

# The cranial anatomy, ontogeny, and relationships of *Karpinskiosaurus secundus* (Amalitzky) (Seymouriamorpha, Karpinskiosauridae) from the Upper Permian of European Russia

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The Upper Permian seymouriamorph tetrapod *Karpinskiosaurus* from European Russia includes two species: *Karpinskiosaurus secundus* and *Karpinskiosaurus ultimus*. *Karpinskiosaurus secundus* is represented by two specimens with skull lengths of about 75 mm. All specimens of *K. ultimus* are smaller than those of *K. secundus*. Revision of the cranial anatomy of all previously known and several new specimens of *Karpinskiosaurus* shows that the specimens of *K. secundus* and most of the specimens of *K. ultimus* represent the ontogenetic series of one species: *K. secundus*. The holotype specimen of *K. ultimus* requires revision, with the aim to find out whether it represents a second species of *Karpinskiosaurus* or not. The available material permits new reconstructions of the largest, holotype skull, and one smaller skull with a length of about 36 mm. *Karpinskiosaurus secundus* is included in a cladistic analysis for the first time here. The analysis shows it to form a sister taxon to Discosauriscidae. The clade comprising *Karpinskiosaurus secundus* plus Discosauriscidae forms a sister group to Seymouriidae. *Karpinskiosaurus secundus* has a large postorbital and a short preorbital region, and the orbits are placed in the posterior portion of the anterior half of the skull length. Among all seymouriamorphs, such cranial proportions are exhibited only by the largest known specimens of *Discosauriscus austriacus*. None of the specimens of *K. secundus* described here exhibits the presence of sensory grooves; thus, all specimens composing the ontogenetic sequence of *K. secundus* are considered to be terrestrial.

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## INTRODUCTION

The group Seymouriamorpha was erected by Watson (1917) as an order of the class Reptilia. Watson (1917) placed the Lower Permian North American tetrapod *Seymouria baylorensis* (Broili, 1904) in this group. Since that time, the definition of the group Seymouriamorpha and its taxonomic composition has substantially changed (e.g. Romer, 1947; Heaton, 1980; Panchen, 1980; Ivakhnenko, 1987; Panchen & Smithson, 1988). Recently, the group Seymouriamorpha has

been revised by Laurin (2000) and Bulanov (2003). According to Laurin (2000), as well as the Upper Carboniferous–Lower Permian *Utegenia* from Kazakhstan, and the Lower Permian taxa *Seymouria* (North America and Europe), *Discosauriscus* (Europe), and *Ariekanerpeton* (Tadzhikistan), the group Seymouriamorpha also included *Kotlassia*, and probably *Karpinskiosaurus*, from the Upper Permian of Russia. Laurin (1996a) tentatively included *Kotlassia* in his phylogenetic analysis, and his cladogram showed a dichotomy of *Kotlassia* and *Utegenia*. Laurin (1996a) used characters of *Kotlassia* taken from Bystrow (1944) and Ivakhnenko (1987), but

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*Kotlassia* of Bystrow (1944) represents a mixture of the material of two different taxa: *Kotlassia* and *Karpinskiosaurus* (Ivakhnenko, 1987; Bulanov, 2003).

*Kotlassia prima* (Amalitzky, 1921) is known on the basis of the entire skeleton and one additional skull (Amalitzky, 1921; Ivakhnenko, 1987; Bulanov, 2003). According to Bulanov (2003), the genus *Karpinskiosaurus* consists of two species: *Karpinskiosaurus secundus* (Amalitzky, 1921) and *Karpinskiosaurus ultimus* (Tehudinov & Vyushkov, 1956). The species *Karpinskiosaurus secundus* is represented by two large skulls with length of about 75 mm. All specimens considered to represent *Karpinskiosaurus ultimus* are smaller: the largest, partially articulated skull of *Karpinskiosaurus ultimus* is about 40-mm long. According to Bulanov (2003), besides *Kotlassia* and *Karpinskiosaurus*, the taxon Seymouriamorpha also includes three other forms from the Upper Permian of Russia: *Biarmica*, *Leptorophya*, and *Microphon*. In contrast to *Kotlassia* and all other seymouriamorphs, all three latter genera possess tricuspid or multicuspid teeth. According to Bulanov (2003), however, the larval stages of *Karpinskiosaurus ultimus* possess tricuspid teeth, whereas larger, postmetamorphic stages of this species have only monocuspid teeth.

All Upper Carboniferous–Lower Permian seymouriamorphs have been revised recently: *Utegenia* (Bulanov, 2003; Klembara & Ruta, 2004a, b), *Disco-sauriscus* (Klembara, 1997; Klembara & Bartík, 2000), *Ariekenerpeton* (Bulanov, 2003; Klembara & Ruta, 2005a, b), *Seymouria sanjuanensis* (Berman *et al.*, 2000; Klembara *et al.*, 2005, 2006, 2007), and two new genera have been described, namely *Makowskia* (Klembara, 2005) and *Spinarerpeton* (Klembara 2009a), both from the Boskovice Basin in the Czech Republic. Bulanov (2003) revised all Upper Permian taxa that he included in Seymouriamorpha; however, his systematics of Seymouriamorpha has not been tested by phylogenetic analysis using the principle of parsimony.

The aim of this paper is: (1) to provide a detailed revision of the cranial anatomy of the Upper Permian seymouriamorph from European Russia, *Karpinskiosaurus secundus*, based on the original and well-preserved new specimens; (2) to analyse its cranial ontogenetic changes; and (3) to analyse its relationships.

The term skull is used here in the sense of Romer and Parsons (1977).

## MATERIAL AND METHODS

Most of the specimens of *Karpinskiosaurus secundus* studied here have been mechanically prepared. Only the holotype PIN 2005/81 of *Karpinskiosaurus secundus* and specimen PIN 2005/82 are partially chemi-

cally prepared. The skull reconstructions presented here were based on wax-plasticine models. Where possible, every bone was measured and modelled at four (in the case of PIN 2005/81) and six (in the case of PIN 4617/200) times their natural size, and were joined together using flat metal bars. The model of the large skull was made on the basis of specimens PIN 2005/81 (holotype) and PIN 2005/82; the skull length (SL) of both these specimens is about 75 mm. The morphology of only several detailed structures was added using smaller specimens. The sutures painted in black in the skull roof of the holotypic skull are of unknown provenance, and are not fully followed here.

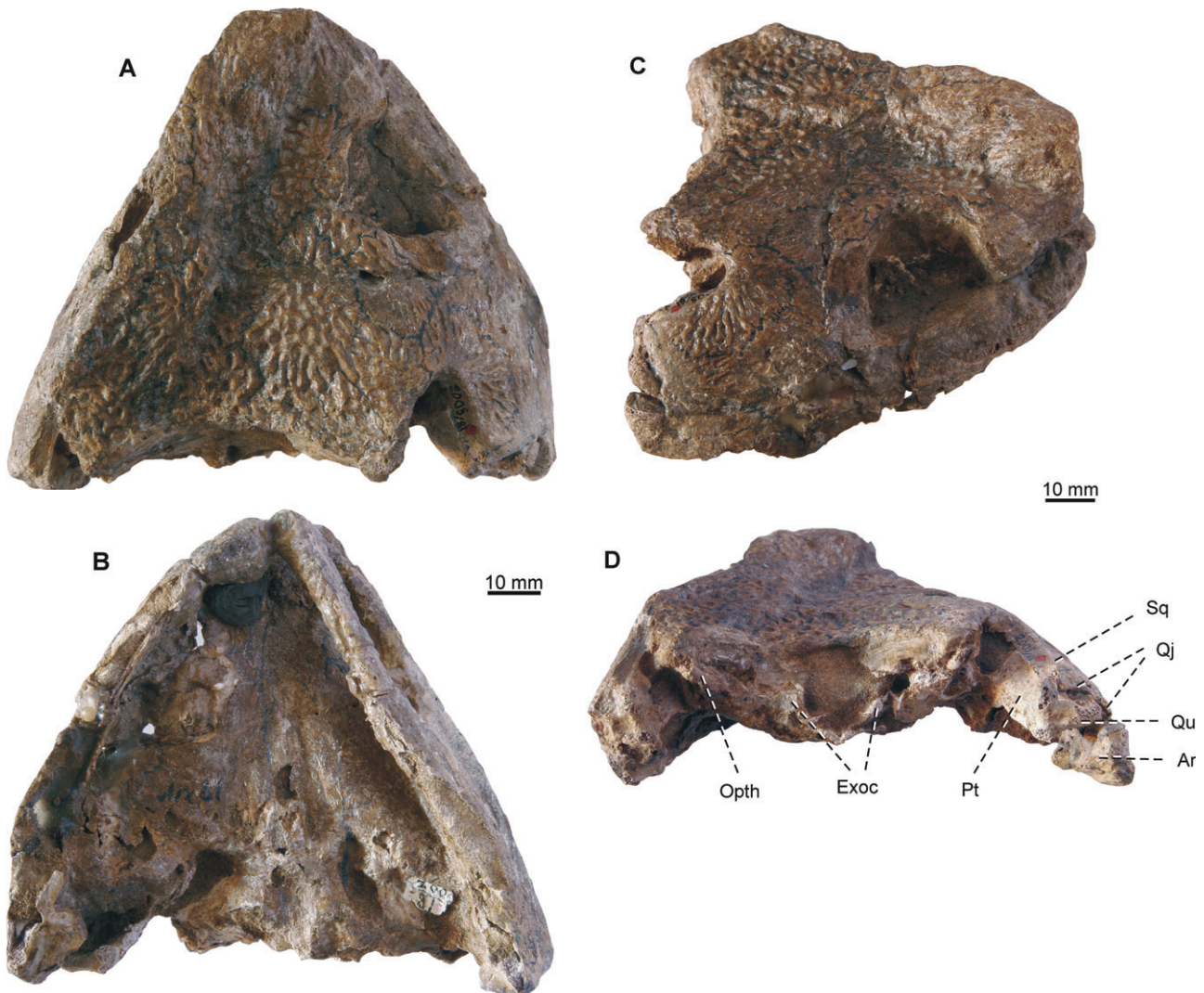
The model of the small skull was mostly based on PIN 4617/200 (SL about 36 mm) and PIN 4617/158 (SL about 40 mm). Some of the palatal bones were reconstructed on the basis of slightly smaller specimens PIN 4617/188, PIN 4617/201, SGU 104B/2009, and PIN 104B/2032. The lower jaw was reconstructed on the basis of PIN 4617/158 and PIN 4617/188.

## INSTITUTIONAL ABBREVIATIONS

PIN, Palaeontological Institute, Russian Academy of Sciences, Moscow, Russia; SGU, Saratov State University, Saratov, Russia; SNM, Slovak National Museum, Bratislava, Slovakia.

## ANATOMICAL ABBREVIATIONS

al.pr, alar process of vomer; am.l, anteromedial lamina of dentary; An, angular; an.fe, anterior fenestra of mandible; Ar, articular; ar.Pmx, premaxillary articulation; ar.po, articular portion of pterygoid; as.l, ascending lamina of pterygoid; as.pr, ascending process of maxilla; a.Sq, area overlapped by squamosal; Boc, basioccipital; bp.pr, basipterygoid process of basisphenoid; clt.pr, cultriform process of parasphenoid; De, dentary; d.f, depression with foramina; Ecpt, ectopterygoid; Exoc, exoccipital; f.ch.t, foramen for chorda tympani; Fr, frontal; in.l., internal lamina of lacrimal; ip.fe, interpremaxillary fenestra; It, intertemporal; Ju, jugal; La, lacrimal; m.c.e, mesial cutting edge; me.l, medial lamina of palatine; Mx, maxilla; Na, nasal; oc.fl, occipital flange; Opth, opisthotic; ot.fl, otic flange (unornamented portion) of squamosal; Pa, parietal; Pal, palatine; pal.r, palatal ramus of pterygoid; Par, prearticular; Pas, parasphenoid; p.Cor, posterior coronoid; Pfr, prefrontal; p.M.fe, posterior Meckelian fenestra; Pmx, premaxilla; Po, postorbital; Pofr, postfrontal; Pp, postparietal; pq.f, paraquadrate foramen; Psp, postsphenial; Pt, pterygoid; Qj, quadratojugal; Qu, quadrate; qu.r, quadrate ramus of pterygoid; ro.fl, rounded unornamented flange of quadratojugal; San, surangular; sd.s, supradental shelf; Smx, septomaxilla; Sp, splenial; Sq, squamosal;



**Figure 1.** *Karpinskiosaurus secundus* (Amalitzky, 1921), PIN 2005/81 (holotype). Photographs of skull in dorsal (A), ventral (B), dorsolateral (C), and ventral (D) views.

St, supratemporal; Ta, tabular; tr.pr, transverse process of pterygoid; u.l.Ta, underlying lamina for tabular; Vom, vomer.

#### SYSTEMATIC PALAEOLOGY

SEYMOURIAMORPHA WATSON, 1917

KARPINSKIOSAURIDAE SUSHKIN, 1925

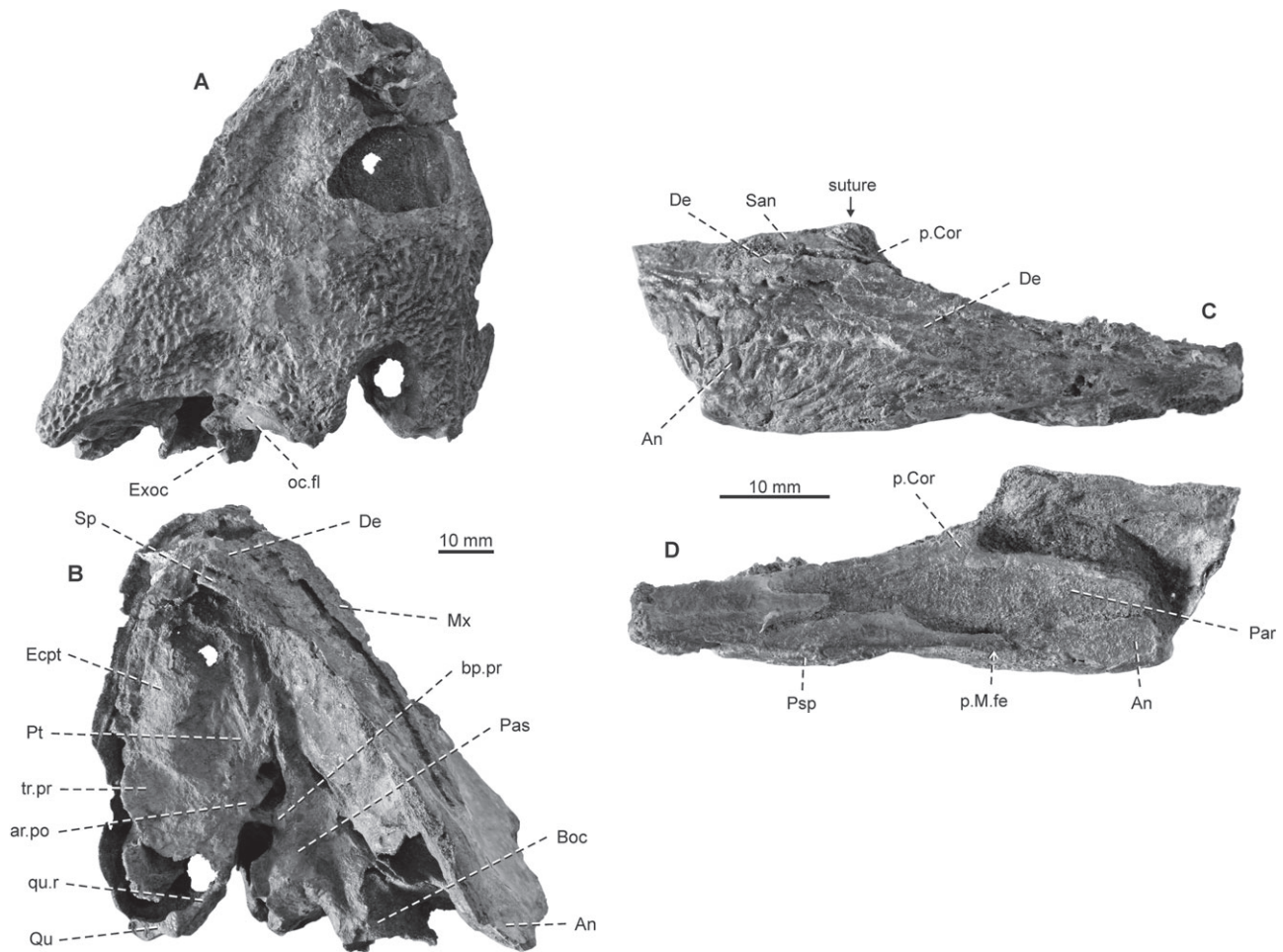
KARPINSKIOSAURUS SUSHKIN, 1925

*KARPINSKIOSAURUS SECUNDUS* (AMALITZKY, 1921)

(FIGS 1–12)

**Taxonomic remarks:** The species *Karpinskiosaurus ultimus* was originally described as *Nycteroleter ultimus* by Tchudinov & Vyushkov (1956). The holotype of *N. ultimus* is an anterior portion of the left dentary with several teeth preserved. The paratypes are exclusively fragments of jaw elements. All jaw

material comes from the locality Pron'kino in the Orenburg region. Ivakhnenko (1987) recognized that this species does not belong to the genus *Nycteroleter*, and, on the basis of an additional new skull and jaw material from the locality Babintsevo, assigned it to a new genus *Raphanodon* and placed it in the family Leptorophidae. In the revised paper on this species, Bulanov (2002) concluded that several specimens from the Babintsevo locality plus all jaw material including the holotype dentary of *Raphanodon* (= *Nycteroleter*) *ultimus* from the locality Pron'kino represent the second species of the genus *Karpinskiosaurus*: *Karpinskiosaurus ultimus*. However, according to the personal communication of Dr V.V. Bulanov (Palaeontological Institute, Russian Academy of Sciences, Moscow), the identity of the original holotypic dentary of *N. ultimus* of Tchudinov & Vyushkov

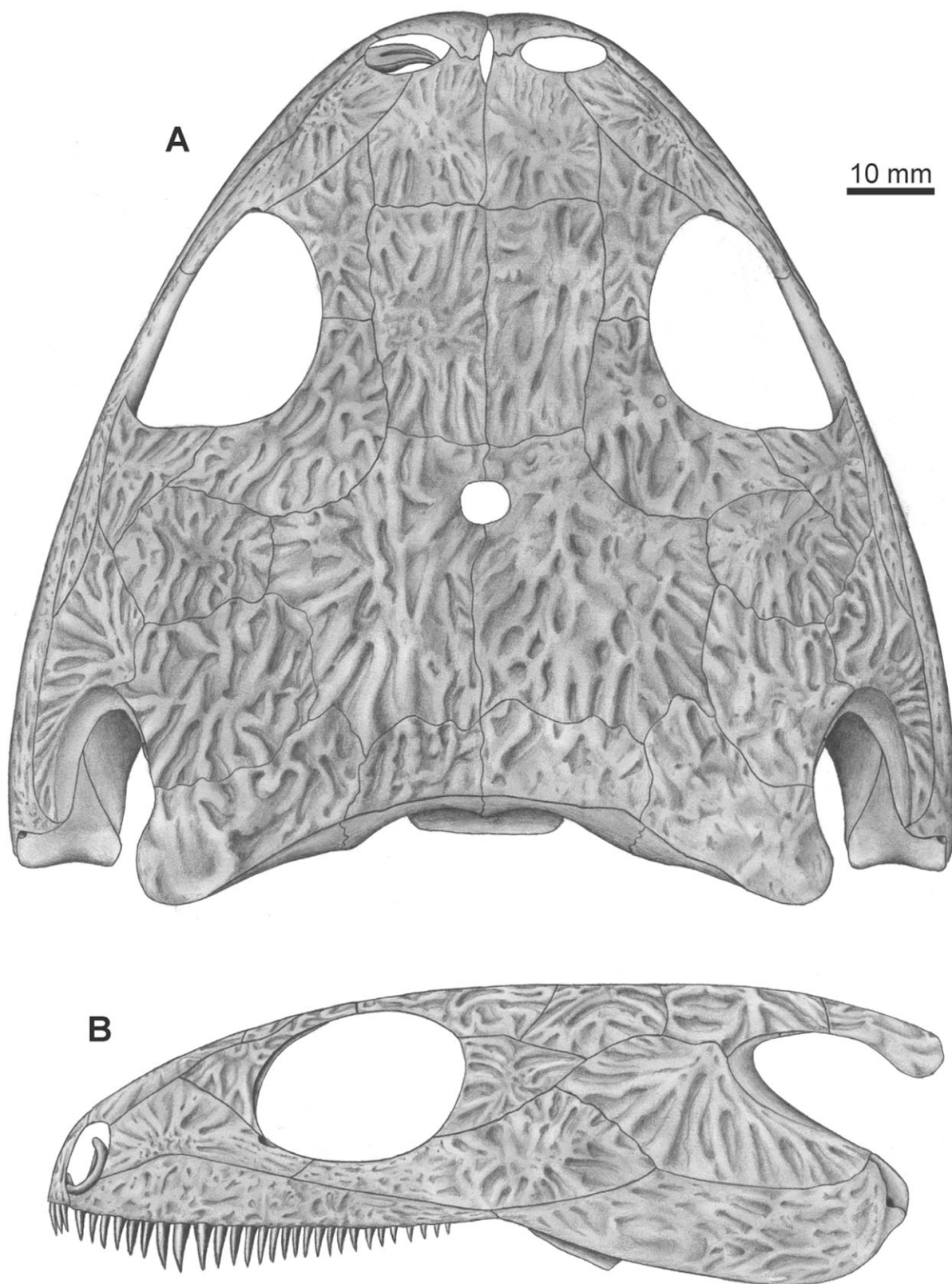


**Figure 2.** *Karpinskiosaurus secundus* (Amalitzky, 1921), PIN 2005/82. Photographs of skull in dorsal (A) and ventral (B) views. Partial lower jaw in external (C) and internal (D) views (anterior and posterior portions are missing).

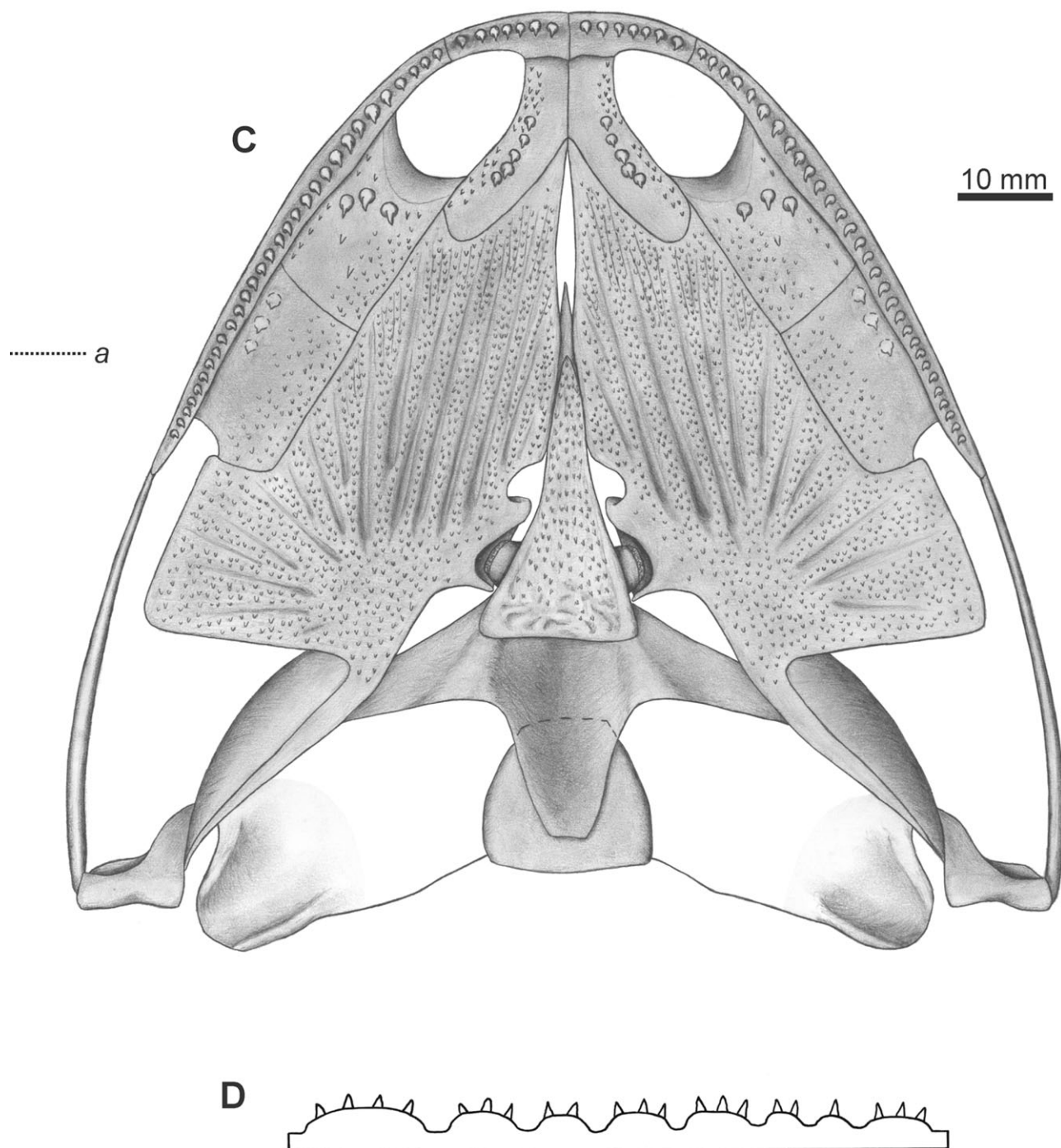
(1956) from the locality Pron'kino, and the specimens from the Babintsevo locality secondarily attributed to *Raphanodon* (= *Nycteroleter*) *ultimus* from the locality Pron'kino (Ivakhnenko, 1987; Bulanov, 2002), is not sufficiently proved, and requires revision. Only additional preparation of new material from the locality Pron'kino, which will be performed by Dr V.V. Bulanov, should reveal whether the species *Karpinskiosaurus ultimus* is or is not a valid species of the genus *Karpinskiosaurus*.

Here, two skulls of *Karpinskiosaurus secundus* (Amalitzky, 1921; Ivakhnenko, 1987; Bulanov, 2003), several specimens from the locality Babintsevo attributed previously to *Karpinskiosaurus ultimus* (Bulanov, 2002), several new specimens from the locality Babintsevo, and three maxillae from the locality Adamovka are considered to represent a single species: *Karpinskiosaurus secundus* (Amalitzky, 1921). All these specimens exhibit the distinguishing features of *Karpinskiosaurus secundus*.

*Kotlassia secunda*: Amalitzky, 1921: 13, pl. 1; fig. 1.  
*Karpinskiosaurus*: Sushkin, 1925: 180.  
*Karpinskiosaurus neglectus*: Sushkin, 1926: 339.  
*Kotlassia prima*: Efremov, 1940: 379 (in part).  
*Kotlassia prima*: Bystrow, 1944: 380 (in part).  
*Karpinskiosaurus secundus*: Watson, 1954: 408.  
*Kotlassia prima*: Efremov & V'yushkov, 1955: 18 (in part).  
*Karpinskiosaurus secundus*: Kalandadze, Ochev, Tatarinov, Tchudinov & Shishkin, 1968: 79.  
*Kotlassia secunda*: Tatarinov, 1972: 71.  
*Karpinskiosaurus secundus*: Ivakhnenko, 1987: 33.  
*Raphanodon ultimus*: Ivakhnenko, 1987: 41 (in part).  
*Karpinskiosaurus secundus*: Ivakhnenko, Golubev, Gubin, Kalandadze, Novikov, Sennikov & Rautian, 1997: 15.  
*Raphanodon ultimus*: Ivakhnenko, Golubev, Gubin, Kalandadze, Novikov, Sennikov & Rautian, 1997: 15 (in part).



**Figure 3.** *Karpinskiosaurus secundus* (Amalitzky, 1921). Reconstructions of skull in dorsal (A), lateral (B), and ventral (C) views. D, schematic drawing of transverse section of palatal ramus of pterygoid at level *a* in (C).



**Figure 3.** *Continued*

*Karpinskiosaurus ultimus*: Bulanov, 2002: 73 (in part).

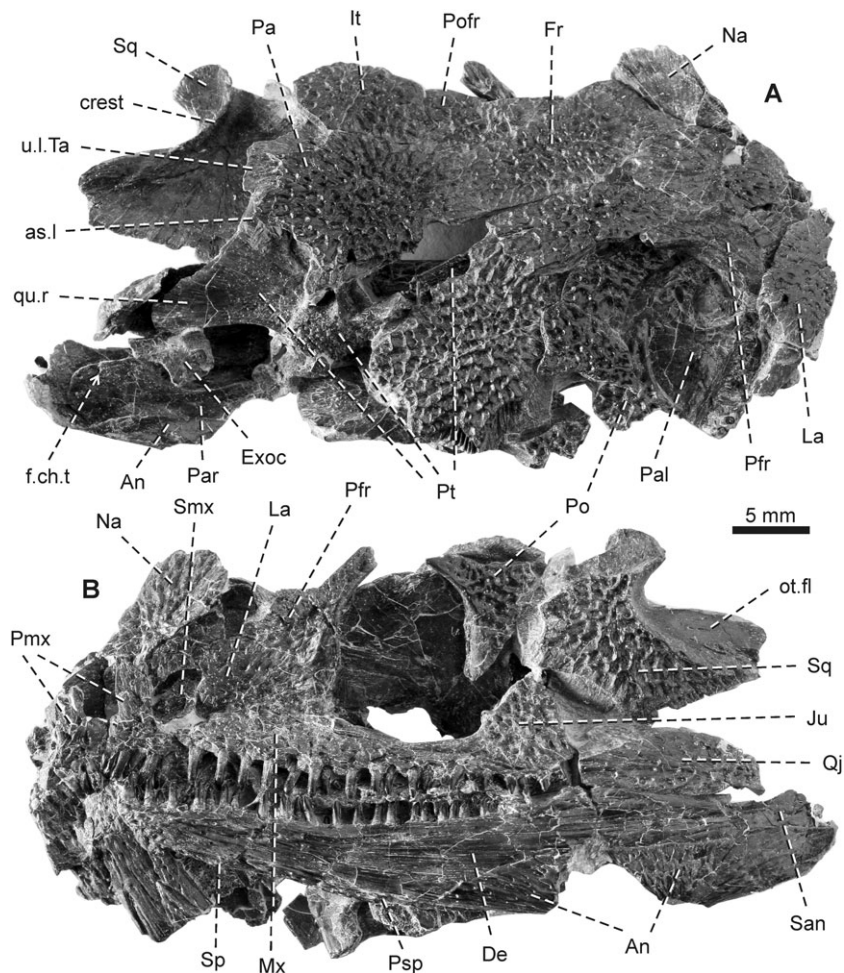
*Karpinskiosaurus ultimus*: Bulanov, 2003: 62 (in part).

*Karpinskiosaurus secundus*: Bulanov, 2003: 69.

*Holotype*: PIN 2005/81, skull (SL 75 mm; Fig. 1) and postcranial skeleton. Sokolki locality, Vyatkian

Regional Stage, Vyatka Horizon, Arkhangelsk Region, European Russia, Upper Permian.

*Referred material, localities, and horizon*: All localities are in the Upper Permian deposits of European Russia: PIN 2005/82 (SL 75 mm) – Sokolki locality, Vyatkian Regional Stage, Arkhangelsk Region; SGU 104B/321–323 (maxillae) – Adamovka locality, Vyat-



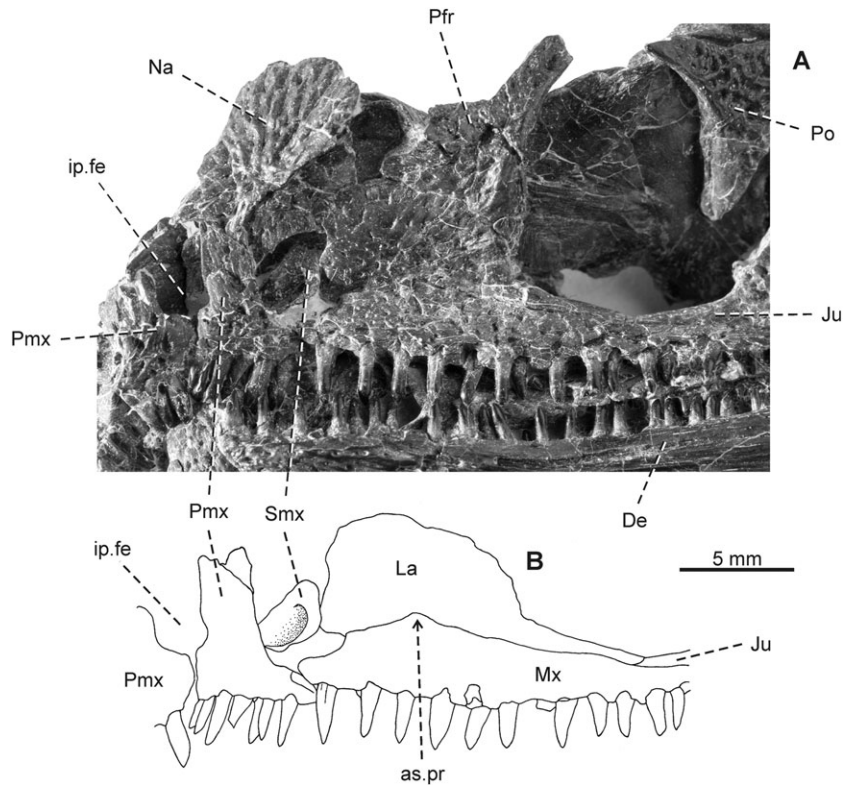
**Figure 4.** *Karpinskiosaurus secundus* (Amalitzky, 1921), PIN 4617/158. Photographs of partly disarticulated skull in dorsal (A) and lateral (B) views.

kian Regional Stage, Orenburg Region; SGU 104B/2008–09 (disarticulated skulls), SGU 104B/2032 (disarticulated skull), PIN 4617/158 (partially disarticulated skull, SL 40 mm), PIN 4617/188 (disarticulated skull), PIN 4617/200 (skull roof and partial palate, SL 36 mm), PIN 4617/201 (partial skull) – Babintsevo locality, Severodvinian Regional Stage, Orenburg Region.

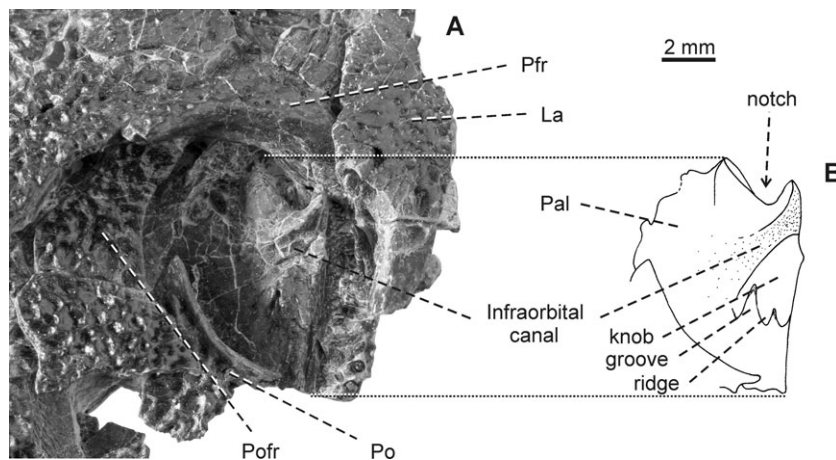
**Diagnosis:** Autapomorphies of *Karpinskiosaurus secundus* (relative to *Utegenia*, *Ariekanerpeton*, *Discosauriscus*, *Makowskia*, *Spinarerpeton*, and *Seymouria*) are irrespective of the skull size: interpremaxillary fenestra present; distinct posterior process of parietal wedged between tabular and postparietal; parietal with underlying lamina for tabular; dorsomedial margin of squamosal wedged between supratemporal and intertemporal; presence of lateral process of supratemporal wedged into squamosal; otic notch encroaching upon posterolat-

eral margin of skull table; rounded or oval otic notch in dorsal view reaching anteriorly mid-length of supratemporal; anteromedial corner of tabular extending into a distinct process fitting between parietal and supratemporal, and reaching about mid-length of supratemporal; absence of tabular process; presence of small, but distinct ascending process on anterodorsal margin of maxilla fitting into a notch in ventral margin of lacrimal; jugal–postorbital suture longer than postorbital–squamosal suture; most of external surface of dentary bearing many horizontally coursing grooves divided by intervening ridges; with exception of apical portion, marginal teeth are labiolingually expanded and mesiodistally narrow.

**Remarks:** The lengths of the skulls ( $SL = Na + Fr + Pa + Pp$ , measured along the midline) described here spans from an estimated 25 mm (SGU 104B/2008) to about 75 mm (PIN 2005/81 and PIN 2005/82).



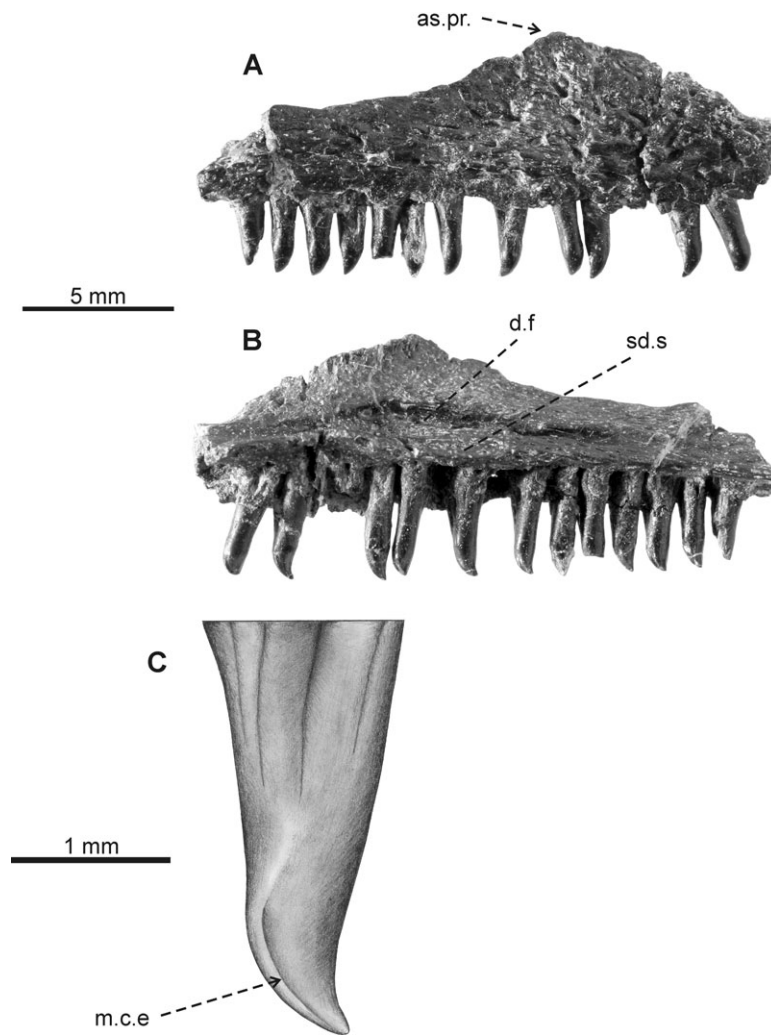
**Figure 5.** *Karpinskiosaurus secundus* (Amalitzky, 1921), PIN 4617/158. A, photograph of anterolateral portion of skull in lateral view. B, outlines of several bones of the same specimen.



**Figure 6.** *Karpinskiosaurus secundus* (Amalitzky, 1921), PIN 4617/158. A, photograph of palatine through right orbit in dorsal view. B, outline of palatine of the same specimen in dorsal view.

The very small specimen SGU 104B/2031 of *Karpinskiosaurus ultimus* (Bulanov, 2003: 67; fig. 38), considered to be larval by Bulanov (likewise SGU 104B/2033–34; Bulanov, 2003: 62), are not attributed to *Karpinskiosaurus secundus* here because they do not exhibit the diagnostic features typical for *Karpinskiosaurus secundus* (see below) and possess tricuspid teeth.

Bulanov (2002) recorded three features that should distinguish *Karpinskiosaurus ultimus* from *Karpinskiosaurus secundus*: (1) larger size of intertemporal; (2) absence of ascending lamina of maxilla; and (3) smaller lingual curvature of marginal tooth apices. First, although the left intertemporal of PIN 4617/158 is large relative to the presumed size of the left supratemporal, which is missing in this specimen, it



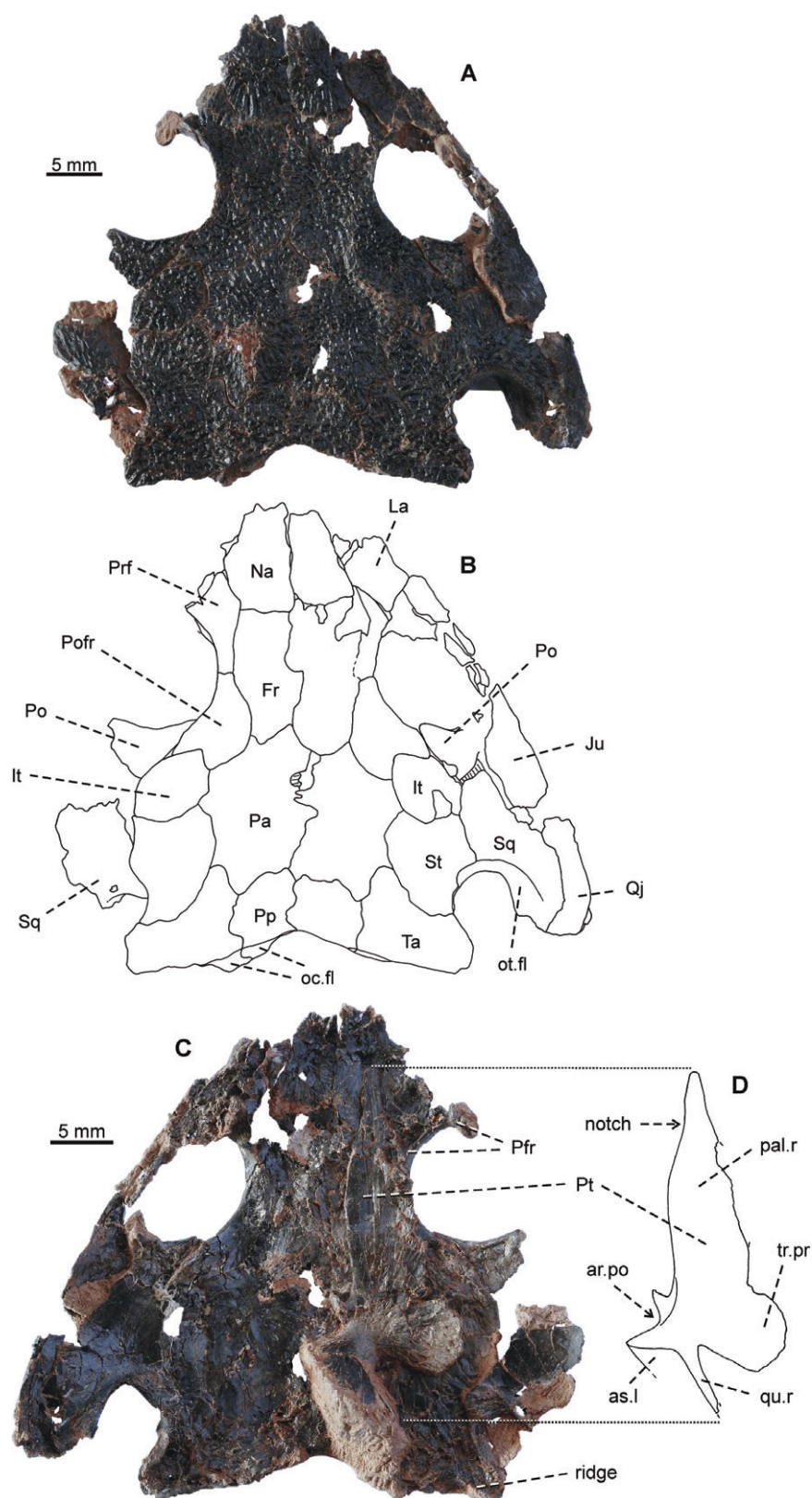
**Figure 7.** *Karpinskiosaurus secundus* (Amalitzky, 1921), SGU 104B/323. Right maxilla in external (A) and internal (B) views. C, reconstruction of maxilla tooth in mesiolingual view (on basis of SGU 104B/323).

is not true that the intertemporal is the principally larger element than the supratemporal in all specimens of this species (see below). Similar conditions also exist in *Discosauriscus austriacus* (Makowsky, 1876). In the latter species, the supratemporal is always larger than the intertemporal; however, in some specimens the size of the intertemporal approaches the size of the supratemporal (Klembara & Janiga, 1993: figs 9A, 10A). Second, the presence or absence of the ascending lamina of maxilla is not considered to be a distinctive character of both species, and its occurrence in a given specimen depends on the ontogenetic stage (Dr V.V. Bulanov, pers. comm.). Third, I consider the smaller lingual curvature of marginal tooth apices in *Karpinskiosaurus ultimus* as only a size-related character. Fourth, according to Bulanov (2005), both species differ in the

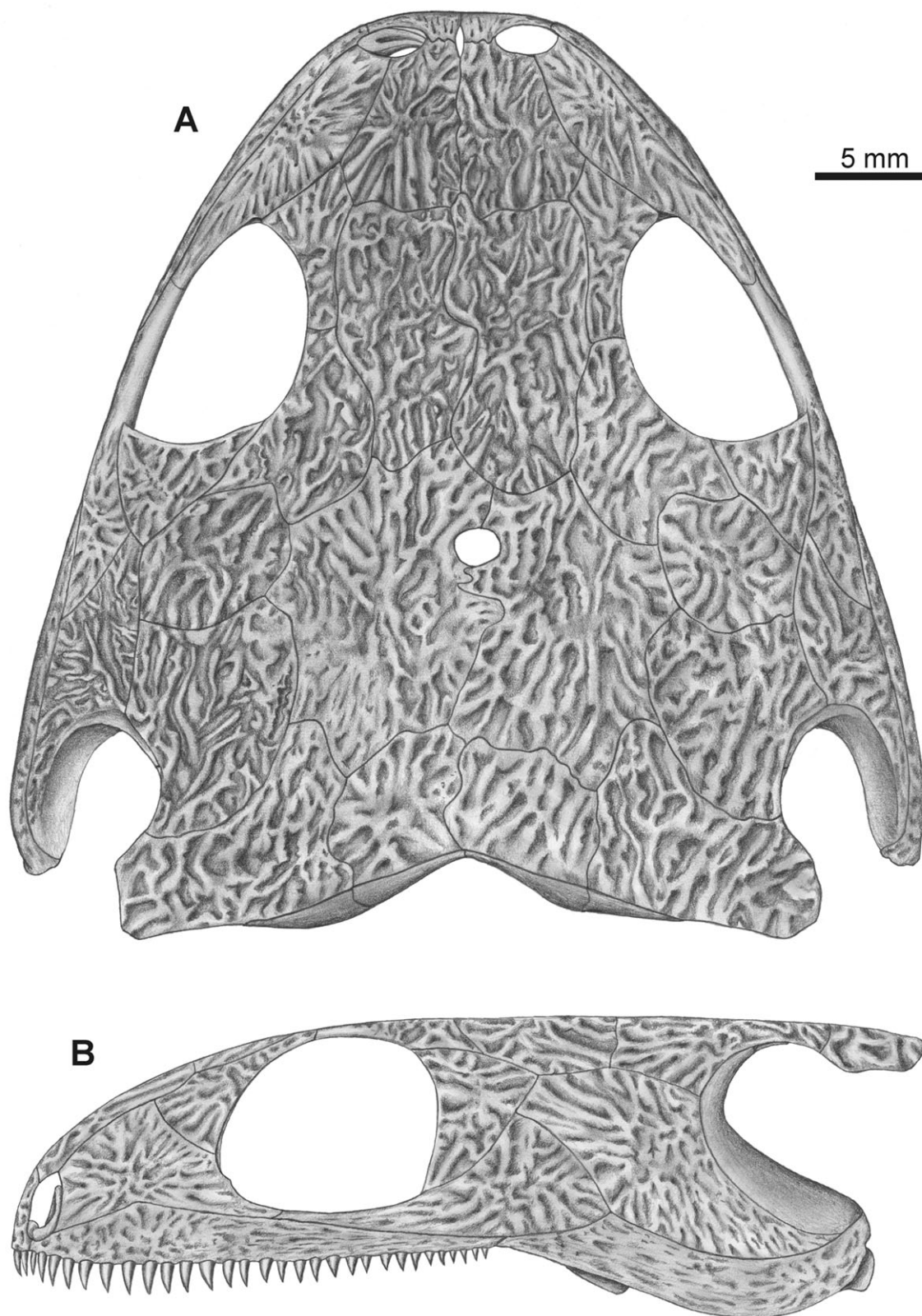
depth of the otic notch. However, as is demonstrated below, the depth of the otic notch remains the same in small and large specimens, apart from the fact that in smaller specimens the otic notch is rounded, whereas in large specimens it is oval, similar to those in other early tetrapods such as *Seymouria sanjuanensis* (Klembara *et al.*, 2007).

## DESCRIPTION

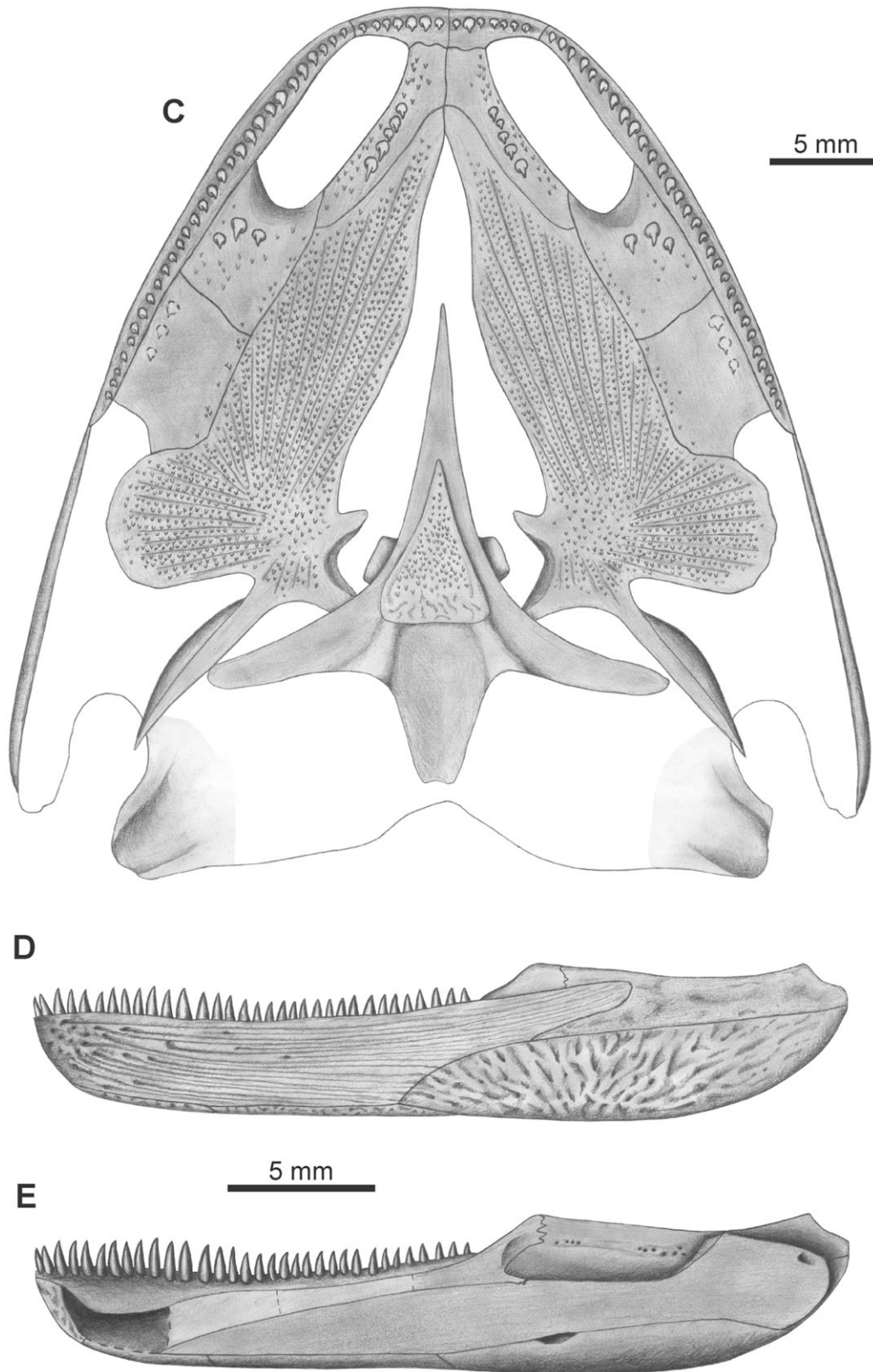
The description of the skull and lower jaw below is based mostly on the largest articulated skulls. When the individual bone or structure exhibits a relevant grade of variability in its shape, this is emphasized in the text and figures. The ontogenetic changes are described in a separate section below.



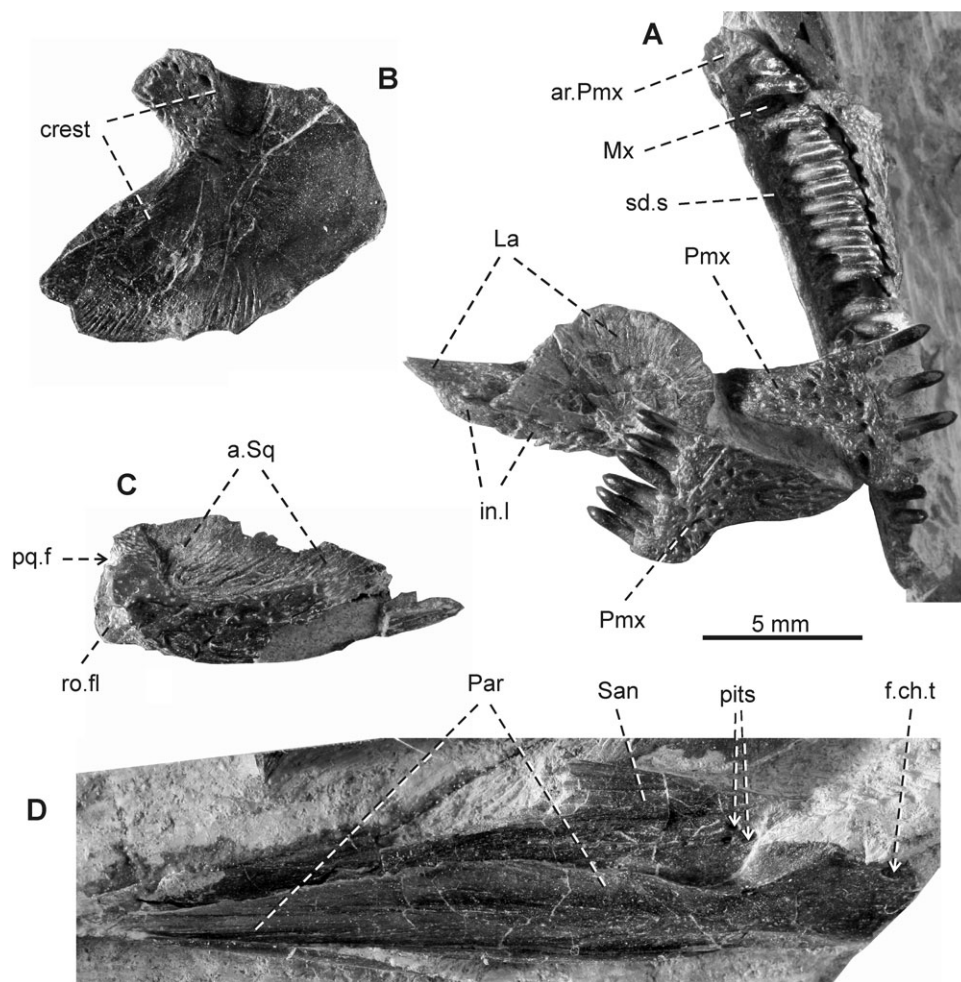
**Figure 8.** *Karpinskiosaurus secundus* (Amalitzky, 1921), PIN 4617/200. Photograph of skull (A) and outlines of its individual bones (B) in dorsal view. C, photograph of skull in ventral view. D, outline of pterygoid in dorsal view.



**Figure 9.** *Karpinskiosaurus secundus* (Amalitzky, 1921). Reconstructions of skull in dorsal (A), lateral (B), and ventral (C) views. Left lower jaw in external (D) and right lower jaw in internal (E) views.



**Figure 9.** *Continued*



**Figure 10.** *Karpinskiosaurus secundus* (Amalitzky, 1921), PIN 4617/188. Photographs of disarticulated specimen. A, maxilla and lacrimal in internal views, premaxillae in external view. B, squamosal in internal view. C, quadratojugal in external view. D, prearticular in internal view.

### SKULL

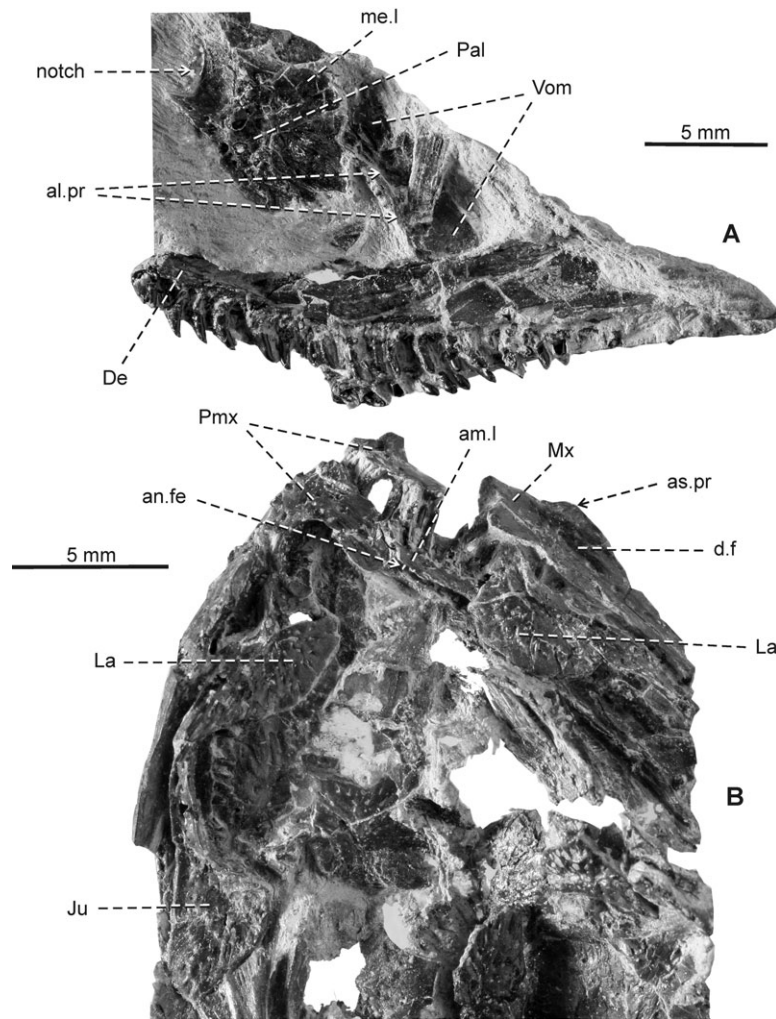
The ornamentation of the skull roofing bones consists of anastomosing ridges and grooves radiating from the ossification centre of each bone. In the region of the ossification centre, the deep pits and ridges form a polygonal pattern of ornamentation. The ridges and grooves are present on bones of all sizes of the skull, although not in the same grade of intensity. In the smallest specimen described here, SGU 104B/2008, such a type of ornamentation is already indicated: pits are located in the ossification centres of the bones, and shallow grooves and low ridges radiating from the centres are present. The sutures are simple in small specimens and irregular in large specimens.

#### *Skull roof*

The nasal ramus of the premaxilla is long and wide, and overlapped the anterior process of the nasal (Figs 3A–C, 4B, 5, 9A–C, 10A, 11B). Its medial

margin is slightly concave, indicating the presence of the interpremaxillary fenestra. The maxillary ramus is long and was slightly overlapped by the premaxillary process of the maxilla (Figs 5, 10). The maxillary ramus forms most of the anterior margin of the exonarial fenestra (external naris). On the inner surface of the premaxilla, the distinct supradental shelf is present. The anterior wall of the septomaxilla abuts the dorsal surface of the supradental shelf and the inner surface of the maxillary ramus of the premaxilla. The supradental shelf of the premaxilla forms the anterior margin of the exochoanal fenestra (choana). The medial portion of the supradental shelf extends posteriorly into a distinct vomerine process (SGU 104B/2008–09). The premaxilla bears up to seven teeth.

The nasal is longer than wide (Figs 1A, 3A, 4, 5A, 8A, B, 9A, B). It is widest at the point where the nasal, prefrontal, and lacrimal meet. The anterior process of



**Figure 11.** *Karpinskiosaurus secundus* (Amalitzky, 1921). A, PIN 104B/2032, disarticulated partial skull: right palatine in ventral view; left vomer in dorsal view; left lower jaw in internal view. B, PIN 104B/2008, partially disarticulated skull in dorsal view (right maxilla in internal view).

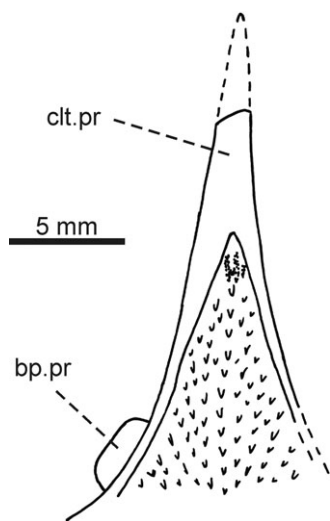
the nasal is about the same width as the nasal process of the premaxilla. The nasal forms the posteromedial margin of the exonarial fenestra. The suture between the nasals is slightly undulating. The nasal has a simple suture with the lacrimal and prefrontal.

The septomaxilla is preserved in PIN 4617/158 (Figs 3A, B, 4B, 5, 9A, B) and SGU 104B/2008. The septomaxilla is a trough-shaped bone situated in the exonarial fenestra. It abuts the anterolateral margin of the lacrimal, anteromedial wall of the maxilla, and the medial wall of the premaxilla. The dorsal margin of the septomaxilla that adjoins the maxilla and lacrimal is very slightly ornamented, anteroposteriorly very short, and forms a part of the skull roof. Immediately below the ornamented surface of the septomaxilla, a septomaxillary foramen is located. The bottom of the inner septomaxilla surface is rugose.

The medial portion of the septomaxilla is extended, and indicates that the septomaxilla contacted the vomer as in *D. austriacus* (Klembara, 1997) and *Makowskia laticephala* (Klembara, 2005). The exonarial fenestra is surrounded by the maxilla, premaxilla, lacrimal, and nasal.

The frontal is a long bone, being slightly wider anteriorly than posteriorly (Figs 1A, 2A, 3A, 4A, 5A, 8A, B, 9A). In the largest specimens, the median suture is almost straight; however, in small specimens the suture is mostly undulating or irregular.

The prefrontal is of triangular shape and forms the anteromedial margin of the orbit (Figs 4, 5A, 6A, 8A, B, 9A, B). The anterolateral portion of the bone extends into a long ventrolateral lamina that underlies the lacrimal (clearly visible in PIN 4617/200) and terminates in an anteroposteriorly elongated process



**Figure 12.** *Karpinskiosaurus secundus* (Amalitzky, 1921): PIN 4617/201, partial parasphenoid; dashed line indicates imprint of anteriormost portion of cultriform process in matrix.

with a distinctly roughened surface at its end (Fig. 8C; the dorsal portion of the process is embedded in matrix and not visible in dorsal view). In *D. austriacus* (Klembara, 1997), a similar process probably contacted the dorsal surface of the palatine, immediately anterolateral to the infraorbital canal (Klembara, 1997: fig. 26). This was probably also the case in *Karpinskiosaurus secundus* (Fig. 6). The posterior ramus of the prefrontal is mediolaterally broad and meets the postfrontal in a horizontal suture. The prefrontal–postfrontal suture lies in the middle of the length of the frontal. In PIN 4617/188, a small ventral lamina is present at the posteromedial tip of the posterior ramus of the prefrontal underlying the frontal (similar to that in *D. austriacus*; Klembara, 1997: fig. 5). In PIN 4617/158, the orbital margins of the prefrontal, postfrontal, and jugal form a high, sharp, and smooth wall, similar to that in *Discosauriscus* (Klembara, 1997) and *Makowskia* (Klembara, 2005).

The postfrontal is a large crescent-shaped bone (Figs 3A, B, 4A, 6A, 8A–C, 9A, B). Its lateral portion is anteroposteriorly broad, and its suture with the postorbital is long and almost straight. It has a long suture with the parietal. The posterolateral margin of the postfrontal is slightly notched anteriorly to articulate with the intertemporal. This notch is more pronounced in smaller specimens (e.g. PIN 4617/200).

The parietal is large, plate-like, and slightly longer than wide (Figs 1A, 2A, 3A, 4A, 8A, B, 9A). It extends into two short processes anterolaterally: (1) between the postfrontal and intertemporal; and (2) between the intertemporal and supratemporal. A distinct,

elongated process extends between the supratemporal and tabular. A typical feature for *Karpinskiosaurus secundus* is a pronounced process fitting between the tabular and postparietal. This process is distinctly developed in the middle-sized specimens (PIN 4617/158 and PIN 4617/200, in Figs 4, 8, respectively), but it is also clearly recognizable in the largest skulls (Fig. 3A). A rounded parietal foramen lies at the level of the anterior portions of the intertemporals. The median suture lying anterior to the parietal foramen is more or less straight; behind the foramen it is undulating in smaller specimens, but almost straight in large specimens. The anterior and lateral margins of the parietal bear ventral laminae (PIN 4617/158; Fig. 4A) that are in a similar position to those in the parietal of *D. austriacus* (Klembara, 1997: fig. 5); however, in contrast to *D. austriacus*, the parietal of *Karpinskiosaurus secundus* also bears the ventral lamina for the anteromedial portion of the tabular. On the ventral surface, the posteromedial portions of both parietals and medial portions of the postparietals are more massively constructed relative to the remaining portions of the bones.

The intertemporal is oval in shape (Figs 1A, C, 3A, 4A, 8A, B, 9A). It has a long suture with the squamosal coursing in an anterolateral–posteromedial direction.

The supratemporal is of quadrangular shape (Figs 1A, C, 2A, 3A, 8, 9A). The suture with the ornamented portion of the squamosal is long and courses in an anteromedial–posterolateral direction, whereas the suture with the posterodorsal unornamented portion of the squamosal courses in an anterolateral–posteromedial direction, as a consequence of the encroachment of the medial portion of the otic notch into the posterolateral margin of the skull table. The lateral margin of the supratemporal extends into a process that fits between the ornamented portion of the squamosal lying anteriorly and the unornamented portion of the squamosal extending posteriorly. The posterolateral margin of the supratemporal is concave and participates on the formation of the medial embayment of the otic notch. The ventrolateral margin of the supratemporal bears a vertical flange that is sutured with the posterodorsal portion of the squamosal otic flange. The suture between both flanges reaches the level between a third and two-thirds of the supratemporal length, regardless of the size of the specimen. This is unlike the conditions in *Discosauriscus*, in which the supratemporal–squamosal suture lies at the level of the supratemporal mid-length (Klembara, 1997).

The postparietal is of quadrangular shape (Figs 1A, 2A, 3A, 8A, B, 9A). It is always slightly wider than long. The posterior margin of the postparietal extends into a large occipital flange, which is sutured with the

tabular occipital flange in an interdigitating suture coursing in the anterolateral–posteromedial direction. The occipital flange is anteroposteriorly longest laterally and shortest medially.

The tabular is a mediolaterally elongated plate (Figs 1A, 2A, 3A, 8A, B, 9A). Its anterolateral margin is slightly concave and participates in the formation of the posteromedial margin of the otic notch. The posterolateral margin of the tabular is rounded. The posterolateral corner of the tabular extends further laterally than the posterolateral corner of the supratemporal. The anterolateral corner of the tabular forms a small process. The anteromedial corner of the tabular forms a distinct process fitting between the parietal and supratemporal. This process is better developed in smaller specimens in which the sutures are simpler in comparison with large specimens. In PIN 4617/200, the process is distinctly developed and reaches about the mid-length of the supratemporal. The tabular in PIN 4617/158 is not preserved, but the perfectly preserved posterior margins of the parietals clearly indicate the presence of this process of the tabular (Fig. 4A). In the large skull PIN 2005/82, this process is clearly recognizable on the left side of the skull. Although the sutures in the holotype skull are complicated, and in some places difficult to trace, the process is readily traceable on the right side of the skull. The occipital flange is well developed and extends laterally almost to the posterolateral corner of the tabular. The surface of the occipital flange is finely mediolaterally striated. In the small skull PIN 4617/200, the occipital flange is mediolaterally shorter, and fades out laterally at about the mid-width of the tabular. The tabular process, the typical feature of all Upper Carboniferous–Lower Permian seymouriamorphs, is absent. On the ventral surface of the tabular of PIN 4617/200, two mediolaterally coursing ridges, one anterior and one posterior, and the depression between them, are present (Fig. 8C). The posterior ridge bears a distinct posteroventrally inclined surface that abutted the paroccipital process of the opisthotic (clearly visible in PIN 2005/82).

The maxilla is highest in its anterior portion, at about the level of the fifth or sixth tooth (Figs 2B, 3A, B, 4B, 5, 7, 9A–C, 10A, 11B). Here, its dorsal margin forms a small, but distinct, ascending process that fits into a notch in the ventral margin of the lacrimal. The posterior end of the maxilla has a short contact with the anterior tip of the quadratojugal. At the anterior end, the maxilla is notched and joins the septomaxilla. The internal surface of the maxilla is longitudinally striated and bears a longitudinal groove. Below this groove lies the supradental shelf. The shelf is widest at the level where the maxilla is the highest. Here, immediately

above the supradental shelf, several large foramina are located in the longitudinal groove (Fig. 7B). The maxilla bears up to 30 teeth.

The lacrimal is a dorsoventrally broad plate posteriorly extending into a suborbital process (Figs 3A, B, 4B, 5, 6A, 8A, B, 9A, B, 10A, 11B). The lacrimal canal is present and is located immediately dorsal to the ventral margin of the bone. In all specimens studied here, the nasolacrimal canal is dorsally closed. The lacrimals of SGU 104B/2032 and PIN 4617/188 (Fig. 10A) show the presence of the internal lamina extending from the posterior section of the ventromedial margin of the lacrimal, similar to *D. austriacus*, in which this lamina fits between the maxilla and the palatine (Klembara, 1997: fig. 11). The anterior portion of the suborbital process of the lacrimal is mediolaterally wide, and its posterior tip dorsally overlaps the suborbital process of the jugal (clearly visible in PIN 4617/158 and PIN 4617/201; Fig. 5). In lateral view, the suture between both bones courses in the posterodorsal–anteroventral direction, as in *Seymouria sanjuanensis* (Klembara *et al.*, 2005, 2006), but in contrast to discosauriscids (Klembara, 1997, 2005, 2009a; Klembara and Ruta, 2005a) and *Utegenia* (Klembara and Ruta, 2004a).

The jugal is a triangular plate with a dorsoventrally broad postorbital portion and long suborbital ramus that forms the almost complete ventral margin of the orbit (Figs 1C, 3A, B, 4B, 5, 8A, B, 9A, B, 11B). The whole dorsal surface of the suborbital ramus is smooth. The jugal has a long, oblique suture with the postorbital, and a relatively shorter suture with the squamosal. The posterior process of the jugal reaches to about the level of the intertemporal–supratemporal suture in small and large skulls.

The postorbital is a large triangular plate (Figs 1A, 3A, B, 4, 5A, 8A, B, 9A, B). Its anterior margin forms most of the posterior wall of the orbit. Posteriorly, the postorbital extends into a pointed process that fitted between the intertemporal and squamosal. The medial ramus of the postorbital has a long suture with the postfrontal.

The squamosal is a large and elongated plate (Figs 1A, C, D, 2A, 3A, B, 4, 8A, B, 9A–C, 10B). The ornamented portion is larger than the smooth otic flange. Anteriorly, the squamosal extends into a plate-like (in small skulls) or pointed (large skulls) process, fitting between the postorbital and jugal. Large ventral lamellae for the postorbital and jugal are well preserved in PIN 4617/158 (Fig. 4B). The squamosal is sutured with the quadratojugal ventrally and with the quadrate posteromedially. The smooth otic flange of the squamosal becomes mediolaterally wider in the posteroventral direction. The otic flange is distinctly concave and completely encloses the rounded (in

small skulls) or oval (in large skulls) otic notch ventrolaterally. On the internal surface of the squamosal, there is a prominent crest coursing along the posterior margin of the otic flange (Figs 4A, 10B). The ascending lamina of the pterygoid abutted the crest, similar to the condition in *D. austriacus* (Klembara, 1997: fig. 13).

The quadratojugal is a massive and long element (Figs 1C, D, 2A, 3A, B, 4B, 8A–C, 9A–C, 10C). Anteriorly, it has a long and almost straight suture with the jugal coursing in the anteroventral–posterodorsal direction. The quadratojugal has a large ventral lamina for the squamosal and a small ventral lamina for the jugal (well preserved in PIN 4617/158 and PIN 4617/188; Fig. 10C). The posterior portion of the quadratojugal forms a medially extending smooth flange; between it and the ornamented portion, a distinct notch forming a lateral wall of the paraquadrate foramen is located (Fig. 10C). The medial wall of the foramen is formed by the quadrate.

#### Palate

The vomer is a long and narrow element (Figs 3C, 9C, 11A). It forms the whole medial margin of the exchoanal fenestra (SGU 104B/2009). The exchoanal margin of the vomer forms a high, dorsally extending alar process bearing many small sharp teeth (SGU 104B/2032 and PIN 4617/201). Both vomers meet anteriorly in a median suture. The posterior portion of the vomer is slightly notched in the pterygoid. The posterolateral margin of the vomer is sutured with the palatine. At about the middle section of the ventral surface of the vomer, five tusks arranged one after another in anteromedial–posterolateral direction are located (SGU 104B/2009). Anterior to them, the surface of the vomer is covered by small, sharp denticles. The denticles also lie laterally to the tusks, along the whole exchoanal margin, and continue to the anterior surface of the palatine.

The palatine is an elongated, quadrangular bone with a deeply incised anterior margin (well preserved in PIN 104B/2032, SGU 104B/2009) (Figs 3C, 4A, 6, 9C, 11A). This margin is posteriorly lined with small and sharp denticles. Immediately posteriorly to these small teeth, one, and further posterolaterally, two, tusks are located. The remaining ventral surface of the palatine is covered with small denticles extending up from the pterygoid. It is visible in dorsal view in PIN 4617/201 that the palatine–ectopterygoid suture is almost straight and courses in an anterolateral–posteromedial direction. The palatine of SGU 104B/2032 (Fig. 11A) shows a large medial lamina that overlapped the pterygoid from the dorsal side (a similar condition is also present in *D. austriacus*; Klembara, 1997: fig. 26). On the dorsal surface of the right palatine of PIN 4617/158, the infraorbital canal

is present (Fig. 6), as in *Discosauriscus* (Klembara, 1997) and *Utegenia* (Klembara & Ruta, 2004a). Immediately behind it, a well-developed knob, ridges, and grooves are positioned.

The ectopterygoid is a quadrangular plate: it is longer than wide (Figs 2B, 3C, 9C). The posterolateral corner of the ectopterygoid is anteriorly notched. There are indications in PIN 2005/82 that three tusks lined the anterolateral margin of the bone. The remaining ventral surface is covered with oblique rows of small denticles extending up from the pterygoid.

The pterygoid is the largest palatal bone: it consists of the palatal ramus, transverse process (flange), articular area, and quadrate ramus (Figs 1D, 2B, 3C, D, 4A, 8C, D, 9C). The anterior tips of the palatal rami meet in the midline. The medial margin of the palatal ramus is slightly concave in the anterior half of its length (visible in PIN 4617/200 and PIN 2005/82), as in *Seymouria sanjuanensis* (Klembara *et al.*, 2005, 2006, 2007). The remaining section of the medial margin is straight, but immediately anterior to the articular area, a distinct lateral notch is present. The sutures with the palatine and ectopterygoid are straight. The transverse process is well developed and is of quadrangular shape. Its anterior and posterior margins are parallel. The lateral margin of the transverse process is flexed ventrally, and is distinctly sculptured. As a whole, the transverse process is flexed ventrally (PIN 2005/82) and extended slightly below the lateral margin of the cheek. The transverse process bears no tusks. The basicranial fossa lies at the level of the anterior half of the transverse process. The articular surface is slightly rugose. The surface of the central portion of the pterygoid, immediately lateral to the articular portion, is sculptured. The sculpturing consists of pits, short grooves, and ridges. From here, distinct rounded ridges bearing many small denticles separated by intervening grooves diverge on the ventral surface of the palatal ramus and transverse flange of the pterygoid (Fig. 3C, D). The rows of denticles continue to the ventral surface of the palatine, ectopterygoid, and anterior portion of the quadrate ramus of the pterygoid. The ascending lamina of the quadrate ramus is high and obliquely oriented. Its dorsal margin lies close to the ventral surface of the skull roof (PIN 2005/82 and PIN 4617/158). The ascending lamina is deeply excavated anteriorly. The posterior-most section of the quadrate ramus is dorsoventrally low and articulates with the quadrate laterally. The dorsal surface of the pterygoid is preserved in PIN 4617/200: it is smooth and bears a series of narrow, anteroposteriorly coursing grooves (Fig. 8C).

The parasphenoid is a large plate consisting of a median, triangular parasphenoidal plate and two pos-

terolateral processes (Figs 2B, 3C, 9C, 12). The parasphenoidal plate projects anteriorly into a stout cultriform process bearing a faint median crest on its smooth ventral surface (PIN 4617/201). The parasphenoidal plate bears a triangular field of small and pointed denticles on its ventral surface. The field is limited by distinct margins. The transversely directed posterior margin lies immediately behind the posterior level of the basiptyergoid processes. The rows of denticles radiate from the region located between the basiptyergoid processes. The remaining surface behind the denticles is finely sculptured. The ventrolateral crests are pronounced, rounded, and divided by the median depression. The morphology of the parasphenoidal plate is very similar to that in *Seymouria sanjuanensis* (Klembara *et al.*, 2005, 2006, 2007). The posterolateral processes are stout and long. Posteriorly, the parasphenoid forms a large triangular process. Its posterior margin is slightly anteriorly notched. This process underlies the ventral portion of the basioccipital.

#### *Ossifications of palatoquadrate and stapes*

The quadrate is ossified only in the largest specimens: PIN 2005/81 and PIN 2005/82 (Figs 1D, 2B, 3). The bone interpreted by Bulanov (2003) as an articular in PIN 4671/158, is the exoccipital (Fig. 4A). The quadrate is of triangular shape. The condylar portion is robust, and gradually narrows dorsally into a wedge fitting between the quadratojugal and squamosal laterally and the quadrate ramus of the pterygoid medially.

In PIN 2005/82 there is a vertical lamina present immediately dorsally to the right pterygoid, which probably represents the epiptyergoid. However, no diagnostic morphological features are visible, and this region of the skull would require additional preparation to confirm this identity. There are several elongated bony fragments located in the left otic notch in both PIN 2005/81 and PIN 2005/82. According to Dr V. V. Bulanov (pers. comm.), additional chemical preparation revealed the presence of the elongated stapes in PIN 2005/82.

#### *Neural endocranium*

The ossifications of the neural endocranium are preserved almost exclusively in the largest specimens, but several endochondral elements of the neural endocranium are also preserved in smaller specimens. The basiptyergoid processes of the basisphenoid are preserved in specimens of various sizes, but the remaining portion of the basisphenoid is not accessible (Figs 2B, 3C, 12). A partial basioccipital is preserved (Figs 2B, 3C). It is a plate with a straight posterior margin and anteromedially converging lateral margins. The basioccipital articulates with

the exoccipitals. The ventral surface of the basioccipital is smooth; the dorsal surface is strongly rugose. The smallest specimen in which the exoccipital is preserved is PIN 4617/158 (SL 40 mm; Fig. 4A). Both exoccipitals are preserved in PIN 2005/81 (SL 75 mm; Fig. 1D) and PIN 2005/82 (SL 75 mm; Fig. 2A). The overall morphology of the exoccipital is similar to that in *Discosauriscus* (Klembara, 1997: figs 21, 24); however, it is much more slender and longer than that in the latter taxon. Both ends of the exoccipital are unfinished. The ventral end is broader than the dorsal end, and all its three articulation surfaces are distinguishable: the anterior facet for the junction with the opisthotic, the middle facet for the junction with the basioccipital, and the posterior facet participating in the formation of the occipital condyle. The dorsal end articulated with the occipital flanges of the tabular and postparietal, and the posterior wall of the opisthotic. The foramen for the nervus hypoglossus is located in the ventral portion of the exoccipital. The opisthotics and prootics are also present, but their state of preservation does not allow their detailed description. The lateral end of the massively constructed opisthotic abuts the ventrolateral surface of the tabular (Fig. 1D). The otic tube is preserved and its rounded lateral opening is well preserved at the right side of PIN 2005/82.

#### LOWER JAW

The lower jaw (Figs 1B–D, 2B–D, 4B, 9D–E, 10D, 11) is deepest at about the level of the posterior coronoid–surangular suture. Its overall morphology is similar to that of Upper Carboniferous–Lower Permian seymouriamorphs, like *Utegenia* (Klembara & Ruta, 2004a), *Seymouria* (White, 1939; Laurin, 1996c), and *Discosauriscus* (Klembara, 1997).

The dentary is completely preserved in PIN 4617/158 (Fig. 4B) and PIN 4617/188. In SGU 104B/2008, the dorsal portion of the internal surface of the anteriormost portion of the right dentary is preserved (Fig. 11B). It exhibits the presence of the ventrally projecting anteromedial lamina and an elongate anterior mandibular fenestra located between the anteromedial lamina dorsally and the splenial ventrally; both lamina and fenestra are also present in *D. austriacus* (Klembara, 1997) and *Ariekanerpeton sigalovi* (Klembara & Ruta, 2005a). The external surface of the dentary is strongly horizontally grooved; only in its anterior portion are distinct pits present (Figs 4B, 9D). The posteriormost portion of the dentary is narrow and pointed, and does not reach the dorsal margin of the lower jaw. Hence, the vertically coursing angular–posterior coronoid suture is exposed in lateral view. Ventrally, the dentary joins the splenial

and postsplenial, and posteriorly it overlaps the anterior lamina of the angular. The dentary bears up to 40 teeth.

The surangular is an elongated bone that has a straight horizontal suture with the angular (Figs 2C, 4B, 9D, E, 10D). The dorsal margin of the surangular is massive and is shallowly concave to accommodate the posterior portion of the cheek (well preserved in PIN 4617/158, Fig. 4B). On its internal surface, immediately below this massive dorsal wall, an elongated groove with large pits and foramina at its bottom is present (Fig. 9E). The posterior margin of the angular courses in an anterodorsal–posteroventral direction in lateral view. The anterodorsal portion of the surangular is massive, and was joined with the ascending ramus of the posterior coronoid in a vertically oriented and strongly interdigitating suture (Fig. 2C, D).

The splenial is a narrow splint of bone (Figs 2B, 4B, 9D, E). Its anteriormost portion forms the ventral part of the symphysis. The posterior end of the splenial underlies the anterior portion of the postsplenial.

The postsplenial is longer and deeper than the splenial (Figs 4B, 9D, E). The anterior end of the postsplenial fitted between the splenial and dentary; the suture with the dentary is much longer. The posterior end of the postsplenial underlies the anterior portion of the angular. The splenial, postsplenial, and angular have ornamented external surfaces and smooth ventral and internal walls. The ornamentation of the splenial and postsplenial consists of small pits, tubercles, short ridges, and grooves.

The angular is a large, anteroposteriorly elongated plate forming the posteroventral wall of the lower jaw (Figs 2B, C, 4B, 9D, E). Its narrow and pointed anterior process fits between the postsplenial and dentary. The external surface of the angular is pronouncedly ornamented. The ornamentation consists of pits and tubercles located in the ossification centre of the bone, which lies close to the ventral margin of the bone; from here, the grooves and ridges radiate anteriorly, dorsally, and posteriorly. The angular has a high medial wall overlapping from outside the large, ventrally extending, and far-overlapping area of the prearticular (PIN 4617/188; Fig. 10D). The anterodorsal margin of the medial wall of the angular, near to the suture with the postsplenial, is shallowly ventrally notched, indicating the presence of the posterior Meckelian fossa (Fig. 9E).

The prearticular is completely preserved in PIN 4617/188 (Fig. 10D). It is a long bone, the posterior portion of which is dorsoventrally broad. The postero-dorsal portion of the prearticular bears a small fossa containing a foramen, presumably for the entry of the chorda tympani (Figs 4A, 9E, 10D). The anterior margin of the broad portion extends into a smooth

and broad lamina forming the posterior wall of the adductor fossa. Immediately anterior to this posterior broad portion, the prearticular is dorsoventrally constricted. Further anteriorly, the prearticular widens dorsoventrally: it is widest at roughly the level of the postsplenial–angular suture. From here, the prearticular gradually narrows dorsoventrally into a long process forming most of the internal surface of the lower jaw.

The posterior coronoid is preserved (Fig. 2C). It has an ascending ramus that joined the surangular in the vertical interdigitating suture (Figs 2C, 9D, E). In PIN 2005/82, the area of at least the middle coronoid is also preserved, but the preservation of this area is very poor, so that the suture between both coronoids and the character of their surfaces are not recognizable.

The articular is located between the posterior portion of the prearticular and the posterior portions of the angular and surangular. The ossified articular is present in the largest specimens: PIN 2005/81 (Fig. 1D) and PIN 2005/82 (Fig. 2B). Its poor preservation does not permit any detailed morphological characteristics to be observed.

#### DENTITION (FIGS 3C, 4B, 5, 7, 9B–E, 10A, 11)

With the exception of the apical portion, the marginal teeth are labiolingually expanded and mesiodistally narrow. The labial wall of the expanded portion of the tooth is slightly concave, whereas the lingual wall is slightly convex (Figs 7, 11A; Bulanov, 2003: fig. 37A, B). The apices of crowns are labiolingually flattened, and curved lingually. They bear mesial and distal cutting edges. The degree of curvature depends on the size of the specimen: it is more distinct in the largest specimens. In the smallest specimen, SGU 104B/2008, the dentine is not infolded on the teeth accessible for observation. In PIN 4617/158, the external surfaces of the tooth bases bear grooves reaching about one-third of the tooth length. In the large specimens (e.g. SGU 104B/322 corresponding to the size of PIN 2005/81 and PIN 2005/82), the grooves reach the level of the mid-length of the crown (see also Bulanov, 2003: fig. 42). The deepest infoldings, leaving grooves on the external surfaces, are one on the mesial and one on the distal surfaces of the crown; all other grooves are much shallower (see also Bulanov, 2003: fig. 37A–C) and present mostly at the lingual surfaces of the tooth base. The premaxilla bears up to seven teeth (SGU 104B/2008 and PIN 4617/188), the maxilla bears up to 30 teeth, and the dentary bears up to about 40 teeth. The number of palatal tusks is as follows: five tusks on the vomer (PIN 104B/2009) and three tusks on the palatine (PIN 104B/2032). I

observed traces of possibly three tusks on the right ectopterygoid of PIN 2005/82, but this region of the bone is badly preserved. The right ectopterygoid (PIN 4828/614) of the related seymouriamorph species, *Kotlassia prima*, bears nine tusks, lining the entire lateral margin of the bone (J. Klembara, pers. observ.). Nevertheless, the exact number of the tusks on the ectopterygoid of *Karpinskiosaurus secundus* remains unknown at present. A row of small pointed teeth is present on the ventral surface of the vomer lining the exochoanal margin. Further posteriorly, such small and pointed teeth line the endochoanal and lateral margins of the palatine. On the ventral surface of the palatal ramus and transverse process of the pterygoid, from the place lateral to the basicranial fossa, rows of small denticles cover broad diverging ridges (Fig. 3C, D). The ridges are divided by narrow intervening furrows. The rows of small denticles also continue onto the ventral surfaces of the palatine and ectopterygoid.

#### GRADE OF OSSIFICATION, RECONSTRUCTED SKULLS, AND ONTOGENETIC CHANGES

The lengths of the skulls ( $SL = Na + Fr + Pa + Pp$ ) described here range from about 25 mm for the smallest specimen (SGU 104B/2008) to 75 mm for the largest specimens (PIN 2005/81 and PIN 2005/82). None of the specimens exhibit the presence of sensory grooves. Thus, all specimens composing the ontogenetic sequence of *Karpinskiosaurus secundus* are considered to be terrestrial dwellers.

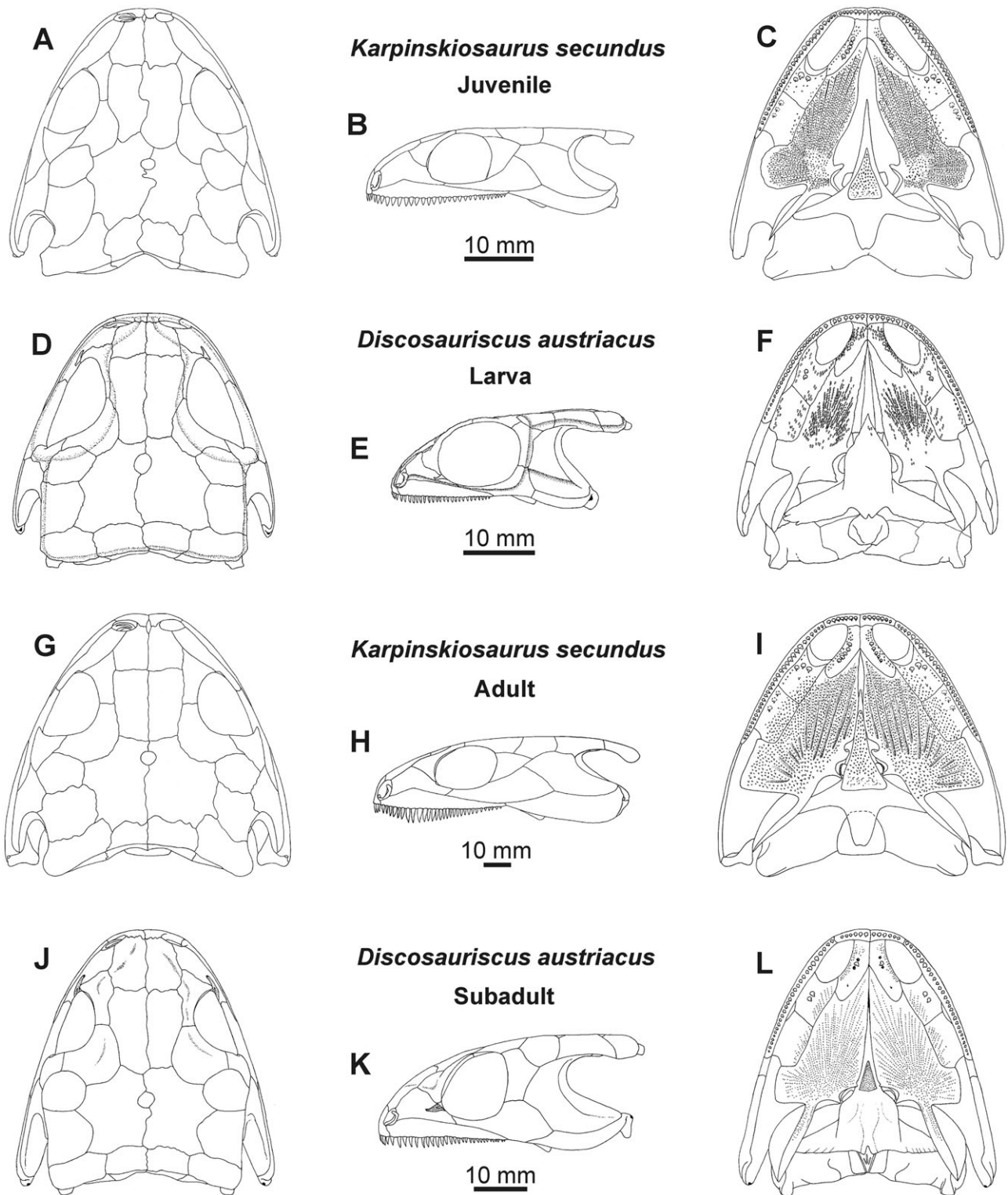
The smallest specimen in which endochondral ossifications are present is PIN 4617/158 (SL about 40 mm), in which the exoccipital is present (Fig. 4A). Although an almost completely preserved lower jaw is preserved in this specimen, the quadrate and articular are not present. These two latter bones are not present in the slightly smaller specimens PIN 4617/200 and PIN 4617/188 either. The fully ossified quadrate and articular are present only in the largest specimens: PIN 2005/81 and PIN 2005/82. In these two largest specimens, all braincase bones are also ossified.

The large skull of *Karpinskiosaurus secundus* (SL about 75 mm) is robustly constructed (Figs 1, 3; cf. the alternative reconstruction of the skull in dorsal view of Bulanov, 2003). In dorsal view, the skull is of semielliptical shape. It is wider than long. The preorbital portion is much shorter than the postorbital region. The orbits are of oval shape and lie in the posterior portion of the anterior half of the skull length. The interorbital region is wide. An anteroposteriorly elongated interpremaxillary fenestra is

present: it also enters between the anteriormost portions of the nasals. The prefrontal–postfrontal suture is wide: its length is about half of the frontal width. The postorbital region is wide and about twice as long as the preorbital region. The pineal foramen lies posterior to the level of the posterior margins of the orbits. The posterior margin of the parietal table is pronouncedly notched anteriorly. The otic notch is of oval shape: in lateral view, it is anteroposteriorly long and dorsoventrally narrow. It is surrounded by the squamosal, supratemporal, and anterolateral margin of the tabular. The jaw joint lies in the level of the mid-length of the tabular. The posterolateral portion of the transverse process of the pterygoid extends slightly below the ventral cheek margin, at the level of the jugal–quadratojugal suture. The suborbital portion of the cheek is high. At the level of the mid-length of the orbit, the height of the suborbital portion of the cheek is almost one half of the orbit height in lateral view. The articulation of the parietal table and the cheek is firm. The sutures are more complicated in the postorbital region relative to the antorbital region of the skull. The palate is closed; however, there is a narrow anteroposteriorly elongated fenestra between the anteromedial margins of the pterygoids. Such a fenestra is also present in *Seymouria sanjuanensis* (Klembara *et al.*, 2005, 2006, 2007). The suborbital fenestra is absent. In contrast to the conditions in *Seymouria* (Klembara *et al.*, 2005, 2006), discosauriscids (Klembara, 1997, 2005; Klembara & Ruta, 2005a), and *Utegenia* (Klembara & Ruta, 2004a), the posterior median process of the parasphenoid is very long in *Karpinskiosaurus secundus*.

The small reconstructed skull (SL about 36 mm) is about as long as it is wide (Fig. 9). During growth, the following morphological and proportional changes can be recognized (Fig. 13).

1. In the smallest specimens, the ornamentation of the skull roofing bones consists of pits located in the ossification centres of the bones, and fine grooves and ridges diverging from the ossification centres of the bones (e.g. lacrimal and jugal in Fig. 11B). During growth, the ridges in the region of the ossification centres join together via the short ridges to enclose the pits or depressions of polygonal shape. From here, the more or less straight ridges and grooves radiate to the margins of the bones.
2. The sutures become progressively more complicated.
3. Progressive infolding of the dentine of the marginal teeth. In the largest specimens, the grooves on the external surface of the teeth, which reflect this infolding, reach the mid-length of the teeth.



**Figure 13.** Comparisons of skulls of *Karpinskiosaurus secundus* (Amalitzky, 1921) with similar sized skulls of *Discosauriscus austriacus*. Outline drawing of skulls in dorsal, lateral, and ventral views: A–C, *Karpinskiosaurus secundus*, based on PIN 4617/200 and PIN 4617/158. D–F, *Discosauriscus austriacus* (Makowsky, 1876), based on SNM Z 15529. G–I, *Karpinskiosaurus secundus*, based on PIN 2005/81 and PIN 2005/82. J–L, *Discosauriscus austriacus* (Makowsky, 1876), based on SNM Z 25744 and SNM Z 15568.

4. Progressive widening of the skull, as in the inter-orbital as in the postorbital region.
5. Widening of the prefrontal–postfrontal suture, and consequent widening of the interorbital width.
6. Shortening of the frontal. In the small skull the frontals extend behind the posterior level of the orbits, whereas in the large skull the frontal–parietal suture lies at the level of the posterior margins of the orbits.
7. Shortening of the postparietals and tabulars. The posterior margin of the skull roof becomes progressively more concave.
8. The suborbital portion of the skull becomes much higher, and the lacrima–jugal suture becomes longer. As a consequence, the orbit becomes slightly smaller and more oval in lateral view.
9. The jugal and quadratojugal become larger relative to the corresponding bones of small specimens, whereas the squamosal becomes smaller.
10. In the small skull, the otic notch is rounded. During growth, the otic notch becomes oval, with the main axis coursing anteroposteriorly. The shape of the otic notch in the large skull is influenced by the progressive dorsal expansion of the quadratojugal.
11. Gradual prolongation of the tabular occipital flange. In the small skull, PIN 4617/200, the occipital flange is mediolaterally short, and extends laterally to the mid-width of the tabular. Hence, between it and the posterolateral corner of the bone a free and narrow gap representing a dorsal portion of the post-temporal fenestra is present. In the large skull, PIN 2005/82, the occipital flange extends almost to the posterolateral corner of the tabular (Fig. 2A). Similar conditions are observable during the growth series of the seymouriamorph *D. austriacus*. In small specimens of *D. austriacus*, the occipital flange is also short and there is a free space between its lateral termination and the tabular process. However, during growth the occipital flange prolongs laterally and extends slightly above the anteromedial portion of the tabular process (Klembara, 1994, 1995, 1997).
12. Progressive closure of the palate.

There are, however, significant proportional similarities displayed by the small and large skulls. The similarities are as follows (Fig. 13).

1. The lengths of preorbital regions, orbits, and postorbital regions are proportionally the same.
2. The length of the preorbital region plus orbit is shorter than the length of the postorbital region.
3. The orbits lie in the posterior portion of the anterior half of the skull.
4. The parietal foramen lies posterior to the level of the posterior margins of the orbits.
5. The otic notch extends to the mid-length of the supratemporal. Hence, the configuration of the elements composing the otic notch region is basically the same in small and large skulls.
6. The position of the jaw joint is about the same.

From the above it is clear that the general proportions of the small (SL about 25 mm) and large (SL 75 mm) skulls are very similar, except that during growth the skull becomes progressively wider. Both small and large skulls lack traces of the sensory grooves, and were apparently fully terrestrial. Only in the largest, fully ossified specimens are the ossified quadrates and articulars present. In the Lower Permian seymouriamorph *Seymouria sanjuanensis*, the growth series from the early juveniles (SL about 20 mm) to adults (SL up to about 95 mm) are known (Klembara *et al.*, 2005, 2006, 2007). In contrast to *Karpinskiosaurus secundus*, the ossified quadrates and articulars are already present in the early juveniles of *Seymouria sanjuanensis*. Likewise, these smallest known skulls of *Seymouria sanjuanensis* do not exhibit the presence of sensory grooves. However, as in the juveniles of *Karpinskiosaurus secundus*, the general skull proportions have already been reached in the late juvenile stage (SL 56 mm) of *Seymouria sanjuanensis*, and fully ossified endocranial elements are present only in the adult specimens of the latter species (Klembara *et al.*, 2006, 2007). Comparison of the ontogenetic sequences of these two seymouriamorphs indicates that both species metamorphosed very early in their ontogeny, and spent much of their life on land. However, in contrast to conditions in *Seymouria sanjuanensis*, the ossified quadrates and articulars are present only in the largest adult skulls of *Karpinskiosaurus secundus*.

The only other seymouriamorph in which the ossified quadrate and articular have been recorded is *Discosauriscus austriacus* from the Lower Permian lake deposits of the Boskovice Basin in the Czech Republic (Klembara, 2009b). Specimens of *D. austriacus* with a skull length of up to about 35 mm had external gills and fully developed sensory grooves (Klembara, 1995). In specimens of skull length 47–52 mm, only remnants of the sensory grooves in the snout region are present (Klembara, 1996, 1997). These specimens are considered to represent juveniles or subadults approaching sexual maturity (Klembara, 1997; Sanchez *et al.*, 2008). They are very rare in the fossil record and probably already lived more or less outside of the lake. Only in the largest skull of *D. austriacus*, of about 62 mm in length, are the ossified quadrate and articular present, and the well-preserved left prefrontal of this

specimen lacks the presence of the sensory groove. This specimen may represent an early adult stage (see analysis of the ontogenetic conditions of *D. austriacus* in Klembara, 2009b). Thus, in contrast to *Karpinskiosaurus secundus* and *Seymouria sanjuanensis*, the individuals of *D. austriacus* spent much longer in the water and metamorphosed later. However, in both species, *D. austriacus* and *Karpinskiosaurus secundus*, the ossified quadrates and articulars appear only at a late ontogenetic stage.

The skull of *Karpinskiosaurus secundus* has a short snout, and the orbits are small and oval, and located in the posterior portion of the anterior half of the skull length. The interorbital portion is wide, and the postorbital portion is long and broad. Comparing skull proportions of *Karpinskiosaurus secundus* with those in other seymouriamorphs, only discosauriscids exhibit similar skull proportions. The skulls of the largest known specimens of *D. austriacus* exhibit the following features: short preorbital region, small oval orbits lying in posterior half of preorbital region, broad interorbital region, and long and broad postorbital region (Klembara, 1997). In all these characters, the skulls of the largest *D. austriacus* correspond very well to the large skulls of *Karpinskiosaurus secundus*. This is in contrast to long-snouted *Seymouria* (White, 1939; Berman *et al.*, 1987, 2000; Laurin, 1995, 1996c; Klembara *et al.*, 2005, 2006, 2007) and *Utegenia* (Klembara & Ruta, 2004a), representing two different families of Seymouriamorpha, respectively.

## PHYLOGENETIC ANALYSIS

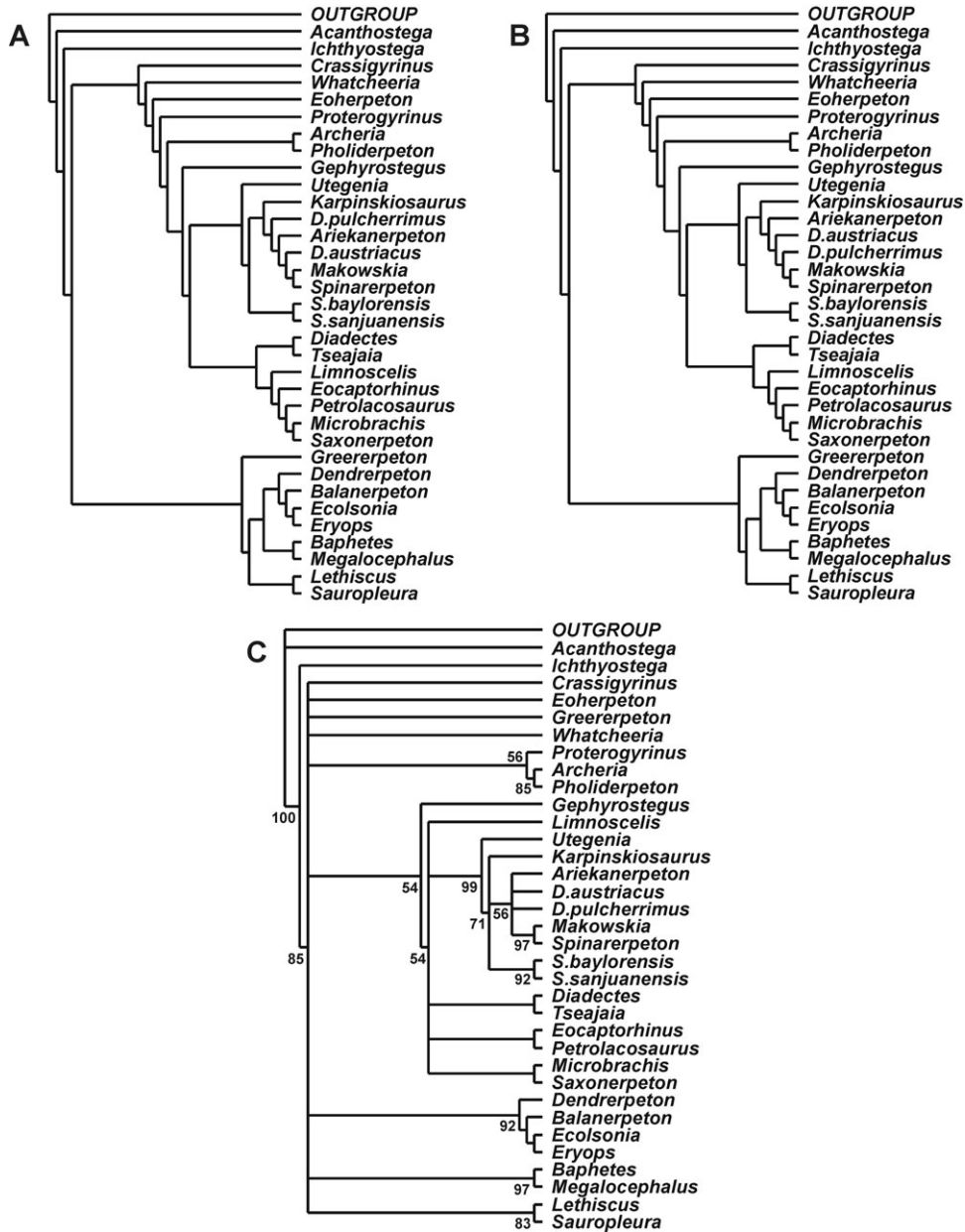
A phylogenetic analysis of Upper Carboniferous–Lower Permian Eurasian and North American seymouriamorphs, as well as several other early tetrapods, was made by Klembara & Ruta (2004b). Using this same data matrix, two further seymouriamorphs have been added: *M. laticephala* (Klembara, 2005) and *Spinarerpeton brevicephalum* (Klembara, 2009a), both from the Lower Permian deposits of the Boskovice Basin in the Czech Republic. The present analysis is based on the data matrix used for *Spinarerpeton* (Klembara, 2009a), which includes 34 taxa and 150 characters. Here, I include *Karpinskiosaurus secundus* in this data matrix. I have added five new characters and have added new states to character 85. Besides this, I have added several additional characters and updated the sources of the data (Appendix S1).

The data matrix of 35 taxa and 155 characters was processed with PAUP\* 4.0b10 (Swofford, 2001) on a Pentium PC (Appendix S2). All characters are unordered and of equal weight. The heuristic search algorithm and ACCTRAN optimization were used to

analyse the data matrix. The results of the analysis are two equally parsimonious trees of 568 steps (consistency index, CI = 0.3856; retention index, RI = 0.6928; rescaled consistency index, RC = 0.2671). The trees obtained were printed using TreeView (Page, 1996). In both trees, *Karpinskiosaurus secundus* is basal and sister taxon to Discosauriscidae (Fig. 14A, B). As for the Seymouriamorpha, the trees only differ in the position of *Ariekanerpeton* relative to two species of *Discosauriscus*. In the first tree, *Karpinskiosaurus secundus* forms a sister taxon to the following succession of the subgroupings (*Discosauriscus pulcherrimus* + (*Ariekanerpeton* + (*D. austriacus* + (*Makowskia* + *Spinarerpeton*)))) (Fig. 14A), whereas in the second tree, the succession of discosauriscids is (*Ariekanerpeton* + (*D. austriacus* + (*D. pulcherrimus* + (*Makowskia* + *Spinarerpeton*)))) (Fig. 14B). The strict consensus tree of two trees shows a trichotomy of *Ariekanerpeton*, *D. austriacus*, and *D. pulcherrimus*, and *Makowskia* plus *Spinarerpeton* as sister taxa. The position of *Karpinskiosaurus secundus* is unresolved relative to the clades of discosauriscids and seymouriids.

In both cladograms, *Karpinskiosaurus secundus* plus all discosauriscids (*Ariekanerpeton*, *D. austriacus*, *D. pulcherrimus*, *Makowskia*, and *Spinarerpeton*) form a clade that is the sister taxon to *Seymouria sanjuanensis* plus *Seymouria baylorensis*. Similarly, in both cladograms the utegeniid *Utegenia* remains basal to both *Seymouria* species; similar topologies of *Utegenia* relative to all other seymouriamorphs are in the cladograms of Klembara & Ruta (2005b) and Klembara (2005, 2009a). A bootstrap analysis shows relatively strong support for the separation of Discosauriscidae and Seymouriidae, and the node that links all seymouriamorphs (*Utegenia*, Seymouriidae, *Karpinskiosaurus secundus*, and Discosauriscidae) is strongly supported (Fig. 14C).

Although the treatment of early tetrapod relationships is beyond the scope of this paper, several points resulting from the topology of taxa on two most parsimonious trees (Fig. 14A, B) are mentioned here. The most unexpected feature of both trees is the paraphyletic position of lepospondyls: *Microbrachis* and *Saxonerpeton* are deeply nested in the amniote stem, whereas *Lethiscus* and *Sauroplorea* are nested in the Temnospondyli. This is in contrast to the topology of these four taxa in the most parsimonious tree of Klembara & Ruta (2004b): in their tree, all four taxa are nested in the Temnospondyli. Two taxa, *Crassigyrinus* and *Whatcheeria*, have a basal stem amniote position, but they usually appear as stem tetrapods (e.g. Ruta *et al.*, 2003). The Upper Carboniferous *Gephyrostegus bohemicus* (Carroll, 1970) constantly preserves its position immediately basal to the clade Seymouriamorpha plus Diadectomorpha and crown



**Figure 14.** Phylogenetic analysis. A, B, two equally parsimonious trees recovered by PAUP\* 4.0b10 from a heuristic search of 35 taxa and 155 characters. C, bootstrap percentages on a 50% majority-rule consensus tree.

group Amniota (see also Klembara & Ruta, 2004b, 2005b; Klembara, 2005, 2009a).

## COMPARISONS AND DISCUSSION

*Karpinskiosaurus secundus* differs from all other seymouriamorphs, including discosauriscids *D. austriacus*, *D. pulcherrimus* (Klembara, 1997, Klembara & Bartík, 2000), *A. sigalovi* (Ivakhnenko, 1981, 1987, Laurin, 1996b; Ivakhnenko *et al.*, 1997; Bulanov, 2003; Klembara & Ruta, 2005a, b), *M. laticephala* (Klem-

bara, 2005), *Spinarepeton brevicephalum* (Klembara, 2009a), both seymouriids *Seymouria baylorensis* and *Seymouria sanjuanensis* (White, 1939; Berman *et al.*, 1987, 2000, Berman & Martens, 1993; Laurin, 1995, 1996c; Klembara *et al.*, 2001, 2005, 2006, 2007), and utegeniid *Utegenia shpinari* (Kuznetsov & Ivakhnenko, 1981; Ivakhnenko, 1987; Laurin, 1996a; Ivakhnenko *et al.*, 1997; Bulanov, 2003; Klembara & Ruta, 2004a, b), in the following characters.

1. Interpremaxillary fenestra present. The interpremaxillary fenestra may be present as a transi-

- tional structure in the larval stage of *Discosauriscus austriacus*; however, during growth the fenestra becomes closed (Klembara, 1997). The interpremaxillary fenestra is not present in the adult stage of any Upper Carboniferous–Lower Permian seymouriamorph.
2. Distinct posterior process of parietal wedged between tabular and postparietal. The posterior process of the parietal is most distinctly developed in the smaller specimens, in which the sutures are not so complicated. In similar sized skulls of *Utegenia* and discosauriscids, as well as in those of all size categories of *Seymouria*, this posterior process of the parietal is never as large.
  3. Parietal has underlying lamina for tabular. This is not visible in the largest articulated skulls; however, because the largest skulls display all other distinctive features of *Karpinskiosaurus secundus*, the presence of this character is supposed in them. This feature is probably connected with the presence of the distinct anteromedial process of the tabular (see character 8 below). In all other Upper Carboniferous–Lower Permian seymouriamorphs, the tabular has the underlying lamina that is overlapped by the posterolateral portion of the parietal (Klembara, 1997: fig. 5).
  4. Dorsomedial margin of squamosal wedged between supratemporal and intertemporal; hence, intertemporal–squamosal suture runs in anterolateral–posteromedial direction, and supratemporal–squamosal suture runs in anteromedial–posterolateral direction. In all Upper Carboniferous–Lower Permian seymouriamorphs, the suture between the squamosal laterally, and the supratemporal plus intertemporal medially, is straight.
  5. Presence of lateral process of supratemporal wedged into squamosal. In all Upper Carboniferous–Lower Permian seymouriamorphs, the entire lateral margins of the supratemporal and squamosal are straight.
  6. Otic notch encroaches upon posterolateral margin of skull table; thus, lateral portion of tabular extends far laterally than otic notch margin of supratemporal. In all Upper Carboniferous–Lower Permian seymouriamorphs, the otic notch margin formed by the posterolateral margin of the skull table is straight.
  7. Rounded or oval otic notch in dorsal view reaching anteriorly mid-length of supratemporal. In *Seymouria* and discosauriscids, the otic notch is anteroposteriorly elongated and anteriorly reaches the level of the supratemporal–intertemporal suture, or extends still more anteriorly. In *Utegenia*, the otic notch is very short and its morphology is quite different from that in *Karpinskiosaurus secundus*, but is comparable with the conditions in *Gephyrostegus* and embolomeres (Klembara & Ruta, 2004a).
  8. Anteromedial corner of tabular extends into a distinct process fitting between the parietal and the supratemporal, and reaching about mid-length of the supratemporal. Such a large process invading the territory of the parietal is not developed in any Upper Carboniferous–Lower Permian seymouriamorph.
  9. Absence of tabular process. The tabular process is present in all Upper Carboniferous–Lower Permian seymouriamorphs. In *Utegenia*, the tabular process is an elongated plate with pointed or rounded posterior end, whereas in *Seymouria* and discosauriscids the tabular process is of rectangular shape. In *Karpinskiosaurus secundus*, the tabular process is absent and the lateral portion of the smooth occipital flange of the tabular reaches almost the posterolateral corner of the tabular, i.e. it extends more laterally than in seymouriamorphs with the tabular process.
  10. Presence of small, but distinct ascending process on anterodorsal margin of maxilla fitting into a notch in ventral margin of lacrimal. Such an ascending process is absent in all Upper Carboniferous–Lower Permian seymouriamorphs.
  11. Jugal–postorbital suture longer than postorbital–squamosal suture. A relatively short and equally running jugal–postorbital suture is present in several seymouriamorph species, such as *Seymouria sanjuanensis*, *Discosauriscus pulcherrimus*, and *Ariekanerpeton sigalovi*; however, it is never longer than the postorbital–squamosal suture.
  12. Most of external surface of dentary bears many horizontally coursing grooves divided by intervening ridges. Several similar horizontally coursing grooves are present on the external surface of the dentary of the largest known specimen of *Ariekanerpeton sigalovi* from the Lower Permian of Tadzhikistan (PIN 2079/262a, SL ~ 48 mm); however, the grooves are not so densely arranged, and occupy approximately the middle section of the dentary length (Klembara & Ruta, 2005a: fig. 1B). In *Karpinskiosaurus secundus*, the horizontal ridges and intervening grooves are very densely arranged, and except for the anteriormost portion occupy the entire external surface of the dentary. This distinctive pattern of ornamentation is already present in the smallest specimens of *Karpinskiosaurus secundus*.
  13. With the exception of the apical portion, the marginal teeth are labiolingually expanded and mesiodistally narrow. In the Upper Carboniferous–Lower Permian seymouriamorphs, the teeth are conical.

Bulanov (2003) included *Discosauriscus* and *Ariekanerpeton* in the subfamily Discosauriscinae, and *Karpinskiosaurus* in the subfamily Karpinskiosaurinae, and both subfamilies into the family Karpinskiosauridae. As shown below, *Karpinskiosaurus secundus* displays many features that are completely absent not only in *Discosauriscus* and *Ariekanerpeton*, but also in all other Lower Permian seymouriamorphs, including, among others: the absence of the tabular process; anteromedial corners of the tabulars extending anteriorly; presence of the medial embayment in the lateral margins of the supratemporal and tabular; rounded, and/or oval, otic notch; etc. (see the complete list of distinguishing characters for *Karpinskiosaurus secundus* above). Besides this, the postcranial skeleton of *Karpinskiosaurus secundus* is preserved, but not yet described. Therefore, I do not see sufficient reason to change the current understanding of the family Discosauriscidae, and I consider both Discosauriscidae (Romer, 1947) and Karpinskiosauridae (Sushkin, 1925) as separate families within Seymouriamorpha, despite of the fact that the general proportions of the skull of *Karpinskiosaurus secundus* and discosauriscids are very similar.

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#### REFERENCES

- Amalitzky A. 1921.** Seymouriidae, North Dvina Excavations of Professor V. P. Amalitzky. *Petrograd Academy of Sciences* 2: 1–14 (in Russian).
- Beaumont EH. 1977.** Cranial morphology of the Loxommataidae (Amphibia: Labyrinthodontia). *Philosophical Transactions of the Royal Society of London, Series B* 280: 29–101.
- Berman DS. 2000.** Origin and early evolution of the amniote occiput. *Journal of Paleontology* 74: 938–956.
- Berman DS, Henrici AC, Sumida SS, Martens T. 2000.** Redescription of *Seymouria sanjuanensis* (Seymouriamorpha) from the Lower Permian of Germany based on complete, mature specimens with a discussion of paleoecology of the Bromacker locality assemblage. *Journal of Vertebrate Paleontology* 20: 253–268.
- Berman DS, Martens T. 1993.** First occurrence of *Seymouria* (Amphibia: Batrachosauria) in the Lower Permian Rotliegend of Central Germany. *Annals of Carnegie Museum* 62: 63–79.
- Berman DS, Reisz RR, Eberth DA. 1985.** *Ecolsonia cutlerensis*, an early Permian dissorophid amphibian from the Cutler Formation of north-central New Mexico. *Circular of the New Mexico Bureau of Mines and Mineral Resources* 191: 1–31.
- Berman DS, Reisz RR, Eberth DA. 1987.** *Seymouria sanjuanensis* (Amphibia, Batrachosauria) from the Lower Permian Cutler Formation of north-central New Mexico and the occurrence of sexual dimorphism in that genus questioned. *Canadian Journal of Earth Sciences* 24: 1769–1784.
- Berman DS, Sumida SS, Martens T. 1998.** *Diadectes* (Diadectomorpha: Diadectidae) from the early Permian of central Germany, with description of a new species. *Annals of the Carnegie Museum* 67: 53–93.
- Bosnyak AK, Milner AC. 1998.** Order Nectridea Miall, 1875. In: Wellnhofer P, ed. *Handbuch der Paläoherpetologie, Teil 1: Lepospondyli*. Munich: Pfeil, 73–212.
- Broili F. 1904.** Permische Stegocephalen und Reptilien aus Texas. *Palaeontographica* 51: 80–84.
- Bulanov VV. 2002.** *Karpinskiosaurus ultimus* (Seymouriamorpha, Parareptilia) from the Upper Permian of European Russia. *Paleontological Journal* 36: 72–79.
- Bulanov VV. 2003.** Evolution and systematics of seymouriamorph parareptiles. *Paleontological Journal* 37 (Suppl 1): 1–105.
- Bulanov VV. 2005.** First data on karpinskiosaurids (Seymouriamorpha, Parareptilia) from the Ishevo faunal assemblage). *Paleontological Journal* 39: 187–191.
- Bystrow AP. 1944.** *Kotlassia prima* Amalitzky. *Bulletin of the Geological Society of America* 55: 379–416.
- Carroll RL. 1970.** The ancestry of reptiles. *Philosophical Transactions of the Royal Society of London, Series B* 257: 267–308.
- Carroll RL, Gaskill P. 1978.** The order microsauria. *Memoirs of the American Philosophical Society* 126: 1–211.
- Clack JA. 1994.** *Acanthostega gunnari*, a Devonian tetrapod from Greenland; the snout, palate and ventral parts of the braincase, with a discussion of their significance. *Meddelelser om Grønland: Geoscience* 31: 1–24.
- Clack JA. 1996.** The palate of *Crassigyrinus scoticus*, a primitive tetrapod from the Lower Carboniferous of Scotland. In: Milner AR, ed. *Studies on Carboniferous and Permian vertebrates*. 55–64. Special Papers in Palaeontology 52, Oxford: Alden Group.
- Clack JA. 1998.** The Scottish Carboniferous tetrapod *Crassigyrinus scoticus* (Lydekker)-cranial anatomy and relationships. *Transactions of the Royal Society of Edinburgh: Earth Sciences* 88 (for 1997): 127–142.

- Clack JA. 2002.** An early tetrapod from 'Romer's Gap'. *Nature* **418**: 72–76.
- Coates MI. 1996.** The Devonian tetrapod *Acanthostegia gunnari* Jarvik: postcranial anatomy, basal tetrapod relationships and pattern of skeletal evolution. *Transactions of the Royal Society of Edinburgh: Earth Sciences* **87**: 363–421.
- Efremov IA. 1940.** Übersicht der Formen der Perm- und Trias Tetrapoden Fauna der UdSSR. *Zentralblatt der Mineralogie, Geologie und Paläontologie, Abhandlungen B* **12**: 372–383.
- Efremov IA, Vyushkov BP. 1955.** Catalogue of localities of Permian and Triassic terrestrial vertebrates from the USSR. *Trudy Paleontologicheskogo Instituta Akademii Nauk* **46**: 1–185 (in Russian).
- Fracasso M. 1987.** Braincase of *Limnoscelis paludis* Williston. *Postilla* **201**: 1–22.
- Godfrey SJ. 1989.** The postcranial skeletal anatomy of the Carboniferous tetrapod *Greererpeton burkemorani* Romer 1969. *Philosophical Transactions of the Royal Society of London, Series B* **323**: 75–133.
- Heaton MJ. 1979.** Cranial anatomy of primitive captorhinid reptiles from the Late Pennsylvanian and Early Permian, Oklahoma and Texas. *Bulletin of the Oklahoma Geological Survey* **127**: 1–80.
- Heaton MJ. 1980.** The Cotylosauria, a reconsideration of a group of archaic tetrapods. In: Panchen AL, ed. *The terrestrial environment and the origin of land vertebrates*. London: Academic Press, 497–551.
- Heaton MJ, Reisz RR. 1986.** Phylogenetic relationships of captorhinomorph reptiles. *Canadian Journal of Earth Sciences* **23**: 402–418.
- Holmes R. 1977.** The osteology and musculature of the pectoral limb of small captorhinids. *Journal of Morphology* **152**: 101–140.
- Holmes RB. 1984.** The Carboniferous amphibian *Proterogyrinus scheelei* Romer, and the early evolution of tetrapods. *Philosophical Transactions of the Royal Society of London, Series B* **306**: 431–527.
- Holmes RB. 1989.** The skull and axial skeleton of the Lower Permian anthracosauroid amphibian *Archeria crassidisca* Cope. *Palaeontographica Abteilung A* **207**: 161–206.
- Holmes RB, Carroll RL, Reisz RR. 1998.** The first articulated skeleton of *Dendrerpeton acadianum* (Temnospondyli, Dendrerpetontidae) from the Lower Pennsylvanian locality of Joggins, Nova Scotia, and a review of its relationships. *Journal of Vertebrate Paleontology* **18**: 64–79.
- Ivakhnenko MF. 1981.** Discosauriscidae from the Permian of Tadzhikistan. *Paleontologicheskij Zhurnal* **1**: 114–128 (in Russian).
- Ivakhnenko MF. 1987.** Permian parareptiles of USSR. *Trudy Paleontologicheskogo Instituta Akademii Nauk* **223**: 1–160 (in Russian).
- Ivakhnenko MF, Golubev VK, Gubin YM, Kalandadze NN, Novikov IV, Sennikov AG, Rautian AS. 1997.** Permian and Triassic tetrapods of Eastern Europe. Moskva: GEOS, 1–216 (in Russian).
- Jarvik E. 1952.** On the fish-like tail in the ichthyostegid stegocephalians with descriptions of a new stegocephalian and a new crossopterygian from the Upper Devonian of East Greenland. *Meddelelser om Grønland* **114**: 1–90.
- Jarvik E. 1980.** *Basic structure and evolution of vertebrates*. London and New York: Academic Press.
- Jarvik E. 1996.** The Devonian tetrapod *Ichthyostega*. *Fossils and Strata* **40**: 1–206.
- Kalandadze NN, Ochev VG, Tatarinov LP, Tchudinov PK, Shishkin MA. 1968.** Catalogue of the Permian and Triassic tetrapods from the USSR. In: Vanin VV, ed. *Upper Palaeozoic and Mesozoic Amphibians and Reptiles from the USSR*. Moscow: Nauka, 72–92 (in Russian).
- Klembara J. 1994.** The sutural pattern of skull-roof bones in Lower Permian *Discosauriscus austriacus* from Moravia. *Lethaia* **27**: 85–95.
- Klembara J. 1995.** The external gills and ornamentation of skull roof bones of the Lower Permian tetrapod *Discosauriscus* (Kuhn 1933) with remarks to its ontogeny. *Paläontologische Zeitschrift* **69**: 265–281.
- Klembara J. 1996.** The lateral line system of *Discosauriscus austriacus* (Makowsky 1876) and the homologization of skull roof bones between tetrapods and fishes. *Palaeontographica Abteilung A* **240**: 1–27.
- Klembara J. 1997.** The cranial anatomy of *Discosauriscus* Kuhn, a seymouriamorph tetrapod from the Lower Permian of the Boskovice Furrow (Czech Republic). *Philosophical Transactions of the Royal Society of London, Series B* **352**: 257–302.
- Klembara J. 2005.** A new discosauriscid seymouriamorph tetrapod from the Lower Permian of Moravia, Czech Republic. *Acta Palaeontologica Polonica* **50**: 25–48.
- Klembara J. 2009a.** The skeletal anatomy and relationships of a new discosauriscid seymouriamorph from the Lower Permian of Moravia (Czech Republic). *Annals of Carnegie Museum of Natural History* **77** (for 2008): 451–484.
- Klembara J. 2009b.** New cranial and dental features of *Discosauriscus austriacus* (Seymouriamorpha, Discosauriscidae) and the ontogenetic conditions of *Discosauriscus*. *Special Papers in Palaeontology* **81**: 61–69.
- Klembara J, Bartík I. 2000.** The postcranial skeleton of *Discosauriscus* Kuhn, a seymouriamorph tetrapod from the Lower Permian of the Boskovice Furrow (Czech Republic). *Transactions of the Royal Society of Edinburgh: Earth Sciences* **90** (for 1999): 287–316.
- Klembara J, Berman DS, Henrici A, Cernanský A. 2005.** New structures and reconstructions of the skull of the seymouriamorph *Seymouria sanjuanensis*, Vaughn. *Annals of Carnegie Museum of Natural History* **74**: 217–224.
- Klembara J, Berman DS, Henrici A, Cernanský A, Werneburg R. 2006.** Comprison of cranial anatomy and proportions of similarly sized *Seymouria sanjuanensis* and *Discosauriscus austriacus*. *Annales of Carnegie Museum* **75**: 37–49.
- Klembara J, Berman DS, Henrici A, Cernanský A, Werneburg R, Martens T. 2007.** First description of skull of Lower Permian *Seymouria sanjuanensis* (Seymouriamorpha: Seymouriidae) at an early juvenile stage. *Annals of Carnegie Museum* **76**: 53–72.

- Klembara J, Janiga M. 1993.** Variation in *Discosauriscus austriacus* (Makowsky, 1876) from the Lower Permian of the Boskovic Furrow (Czech Republic). *Zoological Journal of the Linnean Society* **108**: 247–270.
- Klembara J, Martens T, Bartík I. 2001.** The postcranial remains of a juvenile seymouriamorph tetrapod from the Lower Permian Rotliegend of the Tambach Formation of Central Germany. *Journal of Vertebrate Paleontology* **21**: 521–527.
- Klembara J, Ruta M. 2004a.** The seymouriamorph tetrapod *Utegenia shpinari* from the ?Upper Carboniferous–Lower Permian of Kazakhstan. Part. I: Cranial anatomy and ontogeny. *Transactions of the Royal Society of Edinburgh: Earth Sciences* **94** (for 2003): 45–74.
- Klembara J, Ruta M. 2004b.** The seymouriamorph tetrapod *Utegenia shpinari* from the ?Upper Carboniferous–Lower Permian of Kazakhstan. Part II: Postcranial anatomy and relationships. *Transactions of the Royal Society of Edinburgh: Earth Sciences* **94** (for 2003): 75–93.
- Klembara J, Ruta M. 2005a.** The seymouriamorph tetrapod *Ariekanerpeton sigalovi* from the Lower Permian of Tadzhikistan. Part 1. Cranial anatomy and ontogeny. *Transactions of the Royal Society of Edinburgh: Earth Sciences* **96**: 43–70.
- Klembara J, Ruta M. 2005b.** The seymouriamorph tetrapod *Ariekanerpeton sigalovi* from the Lower Permian of Tadzhikistan. Part II. Postcranial anatomy and relationships. *Transactions of the Royal Society of Edinburgh: Earth Sciences* **96**: 71–93.
- Kuznetsov VV, Ivakhnenko MF. 1981.** Discosauriscids from the upper palaeozoic of South Kazakhstan. *Paleontologicheskij Zhurnal* **3**: 102–110 (in Russian).
- Laurin M. 1995.** Comparative cranial anatomy of *Seymouria sanjuanensis* (Tetrapoda: Batrachosauria) from the Lower Permian of Utah and New Mexico. *PaleoBios* **16**: 1–8.
- Laurin M. 1996a.** A reappraisal of *Utegenia*, a Permian–Carboniferous seymouriamorph (Tetrapoda: Batrachosauria) from Kazakhstan. *Journal of Vertebrate Paleontology* **16**: 374–383.
- Laurin M. 1996b.** A reevaluation of *Ariekanerpeton*, a Lower Permian seymouriamorph (Tetrapoda: Seymouriamorpha) from Tadzhikistan. *Journal of Vertebrate Paleontology* **16**: 653–665.
- Laurin M. 1996c.** A redescription of the cranial anatomy of *Seymouria baylorensis*, the best known seymouriamorph (Vertebrata: Seymouriamorpha). *PaleoBios* **17**: 1–16.
- Laurin M. 2000.** Seymouriamorphs. In: Heatwole H, Carroll RL, eds. *Amphibian biology*, 4, palaeontology. Chipping Norton: Surrey Beatty & Sons, 1064–1080.
- Lombard RE, Bolt JR. 1995.** A new primitive tetrapod *Whatcheeria deltae* from the Lower Carboniferous of Iowa. *Palaeontology* **38**: 471–494.
- Makowsky A. 1876.** Über einen neuen Labyrinthodonten ‘*Archegosaurus austriacus* nov. spec.’. *Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften in Wien* **73**: 155–166.
- Milner AC, Lindsay W. 1998.** Postcranial remains of *Baphetes* and their bearing on the relationships of the Baphetidae (= Loxommatidae). *Zoological Journal of the Linnean Society* **122**: 211–235.
- Milner AR. 1980.** The temnospondyl amphibian *Dendrerpeton* from the Upper Carboniferous of Ireland. *Palaeontology* **23**: 125–141.
- Milner AR, Sequeira SEK. 1994.** The temnospondyl amphibians from the Viséan of East Kirkton, West Lothian, Scotland. *Transactions of the Royal Society of Edinburgh: Earth Sciences* **84**: 331–361.
- Miner RW. 1925.** The pectoral limb of *Eryops* and other primitive tetrapods. *Bulletin of the American Museum of Natural History* **51**: 145–312.
- Moss JL. 1972.** The morphology and phylogenetic relationships of the Lower Permian tetrapod *Tseajaja campi* Vaughn (Amphibia: Seymouriamorpha). *Publications of Geological Sciences of the University of California* **98**: 1–68.
- Moulton JM. 1974.** A description of the vertebral column of *Eryops* based on the notes and drawings of A. S. Romer. *Breviora* **428**: 1–44.
- Page RDM. 1996.** TREEVIEW: an application to display phylogenetic trees on personal computers. *Computer Applications in the Biosciences* **12**: 357–358.
- Panchen AL. 1975.** A new genus and species of anthracosaur amphibian from the Lower Carboniferous of Scotland and the status of *Pholidogaster pisciformis* Huxley. *Philosophical Transactions of the Royal Society of London, Series B* **269**: 581–640.
- Panchen AL. 1980.** The origin and relationships of the anthracosaur amphibians from the Late Palaeozoic. In: Panchen AL, ed. *The terrestrial environment and the origin of land vertebrates*. London: Academic Press, 319–350.
- Panchen AL. 1985.** On the amphibian *Crassigyrinus scoticus* Watson from the Carboniferous of Scotland. *Philosophical Transactions of the Royal Society of London, Series B* **309**: 505–568.
- Panchen AL, Smithson TR. 1988.** The relationships of early tetrapods. In: Benton MJ, ed. *The phylogeny and classification of the tetrapods 1, amphibians, reptiles, birds*. Oxford: Clarendon Press, 1–32.
- Pawley K, Warren A. 2006.** The appendicular skeleton of *Eryops megacephalus* Cope, 1877 (Temnospondyli: Eryopoidea) from the Lower Permian of North America. *Journal of Paleontology* **80**: 561–580.
- Reisz RR. 1981.** A diapsid reptile from the Pennsylvanian of Kansas. *Occasional Papers of the Museum of Natural History, University of Kansas* **7**: 1–74.
- Romer AS. 1946.** The primitive reptile *Limnoscelus* restudied. *American Journal of Science* **244**: 149–188.
- Romer AS. 1947.** Review of the Labyrinthodontia. *Bulletin of the Museum of Comparative Zoology, Harvard College* **99**: 1–368.
- Romer AS. 1957.** The appendicular skeleton of the Permian embolomorphous amphibian *Archeria*. *Contributions from the Museum of Paleontology, University of Michigan* **13**: 103–159.
- Romer AS, Parsons TS. 1977.** *The vertebrate body*, 5th edn. Philadelphia, PA: Saunders College Publishing.
- Ruta M, Coates MI, Quicke DLJ. 2003.** Early tetrapod

- relationships revisited. *Biological Reviews of the Cambridge Philosophical Society* **78**: 251–345.
- Sanchez S, Klembara J, Castanet J, Steyer S. 2008.** Salamander-like development in a stem amniote revealed by palaeohistology. *Biology Letters* **4**: 411–414.
- Sawin HJ. 1941.** The cranial anatomy of *Eryops megacephalus*. *Bulletin of the Museum of Comparative Zoology, Harvard College* **88**: 407–463.
- Smithson TR. 1982.** The cranial morphology of *Greererpeton burkemorani* Romer (Amphibia: Temnospondyli). *Zoological Journal of the Linnean Society* **76**: 29–90.
- Smithson TR. 1985.** The morphology and relationships of the Carboniferous amphibian *Eoherpeton watsoni* Panchen. *Zoological Journal of the Linnean Society* **85**: 317–410.
- Sumida SS, Lombard RE, Berman DS. 1992.** Morphology of the atlas-axis complex of the late Palaeozoic tetrapod suborders Diadectomorpha and Seymouriamorpha. *Philosophical Transactions of the Royal Society of London, Series B* **336**: 259–273.
- Sushkin PP. 1925.** On the representatives of the Seymouriamorpha, supposed primitive reptiles, from the Upper Permian of Russia, and on their phylogenetic relations. *Occasional Papers, Boston Society of Natural History* **5**: 179–181.
- Sushkin PP. 1926.** Notes on the pre-Jurassic tetrapoda from Russia: 3. On Seymouriamorpha from the Upper Permian of North Dvina. *Palaeontologica Hungarica* **1**: 336–344.
- Swofford DL. 2001.** *PAUP\*: Phylogenetic analysis using parsimony (\*and other methods)*. Version 4.0b10. Sunderland, MA: Sinauer Associates.
- Tatarinov LP. 1972.** Seymouriamorphen aus der Fauna der USSR. *Handbuch der Paläoherpetologie* **5**: 70–80.
- Tchudinov PK, Vyushkov BP. 1956.** New data on small cotylosaurs from the Permian and Triassic of the USSR. *Doklady Akademii Nauk SSSR* **8**: 547–550 (in Russian).
- Vallin G, Laurin M. 2004.** Cranial morphology and affinities of *Microbrachis*, and a reappraisal of the phylogeny and lifestyle of the first amphibians. *Journal of Vertebrate Paleontology* **24**: 56–72.
- Watson DMS. 1917.** A sketch classification of the pre-Jurassic tetrapod vertebrates. *Proceedings of the Zoological Society of London* **1917**: 167–186.
- Watson DMS. 1954.** On *Bolosaurus* and the origin and classification of reptiles. *Bulletin of the Museum of Comparative Zoology (Harvard University)* **111**: 297–449.
- Wellstead CF. 1982.** A Lower Carboniferous aistopod amphibian from Scotland. *Palaeontology* **25**: 193–208.
- White TE. 1939.** Osteology of *Seymouria baylorensis* Broili. *Bulletin of the Museum of Comparative Zoology, Harvard College* **85**: 325–409.
- Williston SW. 1911.** *American Permian vertebrates*. Chicago, IL: University of Chicago Press.

## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

### Appendix S1. List of characters used in the cladistic analysis.

The following sources were used for each taxon (asterisked taxa are those for which personal observations were carried out by the author): *Acanthostega* (Clack, 1994, 2002; Coates, 1996); *Archieria* (Holmes, 1989; Romer, 1957); *\*Ariekanerpeton* (Ivakhnenko, 1981, 1987; Laurin, 1996b; Klembara & Ruta, 2005a, b); *Balanerpeton* (Milner & Sequeira, 1994); *Baphetes* (Beaumont, 1977; Milner & Lindsay, 1998); *Crassigyrinus* (Panchen, 1985; Clack, 1996, 1998); *Dendrerpeton* (Milner, 1980; Holmes *et al.*, 1998); *Diadectes* (Berman *et al.*, 1998; Berman, 2000); *\*Discosauriscus austriacus* and *\*Discosauriscus pulcherrimus* (Klembara, 1997; Klembara & Bartík, 2000, and references therein); *Ecolsonia* (Berman *et al.*, 1985); *Eocaptorhinus* (Holmes, 1977; Heaton, 1979, 1980; Heaton & Reisz, 1986); *Eoherpeton* (Panchen, 1975; Smithson, 1985); *Eryops* (Miner, 1925; Sawin, 1941; Moulton, 1974; Pawley & Warren, 2006); *\*Gephyrostegus* (Carroll, 1970); *\*Greererpeton* (Smithson, 1982; Godfrey, 1989); *\*Ichthyostega* (Jarvik, 1952, 1980, 1996); *Lethiscus* (Wellstead, 1982); *Limnoscelis* (Williston, 1911; Romer, 1946; Fracasso, 1987; Berman, 2000); *\*Makowskia* (Klembara, 2005); *Megalocephalus* (Beaumont, 1977); *Microbrachis* (Carroll & Gaskill, 1978; Vallin & Laurin, 2004); *Petrolacosaurus* (Reisz, 1981); *Pholiderpeton* (Clack, 1987); *\*Proterogyrinus* (Holmes, 1984); *Sauroplorea* (Bossy & Milner, 1998); *Saxonerpeton* (Carroll & Gaskill, 1978); *\*Seymouria baylorensis* (White, 1939; Sumida *et al.*, 1992; Laurin, 1996c; Berman, 2000); *\*Seymouria sanjuanensis* (Laurin, 1995; Berman *et al.*, 2000; Klembara *et al.*, 2001, 2005, 2006, 2007); *\*Spinarerpeton* (Klembara, 2009a); *Tseajia* (Moss, 1972); *\*Utegenia* (Kuznetsov & Ivakhnenko, 1981; Ivakhnenko, 1987; Laurin, 1996a; Klembara & Ruta, 2004a, b); *Whatcheeria* (Lombard & Bolt, 1995).

### Appendix S2. Data matrix.

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