



Osteology of the Permian temnospondyl amphibian *Glanochthon lellbachae* and its relationships

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Abstract. The early Permian Meisenheim Formation of the Saar–Nahe Basin (Germany) is famous for its richness in vertebrate fossils, among which the temnospondyls were present with microvores and fish-eating apex predators. The latter trophic guild was occupied exclusively by the genus *Sclerocephalus* in that basin within a long time interval up to M8, whereas in M9, a new taxon, *Glanochthon lellbachae*, appeared. This taxon is defined by (1) a preorbital region 1.8–2.0 times as long as the postorbital skull table, (2) dermal ornament with tall radial ridges, (3) a prefrontal anteriorly wider with straight lateral margin, (4) a squamosal posteriorly only half as wide as the quadratojugal, (5) phalanges of manus and pes long and gracile, (6) carpals unossified in adults, and (7) tail substantially longer than skull and trunk combined. Phylogenetic analysis finds that *G. lellbachae* forms the basal sister taxon of the stratigraphically younger *G. angusta* and *G. latirostre* and that this clade nests within the paraphyletic taxon *Sclerocephalus*, with *S. nobilis* forming the sister taxon of the genus *Glanochthon* (urn:lsid:zoobank.org:act:3038F794-17B9-4FCA-B241-CCC3F4423651; registration date: 15 March 2021).

1 Introduction

The Saar–Nahe Basin ranks among the largest late Paleozoic sedimentary basins in continental Europe and has produced thousands of early Permian tetrapod fossils (Boy et al., 2012; Fig. 1). The largest tetrapod taxa in these lacustrine deposits were eryopiform temnospondyls, which formed the top predatory group that preyed on bony fishes (Boy, 2003). Among these, the most common genus, *Sclerocephalus*, evidently preferred actinopterygians, whereas the more gracile

Glanochthon and *Archegosaurus* preserve acanthodian skeletons in their intestines (Boy, 1994; Kriwet et al., 2008; Schoch and Witzmann, 2009a). For more than 150 years, the three taxa were the only well-known eryopiforms from the Saar–Nahe Basin despite much collecting in numerous localities. The only exceptions formed two isolated finds, the still enigmatic *Palatinerpeton* (Boy, 1996) and a fragmentarily known *Onchiodon*-like eryopid (Schoch and Hampe, 2004).

This changed when private collector Klaus Krätschmer discovered a new site in the Klauswald southwest of Odernheim am Glan (Fig. 1), where large quantities of vertebrates were collected. This locality falls within the Meisenheim Formation, the richest tetrapod-bearing rock sequence in the basin (Boy et al., 2012). He published a large part of his material (Krätschmer, 2004, 2006; Krätschmer and Resch, 2005) and compared it with other samples, providing detailed information also on the various localities and *fossil-lagerstätten*. His taxonomic considerations led him to suggest the existence of various new taxa, most of which turned out to be synonyms of *Sclerocephalus haeuseri* Goldfuss (Schoch and Witzmann, 2009a). Nevertheless, his work highlighted the variation between and within samples of eryopiform temnospondyls, and one of the new morphs from the Klauswald locality that he envisioned clearly forms a separate taxon from the co-occurring *Sclerocephalus nobilis*. This new species was first named *Cheliderpeton lellbachae* by Krätschmer (2006).

The various samples of *Sclerocephalus* and *Glanochthon* span a time range of some 2.5 Myr (Boy et al., 2012; Menning and Bachtadse, 2012), and the morphological and developmental aspects of this endemic evolutionary lineage will be the subject of a research program that seeks to trace the microevolution and cladogenesis between the samples. The

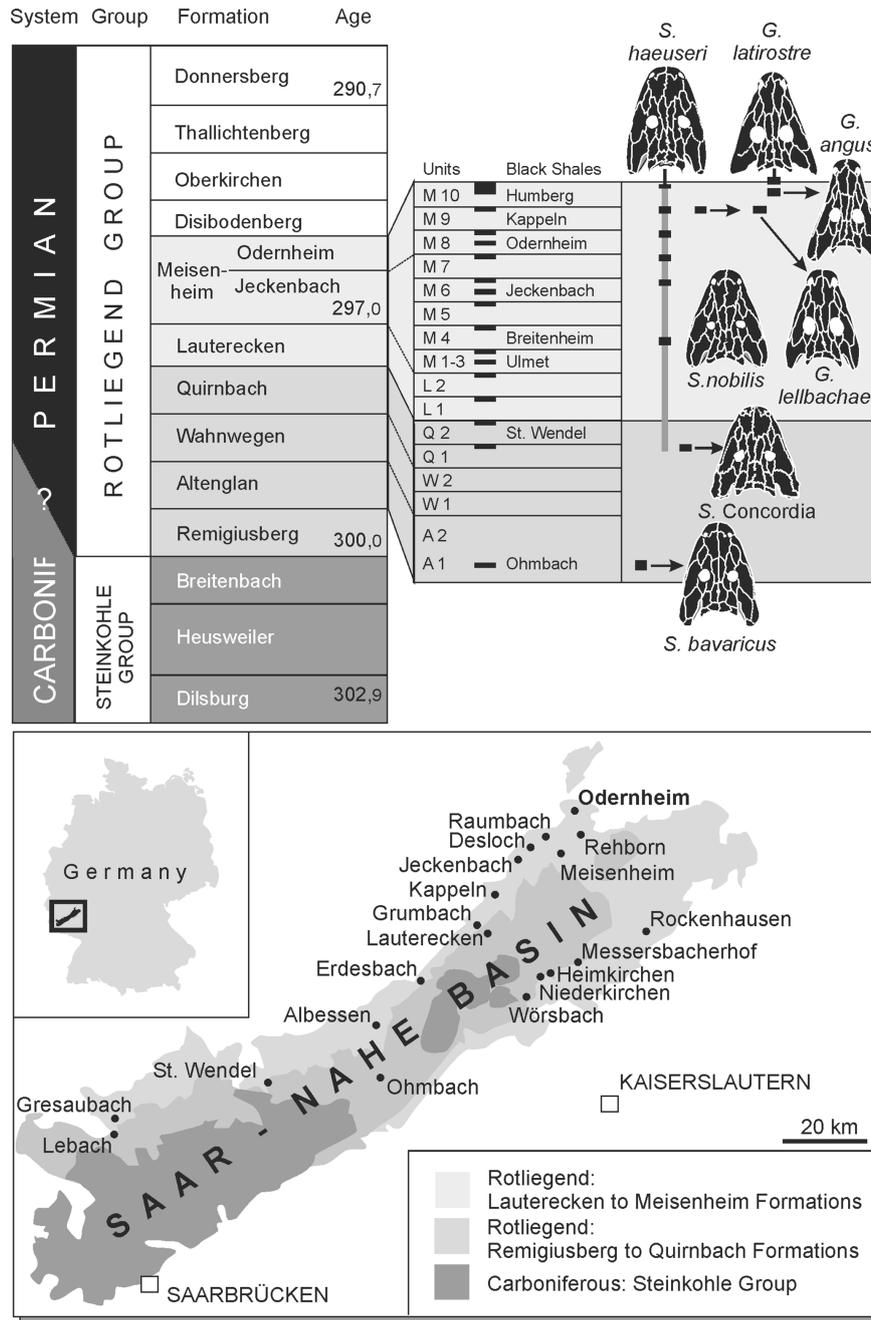


Figure 1. Localities yielding *Sclerocephalus* and *Glanochthon* material and stratigraphy of the Rotliegend sequence with emphasis on the Meisenheim Formation (Autunian, Lower Permian) in the Saar–Nahe Basin of Germany.

present exercise forms only the first step in this program. The objective is to describe and diagnose this taxon, especially in comparison to co-occurring *S. nobilis* from the same locality and to study its phylogenetic relationships.

2 Material and methods

NHMM: Naturhistorisches Museum, Mainz, Germany. NHMM 2006/14 (102 mm SL, SL signifies skull length, complete skeleton with skin preservation; Figs. 2a–c, 3d).

SMNK: Staatliches Museum für Naturkunde, Karlsruhe, Germany. SMNK-TAL 4638a (91 mm SL, complete skeleton); 4638b (91 mm SL, complete skeleton).

SMNS: Staatliches Museum für Naturkunde, Stuttgart, Germany. SMNS 91281 (115 mm SL, complete skeleton; Fig. 3a); 90507 (85 mm SL, palate and postcranium; Figs. 3c, 4c, d).

UGKU: Urmuseum Geoskop, Pfalzmuseum für Naturkunde, Thallichtenberg, Germany. UGKU POL-F 1997/1 (Fund-Nr. ROT 658) (115 mm SL, complete skeleton with skin preservation; Figs. 3b, 4a, b).

Anatomical abbreviations

a – angular; ar – articular; cl – clavicle; cop – coronoid process; d – dentary; ec – ectopterygoid; f – frontal; icl – interclavicle; ju – jugal; la – lacrimal; m – maxilla; n – nasal; na – naris; p – parietal; ptf – postfrontal; pgr – postglenoid region; pl – palatine; pm – premaxilla; po – postorbital; pp – postparietal; prf – prefrontal; ps – parasphenoid; psp – postsphenial; pt – pterygoid; q – quadrate; qj – quadratojugal; sa – surangular; sp – splenial; sq – squamosal; st – supratemporal; t – tabular; vo – vomer.

3 Systematic paleontology

Order **Temnospondyli** Zittel, 1888

Rhachitomi Watson, 1919 sensu Schoch, 2013

Eryopiformes Schoch, 2013

Family **Sclerocephalidae** Jaekel, 1909

Genus *Glanochthon* Schoch and Witzmann, 2009

Diagnosis

(1) Preorbital region 1.8–2.2 times as long as postorbital skull table, (2) tabular horn prominent, (3) postglenoid region posteriorly longer than the articular facet, (4) jugal narrower than greatest orbit width, and (5) interclavicle slender and at least twice as long as wide (modified from Schoch and Witzmann, 2009b).

Type species

Glanochthon latirostre (Jordan, 1849).

Glanochthon lellbachae (Krätschmer, 2006) comb. nov. (Figs. 2–5)

Cheliderpeton lellbachae Krätschmer, 2006

Holotype

NHMM 2006/14, 102 mm SL, complete skeleton with skin impression (Fig. 2).

Type of locality and age

The Klauswald southwest of Odernheim am Glan, Rhineland-Palatinate, Germany (Fig. 1). M9 sequence, Klauswald facies, Odernheim Subformation, Meisenheim Formation, lower Rotliegend, Autunian, lowermost Permian.

Referred material

Altogether, five additional specimens are referred to as *Glanochthon lellbachae* (see material section). There remains a substantial number of specimens in private collections.

Diagnosis

Autapomorphies: (1) preorbital region in adults 1.8–2.0 times as long as postorbital skull table, (2) dermal ornament with continuous and relatively tall radial ridges in the snout, frontals and cheek (contrasting the more polygonal arrangement in *S. nobilis*), (3) prefrontal anterolaterally expanded to form a more equant pentagon, (4) squamosal posteriorly only half as wide as quadratojugal, (5) phalanges of manus and pes slightly longer and more gracile than in *S. nobilis* and (6) tail substantially longer than skull and trunk combined (shorter than that measurement in *S. nobilis*).

Taxonomic assignment

This taxon was originally erected as *Cheliderpeton lellbachae* by Krätschmer (2006), who made reference to its resemblance to *Cheliderpeton latirostre* as described and referred to by Boy (1993). Schoch and Witzmann (2009b) suggested the new genus name *Glanochthon* for *Cheliderpeton latirostre* after the type species *Cheliderpeton vranyi* had been redescribed by Werneburg and Steyer (2002) and was found not to be closely related to *G. latirostre* (Schoch and Witzmann, 2009b). Based on its below-demonstrated close relationship to *G. latirostre*, *Cheliderpeton lellbachae* is also referred to as *Glanochthon* as a new combination.

G. lellbachae co-occurs with *Sclerocephalus nobilis* in the same locality and horizon (Krätschmer and Resch, 2005; Schoch and Witzmann, 2009a). The combined list of autapomorphic characters 1–5 for the genus distinguish this taxon from *S. nobilis* and all other species of *Sclerocephalus*. Hypothetical larvae and small juveniles of *G. lellbachae* and *S. nobilis* may not be distinguished on the basis of the mentioned features, but *S. nobilis* generally has a wider jugal and more rounded orbit even at small stages. The presence of a third eryopiform temnospondyl at the Klauswald locality (suggested by Krätschmer, 2006) cannot be confirmed. With a maximum skull length of 17 cm (specimens in private collections), *G. lellbachae* appears to have been smaller than the more heavily ossified *S. nobilis* (24 cm), but admittedly the number of available specimens is very limited.

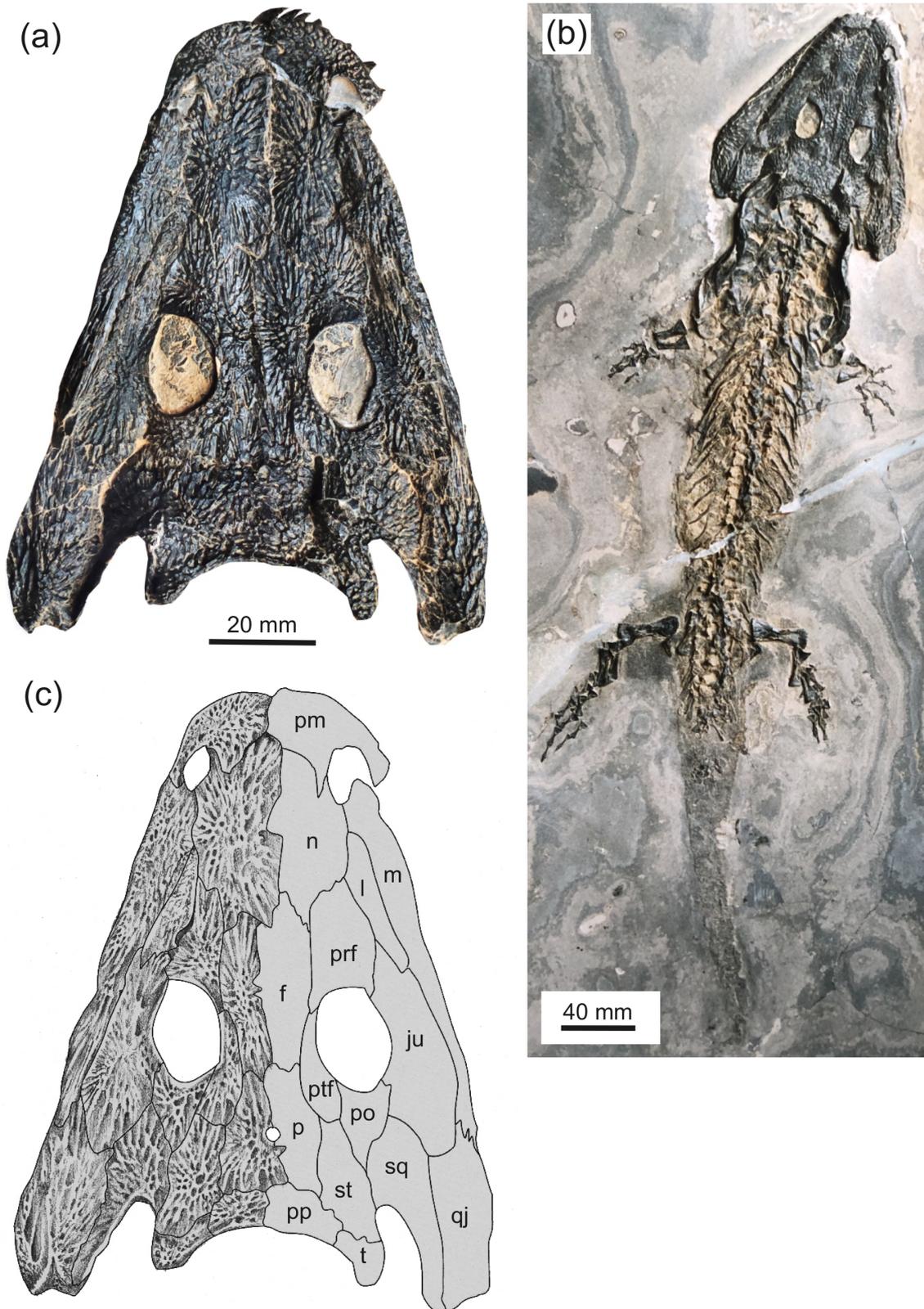


Figure 2. Type specimen of *Glanochthon lellbachae* (Krätschmer, 2006) comb. nov. (NHMM 2006/14). (a, c) Close-up of skull roof and (b) complete skeleton.

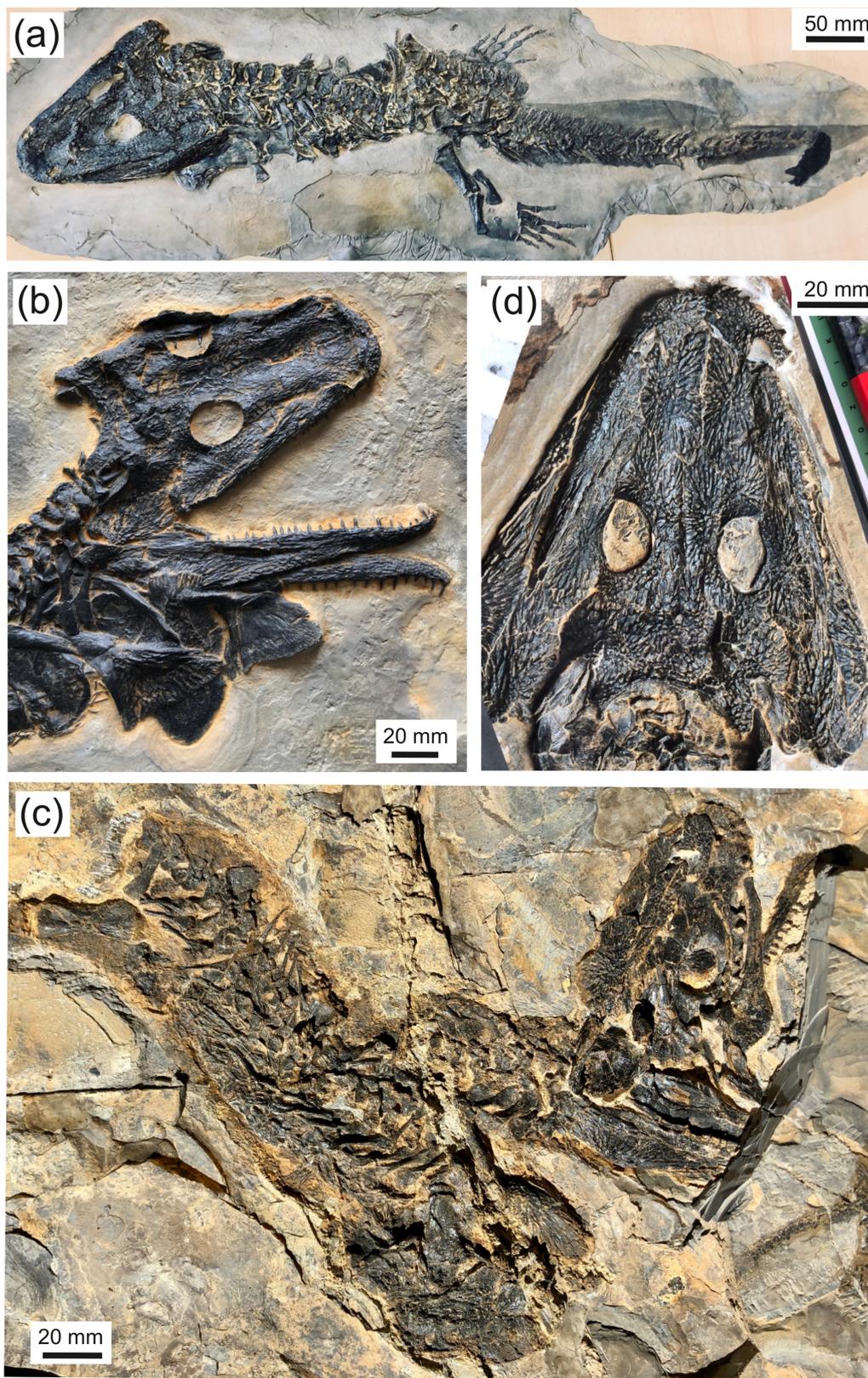


Figure 3. *Glanochthon lellbachae* (Krätschmer, 2006) comb. nov.: (a) SMNS 91281, (b) UGKU POL-F 1997/1, (c) SMNS 90507 and (d) NHMM 2006/14.

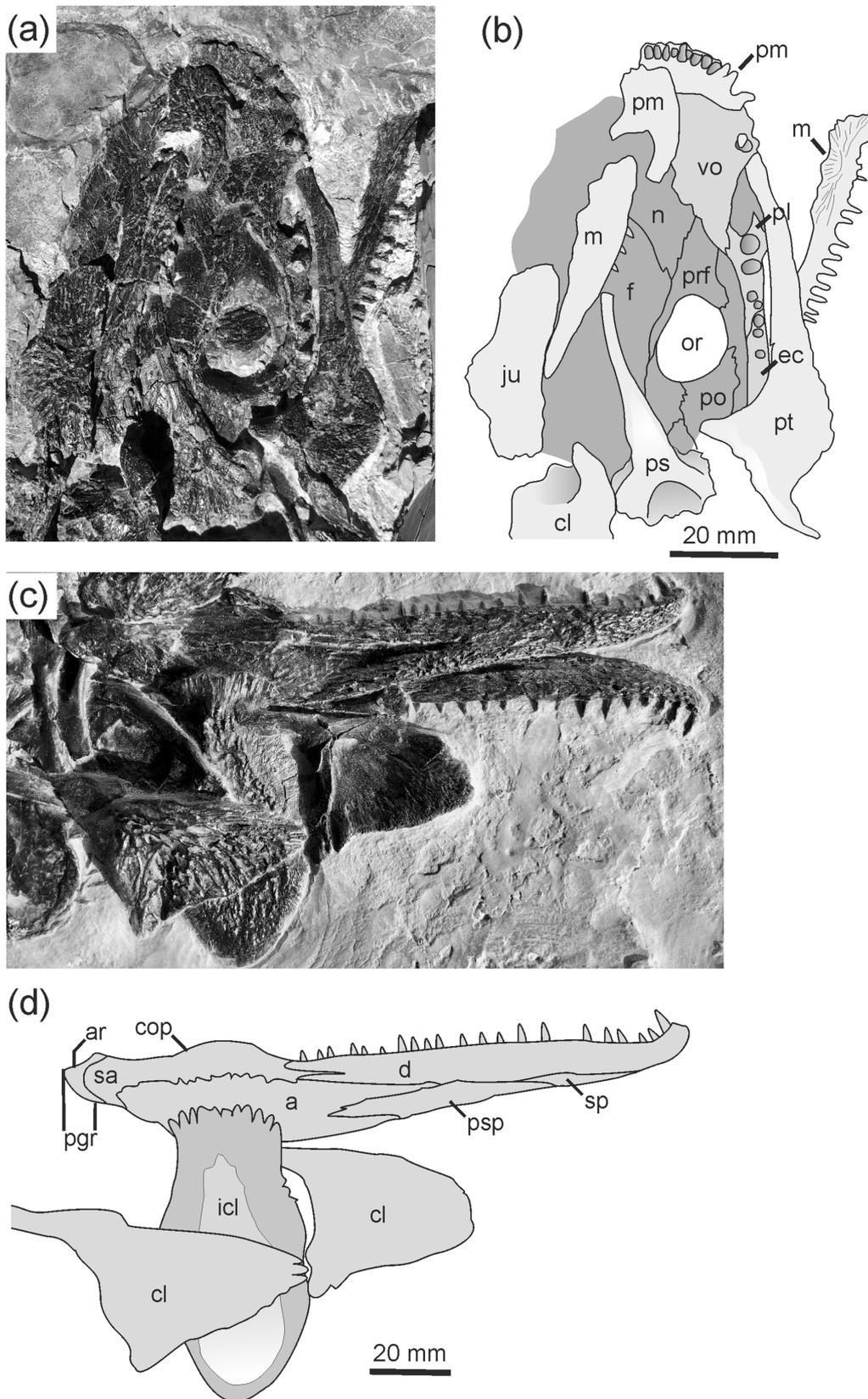


Figure 4. Palate and postcranium of *Glanochthon lellbachae* (Krätschmer, 2006) comb. nov.: (a, b) SMNS 90507 and (c, d) UGKU POL-F 1997/1.

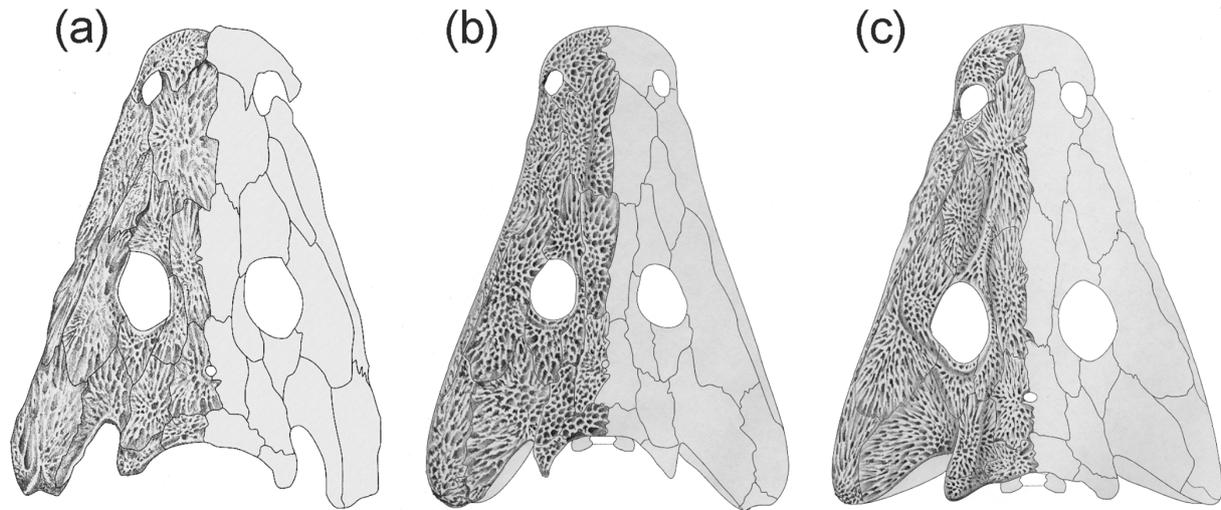


Figure 5. Comparison of *Glanochthon lellbachae* (a) with *G. angusta* (b) and *G. latirostre* (c). (Panels b and c from Schoch and Witzmann, 2009b.)

Phylogeny and taxonomy

In the analysis reported below, *S. nobilis* and the *Glanochthon* clade are found to be sister taxa. This recognized topological pattern leads to the phylogenetically problematic situation that *Sclerocephalus* forms a grade towards *Glanochthon*, which under strict application of cladistic principles would prompt erection of new genera at each node. An alternative option would be to define *Sclerocephalus* more broadly, encompassing all of Sclerocephalidae including *Glanochthon*. At the present stage, I consider any such step premature as long as morphological effects of microevolution cannot be distinguished from other effects, especially plasticity (ecophenotypes), which is beyond the scope of the present study.

Comment

Based on the current phylogenetic findings, *Glanochthon* is referred to as the family Sclerocephalidae, which contains a monophyletic group including a long *Sclerocephalus* grade and a terminal *Glanochthon* clade. The former referral of *Glanochthon* (as *Cheliderpeton latirostre*) within the Intasuchidae (Schoch and Milner, 2000) was based on a suite of characters which appear to be convergent in the present light of evidence.

Occurrence

Although *S. nobilis* and *G. lellbachae* co-occur in the same locality and several successive horizons, they differ in sample size per horizon. Most notably, *G. lellbachae* is more common in the upper fish beds (Obere Fischschiefer, “kalkige Papierschiefer”, K5), whereas *S. nobilis* peaks in the lower fish beds (Untere Fischschiefer, K2) as defined by

Krätschmer (2004). In the other beds (K3, 4), the two taxa co-occur, mostly represented by large juveniles.

4 Description

In the following description, features unique to *G. lellbachae* are highlighted, together with characters shared between *G. lellbachae* and *S. nobilis*, as well as *G. angusta* and *G. latirostre*. *S. nobilis* is consistent in most features with *S. haeuseri*, differing particularly in the synapomorphies shared with *G. lellbachae*. These differences often fall within a wide range of variation, with type specimens of *G. lellbachae* and *S. nobilis* forming end points on a continuum. Comparison with *S. nobilis* refer to specimens of the same size unless specifically stated otherwise because *S. nobilis* attained larger adult size and underwent marked ontogenetic changes in the latest phase of development (Schoch and Witzmann, 2009a). That is to say that the largest adults of *G. lellbachae* and *S. nobilis* differ even more than specimens of similar size.

4.1 Skull roof

The skull is slender with nearly straight lateral margins. Almost all skull-roofing elements are somewhat narrower than in *S. nobilis*. This is most conspicuous in the case of the squamosal, quadratojugal and jugal. The orbits also differ, being sagittally oval in *G. lellbachae* and almost perfectly round in *S. nobilis*. In *G. lellbachae*, the prefrontal and jugal form a markedly angled anterolateral region of the orbit.

The adult dermal ornament consists of elongated radial ridges, especially on the nasal, frontal, prefrontal, jugal and the anterior part of the parietal. Compared with *S. nobilis*, the ridges are taller and more continuous, and the polygons

on the posterior skull table and cheek are larger. In the largest specimens, the ridges are tallest. Like in *S. nobilis* and *G. angusta* and in contrast to *G. latirostre*, lateral line sulci are entirely absent.

The tip of the snout is blunt as in *S. haeuseri* and in contrast to the more rounded outline in *S. nobilis*. The region anterior to the naris is not longer than in *S. nobilis* but shorter than in *G. angusta*. The slightly more elongated preorbital region compared to *S. nobilis* is dominated by a more slender and relatively longer nasal. The lacrimal is often obscured by displaced neighboring elements, especially the maxilla; it does not appear to be substantially smaller than in *S. nobilis*. The prefrontal is markedly distinct from that of *S. nobilis*; its posterior region is narrower, the anterior one is wider than in the sister taxon, and the lateral margin is nearly straight and sagittally aligned in some specimens.

In *G. lellbachae*, the orbits are elongate oval rather than round, and the interorbital distance (0.15–0.17) is slightly smaller than in *S. nobilis* (0.19–0.24), resulting from narrower postfrontals and frontals. The prefrontal–postfrontal contact is nevertheless well established. The posterior skull table is consistent with *S. nobilis* in the proportions and suture patterns, especially the shape of the posterior (occipital) margin of postparietals and tabulars, as well as the elongate shape of the supratemporal, which is more consistent with other *Glanochthon* species than *Sclerocephalus* species.

The cheek differs most conspicuously in some specimens with the more slender squamosal and quadratojugal bones. In *G. lellbachae*, the squamosal is substantially narrower than the quadratojugal, which inverts the condition in all *Sclerocephalus* species. The jugal is clearly narrower in the type of *G. lellbachae* compared with most *S. nobilis* specimens, but there are a range of specimens with intermediate conditions which otherwise group with either *G. lellbachae* or *S. nobilis*.

4.2 Palate

The ventral side of the skull is exposed only in SMNS 90507 (Fig. 4a, b). The palate has little to distinguish it from that of *S. nobilis* or any species of that genus. The vomer is wider than in other *Glanochthon* species, but the tusk pair is relatively larger than in *S. haeuseri*, which is in turn more consistent with *Glanochthon*. The palatine is about twice as wide anteriorly than along its posterior part and bears two large tusks aligned at the lateral margin, and there are at least two smaller teeth posterior to these. The ectopterygoid meets the palatine in an S-shaped suture, and it bears 5–6 large teeth arranged in a straight row. The palatine ramus of the pterygoid is slender and anteromedially stepped, whereas the lateral wing of the pterygoid is laterally expanded much like in *Sclerocephalus* species.

In the parasphenoid, the base of the cultriform process is twice as wide as the anterior two-thirds, and it bears an elongate triangular denticle field that is posteriorly continuous

with that of the basal plate. The plate is wider than in *G. angusta*, which is more consistent with that of *G. latirostre* (Schoch and Witzmann, 2009b). On the basal plate, the denticle field is wedge-shaped, which is most similar to that of *G. angusta*. Laterally, an offset triangular region bears a marked groove, but a foramen is not preserved. Consistent with *Glanochthon*, and in contrast to the situation of *S. haeuseri*, muscular pockets along the posterolateral margin of the basal plate are not present.

4.3 Dentition

The marginal teeth are straight conical and not recurved. Their bases are striated, indicating labyrinthodont infolding of enamel and dentine. The teeth of the premaxilla and maxilla are generally smaller than those of the dentary. In the maxilla, tooth size decreases continuously towards the posterior end. The tooth count of the premaxilla is 11, that of the maxilla is unknown, and the dentary bears 21 teeth (with many irregular distances between) in UGKU POL-F 1997/1.

4.4 Braincase and occiput

There are no elements of the braincase exposed, and in the single specimen exposed in ventral view, the absence of braincase ossifications indicates that the neurocranium remained cartilaginous at least up to that stage. This is consistent with most *Sclerocephalus* and *Glanochthon* species (Boy, 1988).

4.5 Mandible

The mandible has little to distinguish it from *S. haeuseri* and *S. nobilis*, with the exception of the features described as follows. The coronoid process is somewhat more raised than in *S. haeuseri*. The postglenoid region is well established with a rounded posterior end and posteroventrally sloping dorsal margin. The dorsal surface is triangular and markedly concave. The postglenoid region is distinctly longer and more robust than in *S. haeuseri*, and its lateral side is more robustly ornamented than in other taxa.

4.6 Visceral skeleton

Only the distal, undiagnosed end of the stapes is exposed in UGKU POL-F 1997/1 (Fig. 3b). It is slender, apparently without quadrate process and with expanded distal end. No hyobranchial ossification has been identified.

4.7 Axial skeleton

The trunk is consistent in the number of vertebrae (24) with the conditions in *S. nobilis* and other species of *Sclerocephalus* and *Glanochthon*. However, the proportionate length of the trunk with respect to the skull is somewhat greater than in *S. nobilis* and about equal to that of *S. haeuseri*

from both Jeckenbach (M6) and Pfarrwald (M9P). Furthermore, the tail (= preserved skin outline) of *G. lellbachae* is substantially longer than in all *Sclerocephalus* species, reaching the length of skull and trunk combined. The caudal skeleton ossified slowly and in adults reached only 50 % the length of the tail, as revealed by the preserved tail skin. The vertebral centra are consistent in morphology and extent of ossification with those of *S. nobilis*. The first four (cervical) neural arches have the same proportions and relative differences in height as in classical *S. haeuseri* (Boy, 1988). The anterior trunk ribs are long, and at least 6–7 of them have large blade-like uncinat processes which have blunt ends and bear large foramina presumably for blood vessels, a feature also described in large adults of *S. haeuseri* (Schoch and Witzmann, 2009a).

4.8 Appendicular skeleton

The dermal pectoral girdle differs in *G. lellbachae* in having a more slender interclavicle that is twice as long as wide. In *S. nobilis*, the interclavicle width usually reaches two-thirds the length, which is similar to stratigraphically older *Sclerocephalus* samples (Schoch and Witzmann, 2009a). In large *S. nobilis* and *S. haeuseri*, the interclavicle and clavicle are proportionately larger, and the interclavicle is even wider than in juveniles (Boy, 1988). The interclavicle has a well offset ornamented region on the ventral side with ridges most pronounced in the anterior half and a serrated anterior margin which has only half the greatest width of the element. The scapulocoracoid is larger in *S. nobilis* compared to *G. lellbachae* of similar size. This was probably simply a function of ossification, which was slightly higher in *S. nobilis* of the same size as *G. lellbachae* and much higher in adult *S. nobilis*, in which it reached levels nearing those of *Onchiodon* and *Eryops* (Werneburg, 2008).

There is no consistent difference in the shape and relative size of the ilium between the two taxa, although the largest adult of *G. lellbachae* has a markedly downcurved anteroventral margin in the acetabular region. The long axis always measures twice the length of the ventral margin, and the shaft is posterodorsally angled in adults of both taxa. The pubis remained unossified throughout life in *G. lellbachae*, whereas in the large adult of *S. nobilis*, the pubis and ischium formed a vast co-ossified plate.

The limbs are well ossified in adults (10–17 cm skull length), but even the largest specimens lack carpal ossifications. The tarsus contains three small polygonal bones arranged in an oblique row running from the fibula to the first toe (SMNS 90507). Manus and pes are slightly longer relative to skull length than they are in *S. nobilis* of similar size. In addition, the phalanges are markedly more slender with less broadened ends in *G. lellbachae*. The humerus is well differentiated with fully ossified distal condyles but no supinator. Throughout ontogeny, the humerus is substantially

shorter relative to the skull (0.28–0.3 in *G. lellbachae*, 0.33–0.56 in *S. nobilis*).

The scalation of the ventral and lateral regions in the trunk is consistent with that of *Sclerocephalus* as described by Boy (1988) and Witzmann (2007).

5 Phylogenetic analysis

5.1 Data matrix

The original data matrix contained 54 characters (Schoch and Witzmann, 2009b) to which 10 new characters were added (see Appendix A). Six taxa were added: *S. sp. Concordia* (from Lake Concordia deposit, St. Wendel, Quirnbach Formation; Schoch and Sobral, 2021), *S. bavaricus* (Boy, 1988), *S. jogischneideri* (Werneburg, 1992), *S. nobilis* (Schoch and Witzmann, 2009a), *G. lellbachae* and *Sclerocephalus stambergi* (Klembara and Steyer, 2012).

5.2 Analysis

The analysis of 64 characters and 24 taxa found a single most parsimonious tree requiring 121 steps (CI = 0.57, RI = 0.814). The analysis was conducted in the ACCTRAN mode under the New Technology search option. Bremer support values were calculated, revealing some robust support for the *Glanochthon* clade and the more inclusive sister group *G. latirostre* + *G. angusta* (three steps), as well as Eryopiiformes in general (each three steps), a slightly lower support for Sclerocephalidae and Eryopidae (each two steps), but low support for the single nodes of the *Sclerocephalus* grade, as well as the relationship between archegosaurids (each just one step).

5.3 Results

In the obtained topology (Fig. 6), the general branching pattern differs from that of Schoch and Witzmann (2009b) in two major aspects: (1) *Sclerocephalus* forms a grade towards *Glanochthon* and (2) *Cheliderpeton vransyi*, *Melosaurus* and *Intasuchus* form successive sister taxa of the archegosaurids *Archegosaurus*, *Platyoposaurus* and *Australerpeton*. This is the first analysis to obtain *Sclerocephalus* and *Glanochthon* as part of the same clade rather than a grade towards stereospondyls. However, Boy (1987) was already tempted to consider *Glanochthon* (then only known by its stratigraphically youngest species *G. latirostre*) as a close relative of *Sclerocephalus*. The Sclerocephalidae (*Sclerocephalus* + *Glanochthon*) is thus recognized as a relatively speciose basal clade of the Stereospondylomorpha.

The paraphyletic taxon *Sclerocephalus* was found to be a grade with respect to the genus *Glanochthon*, in which *S. stambergi*, *S. bavaricus*, *S. jogischneideri*, *S. sp. Concordia* + *S. haeuseri* and *S. nobilis* form successive sister taxa to

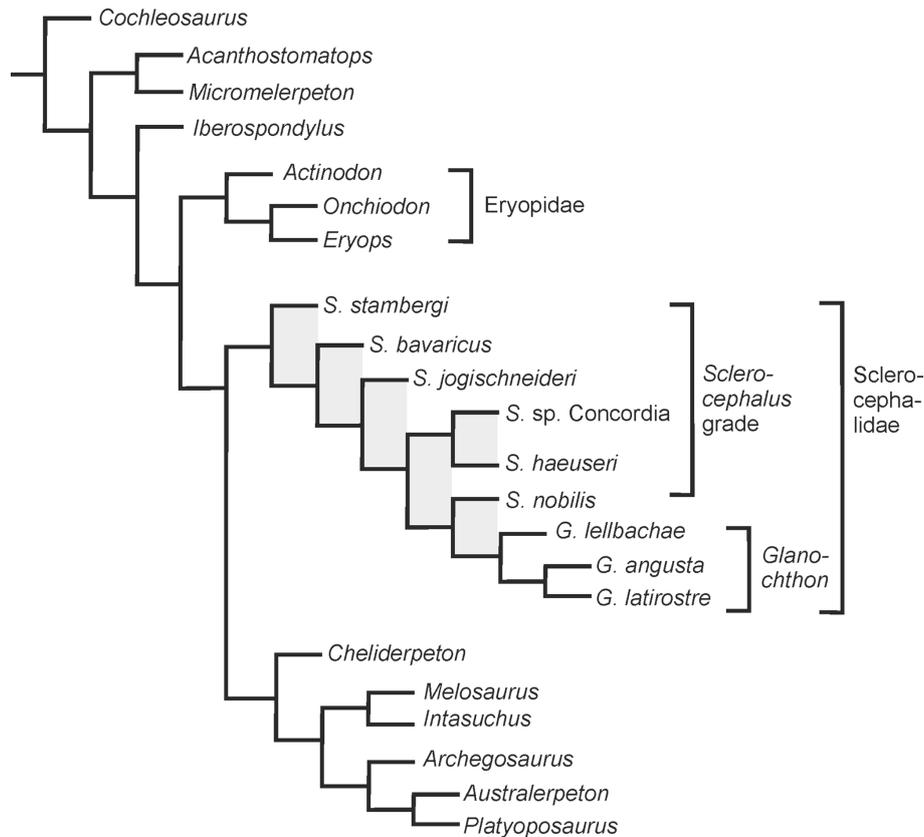


Figure 6. Phylogenetic analysis of eryopiform temnospondyls with emphasis on the position of *Glanochthon lellbachae*.

Glanochthon. In the present analysis, *S. haeuseri* was confined to Boy's subspecies *S. haeuseri haeuseri*.

6 Conclusions

Sclerocephalus was the most common and regionally widespread genus in the lower Rotliegend of the Saar–Nahe Basin, and morphological change through the rock sequence was considerable (Schoch, 2009, 2014; Schoch and Witzmann, 2009a). This was already highlighted by Boy (1988) who paid tribute to the morphological change across stratigraphic levels. He formally defined *S. bavaricus* and *S. haeuseri* as chronospecies and recognized two chronosubspecies within the latter: *S. haeuseri jeckenbachensis* from Lake Jeckenbach (M6) and *S. haeuseri haeuseri* from Lake Pfarwald (M9–P). Throughout the sequence A1–M8, there was only a single taxon present at any preserved time slice.

Before deposition of the M9 sequence, *Sclerocephalus* probably formed an anagenetic lineage spanning some 2 Myr (A1–Q1–M3–M6–M8) as there is no evidence of cladogenesis within the Saar–Nahe Basin. However, the phylogenetic placement of *S. jogischneideri* between *S. bavaricus* and *S. sp. Concordia* suggests the emigration of a post-A1 population which ultimately appeared in the Thuringian Forest

(southwest Saale) Basin. This placement was already suggested by Werneburg (1992). The age of *S. jogischneideri* (upper Oberhof Formation) relative to that of the Saar–Nahe Basin sequence is controversial but probably not older than M9 and possibly much younger (Lützner et al., 2012).

In M9, where two different lakes existed that were separated by a tectonic structure (Kappeln M9–K in the north, Pfarwald M9–P in the south), morphologically distinct samples appear. Whereas Lake Pfarwald harbored classical *S. haeuseri* (*S. haeuseri haeuseri* of Boy, 1988), Lake Kappeln was inhabited by an apparently uniform population similar to *S. haeuseri* in the southwest (St. Wendel locality S-2 of Boy, 1987, clay pit Halseband, and road cut nearby) but two distinct taxa in the northeast (Odernheim and Alsenz regions), here referred to as *S. nobilis* and *G. lellbachae*. The latter two are likely to have diverged within the time interval between the M8 and M9 lake deposits and, as indicated by phylogenetic analysis, evolved from *S. haeuseri*, which is well-known from M8 deposits. These interesting patterns will be analyzed elsewhere.

Speaking within the framework of Boy's chronospecies concept, the ancestor of *S. nobilis* and *G. lellbachae* branched off after *S. h. jeckenbachensis* and before *S. h. haeuseri*. As Boy (1988) noted, *S. h. haeuseri* had evolved a narrow interorbital region and slender posterior skull table, which was

considered a derived character of later *S. haeuseri* (Schoch et al., 2019). However, these features are unique to the population in Lake Pfarrwald, which falls within M9 rather than M10 as originally considered by Boy (1988), a fact that became only apparent after more research had been conducted (Boy et al., 2012). The subsequent, true M10 population of *S. haeuseri* from the lowermost horizons of Lake Humberg (Odernheim region) differs from the M9-P Pfarrwald population (*S. h. haeuseri*), instead sharing more aquatic features with M8 *S. haeuseri* (Schoch, 2009). Hence, Pfarrwald *S. haeuseri* is more likely to form a regionally isolated population, whereas M10 *S. haeuseri* more likely evolved from a population in Lake Kappel, such as the one preserved in the M9-K sample from St. Wendel.

A more detailed assessment of the relationships between all species referred to *Sclerocephalus* will be carried out elsewhere. In the present cladogram, phylogenetic positioning might be hypothesized as being influenced by size disparity and ontogenetic disparity, with *S. stambergi* and *S. jogischneideri* both found to be basal and relatively small taxa. In contrast to the rather adult morphology of *S. jogischneideri*, *S. stambergi* has an immature appearance, probably representing a juvenile, by analogy with the ontogenetically well-sampled *S. haeuseri* (Boy, 1988). Furthermore, both *S. jogischneideri* and *S. stambergi* are known from a single specimen each, whereas the other taxa or samples (“populations”) are represented by dozens or sometimes hundreds of specimens (Schoch, 2009; Krätschmer, 2004), and some stratigraphically (and probably phylogenetically) younger samples (Lake Odernheim, M8; Lake Humberg, M10) are known by small, paedomorphic adults only (Schoch, 2009). Furthermore, as large adults are very rare, they are often found only after many years of continued collecting. Admittedly, this fact also weakens the size disparity between *S. nobilis* and *G. lellbachae* mentioned above.

Phylogenetic analysis indicates that *G. lellbachae* forms the stratigraphically oldest taxon of the *Glanochthon* clade, sharing a range of synapomorphies with its stratigraphically younger relatives *G. angusta* (M10c) and *G. latirostre* (M10d). The three taxa might well form an anagenetic lineage, but speciation events cannot be ruled out. The two different hypotheses can only be tested by more detailed geographic and stratigraphic sampling, which is hardly possible without numerous new additional outcrops.

A new, still to be formally named species of *Glanochthon* was reported by Steyer (1996) from Buxières-les-Mines (Allier basins, France). Boy and Schindler (2012) and Schneider and Werneburg (2012) concur that the corresponding rock unit, the Membre supérieur of the Assise de Buxières-Autunien gris (Steyer et al., 2000), falls within the uppermost part of the Meisenheim Formation. This is consistent with the proposed hypothesis of an origin of *Glanochthon* within the Saar–Nahe Basin and a subsequent emigration into the Allier basins.

The current phylogenetic findings are not readily translated into a taxonomic scheme. The easiest solution would be to grant each sample from a different lake deposit a separate species name. This is practiced here in the straightforward case of *Glanochthon*, but in the vast series of samples of *Sclerocephalus haeuseri*, Boy’s (1988) chronosubspecies approach still remains more appealing. A morphometric study analyzing this interesting problem is under way and will be published elsewhere. Provided that the findings of the present study are correct, *Sclerocephalus* forms a paraphyletic assemblage with respect to the *Glanochthon* clade. The logical and phylogenetically correct approach would be to erect new genera for the successive species, but the close resemblance of most of these taxa would make these difficult to define. The extraordinary detailed stratigraphic and morphological record of the *Sclerocephalus*–*Glanochthon* clade therefore demonstrates the limits of any taxonomic approach to classify evolving lineages.

Appendix A: Character list

1. Premaxilla (alary process). Absent (0) or present (1).
2. Premaxilla (prenarial portion). Short (0) or expanded anteriorly by about the length of the naris (1).
3. Premaxilla (outline). Parabolically rounded (0) or box-like, anteriorly blunt (1).
4. Snout (internarial distance). Narrower than interorbital distance (0) or wider (1).
5. Snout (margin). Straight (0) or laterally constricted at level of naris (1).
6. Rostrum. Absent (0) or present (1).
7. Internarial fenestra. Absent (0) or present (1).
8. Orbits. Round to slightly oval (0) or elongated oval (1).
9. Orbits. Ends rounded (0) or pointed (1).
10. Maxilla (anterior margin). Straight (0) or laterally convex due to enlarged teeth (1).
11. Maxilla (contact to nasal). Absent, separated by lacrimal (0) or present (1).
12. Nasal (lateral margin). Straight (0) or stepped with lateral excursion anterior to prefrontal, accommodating narrower lacrimal (1).
13. Lacrimal (length). As long as nasal (0), shorter than nasal (1) or much abbreviated (2).
14. Lacrimal (width). Lateral suture parallels medial one (0) or lateral suture posterolaterally expanded to give broader preorbital region (1).
15. Preorbital region (length). Less than twice the length of posterior skull table (0) or more (1).
16. Prefrontal-jugal (contact). Absent (0) or present (1).
17. Prefrontal (anterior end). Pointed (0) or wide and blunt (1).
18. Frontal-nasal (length). Frontal as long or longer than nasal (0) or shorter (1).
19. Interorbital distance. Narrower than orbital width (0) or wider (1).
20. Lateral line (sulci). Absent in adults (0) or present (1).
21. Posterior skull table (length). Less than 0.7 times the width (0), 0.7–0.8 times (1) or larger than 0.8 (2).
22. Intertemporal. Present (0) or absent (1).
23. Postorbital. Long triangular, wedged deeply between squamosal and supratemporal (0) or short (1).
24. Squamosal embayment (size). Wide, giving semilunar flange on squamosal (0) or slit-like with thin flange on squamosal (1).
25. Tabular (ventral crest). Absent (0) or present (1).
26. Jugal (preorbital expansion). Absent in adults (0) or present (1).
27. Ornament. Polygons and short ridges (0) or long ridges arranged radially (1).
28. Vomer. Smooth (0) or with paired depressions anteriorly (1).
29. Vomerine tusks. Anterolateral to choana, transverse row (0) or well anterior to choana, sagittal row (1).
30. Anterior palatal openings. Absent (0) or present (1).
31. Choana (width). Elongated oval or slit-like (0) or round (1).
32. Premaxilla. Borders choana (0) or not (1).
33. Palatine, ectopterygoid (continuous tooth row). Absent (0) or present (1).
34. Palatine. Fangs and no more than 3–4 extra teeth (0) or 5 or more extra teeth (1).
35. Ectopterygoid (tusks). Present (0) or absent (1).
36. Parasphenoid. Denticle field on plate triangular (0) or round (1).
37. Basispterygoid ramus (length). Transverse, rod-like (0) or short without medial extension (1).
38. Basicranial articulation. Moveable overlap (0) or tightly sutured (1).
39. Carotid foramina (entrance). Anteromedial on basal plate, close to cultriform process (0) or at posterolateral corner of plate (1).
40. Vomer. Separated by pterygoid from interpterygoid vacuity (0) or bordering that opening (1).
41. Cultriform process (width). Throughout of similar width (0) or posteriorly expanding abruptly to about twice the width (1).
42. Stapes (quadrate process). Absent (0) or present (1).
43. Interclavicle (adult shape). As wide as long (0) or longer than wide (1).
44. Interclavicle (width). As wide or wider than posterior skull table (0) or narrower (1).

"Sclerocephalus"_stambergi

1011000000111001000?2101110????????????????111??
 ??????????00000000

Sclerocephalus_bavaricus

11010000001120010001210111010000?00000110?101
 001?01?12?00000011

Sclerocephalus_haeuseri

101100000112200100002101110100001000001101101
 0010010121010000011

Sclerocephalus_sp._Concordia

101100000112200100002101110100001000011101101
 001001?120100000011

Sclerocephalus_jogischneideri

10110000011220010001210111010000100000110?101
 001?01?121000000011

Sclerocephalus_nobilis

11110000011210010000210111010000100000110?101
 0010010121011100111

Glanochthon_lellbachae

111110001111?01100012101110100001010001100111
 0011010111001110111

Glanochthon_angusta

111110001111?01100012101110100001010001100111
 0011011111001111111

Glanochthon_latirostre

111110001111101100011101111100001010001100111
 0011011111001111111

Intasuchus_silvicola

11010001?0000011010?0101?1110001111010110?????
 ?????????1000000000

Melosaurus_uralensis

1101000100100011010?1101?10????????????????11?0?
 ?1?????1000000000

Cheliderpeton_vranyi

100100000?0000101012101?10????????????????10100
 11011211000000000

Archegosaurus_decheni

110101010010001101012101111110011111101101111
 0011011111000010000

Platyoposaurus_stuckenbergensis

110101000010001101012101110111011111101100111
 0011?11111000000000

Australerpeton_cosgriffi

110101000010001101012101110111011111111100111
 0010?11111000000000

Code availability. Software package available under: <https://cladistics.org/tnt> (Willi Hennig Society, 2021).

Data availability. All underlying research data are provided in the Appendices A and B.

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