PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

The cranial anatomy of *Discosauricsus* Kuhn, a seymouriamorph tetrapod from the Lower Permian of the Boskovice Furrow (Czech Republic)

Jozef Klembara

Phil. Trans. R. Soc. Lond. B 1997 **352**, 257-302
doi: 10.1098/rstb.1997.0021

The cranial anatomy of *Discosauriscus* Kuhn, a seymouriamorph tetrapod from the Lower Permian of the Boskovice Furrow (Czech Republic)

JOZEF KLEMBARA

Faculty of Natural Sciences, Comenius University, Zoological Institute, Mlynská dolina B-2, 842 15 Bratislava, Slovak Republic

CONTENTS

SUMMARY

A detailed description is given of the cranial anatomy of the Lower Permian tetrapod *Discosauriscus*. This material is three-dimensionally preserved and represents one of the best known seymouriamorph tetrapods. Two species, *D. austriacus* and *D. pulcherrimus*, are distinguished in the material from the Boskovice Furrow. *D. austriacus* is abundant, *D. pulcherrimus* is rare. The two species differ in the following features: in (1) the shape of the postorbital and the jugal and the nature of their junction, (2) the shape of the prefrontal and the postfrontal and the position of their contact and (3) the morphology of the ventral surfaces of the palatal bones and the arrangement of the denticles on them. The genus *Discosauriscus* represents larval, metamorphic and early juvenile individuals. Comparison of the cranial structures of *Discosauriscus* with those of *Seymouria baylorensis*, *Seymouria sanjuanensis*, and *Seymouria* cf. *S. sanjuanensis* (which is of similar size to the largest individuals of *Discosauriscus*) shows that (i) *Discosauriscus* and *Seymouria* are structurally similar but different genera, (ii) *Discosauriscus* is a member of the taxon Seymouriamorpha, (iii) *Discosauriscus* and *Ariekanerpeton* comprise the family Discosauriscidae and (iv) *Seymouria* is not a reptile (an amniote animal). *Ariekanerpeton*, *Utegenia*, *Urumquia*, kotlassiids, leptorophids and *Enosuchus* require revision.

1. INTRODUCTION

Since the first description of the Moravian *Archegosaurus austriacus* (Makowsky 1876), the only major revision of the skeletal anatomy of this tetrapod from the Boskovice Furrow was performed by Špinar (1952). He distinguished two genera and four species: *Discosauriscus pulcherrimus* (Fritsch 1879), *D. potamites* (Steen 1938), *Letoverpeton moravicum* (Fritsch 1883) and *L. austriacum* (Makowsky 1876). Most previous studies of the cranium of these Moravian tetrapods (Špinar 1952; Watson 1954; Werneburg 1985, 1988, cf. also 1989*a*, *b*) were based on compressed material, only Švec (1986) studied the braincase on partly chemically prepared three-dimensional specimens.

The new material of *Discosauriscus* from the Lower Permian of the Boskovice Furrow is three-dimensional (Klembara & Meszároš 1992) and permits the complete revision of the cranial anatomy of this genus. Studies of the cranial proportions and selected cranial structures have already been published separately (Klembara 1992, 1993, 1994*a*, *b*, 1995*b*, 1996). Klembara & Janiga (1993) concluded that the proportional differences and the morphological data on which Špinar (1952) distinguished two genera and four species are invalid and that probably only one taxon—*Discosauriscus austriacus* (Makowsky 1876)—exists in the Boskovice Furrow, and that probably the specimens from Ruprechtice (north region of the Czech Republic) and Niederhäslich (Germany), known as *Discosauriscus pulcherrimus* (Fritsch 1879), also belong to this taxon. As shown below, in the light of previously unknown features provided by the new material, it is possible to recognize that *Discosauriscus pulcherrimus* (Fritsch 1879) from Ruprechtice and Germany is a valid species. However, among the several hundred specimens from the Boskovice Furrow at my disposal, only five may be assigned to this species. All others belong to *Discosauriscus austriacus* (Makowsky 1876). Only these two species of the genus *Discosauriscus* are distinguishable at present. The taxa *Discosauriscus sacheti* (Saint-Seine 1949; cf. Heyler (1969)), *Discosauriscus netschaevi* (Riabinin 1911), Lower Upper Permian, cf. Ivakhnenko (1987) and *Letoverpeton thuringiacum* (Werneburg 1988) are insufficiently known and need revision.

In contrast to *D. pulcherrimus*, the postcranial material of *D. austriacus* from the Boskovice Furrow is well preserved and will be described in detail separately.

Klembara (1994*a*, *b*, 1995*a*) concluded that the taxa *Discosauriscus*, *Utegenia*, and *Ariekanerpeton* are represented by larval, metamorphic and early juvenile individuals; the adults are unknown so far (cf. Laurin 1994, 1995 for *Utegenia* and *Ariekanerpeton*). The same is probably true for *Urumquia* (Zhang *et al*. 1984).

2. METHODS

Most of the specimens were completely removed from the rock chemically using acetic acid (for the method, see Klembara & Meszároš (1992)). Although the individual bones are three-dimensionally preserved, the skulls as a whole are more or less dorsoventrally compressed. To reconstruct the original shape of the skull, enlarged, three-dimensional wax-plasticine models were constructed. One model is based mostly on specimen K 13 (*Discosauriscus austriacus*, SL (skull length) = 27 mm, figures 2 and 23–26), representing a late larval or early metamorphic individual; the second model is based largely on K 323 (*D. austriacus*, SL = 49 mm) and K 52 (SL *ca*. 52 mm), both representing probable early juveniles of the same species (figures 27 and 28). The third model is based on K 16 (*D. pulcherrimus*), which probably represents a late metamorphic individual (figures 33 and 34). Every bone of these skulls was individually measured, modelled, enlarged, and then put together. The missing cranial parts were supplemented from other specimens of comparable size.

3. SYSTEMATIC PALAEONTOLOGY

Seymouriamorpha (Watson 1917)
Family Discosauriscidae (Romer 1947)
Genus *Discosauriscus* (Kuhn 1933)

The following diagnoses do not include the type of the ornamentation of the skull roof bones; for its ontogeny (including sensory organs), see Klembara (1995*a*).

Diagnosis

(i) *Larval and metamorphic individuals*

In dorsal view, the skull is semi-elliptical in shape. Short preorbital region. Large rounded orbits placed anteriorly. Pineal foramen lies at or slightly behind the posterior level of the orbital margin and in the anterior half of the length of the interparietal suture. Posterior extent of the jaw joint lies at the level of the supratemporal–tubular suture. Shallow and dorsoventrally broad otic notch. 'Kinetic line' absent. Infraorbital, supraorbital, postotic, main, jugal and supratemporal commissural sensory grooves almost constantly well developed. Pit lines are occasionally preserved on frontal, parietal, postparietal, tabular, supratemporal and intertemporal. Foraminate pits occasionally preserved. Well-developed tubular process of rectangular shape. Jugal exposed on the ventral cheek margin. Jugal–ectopterygoid contact lies behind the posterior end of the maxilla. Trough-shaped septomaxilla with septomaxillary foramen. Septomaxilla–vomer contact present. Prefrontal–palatine junction is in the region of the anterolateral corner of the palatine. Anteromedially running orbital flange of the prefrontal present. Internal lamina of the lacrimal present; it joins the dorsolateral surface of the palatine and the internal surface of the maxilla. About 40 sclerotic plates. Marginal dentition: premaxilla 5–7, maxilla 20–29. Teeth are of a cylindrical shape with slightly recurved tips. Dentine of the basal portions of the teeth starts (in late larval stage) to exhibit labyrinthine infolding. Palatal tusks: vomer 1–4, palatine 1–5, ectopterygoid 0. Arrangement of the tooth rows and presence or absence of the ridges on the ventral surface of the palate differs between species (see below). Interpterygoid vacuities narrow. Transverse flange extends slightly below the level of the ventral margin of the cheek. Suborbital fenestra present. Infraorbital canal on the dorsal palatine surface present. Large posteromedial portions of the vomer and the palatine overlap dorsally the pterygoid. Parasphenoid is triangular in shape; the stem and the posterolateral processes are long. Laterally expanded otic tubes, cartilaginous. Basioccipital is a quadrangular plate, with two ridges on its ventral surface converging posteromedially. Ossified portion of the exoccipital is dorsoventrally short. Two Meckelian fenestrae present. All three coronoids bear small teeth. Dentary bears up to 43 teeth. Crescent-shaped stapes.

(ii) *Early juvenile stage* (known only in *D. austriacus*)

A short-snouted amphibian. Rounded orbits placed relatively far anteriorly; long postorbital region (taking the midpoint of the orbit as a reference, the distance to the posterior end of the postparietals is about 27–30% longer than the distance to the anterior termination of the skull measured at the midline). Pineal foramen lies

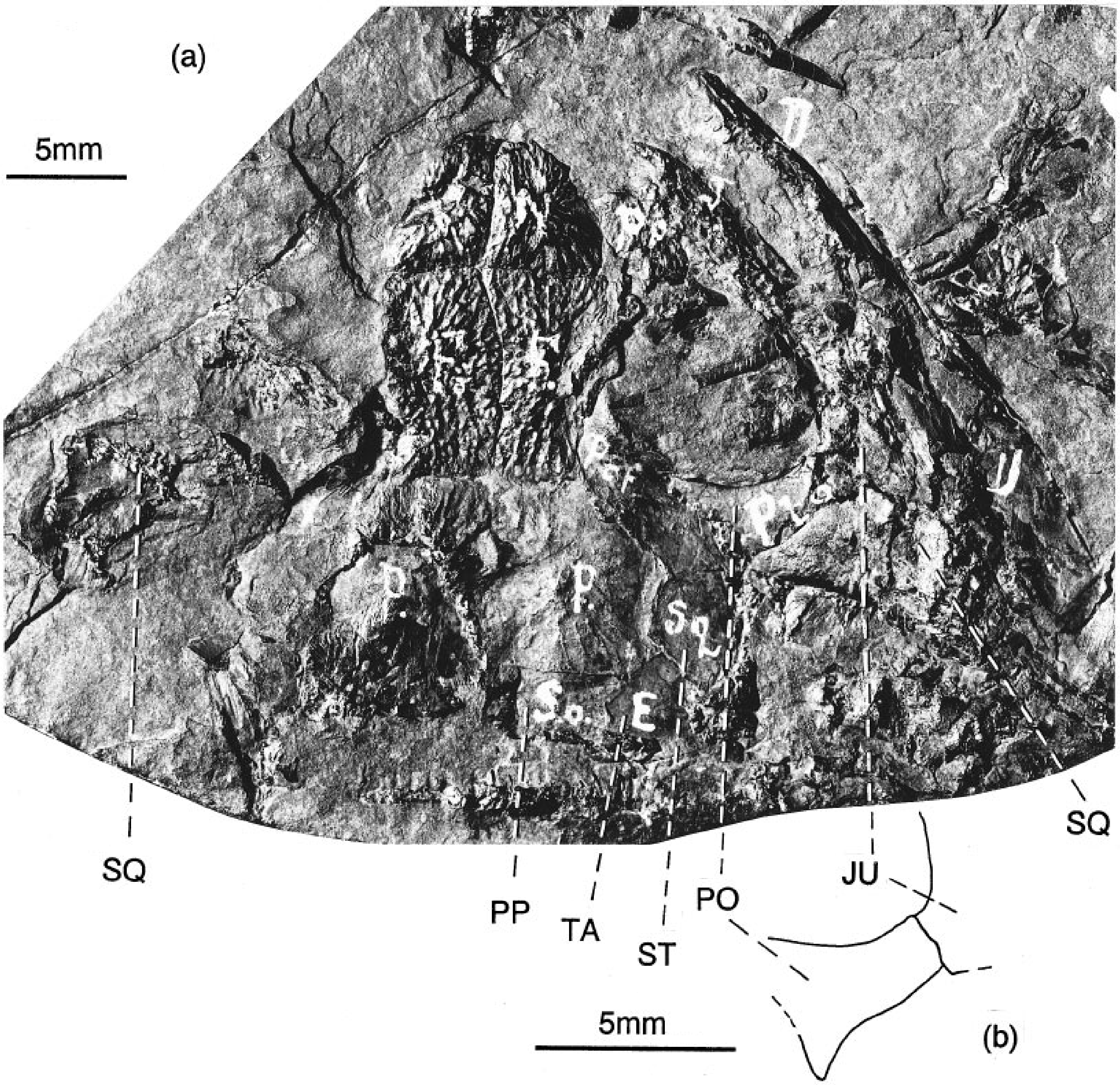

Figure 1. (a) *Discosauriscus austriacus* (Makowsky 1876). Lectotype (MU-P-0010). Some of the skull roof bones are labelled with white ink personally by Makowsky (Augusta 1936). (b) Slightly enlarged partial postorbital and jugal of lectotype.

behind the level of the posterior borders of the orbits. Deep and dorsoventrally relatively broad otic notch. Posterior extent of the jaw joint lies slightly posteriorly to the posterior margin of the postparietals. No fenestra or slit in the region between the nasals and premaxillae. Palate is completely closed. The dentine of the bases of the marginal teeth and palatal tusks is infolded (about one half of the tooth length; however, in some specimens, the individual folds extend to the apex of the crown). Lateral margins of the basioccipital are almost parallel to each other. Other morphological features as in (i).

For further discussion of ontogenetic changes, see §4*b*: '(ii) *early juvenile stage*' of *D. austriacus* and figures 23–28.

Types species: *Discosauriscus pulcherrimus*

In the following text, *D. austriacus* is described first, because the knowledge of its anatomy is the basis for comparisons with the limited material of *D. pulcherrimus*.

4. *DISCOSAURISCUS AUSTRIACUS* (MAKOWSKY 1876)

1876 *Archegosaurus austriacus* (Makowsky p. 155)
1883 *Branchiosaurus moravicus* (Fritsch p. 82)
1883 *Melanerpeton falax* (Fritsch p. 104)
1924 ?*Discosaurus moravicus* (Stehlík p. 17)
1936 *Melanerpeton perneri* (Augusta p. 33)
1936 ?*Melanerpeton longicaudatum* (Augusta p. 36)
1936 ?*Melanerpeton magnum* (Augusta p. 38)
1938 *Melanerpeton potamites* (Steen p. 256)
1947 *Phaiherpeton pulcherrimum* (Romer p. 292, *non* Fritsch 1879)
1952 *Discosauriscus pulcherrimus* (Špinar p. 27, *non* Fritsch 1879)
1952 *Discosauriscus potamites* (Špinar p. 50)
1952 *Letoverpeton moravicum* (Špinar p. 61)
1952 *Letoverpeton austriacum* (Špinar p. 73)

Note: *D. austriacus* and *D. pulcherrimus* differ in several principal characters (see '*Diagnoses*'). Because none of these characters was used by Špinar (1952) in

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Figure 2. *Discosauriscus austriacus* (Makowsky 1876). Skull in dorsal view; based on specimen K 13 (cf. figure 23*a*). Septomaxilla and sclerotic ring only on right side.

his revised paper for distinguishing his two genera and four species (*Discosauriscus pulcherrimus*, *D. potamites*, *Letoverpeton moravicum*, *L. austriacum*), it is difficult to recognize these two species in the material described in his paper (also from the point of view of its preservation): it may include both species. The same is true for all material from the Boskovice Furrow studied by the authors before Špinar (see the detailed synonymy lists at all our taxa there) except for Makowsky (1876) as well as the later studies of Švec (1984, 1986), Ivakhnenko (1987) and Werneburg (1985, 1989*a*, *b*).

1992 *Discosauriscus austriacus* (Klembara & Meszároš p. 305 (except for specimens D 201.I, III, IV, VI–VII, D 208, K 19.I–III, K 170, K 171, K 217 — *Discosauriscus* sp.))

1992 *Discosauriscus austriacus* (Klembara, p. 250)

1993 *Discosauriscus austriacus* (Klembara & Janiga, p. 268 (except for specimens K 9 and K 16 which belong to *D. pulcherrimus*))

1993 *Discosauriscus austriacus* (Klembara, p. 145 (except for specimens K331.III—*Discosauriscus* sp.))

1994*a* *Discosauriscus austriacus* (Klembara, p. 85 (except for specimen D 208—*Discosauriscus* sp.))

1994*b* *Discosauriscus austriacus* (Klembara, p. 609 (except for specimen D 200.III—*Discosauriscus* sp.))

1995*a* *Discosauriscus austriacus* (Klembara, p. 271)

1995*b* *Discosauriscus austriacus* (Klembara, p. 264)

1996 *Discosauriscus austriacus* (Klembara, p. 1)

Lectotype

Because Makowsky (1876) did not designate the holotype, it is necessary to select a lectotype (figure 1): specimen no. MU-P-0010 (designated with the Roman number IV by Makowsky), deposited at the Department of Geology and Paleontology, Faculty of Natural Sciences, Masaryk University, Brno (Czech Republic). Špinar's (1952) lectotype of his *Letoverpeton austriacum* (Makowsky's Roman number VII) is lost.

Paralectotypes

Numbers MU-P-0005/I, MU-P-0008, MU-P-0009, MU-P-0011 (deposited at the same institution as the lectotype). Thirteen further specimens described by Makowsky (deposited also at MU-P) and three in the Moravian Regional Museum in Brno (nos. 21233, 21213, 21230 and 21231) are not determinable to species, and in several cases even to genus, due to their poor preservation.

Type locality

'Příčná zmola' at Malá Lhota (Klein-Lhotta) near Černá hora (Makowsky 1876; cf. Augusta 1936, 1948); Bačov horizon.

Locality

The material from the Boskovice Furrow comes from the following localities:

(1) Vanovice (Drválovice), designated as D (see Klembara & Meszároš 1992).
(2) Kochov-Horka (district of Letovice, see Klembara & Meszároš 1992), designated as K.
(3) Kochov-L, about 500 m north-east of Kochov (district of Letovice), designated as KO.

Horizon

Bačov horizon, zone 6—Lower Saxonian (*sensu* Werneburg 1989*a*, Lower Permian).

Referred specimens

The specimens are deposited at the Zoological Institute, Faculty of Natural Sciences, Comenius University, Bratislava:

D 2–4, 7–9, 12–14, 16, 18–20, 22, 24–26, 28–30, 32, 34, 37–45, 47–49, 52–64, 66–94, 99–100, 103–107, 109, 111, 113, 120, 121, 137, 139, 171–174, 179–180, 183, 185, 189, 192, 193, 195, 196, 198, 201.II, 201.V, 201.VIII, IX, 202.I, II, 204, 207–214, 216, 217, 354.I, II;

K 1–6, 11–15, 17, 18, 20–22, 30–34, 36–43, 45, 47–50.I, II, 51, 52, 54–60, 62–69, 71, 72, 74–78, 80–92, 95, 98–104, 111–113, 115, 117, 118, 120, 121, 123, 126, 127.I, 130–142, 144, 146, 147, 152, 164, 168, 169, 172, 174–182, 184, 185, 187–192, 194–196, 198, 201–203, 205, 206, 208, 210–212, 214, 215.I, 218–220, 222–227, 229–238, 240–251, 253, 254, 256–261, 263–265, 267–273, 276–285, 287.I, II, 289–293, 295–299, 301–303, 305–307, 309, 311–328, 329.I, II, 330, 331.I, II, 332.I, II, 333, 334, 335.I–III, 336, 337, 338.I, II, 339, 340.I, II, 341.I–V, 342–345, 346.I, 347, 348, 349.I–III, 350, 351.II, 352.I, III, 353–358, 360, 362, 364, 378–381, 383, 385–393;

KO 1–34, 37, 38, 41–44, 47, 48, 50–57, 59–71, 74, 77, 79–88, 90–123, 125–137, 140–143, 145, 147, 148, 150–166, 168–179, 181.I, 182–186, 189–212, 214–216, 218–233, 235–240.

Diagnosis

As for genus, with several characters distinguishing it from *D. pulcherrimus*: (1) The prefrontal and the postfrontal meet around the midlength of the frontal. (2) The postorbital is robust; its anteroposteriorly broad lateroventral portion and the complementary dorsomedial portion of the jugal meet in a relatively long, horizontal suture. (3) The region of the skull roof between the posterior orbital margin and the otic notch is anteroposteriorly longer than that of *D. pulcherrimus*. (4) Radially running ridges bearing small denticles are present on the ventral surface of the palatal ramus and on parts of the transverse flange of the pterygoid (the small rows of teeth sometimes extend on the ectopterygoid and palatine) and the central portion of the parasphenoid; in juveniles, the ridges are not as distinct, and radially running rows of denticles are present on most of the ventral surface of the transverse flange of the pterygoid.

Description

In this section, following the description of the lectotype skull, the cranial structures of individuals with skull lengths (SL) of about 17–62 mm are described (several specimens with skull lengths of about 12–17 mm were previously described in connection with the ontogeny of ornamentation (see Klembara 1995*a*). As concluded by Klembara (1995*a*), this size category probably includes: (i) larval stage: SL up to about (?25)–30 mm; (ii) metamorphic stage: SL up to about 50 mm; (iii) early juvenile postmetamorphic stage: SL up to about 62 mm.

In the material from the Boskovice Furrow that was available for this study, specimens with a skull length of up to about 40 mm are common. Specimen K 54 has a skull length of 44 mm. Above this skull size, only six specimens have a skull length of 47–62 mm, representing probably already postmetamorphic, early juvenile individuals (at least specimens K 52, K 323, OB 1, OB 8): the skull lengths of these specimens are as follows: K 52, about 52 mm; K 323, 49 mm; KO 79, 51 mm, KO 80, about 47 mm; OB 1, about 62 mm. Specimens K 52 and K 323 are most robustly constructed; as for specimen OB 1, see Klembara (1995*a*). In the case of OB 1 and OB 8 (SL about 56 mm) it is not possible to distinguish the species of the genus *Discosauriscus*.

(*a*) *Lectotype skull*

Most of the skull roof bones are preserved in an articulated state. However, several bones are missing, and only impressions of these remain (figure 1). This is also true for the right postorbital and jugal; however, their impressions are well preserved, so that the typical broad rami of the contact portions of both bones and their long anteroposterior suture are identifiable. In addition, the small process of the lateral margin of the left frontal lies in the midlength of the bone, indicating the position of the prefrontal–postfrontal suture, typically situated at the frontal midlength in this species. It is possible that the pterygoid is still in the matrix, but the skull is carbonized and not suitable for chemical preparation. However, the two features mentioned above are sufficient for the determination of the skull no. MU-P-0010 as *D. austriacus*. The

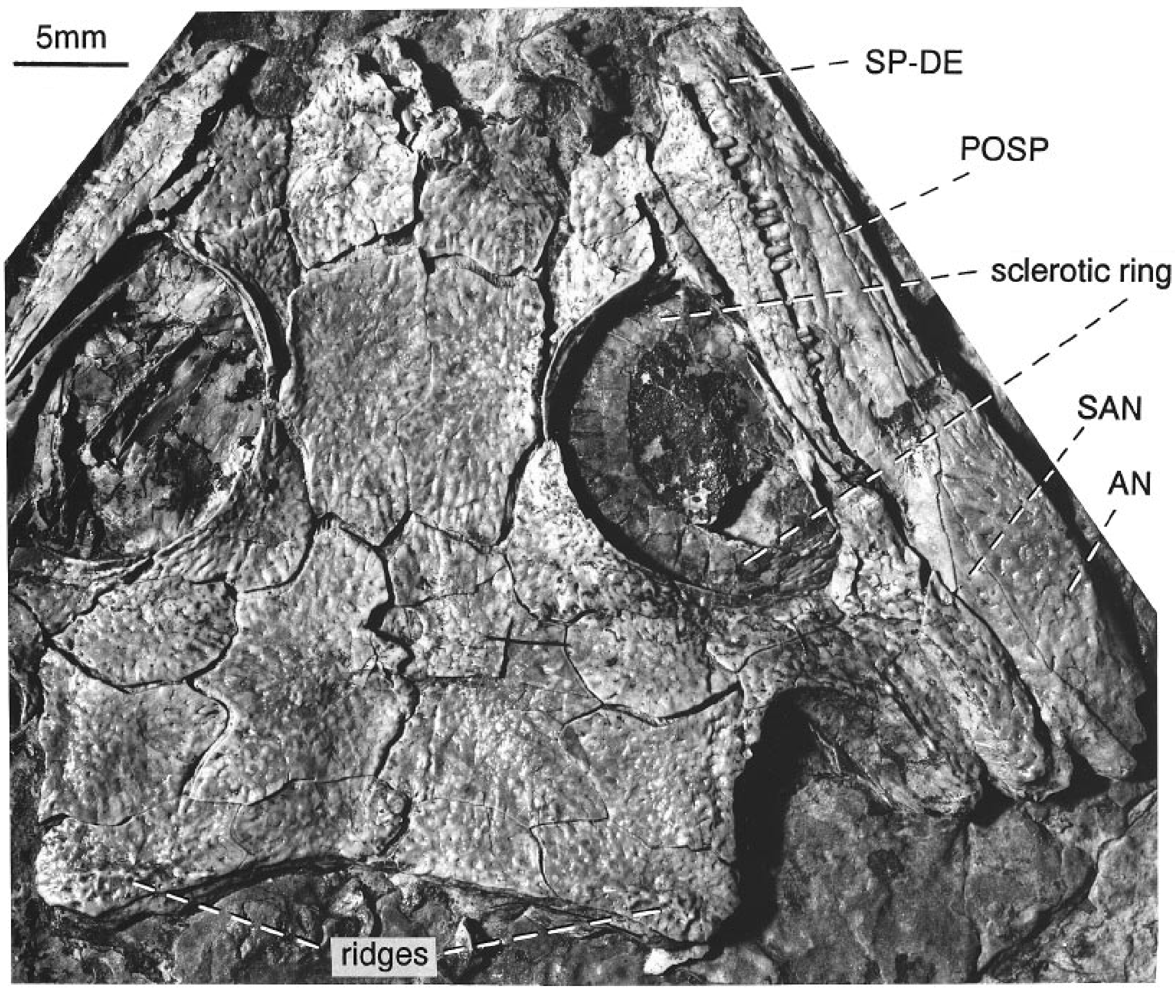

Figure 3. *Discosauriscus austriacus* (Makowsky 1876). K 330; skull in dorsal view.

paralectotypes are also determinable using these features.

The length of the lectotype skull (SL) is 25 mm. This, together with well preserved radiating ornamentation on the nasals and frontals, indicate that this specimen is in the late larval period or in the initial stage of metamorphosis. The sensory grooves on the nasals are deep.

(*b*) *Skulls from Boskovice Furrow*

In the following account, separate descriptions are given of (i) the specimens representing the larval and metamorphic individuals and (ii) the specimens probably representing early juveniles, including proportional changes occurring during metamorphosis. The intention is to emphasize the structural and proportional differences caused by metamorphosis (see also Klembara 1995*a*).

(i) *Larval and metamorphic stage*

Skull roof and sclerotic ring

Structure of bone. The inner structure of the bones of the skull roof (between the ornamented dorsal and smooth ventral compact layers) consists of intricate, interconnected canals, and cavities of variable size. The condition of the right parietal of K 181 shows that the bony partitions between the cavities are arranged in a more or less radial pattern. This pattern, however, is overshadowed by many anastomoses. Some bones, especially the quadratojugal, jugal and squamosal, possess large vacuities. In several specimens, an almost continuous canal can be seen passing along the raised medial margin of the circumorbital bones (K 60, K 84, K 101).

In many specimens, relatively large foramina, pits, depressions and cavities are present on the ventral surface of the ectopterygoids, palatines and vomers.

Intensity of ornamentation. The ontogeny of the ornamentation has been described elsewhere (Klembara 1995*a*). The intensity of ornamentation varies slightly among specimens, but there are no differences in proportionally different skulls. The intensity of ornamentation can differ on individual bones of the same specimen. The ornamentation is often less pronounced on the maxillae, premaxillae and lacrimals than on parietals or the fromtals. In some specimens, the ornamentation of some regions is more pronounced, e.g. along the sensory grooves and margins of those bones which form the medial wall of the orbit, sometimes on the jugal, quadratojugal, squamosal and posterior margins of the tabulars and postparietals. In K 330, there are short but pronounced transverse ridges on the tabulars (figure 3). The margin of the pineal foramen of K 241 (similarly in K 334) is formed by relatively large oval pits and ventrally running grooves.

The ornamentation of the lower jaw is present on the angular, surangular, postsplenial and splenial (figure 3) but not on the dentary.

Foramina. In most pits of the ornamented surface, there is one small foramen; occasionally (K 240, K 247), sporadic small foramina or pores are visible at the base of some ridges. However, the surface of the greater part of the jugal may be perforated by particularly large openings passing into the cavities of these bones (figure 4). The larger openings are often arranged in a row in the region of the sensory lines, mostly on the squamosal and the postorbital (figure 4). The cavities in all bones, and their communication with the surface through the different-sized openings, indicate a rich vascularization of bones and appropriate parts of the skin cover of the skull. This particularly applies to the cheek in the area of the squamosal, quadratojugal and jugal. The nutrient foramina are concentrated on the ventral surfaces of the bones, in the region of their radiating centres.

Sutures. The sutural pattern of the skull roof bones is seen in figure 5. The morphology of the sutured areas of the individual articulating bones is described in the text below. Most of the bones have ventral (or basal) laminae (or lamellae) which are overlapped by the neighbouring bones (cf. also Kathe 1995). These overlapped laminae (as well as the overlapping surfaces) are either relatively smooth or bear distinct grooves and ridges, reflecting the mode of the junction of the given bones. Hence, the size of such bones differs from the size of their ornamented surfaces (Klembara 1994*a*). The position of the ventral laminae is, with several exceptions (by the junctions of the postparietals, parietals and frontals), essentially constant; only the size of the laminae varies slightly.

Premaxilla. This is a triramous structure consisting of the ventral (or maxillary), posterodorsal (or nasal) and posterior (or vomerine) rami; the first two rami form the rim of the exonarial fenestra (figures 2, 4, 5*a*, 6, 23 and 24*a*).

In D 29, K 303, K 388, KO 28, KO 103 and KO 117, premaxillae are well preserved and the medial margin of the nasal ramus forms a right angle with the base of the maxillary ramus (figure 6). These specimens show that premaxillae met in a more or less vertical suture along their entire medial margins, except for the most posterior tips. In some specimens (D 76, D 198, K 22, K 243, K 336, KO 23, KO 117, KO 174), the posterior halves of the premaxillae medial margins are laterally curved, leaving a space for the presence of the 'interpremaxillary fenestra' (Werneburg 1985; Ivakhnenko 1987). There really is a free space between both nasal rami of the premaxillae (Klembara 1994*a*, fig. 7A), when one considers only these two bones independently of the remaining skull. However, the anteriormost parts of nasals of many specimens (KO 4, KO 18, KO 28, KO 61, KO 174, KO 184) bear relatively long digitiform processes which undoubtedly fitted, probably completely, into the space ('fenestra') between the nasal rami of premaxillae or their digitiform processes. A small fenestra may occasionally be present between the premaxillae and nasals, but only as a result of the incomplete ossification of these parts of premaxillae. As will be shown below, there is no free space here in early juvenile specimens (figure 29).

The maxillary ramus of the premaxilla has a sutural contact with the maxilla laterally, by which the premaxilla underlies the maxilla in a short section (K 60). The premaxilla bears 5–7 teeth (K 60, K 336, D 91 respectively). However, the number of teeth may vary within the same specimen (the left premaxilla of KO 18 supports seven teeth, and the right one only six). On the inner surface, a prominent horizontal lamina is present. Its medial, vomerine portion, projects slightly posteriorly into a short ramus.

The medial part of the vomerine ramus forms a short, narrow process (D 54, D 73, K 348) which, with its fellow, fits between the anteromedial margins of the vomers (the corresponding grooves in the vomers are visible in D 52 and K 224). Both vomerine rami, as well as the bodies of both premaxillae, are firmly connected suturally. The vomerine rami of the premaxillae of K 348 are slightly concave. The slightly dorsally flexed anteriormost parts of the vomers extend for a short distance above the vomerine rami of the premaxillae. The vomerine ramus of the premaxilla continues laterally as a narrow and thin horizontal lamina bordering the exochoanal fenestra anteriorly. The anterior wall of the septomaxilla abuts against the dorsal surface of this lamina and the inner surface of the maxillary ramus of the premaxilla.

The inner surface of the premaxilla, above the vomerine rami, may bear a variable number of foramina of different size.

Nasal. This bone is triangular and always longer than it is broad (figures 2–4, 5*a* and 23*a*). With its anterolateral margin, the nasal contributes to the border of the exonarial fenestra. The nasal is broadest where it meets the lacrimal–prefrontal suture. From this point, the lateral edge of the nasal narrows anteriorly and slightly posteriorly. The suture with the lacrimal and the prefrontal is steep, often interdigitating or irregular, mostly with the lacrimal, and sometimes with the prefrontal. The suture between both nasals is steep and its course is mostly simple. Posteriorly, the nasal overlaps a relatively broad area of the frontal.

Septomaxilla. This is a small trough-shaped bone (figures 2, 5*a* and 7). Posteriorly, it is sutured with a lacrimal, its posterodorsal wall fitting into the notch in the anterior margin of the lacrimal. The narrow dorsal surface of the posterior wall of the septomaxilla (immediately above the exit of the nasolacrimal canal) is ornamented and incorporated into the formation of the skull roof. It often bears longitudinal grooves into which the digitiform processes of the anterior margin of the lacrimal fitted (K 246). Medial to this, the posterior wall is short and does not reach the nasal.

The relatively large septomaxillary foramen (dorsally incompletely ossified in KO 184) is located immediately below the narrowed dorsal surface of the septomaxilla. It is continuous with the lacrimal section

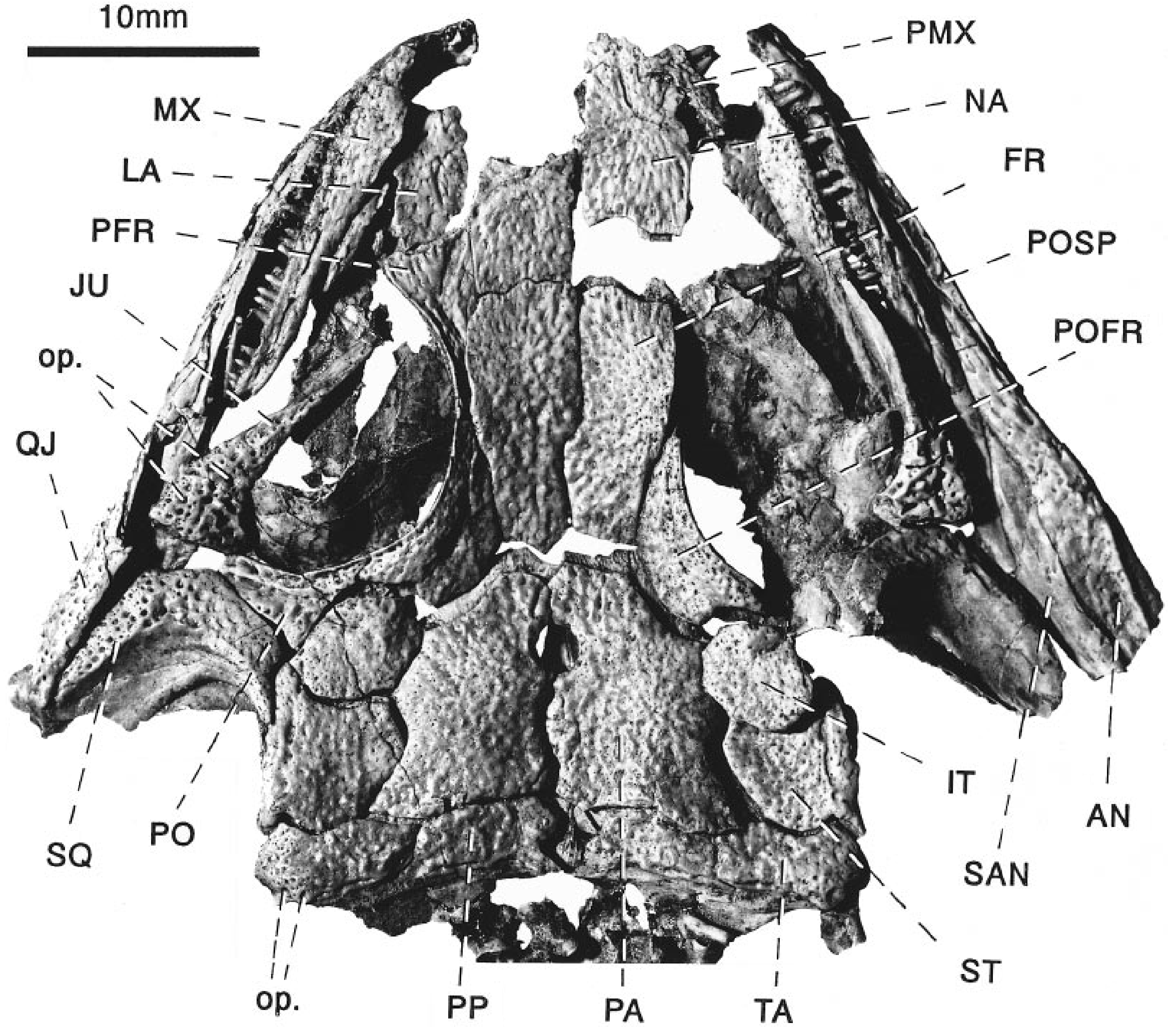

Figure 4. *Discosauriscus austriacus* (Makowsky 1876). K 102; skull in dorsal view.

of the nasolacrimal canal. The wall in the immediate medial surrounding of the septomaxillary foramen may be perforated by foramina or short canals (K 83, K 177, K 246).

Laterally, the septomaxilla rests on the dorsal surface of the horizontal lamina of the maxilla, and anteriorly on the horizontal lamina of the maxillary ramus of the premaxilla, abutting against the inner walls of these two bones. On the ventral, outer surface of the septomaxilla, the border of this contact and of the free basal wall is morphologically expressed as a distinct edge. Immediately laterally to the septomaxillary foramen, the wall is sculptured and perforated by short canals. The bottom of the inner surface of the septomaxilla is roughened or irregularly sculptured, sometimes with deep pits. The ventral (external) surface of the free basal wall is more or less distinctly pitted (K 246). The medial margin of this free basal wall is irregular.

The medial margin of the anteromedial portion of the septomaxilla is short and more or less straight. Its posterodorsal edge is broadened into a plate-like surface (K 177, K 246); in the natural position of the septomaxilla, it slants postero-ventromedially. It is highly probable that the laterodorsally curved anterolateral tip of the vomer abutted against this surface. The existence of the septomaxilla–vomer contact is also supported by three other lines of evidence. (1) As seen in K 348, the anterior portion of the vomer is broader than the width of the vomerine portion of the premaxilla. (2) As described for the premaxilla, the anterior portion of the vomer overlapped dorsally the vomerine portion of the premaxilla. (3) Because the anteromedial end of the septomaxilla extends to the anterolateral margin of the vomerine portion of the premaxilla, the plate-like termination of the septomaxilla should be overlapped by the anterolateral tip of the vomer. This condition is confirmed in the model.

The fenestra exonarina is thus formed by the premaxilla, maxilla, septomaxilla, lacrimal and nasal.

Figure 5. *Discosauriscus austriacus* (Makowsky 1876). Schematic drawings of dorsal part of skull roof (a) and cheek (b) in dorsal view, showing the position of overlapped areas (basal or ventral laminae) and centres of radiation of individual bones.

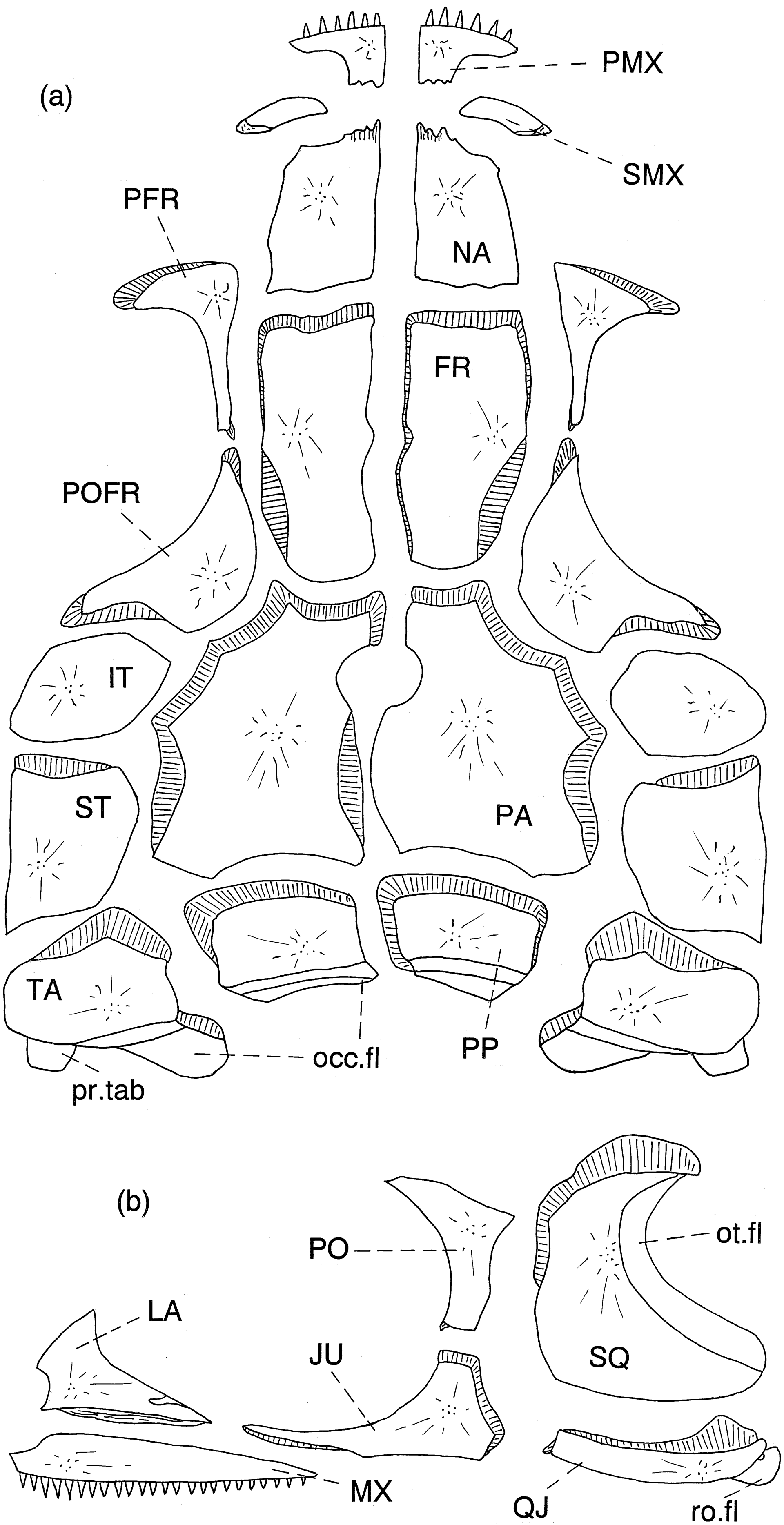

Figure 5. For legend see opposite.

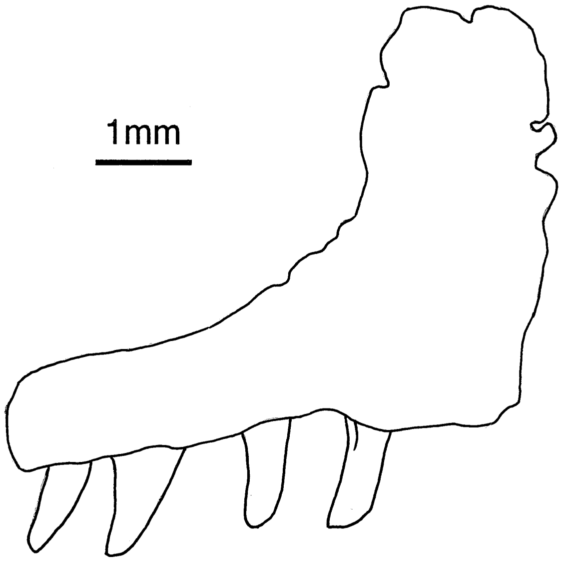

Figure 6. *Discosauriscus austriacus* (Makowsky 1876). K 388; right premaxilla in dorsal view.

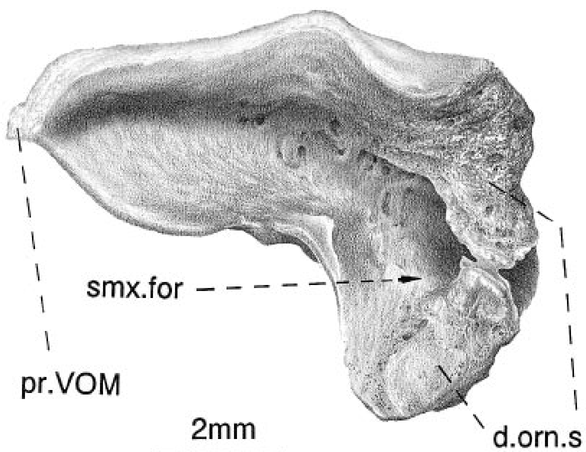

Figure 7. *Discosauriscus austriacus* (Makowsky 1876). K 246; right septomaxilla in dorsal view.

Frontal. This lies between the orbits and is of rectangular shape (figures 2–4, 5*a* and 23*a*). In most specimens, the frontal is broadest in the place of the prefrontal–postfrontal suture; it forms a more or less pronounced process here, fitting between these two bones. Exceptionally (K 206), this part of the frontal is not pronounced, and its lateral edge is more or less straight. From the point of this lateral process, the lateral edge of the frontal narrows posteriorwards and only slightly anteriorwards. The prefrontal has a steep suture with the frontal. The postfrontal overlaps a relatively broad area of the frontal. Posteriorly, the frontal overlaps the parietal. A smooth overlapped area of the medial margin of the frontal is developed on the right (KO 27) or the left (D 87) side.

Prefrontal. The triangular prefrontal forms the anteromedial wall of the orbit, (figures 2–4, 5*a*, 8 and 23). The orbital wall is high and relatively narrow dorsally. In the inner surface of the orbital wall of the right prefrontal of K 83, near the suture with the lacrimal, there is one relatively large and several smaller foramina; in K 282, the large foramen is present in its posteriormost

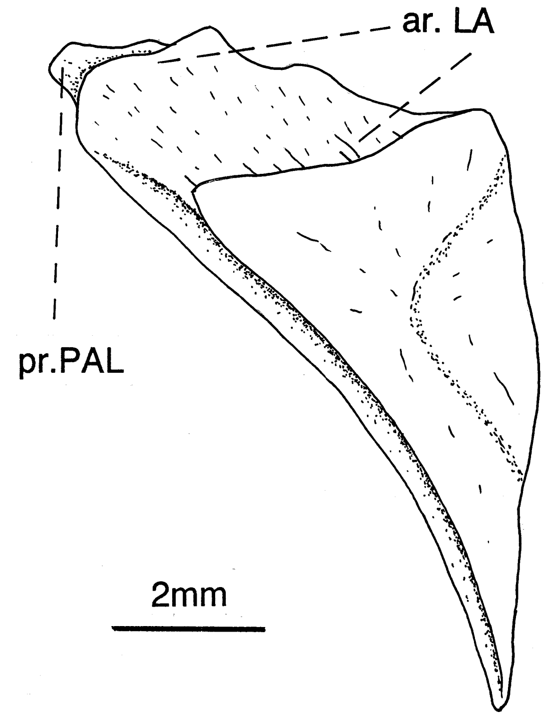

Figure 8. *Discosauriscus austriacus* (Makowsky 1876). KO 63; left prefrontal in dorsal view.

part. Anteriorly, the lacrimal overlaps the large, plate-like, triangular lamina of the prefrontal. Inside the skull, the lateroventrally projecting tip (slightly roughened on its outer surface in K 193) of this lamina (K 316, K 390, KO 27, KO 40 and KO 63) joins the dorsomedial surface of the maxillary process of the palatine (figures 8 and 26). In some specimens (K 330), the lateral (or lower) corner of the ornamented area of the prefrontal is slightly curved anteriorly and notched, so participating in the formation of the upper orbital border of the nasolacrimal canal. The relatively long posterior ramus of the prefrontal forms a small basal process at its posteromedial edge and overlaps the ventral lamina of the postfrontal. In dorsal view, the suture between both latter bones is short and transversely oriented.

On the ventral surface, a prominent, high orbital flange runs anteromedially, close to the orbital margin of the bone, except for its posterior section (KO 25, KO 27). In the anterior surface of the crest, near its connection with the bone itself, a foramen is visible (KO 25). This crest probably served for the attachment of the orbitonasal membrane, dividing the orbital and nasal spaces.

Postfrontal. This is a relatively large, crescentic and convex bone participating in the formation of the posteromedial margin of the orbit (figures 2–4, 5*a* and 23). The medial portion of the postfrontal is wedged between the narrowed parts of the frontal and the parietal. The suture with the parietal is shorter than with the frontal; the postfrontal overlaps the large areas of the parietal and the frontal. However, the middle section of the frontal lateral margin overlaps a small basal lamina of the neighbouring portion of the postfrontal. The intertemporal is wedged into a notch in the posterior margin of the postfrontal, overlapping the small lamina of the latter laterally. Posterolaterally, the postfrontal has a short suture with the postorbital, by which the latter overlaps the small area of the former.

Parietal. The parietal forms a large anteroposteriorly prolonged plate (figures 2–4, 5*a*, 9 and 23, however, see Klembara & Janiga 1993). It is narrow anteriorly and it gradually broadens posteriorly. The parietal meets the frontal anteriorly, the postfrontal anterolaterally, and the intertemporal and the supratemporal laterally. All four bones overlap the broad areas of the parietal. In contrast, the parietal overlaps the broad areas of the postparietal and the tabular posteriorly. The suture with the tabular is shorter than that with the postparietal, although there are exceptions (right side of K 342).

In the median plane, behind the pineal foramen, the right parietal overlaps the ventral lamella of the left one; the lamella is developed (not always distinctly) on the right (KO 173) or the left (D 87) medial margin. The suture between the ornamented surfaces of both parietals is mostly undulating (Klembara 1994*a*). As for the region of the pineal foramen, its size and position, see Klembara (1994*a*). The medial portions of both parietals, behind the pineal foramen, are thickened, and on the ventral surface they form a prominent median ridge continuing onto the postparietals. In this region, dorsally, the parietals are slightly depressed.

Intertemporal. This is usually oval in shape with the long axis in the anteromedial–posterolateral direction (figures 2–4, 5*a*, 9 and 23). Anterolaterally, it overlaps the narrow ventral lamina of the postfrontal. Posteriorly and laterally, it overlaps the supratemporal and the squamosal respectively.

Supratemporal. This is approximately quadrangular in shape (figures 2–4, 5*a*, 9 and 23). Although proportional changes of the supratemporal and intertemporal occur (Klembara & Janiga 1993), the supratemporal is generally larger than the intertemporal. The supratemporal overlaps a large ventral lamina of the tabular. The posterolateral corner of the supratemporal projects into the pointed process (which is an extra bone in several specimens, Klembara 1993), and is slightly flexed ventrolaterally.

On the ventrolateral surface of the bone runs a prominent wall (otic flange); it is broadest anteriorly and gradually tapers in width posteriorly. Anteriorly, the otic flange fitted into a deep groove in the squamosal; the inner wall of this flange may be distinctly obliquely striated (K 6) indicating a firm connection of both bones (figure 25*a*). The suture between the ornamented surfaces of the squamosal and the supratemporal is somewhat interdigitating (Klembara 1994*a*).

Postparietal. This is a broad (mediolaterally) and short rectangular bone (figures 2–4, 5*a*, 9, 23*a* and 24). The suture between the ornamented surfaces of both postparietals is occasionally irregular (as is that between the parietals), so that (1) the size of their ornamented surfaces may differ substantially in the same specimen and (2) in one specimen the right parietal may meet the left postparietal (KO 4), in

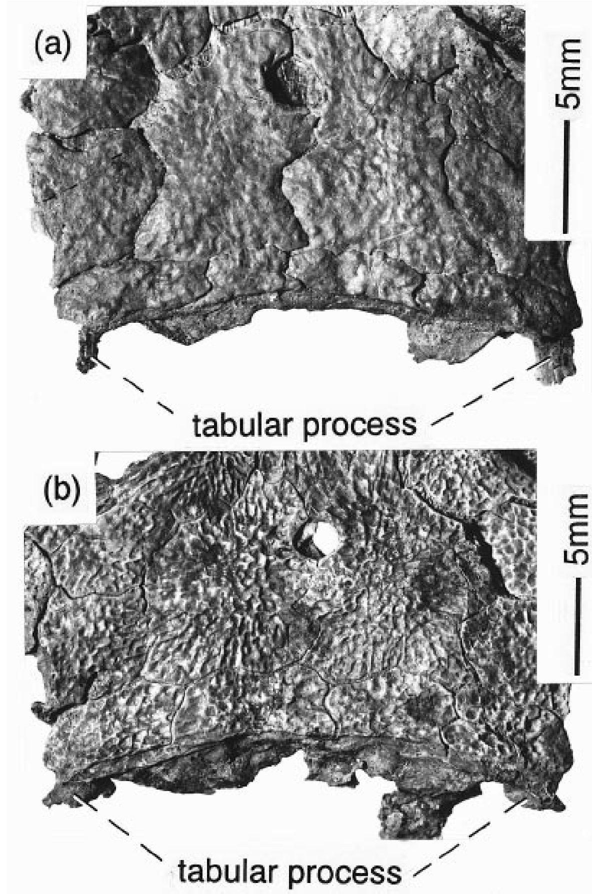

Figure 9. *Discosauriscus austriacus* (Makowsky 1876). K 11 (a), K 313 (b); posterior skull tables in dorsal view.

another one it is vice versa (KO 8). Medially, the overlapped area is sometimes formed by the left (K 177), and sometimes by the right (D 47) postparietal. The suture between the ornamented surfaces of the postparietal and parietal is straight or slightly curved. The tabular overlaps a narrow ventral lamina of the postparietal. In the region of the posterior rims of the ornamented surfaces, both latter bones are joined in an interdigitating suture.

The postparietal and tabular, immediately behind the posterior margins of their ornamented surfaces, form a narrow, horizontal lamina (or shelf or crest). It is most prominent at the level of the suture between the ornamented surfaces of both bones (K 83), and it has a smooth, roughened or mediolaterally striated dorsal surface. Below this lamina, the postparietal forms a smooth, narrow, posteroventrally inclined occipital flange (lappet). It narrows medially and together with its fellow, may form a small, posteroventrally directed process (K 80, K 172) as seen also in *Seymouria* (Holmes 1984, fig. 38*a*, *c*; Laurin 1995, fig. 1B), and some other early tetrapods (Holmes 1984, fig. 8; Clack 1987; Smithson 1985). The occipital flange broadens laterally and joins that of the tabular by which the former overlaps the latter. Between the horizontal lamina and occipital flange, a more or less deep depression remains.

Tabular. This forms the posterolateral corner of the skull table (figures 2–4, 5*a*, 9, 23 and 24). It is of rectangular shape. Its lateral portion is slightly curved ventrolaterally. Although the width (i.e. the mediolateral extent) of the tabular and postparietal differ between specimens (and also in the same specimen), interruption of the tabular–parietal contact has not been recorded so far (Klembara 1994*a*). The large occipital flange projects posteroventrally. The occipital flanges of the tabular and the postparietal form a single posteroventrally inclined flange, most prominent in the level slightly medially to the suture between their ornamented surfaces. The dorsal surfaces of both occipital flanges are mostly smooth or slightly roughened. In K 313, the more or less regular ridges and grooves diverge radially from the lateral regions of the tabular occipital flanges (figure 24*b*).

The typical tabular process (or horn) is present on the tabular of *D. austriacus*. Ivakhnenko (1987) called this structure the 'tabular paroccipital process' because of its presumed relation to the endocranial paroccipital process. According to Ivakhnenko (1987), this cartilaginous endocranial process is covered posterodorsally by the tabular paroccipital process. Ivakhnenko (1987) correctly pointed out that the tabular process is not the posterior prolongation of the posterolateral ornamented corner of the tabular as stated and figured by Špinar (1952).

The tabular process of *D. austriacus* (figures 2, 4, 5*a*, 9, 23, 24 and 25*a*) is a plate-like structure which projects posteriorly or posterolaterally from the ventrolateral surface of the tabular (as in *Proterogyrinus*, Holmes (1984) or *Pholiderpeton*, Clack (1987)); however, it is not homologous with the 'tabular horn' in *Seymouria* (*sensu* Laurin 1995) which is a ventrally prolonged posterolateral corner of the tabular ornamented surface. In *S. baylorensis*, the ornamented surface of the posterolateral corner of the supratemporal also contributes to this 'tabular horn' (White 1939; Laurin 1996*c*). In one specimen (K 248), the posterolateral corner of the ornamented area is slightly extended posteriorly, as seen in the tabulars of some early tetrapods (e.g. in *Eoherpeton*, Smithson (1985), figs 7, 8); this is, however, exceptional and has nothing to do with the tabular process. The tabular process in *D. austriacus*, in contrast to the posteroventrally inclined occipital flanges of the tabular and the postparietal, has a more or less horizontal position. It extends behind the posterior margin of the tabular (with the exception of the incompletely developed process in KO 88). There is a narrow free space between the ventral surface of the tabular and the dorsal surface of the tabular process. The tabular process is quadrangular in shape. It may be wide or narrow; it is occasionally pointed (KO 67, KO 86, KO 88, KO 153). Its shape may differ on the two sides of the same specimen (figure 9*a*). In K 313 it is fan-shaped (figure 9*b*). It has a smooth or slightly roughened dorsal surface. The posterior edge of the tabular process is mostly irregular or digitiform.

Maxilla. This narrow and long bone extends posteriorly approximately to the centre of the orbit (2–4, 5*b*, 10, 23 and 24*a*). It supports 20 (K 177)–29 (K 134) teeth. The maxilla is deepest at the level of about the third to the sixth teeth (the largest teeth). From this point posteriorly, its depth gradually decreases. Its anterodorsal edge is deeply notched and forms the posteroventral rim of the anterior exonarial fenestra. The anteromedial edge and the inner surface of this area is slightly roughened and it contains one or two foramina (K 177, K 206). Here the maxilla joined the septomaxilla, the surface of which is also roughened with foramina. The vessel and nerve branches from the maxilla continued here into the septomaxilla. Along most of its dorsal margin, the maxilla meets the lacrimal in a steep and straight suture, and further posteriorly, it is overlapped by a long suborbital process of the jugal. The posterior tip of the maxilla is free. It does not meet the quadratojugal, and a foramen is present near the posterior tip of the maxilla. The anterior end of the maxilla is narrow and joins the maxillary ramus of the premaxilla, which underlies the former slightly. A relatively deep, not always continuous groove runs above and along the ventral margin of the outer maxilla surface. In the groove, several foramina for nerves and vessels are situated.

On the inner surface of the maxilla (figure 10), the most prominent structure is the horizontal lamina. Anteriorly, it forms the anterolateral margin of the exochoanal fenestra. Further posteriorly, it narrows gradually and joins the palatine (it fits into a groove in the latter) and the ectopterygoid (the ectopterygoid slightly overlaps the horizontal lamina). Above the horizontal lamina, the maxillary wall is longitudinally grooved, especially along the middle third of its length. The similarly grooved and ridged internal lamina of the lacrimal was attached to the upper part of this maxilla portion. In the anterior portion, immediately above the horizontal lamina, the maxilla is laterally vaulted; the posterior portion of this cavity bears irregular grooves, pits and ridges (continuing onto the lacrimal) with two foramina. Three other large foramina are present in the posterior half of the maxilla. The most anterior opening lies approximately in the middle of its length and through this foramen the infraorbital artery and the maxillary ramus of the trigeminal nerve entered the maxilla (see also '*Palatine*' and '*Lacrimal*'). The most posterior one lies near the level of the fourth tooth from the posterior end of the tooth row and the third opening is between the two former foramina. The middle one is very large in K 13 and leads into a canal. In the wall of this canal, and in the vicinity of the openings, several associated foramina are present.

Lacrimal. This is a roughly quadrangular bone posteriorly projecting into the jugal process (figures 2–4, 5*b*, 11 and 23). It extends from the posterior rim of the exonarinal fenestra to the orbit where it forms its anteroventral margin. The posterior tip of the lacrimal underlies the anterior tip of the lacrimal process of the jugal (K 40).

The nasolacrimal canal originates in the orbital wall of the lacrimal. The narrow edge of the lower corner of the ornamented surface of the prefrontal enters into the formation of the upper wall of the nasolacrimal canal. The posterior section of the canal is broad and with the longitudinal partition usually divided into two halves (figure 4). The length of this partition varies slightly among specimens, but in most it is high and short anteroposteriorly. This posterior section of the nasolacrimal canal is uncovered dorsally to various degrees.

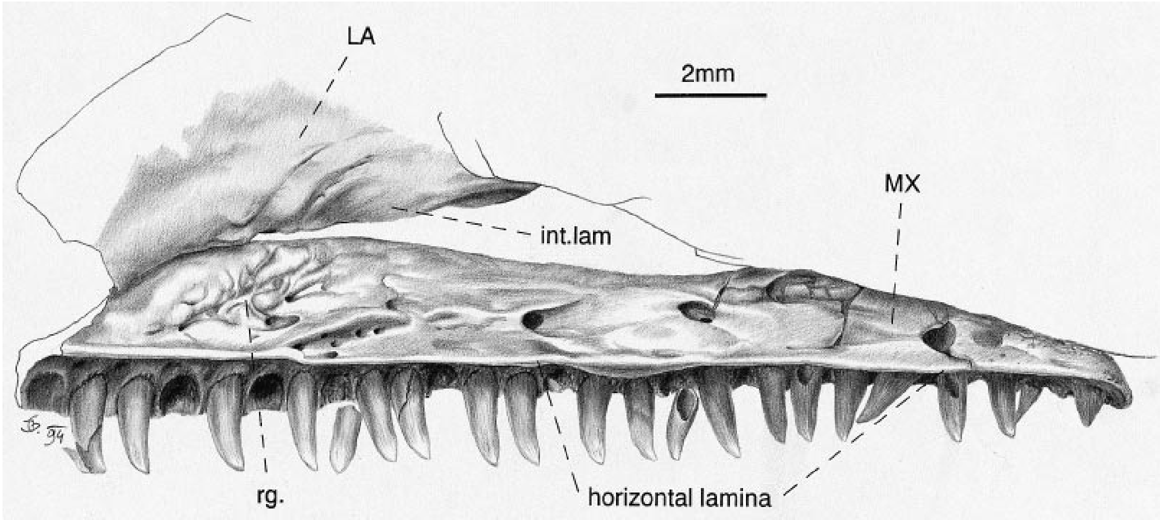

Figure 10. *Discosauriscus austriacus* (Makowsky 1876). K 40; right maxilla and lacrimal in internal view.

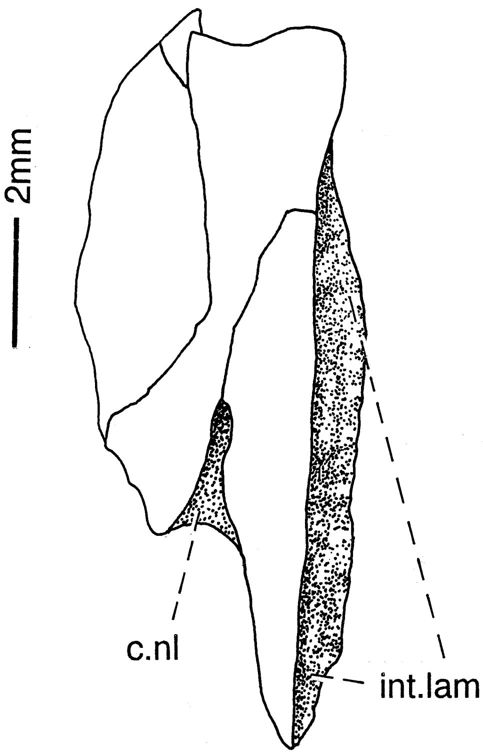

Figure 11. *Discosauriscus austriacus* (Makowsky 1876). K 172; right lacrimal in dorsal view.

The roof of the canal sometimes bears rounded fenestrae or elongated orifices (K 55, K 177, K 320). At the base of the canal, small pits and orifices are sometimes visible (K 83, KO 4). From the orbital margin anteriorwards, the nasolacrimal canal narrows continuously. It runs along the lower (ventral) margin of the lacrimal and opens anteroventrally in a relatively large, round or oval opening. It is continuous with the septomaxillary foramen. This portion of the lacrimal is slightly prolonged and anteroventrally bent (K 83, K 246).

A relatively broad, ventrally projecting internal lamina extends along the posterior two-thirds of the lower edge of the lacrimal. It is broadest anteriorly, narrows gently posteriorly and fades out sharply before reaching the posterior tip of the bone (figures 10 and 11). The longitudinally ridged and grooved outer surface of this lamina was attached to the upper inner surface of the maxilla. The inner surface of the lamina joined the laterodorsal surface of the palatine.

Jugal. This participates in the formation of the posteroventral margin of the orbit (figures 2, 3, 4, 5*b*, 12, 23 and 24*a*). The orbital margin is not as extensive as those of the prefrontal or postorbital. The jugal is a flat bone, projecting anteriorly into a long suborbital process. Its flattened anterior tip overlaps the posterior tip of the posterior process of the lacrimal dorsomedially (K 40, K 339). The middle section of the lower edge of the jugal is free and enters the ventral margin of the cheek. Posteriorly, the jugal is provided with a narrow lamina overlapped by the squamosal and partly by the quadratojugal. Posteroventrally, the jugal overlaps the narrow pointed lamina of the quadratojugal. The dorsomedial portion of the jugal has a short lamina overlapped by the postorbital.

The smooth inner surface of the jugal contains relatively large foramina. Five foramina are seen in the left jugal of K 172; one of them lies posteriorly, four others are arranged in a horizontal row and lie in the middle third of the jugal length, near its ventral edge. They are at approximately the same horizontal level as the foramina in the inner surface of the maxilla. As seen in other specimens (K 65, D 47), the canal passed through the broadened, lower part of the jugal. A large foramen in the inner surface of the jugal occurs in *Eocaptorhinus* (Heaton 1979) and various batrachomorphs (Shishkin 1973). According to Säve-Söderbergh (1936) and Shishkin (1968), branches of the maxillary artery and nerve passed through these foramina.

The ventral part of the inner wall of the jugal, immediately posteriorly to the jugal–maxilla contact, may (D 9, D 25, D 109, D 171, K 332.II) bear (though not always distinctly) a horizontal groove or a prolonged pit which is slightly roughened and contains foramina (figure 12). Into this groove, the posterolateral corner of the ectopterygoid fitted. This interpretation is supported by the model.

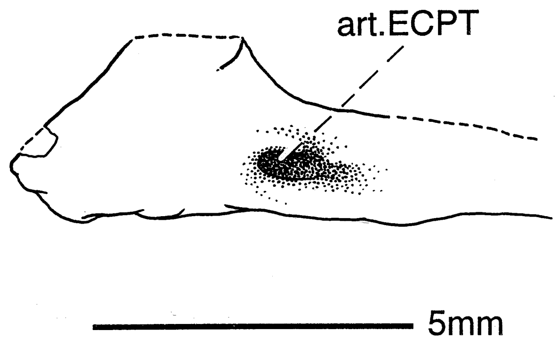

Figure 12. *Discosauriscus austriacus* (Makowsky 1876). K 332.II; left jugal in internal view.

Postorbital. This bone is triangular (figures 2–4, 5*b* and 23). It forms the posterior rim of the orbit. The orbital margin may be as extensive as that of the prefrontal. The posterior portion of the postorbital forms a wedge fitting between the anterolateral part of the intertemporal and the anteromedial part of the squamosal where it overlaps the ventral lamina of the latter. In lateral aspect, the medial margin of the postorbital is not in line with the horizontal upper margin of the squamosal and the lateral margin of the intertemporal, as seen in *Proterogyrinus* (Holmes 1984). In *Discosauriscus*, the postorbital extends into the skull table. An intermediate condition is seen in embolomeres like *Neopteroplax* (Romer 1963) or *Archeria* (Holmes 1989); cf. also Panchen (1964, 1972); Klembara (1985); Clack (1987, 1988).

The medial portion of the postorbital is relatively narrow; in contrast, its lateroventral portion is anteroposteriorly broad, and it has a relatively broad and directly anteroposteriorly running suture with a broad dorsomedial portion of the jugal. Occasionally, the length of this postorbital–jugal suture may be shortened, and its length and form may be partly influenced by the individual variability of the shape and size of the ornamented surface of the squamosal. This condition does not depend on skull proportions and it may vary on the two sides of the skull (KO 42, KO 129). In its anterolateral corner, the postorbital forms a small unornamented process slightly overlapping the orbital margin of the jugal (K 66, KO 79).

The ventral surface of the postorbital is smooth with a single foramen of variable size in the central region (D 18, K 190).

Squamosal. This is a large crescentic bone (figures 2–4, 5*b*, 13, 23 and 24). Posteriorly, it is deeply incised, forming the large squamosal embayment. Ventrally and posteroventrally, it overlaps a large lamina of the quadratojugal. Dorsally, the squamosal bears a relatively large, dorsomedially extending basal lamina and a deep, anteroposteriorly directed groove on its dorsal surface. The intertemporal and the supratemporal overlap the basal lamina and fit into the groove. The ‘kinetic line’ between the cheek and skull table, suggested to be present in embolomeres (Panchen 1964, 1970), is absent in *Discosauriscus* (as in other seymouriamorphs).

The arched, posterior rim of the ornamented surface of the squamosal is relatively high in most specimens. It forms a crest between the sculptured and the posterior unornamented portion (otic flange). In the otic flange, a more or less distinct groove (roughened, with foramina) and ridge run close to the crest. This groove and ridge probably served as a place for the attachment of the tympanic membrane.

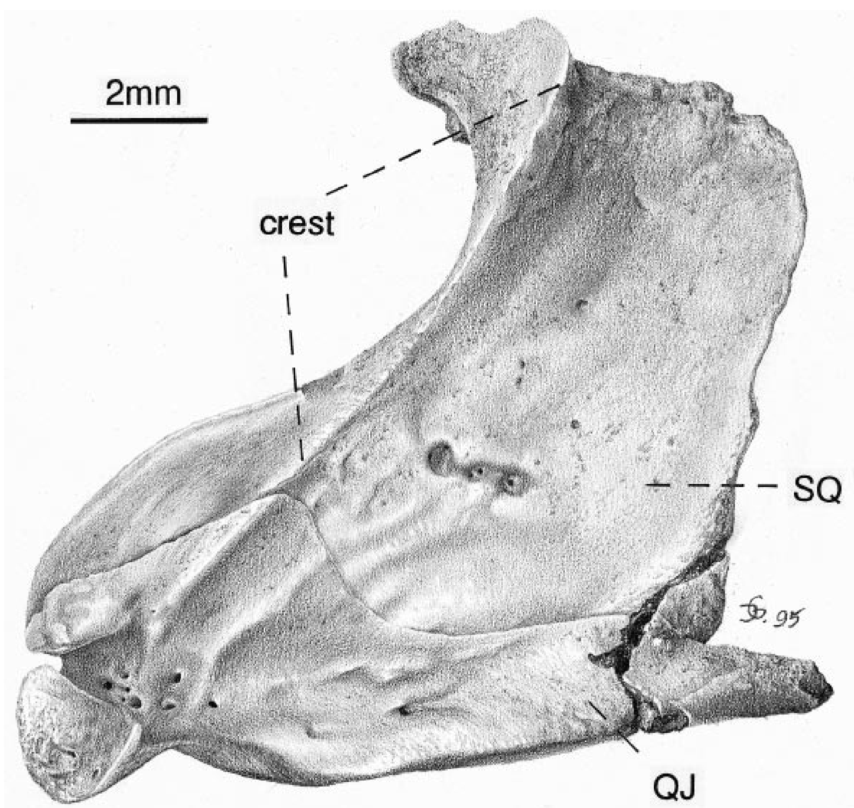

Figure 13. *Discosauriscus austriacus* (Makowsky 1876). K 40; left squamosal and quadratojugal in internal view.

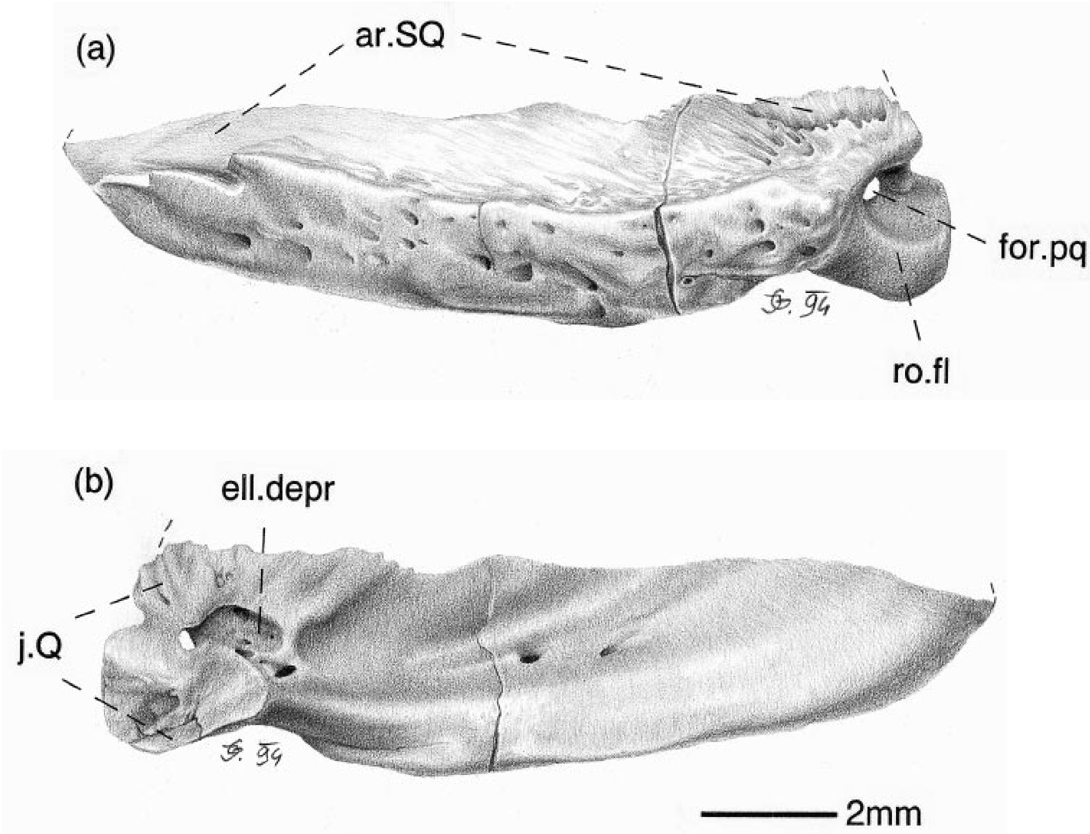

Figure 14. *Discosauriscus austriacus* (Makowsky 1876). K 3; left quadratojugal in lateral (a) and internal (b) views.

On the inner surface of the squamosal (figure 13), a prominent, ventromedially extending crest is present. It starts approximately at the mid-length of the dorsal portion (basal lamina) of the squamosal where it is most prominent, and runs diagonally along its posterior margin. It turns a little anteriorly near the posteroventral portion of the bone and fades out. The dorsal margin of the quadrate ramus of the pterygoid abutted against this crest. The posteriormost section of the crest (from the point where it turns anteriorly and extends on the ventral surface of the quadratojugal) probably marks the dorsolateral extent of the cartilaginous quadrate.

Quadratojugal. This is an elongate bone occupying the posteroventral portion of the cheek (figures 2–4, 5 *b*, 13, 14, 23 and 24). Its ornamented part is narrow. However, a large, ventral lamina underlies the squamosal (K 40, K 383). The posterior portion of the quadratojugal borders the lateral and lateroventral part of the condylar portion of the quadrate. This part of the quadratojugal is a thin, unornamented rounded flange, curved medially at its base. The posteriormost portion of the rounded flange (figures 13 and 14) is perforated in the anteroposterior direction by the paraquadrate foramen (proprium) (concerning this term, see Bystrow (1939)). In some specimens, however, it is open posteriorly and a notch is present (K 18 and K 40 respectively). In these cases, the medial wall of the foramen was completed by the quadrate.

The inner surface of this portion of the quadratojugal, above and below the paraquadrate foramen, is roughened and marks the junction with the cartilaginous quadrate. The paraquadrate foramen opens into an elliptical depression here. A large foramen occurs in the upper wall of this pit, and a small one in its lower wall (figure 14). A little more anteriorly, approximately in the level of the latter foramen, a relatively large pit, with the foramen at its base, is present. There is slight variation in the location of these foramina (figure 13). It is not possible to observe the communication of these foramina. According to Bystrow & Efremov (1940), the foramen paraquaratum proprium and foramen paraquadratum accessorium served for the passage of blood vessels. According to Clack (1987), based on the conditions in *Pholiderpeton*, the paraquadrate foramen probably did not serve for the transmission of the mandibular branch of the seventh cranial nerve.

The lower margin of the quadratojugal is thickened and contains a long canal (K 65, K 172). One (K 206, K 319) or two (K 177) orifices of various sizes in the inner surface of the quadratojugal communicated with this canal. These foramina lay within approximately the middle third of the bone length. Above the thickened lower margin, the inner surface of the quadratojugal is slightly hollowed out and together with a matching structure in the squamosal it forms the thinning of this part of the cheek. The inner surface of the quadratojugal may be slightly longitudinally and obliquely striated (K 180).

Sclerotic ring (figure 2). The most complete sclerotic ring is present in the right orbit of K 330 (figure 3); about one medial (or upper) half of the ring and the carbonized soft parts of the eye are preserved. Each

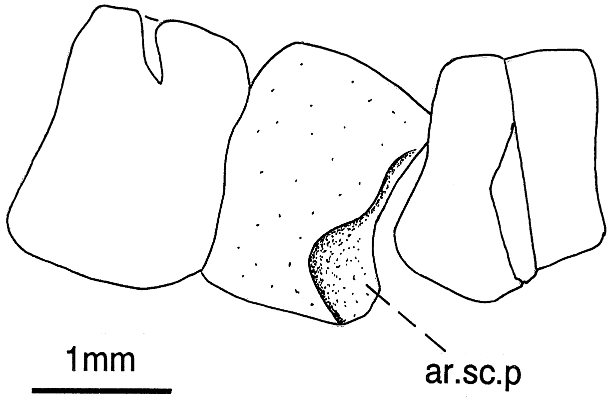

Figure 15. *Discosauriscus austriacus* (Makowsky 1876). D 196; sclerotic plates from left orbit in dorsal view.

sclerotic plate is almost rectangular in shape. One of its proximal corners (relative to the middle of the ring) projects into the more or less broad process which overlaps the neighbouring sclerotic plate (K 102, K 330, D 196, figure 15). There are 19 plates preserved in the right orbit of K 330, so about 40 plates could be present in the complete sclerotic ring of this specimen.

Palate. The palate is of the generalized seymouriamorph type (figure 24*a*). In this stage, narrow interpterygoid vacuities are still present (transient ontogenetic condition, see below). Ivakhnenko (1987) described in *Ariekanerpeton* and figured in *Utegenia* a small foramen for the inferior ramus of the palatal artery situated in the region between the palatine, ectopterygoid and maxilla. This suborbital fenestra probably served for the passage of the lateral palatal ramus of the facial nerve and a branch of the inferior orbital artery (lateral palatine artery). It is also present in *Discosauriscus*, although the degree to which the palatine or the ectopterygoid form its border differs among specimens. Likewise, the degree to which the posterolateral corner of the ectopterygoid is anteriorly notched to form the anterior border of the subtemporal fenestra also differs among specimens.

Vomer. This is an elongated plate, with a dorsally curved lateral margin (alar process, K 224) forming the medial border of the exochoanal fenestra (figures 24*a* and 26). The anteriormost portion of the vomer is trough-shaped and it gradually becomes flat posteriorly. Anteriorly, both vomers meet in the median plane, except for the anteriormost parts where small processes of the premaxillae fit. The median suture occurs in the anterior third of the length of the vomer. Specimen D 73 shows that in the anteriormost section of their median contact, both vomers meet in an interlocking suture; further posteriorly, the left vomer overlaps the right one slightly dorsally. From the posterior end of the median suture, both vomers diverge posterolaterally. The anterior processes of the pterygoids fit into this space, and they are overlapped dorsolaterally by the vomers (KO 61). The posterior end of the vomer is broad and largely overlaps the pterygoid. The ventral exposure is relatively narrow and fits into the notch in the anterolateral wall of the pterygoid. The border between these two parts of the vomer is morphologically expressed as a crest on the ventral surface of the bone (D 70, K 17, K 65, K 234, KO 61, KO 82, KO 84, KO 99). The posterolateral margin of the vomer slightly underlies the palatine (D 70, K 64).

The ventral margin of the exochoanal wall forms a ridge along which runs a row of small, sharp, pointed teeth. This tooth-row is sometimes double and often accompanied by further small teeth (KO 3, KO 18, KO 23, K 358); sometimes the row may be incomplete. Anteriorly, at the beginning of the tooth-row and on the ventral surface of the vomer, two or more rows (K 348) or a patch (K 313) of small teeth are present. In some specimens (K 224, K 227), more small teeth may also be present in the region of the posterior end of the tooth-row. These teeth are in continuity with small teeth on the ventral surface of the palatine (D 70, K 277). At the border between the middle and the posterior thirds of the vomer length, two (D 73, K 313) or three (K 83) tusks (or tusk-positions) are present. In K 60, the right vomer bears two, the left four tusk-positions. In K 14, the right vomer bears two, the left three tusks; in K 180 (probably also in K 224), the left vomer bears three tusks, the right one only one tusk; in KO 23, the right vomer bears two tusks, the left only one tusk. The number of tusks does not depend on the skull proportions (Klembara & Janiga 1993). The tusks lie immediately medial to the row of small teeth, and the teeth within the row are the largest here.

The dorsal surface of the vomer (K 9) bears a distinct shallow groove running in an anterolateral–posteromedial direction. It probably marks the cartilaginous anteromedial rim of the endochoanal fenestra of the nasal capsule. However, no such distinct grooves are visible on the dorsal surfaces of KO 55 and KO 63.

Palatine. This is a broad plate wedged between the maxilla, pterygoid and ectopterygoid (figures 24*a* and 26). Most of its anterior margin is broadly notched and forms the posterior wall of the exochoanal fenestra; the wall is anterodorsally–posteroventrally inclined. The palatine overlaps dorsally the posterolateral margin of the vomer slightly and the pterygoid extensively (K 346.I, KO 31, KO 155, D 70). Except for its medially deflected posterior section participating on the bordering of the suborbital fenestra (KO 1, K 102, K 383), the lateral edge of the palatine bears a groove into which the horizontal lamina of the maxilla fitted. Anterolaterally, the palatine forms a maxillary process. It contains a large foramen in its posterior portion (KO 1, KO 61). The posterior margin of the palatine is transversely oriented; however, the right palatine of KO 7 has a relatively large posteromedial process. The posterior margin of the palatine fitted into a groove in the anterior margin of the ectopterygoid (D 25, K 62, K 169).

The dorsal surface, excellently preserved in KO 1 (also well displayed in K 169, K 202, K 224, KO 7, KO 16), bears more important features (figure 26). The anterior half of its lateral edge bears a ventrolaterally inclined surface which is broadest anteriorly. The inner surface of the internal lamina of the lacrimal was attached to this surface. Immediately anteromedial to this surface, the medial wall of the maxillary process bears a distinctly bordered and slightly roughened area for the tip of the prefrontal. Near the exochoanal border and parallel to it, the dorsal palatine surface bears a distinct transversely oriented canal. It is broadest medially and lateralwards becomes narrower and deeper. The canal penetrates the lateral margin of the palatine and opens in the posterior part of the large antrum present in the lateral wall (the antrum is anteroposteriorly elongated and lies immediately above the anterior section of the groove for the horizontal lamina of the maxilla). A similar canal was described in the procolophonids *Tichvinskia* (Ivakhnenko 1979) and *Procolophon* (Carroll & Lindsay 1985) and is probably homologous with the infraorbital canal or foramen (or maxillo–palatine foramen) in many saurians (Jollie 1960). Through this canal, the maxillary branch of the trigeminal nerve and the infraorbital (or maxillary) artery probably ran, and further anterolaterally they entered the foramen in the inner maxillary wall. In KO 16, the immediate roof of this canal is mediolaterally narrowed to a thin bridge, hence the lamina of the lacrimal also participated on its covering. Because this canal is medially very broad, it is highly probable that in its anterior portion the anastomosing branch ran between the infraorbital and palatal arteries (cf. Ivakhnenko 1979). Immediately anterolaterally to this canal, a relatively large foramen is present. A similar position is occupied by the palatal foramen in captorhinids (Heaton 1979) and the foramen in the anterolateral portion of the palatine in *Procolophon* (Carroll & Lindsay 1985). This large foramen in *Discosauriscus* contains four further foramina (three anteriorly and one posteriorly) which lead into the bone forming four short canals. The posterior one opens in the anterior wall of the infraorbital canal. The medial of the three anterior canals leads ventromedially and opens ventrally, approximately in the mid-width of the exochoanal rim (K 209). The remaining two canals extend anterolaterally. One further small foramen lies in the medial wall of the maxillary process, immediately anteroventral to the facet for the prefrontal. Immediately posterolateral to the infraorbital canal there are two foramina present, one behind the other. The anterior one is smaller, and continues as a canal into the bone to the tusk region. The posterior, larger foramen penetrates the upper portion of the lateral margin of the palatine and opens in its lateral wall, above the maxilla–palatine suture. This foramen is not completely closed laterally in K 169 and KO 7. The third foramen (KO 1) or sulcus (KO 7) lies in the lateral margin of the palatine, immediately posterior to the internal lamina of lacrimal–palatine junction. Posterior to the infraorbital canal, two further foramina leading into the bone are present on the dorsal surface of KO 1.

Unfortunately, the condition in most other early tetrapods is poorly known in this area. In every case, the structure of the palatine and its relationships to the neighbouring bones in *Discosauriscus* is very similar to that in procolophonids and is of the reptilian type.

On the ventral surface, usually two (K 277, K 313) or occasionally three (K 83) tusks (or tusk positions) are present. In K 14, the left palatine bears two, the right one three tusks. The right palatine of KO 22 bears only one tusk. In the left palatines of K 54 and K 209 four tusks are present, the dentition of the right ones is not accessible. The right palatine of D 103 bears five, the left one 2+?1 or 2 tusks; the right palatine of K 335.III bears five tusks. The condition in the three last specimens is rare. The tusks lay near the lateral margin of the palatine and approximately in the middle of its length. Small teeth form a row or patches in the region of the exochoanal fenestra margin (D 70, D 213, K 13, K 83) and lateral (K 313, KO 53) or posterolateral to the tusks (D 76, K 169, KO 33, KO 48). Specimen K 277 shows the more or less continuous row of teeth running from the vomer over the exochoanal fenestra margin of the palatine (also in K 17). The obliquely running rows of small teeth behind the tusks show continuity with the rows of teeth on the pterygoid ventral surface (D 57, K 277, K 306, K 313).

Ectopterygoid. This is a rectangular bone (figures 24*a* and 26). Posteriorly, it broadens slightly and gradually. Medially and posteromedially, it is joined in an interlocking suture with the pterygoid by which the former overlaps dorsally (in various degrees) the latter (K 17). The posterolateral margin may be conspicuously notched (KO 26) and forms the anterolateral rim of the subtemporal fossa; the left ectopterygoid of KO 18 and the right one of KO 7, however, are not distinctly notched. The rim of the notch may be conspicuously thickened (K 224, KO 61). The ectopterygoid meets the maxilla along its straight lateral margin except for the anteriormost section. Here, the ectopterygoid is notched (KO 7, K 357) or medially deflected (K 102) where it participates in the border of the suborbital fenestra. In KO 18 it is evident that the lateral margin of the ectopterygoid is slightly flexed dorsally and its ventral border is faintly grooved; this indicates that it overlapped the horizontal lamina of the maxilla dorsally. The posterolateral corner of the ectopterygoid (readily visible in D 76) fitted into the pit or groove on the inner surface of the jugal, at a level slightly above the posterior end of the maxilla.

The ectopterygoids do not bear tusks. Individual small teeth (K 169, K 206) or patches (K 13, K 227, KO 169) of small teeth may be present on the ventral surface of the bone. The small teeth on the ectopterygoid of D 57 are in continuity with the pterygoid tooth-rows. On the left ectopterygoid of K 337, one row of small teeth runs parallel with the lateral margin of the bone; in KO 33 two, in K 346.I four incomplete, closely spaced rows are present in a similar position.

Werneburg (1988) described one pair of tusks on the left ectopterygoid of his *Letoverpeton thuringiacum*. However, this must be demonstrated in more specimens. I suspect that this bone is the vomer in a shifted position.

Pterygoid. This is the largest palatal bone (figures 24*a* and 26). It is composed of four regions: (1) the palatal ramus, (2) the transverse flange, (3) the central region around the basicranial recess and (4) the quadrate ramus including the ascending lamina.

The palatal ramus forms a plate which widens posteriorly gradually and deepens in a trough-like manner (KO 176). Anteriorly, both pointed rami meet on a short section in the median plane in an

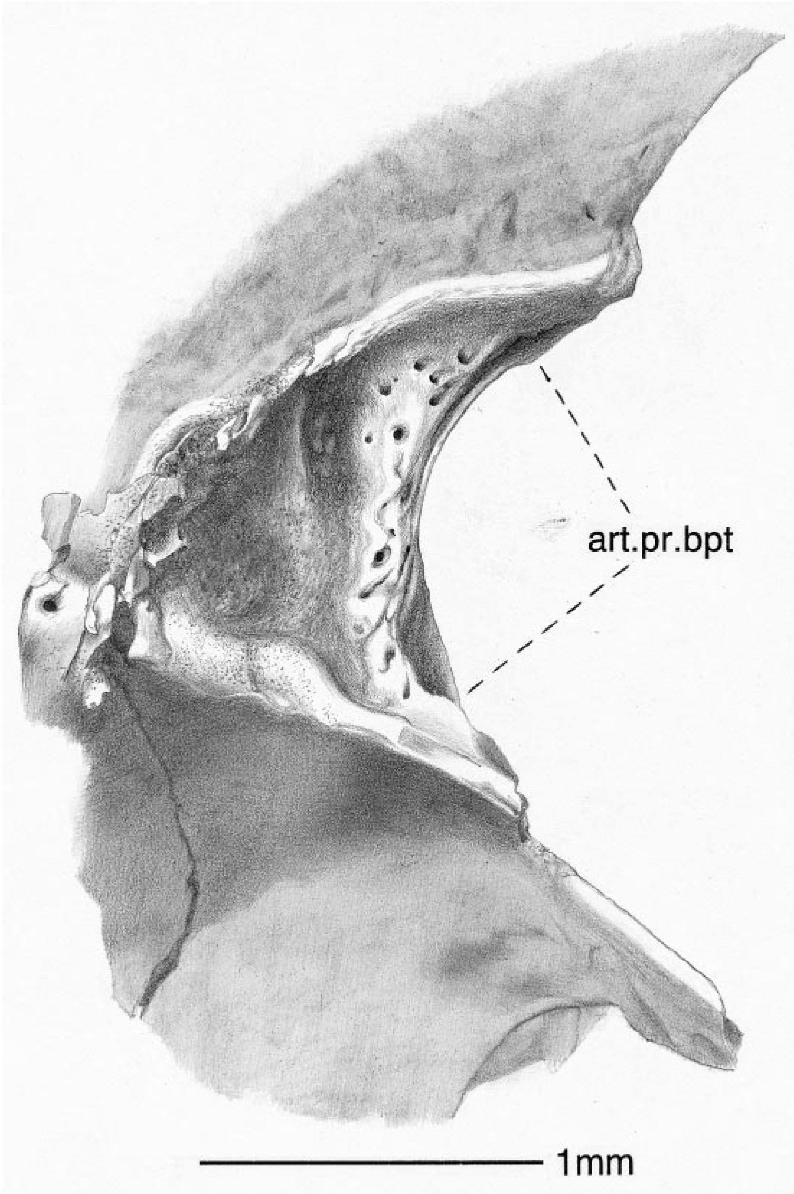

Figure 16. *Discosauriscus austriacus* (Makowsky 1876). D 47; detail of the articular surface of the right pterygoid in ventral view.

overlapping suture (the specimen D 73 indicates that its right pterygoid slightly overlapped the left one). The medial margin of the pterygoid is straight. However, anterior to the articular portion it turns laterally so that a narrow fissure remains between it and the lateral wall of the parasphenoid.

The transverse flange is a distinct structure (*contra* Heaton 1980) projecting laterally at the level of the basipterygoid articulation and forming most of the anterior rim of the subtemporal fossa. It is antero-posteriorly broad and as a whole flexed laterally and posteroventrally below the plane formed by the contact of the palatal ramus with the ectopterygoid and the palatine (KO 176). Hence, viewed laterally, it is slightly exposed below the ventral edge of the cheek (figure 23*b*). The lateral margin of the transverse flange is slightly rounded.

The intensity of the development of the ridges with small teeth on the ventral surfaces of the palatal ramus and the transverse flange differs substantially among specimens; the same is true of the right and the left pterygoid (K 14). However, the basic composition of these structures is consistent: the ridges run radially from the posterior portion of the palatal ramus. This region is massive, the ridges are more or less fused together here, and it also bears various processes, deep grooves, or pits. The ridges may or may not bear a row of small teeth. This pattern may be limited to the ventral surfaces of the palatal ramus and the transverse flange of the pterygoid (K 4), or the tooth-rows may continue onto the ectopterygoid (D 57) and palatine (D 57, D 277). In some specimens (K 1, K 180), the transverse flange (mainly the posterior margin) bears high ridges and deep grooves which continue posteriorly onto the medial (inner) surface of the quadrate ramus.

The basicranial recess lies at the level of the posterior portion of the transverse flange. The recess is crescentic and it is bounded ventrally by walls which are highest antero- and posteromedially. Inside the pit, the extent of the articular area for the basipterygoid (= basitrabecular) process of the basisphenoid is clearly limited laterally by the relatively deep groove and wall. The articular surface (clearly visible in D 47, K 14, K 80, KO 3) consists of the grooves, ridges and pits, and included also the medial (and sometimes also the dorsomedial) surface of the medial edge of the pit. Thus, the basipterygoid process of the basisphenoid leaned partly against the articular edge and most of it fitted into the articular pit of the pterygoid. The character of the articular surface, as seen in D 47 (figure 16), is very similar to the contact surface on the jugal of K 323 for its junction with the squamosal. The articular surface of the articular recess of K 80 mainly bears small deep pits; its medial edge is very narrow. The character of the articular recess surface indicates that it was lined with fibrous tissue or partly also by fibrous cartilage. In all cases, the junction with the basipterygoid process was firm and the joint as a whole was immobile. Immediately lateral to the articular recess, the pterygoid ventral surface is roughened and usually bears one or two foramina (K 66). The dorsal wall of the articular recess is typically striated (K 169). These structures probably mark the ligamentous fixation of the joint.

The quadrate ramus is turned into an almost vertical position and has an arcuate course. The anterior half of the quadrate ramus forms a thin and high plate (ascending lamina *sensu* Bystrow 1944) of quadrangular shape. It is transversely oriented and its upper margin lies near the skull roof in the region of the anterior part of the supratemporal. The lamina extends posterolaterally, gradually narrows, and abuts against the crest on the ventral surface of the squamosal (figure 13). Posteriorly, the squamosal and the pterygoid diverge and the quadrate is wedged between them (figure 24). The ascending lamina is deeply vaulted anteriorly at its base; its anterior (inner) surface is slightly dorsoventrally striated. The posterior (outer) surface of the ventral margin of the whole quadrate ramus is slightly thickened, roughened and longitudinally striated (with a distinct longitudinal ridge in KO 140).

The dorsal surface of the palatal ramus is relatively smooth, and slightly roughened in its anterior region. In the posterior third of its length, the lateral portion of the palatal ramus bears several distinct transverse scars. In the central portion of the pterygoid of K 12, at the level between the anterior margin of the transverse flange and the anterior wall of the articular recess, is a relatively deep heart-shaped pit (figure 26). It has a distinct wall and the relatively smooth base bears small pits. This area, especially anteriorly, is roughened. In exactly the same position in K 38, a circular pit is present. The pit corresponds in size to the larger end of the epipterygoid and it is likely that the cartilaginous end of this bar-like bone fitted into this pit (see '*Epipterygoid*').

The dorsal surface of the transverse flange, especially its lateral portion, is uniformly transversely striated, indicating the pterygoideus muscle attachment. The anteroventral portion of the quadrate ramus bears a deep, elongated depression facing into the subtemporal fossa (K 38). It extends to approximately the mid-length of the lateral wall of the quadrate ramus. The posterior half of the inner surface of the quadrate ramus is strongly longitudinally striated (K 66). With its posteriormost part, the quadrate ramus joined the quadrate.

Parasphenoid. It is described within the neural endocranium with which it is fused (see below).

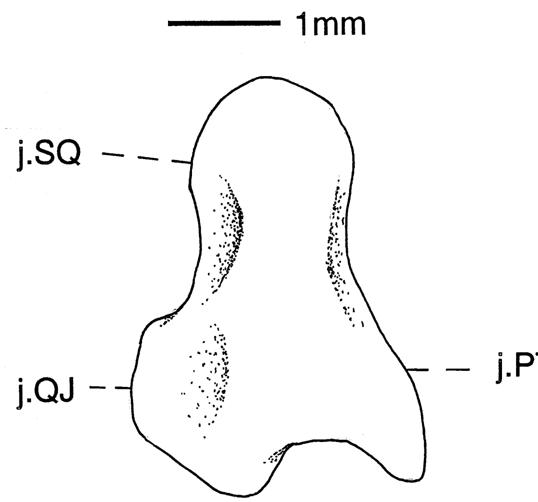

Figure 17. *Discosauriscus austriacus* (Makowsky 1876). K 383; left quadrate in posterodorsal view.

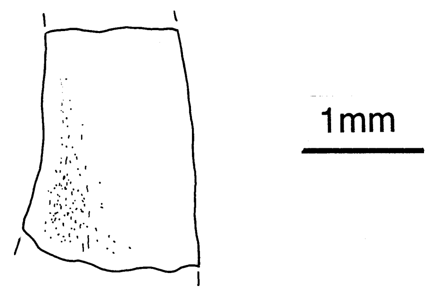

Figure 18. *Discosauriscus austriacus* (Makowsky 1876). K 99; left epipterygoid placed directly on bench.

Ossifications of palatoquadrate

Quadrate. This is not normally preserved and was cartilaginous. According to the construction of the model, the quadrate formed a wedge fitting between the quadratojugal and the squamosal laterally and the posterior end of the quadrate ramus of the pterygoid medially (figure 24). In K 383, however, a triangular element is preserved (figure 17). On one side (presumably the posterodorsal one) it is formed by finished bone, on the inside it is unfinished. Judging by its shape and morphology, it could be a partly ossified probably left quadrate. The lower, broader, articular portion is bilobed with a dorsally directed notch between the lobes; one lobe (probably the lateral one) is larger. The finished posterodorsal surface bears a slightly developed tubercle as in *Seymouria* (White 1939; Heaton 1980). The presence of this partially ossified quadrate is exceptional.

Epipterygoid. This is a short, narrowed bar (K 3, K 55, K 99, K0 1, KO 50, KO 80), slightly longer than wide (figure 18). It is covered by distinct bone but both ends of the elliptical shape are unfinished and continued in cartilage. One end is larger, presumably the lower, fitting into the pit in the dorsal surface of the pterygoid, near its articular portion (K 12, K 38, K 102, K0 11, see '*Pterygoid*', figure 26). The dorsal, narrow, cartilaginous extension of the epipterygoid was probably fixed in the pit in the ventral parietal surface (figure 25*a*). The morphology and the position of the pit in the pterygoid dorsal surface for the lower end of the epipterygoid, as well as the morphology of the epipterygoid itself, indicate that the epipterygoid (in the cartilage–bone condition here) does not participate in the basipterygoid articulation.

Lower jaw

The lower jaw is long, mediolaterally narrow and curved medially in its anterior portion (figure 25*b*, *c*). The original shape and junction of both lower jaws is well preserved in KO 64. The lower jaw is highest at the mid-length of the adductor fossa which faces mediodorsally.

Dentary. This is a long bone, approximately triangular in lateral view. Its anterior end is dorsoventrally the highest and is almost perpendicularly oriented. From this point, it tapers gradually posteriorly. The symphysial area is triangular and its surface is roughened. With its lower edge, the dentary joins the splenial and postsplenial, and posteriorly it overlaps the anterior part of the surangular from the outside. The dental lamina bears up to 43 teeth (K 302).

The anteriormost end of the dentary is crescentic in transverse section. On the inside, at the level of the bases of the first four teeth, the dentary forms a narrow lamina oriented ventromedially. The ventral margin of the lamina forms the dorsal rim of an elongated fenestra. The posterior margin of the lamina sutures with the anterior coronoid and posteroventrally the lamina joins the splenial (K 40, K 313). Further posteriorly, the dental lamina articulates with the middle and posterior coronoids.

The anterior portion of the outer dentary surface bears many small foramina for cutaneous arterial and sensory branches (K 83). Further posteriorly, the surface is smooth with short grooves. Close to the upper margin of the dentary and parallel to it, a groove with foramina at its base runs on the outer surface. It resembles that in the maxilla. Through these foramina, the nerve and arterial branches passed to the outer dentary surface.

Surangular. This is a long, narrow plate. The surangular crest is low, not as high as in embolomeres (e.g. *Pholiderpeton*, Clack (1987)). The uppermost portion of the anterior end of the surangular has a strong interdigitating suture with the posterior ramus of the posterior coronoid. The suture is clearly visible internally but also has a small lateral exposure. The inferior margin of the bone is overlapped by the angular from outside along its whole length. The dorsolateral surface of the surangular crest is slightly grooved for the quadratojugal. The posterodorsal, articular margin is slightly depressed. Ventral to it, on the outer surface, one (K 55) or two (K 180) anteriorly directed foramina are present. The surangular foramen in saurians has a similar position (Skinner 1973) and transmits the cutaneous branch of the inferior alveolar nerve. The posterior margin of the surangular is slightly curved medially (K 172). A conspicuous longitudinal crest is present on the inner surface of the surangular in D 76. It is most massive anteriorly, where it supports the posterior portion of the posterior ramus of the coronoid (K 65), and posteriorly it gradually fades out. The posterior portion of the inner surangular surface is roughened with deep pits (K0 1, KO 173, K 65, K 324, KO 179) indicating the junction with the cartilaginous articular.

Coronoids. Anterior, middle and posterior coronoids are present. All three coronoids bear small teeth on most of their inner surface (the posterior coronoid only on its anterior ramus). The narrow shelf of the dentary bears a deep groove on its medial margin (K 324) into which the anterior and middle coronoids and the anterior ramus of the posterior coronoid fitted.

The anterior coronoid is a narrow, elongated plate interposed between the dentary and the splenial. Posteriorly, it has an oblique (in lingual view) suture with the middle coronoid, which bears the unornamented area overlapped by the former bone.

The middle coronoid is a long and narrow plate, a little longer than the anterior coronoid. Its anteroventral margin is slightly overlapped by the posterior tip of the splenial (K 95, K 313). Similarly, its lower margin is overlapped by the prearticular along its whole length (K 313). Posteriorly, it forms a large area which is overlapped by the posterior coronoid (K 320).

The posterior coronoid consists of an anterior ramus which is posteriorly broadened into a large, triangular plate, and of a posterior ramus. On the internal side, the suture of the posterior ramus with the surangular lies more posteriorly in comparison with its position on the external surface; this is because both bones overlap slightly. The internal surface of the posterior ramus bears strong longitudinal ridges and grooves. On the lingual surface, the triangular plate is overlapped by the prearticular. The angle between the posterior ramus and the triangular plate defines the anterior limit of the adductor fossa.

Splenial. This bone, together with the postsplenial and angular, forms the ventral trough-shaped wall of the lower jaw. In all three bones, the border of the outer ornamented and ventral unornamented area forms a distinct sharp edge.

Anteriorly, the splenial forms the ventralmost corner of the symphysial area. On the outside, the splenial appears as a narrow strip of bone; its posterior end overlies the anterior tip of the postsplenial. Lingually, the dorsal margins of both sutured bones are shallowly ventrally notched; this is the ventral rim of the small, elliptical anterior Meckelian fenestra (K 313). On the lingual side, the splenial forms a relatively broad plate joining the dentary and anterior and posterior coronoids dorsally (K 313, KO 25). The anterodorsal margin of this plate is free and forms the ventral margin of the fenestra probably filled with the Meckelian cartilage. The posterior margin of the splenial joins the anterodorsal margin of the prearticular.

Postsplenial. This is a narrow and long bone, longer than the splenial. On the outer surface, its anterior tip fits between the dentary dorsally and the splenial ventrally. Posteriorly, it underlies the angular on relatively long section. On the lingual surface, the splenial overlaps the prearticular from the outside.

Angular. This is a long and massive bone. Its outer side tapers anteriorly and fits between the surangular dorsally and the postsplenial ventrally. Its lingual portion has a long suture with the prearticular. The upper margin of the narrow lingual wall of the angular bears a relatively deep groove into which the distinct edge of the prearticular fitted (KO 2). The anterodorsal margin of the lingual wall is incised and this elliptical incision continues anteriorly also on the dorsal, posteriormost margin of the postsplenial (D 57, D 76, K 65); in KO 26, however, the incision is only in the angular margin. The incision is the ventral rim of the elongated posterior Meckelian fenestra; it is larger then the anterior Meckelian fenestra. The inner surface of the posteriormost portion of the outer angular wall is roughened (K 313) indicating the junction with cartilaginous articular. The posteroventral margin of the angular is free (KO 175).

Prearticular. This is a long, flat bone occupying most of the lingual surface of the lower jaw. The posterior portion is rectangular and forms the medial wall of the adductor fossa. On the lingual surface, a foramen, probably for the chorda tympani, is present (D 95, K 65); in KO 197, a tiny foramen is situated on the base of the distinct groove running in the posterodorsal–anteroventral direction.

Immediately anteriorly to this large posterior portion, the prearticular is much narrower. The dorsal margin of this part is bevelled and forms a distinct edge medially. Ventral to this edge, an acuminate ridge runs almost parallel, and further anteriorly, the ridge extends approximately to the mid-length of the postsplenial (K 316). Anteriorly, the tip of the prearticular fits into the splenial. Ventrally, the prearticular has a long and broad portion which is overlapped by the angular from the outside (K 172, K 381, KO 2). The posteroventral margin of the prearticular is free; the cartilaginous articular was interposed between it and the free posteroventral margin of the angular. The posteriormost portion of the prearticular did not reach the posterior level of the angular and surangular, and its inner surface is roughened (KO 173, KO 175) because of the junction with the articular.

Articular. This was cartilaginous, interposed between the surangular, the angular and the prearticular. The morphology of the posteriormost portions of these three bones (KO 175) indicates that the articular was exposed posteroventrally, partly laterally, and its posterodorsal portion laterally.

Dentition

The teeth are cylindrical with slightly recurved tips (figure 24*a*). In the larval stage, the teeth possess relatively large pulp cavities and the dentine of their bases starts to infold. In specimens in the stage of metamorphosis, the dentine infolding is variously developed in the basal portion of the teeth. The dentine starts to infold on the largest maxillary and premaxillary teeth. For the ontogeny of the teeth, see Klembara (1995*a*, fig. 9). On the lingual side, near to the crowns, the teeth are faintly longitudinally striated (figure 10).

There are 5–7 premaxillary teeth. In K 348, the left premaxilla bears six teeth, the right one only five. However, two small tooth positions are also present. In most specimens, the second–sixth teeth are larger. The maxilla supports 20–29 teeth (K 177 and K 134 respectively). Anteriorly, at the level where the maxilla is the deepest, the third–fifth teeth are the largest. From this point posteriorly, the tooth length gradually decreases. In some specimens (K 60, K 336, K 348), small replacement teeth are also present. The number of premaxillary and maxillary teeth do not depend on the skull proportions of the individual. The dentary bears up to 43 teeth (K 302). One or two first teeth are relatively small, then follows the largest tooth. From this point, the teeth decrease slowly in height posteriorwards. The distance between the individual teeth of the premaxilla, maxilla and dentary vary among specimens.

The number of palatal tusks is as follows: vomer: 1–4; palatine: 1–5; ectopterygoid: 0. This plasticity in the number of tusks on the vomer and the palatine (also in the same individual) probably indicates larval and metamorphic conditions. However, the most common number of the palatal tusks is: vomer: 2; palatine: 2. The structure and shape of the tusks is basically identical to the marginal dentition. Rows of small teeth border the exochoanal fenestra on the vomer and the palatine, and continue laterally and posteriorly to the palatine tusks, and further on the ectopterygoid parallel with the lateral margin of the latter. Very often, some sections of this vomer–palatine–ectopterygoid tooth-row are accompanied or replaced by the patches of small teeth. The radially diverging ridges (bearing small teeth) on the ventral surface of the palatal ramus of the pterygoid continue sometimes onto the palatine and ectopterygoid.

The ventral surface of the central region of the parasphenoid also bears radially diverging or longitudinal ridges with or without small teeth.

Parasphenoid, neural endocranium and stapes

The parasphenoid is fused with the basisphenoid portion of the ethmosphenoid in the orbitotemporal region, hence this structure may be called the parabasisphenoid (figure 19). Where possible, however, the two components (dermal and chondrogenous) will be described separately. With regard to the otoccipital, only the partly ossified basioccipital and exoccipitals are present; in addition, pieces of chondrogenous bone occasionally occur attached to the ventral surface of the skull table (see below). Because of poor ossification of the endocranium, the position and orientation of individual endocranial ossifications is here derived from the conditions in *Seymouria* (White 1939; Laurin 1995, 1996*c*).

The parasphenoid and the endocranium of *Discosauriscus* were described by Švec (1986). However, Švec described the parasphenoid structures as endocranial

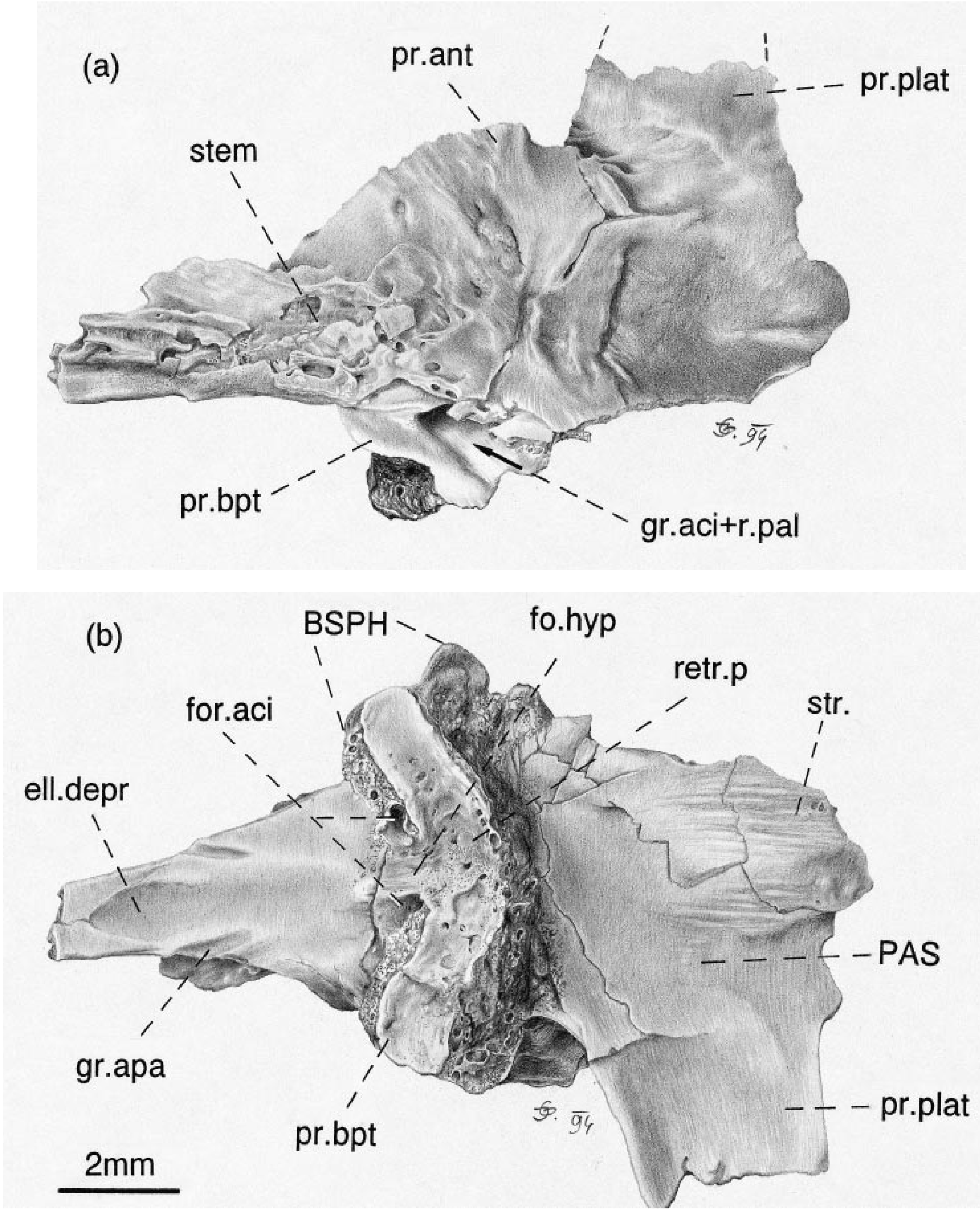

Figure 19. *Discosauriscus austriacus* (Makowsky 1876). K 95; parabasisphenoid in ventrolateral (a) and dorsal (b) views.

ones. He considered the posterior portion of the parasphenoid body and the incomplete part of the posterior parasphenoid plate as ossified prootic plus opisthotic. He interpreted the longitudinal grooves in the parasphenoid body as the canals for the olfactory nerves, etc. Because this represents an almost complete misunderstanding of these structures, Švec's (1986) descriptions and conclusions will not be considered here.

Parasphenoid. As a whole, the parasphenoid is triangular in shape (figures 19, 20, 24*a*). It consists of a long stem (or body) with paired small anterior processes, and a posterior plate with a pair of large posterolateral processes. It sheathes the incompletely ossified basisphenoid portion of the otherwise cartilaginous ethmosphenoid, cartilaginous otic capsules and part of the basioccipital ventrally. The anterior portion of the parasphenoid, up to a level slightly behind the posterior limit of the basipterygoid processes, corresponds to the parasphenoid (parasphenoid stem or body) of osteolepiforms. The parasphenoid stem of *Discosauriscus* is long and triangular; its pointed anterior end reaches to about the level of the posterior margin of the exochoanal fenestra.

The parasphenoid stem has the form of a shallow trough (K 66, K 95). On its posterior dorsal surface, three distinct features are recognizable (figure 19*b*). In the space between and immediately anteriorly to the anterior openings of the internal carotid arteries (see below), a small rounded pit (deep in K 211) is present, which probably represents the hypophysial fossa. From this pit anteriorwards, an ellipsoid depression, bounded with low ridges, is present. Immediately laterally to these ridges, a distinct sulcus is preserved; it is deepest

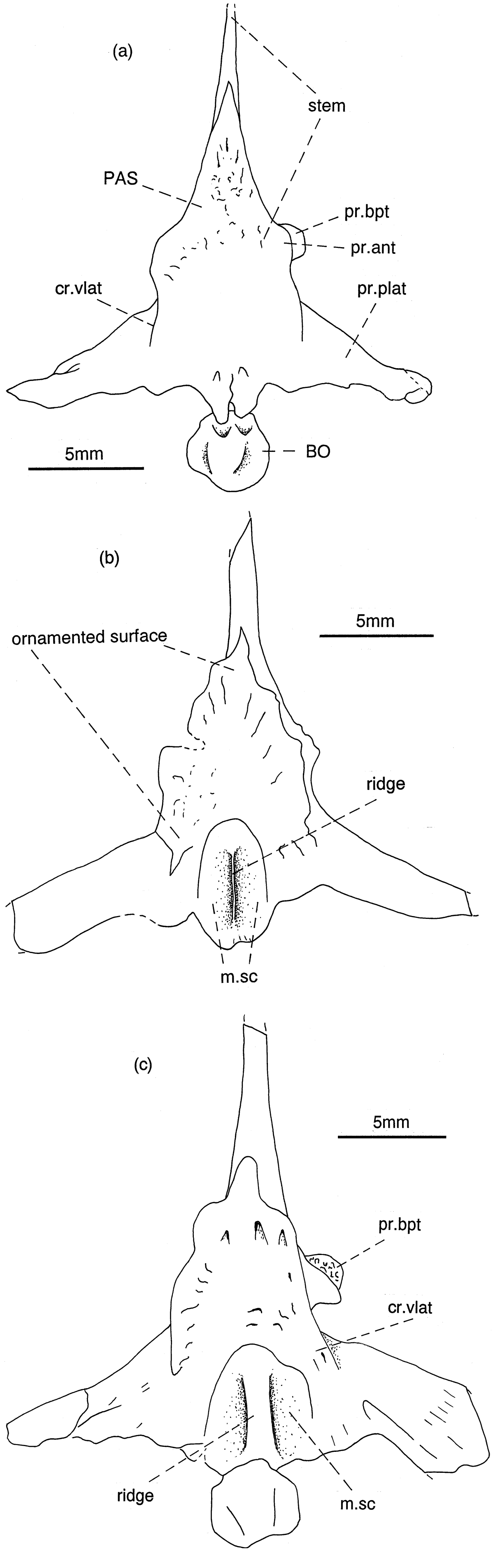

Figure 20. *Discosauriscus austriacus* (Makowsky 1876). KO 26 (a), KO 162 (b), KO 2 (c); parasphenoids and basioccipitals (only in (a), (c)) in ventral views.

on the lateral margin of the parasphenoid stem and it fades out posteriorly. The same structures were recognized by Shishkin (1973) on the dorsal surface of the parasphenoid stem of *Dvinosaurus primus*. Shishkin (1968, 1973) interpreted this structure as the canal carrying the arteria palatina anterior running between the parasphenoid ventrally and trabecular endocranial portion (sometimes penetrating its base) dorsally. It means that the structure interpreted by White (1939) as the presphenoid in *Seymouria* is in fact the parasphenoid. Also, in *Discosauriscus*, this parasphenoid portion is Y-shaped. The median limb is the transition to the ornamented triangular area of the parasphenoid lying between the pterygoids and visible from the ventral side. Between this triangular area and the overlying portion of the parasphenoid stem, the posteromedial parts of the palatal rami of the pterygoids fitted and closed the palate in juveniles. Therefore, the anterior unornamented and more dorsal portion of the parasphenoid stem lies immediately dorsal to the pterygoids, and in the postmetamorphic stage is no longer visible from the ventral side. In *Discosauriscus*, the ventral surface of the posterior half of the parasphenoid stem bears the type of ornamentation corresponding to that portion of the ventral surface of the pterygoid from which the ridges with denticles diverge radially: it may be only slightly roughened (KO 26) or may bear variously intensively developed ridges (mostly longitudinally oriented), grooves, pits or processes. On the surface of these structures, small patches, isolated denticles, rows of denticles or their positions (D 47, D 213, KO 82, KO 83) are present. In the region of the basipterygoid processes, the parasphenoid broadens into the small processes which cover the basipterygoid processes from below (visible in K 241, KO 43, KO 82, KO 323).

Further posteriorly, the parasphenoid continues as a plate from which the large posterolateral processes diverge. This part of the parasphenoid covered the cartilaginous otic capsule ventrolaterally (see below).

The posteriormost median portion of the parasphenoid, behind the posterior limit of the posterolateral processes, forms two small processes. These processes underlay the ventral, anteriormost portion of the basioccipital (the original contact visible in K 3, KO 6, KO 26, KO 110, figure 20*a*).

The dorsal surface of the otoccipital parasphenoid portion is longitudinally striated (KO 27, KO 64), figure 19*b*. Its ventral surface may be relatively smooth (KO 82) but usually it is striated: the striae diverge from the region between and slightly behind the basipterygoid processes posterolaterally. The parasphenoid margins are slightly curved ventrolaterally in the region of the anterior processes, and in the sections slightly behind the basipterygoid processes, they continue posteriorly or slightly posterolaterally in the form of low and rounded (sometimes sharp, KO 82) ventrolateral crests representing the basal tubera (they may be also ornamented, e.g. KO 145, KO 162). Both

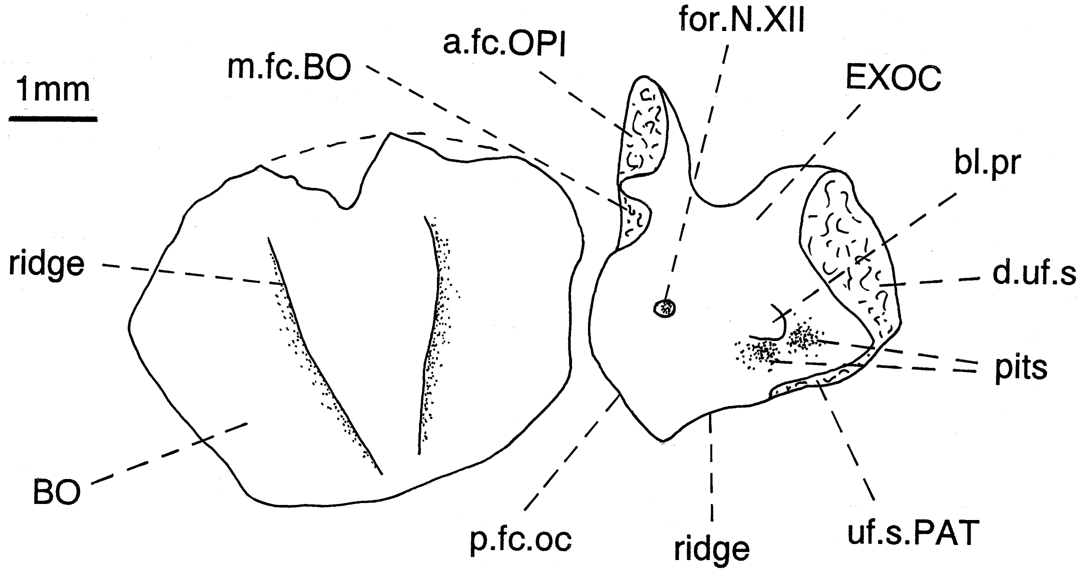

Figure 21. *Discosauriscus austriacus* (Makowsky 1876). KO 133; basioccipital in ventral and left exoccipital in lateral views.

crests bound the muscle scars which are sometimes separated by a distinct median ridge (figure 20). However, in most specimens, the muscle scars are not distinctly separated by a crest.

Ethmosphenoid. Only the incompletely ossified basisphenoid portion is preserved (figure 19*b*). It consists of the crista sellaris which is covered dorsally by finished bone. Mesially, it is depressed, forming a relatively large rounded pit. The pit is roughened with small foramina (KO 6, KO 27) and probably represents the retractor pit present in *Seymouria* and other early tetrapods (Clack & Holmes 1988). The lateral portions of this basisphenoid portion project dorsolaterally. The basipterygoid processes are incompletely ossified but are covered ventrally by finished bone. The parabasal or Vidian canal is visible in many specimens. The internal carotid artery and ramus palatinus of the facial nerve (N. VII) passed along the sulcus between the parasphenoid and the posterior section of the root of the basipterygoid process (i.e. ventromedially to it). Further anteriorly, the internal carotid artery curved medially, penetrated the parabasisphenoid (i.e. the fused region of the basipterygoid process root with the underlying parasphenoid, visible in KO 1, K 16, K 241, KO 6, KO 68, KO 80), and the canal carrying the artery opened at the base of the dorsum sella (KO 68, K 95). The canal follows an anteromedial course and it is traceable in specimens in which the wall of the canal is broken (D 47, KO 27). In the smooth ventral surface of the basipterygoid process of D 47 and KO 80, a distinct anteroposteriorly running groove is present, indicating the further anterior course of the ramus palatinus (from N. VII) and arteria palatina. Between and immediately anterior to the openings for the internal carotids, the shallow depression probably represents the fossa hypophysialis.

Basioccipital. This is a pentagonal plate (figures 20*a*, *c*, 21 and 24). The dorsal surface of the basioccipital is of unfinished bone (KO 28, K 258, K 323). The anteriormost portion of the ventral surface bears distinct triangular impressions of the posteriormost tips of the parasphenoid (KO 26, KO 30, K 320). A median ridge may be present between both impressions (KO 30). The ventral surface bears two relatively massive ridges passing parallel with the lateral margins and converging posteromedially. Between both ridges a shallow trough is formed.

Exoccipital. This is a short bone, expanded and unfinished at both ends (figures 21, 23*b* and 24). Its shaft is broad. The ventral unfinished end is divided into three portions: (i) the posterior, posteromedially facing portion participating in occipital condyle formation; (ii) the largest, medially inclined middle portion joining the basioccipital; and (iii) the anteriormost portion (KO 82, KO 133) facing ventrolaterally and presumably joining, as in *Seymouria* (White 1939), the opisthotic. The dorsal unfinished portion, facing dorsolaterally, joined the postparietal and perhaps also the occipital flange of the tabular. This dorsal unfinished portion continues posteromedially into the small facet which served for the junction with the proatlas. From this facet, the distinct ridge extends posteroventrally. Immediately lateral to it, two relatively deep pits are present. Between them, a blunt process is located (K 204). In KO 162, the pits are not so distinct, but the process is relatively large with a pit at its apex. The posterolateral wall of the exoccipital is medially notched, participating on the formation of the foramen for the exit of the vagus (N. X) and accessorius (N. XI) nerves. The medial exoccipital side forms the lateral wall of the foramen magnum. The lower end of the exoccipital is penetrated transversely by the canal for the hypoglossus (N. XII) nerve (K 323). The small foramen for the exit of this nerve lies in the ventrolateral wall, at the level between the posterior and middle unfinished portions.

Stapes. This is a crescentic bone, at one end narrowed and at the other broadened, indicating the presence of two processes (figure 22). It is poorly ossified. Its shaft is incompletely covered by smooth

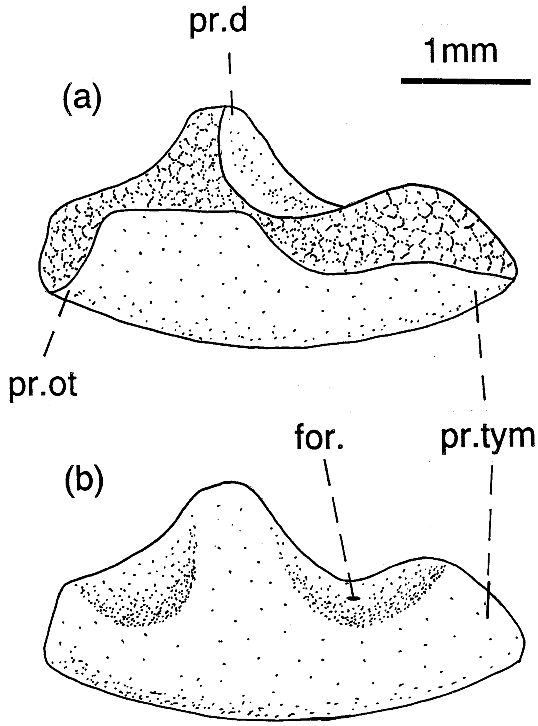

Figure 22. *Discosauriscus austriacus* (Makowsky 1876). K 172; right stapes in posterior (a) and anterior (b) views.

finished bone posteriorly and both ends are unfinished. Because no other structure is recognizable on the stapes, it is difficult to decide on its exact position. I conclude that the broad end of the stapes was the proximal one, as was probably the case in *S. baylorensis* (Laurin 1996*c*). The lower of the processes of this end fitted into the fenestra ovalis and the extent of the dorsally oriented upper process is unknown. The distal process was directed to the tympanic membrane. Between both latter processes, one small foramen is present (KO 82). It is difficult to decide if the hyoid process suggested to be present in *Seymouria* (pars anterior of extracolumella, White (1939); hyostylar cartilage of Heaton (1980)), was or was not present in *Discosauriscus*.

Ventral surface of skull table

The ventral surface of the skull table, especially its posterior portion, presents some structures which partly reflect the outline and the extent of dorsal cartilaginous endocranial portions (figure 25*a*). Lateral to the pineal foramen, anteromedial to the parietal ossification centre, a relatively large and deep pit or foramen (relative to the size of the nutrient foramina) is present (KO 10, KO 27); its surface is roughened. It lies immediately lateral to the presumed outline of the dorsolateral endocranium wall. This pit probably served for the dorsal ligamentous fixation of the cartilaginous epipterygoid portion. In a similar position is the free dorsal 'rod' of the epipterygoid, *Eryops* (Sawin 1941), *Megalocephalus* (Beaumont 1977) and some other early tetrapods (Clack 1987). The condition in K 339 indicates that the outline of the anterior otoccipital wall continued from the lateral wall of the pineal foramen obliquely posterolaterally towards the supratemporal. In the posterolateral corner of the supratemporal, a distinct prolonged and roughened groove (K 6) or irregular roughening (K 256) is present. This is probably the facet for the anterolateral corner of the laterally prolonged otic capsule ('otic tube').

The ventral surface of the tabular is relatively complex. The tabular process projects from its posterolateral corner (see also '*Tabular*'). Along the lateral portion of this process, an arched and high arcuate crest (crista arcuata) is present. The lower part of its lateral wall is slightly roughened, the upper part is smooth (KO 4). At the junction of the thickened base of the crest and the smooth or slightly roughened immediate lateral surface of the tabular, one or two foramina are usually present. Sometimes (K 357), the crest itself contains a foramen. Anteriorly, the crest joins with the otic flange of the supratemporal. Medial to the crest, an anteroposteriorly running groove with a pit lying in its anteriormost section is present. The area around the groove, i.e. most of the tabular process surface, is roughened (K 13, K 313). Such morphology indicates that a slightly laterally directed tabular process, together with the groove, supported muscle (probably of the trapezius group as supposed by Howie (1970) in capitosauroids and Clack (1987) in embolomeres) and its tendon which inserted in the pit.

Between the lateral wall of the tabular process and the medial wall of the tabular occipital flange, a notch remains. This space corresponds to the structure interpreted as the posttemporal fossa or fenestra (Watson 1954; Laurin 1997) or canal for the dorsal capitis vein (Holmes 1984) in *Seymouria*.

Immediately posterior to the tabular–supratemporal and postparietal–parietal sutures, a distinct transverse groove (its anterior wall is pronounced as a ridge) runs along the surface of the postparietal and tabular. The groove, and/or the ridge, is most pronounced in the lateral section of the postparietal. The immediate posterior surrounding of this transverse structure is distinctly roughened in a circular to oval shape; the roughening extends on the occipital flange and slightly on the tabular occipital flange (KO 4). Slightly laterally to the latter roughening, a short crest and groove are present. This ridge and groove, together with the roughening indicate the junctions probably with the exoccipital and opisthotic, as in *Seymouria* (White 1939; Holmes 1984; Laurin 1995, 1996*c*). On the right side of KO 4, the tiny, transversely prolonged and independent bony crest is attached to the transverse ridge (cf. Ivakhnenko 1987). This piece of bone is probably the ossified part of the synotic portion lying between the cartilaginous otic capsules.

On the tabular surface, the transverse groove, and/or ridge, is most distinct laterally where it finishes in the relatively deep pit or short groove lying immediately anterior to the pit for muscle insertion. This pit (paroccipital fossa *sensu* Ivakhnenko (1987)) probably represents the impression of the posterolateral and dorsal corner of the opisthotic (paroccipital process). On the left side of KO 27, inside of this prolonged pit, a piece of bone, probably of the opisthotic, is present (cf. Ivakhnenko 1987).

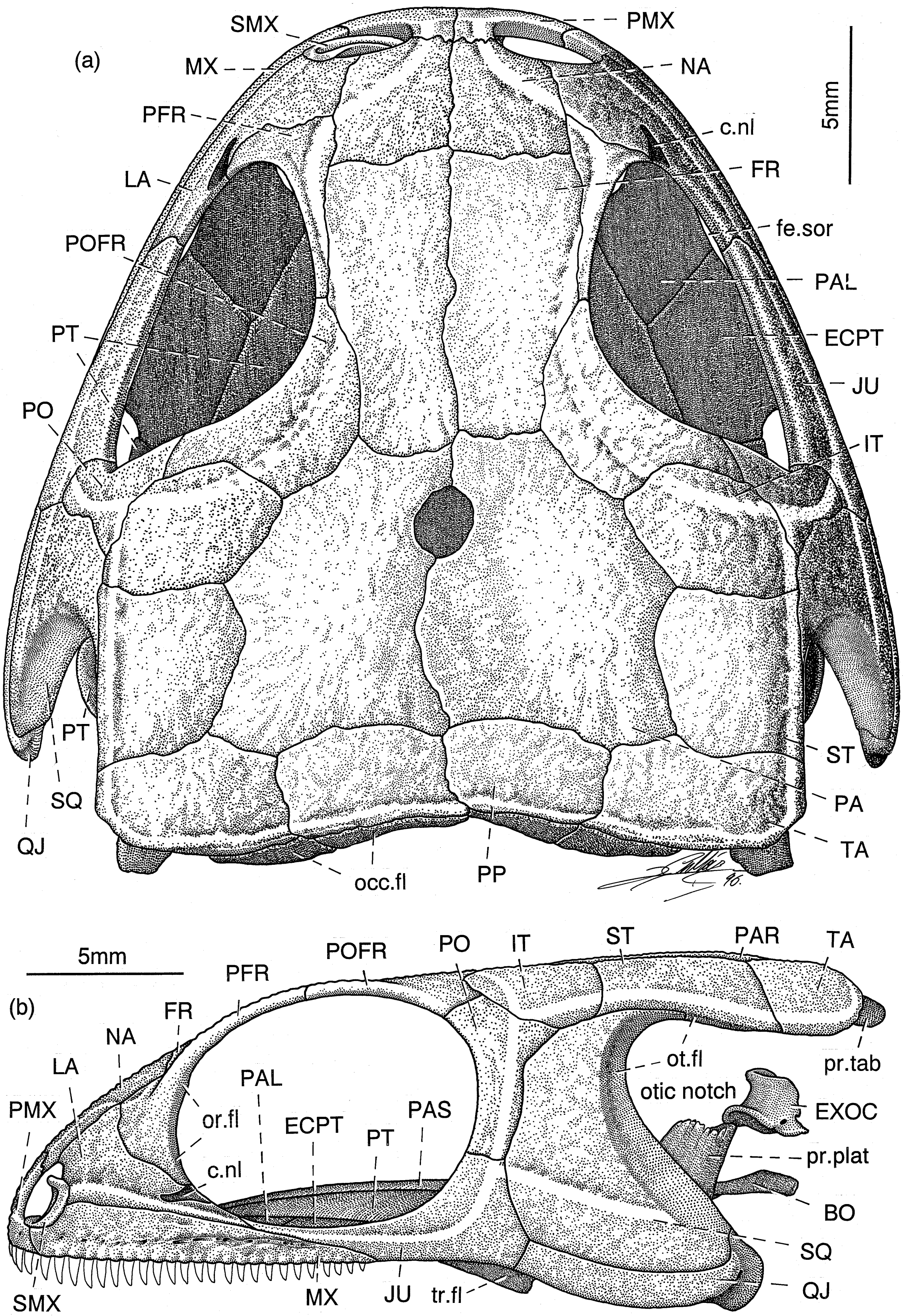

Figure 23. *Discosauriscus austriacus* (Makowsky 1876). Reconstruction of skull (representing late larval and early metamorphic stage) in dorsal (a) and lateral (b) views; based on K 13 (cf. figure 2 and Klembara (1994*a*), fig. 1). In these and following reconstructions are foraminate pits, pit-lines and ornamentation of skull roof bones omitted; as for these, see Klembara (1994*b*, 1995*a*, 1996), respectively.

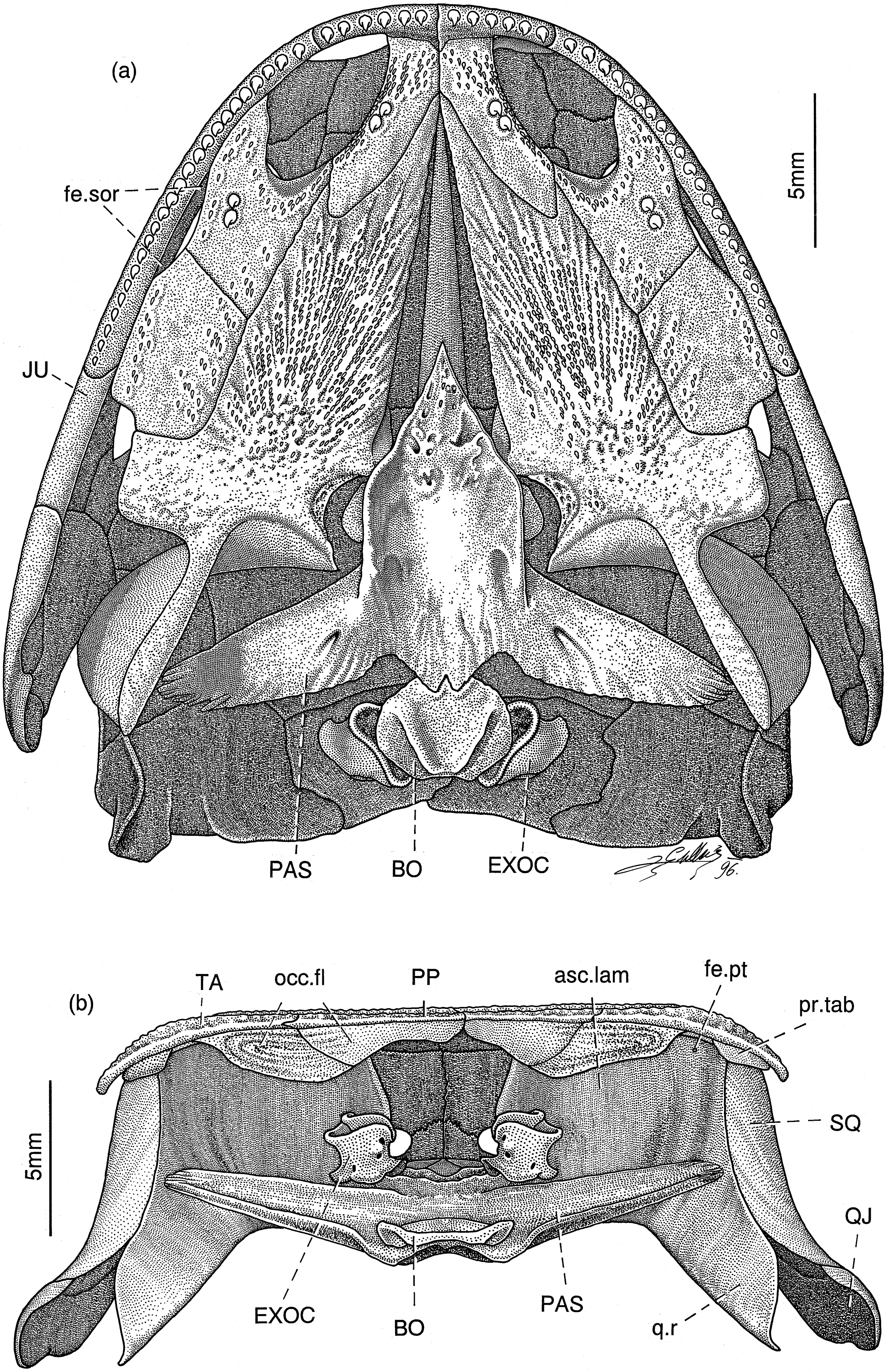

Figure 24. *Discosauriscus austriacus* (Makowsky 1876). Reconstruction of skull (representing late larval and early metamorphic stage) in palatal (a) and occipital (b) views; based on K 13.

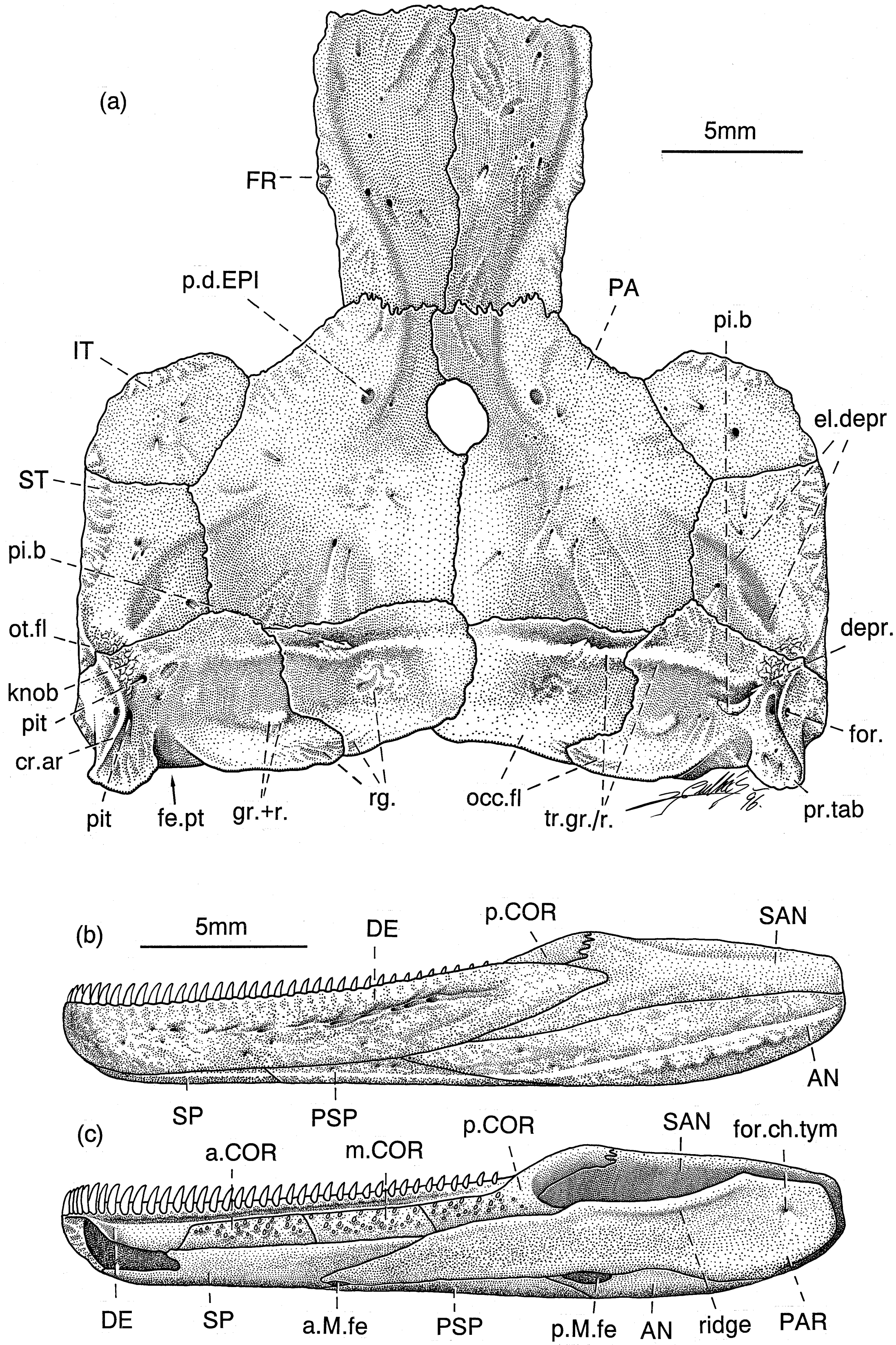

Figure 25. *Discosauriscus austriacus* (Makowsky 1876). (a) Reconstruction of skull table in ventral view (based mostly on metamorphic individuals K 6, KO 4, KO 10, KO 11). Reconstruction of lower jaw (representing late larval and early metamorphic stage) in lateral (b) and lingual (c) views.

On the anterolateral surface of the tabular, im mediately anterior to the pits for muscle insertion and for the paroccipital process, a relatively large grooved and pitted knob, roughly triangular in shape (sometimes slightly extending on the supratemporal, KO 56), is present; immediately medial to it, a pit is present (well visible in KO 4). The function of this structure is unclear, but the character of its surface suggests a

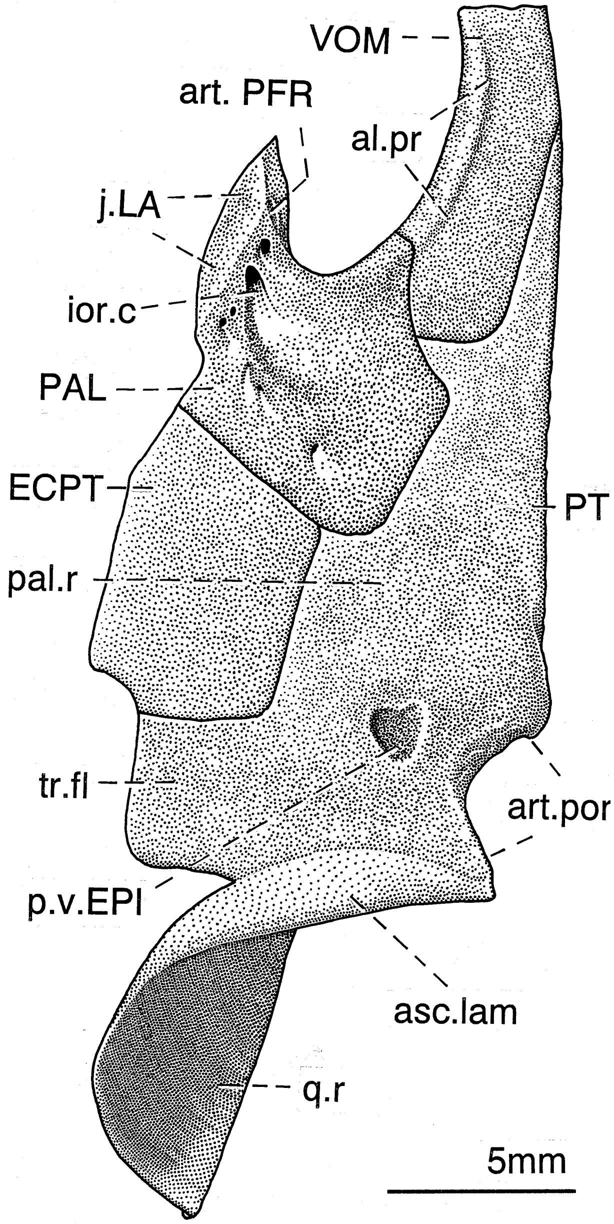

Figure 26. *Discosauriscus austriacus* (Makowsky 1876). Reconstruction of left half of palate (representing late larval and early metamorphic stage) in dorsal view; based mostly on KO 1.

ligamentous attachment. Almost invariably, the stapes is attached to this area in the preserved material.

(*ii*) *Early juvenile stage*

See figures 27 and 28. The proportional changes occurring during metamorphosis are as follows (see also Klembara 1995*a*):

larval and early metamorphic characters (figures 23–26):

- preorbital region is very short,
- nasal and lacrimal are short, frontal long,
- orbits are very large and placed anteriorly,
- relatively narrow interorbital region,
- frontal is longer than parietal,
- anterior margin of pineal foramen lies almost at level of posterior margin of orbit,
- posterior margin of skull table only slightly anteriorly notched,
- occipital flanges of postparietal and tabular only slightly ventrally deflected,
- squamosal and quadratojugal are relatively narrow and short,
- posterior extent of jaw joint lies level with the supratemporal–tabular suture,
- otic notch is broad and shallow,
- marginal teeth with large pulp cavity, without infolding of dentine,
- narrow interpterygoid vacuities present.

postmetamorphic, juvenile characters (figures 27 and 28):

- preorbital region is longer (especially nasal and lacrimal),
- nasal is only slightly shorter than frontal (frontal grows slowly relative to nasal, see Klembara & Janiga (1993)),
- orbits are relatively smaller,
- increased interorbital width,
- postorbital skull length increased (postorbital, postfrontal and jugal are very large); similarly intertemporal (it is more rounded) and anterior portion of squamosal,
- frontal and parietal are of about the same length,
- pineal foramen lies more posteriorly relative to level of posterior margin of orbit,
- posterior margin of skull table more extensively anteriorly notched,
- occipital flanges of postparietal and tabular more ventrally deflected,
- squamosal and quadratojugal are broader and longer,
- posterior extent of jaw joint lies slightly behind the posterior margin of postparietals,
- otic notch is proportionally narrower and deeper,
- distinct dentine infolding of bases of marginal teeth; especially in K 52, individual folds extend to apex of the crown,
- completely closed palate.

As demonstrated elsewhere (Klembara & Janiga 1993, tab. 4; Klembara 1995*a*) and here, the nasal grows progressively during ontogenesis, while the frontal grows very slowly. Hence, the length of the nasal+frontal of both larval and postmetamorphic skulls is about the same (comparing skulls of the same magnification). In the postmetamorphic skull, the orbit is relatively smaller and rounded and its anterior position remains (the midpoint of its length lies in the anterior half of the skull length) despite the progressive growth of the nasal and other bones of the preorbital region.

The bones of early juvenile individuals are massive, without large internal vacuities in cheek or palatal bones. The pineal foramen is completely closed anteriorly. The ornamentation of the skull roof bones was described elsewhere (Klembara 1995*a*). Here it may also be added that the prefrontal of the largest specimen, OB 1 (*Discosauriscus sp.*), is well preserved and its dorsal surface bears distinct polygonal ornaments, as observed in large specimens of *Seymouria sanjuanensis* (Vaughn 1966; Berman *et al.* 1987; Laurin 1995).

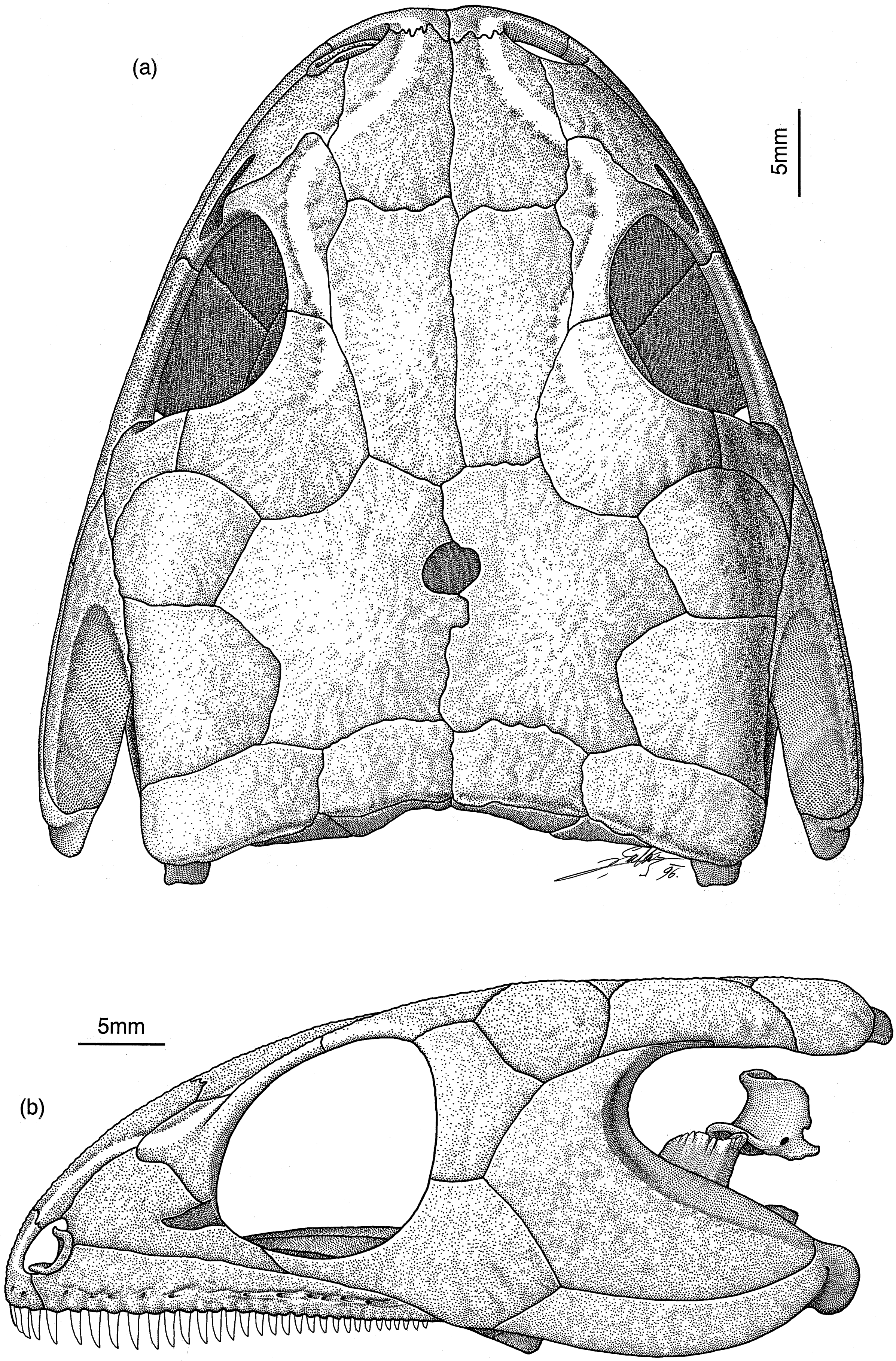

Figure 27. *Discosauriscus austriacus* (Makowsky 1876). Reconstruction of early juvenile skull in dorsal (a) and lateral (b) views; based on K 52 and K 323. For names of bones, see figure 23.

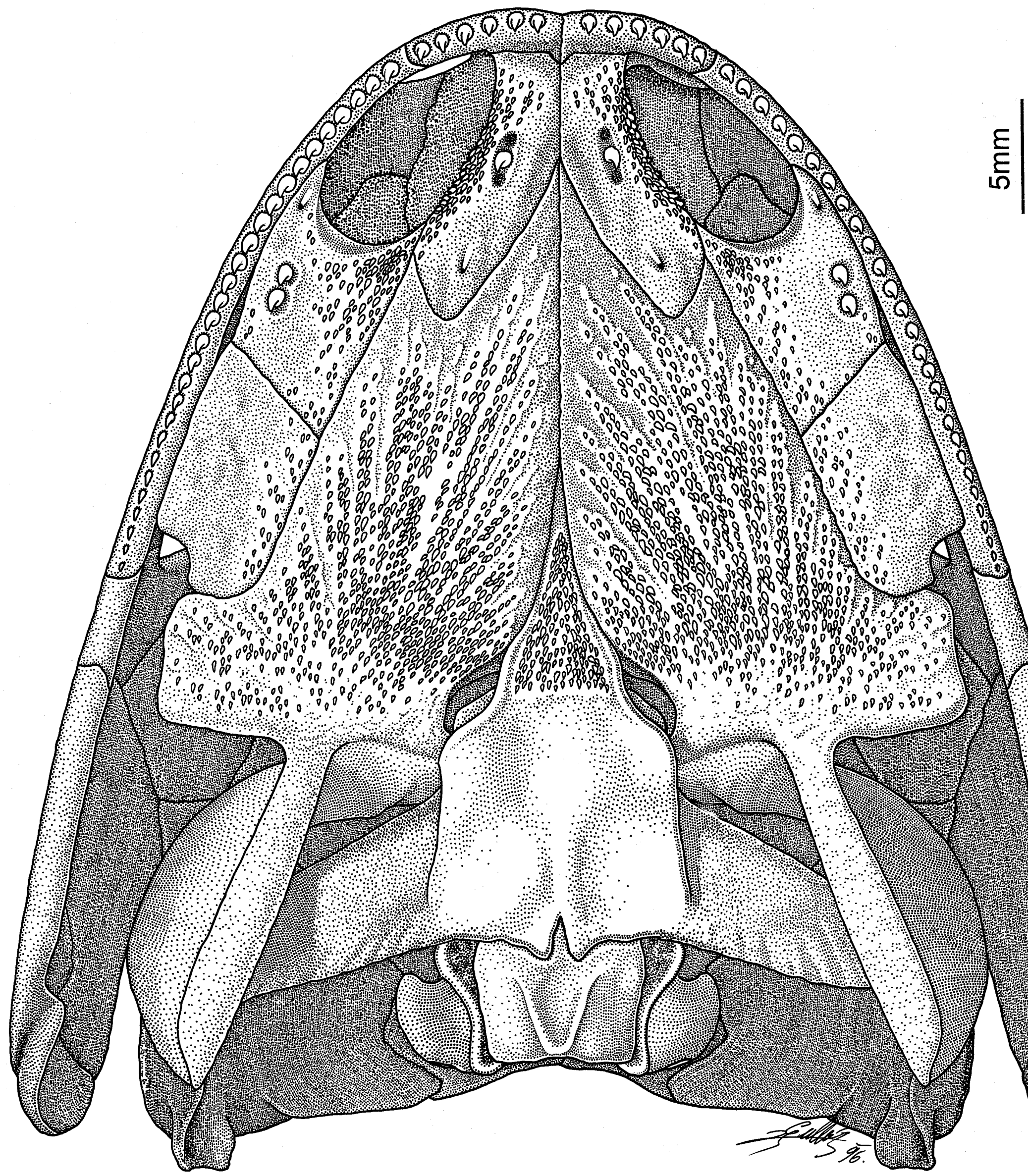

Figure 28. *Discosauriscus austriacus* (Makowsky 1876). Reconstruction of early juvenile skull in palatal view; based on K 52 and K 323. For names of bones, see figure 24*a*.

The ventral surface of the nasals of K 52 bear relatively massive ridges, passing posterolaterally near the lateral margins of the bones (present also in K 16 —*D. pulcherrimus*). Their continuation onto the frontals is, unfortunately, not observable.

Regarding the premaxilla, in K 323 the left nasal ramus is posteriorly slightly broadened and corresponds to the broadened anterior part of the left nasal. The morphology of contact margins of both bones clearly shows that they met in a firm interdigitating suture. The premaxillae and the nasals of this specimen met in the median plane along their whole medial margins. Hence, there is no fenestra in this region of the skull roof. A similar situation is seen in K 52 (figure 29). Conditions here indicate that (1) the posterior end of the nasal ramus of the left premaxilla slightly overlapped the partly smooth dorsal surface of the anteriormost portion of the nasal, and that (2) there was no space for the fenestra here. It may be concluded that no fenestra (as a constant, distinct morphological structure) was situated between the posterior portions of the premaxillae or between them and the anterior portions of nasals in *Discosauriscus austriacus* (cf. Klembara 1994*a*).

In contrast to K 52 and K 323, the postorbital of KO 79 and KO 80 is neither so robust nor anteroposteriorly so long. The two latter specimens are more delicately constructed. These features reflect proportional differences (skull shape trends), individual shape variability of the skull roof bones, and probably also sexual dimorphism (Klembara & Janiga 1993; Klembara 1994*a*, 1995*a*); cf., for example, Boy (1990, pp. 291–293). Two palpebral bones in the orbits of one juvenile individual (OB 1, *Discosauriscus* sp.) have been described by Klembara (1995*a*).

In the palate, the ventral surfaces of the pterygoid palatal rami of KO 79 and KO 80 are badly preserved, but very low ridges are recognizable; distinct ridges are present on the parasphenoid of KO 80. In K 323 and K 52, the ventral surfaces of the palatal rami and

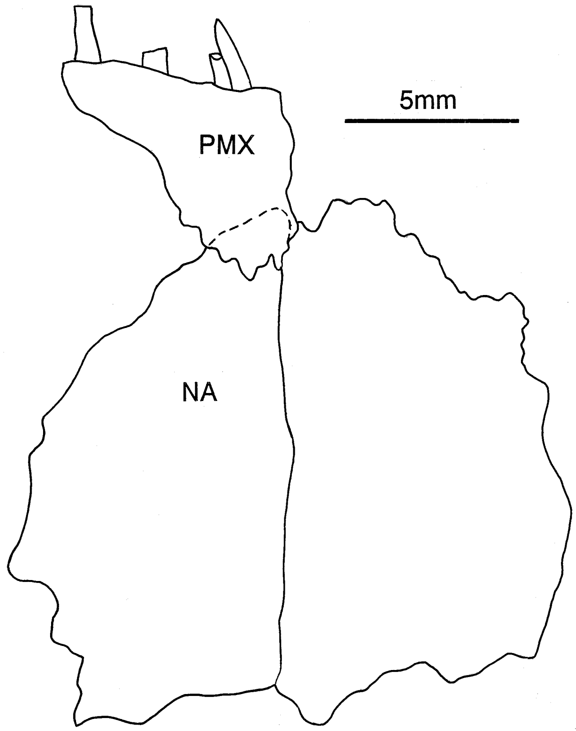

Figure 29. *Discosauriscus austriacus* (Makowsky 1876). K 323; premaxilla and nasals in dorsal view to show their junction.

transverse flanges are covered by rows of small teeth, but the ridges in K 323 are not so distinct. However, the arrangement of the tooth-rows remains different in both species, as given in the diagnoses. In K 52, rows of teeth are present likewise on the ectopterygoid and the palatine. In K 323, a triangular field is present in the central region of the parasphenoid ventral surface (figure 28). The palate is already completely closed. The ventral end of the epipterygoid is more substantially widened (KO 80).

In K 323, the dentine is infolded in about the basal half of the marginal tooth length. In K 52, the well-developed individual folds of dentine extend to the apex of the crown (see also Klembara 1995*a*, fig. 9). The perfectly preserved tusk on the right vomer of K 52 has the dentine infolded in its basal half.

(*iii*) *Reconstructed skull*

Based on the models (see '*Methods*'), the larval skull was shorter (in the median plane) than it was wide (between the posterior tips of quadratojugals), while the length and width of an early juvenile skull were about the same (figures 23–28). However, skull shape trends occur in populations of *Discosauriscus austriacus* (Klembara & Janiga 1993). In dorsal view, the skull has a semielliptical shape. The midpoint of the orbit lies in the posterior portion of the anterior half of the skull length. The large (larvae) and smaller (juveniles) rounded orbits face dorsolaterally; their medial margins are high and sharp. Judging from the morphology of the contacting parts of the maxilla and septomaxilla, the portion of the skull roof leading into the exonarial fenestra is slightly depressed. The size of the pineal (and/or parapineal) foramen is variable (Klembara 1994*a*). The cheeks are relatively steep and form an angle of about 60° with the skull table. The posterior portion of the cheek is emarginated by a large otic notch housing the tympanum. The quadratojugal portion of the cheek is expanded ventrally below the horizontal ventral margin of the maxilla. Viewed dorsally, the parietals bear a flat and rounded depression behind the pineal foramen. The lateral margin of the tabular and the posterolateral corner of the supratemporal are slightly flexed ventrally (similar to *S. sanjuanensis*). The sutures of the skull roof bones are relatively simple. The skull table–check junction is firm and no 'kinetic line' is present. The intertemporal—postorbital and intertemporal—squamosal sutures are simple. However, the supratemporal–squamosal suture may be interdigitating between the ornamented surfaces of both bones (Klembara 1994*a*). The palate is closed. The basipterygoid articulation was immobile. The lower jaw is relatively low in the region of the adductor crest.

5. *DISCOSAURISCUS PULCHERRIMUS* (FRITSCH 1879)

1879 *Melanerpeton pulcherrimum* (Fritsch p. 186; detailed description and figures in)
1883 *Melanerpeton pulcherrimum* (Fritsch p. 99; tab. 14, fig. 1)
1883 *Melanerpeton spiniceps* (Credner p. 289)
1883 *Discosaurus permianus* (Credner p. 294; [recte = *Discosauriscus permianus* (Kuhn 1933 p. 52)])
1985 *?Discosauriscus* cf. *pulcherrimus* (Werneburg p. 128)
1985 *Letoverpeton austriacum* (Werneburg p. 130)
1985 cf. *Letoverpeton austriacum* (Werneburg p. 130)

(However, the revision of the material studied by Werneburg (1985) is needed to confirm the absence of *D. austriacus* here; see also 'note' in the synonymy list of *D. austriacus*.)

1993 *Discosauriscus austriacus* (Klembara & Janiga p. 268 (in this paper, the specimens K 9 and K 16 mentioned as *D. austriacus* belong to *D. pulcherrimus*))
1995*a* *Discosauriscus pulcherrimus* (Klembara p. 272, fig. 5)

Holotype

Specimen M 437—National Museum, Prague (the former number ČGH 3478, see Špinar (1952)); almost complete skeleton (with some parts in state of impressions) figured and described in detail by Fritsch (1883; 99–104, pl. 14, fig. 1); figure 30 here.

Type locality

Ruprechtice (Ruppersdorf) (north Bohemia, Czech Republic), Ruprechtice horizon, zone 5—Upper Autunian (*sensu* Werneburg 1989*a*).

Locality

The material from the Boskovice Furrow comes from the same localities as *D. austriacus*: Kochov-Horka (K) and Kochov-L (KO) (see above).

Horizon

Bačov horizon, zone 6—Lower Saxon (*sensu* Werneburg 1989*a*), Lower Permian.

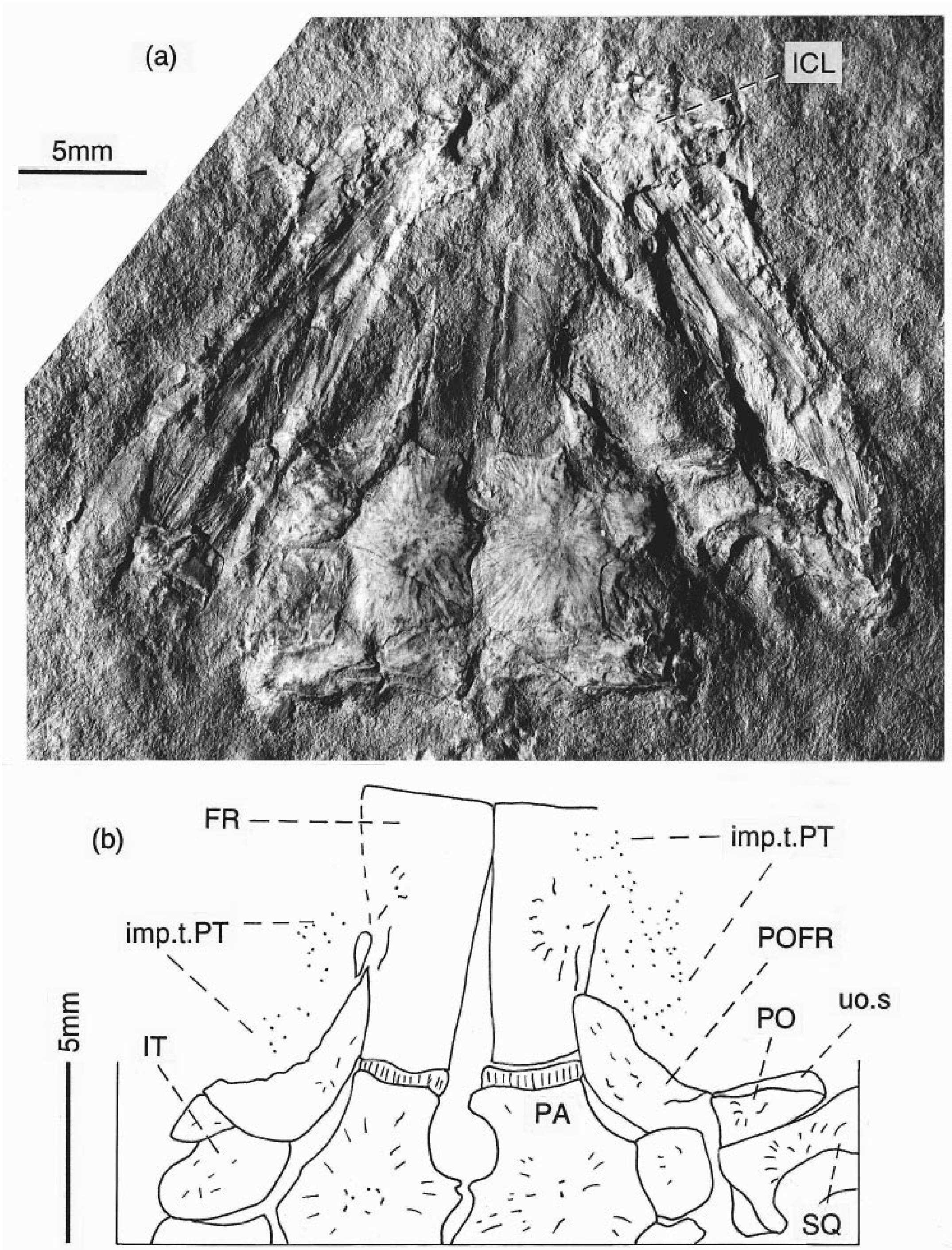

Figure 30. *Discosauriscus pulcherrimus* (Fritsch 1879). M 437 (holotype). (a) Skull in dorsal view. (b) Slightly enlarged central portion of skull in dorsal view.

Referred specimens

The specimens are deposited at the Zoological Institute, Faculty of Natural Sciences, Comenius University under the following numbers: K 9, K 16, KO 78, KO 180, KO 181.II.

Diagnosis

As for genus, with several characters absent in the species *D. austriacus*: (1) The anterior portion of the postfrontal is relatively long and narrow, the prefrontal is relatively short; both bones meet in the first (anterior) third of the frontal length or slightly posterior to this level. (2) The postorbital is relatively gracile bone of a triangular chevron shape. Its lateroventral ramus is narrow and pointed, like the dorsomedial portion of the jugal; both ends of these bones meet in a short horizontal suture, in which the tip of the postorbital lies slightly anterior to the tip of the jugal. (3) The portion of the skull roof between the posterior margin of the orbit and the anterior margin of the otic notch is relatively short. (4) The ventral surface of the palatal ramus and the transverse flange of the pterygoid are covered by densely arranged rows of denticles diverging from the midline of the posterior

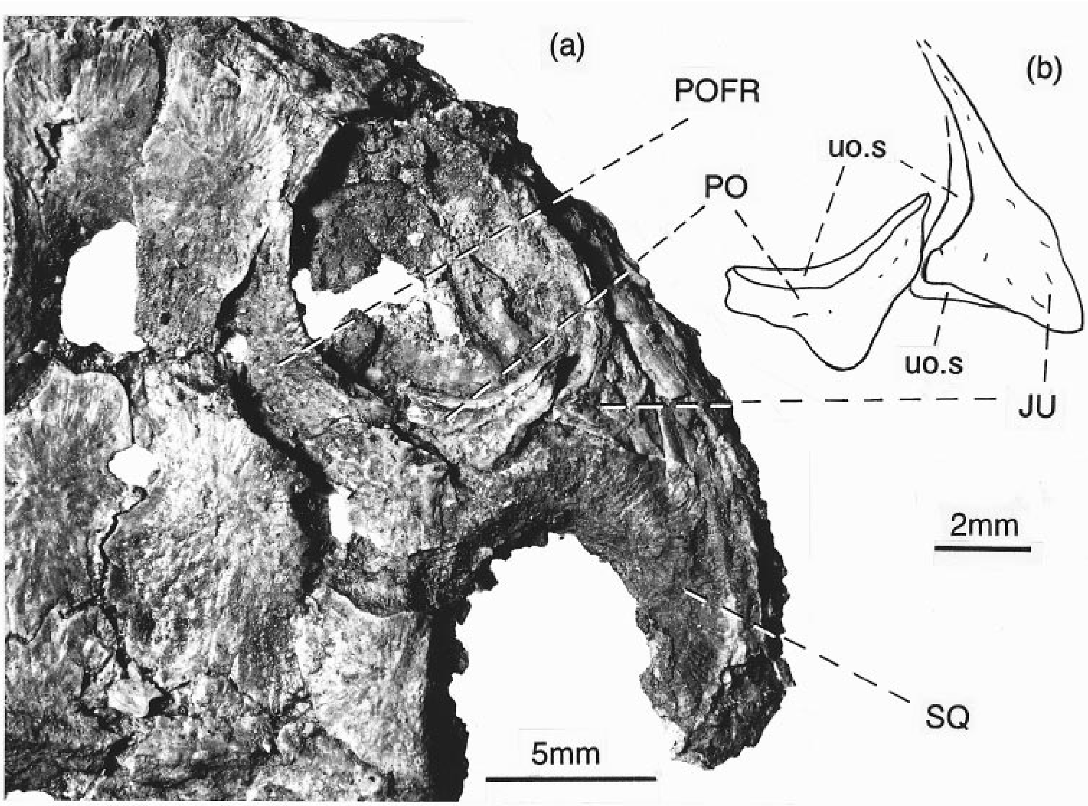

Figure 31. *Discosauriscus pulcherrimus* (Fritsch 1879). KO 78. (a) Right side of skull in dorsal view. (b) Slightly enlarged right postorbital and jugal in dorsal view.

half of the palatal ramus (continuing on the ectopterygoid and the palatine); ridges are absent. Small denticles (individual or in rows) are present also on the smooth ventral surface of the central portion of the parasphenoid.

Description

(*a*) *Holotype skull*

The holotype skull of *D. pulcherrimus* shows three features in which it differs from *D. austriacus* (figure 30):

1. The lateroventral ramus of the right postorbital is relatively well preserved. As seen in the skulls from the Boskovice Furrow, the postorbital portion has relatively broad unornamented orbital margins. This portion of the holotype postorbital is dorsoventrally compressed, giving the impression that this part of the postorbital is broad. However, on the holotype skull, the narrow ornamented and relatively large unornamented surface of the postorbital are clearly distinguishable.

2. The prefrontal–postfrontal suture lies in about the first (anterior) third of the frontal length (the anterior portion of the postfrontal is long).

3. Although the pterygoids are absent in the holotype skull, the impressions of small denticles on the ventral surface of the pterygoid palatal ramus are observed in the matrix. No impressions of ridges are present.

The presence of these three features in the holotype skull as well in the skulls from the Boskovice Furrow justifies *D. pulcherrimus* as a valid species.

The length of the holotype skull (SL) is about 21 mm. On the parietal (and the impressions of the frontal bones), distinct radially diverging grooves and low ridges are present. These characteristics indicate that the holotype represents a late larval individual.

(*b*) *Skulls from the Boskovice Furrow*

Except for the diagnostic features, the skull of *D. pulcherrimus* is structurally identical to that of *D. austriacus*. Although only five specimens of *D. pulcherrimus* from the Boskovice Furrow are available so far, the proportional differences of K 9 (broad skull including a dorsoventrally relatively broad otic notch) and K 16 or KO 78 (narrow skull) indicate the same shape trends of the skull as in *D. austriacus* (Klembara & Janiga 1993), cf. figures 31 and 32. Specimen K 16 is the largest and probably represents a late phase of metamorphosis (Klembara 1995*a*); four additional specimens represent late larval (KO 180, KO 181.II) and early metamorphic (K 9, KO 78) individuals.

As specified in the diagnosis, the postorbital is lateroventrally pointed and has a short, oblique suture with the jugal. The similarly-shaped dorsomedial process of the jugal lies slightly posterior to the pointed process of the postorbital (figures 31 and 32). In comparison with *D. austriacus*, the postorbital of *D. pulcherrimus* is a more gracile, chevron-shaped element, in common with *Seymouria sanjuanensis* (Berman *et al.* 1987; Laurin 1995). This means that the region of the skull roof between the posterior margin of the orbit and the otic notch is anteroposteriorly relatively short and the orbit is relatively large in *D. pulcherrimus* (figure 33). In contrast to *D. austriacus*, the postorbital and jugal

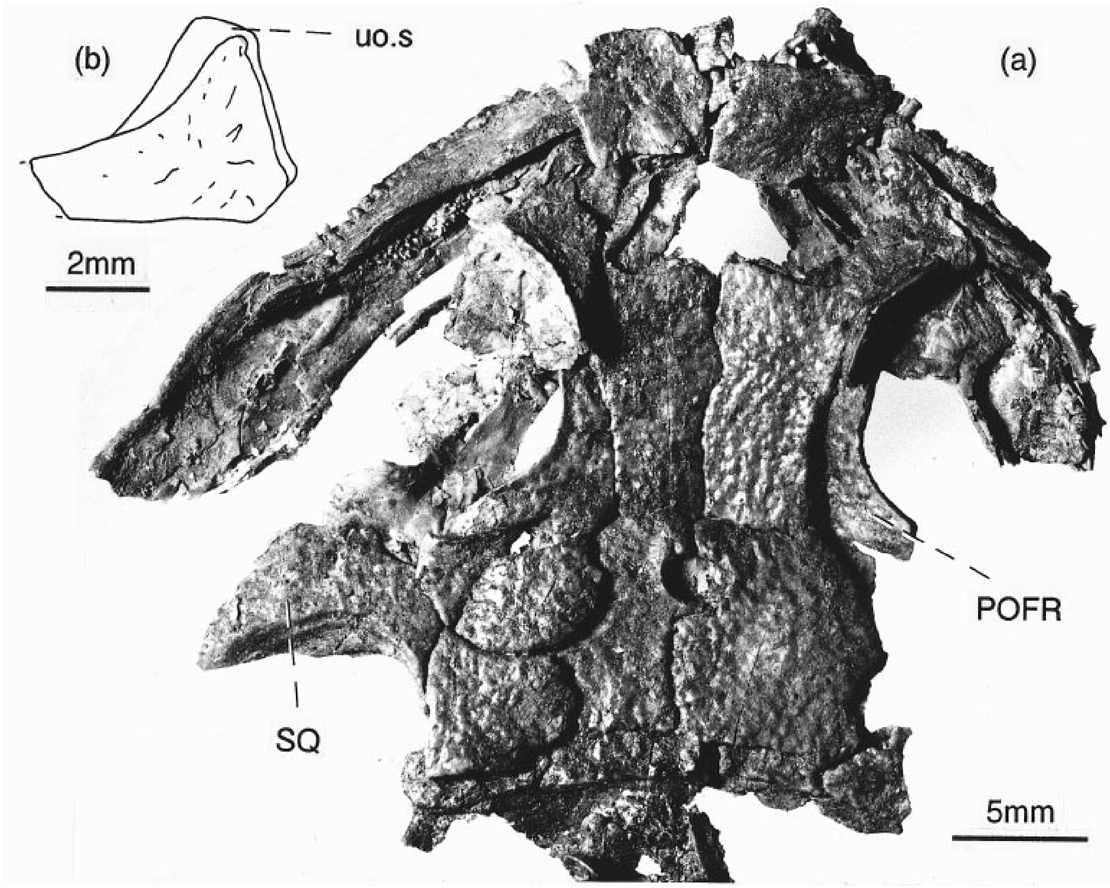

Figure 32. *Discosauriscus pulcherrimus* (Fritsch 1879). K 9. (a) Skull in dorsal view. (b) Left jugal in lateral view.

have relatively broad unornamented orbital margins (figures 31 and 32). In all specimens, the anterior portion of the postfrontal is relatively narrow and long, the posterior portion of the prefrontal is relatively short; both bones meet at about one- (anterior) third of the frontal length. This latter character is more distinct in specimens representing late larval and early metamorphic individuals.

The diagnostic feature of the palate of *D. pulcherrimus* is that the ventral surface of the palatal ramus and the transverse flange of the pterygoid are completely covered by small, sharp, pointed teeth (as is also indicated on the holotype skull, figure 30). These teeth lie on a completely smooth pterygoid surface; no traces of the ridges formed in *D. austriacus* are present (figure 34). In the small individual KO 180, very densely arranged rows of these teeth diverge from the midline of the posterior half of the pterygoid palatal ramus medially, anteriorly, laterally and on the pterygoid flange. In larger individuals (K 9 and K 16), the arrangement of denticles in rows is less distinct. In contrast to *D. austriacus*, the shagreen of teeth on the transverse flange of the pterygoid in *D. pulcherrimus* is present even in the smallest individuals (KO 180, KO 181.II).

Small denticles are present also on the parasphenoid (in the region between, and anteromedially to, the basipterygoid processes). In K 9, a roughly triangular denticle field (similarly in K 323 of *D. austriacus*) is present in this parasphenoid region; in KO 180, only several rows of denticles (as in K 16) are present here. Already the conditions of these several specimens indicate the variation in the arrangement of the denticles in this region of the parasphenoid ventral surface, as in *D. austriacus*. However, in contrast to the latter genus, no ridges are developed on the ventral parasphenoid surface. Small denticles are present also on the ventral surface of the left palatine of K 9. In KO 180, most of the surfaces of the palatine and the ectopterygoid are covered by a shagreen of teeth, and it may be concluded that most of the ventral surface of the palatal bones is more or less covered by such small shagreen teeth (figure 34).

The vomer bears two tusks (both sides of K 9 and the right side of K 16). Two tusks are preserved on the right palatine of K 16. In K 16, the right premaxilla has six and the left maxilla (the posteriormost part not preserved) about 26 teeth.

As for the proportional differences between the palatal bones or their components (e.g. the antero-posterior extent of the transverse flange and other portions of the pterygoid) between *D. austriacus* and *D. pulcherrimus*, see figures 24*a* and 34.

The maxilla of K 16 is relatively high and robust as in the largest specimens of *D. austriacus* (K 52, K 323). The otic notch seems to be relatively shorter dorso-ventrally in some specimens (KO 78, KO 180; though not in K 9) in *D. pulcherrimus*. However, additional material of *D. pulcherrimus* is needed to obtain more knowledge about the individual variability, proportional differences, or further real structural differences relative to *D. austriacus*.

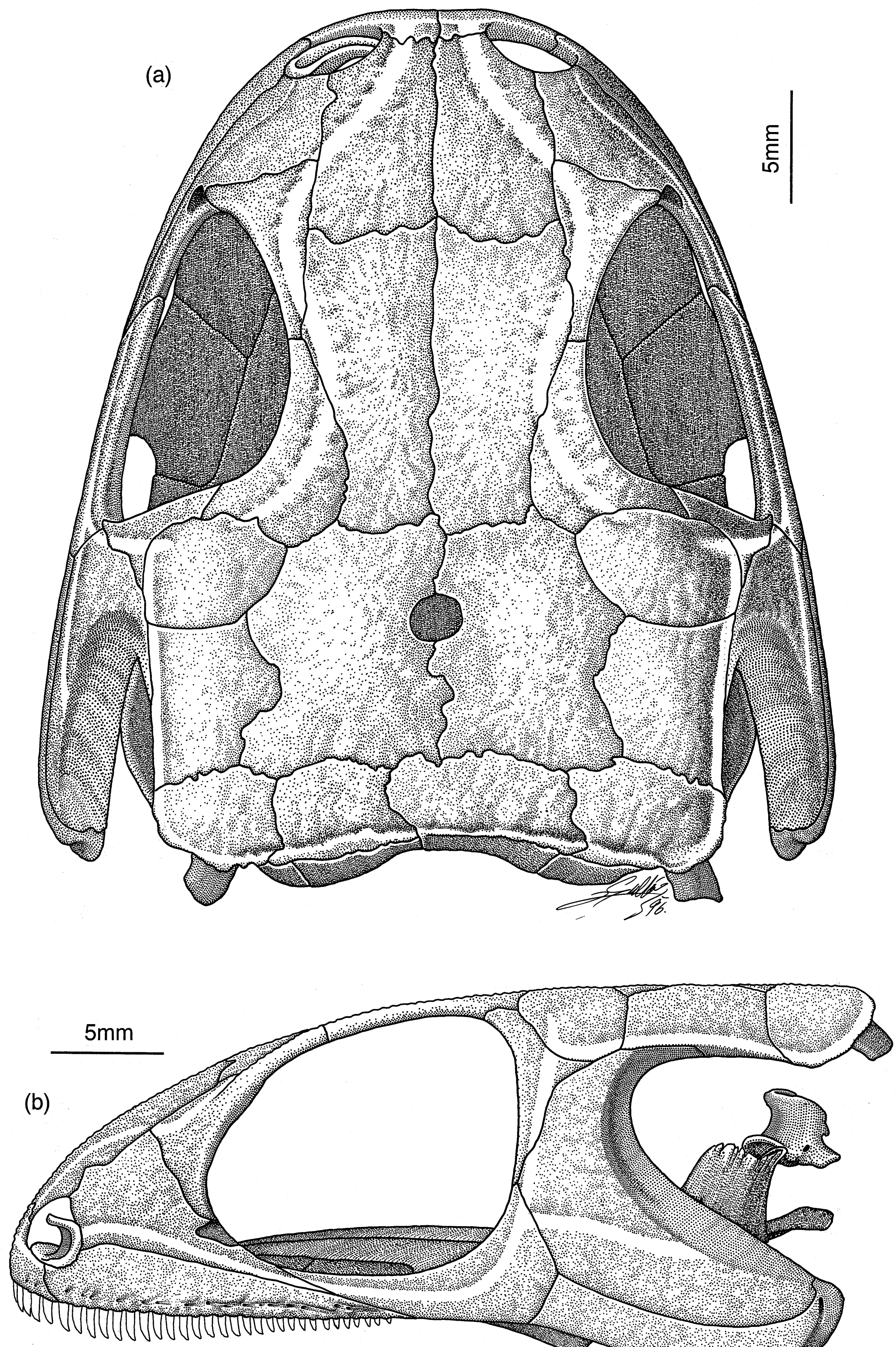

Figure 33. *Discosauriscus pulcherrimus* (Fritsch 1879). Reconstruction of late metamorphic skull in dorsal (a) and lateral (b) views. Based on K 16. For names of bones, see figure 23.

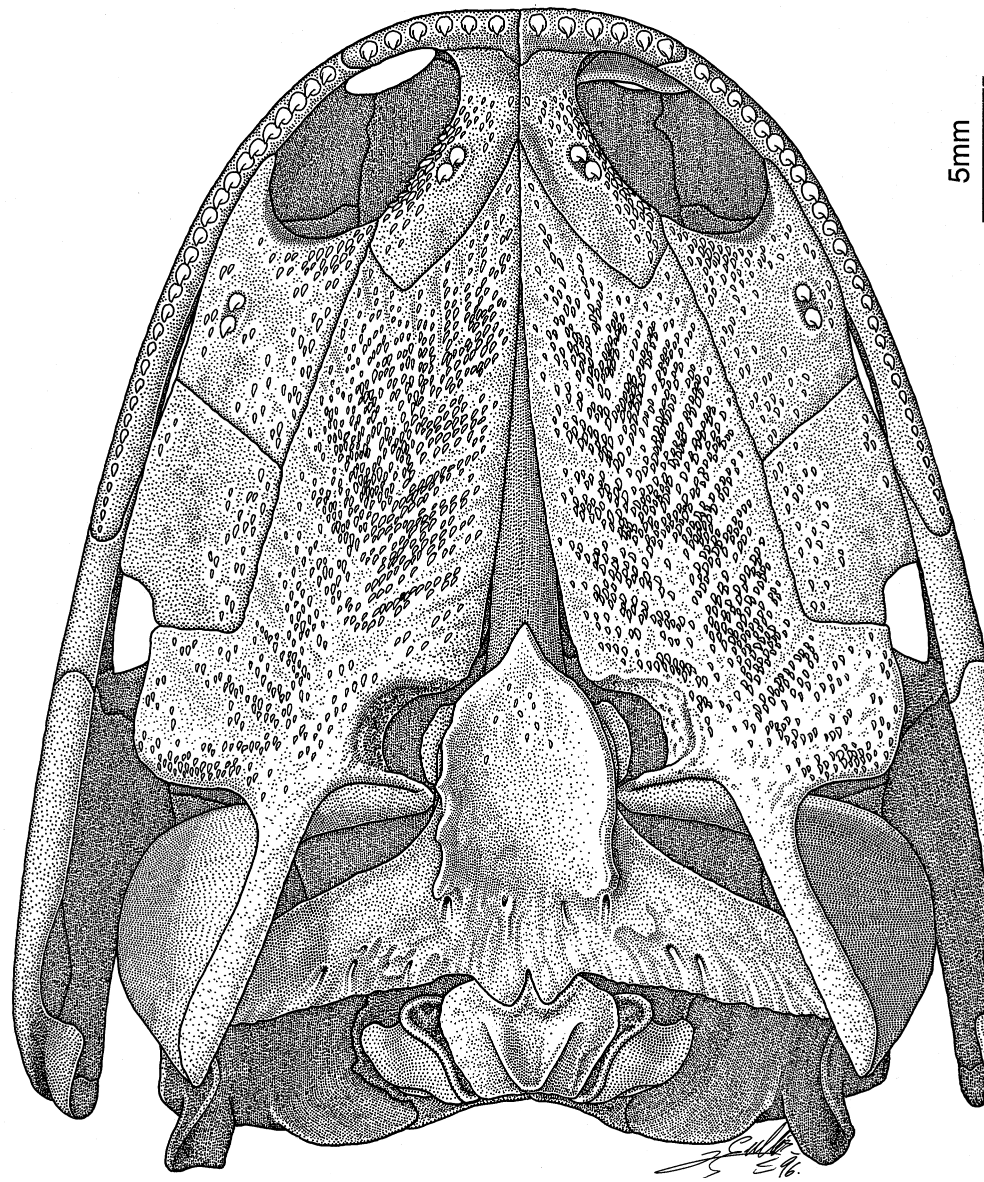

Figure 34. *Discosauriscus pulcherrimus* (Fritsch 1879). Reconstruction of late metamorphic skull in palatal view. For names of bones, see figure 24*a*.

6. COMPARISON AND DISCUSSION

(*a*) *Stratigraphical occurrence*

Discosauriscus austriacus is a common species in the Boskovice Furrow; whereas only five specimens of *D. pulcherrimus* have been found so far. This is important from the stratigraphical point of view and indicates that the latter species occurs in both the Bačov horizon (corresponding to 'Upper Rotliegend', zone 6) and the Uppermost 'Lower Rotliegend', zone 5 (*sensu* Werneburg 1989*a*).

(*b*) *Relationships of Discosauriscus*

The taxonomic content of the taxon Seymouriamorpha (Watson 1917) has been differently interpreted by successive authors (Romer 1947; Watson 1954; Heaton 1980; Holmes 1984; Panchen 1975, 1985; Panchen & Smithson 1988; Smithson 1985, 1986; Ivakhnenko 1987; Werneburg 1989*a*; Carroll 1995; Laurin & Reisz 1995). This is mostly because of insufficient knowledge of the taxa (genera or families) which might compose the Seymouriamorpha. The same is true for the composition of individual families within the Seymouriamorpha (cf. Heaton 1980; Smithson 1985; Ivakhnenko 1987). Fracasso (1987) concluded that *Seymouria* is a reptile. Heaton (1980) excluded the family Discosauriscidae (Kuhn 1933) from Seymouriamorpha and suggested a relationship with gephyrostegids. Švec (1986) suggested that discosauriscids were embolomeres. Here it must be emphasized that, as shown by Klembara (1995*a*), the adults of *Discosauriscus* (together with *Utegenia* and *Ariekanerpeton*) are unknown so far, and it is necessary to understand the previous comparisons and their results on the basis of this lack of information. The first step to resolve this complex problem is to make (where possible) detailed comparisons of the cranial structures (i) within Discosauriscidae and then (ii) of *Discosauriscus* with *Seymouria*.

Table 1

	Discosauriscus	*Ariekanerpeton*	*Utegenia*
1.	short preorbital region (orbits are placed anteriorly relative to middle of skull length)	short preorbital region (orbits are placed anteriorly relative to middle of skull length)	relatively long preorbital region (orbits are placed in middle of skull length)
2.	5–7 premaxillary teeth	?6–7 premaxillary teeth	?4 premaxillary teeth
3.	pineal foramen lies constantly in anterior half of parietal length	pineal foramen lies about in mid-length of parietal in early juveniles (however, conditions in larval and metamorphic individuals are as those in *Discosauriscus* and *Utegenia*)	pineal foramen lies in anterior half of parietal length in largest specimens (they are, however, probably still in the stage of metamorphosis)
4.	ossification centres of parietals lie constantly slightly posteriorly to level of pineal foramen	ossification centres of parietals lie at level of pineal foramen in early juveniles (however, conditions in larval and metamorphic individuals are as those in *Discosauriscus* and *Utegenia*)	ossification centres of parietals lie slightly posteriorly to level of pineal foramen
5.	prefrontal joins palatine anterior to level of palatine tusks	prefrontal joins palatine anterior to level of palatine tusks	?
6.	broad lateroventral portion of postorbital and dorsomedial portion of jugal meeting in relatively long anteroposteriorly running suture (in *D. austriacus*; conditions in *D. pulcherrimus* are similar to those in *Ariekanerpeton*)	relatively narrow lateroventral portion of postorbital and dorsomedial portion of jugal meeting in oblique suture	narrow, pointed and short lateroventral portion of postorbital and dorsomedial portion of jugal meeting in oblique suture
7.	jugal overlaps lacrimal dorsally	jugal overlaps lacrimal dorsally	jugal has ?vertical suture with lacrimal
8.	short posterior process of jugal having a short and oblique suture with quadratojugal	long and pointed posterior process of jugal having horizontal suture with narrow anterior portion of quadratojugal	long and dorsoventrally broad posterior process of jugal
9.	large intertemporal	large intertemporal	small intertemporal
10.	rounded orbit	rounded orbit	oval orbit
11.	short prefrontal–postfrontal suture in metamorphic individuals	short prefrontal–postfrontal suture in metamorphic individuals	long prefrontal–postfrontal suture in largest (probably in late larval and early metamorphic) individuals
12.	prefrontal–postfrontal contact lies in middle (*D. austriacus*) or anterior half (*D. pulcherrimus*) of frontal length	prefrontal–postfrontal contact lies in level of mid-length of frontal	prefrontal–postfrontal contact lies posteriorly to frontal mid-length (prefrontal with long posterior ramus)
13.	broad (mediolaterally) and relatively short postorbital	broad (mediolaterally) and relatively short postorbital	long and narrow postorbital
14.	postorbital–supratemporal contact absent (with some exceptions, Klembara (1994*a*))	postorbital–supratemporal contact absent	postorbital–supratemporal contact present
15.	relatively broad otic flange and narrow ornamented surface of squamosal	relatively broad otic flange and narrow ornamented surface of squamosal	narrow otic flange and broad ornamented surface of squamosal
16.	squamosal–supratemporal suture extends to mid-length of supratemporal	squamosal–supratemporal suture extends to mid-length of supratemporal	squamosal–supratemporal suture long extending posteriorly to mid-length of supratemporal
17.	broad and relatively shallow otic notch	broad and relatively shallow otic notch	broad and very shallow otic notch
18.	posterolateral corner of supratemporal slightly curved ventrally	posterolateral corner of supratemporal slightly curved ventrally	posterolateral corner of supratemporal not curved ventrally
19.	lateral portion of tabular slightly curved ventrally	lateral portion of tabular slightly curved ventrally	lateral portion of tabular not curved ventrally
20.	anteroposteriorly long tabulars and postparietals	anteroposteriorly long tabulars and postparietals	anteroposteriorly short tabulars and postparietals
21.	stem and posterior plate of parasphenoid relatively narrow (with long posterolateral processes)	stem and posterior plate of parasphenoid relatively narrow (with long posterolateral processes)	stem and posterior plate of parasphenoid broad (with indistinct posterolateral processes)
22.	tusks of palatine not placed on ridges	tusks of palatine placed on ridges	tusks of ?vomer and palatine placed on ridges

Table 1—*cont.*

	Discosauriscus	*Ariekanerpeton*	*Utegenia*
23.	presence (*D. austriacus*) of radiating ridges bearing small teeth on ventral surface of palatal ramus and transverse flange of pterygoid and central portion of parasphenoid; in *D. pulcherrimus*, ridges are absent and rows of small teeth diverge from anteroposteriorly lying plane placed about in mid-width of pterygoid palatal ramus (small teeth are present also on central portion of parasphenoid)	absence of ridges on ventral surface of pterygoid palatal ramus and central portion of parasphenoid (as in *D. pulcherrimus*), however, rows of small teeth diverge exactly as in *D. austriacus*	absence of ridges on ventral surface of pterygoid palatal ramus and central portion of parasphenoid (as in *D. pulcherrimus*), however, rows of small teeth diverge exactly as in *D. austriacus*
24.	suborbital fenestra present	suborbital fenestra present	? absence of suborbital fenestra (not described and not figured in Kuznetsov & Ivakhnenko (1981), however, not described and figured in Ivakhnenko (1987))
25.	basioccipital and exoccipital ossified	basioccipital and exoccipital ossified (in largest, probably earliest juveniles—*sensu* Klembara 1995*a*)	basioccipital and exoccipital not ossified in the largest individuals
26.	basioccipital with pair of posteromedially diverging crests on its ventral surface	basioccipital with pair of posteromedially diverging crests on its ventral surface	—
27.	phalangeal formula of manus and pes is 2-3-4-5-3 (Špinar 1952)	phalangeal formula of manus 2-3-4-4-3 and pes 2-3-4-5-4	phalangeal formula of manus 2-3-4-4-3 and pes 2-3-4-5-3
28.	rounded scales with concentric rings (Špinar 1952; Klembara & Meszároš 1992)	rounded scales	spindle-shaped ventral scales (however, rounded lateral and dorsal scales)
29.	24 (exceptionally 23) presacral vertebrae (Špinar 1952; Klembara & Janiga 1993)	24 presacral vertebrae	28 presacral vertebrae

(i) *Comparisons of Discosauriscus, Ariekanerpeton and Utegenia*

The family Discosauriscidae was erected by Romer (1947) on the basis of two characters in *Discosauriscus*: large intercentra and short skull (relative to Seymouriidae (Williston 1911)). Only the second character is valid. This family has been based on specimens representing early ontogenetic stages (Klembara 1995*a*) and comprises *Discosauriscus*, *Ariekanerpeton* and *Utegenia* (*sensu* Ivakhnenko (1987) and Werneburg (1989*a*)) and *Urumquia* (*sensu* Zhang *et al*. 1984; synonymized with *Utegenia* by Ivakhnenko (1987)). Recently Laurin (1995) suggested that discosauriscids represent a paraphyletic taxon, with *Utegenia* and *Kotlassia* as basal seymouriamorphs.

In addition to published data regarding the skeletal anatomy of *Utegenia* (Kuznetsov & Ivakhnenko 1981; Ivakhnenko 1987) and *Ariekanerpeton* (Ivakhnenko 1981, 1987), the following comparison of *Discosauriscus*, *Ariekanerpeton* and *Utegenia* (table 1) is also based on casts of the holotypes of *Ariekanerpeton sigalovi* (no. 2079/1: dorsal and ventral surfaces) and *Utegenia shpinari* (no. 2078/1: dorsal surface only). Specimens of similar size are compared.

The following characters of *Ariekanerpeton* and *Utegenia* apparently differentiate these genera from *Discosauriscus*; but I consider them to be either ontogenetic (presence of interpremaxillary fenestra) or caused by imperfect preservation (presence of fenestra between toothed regions of premaxillaries; triangular dorsal ornamented surface of septomaxilla contacting nasal; absence of transverse flange of pterygoid; prearticular extends to symphysial region; slightly different position of Meckelian fenestrae). The conditions on the cast of *Ariekanerpeton* also indicate that there are about six or seven teeth on the premaxilla. Further, the vomerine tusks of *Ariekanerpeton* are placed on a ridge similar to that in *Discosauriscus*. In every case, the revision of most characters of *Ariekanerpeton* and *Utegenia* is necessary.

(ii) *Comparisons of Discosauriscus and Seymouria*

In all comparisons of *Discosauriscus* with *S. baylorensis* (White 1939; Watson 1954; Romer 1976; Holmes 1984; Laurin & Reisz 1995; Laurin 1996*c* and *S. sanjuanensis* (Vaughn 1966; Berman *et al*. 1987; Berman & Martens 1993; Laurin 1995) which follow below, it is clear that different ontogenetic stages are being compared. However, *Seymouria* cf. *S. sanjuanensis* (Berman & Martens 1993) is of a similar size to the largest specimens (K 52, K 323) of *Discosauriscus austriacus* and both forms represent early juveniles. Hence, the comparison of these two forms is significant from a morphological and taxonomical point of view. For comparisons with *S. baylorensis* and *S. sanjuanensis*, also the largest, earliest juveniles of *D. austriacus* are used (table 2).

In addition to the characters shared with *D. austriacus contra Seymouria* spp., *D. pulcherrimus* exhibits the

Table 2

	Discosauriscus austriacus	*Seymouria* cf. *S. sanjuanensis*	*Seymouria sanjuanensis*	*Seymouria baylorensis*
1.	short preorbital region (orbits are placed anteriorly relative to middle of skull length)	long preorbital region (orbits are placed in middle of skull length)	long preorbital region (orbits are placed in middle of skull length)	long preorbital region (orbits are placed in middle of skull length)
2.	narrow nasal in level of point where PFR-LAC-NA meet	broad nasal in level of point where PFR-LAC-NA meet	broad nasal in level of point where PFR-LAC-NA meet	broad nasal in level of point where PFR-LAC-NA meet
3.	prefrontal joins palatine anterior to level of palatine tusks	?	prefrontal joins palatine posterior to level of palatine tusks	prefrontal joins palatine posterior to level of palatine tusks
4.	rounded orbit	posteroventral and anteroventral notches in oval orbit only slightly indicated	posteroventral and anteroventral notches in oval orbit	posteroventral and anteroventral notches in oval orbit
5.	20–29 maxillary tooth positions	up to 25 maxillary tooth positions	24–30 maxillary tooth positions	16–21 maxillary tooth positions
6.	strip of dorsal ornamented surface of septomaxilla forming part of skull roof	?	absence of ornamented surface of septomaxilla	absence of ornamented surface of septomaxilla
7.	presence of septomaxillary foramen	?	absence of septomaxillary foramen	absence of septomaxillary foramen
8.	orbital flange of prefrontal runs anterolateral–posteromedially	?	orbital flange of prefrontal transversely oriented	orbital flange of prefrontal transversely oriented
9.	posterolateral corner of supratemporal slightly curved ventrally	?	posterolateral corner of supratemporal not curved ventrally	posterolateral corner of supratemporal curved ventrally
10.	lateral portion of tabular slightly curved ventrally	?	lateral portion of tabular moderately curved ventrally	lateral portion of tabular extensively curved ventrally
11.	less prominent caniniform region of maxilla	less prominent caniniform region of maxilla	less prominent caniniform region of maxilla	prominent caniniform region of maxilla
12.	jugal overlaps lacrimal dorsally	lacrimal overlaps slightly jugal	lacrimal overlaps jugal	lacrimal overlaps jugal
13.	jugal does not extend anterior level of orbit	jugal does not extend anterior level of orbit	jugal does not extend anterior level of orbit	jugal extends anterior level of orbit
14.	ventrolateral portion of postorbital and dorsomedial portion of jugal are broad and suture between them runs anteroposteriorly	ventrolateral portion of postorbital and dorsomedial portion of jugal are narrow, pointed and meet in oblique suture	ventrolateral portion of postorbital and dorsomedial portion of jugal are narrow, pointed and meet in oblique suture	ventrolateral portion of postorbital and dorsomedial portion of jugal are broad and suture between them runs anteroposteriorly
15.	absence of maxilla–quadratojugal contact	?	maxilla–quadratojugal contact present	maxilla–quadratojugal contact present
16.	relatively narrow otic flange of squamosal	broad otic flange of squamosal	broad otic flange of squamosal	broad otic flange of squamosal
17.	obliquely (anterodorsal–posteroventrally) running squamosal–jugal suture	vertical jugal–squamosal suture	vertical jugal–squamosal suture	obliquely (anterodorsal–posteroventrally) running squamosal–jugal suture
18.	paraquadrate foramen present	?	?	?
19.	absence of quadratojugal–ectopterygoid contact	?	?	presence of quadratojugal–ectopterygoid contact
20.	broad and shallow otic notch	narrow and deep otic notch	narrow and deep otic notch	narrow and deep otic notch
21.	radiating ridges bearing small teeth on ventral surface of palatal ramus and transverse flange of pterygoid and central portion of parasphenoid	ventral surface of pterygoids covered by shagreen of teeth	ventral surface of pterygoids covered by shagreen of teeth	ventral surface of pterygoids covered by shagreen of teeth
22.	rectangular ectopterygoid	?	rectangular ectopterygoid	triangular ectopterygoid
23.	suborbital fenestra present	?	suborbital fenestra absent	suborbital fenestra absent
24.	infraorbital canal present	?	infraorbital canal absent	infraorbital canal absent

Table 2—*cont.*

	Discosauriscus austriacus	*Seymouria* cf. *S. sanjuanensis*	*Seymouria sanjuanensis*	*Seymouria baylorensis*
25.	unornamented portion of parasphenoid stem lies dorsally to medial margins of pterygoids	cultriform process of parasphenoid lies dorsally to medial margins of pterygoids	?	cultriform process of parasphenoid lies ventrally to medial margins of pterygoids
26.	paired posteromedian process of parasphenoid	—	—	unpaired posteromedian process of parasphenoid
27.	basioccipital with pair of posteromedially diverging crests on its ventral surface	?	?	ventral surface of basioccipital smooth
28.	posteriormost portion of angular not present on lingual surface of mandible	?	posteriormost portion of angular not present on lingual surface of mandible	posteriormost portion of angular present on lingual surface of mandible
29.	presence of anterior and posterior Meckelian fenestrae	?	Meckelian fenestrae absent	Meckelian fenestrae absent

following further differences from all *Seymouria* species, namely the prefrontal–postfrontal suture lies in the anterior third of the frontal mid-length and the tooth-rows on the ventral surface of the palatal ramus, and the transverse flange of the pterygoid diverge from anteroposteriorly lying plane placed about in the mid-width of the pterygoid palatal ramus (small teeth are also on the central portion of the parasphenoid). *D. pulcherrimus* also differs from *S. baylorensis* in that the ventrolateral ramus of the postorbital and the dorso-medial portion of the jugal are narrow and pointed.

As already described above ('*Tabular*'), *Discosauriscus* possesses (1) a posteriorly protruding (from the ventral surface of the tabular) and horizontally lying tabular process (or horn) which seems to be homologous with a similar process in *Proterogyrinus* (Holmes 1984), *Pholiderpeton* (Clack 1987) and other embolomeres (Panchen 1985), (2) the 'tabular horn' (*sensu* Laurin 1995), i.e. the ventrolaterally inclined posterolateral corner of the supratemporal and the lateral part of the tabular (including ornamented surfaces of these two bones), conditions are identical with those in *S. sanjuanensis* (Laurin 1995) and (3) the occipital flange of the tabular, which I consider to be homologous with the medial occipital flange of the tabular in *S. sanjuanensis* (Laurin 1995), *Proterogyrinus* (Holmes 1984) and *Pholiderpeton* (Clack 1987). The question remains, are the tabular process of *Discosauriscus* and the lateral occipital flange of *Seymouria* (Laurin 1995, 1996*c*) homologous structures? In large specimens (KO 183, KO 80) of *Discosauriscus austriacus*, the tabular process is mediolaterally broad and convex. I suppose that during ontogeny the dorsal wall of the tabular process (lying laterally to the posttemporal fenestra) fuses with the ventral surface of the tabular, and the posterior portion of the tabular process deflects ventrally (similar to the occipital flanges of the tabular and the postparietal; better visible on the ventral side of the bones) to give a similar condition seen in *Seymouria* (Laurin 1995, fig. 1B and 1996*c*). If so, then the lateral occipital flange of the tabular of *Seymouria* (lying lateral to the posttemporal fenestra) should be homologous to the tabular process in *Discosauriscus*. Therefore, *Seymouria* can be considered as possessing a modified tabular horn (*contra* Panchen (1975) and Smithson (1985)), a conclusion I share with Holmes (1984). Therefore, the condition of having the horizontally lying tabular process in *Discosauriscus* and the ventrally flexed lateral occipital flange in *Seymouria* is not considered to be a principal difference between these two genera here because it may be connected with ontogeny.

All the above data show that: (1) As well as the typical otic tubes and the small posttemporal fenestrae, readily visible in mature specimens of *Seymouria* (White 1939; Holmes 1984; Laurin 1996*c*), a further possible synapomorphy uniting *Utegenia*, *Ariekanerpeton*, *Discosauriscus* and *Seymouria* is a rectangular, plate-like tabular process, modified in *Seymouria*. It is not known whether the infraorbital canal found in *Discosauriscus* is present also in *Utegenia*, *Ariekanerpeton* and *Seymouria*. According to Smithson (1985), the otic tubes and the squamosal–intertemporal contact are synapomorphies uniting Seymouriidae, Kotlassiidae and Discosauriscidae. However, the second character is not unique for Seymouriamorpha (Klembara 1994*a*, *b*, 1996).

(2) *Utegenia* shares with *Ariekanerpeton* two cranial characters: palatine tusks situated on ridges and the presence of diverging tooth-rows (not on ridges as in *D. austriacus*) on the ventral surface of the pterygoid palatal ramus (ridges are absent also in *D. pulcherrimus*, however, rows of small teeth diverge in this species from anteroposteriorly lying plane placed in the mid-width of the pterygoid palatal ramus).

As well as the same position of the pineal foramen and the ossification centres of parietals in *Discosauriscus* and *Utegenia*, which are primitive features, no derived character uniting these two genera can be found at present (it is not clear now, if the suborbital fenestra is present or not in *Utegenia*).

The characters of *Utegenia* like the long and narrow postorbital, narrow otic flange and broad ornamented surface of squamosal, squamosal–supratemporal suture long extending posteriorly to mid-length of supratemporal, posterolateral corner of supratemporal, and lateral portion of tabular not curved ventrally, spindle-shaped ventral scales (gastralia) and 28 presacral vertebrae, are shared with more primitive tetrapods like *Proterogyrinus* (Holmes 1984), and support the conclusion of Laurin (1995) that *Utegenia* is a basal seymouriamorph.

(3) According to Laurin (1995), five synapomorphies unite *Ariekanerpeton*, *Discosauriscus* and *Seymouria*: postorbital–supratemporal contact absent (however, with some exceptions, Klembara (1994*a*)); mediolaterally broad postorbital; otic flange of squamosal broad; presacral count of 24 vertebrae; gastralia absent. *Ariekanerpeton*, *Discosauriscus* and *Seymouria* share one further character: long posterolateral processes of the parasphenoid. The presence of the elongated internal lamina of the lacrimal interposed between the palatine and the maxilla unites *Discosauriscus* and *Seymouria* but its presence in *Ariekanerpeton* is to be expected. According to Laurin (1995), the rectangular gastralia which are present in *Utegenia*, are absent in *Ariekanerpeton*, *Discosauriscus* and *Seymouria*, uniting these three taxa. The rounded ventral scales are present in *Discosauriscus* (Špinar 1952; Klembara & Meszároš 1992), however, the rectangular chevron-shaped gastralia are probably absent in this genus. In *Seymouria*, no scales have been recorded so far.

(4) Despite several differences, the above comparisons indicate that *Ariekanerpeton* and *Discosauriscus* are similar in most respects. There are six or seven characters uniting *Ariekanerpeton* and *Discosauriscus*: short preorbital region with narrow nasals (orbits are placed anteriorly to middle of skull length); prefrontal joins palatine anterior to level of palatine tusks; jugal overlaps lacrimal dorsally (condition not completely clear in *Utegenia*); rounded orbit; broad and relatively shallow otic notch; basioccipital with pair of posteromedially diverging crests on its ventral surface and rounded scales. Unfortunately, many features are unknown in *Ariekanerpeton*, and more shared characters may be expected (e.g. presence of septomaxillary foramen; presence of infraorbital canal, etc.). According to Laurin (1995, fig. 4), *Ariekanerpeton* is more closely related to *Seymouria* than to *Discosauriscus* on the basis of the absence of the interpterygoid vacuities and the maxillary tooth count. However, in *Discosauriscus* as in *Ariekanerpeton*, the maxillary tooth count is 20–29 and the interpterygoid vacuities are absent. I suspect that the interpterygoid vacuities are absent also in *Utegenia*; the skulls of *Ariekanerpeton* and *Utegenia* are reconstructed as being extremely broad by Ivakhnenko (1987). Because the maxillary tooth count in *Utegenia* is 25–30 (Ivakhnenko 1987) and in *Seymouria sanjuanensis* it is 24–30, the maxillary tooth count and the presence of the interpterygoid vacuities are not valid characters for testing the interrelationships of these seymouriamorphs.

Although very incomplete, the above data suggest that in contrast to *Utegenia*, both *Ariekanerpeton* and *Discosauriscus* are short-snouted, their skulls being about as long as they are wide, and these two genera are considered here to be members of the family Discosauriscidae.

(5) *Discosauriscus* species differ from *Seymouria* species in the following characters: short preorbital region (orbits are placed anteriorly relative to middle of skull length); narrow nasal in level of point where prefrontal–lacrimal–nasal meet; prefrontal joins palatine anterior to level of palatine tusks; rounded orbit; strip of dorsal ornamented surface of septomaxilla forming part of skull roof; presence of septomaxillary foramen; orbital flange of prefrontal runs anterolateral–posteromedially; jugal overlaps lacrimal dorsally; absence of maxilla–quadratojugal contact; relatively narrow otic flange of squamosal; ?absence of paraquadrate foramen; absence of quadratojugal–ectopterygoid suture; broad and shallow otic notch; radiating ridges bearing small teeth on ventral surface of palatal ramus and transverse flange of pterygoid and central portion of parasphenoid; suborbital fenestra present; infraorbital canal present; paired posteromedial process of parasphenoid; basioccipital with pair of posteromedially diverging crests on its ventral surface; presence of anterior and posterior Meckelian fenestrae. These differences (valid also for most characters in *Ariekanerpeton*) justify the acceptance of the existence of two different families: Discosauriscidae and Seymouriidae.

Discosauriscus austriacus shares with *S. baylorensis* one character: ventrolateral portion of postorbital and dorsomedial portion of jugal are broad and suture between them runs anteroposteriorly. The type of the postorbital–jugal suture and the shape of the postorbital are basically the same in *D. pulcherrimus* and *S. sanjuanensis* and *S.* cf. *S. sanjuanensis*. *D. pulcherrimus* seems to be the closest to *S. sanjuanensis* and *S.* cf. *S. sanjuanensis*.

(6) The radiating ridges (bearing small teeth) on the ventral surface of the palatal ramus of the pterygoid and the central portion of the parasphenoid found in *D. austriacus* are absent in *Utegenia*, *Ariekanerpeton*, *D. pulcherrimus* and *Seymouria*.

(7) Heaton (1980) excluded 'discosauriscids' from being related to Seymouriamorpha on the basis of three characters. Two of them concern the postcranial skeleton and the cranial in the absence of the pterygoid flange. However, the pterygoid flange is very well developed in *Discosauriscus*. Despite the differences listed above, *Discosauriscus* is structurally close to *Seymouria* and it may be concluded that *Discosauriscus* is a seymouriamorph.

(8) *Seymouria* is not a reptile (i.e. a crown-group amniote tetrapod) (cf. Klembara 1995*a*; Laurin & Reisz 1997) as suggested by Fracasso (1987).

(9) According to Panchen & Smithson (1988) and Smithson *et al.* (1994), two out of four autapomorphies characteristic for the reptiliomorph clade should be the absence of posttemporal fenestra and the pedal phalangeal formula 23454 or 5. As seen from above, *Discosauriscus* possessed the same type of posttemporal fenestra as *Seymouria* (Holmes 1984; Laurin 1996*c*) and the phalangeal pedal formula in *Discosauriscus* is 23453 (Špinar 1952).

As seen above, it is difficult to create an extensive list of synapomorphies uniting all seymouriamorph genera or to find the synapomorphies uniting individual genera at present simply because of the absence of knowledge of their detailed anatomy. More light on the phylogeny of seymouriamorphs should result from the revision of *Utegenia* and *Ariekanerpeton* (Laurin 1996*a*, *b*) and the description of the postcranial skeleton of *Discosauriscus* which is under preparation by the author. Moreover, the revision of *Urumquia*, kotlassiids (*sensu* Ivakhnenko 1987), leptorophids and *Enosuchus* (Ivakhnenko 1987), as well the discovery of the adults of *Discosauriscus*, *Ariekanerpeton* and *Utegenia* is necessary.

I am indebted to Professor Dr R. Brzobohatý (Masaryk University, Brno) for allowing me to study the original series of Makowsky's specimens and to Dr P. Hudec (Moravian Regional Museum, Brno) and Dr V. Petr (Faculty of Natural Sciences, Prague) for help in searching for Špinar's lectotype (specimen no. VII of Makowsky) of *Letoverpeton austriacum*. For the illustrations (figures: 2, 7, 10–14, 16, 19, 23–28, 33, 34) and the contribution in producing the reconstructed skulls I am grateful to Mr J. Gullár (Muškátová 32, 821 01 Bratislava, Slovak Republic). For useful discussion concerning the anatomy and phylogeny of seymouriamorphs, I thank the late Professor Dr Z. V. Špinar (Prague), Dr M. Laurin (University of California, Berkeley), Dr R. Werneburg (Schloss Bertholdsburg, Schleusingen), Dr T. Martens (Museum of Nature, Gotha), Dr M. F. Ivakhnenko (Palaeontological Institute, Moscow) and Mr Š. Meszároš (Bratislava). For critically reading the manuscript and grammar and stylistic corrections I am indebted to Dr M. Laurin, Dr R. L. Carroll (Redpath Museum, McGill University, Montreal) and Dr A. R. Milner (Birkbeck College, London). Dr M. Laurin also lent me an unpublished typescript of his work on *S. baylorensis*. For the preparation of the material, photographic assistance and help with the construction of the wax-plasticine models I thank Mrs Z. Šulavíková (Faculty of Natural Sciences, Bratislava). For access to several important specimens for this study, I thank Dr M. Hornáček (Vlastivedné múzeum, Trnava). This project was partly supported by the Grant Agency for Science, Grant project no. 1/1143/94.

APPENDIX. LIST OF ABBREVIATIONS

a.COR	anterior coronoid
a.fc.OPI	anterior facet (for junction with opisthotic)
al.pr	alar process
a.M.fe	anterior Meckelian fenestra
AN	angular
ar.La	area overlapped by lacrimal
ar.sc.p	area overlapped by neighbouring sclerotic plate
ar.SQ	area overlapped by squamosal
art.ECPT	articular pit or groove for ectopterygoid
art.PFR	articular pit for prefrontal
art.por	articular portion of pterygoid
art.pr.bpt	articular surface for basipterygoid process of basisphenoid
asc.lam	ascending lamina of quadrate ramus of pterygoid
bl.pr	blunt process
BO	basioccipital
BSPH	basisphenoid
c.nl	nasolacrimal canal
cr.ar	arcuate crest
cr.vlat	crista ventrolateralis
DE	dentary
depr.	depression (deep pit or groove)
d.orn.s	dorsal ornamented surface
d.uf.s	dorsal unfinished surface
ECPT	ectopterygoid
el.depr	elongated depression
ell.depr	elliptical depression
EXOC	exoccipital
fe.pt	posttemporal fenestra
fe.sor	suborbital fenestra
fo.hyp	fossa hypophysialis
for.	foramen
for.aci	foramen for internal carotid artery
for.ch.tym	foramen for chorda tympani
for.N.XII	foramen for hypoglossus nerve (N.XII)
for.pq	paraquadrate foramen
FR	frontal
gr.aci+r.pal	groove for internal carotid artery and ramus palatinus (from N.VII)
gr.apa	groove for anterior palatine artery
gr.+r.	groove and ridge
ICL	interclavicle
imp.t.PT	impressions of small teeth on pterygoid ventral surface
int.lam	internal lamina of lacrimal
ior.c	infraorbital canal
IT	intertemporal
j.LA	surface for junction with lacrimal
j.PT	place of junction with quadrate ramus of pterygoid
j.Q	surface for junction with quadrate
j.QJ	place of junction with quadratojugal
j.SQ	place of junction with squamosal
JU	jugal
LA	lacrimal
m.COR	middle coronoid
m.fc.BO	middle facet (for junction with basioccipital)
m.sc	muscle scar
MU-P	Department of Geology and Palaeontology, Faculty of Natural Sciences, Masaryk University, Brno
MX	maxilla
NA	nasal
occ.fl	occipital flange
op.	openings
or.fl	orbital flange
ot.fl	otic flange
PA	parietal
PAL	palatine
pal.r	palatal ramus of pterygoid
PAR	prearticular
PAS	parasphenoid
p.COR	posterior coronoid
p.d.EPI	pit for dorsal extension of epipterygoid
p.fc.oc	posterior facet (participating on formation of occipital condyle)
PFR	prefrontal
pi.b	piece of bone
p.M.fe	posterior Meckelian fenestra
PMX	premaxilla
PO	postorbital
POFR	postfrontal
POSP	postsplenial
PP	postparietal
pr.ant	anterior process of parasphenoid
pr.bpt	basipterygoid process of basisphenoid
pr.d	dorsally projecting process
pr.ot	process fitting into fenestra ovalis
pr.PAL	process contacting palatine
pr.plat	posterolateral process of parasphenoid
pr.tab	tabular process (horn)
pr.tym	process directed to tympanic membrane

pr.VOM	process contacting vomer
PSP	postsplenial
PT	pterygoid
p.v.EPI	pit for ventral extension of epipterygoid
QJ	quadratojugal
q.r	quadrate ramus of pterygoid
retr.p	retractor pit
rg.	rugosity
ro.fl	rounded flange
SAN	surangular
SL	skull length (PP+PA+FR+NA)
SMX	septomaxilla
smx.for	septomaxillary foramen
SP	splenial
SP-DE	splenio-dentary
SQ	squamosal
ST	supratemporal
str.	longitudinal striation
TA	tabular
tr.fl	transverse flange of pterygoid
tr.gr./r.	transverse groove and/or ridge
uf.s.PAT	unfinished surface (for junction with proatlas)
uo.s	unornamented surface
VOM	vomer

REFERENCES

Augusta, J. 1936 Die Stegocephalen aus dem unteren Perm der Boskovicer Furche in Mähren. *Práce geol.-paleont. ústavu KU v Praze*, 1–64.

Augusta, J. 1948 Our present knowledge of the Stegocephali in the Lower Permian of Moravia. *Přírodovědní sborník ostravského kraje* (*Opava*) **IX**, 82–101. (In Czech.)

Beamount, E. H. 1977 Cranial morphology of the Loxommatidae (Amphibia: Labyrinthodontia). *Phil. Trans. R. Soc. Lond.* B **280**, 29–101.

Berman, D. S. & Martens, T. 1993 First occurrence of *Seymouria* (Amphibia: Batrachosauria) in the Lower Permian Rotliegend of Central Germany. *Ann. Carnegie Mus.* **62**, 63–79.

Berman, D. S., Reisz, R. R. & Eberth, D. A. 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. *Canad. J. Earth Sci.* **24**, 1769–1784.

Bjerring, H. C. 1989 Apertures of craniate olfactory organs. *Acta zool., Stockh.* **70**, 71–85.

Boy, J. A. 1990 On some representatives of the Eryopoidea (Amphibia: Temnospondyli) from the European Rotliegend (?uppermost Carboniferous–Permian) 3. *Onchiodon. Paläont. Z.* **64**, 287–331.

Bystrow, A. P. 1939 Blutgefässystem der Labyrinthodonten (Gefässe des Kopfes). *Acta zool., Stockh.* **20**, 125–155.

Bystrow, A. P. 1944 On *Kotlassia prima* (Amalitsky). *Bull. geol. Soc. Am.* **55**, 379–416.

Bystrow, A. P. & Efremov, J. A. 1940 *Benthosuchus sushkini* Efr. A labyrinthodont from the Eotriassic of Sharjenga River. *Trudy Paleont. Inst.* **10**, 1–152. (In Russian.)

Carroll, R. L. 1995 Problems of the phylogenetic analysis of Paleozoic choanates. In *Proceedings of the 7th international symposium on early vertebrates* (ed. P. Janvier & M. Arsenault), *Bull. Mus. natl. Hist. nat., Paris, ser. 4*, **17**, pp. 389–445.

Carroll, R. L. & Lindsay, W. 1984 Cranial anatomy of the primitive reptile *Procolophon. Can. J. Earth Sci.* **22**, 1571–1587.

Clack, J. A. 1987 *Pholiderpeton scutigerum* (Huxley), an amphibian from the Yorkshire coal measures. *Phil. Trans. R. Soc. Lond.* B **318**, 1–107.

Clack, J. A. 1988 New material of the early tetrapod *Acanthostega* from the Upper Devonian of East Greenland. *Palaeontology* **31**, 699–724.

Clack, J. A. & Holmes, R. 1988 The braincase of the anthracosaur *Archeria crassidisca* with comments on the interrelationships of primitive tetrapods. *Palaeontology* **31**, 85–107.

Credner, H. 1883 Die Stegocephalen aus dem Rothliegenden des Plauen'schen Grundes bei Dresden. *Zeitschrift der deutschen geologischen Geselschaft*, 4. Theil, 276–300.

Fracasso, M. A. 1987 Braincase of *Limnoscelis paludis* Williston. *Postilla* **201**, 1–22.

Fritsch, A. 1879 Neue Übersicht der in der Gaskohle und den Kalksteinen der Permformation in Böhmen vorgefundenen Tierreste. *Sitzungsberichte der königlichen böhmischen Geselschaft der Wissenschaften* (*Prag 1879*), 184–195.

Fritsch, A. 1883 *Fauna der Gaskohle und der Kalksteine der Permformation Böhmens*. Selbstverlag, Prag 1883, Bd. **I**, pp. 1–182.

Heaton, M. J. 1979 Cranial morphology of primitive captorhinid reptiles from the late Pennsylvanian and early Permian, Oklahoma and Texas. *Bull. Oklahoma Geol. Survey* **127**, 1–84.

Heaton, M. J. 1980 The Cotylosauria: a reconsideration of a group of archaic tetrapods. In *The terrestrial environment and the origin of land vertebrates* (ed. A. L. Panchen) (*System. Ass. Spec. Vol.* **15**), pp. 497–551. London and New York: Academic Press.

Heyler, D. 1969 Vertébrés de l'Autunien de France. *Cahiers de Paléont. du CNRS* **15**, 1–225.

Holmes, R. 1984 The Carboniferous amphibian *Proterogyrinus scheelei*, Romer, and the early evolution of tetrapods. *Phil. Trans. R. Soc. Lond.* B **306**, 431–527.

Holmes, R. 1989 The skull and axial skeleton of the Lower Permian anthracosauroid amphibian *Archeria crassidisca* Cope. *Palaeontographica* A **207**, 161–206.

Ivakhnenko, M. F. 1979 The Permian and Triassic procolophons of the Russian Platform. '*Nauka*', *Trudy paleontologicheskovo Instituta AN* **164**, 1–80. (In Russian.)

Ivakhnenko, M. F. 1981 Discosauriscidae from the Permian of Tadzhikistan. *Paleontologicheskij zhurnal* **1**, 114–128. (In Russian.)

Ivakhnenko, M. F. 1987 Permian parareptiles of USSR. '*Nauka*', *Trudy paleontologicheskovo Instituta AN* **223**, 1–160. (In Russian.)

Jollie, M. T. 1960 The head skeleton of the lizard. *Acta zool., Stockh.* **41**, 1–64.

Kathe, W. 1995 Morphology and function of the sutures in the dermal skull roof of *Discosauriscus austriacus* (Makowsky 1876) (Seymouriamorpha; Lower Permian of Moravia) and *Onchiodon labyrinthicus* (Geinitz 1861) (Temnospondyli; Lower Permian of Germany). In *Premiers vertébrés et vertébrés inférieurs* (ed. H. Leliévre, S. Wenz, A. Blieck & R. Cloutier) (*Geobios mémoire spécial no. 19*), pp. 255–261.

Klembara, J. 1985 A new embolomerous amphibian (Anthracosauria) from the Upper Carboniferous of Florence, Nova Scotia. *J. Vert. Paleont.* **5**, 293–302.

Klembara, J. 1992 The first record of pit-lines and foraminal pits in tetrapods and the problem of the skull roof bones homology between tetrapods and fishes. *Geologica carpathica* **43**, 249–252.

Klembara, J. 1993 The subdivisions and fusions of the exoskeletal skull bones of *Discosauriscus austriacus* (Makowsky 1876) and their possible homologues in rhipidistians. *Paläont. Z.* **67**, 145–168.

Klembara, J. 1994*a* The sutural pattern of skull-roof bones in Lower Permian *Discosauriscus austriacus* from Moravia. *Lethaia* **27**, 85–95.

Klembara, J. 1994*b* Electroreceptors in the Lower Permian tetrapod *Discosauriscus austriacus* (Makowsky 1876). *Palaeontology* **37**, 609–626.

Klembara, J. 1995*a* The external gills and ornamentation of skull roof bones of the Lower Permian tetrapod *Discosauriscus* (Kuhn 1933) with remarks to its ontogeny. *Paläont. Z.* **69**, 265–281.

Klembara, J. 1995*b* Some cases of fused and concrescent exocranial bones in the Lower Permian seymouriamorph tetrapod *Discosauriscus* (Kuhn 1933). In *Premiers vertébrés et vertébrés inférieurs* (ed. H. Leliévre, S. Wenz, A. Blieck & R. Cloutier) (*Geobios mémoire spécial no. 19*), pp. 263–267.

Klembara, J. 1996 The lateral line system of *Discosauriscus austriacus* (Makowsky 1876) and the homologization of skull roof bones between tetrapods and fishes. *Palaeontographica* A **240**, 1–27.

Klembara, J. & Janiga, M. 1993 Variation in *Discosauriscus austriacus* (Makowsky 1876) from the Lower Permian of the Boskovice Furrow (Czech Republic). *Zool. J. Lin. Soc.* **108**, 247–270.

Klembara, J. & Meszároš, Š. 1992 New finds of *Discosauriscus austriacus* (Makowsky 1876) from the Lower Permian of the Boskovice Furrow (Czecho-Slovakia). *Geologica carpathica* **43**, 305–312.

Kuhn, O. 1933 Labyrinthodontia. In *Fossilium Catalogus, I. Animalia* (ed. W. Quenstedt), **61**, pp. 1–114.

Kuznetsov, V. V. & Ivakhnenko, M. F. 1981 Discosauriscids from the Upper Palaeozoic of South Kazakhstan. *Paleontologicheskij zhurnal* **3**, 102–110. (In Russian.)

Laurin, M. 1994 A new study of discosauriscid anatomy using digital image editing software. (Abstract.) *J. Vert. Paleont.* **14**, Suppl. to No. 3.

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. 1996*a*. A reappraisal of *Utegenia*, a Permo-Carboniferous seymouriamorph (Tetrapoda, Batrachosauria) from Kazakhstan. *J. Vert. Paleont.* **16** (3), 374–383.

Laurin, M. 1996*b* A re-evaluation of *Ariekanerpeton*, a Lower Permian seymouriamorph (Tetrapoda: Seymouriamorpha) from Tatzhikistan. *J. Vert. Paleont.* **16** (4), 653–665.

Laurin, M. 1996*c* A redescription of the cranial anatomy of *Seymouria baylorensis*, the best known seymouriamorph (Vertebrata: Seymouriamorpha). *PaleoBios* **17** (1), 1–16.

Laurin, M. & Reisz, R. R. 1995 A reevaluation of early amniote phylogeny. *Zool. J. Lin. Soc.* **113**, 165–223.

Laurin, M. & Reisz, R. R. 1997 A new perspective on tetrapod phylogeny. In *Amniote origins—completing the transition to land* (ed. S. Sumida & K. Martin), pp. 9–59. London: Academic Press.

Makowsky, A. 1876 Über einen neuen Labyrinthodonten '*Archegosaurus austriacus* nov. spec.'. *Sitzungsber. d.k. Akad. d. Wissenschaft* **73**, 155–166.

Panchen, A. L. 1964 The cranial anatomy of two Coal Measure anthracosaurs. *Phil. Trans. R. Soc. Lond.* B **247**, 593–637.

Panchen, A. L. 1970 *Handbuch der Paläoherpetologie*, part 5a (*Anthracosauria*), Fischer Verlag, Stuttgart.

Panchen, A. L. 1972 The skull and skeleton of *Eogyrinus attheyi* (Watson) (Amphibia: Labyrinthodontia). *Phil. Trans. R. Soc. Lond.* B **263**, 279–326.

Panchen, A. L. 1975 A new genus and species of anthracosaur amphibian from the Lower Carboniferous of Scotland and the status of *Pholiderpeton pisciformis* (Huxley). *Phil. Trans. R. Soc. Lond.* B **269**, 581–637.

Panchen, A. L. 1985 On the amphibian *Crassigyrinus scoticus* (Watson) from the Carboniferous of Scotland. *Phil. Trans. R. Soc. Lond.* B **309**, 461–568.

Panchen, A. L. & Smithson, T. R. 1988 The relationships of earliest tetrapods. In *The phylogeny and classification of the tetrapods. Volume 1: amphibians, reptiles, birds.* (ed. M. J. Benton), Systematics Association Special Volume **35**A, pp. 1–32. Oxford: Clarendon Press.

Riabinin, A. N. 1911 Débris de stégocephales trouvés aux mines de Kayrgal, gouverment d'Orenbourg. *Bull. Com. Géol.* **20**, 25–35.

Romer, A. S. 1947 Review of the Labyrinthodontia. *Bull. Mus. comp. Zool. Harv.* **99**, 1–368.

Romer, A. S. 1963 The larger embolomerous amphibians of the American Carboniferous. *Bull. Mus. comp. Zool. Harv.* **128**, 415–454.

Romer, A. S. 1976 *Osteology of the reptiles.* Chicago and London: University of Chicago Press.

Sainte-Seine, P. de 1949 Vertébrés autuniens de Bourbon l'Archambault. *Ann. Paleont.* **35**, 133–140.

Säve-Söderbergh, G. 1936 On the morphology of Triassic stegocephalians from Spitsbergen and the interpretation of the endocranium in the Labyrinthodontia. *K. svenska VetenskAkad. Handl.* **16**, 1–181.

Sawin, H. J. 1941 The cranial anatomy of *Eryops megacephalus*. *Bull. Mus. comp. Zool. Harv.* **88**, 407–463.

Shishkin, M. A. 1968 On the cranial arterial system of labyrinthodonts. *Acta zool. Stockh.* **49**, 1–22.

Shishkin, M. A. 1973 Morphology of early amphibians and problems of evolution of lower tetrapods. *Trudy Paleont. Inst.* **137**, 1–260. (In Russian.)

Skinner, M. M. 1973 Ontogeny and adult morphology of the skull of the South African skink, *Mabuya capensis* (Gray). *Ann. Univ. Stellenbosch* **48**, 1–116.

Smithson, T. R. 1985 The morphology and relationships of the Carboniferous amphibian *Eoherpeton watsoni* (Panchen). *Zool. J. Linn. Soc.* **85**, 317–410.

Smithson, T. R. 1986 A new anthracosaur amphibian from the Carboniferous of Scotland. *Palaeontology* **29**, 603–628.

Smithson, T. R., Carroll, R. L., Panchen, A. L. & Andrews, S. M. 1994 *Westlothiana lizzie* from the Viséan of East Kirkton, West Lothian, Scotland, and the amniote stem. *Trans. R. Soc. Edinb.: Earth Sci.* **84**, 383–412.

Steen, M. C. 1938 On the fossil Amphibia from the Gas Coal of Nýřany and other deposits in Czechoslovakia. *Proc. zool. Soc. Lond.* B **108**, 205–283.

Stehlík, A. 1924 New Stegocephali from Moravian Permian Formation and additions to the knowledge of Stegocephali from Nýřany. *Acta soc. scient. nat. Mor.* **1**, 199–283. (In Czech.)

Špinar, Z. V. 1952 Revision of some Moravian Discosauriscidae (Labyrinthodontia). *Rozpravy ÚÚG* **15**, 1–115. (In Czech.)

Švec, P. 1984 The vertebrae of the Lower Permian genus *Discosauriscus* (Kühn 1933) (Amphibia, Discosauriscidae); notes on their morphology and evolution. *Věstník ÚÚG* **59**, 291–297.

Švec, P. 1986 The braincase of the family Discosauriscidae (Amphibia: Labyrinthodontia). *Věstník ÚÚG* **61**, 273–279.

Vaughn, P. P. 1966 *Seymouria* from the Lower Permian of south-eastern Utah, and possible sexual dimorphism in that genus. *J. Paleont.* **40**, 603–612.

Watson, D. M. S. 1917 A sketch classification of the pre-Jurassic tetrapod vertebrates. *Proc. Zool. Soc. Lond. 1917*, 167–186.

Watson, D. M. S. 1954 On *Bolosaurus* and the origin and classification of reptiles. *Bull. Mus. comp. Zool. Harv.* **111**, 295–449.

Werneburg, R. 1985 Zur Taxonomie der jungpaläozoischen Familie Discosauriscidae (Romer 1947) (Batrachosauria, Amphibia). *Freib. Forsch.-H.*, **C 400**, 117–133.

Werneburg, R. 1988 Die Amphibienfauna der Oberhöfer Schichten (Unterrotliegendes, Unterperm) des Thüringer Waldes. *Veröff. Naturhist. Mus. Schloss Bertholdsburg Schleusingen* **3**, 2–27.

Werneburg, R. 1989*a* Labyrinthodontier (Amphibia) aus dem Oberkarbon und Unterperm Mitteleuropas – Systematik, Phylogenie und Stratigraphie. *Freib. Forsch.-H.*, **C 436**, 7–57.

Werneburg, R. 1989*b* Some notes to systematic, phylogeny and biostratigraphy of labyrinthodont amphibians from the Upper Carboniferous and Lower Permian in Central Europe. *Acta Musei Reginaehradecensis S.A.: Scientiae Naturales* **XXII**, 117–129.

White, T. E. 1939 Osteology of *Seymouria baylorensis* (Broili). *Bull. Mus. comp. Zool. Harv.* **85**, 325–409.

Williston, S. W. 1911 A new family of Reptiles of the Permian of New Mexico. *Amer. Jour. Sci.* **31**, 378–398.

Zhang, F., Li, Y. & Wan, X. 1984 A new occurrence of Permian seymouriamorphs in Xinjiang, China. *Vertebrata Palasiatica* **22**, 294–304. (In Chinese, English abstract.)

Received 3 June 1996; accepted 15 August 1996

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES