Paläont. Z.	69	1/2	265–281	10 Abb.	Stuttgart, März 1995

The external gills and ornamentation of skull roof bones of the Lower Permian tetrapod *Discosauriscus* (KUHN 1933) with remarks to its ontogeny

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With 10 figures

Kurzfassung: Bis jetzt sind die größten Individuen von *Discosauriscus* (wie auch *Utegenia* und *Ariekanerpeton*, unterpermische Mitglieder der Familie Discosauriscidae) für adulte Individuen gehalten worden. Die größten Exemplare von *Discosauriscus*, die noch äußere Kiemen besitzen, haben eine Schädellänge von etwa 22–25 mm. Es ist vorausgesetzt worden, daß die Metamorphose bei Discosaurisciden ungefähr bei dieser Größe anfing und daß die Individuen mit einer Schädellänge von etwa 50–54 mm schon adult oder senil waren.

Neue Funde von *Discosauriscus* zeigen die Anwesenheit von äußeren Kiemen in Exemplaren mit einer Schädellänge bis zu 32 mm. Diese Beobachtung, die Ornamentierung der Schädeldachknochen und osteologische Merkmale der neuen, großen Individuen legen nahe, daß 1) *Discosauriscus* die larvalen, metamorphosierenden und frühjuvenilen Stadien eines reptiliomorphen Tetrapoden repräsentiert, dessen Adultindividuen noch nicht bekannt sind und daß 2) die zwei anderen Discosauarisciden (*Ariekanerpeton* und *Utegenia*) ebenfalls frühontogenetische Stadien darstellen.

Abstract: Until now, the largest specimens of *Discosauriscus* (and also *Utegenia* and *Ariekanerpeton* – the Lower Permian members of the family Discosauriscidae) have been considered to be adult individuals. The largest specimens of *Discosauriscus*, in which the external gills are still present, had skull lengths of about 22–25 mm. Metamorphosis was believed to have commenced at this size in discosauriscids and specimens with skull lengths of about 50–54 mm were considered to be already adult or senile.

New finds of *Discosauriscus* demonstrate the presence of external gills in specimens with skull lengths of up to 32 mm. On the base of this, together with the ornamentation of the skull roof bones and osteological features of new large specimens, it is here concluded that 1) *Discosauriscus* represents the larval, metamorphic and early juvenile stages of a reptiliomorph tetrapod, the adults of which are yet unknown and 2) two other discosauriscids (*Ariekanerpeton* and *Utegenia*) also represent early ontogenetic stages.

Introduction

The Lower Permian tetrapod *Discosauriscus austriacus* was first described by MAKOWSKY (1876 as "*Archegosaurus*" *austriacus*) from the Boskovice Furrow in Moravia (Czech Republic). Because the names "*Archegosaurus*" and "*Discosaurus*" (CREDNER 1882) were both preoccupied, KUHN (1933) introduced the name *Discosauriscus* for this species. ŠPINAR (1952) distinguished two genera and four species (*Discosauriscus pulcherrimus*, *D. potamites*, *Letoverpeton austriacum*, and *L. moravicum*). ŠPINAR (1952) was the first worker to observe the external gills in several specimens which became very important in the discussion about the taxonomic status of the Seymouriamorpha WATSON 1917. The family Discosauriscidae was established by ROMER (1947) and placed within the Seymouriamorpha.

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0031-0220/95/0069-0265 $ 4.25

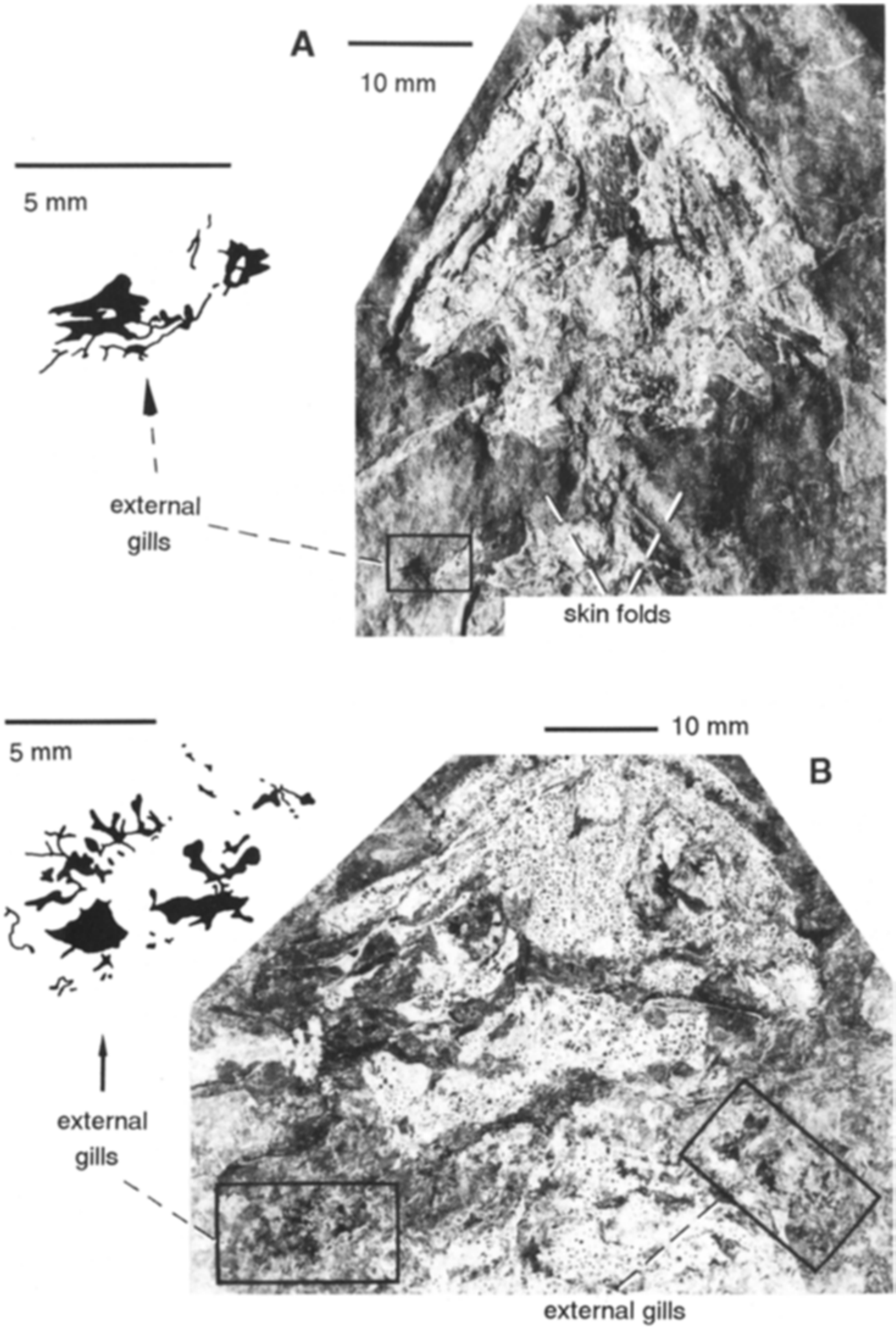

Fig. 1. *Discosauriscus.* A: K 359. B: K 361. Skulls, part of postcranial skeleton and external gills.

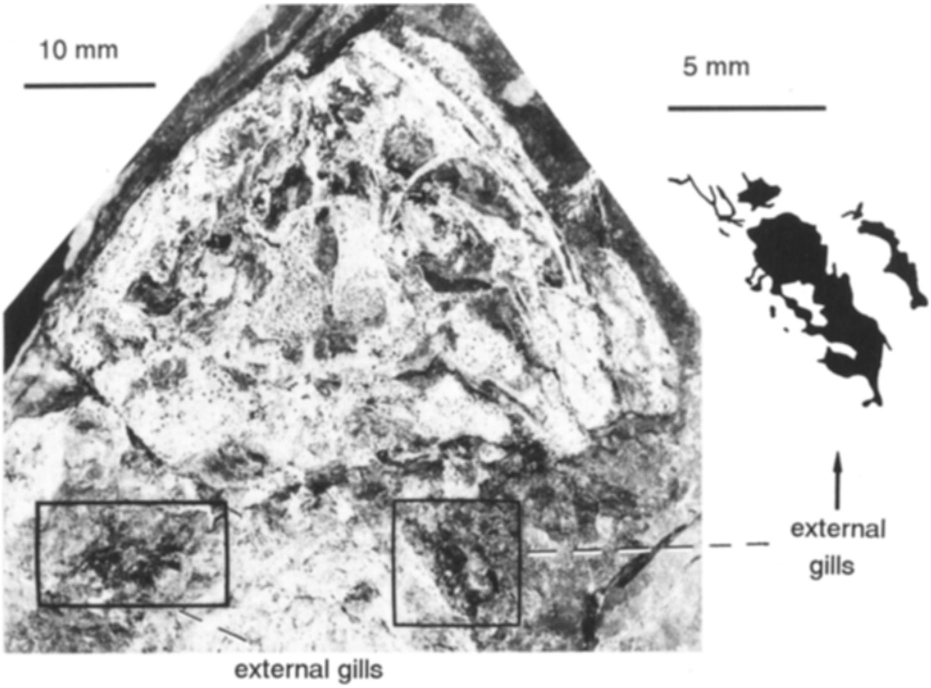

Fig. 2. *Discosauriscus.* K 370. Skull, part of postcranial skeleton and external gills.

The relatively large proportional differences of the crania of *Discosauriscus* represent various shape trends (KLEMBARA & JANIGA 1993) and have been recognized also in *Seymouria* (cf. WHITE 1939; VAUGHN 1966; BERMAN et al. 1987).

According to ŠPINAR (1952), the largest discosauriscids, in which the external gills were still observable, had skull lengths of about 25 mm. IVAKHNENKO (1987) stated that external gills in *Utegenia* are absent in specimens with skulls longer than 15 mm. However, in these specimens, IVAKHNENKO (1987, 1990) recorded structures behind the skull and lateral to the cervical vertebral column which he interpreted as skin infoldings covering probably functional internal gills. IVAKHNENKO (1987) also found thickened skin in this portion of the body in *Ariekanerpeton*. The above data imply that the large members of the family Discosauriscidae probably represent completely aquatic animals which were nevertheless adult.

As for the ornamentation of skull roof bones in *Discosauriscus*, some data were given by ŠPINAR (1952).

During 1993, several specimens of *Discosauriscus* were found, among which 1) some possess external gills and have a skull length greater than 25 mm and 2) some specimens represent the largest individuals found in the Boskovice Furrow up to now; the preserved skull length of the largest is at least 62 mm and it is therefore the largest specimen of a Euroasiatic discosauriscid.

The terms 'reptiliomorphs' and 'batrachomorphs' are used here in the sense of SÄVE-SÖDERBERGH (1934, 1935).

Abbreviations

FR	frontal	NA	nasal	QJ	quadratojugal
JU	jugal	PFR	prefrontal	SQ	squamosal
LA	lacrimal	PP	postparietal	c.rad	centre of radiation

Localities, material and methods

The material is from four Lower Permian localities in Boskovice Furrow (Czech Republic):

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 northeast of Kochov (district of Letovice), designated as KO.
4) Obora (near the towns of Skalice nad Svitavou); shales in the field on the left side of the road from Obora to Jabloňany, about 60 m NW of the insect locality (e.g. KUKALOVÁ 1963). It is designated as OB.

Specimens (deposited at the Zoological Institute, Faculty of Natural Sciences, Comenius University) are used: D 91, D 209, K 1, K 16, K 19.I, K 41, K 52, K 72, K 144, K 313, K 323, K 329.II, K 338.II, K 342, K 359, K 361, K 362, K 370, K 371A,B (counterparts), KO 35A (incomplete positive), KO 35B (incomplete negative), KO 79, KO 80, KO 131, OB 1, OB 2.

The skull lengths (postparietal+parietal+frontal+nasal) of the new specimens are as follows: KO 79–51 mm, KO 80– about 47 mm (the tips of the nasals are absent), OB 1– about 62 mm. The skull lengths of two other large specimens are: K 52– about 52 mm, K 323–49 mm.

In this paper, specimens with skull lengths (SL) from 13–62 mm from Moravian localities are considered. Some data on the skeletal anatomy of smaller specimens are given by ŠPINAR (1952); for *Utegenia* see KUZNETSOV & IVAKHNENKO (1981) and IVAKHNENKO (1987), and for *Ariekanerpeton* see IVAKHNENKO (1981, 1987).

Recently, BERMAN & MARTENS (1993) described two specimens of *Seymouria* cf. *sanjuanensis* from the Bromacker locality in Germany. The skull lengths of these specimens are: MNG 7727 – about 56 mm, MNG 8759 – about 21 mm. The specimen MNG 7727 is used here for the comparative purposes and designated as the Bromacker *Seymouria*; according to the authors, the individual which it represents was not fully mature. Specimen MNG 8759, considered by the authors to be very immature, probably postlarval stage, is not considered here because of the insufficient published morphological data.

The skulls restorations on figures 9A–D are based on enlarged wax-plasticine models of specimens K 13 and K 323.

External gills

In all specimens, the external gills are preserved as bushy structures situated behind the skull, lateral to the neck and shoulder girdle. Between the gills and the skull, the imprints of skin folds are present in some specimens (KO 35A, K 359), Fig. 1 A.

The largest specimen in which external gills are present (K 370) has a skull length of about 32 mm (Fig. 2). Here, the gills are preserved on both sides, likewise in K 361 (SL = about 30–31 mm, Fig. 1 B) and K 371B (SL = about 20 mm). In K 362 and K 359 (both SL = about 31 mm) the remains of the right external gills are present (Fig. 1 A).

The external gills are present as carbonized remains, as are the soft eye structures (K 371). From the osteological point of view, the skeletons of these specimens are badly preserved; gills are visible only on the surface of the split shale. Specimens OB 1 and OB 2 (skull length about 30 mm) are also carbonized; they lay on the same block surface. The external gills are very well observable in alcohol.

Ornamentation

Well preserved skulls of small *Discosauriscus* individuals are rare. In specimens with a skull length of about 13 mm (K 41, D 209), the region of the centre of radiation is elevated and

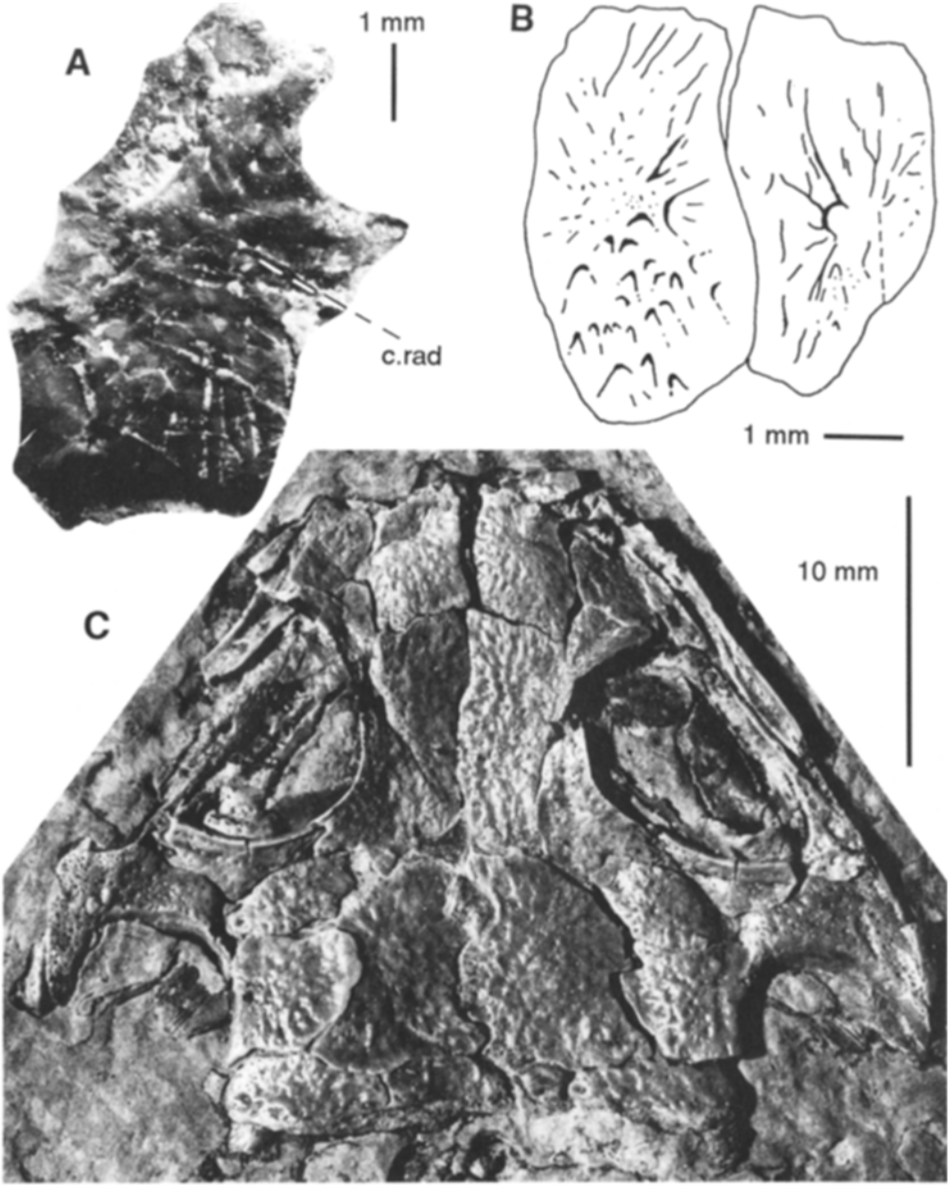

Fig. 3. *Discosauriscus austriacus* (MAKOWSKY 1876). A: K 144, left parietal in dorsal view. B: K 41, frontals in dorsal view. C: K 342, skull in dorsal view.

several foramina are present in it. From these foramina the narrow grooves and broad, low ridges of different lengths pass radially (Fig. 3 B). In the left parietal of K 144 (estimated SL = 15 mm), low protuberances are already present in the region of the radiating centre and the anterior half of the bone, whereas in the posterior part, there are distinct, narrow, radially diverging grooves along the smooth surface (Fig. 3 A). In specimens with a skull length of about 20–25 mm, the low protuberances cover a greater part of the central bone surface and the grooves and ridges lie more or less peripherally (Fig. 3 C). During further growth, the pits broaden round the foramina (starting in the region of the centre of radiation) so that ridges arise round the pits and grooves. In this way a polygonal type of ornamentation is formed; it is most intensively developed in the largest specimen K 52 (Fig. 7 B). It must be emphasized, however, that in specimens with skull lengths of about 25–52 mm the preservation of the radial orientation of pits, grooves and ridges varies considerably among specimens. In specimens with the same skull length the radial ornamentation may be preserved or almost completely suppressed (see comparisons in Figs. 4, 5, 7). This is an individual variation, as is the intensity of ornamentation in specimens of the same size and it does not depend on skull proportions. In K 313 (SL = about 34 mm), the centres of radiation are visible in almost all bones (Fig. 4 B); similarly in KO 131 (skull length about 29 mm). The skull preservation of small individuals does not allow the process of suppression of radial ornamentation in individual bones to be followed; however, traces of radial grooves and ridges persist longest on the nasal and then the frontal and parietal.

Skull roof of the largest specimens

Despite the skull shape trends existing in *Discosauriscus* (Klembara & Janiga 1993), in the skulls of the largest specimens (KO 80, K 323, KO 79, K 52) the nasals are about 1–1.5 mm shorter relative to the frontals (Figs. 6, 7). In OB 1, however, the lengths of the left frontal and nasal seem to be almost the same (Fig. 8). These specimens, together with all other smaller specimens, demonstrate the progressive lengthening of the nasal relative to the frontal with growth.

The carbonized specimen OB 1 (Fig. 8) is slightly compressed anteroposteriorly. Most of the bones of the skull roof remain in their original position but individual sutures are not readily traceable. However, the outlines of frontals, left nasal and left prefrontal are readily recognizable. In both orbits of OB 1, an ellipsoid structure is present. The outline of both ellipsoid elements is relatively clear and their shape and size are identical. The structure and shape of the ellipsoids do not permit them to be interpreted as the remains of the eye pigments or palatal bones. However, an element almost identical in shape and position has been recorded in the Bromacker *Seymouria* and interpreted as the part of the palpebral cup (Berman & Martens 1993). It is very probable that these structures correspond to the palpebral bones found in various lacertilians (see below).

The shapes of nasal and frontal as well as the entire anatomy of the skull roof of the Bromacker *Seymouria* (as well as North American *S. sanjuanensis*, Berman et al. 1987), OB 1 and other four large specimens of *Discosauriscus* are similar. In skull size, the Bromacker *Seymouria* fits between the largest *Discosauriscus* specimens K 52 and OB 1 and it will be used for comparisons especially from the point of view of ontogenetic development. As will be discussed below, no adult specimen of *Discosauriscus* has been found in the Boskovice Furrow so far.

Comparisons, discussion and conclusions

These new discoveries of specimens with external gills, together with large specimens, have a profound influence on the taxonomic status of *Discosauriscus* because: (a) discosauriscids have

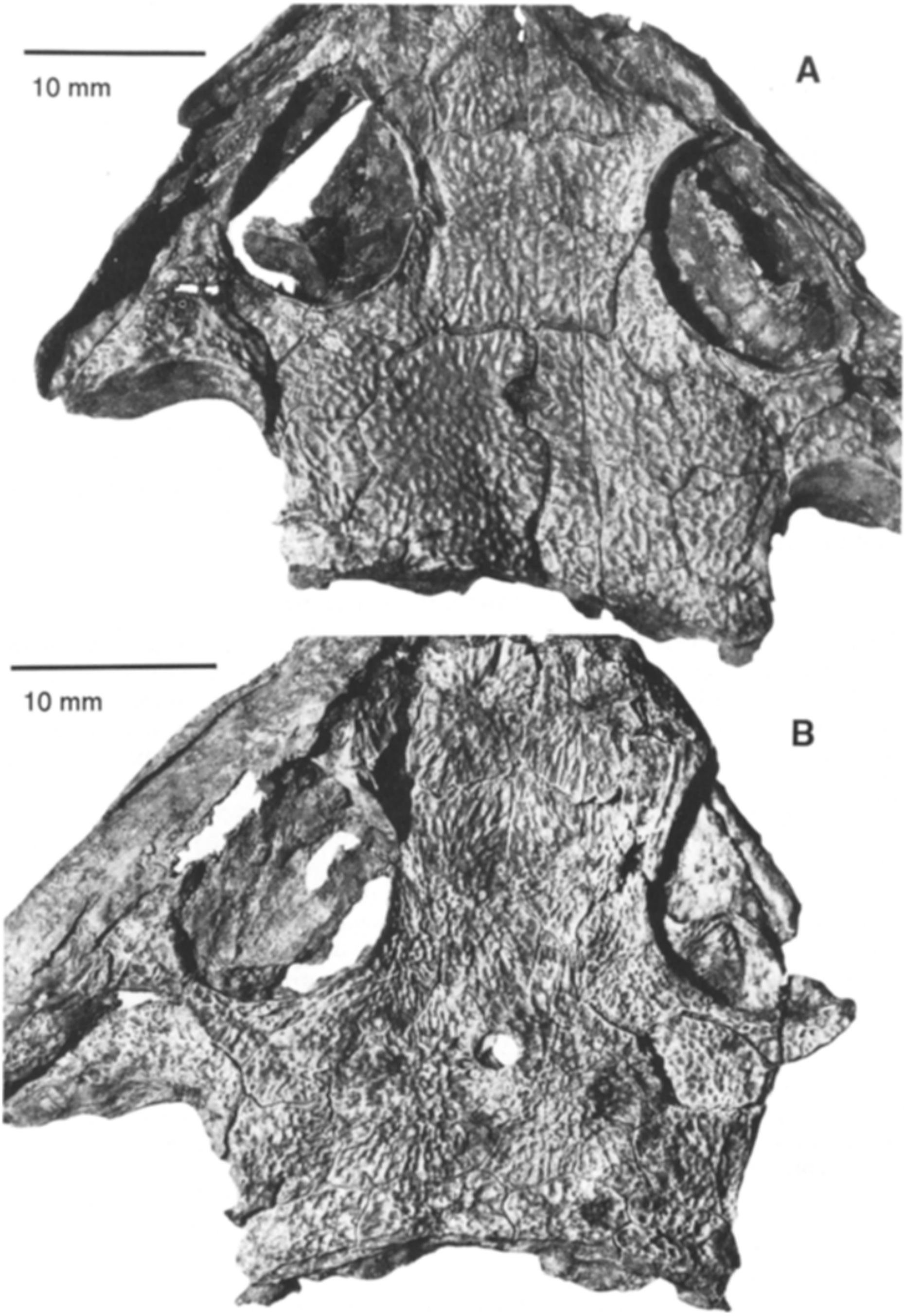

Fig. 4. *Discosauriscus austriacus* (MAKOWSKY 1876), skulls in dorsal view. A: K 1. B: K 313.

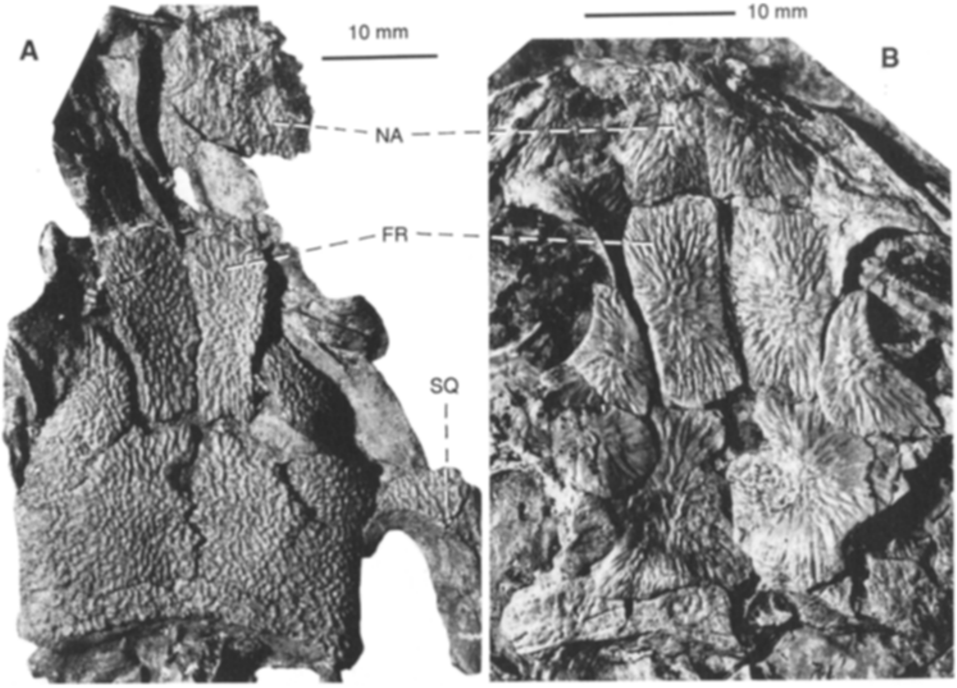

Fig. 5. A. *Discosaurisens pulcherrimus* (Fritsch 1879), B. *Discosauriscus austriacus* (Makowsky 1876), skulls in dorsal view. A: K 16. B: K 329.II.

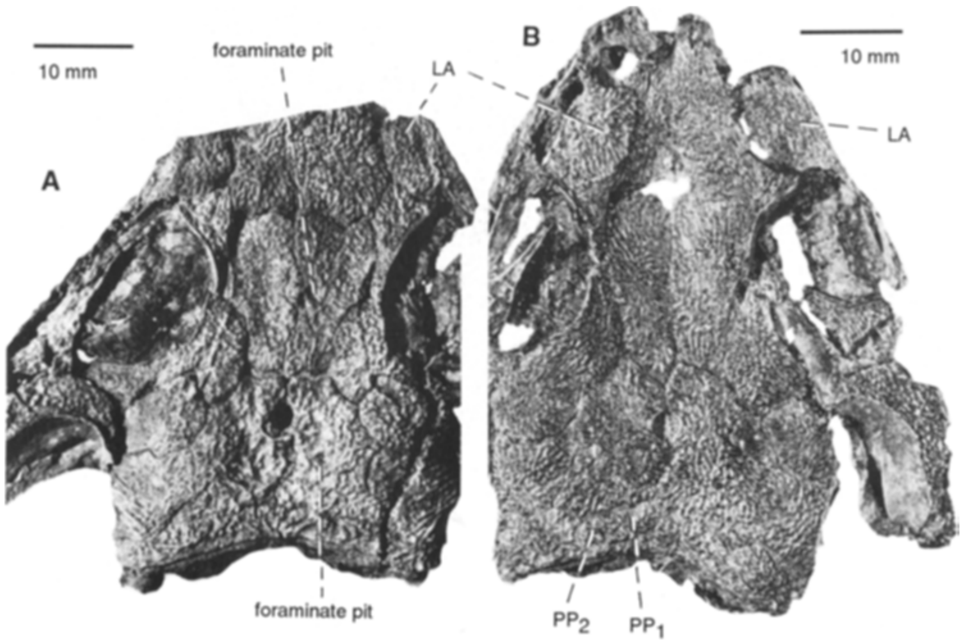

Fig. 6. *Discosauriscus austriacus* (Makowsky 1876), skulls in dorsal view. A: KO 80. B: KO 79.

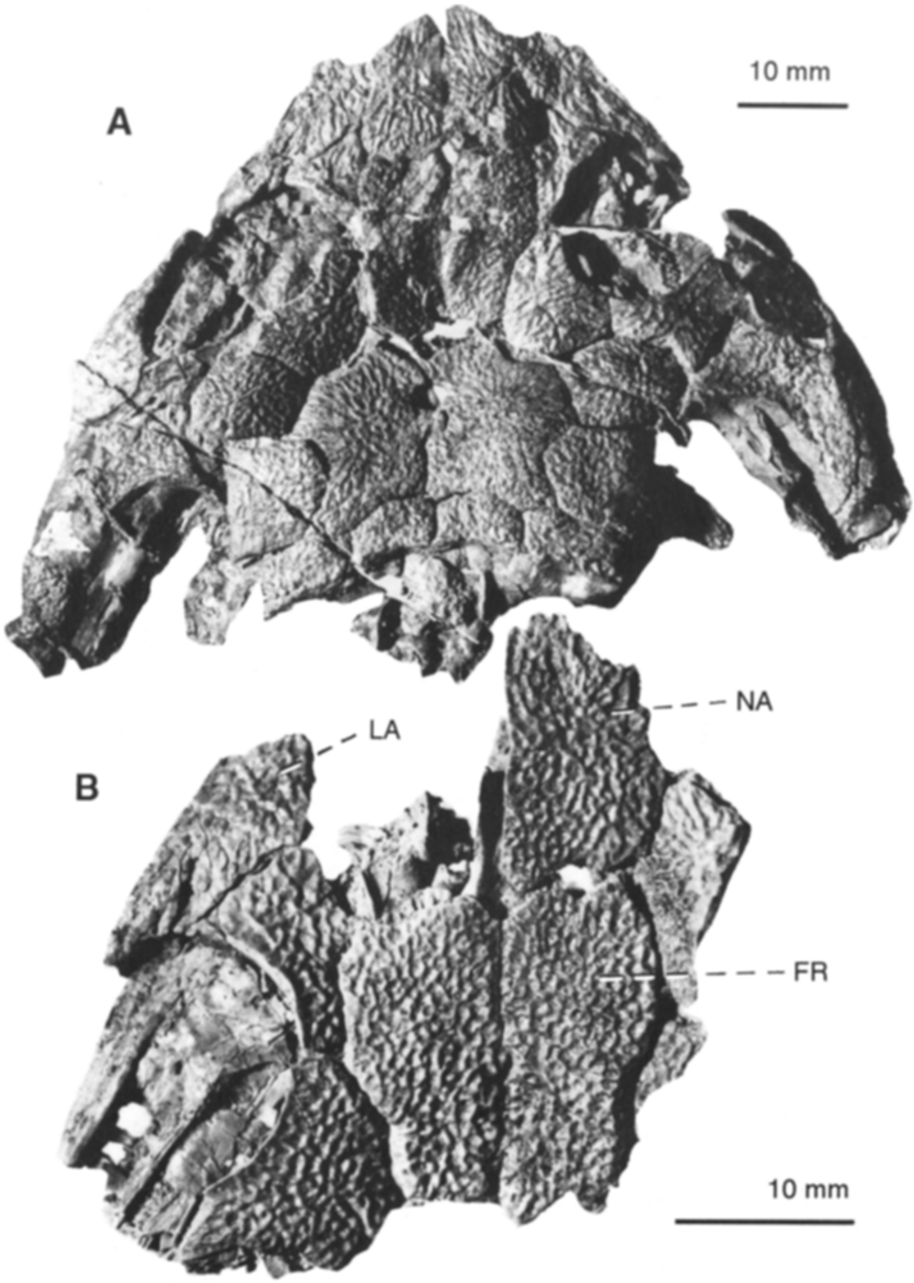

Fig. 7. *Discosauriscus austriacus* (Makowsky 1876). A: K 323, skull in dorsal view (cf. Figs. 9C, D). B: K 52, partial anterior half of skull in dorsal view (cf. Fig. 10E).

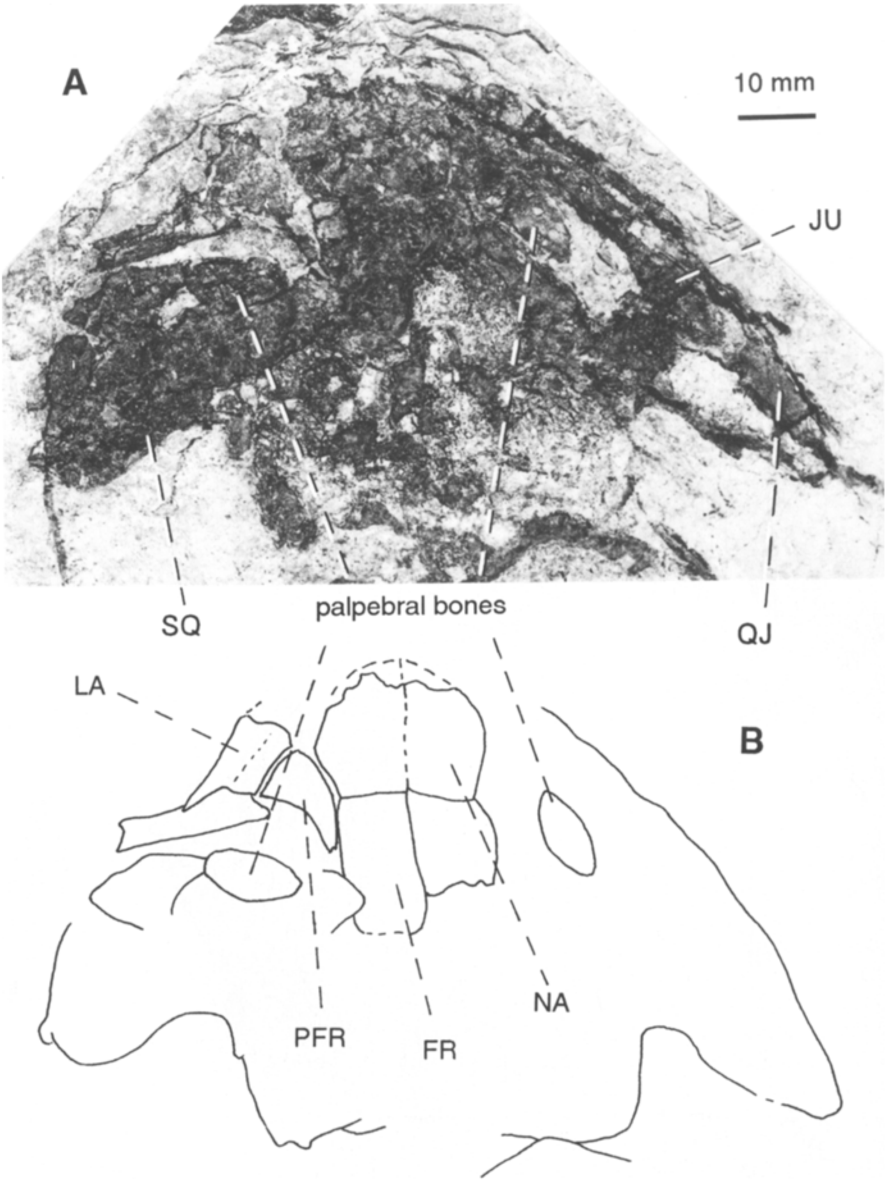

Fig. 8. *Discosauriscus* sp. A: OB 1, skull in dorsal view. B: Outlines of some cranial bones of the same specimen.

traditionally been considered to be seymouriamorphs (since ROMER 1947), (b) HEATON (1980) excluded them from the latter group, (c) ŠVEC (1986) suggested that discosauriscids are embolomeres, (d) FRACASSO (1987) concluded that *Seymouria* is a reptile and (e) according to HOLMES (1984) and SMITHSON (1985), the discosauriscids are a group of neotenic amphibians (based on IVAKHNENKO's (1981) results).

According to IVAKHNENKO (1987), external gills are absent in specimens of *Utegenia* and *Ariekanerpeton* of skull lengths greater than 15 mm. The largest specimens of *Discosauriscus* in which ŠPINAR (1952) recorded external gills, had skull lengths of 22–25 mm. This means that above this size threshold, the individuals started to metamorphose (IVAKHNENKO 1981; KUZNETSOV & IVAKHNENKO 1981). According to IVAKHNENKO (1987), individuals of *Ariekanerpeton* reach their definitive form at a skull length of about 25–30 mm, and specimens with a skull length about 50 mm are already senile.

The specimens of *Discosauriscus* with external gills considered in this paper have skull lengths from 20-32 mm. This means that this size category of *Discosauriscus* is represented by larval individuals. However, because there is no substantial difference in the skull anatomy of the individuals with skull lengths from 17–52 mm, apart from the changes associated with the larva-metamorphic stage transition (see below), it is very probable that the specimens of *Discosauriscus* in this size category include only larval and metamorphic, still aquatic, individuals; however, adult or senile specimens remain unknown.

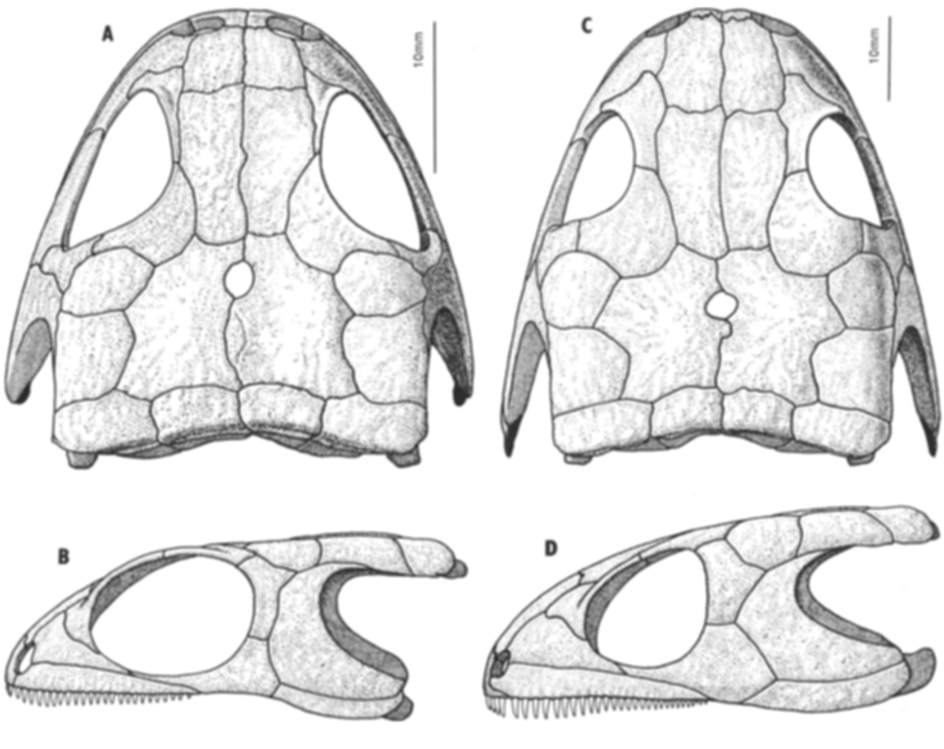

Fig. 9. *Discosauriscus austriacus* (MAKOWSKY 1876). Skull roof in dorsal (A, C) and lateral (B, D) views of a larval stage (A, B, based on specimen K 13 (SL = 27 mm) – cf. Fig. 3C; for ornamentation see KLEMBARA 1993: fig. 1) and an early juvenile stage (C, D, based on K 323 and K 52 – cf. Fig. 7).

Although the detailed skeletal anatomy of *Discosauriscus* will be described elsewhere, some data supporting this assumption will be given here (cf. Figs. 9 A, B and 9 C, D):

A. The larval characters of *Discosauriscus* (the specimens with a skull length up to 25–30 mm) are as follows (Figs. 3 C, 9 A, B):
- 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 (see also KLEMBARA & JANIGA 1993);
- anterior margin of pineal foramen lies almost at the level of the posterior margin of the orbit;
- squamosal and quadratojugal are relatively narrow and short;
- posterior extent of jaw joint lies in level of the supratemporal-tabular suture;
- otic notch is broad and shallow;
- marginal teeth with large pulp cavity, without infolding of dentine (Fig. 10 A).

B. The characters of the largest *Discosauriscus* specimens (up to about 52 mm skull length) which indicate the completion of metamorphosis (see below) are as follows (Figs. 7, 9 C, D):
- 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 the level of the posterior margin of the orbit;
- 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 (Fig. 10 E).

The above listed larval and postmetamorphic characters seem to be common for reptiliomorphs (i. e. *Discosauriscus*) and batrachomorphs (e. g. *Sclerocephalus* BOY 1988 or *Onchiodon* BOY 1990) and show that the largest specimens of *Discosauriscus* do not represent adult or senile individuals. As for the ontogeny of the earliest stages of *Ariekanerpeton* (up to 25 mm skull length), see IVAKHNENKO 1981.

To the larval and postmetamorphic characters of *Discosauriscus*, the other data regarding its cranial anatomy must be added:

1) IVAKHNENKO (1987) stated that in the senile specimens of *Ariekanerpeton* (SL = 48–50 mm) the ossification of the basioccipital and, in the largest specimens (to SL = 54 mm), ossified exoccipitals appear. Because *Ariekanerpeton* is extremely similar to *Discosauriscus*, these observations seem unlikely. In *Discosauriscus*, the small specimens (e. g. K 338.II, SL = about 17 mm, see KLEMBARA & MESZÁROŠ 1992: fig. 6) and the largest ones (e. g. KO 79) have the basioccipital and the exoccipitals ossified approximately to the same degree.
2) The quadrate, the articular and a substantial portion of the otoccipital region of the neural endocranium are cartilaginous (as well as many parts of the postcranial skeleton); cf. similar conditions in batrachomorphs (e. g. BOY 1974, 1988).
3) Radial ornamentation on some bones may occur in the largest specimens (see above and Figs. 6 B, 7 A); cf. the similar conditions in *Cheliderpeton* (BOY 1993) and some specimens of adult *Seymouria* (e. g. BROILI 1904).
4) Simple sutures are present even in the largest specimens (Figs, 5 B, 6, 7), although some exceptions exist (e. g. K 72, KLEMBARA 1994).
5) Incompletely ossified bones around the pineal foramen and possibly in the region of the "interpremaxillary fenestra" (KLEMBARA 1994) in specimens with skull length up to about 40 mm. In the largest K 323 and K 52, the region of the "interpremaxillary fenestra" is completely closed.
6) The posterior portion of the nasolacrimal canal roof is incompletely ossified in the largest specimens such as K 52 and K 323. The left nasolacrimal canal of KO 80 is closed, but the right one is still open (Fig. 6 A); in KO 79, the posterior portion of the left lacrimal is not well preserved but the right nasolacrimal canal is closed (Fig. 6 B). In *Sclerocephalus* (BOY 1988), the nasolacrimal canal becomes

closed dorsally during the larval stage, while in *Acanthostomatops* (BOY 1989) and *Onchiodon* (BOY 1990), the dorsally opened nasolacrimal canal persists through metamorphosis and it becomes completely closed in the middle and early juvenile period respectively.

7) The large number of extra or subdivided skull roof bones (KLEMBARA 1993). Extra bones are present also in one of the largest specimens – KO 79 (Fig. 6 B).
8) Sensory grooves are preserved on nasal and prefrontal also in large specimens (K 323, KO 79, KO 80); in the largest K 52, however, the distinct traces of sensory grooves are visible only on nasals (Figs. 6, 7). Pit-lines (KLEMBARA 1992) are also present in specimens with a skull length of 38 mm (e.g. D 91). The same is true for the foraminate pits (KLEMBARA 1992); in the large specimen KO 80, the foraminate pit is present in the right parietal and frontal (Fig. 6 A).
9) Strong vascularisation of the skin on the skull roof surface (there are many foramina in the external surface of the skull roof bones, Fig. 3 C); cf. the conditions in batrachomorphs (BOY 1974).

The above listed cranial features indicate that this size category of *Discosauriscus* includes larval, metamorphic and early juvenile (see also below) individuals.

Discosauriscus thus represents the early ontogenetic stages of a reptiliomorph amphibian. It should be emphasized that in the larva of *Discosauriscus*, with the exception of the stapes, ossified hyobranchial elements and dental ossicles (associated with the ceratobranchials) have not been recorded so far. The same conditions were recorded by IVAKHNENKO (1981) in *Ariekanerpeton* and by KUZNETSOV & IVAKHNENKO (1981) in *Utegenia*. This is different from the conditions found in larvae of various batrachomorph amphibians in which the hyobranchial skeleton is ossified or at least some hyal elements and the dental ossicles are always present (e.g. NILSSON 1946; HEYLER 1957; BOY 1972, 1988, 1990; BERMAN 1973; CARROLL & GASKILL 1978; MILNER 1982; HOOK 1983). The criterion of the absence of the dental ossicles in late metamorphic individuals in various batrachomorph amphibians (see e.g. BYSTROW 1939; Boy 1974, 1988, 1990) cannot be used in the reptiliomorph *Discosauriscus* for distinguishing larval and late metamorphic or early juvenile stages.

To determine the onset and completion of metamorphosis, the cranial characters listed above (paragraphs A, B and 1–9) as well as the conditions in the Bromacker *Seymouria* will be considered in a further analysis together with those in batrachomorphs (in which more or less complete ontogenetic series are recorded; e.g. BOY 1988, 1989, 1990, 1993).

Specimen KO 79 (preserved SL = 51 mm, Fig. 6 B) possesses residual traces of a radial ornamentation (mainly on the parietal and frontal), sensory grooves (clearly visible on nasals and prefrontals), and a closed nasolacrimal canal (visible in the right lacrimal). In KO 79, the nasals are slightly shorter than the frontals and the quadrates and articulars are not preserved (still cartilaginous). In the two largest and most robust specimens (K 52, K 323) the orbits are rounded and relatively small (Figs. 7, 9). In K 52, a polygonal ornamentation is present and its nasals are almost the same length as the frontals. Despite this, the orbits are placed relatively anteriorly (also in K 323) resembling the conditions in adult *Kotlassia* or *Karpinskiosaurus* (sensu IVAKHNENKO 1987) (Figs. 7, 9 C, D). In K 52 and K 323, the posteriormost portion of the nasolacrimal canal still remains open dorsally. The lateral line system is not strikingly developed in K 52 and K 323 (see above and Fig. 7). In K 323, the bases of the teeth are infolded; in K 52, the individual folds extend to the apex of the crown (Fig. 10 E). The latter condition is typical for the juvenile individuals in *Onchiodon* (BOY 1990). In the Bromacker *Seymouria* (SL = 56 mm), however, the sensory grooves appear to be completely absent, the ornamentation is moderately developed (unfortunately no further data are given), the nasolacrimal canal is closed (visible on the left side; the right lacrimal is not well preserved) and the length of nasals and frontals is almost equal (cf. the same prolongation of the preorbital region in many batrachomorphs: e.g. BOY 1988, 1989, 1990, 1993). The articular, however, is already ossified and the palpebral bone has appeared. These data indicate that the Bromacker *Seymouria* probably represents an already postmetamorphic, early juvenile individual. The above results also suggest that the largest specimens (KO 79, KO 80, but mostly K 52 and

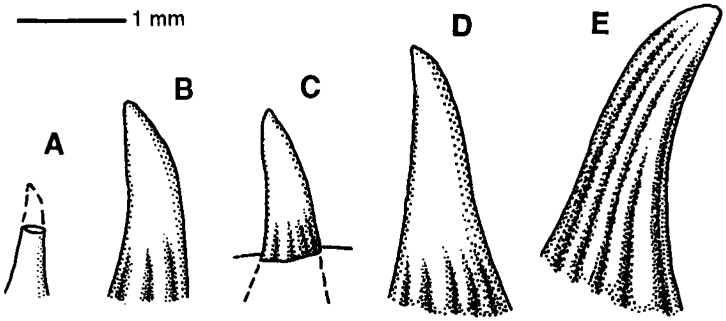

Fig. 10 A–C, E; *Discosauriscus austriacus* (MAKOWSKY 1876). D; *D. pulcherrimus* (FRITSCH 1879). Marginal teeth. A: K 337 (left maxillar tooth lingually; SL = 23.5 mm). B: KO 1 (left maxillar tooth from outside; SL = 31 mm). C: KO 129 (left maxillar tooth from outside; SL = 37 mm). D: K 16 (right premaxillar tooth lingually; SL = 44 mm). E: K 52: (left premaxillar tooth lingually; SL = about 52 mm).

K 323 – see also above listed characters in paragraph B and Figs. 6, 7) have basically completed their metamorphosis and represent already early juvenile individuals.

It is more difficult, however, to determine the onset of metamorphosis. In K 16 (SL = 44 mm, Fig. 5 A), the length of the nasal is 13 mm and of the frontal 17 mm. This, together with measurements of various individuals with skull length between 25–47 mm (KLEMBARA & JANIGA 1993) and of the largest ones given here, indicate the progressive prolongation of nasal relative to frontal. The degree of development of the polygonal pattern of ornamentation varies substantially with a skull length from 25 to 52 mm. The largest skull, in which the external gills have been recorded, is about 32 mm long. Therefore, without dental ossicles it is difficult to use these characters to determine unambiguously the onset of metamorphosis. As demonstrated above, the polygonal type of ornamentation starts to form on some bones in skulls with a midline length of about 25–30 mm. Up to this skull length, the nasals are very short (Fig. 3 C and data in KLEMBARA & JANIGA 1993) and about at this size the dentine of some marginal teeth starts to infold (Fig. 10). Hence, it may be that, by analogy with the conditions in eryopoids (e.g. BOY 1988, 1990, 1993), individuals of *Discosauriscus* with skull lengths of about (? 25)–30 mm had started to metamorphose. However, this undoubtedly varied among individuals and populations, depending on many factors, judging from the conditions in Recent amphibians (WILBUR & COLLINS 1973; DUELLMAN & TRUEB 1986) and, for example, from the different degrees of development of the polygonal type of ornamentation in the largest *Discosauriscus* specimens with skull lengths between 30–52 mm. It is clear that in the case of *Discosauriscus*, the populations of various year groups are compared. It may be concluded, on the base of ornamentation, that metamorphosis in *Discosauriscus* probably occurred in individuals of a skull length of about (? 25)30–50 mm (cf. the large variability of body sizes of individuals of the given population at metamorphosis, i.e. between the minimum and maximum size thresholds at which the metamorphosis undergoes in Recent amphibians; WILBUR & COLLINS 1973).

Specimen OB 1 (SL = 62 mm, Fig. 8) from the Boskovice Furrow would thus represent a juvenile individual living near or already outside of the water body. OB 1 is the largest specimen of *Discosauriscus* found since the first discovery in the Boskovice Furrow in 1872 (AUGUSTA 1948). Specimens of skull length 45–52 mm are rare (apart from the four large specimens discussed above, K 19.I, KLEMBARA & MESZÁROŠ 1992, is in this size category), while those below this size category are relatively abundant.

The assumption that K 52 and K 323 had completed metamorphosis and that larger individuals were already juveniles is supported by the presence of the palpebral bones in the Bromacker *Seymouria* and in OB 1. According to BELLAIRS & KAMAL (1981), the intradermal osteoderms, which include the supraoculars, supraorbitals, supraciliars or palpebrals, develop in postnatal life in saurians (however, see the discussion as for the ontogeny of palpebral in *Varanus* in JOLLIE 1960). In Recent salamanders and anurans, the eyelids only develop at metamorphic climax and in caecilians, the eyes are covered by bone or a thin layer of skin also in this period of ontogenesis (DUELLMAN & TRUEB 1986). Based on the above analysis, the palpebral bone in the Bromacker *Seymouria* also develops relatively late, during the last phases of metamorphosis or in the early juvenile period (probably as preparation for terrestrial life).

The recognition that at least the four largest specimens had completed their metamorphosis and the appearance of palpebral bones in OB 1 indicate that *Discosauriscus* was not a paedomorphic (at least obligate) animal. However, the facultative paedomorphosis of some populations cannot be excluded. For example, specimen K 329.II (Fig. 5 B) is relatively large (SL = 40 mm) and the ornamentation is of larval type.

In the case that individuals of *Discosauriscus* completed their metamorphosis at a skull length of about 50 mm, it must be expected that such large larvae would need several years to reach metamorphosis. However, this probably also occurred in *Archegosaurus* (BOY 1974, metamorphosis completed in specimens with a skull length about 70 mm) and *Cheliderpeton* (BOY 1993, the smallest juveniles had a skull length of about 50 mm); cf. also conditions in *Onchiodon* (BOY 1990).

The above results suggest that the genera *Utegenia* (KUZNETSOV & IVAKHNENKO 1981; IVAKHNENKO 1987) and *Ariekanerpeton* (IVAKHNENKO 1981, 1987) are also based on larval animals (*Ariekanerpeton* may also include early juvenile individuals) and hence the revision of both genera as well as the whole family Discosauriscidae is needed. Similarly, all comparative analyses in which *Discosauriscus* was compared with various adult early tetrapods to establish the interrelationships (e.g. HEATON 1980; ŠVEC 1984, 1986) must be revised.

The recognition of *Discosauriscus* as representing early ontogenetic stages is very important because such characters as the presence of subdivided or fused bones (KLEMBARA 1993), pit lines and foraminate pits (KLEMBARA 1992) are ontogenetic, not paedomorphic; hence, more probably reflect the primitive ancestral conditions. Therefore, it has considerable meaning in the solution of the problem of homology of the skull roof bones in tetrapods and fishes (KLEMBARA 1992, 1993).

Acknowledgements

For critically reading the manuscript and its linguistic correction I am indebted to Dr. A. R. MILNER (Birkbeck College, London). I thank Mr. JURAJ GULLÁR (Bratislava) for the drawings of the figures 9 and 10. For collecting and preparation specimens studied in this paper I thank Dr. M. HORNÁČEK (Smolenice), Mrs. Z. ŠULAVÍKOVÁ (Comenius University, Bratislava) and Mr. Š. MESZÁROŠ (Bratislava).

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Eingang des Manuskriptes am 7. Januar 1994;
Annahme durch die Schriftleitung am 15. April 1994.