

THE FIRST RECORD OF PIT-LINES AND FORAMINAL PITS IN TETRAPODS AND THE PROBLEM OF THE SKULL ROOF BONES HOMOLOGY BETWEEN TETRAPODS AND FISHES

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Abstract: Two types of completely new structures for tetrapods - pit-lines and foraminal pits - are present in the exocranial bones of Lower Permian *Discosauriscus austriacus*. The morphology and position of these sensory structures are basically identical with those in the exocranial bones of osteolepiform fishes. These structures as well as the bones which bear them are considered to be homologous both in *Discosauriscus* and osteolepiforms. These conditions indicate that bones enclosing the pineal foramen in osteolepiforms are frontals.

Key words: Amphibia: *Discosauriscidae*, Lower Permian, sensory structures, pit-lines, foraminal pits, tetrapods and fishes - homologization of skull roof bones.

Introduction

Since the 1940s, workers in lower vertebrate paleontology have been divided into two camps concerning the terminology of the skull roof bones in Palaeozoic lobe-finned fishes - osteolepiforms (Westoll 1938, 1943; Romer 1941; Jarvik 1967). These fishes are considered by most authors to be ancestral to the majority of tetrapods. According to the traditional or "orthodox" terminology the bones enclosing the pineal foramen in osteolepiforms are frontals (cf. Jarvik 1967; Borgen 1983). But following his find of *Elpistostege*, Westoll (1938, 1943) and later Romer (1941), suggested that the traditional terminology be changed. This was based upon the view that *Elpistostege* is intermediate between osteolepiforms and ichthyostegid amphibians (Westoll 1938, 1943). Accordingly both workers concluded that the position of the pineal foramen is constant in tetrapods and fishes and always lies between the parietals.

The existence of pit-lines and foraminal pits in the Lower Permian tetrapod *Discosauriscus* from Czecho-Slovakia are described here as the first records of these structures in tetrapods. Their position within the skull roof is identical with those in osteolepiforms and therefore shows that bones enclosing the pineal foramen in osteolepiforms are frontals.

A complete description of these new structures is in preparation.

Material, methods and localities

The material, methods and localities were described by Klembara & Meszároš (in press). The specimens used here: D 52 - skull and anterior trunk; K 30 - skull; K 60 - skull; K 80 - skull and partly disarticulated postcranial skeleton; K 102 - skull and almost complete postcranial skeleton; K 206 - skull; K 224 -

partial skull; K 279 - partial skull and a few postcranial elements; K 327 - skull and anterior part of presacral vertebral column.

Description, discussion and conclusions

Sensory organs - pit-lines - are common in fishes, however, among tetrapods the neuromasts which could represent the pit-lines have been recognized only in larvae of some Recent urodeles (Schmalhausen 1955, 1957; Jarvik 1972). In these urodeles the neuromasts lie in the skin and do not leave traces in the bone surface.

In some ornamented skull roof bones of *Discosauriscus* the distinct grooves with small foramina at their bases are present (Fig. 1A). They cross or lay close to the centre of radiation of the bone and have a more or less constant position within the bone. Morphologically and positionally these grooves correspond to the pit-lines of osteolepiforms and other groups of fishes (see in Säve-Söderbergh 1933; Jarvik 1948; Jessen 1966; Chang 1982; Andrews 1985; Long 1989) and I consider them to be homologous structures. Figures 1B and 2B show pit-lines of *Discosauriscus* in frontal, parietal, supratemporal, tabular and postparietal bones.

A striking similarity in position is seen between the pit-lines of *Discosauriscus* and Middle Devonian osteolepids, such as *Osteolepis macrolepidotus* (Fig. 2). In *Discosauriscus* specimen K 60, the groove of the frontal pit-line lies in the posterior two thirds of the frontal bone (Fig. 1B). It crosses the centre of radiation, at which point it is bent. The anterior part of the pit-line runs anterolaterally, crosses the supraorbital sensory groove and ends at the lateral margin of the bone. Its posterior part runs obliquely posteromedially and ends in the posteromedial corner of the bone. Exactly the same position is seen in the frontal pit-

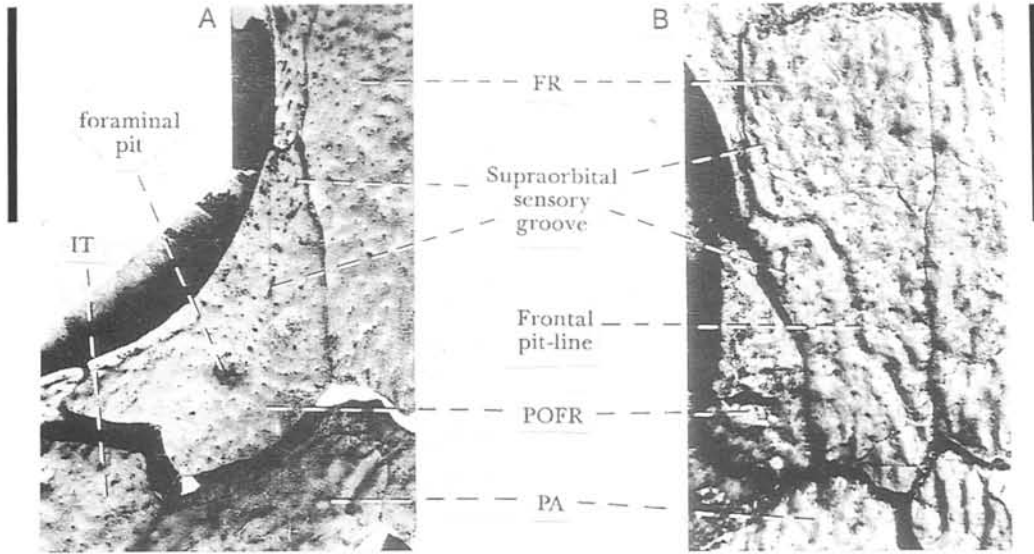


Fig. 1. *Discosauriscus austriacus* (Makowsky, 1876) showing frontal pit-line in specimen K 60 (A) and foraminal pit in specimen K 102 (B). Scale bar, 5 mm.

Abbreviations: FR - frontal, IT - intertemporal, PA - parietal, POFR - postfrontal.

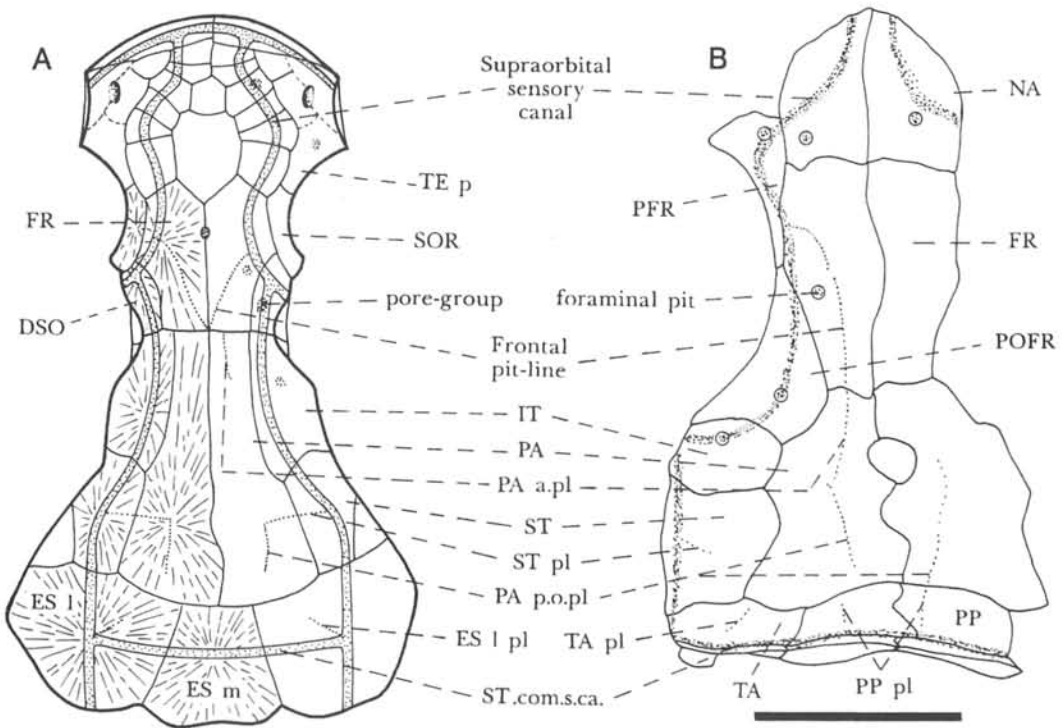


Fig. 2. Position of homologous bones, sensory canals, pit-lines and groups of foramina within skull roofs in: A. *Osteolepis macrolepidonus* (from Jarvik 1948, Fig. 16A, pore-groups and extrascapular lateral pit-lines completed from other osteolepid specimens); pore-groups of dermosphenotic and intertemporal completed from Jessen (1966); anterior parietal pit-line completed from Watson 1926). B. *Discosauriscus austriacus* (composite based on specimens K 69, D 52, K 30, K 80, K 102, K 206, K 224, K 279, K 327), scale bar, 10 mm. Tabular pit-line of *Discosauriscus* is based on D 52 in which specimen it is on right tabular.

Abbreviations: DSO - dermosphenotic, ES l pl - extrascapular lateral pit-line, ES m - extrascapular medial, FR - frontal, IT - intertemporal, NA - nasal, PA - parietal, Pa a.pl - anterior parietal pit-line, PA p.o.pl - posterior parietal oblique pit-line, PFR - prefrontal, POFR - postfrontal, PP - postparietal, PP pl - postparietal pit-line, SOR - supraorbital, ST - supratemporal, ST.com.s.ca - supratemporal commissural sensory canal; ST pl - supratemporal pit-line, TA - tabular, Ta pl - tabular pit-line.

-line in *Osteolepis* (Fig. 2). A similar course of the frontal pit-line is seen in *Discosauriscus* K 69 (Fig. 2B). In this specimen the frontal pit-line continues onto the parietal bone. Here both anterior and posterior oblique parietal pit-lines end with one end in the region of the radiation centre of the bone. The anterior parietal pit-line corresponds to the pit-line in the anterior portion of parietal of *Osteolepis* described by Watson (1926, 1954), (Fig. 2). The posterior oblique parietal pit-line of *Discosauriscus* corresponds to those in *Osteolepis*; similarly as the supratemporal and tabular pit-lines (Fig. 2). In contrast to *Discosauriscus*, the pit-line of median extrascapular of *Eusthenopteron* (Jarvik 1980 I: Fig. 121A) has a transverse course which is probably the result of the compound character of this bone in osteolepiforms (cf. Jarvik 1948 and Klembara in press). It is seen that the position of pit-lines, both in *Discosauriscus* and *Osteolepis*, is basically identical. This means that the bones which bear them must be homologous (the definitions and names of cranial bones were first applied to tetrapods and later extended to fishes). Hence, bones enclosing the pineal foramen are frontals in *Osteolepis* and the tabulars and parietals (or median postparietal) in *Discosauriscus* (Klembara in press) are homologous with the extrascapular series of bones in *Osteolepis*. This conclusion is supported by the observation that the course of the supratemporal (or occipital) commissural sensory canal both in *Discosauriscus* and osteolepiforms are essentially identical (Fig. 2). The occurrence of this sensory canal in discosauriscids is unique among reptiliomorph tetrapods.

The correct identification of homologous skull roof bones in *Discosauriscus* and *Osteolepis* enables the positioning of pits with groups of foramina at their bases - here called the foraminal pits - in *Discosauriscus* (Figs. 1A, 2B). Such foraminal pits are completely new structures in tetrapods and positionally correspond exactly to the pore-groups in osteolepids (Fig. 2). Especially conspicuous is the position of groups of foramina on frontals both in *Discosauriscus* and *Osteolepis*. They are bordered by the pit-line anteromedially and the supraorbital sensory canal laterally (Fig. 2). Probably both structures are homologous.

Moreover, the subdivisions and fusions of exocranial bones found at the same locations within the skull roof in *Discosauriscus* (Klembara in press) and osteolepiforms (Jarvik 1948) support the identification of homologous bones based on the pit-lines and foraminal pits. All these facts demonstrate that the "orthodox" terminology of skull roof bones used in osteolepiforms is correct.

The conditions in osteolepiforms described above make clear which characters are primitive (plesiomorph) and which are derived (apomorph) when testing relationships between fishes and tetrapods. Hence, the tabular - parietal contact ("anthracosaur condition") is primitive and the absence of this contact ("temnospondyl condition") is derived for tetrapods and not *vice versa* as stated by Panchen & Smithson (1988) and Gauthier, Kluge & Rowe (1988). Similarly, the squamosal - intertemporal contact is also a primitive character for tetrapods.

The earliest tetrapods, *Ichthyostega* (Jarvik 1980 I) and *Acanthostega* (Jarvik 1980 I; Clack 1988) from Upper Devonian of East Greenland, are in many respects very similar to Devonian osteolepiform fishes. From the above results it seems that the identification of bones enclosing the pineal foramen in these tetrapods as frontals (Jarvik 1967, 1980 I) is basically correct; the frontals in *Ichthyostega* include probably also the dermosphenotics.

In *Discosauriscus* and *Osteolepis*, the arrangement of dermal skull roof bones, the position of sensory grooves, pit-lines, foraminal pits and subdivided or fused bones are basically identical. These conditions clearly show the phylogenetic continuity and relationships between osteolepiforms and *Discosauriscus* and are further evidence that tetrapods (at least reptiliomorph) ori-

ginated from osteolepiforms. The conditions found in *Discosauriscus* are not derived from dipnoans, the group considered by some workers (Rosen et al. 1981; Forey 1987) the closest sister group of tetrapods.

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