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A NEW SPECIES OF *SCLEROCEPHALUS* (TEMNOSPONDYLI: STEREOSPONDYLOMORPHA) FROM THE EARLY PERMIAN OF THE BOSKOVICE BASIN (CZECH REPUBLIC)

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ABSTRACT—A new species of the temnospondyl tetrapod, *Sclerocephalus stambergi* n. sp., is described from the early Permian deposits of the Boskovice Basin in Moravia (Czech Republic). The length of the skull of the only known specimen is about 50 mm. Characters including the well-ossified quadrate, septomaxilla and scapulocoracoid, presence of the maxilla-nasal suture and a free posterolateral margin of the supratemporal suggest an early adult age. This new species of *Sclerocephalus* is distinguished from the others on the basis of the following characters: nasal and maxillary processes of the premaxilla of equal width; absence of the alary process of the premaxilla; distinct pointed process on the lacrimal between the maxilla and jugal; narrow interclavicle; and very peculiar tabular presenting a quadrangular, plate-like process extending from its posterolateral portion, an almost right angle between its lateral and posterior margins, and a long posteromedial process. The new species represents the smallest and possibly the most basal *Sclerocephalus* species. The specimen described here sheds new light on the anatomy and taxonomy of *Sclerocephalus*. It completes the biodiversity of the tetrapod fauna from the Boskovice Basin, and our knowledge on the evolution of the European Paleozoic temnospondyls.

INTRODUCTION

THE BOSKOVICE Basin (formerly the Boskovice Furrow) in Moravia (Czech Republic) is filled by lake depositional sequences of early Permian age (Jaroš, 1963; Zajíc and Štamberg, 2004; Štamberg and Zajíc, 2008). The first finds of tetrapods from this region were made near the town of Malá Lhota in 1872 (Augusta, 1948). These tetrapods were described by Makowsky (1876) as *Archegosaurus austriacus*. Later studies showed that this species belongs to a different genus, the seymouriamorph *Discosauriscus austriacus* (for review see Špinar, 1952; Klembara, 1997). Since that time, the deposits of various localities in the Boskovice Basin have yielded mostly specimens of seymouriamorph tetrapods (e.g., Špinar, 1952; Klembara and Meszároš, 1992). Among them, the most abundant species is *Discosauriscus austriacus*, which is known from hundreds of specimens (Klembara, 1997; Klembara and Bartík, 2000). The other species of *Discosauriscus*, *D. pulcherrimus* (Fritsch, 1879), is known from a few specimens from the Boskovice Basin (Klembara, 1997). Aside from *Discosauriscus*, two other taxa have been described, each on the basis of a single specimen: *Makowskia laticephala* Klembara, 2005 and *Spinarerpeton brevicephalum* Klembara, 2009. Within the temnospondyls, several poorly preserved branchiosaurs were reported from the basin by Augusta (1947), and only one other temnospondyl, an zatracheid cf. *Dasyceps* was described 60 years later (Milner et al., 2007) on the basis of a single specimen.

The specimen described here belongs to the stereospondylomorph temnospondyls. The aim of this paper is to present a detailed osteological description of this new find as well as an up-to-date paleobiogeographical scenario of the genus *Sclerocephalus*.

Institutional acronyms include: DE, Department of Ecology, Comenius University in Bratislava, Faculty of Natural Sciences, Bratislava, Slovakia; MHK, Museum of Eastern Bohemia, Hradec Králové, Czech Republic; SNM, Slovak National Museum, Bratislava, Slovakia.

MATERIAL AND METHODS

The specimen described here is preserved in two slabs, the part MHK 81460/1 and counterpart MHK 81460/2 (Figs. 1.1, 2.1). It is preserved in a laminated limestone, in the same manner as other tetrapods and fishes of various localities in the Boskovice Basin (Klembara and Meszároš, 1992). Several skeletons of branchiosaurs, including skulls, are also preserved on both slabs and are well visible under ultraviolet light. The specimen described here consists of a nearly complete skull with several associated postcranial elements. The cranial anatomy is shown by the skull roof, several palatal fragments, and the lower jaw. The skull length (SL) is about 50 mm. The length of skull is the sum of lengths of the nasal, frontal, parietal and postparietal measured, where possible, in the median plane; the length of the premaxilla is not included. Although the skull is dorsoventrally compressed and several bones are damaged or missing (e.g., right posterolateral portion of the skull table) as a consequence of the splitting, the individual bones are more or less three-dimensionally preserved. To reconstruct the original shape of the skull, all the dorsal bones were measured, modeled in a wax-plasticine matrix at seven times their natural size and assembled in anatomical position using flat metal bars. In this cranial reconstruction, the missing bones of the right side (supratemporal, tabular and postparietal) have been reconstructed on the basis of the shape of the left ones (Fig. 3). All the drawings, except the cranial reconstruction, have been made using a Leica MZ75 stereomicroscope equipped with a camera lucida.

SYSTEMATIC PALEONTOLOGY

Order TEMNOSPONDYLI Zittel, 1888
Unranked clade STEREOSPONDYLOMORPHA Yates and Warren, 2000
Family SCLEROCEPHALIDAE Jaekel, 1909
Genus SCLEROCEPHALUS Goldfuss, 1847

Diagnosis.—See Schoch and Witzmann (2009, p. 137–139).

Type species and type locality.—*Sclerocephalus haeuseri* Goldfuss, 1847 from the lower Permian of Pfarrwald near Heimkirchen, Germany.

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Other species.—*Sclerocephalus bavaricus* (Branco, 1887), "*S. jogischneideri*" Werneburg, 1992, and *S. nobilis* (Krätschmer and Resch, 2005).

Occurrence.—Lower Permian of Germany and Czech Republic.

SCLEROCEPHALUS STAMBERGI new species
Figures 1–5

Etymology.—Named for Dr. Stanislav Štamberg (Museum of Eastern Bohemia, Hradec Králové, Czech Republic) who discovered the specimen and for his valuable contribution to vertebrate paleontology.

Holotype.—Part MHK 81460/1 and counterpart MHK 81460/2, skull and associated postcranial elements (Figs. 1.1, 2.1). It is the only known specimen. It is deposited in the collections of the Museum of Eastern Bohemia in Hradec Králové (Czech Republic).

Locality and horizon.—Boskovice Basin (formerly Boskovice Furrow) in Moravia (Czech Republic). Locality Zbraslavec: limestone slabs outcropping in a field located above the road between the villages Zbraslavec and Drnovice, about 400 m south from the margin of Zbraslavec. *Acanthodes gracilis* (Beyrich, 1848) Biozone, lower Letovice Formation, lower Permian (Asselian) (Zajíc and Štamberg, 2004; Štamberg and Zajíc, 2008).

Diagnosis.—*Sclerocephalus* with the following combination of character states: nasal and maxillary processes of the premaxilla of equal width; absence of the alary process of the premaxilla; distinct pointed process in the posterolateral region of the lacrimal between the maxilla and jugal; relatively narrow interclavicle; and very peculiar tabular presenting a quadrangular, plate-like process extending from its posterolateral portion, an almost right angle between its lateral and posterior margins, and a long posteromedial process.

DESCRIPTION

The skull is subtriangular (Figs. 1–3). The orbits are rounded and located slightly posterior to the skull mid-length. The jaw joint is posterior to the level of the posterior margin of the skull table. The posterior margin of the skull table is slightly embayed anteriorly in its mid-portion. Because the skull is split into two slabs, the ornamentation is slightly damaged on the individual bones. However, the ossification centers and the dorsal ornamentation are well recognizable on most of the bones: the ornamentation consists of well developed ridges alternating with relatively deep pits and grooves radiating from the ossification centers (Figs. 1, 2). The ridges present an anastomosing pattern. The sensory grooves are not distinctly visible. Only on the jugal, a deep interrupted groove could mark a potential sensory groove. Numerous sutures are complicated and interdigitated.

Skull roof.—The premaxillae are heavily constructed (Figs. 1–3). The nasal process is wide and short. Its width is the same than that of the maxillary process. The entire posteromesial surface of the premaxilla formed a wall of the exonarial fenestra. Neither premaxilla exhibits an alary process.

The nasal is elongate and broad. The left nasal differs in shape from the right nasal (Figs. 1–3). The suture between both nasals is S-shaped. The anterior half is broader than the posterior half. The posterolateral corner of the left nasal forms a wedge between the prefrontal and frontal. The nasal forms the posteromedial wall of the exonarial fenestra. The nasal has short sutures with the septomaxilla anterolaterally and with the maxilla posteriorly. The nasal has long sutures with the lacrimal and prefrontal. The nasal-frontal suture has a transverse course at the right side of the skull whereas at the left side the suture has an oblique course.

The dorsal portion of the left septomaxilla is well preserved (Figs. 1–3). It is triangular, its posterior process fitting as a wedge between the maxilla and nasal. The dorsal surface of the septomaxilla forms part of the skull roof. The anterior margin of the septomaxilla forms the posterior wall of the exonarial fenestra.

The frontal is long and narrow (Figs. 1–3). The left frontal is slightly longer than the right frontal; however, the anteriormost portion of the frontal is not well preserved. The frontal is longer than the parietal and nasal. It has long sutures with the prefrontal and postfrontal. The frontal-parietal suture lies about at the level of the mid-length of the postfrontal.

The prefrontal is triangular, and forms a rounded orbital margin (Figs. 1–3). The anterior portion of the prefrontal is a large wedge between the nasal and lacrimal. The prefrontal-nasal suture is not well preserved on the right side of the skull. The lateral portion of the prefrontal forms a narrow process that shares a short suture with the jugal, therefore excluding the lacrimal from the orbital margin. The posteromedial process of the prefrontal is mediolaterally narrow and joins the postfrontal in a short suture. This suture lies about at mid-length of the frontal.

The postfrontal is crescent-shaped with a raised orbital margin (Figs. 1–3). It has a long and mediolaterally narrow anterior ramus. The posterior portion of the postfrontal, relatively broader than the anterior one, deeply invades the parietal. The postfrontal has a long suture with the postorbital laterally.

The parietal is elongate (Figs. 1–3). Its anterior portion meeting the frontal is mediolaterally narrow. The pineal foramen is rounded, small, and located posterior to the posterior orbital margin, at the level of the posterior portion of the postfrontal. The suture between both parietals posterior to the pineal foramen is undulating but straight anterior to the foramen.

Most of the left supratemporal is preserved (Figs. 1–3). It is elongate and quadrangular. Posteriorly, the supratemporal-squamosal suture reaches the level of about three quarters of the supratemporal length. The posterolateral margin of the supratemporal is free. The suture between the supratemporal and parietal is the longest relative to the length of the sutures of the supratemporal with other neighboring bones. The supratemporal-postorbital suture is not visible and its length can only be estimated (Fig. 4). The suture with the postparietal is slightly longer than that with the tabular.

The left postparietal is nearly complete (Figs. 1–3). It is larger than the tabular and most of its suture with the supratemporal is well preserved. The course of the suture is irregular.

The left tabular is well preserved (Figs. 1–3). It is rectangular, with a large, pointed process extending posteromedially. Hence, the process has an anterolaterally-posteroventrally oriented suture with the postparietal. The surface of the process bears strong mediolateral grooves and ridges. This portion probably represents the occipital flange of the tabular which was probably inclined posteroventrally in the intact skull. The posterior and lateral margins of the tabular form almost a right angle. The tabular-supratemporal suture is irregular and mediolaterally oriented. A distinct, elongate tabular process extends from the posterolateral portion of the tabular. It has a posterolateral orientation. The process

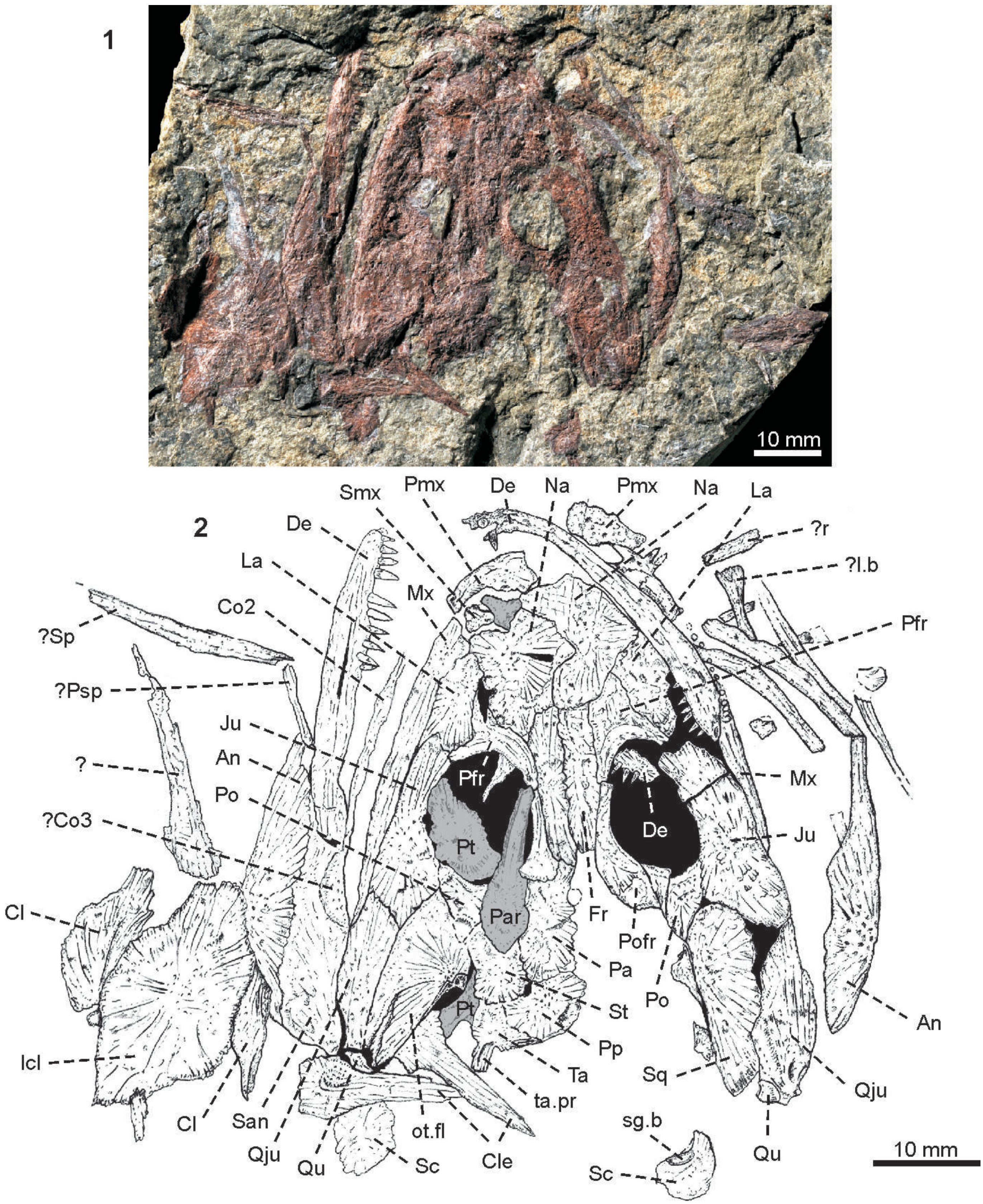

FIGURE *1*—*Sclerocephalus stambergi* n. sp., MHK 81460/1 (part), holotype, lower Permian of Czech Republic. *1*, photograph; *2*, interpretive drawing of skull and postcranial elements (palatal bones in gray). Abbreviations: An=angular; Cl=clavicle; Cle=cleithrum; Co2=middle coronoid; Co3=posterior coronoid; De=dentary; en.fe=exonarial fenestra; Fr=frontal; Icl=interclavicle; Ju=jugal; La=lacrimal; l.b=limb bone (?humerus); Mx=maxilla; Na=nasal; ot.fl=otic flange of squamosal; Pa=parietal; Par=parasphenoid; Pmx=premaxilla; Po=postorbital; Pofr=postfrontal;

consists of a quadrangular plate with a crenulated posterior margin. It is well visible that the lateral margin and the dorsal surface of the tabular process are continuous with the dorsal surface of the tabular. The ornamentation on the dorsal surface of the tabular is partially preserved: ridges and grooves course from the tabular to the dorsal surface of the tabular process. This indicates that the tabular process is not the outgrowth from the ventral surface of the tabular but rather from its posterolateral margin.

Both maxillae are preserved, the left one being complete (Figs. 1–3). Its anterior portion extends into a process which joined the premaxilla. The internal surface of this process formed the lateral wall of the exonarial fenestra. The anterior portion of the maxilla is deep and its entire dorsal margin is sutured with the lacrimal. Anterior to the maxilla-lacrimal suture, a short maxilla-nasal suture is visible. Immediately anterior to this suture, the wedge-like process of the septomaxilla fits between these two bones. Most of the dorsal margin of the maxilla is sutured to the jugal. The posterior end of the maxilla underlies the anteroventral portion of the quadratojugal.

The lacrimal is elongate and surrounded by the maxilla, jugal, prefrontal and nasal (Figs. 1–3). A distinct and pointed process between the maxilla and jugal extends from the posterolateral margin of the lacrimal. The nasolacrimal canal is not visible.

The jugal is the largest element of the cheek. The right jugal is larger than the left jugal, and its suborbital depth is greater (Figs. 1–3). Its anterior margin bears a shallow notch for the accommodation of the lacrimal. Posteriorly, the jugal has a wedge-like process between the quadratojugal and squamosal.

Both postorbitals are preserved (Figs. 1–3). The postorbital is triangular and has a robust, raised orbital margin. The postorbital fits between the postfrontal and supratemporal medially and between the jugal and squamosal laterally.

The squamosal is large and elongate (Figs. 1–3). It has a long, almost straight suture with the quadratojugal. The dorsal portion of the squamosal has a medially extending lamina, which was overlapped by the supratemporal in the intact skull (the lamina is completely exposed on the right squamosal; Fig. 2.2). The posterodorsal margin of the squamosal is almost straight. A smooth otic flange is partially visible on the posterodorsal wall of the squamosal. The squamosal embayment is wedge-shaped.

The quadratojugal is narrow and elongate (Figs. 1–3). It is deepest at mid-length. Anteriorly, it has a long anteroventrally-posterodorsally oblique suture with the jugal. The quadratojugal has a large, dorsally extending triangular lamina, which underlies the posteroventral portion of the squamosal. The posterior end of the quadratojugal is enlarged and spoon-shaped.

Palate.—Several fragments of palatal elements are preserved. They can be tentatively identified on the basis of their position. The smooth bone within the left exonarial fenestra probably represents a portion of the left vomer in dorsal aspect (Fig. 2). A large fragment within the left orbit may represent a portion of the palatal ramus of the left pterygoid (Figs. 1, 2). The fragments between the left squamosal and the lateral margin of the skull table probably represent portions of the left quadrate ramus of the pterygoid (Figs. 1, 2). A long bone in the medial portion of the left orbit and continuing posteriorly may represent a portion of the cultriform process and part of the parasphenoidal plate (Figs. 1, 2).

Quadrate.—The ossified quadrate is preserved on both sides of the skull (Figs. 1, 2). Its exposed external surface is located between the posterior ends of the squamosal and quadratojugal. It is subtriangular.

Lower jaw.—Except for the left angular and surangular, all other elements of the lower jaw are more or less disarticulated.

The dentary is long (Figs. 1, 2) and gradually tapers to a pointed end posteriorly. A small fragment with three teeth is located in the anterior portion of the right orbit, and probably represents a portion of the right dentary.

The angular is large and ovoid, with strong ornamentation on its external surface (Figs. 1, 2). This ornamentation consists of pits, grooves and ridges radiating from the posteroventral portion of the bone. The angular-surangular suture is rather complicated and has an anteroposterior course.

The surangular is large (Figs. 1, 2). Its posterior margin is slightly dorsally elevated. On MHK 81460/1, the left surangular has a posterodorsally-anteroventrally extending suture with the posterior end of the posterior coronoid (Fig. 1). This posterior coronoid has a suture with a bony fragment immediately anterior to it. This more anterior element probably represents the middle coronoid (assuming that *S. stambergi* has three coronoids, the anterior one not preserved). However, both coronoids are fragmentary and do not provide any other morphological information.

On both sides of the skull, two elongate elements, one short and slender and one much longer and robust, are present. They probably represent the splenial and postsplenial respectively (Figs. 1, 2).

Dentition.—Several marginal teeth are well preserved, especially on the left dentary and partially on the right dentary and right maxilla (Figs. 1, 2). The teeth are conical, pointed, and not recurved. On the basal portions of the crowns, vertical grooves indicating the inner infolding of the dentine are present. These grooves extend for about two thirds of the crown height (Fig. 4).

Postcranial skeleton.—Several postcranial elements are preserved. They include the elements of the pectoral girdle, several fragments of ribs and possibly one long bone (Figs. 1, 2).

The interclavicle is mostly preserved in ventral view. It is rhombic (Figs. 1, 2) and relatively narrow. Its ornamented surface is slightly longer than wide. The ossification center lies slightly anterior to the mid-length of the bone. The anterior portion of the interclavicle is enlarged and its posterior end is wedge-shaped. The articulation areas with the clavicles are broad and occupy most of the surface of the anterior half of the interclavicle. The posterolateral margins and the middle portion of the posterior end are unornamented.

The left clavicle is preserved in situ; the right clavicle is slightly disarticulated from the interclavicle (Figs. 1, 2). The ventral plate of the clavicle is broad and ornamented, but no other morphological data is apparent. The proximal portion of the left dorsal process is preserved but its distal portion is broken.

←

Pp=postparietal; Prf=prefrontal; Psp=postsplenial; Pt=pterygoid; Qu=quadrate; Qju=quadratojugal; r=rib; San=surangular; Sc=scapulocoracoid; sg.b=supraglenoid buttress; Smx=septomaxilla; Sp=splenial; Sq=squamosal; sq.la=squamosal lamina; St=supratemporal; Ta=tabular; ta.pr=tabular process; Vom=vomer.

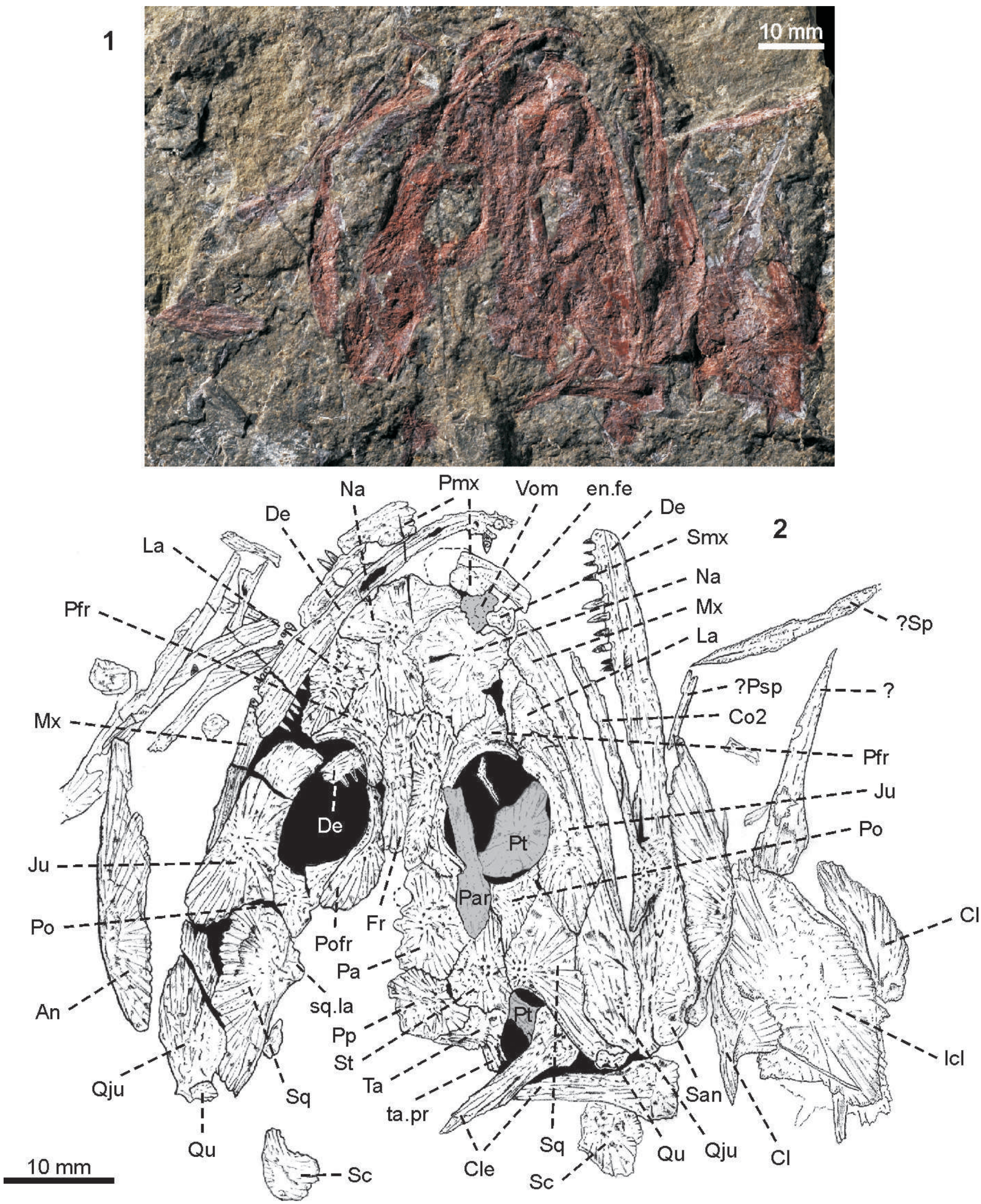

FIGURE 2—*Sclerocephalus stambergi* n. sp., MHK 81460/2 (counterpart), holotype, lower Permian of Czech Republic. *1*, photograph; *2*, interpretive drawing of skull and postcranial elements (palatal bones in gray). Abbreviations as in Figure *1*.

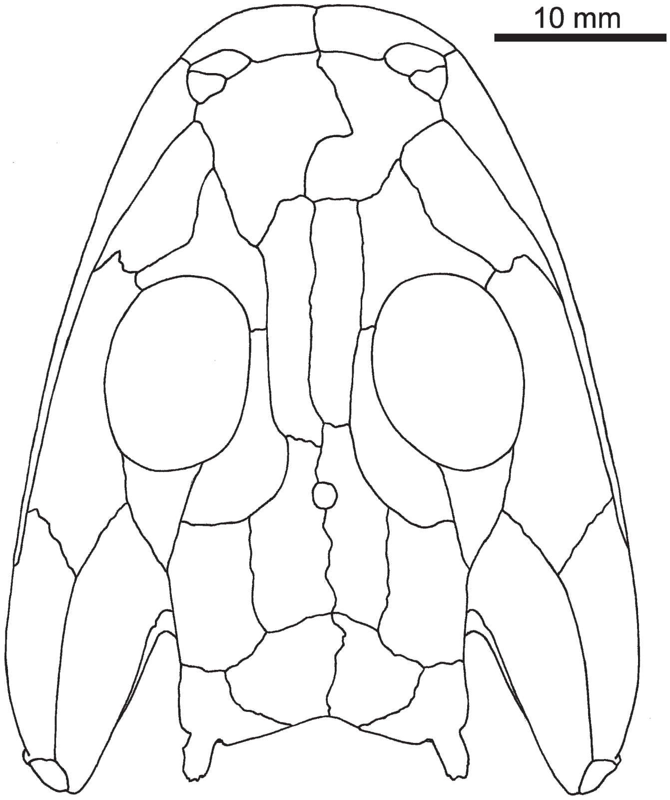

FIGURE 3—*Sclerocephalus stambergi* n. sp., holotype, lower Permian of Czech Republic, MHK 81460. Cranial reconstruction in dorsal view.

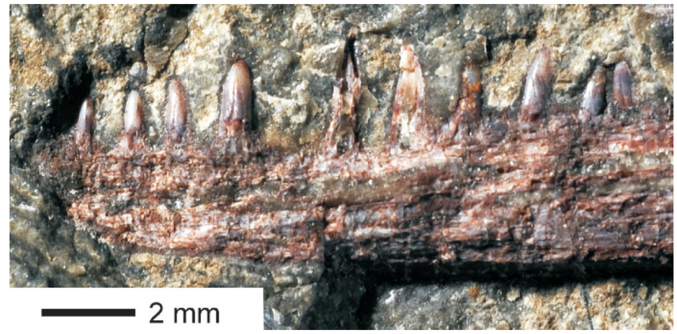

FIGURE 4—*Sclerocephalus stambergi* n. sp., MHK 81460/1 (part), holotype, lower Permian of Czech Republic. Close up view of anterior portion of left dentary.

Both cleithra are preserved (Figs. 1, 2). The cleithrum is elongate and consists of the proximal and distal portions. The distal portion is broad and subquadrangular. The proximal portion is the largest one dorsally, but becomes gradually narrow ventrally. Its ventral end is pointed.

Both scapulocoracoids are present: one lies immediately posterior to the cleithra on the left side of the skull, the other posterior to the squamosal on the right side of the skull (Figs. 1, 2). The ventral side of the right scapulacoracoid is well preserved (Fig. 1). It is almost crescent-shaped, but its posterior portion is much broader than its anterior one. At mid-length, a well developed, elongate glenoid portion is visible. The supraglenoid buttress is distinct. Unfortunately, the preservation of the bone does not allow the identification of the foramina in the glenoid region.

INDIVIDUAL SIZE OF SPECIMEN

According to a recent study about the development of *Sclerocephalus haeuseri* (Schoch and Witzmann, 2009), specimens with a skull length up to 40 mm represent larvae, specimens with a skull length between 40 and 110 mm are juveniles, and specimens with a skull length of 110–120 mm are early adults. The specimen described here exhibits features that are typical for the late juvenile to early adult ontogenetic stage of *S. haeuseri* (Schoch and Witzmann, 2009; cf. also Boy, 1988; Schoch and Milner, 2000; Steyer, 2000a). The characters indicating the late juvenile to early adult ontogenetic conditions of *S. stambergi* are as follows.

Presence of the well ossified septomaxilla separated from the lacrimal by the nasal-maxilla suture.—According to Boy (1988), in *S. haeuseri* the septomaxilla starts to ossify at the juvenile stage and has a short contact with the lacrimal. Only in the adult skulls, the lacrimal is fully developed and separated from the septomaxilla by the maxilla-nasal suture. The separation of the septomaxilla by the nasal-maxilla suture is established only in the adult stage (Boy, 1988).

Presence of the well ossified quadrate.—According to Schoch and Witzmann (2009, p. 148, fig. 2A), in *S. haeuseri* the quadrate is generally ossified in skulls with lengths of 100 mm or more, i.e., in the late juvenile and adult specimens.

Orbits lie slightly posterior to the mid-length of the skull.—This condition is seen only in the late juveniles and adults of *S. haeuseri* (Boy, 1988; Schoch and Milner, 2000; Schoch and Witzmann, 2009).

Jaw joint lies posterior to the posterior margin of the skull table.—Such position of the jaw joint is present in the late juveniles and adults of *S. haeuseri* (Boy, 1988; Schoch and Witzmann, 2009).

Presence of the well developed tabular process.—In *S. haeuseri*, the tabular horn is fully developed only in the adult specimens with the skull length of about 130–140 mm (Schoch and Witzmann, 2009, fig. 2A).

Skull roof sutures are rather complicated and interdigitated.—The complicated sutures are visible in the late juveniles and the adult specimens of *S. haeuseri* (Boy, 1988; Schoch and Witzmann, 2009).

Vertical grooves on the basal portions of the tooth crown of about two thirds of the crown height.—This condition is typical for only adult specimens of *S. haeuseri* (Boy, 1988).

As for the postcranial skeleton, the scapulocoracoid is well ossified in *Sclerocephalus stambergi* with a well developed glenoid region. According to Boy (1988) and Meckert (1993), the scapulocoracoid became fully ossified at the early adult stage. According to Schoch and Witzmann (2009), the glenoid region is fully formed only in the adult specimens of *S. haeuseri*. In *S. stambergi*, the glenoid region is well developed and the morphology of the scapulocoracoid corresponds to the scapulocoracoid of an early adult specimen of *S. haeuseri* (Boy, 1988, fig. 8B).

All these features indicate that the specimen described here represents a late juvenile or more likely an early adult ontogenetic stage. It is interesting to note that, for a subadult *Sclerocephalus*, the skull of *S. stambergi* is rather small: its length is only 50 mm, versus 90 to 140 mm for the juveniles to early adults of *S. haeuseri*. Pending the discovery of further individuals of *S. stambergi*, we prefer to exclude the relative small size of the holotype from the diagnosis.

DISCUSSION

The general anatomy of the skull and postcranial bones of the specimen described here fits with the Permo–Carboniferous

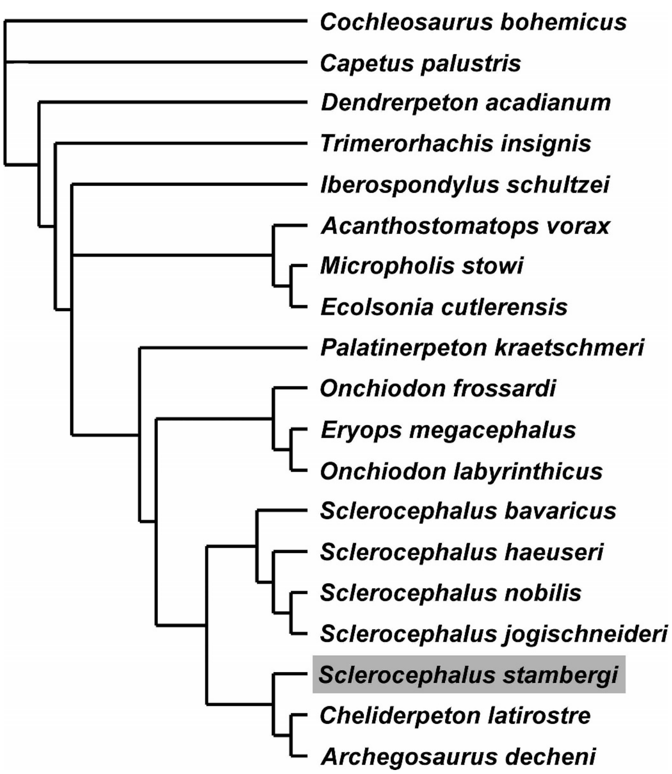

FIGURE 5—Preliminary phylogenetic analysis; strict consensus tree recovered by PAUP v. 3.1 from a heuristic search of 54 characters and 19 taxa.

temnospondyl *Sclerocephalus*. According to the most recent revision of the genus (Schoch and Witzmann, 2009), *Sclerocephalus* included four species: *S. haeuseri* Goldfuss, 1847; *S. bavaricus* (Branco, 1887); *S.* "*jogischneideri*" Werneburg, 1992; and *S. nobilis* (Krätschmer and Resch, 2005). However, we question here the validity of *S.* "*jogischneideri*" because its diagnosis is based on doubtful characters. The absence of suture between the basipterygoid and parasphenoid could be the result of poor preservation, and the interorbital distance (considered as wide in the previous diagnosis) is a highly variable character (e.g., Boy, 1988; Steyer, 2000b) that depends on the orbit size (Schoch and Witzmann, 2009).

The new species *S. stambergi* is placed in the genus *Sclerocephalus* because the specimen described here presents the following diagnostic characters of the genus *Sclerocephalus* (Schoch and Witzmann, 2009, p. 137–139): a slender and elongated supratemporal (the length/width ratio of 2.1 for *S. stambergi* fits within the range for *Sclerocephalus*, 1.7 to 2.4) and a posteriorly triangular interclavicle. Other characters given in the diagnosis of *Sclerocephalus* by Schoch and Witzmann (2009, p. 137–139) are either not preserved (one is relative to the palatal view) or not expressed here (because of the not fully adult developmental stage of *S. stambergi*).

The new species *Sclerocephalus stambergi* differs from all the other species of *Sclerocephalus* in the following features: 1) Equal width of the nasal and maxillary processes of the premaxilla. In the subadult and adult specimens of the other species, the maxillary process of the premaxilla is very short; the nasal process may be up to three times wider than that of the maxillary process (Boy, 1988; Werneburg, 1992; Schoch and Milner, 2000; Schoch and Witzmann, 2009); 2) Absence of the alary process of the premaxilla. This small, posterodorsally extending process from the posterior margin of the nasal process is always present in other species of *Sclerocephalus,* including larval specimens (Boy, 1988; Schoch, 2003). However, the posterior margin of the nasal process of the right premaxilla in *S. stambergi* is well preserved and clearly visible. This margin is almost straight mediolaterally and does not show any alary process; 3) The lacrimal extends into a distinct and pointed posterolateral process fitting between the maxilla and jugal. Such process is absent in the other species of *Sclerocephalus*; 4) The posterior and lateral margins of the tabular form an almost right angle. In the other species of *Sclerocephalus*, the posterolateral corner of the tabular extends into a wedge-like process and the lateral and posterior margins have a sharp angle (Schoch and Milner, 2000; Schoch and Witzmann, 2009, fig. 5); 5) The tabular extends into a long posteromedial process posterior to the posterolateral corner of the postparietal. The posteriormost portion of this process may represent the occipital flange of the tabular. It is not ornamented as the tabular itself, but bears lateromesially coursing ridges. Such process is not present in any other species of *Sclerocephalus* (Schoch and Milner, 2000; Schoch and Witzmann, 2009, fig. 5); 6) Presence of an elongate, quadrangular tabular process. The tabular process is present in *Sclerocephalus haeuseri* in the form of an elongated and pointed horn (Schoch and Witzmann, 2009, figs. 3A, B, 4A, 5A). However, the plate-like tabular process as preserved in *Sclerocephalus stambergi* has not been identified in temnospondyls previously, and is similar to those in seymouriamorphs such as *Discosauriscus* (Klembara, 1997), *Ariekanerpeton* (Klembara and Ruta, 2005) and *Makowskia* (Klembara, 2005). In *Discosauriscus*, the tabular process has basically an identical shape and position as that of *S. stambergi*, but in *D. austriacus* it represents an outgrowth from the posteroventral surface of the tabular (Klembara, 1997); and 7) The interclavicle is relatively narrow (width/length ratio of 0.55) compared with that of the other species of *Sclerocephalus* (width/length between 0.6 and 0.65, Schoch and Witzmann, 2009, p. 139).

All the above show that the specimen described here does not fit with previously known species of *Sclerocephalus* but represents a new, and probably the smallest, species.

Sclerocephalus is one of the best known and abundant tetrapods from the non-marine Permo–Carboniferous of Europe (Schoch and Witzmann, 2009) and one of the most basal stereospondylomorphs (Yates and Warren, 2000). Although *Sclerocephalus* may be present in France (Steyer et al., 1997), *S. stambergi* represents the first definite occurrence of the genus outside Germany.

PRELIMINARY PHYLOGENETIC ANALYSIS

In order to assess the phylogenetic position of *Sclerocephalus stambergi* within late Paleozoic temnospondyls including all the other species of *Sclerocephalus*, a preliminary cladistic analysis was performed. We used the recent character-taxon matrix by Schoch and Witzmann (2009, p. 168, table A1) and added the new taxon, *Sclerocephalus stambergi* (see Appendix 1 for the character states for *S. stambergi*). The modified matrix comprises 54 characters and 19 taxa. We refer to Schoch and Witzmann (2009, appendix, p. 166, 167) for the character list used here. The software PAUP v. 3.1 (Swofford, 1992) was used with the same options and modes as in the cited study: all the characters are treated as unordered, the two outgroups *Cochleosaurus bohemicus* and *Capetus palustris* formed a basal polytomy, and the analysis was run in the branch-and-bound mode under ACCTRAN. The analysis yielded three most parsimonious trees (L=90 steps, CI=0.62, RI=0.82), the strict consensus of which is illustrated on Figure 5. The result is the same by using WinClada 1.00.08.

The topology of the strict consensus tree obtained here is the same as that of Schoch and Witzmann (2009, fig. 10A, B, p. 161): *Sclerocephalus bavaricus* is sister-taxon of the clade (*S. haeuseri* + (*S. ''jogischneideri''* + *S. nobilis*)). Unfortunately, the new *S. stambergi* added in the analysis does not fall within the previous clade *Sclerocephalus* but rather as the sister-taxon of the closely related stereospondylomorph clade (*Archegosaurus decheni* + *Cheliderpeton latirostre*). However, this relationship is only supported by a single non-ambiguous synapomorphy—a narrow interclavicle (character 50, state 1). This apparent position of *S. stambergi* outside but close to the *Sclerocephalus* clade may be due to the fact that: 1) the holotype of *S. stambergi* is not a fully adult individual and therefore does not express all *Sclerocephalus* characters (as noted above); and 2) numerous characters of *S. stambergi* related to the palatal and postcranial regions are unfortunately not preserved in the holotype and thus can only be coded as ''?'' in the matrix (39 percent).

Additional specimens of *Sclerocephalus stambergi* are needed to determine more precisely its relationships. *Sclerocephalus* remains the most basal known stereospondylomorph temnospondyl. It is possible that *S. stambergi* will eventually emerge as the sister-taxon of the clade (*S. bavaricus* + (*S. haeuseri* + (*S. ''jogischneideri''* + *S. nobilis*))). Its smallest size compared with the other species of *Sclerocephalus* may suggest that it could be the most basal *Sclerocephalus* in accordance with Cope's rule (which suggests an increasing of size during evolution; cf. Cope, 1880; Depéret, 1907).

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APPENDIX

Character states attributed to *Sclerocephalus stambergi* (lower Permian of Czech Republic) in the preliminary phylogenetic analysis and following the matrix of Schoch and Milner (2009, Table A1, p. 167, 168). See this reference for the character list and definition. Abbreviations: Char=character number; S.s.=*S. stambergi*, +=polymorphic character.

```
Char          111111111122222222223333333333444444444455555
     123456789012345678901234567890123456789012345678901234
-----------------------------------------------------------
S.s. 1011111+000100001110101100?????????????00????011?10???
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