

# Anatomy and relationships of the Triassic temnospondyl *Sclerothorax*

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Recently, new material of the peculiar tetrapod *Sclerothorax hypselonotus* from the Middle Buntsandstein (Olenekian) of north-central Germany has emerged that reveals the anatomy of the skull and anterior postcranial skeleton in detail. Despite differences in preservation, all previous plus the new finds of *Sclerothorax* are identified as belonging to the same taxon. *Sclerothorax* is characterized by various autapomorphies (subquadrangular skull being widest in snout region, extreme height of thoracal neural spines in mid-trunk region, rhomboidal interclavicle longer than skull). Despite its peculiar skull roof, the palate and mandible are consistent with those of capitosauroid stereospondyls in the presence of large muscular pockets on the basal plate, a flattened edentulous parasphenoid, a long basicranial suture, a large hamate process in the mandible, and a falciform crest in the occipital part of the cheek. In order to elucidate the phylogenetic position of *Sclerothorax*, we performed a cladistic analysis of 18 taxa and 70 characters from all parts of the skeleton. According to our results, *Sclerothorax* is nested well within the higher stereospondyls, forming the sister taxon of capitosauroids. Palaeobiologically, *Sclerothorax* is interesting for its several characters believed to correlate with a terrestrial life, although this is contrasted by the possession of well-established lateral line sulci.

**Key words:** *Sclerothorax*, Temnospondyli, Stereospondyli, Buntsandstein, Triassic, Germany.

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## Introduction

The Central European Buntsandstein represents a crucial time for the evolution of terrestrial vertebrates, spanning some 6–7 million years within the Early and Middle Triassic. This sequence of continental red-beds has produced a range of land-living vertebrates most of which are poorly preserved and tantalizingly difficult to interpret. These include various temnospondyls, procolophonids, pareiasaurs, basal diapsids, and archosaurs (Meyer 1858; Jaekel 1910; Huene 1914, 1920; Wild 1998).

One of the most intriguing Buntsandstein vertebrates is a remarkable temnospondyl, originally based on a single set of two articulated specimens. These were uncovered in a sandstone quarry near Queck, located in the north-central German state of Hesse (Hessen). The discovery of this material dates back to the mid-1920s, and it was first studied by Friedrich von Huene who erected a new genus and species, *Sclerothorax hypselonotus* (Huene 1932). Although the material comprised two skeletons of diverging modes of preservation, Huene was convinced that there was only one taxon, and he

undertook a meticulous preparation and casting of the material to prove this hypothesis.

His first specimen includes a vertebral column in lateral aspect, “ranging from the anteriormost vertebrae” to the base of the tail, but lacking any trace of the skull and otherwise revealing only scarce information on the girdles. That animal had elongated neural spines being highest at a level anterior to the mid of the trunk and becoming continuously lower both cranially and caudally. By itself, this find was readily identified as a temnospondyl because of its rhachitinous vertebral arrangement, and the peculiar morphology as well as the articulated nature of the find constitute a most interesting discovery. This find forms the most complete evidence of a temnospondyl postcranium in the Buntsandstein, and in the German Triassic ranks among the Lower Keuper material of *Trematolestes* and the plagiosaurids.

Conversely, Huene’s second specimen comprises a complete skull and pectoral girdle in dorsal exposure, along with the posterior part of a vertebral column embedded with the spines of the neural arches pointing dorsally. This was also clearly a temnospondyl, having a very wide, flattened skull and an extensive dermal shoulder girdle. At first sight, this

specimen seemed so different from the first find that Huene himself was struck. Yet his efforts in further preparing the second specimen revealed the morphology of the dorsal spines which he found similar to the first specimen, albeit affected by compaction and consequently distorted. As there was also an overlap in the ribs and pectoral girdle, showing no morphological differences, Huene concluded that there was just one taxon. This view has been adopted ever since (Romer 1947, 1966; Carroll 1988; Schoch and Milner 2000), but eventually a further specimen was found at the Queck locality.

The third specimen, discovered in 1967, was reported only very recently by Fastnacht (2004). It is similar to Huene's first find in exposing the axial skeleton laterally, and all preserved elements are identical to the latter. However, there is a mandible anterior to the first vertebra, and Fastnacht (2004) also reported a potential steinkern (infilling) of a palate. The latter appeared to have an outline similar to the Buntsandstein temnospondyl *Trematosaurus brauni*, thereby differing boldly from the skull of Huene's second, broad-headed find. Fastnacht consequently concluded that Huene's finds 1 and 2 constituted entirely different taxa. However, reexamination of the original material reveals that there are no clearly identifiable cranial remains besides the mandible in the third specimen.

Recently, a further series of three specimens emerged in the collection of the Kassel Natural History Museum, noticed by Jürgen Fichter. This sample includes three skulls supplementing one another to give a very detailed picture of most parts of the cranium, including the braincase. The overlap of these finds with both Huene's first and second specimen is extensive and compelling, prompting thorough analysis of all the available material. At the same time, the postcranial remains associated with the crania are consistent with those of both original finds of Huene (1932) and the Mainz specimen.

The goal of the present paper is to review all available evidence on the identity, taxonomy, and anatomy of the material referred to *Sclerothorax*. Our conclusion that all of the now available specimens in fact do belong to one and the same taxon will guide us to a detailed description of that taxon and an analysis of its phylogenetic and evolutionary significance.

*Institutional abbreviations.*—GPIM-N, Geologisch-Paläontologisches Institut, University of Mainz, Germany; HLD-V, Hessisches Landesmuseum, Darmstadt, Germany; NMK-S, Naturhistorisches Museum, Kassel, Germany; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany.

## Material and interpretation

*HLD-V 607:* Huene's find 2 (Fig. 1B).—The only Queck specimen preserving the skull, also having a good pectoral girdle, a right humerus, a left femur, and most of the rear part of the presacral vertebral column. The specimen is exposed in dorsal view. The neural spines, described and figured by

Huene (1932: blocks B1–2), are lost today. Excellent plaster casts of most slabs exist in the collection of the Staatliches Museum für Naturkunde Stuttgart (SMNS 1193a–k).

*HLD-V 608:* Huene's find 1 (Fig. 1A).—A nearly complete vertebral column preserved in lateral view, consisting of 24 presacral and at least eight caudal vertebrae and ribs. In addition, the left clavicle, cleithrum, and scapula are preserved as well as the complete right pelvis, then reprepared by Huene to expose the ilium. There are no diagnostic remains of skull, mandible, or limb elements.

*GPIM-N 2045* (Fig. 5C).—The largest specimen similar to HLD-V 608 in mode of preservation and anatomical regions exposed. In contrast to HLD-V 608, shortly anterior to the first vertebrae there is an imprint of a right mandible in lingual view and a structure that was interpreted as a very poorly preserved steinkern of the skull. Indeed, in casts of this specimen the imprint of this structure has some resemblance with the palate of a slender-headed stereospondyl. However, our interpretation of the GPIM specimen differs from that of Fastnacht (2004) in one critical point: we conclude that the hypothesized steinkern of a palate does actually not form part of the specimen. In the original specimen, the palate-like structure described by Fastnacht (2004) is formed by a large block of coarse sandstone that, after closer inspection, we interpret as a conglomerate component. This inclusion differs boldly from the surrounding sediment, and there are no imprints or remnants of bone whatsoever. Assuming that it really was an infilling (steinkern) of the interpterygoid vacuities as was suggested, the lack of any traces of the palate or the ventral side of the skull roof, which would have to be present in such a kind of preservation, are inexplicable. As GPIM-N 2045 is embedded in a block containing numerous conglomeratic pebbles of various sizes and lithologies, the presence of such a large coarse-grained component is not unexpected. The mandible is definitely present and the preserved details are consistent with the lower jaw in both HLD-V 607 and NMK-S 117. The original material included the counterpart which was reported by excavation team members to have comprised parts of a skull. The counterpart is lost today.

*NMK-S 117* (Fig. 2B).—The posterior half of a skull in ventral aspect, exposing palatal and occipital elements, and the anterior region of the vertebral column (neural arches, ribs). This specimen is most interesting in preserving the atlas intercentrum in articulation with the paired and well-separated exoccipitals. In addition, the pterygoids and basal plate of the parasphenoid are present, matching the outlines of the palate in HLD-V 607. The left humerus is present in 3d, having weakly ossified ends and resembling the humerus exposed in HLD-V 607 (Fig. 6F).

*NMK-S 118a* (Figs. 2A, 3B, D).—Two thirds of a large skull in dorsal exposure with well-preserved ornament and sutures. All skull roofing elements except the anterior part of the nasals, lacrimals, maxillae, and premaxillae are present. The sutures and ornament agree with that of Huene's skull (HLD-V 607).

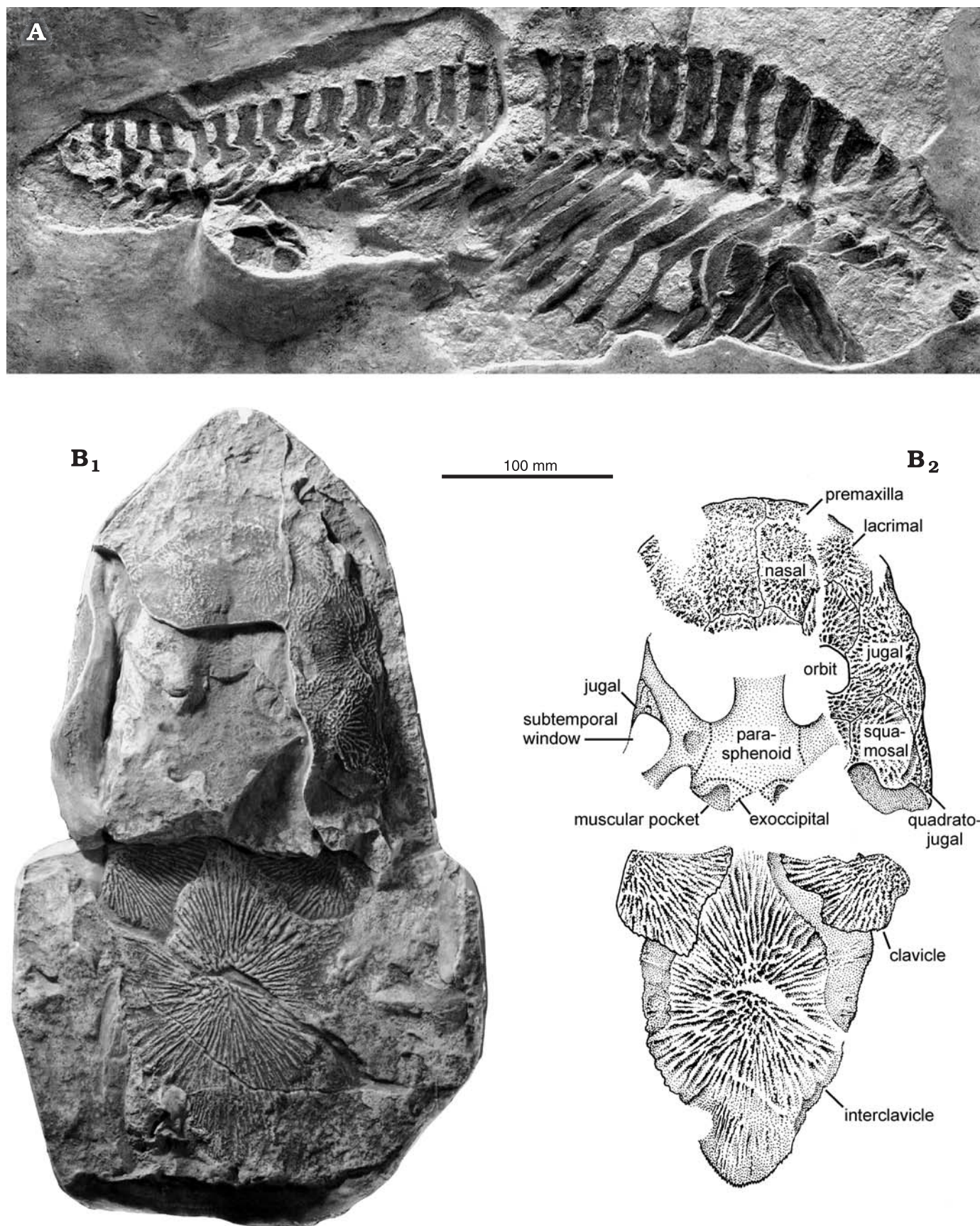


Fig. 1. Original material of *Sclerothorax hypselonotus* Huene, 1932 described by Huene (1932) from Buntsandstein of Queck, Hessen, Germany. A. HLD-V 608, lateral view (right side). B. HLD-V 607 (lectotype) in dorsal view (B<sub>1</sub>) with interpretive drawing (B<sub>2</sub>).

*NMK-S 118b* (Figs. 2A, 3C).—A small skull in dorsal exposure, lacking the medial regions and posterior skull table, thereby exposing the dorsal side of the basicranium and cultriform process. Most of the outline of the skull is preserved, matching the observations in HLD-V 607 and NMK-S 118a. The exposed dorsal part of the palate agrees with that of NMK-S 117. The specimen includes a range of disarticulated postcranial elements, among them two clavicles, a femur, several ribs, two neural arches from the anterior trunk, and three intercentra. In addition, the bedding plane is covered by numerous bony plates, some of which are exposed in what probably represents the external view, revealing a coarse ornament. These ossicles are irregular in size and outline, but match bonelets preserved in both NMK-S 117 and HLD-V 608, the latter was already mentioned by Huene (1932).

## Systematic palaeontology

Temnospondyli Zittel, 1888

Stereospondyli Zittel, 1888

Capitosauria Schoch and Milner, 2000

Sclerothoracidae Huene, 1932

*Sclerothorax* Huene, 1932

*Sclerothorax hypselonotus* Huene, 1932

*Lectotype*: HLD-V 607 (Fig. 1B). Skull length 170 mm, total length of preserved parts of specimen 480 mm. The lectotype was designated by Fastnacht (2004).

*Type locality*: Sandstone quarry near Queck in the Fulda Valley (r: 35/41.525; h: 56/20.300).

*Type horizon*: Eichsfeld Sandstein, lower part of Middle Buntsandstein section (Volpriehausen Folge, S4), Olenekian, Lower Triassic (Huene 1932; Laemmlen 1963; Fastnacht 2004).

*Referred material*.—HLD-V 608 and GPIM-N 2045 from the type locality at Queck, NMK-S 117, 118a, b from top of Hardeggen Sandstein (S 6) of Heimarshausen near Naumburg (see Appendix 1).

*Stratigraphic range*.—Lower (S4) to upper part (S6) of Middle Buntsandstein section, probably spanning a large part of the Olenekian, which equals 4–5 Ma (Deutsche Stratigraphische Kommission 2002).

*Diagnosis*.—Autapomorphic character-states, diagnosing *S. hypselonotus* from all other temnospondyls: (1) Skull very wide with quadrangular outline, anterior third of skull as wide as cheek, with convex lateral projections. (2) Margin of snout heavily ornamented by gross ridges that form high tubercles. (3) Medial skull roofing elements laterally extended, with frontals and parietals being as wide as long and postparietals being two times wider than long. (4) Neural spines differing in height, converging towards a highest point well anterior to the mid-level of the trunk (Fig. 5). (5) Interclavicle extensive, longer than the skull and nearly as wide, thereby proportionately larger than in any other temnospondyl (Fig. 1B). (6) Glenoid area forming a prominent process

that raises well from the lateral face of the scapulocoracoid (Fig. 6D). (7) Postcranium covered with numerous irregular and small, heavily ornamented ossicles (Fig. 6H).

## Description

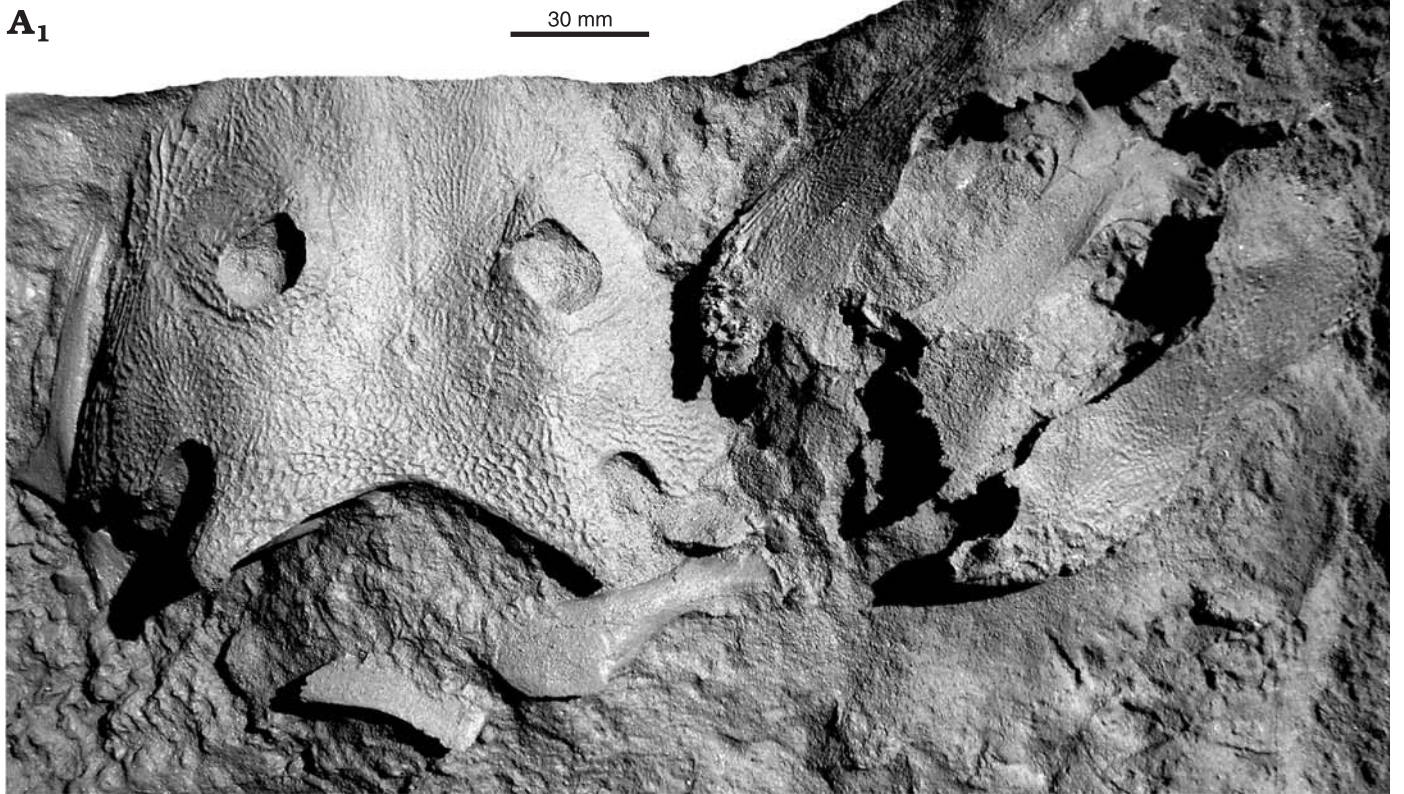
### Skull

*Preservation*.—Significant parts of the skull are preserved in HLD-V 607, NMK-S 117, and NMK-S 118. In the lectotype specimen two thirds of the cranium are still present, exposed in dorsal view. It includes three quarters of the skull roof as rather weak imprints (natural moulds) and conversely one third of the palate in a similar state. The skull roof preserves the right cheek, nearly the whole orbital region, and the snout, while the palate shows the basicranial region, left pterygoid, left choanal region, and marginal tooth row.

*General appearance*.—The skulls of HLD-V 607 and NMK-S 118b both have a nearly perfect quadrangular outline, with the greatest width approaching 92% of the greatest length. The tip of the snout is blunt and has a nearly straight transverse margin, while further posterior there are irregular lateral projections borne by the rim of the maxilla. This resembles the situation in *Eryops* (Sawin 1941) and *Sclerocephalus* (Boy 1988) where a similar lateral widening of the maxilla supports a set of enlarged teeth. In *Sclerothorax*, however, no such teeth are present, as the left side of HLD-V 607 reveals. Instead, the maxilla houses a series of small teeth that are all of similar size. This is confirmed by NMK-S 118b where a short series of teeth is preserved in the anterior region of maxilla. The lateral margins are otherwise curved rather than straight, with convex margins in the snout and cheek regions, and a markedly concave region between them at hind-level of the orbits. This pattern is present in all three dorsally exposed specimens (HLD-V 607, NMK-S 118a, b). The posterior rim of the skull table is strongly concave. Otherwise, the posterior ends of postparietals and tabulars are straight.

*Skull roof*.—The ornamentation of the skull roof is heterogeneous, consisting of small, reticulate ridges in the central parts of the skull table and larger, deeper pits and grooves at the peripheral regions, particularly in the snout. Most of the ornament is untypically small-scale for a temnospondyl of this size. Only a few zones of supposedly more intense positive allometry bear elongated, parallel ridges (the “zones of intensive growth” *sensu* Bystrow 1935) (lateral part of squamosal, most of the jugal, alary shelf of maxilla), whereas most of the other regions house small polygons. In both NMK-S 118a and 118b, there are well-established lateral line

Fig. 2. New original material of *Sclerothorax hypselonotus* Huene, 1932 from Heimarshausen near Naumburg, Hardeggen Sandstein, Lower Triassic. A. NMK-S 118a, b. A1, two skulls in dorsal view, NMK-S 118a (right) and -118b (left); A2, close-up of NMK-S 118b. B. NMK-S 117, skull in ventral view and anterior trunk vertebrae. →



sulci in several regions of the skull roof: the squamosal and jugal bear a wide and deep infraorbital sulcus, while the postorbital, postfrontal, and posteromedial region of the prefrontal have a rather narrow supraorbital sulcus. The infraorbital sulcus is deep and forms a smallish flexure not on the lacrimal, but at the very margin of the preorbital region, still on the alary shelf of the maxilla.

The premaxilla and maxilla have wide lateral and anterior shelves that are heavily ornamented by enlarged, radially arranged pits, short grooves, and manifold tuberosities. The size and position of the nares is unclear; in the lectotype specimen, paired depressions between the premaxillae and nasals were interpreted by Huene (1932) as nares. In NMK-S 118b, the posterolateral rim of the naris is preserved on both sides, suggesting larger openings than in Huene's interpretation. Still, their medial expansion remains unknown, and the reconstruction attempted in Figs. 3D and 4A remains conjectural.

Most of the anterior and lateral extensions of the premaxilla and maxilla are formed by a thin and flat shelf, whose marginal areas only are tooth-bearing. The suture between the premaxilla and maxilla is not preserved and can only be approached by differences in ornamentation (Figs. 1B, 3D). Likewise, the suture between the premaxilla and nasal is hard to ascertain, with too much equivocal evidence from ornamentation and overall relief. Like in most other stereospondyls, the alary shelf of the maxilla is hardly wider than the posterior process.

The nasal is as long as the frontal (HLD-V 607) or 10% longer (NMK-S 118b) and reaches the same width, although the suture with the lacrimal is poorly defined in all three specimens. Both nasal and frontal have a crudely rectangular outline as single elements, while in each case the paired elements together cover a quadrangular area. The nasal is evenly ornamented with polygonal and (posteriorly) short radial ridges. The lacrimal is as long as the nasal and nearly as wide, suturing with the latter medially, the prefrontal posteromedially, the jugal both posteriorly and laterally, and the maxilla anterolaterally. While the other sutures are mostly straight, that with the jugal is markedly serrated. As with the nasal and frontal, the ornament is poorly defined with low ridges and a simple radial pattern. There is no lacrimal flexure of the infraorbital sulcus, and in general there are no unambiguous traces of any lateral line sulcus on the lacrimal.

The rim of the orbit is raised in the prefrontal, frontal, and postfrontal regions. The shape of the orbit is that of a sagittally elongated oval with a pronounced lateral projection. The prefrontal is slightly longer than the lacrimal, having a pointed anterior end that wedges in between the nasal and lacrimal. Posterolaterally, it forms a pronounced projection indentating into the jugal. There is no suture with the postfrontal, which allows the frontal to make a short contribution to the orbit rim. The jugal is very wide and also forms by far the longest skull element. It has a straight suture with the maxilla and in places a serrated contact with the prefrontal, postorbital, and lacrimal.

By area, the postfrontal is the smallest element in the skull roof, having a wedge-shaped outline. It contacts the postorbital by a serrated suture. The latter is considerably wider than the postfrontal, largely due to the hypertrophic lateral wing that projects deeply into the jugal. The postorbital also bears the most deeply incised portion of the lateral line sulci. It is generally not longer than the postfrontal, and its posterior portion forms a small projection ending in a pointed tip. The parietal is markedly shorter than the frontal and nasal, being only slightly longer than wide. The small pineal foramen is located in the anterior half of the element. The postparietal is markedly wider but reaches only half the length of the parietal, being more coarsely ornamented, i.e. the polygons are larger and the ridges higher. The supratemporal has the typical pentagonal outline observed especially in capitosauroids, with the posterior portion having three and the anterior one two corners. Although there are no traces of lateral line sulci, the region where they might be expected is markedly raised to form a broad ridge (Fig. 3B). This ridge continues posteriorly onto the proportionately large tabular to end in the pronounced horn, and anteriorly onto the postfrontal and further on the prefrontal to merge run along the nasal-lacrimal boundary; these details are only preserved in NMK-S 117. As the postparietal, it has a narrow unornamented rim at the posterior margin, while the other areas are coarsely pitted. In uncrushed specimens, the tabular horn forms the highest elevation of the element and the skull as a whole (NMK-S 118a).

In the cheek, the squamosal forms an unusually short element, reaching only to the level of the posterior margin of the supratemporal. Its suture with the jugal is set far anterior, limiting the posterior extension of the latter. On the posterolateral end of the squamosal, the infraorbital sulcus ends in a widened and more deeply incised trough that curves medially as it approaches the falciform crest. The latter is extensive, forming a broad projection into the squamosal embayment. In dorsal view, the otic notch is markedly set off from the posterolateral part of the embayment. The quadratojugal is narrow having a serrated suture with the squamosal, tapering anteriorly to meet the maxilla in a narrow contact, and forming a posterior process bearing the facet for the lateral end of the quadrate trochlea.

*Palate.*—Although the available exposure of the palate is less complete than that of the dermal skull roof, the preserved regions are quite informative. The basicranium is completely exposed and excellently preserved in the two new specimens (NMK-S 117, 118b; Fig. 3A, C), and the few details preserved in HLD-V 607 are entirely consistent with these (Fig. 1B). The new specimens reveal much information on the pterygoids, subtemporal windows, quadrate trochleae, and the cultriform process. In addition, the palate of NMK-S 118b preserves small platelets located within or at the margins of the interpterygoid vacuities; these are probably homologous to the dentigerous ossicles known from the interpterygoid vacuities of other temnospondyls (Boy 1988). At the posterolateral margin of the parasphenoid plate, at the

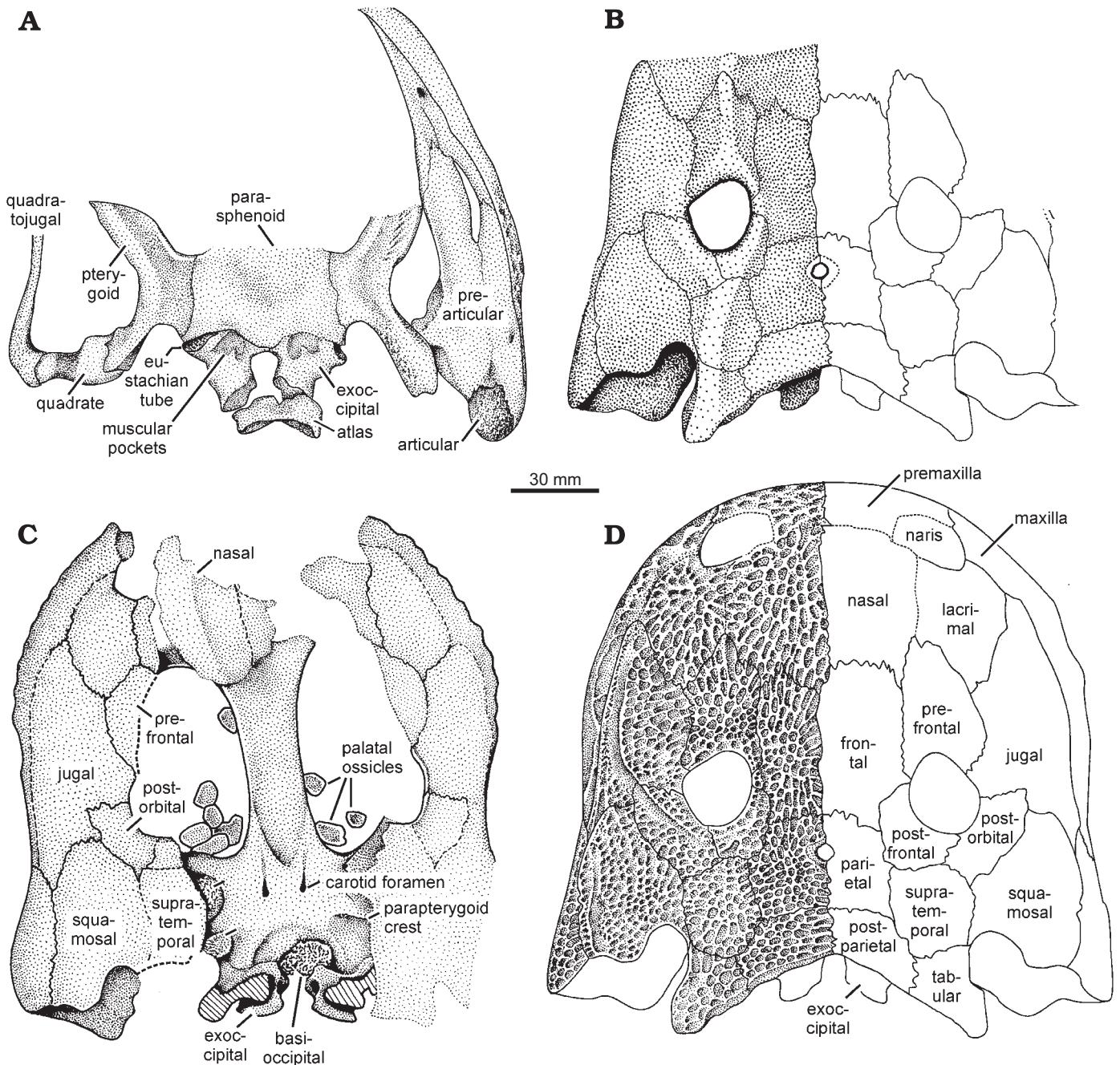


Fig. 3. Original skull specimens and ornamentation of *Sclerothorax hypselonotus* Huene, 1932 from Heimarshausen near Naumburg, Hardegsen Sandstein, Lower Triassic. **A.** NMK-S 117, palate in ventral view. **B.** NMK-S 118a, skull roof in dorsal view, with 3d structure shown on left side. **C.** NMK-S 118b, marginal parts of skull roof and medial region of palate and braincase in dorsal view. **D.** Reconstructed skull roof with ornament mapped on left side, based on NMK-S 118a, b.

narrow region that separates the exoccipital from the pterygoid, there is an opening. A similar opening was described in *Mastodonsaurus*, where it has been suggested to form the ventral entrance into the eustachian tube (Schoch 2000b).

Apart from the marginal dentition of maxilla, palatine, and ectopterygoid, all other preserved regions are edentulous. In particular, the tooth patches or *areae asperae sensu* Bystrow and Efremov (1940) are entirely absent. The cultriform process of the parasphenoid is extremely broad, being

only slightly narrower than the likewise unusually wide basal plate. While the process is completely flat on the ventral side (HLD-V 607), the basal plate bears a faint central depression similar to that of most basal capitosauroids. Dorsally, the basal plate is crested in the same way as reported in other stereospondyls (Fig. 3C; Shishkin 1973; Schoch 1999b; Schoch and Milner 2000). Both of the paired crests running towards the lateral margins of the basal plate are well established, the transverse parapterygoid crest anteriorly and the

oblique paroccipital crest posteriorly. The parapterygoid crest is as high as in *Mastodonsaurus*, where an abutting of the stapedial ventral process has been reported (Schoch 2000b). Unfortunately, the stapes is not preserved in any of the *Sclerothorax* specimens. On the dorsal side, the centre of the basal plate houses paired openings for the internal carotid artery, permitting the vessel to leave the bone in anterodorsal direction. This agrees with the anatomy of most stereospondyls (Shishkin 1968; Boy 1990), where the openings for the internal carotid are almost throughout on the dorsal side, contrasting the plesiomorphic situation in other temnospondyls and lower tetrapods (Schoch 1999b). The posterior entrance foramina of the carotids are not preserved, but probably were located near the parasphenoid-exoccipital suture. The basioccipital (= posterior) region of the basal plate is concave and preserves a shagreen of bony matrix that may pertain to the basioccipital. As in some other stereospondyls, the basioccipital appears to have started to ossify in small areas (Schoch 1999a). There is a wide gap between the condylar facets of the exoccipitals, although their medially facing parts are roughened, which suggests they were continued by cartilage. A similar morphology is observed in *Wetlugasaurus angustifrons* (Schoch and Milner 2000: fig. 73). The pterygoid is separated from the exoccipital by a short lateral projection of the parasphenoid (NMK-S 117, Fig. 3A); the projection is also well preserved in the lectotype specimen. The suture between the parasphenoid and exoccipital encircles a large ventrolateral opening, similar in location and relative size to that described in *Mastodonsaurus* (Schoch 2000b). The main basicranial suture, formed by the parasphenoid and pterygoid, is extensive and aligned mainly in parasagittal fashion. The length of this contact is similar to that of capitosauroids and trematosauroids, while the marked posterior projection formed by the pterygoid is found mostly in some of the more advanced capitosauroids such as *Eryosuchus* and *Cyclotosaurus* (Schoch and Milner 2000; Sulej and Majer 2005). The pterygoid has a very short basipterygoid ramus and—correlating with the far anterior position of the quadrate condyles—a relatively short quadrate ramus, as well. The palatine ramus is at least twice as long as the quadrate ramus, having entirely straight medial and lateral margins and being aligned obliquely at an angle of 40° to the sagittal axis. In HLD-V 607 it forms a broad suture with the triangular ventral projection of the jugal (the “jugal isle” or insula jugalis of Bystrow and Efremov 1940), and the ectopterygoid. Yet there is no evidence whether the pterygoid contacted the palatine or not. The main body of the palatine ramus is thickened, forming a broad ventral ridge running along the lateral part of the ramus. As in some metoposauroids and parotosuchid capitosauroids, the most ventrally exposed regions of this ridge are ornamented. The cultriform process becomes continuously wider both anteriorly and posteriorly (Fig. 3C). The nature and geometry of the suture with the vomers remains poorly understood, as the only specimen preserving the anteriormost portion of the parasphenoid is exposed in dorsal view (NMK-S 118b); a faint line on the right

side of the specimen suggests a ventrolateral overlap of the cultriform process by the vomer. Given the latter observation holds, the suture topology would match that of the majority of stereospondyls in that paired posteromedial processes of the vomer frame the ventral surface of the cultriform process on both sides (Fig. 4B). In contrast to the mostly flat anterior portion, the posterior end of the cultriform process is markedly thickened along its dorsolateral margins, probably forming sites of attachment for the laterosphenoid and/or sphenethmoid regions of the braincase. However, the anterior neurocranium itself remained entirely unossified. Remains of the otic capsule are present with two separate, poorly defined masses of endochondral bone. By their positions, they probably represent the prootic (anterior) and opisthotic (posterior) portions of the capsule (Welles and Cosgriff 1965; Schoch 2002). The prootic portion partially fills a large concavity between the parapterygoid crest and the anterior margin of the basal plate, where the (probably cartilaginous) epipterygoid was attached.

In the anterior palate, there are only two small regions preserved in NMK-S 118b. (i) A small exposure of what appears to be the posterior margin of the vomer lateral to the cultriform process, marking the most anterior extension of the interpterygoid vacuity. This is located unusually far posterior and also strikes by being aligned transversely. (ii) The anterolateral rim of the snout is exposed preserving part of the maxillar tooth arcade, the bases of six teeth and seven tooth sockets alternating with one another, and neighbouring parts of the palatal tooth arcade. The latter includes the palatine posterior to the choanae which are not preserved. The exposed part of the palatine has seven teeth and sockets that are markedly larger than those of the maxillar dentition, characterized by laterally extended bases as typical of stereospondyls (Schoch and Milner 2000).

The anteriormost margin of the subtemporal window is formed by the insula jugalis which probably separated the ectopterygoid entirely from the opening. The shape of the subtemporal window is rather common among stereospondyls, having a straight parasagittal lateral margin and a medial expansion at mid-level (Fig. 3A). The quadrate trochlea includes a larger medial and a smaller lateral tuber and is relatively wide, in which it is consistent with the quadrate of capitosauroids (Schoch 2000a).

*Occiput.*—Three specimens preserve details of the occiput (HLD-V 607, NMK-S 118a, b), together giving a complete picture of that region (Fig. 4C). In the occipital cheek region, the pterygoid and squamosal make similarly large contributions, while the quadratojugal and quadrate are restricted to small rims. The quadratojugal houses a large opening, the paraquadrate foramen, close to its lateral occipital margin. The entire lateral rim of the occipital face of the cheek is framed by a prominent bulge that culminates in the large falciform crest of the squamosal. The quadrate forms a narrow transverse strip of bone in occipital view. The squamosal and pterygoid are firmly sutured along their entire margin, and the latter forms a well-developed oblique crest mounting



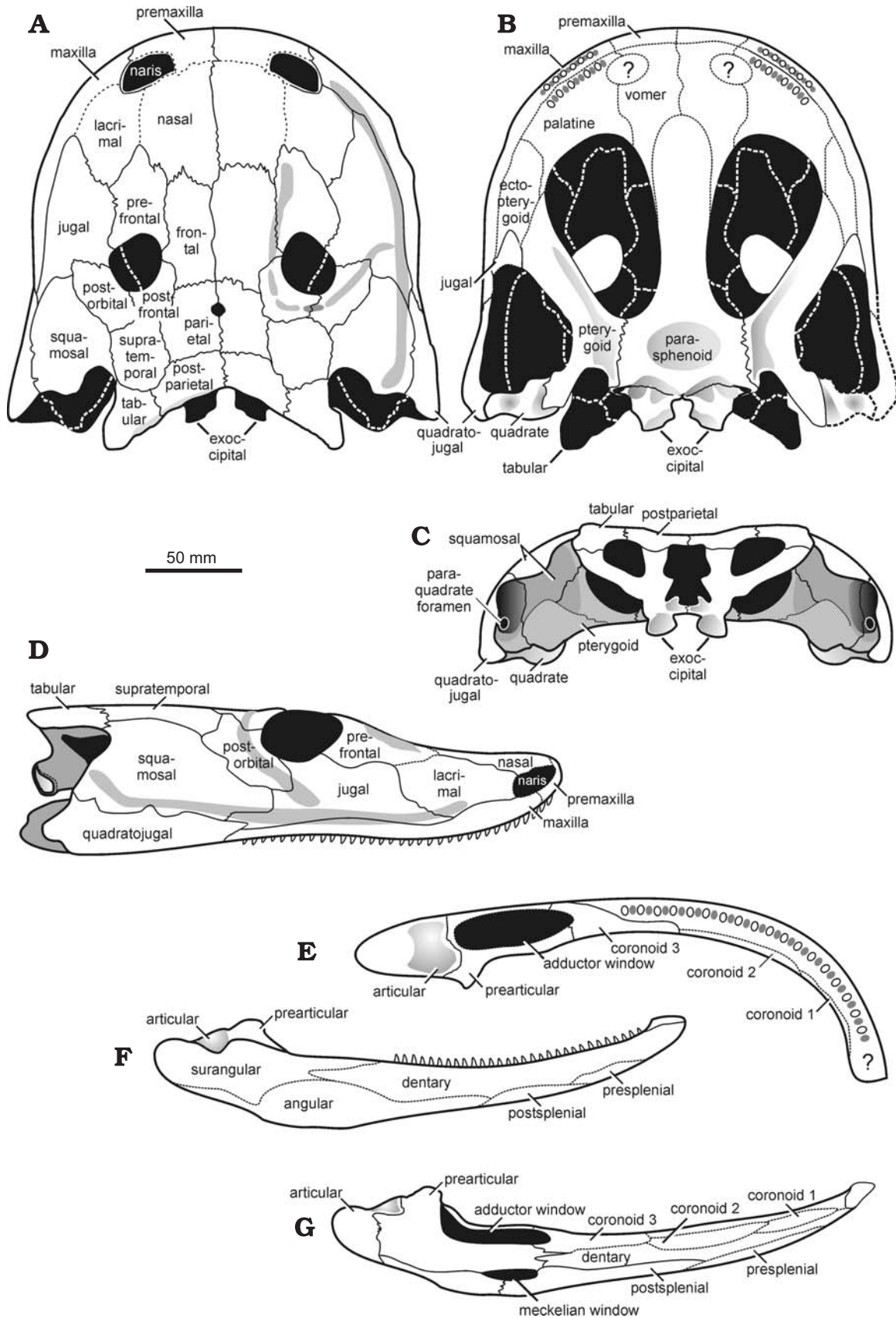


Fig. 4. Reconstruction of skull and mandible of *Sclerothorax hypselonotus* Huene, 1932. **A.** Skull roof in dorsal view (based on NMK-S 118a, b). **B.** Palate in ventral view (based on NMK-S 117, 118b). **C.** Occiput in posterior view (based on NMK-S 118b). **D.** Skull in lateral view (same as A). **E–G.** Mandible in dorsal (**E**), labial (**F**), and lingual (**G**) views (based on HLD-V 607, NMK-S 117).

to a 5 mm tall sheet of bone that projects from the occipital slope of the pterygoid. The exoccipital has a tall and stout vertical column attaching to the postparietal which exceeds the height of that of most other stereospondyls, revealing that the posterior skull of *Sclerotherax* is relatively high. The widely separate exoccipital facets are at the same horizontal plane as the quadrate trochleae, and they also fall into the same transverse plane. By that, *Sclerotherax* differs boldly from many more basal stereospondyls and bears close resemblance to mastodontosaurid or cyclotosaurid capitosauroids.

**Mandible.**—There are three specimens in which nearly complete mandible halves are preserved (HLD-V 607, GPIM-2045, NMK-S 117). The best-preserved region is the posterior portion of the mandible in lingual view, as exposed in NMK-S 117. The lower jaw is generally slender and even in the posterior third it is relatively low (Fig. 4E–G). There is a large postglenoid area (PGA) that reaches the depth of the mandible at mid-level. The posterior end of the PGA is rounded, and the dorsal and ventral margins are roughly parallel, aligned horizontally. The prearticular forms a pronounced hamate process anterior to the articulation facet, similar to that of moderately advanced capitosauroids. The (posterior) Meckelian window is elongate, exceeding the length of the PGA. There is a small Meckelian foramen anterior to it, located within the post-splenic. The dentition is extremely poorly preserved, the teeth were small (5–8 mm length), of similar size throughout, and closely set, matching the described pattern on the maxilla. In addition to the glenoid facet, the articular makes a large contribution to the mandible, covering the complete PGA region of the lingual side.

## Axial skeleton

With the exception of the posterior part of the tail, the vertebral column and rib cage are present (Figs. 1A, 5B, C). While the skull has many affinities to capitosauroids and other “higher” stereospondyls, the postcranium reveals a most unique mix of features. The axial skeleton is particularly surprising. On a crude scale, the closest similarities exist with the axial skeletons of *Eryops*, *Sclerocephalus*, and *Cacops* (Williston 1910; Moulton 1974; Boy 1988; Schoch and Milner 2000), which agree well with the relative size and structure of the intercentrum, the parapophysis, the transverse process, and the general morphology of the neural arch. The pleurocentrum, here reported for the first time in *Sclerotherax*, is considerably larger than in most other Permo-Triassic temnospondyls.

In studying both HLD skeletons, Huene (1932) counted 24 presacral vertebrae, and we came to the same conclusion for HLD-V 608. However, in HLD-V 607, we are not sure how Huene identified the position of the sacrum as well as the first vertebrae, because these regions were preserved on blocks B which are lost. As GPIM-N 2045 is not entirely complete either, Huene’s find 1 remains the only source for the vertebral count to date. The minimal number of caudal vertebrae, given by HLD-V 608, is eight. None of these pre-

serves a haemal arch, while the first six caudals have slender ribs preserved mostly still in place.

Our examination of GPIM-N 2045, which is more completely exposed in the region of the vertebral centra, revealed large pleurocentra preserved in place. These pleurocentra are unusually large and closely set with the other elements, nearly filling the space given by the intercentrum and neural arch (Fig. 5D). This comes quite close to situation described by Moulton (1974) for large specimens of *Eryops*. In GPIM-N 2045, the pleurocentra of each vertebral segment and the intercentrum of the succeeding segment are tightly attached to each other. Again, this has been reported in *Eryops* by Moulton (1974), and our personal observation in *Sclerocephalus* revealed a similar situation in large adults of that genus. Despite their large size, the pleurocentra do never participate in the articulation with ribs. In the mid-trunk region, they are preserved in 3d, showing they have a substantial ventral part wedging in between the intercentrum and neural arch. The dorsal parts of the countersided pleurocentra have large medial projections which fail to meet in the midline. In the posterior half of GPIM-N 2045, the intercentra are preserved in full articulation, alternating with the neural arches throughout the column. This matches exactly the structure described in detail by Howie (1970), Moulton (1974), and Warren and Snell (1993), whereas the pleurocentra are enlarged, reaching the size and degree of ossification of the intercentra. In turn, the intercentra are also higher than in *Eryops*, resembling those of the stereospondyls *Australerpeton*, *Paracyclotosaurus*, and *Stanocephalosaurus pronus* more closely. The parapophysis is round or slightly oval, as usual located at the posterodorsal edge of the intercentrum. This facet is well separated from that of the diapophysis. The transverse processes attain their greatest length in the mid-trunk region (GPIM-N 2045), and consequently the morphology of the rib head should be most asymmetrical there. NMK-S 117 preserves the first ribs with their heads exposed to show widely divergent articular morphologies even in closely neighboured ribs (Figs. 2B, 6B). Starting with the axis, the first four following diapophyses are transversely narrow and have rather short, vertically aligned facets. The diapophysis and parapophysis of the axis are aligned in the same vertical axis, while from the third vertebra on backwards, the parapophysis lies slightly anterior to the diapophysis (Fig. 6A).

The dorsal spines of the neural arches are very robust (Fig. 1A). They have mostly smooth lateral surfaces, lacking the prominent muscle crests reported in *Eryops* (Moulton 1974). Only in GPIM-N 2045, there are faint ridges on the anterior and posterior edges. In the entire vertebral column, the dorsal spines are at least two times taller than the distance between pre- and postzygapophysis. The dorsal ends of the spines are markedly irregular in shape, width, and the morphology of their dorsal faces, which are rugose as in adult *Sclerocephalus* (observation by authors). The general morphology of the neural arches is similar from the third through the 18<sup>th</sup> vertebra, the single most outstanding feature that varies being their height. Further posterior, the neural arches

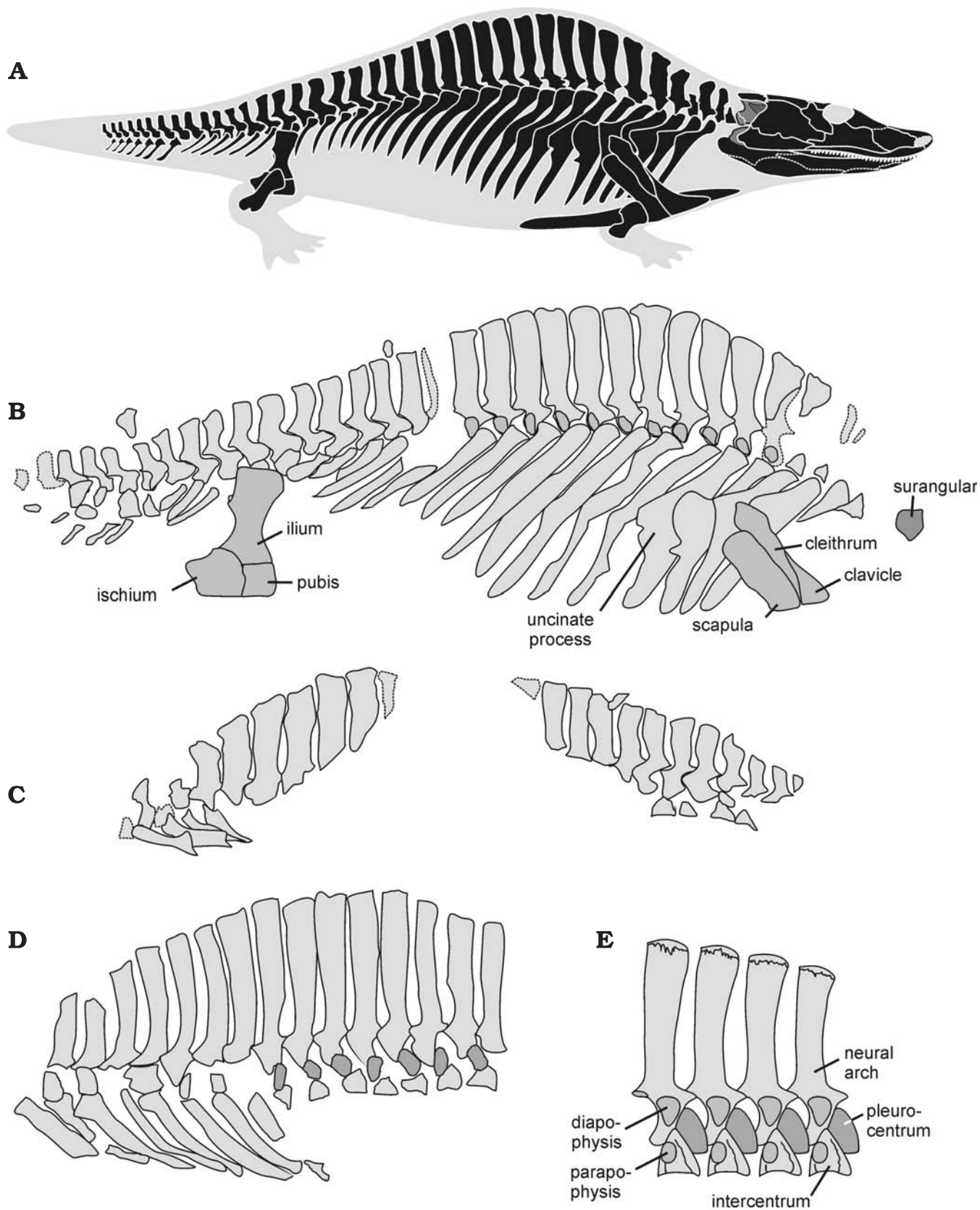


Fig. 5. *Sclerothorax hypselonotus* Huene, 1932. **A.** Reconstruction of complete skeleton in lateral view (based largely on HLD-V 608, GPIM-N 2045). **B.** HLD-V 608, original material. **B<sub>1</sub>**, postcranial skeleton in right lateral view, exposing ribs and parts of the pectoral and pelvic girdle, **B<sub>2</sub>** same skeleton in left lateral view. **C.** GPIM-N 2045, anterior trunk skeleton in left lateral view, exposing pleurocentra. **D.** Reconstruction of vertebrae in the mid-trunk region, based on GPIM-N 2045.

have a distinctly longer distance between the pre- and postzygapophyses, while the height of the spines is still decreasing continuously up to the level of the last preserved tail vertebra. In sum, the neural spines attain their greatest height at the 10<sup>th</sup> through 12<sup>th</sup> vertebra, to become continuously lower from that level on. The dorsal spine of the sacrum is much lower than that of the axis or third vertebra. The dorsal spine of the 11<sup>th</sup> vertebra is two times higher than that of the axis and almost three times higher than that of the sacral vertebra.

The trunk ribs are all preserved in the available material, and in HLD-V 608 they were uncovered partially on both sides (Huene 1932). There, the anteriormost ribs are preserved in tight articulation, revealing the following sequence of morphologies (Figs. 1A, 5B<sub>1</sub>): the first ribs have prominent blade-like uncinat processes rising from the shaft in a relatively far proximal position compared to the succeeding ribs. Posteriorly, the ribs become successively longer with the uncinat processes increasing slightly in length and overall area. The ribs of the 4<sup>th</sup> to 8<sup>th</sup> vertebrae have the largest uncinat processes, which become abruptly shorter and less differentiated from the 9<sup>th</sup> vertebra on and are essentially absent from the 15<sup>th</sup> vertebra backwards. The ribs become continuously shorter from the 11<sup>th</sup> vertebra on in posterior direction.

The sacral rib is not preserved in articulation, but there is a potential sacral rib exposed in SMNS 1193k cast (HLD original apparently lost) that reveals a highly peculiar morphology. The element is preserved as one bone in a series of obviously rather short, rod-like ribs, itself being expanded both distal and proximal to the single "head". In HLD-V 608, at least three caudal ribs are associated with caudal vertebrae 1–3, and posterior to that level there are four shorter rod-like elements in succession, preserved ventral to the intercentra; these are more likely to represent haemal arches rather than caudal ribs. In conclusion, there is no evidence for the existence of ribs posterior to the third caudal vertebra. Provided the four shorter bars are indeed haemal arches, the tail was relatively short and low as compared with other temnospondyls, even *Eryops* (Moulton 1974).

## Appendicular skeleton

A substantial portion of the pectoral and pelvic girdles is preserved, and in addition one right humerus (Fig. 6E) and a left femur (Fig. 6F). There are no remains of other parts of the limbs. In the pectoral girdle, the interclavicle, clavicles, cleithra, and scapulocoracoids are all well ossified and nearly completely preserved, and in the pelvis there are substantial ossifications of the ilium, ischium, and pubis which are completely exposed in HLD-V 608 (Figs. 5B<sub>1</sub>, 6G).

The interclavicle exceeds the length of the skull (185 mm versus 170 mm in the lectotype specimen, see Fig. 1B). It is a flat, rhomboidal element almost as wide as the skull and with its widest part at mid-level. This is also the centre of ornamentation, covered by relatively few reticulate ridges from which very long parallel ridges arise in all directions. Apart from the wide areas anterior to the mid-level that were cov-

ered by the clavicles, there are no other regions that were free of ornament, although in the posterior third the ridges become very faint. The anterior tip of the interclavicle is unknown, but according to the depressions that indicate ventral overlap by the clavicles, the clavicles contacted one another at the anterior end of the interclavicle, or at least must have come very close (restoration given in Fig. 6C). The clavicles are slightly longer than half the length of the interclavicle, and their widest parts are well anterior to the mid-level of the latter. Their ornament originates from short reticulate ridges at the lateral margin, in the posterior third of the clavicular blades. Consequently, in that region the ridges run in posteromedial direction to meet the ridges of the interclavicle at almost exactly a right angle (Fig. 6C). The dorsal projection of the clavicle is long, reaching more than half the dorsal extension of the pectoral girdle, and has the outline of an elongated triangle. The dorsal process articulates with the elongated cleithrum dorsally and the scapular blade ventrally. The cleithrum is longer than the dorsal process of the clavicle and has a posteriorly broadened head region, which comprises one fourth the length of the whole element (Fig. 6D). The head is not expanded at the anterodorsal margin, however, thereby differing from *Eryops*, *Sclerocephalus* and the dissorhoids. In most features, the cleithrum is similar to that of capitosauroids, which includes the rugged dorsal end and the very modest posterior projection of the head. The scapular portion of the scapulocoracoid is slightly shorter than the cleithrum in HLD-V 608, whereas in HLD-V 607 they form a continuous dorsal margin. In lateral view, the scapular blade is more similar to that of *Mastodonsaurus* or *Sclerocephalus* than to *Eryops* (which is much higher, see Pawley and Warren 2006), but posteriorly the posterior rim of the supraglenoid groove develops into a high crest running dorsally to end in a pronounced buttress at the dorsal end of the scapular portion. The glenoid is only preserved with a relatively small exposure of the facet, and the ventromedial portion of the coracoid remains unknown.

The humerus is partially preserved in both HLD-V 607 (Fig. 6E) and NMK-S 117, each specimen revealing different parts of the bone. In the former, the humerus is preserved at some distance to the glenoid facet of the scapulocoracoid, but still in life orientation. The most striking feature is the contrast between proximal and distal ends; while the former appears narrow and poorly differentiated, the latter is broadened and bears a range of rugosities suggesting muscle various attachments and cartilaginous cover of condyles. Probably the main axis of the proximal end was aligned at a right angle to that of the distal, as it is in *Eryops* and other more terrestrial temnospondyls. However, in the second specimen (NMK-S 117), in which the proximal end is well exposed, the proximal head region is stout with a rounded rather than widened outline. The more complete specimen (HLD-V 607) is poorly preserved, and neither a supinator process nor a deltopectoral projection are preserved in any specimen. An ectepicondylar foramen mentioned by Huene (1932) cannot be confirmed.

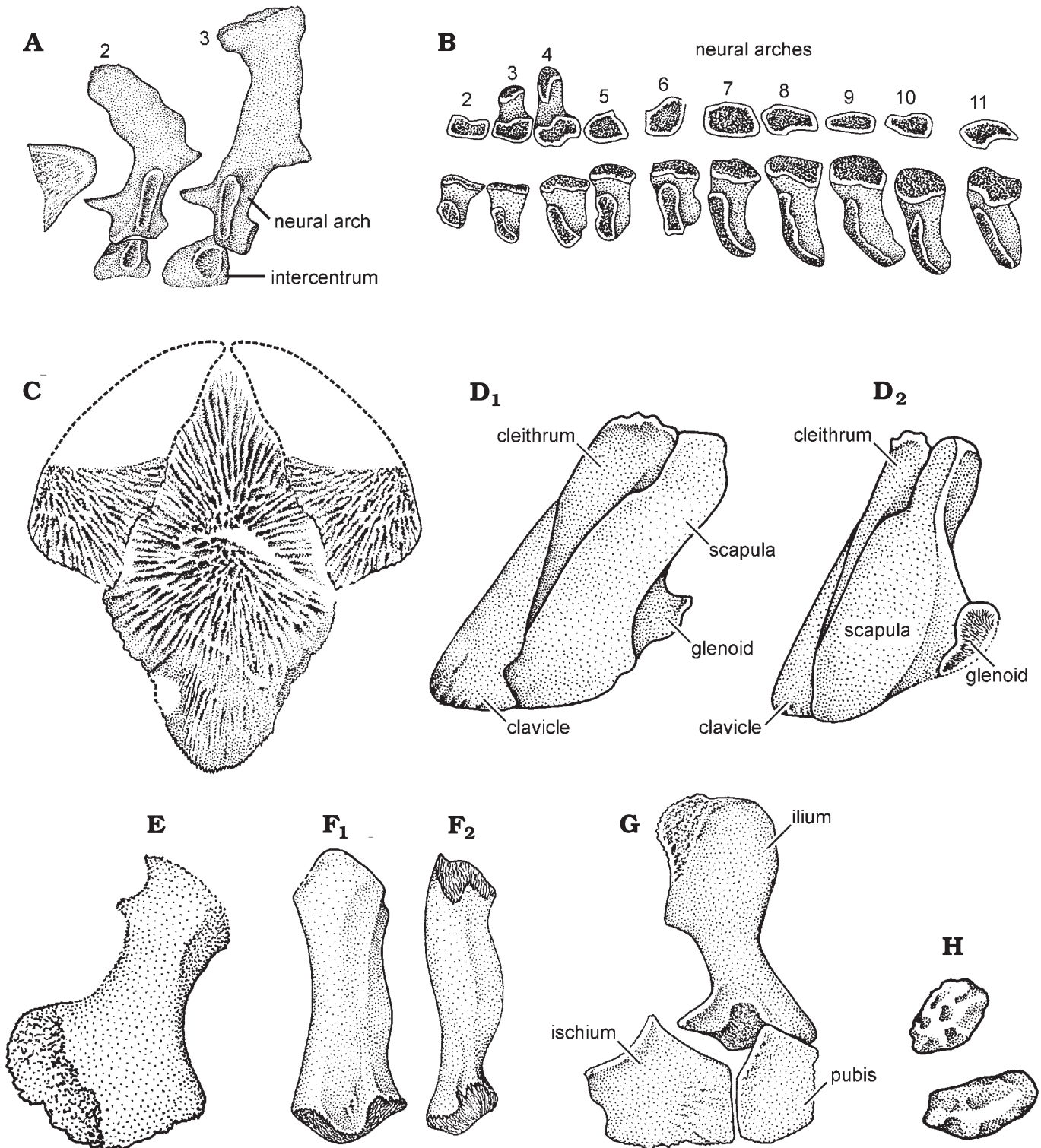


Fig. 6. *Sclerothorax hypselonotus* Huene, 1932. Postcranial skeleton, based on material from Queck and Heimarshausen, Middle Buntsandstein. **A.** Cervical region, with second and third vertebra exposed (HLD-V 608). **B.** Neural arches in ventral view (NMK-S 117; numbers mark position within column). **C.** Dermal elements of pectoral girdle in ventral view (based on HLD-V 607). **D.** Pectoral girdle as preserved (HLD-V 607) in lateral (D<sub>1</sub>) and posterolateral (D<sub>2</sub>) views. **E.** Right humerus (HLD-V 607). **F.** Left femur (NMK-S 118) in dorsal (F<sub>1</sub>) and posterior (F<sub>2</sub>) views. **G.** Right pelvis (HLD-V 608). **H.** Dermal ossicles.

The pelvis is completely ossified, with the ilium being very stout and dorsally expanded, the ischium forming a large blade and the pubis an anteriorly abbreviated, quadrangular element (Fig. 6I). Being similar to the ilia of the

stereospondyls *Benthosuchus* and *Mastodonsaurus*, that of *Sclerothorax* differs in having a prominent anterolateral outgrowth, a small posterodorsal projection, and a blunt dorsal end with a rugged posterolateral surface. The orientation and

geometry of the shaft, as well as the acetabular region are otherwise very similar to that of the mentioned stereospondyls. The ischium is a pentagonal plate of two-thirds the height of the ilium, while the ossified part of the pubis reaches only half the size of the former(?) and has a blunt anterior margin that does not project beyond the anteriormost margins of the ilium.

The femur—preserved in HLD-V 607 (Huene 1932: fig. 11) and NMK-S 118b (Fig. 6F)—is a robust and differentiated element with a pronounced ventral crest and a distally unusually expanded end into which the ventral crest merges. While the proximal end is not different from that of other stereospondyls, the distal one is peculiar in having a posteriorly enlarged condyle.

## Relationships of *Sclerotherax*

### Previous hypotheses

In modern cladistic parlance, *Sclerotherax* was considered a basal stereospondylomorph temnospondyl by Huene (1932), and subsequent authors have followed him in that consideration (Romer 1947; Schoch and Milner 2000). Huene referred especially to palatal characters, such as the palatine ramus of the pterygoid and the relatively narrow interpterygoid vacuities, but also mentioned the small orbits and the shape of the postorbital as diagnostic. He concluded that, despite a few palatal features shared with metoposaurids and brachyopids, *Sclerotherax* was most similar to *Sclerocephalus* (= *Onchiodon*) *frossardi* and *Sclerocephalus haeuseri*, and therefore placed the taxon within the family Actinodontidae.

True stereospondyls, at that time defined by the structure of their more fully ossified disc-shaped vertebral segment, seemed too different from *Sclerotherax* to be considered close relatives, although similarities with capitosauroids were explicitly highlighted by Huene (1932). Later, Romer (1947) listed *Sclerotherax* as a “sterile side branch” of his “neorhachitomes”, a group comprising rhinesuchids and lydekkerinids. In a review of the clade, Schoch and Milner (2000) attempted to place *Sclerotherax* within the Stereospondyli, albeit as *incertae sedis* and within its own family Sclerotheracidae as suggested by Huene (1932).

In the following analysis, some of the characters employed by the above listed authors to characterize the taxon turned out to be synapomorphies shared by *Sclerotherax* and stereospondyls, but their largely diagrammatic reconstruction of the skull was partially erroneous and based on only a fraction of the actual material, which was presumed lost but reappeared due to the active search of one of us (TK).

### Phylogenetic analysis

*Taxa*.—Outgroup: *Dendrerpeton acadianum* (we exclusively refer to the single find described by Holmes et al. 1998). Dissorophidae—here represented by only two species, *Ca-*

*cops aspidephorus* and *Dissorophus multicinctus*, complementing one another (Williston 1910; DeMar 1968), the Zatrachydidae represented by *Acanthostomatops vorax* (Boy 1989), the Eryopidae represented by *Eryops megacephalus* (Miner 1925; Sawin 1941; Moulton 1974; Pawley and Warren 2006). All other taxa fall into the Stereospondylomorpha of Yates and Warren (2000): *Sclerocephalus haeuseri* (Boy 1988), *Peltobatrachus pustulatus* (Panchen 1959), *Australerpeton cosgriffi* (Barberena 1998; Dias and Schultz 2003), *Uranocentrodon senekalensis* (Van Hoepen 1915), *Lydekkerina huxleyi* (Pawley and Warren 2005), *Laidleria gracilis* (Kitching 1957; Warren 1998), *Siderops kehli* (Warren and Hutchinson 1983), *Gerrothorax pustuloglomeratus* (Hellrung 2003), *Paracyclotus davidi* (Watson 1958), *Mastodonsaurus giganteus* (Schoch 1999a), *Trematolestes hagdorni* (Schoch 2006), the Metoposauridae (Dutuit 1976; Hunt 1993). Finally, we included *Sclerotherax hypselonotus*, based on the findings of the present study.

The choice of taxa followed several general considerations. First, we had to include representatives of all major stereospondyl clades (Rhinesuchidae, Lydekkerinidae, Brachyopoidea, Plagiosauridae, Capitosauroidea, and Trematosauroidea *sensu* Schoch and Milner 2000). Second, we added two enigmatic temnospondyls, *Peltobatrachus* and *Laidleria*, whose phylogenetic whereabouts are far from clear but which both share interesting postcranial features with *Sclerotherax* such as dermal armour. Finally, as *Sclerotherax* has some “terrestrial” features in the postcranial skeleton, we included zetracheids, dissorophids, and eryopids, although they all fall well outside the stereospondylomorphs (Boy 1990; Yates and Warren 2000). We have omitted *Lapillopsis*, as there are no articulated postcranial skeletons known of that taxon.

*Characters*.—Seventy characters from all parts of the skeleton were analyzed. All character-states are listed and defined in the Appendix 1 and scored in Table 1. Most of them are taken from the literature, sources are throughout indicated. As most of the considered taxa are not represented by juveniles or larvae, early ontogenetic stages (e.g., in eryopids, zetracheids, or *Sclerocephalus*) have been ignored.

*Details of analysis*.—The programmes PAUP 3.1 (Swofford 1991) and MacClade 3.0 (Maddison and Maddison 1992) have been employed to analyze the character distribution, run in the heuristic mode. Throughout, binary character-codings were preferred, but in five cases (characters 25, 42, 43, 52, and 53) multiple states had to be coded, treated as unordered in PAUP. The analysis (using both outgroups) gave one most parsimonious topology, requiring 163 steps. The consistency index of that tree is 0.485, the retention index 0.690, and the rescaled consistency index is 0.334. We performed analyses of node stability (Bremer Decay Index), their results are listed in the following section. Variation of outgroups (inclusion of both outgroup taxa versus use of either of the two) did not cause any change to the result of the analysis, giving the same topology. Exclusion of the poorly known *Peltobatrachus* gave the same result, a completely re-

Table 1. Character-taxon matrix. *DE*, *Dendrerpeton*; *DI*, Dissorophidae; *ZA*, Zatrachydidae; *ER*, Eryopidae; *SC*, *Sclerocephalus*; *PB*, *Pelto-*  
*batrachus*; *AU*, *Australerpeton*; *UR*, *Uranocentron*; *LY*, *Lydekkerina*; *LA*, *Laidleria*; *SI*, *Siderops*; *GT*, *Gerrothorax*; *ST*, *Sclerothorax*; *PC*,  
*Paracyclotossaurus*; *MA*, *Mastodonsaurus*; *BE*, *Benthosuchus*; *TR*, *Trematolestes*; *ME*, *Metoposauridae*.

Charac- ter	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
	DE	BA	DI	ZA	ER	SC	PB	AU	UR	LY	LA	SI	GT	ST	PC	MA	BE	TR	ME
1	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	1
2	0	0	0	0	1	1	1	0	0	0	0	0	0	1	0	0	0	0	0
3	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0
4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
5	0	0	1	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0
6	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1
7	—	—	—	—	—	0	—	0	0	0	0	0	0	1	1	1	0	0	1
8	—	—	—	—	—	0	—	0	0	0	0	0	0	0	0	1	1	0	0
9	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
10	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1
11	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0
12	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0
13	0	0	0	0	1	1	?	0	1	1	0	0	0	1	1	0	1	0	0
14	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0
15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
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18	0	0	0	0	1	1	1	1	1	1	0	0	1	1	1	1	1	0	0
19	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1
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22	0	0	1	1	1	1	0	1	1	0	0	0	0	1	1	1	1	1	1
23	0	0	1	1	0	0	0	0	0	0	1	1	1	0	1	1	0	0	1
24	0	0	1	1	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1
25	0	?	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1
26	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1
27	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1
28	0	0	0	0	0	0	?	1	0	1	1	1	1	1	1	1	1	1	1
29	0	0	0	0	0	0	?	0	0	0	0	0	0	?	0	0	1	1	0
30	0	0	0	0	0	0	0	0	0	0	1	1	0	1	1	1	0	0	1
31	0	0	0	0	0	1	?	1	0	1	0	0	1	?	1	1	1	1	1
32	0	0	0	0	0	0	?	1	1	1	1	1	0	?	1	1	1	1	1
33	0	0	0	0	0	0	?	1	1	1	1	1	0	?	1	1	1	1	1
34	0	0	0	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1
35	—	—	—	—	—	—	—	—	0	0	1	1	1	1	1	1	1	1	1
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38	0	0	0	0	0	0	1	1	1	1	?	1	1	1	1	1	1	1	1
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40	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1
41	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2	1	1	0
42	0	0	0	0	0	0	1	1	1	1	2	2	2	1	1	1	1	1	1
43	0	0	0	0	0	0	1	1	1	1	0	0	0	1	1	0	0	0	0
44	0	0	1	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1
45	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	1
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47	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	1	0	1	1
48	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0
49	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1
50	0	0	0	0	0	0	?	?	1	1	1	1	1	1	1	1	1	1	1
51	0	0	0	0	0	0	0	0	1	1	1	1	1	2	2	2	1	1	1
52	0	0	0	0	0	0	?	?	1	1	2	0	2	0	1	1	?	0	0
53	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1
54	0	0	1	?	1	1	1	1	0	0	0	0	0	1	0	0	0	0	0
55	0	0	1	?	1	1	1	1	0	0	0	0	0	1	0	0	0	0	0
56	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0	0	1
57	0	0	0	0	0	0	0	0	0	0	1	?	1	0	0	0	0	0	0
58	0	0	1	1	1	0	?	0	0	0	?	0	0	0	0	0	0	0	0
59	0	0	0	0	0	0	?	1	1	1	?	1	1	1	1	1	1	1	1
60	0	0	0	0	0	1	?	1	1	1	?	0	1	1	1	1	1	1	1
61	0	0	0	0	0	0	?	0	0	0	?	1	1	1	1	1	1	1	1
62	0	0	1	?	1	0	0	0	0	0	?	0	0	1	0	0	0	0	0
63	0	0	0	?	0	0	0	0	0	0	?	1	0	0	1	0	1	1	1
64	0	0	1	?	0	0	0	0	1	0	1	1	0	1	1	0&1	0	1	0&1
65	0	0	1	?	1	1	1	?	0	1	0	0	0	1	0	0	0	0	0
66	0	0	1	?	1	0	0	0	0	1	?	0	0	1	0	0	0	0	0
67	0	0	0	?	0	1	0	1	1	0	?	1	0	0	1	0&1	1	1	1
68	0	0	0	0	0	0	0	0	1	1	?	1	1	1	1	1	1	1	1
69	0	0	0	0	0	0	0	0	0	0	?	0	0	1	1	1	1	1	1
70	0	0	1	0	0	0	1	0	0	0	1	0	1	1	0	0	0	0	0

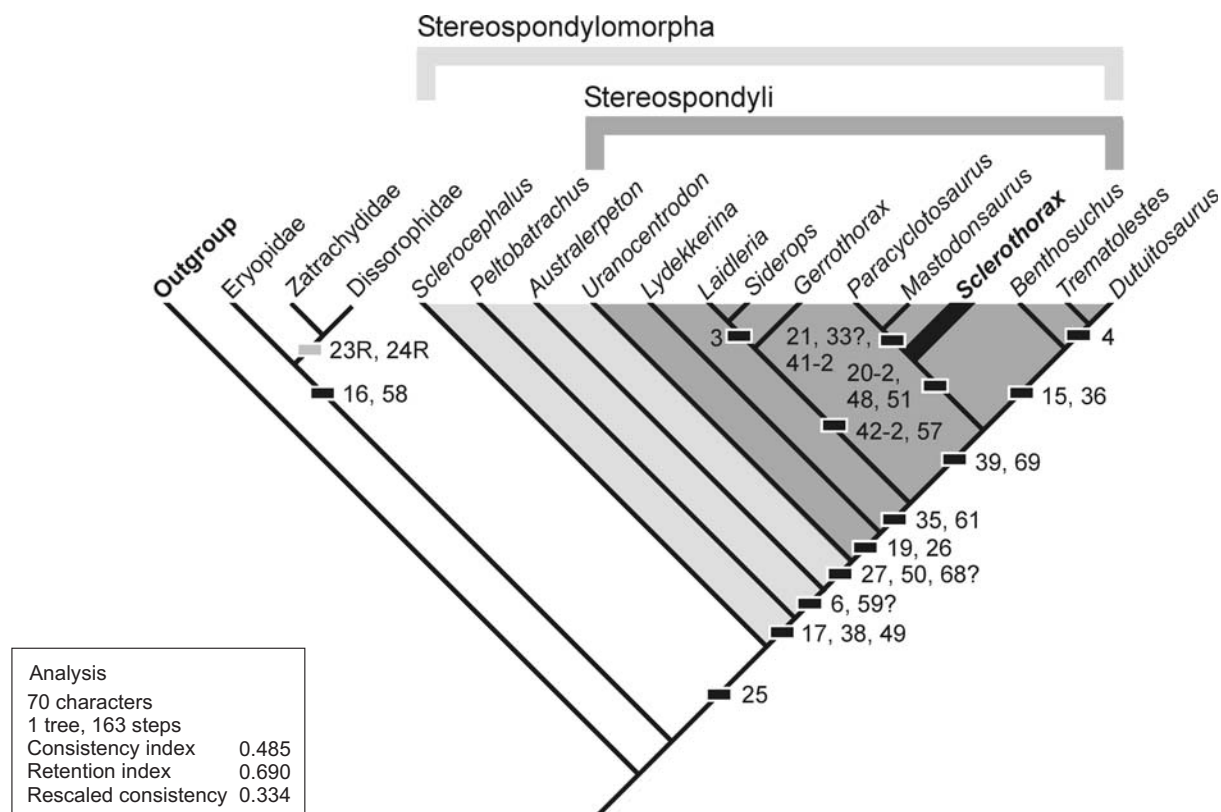


Fig. 7. Results of phylogenetic analysis. *Sclerotherax* is deeply nested within the higher Stereospondyli, forming the sister taxon of the two best-known capitosauroids. Interestingly, plagiosaurids (*Gerrothorax*), *Laidleria*, and brachyopoids (*Siderops*) are found to be monophyletic, which is in accordance with Yates and Warren (2000), while in contrast to the findings of these authors, the latter clade is only remotely related to trematosaurids and metoposaurids. *Peltobatrachus*, another enigmatic terrestrial temnospondyl, is here found to be a primitive stereospondylomorph. Numbers below each node refer to synapomorphies supporting them.

solved tree requiring 159 steps, a consistency index of 0.497, a retention index of 0.686, and a rescaled consistency index of 0.341. As the states of characters 1 and 58 are known to be subject to ontogeny, we have alternatively omitted these, receiving the same topology as with the full set of characters.

## Results

- Our results (Fig. 7) principally corroborate Yates and Warren's (2000) Stereospondylomorpha as a monophylum, and differ from the concept of Schoch and Milner (2000) by the inclusion of *Peltobatrachus* and the plagiosaurids. The Stereospondylomorpha as represented here is supported by one synapomorphy (25) and three-steps Bremer Support.
- The relationships of the three Euskelian clades (Dissorophidae, Zatracheidae, Eryopidae) are resolved, but the support of these successive clades is weak. We found the Zatrachyidae and Dissorophoidea to form a clade, with the Eryopidae nesting as their shared sister group, each supported by one step Bremer Support. While the clade as a whole is supported by two synapomorphies (16, 58), zatracheids and dissorophoids are not supported by synapomorphies but two homoplasies (23, 24) and one step Bremer Support.
- *Peltobatrachus* is found to nest more basally than even *Australerpeton*, which is not necessarily in contradiction to Yates and Warren (2000) and the more recent analysis of Pawley and Warren (2005) who suggested it be nested between *Sclerocephalus* (plus the archegosaurids which we did not consider) and the rhinesuchids; these authors did not code *Australerpeton* which was then still poorly known. *Peltobatrachus* itself is poorly known for many parts of the skull (margins, snout, anterior palate) and unknown for others (interclavicle), so that its relationships may remain obscure to some extent. In our analysis, the position of *Peltobatrachus* is supported by three synapomorphies (17, 38, 49) and three-steps Bremer Support. Omitting *Peltobatrachus* did not critically change the topology of the cladogram.
- *Australerpeton*, the rhinesuchids (*Uranocentrodon*), and lydekkerinids (*Lydekkerina*) are found to be successive sister taxa, together forming the basalmost grade of the Stereospondyli *sensu stricto* (Yates and Warren 2000; Schoch and Milner 2000). These successive nodes are supported as follows: *Australerpeton* crownwards (6, 59, one-step Bremer Support), *Uranocentrodon* crownwards (27, 50, 68, four-steps Bremer Support), and *Lydekkerina* crownwards (19, 26, one-step Bremer Support). This hypothesis is consistent with those of Yates and Warren



(2000) and Pawley and Warren (2005) in the general order of succession, but it differs from Yates and Warren in that *Benthosuchus* and *Mastodonsaurus* are not nested with *Lydekkerina*, a group also not found by Damiani (2001) or Pawley and Warren (2005).

- *Laidleria*, *Siderops*, and *Gerrothorax* as a monophylum. This is interesting, as it shares the view put forward by Yates and Warren (2000) that the short-faced stereospondyls may form a clade. It certainly differs from Schoch and Milner's (2000) concept, in which the former two were nested with lydekkerinids, and the plagiosaurids were no stereospondyls at all. On the other hand, there are two major differences between our result and that of Yates and Warren: (1) our short-faced clade is nested well below the capitosauroid-trematosauroid dichotomy, whereas it nests within the "trematosaur" clade of Yates and Warren (2000); (2) *Laidleria* and *Siderops* are here found to be monophyletic with the plagiosaurids forming their sister group, while Yates and Warren found *Laidleria* and plagiosaurids to be sister taxa with *Siderops* (and all other brachyopoids) their sister taxon. In our analysis, the monophyly of *Laidleria*, *Siderops*, and *Gerrothorax* is supported by two synapomorphies (42-2, 57), and four-steps Bremer Support, while the relationship between *Laidleria* and *Siderops* is indicated by one character (3) and one-step Bremer Support. The (*Laidleria* + *Siderops*) + *Gerrothorax* clade nested above *Lydekkerina* and below the capitosauroid-trematosauroid dichotomy is supported by two synapomorphies (35, 61) and one-step Bremer Support.
- The basal capitosauroid-trematosauroid dichotomy suggested by all more recent authors (Yates and Warren 2000; Schoch and Milner 2000; Damiani 2001; Pawley and Warren 2005) is also found here. Most interestingly, *Sclerothorax* is here supported as the sister taxon of capitosauroids (*Mastodonsaurus* plus *Paracyclotosaurus*), while *Benthosuchus* forms the sister group to *Trematolestes* and the Metoposauridae. *Sclerothorax* plus the capitosauroids is supported by three synapomorphies (20-2, 48, 51) and two-steps Bremer Support; the two capitosauroids are indicated as a monophylum by three characters (21, 33, 41-2) and a two-step Bremer Support. The trematosauroid clade plus *Benthosuchus* is supported by two synapomorphies (15, 36) and one-step Bremer Support, while the monophyly of *Trematolestes* and the Metoposauridae is indicated by two characters (4) and one-step Bremer Support.

## Conclusions

The new finds of *Sclerothorax hypselonotus*, along with a re-examination of the previously existing ones, provide a more detailed picture of this taxon which now permits its definitive assignment to the Triassic Stereospondyli. In contrast to Huene's (1932) and Schoch and Milner's (2000) concepts, *Sclerothorax* nests much higher within the "derived" stereospondyls, highlighted by numerous capitosauroid features

apparent especially in the three new specimens. However, the present analysis is far from inclusive—for instance, the poor knowledge of capitosauroid postcrania in general precludes a more broad-scale analysis. In addition, the gaps in the anterior and marginal palate and snout rim of *Sclerothorax* have produced numerous missing data in the analysis, which render a phylogenetic analysis of this taxon even more problematic.

Some features of *Sclerothorax* have been argued to indicate a terrestrial mode of life, among them the extremely broad skull table (Schmalhausen 1968), the structure of the neural arches and dorsal spines (Fastnacht 2004), the full ossification of the endochondral pectoral and pelvic elements, the proportions of these bones, and the dermal armour. These features are all found in temnospondyls with terrestrial species such as eryopids, dissorophids, and *Peltobatrachus*. Their presence in a member of the otherwise fully aquatic Capitosauria is unexpected and would suggest that within temnospondyls, terrestrial lineages may be poorly or inadequately represented in the fossil record. However, the possession of lateral line sulci in *Sclerothorax* contradicts the idea of a fully terrestrial existence, suggesting this animal might have led a more complex, amphibious mode of life. Eventually, the strong seasonality of the Middle Buntsandstein in central Germany may have favoured such an amount of flexibility among lower tetrapods.

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## Appendix 1

### Characters analyzed

Characters marked with “B” from Boy (1996), “D” from Damiani (2001), with “Y+W” from Yates and Warren (2000), with “S” from Schoch (2000a), “S+M” from Schoch and Milner (2000), and “P+W” (Pawley and Warren 2005).

1. Orbits, location. Medial, framed by wide jugals laterally (0), or lateral emplacement, framed by very slender jugals (1).
2. Orbits, margins. Raised well above skull plain (0), or flush with roof (1). (D)
3. Lacrimal. Present (0), or absent (1). (Y+W)
4. Lacrimal, position. Long element anterior to orbit (0), or small and confined to lateral orbit margin (1).
5. Medial skull table. Medial elements longer than wide (0), or quadrangular (1).
6. Lateral line sulci in adults. Absent (0), present (1). (Y+W)
7. Infraorbital sulcus. With simple curve on lacrimal (0), or with pronounced S-shaped lacrimal flexure (1). (D)
8. Supraorbital sulcus. Passing medial to lacrimal (0), or entering lacrimal (1). (D, S)
9. Maxilla, stepped margin. Margin of maxilla straight, continuous (0), or stepped, correlating with enlarged teeth, and abruptly narrowing anteriorly (1).
10. Maxilla-nasal. Maxilla separated from nasal by lacrimal (0), or contacting nasal anterior to lacrimal (1). (Y+W)
11. Prefrontal-postfrontal. Sutured (0), or separated by frontal (1). (D, S)
12. Prefrontal-jugal. Separated by lacrimal (0), or in contact (1). (Y+W, S+M)
13. Postorbital. Not wider than orbit (0), or with substantial lateral process (1). (Y+W, D)
14. Otic notch. Semicircular embayment between squamosal and posterior skull table (0), or straight transverse posterior skull margin without embayment between cheek and table (1). (Y+W)
15. Ornament, intensive growth. Elongated ridges (“zones of intensive growth”) confined to snout only (0), or prepineal growth zone established on extended anterior parietal and postorbital (1). (Y+W)
16. Posterior skull. Parietals and supratemporals longer than wide (0), or quadrangular, giving a foreshortened posterior skull table (1).
17. Jugal, ventral portion. No ventral outgrowth (0), or insula jugalis framing subtemporal window (1). (B)
18. Jugal, extension. Jugal ending at or behind level of anterior orbit margin (0), or extending anteriorly (1). (Y+W)
19. Squamosal-tabular. Separated by supratemporal (0), or sutured (1). (Y+W, S+M)
20. Squamosal, falciform crest. Posterior rim of squamosal straight (0), or with a long crest (falciform crest type 1) (1), or with a large convex projection (falciform crest type 2). (S+M, D)
21. Tabular, orientation. Posteriorly directed (0), or laterally (1). (S+M, D)
22. Tabular, ventral surface. Tabular horn ventrally smooth (0), or bearing ventral crest terminating at posterior tip (1). (Y+W)
23. Posterior skull rim. Cheek posterior to tabular horns (0), or at one level (1). (Y+W, D)
24. Quadrate, occipital condyles. Quadrate condyles posterior to occipital ones (0), or at same level (1), or even well anterior (2). (Character-states not ordered).
25. Paraquadrate foramen. Absent (0), or present (1). (Y+W)
26. Dentition, marginal. Heterogenous, varying sizes and distances (0), or homogeneous, small teeth, equidistant (1). (S+M, D)
27. Dentition, tooth bases. Round or oval (0), or forming transversely broadened ovals (1). (S+M, D)
28. Dentition, vomer. Tooth patches present (0), or dentition restricted to vomerine fangs (1). (S+M, D)
29. Dentition, transvomerine. Tooth row transverse (0), or V-shaped (1). (Y+W, S+M, D)
30. Dentition, basicranium. Tooth patches present (0), or teeth entirely absent (1). (Y+W, S+M, D)
31. Dentition, ectopterygoid. Fang pair present (0), or absent (1). (Y+W, D)
32. Anterior palatal depression. Forming a continuous fossa on the vomer (0), or perforated to accommodate symphyseal fangs (1). (Y+W)
33. Anterior palatal depression. Posterior rim round (0), or straight transverse (1). (S)
34. Basicranium, contact. Joint between basal plate and pterygoid (0), or sutural contact (1). (Y+W)
35. Basicranium, suture. Suture much shorter than basal plate, reaching at best 40% its length (0), or suture almost as long as basal plate (1).
36. Parasphenoid. Suturing with exoccipitals (0), or underplating exoccipitals (1). (Y+W)
37. Basicranium, carotids. Internal carotids entered basicranium ventrally near base of cultriform process (0), or at posterolateral corner of bone (1). (B)
38. Maxilla-vomer. Separated by premaxilla (0), or in contact (1). (Y+W)
39. Parasphenoid, plate. Basal plate short, reaching less than 30% of the posterior skull table (0), or anteriorly extended to reach 50–70% of the length posterior skull table (1).
40. Parasphenoid, process. Cultriform process much narrower than basal plate (0), or almost as wide (1).
41. Parasphenoid, process. Cultriform process ventrally flat (0), knife-edged and keel-shaped (1), or with ridge emplaced on broader base (2). (Character-states not ordered). (Y+W)
42. Parasphenoid, muscular pockets. Posterolateral corner with faint depressions or smooth (0), or housing large pockets (1), or pockets entirely absent (2). (Character-states not ordered). (Y+W)
43. Parasphenoid, posterolateral process. Posterolateral margin straight (0), or with lateral wing (1).
44. Pterygoid-vomer. Pterygoid and vomer in contact (0), or separated by palatine (1). (Y+W)
45. Pterygoid, ventral ornament. Palatine ramus of pterygoid smooth (0), or ornamented with reticulate ridges (1).
46. Pterygoid, exoccipital. No contact (0), or sutured lateral to parasphenoid (1). (S+M, D)

47. Palatine-ectopterygoid. Suture roughly transverse (0), or palatine forming posteromedial process medial to ectopterygoid (1). (S+M, D)
48. Quadrate trochlea. Formed by quadrate only (0), or laterally extended to include a ventral portion of quadratojugal (1). (S, D)
49. Occipital condyle. Trilobed, with basioccipital forming ventral part of facet (0), or bilobed exoccipital condyle with reduced basioccipital contribution (1). (Y+W)
50. Retroarticular process. Absent or present as very faint outgrowth (0), or longer than glenoid facet (1). (Y+W)
51. Hamate process. Anterior margin of lower jaw articulation facet not raised (0), or raised slightly above the level of the facet (1), or prearticular forming a high hamate process (2). (S+M, D)
52. Presacral count. Twenty-four or fewer vertebrae (0), or twenty-eight (1), or twenty-one (2) (Character-states not ordered).
53. Neural arch, transverse process. Short, directed posteriorly (0), or distally extended with diapophysis pointing laterally (1).
54. Neural arch, dorsal end. Originally covered by cartilage, as indicated by rugose dorsal surface (0), or dorsally fully ossified (1).
55. Neural arch, height. Low throughout the trunk (not higher than distance between zygapophyses) (0), or dorsally well extended beyond that measure, at least in some positions in the trunk (1). (Y+W)
56. Intercentrum. Presacral intercentra form simple wedges (0); or dorsally closed discs (1). (Y+W)
57. Pleurocentrum. Ossified (0), unossified (1). (Y+W)
58. Interclavicle, outline. Rhomboidal (0), or pentagonal (1).
59. Interclavicle, proportions. As long as broad (0), or 1.3 times as long as wide (1).
60. Interclavicle, length. Smaller than skull, less than 50% of the area (0), or 70–100% (1).
61. Interclavicle, clavicles. Clavicles broadly separated by interclavicle ventrally (0), or in contact (1).
62. Scapula, length. Ossified portion low, not reaching level of axial skeleton (0), or dorsally extended and almost reaching that level (1).
63. Scapula, glenoid facet. Ossified (0), or unossified (1).
64. Humerus, supinator. Present (0), or absent (1). (Y+W)
65. Humerus, condyles. Distal end narrow (0), or broadened to give extensive condyles (1).
66. Ilium, dorsal end. Not wider than shaft (0), or significantly broadened (1).
67. Pubis. Ossified (0), unossified (1).
68. Femur. Intercondylar fossa forming deep and elongated trough (0), or reduced to short depression (1). (Y+W)
69. Gastral squamation. Ossified dermal scutes (0), or dermis naked (1).
70. Dorsal squamation. Dorsal region naked (0), or covered by dermal ossicles (1).