

Redescription and phylogenetic relationships of *Solenodonsaurus janenschi* Broili, 1924, from the Late Carboniferous of Nýřany, Czech Republic

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Abstract

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The basal tetrapod *Solenodonsaurus janenschi* Broili, 1924, from Nýřany (Westphalian D, Late Carboniferous), Czech Republic, is redescribed and its phylogenetic position re-evaluated. A distinct groove at the base of the maxillary teeth is regarded as an autapomorphic character, which is present in both the large and small specimens. Other characteristic features, which are not unique to *S. janenschi*, are: an extension of the lacrimal that forms the anteroventral margin of the orbit; a long posterior extension of the jugal; spool-shaped vertebrae, and small, wedge-like intercentra. A phylogenetic analysis based on the data matrix of Ruta, Coates and Quicke suggests that *S. janenschi* is the sister taxon of the Lepospondyli. Shared characters include the shape of the vertebrae, non-swollen neural arches, and absence of an intertemporal. Although nested within the amniote stem, *S. janenschi* is not as closely related to basal amniotes as previously suggested. A rather long, slender humerus argues for a predominantly terrestrial mode of life, and the curved, slender ribs, as well as the comparatively small skull, suggest costal ventilation of the lungs similar to that in amniotes, rather than buccal pumping. The morphology of the shallow squamosal embayment in which an ossified dorsal margin is absent, renders the presence of a tympanum unlikely.

Key Words

“anthracosaurs”
lepospondyls
spool-shaped vertebral centra
stem-amniote
tetrapod

Introduction

Solenodonsaurus janenschi Broili, 1924 is a basal tetrapod only known from the Late Carboniferous (Westphalian D) Gaskohle of Nýřany, Czech Republic. During the last century *S. janenschi* has played an important role in discussions about the origin of amniotes. Broili (1905) was the first study of *S. janenschi* based on a slab from Nýřany preserving a skull and postcranial elements of a tetrapod, which he interpreted to be the temnospondyl *Cochleosaurus bohemicus* based on a description by Frič (1876). This specimen belonged to the Palaeontological Institute in Munich and was lost during the Second World War. In 1924, Broili studied the counterpart of the Munich specimen, which is stored at the Museum of Natural History in Berlin. Broili recognized that the specimen was not a temnospondyl, but rather belonged to a new species of basal

“reptiles,” *Solenodonsaurus janenschi* (Broili 1924). Pearson (1924) investigated a much smaller individual of *S. janenschi* derived from the same deposits in Nýřany and housed at the Museum of Zoology in Cambridge, UK. Several features, such as a temporal notch led Pearson to classify *S. janenschi* as a seymouriamorph. Brough & Brough (1967) doubted the validity of *S. janenschi* and regarded all known specimens as belonging to the gephyrostegid “anthracosaur” *Gephyrostegus bohemicus* Jaekel, 1902. Carroll (1970) examined different taxa from Nýřany collectively termed “anthracosaurs,” which included *S. janenschi*. Apart from the specimens already published by Broili (1924), Pearson (1924), and Brough & Brough (1967), Carroll (1970) provided a description of the counterpart of Pearson’s specimen that is housed in the Museum of Natural History in Berlin. He classified *S. janenschi* as a basal amniote with several “anthracosaurian” char-

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acters. Therefore, *S. janenschi* apparently supported the view that the origin of amniotes took place among “anthracosaurs” (Carroll 1970). Gauthier et al. (1988) questioned the phylogenetic position of *S. janenschi* as a basal amniote. Their phylogenetic analysis suggested a sister-group relationship between *S. janenschi* and Cotylosauria, the latter consisting of the sister-groups Diadectomorpha and Amniota. Thus, *S. janenschi* was not a basal amniote but rather laid on the amniote stem. A new phylogenetic approach of Laurin & Reisz (1997) prompted them to re-evaluate the phylogenetic relationships of *S. janenschi* based on a restudy of the holotype (Laurin & Reisz 1999). In their analysis *S. janenschi* resolved as a stem-amniote rather than a basal amniote, similar to the analysis of Gauthier et al. (1988). Also in the comprehensive phylogenetic analysis of basal tetrapods performed by Ruta et al. (2003a), *Solenodonsaurus* came to lie on the amniote stem rather than being a basal amniote; it represented the sister-group to seymouriamorphs, diadectomorphs, amniotes and lepospondyls.

In the present study all the known specimens of *S. janenschi* are redescribed and an analysis is performed to clarify its phylogenetic position. Furthermore, different aspects of the life-style and palaeobiology of *S. janenschi* are discussed.

Material and methods

All the specimens of *Solenodonsaurus janenschi* are derived from the Gaskohle of Nýřany, Czech Republic and are cataloged into the collections of the Museum für Naturkunde, Berlin, Germany, and the University Museum of Zoology, Cambridge, United Kingdom. The following specimens were studied: MB. Am. 988 (formerly MB. R. 890), detached, disarticulated vertebral centra; MB. Am. 989.1 (holotype), a large, articulated skeleton consisting of skull, parts of the pectoral girdle and the forelimb, and several articulated vertebrae and ribs; MB. Am. 990.1 (formerly MB. 1901.1380), elements of the axial skeleton that include some vertebrae and ribs (size of vertebrae and ribs comparable to those of holotype); MB. Am. 991.1 (formerly MB. 1898.1038), disarticulated bones of skull, lower jaw, and pectoral girdle (smaller than holotype); UMZC T 693 (formerly DMSW R15), parts of skull, vertebrae and ribs, and forelimb (counterpart of MB. Am. 991.1). Plaster casts of the following were also studied: skull of the lost Munich specimen, which is the counterpart of the holotype MB. Am. 989.1; MB. Am. 991.2: cast of MB. Am. 991 before the humerus was removed. All the specimens were drawn using a camera lucida, scanned, and edited using Adobe Photoshop CS5. A phylogenetic analysis was performed using the data matrix of Ruta et al. (2003a).

Institutional abbreviations. DMSW – D. M. S. Watson collection, now part of UMZC; MB – Museum of Natural History, Berlin, Germany; UMZC – University Museum of Zoology, Cambridge (United Kingdom).

Anatomical abbreviations. ar – articular; cla – clavicle; clei – cleithrum; cor – coracoid; cr – crest; cri – caudal rib; d – dentary; ect – ectepicondyle; ent – entepicondyle; f – frontal; For ent – entepicondylar foramen; glen – glenoid; gs – gastral scales; ha – haemal arch; hu – humerus; ic – intercentrum; icl – interclavicle; j – jugal; la – lacrimal; m – maxilla; n – nasal; na – neural arch; orb – orbit; p – parietal; pc – pleurocentrum; pf – postfrontal; pfo – pineal foramen;

pm – premaxilla; po – postorbital; poz – postzygapophysis; pp – postparietal; prf – prefrontal; prz – prezygapophyses; ps – parasphenoid; q – quadrate; qj – quadratojugal; ra – radius; ri – rib; sc – scapula; scl – sclerotic ring; soc – supraoccipital; sq – squamosal; sri – sacral rib; st – supratemporal; sur – surangular; sv – sacral vertebrae; t – tabular; trp – transverse process; ul – ulna.

Systematic palaeontology

Tetrapoda Goodrich, 1930

Solenodonsaurus janenschi Broili, 1924

1905 *Cochleosaurus bohemicus* Fritsch – Broili, fig. 3a, plate 1

1924 *Solenodonsaurus janenschi* – Broili, p. 10

1924 *Solenodon janenschi* – Broili, figs 1, 2, plate

1924 *Solenodonsaurus janenschi*, Broili – Pearson, pp. 338–342, figs 1–3

1967 *Gephyrostegus bohemicus* Jaekel – Brough & Brough, pp. 147–165

1970 *Solenodonsaurus janenschi* – Carroll, pp. 292–301, figs 14–18

1999 *Solenodonsaurus janenschi* – Laurin & Reisz, pp. 1239–1255, figs 2–4

Holotype. MB. Am. 989.1; original to Broili 1924: figs 1, 2, plate; Carroll 1970: fig. 14b; Laurin & Reisz 1999: figs 3, 4

Stratum typicum. Gaskohle, Nýřany Series, Westphalian D, Silesian, Late Carboniferous

Locus typicus. Nýřany, Czech Republic

Referred specimens. MB. Am. 988; MB. Am. 990.1 (formerly MB. 1901.1380); MB. Am. 991.1 (formerly MB. 1898.1038); UMZC T 693 (formerly DMSW R15)

Diagnosis

Autapomorphy. Broad, vertical groove at the base of the maxillary teeth.

Derived characters which are not unique to *S. janenschi*. Curved, long ribs without uncinat processes; humerus with long, slender shaft; lacrimal extends posterolaterally along the orbital margin; anterior process of the prefrontal is long and slender.

Derived characters which are not unique to *S. janenschi* (only observable in large specimens MB. Am. 989.1 and MB. Am. 990.1, but unknown in the small specimen MB. Am. 991/UMZC T 693). Small, wedge-like intercentrum; articulation between diapophysis and both rib heads; jugal extends posteriorly between squamosal and quadratojugal; tabular horn absent; contact between parietal and tabular.

Derived characters which are not unique to *S. janenschi* (only observable in small specimen MB. Am. 991/UMZC T 693, but unknown in large specimens MB. Am. 989.1 and MB. Am. 990.1). Maxillary teeth are larger than dentary teeth.

Derived adult characters which are not unique to *S. janenschi* (ontogenetic character, not yet developed in the juvenile specimen). Spool-shaped pleurocentrum; neural arch fused to pleurocentrum.

Results

Description of the holotype

General. As preserved, the holotype of *Solenodonsaurus janenschi* (MB. Am. 989.1) measures 360 mm from the incomplete tip of the snout to the last preserved vertebra and consists of the greater part of the skull, disarticulated elements of the right pectoral girdle, left forelimb, parts of the presacral vertebral column, and several ribs (Fig. 1). The postcranial bones

are preserved as casts and are of greater fidelity than the skull, which was not prepared away using acid.

The skull. The poorly preserved skull is approximately 140 mm long, measured from the anterior margins of the nasals to the level of the posterior end of the squamosals (Fig. 2A, B). In addition to the skull of specimen MB. Am. 989.1, a cast of the lost Munich counterpart is cataloged into the Berlin collections, and both showing the skull roof in dorsal aspect. The skull increases in width posteriorly and the original curvature is preserved. Both orbits are preserved, although the left is poorly de-

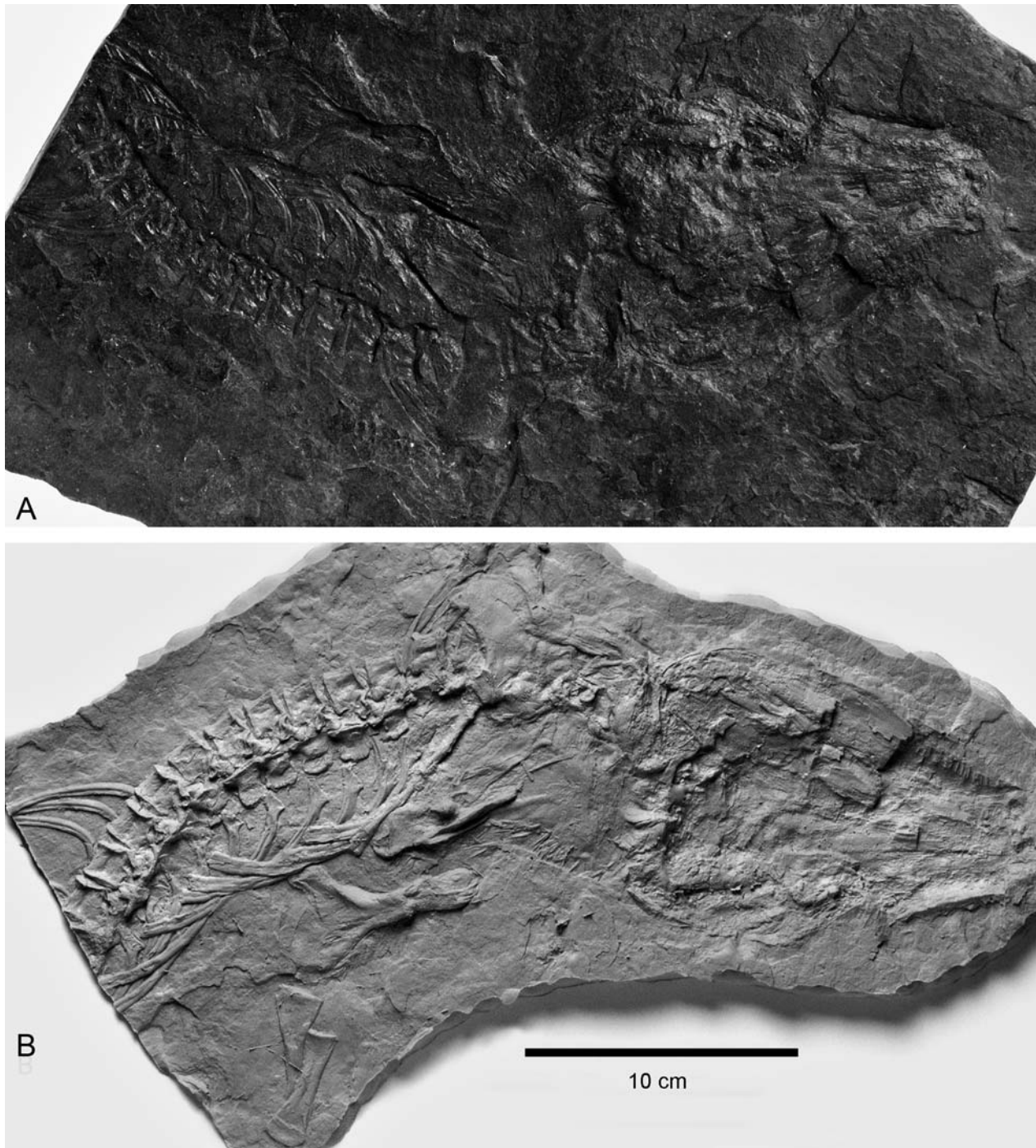


Figure 1. *Solenodonsaurus janenschi* Broili, 1924, photographs. **A.** Holotype MB. Am. 989.1; **B.** Plaster cast of the holotype.

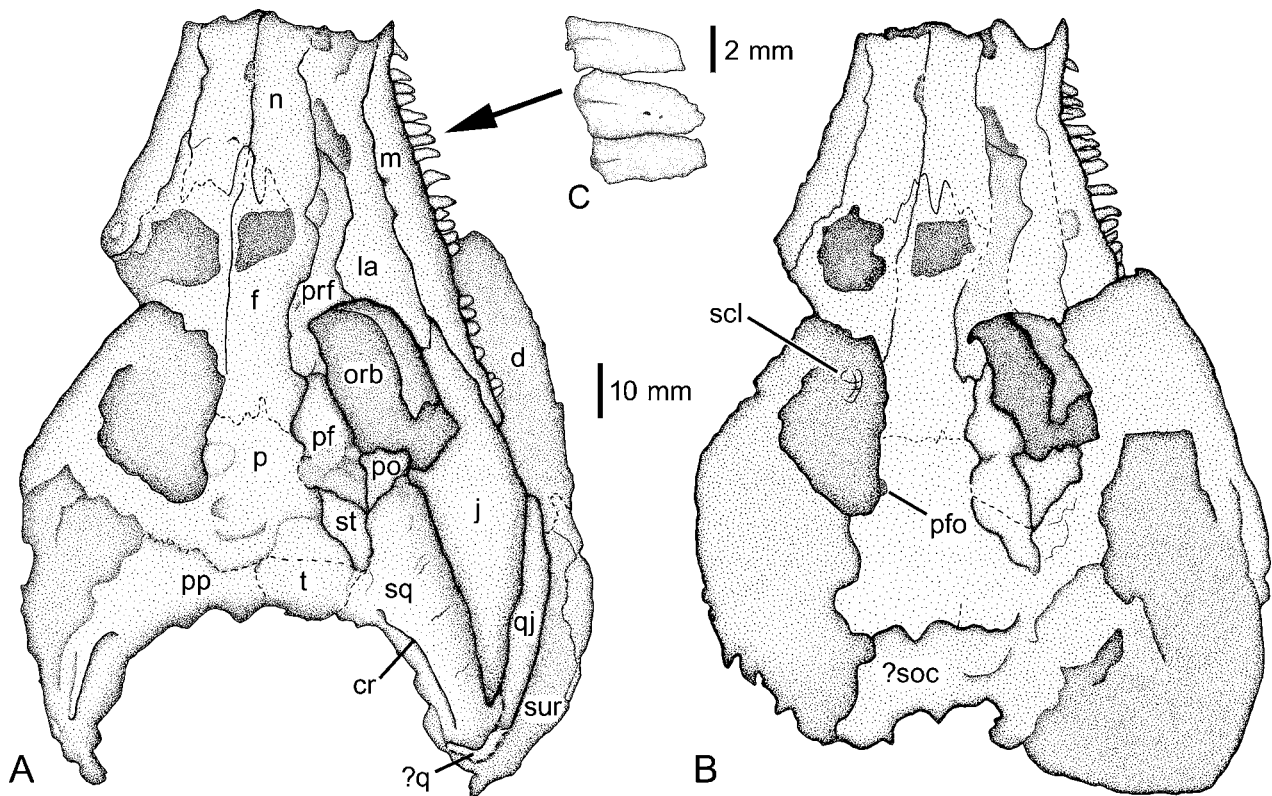


Figure 2. *Solenodonsaurus janenschii* Broili, 1924; interpretative drawings of the skull. **A.** Plaster cast of the skull of the lost Munich specimen, which is the counterpart of the holotype MB. Am. 989.1; **B.** Skull of the holotype MB. Am. 989.1; **C.** Close up of maxillary teeth, showing broad, vertical groove at the tooth bases.

fined. The right orbit is ovate in outline and large (21% in relation of the skull's length). Small, quadrangular bones preserved in the left orbit represent platelets of the sclerotic ring (Fig. 2B). The ornamentation of the dermal skull is weakly developed and irregular. Elongated grooves on the squamosal and nasal radiate outward from an ossification centre. Small and irregular pits are distributed all over the surface of the maxilla.

Only the right maxilla is well preserved, which is long and slender, becoming gradually smaller anteriorly and posteriorly. The maxilla extends posteriorly to the level of the posterior orbital margin. Twenty teeth can be counted on the maxilla, but the total number was undoubtedly greater. The teeth have posteriorly curved, apical cusps, and a broad, vertical groove at their base, as noted by Broili (1924) (Fig. 2C). The largest teeth are located in the anterior third of the maxilla. The nasal is rectangular, with a deeply interdigitating suture with the frontal. The frontal is rectangular and elongated and equal in width to the nasal but slightly longer. The prefrontal forms the anterodorsal rim of the orbit. As in *Gephyrostegus bohemicus* (Carroll 1970) and the microsauro *Asaphestra* (Carroll & Gaskill 1978), a long, slender process extends anteriorly between lacrimal and nasal. Another, shorter process extends posteriorly to form part of the medial orbital margin and contacts the postfrontal posteriorly, thus excluding the frontal from participation in the orbital margin.

The lacrimal is elongated and becomes gradually wider anteriorly and posteriorly. A nasolacrimal duct cannot be detected. The lacrimal extends posteriorly to the orbit and forms its anterolateral margin. A small process extends posterolaterally and contacts the jugal. Only the right parietal is preserved, which is approximately as wide as it is long and distinctly broader than the frontal. A small notch on its medial margin indicates the position of the pineal foramen, which is located anterior to the midlength of the parietal. As in embolomeres and gephyrostegids (Carroll 1970; Holmes 1984), "microsaurs" (Carroll 2000), diadectomorphs (Carroll 1967; Berman & Sumida 1990), and basal amniotes (Carroll & Baird 1972), the parietal contacts the tabular. Due to the poor preservation of the region posteromedial to the orbits, different sutural patterns of the bones were proposed in previous studies. According to Carroll (1970, fig. 14a, b), the postfrontal has a conspicuous posterior extension, whereas in contrast, Laurin & Reisz (1999) suggested that the postfrontal is short, and a broad process of the parietal contacted the postfrontal. We, on the other hand, interpret the postfrontal as forming the greater portion of the medial orbital margin and as having a point-like contact with the squamosal. In contrast to gephyrostegids and embolomeres (Carroll 1970; Boy & Bandel 1973; Holmes 1984, 1989), the intertemporal appears to be absent, and consequently the postfrontal has a wide posterior extension.

The intertemporal is also absent or fused to other bones in diadectomorphs (Berman et al. 1992), basal amniotes (Clark & Carroll 1973; Carroll 1991), lepospondyls (Carroll 2000), and derived temnospondyls (Holmes 2000). The postorbital is a small, triangular bone at the posterior margin of the orbit and has approximately the same size as the small supratemporal (Figs 2A, B). There is no indication of a posterior extension of the supratemporal, as suggested by Carroll (1970).

The postorbital region of the skull table is poorly preserved. The tabular appears to have the outline of an equal-sided rectangle and lacks a tabular horn seen in gephyrostegids (Carroll 1970; Boy & Bandel 1973) and embolomeres (Holmes 1984, 1989). The exact outline of the postparietal cannot be discerned. The jugal is long and trapezoidal in outline with a small, anteriorly directed process that extends between lacrimal and maxilla and a long, slender posteriorly directed process that extends deeply between squamosal and quadratojugal. A comparable posterior extension is not present in embolomeres, gephyrostegids, and seymouriamorphs (White 1939; Carroll 1970; Holmes 1984, 1989; Klembara & Ruta 2005a) but does resemble the pattern in diadectomorphs (Berman & Sumida 1990; Laurin & Reisz 1999).

The squamosal is a large, triangular bone that bears a small crest-like ridge that curves slightly as it follows the posterior margin of the posttemporal embayment (Fig. 2A). A slender quadratojugal extends from the level of the midlength of the jugal to the squamosal. The quadratojugal and maxilla do not contact one another. The lower jaw is represented by only a fragment of the dentary with no visible teeth.

A reconstruction of the skull of *Solenodonsaurus janenschi* is shown in Figure 3.

Pectoral girdle. The pectoral girdle is incompletely preserved and includes the right scapula, clavicle, cleithrum and interclavicle (Fig. 4). The interclavicle is rhomboid in outline and narrows posteriorly into the parasternal process, but the latter is overlain by an unidentified bone, obscuring its length and shape. The ornamentation of the ventral surface consists of numerous fine grooves radiating outward from the bone centre. The clavicle has the typical L-shape in anteroposterior view, a ventral blade and dorsal process meeting in a right angle. The ventral surface of the narrow, rectangular ventral blade bears irregular, densely arranged grooves that diverge outward from the base of the slender dorsal process. The cleithrum is poorly preserved by a stout rod that probably presents a part of the clavicular stem (Fig. 4). The external surface of the reniform scapula is smooth. Ventrally a roughened, unfinished ovate area indicates the position of the glenoid, which lies at its posteroventral margin. A small bone lying near the ventral margin of the scapula may represent the coracoid, but poor preservation prevents description of its original shape.

Forelimb. The forelimb is represented by the closely associated left humerus, radius, and ulna (Fig. 4). The humerus is closely similar to those of basal amniotes

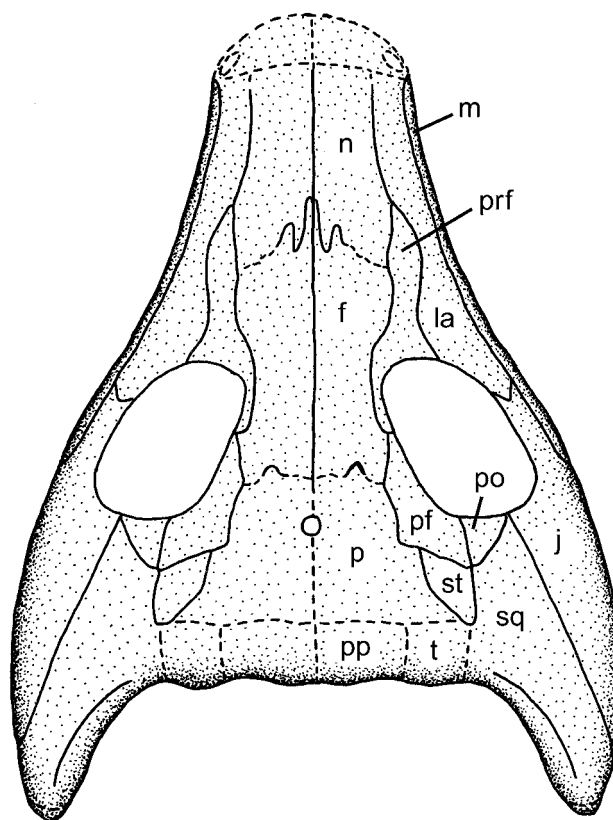


Figure 3. *Solenodonsaurus janenschi* Broili, 1924. Reconstruction of the skull based on the holotype MB. Am. 989.1 and the lost Munich specimen.

(Fox & Bowman 1966; Heaton & Reisz 1986), “microsaurs” (Carroll 2000) or *Westlothiana* (Smithson et al. 1994) in being slender (Figs 4, 5A) and not L-shaped as in gephyrostegids (Boy & Bandel 1973) or embolomeres (Holmes 1984). It measures 78 mm in length. The proximal and distal ends are rotated at about 90° around the long axis so as to lie in planes normal to one another. As preserved only the slender outer margin of the proximal head is visible, with a width of only 13 mm. The shaft of the humerus is elongated and a supinator process is absent. The expanded distal end has a width of 37 mm. The entepicondyle is large and broad, whereas the ectepicondyle is smaller. The articulation facets for the radius and ulna are separated by a notch. A low ridge extends proximally from the ectepicondyle, but is smaller than in embolomeres (Holmes 1984) or gephyrostegids (Carroll 1970). According to the plate in Broili (1905), an entepicondylar foramen is visible on the Munich counterpart. Furthermore, a small depression in MB. Am. 989.1 indicates the presence of the foramen (see also Laurin & Reisz 1999) (Fig. 5A).

Radius and ulna are much shorter than the humerus, with the radius measuring 42 mm in length. Thus, the radius to humerus ratio is 0.5 in *S. janenschi*. Similar values are seen in embolomeres, such as *Pholiderpeton* (Clack 1987) and *Archeria* (Carroll 1970) and in the gephyrostegid *Gephyrostegus* (Carroll 1970). The proximal and distal ends of the radius are expanded. The ra-

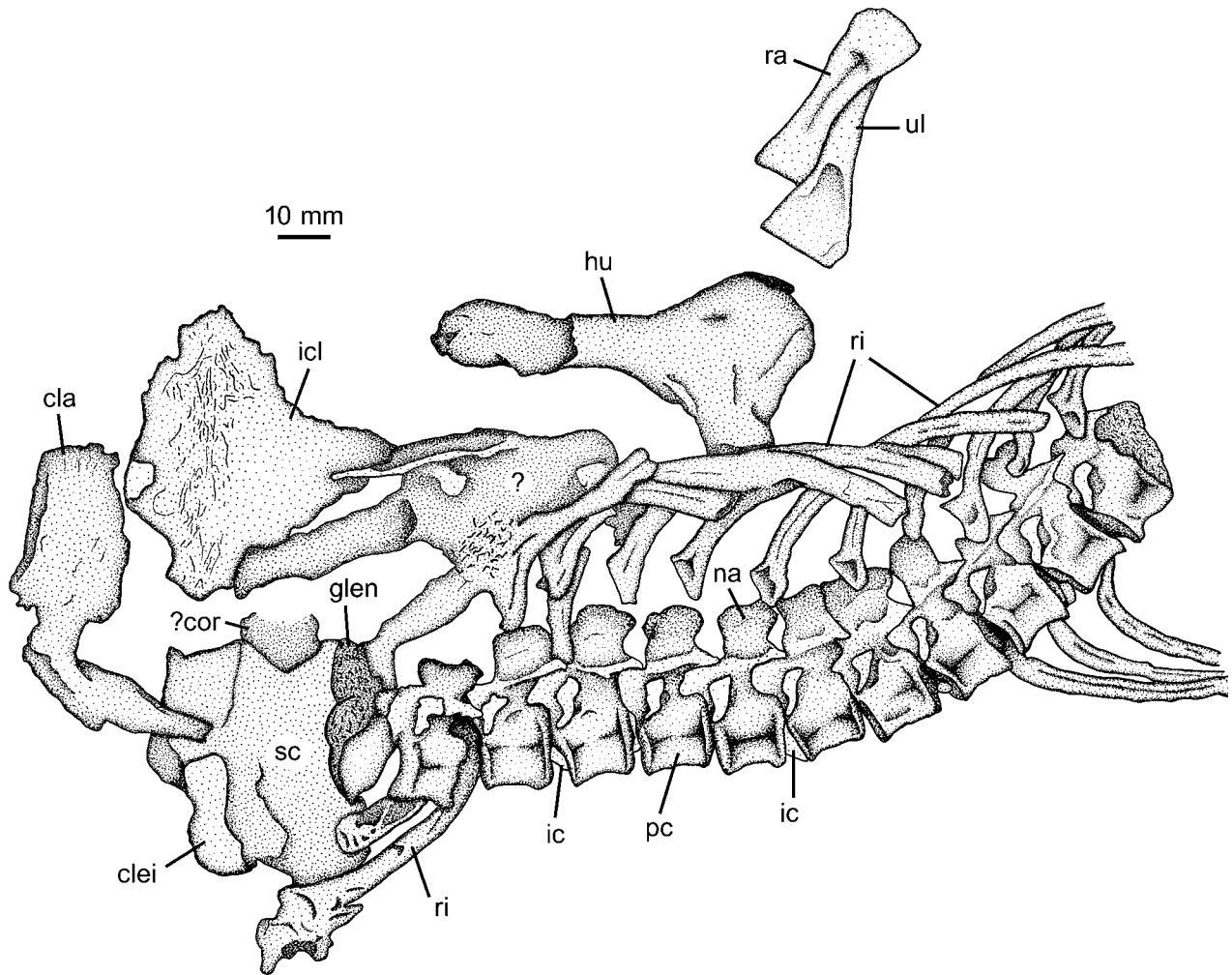


Figure 4. *Solenodonsaurus janenschii* Broili, 1924. Holotype MB. Am. 989.1, interpretative drawing of the postcranial skeleton.

dius overlaps the distal end of the ulna and prevents an exact length measurement of the ulna. The ulna lacks an olecranon process.

Axial skeleton. A series of twelve articulated presacral vertebrae is preserved in MB. Am. 989.1 (Figs 4, 6). In contrast to seymouriamorphs (White 1939; Bystrow 1944; Laurin 2000), diadectomorphs (Carroll 1967; Berman & Sumida 1990) and certain basal amniotes (Fox & Bowman 1966), the neural arches in *S. janenschii* are not swollen. Neural arch and pleurocentrum are solidly fused, with no evidence of a neurocentral suture. In some vertebrae the area of the neurocentral fusion is swollen. The neural spines are positioned slightly posterior to being directly above the pleurocentrum. The pre- and postzygapophyses are well preserved. The ventral projection of the transverse processes lateral to the pleurocentra is reminiscent of some captorhinomorphs (Clark & Carroll 1973). The diapophyses are elongated and narrow ventrally in cross-section. The amphicoelous, spool-shaped pleurocentrum is considerably larger than the intercentrum. In the anterior portion of the vertebral column the pleurocentra gradually increase in length serially posteriorly. Five intercentra are preserved in MB. Am. 989.1. The intercentra are crescent-shaped

in anterior and posterior view, and wedge-shaped in lateral view. The small size of the intercentrum precludes an articulation with one of the rib heads.

Ribs. Several well-preserved, slender, curved ribs lie adjacent to the vertebral column (Fig. 4). They lack uncinate processes. A regional differentiation of the ribs is not apparent. The expanded proximal heads are bicapital, although a distinct notch between tuberculum and capitulum is absent, as in gephyrostegids (Carroll 1970; Boy & Bandel 1973), some captorhinomorphs (Carroll & Baird 1972) and microsaurids (Carroll & Gaskill 1978). The distal end is only slightly expanded compared to the proximal end and consists of unfinished bone.

Bones of uncertain identity. Several bones lying between the interclavicle and the humerus cannot be identified with certainty. One is rib-like in being straight and elongated except for being slightly wider. According to Laurin & Reisz (1999) the bone could be a broadened cervical rib. A second unidentified bone, overlapping the parasternal process of the interclavicle, is strongly deformed with poorly defined margins. Laurin & Reisz (1999) suggested that this bone might represent the parasternal process proper, but this cannot be verified due to poor preservation.

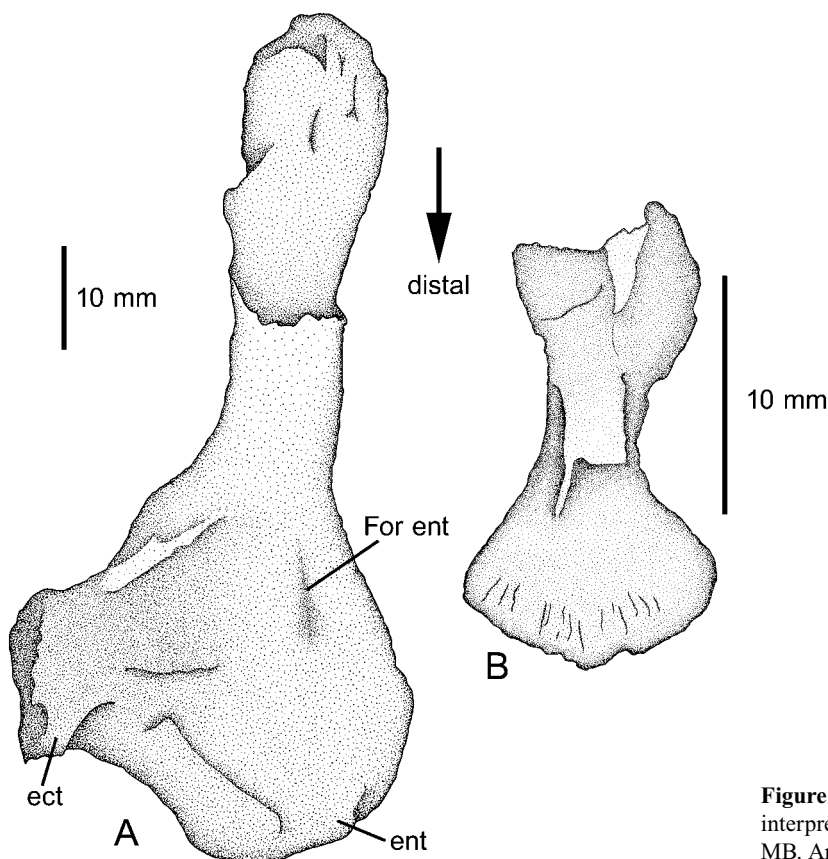


Figure 5. *Solenodonsaurus janenschi* Broili, 1924, interpretative drawings of the humerus. **A.** Holotype MB. Am. 989.1; **B.** MB. Am. 991.2.

Description of sacral region of MB. Am. 990.1

Specimen MB. Am. 990.1 belongs to an individual approximately the same size as the holotype. The bones are represented as natural casts and consist of the sacral vertebra with a right rib, the posteriormost four presacral vertebrae, and the first four caudals with two ribs (Fig. 7). The shape of the presacral neural spines is broadly rectangular and, as in MB. Am. 989.1, the spine is located slightly posterior to the midlength of the spool-shaped, amphicoelous pleurocentrum. Two small, crescent-shape intercentra are preserved between the pleurocentra. No trunk ribs are preserved. The sacral

neural spine is round in lateral view and small compared to that of the postsacral vertebrae. A small intercentrum lies anterior to the large, strongly deformed pleurocentrum. The right sacral rib consists of the capitulum and a fan-shaped extension of the distal end similar to *Kotlassia* (Bystrow 1944). The four caudals are in general smaller than the posterior trunk vertebrae. The neural spines are triangular in lateral view, and the neural arch and the spool-shaped pleurocentrum are solidly fused. Two ribs and the first haemal adjoin their respective vertebrae. The haemal arch is distinctly smaller and less massive than the two ribs and is not fused to the pleurocentrum.

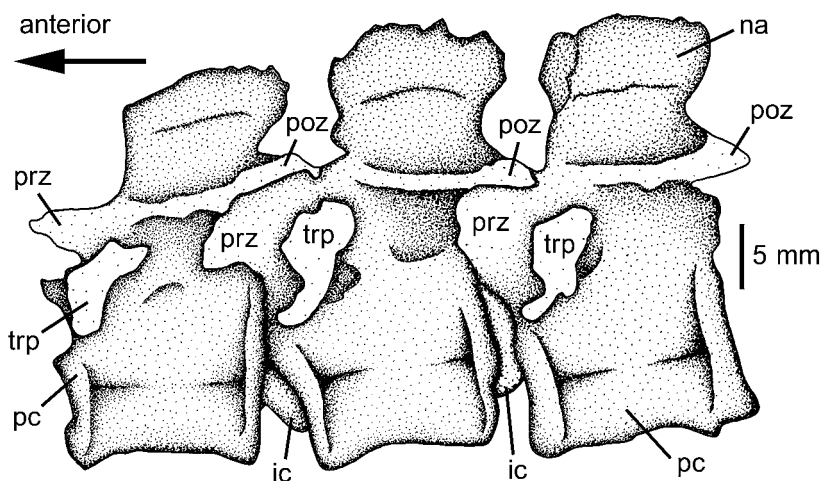


Figure 6. *Solenodonsaurus janenschi* Broili, 1924, interpretative drawing of three trunk vertebrae of the holotype MB. Am. 989.1.

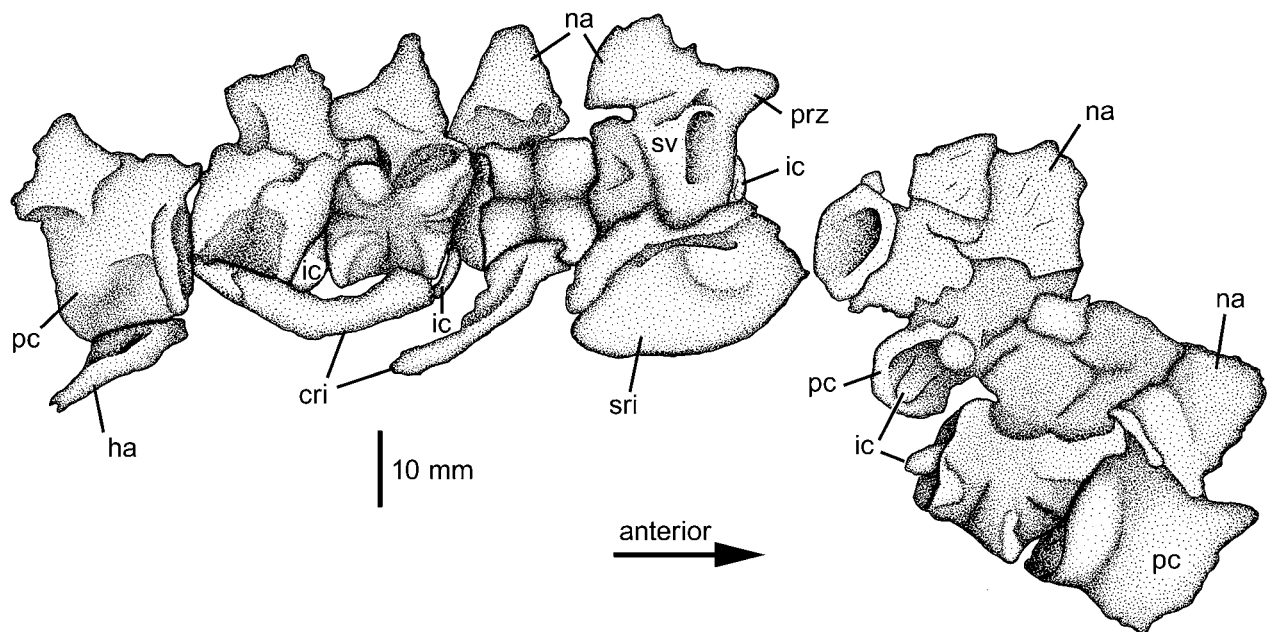


Figure 7. *Solenodonsaurus janenschi* Broili, 1924, interpretative drawing of the sacral region of the vertebral column MB. Am. 990.1.

Description of isolated vertebrae of MB. Am. 988.1

MB. Am. 988.1 is preserved as skeletal remains. Only a small number of disarticulated, spool-shaped pleurocentra can be identified with certainty. Their lengths vary between 13.3 and 18.5 mm.

Description of small specimens

MB. Am. 991.1/ UMZC T 693.

MB. Am. 991.1 and UMZC T 693 represent part and counterpart of a distinctly smaller individual than the holotype. Collectively they include parts of the skull, pectoral girdle, and vertebrae preserved as natural casts. Specimen MB. Am. 991.1 is described first, as UMZC T 693 provides only supplementary information.

MB. Am. 991.1. The incomplete, disarticulated skull of MB. Am. 991.1 is shown in dorsal aspect (Fig. 8A). The dermal ornamentation is weakly developed and consists of shallow pits and grooves that radiate from an ossification centre. The premaxillae are represented only by small fragments. The maxilla is elongated and rectangular, becoming gradually more slender anteriorly and posteriorly, though its posterior extent is not preserved. The nasal is slenderly rectangular and is slightly shorter than the frontal, and as in MB. Am. 989.1, the frontal and nasal suture is deeply interdigitating. The prefrontal has a triradiant outline with the posterior process forming part of the medial orbital margin and is proportionally slightly longer than in the holotype. There is no evidence that the frontal entered the orbital margin as in *Gephyrostegids* (Carroll 1970; Boy & Bandel 1973). In contrast, Carroll (1970) suggested that the slenderness of the process precluded a contact between prefrontal and postfrontal. However, Laurin & Reisz

(1999) suggested that the prefrontal has rotated and is preserved in lateral aspect. This, they argue, would explain the apparent slenderness of the process and the exclusion of the frontal from the orbital margin. However, there is no evidence of rotation of the bone; rather, it is preserved in dorsal view. As in the holotype, the elongated lacrimal extends to the orbit and forms its anterolateral margin. Both parietals are displaced and the right one is better preserved. The parietal is substantially wider than the frontal or nasal. As pointed out by Carroll (1970), the left parietal is overlain by the parasternal process of the interclavicle. Only one jugal is preserved, displaced, and in contrast to that in the holotype is ovate in outline and narrows anteriorly. The parasphenoid, measuring approximately 30 mm in length, is also displaced. The cultriform process is slender and rod-shaped, whereas the basal plate is triangular. At the base of the cultriform process numerous denticles form a triangular, anteriorly tapering field. The basiptyergoid processes are not evident (Fig. 8A), they might have been confined to the basisphenoid which is not visible. An elongated surangular is preserved in medial view. Fifteen teeth can be counted on the maxilla and 23 on the dentary. The maxillary teeth are distinctly larger than those on the dentary, and, as in the holotype, the cusp tips are curved posteriorly and there is a broad, vertical groove on the base of the teeth (Fig. 8C).

The pectoral girdle is incomplete and consists of the interclavicle and right clavicle. The T-shaped interclavicle is broken into two fragments. As in the holotype, the ornamentation consists of numerous grooves that radiate from the center of the bone. The slender parasternal process resembles those of basal amniotes (Fox & Bowman 1966; Clark & Carroll 1973) and some mi-

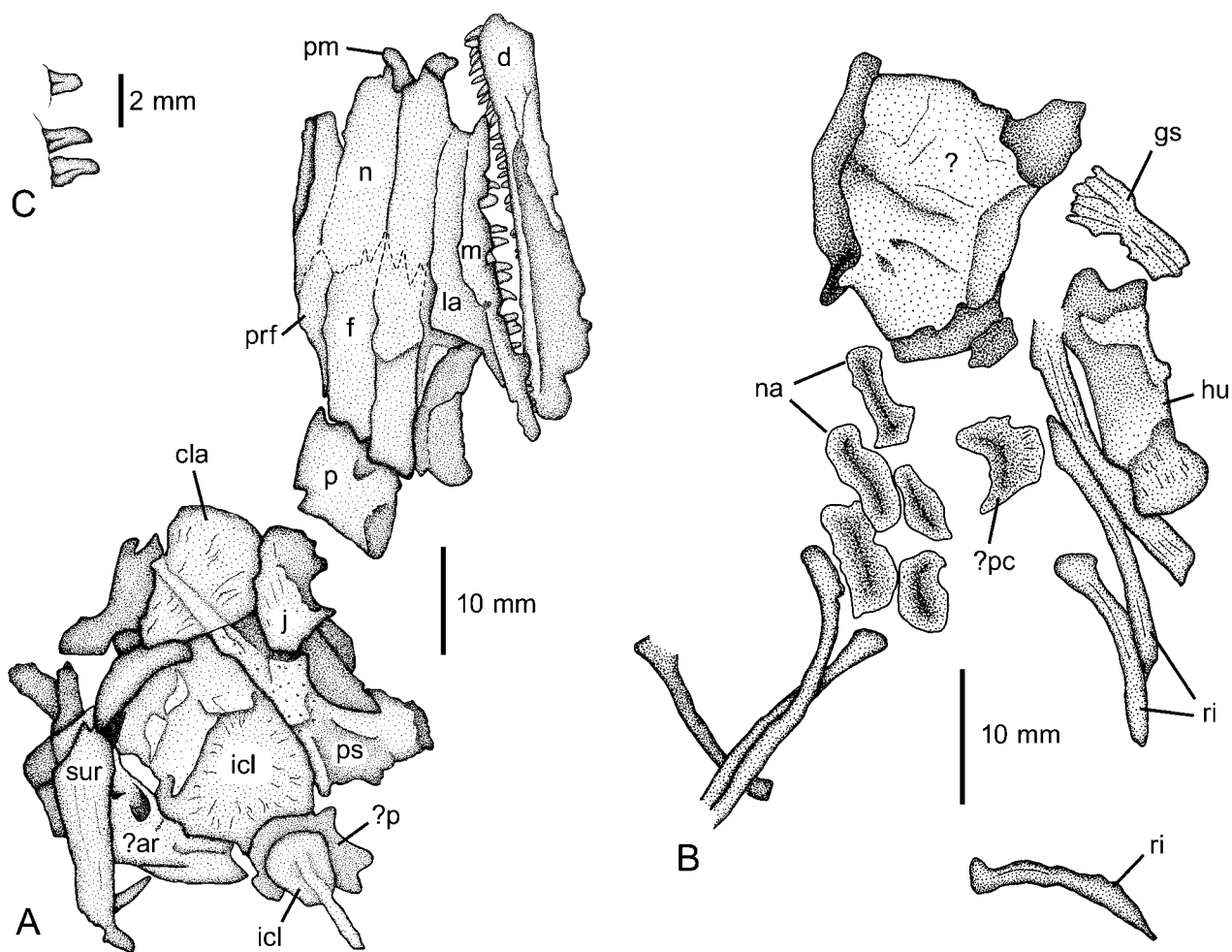


Figure 8. *Solenodonsaurus janenschi* Broili, 1924, interpretative drawings of small individual. **A.** MB. Am. 991.1, skull fragments plus parts of pectoral girdle; **B.** UMZC T 693, counterpart of MB. Am. 991.1, elements of pectoral girdle, forelimb, and vertebral column; **C.** MB. Am. 991.1, close up of maxillary teeth, showing broad vertical groove at the tooth bases.

crocodiles (Carroll & Gaskill 1978). Compared to the holotype, the ventral blade of the clavicle is broader and more rounded, and the dorsal process is not preserved. MB. Am. 991.2 is a plaster cast of the whole slab MB. Am. 991 before the humerus was removed. The humerus measures 18 mm in length and is slightly damaged. The short, slender shaft is expanded at both ends (Fig. 5B), processes or foramina are not preserved. Entepicondyle and ectepicondyle are separated by a well-defined notch as in the holotype.

UMZC T 693. The once excellent condition of this specimen, as seen in drawings of Pearson (1924, fig. 1) and Carroll (1970, fig. 17a) is no more present. Both the top side and the underside of the plate UMZC T 693 were prepared, the latter is protected by a pane of glass. At the top side, the skull is preserved in dorsal view with its original bone substance, whereas the postcranial bones are preserved as natural casts. In the following, only those aspects of the specimen are described that are not visible in MB. Am. 991.1. The slender humerus bears shallow, diverging grooves. Additionally, disarticulated elements of the autopodium are preserved, including four metacarpalia and two phalanges. Seven,

poorly preserved, slightly disarticulated ribs are represented as natural casts (Fig. 8B). In contrast to larval seymouriamorphs (Klembara & Ruta 2005b) and larval temnospondyls (Boy & Sues 2000), the slender ribs are curved rather than straight. As in the holotype, the expanded proximal head of the ribs do not possess a distinct notch between the tuberculum and capitulum. Five neural arches are preserved as casts. They are paired structures not fused in the midline. The identification of vertebral centra, as suggested by Carroll (1970, fig. 7b), remains ambiguous. Carroll (1970), who was able to investigate the now glass-covered underside (ventral side) of the specimen, identified the palatine in the left orbit on the basis of a row of denticles on the bone surface. Additional disarticulated elements in the region of the pectoral girdle cannot be identified with certainty, however Pearson (1924, figs 1, 2) and Carroll (1970) offered different identities for these bones. Pearson (1924) identified the bones as the supratemporal, tabular, postorbital, jugal, quadratojugal, and squamosal. The tabular, according to Pearson (1924) bears a horn, comparable to the tabular horn of some seymouriamorphs (Klembara & Ruta 2004) or embolo-

meres (Holmes 1989). In Pearson's interpretation, the tabular forms an otic notch with the squamosal. Carroll (1970) identified the same bones as the clavicle, pterygoid, and epityergoid. The position of the clavicle on the counterpart MB. Am. 991.1 supports Carroll's interpretation. The tabular horn, *sensu* Pearson (1924), was identified by Carroll (1970) as the transverse flange of the pterygoid. Unfortunately, the presence of the pterygoid cannot be verified due to the poor preservation.

Phylogenetic analysis

Both the large and the small specimens of *Solenodonsaurus janenschii* (MB. Am. 989, MB. Am. 990, MB. Am. 991, UMZC T 693) were used for character coding in the phylogenetic analysis, since it is supposed here that the material belongs to a single species (see discussion below). A phylogenetic analysis was undertaken using PAUP* (Swofford 2003). The list of coding for *S. janenschii* (see Appendix) based on our first-hand examination was added to the data matrix of Ruta et al. (2003a), consisting of 90 taxa and 319 cranial and postcranial characters. In the present analysis the taxa have been coded for 308 characters, the fishlike sarcopterygian *Eusthenopteron* served as the outgroup. The analysis (heuristic search option, using random stepwise addition, TBR branch-swapping, multistate taxa interpreted as polymorphism, excluding parsimony-uninformative characters, and all the characters unsorted) resulted in 64 trees (1418 steps) for which a strict consensus tree is presented here, with a consistency index (CI) of 0.2659, a rescaled consistency index (RC) of 0.1787, a retention index (RI) of 0.6721, and a homoplasy index (HI) of 0.7701.

The phylogenetic analysis suggests that *S. janenschii* is the sister group of lepospondyls (Fig. 9), which is supported by four unequivocal character states: 103 (ci = 0.11; 2 → 0), "Interorbital distance greater than half skull table width"; 171 (ci = 0.14; 1 → 0), "Parasphenoid without single median depression"; 239 (ci = 0.13; 1 → 0), "Absence of distinct supinator process projecting anteriorly"; 295 (ci = 0.5; 1 → 0), "Neural spines without distinct convex lateral surfaces". The character states 103, 171, and 239 have a consistency index (ci) of less than 0.15. Only character state 295 (ci = 0.5; 1 → 0), the presence of unswollen neural arches, is greater. The absence of an intertemporal, 60; (ci = 0.43; 0 → 1) is a synapomorphy with lepospondyls, *S. janenschii*, *Westlothiana*, diadectomorphs, and amniotes. Character states distinguishing *S. janenschii* from lepospondyls are: 22 (ci = 0.5; 0 → 1), "Prefrontal contributes less than half of anteromesial orbit margin"; 38 (ci = 0.14; 0 → 1), "Presence of condition: anterior margin of frontals deeply wedged between posterolateral margins of nasals"; 56 (ci = 0.25; 0 → 1), "Nasals smaller than postparietals"; 169 (ci = 0.17; 0 → 1), "Parasphenoid with elongate, strut-like cultri-

form process"; 231 (ci = 0.13; 1 → 0), "Absence of condition: Interclavicle wider than long"; 233 (ci = 0.1; 0 → 1), "Presence of separate scapular ossifications"; 304 (ci = 0.2; 1 → 0), "Absence of condition: Tallest ossified part of neural arch in posterior trunk vertebrae lying above posterior half of vertebral centrum".

As in the analysis by Ruta et al. (2003a), diadectomorphs resolve as sister group of amniotes. This relationship is supported by the following character states: 51 (ci = 0.2; 1 → 0), "Absence of postparietal/exoccipital suture"; 52 (ci = 0.1; 0 → 1), "Postparietals entirely on occipital surface"; 109 (ci = 0.75; 1 → 2), "Small fossa near ventrolateral corner of occiput bordered laterally by ventromedial flange of tabular, roofed over by dorsal portion of lateral margin of supraoccipital-opisthotic complex and floored by lateral extension of opisthotic"; 166 (ci = 1.0; 0 → 1), "Articular surface of basioccipital convex"; 168 (ci = 0.33; 0 → 1), "Presence of condition: opisthotic forming thick plate with supraoccipital, separating exoccipitals from skull table".

Among "anthracosaurs", only the embolomeres form a monophyletic group, supported by the following character states: 10 (ci = 0.33; 1 → 0), "Absence of septomaxilla"; 24 (ci = 0.11; 0 → 1), "Lacrimal allowing contact between prefrontal and jugal"; 94 (ci = 0.18; 0 → 1), "Jugal extending anterior to anterior orbit margin"; 109 (ci = 0.75; 1 → 3), "Absence of fossa"; 128 (ci = 0.07; 1 → 0), "Palatine without denticles"; 138 (ci = 0.13; 1 → 0), "Ectopterygoid with tooth row"; 168 (ci = 0.33; 0 → 1), "Presence of condition: Opisthotic forming thick plate with supraoccipital, separating exoccipitals from skull table". Contrary to the analysis by Ruta et al. (2003a), the seymouriamorphs and gephyrostegids are paraphyletic groups, with both groups being members of the amniote stem line.

The statistical support for the grouping is fairly low, which is not surprising given the data set contains a high amount of homoplasies and missing characters. When relaxing the parsimony run by one step, the clade Lepospondyli collapses, and so does necessarily the position of *S. janenschii*. In addition, a bootstrap analysis (100 replicates; for computational reasons the "fast stepwise-addition" option was implemented) did not show support of >50% for any major clade and the respective sister taxa.

Discussion

Assignment of the material to *Solenodonsaurus janenschii*

Previous studies of *Solenodonsaurus janenschii* did not ascertain if the small individual housed in Berlin and Cambridge belongs to the same taxon as the holotype, i.e. if the *Solenodonsaurus* material represents a partial growth series or different taxa (Carroll 1970; Laurin & Reisz 1999). Schultze (1984) has defined those features necessary to recognize a growth series: 1) all the speci-



Figure 9. Phylogenetic position of *Solenodonsaurus janenschi* Broili, 1924 based on new morphological observations included into the data matrix of Ruta et al. (2003a). The clade containing lepospondyls and *Solenodonsaurus janenschi* is shaded in grey.

mens must come from the same locality; 2) all the specimens should occur in the same horizon; and 3) they must show the same autapomorphies independent of their size. Based on this set of conditions all the specimens of *S. janenschi* (MB. Am. 989.1, MB. Am. 990.1, MB. Am. 988.1, MB. Am. 991.1, UMZC T 693) can be assigned to a single species, with the small specimen representing a juvenile. The complete material is derived from the Gaskohle (Westphalian D) of Nýřany. The unique vertical groove of the maxillary teeth is present in both the large and small specimens of *S. janenschi*. This character is absent in all other known basal tetrapods (Boy & Bandel 1973; Clack 1987; Holmes 1989) and can thus be regarded as an autapomorphy of *S. janenschi*. Furthermore, the derived characters supporting this interpretation are (although not unique to *S. janenschi*): the spool-shaped vertebrae (not ossified in the juvenile); posterolateral extension of the lacrimal along the orbital margin; long, slender, anterior process of the prefrontal; and long, curved ribs without uncinate processes. Juvenile characters of the small specimen MB. Am. 991/UMZC T 693 can be found in the skull, the vertebral column and the humerus. The skull is preserved two-dimensionally, indicating that the neurocranium was still largely cartilaginous. As in most temnospondyls (Boy & Sues 2000; Witzmann 2006) and seymouriamorphs (Klembara & Ruta 2005a, b), the ossification of the neurocranium of *S. janenschi* was apparently delayed with respect to the dermal skull elements. This can be regarded as a plesiomorphic character of early tetrapods, since this pattern of ossification occurs also in the sarcopterygian *Eusthenopteron* (Schultze 1984; Cote et al. 2002). In contrast, the skull of *S. janenschi* is preserved three-dimensionally in the large specimen, indicating that the neurocranium was already ossified to a large degree. However, allometric changes in skull proportions, related to ontogeny, cannot be diagnosed due to the poor preservation of the small specimen.

A further juvenile character of MB. Am. 991/UMZC T 693 is seen in the paired neural arches, which are not fused in the midline. As in larval temnospondyls (Carroll 1989; Boy & Sues 2000; Witzmann & Pfretzschner 2003) or larval seymouriamorphs (Klembara & Bartík 2000; Klembara & Ruta 2005a, b), the axial skeleton of *S. janenschi* appears to have ossified gradually, with late ontogenetic fusion of the paired neural arch halves. The vertebral centra are also not yet fused or sutured to the neural arches. In this respect *S. janenschi* is more plesiomorphic than most lepospondyls and basal amniotes, in which the ossification and fusion of neural arches and centra was rapid and occurred almost concomitantly very early in ontogeny (Carroll 1989; Carroll & Chorn 1995; Carroll et al. 1999). Also the undifferentiated, weakly ossified humerus is in accordance with the interpretation of the small specimen MB. Am. 991/UMZC T 693 as a juvenile.

The systematic position of *Solenodonsaurus janenschi*

The present phylogenetic analysis suggests that *Solenodonsaurus janenschi* is the sister taxon of lepospondyls, a morphological and ecological diverse group of Palaeozoic non-amniote tetrapods (Carroll 2000, 2009). This result is consistent with "Analysis II" in Ruta et al. (2003b), in which *Solenodonsaurus* also appears as sister taxon of lepospondyls. Shared derived characters of *S. janenschi* and nearly all lepospondyls are the shape of the vertebrae and the absence of an intertemporal. However, as outlined above, the mode of vertebral ontogeny apparently differs between *S. janenschi* and lepospondyls and is more plesiomorphic in the former. The present analysis supports the thesis of Gauthier et al. (1988) and Laurin & Reisz (1999), who argued that *S. janenschi* lies on the amniote stem, rather than being a basal amniote, as proposed by Broili (1924) and Carroll (1970). However, the result of the present analysis differs from those of Gauthier et al. (1988) and Laurin & Reisz (1999) in the position of *S. janenschi* with regard to diadectomorphs and basal amniotes. In their studies *S. janenschi* is the sister taxon to the Cotylosauria, which includes the diadectomorphs and amniotes. In the present analysis *S. janenschi* is more closely related to lepospondyls than to cotylosaurs.

Palaeobiology

Aquatic versus terrestrial mode of life. Referring to Carroll's (1970) description of *Solenodonsaurus janenschi*, Milner (1980) regarded it as a largely terrestrial tetrapod without mentioning specific characters that would support this interpretation. Several morphological characters suggesting that *S. janenschi* had a terrestrial lifestyle are listed and discussed here. Unfortunately, due to the incomplete preservation important source of potential characters, such as in the hindlimbs, pelvis, tail, length of axial skeleton, and possible ossification of tarsals and carpals are absent and cannot be explored in terms of their biological interpretation. The humerus of *S. janenschi* has a long and slender shaft and its proximal and distal ends are rotated at about 90° to one another, as in certain terrestrial temnospondyls like amphibamids (Daly 1994; Sigurdson & Bolt 2010), "microsaurs" (Carroll & Gaskill 1978), and basal amniotes (Fox & Bowmann 1966). This morphology suggests the presence of rather long limbs, well suited for locomotion on land. Different skull and snout types of basal tetrapods are characteristic of aquatic prey capture (Taylor 1987). Some aquatic temnospondyls had a long, slender snout for fish capture (Boy 1993; Witzmann 2006), whereas other mainly aquatic forms had large parabolic or broad skulls, enabling effective suction feeding (Boy 1993; Warren 2000; Damiani et al. 2008). The skull of *S. janenschi* is rather short and triangular and does not fit either pattern, indicating mainly terrestrial prey capture. The absence of lateral line sulci

on the skull roof of *S. janenschii* might suggest a primarily terrestrial lifestyle. However, the absence of sulci in fossil tetrapods is of limited value for assessing a terrestrial or aquatic lifestyle. If present, these sulci imply an aquatic lifestyle, but their absence in turn cannot be regarded as evidence for a terrestrial existence (Valin & Laurin 2004; Witzmann et al. 2010).

Squamosal embayment. Different lineages of basal tetrapods evolved an impedance-matching middle ear that was able to perceive aerial sound (Clack 2002; Müller & Tsuji 2007). Several groups of early tetrapods, however, such as *Acanthostega* (Clack 1992), embolomeres (Clack 1983), and lepospondyls (Carroll 2000) did not have a tympanum, and the stout morphology of the stapes precluded aerial transmission of sound waves. In contrast, other basal tetrapods, such as many temnospondyls (Lombard & Bolt 1988) and seymouriamorphs (Carroll 2009; Laurin 2010) have a large otic notch that presumably supported a tympanum and a slender stapes. As already described by Carroll (1970) and Laurin & Reisz (1999), the squamosal of *S. janenschii* bears a shallow, curved crest that extends along the margin of the shallow squamosal embayment. Carroll (1970) suggested that *S. janenschii* possessed an impedance matching middle ear and that a tympanum was attached to this crest. In contrast, Laurin & Reisz (1999) challenged the presence of a tympanum in *S. janenschii*, because the squamosal embayment is too shallow. In most temnospondyls and seymouriamorphs that possessed a tympanum the embayment is much deeper, and the tympanum must have been attached also to the supratemporal and tabular dorsally (Reisz et al. 2010; Laurin 2010). In *S. janenschii*, however, a dorsal margin of the squamosal embayment formed by supratemporal and tabular is not developed. Thus, the present study supports the view of Laurin & Reisz (1999) that argues for the absence of a tympanum in *S. janenschii*. Therefore the function of the shallow embayment remains unknown. For a better understanding of the middle ear region in *S. janenschii*, knowledge of stapes and otic capsule would be necessary which are unfortunately not preserved.

Ribs and thorax. Within basal tetrapods, two modes of lung ventilation can usually be distinguished (Janis & Keller 2001). One is buccal pumping, which is recognized in temnospondyls and extant amphibians and is probably plesiomorphic for tetrapods. Morphological characters for buccal pumping are short, straight ribs that are largely immobile and a broad skull. The second mode of lung ventilation is costal. Morphological characters suggestive of this mechanism are slender, long, curved ribs and a relatively small skull. Furthermore, the capitulum and tuberculum of the rib head are clearly separated. Costal lung ventilation can be attributed to basal amniotes and probably also to a certain degree to stem-amniotes such as embolomeres and microsaurs (Janis & Keller 2001; Clack 2002). The skull of *S. janenschii* is rather small and the ribs are slender and curved without uncinata processes. Furthermore, the

unfinished distal end of the ribs suggests that they may have extended to a cartilaginous sternum, a feature not present in buccal pumping tetrapods. These features suggest strongly that *S. janenschii* relied, at least to a certain degree, on a kind of costal lung ventilation similar to that in amniotes.

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Appendix

List of the coding for *Solenodonsaurus janenschi*

?????	?????	?1000	10000	01000	00100	00?11	00111	21101	10???	?0000	10001	??000
0000?	?0100	00100	00100	0?01?	10000	00?1?	??000	020?1	00004	4????	?????	?????
?????	?????	?????	?????	?????	?????	?????	???1?	00?00	?????	?1100	0????	?????
??01?	?????	?????	?????	??000	0000?	?1?11	0?1??	?1?0?	?0101	21?01	11?1?	1????
?????	?????	?????	???01	000??	00000	01110	100?0	?0001	111??	011??	?1?1	