A new discosauriscid seymouriamorph tetrapod from the Lower Permian of Moravia, Czech Republic

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A new genus and species, *Makowskia laticephala* gen. et sp. nov., of seymouriamorph tetrapod from the Lower Permian deposits of the Boskovice Furrow in Moravia (Czech Republic) is described in detail, and its cranial reconstruction is presented. It is placed in the family Discosauriscidae (together with *Discosauriscus* and *Ariekanerpeton*) on the following character states: short preorbital region; rounded to oval orbits positioned mainly in anterior half of skull; otic notch dorsoventrally broad and anteroposteriorly deep; rounded to oval ventral scales. *Makowskia* is distinguished from other Discosauriscidae by the following characters: nasal bones equally long as broad; interorbital region broad; prefrontal-postfrontal contact lies in level of frontal mid-length (only from *D. pulcherrimus*); maxilla deepest at its mid-length; suborbital ramus of jugal short and dorsoventrally broad with long anterodorsal-posteroventral directed lacrimal-jugal suture; postorbital anteroposteriorly short and lacks elongated posterior process; ventral surface of basioccipital smooth; rows of small denticles placed on distinct ridges and intervening furrows radiate from place immediately laterally to articular portion on ventral surface of palatal ramus of pterygoid (only from *D. pulcherrimus*); oblique anterior margin of transverse flange of pterygoid directed anteromedially-posterolaterally; cultriform process of parasphenoid relatively short and slightly rounded; ventral surface of the posterior plate of parasphenoid heavily sculptured (only from *D. pulcherrimus* and *Ariekanerpeton*); distal ends of fourth and fifth presacral ribs distinctly anteroposteriorly broadened, and extend into the hook-like, posteriorly directed processes; shaft of ?last caudal rib anteroposteriorly broadened; posterior stem of interclavicle narrows anteriorly and posteriorly from broadened mid-length section.

Key words: Skeletal anatomy, Discosauriscidae, Seymouriamorpha, Permian, Boskovice Furrow, Moravia, Czech Republic.

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Introduction

The first discoveries of stegocephalians from the Boskovice Furrow in Moravia (Czech Republic) were made in 1872 near the town of Malá Lhota (Augusta 1948). Makowsky (1876) described these finds as *Archegosaurus austriacus*. Because the name *Archegosaurus* was preoccupied, Kuhn (1933) introduced the new generic name *Discosauriscus* for this species. A comprehensive revision of all finds of discosauriscid tetrapods since Makowsky's first description was made by Špinar (1952). Špinar (1952) recognized two genera, each containing two species, from the region of the Boskovice Furrow and confirmed their position within Seymouriamorpha Watson, 1917: *Discosauriscus pulcherrimus* (Fritsch, 1879), *D. potamites* (Steen, 1938), *Letoverpeton austriacum* (Makowsky, 1876), and *L. moravicum* (Fritsch, 1883). Klembara and Meszároš (1992) presented a new, chemically prepared, three-dimensional material of discosauriscids from the Boskovice Furrow. A subsequent revision by Klembara (1997) reduced the number of discosauriscid taxa from the Lower Permian deposits of the Boskovice Furrow to only one genus and two species: *Discosauriscus austriacus* (Makowsky, 1876) and *D. pulcherrimus* (Fritsch, 1879). The taxa *Discosauriscus potamites* (Steen, 1938) and *Letoverpeton moravicum* (Fritsch, 1883) are junior synonyms of *Discosauriscus austriacus* (see discussion in Klembara 1997). *D. austriacus* is very abundant, whereas only five specimens of *D. pulcherrimus* have been recorded (Klembara 1997). The present paper brings a description of a new genus and species, *Makowskia laticephala*, from the Lower Permian deposits of the Boskovice Furrow, thus extending the number of the genera known from this region and strata to two again. The new species is represented by a single specimen (the anterior portion of the skeleton). The three-dimensional preservation of discosauriscids from the Boskovice Furrow has enabled a very detailed knowledge of the skeletal anatomy, integument, and structures of the sensory systems of both species of the genus *Discosauriscus* (Klembara 1994a, 1996, 1997; Klembara and Bartík 2000) and of *Makowskia* (see below). In addition, fossilized soft parts of the body such as skin, eyes, external gills, and notochord have also been described in *D. austriacus* (Klembara and Meszároš 1992; Klembara 1995, 1997; Klembara and Bartík 2000).

According to Klembara (1997), the family Discosauriscidae Romer, 1947 consists of two genera: *Discosauriscus* and *Ariekanerpeton* (the latter genus has been recorded from the

Lower Permian of Tadzhikistan, Ivakhnenko 1981, 1987; Laurin 1996a; Bulanov 2003). *Discosauriscus* and *Ariekanerpeton* share character states such as short preorbital region, rounded to oval orbits positioned mainly in anterior half of the skull, otic notch dorsoventrally broad and anteroposteriorly deep, and rounded or oval ventral scales. These character states are considered to be unique to the aforementioned genera and included into the diagnosis of the family Discosauriscidae. The genus *Makowskia* described herein falls within this family (see below). All the three genera differ from the Seymouriidae (Williston 1911) and Utegeniidae (Bulanov 2003) which display the characteristic long preorbital region of the skull and orbits located about its mid-length.

Zhang et al. (1984) described a new putative discosauriscid, *Urumqia liudaowanensis*, from the Permian deposits of China. Ivakhnenko (1987) synonymized this form with *Utegenia shpinari*. A revision of the original material of this tetrapod is needed, but Klembara and Ruta (2004a, b) placed *Utegenia shpinari* (Kazakhstan) within seymouriamorphs as the sister taxon to the discosauriscids. According to Laurin (1996b, 2000), discosauriscids appear to be a paraphyletic group that includes all known larval and most juvenile seymouriamorph specimens known (genera *Utegenia*, *Discosauriscus*, *Ariekanerpeton* and *Urumquia*). A new phylogeny of Seymouriamorpha along with discussion of Laurin's (1996b, 2000) conclusions has been recently presented by Klembara and Ruta (2004a, b). It supports the existence of the family Discosauriscidae with two genera *Discosauriscus* (Czech Republic, Germany, Poland, and France) and *Ariekanerpeton* (Tadzhikistan).

The aim of this paper is to provide (i) a detailed description of the skeletal anatomy of a new genus and species of the discosauriscid tetrapod, *Makowskia laticephala*, from the Lower Permian of the Boskovice Furrow in the Czech Republic, (ii) a comparison of its skeletal anatomy with those of other Lower Permian members of the families Discosauriscidae and Seymouriidae and the ?Uppermost Carboniferous–Lower Permian tetrapod *Utegenia shpinari* (Utegeniidae); and (iii) the phylogenetic position of *Makowskia* within Seymouriamorpha.

In the description below the detailed knowledge of the skeletal anatomy of *Discosauriscus* (Klembara 1997; Klembara and Bartík 2000) is used as a standard for comparisons.

Institutional abbreviations.—CM, Carnegie Museum of Natural History, Pittsburgh, USA; MNG, Museum der Natur, Gotha, Germany; SNM, Slovak National Museum, Bratislava, Slovakia.

Material and methods

The holotypic specimen (SNM Z 26506) was found preserved in a laminated limestone, exhibiting similar conditions as specimens of *Discosauriscus austriacus* (Klembara and Meszároš 1992), which are relatively abundant at the locality (Klembara 1997). The skeleton was completely removed from the rock chemically using a 10% solution of acetic acid (for the method, see Klembara and Meszároš 1992). Although the individual bones are three-dimensionally preserved, several portions of the skull are slightly compressed dorsoventrally (Figs. 1A, 2A). To reconstruct the original shape of the skull an enlarged, wax-plasticine model was constructed. All the bones of the skull were measured, modelled at seven times natural size, and then reassembled using flat metal bars. The drawing restorations of the skull and lower jaw (Figs. 4, 5) were produced as follows: (i) mostly on the basis of the model; (ii) when only one of the paired bones is preserved, it is used to reproduce its mate (this was employed almost completely for the maxilla, lacrimal, and jugal); (iii) missing bones are depicted in white and their outlines were reconstructed on the basis of the anatomy of the neighbouring bones or on the anatomy of *Discosauriscus austriacus* (Klembara 1997), with the outlines shown as dashed lines (this was employed for the ventrolateral tips of the prefrontals, posterior portions of the squamosals, and most of the quadratojugals); (iv) where only the ornamentation of the skull roof bones is damaged, these areas are restored in grey only (this was employed for central portion of the left jugal and the squamosals). The other drawings have been made using a WILD M8 stereomicroscope equipped with a camera lucida.

Systematic palaeontology

Seymouriamorpha Watson, 1917

Family Discosauriscidae Romer, 1947

Emended and revised diagnosis (Klembara 1997; Klembara and Bartík 2000).—Tetrapods with short preorbital region; rounded to oval orbits positioned mainly in anterior half of skull; otic notch dorsoventrally broad and anteroposteriorly deep; rounded to oval ventral scales.

Genus *Makowskia* nov.

Etymology: In honor of Prof. Alexander Makowsky, professor at the former German Technical University in Brno (Czech Republic). He was the first to describe the first specimens of discosauriscids from the Boskovice Furrow in Moravia (Czech Republic) discovered near the town Malá Lhota in 1872.

Type and only species: *Makowskia laticephala* sp. nov.

Diagnosis.—As for species.

Makowskia laticephala sp. nov.

Figs. 1–9.

Etymology: From Latin *latus*, broad and Greek *kefalé*, head.

Holotype: SNM Z 26506, skull and anterior portion of postcranial skeleton, is the only known specimen, and is deposited in the collections of the Slovak National Museum in Bratislava (SNM).

Locality and horizon: Boskovice Furrow in Moravia (Czech Republic); Kochov-L, about 500 m NE of the village Kochov (near city Letovice)

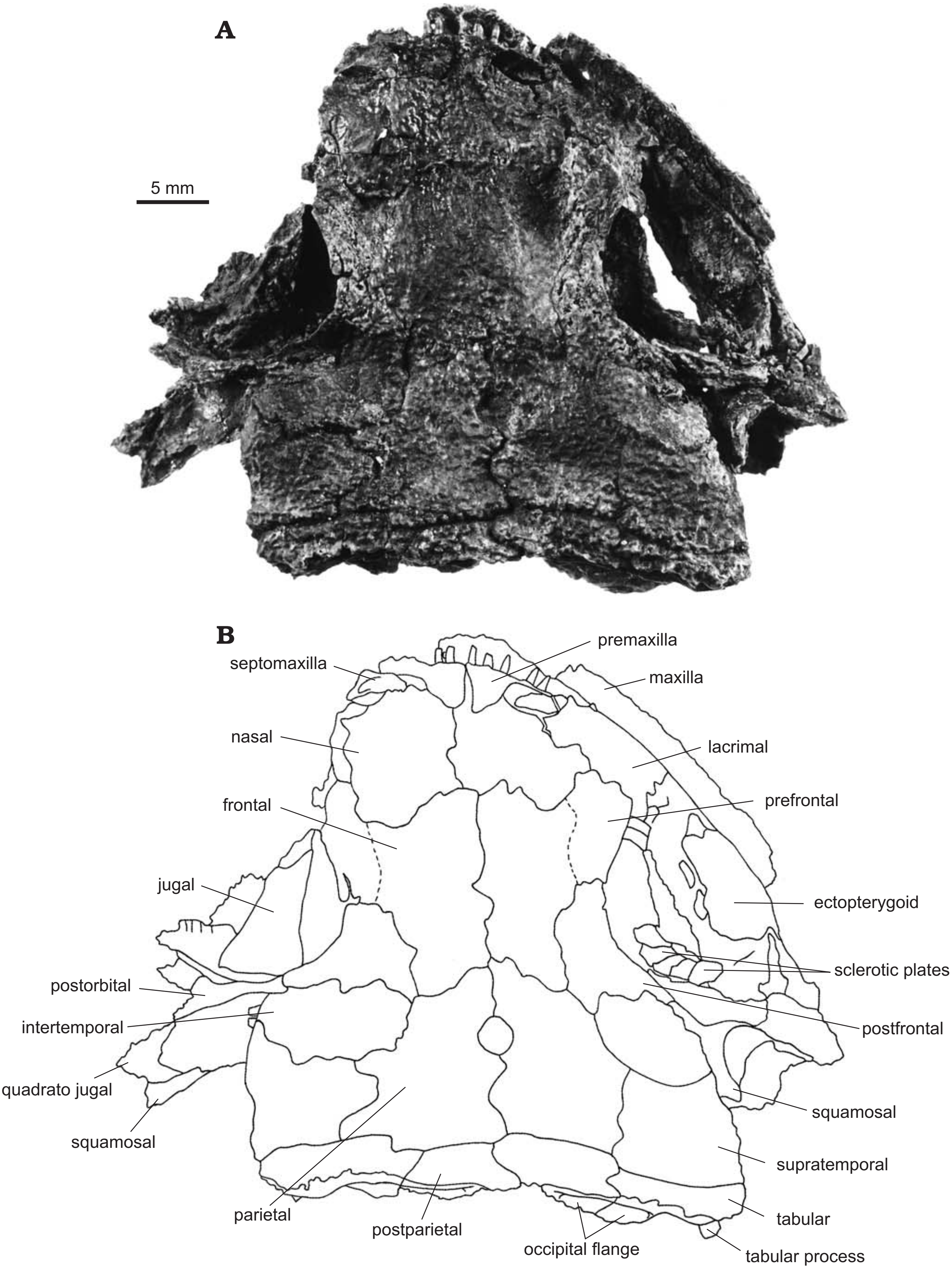

Fig. 1. *Makowskia laticephala* gen. et sp. nov., SNM Z 26506. Photograph of holotype skull (**A**) and explanatory drawing of the same (**B**) in dorsal view.

(Klembara and Meszároš 1992). Bačov horizon, zone 6, Lower Saxonian (*sensu* Werneburg 1989), Lower Permian.

Diagnosis.—Autapomorphies relative to discosauriscids *Discosauriscus* and *Ariekanerpeton* include: nasal bones equally long as broad; interorbital region broad; prefrontal-postfrontal contact lies in level of frontal mid-length (differs only from *D. pulcherrimus*); maxilla deepest at its mid-length; suborbital ramus of jugal short and dorsoventrally broad with long anterodorsal-posteroventral directed lacrimal-jugal suture; postorbital anteroposteriorly short and lacks elongated posterior process; ventral surface of basioccipital smooth; rows of small denticles placed on distinct ridges and intervening furrows radiate from place immediately laterally to articular portion on ventral surface of palatal ramus of pterygoid (only from *D. pulcherrimus*); oblique anterior margin of transverse flange of pterygoid directed anteromedially-posterolaterally; cultriform process of parasphenoid relatively short and slightly rounded; ventral surface of the posterior plate of parasphenoid heavily sculptured (only from *D. pulcherrimus* and *Ariekanerpeton*); distal ends of fourth and fifth presacral ribs distinctly anteroposteriorly broadened, and extend into the hook-like, posteriorly directed processes; shaft of ?last caudal rib anteroposteriorly broadened; posterior stem of interclavicle narrows anteriorly and posteriorly from broadened mid-length section.

Remarks.—The degree of ossification of the skeleton, the type of ornamentation and sutures of skull roof bones of SNM Z 26506 correspond to the similar-sized specimens of *Discosauriscus austriacus* (Klembara 1995, 1997).

Makowskia laticephala is compared with similar-sized specimens of *Discosauriscus austriacus* and *D. pulcherrimus* (Klembara 1997; Klembara and Bartík 2000).

Description and comparison

The skull of *Makowskia laticephala* (SNM Z 26506) is relatively well-preserved, although several bones are missing or variably damaged (Figs. 1, 2). The midline length of skull (Na+Fr+Pa+Pp) is 33 mm. The individual bones of the skull roof are joined via mainly simple, but in some places very sinuous sutures, and therefore paired bones may differ considerably in outline (e.g., supratemporal or parietal, Fig. 1).

The ornamentation of the skull roof bones consists of small tubercles and short ridges concentrated mainly at their centres (best visible on the parietal) (Figs. 1A, 4). Radiating ridges and grooves are present at the periphery of the parietals and frontals, and the posterior portions of the nasals. Otherwise, the ornamentation of most bones consists of tubercles of various size and irregular short ridges and grooves. The ornamentation of the jugal consists of pits of various sizes and weak elevations, as seen in *Discosauriscus austriacus* (Klembara 1997: fig. 4).

The ornamentation of several bones is badly preserved and makes the observation of the presence or course of the sensory grooves impossible. The sensory grooves are observable on the premaxilla, nasal, prefrontal, intertemporal, supratemporal, and postorbital (Figs. 1A, 4). On the right nasal, the sensory groove is very deep, and its morphology resembles the confluent foraminate pits (Klembara 1994a). The distinct ornamentation of the posterior portions of the tabulars and the postparietals does not permit the grooves of the occipital (supratemporal) commissural canal to be identified with certainty.

Skull

Skull roof and sclerotic ring.—The premaxilla is a biramous structure consisting of a ventral (maxillary) and a posterodorsal (nasal) rami; a third, posterior (vomerine) ramus is not distinctly developed (Figs. 1, 4). The bodies of premaxillae are joined only in a short median suture. The nasal ramus is broadest at its base and gradually tapers dorsalwards. Between both nasal rami is an interpremaxillary space, the posterior part of which was probably occupied by anteriormost tips of the nasals. In similar-sized *Discosauriscus austriacus* specimens the presence of the interpremaxillary space is only a transitional, ontogenetic state that reflects the incomplete ossification of the nasal rami of the premaxillae. In larger, juvenile specimens this space is completely closed by the posterior portions of the nasal rami of the premaxillae and the anteromedial tips of the nasals (Klembara 1997: fig. 29). The maxillary ramus is long and dorsoventrally narrow and has a vertical suture with the maxilla, whereas in *D. anstriacus* this suture is oblique. The maxillary ramus forms almost the entire anterior margin of the exonarial fenestra. Each premaxilla bears six conical, sharpely pointed teeth. The inner wall of the maxillary ramus bears a narrow horizontal lamina that forms the anterior margin of the exochoanal fenestra. The anterior wall of the septomaxilla abuts the dorsal surface of the horizontal lamina and the inner surface of the maxillary ramus of the premaxilla. The medial portion of the horizontal lamina extends posteriorly to form a short posterior ramus that meets the vomer.

The nasal is as long as it is wide (Figs. 1, 4), in contrast to the invariably longer nasal in similar-sized *Discosauriscus* (Klembara 1997) and *Ariekanerpeton* (Ivakhnenko 1981; Laurin 1996a; Bulanov 2003). The anteromedial corner of the nasal produces a small process that is slightly overlapped by the dorsal ramus of the premaxilla. The anterior margin of the nasal borders broadly the exonarial fenestra posteriorly and is slightly flexed ventrolaterally creating an anteromedially-posterolaterally directed ridge at the dorsal surface of the bone, which continues onto the prefrontal. The nasal has a zigzag suture with the lacrimal, but an almost straight suture with the prefrontal that is aligned with the frontal-prefrontal suture. The suture between both nasals is irregular.

The septomaxilla, best preserved on the left side of the skull (Figs. 1, 4), is a trough-shaped bone lying in the exonarial fenestra. The septomaxilla joins the lacrimal posterolaterally, the maxilla anterolaterally, and anteriorly it abuts

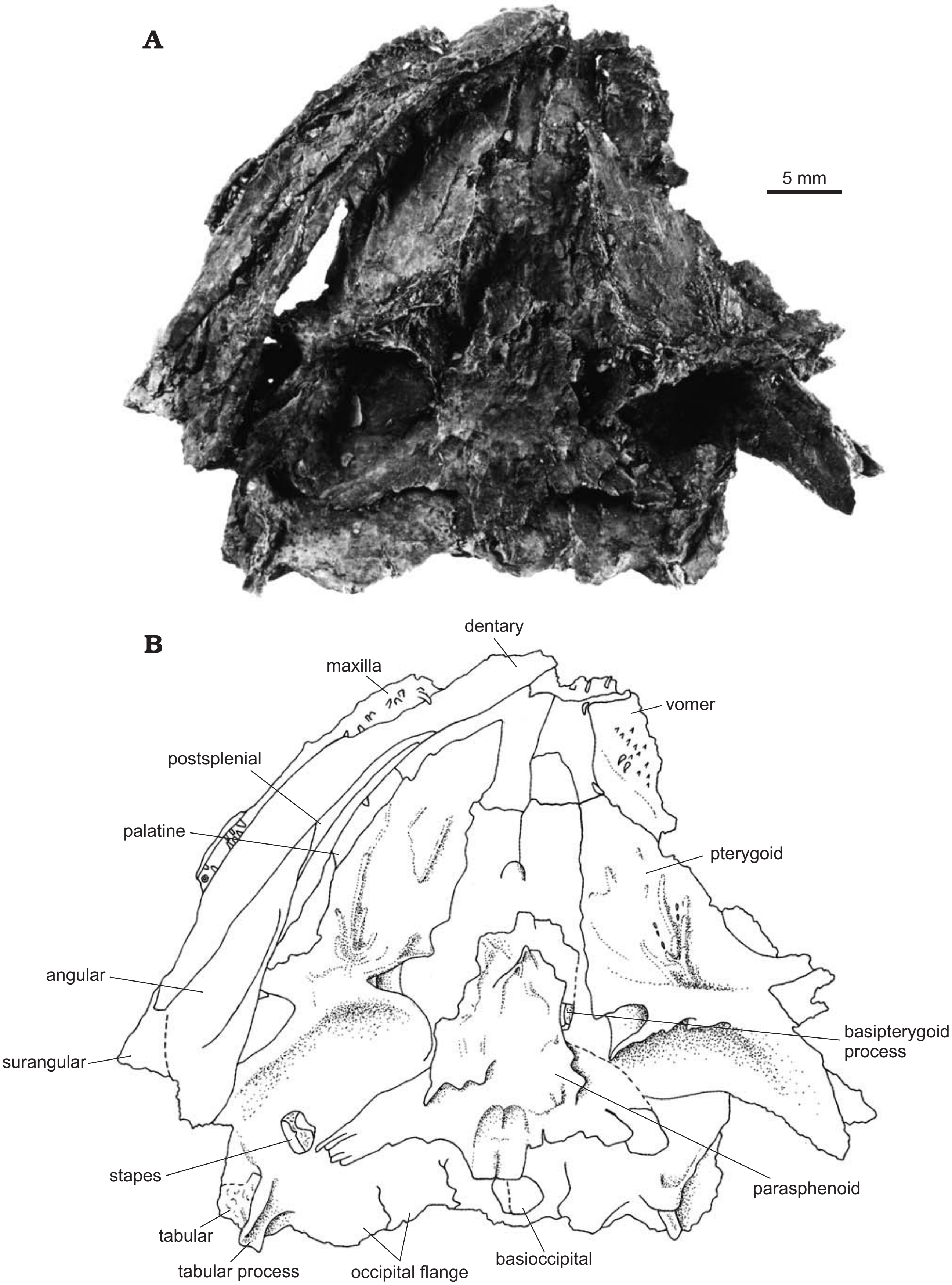

Fig. 2. *Makowskia laticephala* gen. et sp. nov., SNM Z 26506. Photograph of holotype skull (**A**) and explanatory drawing of the same (**B**) in ventral view.

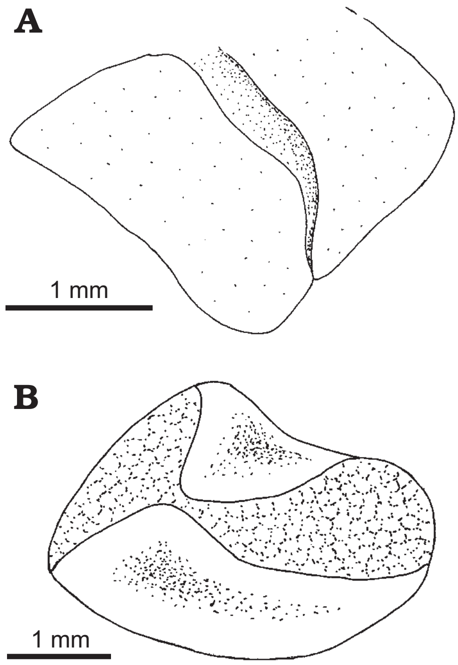

Fig. 3. *Makowskia laticephala* gen. et sp. nov., SNM Z 26506. **A**. Sclerotic plates in anterior part of right orbit. **B**. Right stapes.

the posterior wall of the premaxilla. As in *Discosauriscus* (Klembara 1997), the septomaxilla does not join the nasal. The exonarial fenestra is thus surrounded with the premaxilla, maxilla, septomaxilla, lacrimal, and nasal. The dorsal margin of the septomaxilla that is adjacent to the maxilla and the lacrimal is ornamented. The ornamentation consists of tiny pits and tubercles, and this portion of the septomaxilla participates in the skull roof. The septomaxillary foramen is located in the wall of the septomaxilla, below the ornamented portion. The ventral portion of the inner surface of the septomaxilla adjacent to the septomaxillary foramen is roughened. A small process on the medial surface of the septomaxilla probably joined the vomer as in *D. austriacus* (Klembara 1997).

The frontal is an anteroposteriorly elongate, mediolaterally broad plate (Figs. 1, 4). Its anterior half is mediolaterally broadened, equalling that of the nasal. The suture joining the frontals is undulating.

The prefrontal is triangular in outline and forms the anteromedial margin of the orbit (Figs. 1, 4). Anterolaterally it produces a large ventral lamina that is overlapped by the lacrimal. The posterior ramus of the prefrontal is mediolaterally broad and has a broad contact with the postfrontal. This suture lies at a level of the frontal mid-length. The broad prefrontal-postfrontal suture, together with relatively broad frontal, results in a greatly widened interorbital width, a feature unique to *Makowskia laticephala* among discosauriscids.

The postfrontal is a large, crescent-shaped plate that forms the ventromedial margin of the orbit (Figs. 1, 4). It has a narrow contact with the parietal and an interdigitating suture with the intertemporal.

The parietal is a large, anteroposteriorly elongated plate (Figs. 1, 4). A rounded pineal foramen lies at the level of the intertemporal mid-length. The suture between the parietals is straith anterior to the pineal foramen, whereas posteriorly it has a distinctly undulating shape, as in *Discosauriscus austriacus* (Klembara 1994b, 1997). Also as in *Discosauriscus*, the parietal posesses three lateral processes, though the process wedged between the frontal and postfrontal is very small. A posterolateral process of the right parietal is not developed, eliminating a contact with the tabular but permitting a short contact between the supratemporal and postparietal. This condition probably originated by the secondary fusion of the independently ossified lateral parietal with the supratemporal at an early growth stage. There are several specimens of *D. austriacus* in which several independent bones exist in the region of the lateral and posterolateral processes of the parietal; these have been designated as lateral parietals and represent the subdivisions of the parietals (Klembara 1993; Klembara et al. 2002). The ventral surfaces of the posteromedial margins of the parietals are massive and together they form a rounded crest that continues to the ventral surfaces of the postparietals.

The intertemporal is a mediolaterally broad, elliptical bone with a relatively long, lateral suture with the squamosal (Figs. 1, 4).

The supratemporal is a large, roughly square-shaped element (Figs. 1, 4). Its posterolateral corner, together with the lateral end of the tabular, is slighly flexed ventrolaterally, similar to the condition in *Discosauriscus* (Klembara 1997). On the ventral surface of the supratemporal a stout otic flange runs parallel to lateral margin of the bone before turning medially at its posterior end. Here, it is mediolaterally broadest and shares a digitiform suture with the crista arcuata of the tabular. The otic flange is firmly sutured to the dorsolateral portion of the squamosal.

The postparietal is an anteroposteriorly short, lateromedially broad plate (Figs. 1, 4). The right postparietal is broader and has a suture with the left parietal, a configuration that is occasionally present also in *Discosauriscus austriacus* (Klembara 1997). The postparietals are joined by an oxbow suture. The postparietals and tabulars are distinctly ornamented except for a narrow, smooth, horizontal lamina extending along the occipital margin of the skull table. The lamina exhibits slight transverse striations. Close to the midline suture, the laminae become broader, flex steeply posteroventrally, and unite in a median, ventrally pointed process. The posteroventrally flexed occipital flange of the postparietal is narrowest medially, broadens laterally, and joins the similarly oriented occipital flange of the tabular with the former slightly overlaping the latter. There is a more or less distinct groove between the horizontal lamina and the occipital flanges of the postparietals and the tabulars.

The tabular is a mediolaterally elongated plate and its occipital flange is larger than that of the postparietal (Figs. 1, 4, 5A). There are rounded crests positioned laterally and medially on the external surface of the occipital flange of the

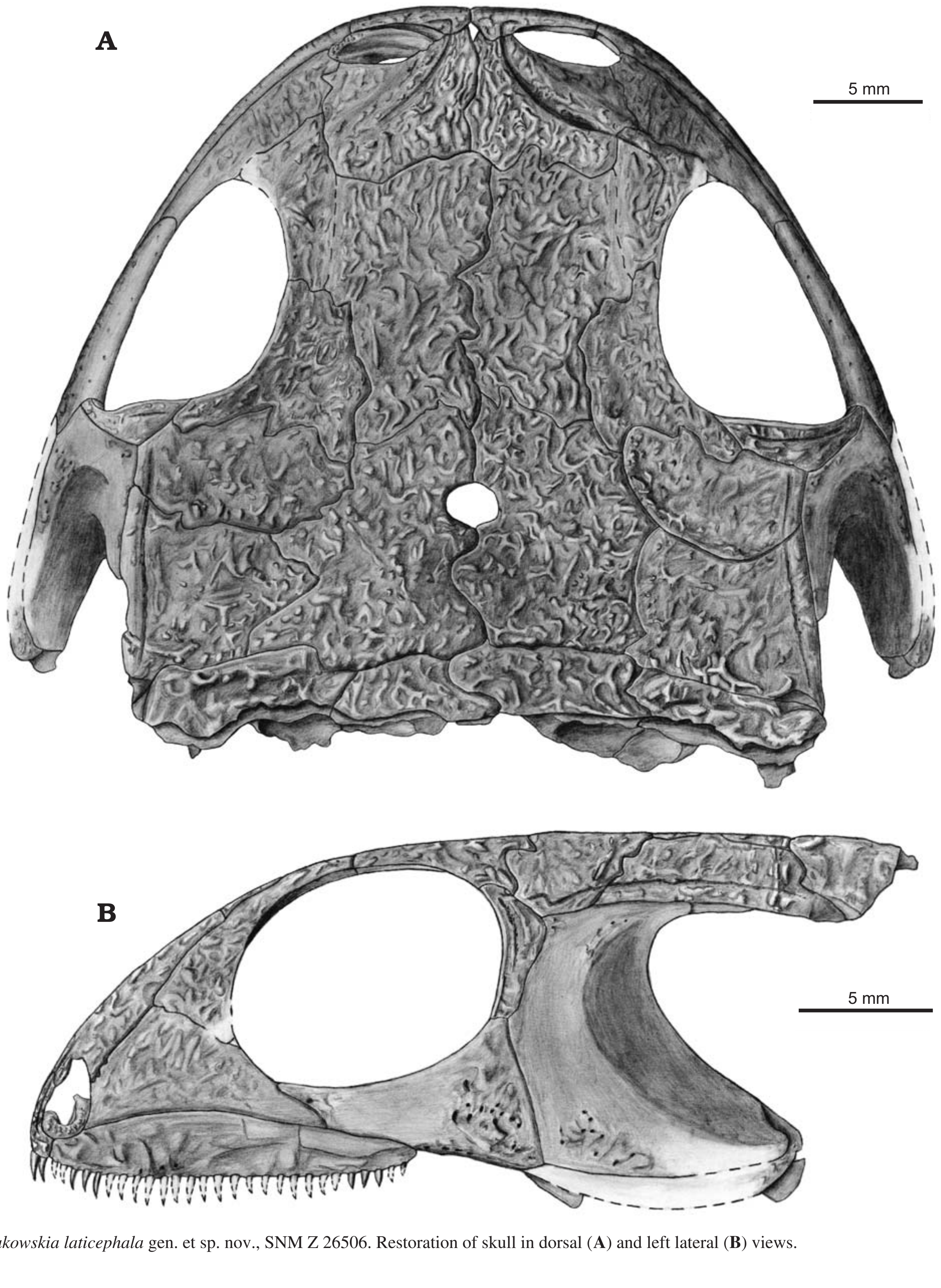

Fig. 4. *Makowskia laticephala* gen. et sp. nov., SNM Z 26506. Restoration of skull in dorsal (**A**) and left lateral (**B**) views.

tabulars and postparietals. The crests surround an elliptical, slightly roughened depression, indicating the place of insertion of the cervical muscles. The right tabular process is a prolonged plate, whereas the left is a horn-like structure, and the dorsal surfaces of both processes are smooth. The ventral surface of both tabulars is well preserved and is basically identical to that of *Discosauriscus austriacus* (Klembara 1997). The crista arcuata is high and, its lateral surface, as well as the surface between it and the lateral margin of the tabular, are roughened. The anterior half of the surface of the tabular process bears a deep sulcus, and immediately anteriorly to it is a deep pit. Anterior to the pit and medially to the crista arcuata there is a distinct elevation bearing a system of grooves, pits and, small crests at its surface.

An almost complete right maxilla and a fragment of the left one are preserved. The maxilla is a long, narrow bone, reaching a level slightly behind the mid-length of the orbit (Figs. 1, 2, 4, 5). Not all teeth are preserved, but on the basis of their spacing the total number can be estimated to be about 25. Contrary to the condition in *Discosauriscus* (Klembara 1997) and *Ariekanerpeton* (Ivakhnenko 1981; Bulanov 2003), the maxilla is the highest at its mid-length. At its anterior end the incision forming the margin of the exonarial fenestra is very shallow, whereas in *Discosauriscus* this portion of the maxilla is more deeply incised (Klembara 1997). The inner surface of the maxilla is not well-preserved, but the presence of the broad horizontal lamina is recognizable.

Most of the right lacrimal is preserved (Figs. 1, 4). Its preorbital part is quadrangular, whereas posteriorly it extends into the suborbital or jugal process that forms the anteroventral margin of the orbit. The jugal process is relatively long and dorsoventrally flattened. Its posteriormost section is broad, which corresponds to the broad articular portion of the suborbital ramus of the jugal.

The left jugal is well-preserved, forming a stout bone of triangular shape (Figs. 1, 4). In contrast to *Discosauriscus* (Klembara 1977) and *Ariekanerpeton* (Ivakhnenko 1981; Laurin 1996a; Bulanov 2003) the suborbital ramus is relatively short and unusually broad dorsoventrally. A broad, anteroventral lamina of the suborbital ramus overlapped a similarly broad, sutural scar on the jugal ramus of the lacrimal. It is readily visible in lateral view that the suture between the ornamented surfaces of the jugal and lacrimal is relatively long, and is directed anterodorsal-posteroventral. The dorsal process of the jugal has the form of a blunt point, similar to that of the postorbital. The suture separating the two bones is very short. The posterior process of the jugal is pointed, and its posteroventral margin has a short suture with the quadratojugal.

The postorbital is a triramous structure; the dorsomedial and ventrolateral rami are of about the same length, whereas the posterior ramus is very short (Figs. 1, 4). The orbital margin is slightly elevated dorsally. The inner surface of the postorbital is smooth and as a such is continuous with the similar surfaces of the postfrontal and prefrontal. The ventrolateral jugal ramus is anteroposteriorly very narrow. The same is true also for the dorsomedial ramus, although it is slightly broader anteroposteriorly and shorter mediolaterally.

Both squamosals are present, although not completely preserved (Figs. 1, 4). On the right squamosal both the ornamented area and the smooth otic flange are partially preserved. On the left squamosal it is observable that the otic flange is much broader than in *Discosauriscus* (Klembara 1997). The morphology of the lateral margin of the supratemporal indicates that its suture with the squamosal reached about the mid-length level of the supratemporal.

Only the posterior portion of the left quadratojugal is preserved (Figs. 1, 4, 5A). A sulcus is present on the posterior margin of the smooth rounded flange. This indicates the presence of the paraquadrate foramen in a similar position to that in *Discosauriscus* (Klembara 1997). The inner surface of this portion of the quadratojugal is roughened, indicating the place of the articulation with the cartilaginous quadrate.

Of the sclerotic ring, only two partially articulated plates in the anterior part and three articulated sclerotic plates positioned in the posteromedial part of the right orbit are preserved (Figs. 1, 3A). Each sclerotic plate is of quadrangular shape. The plates are arranged in such a manner that each plate overlaps or fits into depression of the preceding plate. On the basis of the size of the remaining plates, it is possible to estimate the original number of plates in each sclerotic ring at about 40.

Palate.—The vomer is an elongated plate and forms the whole medial margin of the exochoanal fenestra (Figs. 2, 5A). The anterior thirds of both vomers meet in a short midline suture. The posterior portion of the vomer forms a large lamella that, as in *D. austriacus* (Klembara 1997: fig. 26), is ventrally overlapped by the anterior portion of the pterygoid. The vomer has a short suture with the anteromedial process of the palatine. At about the mid-length of the vomer two tusks are present. Anterior to the tusks and along the exochoanal margin are several small teeth.

The right palatine is relatively well-preserved (Figs. 2, 5A). It is subrectangular in outline and forms the concave margin of the posterior border of the exochoanal fenestra. The palatine is about the same length as the ectopterygoid. The suture with the ectopterygoid is straight. The palatine is notched posterolaterally, but the state of preservation in this area does not permit the unambiguous determination of the presence or absence of the suborbital fenestra, as in *Discosauriscus* (Klembara 1997). In the skull of *Makowskia laticephala* the suborbital fenestra is restored on the basis of the conditions in *Discosauriscus* (Klembara 1997). At about the level of the mid-length of the palatine two tusks are present.

The right ectopterygoid is almost completely preserved, but is visible only in dorsal view (Figs. 1, 5A). It is a subrectangular plate wedged between the maxilla and jugal laterally and the pterygoid medially and posteromedially. The posterolateral corner of the ectopterygoid is obliquely angled.

The pterygoid is the largest palatal bone and all its four parts—palatal ramus, transverse process, central region around the basicranial (articular) fossa, and quadrate ramus—are well-preserved (Figs. 2, 5A). The palatal ramus is mediolaterally broad and its medial margin is almost straight. Immediately anterior to the basicranial articulation the medial margin bears a small notch. Both rami met probably at their anterior tips. There is a noticeable difference in the mediolateral width of the palatal rami. The subrectangular transverse process is well-developed. Its anterior margin is slightly oblique and runs in anteromedial-posterolateral direction. In contrast, the anterior and posterior margins are

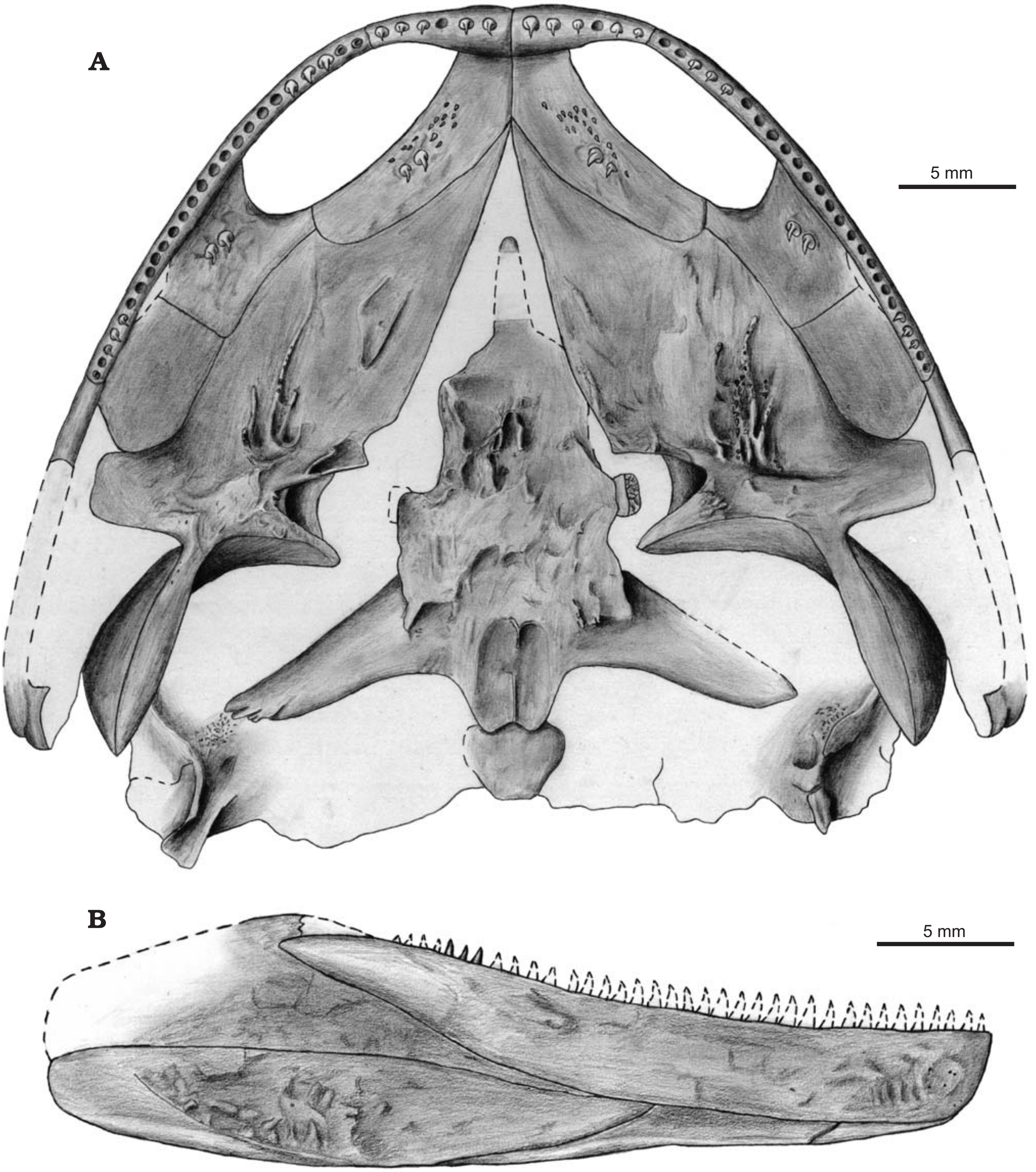

Fig. 5. *Makowskia laticephala* gen. et sp. nov., SNM Z 26506. **A**. Restoration of skull in ventral view. **B**. Restoration of lower jaw in right lateral view.

parallel in *Discosauriscus* (Klembara 1997). The anterior margin is strongly roughened. The transverse process is inclined posteroventrally so that it extends slightly below the ventral margin of the cheek and was probably visible in the lateral view. The articular fossa lies at the level of the transverse process and is surrounded by high walls that reach their greatest hight medially. The dorsomedial surface of the articular fossa is smooth, whereas its dorsolateral and lateral surfaces are sculptured with pits, grooves, and ridges of irregular shape. A similar morphology of the articulating surface is present also in *Discosauriscus* (Klembara 1997), and it indicates a firm articulation with the basipterygoid process of the braincase. Pits, grooves, and ridges are present also immediately laterally to the articular fossa. The morphology of the ventral surface of the palatal ramus is similar to that in *Discosauriscus austriacus*, but dissimilar to that in *D. pulcherrimus* (Klembara 1997). In *Makowskia laticephala* ridges alternating with deep grooves diverge anteriorly from the central region of the pterygoid. The ridges are the highest in the central region, becoming reduced toward the periphery of the palatal ramus. The pattern and extent of the ridges differs between the right and the left pterygoids. The highest ridges bear a row of small denticles, but this also differs between the pterygoids. The central region of the pterygoid is massive and bears pits and irregular grooves and ridges, which continues also onto the transverse process. The quadrate ramus is nearly vertical, and its anterior portion, the ascending lamina, is high and subquadrangular in shape. It is transversely oriented and its dorsal margin lies close to the ventral surface of the skull roof. The basal portion of the ascending lamina is vaulted anteriorly.

The parasphenoid is well-preserved, only the cultriform process is incomplete and the left posterolateral process is broken in several places (Figs. 2, 5A). Preserved parts of the cultriform process show that it was short and rounded slightly anteriorly. The posterior parasphenoid plate is large and forms a high, heavily sculptured, triangular wedge-like process anterior to the level of the basipterygoid processes. The sculpture consists of high ridges bordering deep furrows and pits. Immediately posteriorly to the wedge-like process the parasphenoid plate is also sculptured, but with broad, shallow depressions divided by low rounded ridges. The parallel lateral margins of the ventral parasphenoid plate are sharp and slightly flexed lateroventrally. Posteriorly they extend onto the ventral surface of the posterolateral processes to form the ventrolateral crests or basal tubera. The posterolateral processes of the parasphenoid plate are long and taper slightly laterally. The posteriormost portion of the parasphenoid plate forms two processes adjacent to the midline, the posterior parts of which underlied the anterior margin of the ventral surface of the basioccipital. Both processes bear anteroposteriorly oriented elliptical depressions divided by a narrow and sharp ridge. The depressions probably represent the sites of muscle insertions.

Ossifications of palatoquadrate and stapes.—The quadrate is not ossified, and the epipterygoids are not represented. In similarly sized specimens of *Discosauriscus austriacus*, the epipterygoid is already partially ossified (Klembara 1997). The stapes is crescentic shaped (Figs. 2, 3B). In its shape and grade of ossification the stapes duplicates that in similarly sized *Discosauriscus* specimens (Klembara 1997), except in being slightly more robust. The distal end of the stapes is narrowed, whereas the proximal end broadens and probably continued as two cartilaginous processes, as in *Discosauriscus* (Klembara 1997). The position of stapes relative to the adjacent cranial structures was probably identical to that in *Discosauriscus*.

Neural endocranium.—Only the basipterygoid processes of the basisphenoid are preserved (Figs. 2, 5A). They lie at the level of the posterior portion of the anterior wedge-like process of the parasphenoid. The dorsal and lateral margins of the basipterygoid process are covered by smoothly finished bone, whereas the distal margins of the processes are unfinished, indicating cartilaginous continuation.

The basioccipital is almost completely preserved, although it is broken along in its mid-width and the right side is slightly displaced dorsal to the left side (Figs. 2, 5A). The basioccipital forms a dorsoventrally thin quadrangular plate with anterolaterally rounded corners. In *Makowskia laticephala* the basioccipital is broad anteriorly and its lateral margins converge posteromedially. Its anterior margin is slightly anteriorly convex, whereas the posterior margin is straight and about half of the length of the anterior margin. The ventral surface of the basioccipital is smooth and lacks the posteromedially converging ridges typical of that of *Discosauriscus* (Klembara 1997). The shape of the basioccipital of *Makowskia* is very similar to that in *Utegenia*, however, it is slightly broader in the former species.

The exoccipital is not preserved.

Lower jaw.—Only the incomplete right lower jaw is preserved (Figs. 2, 5B). The individual bones are more or less articulated and best exposed in lateral and ventral views, whereas those of the medial surface are poorly preserved. The relative size of the preserved bones, as well as their intervening sutures, are very similar to those in *Discosauriscus austriacus* (Klembara 1997). The lower jaw is deepest in the region of the anterior end of the surangular.

The dentary is a very long, narrow plate that is broadest anteriorly and narrows gradually to a pointed end posteriorly. Ventrally it joins the splenial and postsplenial, whereas posteriorly it overlaps laterally the anterior portion of the angular. There is a large, anteroposteriorly elongated fenestra between the dentary and splenial on the medial surface of the jaw, as in *Discosauriscus austriacus* (Klembara 1997). Only some of the posteriormost teeth are preserved.

The surangular is a large plate, but its posterodorsal portion is missing and its anterodorsal portion is only partially preserved. The anterior margin of the surangular extends almost perpendicularly and indicates a complicated suture with the posterior coronoid. The posterior end of the dentary lies slightly below this surangular portion, indicating that the surangular-posterior coronoid suture should be visible in lateral view, as in *Discosauriscus austriacus* (Klembara 1997). The coronoids are not preserved.

The splenial is dorsoventrally narrow in lateral view and its ventral surface, together with those of the postsplenial and angular, form a continuous trough-like channel along the ventral margin of the jaw. As in *D. austriacus* (Klembara 1997), the border between the external ornamented and ventral smooth surfaces of all these three bones is demarcated by a sharp and distinct edge. The anteriormost end of the splenial forms the ventral portion of the symphysis. The posterior portion of the splenial overlaps laterally the posterior end of the postsplenial.

In lateral view the postsplenial is dorsoventrally narrow, but dorsally higher than the splenial. Externaly the anterior end of the postsplenial inserts between the splenial and dentary, but the suture with the latter is much longer. The posterior end of the postsplenial underlies the anterior portion of the angular.

The angular is a long and massive plate, whose anterior end narrows and inserts between the postsplenial and dentary. The external surface of the angular is ornamented, with the ventral margin of ornamentation forming a distinct, ventrally convex edge.

Only small fragments of the prearticular are preserved and the articular was cartilaginous.

Dentition.—The teeth are preserved on both premaxillae, maxillae, and vomers and the right palatine; small denticles are preserved on the vomers and pterygoids (Figs. 1, 2, 4B, 5). Several posteriormost teeth are present on the dentary and are cylindrical with slightly posteriorly recurved, sharply pointed crowns. The bases of one anterior maxillary and one of the largest premaxillary teeth bear slightly elongated, fine striations indicating the initial stage of infolding of the dentine. None of the other preserved teeth bears the traces of basal striations. There are six teeth on each premaxilla (several of them are broken). Most of the maxillary teeth are not preserved, but the number of tooth positions indicates a count of about 25 teeth. The number of visible palatal tusks is as follows: two on each vomer and two on the right palatine. The ectopterygoid is not exposed in ventral view. Small pointed denticles are present on the ventral surface of the vomer anterior to the tusks, whereas further posteriorly the denticles are aligned in a row lying laterally to the tusks and marginal to the internal margin of the exochoanal fenestra. Similar small denticles are present also on the ridges on the ventral surface of the palatal ramus of the pterygoid. The denticles are aligned in the rows on the crests of ridges. Only a few denticles were present on the right pterygoid, as indicated by several small tooth positions on the surface of the ridges. Such variation in the number of the denticles on the right and left sides are observable also in *Discosauriscus* (Klembara 1997).

Reconstructed skull.—The skull width exceeds the skull length by about 27%, and the short preorbital length is only about 23% of the skull length (Figs. 4, 5). The nasals are equally long as broad, which is unique within the family Discosauriscidae. The lateral portions of the nasal and the prefrontal are slightly flexed ventrally and aligned with the angle of the adjacent portion of the cheek. As a consequence, this portion of the cheek is morphologically divided from the adjacent dorsal surface of the skull roof by an edge directed anteromedially-posterolaterally. The prefrontal-postfrontal suture is broad. This, together with the relatively broad frontals, accentuates the interorbital width. The intertemporal, supratemporal, and tabular bones are mediolaterally very broad. This is true also for the parietal and thus for the whole parietal table. In dorsal view the skull has a semielliptical shape with the long axis along the midline. The orbits lie in the posterior portion of the anterior half of the skull. They are of oval shaped and face dorsolaterally. The pineal foramen is relatively large and lies at the level slightly posterior to the posterior orbital margins. The jaw joint lies at the level of the supratemporal-tabular suture. The cheek makes an angle of about 60° with the parietal table. The otic notch is anteroposteriorly deep and dorsoventrally broad. The suborbital part of the cheek is very high, contrary to other discosauriscids (Klembara 1997; Klembara and Ruta 2004a). The posterolateral part of the transverse process of the pterygoid is flexed posteroventrally and most probably extended below the ventral cheek margin at the level of the jugal-quadratojugal suture. The posterolateral corner of the supratemporal and the lateralmost portion of the tabular are slightly flexed ventrally, similarly to those in *Discosauriscus* (Klembara 1997) and *Seymouria sanjuanensis* (Laurin 1995). The parietal table-cheek articulation is firm, as in all other seymouriamorphs. The palate is not closed, a condition corresponding to the similar-sized ontogenetic stages of *D. austriacus* (Klembara 1997). The lower jaw was deepest at the level of the posterior coronoid-surangular suture.

Postcranial skeleton

A partial anterior vertebral column with ribs, endoskeletal and dermal pectoral elements and both humeri are preserved in one block (Fig. 6). In addition, the following bones are also present in a more or less disarticulated state: several presacral vertebrae, a short series of caudal vertebrae, right ischium, femur, fibula, left tibia, and one phalanx (Figs. 6–9).

Vertebrae.—A few vertebrae are relatively well-preserved, and their individual structures are easily recognizable. One well-preserved neural arch lies close to the fourth rib (Fig. 6A) and comparison with the vertebral column of *Discosauriscus austriacus* (Klembara and Bartík 2000) indicates that it is probably the 4th presacral neural arch. Its anatomy is similar to that in *D. austriacus*. Several other preserved vertebrae have slightly swollen neural arches halves, which were joined in the median plane via cartilage in life (Fig. 7A). In similarly large specimens of *D. austriacus*, vertebrae with such morphology are present in the posterior half of the presacral vertebral column.

One isolated trunk pleurocentrum and several caudal pleurocentra are present (Fig. 7B_1, B_2, C_1). The isolated pleurocentrum forms a complete ring. A distinct parapophysis is present in the anteroventral portion of its lateral wall. In similar-sized specimens of *D. austriacus* the parapophyses are preserved on first caudal pleurocentra, which form completely ossified rings (Klembara and Bartík 2000: fig. 2). Immediately behind this pleurocentrum is a completely ossified intercentrum (Fig. 7B). It is a bilaterally expanded plate with slightly dorsally curved lateral margins. The neural arches of the caudal vertebrae are flexed posteri-

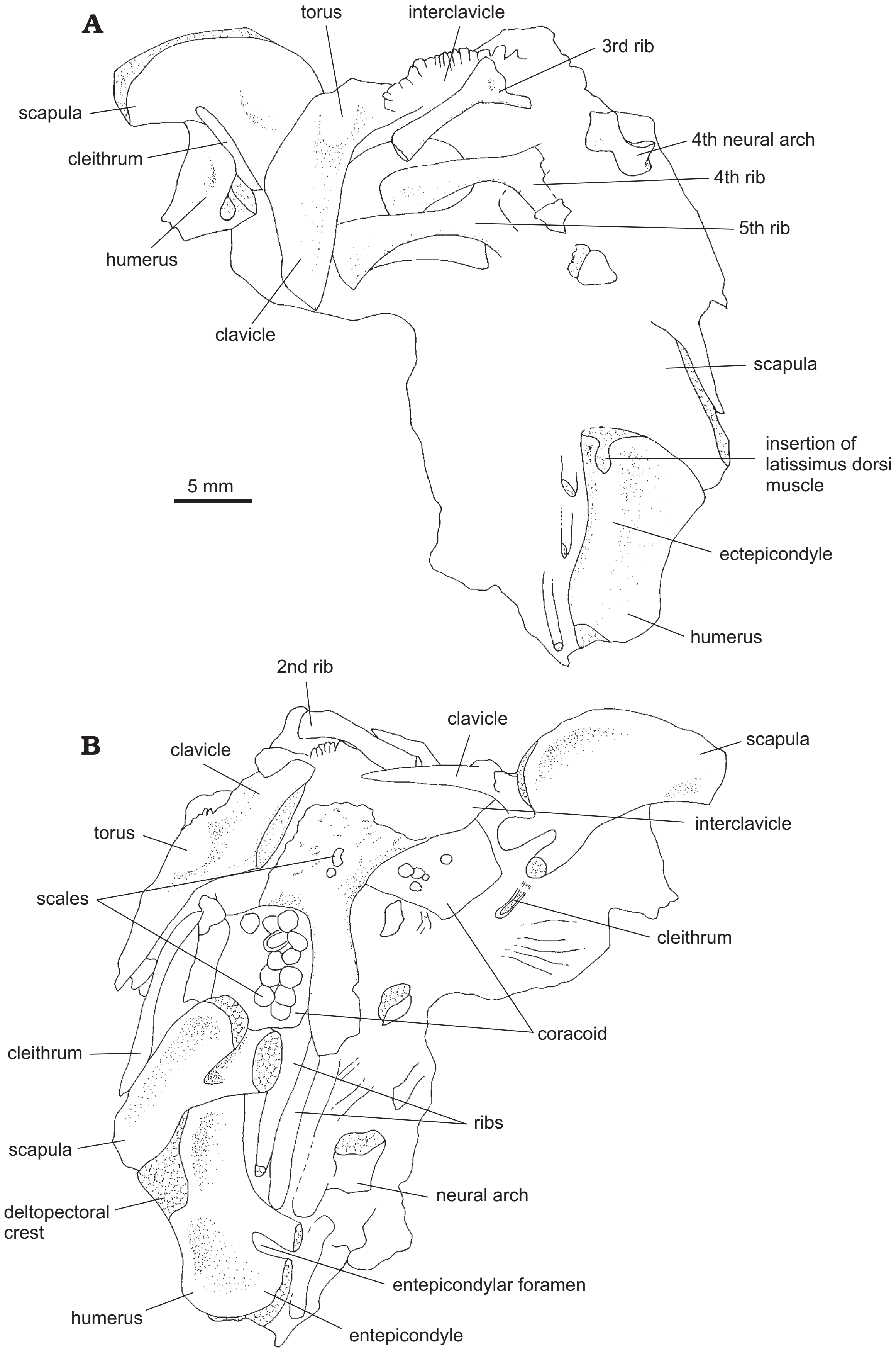

Fig. 6. *Makowskia laticephala* gen. et sp. nov., SNM Z 26506. **A**. Anterior portion of postcranial skeleton in dorsal view. **B**. The same skeleton in ventral view.

orly (Fig. 7C_1) and have a similar shape as those in *D. austriacus*. Several haemal arches are preserved (Fig. 7C). One is almost completely preserved, and it lies posterior to the last caudal rib in the sequence of vertebrae (Fig. 7C_2). Its haemal canal is large, and its distal end is unfinished, indicating a cartilaginous continuation.

Ribs.—On the basis of conditions in *Discosauriscus austriacus* (Klembara and Bartík 2000: fig. 13) it may be inferred that the series including the second to fifth ribs is preserved in *Makowskia laticephala* (Fig. 6). The second rib is a slender oval rod in cross-section. Its unfinished distal end is not broadened. Its proximal end, although partially damaged, is anteroposteriorly expanded and indicates the presence of both a capitulum and tuberculum. The third rib is relatively massive with a slightly flattened shaft. Its distal end is unfinished and slightly broadened. At its proximal end a distinct capitulum and tuberculum are present. The fourth and fifth ribs are dorsoventrally flattened, and their proximal and distal ends are unfinished. However, their distal ends are distinctly anteroposteriorly broadened, and they extend into the hook-like, posteriorly directed processes. A similar morphology of the corresponding ribs is present also in *Seymouria baylorensis* (White 1939: fig. 14), although the ribs have relatively short shafts. Presently, it is not possible to determine, whether the length of the shaft changes during ontogeny in *Makowskia*. In *Discosauriscus*, *Ariekanerpeton*, and *Utegenia* the distal portions of the corresponding ribs are broadened equally anteriorly and posteriorly.

Several caudal ribs are also present, and they correspond to the fourth to sixth caudal ribs of *Discosauriscus austriacus* (Klembara and Bartík 2000) (Fig. 7C_2). The first two are long and approximately circular in cross-section. Their proximal ends bear distinct capitular and tubercular portions. The third rib is probably the last caudal rib, as it is smallest of the series, and the original sequence of vertebrae is preserved. In addition, the vertebrae with haemal arches first appear posterior to the last rib. In contrast to the conditions of *D. austriacus*, the whole shaft of this rib is flattened and anteroposteriorly broad. Its proximal end is broadened and the capitular and tubercular portions are only partially divided. The distal portions of all three ribs are unfinished.

Pectoral girdle and forelimb.—The interclavicle consists of a large anterior plate and a long posterior stem (Figs. 6B, 8A). In contrast to *Discosauriscus*, the anterior plate is transversely very broad, and its anterior margin bears digitiform processes. The external (ventral) surface of the plate, not covered by clavicles, is triangular in outline and slighly ornamented. The ornamentation consists of low ridges and shallow grooves riadiating from the slightly elevated central part of this triangular portion. Except for the posteriormost portion, the posterior stem is well-preserved. The stem is long and its anteriormost section is bilaterally narrow. Further posteriorly the stem gradually broadens before again narrowing. This shape of the posterior stem is unique within Seymouriamorpha.

Both clavicles are present and complete except for lacking the dorsal tips of their ascending processes (Fig. 6). The ventral plate of the clavicle is elliptical in outline. Its anterior margin bears small pointed processes, which are recorded also in *Discosauriscus austriacus* (Klembara and Bartík 2000: fig. 19b). The lateral portion of the ventral plate is massive, and on its external side, at the transition to the ascending process, there is a blunt torus. The ventral portion of the ascending process is massive and anteroposteriorly broad. The ascending process gradually narrows distally and the anterior margin of its external surface forms a sharp edge.

Both cleithra are preserved (Fig. 6). The cleithrum is long and narrow and is hollowed along its entire length. Whereas no other features are recognizable, its general shape is very similar to that in *Discosauriscus austriacus* (Klembara and Bartík 2000).

The scapula is crescent-shaped, consisting of a large plate with a massive supraglenoid buttress that is triangular in shape (Fig. 6). With the exception of the anterior margin, all other margins are unfinished. The supraglenoid fossa is deep, and the supraglenoid foramen remains open ventrally. A similar degree of ossification of the scapula is seen in comparably sized individuals of *Discosauriscus austriacus* (Klembara and Bartík 2000). On the internal surface of the left scapula is a well-developed subscapular fossa.

Both coracoids are present, but are exposed only in external view, revealing a mostly scaled-covered surface (Fig. 6B). The coracoid is a subquadrangular plate with slightly rounded corners. The posterior margin of the left coracoid is of unfinished bone.

A complete right humerus and a proximal portion of the left are preserved (Fig. 6). The morphology of the humerus is in general very similar to that in *Discosauriscus austriacus* (Klembara and Bartík 2000). Both ends of the humerus are unfinished and most of the structures were cartilaginous. The proximal articular surface extends onto the massively developed, L-shaped deltopectoral crest. The shaft is relatively broad, entepicondyle is very short, and the entepicondylar foramen is not enclosed distally. In most of the similarly sized specimens of *D. austriacus* this foramen is already closed (Klembara and Bartík 2000). However, this may also reflect the individual variability in the rate of ossification of the postcranial bones, which occurs in *D. austriacus*. The ectepicondyle is distinctly developed, exhibiting a massive crest at its distal end and a well-developed process on its proximal end for the insertion of the latissimus dorsi muscle. The distal process is joined with the proximal articular surface of the humerus via a narrow strip of bone. The process for the insertion of the subcoracoscapularis muscle is robust, whereas the supinator process is not developed.

Pelvic girdle and hind limb.—Of the pelvis, only the anterior half of the right ischium is present (Fig. 9A). Its morphology is similar to that in *Discosauriscus austriacus* (Klembara and Bartík 2000) except in being much broader mediolaterally.

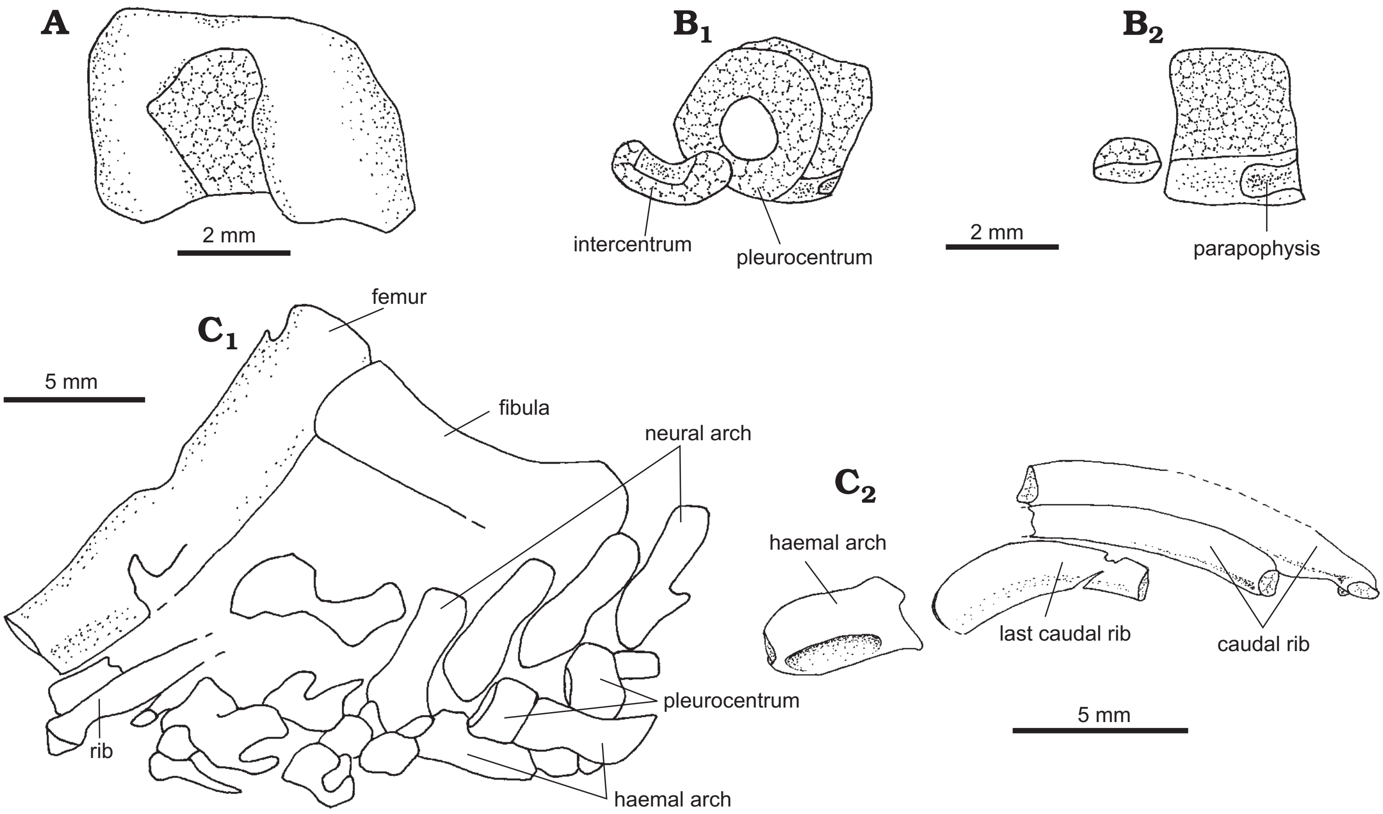

Fig. 7. *Makowskia laticephala* gen. et sp. nov., SNM Z 26506. **A**. Neural arch from the posterior half of the presacral vertebral column in dorsal view. **B**. Pleurocentrum and intercentrum from anterior section of caudal vertebral column in posterolateral (B_1) and right lateral (B_2) views. **C**. Femur, fibula and anterior section of caudal vertebral column in left lateral view (C_1), selected postcranial elements of the same section of vertebral column in right lateral view (C_2).

Most of the right femur is preserved (Fig. 7C_1). Its crescentic-shaped proximal articular surface is of unfinished bone, as is the margin of the well-developed internal trochanter. The intertrochanteric fossa is deep.

The right fibula is compressed (Fig. 7C_1), but its general shape is similar to that in *Discosauriscus austriacus* (Klembara and Bartík 2000: fig. 26).

The left tibia is well-preserved (Fig. 9B). Its proximal end is more robust than the distal end, and both end in unfinished bone. The proximal articulating surface is mediolaterally expanded, whereas the distal articulating surface is oval in outline. The lateral surface of the tibia is concave and bears two prolonged crests separated by a depression between them. These features of the lateral wall of the tibia are not present in *Discosauriscus austriacus* (Klembara and Bartík 2000).

Integument

Several rows and isolated scales are well-preserved (Fig. 6B). They are preserved adhering to the external surface of some elements of the pectoral girdle, particularly the interclavicle and the coracoids. The scales are oval in outline. The diameter of the largest scales varies from 1 to about 1.2 mm. In comparisons with the scales of *Discosauriscus austriacus* (Klembara and Bartík 2000), those of *Makowskia laticephala* are more massive. The external surfaces of the scales are ornamented by concentric elevations separated by grooves of varying depth and width. In addition to the concentric grooves, there are also radially diverging grooves, so that the surface of the scale is divided into small, subquadrangular fields. On the internal surface of the scale, the relatively high concentric ridges are observable. Between them, the fine concentric grooves are present. Fine grooves run also radially. As a whole, a similar morphology of the external and internal surfaces is present also in *D. austriacus* (Klembara and Bartík 2000: fig. 16c, d).

Discussion

Comparisons with discosauriscids and other seymouriamorphs.—The comparisons within the seymouriamorphs below include all ?Upper Carboniferous–Lower Permian taxa known to date: *Utegenia shpinari* Kuznetsov and Ivakhnenko, 1981 (Kuznetsov and Ivakhnenko 1981; Ivakhnenko 1987; Ivakhnenko et al. 1997; Laurin 1996b; Bulanov 2003; Klembara and Ruta 2004a, b), *Seymouria baylorensis* Broili, 1904

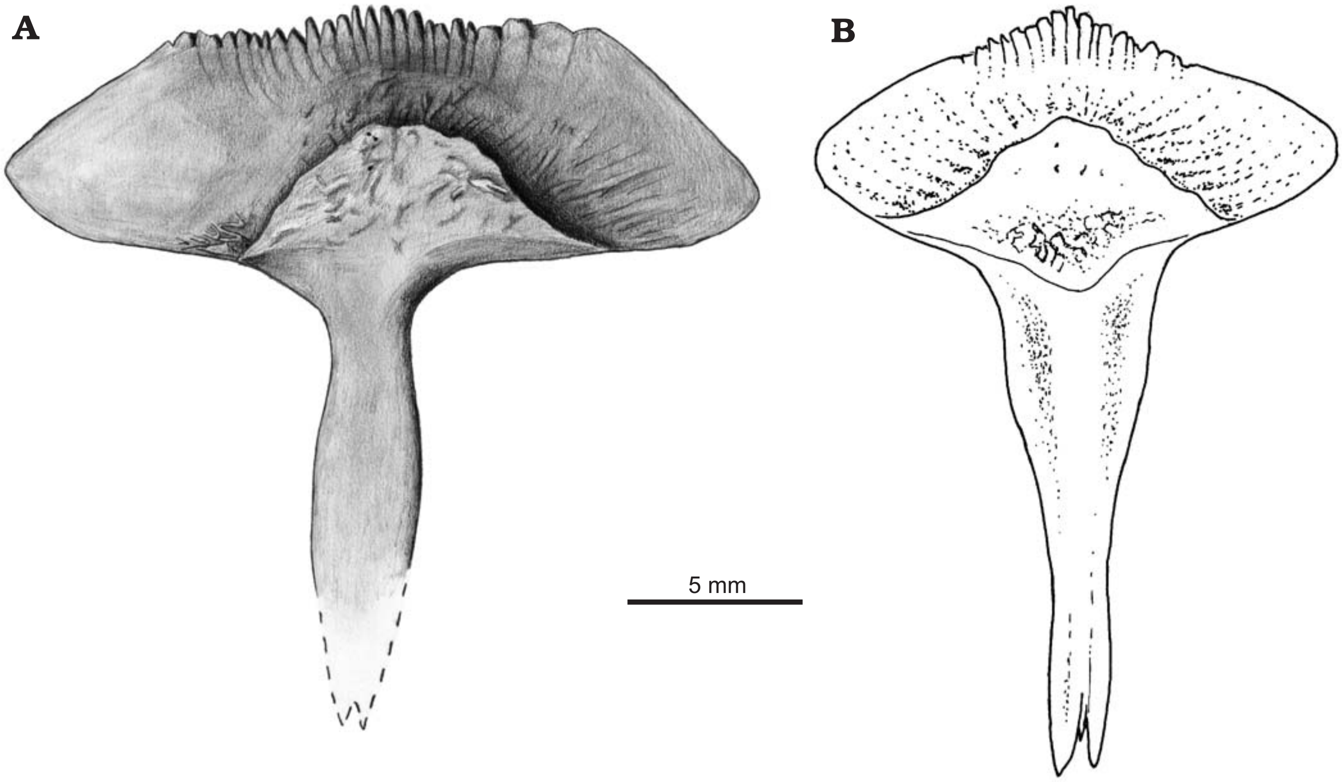

Fig. 8. Interclavicles in ventral views of *Makowskia laticephala* gen. et sp. nov., SNM Z 26506 (**A**) and *Discosauriscus austriacus* (specimen KO 65) (**B**).

(White 1939; Laurin 1996a), *S. sanjuanensis* Vaughn, 1966 (Berman et al. 1987, 2000; Berman and Martens 1993; Laurin 1995, 1996c), *Ariekanerpeton sigalovi* (Tatarinov, 1968) (Ivakhnenko 1981, 1987; Ivakhnenko et al. 1997; Laurin 1996a; Bulanov 2003), *Discosauriscus austriacus* (Makowsky, 1876) and *D. pulcherrimus* (Fritsch, 1879) (Klembara 1997; Klembara and Bartík 2000), and *Makowskia laticephala* gen. et sp. nov. The comparisons do not include the Upper Permian forms from Russia, the kotlassiids and leptorophids, attributed by some authors to Seymouriamorpha (e.g., Ivakhnenko 1987; Bulanov 2003).

Makowskia laticephala gen. et sp. nov. is included in the family Discosauriscidae on basis of the following skeletal and integumentary characters:

(1) Short preorbital region. *Makowskia* is a typical short-snouted discosauriscid. The skulls of *Discosauriscus austriacus* and *Ariekanerpeton* are also short-snouted, being about as long as there are broad; the skull of *D. pulcherrimus* is slightly longer as broad. In *Makowskia* the skull is even broader.

(2) Orbits are positioned mainly in the posterior portion of the anterior half of the skull.

(3) Otic notch is dorsoventrally broad and anteroposteriorly deep. This results in the skull being high in the postorbital region.

(4) Rounded to oval ventral scales.

Those skull proportions that are displayed in all three discosauriscid genera are in contrast with the conditions in the members of two other seymouriamorph genera—*Utegenia* and *Seymouria* in which:

(1) The preorbital region is long and also the whole skull is long.

(2) The orbits lie in the mid-length of the skull.

(3) The otic notch is very shallow in *Utegenia* and its morphology is similar to that in embolomeres (Klembara and Ruta 2004a). In *Seymouria*, the otic notch is anteroposteriorly deep, but dorsoventrally narrow. In *Utegenia* and *Seymouria* the postorbital region of the skull is thus relatively dorsoventrally lower.

(4) In *Seymouria* the ventral scales are absent. In *Utegenia* the ventral scales are elongated and arranged in the chevron-like pattern. Such an arrangement is present in embolomeres (e.g., *Proterogyrinus scheelei*, Holmes 1984).

Makowskia laticephala differs from both species of the genus *Discosauriscus* (Klembara 1997; Klembara and Bartík 2000) and *Ariekanerpeton sigalovi* (Ivakhnenko 1981, 1987; Ivakhnenko et al. 1997; Laurin 1996a; Bulanov 2003) in the following characters:

(1) Nasal equally long as broad. In known size range of *Makowskia* the nasal is longer than broad in *Discosauriscus* and *Ariekanerpeton*. The broad nasal, together with the wide interorbital region, result in a very broad preorbital region in *Makowskia*.

(2) Broad interorbital region. The width of the frontal and that of the prefrontal-postfrontal suture are together much broader than those in *Discosauriscus* and *Ariekanerpeton*.

(3) Prefrontal-postfrontal contact lies in level of frontal mid-length. This difference is only relative to the condition in *Discosauriscus pulcherrimus* in which the prefrontal-post-

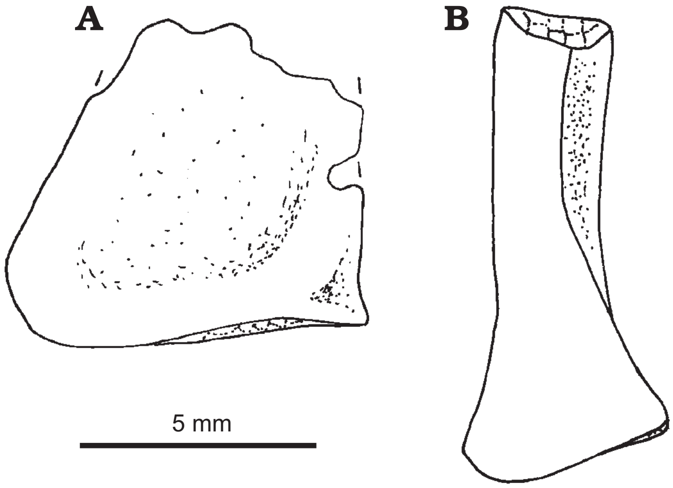

Fig. 9. *Makowskia laticephala* gen. et sp. nov., SNM Z 26506. Right ischium in ventral view (**A**), left tibia in anterior view (**B**).

frontal contact lies at the level of the anterior third of the frontal.

(4) Maxilla is deepest at mid-length. The maxilla in *Discosauriscus* and *Ariekanerpeton* is deepest in its anterior portion.

(5) A relatively short, dorsoventrally broad suborbital ramus of jugal. In *Makowskia* the jugal is stout and together with the stout suborbital ramus of the lacrimal produce a relatively high suborbital wall, and their long contact extends in an anterodorsal-posteroventral direction. A high suborbital wall is not present in similarly sized specimens of *Discosauriscus* and *Ariekanerpeton*. In *Discosauriscus* and *Ariekanerpeton* the jugal-lacrimal suture is relatively short between the tips of both bones.

(6) Postorbital anteroposteriorly short and without an elongated, pointed posterior process. The postorbital in *Makowskia* is relatively short compared to those in *Discosauriscus* and *Ariekanerpeton* in which the postorbital forms a distinct, posteriorly directed pointed process.

(7) Ventral surface of basioccipital smooth. In *Discosauriscus* and *Ariekanerpeton* the ventral surface of the basioccipital carries strong oblique ridges running anterolaterally to posteromedially, and delimiting a weakly concave depression.

(8) Rows of small denticles placed on distinct ridges and intervening furrows radiate from place immediately laterally to the articular portion on the ventral surface of the palatal ramus of the pterygoid. This difference is relative only to *Discosauriscus pulcherrimus* in which rows of small denticles radiate from the midline of the posterior half of the ventral surface of the palatal ramus of the pterygoid, and the ridges are absent.

(9) Anterior margin of transverse flange of pterygoid extends obliquely anteromedially-posterolaterally. In *Discosauriscus* and *Ariekanerpeton* the anterior and posterior margins of the transverse flange are in parallel to one another.

(10) Relatively short and slightly rounded cultriform process of parasphenoid. In *Discosauriscus* and *Ariekanerpeton* the cultriform process is relatively longer and pointed.

(11) Ventral surface of posterior plate of parasphenoid heavily sculptured. This difference is relative only to *Discosauriscus pulcherrimus* and *Ariekanerpeton*. In *D. pulcherrimus* the ventral surface of the parasphenoid plate is smooth and bears small denticles arranged in rows or scattered. In *Ariekanerpeton*, the ventral surface of the parasphenoid plate is smooth.

(12) Distal ends of fourth and fifth presacral ribs distinctly anteroposteriorly broadened, and extend into the hook-like, posteriorly directed processes. In *Discosauriscus* and *Ariekanerpeton* the distal portions of the corresponding ribs are broadened equally anteriorly and posteriorly.

(13) Shaft of ?last caudal rib flattened and anteroposteriorly broad. In *Discosauriscus* the lst caudal rib is narrow. The caudal ribs are not preserved in *Ariekanerpeton*.

(14) Posterior stem of interclavicle narrows anteriorly and posteriorly from broadened mid-length section. In *Discosauriscus* and *Ariekanerpeton* the anterior half of the posterior stem is broader than its posterior half (Fig. 8). The broader, mid-length section is delimited by shallow lateral constrictions.

Makowskia laticephala differs from both species of the genus *Discosauriscus*, *Ariekanerpeton sigalovi* and other seymouriamorphs—*Utegenia shpinari* (Kuznetsov and Ivakhnenko 1981; Ivakhnenko 1987; Ivakhnenko et al. 1997; Laurin 1996b; Bulanov 2003; Klembara and Ruta 2004a, b), and both species of *Seymouria* (White 1939; Berman et al. 1987, 2000; Berman and Martens 1993; Laurin 1995, 1996c) in the following characters:

(1) Nasal equally long as broad. In *Utegenia* and *Seymouria* the nasal is always longer than broad.

(2) Broad interorbital region. The width of the frontal and that of the prefrontal-postfrontal suture are together much broader than those in *Utegenia* and *Seymouria*. The prefrontal-postfrontal suture is broad in similar-sized *Utegenia* and larger *Discosauriscus austriacus* (Klembara 1997) and *Seymouria sanjuanensis* (Berman and Martens 1993), however, the frontal is relatively narrow in all these forms. The prefrontal-postfrontal suture is very short in the smallest known *S. sanjuanensis* specimen (MNG 7859, skull length about 20 mm) from Germany mentioned by Berman and Martens (1993) (personal observation). The length of the suture in this specimen correspons to that in similar-sized specimens of *Discosauriscus*, *Ariekanerpeton*, and *Utegenia*.

(3) Maxilla is deepest at mid-length. The maxilla in *Utegenia* and *Seymouria* is deepest in its anterior portion.

(4) A relatively short, dorsoventrally broad suborbital ramus of jugal. A high suborbital wall is not present in similarly sized specimens of *Utegenia* and the juvenile specimen of *S. sanjuanensis* from Germany (Berman and Martens 1993). In *Utegenia* the jugal-lacrimal suture is relatively short between the tips of both bones. In larger *S. baylorensis* and *S. sanjuanensis* specimens this suture is relatively long, but extends in an anteroventral-posterodorsal direction.

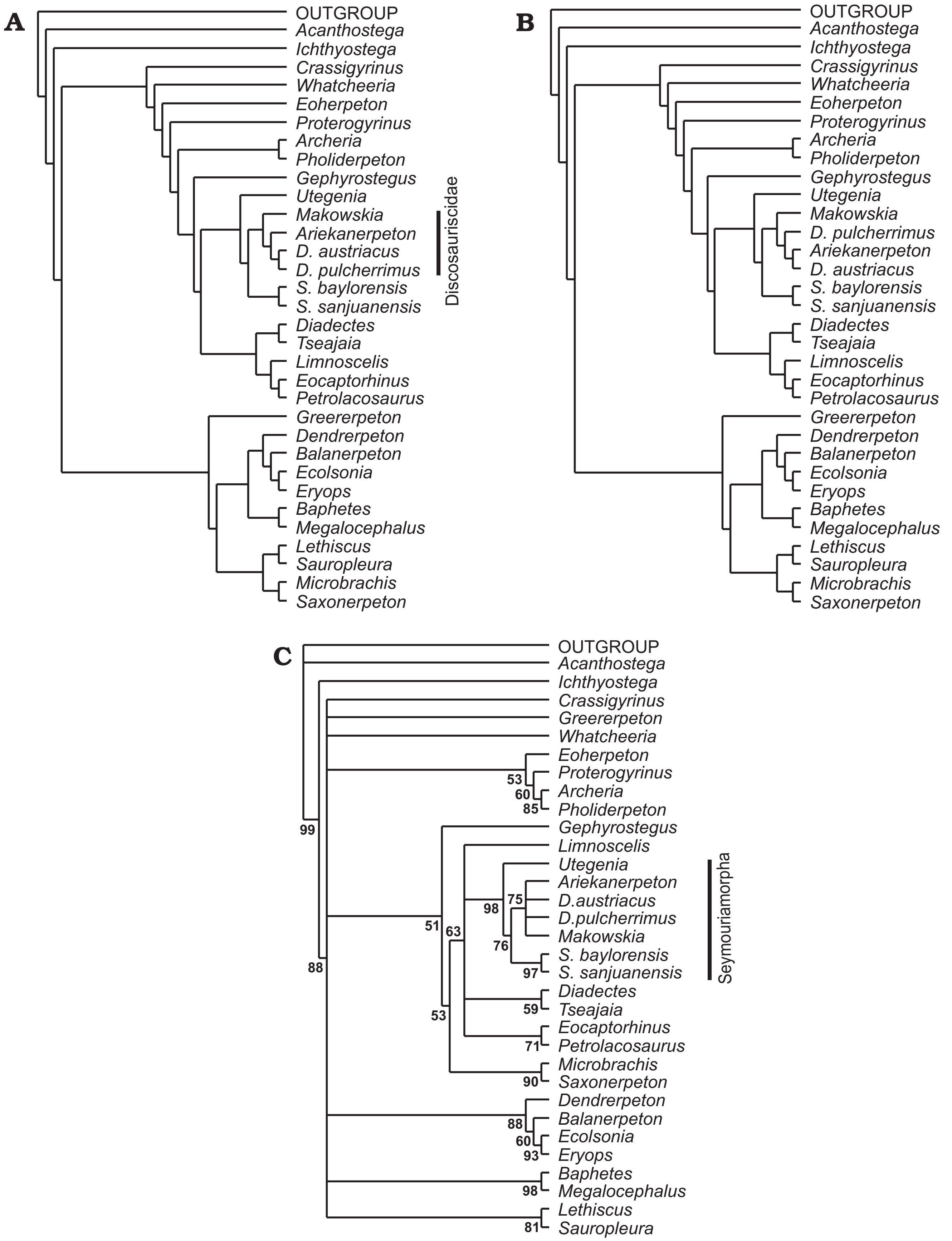

Fig. 10. Phylogenetic analysis. **A**, **B**. Two of six most parsimonious trees recovered by PAUP* 40b10 from a heuristic search of 33 taxa and 150 characters. **C**. Bootstrap percentages on a 50% majority-rule consensus tree.

(5) Postorbital anteroposteriorly short and without an elongated, pointed posterior process. The postorbital is relatively short compared to those in *Utegenia* and juvenile *Seymouria sanjuanensis* in which the postorbital forms a distinct, posteriorly directed pointed process.

(6) Anterior margin of transverse flange of pterygoid extends obliquely anteromedially-posterolaterally. In *Utegenia* and *Seymouria sanjuanensis* the anterior and posterior margins of the transverse flange are in parallel to one another. In *S. baylorensis* (in the sense of White 1939) the margins are parallel one to another. However, according to Laurin (1996b), the lateral half of the anterior margin in *S. baylorensis* is redirected anterolaterally-posteromedially so as to form a wedge-like suture with the ectopterygoid.

(7) Relatively short and slightly rounded cultriform process of parasphenoid. In *Utegenia* and *Seymouria* the cultriform process is relatively longer and pointed.

(8) Shaft of ?last caudal rib flattened and anteroposteriorly broad. In *Seymouria* the last caudal rib is narrow and pointed. The caudal region of the vertebral column is not well-preserved in *Utegenia* but several caudal ribs preserved are not broadened.

(9) Posterior stem of interclavicle narrows anteriorly and posteriorly from broadened mid-length section. In *Utegenia* the stem is very broad anteriorly, then narrows posteriorly, but with its posterior end slightly broadened. In *Seymouria baylorensis* the stem is broadest anterorly, gradually narrows posteriorly before slightly broadening at its posterior end (White 1939). In *S. sanjuanensis*, however, the posterior end of the stem (completely preserved in CM 28597) is not broadened, but is of the same width as the stem in the level of its mid-length. Outlines of the stems of *Utegenia* and *Seymouria baylorensis* are similar except for the stem of *Utegenia* being relatively short, with a length subequal to the anterior plate.

Phylogenetic analysis.—Phylogenetic analysis of ?Upper Carboniferous–Lower Permian seymouriamorphs has been recently made by Klembara and Ruta (2004b). As well as seymouriamorphs, their analysis includes also several other early tetrapods, 31 taxa in total and one hypothetical, all-zero outgroup. The taxa were coded for 150 morphological characters.

Here I included *Makowskia laticephala* into the data matrix of Klembara and Ruta (2004b), and retained their 150 characters; as for the discussion of topology of other taxa than those belonging into Seymouriamorpha, see Klembara and Ruta (2004b). I have made several changes in the definitions of the characters here; these are as follows: (i) definition of character 6 is emended; (ii) new states are added to characters 3, 47, and 56 (Appendix 1). Besides this, I have recoded several characters of seymouriamorph taxa (Appendix 2). The data matrix was processed with PAUP* (v. 40b.10; Swofford 2001) on Pentium PC and the obtained trees printed using TreeView (Page 1996). Characters are unordered and of equal weight. The matrix was analysed using the heuristic search algorithm and ACCTRAN optimization. The result of analysis are six most parsimonious trees of 525 steps (CI = 0.4019; RI = 0.6948; RC = 0.2793). In all six trees, *Makowskia* forms a sister taxon to *Ariekanerpeton*, *Discosauriscus austriacus*, and *D. pulcherrimus*. In three of them *D. austriacus* and *D. pulcherrimus* are sister taxa to *Ariekanerpeton* (Fig. 10A), and in three other trees, *Ariekanerpeton* and *D. austriacus* are sister taxa to *D. pulcherrimus* (Fig. 10B). The strict consensus tree of six trees shows a trichotomy of *Ariekanerpeton*, *D. austriacus*, and *D. pulcherrimus*. To resolve this trichotomy, additional material especially of the postcranial skeleton of *Ariekanerpeton* and *D. pulcherrimus* is required.

Contrary to the cladogram of Klembara and Ruta (2004b), *Makowskia*, *Ariekanerpeton*, *Discosauriscus austriacus*, and *D. pulcherrimus* form a clade, which is the sister taxon to both species of *Seymouria*, and *Utegenia* is basal to both *Seymouria* species. A bootstrap analysis shows a strong support for separation of Discosauriscidae and Seymouriidae, and the node linking *Utegenia* with Seymouriidae plus Discosauriscidae is also strongly supported (Fig. 10C).

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Appendix 1

Data matrix

OUTGROUP
0000000000 0000000000 0000000000 0000000000 0000000000 0000000000
0000000000 0000000000 0000000000 0000000000 0000000000 0000000000
0000000000 0000000000 0000000000

Acanthostega gunnari
2000000000 00000000?? 00???00010 0?00000000 1100100?0 00000?0000
0000010000 0000000000 ?000000000 0000000000 0000000111 0000001100
0000000000 0000000000 00000?0000

Archeria crassidisca
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???????01? 00?0?00000 00?2100001 0?01011111 1100111111 1220000111
1112200000 0010112101 0111?10001

Ariekanerpeton sigalovi
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1001110111 1111111110 0111211111 0112001111 1??0111111 ?1?011??11
1142010 1?0 21?1012100 0??1?????1

Balanerpeton woodi
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1011101110 0000100000 000?000001 ?100001010 0010111111 000001??11
1040100000 20001?2101 01020??000

Baphetes kirkbyi
2100000000 0000010100 1000011000 0111000000 03100100?? 1101000011
1011101110 0000000000 ?000?01?00 ?????????? ?????????? ??????????
????0?0??? ???0002100 0?????????

Crassigyrinus scoticus
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1000100010 0000000000 ?00??00?01 ?000000011 0000000111 ?001000111
?01?10?00? 0000011000 00????0??1

Dendrerpeton acadianum
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??4010000? 20101?2100 110?0????0

Diadectes absitus
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1011101110 0001200000 00?1201001 020221??11 1001?11??1 000111????
0142010111 1120112100 0111011111

Discosauriscus austriacus
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1001110110 1111111110 0111211111 0112011111 1000111111 111011??11
1142010110 2121012101 0??110?000

D. pulcherrimus
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1142010110 ???1012101 0??11?????

Ecolsonia cutlerensis
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11?030000? 220011211? 010??????0

Eocaptorhinus laticeps
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0142010111 2200?????1 1111010111

Eoherpeton watsoni
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Eryops megacephalus
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1020100000 2000011100 0101000000

Ichthyostega stensioei
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Lethiscus stocki
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Limnoscelis paludis
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Megalocephalus pachycephalus
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00???????? ?????????? ??????????

Microbrachis pelikani
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1111111111 1100200000 ?000201011 0?13001011 1000111111 010001??11
1012?00110 3000???101 10?3010001

Petrolacosaurus kansensis
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Pholiderpeton scutigerum
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Proterogyrinus scheelei

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1014100000 0010111101 0111?00001

Sauropleura pectinata/scalaris

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1100110010 0000?00000 ?00?000001 ?00310??11 0001?01??1 000001????
?142?01000 20000??110 01?2?10100

Saxonerpeton geinitzi

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11111????0 0?0??00000 ?00?201011 0?13?????? ?????????? ??????????
??42??0110 20001??101 1102?10001

Seymouria baylorensis

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1011111110 00011?0010 ?1?1201111 1212011111 1000111111 ?11011??11
1142010111 0121012100 0?01110000

S. sanjuanensis

1000010010 11223001?? 3101100101 1111100011 3210010201 1112331011
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Tseajaia campi

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1142010111 1120112100 0101011111

Utegenia shpinari

1000010000 1012200101 2100101001 1111010012 1110111201 1122231001
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11320?0??0 21???????? ???1?????1

Whatcheeria deltae

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?0?0?0?0?? ?????????? ????200101 ??000????? 0??00??111 0000?01011
1013100000 0000001100 01???????1

Appendix 2

Character list

For sources of each taxon, see Klembara and Ruta (2004b).

1. Position of mid-point of maximum anteroposterior orbit diameter: closer to tip of snout than to posterior end of skull (0); in the middle of skull length (1); closer to posterior end of skull than to tip of snout (2).
2. Absence (0) or presence (1) of antorbital vacuities.
3. Skull longer than broad (0) as broad as long (1) or broader than long (2).
4. Preorbital region of skull less than twice as wide as long (0) or at least twice as wide as long (1).
5. Absence (0) or presence (1) of condition: nasals much shorter than frontals (less than one-third as long as frontals).
6. Total width of premaxillae more (0) or less (1) than two-thirds of the width of the skull table.
7. Absence (0) or presence (1) of distinct, triangular or digitiform, dorsal alary processes of premaxillae, widely separated by intervening nasals.
8. Presence (0) or absence (1) of prefrontal-postfrontal suture.
9. Position of prefrontal-postfrontal suture relative to the mid-length of the frontal: posterior (0); at the same level (1); anterior (2).
10. Broad (0) or point-like (1) prefrontal-postfrontal contact.
11. Postorbital medial margin straight for most of its length or very gently curved (1), irregularly sinuous (0).
12. Postorbital not broader than long (0) or broader than long (1).
13. Postorbital without distinct ventrolateral (jugal) ramus (0), with incipient ramus (1), with well-developed and elongate ramus (2).
14. Postorbital without distinct dorsomedial ramus for postfrontal (0), with incipient ramus (1), with elongate ramus (2).
15. Absence of outgrowth from posterolateral ventral surface of tabular (0), presence of outgrowth in the form of spike-like unornamented component (1), elongate and recurved blade (2), rectangular, plate-like process (3), presence of conical extension of unornamented portion of posterolateral corner of tabular (4).

16. Absence (0) or presence (1) of tabular buttons.
17. Absence (0) or presence (1) of prolonged posterolateral ornamented surface of tabular.
18. Septomaxilla absent (0) or present (1).
19. Septomaxilla forming part of skull roof (0) or not (1).
20. Septomaxilla touching nasal (0) or not (1).
21. Nostrils slit-like (0), round (1), elliptical and wide (2), elliptical and elongate (3), keyhole-shaped and longer than premaxilla (4).
22. Maximum diameter of nostril less wide than (0) or almost as wide as premaxilla (1).
23. Intertemporal present (0) or absent (1).
24. Intertemporal smaller than supratemporal (0) or larger than/comparable in size with supratemporal (1).
25. Parietal-tabular contact absent (0) or present (1).
26. In lateral view, quadratojugal underlies jugal (0), jugal-quadratojugal suture is oriented approximately dorsoventrally (1), jugal underlies quadratojugal (2).
27. Jugal not interposed between maxilla and quadratojugal (0) or interposed (1).
28. Absence (0) or presence (1) of flange-like, ventrolateral sheet of bone formed by tabular and supratemporal.
29. Prefrontal-jugal suture absent (0) or present (1) (lacrimal not entering orbit).
30. Dorsalmost part of quadratojugal above (0) or below (1) highest point of maxilla.
31. Absence (0) or presence (1) of posteromedial extensions of unornamented portions of postparietals projecting posteroventrally (presence of a rearward process).
32. Suborbital ramus of lacrimal present and long (0) (more than one third of ventral half of orbit rim), present and short (1) (less than one third of ventral half of orbit rim), absent (2).
33. Postorbital region of jugal longer (0) or shorter (1) than suborbital region.
34. Depth of suborbital region of jugal more (0) or less (1) than half of the length of anteroposterior orbit diameter.
35. Length of postorbital region of jugal more (0) or less (1) than one third of the length of the postorbital cheek region.
36. Postorbital process of jugal rectangular, with bluntly terminated posterior end (1) or not (0).
37. Broad (0) or narrow (1) postorbital-jugal contact (length of suture less than three times the distance between dorsalmost and ventralmost point of orbital edge of postorbital).
38. Posterior apex of postorbital lying posterior to (0) or anterior to/at same level as rearmost part of postfrontal (1).
39. Together, parietals not (0) broader than long or broader (1).
40. Lateral margins of skull table irregular (0), straight or gently concave (1), convex at level of supratemporals (2).
41. Squamosal embayment absent (0), shallow (squamosal straight) (1), deep and dorsoventrally broad (squamosal semicircular) (2), deep and dorsoventrally narrow (3).
42. Unornamented otic flange of squamosal absent (0), narrow (1), broad ventrally (2), narrow ventrally and broad dorsally (3).
43. Squamosal-tabular suture present (0) or absent (1).
44. Maxilla highest point in anterior third of its length (0) or in the middle (1).
45. Palatal vacuities absent (0), present narrow (1), present broad (2).
46. Shape of cultriform process biconvex (0), narrow triangular (1), parallel-sided (2), with proximal constriction followed by swelling (3).
47. Ventral surface of pterygoid palatal ramus covered with shagreen (0), with radiating, densely spaced low ridges with denticle rows (1), with radiating sharp ridges with denticles (2), with densely spaced denticle rows radiating from posterior mid-length of palatal ramus (3), with tooth row(s) along medial margin (4), with multiple rows running mostly parallel to mesial and lateral margins of palatal ramus (5), smooth (6).
48. Transverse pterygoid flange absent (0), present as an incipient downturning [torus transiliens] (1), present as a distinct ridge (2).
49. Absence (0) or presence (1) of teeth on transverse pterygoid flange.
50. Pterygoids not visible in lateral aspect below ventral margin of jugal and quadratojugal (0) or visible (1).
51. Absence (0) or presence (1) of posterior plate of parasphenoid.
52. Absence (0) or presence (1) of ventrolateral crests of parasphenoid.
53. Median posterior process of parasphenoid absent (0), present and unpaired (1), present and paired (2).
54. Parasphenoid posterolateral processes absent (0), present and short (1), present, elongate and wing-like (2).
55. Parasphenoid cultriform process with shagreen (0), with patch of denticles (1), with radiating ridges and denticle rows (2), smooth (3).
56. Posterior plate of parasphenoid behind cultriform process with shagreen (0), with denticulated field (1), sculptured with or without denticles (2), with light striations (3), smooth (4), smooth with denticles arranged in rows or scattered (5).
57. Ventral, exposed surface of vomers narrow, elongate and strip-like (1) or not (0).
58. Presence (0) or absence (1) of fangs on vomer.
59. Absence (0) or presence (1) of shagreen on vomer.
60. Presence (0) or absence (1) of subcentral tooth row (teeth comparable in size to marginal series, often aligned with fangs) on vomer, or presence of row along medial margin (2).
61. Presence (0) or absence (1) of denticle row (line of small teeth between tooth row and lateral margin of the bone) on vomer.
62. Presence (0) or absence (1) of fangs on palatine.
63. Absence (0) or presence (1) of shagreen on palatine.
64. Presence (0) or absence (1) of tooth row on palatine.
65. Presence (0) or absence (1) of denticle row on palatine.
66. Presence (0) or absence (1) of fangs on ectopterygoid.
67. Absence (0) or presence (1) of shagreen on ectopterygoid.
68. Presence (0) or absence (1) of tooth row on ectopterygoid.
69. Presence (0) or absence (1) of denticle row on ectopterygoid.
70. Denticle rows on vomer (continuation of rows on pterygoid) absent (0) or present (1).
71. Denticle rows on palatine (continuation of rows on pterygoid) absent (0) or present (1).
72. Denticle rows on ectopterygoid (continuation of rows on pterygoid) absent (0) or present (1).
73. Row(s) of denticles lining the exochoanal margin absent (0) or present (1).
74. Ectopterygoid partly separated from cheek (1) or not (0).
75. Ectopterygoid longer than (0), as long as (1), shorter than (2) palatine.
76. Anterior, triangular, wedge-like, more or less distinct process immediately anterior to basipterygoid processes absent (0) or present (1).
77. Lateral margins of posterior plate of parasphenoid not sharp (0) or sharp (1).
78. Lateral margins of posterior plate of parasphenoid raised all around (1) or not (0).
79. Lateral margins of posterior plate of parasphenoid confluent with anterior wedge-like process (1) or not (0).
80. Jagged margins of posterior plate of parasphenoid behind basipterygoid processes present (1) or absent (0).
81. Posterolateral angles of posterior plate of parasphenoid extending laterally on medioventral part of posterolateral processes (0) or not (1) (forming acute angles with horizontal plane).
82. Absence (0) or presence (1) of otic tubes.
83. Absence (0) or presence (1) of suborbital fenestra.

84. Posttemporal fossae large (0) (dorsal surface of fossa occupying more than half of maximum width of tabular ornamented surface), small (1), absent (2).
85. Interclavicular stem absent (0), elongate and subtriangular with blunt posterior end (1), elongate and rod-like but without expansion along its shaft (2), elongate and rod-like and with broadened posterior portion (3), elongate and rod-like and with middle expansion along its shaft (4).
86. Anterior margin of ventral plate of clavicle without (0) or with (1) fimbriate indentations.
87. Clavicle ventral plate with anterior expansion (0) or anteroposteriorly narrowed (1).
88. Scapular and coracoid not separate (0) or separate (1).
89. Cleithrum with (0) or without dorsal expansion (1).
90. Cleithrum with (0) or without (1) branchial lamina.
91. Atlantal rib present (0) or absent (1).
92. Chevron-like rectangular gastralia present (0), round gastralia present (1), absence of gastralia (2).
93. Angular reaches rear end of jaw (1) or not (0) in lateral aspect.
94. Adductor ("surangular") crest absent (0), formed only by surangular (1), formed by third coronoid and surangular (2), formed by dentary (3).
95. Three (0) or one (1) coronoids.
96. Posterior coronoid not exposed in lateral view (0) or exposed (1).
97. Contact between anterior coronoid and mesial lamina of splenial absent (0) or present (1).
98. Contact between middle coronoid and mesial lamina of splenial absent (0) or present (1).
99. Mesial lamina of angular absent (0) or present (1).
100. Rearmost part of mesial lamina of splenial closer to adductor fossa (1) than to anterior margin of lower jaw (0).
101. Posterior coronoid without (0) or with (1) posterodorsal process.
102. Suture between prearticular and surangular absent (0) or present (1).
103. Suture between prearticular and splenial present (0) or absent (1).
104. Postsplenial present (0) or absent (1).
105. Mesial lamina of postsplenial absent (0) or present (1).
106. Denticles on prearticular absent (1) or present (0).
107. Adductor fossa faces dorsally (0) or mesially (1).
108. Fangs on anterior coronoid present (0) or absent (1).
109. Fangs on middle coronoid present (0) or absent (1).
110. Fangs on posterior coronoid present (0) or absent (1).
111. Mesially projecting flange on dorsal edge of prearticular absent (0) or present (1).
112. Relatively small posterior Meckelian fenestra between prearticular and angular absent (0), present and small (1), present and large (2) (depth comparable with size of adductor fossa; occasionally shifted slightly anteriorly to involve postsplenial).
113. Relatively small anterior Meckelian fenestra between splenial, postsplenial and prearticular absent (0), present and small (1), present and large (2) (depth comparable with size of adductor fossa; occasionally shifted slightly anteriorly to involve postsplenial).
114. Single, large elongate Meckelian fenestra leaving narrow mesial exposure of splenial (diadectid pattern) absent (0) or present (1).
115. Anterior elongate fenestra between ventromedial anterior lamina of dentary and splenial absent (0) or present (1).
116. Parasymphysial plate present (0) or absent (1).
117. Tooth row of parasymphysial plate absent (0) or present (1).
118. Fang pair of parasymphysial plate absent (0) or present (1).
119. Denticle field on anterior coronoid absent (0) or present (1).
120. Denticle field on middle coronoid absent (0) or present (1).
121. Denticle field on posterior coronoid absent (0) or present (1).
122. Anterior fang pair on dentary present (0) or absent (1).
123. Number of presacral vertebrae: 30 (0), 30–38 (1), more than 38 (2), 30–28 (3), fewer than 28 (4).
124. Pleurocentra paired (0), fused ventrally but forming incomplete rings dorsally (1), forming complete rings (2), fused dorsally but not ventrally (3), with dorsal extremities in contact but not fused (4).
125. Intercentra low (0), crescent (1), disc-like (2), with dorsal extremities in contact but not fused (3).
126. Swollen neural arches absent (0) or present (1).
127. Absence (0) or presence (1) of laterally compressed, rectangular to fan-shaped neural arches.
128. Absence (0) or presence (1) of condition: dorsalmost extremity of ossified part of neural spine aligned vertically with posterior level of pleurocentrum of the same vertebral segment.
129. Absence (0) or presence (1) of condition: height of ossified portion of neural spine plus arch reduced (less than the distance between pre- and postzygapophysis).
130. One (0) or two (1) sacral ribs.
131. Dorsal process of iliac blade high (0), low rounded (1), absent (2), with dorsal notch dividing the blade into small anterior and posterior processes (3).
132. Posterodorsal process of iliac blade elongate and slender (0), stout and abbreviated posteriorly (1), stout and broad posterodorsally (2).
133. Transverse line of ilium absent (0), present (1), presence of iliac shelf (2).
134. Absence (0) or presence (1) of condition: deltopectoral crest L-shaped.
135. Deltopectoral crest in the middle of humerus length (0), more or less halfway between caput humeri and radial condyle, or more proximal (1).
136. Ectepicondyle offset relative to latissimus dorsi process (0) or aligned with the latter (1).
137. Distal extremity of ectepicondyle aligned with ulnar facet (0), between ulnar and radial facets (1), aligned with radial facet (2).
138. Presence (0) or absence (1) of ectepicondylar foramen.
139. Presence (0) or absence (1) of entepicondylar foramen.
140. Distance from most proximal point of articular surface of caput humeri to radial condyle smaller (0) or greater than twice the width of caput humeri (1) in extensor view.
141. Entepicondyle about half as long as humeral shaft (0) or less (1).
142. Olecranon process absent (0) or present (1).
143. Tarsus without (0) or with (1) L-shaped proximal element.
144. Manus with more than five (0), five (1), four (2), three (3) digits.
145. Stapedial foramen present (0) or absent (1).
146. Atlantal pleurocentrum paired (0) or fused (1) in mature individuals.
147. Absence (0) or presence (1) of anteriorly directed, midventral process of axial intercentrum-atlantal pleurocentrum complex.
148. Axial neural arch and pleurocentrum unfused (0) or fused (1).
149. Axial intercentrum and atlantal pleurocentrum unfused (0) or articulated/fused (1).
150. Longest mid-trunk ribs shorter than (0) or at least as long as (1) four mid-trunk vertebrae.