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NEW FINDS OF *DISCOSAURISCUS AUSTRIACUS* (MAKOWSKY 1876) FROM THE LOWER PERMIAN OF BOSKOVICE FURROW (CZECHO-SLOVAKIA)

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Abstract: The excavations at two localities in the Boskovice Furrow have produced new, abundant skeletal material of the Lower Permian discosauriscid tetrapods. The specimens are three-dimensionally preserved and the carbonized remains of the soft parts are present. The stratigraphy and palaeoecological situation of both localities is discussed. The rock of the *Discosauriscus* horizon may be characterized as a highly bituminous, laminated limestone or rhythmite. The situation at both localities suggests that the places in which the animal bodies have been deposited after death were not the original life environment of *Discosauriscus*. The content of the coprolite lying in the abdominal region of one large specimen demonstrates unambiguously the cannibalism in *Discosauriscus*.

Key words: discosauriscids (*?Seymouriamorpha*), Lower Permian, stratigraphy, lithology, palaeoecology, cannibalism.

Introduction

The first discovery of discosauriscids from the Boskovice Furrow in Moravia was made in 1872 at the locality Malá Lhota near Černá hora (cf. Augusta 1948). The skeletons of discosauriscids were found together with plant remains, in dark, Lower Permian shales. These first amphibian remains were described by Makowsky (1876) as *Archegosaurus austriacus*. Subsequently, several localities have been found in the Boskovice Furrow, providing abundant material of variable quality of these Lower Permian tetrapods. Špinar (1952) in his major revision reviewed the anatomy and taxonomy of the Moravian discosauriscids, summarising the history from the earliest research up to 1951. Subsequently, Kuznetsov & Ivakhnenko (1981), Ivakhnenko (1981, 1987), Švec (1984, 1986) and Werneburg (1985, 1988, 1989) have each dealt with some aspects of the taxonomy and morphology of the Moravian discosauriscids.

Discosauriscids are relatively abundant members of the Eurasian (?Upper Carboniferous) - Permian tetrapod fauna. According to Ivakhnenko (1987), the discosauriscids are represented on the Eurasian continent by three genera: *Discosauriscus* Kuhn 1933, *Ariekanerpeton* Ivakhnenko 1981 and *Utegenia* Kuznetsov and Ivakhnenko 1981, forming the family *Discosauriscidae* Romer 1947. This was also accepted by Werneburg (1985, 1988, 1989). Ivakhnenko (1987) divided the family *Discosauriscidae* into two subfamilies: *Utegeninae* Ivakhnenko 1987 (including the single genus *Utegenia*) and *Discosauriscinae* Romer 1947 (including the genera *Discosauriscus* and *Ariekanerpeton*). Werneburg (1989) accepted the existence of these subfamilies, but he included the genera *Discosauriscus* and *Letoverpeton* in the subfamily *Discosauriscinae* and the genera *Utegenia* and *Ariekanerpeton* in the subfamily *Utegeninae*. According to Heaton (1980) the systematic position of discosauriscids is unclear; Smithson (1985; cf. Romer 1947) included them in the suborder *Seymouriamorpha* of the order *Anthracosauria*.

In a detailed study of the Moravian discosauriscids, Špinar (1952) also described the genus *Letoverpeton*, which differs from *Discosauriscus* in the proportions of different skeletal elements and of the entire body. According to Špinar (1952) each genus comprises two species: *D. pulcherrimus* (Fritsch 1879), *D. potamites* (Steen 1938), *L. moravicum* (Fritsch 1883) and *L. austriacum* (Makowsky 1876). This conclusion was not accepted by Ivakhnenko (1981 1987), who regarded the differences between these species as the result of compressional deformation and he aggregated all Moravian discosauriscids as one species - *Discosauriscus austriacus* (Makowsky 1876). However, Werneburg (1985, 1988, 1989), in an evaluation of the German material, accepted Špinar's conclusions (with the exception of *D. potamites*) and moreover described a new species *L. thuringiacum* (Werneburg 1988). Other Eurasian records of discosauriscids are: *D. "sacheti"* (Saint-Seine 1949) - cf. Heyler (1969), Werneburg (1989), *Urumquia lindaowanensis* (Fakui, Yaozeng & Xungang 1984) and *Discosauriscus netschaevi* (Riabinin 1911), which probably comes from the Upper Permian (Ivakhnenko 1981, 1987).

Since 1986, animal and plant material has been systematically collected in two localities of the Boskovice Furrow, rediscovered by Š. Meszároš. The discosauriscid material is relatively abundant and will be published in several papers. As will be shown elsewhere (Klembara & Janiga in press), the discosauriscids from the Boskovice Furrow described up to now represent probably only one genus and species: *Discosauriscus austriacus* (Makowsky 1876). This conclusion was made on the basis of the statistical analysis of seventeen variable characters on seventy skulls (Klembara & Janiga op. cit).

Abbreviations used in figures:

IS - ischia, PFR - prefrontal, PP - postparietal, S - stapes, TA - tabular, f - femur, h - humerus, m - manus, r + ver I - ribs + vertebrae (specimen K 19.I), s.g. - shoulder girdle, ver II - vertebrae (specimen K 19.II).

Material and methods

To date, about 300 specimens have been collected. The adult middle sized specimens (Figs. 6, 7, 12) together with a few relatively poorly preserved larval stages are commonest. A few large specimens are present; an almost complete skull of one of them - K 323 - is 51 *mm* long (nasals - postparietals), Fig. 1. The size of the skull bones and vertebrae of K 52 indicate that its skull was larger than that of K 323, although, the vertebrae are more gracile.

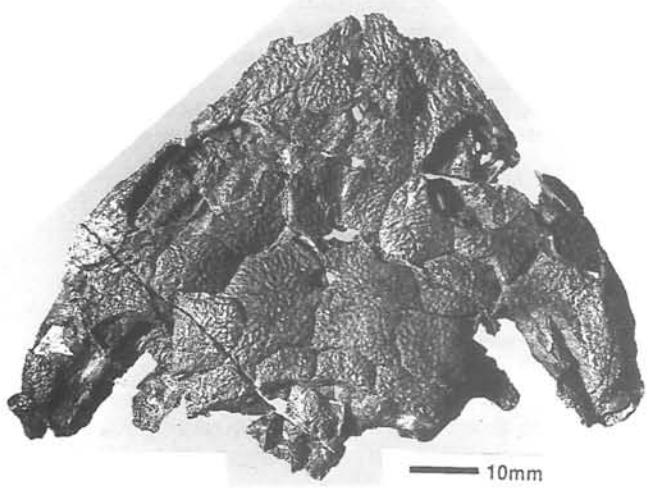

Fig. 1. *Discosauriscus austriacus* (Makowsky 1876), K 323. Skull in dorsal view.

In both localities, the remains of *Discosauriscus* are usually embedded in the rock, more rarely they lie on the surface of the shale. At Letovice (Kochov) they can often be found immediately under the split surfaces of the blocks, overlain by a thin layer of sediment. The rock was dissolved in an 8 % solution of acetic acid, and the bones with calcium phosphate, were saturated with the acetone glue. The bituminous layers had to be removed mechanically. In this way the skull remains were removed from the rock entirely (Fig. 1) or partially (Figs. 2, 6, 7, 12). On the bedding plane of some partly preserved specimens, the carbonized soft parts of the bodies are clearly visible. The skeletal material of *Discosauriscus* is three-dimensional unlike the material from previously known localities in the Boskovice Furrow. Numerous details of structure are preserved such as the openings for blood vessels and nerves and the character of the articular surfaces. It is nevertheless necessary to be careful in the study of material preserved in this way because in the study of compressed elements of skull, false interpretations of the morphology of individual bones and detailed structures can be made.

The material of *Discosauriscus* will be deposited after study in the Slovak National Museum in Bratislava. It is deposited currently in the Zoological Institute, Faculty of Natural Sciences, Comenius University, Bratislava.

The list of the *Discosauriscus* specimens and other animals from the both localities (D - Drválovice, K - Kochov) used in this paper:

D 201.I-IX - one block with skeletal remains of nine specimens; D 208 - partial skull of juvenile individual; D 209 - skull; K 18 - skull and shoulder girdle; K 19.I - greater part of presacral vertebral column with ribs of large individual and coprolite in its abdominal part, scales; K 19.II - posterior part of skull and incomplete postcranial skeleton of relatively small individual; K 19.III - content of coprolite K 19.I: right prefrontal, ?neural arch and big amount of bone pieces; K 47 - skull roof; K 52 - partial skull and postcranial skeleton of a large individual; K 110.I - badly preserved skull and anterior part of vertebral column; K 110.II - insect; K 140 - badly preserved skull and postcranial skeleton; K 141 - disarticulated skull; K 170 - several fragments of skull bones; K 171 - disarticulated skull; K 215.I - skull, ante-

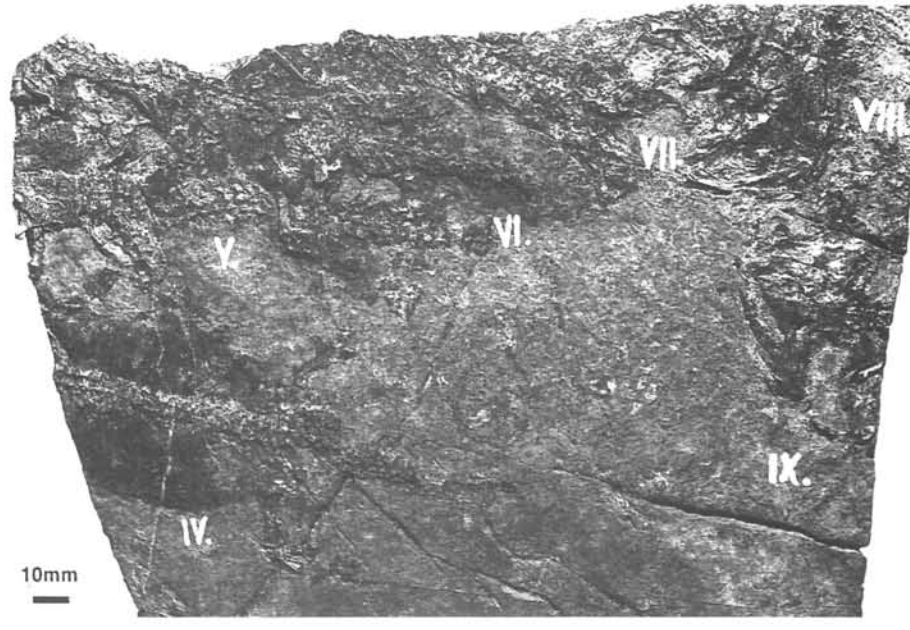

Fig. 2. *Discosauriscus austriacus* (Makowsky 1876), skeletal remains of six specimens D 201.IV - IX on one block surface.

rior postcranial skeleton; K 215.II - complete fish skeleton (probably *Paramblypterus*); K 216 - skeletal remains (probably *Xenacanthus decheni*); K 217 - disarticulated skull; K 249 - some mostly disarticulated skull bones and fragments of interclavicle and right clavicle; K 323 - skull and relatively complete postcranial skeleton; K 329.I - skull and partly disarticulated postcranial skeleton (plus coprolite in abdominal portion) of small individual; K 329.II - skull and anterior portion of postcranial skeleton; K 338.I - skull and articulated postcranial skeleton; K 338.II - skull and articulated postcranial skeleton of small individual; K 347 - skull and articulated postcranial skeleton.

Localities and stratigraphy

The material of *Discosauriscus* comes from two localities (Fig. 3):

1 - The first locality is southwest of the village of Vanovice (district Drválovice) at the private estate of the family Kubík, in the vicinity of a former windmill (Špinar 1952). The excavation site is situated about 40 *m* west of the family house, at the beginning of the walnut-tree alley.

2 - The second locality is situated at the western margin of the town of Letovice (district Kochov). The excavation was carried out at the top of a hill called "Horka", east of the road between Kladoruby (a district of Letovice) and Kochov (about halfway between them).

The lithological profiles of both localities are represented in Fig. 4.

The remains of *Discosauriscus* mainly derive from the key horizon of the upper grey formation, zone II B_3 (Havlena & Špinar 1956), characteristic of the Boskovice Furrow sedimentary cycle. This formation is designated as the ťBačov Bedsť in the literature and is known from several occurrences in the area of the Boskovice Furrow. It forms a significant lithofacial cycle in Lower Permian red sediments here.

The horizon with *Discosauriscus* remains is in the lower part of the grey formation (Fig. 4, horizons 7 - Drválovice and 16 - Kochov). Its thickness varies from 24 to 28 *cm*. The rock may be characterized as a highly bituminous limestone or rhythmite. In places where it is considerably microtectonically disturbed, it may be designated as stylolaminite. Wider fissures are filled up with calcite, more rarely with quartz or asphalt. The colour of the unweathered rock is light-brown (Drválovice) or greyish-blue to greyish-black (Kochov). In transverse thin section, fine lamination can be seen. Thicker, light-coloured laminae alternate with thinner darker ones. Dark laminae are formed by micritic fine-grained carbonate mud with higher content of organic substance (bitumens). Light-coloured laminae are formed by microsparite to sparite. The maximum thickness of dark laminae is 0.25 *mm*, and the maximum thickness of light-coloured laminae is 1 *mm*. Dark laminae often show lenticular development and the occurrence of skeletal remains is usually associated with them or with the boundary of dark and light-coloured laminae. Small fragments of bones are also found rarely in light-coloured laminae. Apart from the skeletal material, the rock contains almost no organic remains. In thin section, only two possible zoospores were found. In ligth-coloured laminae, minute micrite grains and clastic quartz grains of silt size are occasionally present. The sedimentation is probably the result of seasonal changes throughout the year, with light-coloured laminae deposited in a warmer period with higher evaporation, while the darker laminae reflected cooler climatic periods, poorer living conditions for *Discosauriscus*.

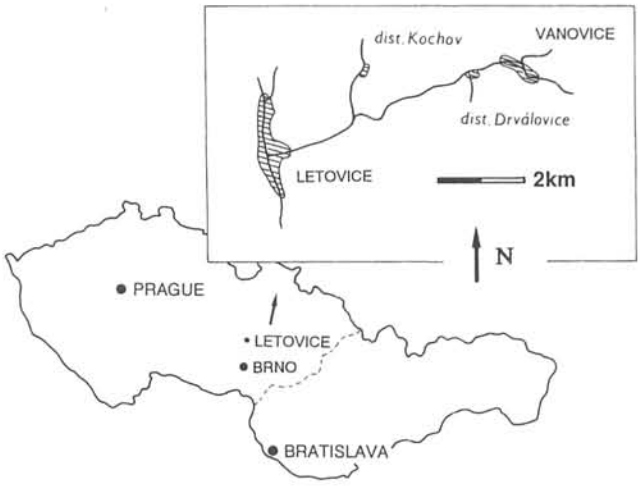

Fig. 3. Schematic map of the Drválovice and Kochov localities.

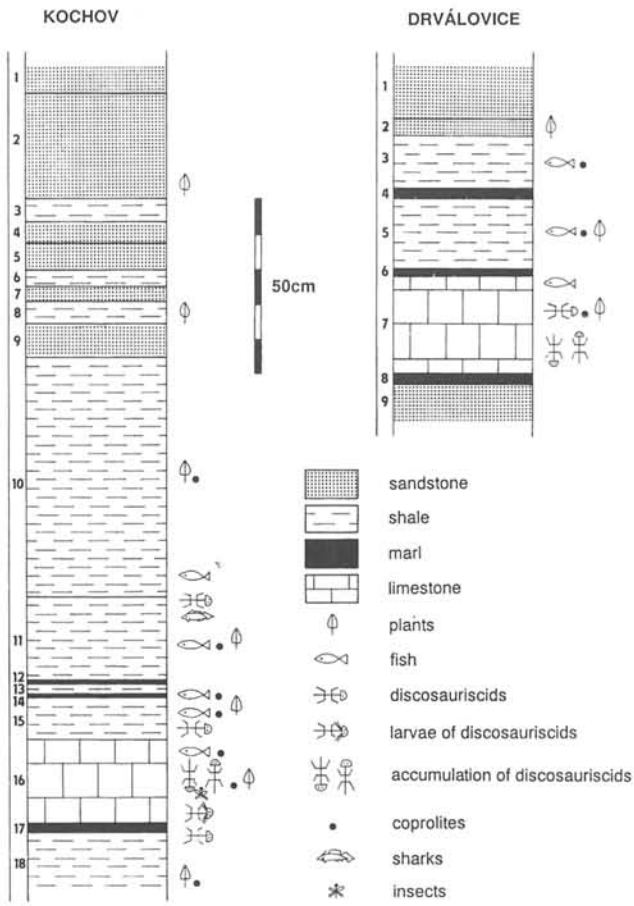

Fig. 4. Schematic lithological profiles of the test pits at the Drválovice and Kochov localities.

At Drválovice, the greatest accumulation of *Discosauriscus* was in the lower part of the horizon, in three layers, about 3 to 4 *cm* far from one another (Fig. 4). Deposition of 50 individuals in the uppermost layer in the larger part of an area 160 x 120 *cm* is chaotic (Fig. 5). A hundred metres north of this locality, where

the horizon was also uncovered in the excavation for a water pipe, discosauriscids were very scarce. At Drválovice, mostly adult forms are found. The find of two individuals D 208 and D 209 may be considered as exceptional so far. Specimen D 209 represents a skull of a large animal whereas D 208 is a larval skull. This small skull was lying close behind and to the right of the large skull.

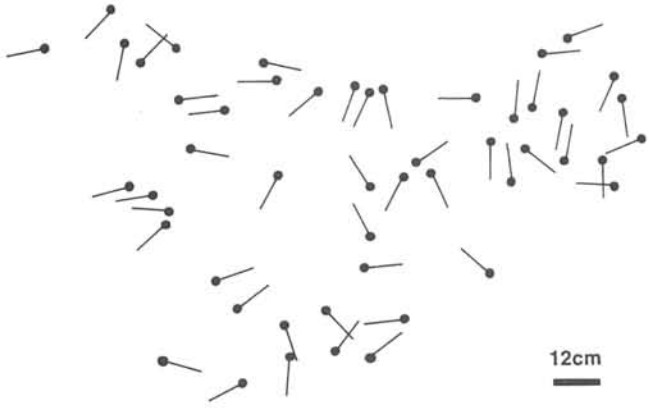

Fig. 5. Diagram to illustrate distribution and arrangement of *Discosauriscus* skeletons on a bedding plane of approximately 160 x 120 *cm*. For explanation see text.

Fig. 6. *Discosauriscus austriacus* (Makowsky 1876). Skull and postcranial skeleton in dorsal view of large specimen K 338.I and skull and postcranial skeleton in ventral view of small specimen K 338.II.

At Kochov (Fig. 4) remains of *Discosauriscus* are not found in such a high concentration as in Drválovice. They are, however, less pressure-deformed. The largest specimens are from Kochov. At a height of about 1 *cm* from the lower surface of the horizon, relatively abundant larvae are found, otherwise they are scarce. It is interesting that almost all larvae are lying with the dorsal side of body in rock. Apart from this horizon *Discosauriscus* was also found in bed 11 (very poorly preserved remains of carbonised specimens: block K 140) and several poorly preserved specimens in beds 15 (K 47) and 17 (K 141, K 170, K 171, K 217), Fig. 4. The discovery of an insect fossil together with *Discosauriscus* (K 110.I, II) in the lower part of the horizon, in which insects had not previously been found, is also interesting.

Fish, probably of the genus *Paramblypterus* (pers. comm. Dr. S. Štamberg) (Fig. 8), are quite abundant at both localities. They are found in the upper part of the horizon with *Discosauriscus*, but mainly in the overlying beds, called ŕfish bedsŕ by Špinar (1952). At Kochov, shark remains were also found, probably of the species *Xenacanthus decheni* (K 216). As for remains of plants and coprolites - see Fig. 4.

Palaeoecology

The Boskovice Furrow is manifested morphologically as a relatively narrow depression exposed toward the NNE - SSW. It is an asymmetrical graben filled with Permo-Carboniferous sediments (Jaroš 1963; Holub 1972). The sedimentation filling of the depression is broadest in the region of Letovice, about 12 *km*.

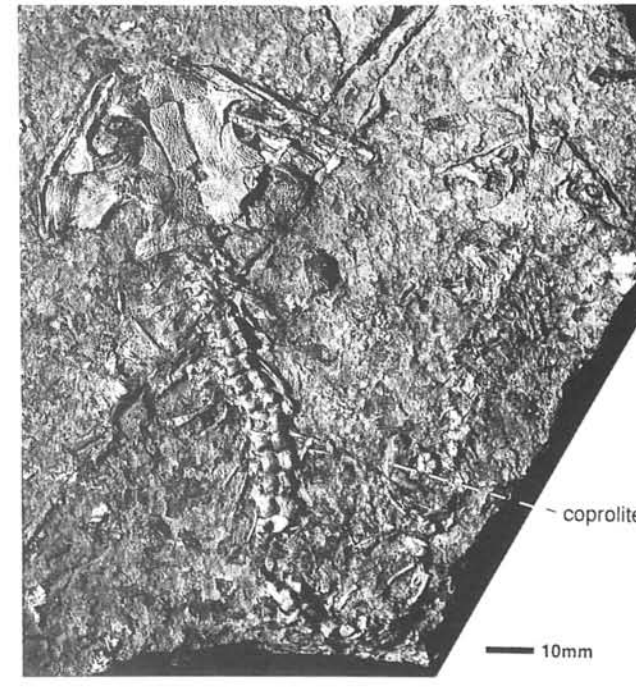

Fig. 7. *Discosauriscus austriacus* (Makowsky 1876). Skulls and parts of postcranial skeletons in dorsal view of smaller - K 329.I and larger - K 329.II specimens.

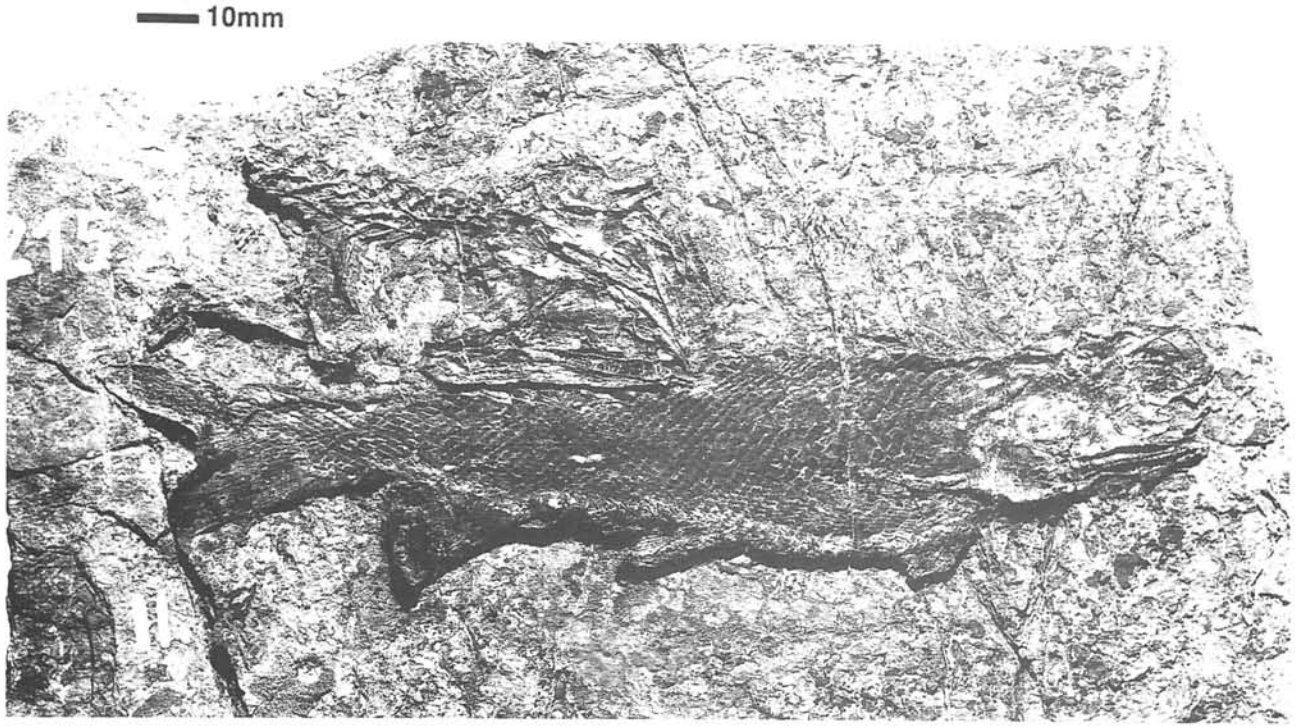

Fig. 8. *Discosauriscus austriacus* (Makowsky 1876). K 215.I, skull and anterior postcranial skeleton in ventral view; K 215.II, complete fish skeleton (? = *Paramblypterus*).

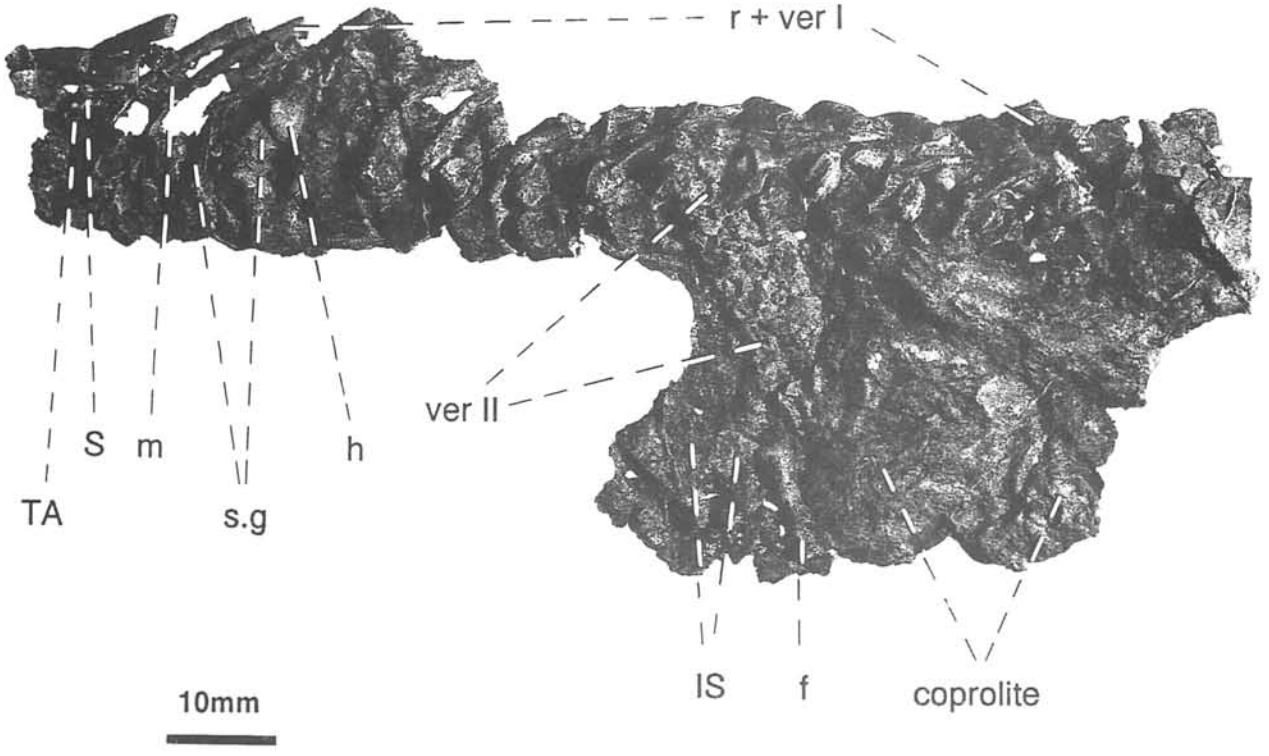

Fig. 9. *Discosauriscus austriacus* (Makowsky 1876). Ribs, vertebral column and coprolite of large individual K 19.I; other skeletal remains belong to smaller individual K 19.II. Right prefrontal of K 19.III (see Fig. 10) is visible on opposite side of coprolite.

According to Špinar (1952), the depression of the Boskovice Furrow probably represents a part of the region periodically filled with the broad desert river overflowing deposits. This river probably also formed extensive shallow basins in the rainy periods of the Permian, overgrown with abundant vegetation (12 plant species have been identified). According to Špinar, these places represented the life environment of the *Discosauriscus*, where it was feeding; its sudden disappearance was probably caused by changes in the environment in which it lived.

The situation at Drválovice and Kochov suggests that the places in which the animal bodies have been deposited were not original life environment of *Discosauriscus*. The environment in which the animals were buried was strongly anoxic, or probably disoxic. This is indicated by the high content of bituminous component. Although these beds have produced tetrapod remains, fish, an insect and a small amount of plant debris; scavenging benthic animals were absent, despite the relatively large amount of potential food. Coprolites of *Discosauriscus* are rare here (in two specimens K 19 and K 329.I coprolites were found in the body - Figs. 7, 9); but fish coprolites are abundant. Also a slightly laminated sediment (see above) suggests the presence of deeper, more distant places from the bank of the lake or larger water basin. The sediment is very fine, implying a low energetic environment. The skeletons (or their parts) are mostly articulated, and isolated bones are rare. The location of bodies of 50 specimens on the layer surface in Drválovice shows no bias in orientation (Fig. 5, the specimens are partly prepared and were contained in more laminae). At both localities, skeletons of almost equal size mostly occur (mostly middle-sized specimens); large specimens are almost absent (also observed by Špinar in 1952). The specimens of different size, occurring one by another (Figs. 6, 7) are rare. At Kochov, the larvae are more abundant in the lower part of horizon; in higher positions they are rare. It may be relevant to note the gradual widening of the lake in the space of the former graben. It appears that the specimens were, to a certain degree, sorted into size categories. After death the carcasses were probably transported by flotation to various distance from the bank, according to their size.

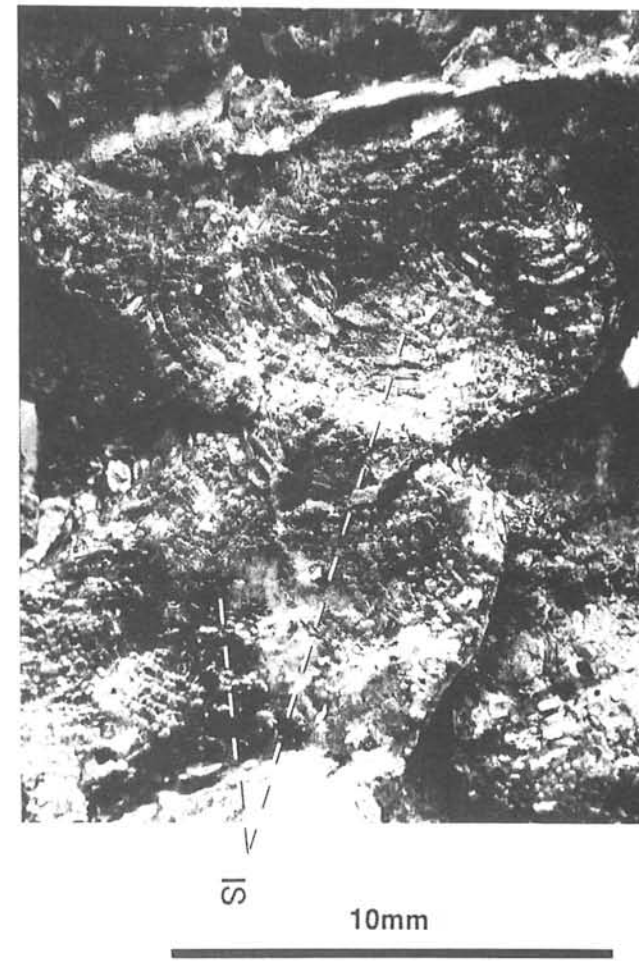

Fig. 11. *Discosauriscus austriacus* (Makowsky 1876). Large scales of K 19.I on ischial surfaces of smaller specimen K 19.II (cf. Fig. 9).

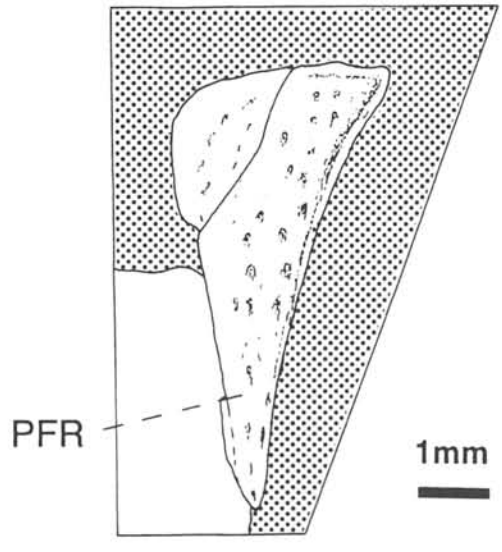

Fig. 10. *Discosauriscus austriacus* (Makowsky 1876), K 19.III. Right prefrontal of small specimen in dorsal view contained in the coprolite of big specimen K 19.I (cf. Fig. 9).

Cannibalism

In this connection, the discovery of two specimens K 19.I, II from Kochov is very interesting. The specimen represents a part of the vertebral collumn (17 presacral vertebrae) with the ribs of one of the largest skeletons (Fig. 9). Close to the hind half of this incompletely preserved presacral part of the column (K 19.I), in the abdominal region, a large compressed coprolite, containing many fragments of mostly undeterminable bones, is present. Among them, however, it is possible to identify one well preserved larger fragment of bone, which could represent part of a neural arch. Anteriorly to it a well-preserved and ornamented flat bone is situated. Its shape and type of ornamentation indicate a slightly compressed right prefrontal (Fig. 10). When compared with other specimens, the lenght of the skull of the specimen with the prefrontal (K 19.III) can be estimated as about 25 *mm*.

Close to the coprolite, almost perpendicularly to the vertebral column of the large specimen (K 19.I) lies a well preserved, substantially smaller specimen (K 19.II, Fig. 9). It is represented by the incompletely articulated vertebral column, ribs, pelvic girdle and several bones of the hind extremities. Further anteriorly also lie, pressed to the vertebrae of the large specimen, the remains of the shoulder girdle, anterior extremity and the remains of the posterior part of the skull (e.g. a well preserved left

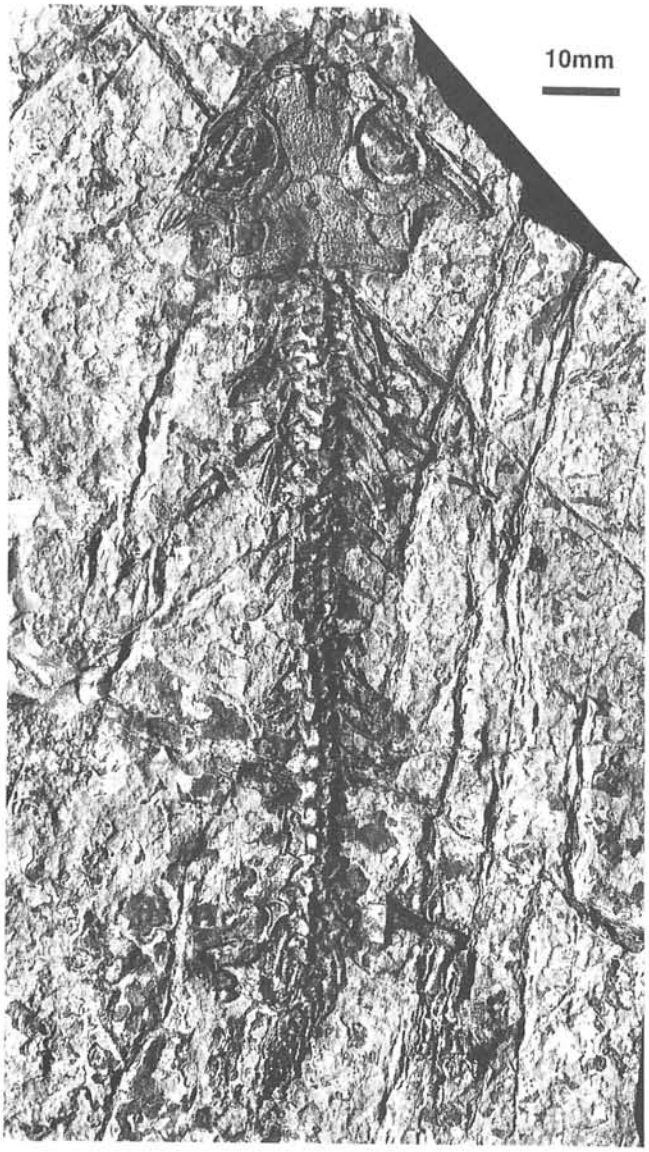

Fig. 12. *Discosauriscus austriacus* (Makowsky 1876), K 347. Skull and postcranial skeleton in dorsal view.

tabular and stapes), Fig. 9. The position and size of these remains indicate that they are the anterior part of the skeleton of the smaller specimen (K 19.II). All parts of the smaller skeleton lying by the vertebrae column of the large specimen, as well as the abuting part of the coprolite, are overlain by the ribs of the large specimen. It is evident that the smaller specimen and coprolite lay in the abdominal cavity. This is also shown by the larger scales covering the skeleton of the smaller specimen and coprolite from both sides. These larger scales can be readily identified on the surface of the pelvic girdle of the smaller specimen (Fig. 11). The longest distance of the uncovered surface of the scale is about 4.5 *mm*. Špinar (1952) stated the average of the scale to be about 2 *mm* in adult discosauriscids. This can be observed also in several specimens in the new material (e.g. K 18, K 249). The remains of the trunk of the smaller specimen are covered with these large scales and are well visible on the surface of the interclavicle stem. From the observation of the size of the concentric lines of large scales and those pressed to the specimens K 18 and K 249 it is evident that the scales, from both sides covering the smaller specimen, the coprolite and the adjacent surfaces, had to belong to the large specimen (K 19.I). The content of the coprolite of this large specimen demonstrates unambiguously the occurrence of cannibalism in discosauriscids.

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