Variation in *Discosauriscus austriacus* (Makowsky, 1876) from the Lower Permian of the Boskovice Furrow (Czech Republic)

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Two genera and four species of discosauriscids, *Discosauriscus potamites*, *D. pulcherrimus*, *Letoverpeton austriacum* and *L. moravicum*, have previously been described from the Boskovice Furrow in Moravia. These taxa were differentiated primarily on the basis of proportional differences of the skull together with other morphological characters.

Excavations at two localities in the Boskovice Furrow have produced new, relatively abundant, skeletal material. The specimens are preserved three-dimensionally. In order to evaluate the differences in skull proportions, 17 variable characters on 70 skulls were measured. Statistical analysis demonstrates the existence of several morphological trends in the shape of the skull. However, no trend permits the division of this set of specimens into two clearly differentiated groups. The morphological differences used previously to define genera and species seem to be incorrect. Pending the discovery of distinct morphological differences, the Moravian discosauriscids can be considered as belonging to only one taxon: *Discosauriscus austriacus* (Makowsky, 1876).

ADDITIONAL KEY WORDS:—Tetrapoda – discosauriscids' cranial measurements – morphometrics – taxonomy.

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INTRODUCTION

Discosauriscids are relatively abundant members of the Eurasian Permian tetrapod fauna. According to Heaton (1980; cf. Holmes, 1984), their systematic position is unclear. Most authors, however, consider that they are representatives of the Seymouriamorpha (e.g. Romer, 1947; Špinar, 1952; Smithson, 1985; Ivakhnenko, 1987; Werneburg, 1989).

According to Ivakhnenko (1987) the discosauriscids are represented by three genera: *Discosauriscus* Kuhn, 1933, *Ariekanerpeton* Ivakhnenko, 1981 and *Ulegenia* Kuznetsov & Ivakhnenko, 1981, forming the family Discosauriscidae Romer, 1947. Špinar (1952) described new material from localities in the Boskovice Furrow. In addition to *Discosauriscus*, Špinar also described the new genus *Letoverpeton*, which differs in the proportions of its skull from the former; each genus comprises two species: *D. pulcherrimus* (Fritsch, 1879), *D. potamites* (Steen, 1938), *L. moravicum* (Fritsch, 1883) and *L. austriacum* (Makowsky, 1876). These conclusions were not accepted by Ivakhnenko (1981, 1987), who regarded the differences between these genera only as a result of compressional deformation; he considered all Moravian discosauriscids to be one species: *Discosauriscus austriacus* (Makowsky, 1876). Werneburg (1985, 1988, 1989), in a review of the German discosauriscids, accepted Špinar's (1952) conclusions (with the exception of *D. potamites*) and described a new species *L. thuringiacum* (Werneburg, 1988).

MATERIAL

Two localities of the Boskovice Furrow provided three-dimensionally preserved material of discosauriscids (Klembara & Meszároš, 1992). The material was chemically prepared and consequently the skulls could be readily measured.

The following is a list of *Discosauriscus* specimens (D—locality Drválovice, K—locality Kočov) used in this paper (except for the specimens used for the skull measurements used in Table 1; this material will be described in detail in future papers dealing with morphology):

D 20, 45, 73, 74, 80, 81, 100, 106, K 9, 14, 16—skulls only; K 20—skull, incomplete shoulder girdle and a few presacral vertebrae; K 58—partial skull and a few postcranial remains; K 74—skull; K 83—skull with a few postcranial elements; K 323—skull and relatively complete postcranial skeleton; K 328—skull and postcranial skeleton, K 337, 338.I, 339—skulls and articulated postcranial skeletons; K 341.I—skull and almost complete postcranial skeleton; K 346.I, 347—skulls and articulated postcranial skeletons.

MEASUREMENTS AND METHODS

Measurements. For the computer calculation, 14 characters (variables) were measured to an accuracy of 0.5 mm on 70 skulls (Fig. 1; Table 1). The next three characters, 15, 16 and 17 are totals of some of the characters (see Table 1). All 17 (i.e. 14+3) characters were present. Some explanatory notes concerning these skull measurements follow.

(1) Individual characters were measured only on the ornamented surfaces of

Figure 1. Diagram to illustrate *Discosauriscus* skull measurements; 14 characters (variables; cf. Table 1 and 'Measurements and methods'). (For key to abbreviations see p. 270.)

the dermal bones. Whenever possible, the total lengths were obtained by the total of individual bones (to eliminate the possible gaps between them caused by greater or lesser compression).

(2) It was not possible to measure the midline length (snout-tip–postparietal) because the premaxillary is mostly absent or displaced from its original position by varying degrees of compression. In the more strongly pressure-deformed skulls found at other localities in the Boskovice Furrow (Špinar, 1952), the exact measurements of some lengths is impossible. Therefore the measurements used by Špinar (1952) (e.g. 'length of skull', 'width of skull', 'middle height of orbit') are omitted. Moreover, such material has been mostly found on the bedding planes of split shale (i.e. not as fully preserved positives and negatives), which can prevent correct determination of the real shape of bone, or the differentiation of ornamented from unornamented surface. Also, in the new three-dimensional material from Drvňovice and Kočov, the lateral portion of the orbit is almost always disturbed.

(3) The length of the parietal is taken to be the distance between its anteromedial and posteromedial edge. The width of the parietals is the distance of their posterolateral edges (i.e. in the region of the junction of the parietal with the tabular and supratemporal). The lengths of the postparietal, frontal and nasal were measured in the same way as the length of the parietal.

TABLE 1. *Discosauriscus austriacus* skull

		Characters							
Specimen number		V1	V2	V3	V4	V5	V6	V7	V8
		Parietal foramen—postparietal	Width of skull table at mid-supra temporal	Length of parietal	Width of parietals	Length of frontal	Length of nasal	Width of nasal	Connecting line of lateral tips of prefrontals
K1	1	10.0	26.5	11.0	8.5	11.0	8.0	4.5	18.5
K5	2	7.5	20.0	8.0	12.5	10.0	6.0	4.0	16.0
K9	3	8.0	24.5	8.0	13.5	9.5	6.0	4.0	16.0
K13	4	9.0	21.5	9.0	13.5	10.5	5.0	4.0	15.0
K14	5	9.5	29.0	9.5	19.0	11.5	7.0	4.0	17.0
K17	6	5.0	23.0	8.0	14.0	9.0	5.0	4.0	14.5
K18	7	9.0	23.5	9.5	14.0	9.5	6.5	4.5	14.0
K20	8	9.0	24.5	8.5	14.5	11.0	7.0	5.0	17.0
K31	9	7.5	18.0	8.5	11.5	9.5	5.5	3.5	13.0
K36	10	8.0	21.5	8.5	14.0	10.0	7.0	4.0	14.0
K40	11	10.0	27.0	10.5	16.0	13.0	7.5	4.0	16.0
K47	12	9.0	23.5	10.0	15.0	10.0	7.0	4.0	17.0
K49	13	9.5	25.0	11.0	16.0	10.5	6.0	4.5	18.5
K50.I	14	8.5	21.5	9.0	13.0	9.5	5.5	3.5	14.0
K54	15	12.0	28.0	13.5	18.5	16.0	11.5	5.0	23.0
K55	16	9.0	23.0	8.0	14.0	10.0	8.5	4.0	16.0
K57	17	9.0	24.0	9.0	14.5	10.5	7.0	4.0	13.0
K60	18	9.0	22.0	11.0	14.0	10.5	7.0	4.0	17.5
K64	19	8.5	22.0	9.0	15.0	9.0	6.0	3.5	14.5
K69	20	9.0	25.0	11.0	14.0	11.5	7.0	4.5	16.5
K72	21	8.5	24.0	9.0	15.5	11.5	8.0	4.5	18.0
K83	22	8.5	22.5	8.5	14.5	11.5	7.0	3.5	14.5
K84	23	9.0	27.0	10.0	16.0	10.5	6.5	4.0	16.5
K98	24	8.5	22.0	8.5	14.0	10.0	5.5	4.0	13.5
K99	25	9.0	22.0	9.0	14.5	10.0	4.5	4.0	15.5
K100	26	7.5	20.0	7.5	12.0	8.5	5.0	4.0	15.0
K102	27	8.5	27.0	10.0	17.0	10.0	8.0	4.5	16.5
K113	28	8.0	26.5	8.0	17.0	11.0	7.0	4.0	16.0
K172	29	11.5	27.5	12.5	17.5	11.5	8.5	5.5	19.5
K194	30	7.5	22.5	8.0	14.5	10.0	6.5	4.0	15.0
K206	31	9.0	25.0	10.0	15.5	10.5	7.0	3.5	15.0
K208	32	8.0	23.0	9.0	13.5	9.5	5.5	4.5	15.0
D4	33	10.0	22.0	11.0	14.5	10.0	7.0	4.0	14.0
D7	34	8.0	24.0	8.0	14.0	9.0	6.0	4.0	19.5
D9	35	9.0	22.5	8.5	14.5	11.0	6.0	4.0	19.0
D20	36	10.5	24.5	13.0	15.5	12.5	7.0	3.5	16.0
D22	37	9.5	28.5	9.5	17.5	10.0	7.0	5.0	19.0
D39	38	8.5	27.5	10.0	18.0	10.5	7.0	4.5	18.5
D40	39	8.0	27.0	8.5	18.5	12.0	5.5	4.5	18.5
D42	40	10.0	27.0	9.5	16.0	12.0	7.0	4.5	15.0
D53	41	10.5	26.5	10.5	16.0	12.0	7.5	5.0	20.0
D61	42	8.5	23.0	8.5	15.5	10.5	6.0	4.0	15.0
D64	43	7.5	25.0	8.0	14.5	10.0	6.0	4.0	13.5
D69	44	8.5	30.0	11.0	16.0	11.0	7.5	5.0	17.5
D70	45	9.0	27.5	10.5	17.0	9.0	7.0	5.0	19.0
D72	46	9.5	27.0	9.5	16.5	12.0	6.0	5.0	18.0
D73	47	9.0	23.5	10.0	15.0	10.5	6.5	4.5	16.0
D74	48	11.0	27.0	11.0	16.5	11.5	7.0	5.0	20.0
D76	49	10.0	32.5	10.5	21.0	10.0	6.5	5.0	20.0
D82	50	7.5	27.0	10.0	17.0	9.0	6.0	4.5	16.0
D89	51	8.0	31.0	9.5	18.0	10.0	6.5	5.0	19.5
D91	52	10.0	28.0	12.0	17.0	13.5	9.0	6.0	20.5
D94	53	9.0	33.0	10.0	20.0	11.0	7.0	5.0	19.5
D100	54	10.0	30.0	10.0	20.0	11.0	7.0	4.5	18.0

measurements (in mm) (cf. Fig. 1)

(variables)

V9	V10	V11	V12	V13	V14	V15	V16	V17
Interorbital width*	Connecting line of level 9†— nasal	Connecting line of orbit‡— postparietal	Length of postparietal	Connecting line of lateral tips of postfrontals	Squamosum§	Total of 12 + 3 + 5 + 6	Total of 12 + 3	Total of 5 + 6
12.5	13.0	26.5	2.5	19.0	11.0	22.5	13.5	19.0
7.5	11.5	21.0	2.5	14.0	8.5	26.5	10.5	16.0
11.5	10.0	21.0	2.0	16.5	9.0	25.5	10.0	15.5
9.0	10.5	22.5	2.5	16.0	8.5	27.0	11.5	15.5
12.0	14.0	26.0	3.0	18.5	10.0	30.0	11.5	18.5
9.0	10.0	11.0	3.0	15.5	8.5	25.0	11.0	14.0
10.0	12.5	23.5	2.5	24.0	10.0	28.0	12.0	16.0
11.0	13.5	23.5	2.0	19.0	11.0	28.5	10.5	18.0
7.5	10.0	20.0	2.0	12.0	8.0	25.5	10.5	15.0
9.5	15.0	23.0	2.0	14.5	7.0	27.5	10.5	17.0
11.5	15.5	29.0	1.5	18.5	10.5	32.5	12.0	20.5
10.5	13.5	28.0	1.5	19.5	9.5	18.5	11.5	17.0
10.5	12.5	23.0	2.5	20.0	11.5	30.0	13.5	16.5
9.5	11.5	24.5	2.0	16.0	9.0	26.0	11.0	15.0
12.5	19.5	35.5	2.5	22.5	12.0	42.5	16.0	26.5
9.5	14.5	26.5	2.5	16.0	11.5	29.0	10.5	18.5
11.5	12.0	22.5	2.0	18.0	11.0	28.5	11.0	17.5
9.0	12.5	25.0	2.0	15.0	10.0	30.5	13.0	17.5
9.0	10.0	21.5	2.0	16.0	9.5	26.0	11.0	15.0
10.0	13.5	26.0	2.5	17.0	10.0	32.0	13.5	18.5
12.0	14.5	26.5	1.5	17.5	9.5	30.0	10.5	19.5
9.5	11.5	23.0	2.5	17.0	9.5	29.5	11.0	18.5
9.5	12.5	23.5	2.5	17.5	8.5	29.5	12.5	17.0
9.0	8.5	22.5	2.0	18.0	8.0	26.0	10.5	15.5
10.5	11.0	23.0	2.5	18.0	9.0	26.0	11.5	14.5
7.5	10.5	19.0	2.0	13.0	7.0	23.0	9.5	13.5
9.5	12.5	26.0	2.0	19.0	9.5	30.0	12.0	18.0
11.5	12.5	24.0	1.5	18.5	9.5	27.5	9.5	18.0
13.0	14.5	29.5	3.0	22.0	11.5	35.5	15.5	20.0
9.0	12.0	21.5	2.0	15.5	10.5	26.5	10.0	16.5
9.5	12.0	23.5	2.0	17.0	11.0	27.5	12.0	17.5
8.5	10.5	21.5	2.0	14.0	8.5	26.0	11.0	15.0
10.0	12.5	25.5	2.5	16.0	6.0	30.5	13.5	17.0
11.0	11.0	20.0	2.0	19.0	9.5	26.0	11.0	15.0
10.0	11.0	25.0	2.5	17.0	9.0	28.0	11.0	17.0
11.0	13.0	30.0	2.5	18.5	8.5	35.0	15.5	19.5
11.5	12.0	24.0	2.5	21.0	11.0	29.0	12.0	17.0
11.0	12.5	24.5	2.5	18.5	12.0	30.0	12.5	17.5
11.0	12.0	24.0	2.0	20.0	11.0	28.0	10.5	17.5
11.5	13.0	27.5	3.0	20.0	10.0	31.5	12.5	19.0
12.0	13.5	29.0	2.0	20.0	10.0	32.0	12.5	19.5
9.0	12.5	22.0	2.0	16.0	9.0	27.0	10.5	16.5
10.5	12.0	22.0	2.0	19.0	9.0	26.0	10.0	16.0
11.5	13.0	25.0	2.0	19.0	10.0	31.5	13.0	18.5
11.0	13.0	24.0	2.0	21.0	11.0	28.5	12.5	16.0
11.0	11.5	26.5	3.0	20.0	11.0	29.5	11.5	18.0
10.0	10.0	28.0	3.0	16.0	9.0	30.0	13.0	17.0
10.5	14.5	30.0	3.5	19.5	10.0	33.0	14.5	18.5
13.0	11.5	25.0	2.5	24.0	12.0	29.5	13.0	16.5
10.5	12.0	23.0	2.5	17.5	9.0	27.5	12.5	15.0
12.0	12.5	23.0	1.5	19.5	9.5	28.5	12.0	16.5
13.0	16.0	29.0	3.0	22.0	12.0	37.5	15.0	22.5
13.0	12.5	25.0	3.0	20.0	11.5	31.0	13.0	18.0
11.0	14.0	25.0	2.5	20.0	11.0	30.5	12.5	18.0

TABLE 1.

Specimen number	Characters							
	V1	V2	V3	V4	V5	V6	V7	V8
	Parietal foramen-postparietal	Width of skull table at mid-supra-temporal	Length of parietal	Width of parietals	Length of frontal	Length of nasal	Width of nasal	Connecting line of lateral tips of prefrontals
D107	55	8.5	25.5	9.0	16.5	11.5	7.5	4.5
K323	56	14.0	39.0	13.0	23.5	17.0	12.0	7.0
K325	57	10.0	25.5	10.0	14.5	13.0	7.5	4.5
K329.I	58	6.5	23.0	6.5	13.0	6.5	4.0	4.0
K340.I	59	9.0	29.0	9.5	18.0	11.0	7.0	5.5
K330	60	10.0	29.0	11.0	17.0	10.0	6.5	5.0
K331.I	61	9.5	21.5	9.5	14.0	12.0	5.5	4.5
K331.II	62	9.0	25.5	8.0	16.0	11.5	8.0	4.5
K326	63	8.5	28.0	9.0	16.5	13.0	8.5	4.5
D354.I	64	9.5	24.0	10.0	14.0	11.0	7.5	4.5
K344	65	7.0	23.5	7.5	13.5	9.5	6.5	3.5
K345	66	10.0	20.5	9.5	16.0	13.0	8.0	4.5
K342	67	7.0	20.0	7.5	12.5	9.5	4.5	3.5
K334	68	10.0	26.0	9.5	16.5	12.0	7.0	5.0
K335	69	8.5	22.5	9.5	15.0	10.5	9.0	5.0
K347	70	8.0	22.5	8.5	14.0	8.5	4.5	3.5

*Interorbital width is measured at level of contact of prefrontal with postfrontal.

†This connecting line is measured from level at which interorbital width was measured.

‡Orbit is measured from its anterior margin.

§Connecting line between posteromedial and posterolateral tips of squamosal.

Analysis of within-group variation. The pattern of character variation within a measured group of *Discosauriscus* specimens is described using principal component analysis. Because the principal component analysis (PCA) with the correlation matrix of log_e-transformed data tends to incorporate less shape into the first component (PC1) than PCA with covariance matrix (Sommers, 1986), we applied the correlation matrix in the analysis of within-group variation (Jolicoeur, 1963a).

Principal components (PCs) are linear combinations of the measured original variables, and so their orientations are defined by the vectors of coefficients (eigenvectors) in those combinations. PC2 describes the largest shape variance. Other components follow similarly but in other directions of data variation than PC2. Closely related is the problem of how many PCs should be interpreted. We think that the procedure does not depend on a file of limiting assumptions and we try to explain 95% of data variance (cf. Jolicoeur, 1963a). Because the PC1 could be considered as a growth trend (cf. Jolicoeur, 1963b) we use it to analyse the trends in the development of measured animals.

Ontogenetic analysis. For this purpose we used the PC1 but from a covariance matrix (Jolicoeur, 1963b,c) of log_e-transformed data. Our preference for the lognormal model is based on the reasons described by Mosimann & James (1979). The eigenvector (PC1) extracted from such a covariance matrix describes relative changes in the measured characters during growth (Strauss, 1985) and partially characterize the ontogenetic level of the examined animals (Jolicoeur, 1984), for example, if the proportions of an *i*th variate to a *j*th variate were to remain constant as the size of a living organism increases, that is, if the

continued

(variables)								
V9	V10	V11	V12	V13	V14	V15	V16	V17
Interorbital width*	Connecting line of level 9†- nasal	Connecting line of orbit‡	Length of postparietal	Connecting line of lateral tips of postfrontals	Squamosum§	Total of 12 + 3 + 5 + 6	Total of 12 + 3	Total of 5 + 6
10.5	12.0	24.0	1.5	19.0	9.0	29.5	10.5	19.0
20.0	20.0	38.0	4.5	35.0	18.0	46.5	17.5	29.0
10.5	13.0	27.0	2.5	19.0	10.0	33.0	12.5	20.5
9.0	8.0	16.5	1.5	13.5	7.0	18.5	8.0	10.5
11.0	13.0	24.0	2.5	21.0	12.0	30.0	12.0	18.0
13.0	14.0	25.0	3.0	21.5	10.5	30.5	14.0	16.5
9.0	12.0	24.5	2.5	17.0	9.5	29.5	12.0	17.5
11.0	13.5	23.5	2.5	18.5	10.5	30.0	10.5	19.5
11.0	14.0	25.5	2.0	20.0	10.0	32.5	11.0	21.5
9.5	14.0	28.0	3.0	20.0	9.0	31.5	13.0	18.5
8.0	10.5	21.5	2.0	16.0	9.0	25.5	9.5	16.0
11.5	17.0	27.0	2.5	18.0	10.5	33.0	12.0	21.0
8.5	8.0	19.5	1.5	13.0	7.0	23.0	9.0	14.0
11.5	13.5	25.5	2.5	18.0	11.5	31.0	12.0	19.0
10.0	14.5	26.0	2.0	17.5	11.0	31.0	11.5	19.5
9.0	10.0	20.0	2.0	16.0	8.5	23.5	10.5	13.0

relative growth of the two dimensions were isometric. In our case the hypothesis that the i th variate is isometric could thus be expressed as: eigenvector = $1/\sqrt{17} = 0.2425356$, because we used 17 variables.

Analysis of between-group variation. To examine a between-group separation we applied discriminant analysis (Jolicoeur, 1959). From the scatter of the PC2 and PC3 of the correlation matrix we identified the structure associated with the shape differences among groups with the help of cluster analysis (Humphries *et al.*, 1981). In palaeobiological data we did not suggest the existence of groups *a priori*; hence we used the hierarchical ordination (Euclidean matrix, maximum distance method—see Šarmanová & Lukasová, 1985). To determine a parallel between PCA and discriminant analysis we computed ten clusters (the first ten components accounted for approximately 95% of the data variation in the PCA). For these ten groups we computed the standardized loadings and discriminant scores from the data matrix of the first 14 measured variables (Table 1). Because the shape components from PCA are the types of discriminators we compared them to the usual linear discriminant function (Humphries *et al.*, 1981).

STATISTICAL ANALYSES: RESULTS

Taxonomic notes and skull proportions

Špínar (1952) has at his disposal an extensive collection of different ontogenetic stages of discosauriscids, from several localities of the Boskovice

Furrow. The specimens were found on the bedding plane surfaces, dorsoventrally compressed and often distorted. Using this material, Špinar distinguished two genera and four species: *Discosauriscus pulcherrimus*, *D. potamites*, *Letoverpeton moravicum* and *L. austriacum*. The diagnoses of both genera (Špinar, 1952: 23 for *Discosauriscus*, Špinar, 1952: 59 for *Letoverpeton*) are based entirely on differences in proportions. *Discosauriscus* has a narrow and elongated skull and is more gracile. Furthermore, the individual bones of the skull are narrower and longer. Postcranially, the interclavicle is long and the ischium is narrow and posteriorly elongated; the body length reaches 350 mm. *Letoverpeton* has a broader, shorter and more robust skull. The skull bones are relatively shorter and broader (the parietal is never broader than long). Postcranially, the interclavicle is short and stout and the ischium is broad and triangular; body length is c. 250 mm.

The orbit of *Discosauriscus* has the shape of an irregular oval whereas in *Letoverpeton* it is broad with a longer posterolateral axis. From Špinar's diagnoses, it follows that there are no morphological differences apart from proportional ones.

Considering the diagnoses of the four species (Špinar, 1952: 28, 50–52, 61, 73–74), the differences between them are also only proportional and the value of other characters is problematic.

(1) These characters are common for both genera and have no taxonomic value (e.g. width of interpterygoid vacuities, presence of the small laterocaudal processes of the parietal, junction of the parietal with the tabular, number of digits per limb, phalangeal formula, number of type of bones of the pectoral and pelvic girdles, shape of scales, etc.).

(2) Because of a considerable degree of dorsoventral compression it is impossible to regard proportional characters as unambiguously diagnostic, and it is necessary to be very careful (e.g. degree of vaulting of the squamosal, shape of orbit, etc.); this throws doubt on the possibility of exact measuring.

(3) It is impossible to compare them in all four species because of imperfect preservation (e.g. number of caudal ribs, number of caudal vertebrae). Apart from proportional differences (e.g. 'narrow' vs 'broad' skulls), which, however, can now be reinterpreted (see below), it is impossible to determine unambiguous morphological differences between individual species.

In his redescription of the German discosauriscids, Werneburg (1985, 1989) accepted the existence of three of Špinar's species although he cast doubt upon the existence of *D. potamites*, which he considered to be synonymous with *D. aff. pulcherrimus*—cf. Werneburg (1989: 34). Werneburg denoted, as *D. pulcherrimus*, the type material from Ruprechtice (North Bohemia) and two German localities (Niederhässlich and Wintersbrunnen). On the palate of the specimens from Niederhässlich, he described two basic characters: the sharply triangular denticle field on the parasphenoid and only one pair of tusks on the vomers. According to Werneburg (1989), these characters have not been demonstrated on the specimens from the Boskovice Furrow, and therefore he identified them as *D. aff. pulcherrimus*. However, Werneburg's statements are not correct for the following reasons: (1) in the majority of well-preserved specimens from the Boskovice Furrow, the lateral margin of the vomer is bordered by a row (one or more) of small denticles and medially from it three pits for tusks are situated in one line (mostly two tusks are present), e.g. in K 83; (2) on the ventral side of the

parasphenoid of K 9 and K 323 (but known only in these two specimens) the triangular denticle field is present.

Apart from the differences between *Discosauriscus* and *Letoverpeton*, Werneburg (1985, 1989) on the basis of the length, width, massiveness, gracility and size of individual bones, the shape of orbit or proportions of some parts of the skull also presented other differences between these genera. These include the structure and form of the parasphenoid, vomer, mandible, interclavicle, ischium and the number of vertebrae. The new material of *Discosauriscus* from the Boskovice Furrow, however, permits us to present preliminary statements (a detailed description of the skeleton and complete documentation will be given in later papers) about all of these characters.

Parasphenoid. The shape of the parasphenoid is identical in 'narrow' (e.g. D 73) and 'broad' (e.g. D 100) skulls, i.e. in both marginal cases the parasphenoid has a long posterolateral processes, reaching up to the region of quadrate (they probably covered from the ventral side the posterolaterally-widened endocranial 'otic tubes'). The type of parasphenoid which Werneburg (1989: Fig. 12) illustrated for *Discosauriscus* has never been found in our material. The posterolateral processes of the parasphenoid are fragile, which is why they are often broken, or 'pressed' to the ventral wall of the skull roof.

Vomerine dentition. According to Werneburg (1989: 35, Fig. 12), *Letoverpeton austriacum* differs from *L. thuringiacum* in the absence of the tusks. Here it must be emphasized that the vomerine dentition is the same in both 'narrow' (e.g. D 73) and 'broad' (e.g. K 14, K 339) skulls. In these specimens the lateral margin of the vomer is bordered by a row of denticles (sometimes they are more abundant, or the denticles form clusters, mostly in the anterior part) and closely medially from it three tusk positions are visible (see above).

Mandible. In the mandible, it has proved impossible to determine unambiguously the boundary between the 'large coronoid and small surangulare' in *Discosauriscus* and the 'small coronoid and large surangulare' in *Letoverpeton* (Werneburg, 1985: Table 3).

Interclavicle. In the interclavicles, there are proportional differences as in the skulls, especially in the comparison of the specimens with the 'narrowest' and the 'broadest' skulls. As Špinar (1952) found, the former are longer and more gracile specimens, the latter are shorter, more plump and more robust. Werneburg (1985: Table 3) suggested that the interclavicle in *Discosauriscus* has a relatively narrower stem and longer and narrower anterior plate, whereas in *Letoverpeton* there is the opposite situation. Figure 3 shows that in the specimen with the 'broad' skull (K 339), the anterior half of the posterior stem is only slightly broader when compared with 'narrow' skull of the specimen K 337. However, it is not the case that the posterior stem in specimens with 'narrow' skulls is longer than in specimens with 'broad' skulls. The posterior stem of the interclavicle of D 100 (broad skull) is substantially longer than that of D 106 (narrow skull); both specimens are of almost equal size. In the anterior plate of the interclavicle, the 'differences' are ambiguous. In '*Letoverpeton*' specimens with 'broad' skulls (e.g. K 346.I), the anterior plate is not always shorter and broader in comparison with the interclavicles of *Discosauriscus* (Fig. 2, and Werneburg, 1985: fig. 8 and pl. 6, figs 1–5; Špinar, 1952: pl. 33).

Ischium. Werneburg (1985: Table 3) argued that the ischium of *Letoverpeton* was broad with a short posterior laterocaudal corner, unlike the long, narrow

Figure 2. *Discosaurus austriacus* (Makowsky, 1876), K 346.I. Skull in ventral aspect and disarticulated shoulder girdle. (For key to abbreviations see p. 270.)

ischium with a long laterocaudal corner in *Discosaurus*. The ischium in the specimens with 'narrow' skulls is indeed narrower; however, this shape of ischium and its caudal corner, as illustrated by Werneburg (1985: Fig. 10n—*Letoverpeton austriacum*) has not been found in the new material. In a specimen with a 'broad' skull (K 341.I), which corresponds to the species *L. austriacum* (Fig. 4), the shape and posterior ending of the ischium is virtually identical to the specimens with the 'narrow' skulls (e.g. K 328).

Vertebrae. Unfortunately no specimen with an explicitly 'narrow' skull was found in which the number of the presacral vertebrae could be unambiguously determined. In K 347, the skull of which corresponds to the transition between *D. pulcherrimus* and *L. austriacum*, there are 24 presacral vertebrae, as in the 'broad' skulls (e.g. K 323, K 338.I).

Within-group variation

The nature and importance of the trend of variation corresponding to each PC can be judged from the signs and the numerical values of its eigenvectors (Table 2) and from the amounts of variance associated with each component (Table 3). PC 1 was a strong size vector, accounting for more than 64% of the variance. It has consistently positive loadings and because it also represents the general growth trend we discuss it below under 'Growth allometry'.

PC 2 is also substantial, accounting for more than 9% of variation. This

Figure 3. *Discosauriscus austriacus* (Makowsky, 1876). A, K 337; B, K 339. Skulls and parts of postcranial skeletons of two proportionally different specimens in ventral aspects. Scale bars = 10 mm.

component refers to the contrast between the width and length of the skull and represents the trend which connects with the present understanding of the importance of the proportional differences within *Discosauriscus* specimens. The length-width contrast is not even; the greater increase in the width of the posterior part of skull (V2 and V4) is reflected in the length (V5).

Also the next shape trend obtained by PCA was discussed in the literature (Berman, Reisz & Eberth, 1987) on the example of the length of the postparietal in *Seymouria* (see below). PC 3 represents an almost unipolar shape trend of elongation or shortening of skull in the region of the parietal (V3), especially in the region of the postparietal (V12). In other words, there are specimens with lengthened postparietals as well as others with proportionately short postparietals. The data in Table 2 show a significant independence between this and preceding length-width trend. The trend (PC 3) refers rather to the contrast between the length of the anterior and posterior parts of skull. The skulls with proportionally long postparietals have partly proportionally shortened nasals (V6).

The next trend (PC 4) is the shortening or elongation of the postparietal, but this time in contrast with the length of the adjoining bone—the parietal. As Jolicœur & Mosimann (1960) stated, a positive deviation of 100 units in this

TABLE 2. Eigenvectors of principal axes of correlation matrix using log_e data in 70 specimens. Variables are identified in 'Measurements and methods' and Table 1

	Principal components (PC)																
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
V1	0.254	-0.210	0.132	-0.299	0.051	0.439	-0.172	0.039	0.238	-0.025	-0.065	-0.135	0.154	-0.299	-0.604	0.024	0.007
V2	0.229	0.428	-0.011	-0.143	-0.136	-0.079	0.155	-0.163	-0.109	0.067	0.524	-0.100	-0.402	-0.448	0.067	0.020	0.008
V3	0.244	-0.182	0.314	-0.388	-0.033	-0.330	0.118	0.178	-0.234	-0.071	-0.081	-0.023	-0.122	0.159	-0.048	-0.627	0.016
V4	0.205	0.352	-0.076	-0.004	-0.702	-0.056	-0.136	0.164	0.302	-0.028	-0.127	-0.005	-0.026	0.386	-0.161	0.050	-0.002
V5	0.248	-0.255	-0.191	0.232	-0.140	0.213	-0.232	-0.115	-0.506	0.041	-0.120	0.078	-0.367	0.093	-0.111	0.039	-0.465
V6	0.250	-0.187	-0.314	0.096	0.131	-0.267	0.323	-0.043	0.203	-0.040	0.431	0.092	0.336	0.215	-0.235	-0.016	-0.386
V7	0.234	0.259	0.067	0.105	0.436	-0.270	-0.382	-0.299	0.174	-0.505	-0.137	-0.078	-0.171	0.130	-0.084	0.033	-0.010
V8	0.248	0.221	-0.045	0.060	0.233	-0.156	-0.539	0.344	-0.085	0.515	0.112	0.183	0.247	-0.081	0.061	-0.081	0.010
V9	0.253	0.260	-0.075	-0.174	0.091	0.185	0.163	-0.416	-0.215	0.286	-0.193	-0.487	0.325	0.244	0.148	-0.017	-0.003
V10	0.254	-0.181	-0.228	0.093	0.073	-0.246	0.224	-0.032	0.424	0.365	-0.471	-0.050	-0.328	-0.265	0.096	-0.010	0.003
V11	0.163	-0.033	0.634	0.558	0.003	0.225	0.104	-0.133	0.219	0.210	0.182	0.002	-0.067	0.142	0.031	-0.173	-0.001
V12	0.257	0.263	0.017	-0.116	0.040	0.252	0.252	-0.164	-0.038	-0.124	-0.230	0.762	0.147	-0.090	0.106	-0.059	-0.001
V13	0.239	0.220	-0.109	0.227	0.232	0.266	0.308	0.666	-0.101	-0.280	-0.081	-0.252	-0.061	-0.005	0.080	0.022	-0.009
V14	0.260	-0.174	0.033	0.258	-0.367	-0.165	-0.123	-0.075	-0.087	-0.319	-0.057	-0.152	0.433	-0.486	0.295	-0.078	0.004
V15	0.250	-0.143	0.432	-0.180	0.0002	-0.274	0.124	0.119	-0.170	0.047	-0.048	0.044	0.022	0.075	0.036	0.742	-0.012
V16	0.268	-0.239	-0.265	0.186	-0.011	0.004	0.023	-0.090	-0.189	-0.010	0.138	0.087	-0.055	0.174	-0.162	0.041	0.796

Figure 4. *Discosauriscus austriacus* (Makowsky, 1876), K 341.I. Pelvic girdle.

trend of shape would correspond to deviation of +55 mm in the postparietal length and -39 mm in the parietal length or *vice versa*.

It is interesting that the posterior part of the skull is mainly 'responsible' for the distinct shape variability of the skull in *Discosauriscus*. PC 5 also relates to the shape variability of the posterior part of the skull, in this case with the width of the parietals (V4). It is an almost unipolar vector which provides information on the proportional decrease of the width of parietals in some specimens, whereas the other specimens have the width of nasals (V7) proportionally greater in comparison with other bones of skull.

TABLE 3. Eigenvalues and percentage variance accounted by each principal component (correlation matrix)

PC	Eigenvalues	Percent of variance
1	11.01	64.8
2	1.59	9.4
3	1.09	6.4
4	0.66	3.9
5	0.56	3.3
6	0.42	2.5
7	0.33	2.0
8	0.29	1.7
9	0.27	1.6
10	0.20	1.2
11	0.17	1.0
12	0.13	0.8
13	0.12	0.7
14	0.08	0.4
15	0.06	0.3
16	0.01	0.0
17	0.00	0.0

TABLE 4. Eigenvectors of first four principal axes of covariance matrix using $\log_e$ data in 70 specimens. Variables are identified in 'Measurements and methods' and Table 1

	Principal components			
	1	2	3	4
V1	0.237	0.011	-0.179	-0.362
V2	0.193	0.015	0.385	-0.089
V3	0.220	0.067	-0.160	-0.459
V4	0.194	-0.007	0.370	-0.030
V5	0.226	-0.115	-0.202	0.153
V6	0.315	-0.324	-0.202	0.324
V7	0.206	0.066	0.227	0.052
V8	0.229	-0.012	0.226	0.042
V9	0.251	-0.049	0.302	-0.123
V10	0.274	-0.204	-0.169	0.204
V11	0.262	-0.175	-0.250	-0.343
V12	0.245	0.850	-0.197	0.283
V13	0.267	0.028	0.310	-0.122
V14	0.252	-0.010	0.264	0.284
V15	0.243	0.024	-0.161	0.108
V16	0.223	0.192	-0.146	0.328
V17	0.257	-0.192	-0.199	0.219

PC 6 also corresponds with variation in the bones of the posterior part of skull. The variation is expressed especially by the complementary changes in the length of the parietal foramen—postparietal (V1) and parietal (V3). When V3 proportionally increases in relation to the total size of skull, V1 decreases, and *vice versa*.

PC 7 is the first trend, which 'represents' the greater width-length changes in the anterior part of skull, mainly in the region of the nasal. It is interesting that this trend, in comparison with the preceding ones, partially correlates with size (correlation between PC 1 and PC 7 = 0.3).

PC 8 (always *c.* 2% of the total data variance) corresponds to the variation in the width of the squamosal (V14).

Other trends in the shape of *Discosauriscus* skulls are given in Table 2. Although a lower percentage of the total data variability, in terms of phylogeny (cf. Jolicoeur, 1963a) they may be important and they are therefore given here (see Table 2) in full.

Growth allometry

Because the discosauriscids were probably neotenic animals (Holmes, 1984; Smithson, 1985), it is necessary to define the stages of their ontogenetic development for better determination of the shape variability of the skull.

PC 1 corresponds to a direction of size increase and can therefore be interpreted as a growth trend. Use of the covariance matrix preserves allometries (Tables 4, 5). In our case, the very divergent variable in the shape—the length of postparietal (V12)—grows isometrically, like the total skull length (V15), but both are positively allometric to the widths of V4 or V2. The nasal length (0.31) is also positively allometric to the nasal width. PC 1 corresponds to the overall

TABLE 5. Percent of variance accounted for by each PC using covariance matrix

PC	Percent of variance
1	63.03
2	9.79
3	8.51
4	4.08
5	2.94
6	2.35
7	1.84
8	1.69
9	1.49
10	1.14
11	1.09
12	0.79
13	0.62
14	0.38
15	0.31
16	0.04
17	0.03

tendency, that the length of skull increases (during growth) at a greater relative rate than the skull width.

Between-group variation

To each variance component in the discriminant analysis correspond 14 standardized canonical discriminant function coefficients; the numerical values of the first four coefficients are given in Table 6. More than 95% of between-group variance was accounted for by the first three functions (Table 7).

The pattern of dispersion of the groups in the plane of the first and second discriminant axes is shown in Fig. 5. Group 9 tends to congregate in the left side of the graph.

As the data in the Tables 6 and 8 show, the proportional changes in the length of the postparietal (and partially in the length of nasal, but in contrast to the

TABLE 6. Standardized canonical discriminant function coefficients

	FUNC 1	FUNC 2	FUNC 3	FUNC 4
V1	1.04	-0.39	-1.71	0.95
V2	-0.17	0.76	-0.60	-0.98
V3	1.22	-0.85	0.89	-0.23
V4	0.01	0.86	-0.07	0.86
V5	-1.51	-1.04	0.57	-0.64
V6	-1.13	-0.91	-1.82	0.56
V7	0.50	0.18	-0.29	0.22
V8	0.07	0.77	0.52	0.54
V9	-0.26	0.39	0.65	0.47
V10	-1.04	-0.09	1.43	0.31
V11	-0.47	-0.18	0.34	-0.48
V12	2.06	-0.47	0.04	0.10
V13	-0.52	0.54	0.59	-0.50
V14	0.62	0.69	-0.51	-0.51

TABLE 7. Multiple discriminant analysis

Discriminant function	Eigenvalues	Relative percentage	χ^2	dF	Significance level
1	13.34	56.61	370.77	126	0.00
2	8.15	34.60	218.98	104	0.00
3	0.99	4.20	92.80	84	0.24
4	0.51	2.18	53.61	66	0.86
5	0.26	1.11	30.02	50	0.99
6	0.12	0.51	16.76	36	0.997
7	0.11	0.45	10.29	24	0.99
8	0.06	0.25	4.59	14	0.99
9	0.02	0.10	1.28	6	0.97

postparietal) are the most distinct differentiating characters between groups. The first component is markedly larger (57%) than the next (proportional variability in the length and width of skull) and except for group 9 the variability in the length of the postparietal also separates groups 2, 3, 5, 6, 7, and 8. The 'length-width' trend differs mainly between group 1 and groups 10 and 4 (Fig. 5A, Table 8). We compared the first function discriminant scores and the component scores from the PC analyses (PC 2—covariance matrix and PC 3—correlation matrix) and, as can be seen in Figs 5B, C, D_1 achieves some discrimination between two possible groups. One group (shorter postparietal) comprises the animals from groups 9, 10, 5, 3 and 7; in the second group are the specimens from other groups. Level D_1 , in which the specimens can be differentiated, has an approximate value 0. It can be seen from the frequency histogram (Fig. 5D), that after division of 70 specimens into 30 groups (according to the value of discriminant scores), the group on level 0 is absent. The relation between the postparietal length (V12) and the frontal length (V5) could represent a certain distinguishing but unsteady criterion in this point 0 of D_1 , because they mostly vary in the discriminant function 1, and a decrease in the frontal length is accompanied by an increase in the postparietal length. For the reasons given below, however, it is impossible to consider such separation as a valuable taxonomic criterion. It is still more doubtful in the other trends (D_2 , D_3 , D_4 —Table 6, Fig. 5A), in which values of the discriminant scores coincide much more (Fig. 6).

TABLE 8. Group centroids of first two discriminant functions. Numbers of groups correspond to those in Fig. 5A–C.

	FUNC 1	FUNC 2
Group 1	1.03	−3.77
Group 2	1.47	−0.57
Group 3	−1.89	−0.72
Group 4	1.85	4.22
Group 5	−4.14	−3.46
Group 6	4.26	1.55
Group 7	−2.15	0.86
Group 8	5.00	−1.67
Group 9	−7.73	0.70
Group 10	−3.98	5.49

Figure 5A–D. A, Scatter of scores computed from first (D_1) and second (D_2) discriminator (see also Tables 2–8). Numbers of groups are derived from hierarchical cluster analysis. B, Principal component 3 (derived from correlation matrix) and C, PC 2 (from covariance matrix) scattered against the first discriminator (D_1). D, Frequency histogram derived from the scores of the first discriminator (D_1) divided into 30 frequency groups (n = Number of specimens).

DISCUSSION

The statistical analysis indicates that in this assemblage of *Discosauriscus* specimens there are several trends in variability of skull shape, as in the populations of other animals. As the independent shape trends in PCA show, it is impossible to divide this material into narrow and long ('*Discosauriscus*') or broad and short ('*Letoverpeton*') skulls, i.e. that all length characters would proportionally equally lengthen, and broad characters would equally shorten or *vice versa*, as understood hitherto (Špinar, 1952; Werneburg, 1985, 1989; see above). Multivariate PCA shows that the relationships between the proportions of individual bones are more complicated, although it is possible to find specimens in these collections which are notably proportionally different in a given region of the skull (e.g. the skull table, Fig. 8). Specimen K 58 (Fig. 8B) is one in which the parietal is broader than it is long. It is evident that, for

Figure 6. Scores of the fourth discriminator (D_4) scattered against the scores of the third discriminator (D_3). For more detailed explanation of the shape variation see Table 6.

example, a particular proportionally narrow bone can be on both 'broad' and 'narrow' skulls (this also follows from PCA). The division of the specimens into 'narrow' and 'broad', on the basis of skull proportions, is incorrect. We follow Jolicoeur (1959), who applied discriminant analysis to the shape variability in the skull of Recent populations of *Canis lupus*. Although studying a very different group of animals, the author found significant length-width variability in the shape of the skull, which correlated significantly with occurrence in different geographical regions. Theoretically it means that although it may be possible to distinguish (on the basis of measurements of the shape changes of bones) several groups from the characteristics obtained (using the component scores, some groups of wolves did not overlap in Jolicoeur's graphs), within the Moravian discosauriscids, this also does not imply the existence of two or more species.

The only trend which markedly differentiates the analysed collection of specimens is the variability in the length of the postparietal and, in part, the nasal. However, in the specimens with the short postparietal (Fig. 5A, group 9), this bone elongates significantly laterally from the median plane (where it was measured), similar to the parietal, frontal and nasal. The difference can be up to 1 mm, in contrast to other specimens, in which this difference is almost zero (Fig. 9). These shape differences in the postparietal also influenced the results of discriminant analysis.

The only character on which Vaughn (1966) differentiated the new species *Seymouria sanjuanensis* from Broili's (1904) species *S. baylorensis* (cf. White, 1939), was the greater anteroposterior length of the postparietal and tabular in the former. Vaughn (1966) had only two specimens of *S. sanjuanensis* for measurement of these bones. Berman, Reisz & Eberth (1987) confirmed Vaughn's differentiating character for these two species and demonstrated other characters. These authors measured the length of the postparietal on three

Figure 7. *Discosauriscus austriacus* (Makowsky, 1876), K 20. Skull in dorsal view. Scale bar = 10 mm. (For key to abbreviations see p. 270.)

Figure 8. *Discosauriscus austriacus* (Makowsky, 1876). A, K 16; B, K 58. Skulls of two proportionally different specimens in dorsal aspect. (For key to abbreviations see p. 270.)

Figure 9. *Discosauriscus austriacus* (Makowsky, 1876). A, D 74; B, D 81. Skulls in dorsal view. Scale bars = 10 mm. (For key to abbreviations see p. 270.)

additional specimens of *S. sanjuanensis* and three specimens of *S. baylorensis*. The statistical analysis and Figs 7, 8, 9 and 11 indicate that the length or width of the postparietal (and the tabular) does not always change proportionally with other length characteristics. For example, in two large specimens with different width of skull table—K 16 ('narrow' skull, Fig. 8A) and K 323 ('broad' skull, Fig. 11), the length of the post parietals is about the same. Additionally, as already mentioned, on the specimen D 81 (with approximately the same width of the skull table as in D 74) the length of the postparietal and tabular is laterally enlarged in the direction from the median plane (Fig. 9).

Although some possibilities for discriminating the collection of Moravian *Discosauriscus* specimens into two groups were found on the basis of parameters such as postparietal length, no important morphological differences have been ascertained up to now. However, the differentiation into groups based on shape variability of the skull does not justify classification into genera or species. Alternative explanations could be sexual dimorphism or other phenomena. Jolicœur (1959) found on the basis of measurement of skulls of the wolf (*Canis lupus*) that Arctic wolves do not overlap with those of the Rockies (with the exception of one juvenile specimen). Similar measurements of skulls have been performed for the detection of intraspecies differentiation in other Recent animals (Baker, 1980; Gibson, Baker & Moeed, 1984). On the other hand, however, in measuring the shape changes of bones the characteristics obtained (e.g. component scores) can overlap in multivariate analyses in several species (e.g. Strauss, 1985). This means that the existence of two or more species of Moravian discosauriscids cannot be excluded. Such a distinct separation as Humphries *et al.* (1981) found among different species was not confirmed by us

Figure 10. *Discosauriscus austriacus* (Makowsky, 1876). A, D 20; B, D 45; C, D 80. Skulls in dorsal aspect. Scale bars = 10 mm. (For key to abbreviations see p. 270.)

using similar techniques. More distinct morphological differences should exist for the differentiation of several species.

In connection with these proportional changes it is notable that within a given region of approximately proportionally equal skulls, the relative size of individual bones can vary. Thus, within the parietal table in D 20, D 45 and D 80 it is possible to observe the elongation of the supratemporal at the expense of the intertemporal (Fig. 10). The relationship of these two bones can differ on the right and left sides of skull of one specimen. However, sometimes the size of two bones may differ in dorsal view but be dependent only on the course of the suture between their ornamented surfaces (e.g. in parietals, Fig. 9B). Such differences should be regarded as individual variability, which, from this aspect, is relatively great in the Moravian *Discosauriscus* (this will be discussed in a later work).

The above results of statistical analysis and the absence of distinct morphological differences indicate that, at present, there exists no reliable criterion for the differentiation of more than one taxon within the Moravian discosauriscids. Proportional differences alone are not sufficient and cannot be considered to be taxonomically significant. Therefore the Moravian discosauriscids (and probably the other specimens, hitherto assigned to *Discosauriscus* and *Letoverpeton*) will be considered as one genus and species: *Discosauriscus austriacus* (Makowsky, 1876).

The presence of differences in skull proportions and the absence of distinct morphological differences are recorded in other early tetrapods, where more specimens are present (e.g. in embolomeres such as *Proterogyrinus*, Holmes, 1984, *Archeria*, Clack, 1987 or in *Acanthostega*, Clack, 1988). According to these authors, in none of these cases can the presence of more taxa be excluded but the absence of distinct morphological differences does not enable us to distinguish them; they

Figure 11. *Discosauriscus austriacus* (Makowsky, 1876), K 323. Skull in dorsal aspect. (For key to abbreviations see p. 270.)

are understood as individual variation in skull proportions. However, the existence of morphological trends was recorded in the genus *Seymouria* (Berman, Reisz & Eberth, 1987), which is morphologically close to discosauriscids.

Systematic position. On the basis of above data it follows that from the previously described and the new material from the Boskovice Furrow in Moravia it is possible to recognize only one genus and species: *Discosauriscus austriacus* (Makowsky, 1876). Ivakhnenko (1987, cf. Ivakhnenko, 1981) came to the same conclusion, although on the base of completely different criteria. The synonymy (see also Ivakhnenko, 1987) is as follows.

Discosauriscus austriacus (Makowsky, 1876)

- 1876 *Archegosaurus austriacus*—Makowsky, p. 155
(For the complete synonymy up to 1952, see Špinar, 1952.)
- 1952 *Discosauriscus pulcherrimus*—Špinar, p. 27
- 1952 *Discosauriscus potamites*—Špinar, p. 50
- 1952 *Letoverpeton moravicum*—Špinar, p. 61
- 1952 *Letoverpeton austriacum*—Špinar, p. 73
- 1981 *Discosauriscus permianus*—Ivakhnenko, p. 117
- 1989 *Discosauriscus pulcherrimus*—Werneburg, p. 34
- 1989 *Discosauriscus aff. pulcherrimus*—Werneburg, p. 34
- 1989 *Letoverpeton austriacum*—Werneburg, p. 35
- 1989 *Letoverpeton moravicum*—Werneburg, p. 35

For diagnosis, see Špinar (1952), Ivakhnenko (1987) and Werneburg (1989). However, these diagnoses will be revised on the basis of anatomical studies of the new material of *Discosauriscus* presented in this paper.

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ABBREVIATIONS USED IN FIGURES

FR—frontal	PFR—prefrontal
IC—interclavicle	POFR—postfrontal
IS—ischia	PMX—premaxillary
IT—intertemporal	PO—postorbital
IT ₁ —intertemporal 1	PP—postparietal
IT ₂ —intertemporal 2	QJU—quadratojugal
JU—jugal	SMX—septomaxillary
LAC—lacrimal	SQ—squamosal
MX—maxillary	ST—supratemporal
NA—nasal	TA—tabular
PA—parietal	