractive than larger or deeper water bodies that provided sufficient resources for several temnospondyls, and juvenile specimens have been identified from all of them. The diverse actinopterygian fish fauna provided prey for all growth stages of the large temnospondyl predators.

Key Words

Capitosauria, lower Keuper, ontogeny, Stereospondyli

Introduction

From the Carboniferous well into the Triassic, the temnospondyls formed a speciose clade of early tetrapods, and relic forms are known in Jurassic and Early Cretaceous strata of Asia and Australia (Warren and Hutchinson 1983; Warren et al. 1997; Schoch 2014). Temnospondyls probably include the stem-group of lissamphibians (Milner 1993; Anderson 2008; Schoch 2014), although in contrast to extant salamanders and frogs, temnospondyls were relatively large predators within or along the shores of rivers, lakes, and lagoons and many exceeded one metre in body length (Schoch and Milner 2000; Steyer and Damiani 2005). During the Triassic, a clade of large-growing and predominantly aquatic forms, the stereospondyls, diversified and populated numerous water bodies. Their robust bones form abundant finds in lacustrine and fluvial deposits around the world. The Lower Keuper (Erfurt Formation) of southern and central Germany yielded many deposits in which a variety of stereospondyls are preserved (Schoch and Seegis 2016; Schoch et al. 2022).

One of these deposits, a small coal and alum mine at Gaildorf, had yielded the historically first remains of temnospondyls (Jaeger 1828; Weber 1992). The heavy coaly siltstones contained 60 cm long skulls and articulated skeletons of the up to 5 m long capitosaur *Mastodonsaurus giganteus*, which soon became an iconic taxon for Triassic deposits (Owen 1841; Meyer and Plieninger 1844; Fraas 1889; Schoch et al. 2023). Based on the complex folds in their large fang teeth, first recognised in *Mastodonsaurus*, the temnospondyls and other early tetrapods became known as labyrinthodonts (Meyer 1842), and they were eventually recognised as relatives of extant amphibians (Quenstedt 1850). After the monographic descriptions of *M. giganteus* by Meyer and Plieninger (1844), subsequent authors added further observations on new material from Baden-Württemberg (Fraas 1889; Huene 1922; Schmidt 1928) and Thuringia (Schmidt 1931; Rühle von Lilienstern 1935), and material attributed to the genus *Mastodonsaurus* was later reported from coeval deposits of Russia (Konzhukova 1955) and Poland (Czepinski et al. 2023), as well as from Anisian lagerstaetten in Germany and arguably southern England (Schoch et al. 2023). A more complete picture of the adult skeleton of this largest temnospondyl could only emerge after new finds had accumulated (Schoch 1999). However, the ontogeny and life history of the taxon remained inadequately known.

This changed with the collection of much additional material as well as numerous data gathered during excavations. This most recent period started with the discovery of the rich fossillagerstätte exposed along a road-cut near Kupferzell-Bauersbach. Located about 22 km north of Gaildorf, this 500 m long section exposed scores of temnospondyl bones, among which were numerous skulls and postcranial remains of *M. giganteus* (Wild 1980; Urlichs 1982; Schoch et al. 2022). The same highway construction exposed further fossillagerstätten near Ilshofen and Wolpertshausen, as did housebuilding at Michelbach an der Bilz (Hagdorn et al. 2015). Finally, the Schumann limestone quarry at Vellberg-Eschenau also yielded large quantities of temnospondyl remains, among which *M. giganteus* is especially common (Schoch and Seegis 2016). The Lower Keuper also yielded material at Bedheim (Rühle von Lilienstern 1935) and Arnstadt, Thuringia (Werneburg and Witter 2005). At closer inspection, these localities preserve slightly different lake faunas, wherein *M. giganteus* is present with specimens of different sizes. These rich finds and the numerous locality data provide a unique opportunity to study the ontogeny and palaeoecology of this largest known temnospondyl. The objectives of the present study are (1) to document the ontogenetic changes in *M. giganteus* and (2) analyse the size distribution of this taxon in the different fossillagerstätten and its palaeoecological implications.

Materials and methods

Material

The material on which the present study is based was collected over a period of almost 200 years (Jaeger 1828; Weber 2013; Schoch and Seegis 2016; Schoch et al. 2022). In the 1820s to 1860s, the Gaildorf locality yielded five skulls of large to giant size (Meyer in Meyer and Plieninger 1844; Meyer 1855). One of them was associated with an articulated postcranial skeleton that was partially figured by Plieninger in Meyer and Plieninger (1844). The surviving material is housed in the collections at Tübingen (GPIT) and Stuttgart (SMNS), and the now-lost giant snout was fortunately described and figured by Meyer (1855).

The skull from Bedheim in Thuringia collected by Rühle von Lilienstern (1935) is housed in the Natural History Museum Berlin (MB), whereas the more recent finds from Arnstadt are housed in the Natural History Museum Schleusingen (NHMS).

Further material accumulated from deposits in Baden-Württemberg are now housed at the SMNS, as is the entire collection from the Kupferzell excavation of 1977 (Schoch et al. 2022). In the 1980s, finds from Michelbach an der Bilz and Wolptershausen came into the MHI collection at the Muschelkalkmuseum Ingelfingen, as did the bulk of the material collected by private collector Werner Kugler in Vellberg-Eschenau (Schoch and Seegis 2016). Since 1998, much additional material was collected by the first author and colleagues at Vellberg that is now housed at the SMNS.

Ontogeny

Analyzing ontogenetic changes in extinct taxa faces a range of challenges, such as incomplete specimens, poor preservation of small stages, taxonomic identification of all growth stages and variation of the studied samples in space and time. Even if restricted to samples collected at the same locality and within one horizon, time averaging is unavoidable in most cases (Boy 2003; Schoch 2009).

The studied material of *Mastodonsaurus giganteus* was collected at numerous localities, nine of which yielded diagnostic skull material (Gaildorf, Markgröningen, Hoheneck, Kupferzell, Vellberg, Michelbach an der Bilz, Wolpertshausen, Bedheim and Arnstadt). Among the diagnostic finds, only Vellberg and Kupferzell produced samples that are rich enough to study ontogenetic changes, whereas the other localities gave only adult or relatively large juvenile specimens. Larval specimens are known from Kupferzell K3 and Vellberg E6, whereas juvenile and subadult specimens are known from Vellberg E6 and E7.

Our focus on the ontogenetic changes in the skeleton of *M. giganteus* is therefore entirely based on the sample from Kupferzell K3, K4 and Vellberg E6 and E7. These two localities represent coeval and regionally neighbouring lake deposits, separated by 25 km distance. They both fall within the topmost units of the Untere Graue Mergel, and the lacustrine facies have been studied in detail (Schoch and Seegis 2016; Schoch et al. 2022).

All the studied specimens referred to *Mastodonsaurus giganteus* were identified on the basis of autapomorphies (see diagnosis). The samples from Vellberg (E6, E7) and Kupferzell (K3, K4) were thoroughly examined for differences between all preserved stages of ontogeny, but we identified only individual variation rather than geographically consistent clusters. We therefore conclude that the samples from Kupferzell and Vellberg, on which our ontogenetic study rests, likely represent the same species and are coeval within the limits of time averaging.

Abbreviations

Anatomical

ap, anterior process; **apv**, anterior palatal vacuity; **ch**, choana; **d**, dentary; **eo**, exoccipital; **f**, frontal; **HHL**, posterior skull length; **HHW**, posterior skull width; **IOW**, interorbital width; **ipv**, interpterygoid vacuity; **ju**, jugal; **la**, lacrimal; **m**, maxilla; **n**, nasal; **nar**, naris; **ORL**, orbit length; **p**, parietal; **pap**, parapophysis; **pf**, postfrontal; **pl**, palatine; **pm**, premaxilla; **pmf**, premaxillar fenestra; **po**, postorbital; **pop**, posterior process; **pp**, postparietal; **prf**, prefrontal; **ps**, parasphenoid; **pt**, pterygoid; **q**, quadrate; **qj**, quadratojugal; **SL**, skull length; **sq**, squamosal; **st**, supratemporal; **stf**, subtemporal fenestra; **ta**, tabular; **vo**, vomer.

Institutional

GPIT, Institut für Geologie Tübingen; **MB**, Museum für Naturkunde Berlin, Leibniz-Institut für Evolutions- und Biodiversitätsforschung; **MHI**, Muschelkalkmuseum Hagdorn Ingelfingen, **NHMS**, Naturhistorisches Museum Schloss Bertholdsburg, Schleusingen, **SMNS**, Staatliches Museum für Naturkunde Stuttgart.

Systematic Palaeontology

Temnospondyli Zittel, 1888
Eutemnospondyli Schoch, 2013
Stereospondyli Zittel, 1888
Capitosauria Yates & Warren, 2000 sensu Damiani & Yates, 2003
Capitosauroidea Säve-Söderbergh, 1935 sensu Schoch, 2008
Mastodonsauridae Lydekker, 1885

Genus *Mastodonsaurus* Jaeger, 1828

Type species. *Mastodonsaurus giganteus* Jaeger, 1828.

Diagnosis. Autapomorphies (Figs 2–6): (1) Premaxilla with openings for symphyseal tusks, set well anterior to naris; (2) orbits large, reaching one-fifth of skull length; (3) jugal slender lateral to orbit; (4) parietal elongated anterior to pineal foramen; (5) lateral line sulci very wide; (6) epipterygoid massive and complex, with six distinct processes (footplate, pr. anterior, pr. dorsalis, pr. sphenethmoidalis, pr. basalis, pr. posterior). Characters shared with other capitosaurs: (a) interclavicle with elongated anterior process; (b) elongate postglenoid area; (c) tall hamate process.

Comment. Character (1) is shared with *C. naraserluki* and *C. mordax* (Fraas 1913; Marzola et al. 2017) and also occurs in one specimen of *C. robustus* (Schoch and Moreno 2024). However, *Mastodonsaurus* differs from all these in having a more elongated premaxilla anterior to the naris and a more lateral and posterior emplacement of the opening with respect to the anterior snout margin (Schoch and Moreno 2024). Character (4) is shared with metoposaurids, but no other taxon with Capitosauroidea.

***Mastodonsaurus giganteus* Jaeger, 1828**

1828 *Mastodonsaurus* Jaeger: p. 35, nomen imperfectum.
*1828 *Salamandroides giganteus* Jaeger: p. 38.
1841 *Labyrinthodon jaegeri* Owen: p. 227
1844 *Mastodonsaurus jaegeri* Meyer: p. 11. pls. 6–7.
1844 *Mastodonsaurus jaegeri* Plieninger: p. 57, pls. 3–7.
1850 *Mastodonsaurus giganteus* Quenstedt: p. 2.
1889 *Mastodonsaurus giganteus* Fraas: p. 32, figs 1–5.
1922 *Mastodonsaurus giganteus* Huene: p. 400, figs 1–12.
1999 *Mastodonsaurus giganteus* Schoch: p. 42, figs 8–49.
2007 *Mastodonsaurus giganteus* Moser and Schoch: p. 1245, figs 2, 3, 5–9.

Holotype. GPIT Am 678, an occiput with exoccipital condyles and posterior portion of parasphenoid, estimated skull length about 61 cm (Moser and Schoch 2007, fig. 9).

Type locality and age. Alum mine with main entrance at Parkschule north of the Kocher River, Gaildorf (Baden-Württemberg, Germany) (Meyer and Plieninger 1844). The fossiliferous sequence was locally restricted and remained poorly constrained for a long time within the Lower Keuper (Fig. 2; Weber 1992; Hagdorn et al. 2015). It encompassed coal, coaly mudstones and siltstones (Plieninger in Meyer and Plieninger 1844; Kurr 1852; Quenstedt 1880). Recent sections measured at briefly exposed outcrops in the vicinity of the type locality confirmed that the sequence was stratigraphically immediately below the Hauptsandstein or main sandstone unit of the Lower Keuper, corresponding to the Estherienschichten (Hans Hagdorn and Theo Simon, pers. comm. 2022), as had been suggested by Weber (1992). The age of the Lower Keuper is considered Longobardian (late Ladinian, late Middle Triassic).

Referred material. Fig. 2 provides an overview of the samples of *M. giganteus* studied in the present paper.

Gaildorf G2 (locus typicus, top of Estherienschichten, below Hauptsandstein). GPIT 1824, occiput (61 cm skull

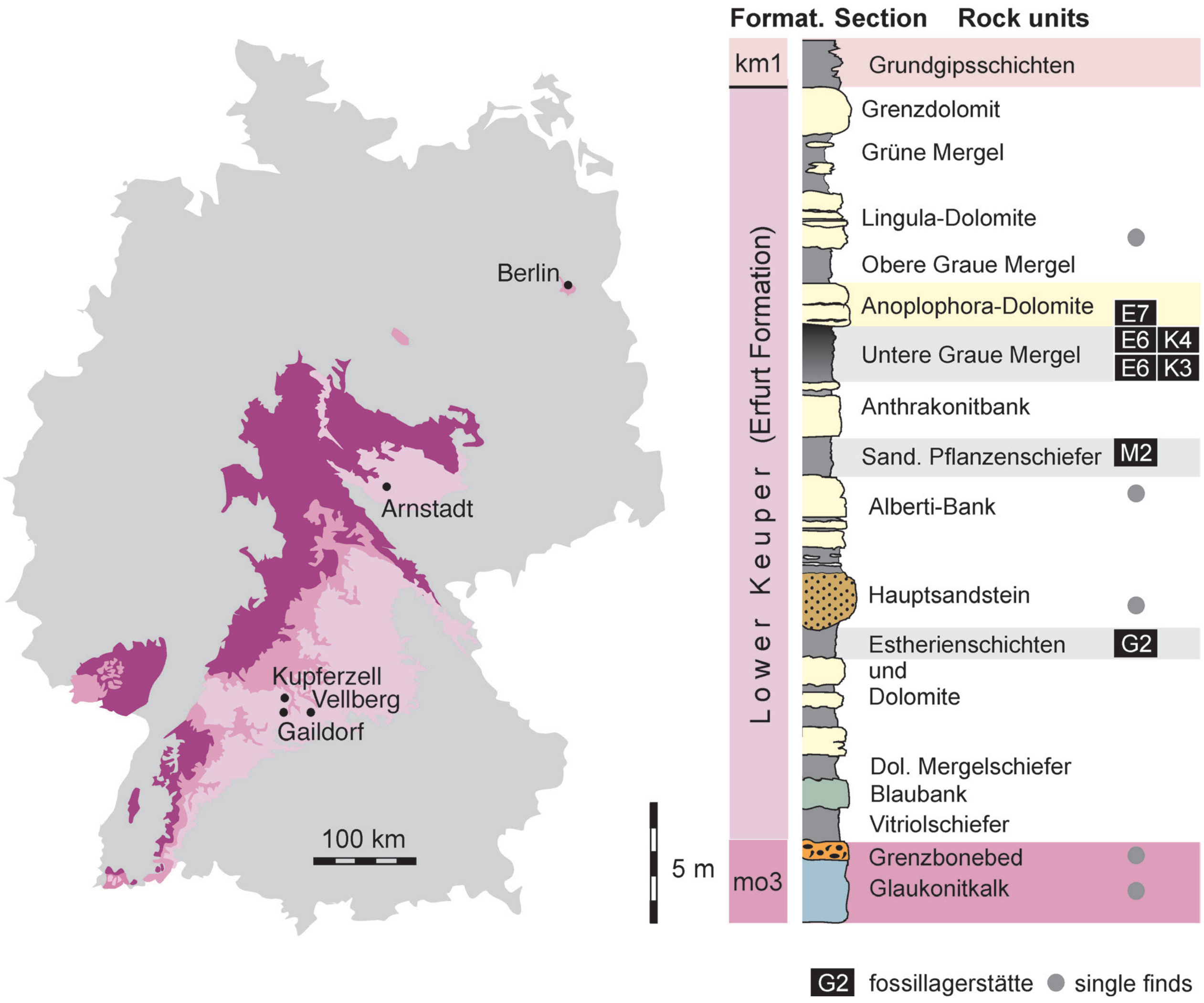

Figure 1. Localities and stratigraphic range of *Mastodonsaurus giganteus* Jaeger, 1828 in Germany. Abbreviations of major localities: G2, Gaildorf (type locality), E5, 6, 7, Vellberg-Eschenau, K3, 4, Kupferzell-Bauersbach, M2, Michelbach an der Bilz.

length). SMNS 4698, complete skull with mandibles (62 cm SL). SMNS 4707, complete skull with mandibles (68 cm SL) and anterior part of vertebral column (9 intercentra). SMNS 4938, tip of snout (estimated 65 cm SL). SMNS 54679, complete skull with mandibles (60 cm SL; this specimen was erroneously reported by Moser and Schoch (2007) as measuring 74 cm). A large snout (about 107 cm SL, described in Meyer and Plieninger 1844 and figured by Meyer 1855), reported as heavily damaged by Fraas (1889), has long been lost (Schoch 1999); here we provide an interpretation of Meyer's (1855) figure in Fig. 5D.

Michelbach an der Bilz M1 (Sandige Pflanzenschiefer, layer M1). MHI 1070, series of intercentra of juvenile specimen.

Kupferzell K3 (Untere Graue Mergel, green layer K3 of Schoch et al. 2022). SMNS 54675, complete skull (60.5 cm), almost undistorted, with perfect braincase. SMNS 54678, complete skull (54.5 cm). SMNS 80704, complete skull (55 cm) with mandible. SMNS 80889, complete skull (59 cm) with mandible. SMNS 80890, postorbital part of skull (45.5 cm). SMNS 80905, disarticulated skull (about 45 cm). SMNS 80945, disarticulated skull (60 cm). SMNS 81075, disarticulated skull (48 cm). SMNS 81310, giant specimen, including complete mandible (110 cm; 88.5 cm SL) with few remnants of the palate and a total of 28 presacral and 6 caudal vertebrae. SMNS 81368, posterior part of palate. SMNS 84030, posterior margin of skull (estimated 65 cm SL). Symphyses of tiny specimens (SMNS 97035, approx. 12–15 mm mm SL; SMNS 97036, 25 mm SL). Isolated material: supratemporal: SMNS 80886, 81153–81156; postorbital: SMNS 81161–81162; squamosal: 80946, 80947, 81164; pterygoid: SMNS 81316, 81318, 81324–81325; parasphenoid: SMNS 81326, 81328, 81330–81332; exoccipital: 80980–80988, 81002–81005, 81013, 81018–81024; interclavicle: SMNS 81282–91; clavicle: SMNS 81298; cleithrum: SMNS 81208–81209, 81257, 81264; intercentra: SMNS 84172 (13), 84173, 84194 (4), 84195, 84206, 84208, 84212 (10), 84213 (11), 84291 (5).

Kupferzell K4 (Untere Graue Mergel, yellow-brown layer K4 of Schoch et al. 2022). SMNS 54676, complete skull (56 cm). SMNS 54677, complete skull (51 cm) with mandible. SMNS 80249, posterior rim of skull (65 cm). SMNS 80878. Near-complete skull (about 65 cm) with

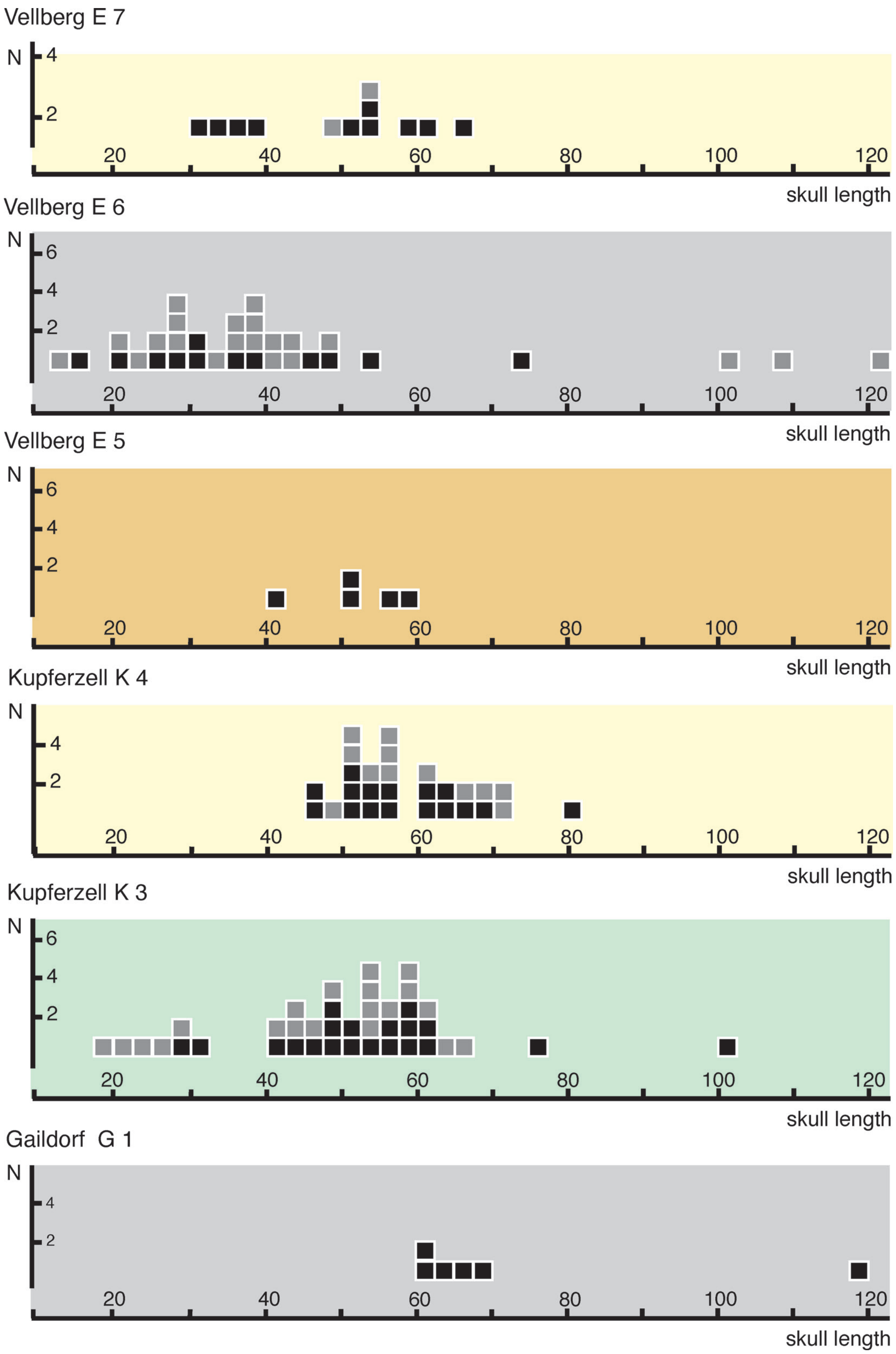

Figure 2. *Mastodonsaurus giganteus* Jaeger, 1828. Frequency and size distribution of specimens in six different localities and horizons of the Lower Keuper in northern Baden-Württemberg (Germany). Black squares: skulls or semi-articulated skeletons; Grey squares: single bones.

parts of mandible. SMNS 80887, snout fragment (54 cm SL). SMNS 80913, fragmentary skull (65 cm total length) with 28 presacral vertebrae. SMNS 83293, fragmentary skull (60 cm). SMNS 83312, fragmentary skull (45 cm). SMNS 97038–97042, skull fragments (68, 50, 47, 50, 57 cm SL, respectively). Isolated material: supratemporal: SMNS 80865, postparietal: 81000, 83260; tabular: SMNS 81091–81098; exoccipitals: SMNS 80917, 80926,

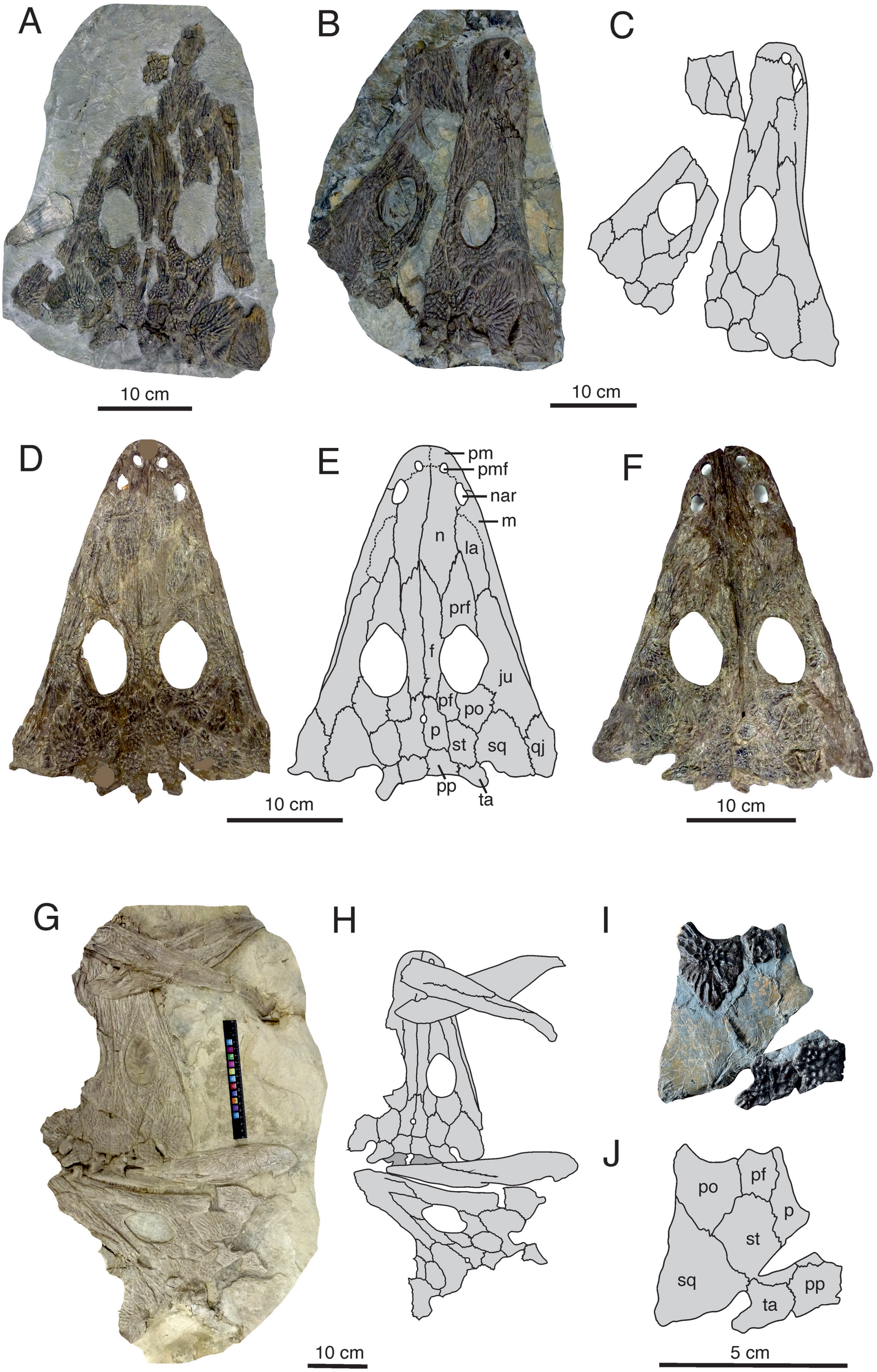

Figure 3. *Mastodonsaurus giganteus* Jaeger, 1828. **A.** MHI-Ku 1992/22 (Vellberg, E6); **B, C.** MHI-Ku 1992/21 (Vellberg, E6); **D, E.** MHI-Ku 1992/31 (Vellberg, E6); **F.** MHI-Ku 1992/42 (Vellberg, E6); **G, H.** MHI 1991-4 (Vellberg, E7); **I, J.** SMNS 97037 (Vellberg, E6).

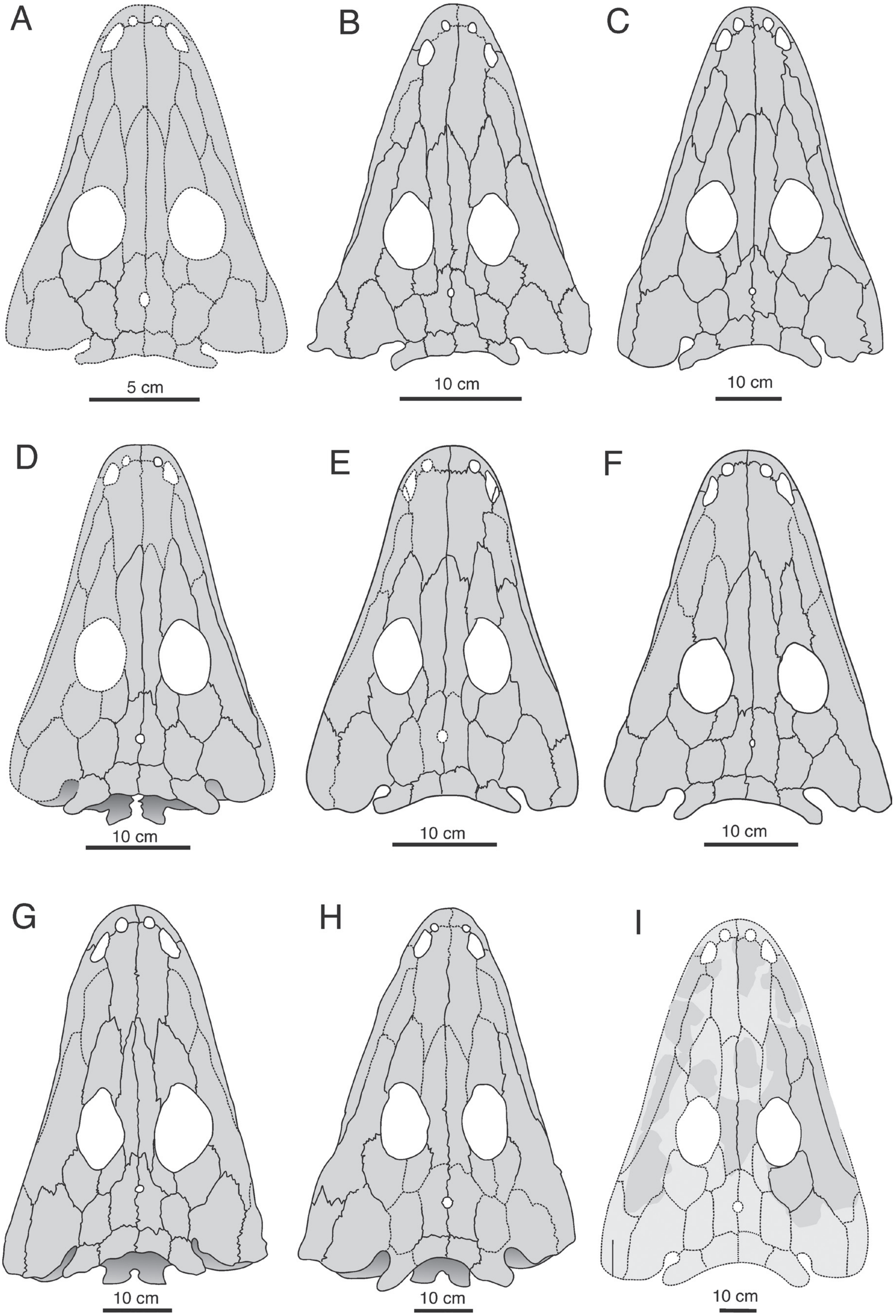

Figure 4. *Mastodonsaurus giganteus* Jaeger, 1828. Skull reconstructions in dorsal view. **A.** Restoration of incomplete specimen SMNS 97037 (Vellberg, E6); **B.** MHI-Ku 1992/31 (Vellberg, E6); **C.** SMNS 54678 (Kupferzell, K3; original figured in Schoch 1999, pl. 3); **D.** MHI-Ku 1991/4 (Vellberg, E6); **E.** MHI-Ku 1992/21 (Vellberg, E6); **F.** MHI-Ku 1992/42 (Vellberg, E6); **G.** SMNS 4698 (Gaildorf, G2; original figured in Schoch 1999, pl. 1); **H.** SMNS 54679 (Gaildorf, G2; original figured in Moser and Schoch 2007, fig. 6c); **I.** Restoration of largest skull, NHMS-WT3323-3368 (Arnstadt), restored regions in light grey.

80956, 80957, 80979, 80980, 80982, 80989, 80990, 80994, 80996, 80998, pterygoid: SMNS 81320, 81321; interclavicle: SMNS 81270–81276; cleithrum SMNS 81210, 81261, 81262; intercentra: SMNS 84138, 84139 (14), 84145 (7), 84200, 84207 (6), 84210, 84211.

Markgröningen (Fraas 1889, p. 5: "10 m above Hauptsandstein" = Untere Graue Mergel). SMNS 4974. Skull without cheek regions (71.3 cm SL).

Vellberg E5 (Untere Graue Mergel, brown layer E5 of Schoch and Seegis 2016). MHI 1991/22, complete skull (50.5 cm). MHI 1992/20, complete skull (59.5 cm). MHI 1992/41, complete skull (42 cm). MHI Ku/UC53le1 (53 cm). MHI Ku/UC53le2 (34.6 cm). SMNS 81966, complete skull (51 cm) with mandible.

Vellberg E6 (Untere Graue Mergel, grey layer E6 of Schoch and Seegis 2016). MHI 1992/1, complete large skull (72 cm) with mandible detached. MHI 1992/31, complete juvenile skull (30 cm). MHI 1992/42, complete juvenile skull (28.6 cm). MHI-Ku 1993/4, tiny interclavicle. MHI-Ku 1993/5, juvenile interclavicle. SMNS 97043, complete skull (39 cm). MHI Ku/UC54le1, mandible (24.1 cm). MHI Ku/UC54le2, mandible (20 cm). MHI Ku/UC54le3, mandible (35 cm). MHI Ku/UC1, mandible (SL approx.: 37 cm). MHI Ku/UC2, mandible (100.8 cm SL). SMNS 92128, complete, highly fractured skull (60 cm length). SMNS 97037, posterior portion of juvenile skull (15 cm SL).

Vellberg E7 (Anoplophora Dolomite, pale yellow dolostone unit E7 of Schoch and Seegis 2016). MHI 1794/3, complete, slightly deformed skull (62 cm). MHI 1991/1, complete skull in 3D with mandible (54.2 cm). MHI 1991/4, two partial skulls (32 and 34 cm). MHI 1991/5, snout (estimated 66.6 cm SL). MHI 1991/6, partial skull (53.9 cm). MHI 1991/7, snout (estimated 35 cm SL). MHI 1991/8, mandible (estimated 58.3 cm SL). MHI 1991/11, complete skull with deformed snout (38 cm). MHI Ku/UC54le, mandible (52.7 cm). MHI Ku/UC54le1, skull (54.4 cm). MHI Ku/UC, skull (54 cm).

Arnstadt (Oberes Dunkles Band, layer 42, dark coaly siltstone of Werneburg in Hagdorn et al. 2015). NHMS-WT3323-3368, partial skull and mandible (estimated 101 cm SL; Werneburg and Witter 2005).

Hoheneck H1 (Lingula-Dolomit, Hoheneck facies). SMNS 740, palate (52 cm; Fraas 1889). SMNS 4194 (66 cm; skull roof in internal view; Fraas 1889).

Diagnosis. Autapomorphies (in contrast to *M. cappelensis*, see Schoch et al. 2023): (1) Orbits with pointed anterior end and narrow interorbital distance (Figs 3, 4; IOW:SL = 0.095); (2) medial premaxillary teeth enlarged (Fig. 5C, D); (3) tusks in palate and especially in the symphysis greatly enlarged (Figs 5, 6), (4) postorbital larger than supratemporal; (5) squamosal wide to give broadened cheek; (6) interclavicle with elongate anterior process; (7) intercentra of the trunk dorsally closed in juveniles and adults (Fig. 6N–Q).

Comment. The three complete skulls from Gaildorf G2 and most specimens from Vellberg E5–7 are all heavily affected by crushing and distortion, whereas the Kupferzell specimens are preserved almost in 3d thanks to early cementation of sediment. Morphological differences especially in the squamosal embayment and cheek may therefore be caused by post-mortem processes rather than reflect morphological variation. We did not spot consistent differences between the Gaildorf G2 sample and other samples described here, therefore consider all samples as belonging to the type species.

The Kupferzell and Vellberg samples are morphologically very similar and stratigraphically well constrained (both fall within above the lagoonal deposit K1 = E4 and below the base of the Anoplophora Dolomite at the top of the Untere Grauel Mergel).

Ontogeny of *Mastodonsaurus giganteus*

Smallest growth stages

The smallest specimens comprise symphyses that were identified in screen-washed samples from Kupferzell (K3) and small elements of the pectoral girdle from Vellberg (E6). As the two localities are coeval, both yield adult specimens of *M. giganteus* that do not show consistent morphological differences, and the two lake environments were very probably interconnected, we consider the Kupferzell (K3) and Vellberg (E6) samples as part of the same species. We did not identify small growth stages of *M. giganteus* in older or younger deposits.

The symphyses are well-preserved and measure 1 mm and 2 mm in length, respectively (Fig. 6A, B). They rank among the smallest identified stereospondyl specimens worldwide, third only to *Rewanobatrachus aliciae* (Warren and Hutchinson 1988) and *Trematolestes hagdorni* (Schoch and Mujal 2022).

The smallest symphysis stems from a specimen with approximately 12–15 mm skull length (SMNS 97035, Fig. 6A). The larger symphysis (SMNS 97036, Fig. 6B) is about double the size but has proportionately similar-sized fangs. The size of the marginal teeth decreased gradually in proportion from the smallest specimen over the next larger to the juvenile and adult symphyses (Fig. 6A–D).

Both symphyses can be easily distinguished from all other temnospondyls: they differ from *Tatrasuchus* (Fig. 6E, F) by the absence of a transverse row of teeth posterior to the fangs and the larger size of these, from *Callistomordax* (Fig. 6G) in the presence of a continuous dentary tooth row anterior to the fangs and from *Trematolestes* (Fig. 6H) in the different outline of the bone, the absence of a sagittally extended symphysis and the different arrangement of the fangs with the medial one being well anterior. The symphyses of plagiosaurids are still more different, especially in the absence of tusks and the outline of the dentary (Hellrung 2003; Damiani et al. 2009; Witzmann and Schoch 2024).

Likewise, we identified a range of small and tiny interclavicles in the Vellberg (E6) sample. These

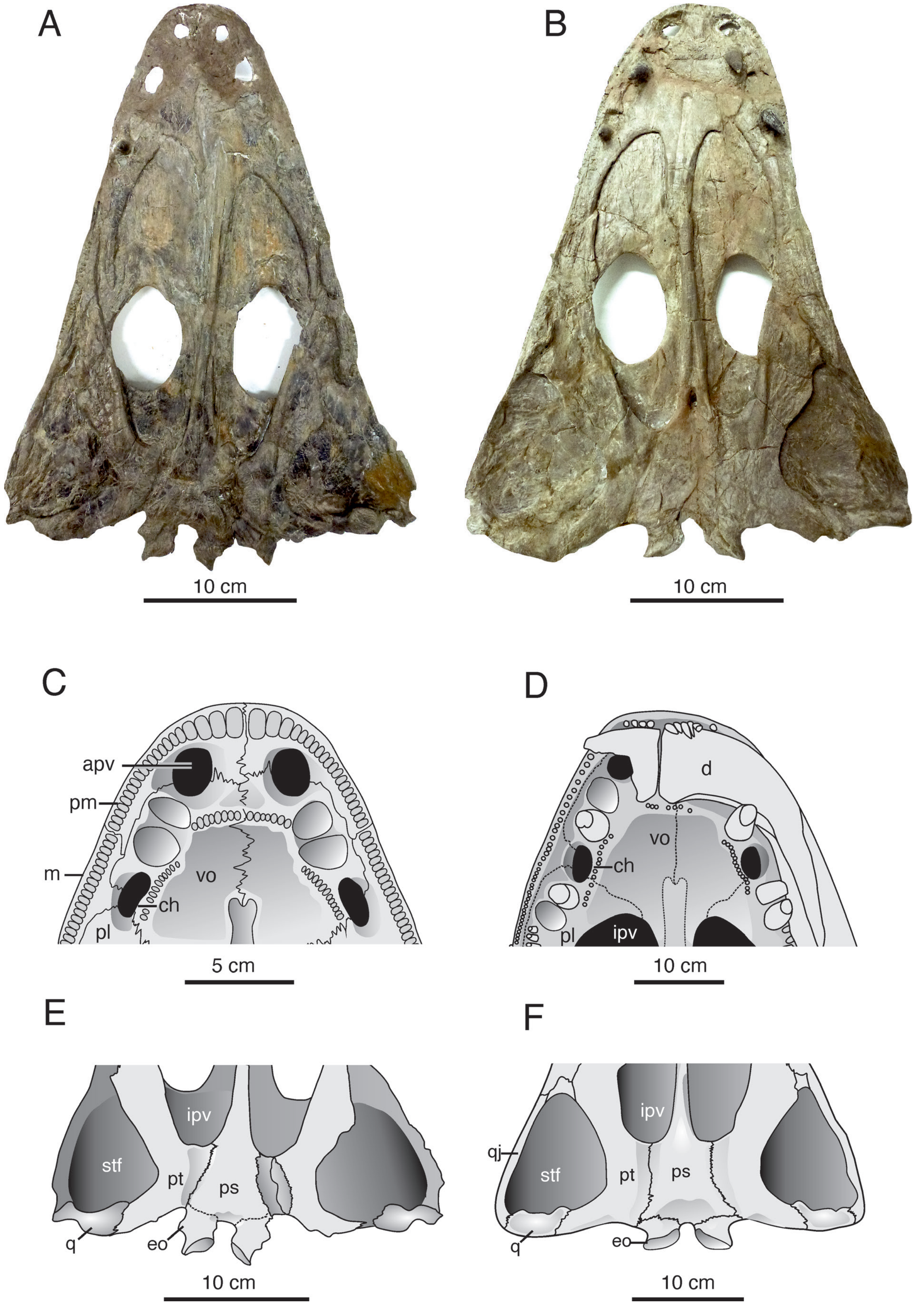

Figure 5. *Mastodonsaurus giganteus* Jaeger, 1828. Palate. **A.** MHI-Ku 1992/31 (Vellberg, E6); **B.** MHI-Ku 1991/11 (Vellberg, E6); **C.** SMNS 54678 (Kupferzell, K4); **D.** giant specimen from Gaildorf G2, based on Meyer (1855)(Gaildorf, G2); **E.** MHI-Ku 1992/42 (Vellberg, E6); **F.** SMNS 54675 (Kupferzell, K3).

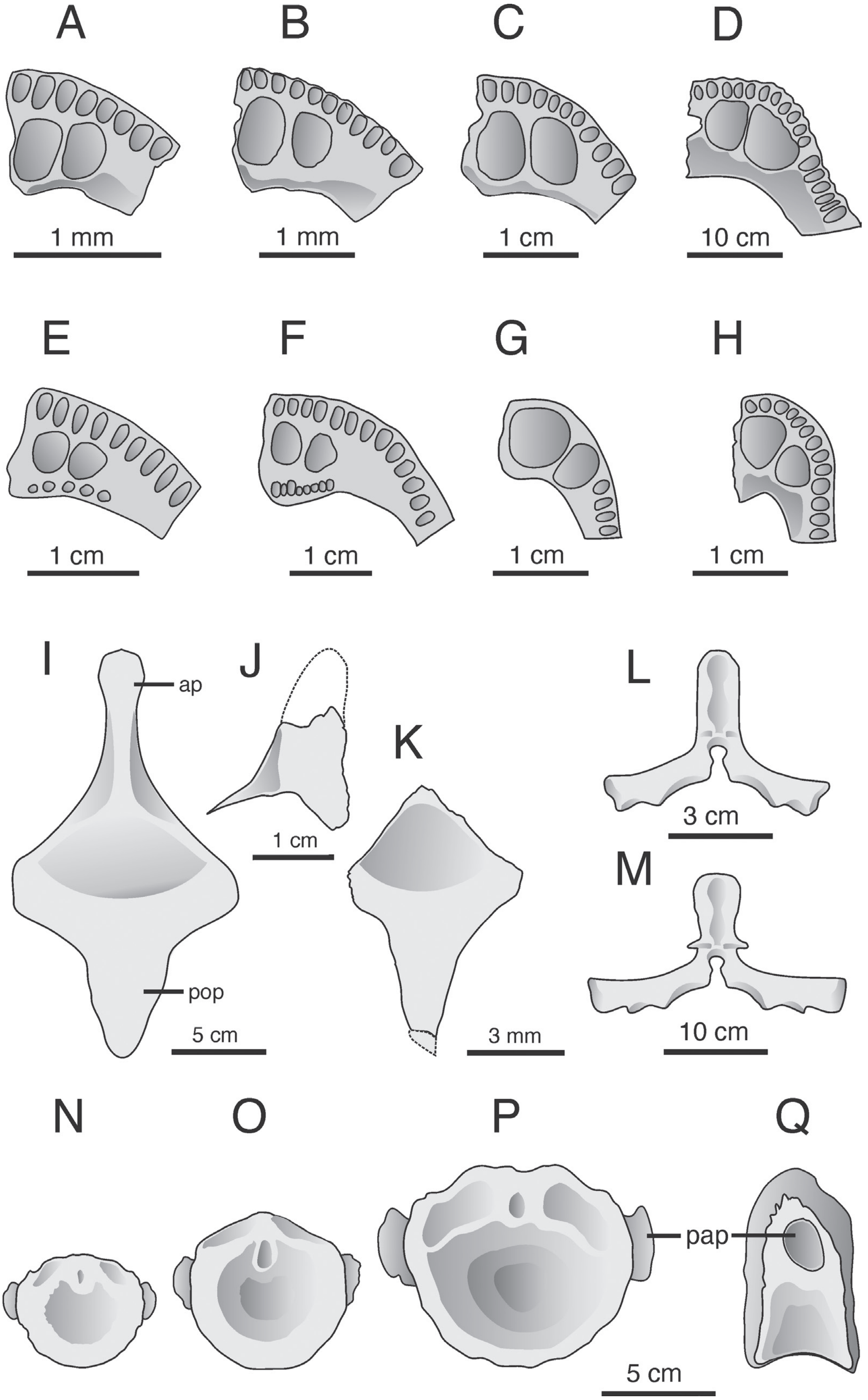

Figure 6. Mandibles and postcranial material of Lower Keuper temnospondyls. **A–H.** Symphyses. **A.** *M. giganteus*, SMNS 97035 (Kupferzell, K3); **B.** *M. giganteus*, SMNS 97036 (Kupferzell, K3); **C.** *M. giganteus*, MHI 1992/32 (Vellberg, E6); **D.** *M. giganteus*, SMNS 81310 (Kupferzell, K3); **E.** *Tatrasuchus wildi*, MHI-Ku 1992/42 (Vellberg, E6); **F.** *Tatrasuchus wildi*, SMNS 54670 (Kupferzell, K3); **G.** *Callistomordax kugleri*, SMNS 90520; **H.** *Trematolestes hagdorni*, SMNS 97034; **I.** *M. giganteus*, adult interclavicle in dorsal view, SMNS 97132 (Kupferzell, K3); **J.** *M. giganteus*, small juvenile clavicle, SMNS 97044 (Vellberg, E6); **K.** *M. giganteus*, tiny interclavicle in dorsal view, SMNS 97131 (Vellberg, E6); **L.** *M. giganteus*, adult neural arch, SMNS 80913; **M.** *M. giganteus*, giant neural arch, SMNS 81310; **N-Q.** *M. giganteus*, intercentra in anterior view; **N.** MHI 1046; **O.** MHI 1079; **P, Q.** SMNS 80913.

are consistent with juveniles and adults of *M. giganteus* in the slender posterior process and the overall proportions; they differ from small interclavicles of *Tatrasuchus* in the slenderer posterior process and from *Callistomordax* and *Trematolestes* in the greater width of the lateral process.

Despite their fragmentary nature, the small specimens here attributed to *M. giganteus* are highly informative in their great consistency with the juvenile and adult morphologies. At least regarding the interclavicle, this agrees with the ontogenetically rather conservative Palaeozoic eryopiforms (Boy 1988; Witzmann 2006).

Juveniles

The smallest juveniles are known from partial skulls, mandibles, and interclavicles (Fig. 6). Juvenile bones from other regions are also present but unambiguous referral to *M. giganteus* remains impossible because the postcranium of the closely related *Tatrasuchus wildi* remains largely unknown.

Skull roof

The best small juvenile specimen of *M. giganteus* is a partial postorbital skull (SMNS 97037) from Vellberg (E6) that preserves the left half of the posterior skull table and squamosal (Fig. 3I, J). This skull shares all features of the ornament of adults, and in comparison to other temnospondyl taxa of similar size, the bones are much thicker. This is especially obvious along the occipital margin. The small juvenile differs from all larger specimens in having a shorter squamosal and a longer supratemporal. The orbit is somewhat larger with respect to the postorbital skull compared with adult specimens; this is interesting, because larger juveniles have relatively small orbits (Fig. 8). Larger juvenile skulls, which are especially well preserved at Vellberg (E6, E7), are remarkably consistent with adults in proportions and suture topologies (Fig. 4). A few trends are apparent from morphometric analysis, in which juveniles have among the widest interorbital distances, the smallest orbit lengths and the narrowest postorbital skulls (Fig. 8). This said, there is substantial variation, especially in Vellberg E6.

Palate

The palate is well preserved in MHI 1992/31 (30 cm SL; Fig. 5A, E) and MHI 1991/11 (38 cm SL). The proportions of the palate elements are similar to those of adults, and the pattern and size of dentition is consistent with later stages. The basal plate of the parasphenoid is slightly shorter and the deltoid area in its anterior part is not yet established. However, its sutures with the pterygoid and exoccipital are consistent with the adult stages, as is the relative size of the exoccipital and its condyle.

Mandible

The Kupferzell and Vellberg localities yielded a wide range of juvenile mandibles that are readily distinguished from those of *Tatrasuchus wildi* by the following features in those of *M. giganteus*: (1) no transverse row of small teeth posterior to the symphyseal fangs, (2) larger size of the symphyseal fangs, (3) Meckelian window elongate and low, reaching 25% the length of the mandible, and (4) long and tall postglenoid area. The juvenile mandibles differ hardly from those of adults, with the postglenoid area only slightly shorter and the hamate process only gently lower in juveniles.

Vertebrae

The morphological consistency of the trunk intercentra is remarkable (Figs 6N–Q, 7K–N). In contrast to the close relative *M. cappelensis*, *M. giganteus* had closed disc-shaped intercentra already in juvenile stages. Intercentra of this type range in transverse width between 4 cm and 12 cm, representing sizes between 30 and 100 cm skull length. Smaller intercentra were found but cannot be distinguished from those of *Tatrasuchus wildi*.

Pectoral girdle

A wide range of clavicles and interclavicles were collected in Vellberg E6, spanning a full range from the smallest to various juvenile stages. These are consistent with adult interclavicles of *M. giganteus* in the slender posterior process, the much-elongated anterior process, and the shape of the clavicular facet (Fig. 7E–G). Independent of size, these features are distinct from all other temnospondyls of the Lower Keuper and especially *Tatrasuchus*. The clavicle of *M. giganteus* has a large convex dorsolateral flange anterior to the ascending process (Fig. 7H, I) that is not present in *Tatrasuchus*. In contrast to the dermal pectoral girdle, diagnostic and undisputed juvenile humeri or other limb elements have not been identified in the studied material.

Pelvic girdle

Small ilia consistent with the morphology of the adult ilium of *M. giganteus* were collected in Kupferzell K3 and figured in Schoch (1999, fig. 46), but their distinction from the yet unknown ilium of *Tatrasuchus* is unknown; the ilia of all other temnospondyls of the Lower Keuper are very different (Schoch 2006, 2008).

Adults

Here we define an arbitrary adult stage beginning with a skull length of 50 cm onwards. As depicted in Fig. 2, adult specimens ranging from 50–60 cm form the bulk of the samples Kupferzell (K3, K4) and Vellberg (E5, E6). Their morphology has been described and figured in detail by Schoch (1999).

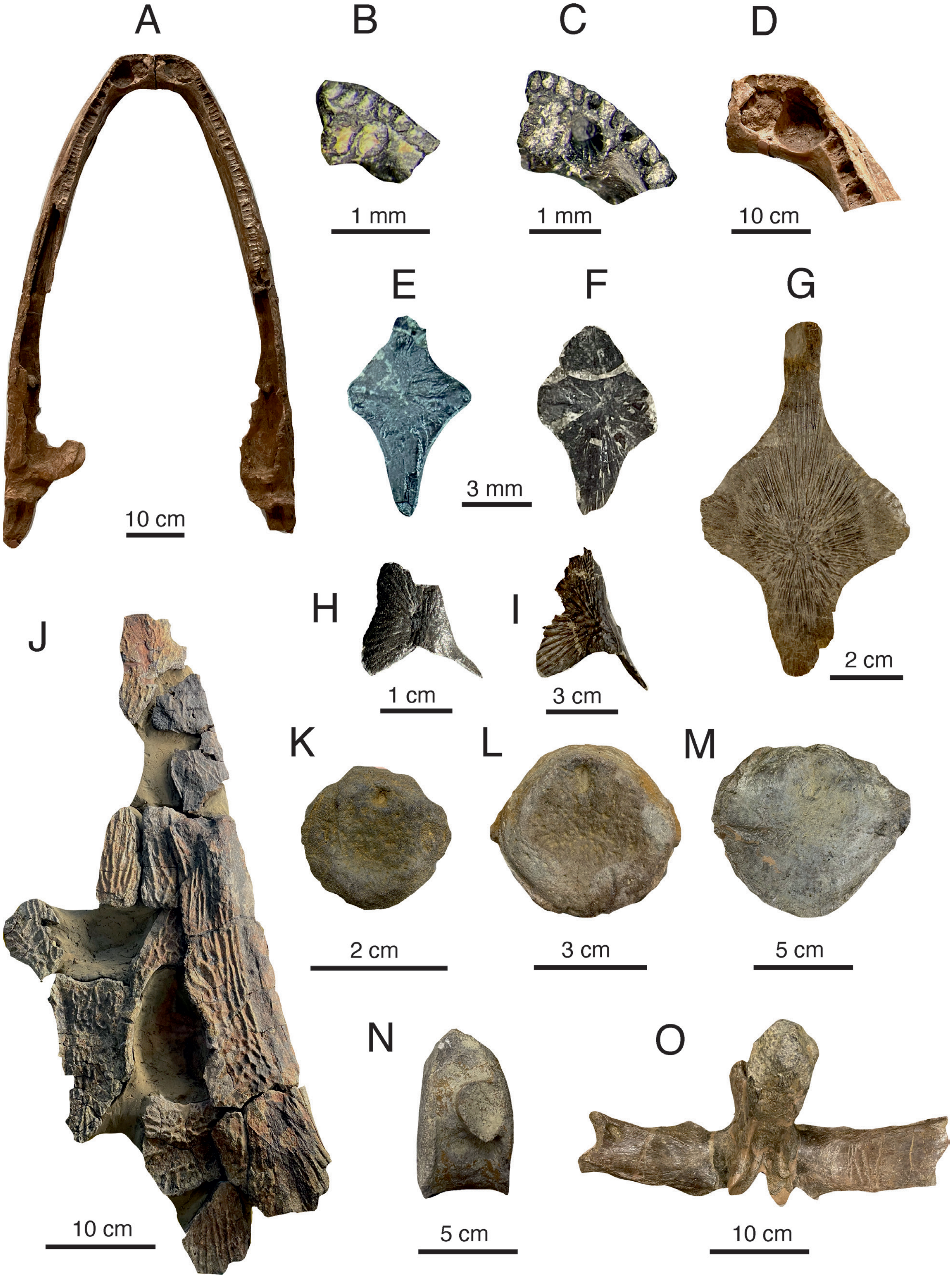

Figure 7. Original material of *Mastodonsaurus giganteus*. **A–D.** Mandibles (**B–D.** Symphyseal region in dorsal view). **A.** SMNS 81310 (Kupferzell, K3); **B.** SMNS 97035 (Kupferzell, K3); **C.** SMNS 97036 (Kupferzell, K3); **D.** SMNS 81310 (Kupferzell, K3); **E–G.** Interclavicles. **E.** SMNS 97131 (Vellberg, E6); **F.** MHI-Ku 1993/4 (Vellberg, E6); **G.** MHI-Ku 1993/5 (Vellberg, E6); **H–I.** Clavicles. **H.** SMNS 97044 (Vellberg, E6). **I.** SMNS 97044 (Vellberg, E6). **J**, large skull, NHMS-WT3323-3368 (Arnstadt). **K–N.** Intercentra (**K–M.** Anterior view; **N.** Lateral view). **K.** SMNS 97044 (Kupferzell, K3). **L.** SMNS 97044 (Kupferzell, K3). **M.** SMNS 84138 (Kupferzell, K3). **N.** SMNS 84139 (Kupferzell, K3). **O.** Neural arch, SMNS 81310 (Kupferzell, K3).

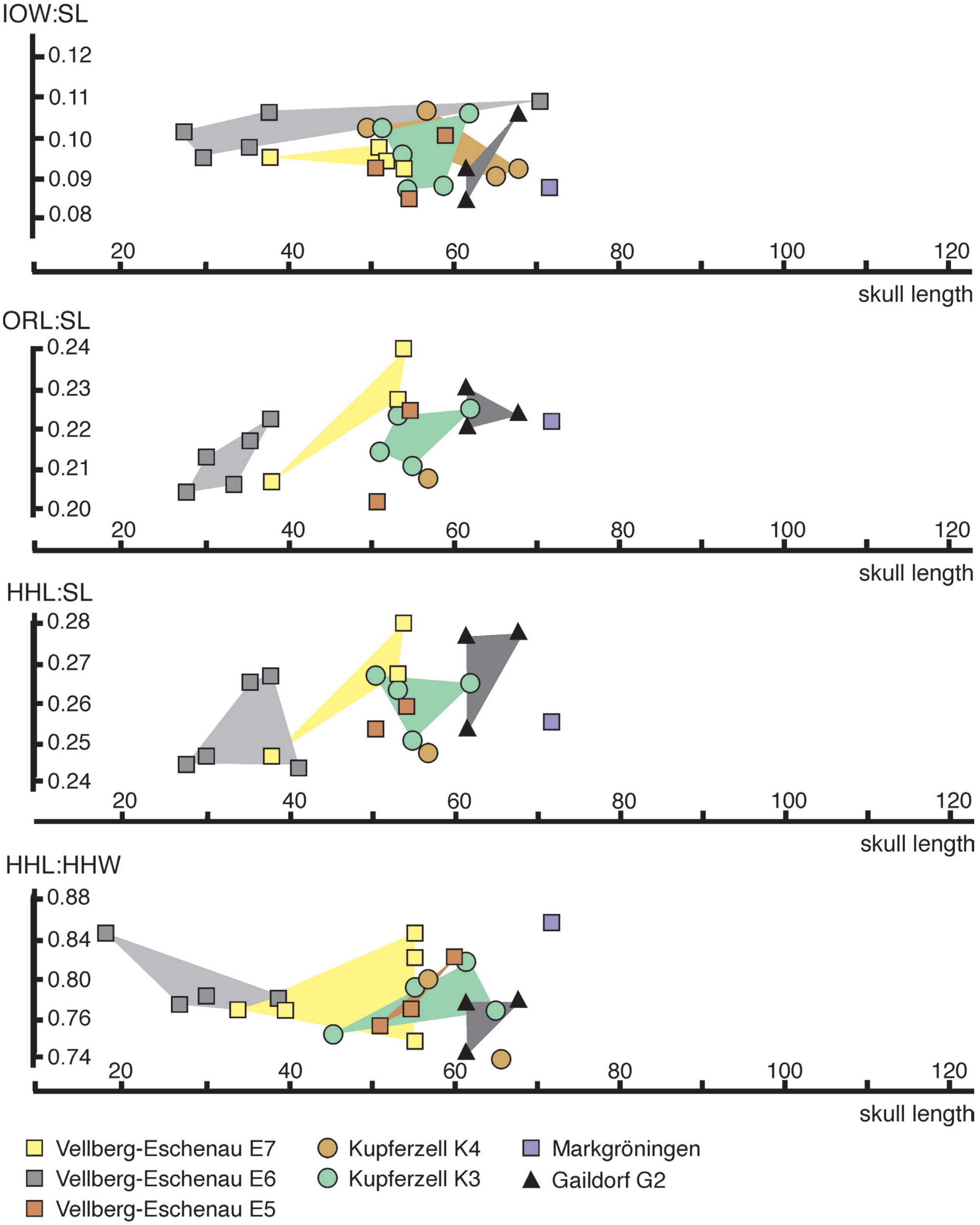

Figure 8. *Mastodonsaurus giganteus* Jaeger, 1828. Morphometrics of skull proportions in the different samples.

Giant specimens

Skull roof

The large specimens from Gaildorf (G2) were described by Meyer and Plieninger (1844), Fraas (1889) and Moser and Schoch (2007). The three complete skulls range from 60 to 68 cm skull length (Fig. 4; Moser and Schoch 2007). Fraas (1889) further described and figured a large skull without cheeks from Markgröningen (SMNS 4974), found in a dark mudstone that was roughly equivalent to the Untere Graue Mergel of Vellberg and Kupferzell.

The grey mudstones of Vellberg E6 yielded numerous isolated bones of giant specimens. These include intercentra, humeri, mandibles, and fragments of skulls in the 100–120 cm size range. It is unknown from how many specimens these bones stem, but a minimum assessment identifies at least three giant individuals collected over 30 years (Werner Kugler, pers. comm. 2016). The Kupferzell fossillagerstätte (K3) gave only a single very large skeleton, referred to as giant specimen ("Riesenexemplar", SMNS 81310). It encompasses a palatine, tabular, complete mandible and 34 vertebrae plus a series of associated ribs (Schoch 1999), representing a specimen with 88.5 cm skull length.

At a highway construction site near Arnstadt in central Thuringia (Erfurter Kreuz, see Werneburg in Hagdorn et al. 2015), a large partial skull was collected (NHMS-WT3323-3368, see Werneburg and Witter 2005) in the upper part of the Lower Keuper. The complete skull measured around 101 cm in length and preserves a good portion of the skull roof (restored in Fig. 4I). This includes portions of the preorbital, interorbital and cheek regions. It is consistent with the large Kupferzell and Vellberg material in that ornament is coarser than in 40–70 cm skulls, meaning that the size of the polygons is proportionately larger in these specimens. In turn, the ridges are low and thinner than in smaller skulls, whereas the lateral line sulci are proportionately of similar width as in smaller specimens.

The orbit of the largest skull is proportionately somewhat smaller, albeit retaining its characteristic outline with the pointed anterior end. In the other material, the length of the orbit varies broadly, with the Gaildorf and Markgröningen specimens ranking among those with the longest orbits. Such variation was also reported by Sulej (2007) on *Metoposaurus krasiejowensis*. The large size of the orbits in *M. giganteus* has been hypothesized to correlate with large adductor musculature (Schoch et al. 2023), which might explain that the size did not essentially change between juveniles and adults.

A rather clear trend was found in the length/width ratio of the postorbital skull table, which is smaller in larger specimens, except for the Markgröningen skull. Conversely, the ratio length of the postorbital skull through skull length increases slightly from juveniles to large adults (Fig. 8).

The area of the postorbital increases markedly between juveniles (30 cm) and small adults (40–50 cm) but remains constant throughout later stages. Likewise, the width of the squamosal increases between juveniles and adults. Both features are typical of adult *M. giganteus*, whereas juveniles retain the plesiomorphic condition seen in adult *M. cappelensis* (Schoch et al. 2023).

In the Thuringian and Gaildorf specimens, the postorbital is still proportionately large. The interorbital distance varies more broadly in the largest skulls, with the Markgröningen and two of the Gaildorf specimens ranking among the narrower skulls, together with K4 specimens from Kupferzell (Fig. 8). The occipital condyles are more massive than in smaller stages and the occipital margin of the postparietals is more strongly concave, especially in the Gaildorf and Markgröningen specimens.

Palate

Meyer (1855) figured the now-lost snout of a giant specimen from Gaildorf (G2) in original size, which measured approximately 107 cm in total skull length (Meyer and Plieninger 1844). Based on Meyer's drawing (modified in Fig. 5D), the marginal and vomerine teeth are throughout proportionately smaller than in 50–60 cm long skulls, whereas the fangs especially of the symphyseal region are enlarged (SMNS 81310). The choana was drawn rounded by Meyer (1855) but reported to be rather oval by Fraas (1889); we suppose that Meyer referred to the outline of the opening within the main plane of the vomer, whereas Fraas described the outline of the opening, which is more deeply emplaced in the dorsal portion of the narial capsule. At any rate, the choana is distinctly shorter and smaller in the giant Gaildorf specimen than in smaller adult stages (Fig. 5C, D).

Vertebrae

The largest vertebrae are mostly heavily crushed, sometimes even more flattened than intercentra of adults in the 50–60 cm skull range. This probably results from a higher porosity of the bones. This is particularly obvious at the top of layer K3 in Kupferzell, which contained both the giant specimen (SMNS 81310) and several smaller disarticulated vertebral columns; in the smaller specimens, the intercentra are hardly crushed at all and retained most of their 3D structure. Apart from the higher porosity, the parapophyses are proportionately larger by area in the giant specimen. The caudal vertebrae are low and wedge-shaped but very massively ossified, not as porose as the trunk vertebrae and consequently less affected by compaction. The neural arches are peculiar in giant specimens by having disproportionately large transverse processes; their length was subject to strong positive allometry from adult to giant size classes (Fig. 6L–M).

Pectoral girdle

Several huge clavicles and interclavicles are housed in the MHI and SMNS collections, among which the giant specimen (SMNS 81310) from Kupferzell (K3) permits the calibration of mandible size and interclavicle length. The proportions appear not to have changed, whereas the ornament underwent a similar coarsening as reported from the skull roof. The ontogenetic changes of the cleithrum involved a broadening of the dorsal head region and an area increase of the scapular facet, well preserved in the K3 sample (Schoch 1999, fig. 41). The humerus of large specimens differs between the Gaildorf and other samples. Large humeri in the 20–24 cm range are known from Vellberg, where they are poorly differentiated without a clear supinator and poorly defined, mostly cartilage-capped condyles. In contrast, the giant Gaildorf humerus (SMNS 4706) figured by Meyer and Plieninger (1844) has a prominent supinator process and a large fully ossified radial condyle. (Schoch 1999, fig. 43). As preserved in one Gaildorf specimen (SMNS 4706), the carpal region contained at least a few ossified carpals (Schoch 1999, p. 17 and fig. 45).

Pelvic girdle. This region is again best represented by the small Gaildorf sample, which preserves three divergent size classes. Interestingly, the smallest of these includes an ilium with attached ischium and pubis (Schoch 1999, fig. 46), being much more fully ossified than all other specimens from Vellberg and Kupferzell.

Paleoecology and life history of *Mastodonsaurus giganteus*

In Fig. 2, we mapped the frequency of *M. giganteus* in six different localities and horizons: Gaildorf (G2), Kupferzell (K3, K4) and Vellberg-Eschenau (E5, E6, E7). The basis of these distributions form registered finds of skulls, articulated skeletons, and isolated elements that together give a minimum number of individuals. To avoid counting isolated bones from the same disarticulated individual twice, we constrained the sample of single elements to the most robust and common bones, the exoccipitals. Especially at Kupferzell the number of interclavicles and mandibles, the other two common elements, matched the distribution of exoccipitals.

Lake Gaildorf G2

The Gaildorf sample is the smallest and most difficult to interpret because the locality is currently poorly accessible. It includes three complete large skulls (60–68 cm), two skull fragments (61–65 cm), one lost giant specimen (107 cm), and articulated as well as isolated postcranial bones. The minimal number of specimens is difficult to assess, because the belonging of cranial and postcranial material remains unclear. As in most other tetrapod fossillagerstätten in the Erfurt Formation, the fossiliferous horizon was restricted to a small area, and in currently accessible neighbouring outcrops it is absent.

The Gaildorf specimens of *M. giganteus* stem from a hard coaly siltstone rich in pyrite, sphalerite, and alum (Kurr 1852). This layer occurs immediately above a light grey mudstone (G1) containing a bonebed and below a 25–30 cm thick coal seam (G3) that was rich in plants, a coaly mudstone poor in fossils (G4), and a dark grey sandstone that yielded occasional plant debris and vertebrate bones (G5). This succession might have formed in a lake that provided good conditions for life, harbouring a fish fauna that is preserved in the 25 cm-thick bonebed-bearing mudstone (G1).

The 30 cm thick pyrite-rich type horizon G2 yielded the skulls and articulated skeletons of *M. giganteus*, along with a skeleton of *Plagiosuchus pustuliferus*, a skull fragment of the small capitosaur *Tatrasuchus wildi* (Schoch 1997) and mass accumulations of bivalves (*Unionites letticus*). A jaw and vertebra of the enigmatic archosauriform *Zanclodon laevis* further documents the presence of terrestrial predators (Schoch 2011), whereas isolated bones of the marine reptile *Nothosaurus* sp. (Meyer and Plieninger 1844) suggest the presence of lagoonal environments in the vicinity. The articulated state of the aquatic tetrapods in G2 indicates a calmer environment than in the preceding unit G1, and the abundant pyrite must have formed under euxinic conditions.

According to Nitsch (2015), many coal deposits of the Lower Keuper are associated with channel sandstones and probably formed in oxbow lakes. At Gaildorf, the reported sequence of mudstones, pyrite-bearing siltstones, coal, and dark grey sandstones is consistent with this interpretation. Weber (2013) cited historical sources that described the setting of the coal seam as lenticular with 1200 m longitudinal extension and 40 m width.

The lateral variation of the horizons is well documented in the three different sections that were published over a range of 36 years (Plieninger in Meyer and Plieninger 1844; Kurr 1852; Quenstedt 1880). These were probably measured in successively exposed sections of the mine.

Plieninger (1844) noted the presence of a second, thinner coal seam at the top immediately below the first sandstone unit, and he highlighted the occurrence of estherians in G1 and coaly clasts in G2 and teeth in G4. Quenstedt (1880) reported the horizons G2, G3 and G5, but noted the absence of G4 in the section available to him, he also mentioned estherians and reddish ironstone nodules in G2. In sum, these sections provide evidence of a freshwater lake environment that developed into a peat lake with calm, euxinic conditions, relatively similar to layers K1 and K2 from Kupferzell (see Schoch et al. 2022). The abundance of freshwater bivalves indicates good living conditions in G2, and the presence of four temnospondyl predators provides evidence of a rich ecosystem (*Mastodonsaurus*, *Tatrasuchus*, *Plagiosuchus*, *Trematolestes*).

Plagiosuchus probably was a bottom-dwelling sit-and-wait predator that, together with the abundance of *Unionites*, indicates a well-aerated lake floor of G2. At the same time, the abundance of pyrite and the dark colour of the sediment probably formed after seasonal poisoning of lake water, most probably by algal blooms, whereas the occurrence of coaly clasts suggest either the presence of already existing peat deposits in the vicinity or, alternatively, the input of larger quantities of plant material from the lake shore. Plieninger (Meyer and Plieninger 1844) reported that the skulls and skeletons of *M. giganteus* were found in the top of G2, with the bones reaching into the coal seam. This might indicate a drying up of Lake G2 (somewhat similar to Lake K3 in Kupferzell, see Schoch et al. 2022), followed by a peat lake preserved in the coal seam of G3 which contains *Taeniopteris*, *Calamites* and *Equisetites* (Kurr 1852).

The large size of most specimens of *M. giganteus* in G2 is remarkable; the complete skulls all fall into the 60–68 cm size range, as do most of the postcranial elements, with few bones stemming from individuals with a skull length of 50–60 cm, and several finds (humerus, ilium, fang, giant snout reported by Meyer and Plieninger 1844) of very large individuals in the 100–120 cm size range. The sample also includes three ilia of very different size, probably matching the three size classes (50, 60, and 110 cm skull length). Among all occurrences of *M. giganteus*, these finds are the most fully articulated, consistent with the find of a *Plagiosuchus* skeleton in G2 (Huene 1922).

Within this relatively small sample, the dominance of large and giant specimens is unparalleled among Lower Keuper deposits (Fig. 2). This may point at differences in life histories: either the Gaildorf population of *M. giganteus* had a longer life span or specimens reached large sizes more often than the later populations due to more favourable conditions. Two anatomical features are further noteworthy: the largest humerus is more heavily ossified than that of other samples and bears a prominent supinator process that is not developed in any other specimen, and the pelvis of some specimens includes an ossified pubis, which is unique among capitosauroid taxa except for *Sclerothorax* (Schoch et al. 2007). Ongoing analysis of bone microanatomy might shed more light on this interesting difference to the Vellberg and Kupferzell samples.

These data coincide with the occurrence of the smaller capitosauroid *Tatrasuchus*. The unusually large size of *M. giganteus* might be a result of character displacement, with *Mastodonsaurus* forming the apex predator and *Tatrasuchus* representing the guild of smaller ambush predators at this locality. At Gaildorf, *M. giganteus* appears to have invaded the lake at later ontogenetic stages and larger sizes than in other lakes, and its huge size might be a result of either plasticity or separate microevolution. Since *Tatrasuchus* probably occupied the same ecological niche as small adults of *M. giganteus*, the latter could have undergone an ontogenetic niche shift between juveniles and small adults. *M. giganteus* might have targeted larger prey and thus developed a stronger bite by proportionately increasing the area of the postorbital and the size of the squamosal (differing from *M. cappelensis*) in order to accommodate larger adductor musculature.

Lake Kupferzell K3

At Kupferzell-Bauersbach, a thick greenish mudstone (K3) has yielded a rich sample of tiny, juvenile, and adult specimens of *M. giganteus*. By the sheer quantity and density of bones, this deposit forms the richest tetrapod fossillagerstätte in the Lower Keuper and well beyond. Especially considering the excavated area, the temnospondyl specimens collected in that horizon by far outnumber those collected at the much larger excavated areas of Vellberg (E5, E6, E7). K3 yielded a loosely articulated giant specimen but otherwise contained mostly smaller adults, juveniles, and tiny specimens (Fig. 2).

The unit K3 has been interpreted as littoral facies of a lacustrine system (Schoch et al. 2022). This is also in line with the high number of bones with bite marks inflicted by the pseudosuchian archosaur *Batrachotomus kupferzellensis*, a more terrestrial predator feeding on carcasses of *M. giganteus* (Mujal et al. 2022), probably stuck in drying-up lakes (Schoch et al. 2022). Characeans and ostracods indicate well-aerated water in a basin less than 10 m deep. This water body spanned probably several km, but bone accumulations are restricted to only 500 m. The lake was subject to pulses of higher energy that produced currents, disarticulated skeletons, and transported the bones (Schoch et al. 2022). The absence of dark components and the light green colour of the sediment suggest that organic components were not as abundant as in other lakes, probably indicating a somewhat less nutrient-rich environment. Salinity fluctuations are indicated by euryhaline ostracods (Urlichs 1982) and histological evidence in bones of *Gerrothorax* point at an environment with fluctuating conditions (Sanchez and Schoch 2013). These fluctuations may have been caused by the occasional contact to a lagoonal water body in the vicinity (Schoch et al. 2022). Conversely, the poor carbonate content of the sediment was probably caused by inflowing streams that also produced channel-like erosions (Urlichs 1982). Only in the last phase of Lake K3, a diverse fish fauna (14 taxa) similar to, but not identical with E5 and E6 at Vellberg was established, and the accumulation of tetrapod bones is confined to that horizon (Schoch et al. 2022).

Despite the diverse fish assemblage, only aquatic tetrapod predators were present, *M. giganteus* and *Gerrothorax pulcherrimus*. The latter was distinctly smaller than *Plagiosuchus pustuliferus* of Gaildorf G2 and Vellberg E5. However, the abundance of this taxon in K3 concurs with the above-cited evidence of clear and well-aerated bottom water.

Within K3, the frequency distribution of *M. giganteus* is bimodal with specimens clustering in the 18–32 as well as 40–65 cm range (skull length; Fig. 2). Apart from that, tiny specimens were identified in the screen-washed fraction, and a single very large specimen (88.5 cm skull length) was found, but the giants in the range of Vellberg and Gaildorf specimens are absent. In Lake K3, *M. giganteus* must have primarily fed on *Gerrothorax* and large bony fishes such as dipnoans, actinistians and scanilepiforms.

Occasionally, *M. giganteus* may also have predated the smaller capitosaur *Tatrasuchus wildi* whose remains are always completely disarticulated and less common; this taxon probably dwelled in neighbouring habitats, and the disarticulated bones were washed in from there. The mass accumulation of bones and skulls of *M. giganteus* and *G. pulcherrimus* was probably caused by the final drying-up of Lake K3, which is documented by mud cracks; of note, bones are often found in the interface between layers K3 and K4, i.e., remaining half buried and thus exposed for a relatively prolonged time after the lake dried up (Schoch et al. 2022). At the same time, carcasses of *M. giganteus*, including that of the giant specimen, were scavenged by *Batrachotomus kupferzellensis*, which occasionally probably also actively hunted *M. giganteus* individuals (Mujal et al. 2022).

Lake Kupferzell K4

The deposit K4 encompasses yellow to brown, dolomitic marlstones. The yellow mud also fills desiccation cracks on top of layer K3, preserving equal amounts of characeans but much larger quantities of ostracods and microvertebrates than K3 (Schoch et al. 2022). Lake K4 represents a shallow, carbonate-rich environment that harboured a rich benthos. It probably formed in a more protected sub-basin that was not subject to frequent currents and therefore less siliciclastic input than K3. The oligohaline ostracod *Darwinula* was accompanied by the 14 fish taxa that also occur in K3 (Urlichs 1982; Schoch et al. 2022). The high abundance of small actinistian bones has been interpreted as evidence of a nursery ground of these fishes (Schoch et al. 2022). This lake probably existed within the same basin as K3, probably on a carbonate mudflat. Like K3, it is rich in ostracods and characeans, thus indicating the persistence of shallow water conditions.

In contrast to K3, the deposits of Lake K4 preserve skeletons rather than accumulations of single bones, indicating lower energy conditions and the preservation of skeletons after short-term droughts which are preserved as minor desiccation cracks. *Gerrothorax* was distinctly less abundant and *Tatrasuchus* more common than in K3 (Schoch 1997). In contrast to K3, *Tatrasuchus* is represented with several well-preserved skulls, suggesting that this sub-basin was inhabited by that taxon. *M. giganteus* was present with specimens in the 50–70 cm range (skull length), whereas giant specimens are entirely absent. The absence of juveniles and the slightly larger mean size compared with K3 coincide with the occurrence of *Tatrasuchus* (size range 25–40 cm skull length). Like at Gaildorf (see above), character displacement may explain this distribution (Schluter and McPhail 1992).

In K4, *M. giganteus* primarily fed on *Gerrothorax* and lungfishes such as the 2 m long *Ptychoceratodus* which is present both with skeletons and large teeth with traces of gastric acids. As in K3, *Batrachotomus kupferzellensis* primarily fed on carcasses of *M. giganteus* (Mujal et al. 2022). Littoral or marine influence in Lake K4 is indicated by the presence of a partial skeleton of *Nothosaurus* sp. (Schoch et al. 2022).

Lake Vellberg E5

In the Schumann quarry of Vellberg-Eschenau, the brown silty mudstones of E5 have been excavated by private collectors in concert with the more fossiliferous horizon E6. The horizon E5 formed in a small lake basin that developed after the retreat of a large brackish lagoon (Schoch and Seegis 2016). It is associated with autochthonous coal and roots at least in the northwestern area of its occurrence (Ummenhofen and northern Eschenau quarries). Its fauna includes a diverse fish assemblage (15 taxa) in which juvenile lungfishes and small polzbergiid actinopterygians form the bulk of the sample. Juvenile actinistians are present but much less abundant than in K4. Together with the occurrence of larval and juvenile temnospondyls (*Callistomordax*, *Trematolestes*, *Plagiosuchus*), these finds suggest the prevalence of well-structured, protected areas of a lake. The dominance of the ostracod *Speluncella* over *Darwinula* points to slightly brackish water (Schoch and Seegis 2016). The large predators in this habitat were the bottom dwelling *Plagiosuchus* and the medium-sized predator *Tatrasuchus*, both present with numerous well-preserved specimens. In contrast, *M. giganteus* is represented by relatively few skulls in the narrow range of 50–60 cm skull length (Fig. 9). This setting formed in a small lake in which *M. giganteus* was probably only occasionally present due to the dominance of competing *Tatrasuchus*. Adult *Trematolestes* and *Callistomordax* probably visited the lake only during the breeding season. In contrast to the other deposits studied by us, Lake Vellberg E5 probably could not support a population of adult *M. giganteus*.

Lake Vellberg E6

The grey clayey mudstones of E6 have been excavated over a period of 35 years and during all field seasons yielded large quantities of vertebrate remains (Schoch and Seegis 2016). They contain thin bonebeds as well as articulated skeletons and probably formed in a stratified lake (>5 km) that was at least seasonally subject to euxinic conditions.

Like in E5, baby lungfishes and two polzbergiids dominate the fish fauna, which also encompasses redfieldiids and semionotids, as well as medium-sized predators (*Saurichthys*, scanilepiforms). The high-bodied polzbergiids indicate that the lake floor was differentiated and offered protected areas, consistent with the presence of small juvenile temnospondyls (*Trematolestes*, *Callistomordax*, *Mastodonsaurus*). Layer E6 is rich in remains of the temnospondyl *Callistomordax*, an elongate eel-like form with large, keeled fangs that is only known from Vellberg. This taxon might have dwelled in protected places because it is the only aquatic tetrapod in this deposit to be preserved with fully articulated skeletons.

M. giganteus is present with specimens of all size classes, and the largest quantities of specimens fall in the 20–50 cm size range (Fig. 2). Notably, there are also remains of giant specimens up to 120 cm skull length, whereas the large adults (60–70 cm range) are much rarer than at Gaildforf G2. In contrast to *Callistomordax*, the remains of *M. giganteus* are nearly always disarticulated and often heavily damaged by predation.

In contrast, *Tatrasuchus* and *Trematolestes* are much less frequent, and only two remains of *Plagiosuchus* were found. Traces on adult remains of all taxa suggest predation by *M. giganteus* (regurgitates, bite marks, lungfish teeth and vertebral centra of temnospondyls corroded by gastric acids). Lake E6 also forms the only deposit so far to evidence cannibalism in *M. giganteus* (Schoch and Seegis

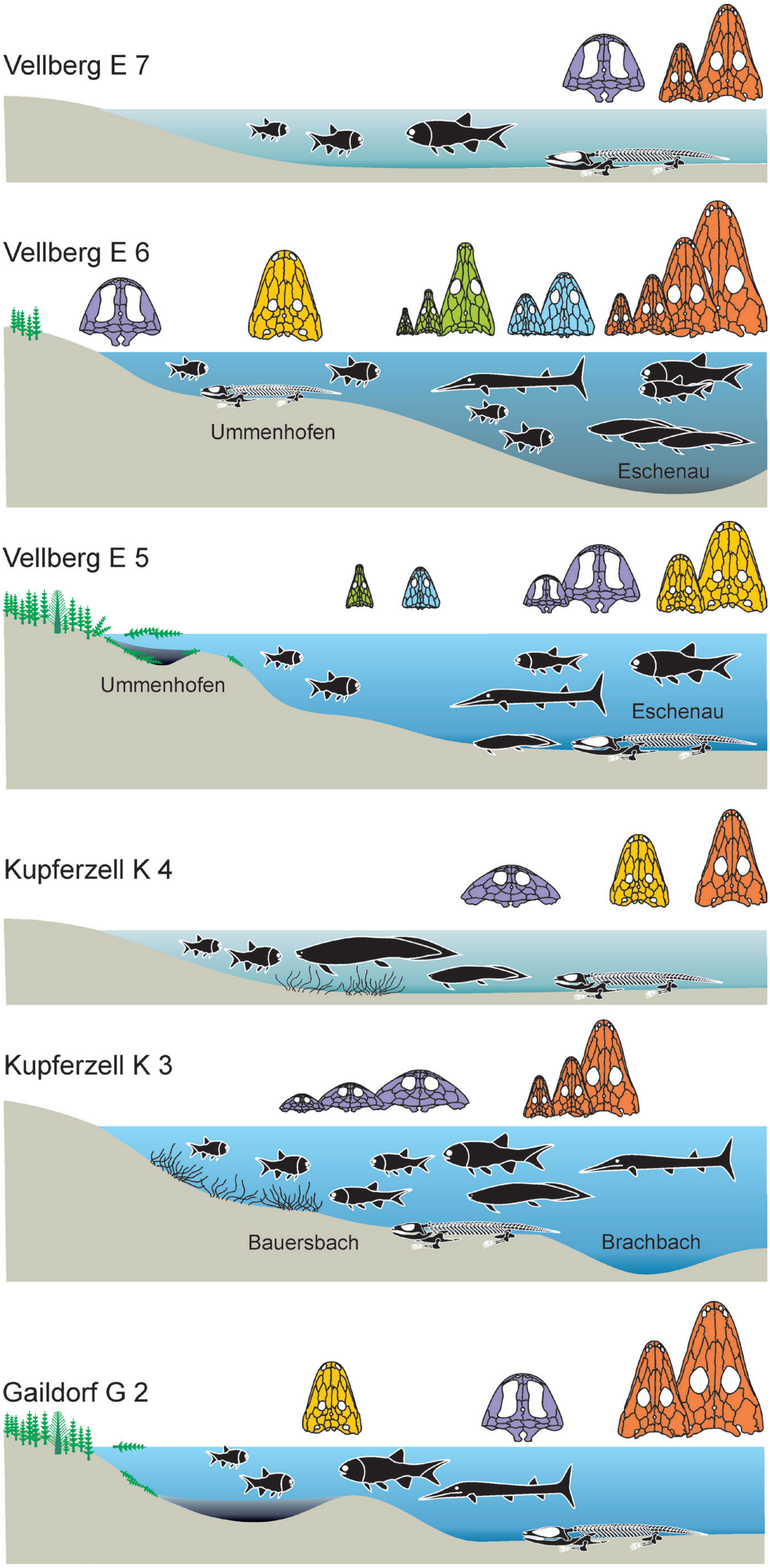

Figure 9. Faunal composition and properties of the six lake deposits with the largest samples of *M. giganteus*. Different size of skulls indicates presence of different growth stages in the same habitat.

2016; Mujal et al. 2022), including a 60 cm skull plus mandibles with bite marks of a much larger conspecific. At the same time, a reduced number of bones of *M. giganteus* display bite marks produced by *Batrachotomus kupferzellensis*, indicating scavenging as in the Kupferzell lakes, but in lesser frequency (Mujal et al. 2022), possibly because the lakes in Vellberg persisted for longer periods, so that the large pseudosuchian archosaurs could not frequently reach the large carcasses of *M. giganteus*.

These data indicate that Lake E6 formed a protected and nutrient-rich nursery ground for lungfishes and temnospondyls, with adult *Ptychoceratodus*, *Trematolestes* and *Tatrasuchus* appearing only during the mating season to lay eggs. In contrast, *Callistomordax* and *M. giganteus* were autochthonous throughout their life cycles and sufficiently different to avoid direct competition as adults. The numerous regurgitates preserved in E6 fall into two different size classes: 5–20 cm long skeletons of juvenile lungfishes and small archosauromorphs (potentially produced by *Callistomordax*) and 1–2 m long skeletons of archosauriforms (especially the amphibious *Jaxtasuchus salomoni*, Schoch and Sues 2013) and pseudosuchians (likely produced by *Mastodonsaurus*). Nevertheless, it cannot be discounted that some of the regurgitates were produced by *Batrachotomus kupferzellensis* (Mujal et al. 2022).

Lake Vellberg E7

The pale yellow micritic dolostones of E7 (Anoplophora Dolomite) form a 70–90 cm thick unit that is subdivided by thin horizons of greyish-brown mudstones. The basal unit has yielded skeletons of the terrestrial apex predator *Batrachotomus kupferzellensis* (thus the unit was coined *Batrachotomus* dolomite) skulls and disarticulated skeletons of *M. giganteus*, occasional finds of large adult *Plagiosuchus* and two juvenile skulls of *Tatrasuchus*. Fish remains are confined to single scales and teeth, with dominance of large polzbergiids (*Serrolepis*).

Like the Kupferzell facies, E7 was probably a clear water environment, although characeans have not been found. The dolostones formed under very shallow water conditions (Schoch and Seegis 2016). Like most of the aforementioned lakes, E7 developed in a sabkha-like setting, emplaced on a tidal flat that underwent frequent periods of desiccation. This is evidenced by the relative abundance of well-preserved skulls and skeletons of *M. giganteus* as well as *Batrachotomus*.

Lake Arnstadt A42

During highway construction near Arnstadt (north of the bridge at the Autobahn exit “Arnstadt Nord”), a large exposure that was open in 2003 yielded tetrapods in several horizons of the Lower Keuper (Werneburg and Witter 2005). The stratigraphically higher one yielded *M. giganteus*, among them the giant specimen restored in Fig. 4I. This horizon (Oberes Dunkles Band, Bed A42 within the upper sandstone S2o) forms a succession of dark coaly siltstones grading into dark grey mudstones. The disarticulated, large skull of *M. giganteus* was found below a bed rich in fossil wood, in a coaly and pyrite-rich layer. The preservation of bones closely resembles that of the Gaildorf specimens (Werneburg in Hagdorn et al. 2015), as does the stratigraphic association of the coaly siltstones with channel sandstones. Bed A42 also contained remains of the marine-lagoonal tetrapods *Plagiosternum* and *Nothosaurus*, as well as vertebrae of large pseudosuchians (Werneburg and Witter 2005). This setting might have formed in a lagoonally-influenced, stagnant water body with terrestrial input (reworked pseudosuchian bones). The occurrence of very large specimens of *M. giganteus* in similar facies at Gaildorf and Arnstadt is noteworthy and might either indicate a preference of swampy environments or simply a wider distribution of such giants.

Conclusions

Mastodonsaurus giganteus was a common predator in Middle Triassic freshwater environments (Hagdorn et al. 2015). The vast majority of Ladinian (Lower Keuper) occurrences stems from lake deposits, but occasional finds in river channels and lagoonal or shallow marine environments document its presence in a wide range of habitats (Schmidt 1928; Schoch 1999; Werneburg and Witter 2005). In the Lower Keuper sequence, *M. giganteus* inhabited a variety of water bodies on a large sabkha plain, including coastal and central parts of various freshwater lakes (Schoch and Seegis 2016; Schoch et al. 2022).

The currently known ontogeny of *M. giganteus* spans the enormous range of 12–15 mm to 1200 mm skull length, with a 100-fold increase in metric size. Although this range is unparalleled among temnospondyls or even lower tetrapods, it does not involve many substantial morphological changes. This agrees with the findings of Schoch and Witzmann (2024) on stereospondyl juveniles.

The smallest specimens are only known from fragmentary symphyses and interclavicles, which already show the main features of the taxon and clearly differ from small juveniles of other taxa. Proportional changes were most profound in the early juvenile phases, involving size differentiation of teeth and fangs and the size of the orbit. Early juveniles (12–20 cm skull length) already had a fully developed dermal ornament with low ridges spanning a wide network. Large adults had a longer postorbital skull table and a more deeply concave occipital margin and in giant specimens the orbit was slightly smaller, compensated by a broader jugal, and the symphyseal fangs were disproportionately large.

The frequency distribution of *M. giganteus* in the Lower Keuper provides interesting insight into the habitat preferences of this species in different phases of its life cycle. In lake shore facies (K4, E7), it was mostly present with larger specimens and juveniles are absent. These environments were probably only visited by adults because they did not provide sufficient protection for immature animals. Larvae and juveniles evidently dwelled in calmer environments within lakes. Among the latter, smaller lakes such as E5 were apparently less attractive than larger or deeper lakes such as K3 and E6. The latter evidently provided sufficient resources for breeding, and tiny specimens of *M. giganteus* have been identified in both deposits. In these rich ecosystems, a diverse actinopterygian fish fauna with taxa ranging between 3 cm (*Dipteronotus*) and 30 cm body length (scanilepiforms) provided prey for all growth stages of the large temnospondyl predators.

Adult *M. giganteus* was most common in lakes with abundant large prey, but the variation of tetrapod and sarcopterygian taxa between lakes indicates that this giant capitosaur was not restricted to a particular group of prey taxa. At Gaildorf, its most likely prey formed the relatively large *Plagiosuchus* whereas at Kupferzell (K3–4) it probably included the smaller *Gerrothorax* together with actinistians and lungfishes. At Vellberg, only adult *M. giganteus* visited the small lake E5, where *Plagiosuchus* and *Tatrasuchus* were preyed upon, as bite marks show. Heavy, predation-induced damage has been identified on several skulls of *Tatrasuchus*. *M. giganteus* also shows cannibalistic behaviours, as crushed and bite-marked skulls and mandibles indicate. At the same time, *M. giganteus* carcasses fed the pseudosuchian archosaur *Batrachotomus kupferzellensis*.

Mastodonsaurus giganteus was not only flexible enough to feed on a wide range of prey taxa, but also occurred in divergent habitats (Fig. 9). This is best exemplified by its abundance at both Kupferzell K3 and Vellberg E6. In these very different water bodies, its babies hatched and grew up to large adult size, whereas in Kupferzell K4 and Vellberg E7, it visited the habitats only during well-defined phases of juvenile and adult life. We conclude that its presence was apparently more restricted by the presence of competitors than by the stability of living conditions. Probably the question of which capitosaur first settled in a lake made the difference. In rich habitats, *M. giganteus* managed to partition niches with *Tatrasuchus*, whereas in most others it failed to do so.

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