

ELECTRORECEPTORS IN THE LOWER PERMIAN TETRAPOD *DISCOSAURISCUS AUSTRIACUS*

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ABSTRACT. In most ornamented dermal cranial bones of the larvae of the Lower Permian tetrapod *Discosauriscus austriacus* from Moravia, distinct rounded or oval pits are present. They are situated in, or close to, the sensory grooves and pit-lines. The diameter of each pit is *c.* 1 mm. The inner surface is sometimes smooth and consists mainly of smaller pits, depressions, or short canals which have small foramina at their bases. Such structures, designated as foraminate pits, have not previously been found in tetrapods. Positionally and structurally, the foraminate pits are comparable with the so-called pore-groups of some rhipidistians, in particular the osteolepids. It is concluded here that these structures are homologous and that the bones which bear them must therefore also be homologous. Thus the bones enclosing the pineal foramen in osteolepiforms are frontals. On the basis of comparisons with Recent urodeles, the foraminate pits are interpreted as structures which may have housed the ampullary electroreceptive organs. If so, *Discosauriscus*, like the rhipidistians, was an electroreceptive animal.

As reported elsewhere (Klembara 1992, 1993, 1994; Klembara and Meszároš 1992; Klembara and Janiga 1993) the Lower Permian localities in the Boskovice Furrow in Moravia (Czech Republic) have produced well preserved three-dimensional material of the tetrapod *Discosauriscus austriacus* (Makowsky, 1876). The most recent finds are of large specimens, and smaller individuals with external gills, showing that *Discosauriscus* is represented by larval and metamorphic individuals (Klembara, in press a). The material reveals many detailed structures. The pit structures, already briefly reported as foraminal pits (Klembara 1992), occur in constant positions in dermal cranial bones, always in relation to the sensory line system. They have not previously been recorded either in early tetrapods ('stegocephalians') or in Recent ones. In this paper, specimens of *Discosauriscus* with skull lengths in the range 17–52 mm are considered.

The term 'Rhipidistia' is used *sensu* Jarvik (1980, p. 202) in this work. The term 'orthodox' terminology, as applied to dermal cranial bones of osteolepiforms, is used here in the sense of Westoll (1943; cf. Borgen 1983); according to this terminology, the bones which enclose the pineal foramen in osteolepiforms are frontals.

MATERIAL, METHODS AND LOCALITIES

The methods of study and the localities for *Discosauriscus austriacus* from the Lower Permian of the Boskovice Furrow were described by Klembara and Meszároš (1992). A third and new locality lies about 500 m northeast of Kochov (district of Letovice). Abbreviations for the localities are: D, Vanovice (Drválovice); K, Kochov; KO, Kochov-L.

The foraminate pits occur on the bones of following specimens which are deposited in the Faculty of Natural Sciences, Zoological Institute, Comenius University, Bratislava: premaxillary, D54, D91; nasal, K224, K327; prefrontal, K80; frontal, K206, KO80, KO111; postfrontal, D47, D137, K3, K102, KO12; intertemporal, K57, K279; supratemporal, KO13, KO25; parietal, D3, D19, D43, D56, D70, D75, D192, D200.III, K13, K18, K20, K48, K63, K185, K205, K227, K231, K241, K316, K320, K325, KO10, KO41, KO60, KO63, KO80; postparietal, D3, D43, D48, D60, D63,

D69, D75, D79, D82, D104, K3, K5, K13, K18, K63, K65, K98, K182, K185, K227, K256, K278, K279, K324, K325, K326, KO7, KO77; tabular, D72, D86, D87, D137, K241; K256, K325, K326, KO7, KO8, KO10, KO11, KO41; maxillary, K180, K257, K316; lacrimal, D54, D73, D81, K195, K328; jugal, K180, K325; squamosal, D53, K98, K256; dentary, D28, K257. Other specimens used: K60, K69, K172.

DESCRIPTION

On the external surface of most dermal cranial bones of *Discosauriscus austriacus*, pit structures – called the foraminate pits (FPs, *fossulae foraminosae*) (Klembara 1992) – are present. Such structures have been found in the premaxillary, prefrontal, nasal, frontal, postfrontal, intertemporal, supratemporal, parietal, postparietal, tabular, maxillary, lacrimal, jugal, squamosal and dentary.

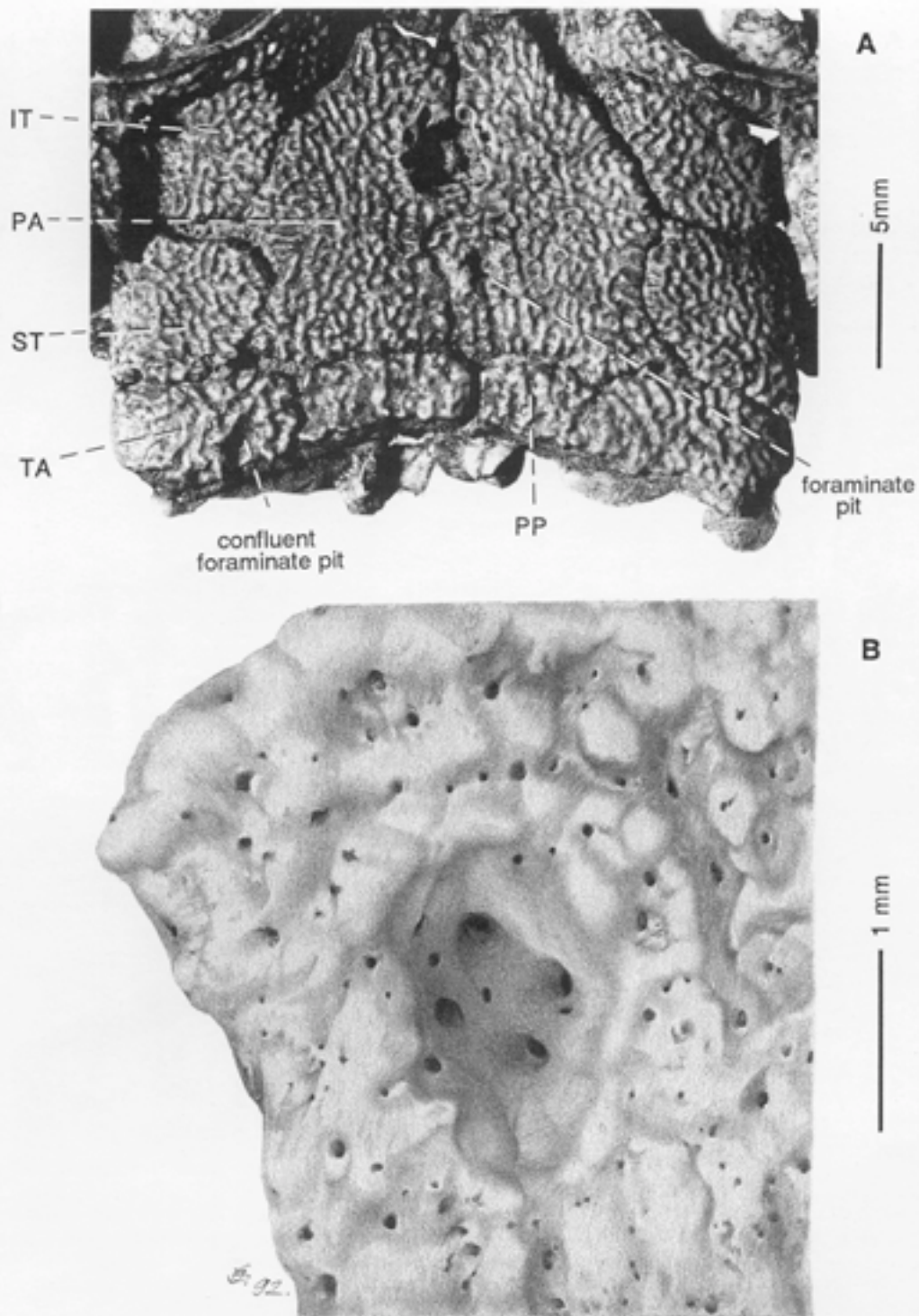
The FPs are generally round, oval or elliptical (Text-figs 1; 2B–C, E, G; 3A, C–E; 5; 6D; 7C–D; F; 8H–I). Their size does not depend on the size of the individual. They vary in depth and may be narrow and relatively deep (Text-fig. 1), or relatively wide and shallow (Text-fig. 6D). The diameter of the shallow and oval FPs may reach up to 1.3 mm, although most of them attain a maximum diameter of 1.0 mm.

The morphology of the inner surface of the FPs is not uniform, although there is a common basic structure. The inner structure of a typical FP is irregular and consists of smaller pit structures (depressions, short grooves, pits and vertical or oblique canals). These pit structures are of various sizes and shapes, and every pit has a tiny foramen (or pore) at its base, leading into the bone (Text-figs 1, 5). The number of foramina in one FP varies from two to ten (it is sometimes difficult to distinguish between a minute pit and the foramen), but there are usually four to seven foramina in one FP. The small pit structures lie mostly in the bottom and in the lower portion of the wall of the FP. However, they are not always clearly developed, so that in some specimens the foramina lie in the almost smooth inner surface of the FP (Text-figs 3A, C–D; 6B, D; 7C; 8H). On the other hand, in the FP of the right parietal of K241, short bulbous and funnel-shaped pits or canals are present, narrowing down into the bone. At the base of these structures, the tiny foramina are clearly visible. It should be emphasized that the morphology of the inner surface within one FP varies so that within a single FP, pits or depressions of various size, canals or foramina in the smooth surface may be simultaneously present (Text-fig. 5B). The location of foramina within the FP surface is irregular, although in K324, the inner surface of the right postparietal FP is relatively smooth and a ring of foramina lies in the basal portion of its wall (Text-fig. 7D; this is also seen in other specimens, such as the posterior FP of the left parietal of D75). The same structural variability seen in the FPs is also observable in the sensory grooves and pit-lines (Klembara 1992, in press b).

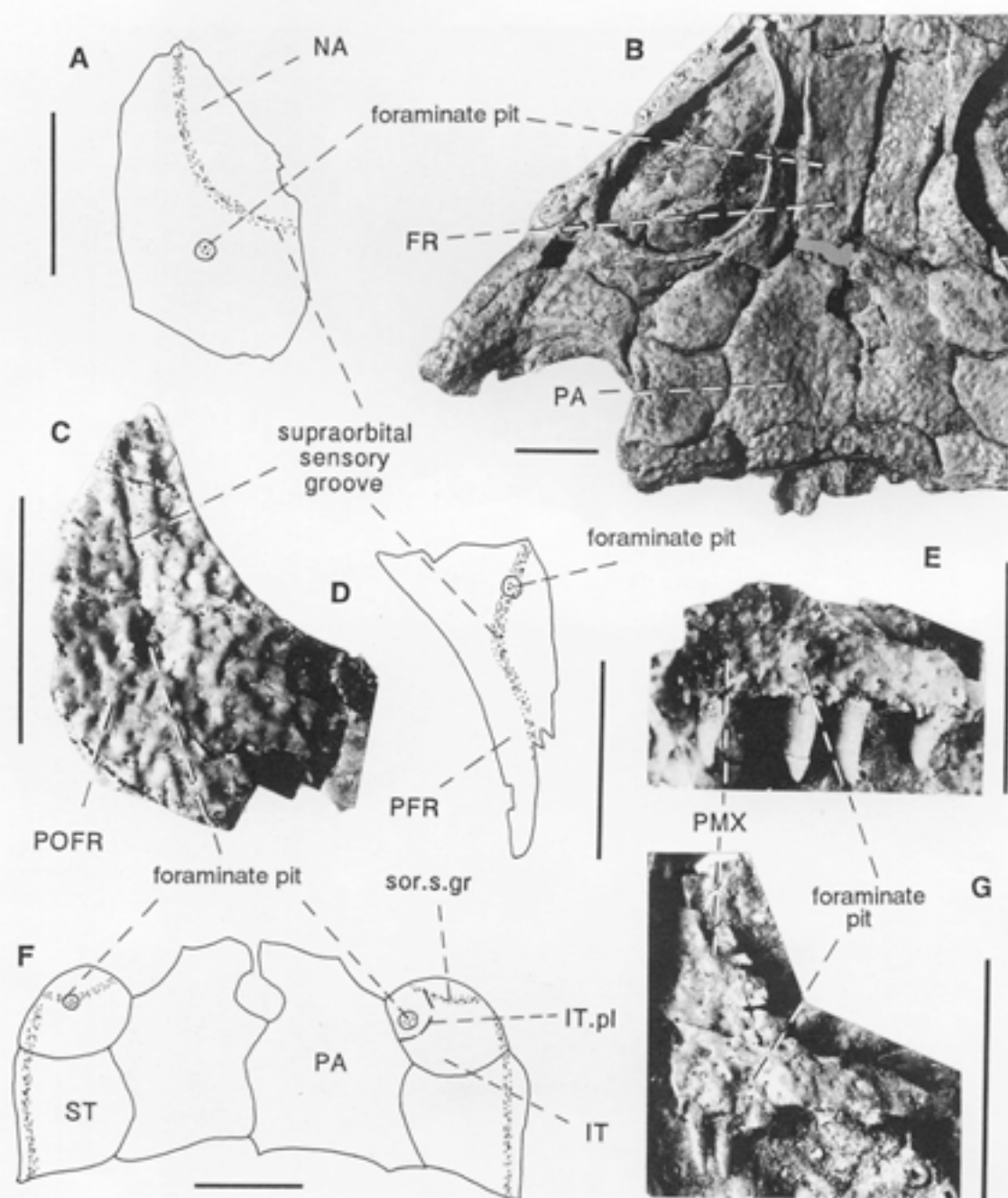
On the ventral surface of the bone, immediately below the FP, a foramen is present in some specimens (e.g. right postparietal of D75, left postparietals of K18 and K278, and left tabular of K256). Although it is probable that this foramen served for the passage of a nerve which ramified inside the bone into small branches passing through the foramina in the FP, this cannot be verified without information from histological sections (this is, however, difficult because the bones contain many relatively large cavities and canals). Because such foramina, like the FP, lie more or less in the central or posteromedial parts of bone in these specimens, the foramen could also be nutritive in function or serve for the nerve of the lateralis system. This is supported by the fact that in those specimens without FP's, foramina are present in the corresponding regions of the bones. An interesting condition is seen in K20, in which the FP lies in the posteriormost part of the right parietal which overlaps the unornamented area of the postparietal. On the ventral surface of this postparietal, there is a group of three foramina which may correspond to the group of foramina in the inner surface of the parietal FP (Text-figs 3A–B). The two groups of foramina do not coincide dorsoventrally; the ventral one is situated slightly more posteriorly. If both groups of foramina were functionally connected, this would imply that the nerve had ramified (at least in this specimen) before entering the bone.

There is usually one FP in each bone. The occurrence of two FPs in immediate proximity is rare (Text-figs 4G; 6A, C–D). In K227, the FP is mediolaterally prolonged. The distribution of foramina on the inner surface of this more or less elliptical depression suggests that it represents two confluent FPs (Text-fig. 5). Two more or less confluent FPs are present also in some left and right postparietals (Text-figs 4B; 6B; 7E (in which two pits are arranged in an anteroposterior orientation with the anterior pit extending slightly into the right parietal)) and in either left (Text-figs 1A; 4G; 7A) or right (Text-fig. 4H) tabulars.

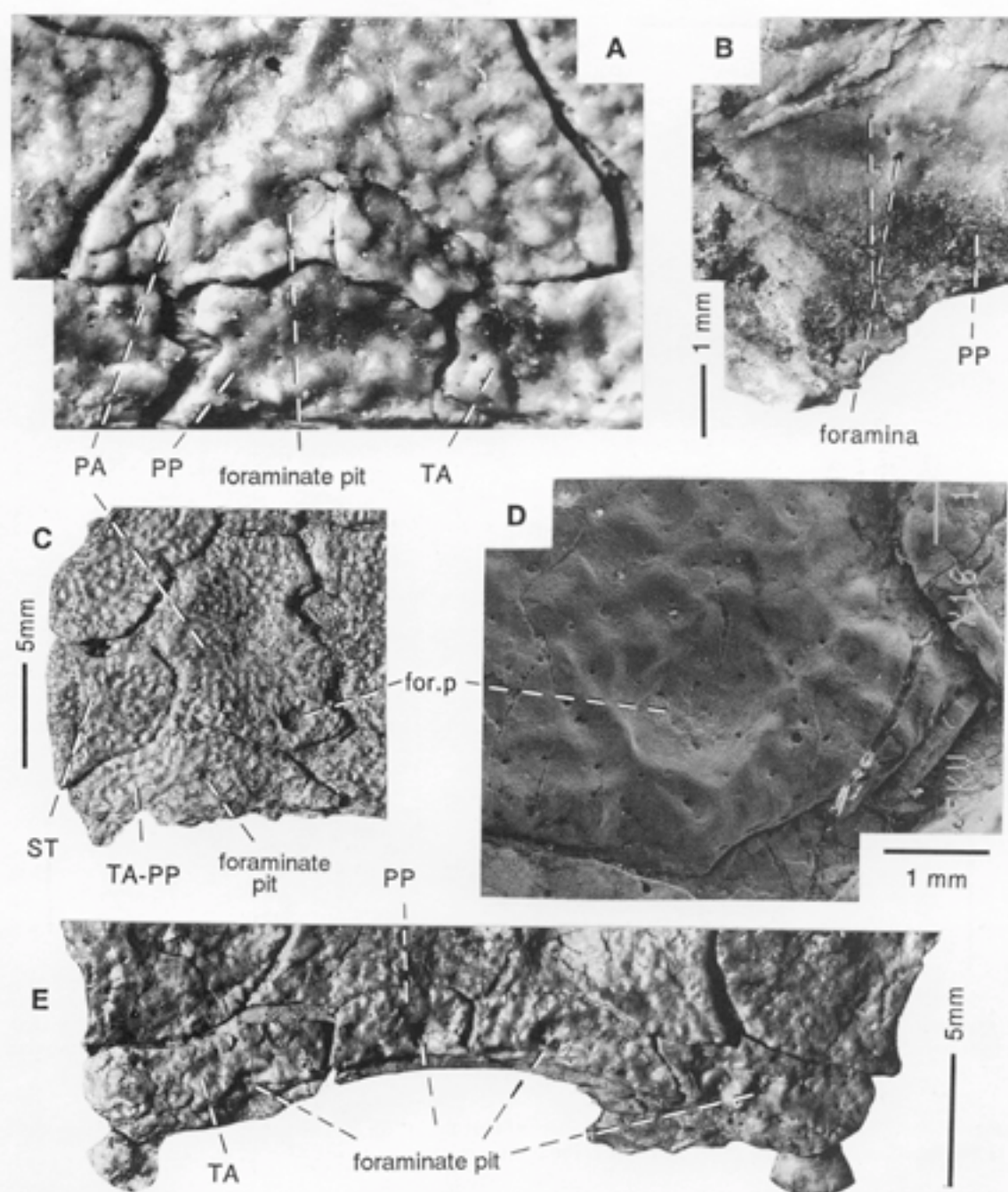
The FPs lie characteristically in or close to the sensory grooves and pit-lines (Text-figs 4E, 9). The lateral line system of *Discosauriscus* has been described elsewhere (Klembara 1992, in press b) and includes sensory grooves (or canals) and pit-lines (the first record in fossil amphibians). The FP also has a more or less constant position within the bone (see also Text-fig. 9).



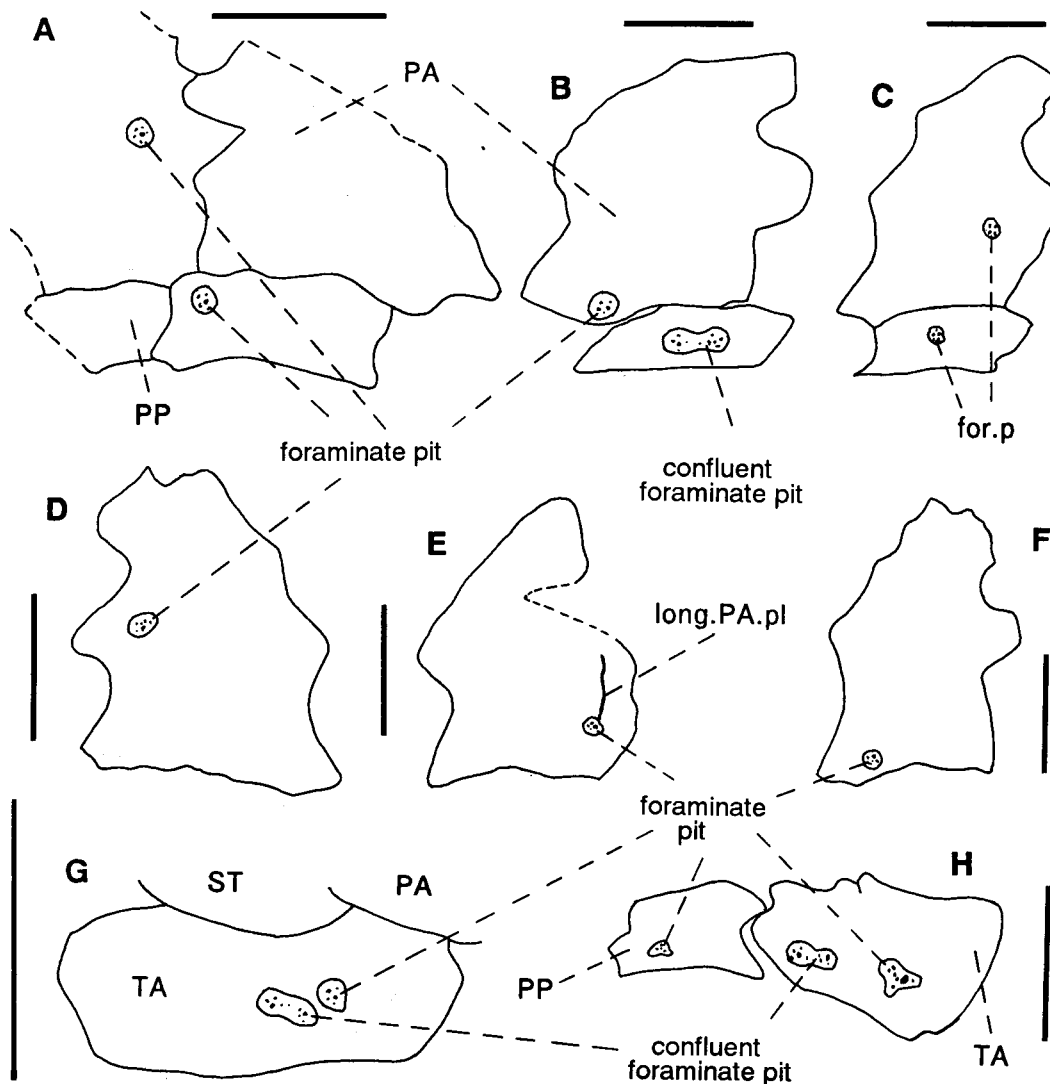
TEXT-FIG. 1. *Discosauriscus austriacus* (Makowsky); K241. A, posterior portion of skull table in dorsal view. B, illustration of enlarged foraminated pit of right parietal of the same specimen.



TEXT-FIG. 2. *Discosauriscus austriacus* (Makowsky). A, K224; right nasal. B, K206; skull roof. C, D47; right postfrontal. D, K80; left prefrontal. E, D54. G, D91; left premaxillaries. F, K57; posterior part of skull table. All figures in dorsal view. Scale bars represent 5 mm.



TEXT-FIG. 3. *Discosauriscus austriacus* (Makowsky). A, K20; foraminated pit in posterior part of right parietal. B, group of three foramina in ventral surface of right postparietal of the same specimen as 3A. C, D43; left side of posterior part of skull table. D, enlarged foraminated pit of left parietal of the same specimen as 3C. E, K326; foraminated pits in posteriormost bones of skull table. All figures in dorsal view except for 3B.



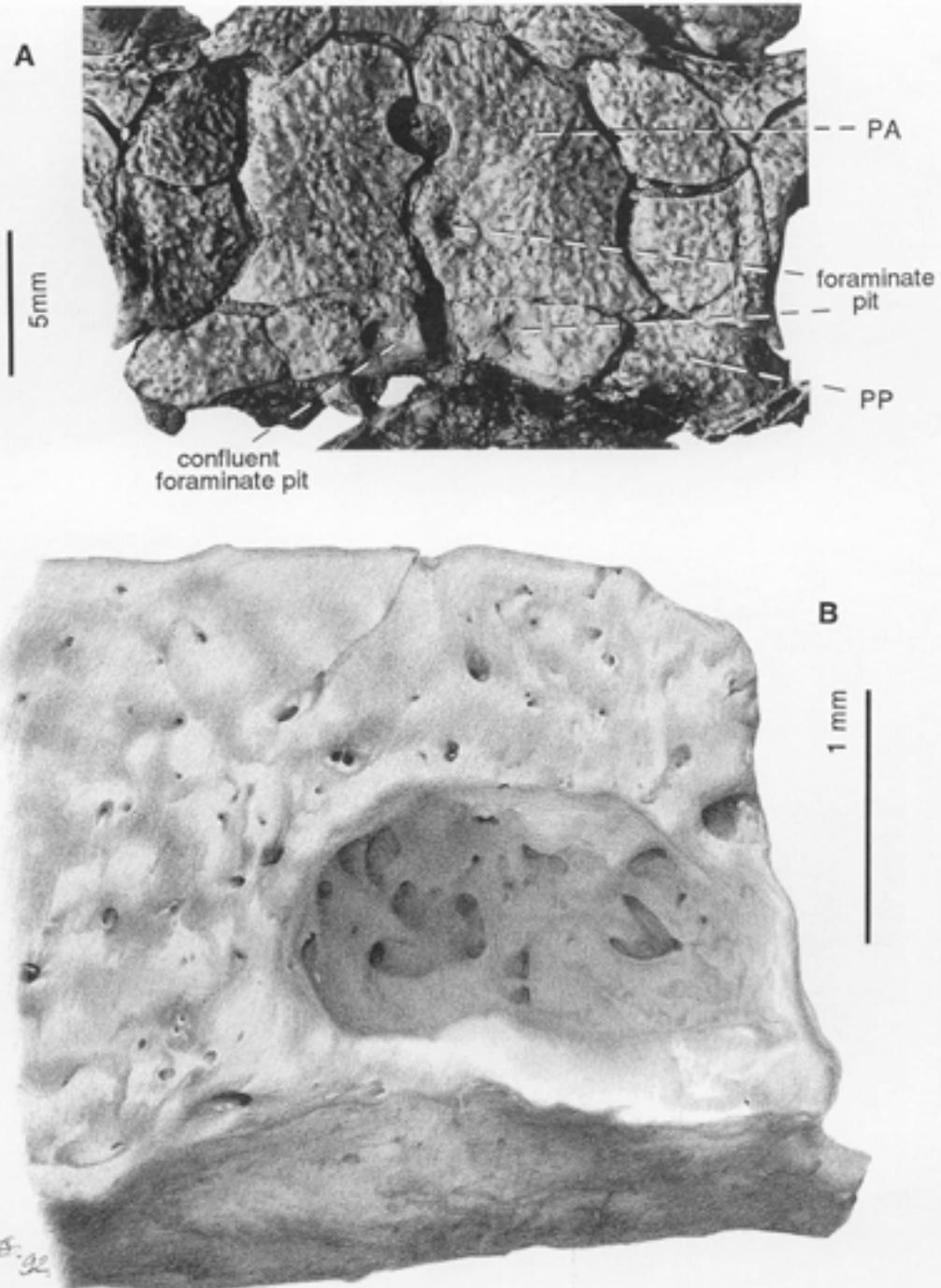
TEXT-FIG. 4. *Discosauriscus austriacus* (Makowsky); outlines of dorsal surfaces of some exocranial bones with foraminatate pits. A, K185; parietals and postparietals. B, K63. C, K18; left parietals and postparietals. D, D70; right parietal. E, K231. F, D200.III; left parietals. G, D86; left tabular. H, KO7; right postparietal and tabular. Scale bars represent 5 mm.

Premaxillary. FPs are visible in two left premaxillaries (Text-fig. 2E, G). In both specimens, the FP lies very close to the junction of the infraorbital and supraorbital sensory grooves.

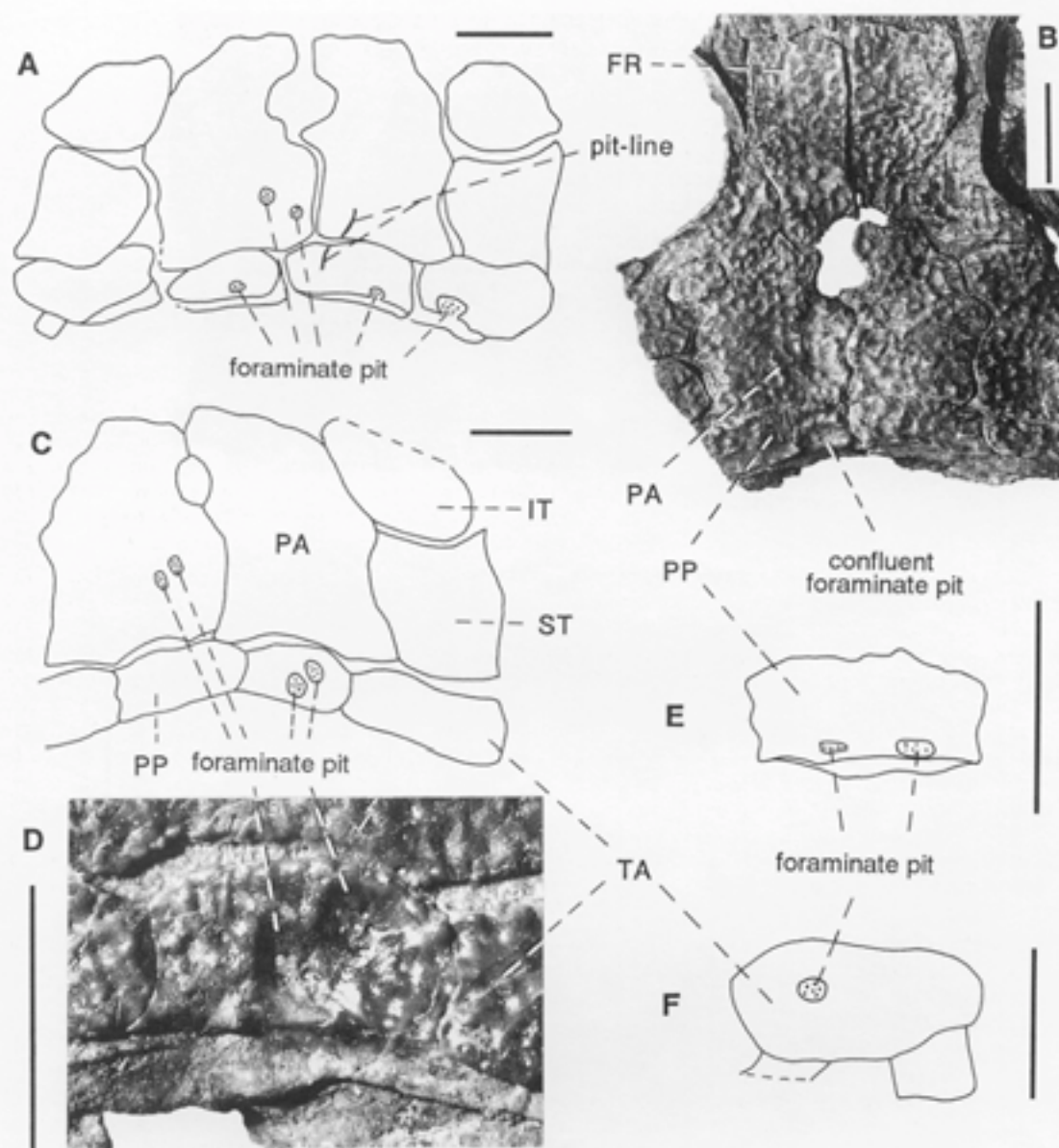
Nasal. In the nasals, the FP is situated close to the lacrimal section of the supraorbital sensory groove (Text-figs 2A, 9).

Prefrontal. A prefrontal FP was found only in the left prefrontal of K80. It lies directly on the path of the sensory groove (Text-fig. 2D).

Frontal. The FP in the left frontal of K206 is situated in the corner formed by the supraorbital sensory groove laterally and the anterolateral part of the frontal pit-line anteromedially (Text-fig. 2B). Although the frontal



TEXT-FIG. 5. *Discosauriscus austriacus* (Makowsky); K227. A, posterior part of skull roof in dorsal view; B, enlarged confluent foraminiate pit in left postparietal of the same specimen.



TEXT-FIG. 6. *Discosaurus austriacus* (Makowsky). A, K325; posterior part of skull table. B, D48; skull table. C, D75; partial posterior skull table. D, two foraminatopits of right postparietal of the same specimen as C. E, K5; right postparietal. F, KO8; right tabular. All figures in dorsal view. Scale bars represent 5 mm.

pit-line is absent in this specimen, its course is clearly visible in other specimens (e.g. K60, K69; see Klembara 1992, in press b). The FPs in K111 and KO80 are in similar positions.

Postfrontal. The FPs in the left and right postfrontals lie directly in the sensory groove (Text-fig. 2c; Klembara 1992, fig. 1b).

Intertemporal. FPs occur in the left intertemporals of K57 and K279. They are situated directly in the sensory grooves. The FP in the right intertemporal of K57 lies immediately medially to the intertemporal pit-line (Text-fig. 2F).

Supratemporal. The supratemporal FP of KO13 lies in the anteromedial portion of the right supratemporal, close to the supratemporal pit-line. In KO25, the FP lies directly in the posterior section of the postotic sensory groove of the right supratemporal (Text-fig. 9).

Parietal. Within the parietals, FPs occur in four basic positions.

- (1) Immediately posterolaterally to the pineal foramen (Text-fig. 4A, D).
- (2) Mid-way between the pineal foramen and the posterior margin of the bone (Text-figs 1, 4C, 5).
- (3) Slightly anterior to the posterior margin of the bone (Text-figs 3A, C-D, 4E).
- (4) In the region of the posterolateral corner of the bone (Text-fig. 4B, F).

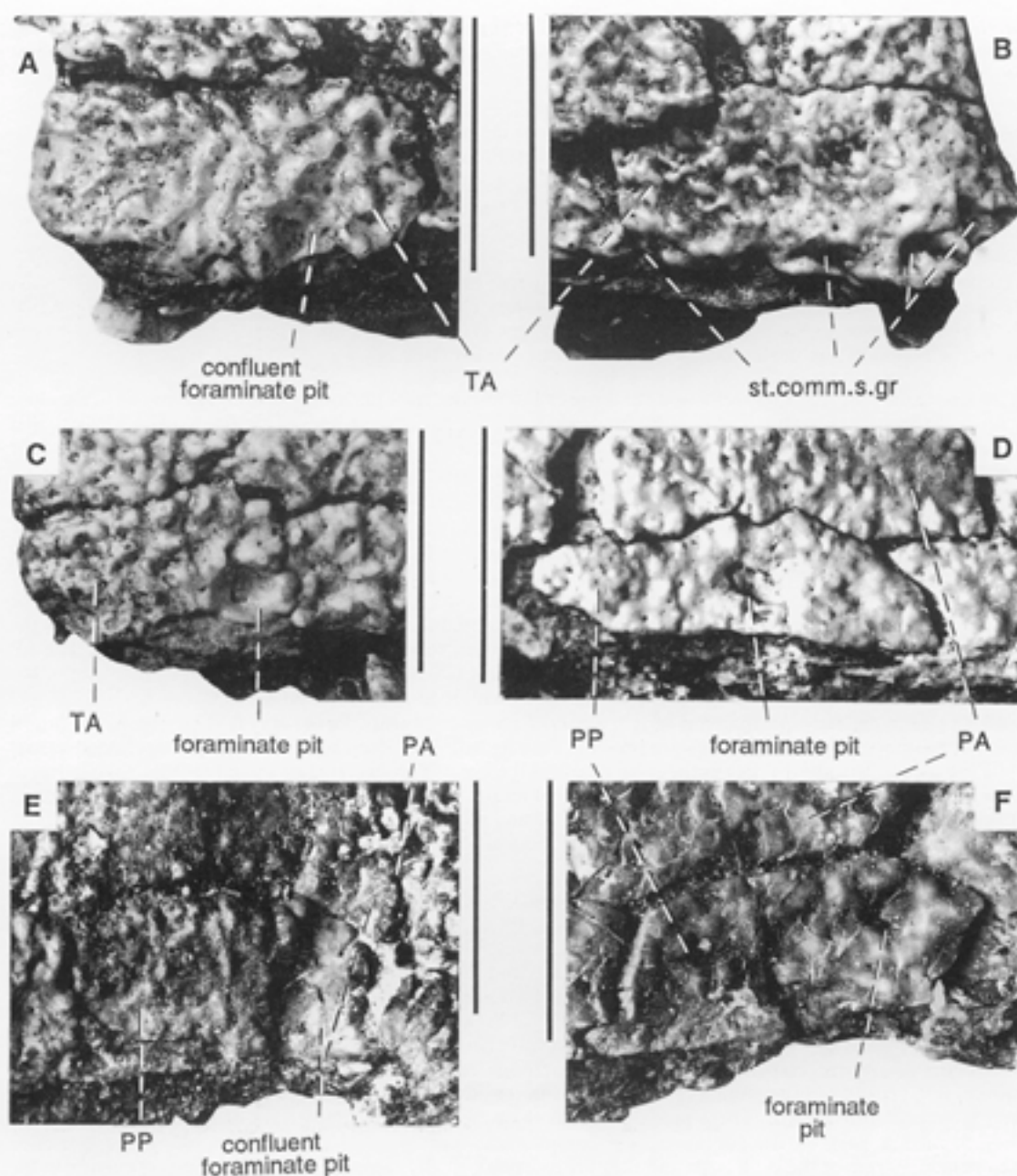
In the first three positions (and sometimes in more or less intermediate positions), the FPs always lie in the close vicinity of the median suture and directly in, or close to, the parietal pit-lines (Text-fig. 9). The FPs situated in the posterolateral corner of the parietal are approximately equidistant between the oblique (and/or theoretically transverse) parietal pit-lines and the supratemporal commissural sensory groove. As already mentioned, a pair of FPs sometimes occurs in the posterior portion of one parietal (Text-fig. 6A, C).

Postparietal. Most of the postparietal FPs are concentrated in the central and posteromedial portion of the ornamented part of the bone, directly in, or close to, the supratemporal commissural sensory groove or postparietal pit-lines (Text-figs 3E, 4H, 5A, 6A, 7D). More rarely, the FP lies in the anterior portion of the postparietal (Text-figs 4A, 7F). In D43, the left postparietal and tabular are fused as one element and here the FP lies in the lateral region of the postparietal component of this tabulo-postparietal (Text-fig. 3C). The FP in the left postparietal of K182 is in a similar position. In D75, one of the FPs in the right postparietal, lies in its anterolateral region (Text-fig. 6C-D). As already mentioned, in the left postparietals of K63, K227, D3 and D48 and in the right postparietal of K3, a pair of partly confluent PFs occurs (Text-figs 4B, 5, 6B, 7E). In the right postparietal of K5, two FPs are present (Text-fig. 6E): the lateral one lies in the posterolateral corner while the second, smaller FP lies in the medial half of the bone. The structure of these two FPs, together with those in the right postparietal of K324 (Text-fig. 7D) and in the left postparietal of D60 (Klembara, in press b), is very similar: elliptical shape, steep, distinct wall and relatively smooth bottom surface. In K5 and K324, the foramina are situated in the basal portions of the wall of FPs.

Tabular. Like most of the postparietal FPs, the tabular FPs are situated in the central, medial or posteromedial portion of the ornamented part of bone (Text-figs 3E, 4G, 6A, 7C), i.e. directly in or close to the supratemporal commissural sensory groove. There are exceptions to this. The FP in KO8 lies in the anteromedial part of the right tabular (Text-fig. 6F). The left tabular of D86 and the right tabular of KO7 bear two FPs. In both specimens, the left FP is confluent (Text-fig. 4G-H). Two almost confluent FPs are in the left tabular of K241 (Text-figs 1A, 7A).

The posterior margin of the ornamented surfaces of the tabulars and postparietals in most specimens of *Discosauriscus* are irregular and relatively large foramina occur in them. They are generally situated in the posterolateral corners of the tabulars (Text-fig. 7B) but they are also present in other regions of the ornamented skull table posterior margin. These pits are smaller than the FPs and usually have one foramen at the base. They formed a part of the supratemporal commissural sensory groove which ran along the posterior ornamented margin of the skull table and they are morphologically comparable to similar pits occurring in the floors of the sensory canals in other regions of the skull. Therefore, although distinction is sometimes difficult, these pits should not be misinterpreted as the FPs lying directly or very close to the supratemporal commissural sensory groove.

Maxillary. In the anterior part of the right maxillary of K316, one relatively small and deep FP is present (Text-fig. 8B). It is situated close to the lacrimal section of the infraorbital sensory groove. The FP in the left maxillary of K180 is in the same position. In the right maxillary of K257, a typical (more shallow) FP is present (Text-fig. 8A), and lies a little more anteriorly and closer to the tooth row in comparison with the FPs of K316 and K180.



TEXT-FIG. 7. *Discosauriscus austriacus* (Makowsky). A, K241; left tabular (cf. Text-fig. 1A). B, K172; right tabular. C, K256; left tabular. D, K324; right postparietal. E, D3; left postparietal. F, D104; left postparietal. All figures in dorsal view. Scale bars represent 5 mm.

Lacrimal. In the right lacrimals of K195 and D81, round and deep FPs are present. They lie close to the lacrimal section of the infraorbital sensory groove (Text-fig. 9). In the left lacrimals of D54 and D73, the FP lies in the anteriormost part of the lacrimal section of the infraorbital sensory groove (Text-fig. 8c) and in the left lacrimal of K328, the FP lies in its posterior part.

Jugal. Two closely spaced FPs are present in the right jugal of K325 (Text-fig. 8i). The more medial one is situated at the point where the jugal and infraorbital sensory grooves meet; the more lateral one is situated on the jugal section of the infraorbital sensory groove. An FP in the left jugal of K180 also occurs in the latter position (Text-fig. 8G).

Squamosal. In the right squamosal of K256, two closely spaced FPs are present (Text-fig. 8H); the more anterior one is smaller, the posterior one is larger. This pair of FPs lies in the area of the squamosal section of the jugal sensory groove. Single FPs in the right (Text-fig. 8F) and in the left (D53) squamosals are situated in similar positions.

Dentary. One deep FP is present midway along the right dentary of D28 (Text-fig. 8D). In the anterior parts of both dentaries of K257 two FPs are situated respectively. The FP in the left dentary is prolonged and probably represents two confluent FPs (Text-fig. 8E).

COMPARISON AND DISCUSSION

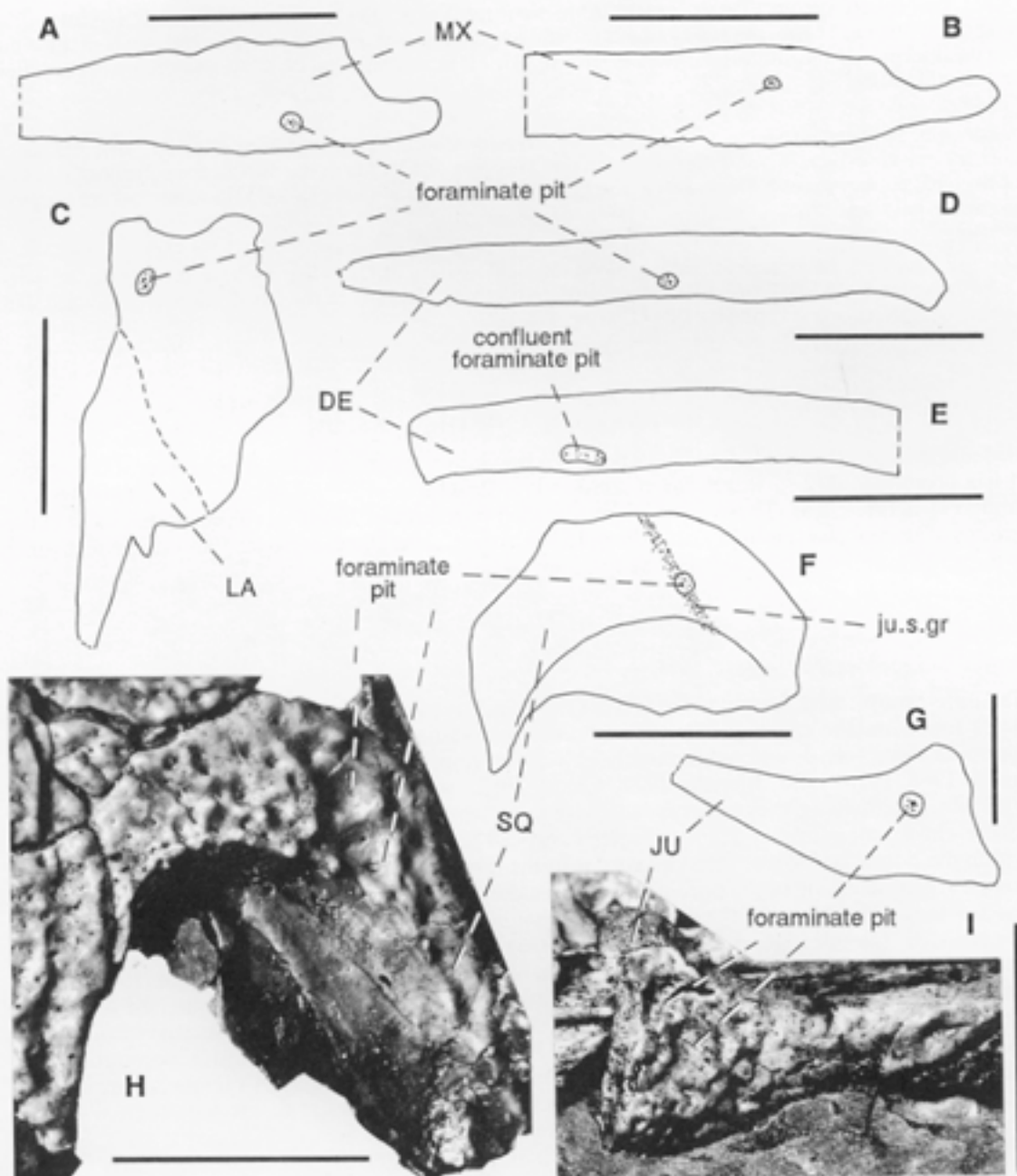
Because the FPs described above have not been previously recorded in fossil or in Recent tetrapods, it has been necessary to search for corresponding structures in fishes. Among them, two types of similar structure occur. These are: (1) the so-called pore-groups found in rhipidistians; and (2) the groups of cranial pits found in arthrodires. In both cases, as in *Discosauriscus*, they comprise distinct groups of foramina lying close to one another.

Pore-groups

The pore-groups, first described by Jarvik (1948) in Devonian osteolepids, are the groups of small pores found on the external faces of some dermal cranial bones. Such distinct groups of small foramina have been found subsequently in various rhipidistians (Gross 1956; Ørving 1960, 1961; Jessen 1966, 1975, 1980; Bjerring 1972; Chang 1982; see also 'cutaneous sense organs' of Ørving 1961). In rhipidistians, they occur mostly within the frontoethmoidal shield but also in some bones of the cheek, mandible and branchiostegal rays. The posteriormost occurrence of pore-groups within the dorsal portion of the skull roof is in the intertemporal (Jessen 1966; Bjerring 1972). The common characteristic of the pore-groups is that they are 'usually well defined and distinct, but the parts of the external faces of the dermal bones that bear these groups are generally neither depressed nor elevated' (Jarvik 1948, p. 137). However, Bjerring (1972) recorded the intertemporal groups of pores situated in a shallow depression in one Carboniferous osteolepiform and Jessen (1966, p. 318) found that the pore-group in the anterior supraorbital 'lies distinctly slightly immersed relative to the outer surface of the surrounded cosmine layer'. The pore-groups are situated close to the sensory canals or pit-lines. Bjerring (1972, p. 85) proved that the foramina of the pore-group 'are the upper extremities of a narrow, dorsally branching canal which passes obliquely through the intertemporal and opens to the surface of the bone somewhat mesial to the longitudinal row of nerve openings leading into the lateral-line canal system'.

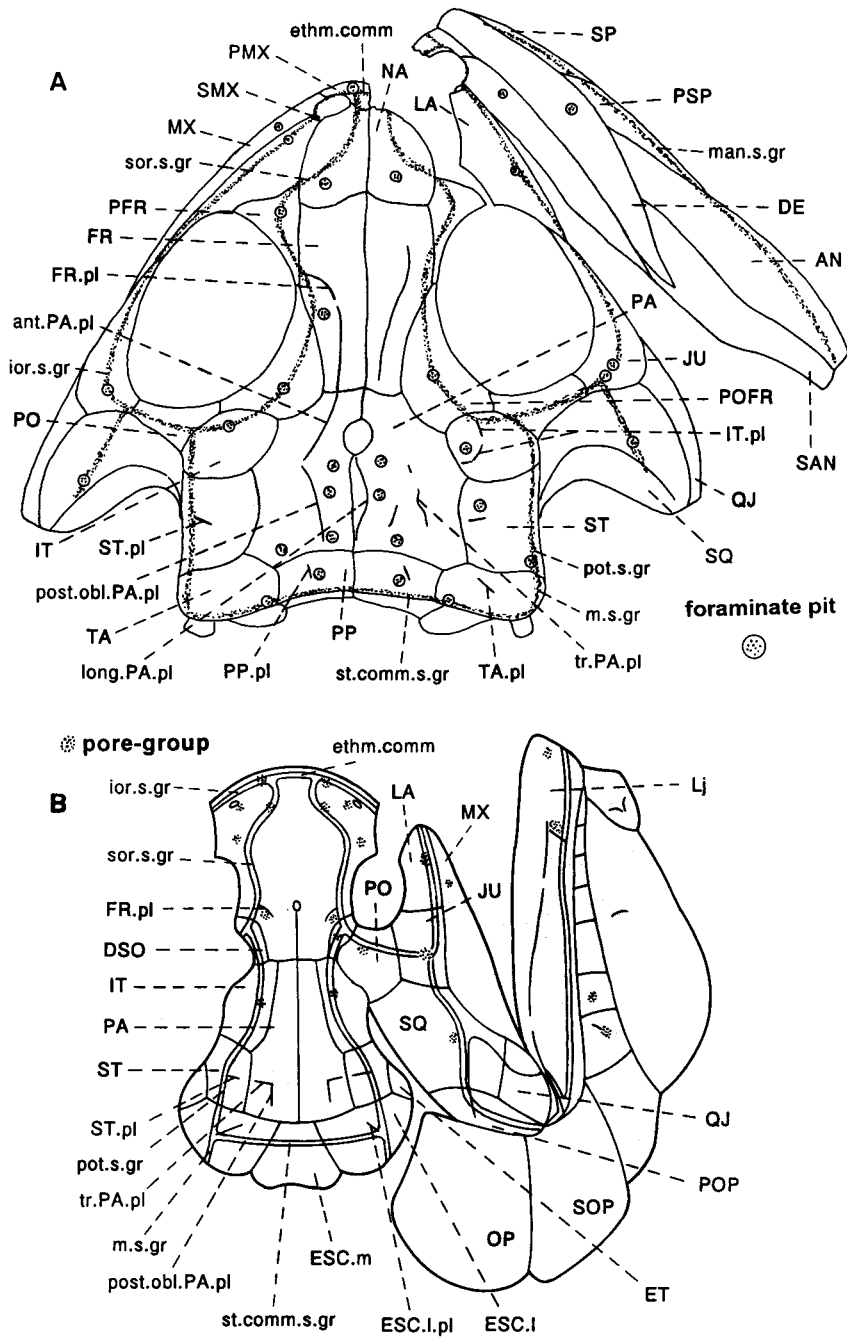
Comparison of the pore-groups of rhipidistians with the FPs of *Discosauriscus* shows striking positional and morphological similarities of both structures.

- (1) The groups of foramina form distinct patches.
- (2) The size (the diameter) of the FP corresponds to the size of the pore-group (always in relation to the size of the skull).
- (3) The corresponding number of foramina in one group: Bjerring (1972) recorded intertemporal pore-groups of eight (left) and seven (right) foramina; in *Discosauriscus* the number of foramina in one FP varies from two to ten.



TEXT-FIG. 8. *Discosauriscus austriacus* (Makowsky). A, K257; right maxillary. B, K316; right maxillary. C, D54; left lacrimal. D, D28; right dentary. E, K257; left dentary. F, K98; right squamosal. H, K256; right squamosal. G, K180; left jugal. I, K325; right jugal. All figures in dorsal view. Scale bars represent 5 mm.

- (4) Only one or two (independent or confluent), exceptionally three (Text-fig. 4G-H) or probably more (Jarvik 1948, fig. 68B) distinct groups of foramina have been observed in one bone. This is, however, judged in the rostral portion of the frontoethmoidal shield in fishes where the bones



TEXT-FIG. 9. A, *Discosauriscus* skull roof (dorsoventrally pressed) showing position of sensory grooves, pit-lines and foraminat pits (based on Klembara 1992, in press b). B, pore-groups, sensory canals and pit-lines observed in exocranial bones of osteolepids from the Middle Devonian of Scotland; combined from several specimens (after Jarvik 1948, fig. 36A); pore-groups in dermosphenotic, intertemporals, maxillary and right lateral extratemporal pit-line based on the Devonian osteolepid *Latvius* (Jessen 1966, fig. 1B-C).

are mostly fused. In all cases, the groups of foramina lie at certain distances to one another and they are not aggregated in larger concentrations in one bone as in arthrodires (see below).

- (5) The presence of two closely spaced groups of foramina (Jarvik 1948, fig. 22F in the right squamosal and in the right squamosal of *Discosauriscus*; Text-fig. 8H) or of two confluent groups of foramina (Jarvik 1948, fig. 23E in the lower jaw; Text-figure 8E).
- (6) The groups of foramina are situated close to the sensory canals and pit-lines. In *Discosauriscus*, the FPs sometimes lie directly in the sensory grooves (Text-fig. 9A) because the latter, contrary to the situation in fishes, lie on the bone surface. However, as seen in osteolepids (Text-fig. 9B), some pore-groups lie directly above the sensory canals.
- (7) The striking position similarity of individual groups of foramina.
 - (a) The premaxillary FPs lie in the region of the junction of infraorbital and supraorbital canals (Text-fig. 2E, G) exactly like the pore-groups of the premaxillary region in osteolepids (Jarvik 1948, fig. 36A), *Powichthys* (Jessen 1975, figs 1D, 2) and *Youngolepis* (Chang 1982, figs 5B, 6C); see also Text-figure 9.
 - (b) The position of nasal FPs (Text-fig. 2A) corresponds well to the position of pore-groups in the region of the nasals and postrostrals in osteolepids (Jarvik 1948, fig. 36A; Jessen 1966, fig. 1A–B), *Powichthys* (Jessen 1975: figs. 1A–C, E; 2); Text-fig. 9.
 - (c) The FP of the prefrontal lies in the same position as the pore-group in the posterior tectal (Text-figs 2D, 9; Gross 1956, fig. 1A; Jarvik 1948, fig. 38K; Jessen 1966, fig. 4B). The position of these groups of foramina supports the view that the posterior tectal is homologous with at least the upper part of the prefrontal of *Discosauriscus* (Klembara, in press b).
 - (d) The FP of the left frontal is situated in exactly the same place as the pore-group of some osteolepids, i.e. in the corner formed by the supraorbital sensory canal laterally and the anterolateral portion of the frontal pit-line medially (Text-figs 2B, 9; Jarvik 1948, fig. 79F). Such a position of the frontal FP provides further evidence that the frontal bone of *Discosauriscus* is homologous with the bone called frontal in the 'orthodox' or 'traditional' terminology in osteolepiforms (Klembara 1992, in press b); it supports the view that the frontals in *Discosauriscus* are homologous with the bones enclosing the pineal foramen in osteolepiforms (Text-fig. 9).
 - (e) The position of the FP in the postfrontal corresponds very well to the position of the pore-group in the dermosphenotic (Text-figs 2C, 9; Jarvik 1948, pl. 22, fig. 3; Jessen 1966, fig. 1A–B). As for the different position of the junction of infraorbital and supraorbital sensory canals in osteolepiforms and *Discosauriscus* see Klembara (in press a).
 - (f) The FP in the intertemporal of *Discosauriscus* lies in the sensory groove or close to the intertemporal pit-line. The same situation occurs in rhipidistians, although the pore-group of the intertemporal lies in the region of different section of sensory canal system (Text-figs 2F, 9; Gross 1956, figs 2B, G; Jessen 1966, figs 4A, C; Bjerring 1972, figs 1A, 2, 3, 4C, 6).
 - (g) The position of the FPs in the lacrimals of D54, D81 and K195 (Text-figs 8C, 9) corresponds to the position of the lacrimal pore-group in osteolepids (Jarvik 1948, figs 22E–F, 36A, 39E, G, 67A; Jessen 1966, fig. 1A; Text-fig. 9).
 - (h) The maxillary FPs lie in the anterior portion of the bone (Text-fig. 8A–B), in exactly the same place as the pore-group in the osteolepid *Latvius* (Jessen 1966, fig. 1A; Text-fig. 9).
 - (i) The FPs in the jugals lie in close vicinity to the junction of the infraorbital and jugal sensory grooves (Text-fig. 8G, I) which is identical in position to those of the pore-groups of jugals in osteolepids (Jarvik 1948, figs 22E, 36A, 67A; Jessen 1966, fig. 1A; Text-fig. 9).
 - (j) The FPs of the squamosal lie in the posterior section of the jugal sensory groove on the ornamented surface of the squamosal, i.e. in the posterior part of the anterior half of the squamosal length (Text-fig. 8F, H). This corresponds to the position of squamosal pore-groups found in osteolepids (Jarvik 1948, figs 22F, 36A, 73A; Jessen 1966, fig. 1A), although the squamosal (or temporal) embayment is absent in the latter (Text-fig. 9).
 - (k) The position of FPs in the dentaries (Text-fig. 8D–E) is comparable to the pore-groups of the anterior regions of the lower jaws of osteolepids (Jarvik 1948, figs 36A, 59F; Text-fig. 9).

From the above results, it can be seen that the only distinct morphological difference between the pore-group of rhipidistians and the FP of *Discosauriscus*, is that in the latter the group of foramina lies in a more distinctly developed pit and that, inside this pit, these foramina lie in still smaller pit structures. Unlike the pore-groups, the FPs occur also in parietals, supratemporals, tabulars and postparietals. Many striking similarities indicate, however, that the FPs and the pore-groups could be homologous structures and that they housed functionally identical organs.

The cranial pits of arthrodires

The groups of pits in the ornamented surface of some cranial bones of relatively small individuals of the arthrodire *Ctenurella*, were preliminarily described by Ørvig (1971, p. 30, fig. 6A). They are distinct, rounded pits arranged in a more or less pronounced reticular pattern. At the bottom of each pit, the foramen or foramina are observable. According to Ørvig (1971, p. 31) '... the 'pitted' areas seem to bear definite relations to the lateral line canals'.

In *Ctenurella*, as in *Discosauriscus*, the foramen or the groups of foramina are situated in distinct, rounded pits which lie close to the lateral line canals (Ørvig 1971, fig. 6A; Text-fig. 9). Although Ørvig did not give much information about the size, the morphology of the inner surface of the pit, or the number of foramina in the bottom of the pits, it seems that the whole morphology and the position of these pits in *Ctenurella* and the FPs of *Discosauriscus* are very similar. This suggests that the structures in the two animals may have had the same function.

INTERPRETATION AND CONCLUSIONS

On the basis of the position of the pore-groups, Jarvik (1948) and Bjerring (1972) deduced that the pore-group canals probably carried small peripheral nerves of the lateralis system. Jarvik (1948, p. 137) proposed, therefore, that the groups of pores 'mark the position of groups of some cutaneous sensory organs of somewhat the same type as the ampullae of Lorenzini in Elasmobranchs, the nerve-sacs of Teleostomian fishes ... and 'die Flaschenförmige Organe' of Dipnoi...' (Jarvik 1980, p. 205). Bjerring (1972) suggested that the peripheral nerves of the lateralis system might have supplied a specific epidermal sensory area which perhaps was responsible for the reception of thermal stimuli (however, according to Bjerring 1986, the pore-groups are evidence for electroreception in osteolepids).

Ørvig (1971, p. 31) regarded the groups of pits in some dermal cranial bones in *Ctenurella*, 'as the sites of comparatively large groups of cutaneous sense organs resembling, or closely related to, ampullae of Lorenzini'. According to Ørvig (1971), the individual pits originally could have housed the ampullae of Lorenzini or clusters of these (similar to those in extant selachians and holocephalians).

As well as fishes, ampullary organs have also been found in representatives of two groups of extant tetrapods: the caecilian *Ichthyophis* (Hetherington and Wake 1979) and the urodeles *Triturus*, *Salamandra* and *Ambystoma* (Fritsch and Wahnschaffe 1983; Northcutt 1989). However, as in extant fishes, the ampullary organs of urodeles do not leave traces in the external surface of the dermal cranial bones. As was shown by Fritsch and Wahnschaffe (1983), the ampullary organ, unlike the neuromast organ, is more or less recessed below the epidermis (usually below the basement membrane) and connected to the surface by a canal (Fritsch and Wahnschaffe 1983, p. 491, figs 6-7, 10, 20). This canal may be relatively long and is delineated by epidermal cells. The diameter of the ampullary organs ranges from 60-80 μm . The ampullary organs form groups of two to five organs (never linearly arranged) and sometimes three to five organs are found at the base of one canal (Fritsch and Wahnschaffe 1983, fig. 8). They accompany the rows of neuromast organs. Unlike the neuromast organs, only one afferent fibre innervates each ampullary organ or groups of organs. During the terrestrial phases of the urodele's life, the canal of the ampullary organ is closed by the outer epidermal layer.

From the comparisons of the ampullary organs of urodeles and FPs of *Discosauriscus*, it is here concluded that the FPs probably housed groups of ampullary organs as found in urodeles and caecilians. This conclusion is supported by morphological and positional similarities of the compared structures. The structure of the inner surface of the FPs is entirely consistent with the possibility of housing such groups of ampullary organs. The inner surface of the FP is smooth or more or less irregular consisting of various pits, depressions, short grooves or canals, each having one small foramen at the base. These structures probably housed the groups of ampullary organs supplied by peripheral nerves of the lateralis system. The size of a group of ampullary organs corresponds very well to the size of one pit structure in the inner surface of the FP. If this interpretation of the *Discosauriscus* FPs is correct, the osteolepiform pore-groups also mark the possible presence of ampullary organs.

The ampullary organs within the head of *Salamandra* occur mostly around the external nares and eyes, although in *Ambystoma mexicanum* they occur also at the base of the gills (Fritsch and Wahnschaffe 1983). In *Ichthyophis*, however, they are also present in the posterodorsal region of the head (Hetherington and Wake 1979), as in *Discosauriscus*. The distribution of the ampullary organs within the head in urodeles differs from the condition in *Discosauriscus* where the FPs are not so abundant and occur mostly in the posterior part of the skull table. In osteolepiforms, the individual pore-groups are also less abundant (as in *Discosauriscus*), but occur, as in urodeles and *Ichthyophis*, mostly in the frontoethmoidal region of the skull. However, the position of most of the pore-groups in the individual skull roof bones of osteolepiforms and of the FPs in *Discosauriscus* is conspicuous (see above and Text-fig. 9) and, together with the morphological similarities, indicate the homology of both structures as well as of the bones which bear them. This is in agreement with the conclusions based mostly on the morphology and position of pit-lines in the dermal skull roof bones in *Discosauriscus* that the 'orthodox' terminology of the skull roof bones used in osteolepiforms (and related fish groups) is correct (Klembara 1992, in press b; Text-fig. 9). It implies that the bones enclosing the pineal (and/or parapineal) foramen are the frontals. The distribution of FPs and pore-groups in skull roofs of *Discosauriscus* and rhipidistians (especially osteolepids but also *Powichthys* and *Youngolepis*) clearly indicates their evolutionary relationship.

It has been shown that, in Recent urodeles, the lateral line system consists of two types of receptors with two different properties: mechanoreceptive neuromasts and electroreceptive ampullary organs (e.g. Fritsch 1981a, 1981b; Münz *et al.* 1982, 1984; Bullock 1982; Himstedt *et al.* 1982; Fritsch and Wahnschaffe 1983). Münz *et al.* (1982) showed that the axolotl (*Ambystoma mexicanum*) was able to detect weak electrical fields. Himstedt *et al.* (1982) observed in the axolotl, changes in prey capture behaviour during electrical stimulation (however, this phenomenon appeared only after visual and mechanical stimuli). They concluded 'that the electrosensory system may help to localize prey objects which produce electrical fields...'. According to Münz *et al.* (1984, p. 42), 'the feeding behavior may normally be guided not by the electroreceptive system alone, but rather by cooperation of the electroreceptive, mechanoreceptive, and olfactory systems'. The possession of electrical fields in insect larvae, snails, tadpoles and fish was recorded by Peters and Bretschneider (1972). If the FPs in *Discosauriscus* housed ampullary organs, this implies that this Early Permian tetrapod was electroreceptive and used this ability in a similar way to Recent urodeles. Likewise, the same is true for rhipidistians. The presence of the FPs in *Discosauriscus* also supports the recognition of this tetrapod (in the size category considered here) to be larval (Klembara 1993, 1994, in press a, b). The possible existence of the electroreceptive ampullary organs in *Discosauriscus* supports the view of Bullock, Northcutt and Bodznick (1982) that electrosensitivity is phylogenetically as old as the major vertebrate sensory systems.

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REFERENCES

- BJERRING, H. C. 1972. The nervus rarus in coelacanthiform phylogeny. *Zoologica Scripta*, **1**, 57–68.
- 1986. Electrical tetrapods? 29–36. In ROČEK, Z. (ed.). *Proceedings of the European Herpetological Meeting (3rd Ordinary General Meeting of the Societas Europaea Herpetologica) Prague 1985*. Prague, 754 pp.
- BORGEN, U. J. 1983. Homologizations of skull roofing bones between tetrapods and osteolepiform fishes. *Palaeontology*, **26**, 735–753.
- BULLOCK, T. H. 1982. Electroreception. *Annual Review of NeuroSciences*, **5**, 121–170.
- NORTH CUTT, R. G. and BODZNICK, D. A. 1982. Evolution of electroreception. *Trends in NeuroSciences*, **5**, 50–53.
- CHANG MEE-MAN. 1982. The braincase of *Youngolepis*, a Lower Devonian crossopterygian from Yunnan, South-Western China. Ph.D. thesis, University of Stockholm.
- FRITZSCH, B. 1981a. The pattern of lateral-line afferents in urodeles. A horseradish-peroxidase study. *Cell and Tissue Research*, **218**, 581–594.
- 1981b. Electroreceptors and direction specific arrangements in the lateral-line system of salamanders? *Zeitschrift für Naturforschung*, **36C**, 493–495.
- and WAHNSCHAFFE, U. 1983. The electroreceptive ampullary organs of urodeles. *Cell and Tissue Research*, **229**, 483–503.
- GROSS, W. 1956. Über Crossopterygier und Dipnoer aus dem baltischen Oberdevon im Zusammenhang einer vergleichenden Untersuchung des Porenkanalsystems paläozoischer Agnathen und Fische. *Kungliga Svenska Vetenskapakademiens Handlingar*, **5**, 1–140.
- HETHERINGTON, T. E. and WAKE, M. H. 1979. The lateral-line system in larval *Ichthyophis* (Amphibia: Gymnophiona). *Zoomorphology*, **93**, 209–225.
- HIMSTEDT, W., KOPP, J. and SCHMIDT, W. 1982. Electroreception guides feeding behaviour in amphibians. *Naturwissenschaften*, **69**, 552.
- JARVIK, E. 1948. On the morphology and taxonomy of the Middle Devonian osteolepid fishes of Scotland. *Kungliga Svenska Vetenskapakademiens Handlingar*, **25**, 1–301.
- 1980. *Basic structure and evolution of vertebrates. Volume 1*. Academic Press, New York, 575 pp.
- JESSEN, H. 1966. Die Crossopterygier des Oberen Plattenkalkes (Devon) der Bergisch-Gladbach-Paffrather Mulde (Rheinisches Schiefergebirge) unter Berücksichtigung von amerikanischem und europäischem *Onychodus*-Material. *Arkiv för Zoologi*, **18**, 305–389.
- 1975. A new choanate fish, *Powichthys thorsteinssoni* n.g., n.sp., from the early Lower Devonian of the Canadian Arctic Archipelago. *Colloques internationaux du Centre National de la Recherche Scientifique*, **218**, 213–222.
- 1980. Lower Devonian Porolepiformes from the Canadian Arctic with special reference to *Powichthys thorsteinssoni* Jessen. *Palaeontographica, Abteilung A*, **167**, 180–214.
- KLEMBARA, J. 1992. The first record of pit-lines and foraminal pits in tetrapods and the problem of the skull roof bones homology between tetrapods and fishes. *Geologica Carpathica*, **4**, 249–252.
- 1993. The subdivisions and fusions of the exoskeletal skull bones of *Discosauriscus austriacus* (Makowsky 1876) and their possible homologues in rhipidistians. *Paläontologische Zeitschrift*, **67**, 145–168.
- 1994. The sutural pattern of skull-roof bones in Lower Permian *Discosauriscus austriacus* from Moravia. *Lethaia*, **27**, 85–95.
- in press a. The external gills and ornamentation of the skull roof bones of the Lower Permian tetrapod *Discosauriscus austriacus* (Makowsky 1876) with remarks on its ontogeny. *Paläontologische Zeitschrift*.
- in press b. The lateral line system of *Discosauriscus austriacus* (Makowsky 1876) and the homologization of skull roof bones between tetrapods and fishes. *Palaeontographica, Abteilung A*.
- and JANIGA, M. 1993. Variation in *Discosauriscus austriacus* (Makowsky 1876) from the Lower Permian of the Boskovic Furrow (Czecho-Slovakia). *Zoological Journal of the Linnean Society*, **108**, 247–270.
- and MESZÁROŠ, Š. 1992. New finds of *Discosauriscus austriacus* (Makowsky 1876) from the Lower Permian of the Boskovic Furrow (Czecho-Slovakia). *Geologica Carpathica*, **5**, 305–312.
- MÜNZ, H., CLAAS, B. and FRITZSCH, B. 1982. Electrophysiological evidence of electroreception in the axolotl *Siredon mexicanum*. *Neuroscience Letters*, **28**, 107–111.
- — — 1984. Electroreceptive and mechanoreceptive units in the lateral line of the axolotl *Ambystoma mexicanum*. *Journal of Comparative Physiology*, **A154**, 33–44.

- NORTHCUTT, R. G. 1989. The phylogenetic distribution and innervation of craniate mechanoreceptive lateral lines. 17–78. In COOMBS, S., GÖRNER, P. and MÜNZ, H. (eds). *The mechanosensory lateral line: neurobiology and evolution*. Springer-Verlag, New York.
- ØRVIG, T. 1960. New finds of acanthodians, arthrodires, crossopterygians, ganoids and dipnoans in the Upper Middle Devonian calcareous flags (Oberer Plattenkalk) of the Bergisch Gladbach-Paffrath Trough. 1. *Paläontologische Zeitschrift*, **34**, 295–335.
- 1961. New finds of acanthodians, arthrodires, crossopterygians, ganoids and dipnoans in the Upper Middle Devonian calcareous flags (Oberer Plattenkalk) of the Bergisch Gladbach-Paffrath Trough. 2. *Paläontologische Zeitschrift*, **35**, 10–27.
- 1971. Comments on the lateral line system of some brachyothoracid and ptyctodontid arthrodires. *Zoologica Scripta*, **1**, 5–35.
- PETERS, R. C. and BRETSCHNEIDER, F. 1972. Electric phenomena in the habitat of the catfish *Ictalurus nebulosus*. *LeS. Journal of Comparative Physiology*, **A81**, 345–362.
- WESTOLL, T. S. 1943. The origin of tetrapods. *Biological Reviews*, **18**, 78–98.

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ABBREVIATIONS

AN	angular	PA	parietal	TA	tabular
DE	dentary	PFR	prefrontal	TA.pl	tabular pit-line
DSO	dermosphenotic	PMX	premaxillary	TA-PP	tabulo-postparietal
ET	extratemporal	PO	postorbital	ant.PA.pl	anterior parietal
ESC.l	lateral extrascapular	POFR	postfrontal		pit-line
ESC.l.pl	lateral extrascapular pit-line	POP	preopercular	ethm.comm	ethmoidal commissure
ESC.m	median extrascapular	PP	postparietal	for.p	foraminate pit
FR	frontal	PP.pl	postparietal pit-line	ior.s.gr	infraorbital sensory groove
FR.pl	frontal pit-line	PSP	postsplenial	ju.s.gr	jugal sensory groove
IT	intertemporal	QJ	quadratojugal	long.PA.pl	longitudinal parietal
IT.pl	intertemporal pit-line	SAN	surangular	m.s.gr	main sensory groove
JU	jugal	SMX	septomaxillary	man.s.gr	mandibular sensory groove
LA	lacrimal	SOP	subopercular	post.obl.PA.pl	posterior oblique parietal
Lj	lower jaw	SP	splenia		pit-line
MX	maxillary	SQ	squamosal	pot.s.gr	postotic sensory groove
NA	nasal	ST	supratemporal	sor.s.gr	supraorbital sensory groove
OP	opercular	ST.pl	supratemporal pit-line	st.comm.s.gr	supratemporal commissural sensory groove
				tr.PA.pl	transverse parietal pit-line