Actinopterygian fish *Paramblypterus rohani* (Heckel & Kner, 1861) from the Permian sediments of the Bohemian Massif (the Czech Republic) and its relationships to *Paramblypterus duvernoyi* (Agassiz, 1833) and other Amblypteridae

Paprskoploutvá ryba *Paramblypterus rohani* (Heckel & Kner, 1861) z permských sedimentů Českého masivu (Česká republika) a její vztahy k *Paramblypterus duvernoyi* (Agassiz, 1833) a dalším amblypteridům

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Abstract: *Paramblypterus rohani* (Heckel & Kner, 1861) which belongs to the most abundant ray-finned fishes of the Permian sediments of the limnic basins of the Bohemian Massif is redescribed. The study is based on both old material and newly discovered specimens from the Krkonoše Piedmont Basin and Intra-Sudetic Basin. The abundant material shows a great variability of cranial bones, the structure of the rostral part of the skull, the opercular apparatus and the bones of the cheek, including the characteristic maxilla and dentition on the jaws. Attention is paid to the position of the fins and to the determination of the general appearance of the fish body with regard to the considerable pressure affected individuals during fossilization. Arrangement of the scales and great variability of their sculpture is also one of important characters. New knowledge about the anatomy of the skull and the overall body shape allows the reconstruction of *Paramblypterus rohani* and comparison with the closely related species *Paramblypterus duvernoyi* (Agassiz, 1833) from the Lower Permian basins of Germany and the determination of different characters. The relationships to other species of the family Amblypteridae are discussed.

Key words: Actinopterygii, Amblypteridae, Permian, Asselian, Bohemian Massif

Introduction

The actinopterygian fish *Paramblypterus rohani* (Heckel & Kner, 1861) is a very important component of the fish fauna in the Lower Permian sediments of the Krkonoše Piedmont Basin and Intra-Sudetic Basin and is one of the earliest described fish from the Permo-Carboniferous sediments of the Bohemian Massif. HECKEL & KNER (1861) originally described *Paramblypterus rohani* as *Palaeoniscus rohani* together with other species *Palaeoniscus caudatus, Palaeoniscus reussii, Palaeoniscus luridus* and *Palaeoniscus obliquus* from the Lower Permian of the Krkonoše Piedmont Basin. FRITSCH (1894, p. 100) recognized the close resemblance of the above mentioned species to *Amblypterus duvernoyi* (Agassiz, 1833). However, FRITSCH (1894) considered the two individuals figured by AGASSIZ (1833) as two different species, while lacking more detailed descriptions of the head bones, scales and fins. For this reason, he listed the species described by Heckel as certain forms of *Amblypterus duvernoyi* under the generic name *Amblypterus*, namely *A. rohani, A. obliquus, A caudatus*, and *A. luridus*. Only *Palaeoniscus reussii* is listed separately as *Amblypterus reussii*. Later, HEYLER (1969) gives a description of *Paramblypterus rohani* from the Krkonoše Piedmont Basin and subsequently assigns a relatively large amount of osteological material from the Lower Permian of the Autun Basin in France (HEYLER 1971) to *Paramblypterus rohani* as well. The species originally described by Heckel (in HECKEL & KNER1861) have been studied in detail by the author of this paper (ŠTAMBERG 1976). They were classified in the genus *Paramblypterus*, namely as *P. rohani*, *P. caudatus*, *P. reussi, P. luridus* and *P. obliquus*. Subsequently, ŠTAMBERG (1977) placed the species *P. luridus* and *P. obliquus* in the synonymy of *P. rohani*. Differences between *P. rohani*, *P. reussi* and *P. caudatus* were seen (ŠTAMBERG 1977) mainly in differences in the shape of the dermal bones of the skull roof (shape of the parietals and their lateral processes, course of the interparietal suture, shape of the supratemporal), differences in the shape of the maxillary plate and in the shape of the body. Great similarity was noted several times between *P. rohani* from the basins of the Bohemian Massif and *P. duvernoyi* from the Saar-Nahe Basin of Germany (FRITCH 1894, WOODWARD 1891, ŠTAMBERG 1976, 2013a, DIETZE 1999, 2000). The present study, based on material including type specimens studied by HECKEL & KNER (1861), FRITSCH (1894, 1895) and on extensive material collected over the last 50 years, has the following basic objectives:

- the most complete knowledge of the species *P. rohani* which is one of the most abundant actinopterygians in the Permian sediments of the Bohemian Massif;
- searching for identical or different characters between *P. rohani* and *P. duvernoyi* and clarifying whether *P. rohani* and *P. duvernoyi* are two different species or whether *P. rohani* belongs to the synonymy of *P. duvernoyi;*
- comparing osteological and morphological characters with other species of the family Amblypteridae.

Paramblypterus duvernoyi is a species of ray-finned fish in the family Amblypteridae originally described as *Palaeoniscus duvernoy* by AGASSIZ (1833) from Permian strata of the Saar-Nahe Basin from the Münsterappel locality. These strata are assigned by BOY et al. (1990, 2012) to the Kappeln-Schwarzschieferbank Horizon, L-O9 (Meisenheim Formation, Odernheim Subformation, early Permian). The specimens that Agassiz illustrated and were to be deposited in the Munich Museum and the University of Heidelberg were probably lost during World War II. Since Agassiz's description of the species in 1833, no proper revision of the species has been made in many years. This was probably the reason that many more species were added over the course of about 150 years and no proper comparison with the original material was made. In this respect, an attempt was also made in the 1970s by the author of this paper to discover the type material of *P. duvernoyi*, but without success and a study of the material from the Saar-Nahe Basin was not possible for the author of this paper at that time. Only in relatively recent times has Dietze (DIETZE 1999, 2000, 2001) collected a larger amount of material from museums and universities collections from localities in the Saar-Nahe Basin and revised the species *Paramblypterus duvernoyi*.

The following description of *Paramblypterus rohani* is based on the description given by the author of the present paper (ŠTAMBERG 1976, 1977) with substantial additions of newly acquired knowledge. The basis of this work is not only the study of older material deposited in the National Museum, Prague and other museums, but especially the extensive material obtained during more than 50 years of research in the basins of the Bohemian Massif carried out by the author of this work.

Geological setting

The actinopterygians described below, belonging to the species *Paramblypterus rohani*, come from the Krkonoše Piedmont Basin and the Intra-Sudetic Basin. In both basins their occurrence is linked to the Lower Permian strata. The intramontane Krkonoše Piedmont Basin occupies the north-eastern region of the Bohemian Massif. The area of the basin is more than 1100 km^2, and the maximum thickness of the volcano-sedimentary basin fill in the central part is nearly 1800 m. The basin was formed as part of a system of basins that opened in the Bohemian Massif during the late phases of the Variscan orogeny. Deposition within the basin started during the Westphalian D (Moscovian), and it continued with several interruptions to the Early Permian (Sakmarian). The youngest units (Saxonian to Triassic) have been preserved only in the eastern part of the basin (Trutnov – Náchod subbasin) (PROUZA & TÁSLER 2001). The Early Permian filling is represented by the Vrchlabí Formation (Asselian) and Prosečné Formation (Asselian) (Fig. 1). Both formations contain several important fossiliferous horizons from which the Rudník Horizon in the Vrchlabí Formation contains the most common occurence of paramblypterids described below. The Rudník Horizon (after TÁSLER et al. 1981, PROUZA & TÁSLER (2001), PROUZA et al. (2013), also present as Rudník Lake (MARTÍNEK at al. 2006) represents 40–60 m thick succession of lacustrine grey mudstone with minor interbeds of black claystone, carbonate, sandstone and conglomerates. Sediments of the Rudník Horizon can reach a thickness of up to 130 m of grey to black shales along the northern margin of the basin (MARTÍNEK et al. 2006). The occurrence of actinopterygians and other vertebrates is restricted to lacustrine organic rich gray-black calcareous claystone only, which outcrops in one or two beds. The organic rich grey black shales with fauna are characterized by fine lamination, high organic matter content, and represent anoxic offshore sedimentation (MARTÍNEK et al. 2006). Present outcrops indicate the eastwest extent of the Rudník Horizon to be more than 30 km in length, and the surface area to be approximately 300–500 km^2, although it could be much larger, around of 1000 km^2 (MARTÍNEK et al. 2006).

The Prosečné Formation (Asselian) represents 300–400 m thick sediments where dominate red-brown mudstones intercalated with fine-grained sandstones, volcanogenic rocks, laminated grey mudstones and carbonate. The upper part of formation is characterized by sequence of laminated grey and variegated claystones, mudstones and carbonates. This lacustrine unit is called Kalná Horizon (TÁSLER et al.1981) or Kalná Lake (BLECHA et al. 1999). The Kalná Lake extends the area by about 60 km^2 as documented by present outcrops, but the original extent of the lake was much larger (BLECHA et al. 1999). The Kalná Lake sediments contain not only one fossiliferous layer, but two sets of layers which can be distinguished from each other by the presence of actinopterygians and amphibians (ŠTAMBERG 2014). OPLUŠTIL et al. (2016) used the term upper and lower Kalná Horizons (Fig. 1) for these fossiliferous layers. Bituminous sediments of the lower Kalná Horizon occurring in the vicinity of the villages Horní Kalná and Veselá contain xenacanthid sharks *Xenacanthus decheni* (Goldfuss,1847), actinopterygians *Paramblypterus rohani* (Heckel & Kner, 1861), *P. vratislaviensis* (Agassiz, 1833), *P. kablikae* (Geinitz, 1860), *P. feistmanteli* (Fritsch, 1895) and branchiosaurid amphibian *Apateon* sp. Variegated, mostly pinkish dolomitic limestones and laminated calcareous claystones of the upper Kalná Horizon are characterized by the presence of the shark *Xenacanthus*, actinopterygians *Paramblypterus rohani*, *P. zeidleri* (Fritsch, 1895) and Aeduellidae indet., small branchiosaurid amphibians together with seymouriamorph *Discosauriscus pulcherrimus* (Fritsch, 1879) and a large stereospondylomorph *Korkonterpeton kalnense* Werneburg, Štamberg & Steyer, 2020.

The Intra-Sudetic Basin is located on the border of Poland and the Czech Republic and its area extends to about 1,800 km^2. Less than a third of the basin is located on the territory of the Czech Republic (Fig. 2). The filling of the basin is continental with fluvial and lacustrine strata next to short-term interconnection of the basin with the sea in the late Viséan. Massive sedimentary input in connection with volcanic lava flows and pyroclastic rocks produced a thick filling of the basin which in the Czech part is up to 3.500 m (PROUZA & TÁSLER 2001). The basin filling is divided into eight formations from which the Broumov Formation is the most important in terms of the focus of this work. The early Permian Broumov Formation (Fig. 2) is 800–1.000 m thick and is divided into the Nowa Ruda Member (at the base), Olivětín Member and Martínkovice Member (Tásler et al. 1979). The Olivětín Member with a 200 m thick set of colourful rocks with a high proportion of products related to volcanic activity is the most important concerning vertebrate occurrence. It contains two fossiliferous horizons, namely the Ruprechtice Limestone Horizon located in the base of the Upper Olivětín Member and the Otovice Limestone in the upper part of the Upper Olivětín Member. The Ruprechtice Limestone Horizon with a main layer of light grey or pinkish Ruprechtice Limestone contains rich fauna including actinop-

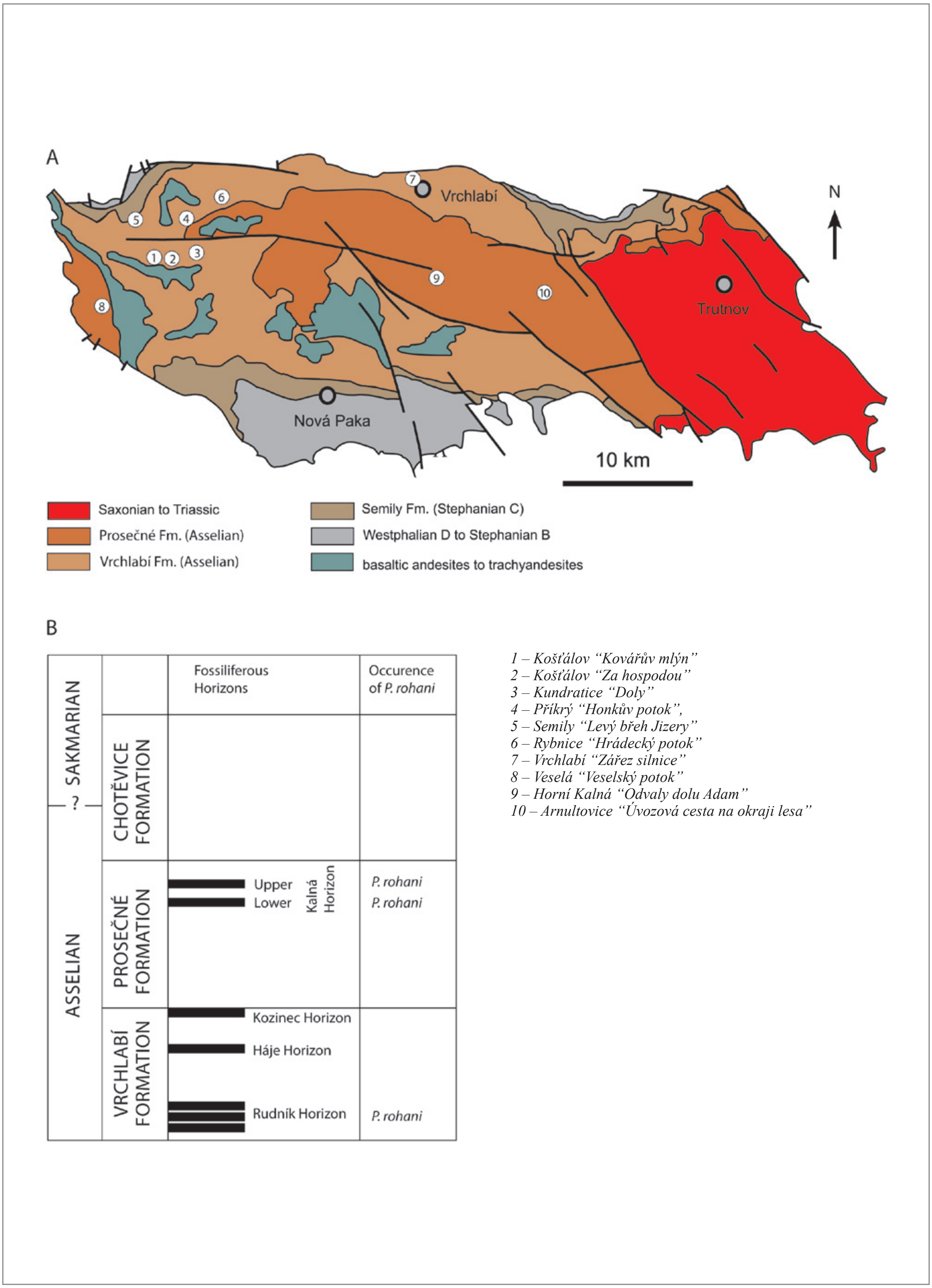
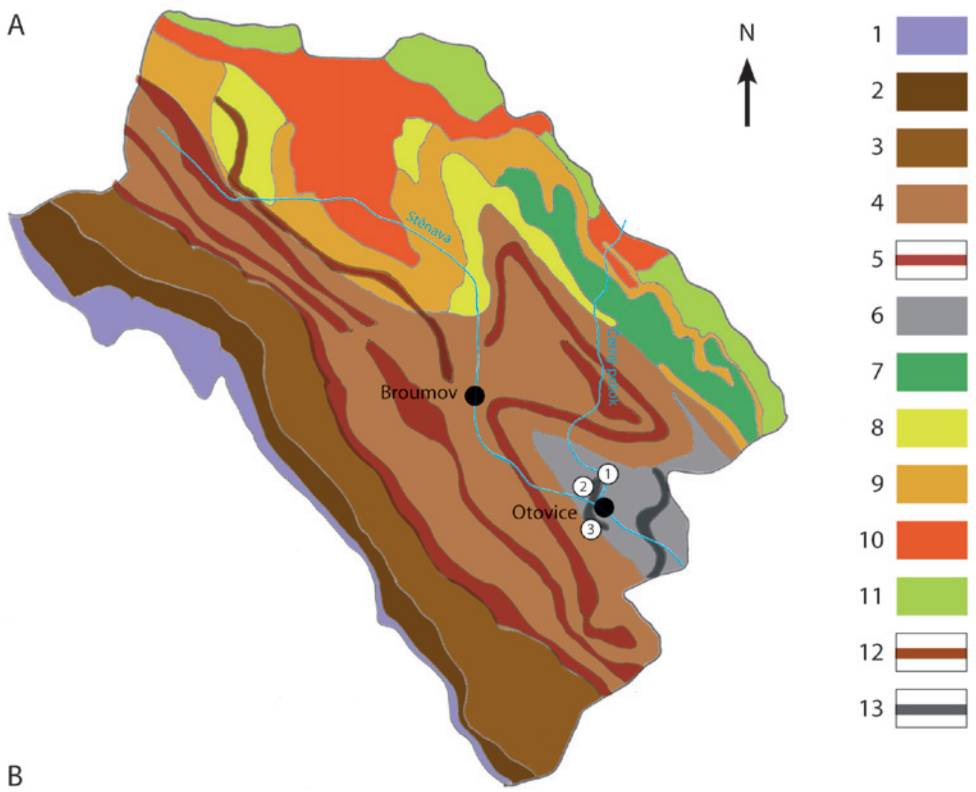
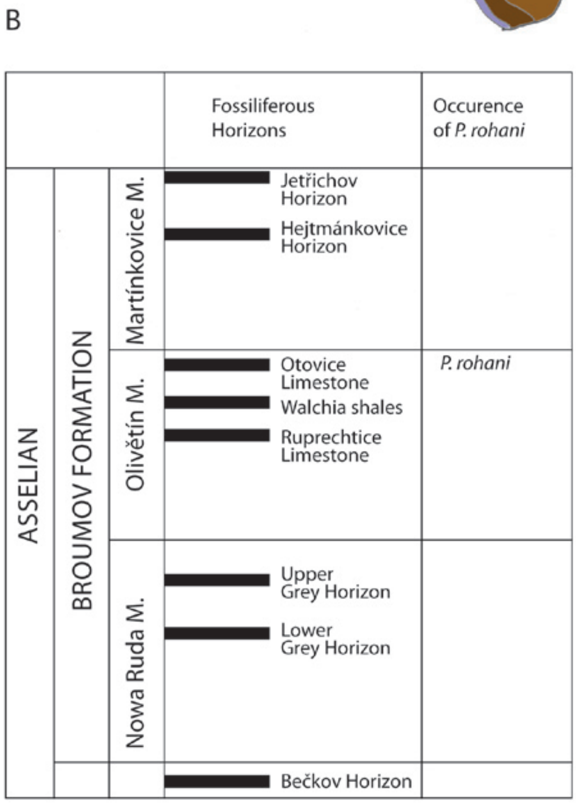


Fig. 1. *A – Simplified geological map of the Krkonoše Piedmont Basin (after BLECHA et al. 1997) with position of the localities with occurence of Paramblypterus rohani. B – Permian units of the Krkonoše Piedmont Basin (after PROUZA & TÁSLER 2001, OPLUŠTIL et al. 2016) with fossiliferous horizons and occurence of Paramblypterus rohani.*
Obr. 1. *A – Zjednodušená geologická mapa podkrkonošské pánve (podle BLECHA et al. 1997) s označením umístění lokalit s výskytem Paramblypterus rohani. B – Jednotky permu podkrkonošské pánve (podle PROUZA & TÁSLER 2001, OPLUŠTIL et al. 2016) s fosiliferními obzory a výskytem Paramblypterus rohani.*





Explanations: 1 – Bohdašín Formation (Triassic), 2 – Bohuslavice Formation (Thuringian), 3 – Trutnov Formation (Saxonian), 4–13 Broumov Formation (Autunian): 4 – Martínkovice Member, 5 – Martínkovice Member with Jetřichovice, Hejtmánkovice and Vižňov horizons, 6–13 – Olivětín Member: 6 – Walchia bone coal facies, 7 – Basaltoides of the Šonov Group, 8 – Volcanoclastic facies, 9 – Aleuropelites, 10 – Ignimbrites, 11 – Rhyolite tuffs, 12 – Ruprechtice Limestone Horizon, 13 – Otovice Limestone Horizon. Localities: O1 – Otovice "Černý potok", O2 – Otovice "Stěnava", O3 – Otovice "Chmelnice".

Vysvětlivky: 1 – bohdašínské souvrství (trias), 2 – bohuslavické souvrství (thuring), 3 – trutnovské souvrství (saxon), 4 – 13 – broumovské souvrství (autun): 4 – martínkovické vrstvy, 5 – martínkovické vrstvy s jetřichovským, hejtmánkovickým a vižňovským obzorem, 6 – 13 – olivětínské vrstvy: 6 – facie walchiových lupků, 7 – bazalty šonovské skupiny, 8 – vulkanoklastické facie, 9 – aleuropelity, 10 – ignimbrity, 11 – ryolitové tufy, 12 – ruprechtický vápencový obzor, 13 – otovický vápencový obzor. Lokality: O1 – Otovice „Černý potok", O2 – Otovice „Stěnava", O3 – Otovice „Chmelnice".

Fig. 2. *A – Geological sketch map of the Intra-Sudetic Basin, here simplified (after PROUZA & TÁSLER 2001) with position of localities with occurrence of Paramblypterus rohani. B – Permian units of the Intra-Sudetic Basin (after OPLUŠTIL et al. 2016) with fossiliferous horizons and occurrence of Paramblypterus rohani.*
Obr. 2. *A – Zde zjednodušená geologická mapa vnitrosudetské pánve (podle PROUZA & TÁSLER 2001) se zakreslením umístění lokalit s výskytem Paramblypterus rohani. B – Jednotky permu vnitrosudetské pánve (podle OPLUŠTIL et al. 2016) s fosiliferními horizonty a výskytem Paramblypterus rohani.*

terygians *Paramblypterus vratislaviensis*, xanacanthid sharks and numerous amphibians of the family Branchiosauridae, Eryopoidae and Discosauriscidae. Grey-black Otovice Limestone contains beside *P. rohani* also actinopterygians of the family Aeduellidae, xenacanthid shark *Xenacanthus* sp. (ŠTAMBERG 2021), but amphibians are missing.

Material and methods

A large collection of specimens that had already been used for the study of FRITSCH (1894, 1895), including the type material described by Heckel (in HECKEL & KNER 1861), which is housed in the National Museum, Prague was now used for the study. The main basis, however, is a collection of 600 specimens obtained by fieldwork carried out by the author of this paper during over the last 50 years. The study material has been supplemented by two new collections of specimens from private collectors, which are now housed in the National Museum, Prague and in the collections of the Faculty of Science, Charles University, Prague.

A Krantz pneumatic needle was used for extracting the fossils from the rock. Photographs were prepared using a Canon EOS 400D camera, and some of the samples were whitened with ammonium chloride or immersed in ethanol for both photographing and drawing. Suitable scales and microsculpture of scales and teeth were documented using a Hitachi S-3700N SEM. Drawing were prepared using a SM 20 stereomicroscope with camera lucida.

Traditional naming convention of the bones of the skull roof is abandoned in this paper and a convention based on the homology of the bones of the skull roof (WESTOLL 1936, SCHULTZE 2008, SCHULTZE et al. 2021) is used in this paper. The descriptive terminology of the other bones of the skull and parts of the body conforms to that used by SCHULTZE et al. (2021). At the end of each of the chapters devoted to individual anatomical units, differences or similarities with other species of the family Amblypteridae are discussed. Species that have not been revised to date (e.g. *Paramblypterus kablikae* (Geinitz, 1860) are not included in these comparative studies.

The local names of the localities of the Krkonoše Piedmont Basin are used according to the work of ZAJÍC (2014), the names of the localities of the Intra-Sudetic Basin are used according to the work of ŠTAMBERG (2021).

Institutional abbreviations

DP: Institute of Geology and Palaeontology, Faculty of Science, Charles University, Prague, the Czech Republic
MHK: Museum of Eastern Bohemia in Hradec Králové, Hradec Králové, the Czech Republic
MNP: Museum of Nová Paka, the Czech Republic
NHMW: Naturhistorisches Museum, Wien, Austria
NM: Department of Palaeontology, National Museum, Prague, the Czech Republic

Systematic palaeontology

***Paramblypterus rohani* (Heckel & Kner, 1861)**

1861 *Palaeoniscus Rohani* Heck. – Heckel & Kner, pp. 51–54, figs 1–3.
1861 *Palaeoniscus luridus* Heck. – Heckel & Kner, pp. 54–56, fig. 4.
1861 *Palaeoniscus obliquus* Heck. – Heckel & Kner, pp.56–58, fig. 5.
1861 *Palaeoniscus caudatus* Heck. – Heckel & Kner, pp. 58–61, fig. 6.
1861 *Palaeoniscus Reussii* Heck. – Heckel & Kner, pp. 61–63, fig. 7.
1891 *Amblypterus reussi* (Heckel) – Woodward, p. 445.
1894 *Amblypterus Rohani* (Heckel). – Fritsch, pp. 104–109; figs 297–301; pl. 123.
1895 *Amblypterus caudatus* (Heck.). – Fritsch, p. 111.
1895 *Amblypterus luridus* (Heckel). – Fritsch, p. 109; fig. 302.
1895 *Amblypterus obliquus* (Heckel) – Fritsch, pp. 109, 111; figs 304, 305.
1895 *Amblypterus Reussi* (Heck.) – Fritsch, p. 112, fig. 307.
1942 *Amblypterus rohoni* Heckel – Lemke & Weiler, pp. 7–16, figs. 2–12.
1942 *Amblypterus reussi* Heckel – Lemke & Weiler, pp. 16–17.
1967 *Janassa lacustris* sp. n. – Zídek, p. 203, pl. 1, figs 1, 2.
1969 *Paramblypterus rohani* Heckel (1861) – Heyler, pp. 72–75; fig. 22; pl. 14, figs 1– 2.
1975 *Paramblypterus rohani* (Heckel, 1861) – Štamberg, pp. 305–308, figs. 1, 2a, pls 1–2.
1976 *Paramblypterus rohani* (Heckel, 1861) – Štamberg, pp. 12–30, figs 1–17, pls 1–2, fig. 1, pls 3–7.
1976 *Paramblypterus caudatus*, Heckel, 1861 – Štamberg, pp. 37–44; figs. 22–24; pl. 2, fig. 2; pls 10–12.
1976 *Paramblypterus luridus* Heckel, 1861 – Štamberg, pp. 44–45, pl. 2, fig. 3.
1976 *Paramblypterus obliquus*, Heckel, 1861 – Štamberg, pp. 45–46.
1976 *Paramblypterus reussii* (Heckel, 1861) – Štamberg, p. 31, figs 19–21, pls 8–9.
1993 *Paramblypterus gelberti* (Goldfuss, 1847) – Štamberg, pp. 84–85, figs 1–2, pl. 1.
1999 *Paramblypterus* sp. – Štamberg, p. 15, fig. 4.
2006 *Paramblypterus rohani* (Heckel 1861) – Štamberg, pp. 225, 227.
2006 *Paramblypterus reussii* (Heckel, 1861) – Štamberg, p. 225, 227.
2007b *Paramblypterus rohani* (Heckel, 1861) – Štamberg, pp. 6–8, figs 1–5.
2007b *Paramblypterus caudatus* (Heckel, 1861) – Štamberg, pp. 8–9, fig. 1.
2008 *Paramblypterus rohani* (Heckel, 1861) – Štamberg & Zajíc, p. 157, Fig. 235
2008 *Paramblypterus caudatus* (Heckel, 1861) – Štamberg & Zajíc, pp. 157–158, fig. 236.
2008 *Paramblypterus reussii* (Heckel, 1861) – Štamberg & Zajíc, p. 158, fig. 237.
2008 *Paramblypterus gelberti* (Goldfuss, 1847) – Štamberg & Zajíc, p 158, fig. 238.
2013a *Paramblypterus rohani* (Heckel, 1861) – Štamberg, p. 172, pl. 1, fig. 1.
2013a *Paramblypterus reussii* (Heckel, 1861) – Štamberg, p. 173, pl. 1, fig. 2.
2020 *Paramblypterus* sp. – Štamberg, p. 16, fig. 10.
2021 *Paramblypterus* cf. *rohani* – Štamberg, p. 86, text-figs 9–12.

Diagnosis: Fusiform body arched in front of the dorsal fin, not exceeding 35 cm total body length. Scales behind the skull bear fine ridges extending posteriorly to denticles. Area of serrated scales above and below lateral sensory line and number of dents on their posterior margin gradually decline and disappears between the pelvic and anal fins. Half of the dorsal fin base on the dorsal body margin is placed anteriorly to the begin of the anal fin base on the ventral body margin. Square postrostral is convex anteriorly. The nasal is not in contact with the intertemporal. Oblong parietals, two times longer than wide, with strongly curved interparietal suture and one or two processes on lateral side of parietals. Postparietals approximately square, two times shorter than the length of the parietals. Triangular intertemporal which is wide posteriorly. Large undivided preorbital is in contact with the intertemporal and dermosphenotic posteriorly. The preorbital and dermosphenotic form together anterior and dorsal edge of the orbit. Supratemporal of oblong shape with a large process posteriorly. Distinct sculpture is formed by ridges on the bones of the skull roof. 6 to 7 suborbital bones. One median extrascapular, one large posterior and two small anterior paired lateral extrascapulars. Spiracular bone of oblong shape is present. Sclerotic ring is present. Preoperculum conspicuously bent anteriorly along posterior and dorsal borders of the deep maxillary plate. Length of the maxillary plate is larger than its deep. Dorsal edge of the maxillary plate is straight. The scale count is following:

$$\frac{28\text{-}31}{9\text{-}11 \quad 23\text{-}26 \quad 38\text{-}40}\ 41\text{-}43$$

Lectotype: Specimen M 849 designated by ŠTAMBERG (1976) from the material figured by Heckel (in HECKEL & KNER 1861) is deposited in the National Museum, Prague.

Type horizon and locality: Košťálov; Rudník Horizon, Vrchlabí Formation, Asselian, Krkonoše Piedmont Basin.

Occurence: (Figs 1, 2) Krkonoše Piedmont Basin, Rudník Horizon of the Vrchlabí Formation Asselian, Krkonoše Piedmont Basin: Čistá; Košťálov; Košťálov "Kovářův mlýn"; Košťálov "Za hospodou"; Dolní Lánov "Kovářsko"; Kundratice "Doly"; Kundratice "Rokle v lese"; Dolní Lánov "Kovářsko"; Prostřední Lánov "Za továrnou"; Příkrý "Honkův potok"; Semily "Levý břeh Jizery"; Rybnice "Hrádecký potok"; Vrchlabí "Zářez silnice".

Krkonoše Piedmont Basin, Kalná Horizon of the Prosečné Formation: Arnultovice; Veselá "Veselský potok"; Horní Kalná "Odvaly dolu Adam".

Intra-Sudetic Basin, Broumov Formation, Otovice Limestone Horizon of the Olivětín Member: Otovice "Černý potok"; Otovice "Stěnava"; Otovice "Chmelnice"; Otovice "Vápenka".

Stratigraphical range: Krkonoše Piedmont Basin: from Rudník Horizon of the Vrchlabí Formation (Asselian) to Kalná Horizon of the Prosečné Formation (Asselian); Intra-Sudetic Basin, Otovice Limestone Horizon of the Olivětín Member, Broumov Formation (Asselian).

Material (List of specimens cited in this thesis with their relevant localities):

***Paramblypterus rohani* (Heckel & Kner, 1861)**

Krkonoše Piedmont Basin, Vrchlabí Formation, Rudník Horizon

Košťálov: MHK-P 19837; MHK-P 80206; MHK-P 81196; NM-M 484; NM-M 490; NM-M 849; NM-M 1252; NM-M 1983; NM-M2695; NM-M 4915; NM-M 4916; NM-M 4920; NM-M 4924; NM-M4928; NM-M 4929; MNP 167; NHMW 1866/XXII/5; NHMW 1901/VII/3.

Košťálov "Kovářův mlýn": MHK-P 64896; MHK-P 64910; MHK-P 64914; MHK-P 64925; MHK-P 80193; MHK-P 80198; MHK-P 80204.

Košťálov "Za hospodou": MHK-P 64834; MHK-P 64842; MHK-P 80153; MHK-P 80156; MHK-P 81423; MHK-P 81450; MHK-P 81490

Kundratice "Doly": MHK-P 64854; MHK-P 64858; MHK-P 80194; MHK-P 80197; MHK-P 83140.

Příkrý "Honkův potok": MHK-P 64821; MHK-P 70075; MHK-P 70084; MHK-P 70091; MHK-P 81437; MHK-P 81442.

Semily "Levý břeh Jizery": MHK-P 64753; MHK-P 64775; MHK-P 64795; MHK-P 64796; MHK-P 64797; MHK-P 64799; MHK-P 64804; MHK-P 64805; MHK-P 64808; MHK-P 64809; MHK-P 64813; MHK-P 64816; MHK-P 81399; MHK-P 81431; MHK-P 81432; MHK-P 81433; MHK-P 81463; MHK-P 82451; NM-M 1215

Rybnice "Hrádecký potok": MHK-G 241; MHK-P 10979; MHK-P 30753; MHK-P 30755; MHK-P 30867; MHK-P 30873; MHK-P 30877; MHK-P 30878; MHK-P 30883; MHK-P 30885; MHK-P 30899; MHK-P 30900; MHK-P 70046; MHK-P 81380; MHK-P 81398; MHK-P 81400; MHK-P 81401; MHK-P 81406; MHK-P 81412; MHK-P 81446; MHK-P 81451; MHK-P 81457; MHK-P 81459; MHK-P 81461; MHK-P 81462; MHK-P 81464; MHK-P 81797; MHK-P 81810; MHK-P 82353; MHK-P 82354; MHK-P 82356; MHK-P 82369; MHK-P 82384; MHK-P 82763; MHK-P 83099; MHK-P 83108; MHK-P 83118; MHK-P 83125; MHK-P 83130; MHK-P 83137.

Vrchlabí "Zářez silnice": MHK-P 64954.

Krkonoše Piedmont Basin, Prosečné Formation, Horní Kalná Horizon

Veselá "Veselský potok": MHK-P 80245.

Horní Kalná "Odvaly dolu Adam": MHK-P 27571.

Arnultovice "Úvozová cesta na okraji lesa": MHK-P 81471.

Intra-Sudetic Basin, Broumov Formation, Otovice Limestone of the Olivětín Member

Otovice "Černý potok": MHK-P 80178.

Otovice "Stěnava": DP 4529.

Otovice "Chmelnice": MHK-P 30945; MHK-P 64665; MHK-P 64673; MHK-P 64687; MHK-P 30945; MHK-P 30947; MHK-P 64661.

***Paramblypterus* sp.**

Krkonoše Piedmont Basin, Vrchlabí Formation, Rudník Horizon

Košťálov "Za hospodou": MHK-P 81420.

Rybnice "Hrádecký potok": MHK-P 30754; MHK-P 81404; MHK-P 81409.

Paramblypterus rohani from the sediments of the Bohemian Massif includes specimens ranging from juveniles 27 mm long (MHK-P 70084) to adults with a total body length 300 mm (MHK-P 81471) and fragments of large specimens. Their fusiform body is slightly arched anteriorly to the dorsal fin at a level perpendicular to the beginning of the pelvic fin. The body length/deep ratio is of about 4.2 but it significantly varies from 4.0 to 4.8 depending upon specimen preservation and degree of deformation. The skull length is of about 5 times in the total body length. The dorsal fin originates immediately behind the middle of the total body length and at least the half of the dorsal fin base is anteriorly to the anal fin base origin. The base of the pelvic fin is closer to the anal fin than to the pectoral.

The vast majority of *P. rohani* specimens from the sediments of the Rudník Horizon of the Krkonoše Piedmont Basin have a markedly arched trunk dorsally at the level of the space between the pectoral and pelvic fins. This arching is sometimes extremely pronounced (NM-M 490, MHK-P 80206, MHK-P 81196 - Fig. 23C). The different arching of the trunk at first gave the impression that it is in fact a species character that distinguishes these individuals from others that do not have such an arched trunk. After studying a large number of specimens, it turns out that the abnormal trunk arching is a deformation that occurred during fossilization.

Skull

Rostral part of the skull

The snout is bluntly rounded in front. The rostral part of the skull is generally very rarely preserved in Permo-Carboniferous actinopterygians, and partially preserved bones of the rostral part of the skull are present on specimens MHK-P 80194, MHK-P 81437, MHK-P 81446, MHK-P 81442, MHK-P 81471 and others. On the studied material (Figs 3, 4), the rostral part is built by a large medially located postrostral, which is laterally flanked by a paired nasal. The nasal is separated from the orbit by a large preorbital with which the nasal sometimes coalesces into a single unit. Anterior to the postrostral lies the paired rostro-premaxillo-lacrymal (Fig. 3A, B).

The postrostral is approximately square in shape with the posterior margin only slightly convex in its central part. The posterior margin of the bone is in contact with the anterior margin of the parietals. The lateral margins of the postrostral are slightly undulating and the anterior nasal aperture can be observed in the anterior part of this margin in MHK-P 80204, MHK-P 81446, MHKP 81437, MHK-P 81471 (Figs 3D, 4A). The anterior edge of the bone is markedly convex. A strong sculpture is developed on the postrostral, formed by mounds parallel to the posterior margin of the bone. The central part of the posterolateral half of the postrostral is without sculpture and at the interface between the posterior and anterior halves of the bone the sculpture is formed by short mounds. The anterior half of the bone is sculptured exclusively by bumps (Figs 3A, D, 4A).

The rostro-premaxillo-lacrymal forms an anterior margin of the rostral part of the skull. Specimen MHK-P 81442 (Fig. 3A, B, C) shows paired lateromedially extended bones with their medial margins in contact. The morphology of the preserved parts suggests that the rostro-premaxillo-lacrymal is composed of three bones, with one of the bones separated and slightly displaced on the specimen. No teeth were found on the anterior margin of these bones, but it can be assumed that they were developed during the animal's lifetime and the bones formed a junction between the right and left jaws. The rostro-premaxillo-lacrymal is thickened at the site of the ethmoid commissure. The sensory canal passes from this thickened point on the anterior margin posteriorly and passes to the nasal. At the point of thickening there is a distinct area on the inner margin of the bone which probably served as an articulation with the ethmoid portion of the neurocranium. The flat medial portion of the outer surface of the bone shows a sculpture consisting of prominent bumps in the negative impression.

The postrostral is laterally flanked by the nasal. The nasal may have sutures laterally with the preorbital. Very often the two bones are fused without sutures, or the nasal may be separated from the preorbital by a suture on one side of the skull but suture is missing between these bones on the other side of the skull.

A well-developed structure of the rostral part of the skull is preserved on the specimen MHK-P 81442 (Fig. 3A, B, C), which shows the inner surface of the bones of the cranial vault and especially those of the rostral part of the skull. The nasal is a narrow, antero-posteriorly elongated bone bearing a prominent supraorbital canal. This canal continues from the parietal through the nasal to the rostro-premaxillo-lacrymal. The detached anterior part of the left nasal shows small prominent bumps forming the external sculpture of the anterior part of the nasal. The preorbital firmly connected to the nasal is stretched antero-posteriorly with a slightly concave lateral margin flanking the orbit. This bone usually bears three sensory pores located just below the border with the nasal. The broken portions of the bone show a distinct sculpture of the outer surface formed by mounds parallel to the edges of the bone (Fig. 3A, B). The preorbital abuts posteriorly with the intertemporal and thus separates the nasal from the intertemporal. The isolated nasal can be observed in MHK-P 81412 (Fig. 4C). It is a narrow, anteroposteriorly elongated bone 9 mm long. The posterior margin is rounded and the anterior margin is divided into small folds and projections. A distinct fold is observed in the anterior part of the medial margin, which is a remnant of the anterior nostril. The surface of the bone is formed by distinct mounds and flat bumps in its posterior part, with small bumps in the anterior part. The remains of the sensory line are preserved as the remains of three pores arranged in an anterio-posterior direction.

The preorbital is a relatively large bone lining the anterior and partly dorsal margin of the orbit (NM-M 1983, MHK-P 81442, MHK-P 30867, MHK-P81399). It is usually separated medially by a suture from the nasal but often fuses with the nasal into a single unit. The preorbital is elongated dorsoventrally, the bone is relatively robust, always showing a consistent shape and sculpture consisting of conspicuous ridges parallel to the margins of the bone. Antero-ventrally and postero-dorsally it is slightly tapered and its posterior margin flanking the orbit is always curved. Three distinct pores which probably form the posterior narinal opening are usually observed on the medial margin of the bone. Posteriorly, the preorbital is in contact with the intertemporal and dermosphenotic, thus separating the nasal not only from the orbit but also from the intertemporal.

The described arrangement of the bones of the rostral part coincides in basic characteristics with the characters described by DIETZE (1999, 2000) in *P. duvernoyi* and *P. gelberti* (Goldfuss, 1847) and also coincides with *Amblypterus latus* (Agassiz, 1833) (ŠTAMBERG 2013b). Rostro-premaxillo-lacrymal in *Paramblypterus vratislaviensis* (Agassiz, 1833) does not participate in delimiting of the orbit anteriorly because it is separated from the orbit by the preorbital and ventral infraorbital (ŠTAMBERG 2021). The *Paramblypterus decorus* (Egerton, 1850), as described by BLOT (1966), shows the postrostral greatly expanded

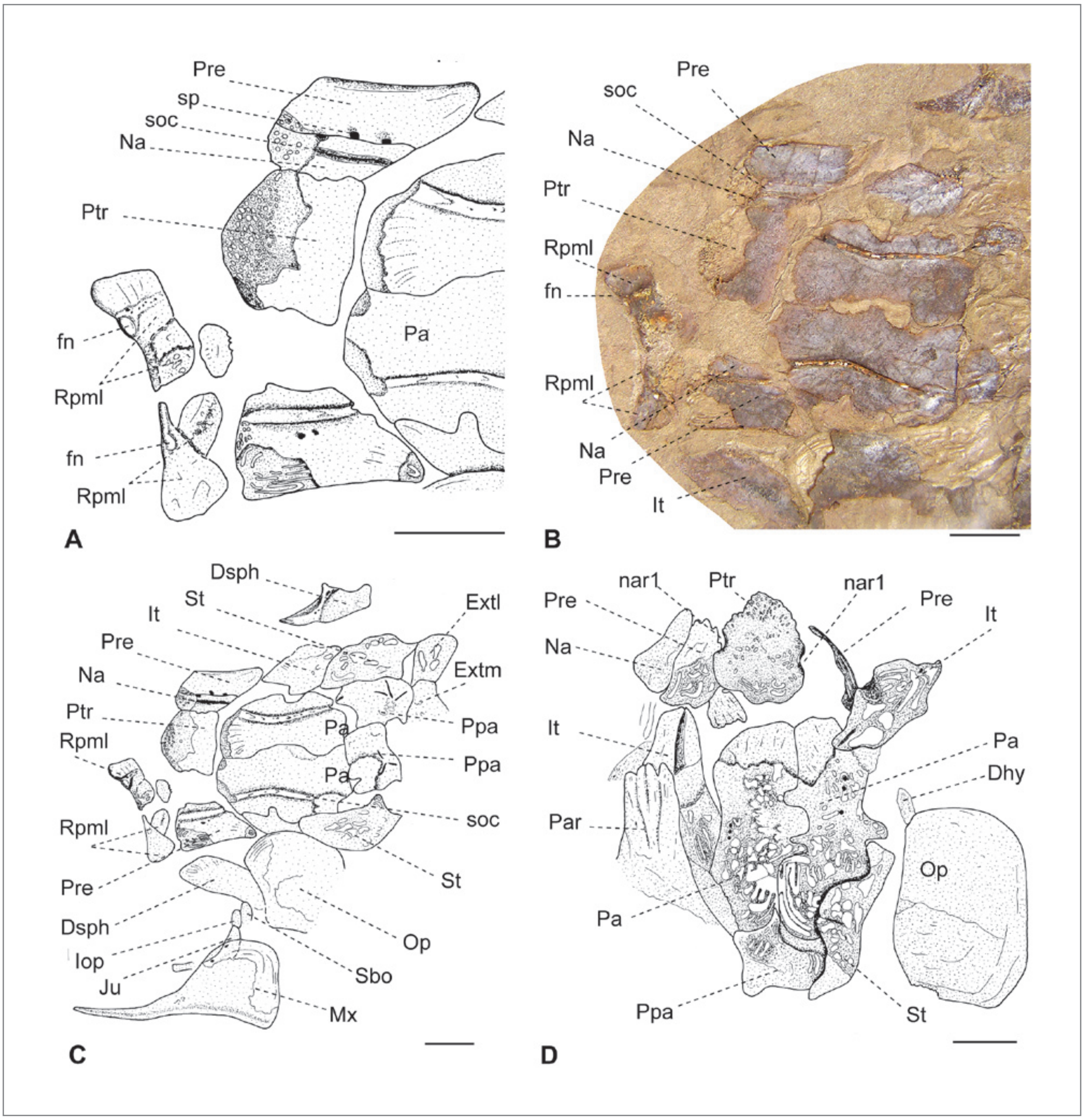


Fig. 3. *Paramblypterus rohani (Heckel & Kner, 1861). Scale bars 5 mm. A, B – Drawing and photograph of the rostral part of the skull in ventral view. MHK–P 81442. C – Whole skull with the bones of the rostral part, the skull roof and cheek. MHK–P 81442. D – Bones of the rostral part and the skull roof in dorsal view. The postrostral with distinct notches of the anterior nasal openings on the lateral margins of the bone. MHK–P 81437.*
Obr. 3. *. Paramblypterus rohani (Heckel & Kner 1861). Měřítka 5 mm. A, B – Perokresba a fotografie rostrální části lebky v pohledu ventrálním. MHK–P 81442. C – Celá lebka s kostmi rostrální části, klenby lebeční a líce. MHK–P 81442. D – Kosti rostrální části lebky a klenby lebeční v pohledu dorsálním. Postrostrale nese na svých laterálních okrajích zářezy předních nasálních otvorů. MHK–P81437.*
Abbreviations: Dhy – dermohyal; Dsph – dermosphenotic; Ext.l – extrascapular lateral; Ext.m – extrascapular medial; fn – facet for articulation with ethmoidal part of the neurocranium; Iop – infraorbital posterior; It – intertemporal; Ju – jugal; Mx – maxilla; Na – nasal; nar1 – anterior nasal opening; Op – operculum; Pa – parietal; Par – parasphenoid; Ppa – postparietal; Pre – preorbital; Ptr – postrostral; Rpml – rostro-premaxillo-lacrimal; Sbo – suborbital; soc – supraorbital canal; sp – sensory pores; St – supratemporal.

in its anterior part and the preorbital (superorbital anteriéur in the sense of BLOT 1966) as a solid bone surrounding the orbit anteriorly and partially dorsally. A revisionary study of this species by DIETZE (2000) shows a postrostral similarly shaped to that of *P. duvernoyi*. At the same time, DIETZE (2000) depicts the preorbital (nasal 2 of DIETZE 2000) in contact with the postrostral in *P. decorus*, thus completely separating the nasal (nasal 1 of DIETZE 2000) from the premaxilla. The nasal (nasal 1 of Dietze) is in contact with the intertemporal (dermosphenotic in the sense of BLOT 1966, dermosphenotic 1 in the sense of DIETZE 2000).

Very important is the preorbital (superorbital antérieur in the sense of BLOT (1966); supraorbital antérieur in the sense of HEYLER (1969); superorbital anterius in the sense of ŠTAMBERG (1976); superantorbital in the sense of GAD (1988), which is part of the rostral region. On the described material, it is always a robust bone of stable shape, which, as said, can fuse with the nasal. DIETZE (1999) described in *P. duvernoyi* the fusion of this bone from two, namely the supraorbital and the preorbital. Similarly, in *Cheirolepis*

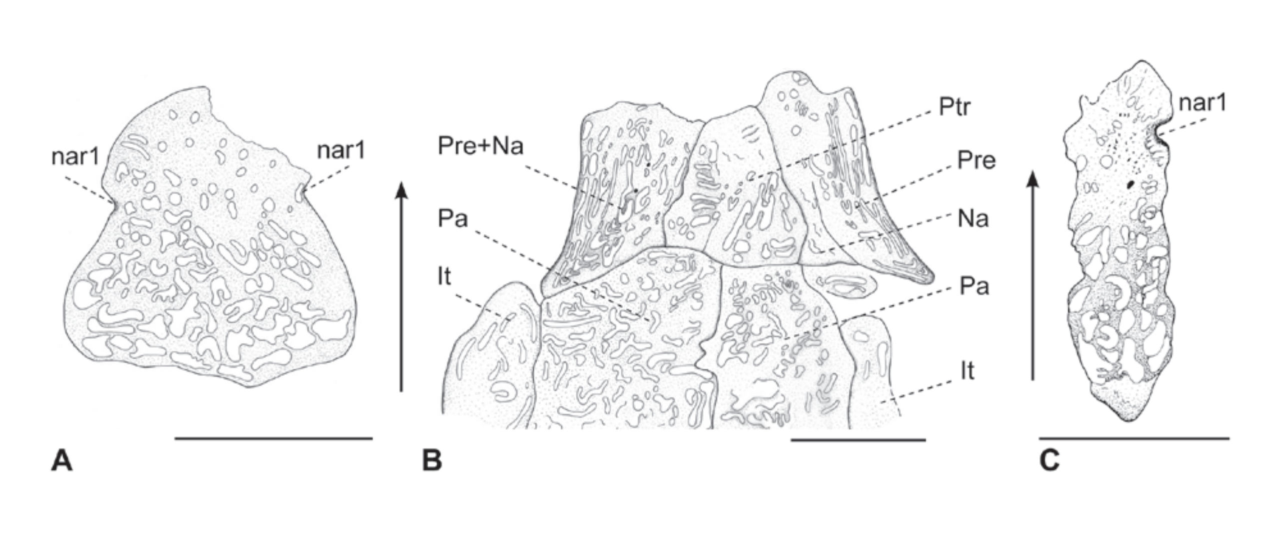


Fig. 4. *Paramblypterus rohani (Heckel & Kner, 1861). Scale bars 5 mm. A – The postrostral in dorsal view with notches of the anterior nasal openings. MHK–P 80193. B – Rostral part of the skull in dorsal view with the preorbital fuses with the nasal on the left side while they are partly separated on the right side. MHK–P 80204. C – Isolated nasal in dorsal view with notch of the anterior nasal opening. MHK–P 81412.*
Obr. 4. *. Paramblypterus rohani (Heckel & Kner, 1861). Měřítka 5 mm. A – Postrostrale v pohledu dorsálním se zářezy předních nasálních otvorů. MHK–P 80193. B – Rostrální část lebky v pohledu dorsálním s preorbitale, které je na levé straně lebky srostlé s nasale, kdežto na pravé straně lebky je částečně oddělené. MHK–P 80204. C – Izolované nasale v pohledu dorsálním se zářezem pro přední nasální otvor. MHK–P 81412.*
Abbreviations: *Na – nasal; nar1 – anterior nasal opening; Pa – parietal; Pre – preorbital; Pre+Na – preorbital fuses with the nasal; Ptr – postrostral; It – intertemporal.*

canadensis Whiteaves, 1881, ARRATIA & CLOUTIER (1996) described two bones in place of the preorbital, namely the more dorsally situated supraorbital and the more ventrally situated preorbital, which form the anterior margin of the orbit. No indication of the division of the preorbital into two bones, or the formation of the preorbital from two bones, has been noted on material described from the basins of the Bohemian Massif. Also the sculpture of this bone, consisting mainly of long ridges running parallel to the ventral margin of the bone and covering the entire outer surface of the bone, indicates growth from a single ossification centre located at the anterior margin of the bone at the site of the large pores.

The preorbital has also recently been described in several species of the family Aeduellidae and it was previously described as the antorbital by WESTOLL (1937) in *Aeduella blainvillei* from Muse in Autun Basin. ŠTAMBERG (2007a) documented the occurrence of this bone in *Bourbonnella hirsuta* Štamberg, 2007a and in *Neslovicella rzehaki* Štamberg, 2007a. It also occurs in *Neslovicella elongata* Štamberg, 2010a and has been documented in material of *Aeduella blainvillei* Westoll, 1937 from the Bourbon-l'Archambault Basin in France (ŠTAMBERG 2018, text-fig. 26d).

Skull roof

The bones of the skull roof form a thick covering of the dorsal side of the skull consisting of paired parietal postparietal, intertemporal, supratemporal and a strip of extrascapular bones (NM-M 4920, MHK-P 64658, MHK-P 64665, MHK-P 64673, MHK-P 81399, NHMW 1901/VII/3 and many others). The skull roof bones tend to be relatively well preserved on the specimens studied, either as a compactly interconnected unit or as isolated bones (Figs 3D, 5, 6, 7, 8).

The parietal is a rectangular bone twice as long as it is wide and twice as long as the length of the postparietal. The anterior margin of the parietal is slightly convex, straight or slightly concave. The medial and lateral margin of the frontal tends to be markedly curved. The interfrontal suture also produces multiple lobed folds (MHK-P 81461 –Fig. 6A) on the right and left parietals, which fit together in a finger-like manner. Also, the lateral margin of the bone forms a lobate process running between the intertermporal and supratemporal (MHK-P 64795, MHK-P 64805) in about one half of its length. This process can be extremely long and extended as in DP 2700, MHK-P 80206, NM-M1983 and other specimens (Fig. 5F) and the variation in the shape of the process is very marked. The different shapes of the frontal bones and other bones of the cranial vault are shown in the accompanying figures (Figs 5, 6). The parietal is distinctly sculptured by mounds and bumps. The shorter mounds of the lateromedial direction are developed mainly in the anterior third of the bone, whereas in the posterior third of the bone the long mounds are paralleled with the lateral and posterior margins of the bone. The entire medial part of the parietal is covered with flat irregularly shaped bumps.

The postparietal is approximately square in shape (e.g., MHK-P 80194 is 4 x 4 mm; MHK-P 64795 is 6 x 6 mm), but may be markedly elongated at the margins and sometimes with anteriorly elongated processes. The suture between right and left postparietal may be strongly curved (MHK-P 64805), and anteriorly there is usually a large prominence (MHK-P 81399, MHK-P 70091) that extends between the parietal and supratemporal. Specimen MHK-P 81433, representing an old individual (Fig. 7A), shows broad articulating surfaces on which the surrounding bones are superimposed, especially the right postparietal and left supratemporal. The outer surface of the bone without articulating surfaces is 10 mm long and 7 mm wide. The bone including the articulating surfaces is 11 mm long and 12 mm wide. The sculpture is made up of irregularly bordered flat bumps.

The intertemporal of triangular shape borders the lateral margin of the parietal from the anterior margin of the parietal to the lateral process of the parietal where it contacts

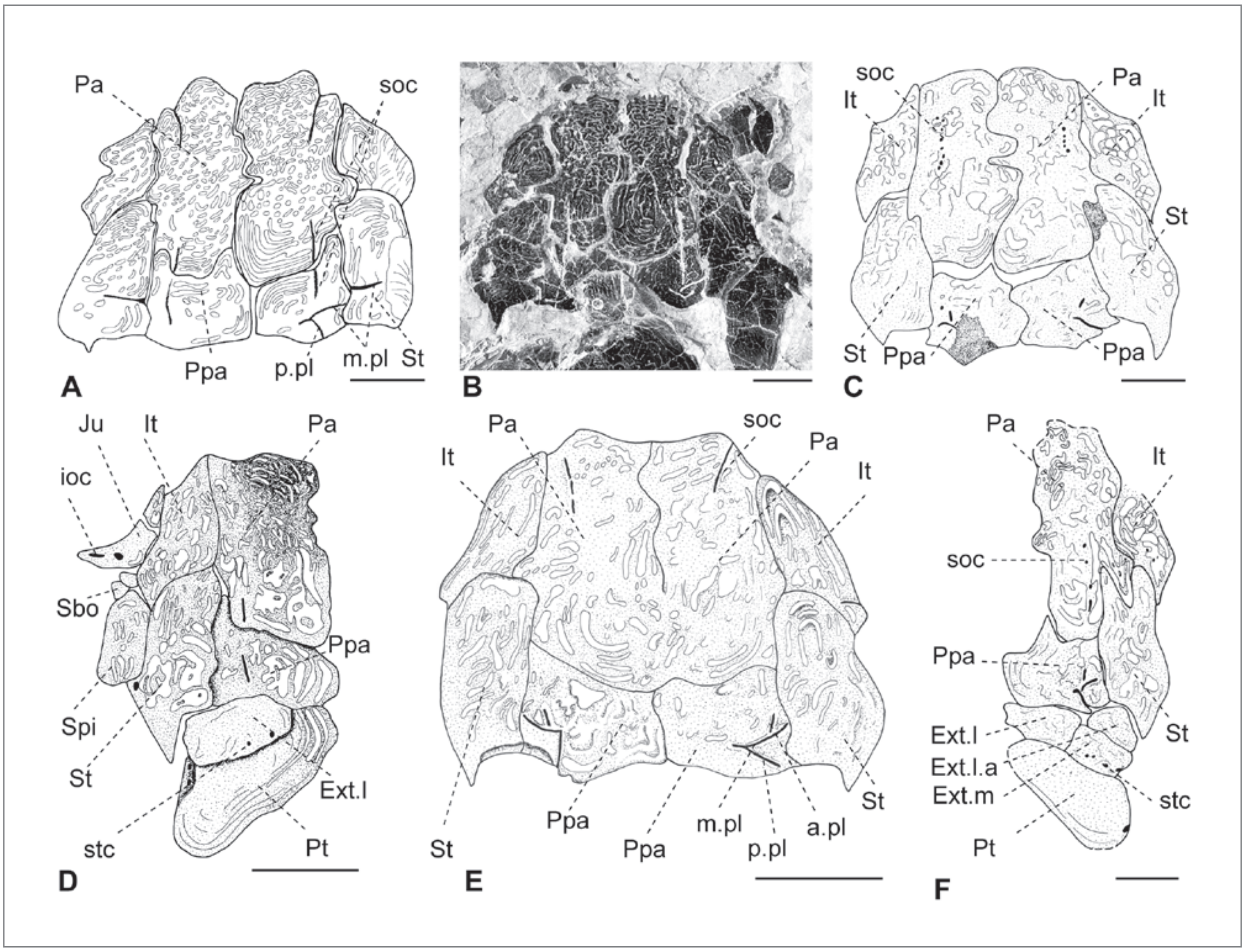


Fig. 5. *Paramblypterus rohani (Heckel & Kner, 1861). The skull roofs in dorsal view. Scale bars 5 mm. A – The parietal where the supraorbital canal passes from the parietal to the postparietal and the medial pit line passes laterally from the postparietal to the supratemporal. NHMW 1901/VII/3. B – Photograph of the skull roof. MHK–P 80198. C – The parietal with conspicuously curved interparietal suture. MHK–P 64805. D – The skull roof with the extrascapular lateral. Large spiracular and the dermosphenotic border the lateral margin of the intertemporal and supratemporal. MHK–P 64665. E – The skull roof with only party visible interparietal suture which is overlaid by the sculpture. MHK-P 81399. F – Right side of the skull roof with large lobate lateral process on the parietal. The extrascapular medial and extrascapular lateral bear pores of the supratemporal commissure. The small accessory extrascapular lateral is without pores of sensory lines. MHK–P 80206.*

Obr. 5. *Paramblypterus rohani (Heckel & Kner, 1861). Kosti klenby lebeční v pohledu dorsálním. Měřítka 5 mm. A – Klenba lebeční se supraorbitálním kanálem přecházejícím z parietale na postparietale a pit line střední na postparietale je protažena laterálně až na supratemporale. NHMW 1901/VII/3. B – Foto kostí klenby lebeční. MHK–P 80198. C – Kosti klenby lebeční s výrazně zprohýbaným interparietálním švem. MHK–P64805. D – Kosti klenby lebeční včetně laterální extraskapulární kosti. Velké spirakulare a dermosphenotikum lemují laterální okraj intertemporale a supratemporale. MHK–P 64665. E – Parietale s pouze částečně viditelným interparietálním švem. Zbylá část švu je překryta silnou skulpturou. MHK–P 81399. F – Pravá část klenby lebeční s výrazným laločnatým laterálním výběžkem na parietale. Extraskapulare mediale a laterale s póry supratemporální komisury a malé přídatné extraskapulare laterale bez smyslových linií. MHK–P 80206.*

Abbreviations: *a.pl – anterior pit line; Ext.l – extrascapular lateral; Ext.l.a – accessory extrascapular lateral; Ext.m – extrascapular medial; ioc – infraorbital canal; It – intertemporal; Ju – jugal; m.pl – medial pit line; Pa – parietal; Ppa – postparietal; p.pl – posterior pit line; Pt – posttemporal; Sbo – suborbital; soc – supraorbital canal; Spi – spiracular; St – supratemporal; stc – supratemporal commissure.*

the supratemporal. The intertemporal is widest in its posterior part and narrows anteriorly. Laterally borders the dermosphenotic and spiracular and anteriorly is in contact with the preorbital, but it is not in contact with the nasal. The sculpture consists of distinct mounds running in the antero-posterior direction (MHK-P 64795, MHK-P 81399).

The supratemporal is rectangular in shape, antero-posteriorly elongated with a rounded anterior margin. The intertemporal and supratemporal meet at the point of the lateral process of the parietal, which partially separates these bones. The lateral margin of the bone is not curved; it does not form a lateral process. Laterally it is in contact with the spiracular and operculum. A prominent posteriorly pointed process forms the supratemporal in its posterior part, and a large area of bone medial to this process is overlain by the extrascapular bones (MHK-P 64665, MHK-P 80206 – Fig. 5D, F). The prominent sculpture of the supratemporal is formed by short or worm-like curved mounds and flat tubercles.

A strip of extrascapular bones formed by paired extrascapular lateral, unpaired extrascapular medial or other accessory extrascapular lateral surround the skull roof posteriorly (Figs 5D, F; 7B, C; 8A). This strip forms the interface between the skull roof and the dermal bones of the pectoral girdle. A band of these bones is delimited laterally by the posterior supratemporal process. The extrascapular lateral is approximately rectangular in shape, mediolaterally elongated and its lateral portion broadly overlies the posterior portion of the supratemporal. The median extrascapular is rectangular in shape, mediolaterally elongated, with a prominent anterior process which is wedged between the right and left postparietals. In some individuals, especially in old individuals, the extrascapular band is enriched with accessory lateral extrascapular

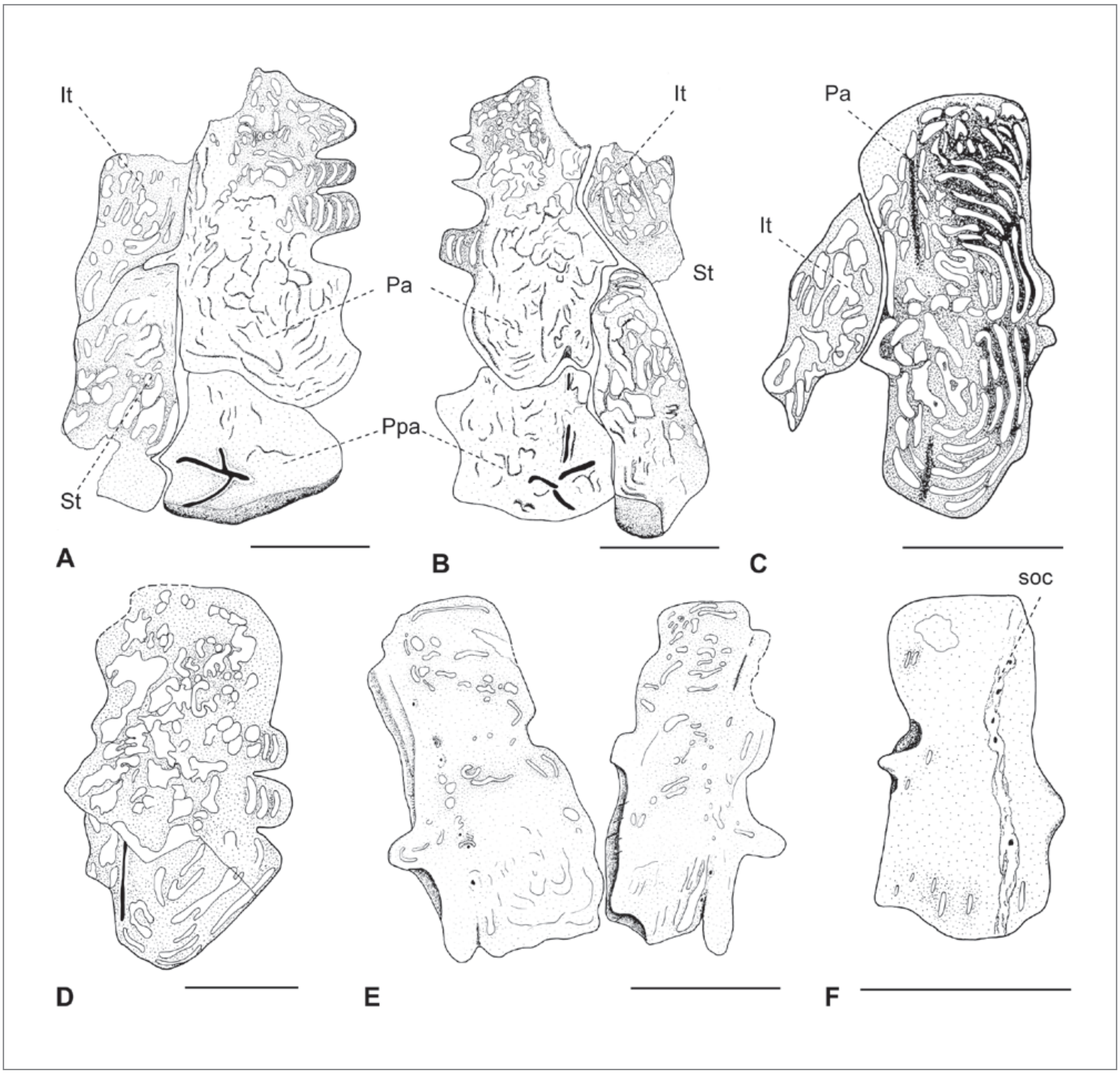


Fig. 6. *Paramblypterus rohani* (Heckel & Kner, 1861). *Variability of the bones of the skull roof and the interparietal suture. Scale bars 5 mm. A, B – Separate right and left sides of the skull roof of the specimen MHK–P 81461 in dorsal view. C – The parietal and intertemporal in dorsal view. MHK–P 64795. D – The parietal in dorsal view with double curved interparietal suture. MHK–P 64896. E – Right and left parietals in dorsal view. MHK–P 81400. F – Left parietal in ventral view with supraorbital canal. MHK–P 30873.*

Obr. 6. *Paramblypterus rohani (Heckel & Kner, 1861). Variabilita kostí klenby lebeční a interparietálního švu. Měřítka 5 mm. A, B – Oddělená pravá a levá část klenby lebeční jedince MHK–P 81461 v pohledu dorsálním. C – Parietale a intertemporale v pohledu dorsálním. MHK–P 64795. D – Parietale v pohledu dorsálním se zdvojeným interparietálním švem. MHK–P 64896. E – Pravé a levé parietale v pohledu dorsálním. MHK–P 81400. F – Levé parietale se supraorbitálním kanálem v pohledu ventrálním. MHK–P 30873.*

Abbreviations: *It – intertemporal; Pa – parietal; Ppa – postparietal; soc – supraorbital canal; St – supratemporal.*

bones. These small anamnestic bones of oval shape are developed in one or two pairs anterior to the extrascapular lateral and medial to the posterior process of the supratemporal. They are separating from the meeting in midline. These small accessory bones of the extrascapular girdle are developed mainly in old adults.

The bones of the skull roof carry a number of pores and pit lines of the sensory canals. The supraorbital and infraorbital sensory canals are mainly applied to the bones. The supraorbital sensory canal continues posteriorly from the nasal along the lateral margin of the parietal. It is manifested by distinct pores lying in the antero-posterior line closer to the lateral margin of the bone. In some individuals, however, these pores are not observable because of the markedly developed covering ganoine sculpture. In the ventral view, a continuous canal (MHK-P 81442, MHK-P 64775) is visible from the nasal through the entire parietal (Fig. 3A, B, C). The continuation of the supraorbital canal in the direction from the parietal posteriorly to the postparietal is observable in a number of bones in the anterior part of the postparietal where the supraorbital canal ends (MHK-P 30867, MHK-P 81461). Distinct pit lines anterior, middle and posterior are present on the postparietal. The posterior pit line is straight or may be arcuate (MHK-P 64795). The medial pit line may also pass as a distinct uninterrupted deep line to the laterally situated supratemporal and continues in a lateromedial direction across this bone (MHK-P 30867, NHMW 1901/VII/3 – Fig. 5A).

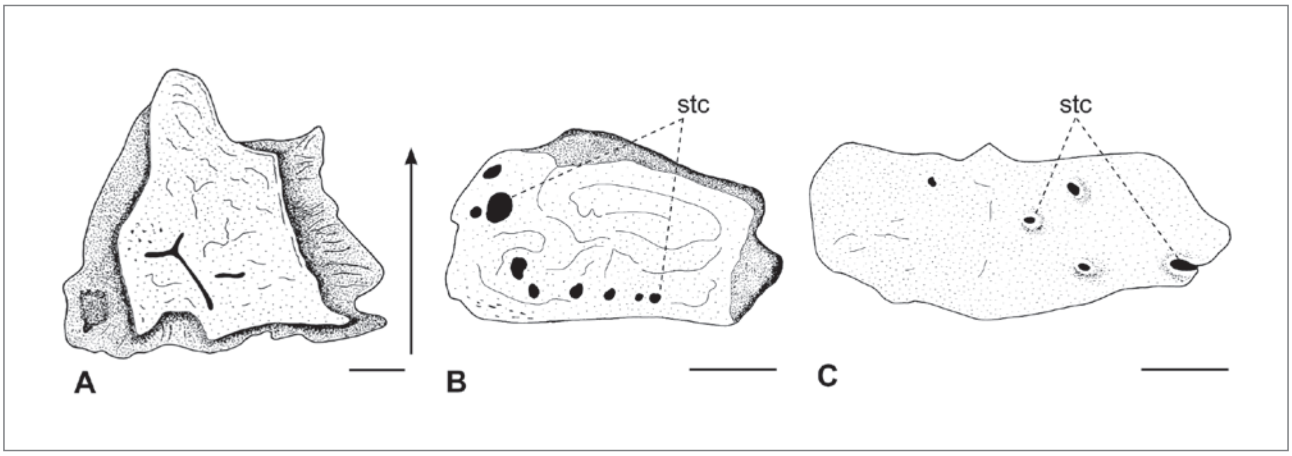


Fig. 7. *Paramblypterus rohani (Heckel & Kner, 1861). Scale bars 2 mm. The arrow indicates the front for all bones. A – Postparietal of old specimen with broad articulating surfaces on which surrounding bones are superimposed. Dorsal view, MHK–P 81433. B – Left extrascapular lateral with pores of the supratemporal commissure. Dorsal view, MHK–P 80153. C – Extrascapular medial with pores of the supratemporal commissure. Dorsal view, MHK–P 80153.*
Obr. 7. *Paramblypterus rohani (Heckel & Kner, 1861). Měřítka 2 mm. Šipka ukazuje přední část všech kostí. A – Postparietale starého jedince se širokými plochami, které se kloubily s okolními kostmi. Pohled dorsální, MHK–P 81433. B – Levé extraskapulare laterale s póry supratemporální komisury. Pohled dorsální, MHK–P 80153. C – Extraskapulare mediale s póry supratemporální komusury. Pohled dorsální, MHK–P 80153.*
Abbreviations*: stc – pores of the supratemporal commissura*

The infraorbital canal passes to the intertemporal from the dermosphenotic, bends markedly at the intertemporal, and points posteriorly to the supratemporal. Pores of the infraorbital sensory canal have also been noted in the anterior half of the intertemporal (MHK-P 30867). Thus, it is clear that from the point of bending of the infraorbital canal near the lateral margin in the posterior third of the intertemporal, the canal also continues to the anterior half of the intertemporal (Fig. 8A). The bend of the infraorbital canal on the intertemporal and exact location of the transition of the canal to the dermosphenotic is not preserved. Caudally from the bend of the infraorbital canal, this canal passes posteriorly to the supratemporal and continues along the lateral margin of the bone to the extracapular lateral as the otic canal. On the supratemporal a cluster of conspicuous pores can be periodically observed in the central part of the bone where the ossification centre of the supratemporal. On the extrascapular lateral, the otic canal branches into two lines. One branch of the otic canal continues from the extrascapular lateral to the supracleithrum and then continues on the scales as the lateral sensory line. The other line is indicated by well-marked pores parallel to the posterior margin of the extrascapular lateral and continues as supratemporal commissure through the median extrascapular. The conspicuous pores of the supratemporal commissure are arranged along the posterior margin and occasionally on the remainder of the dorsal surface of the median extrascapular, thus connecting the right and left branches of the infraorbital canal.

The bones of the skull roof and their sculpture are very characteristic and belong to the most frequently found and relatively well preserved bones. Their shape, and especially the formation of the interparietal suture and lateral parietal processes, has been one of the diagnostic features distinguishing the species *P. rohani*, *P. caudatus* and *P. reussi* from each other (ŠTAMBERG 1976). As shown by the amount of comparative material, this is only a variation of these bones in one species and not a determinative character of different species. The identical position, morphology, sculpture and also the high variability of these bones is also recorded in *P. duvernoyi* from the Saar-Nahe Basin (DIETZE 1999). A lack or less pronounced sculpture compared to *P. rohani* and *P. duvernoyi* is recorded in *P. gelberti* and this difference is also one of the characteristic features of *P. gelberti* (GAD 1988, DIETZE 1999, 2000). The bones of the skull roof of *Paramblypterus vratislaviensis* differ from *P. rohani* not only in the formation of the interparietal suture or sutures between the parietal and intertemporal and supratemporal, but also in the shape of the intertemporal and supratemporal (ŠTAMBERG 2021). The shape of the dermal bones and their arrangement is also different in *Paramblypterus decorus*, where the large parietal process extending between the intertemporal and supratemporal is absent and the interparietal suture is only slightly undulating. In contrast to *P. rohani* and *P. duvernoyi*, in *P. decorus* the intertemporal is in contact with the nasal by its anterior margin and is almost the same size as the supratemporal (BLOT 1966, DIETZE 2000). *Amblypterus latus* possesses the supratemporal with ventrolateral protuberance extending between the spiracular and operculum (DIETZE 2000, ŠTAMBERG 2013b).

The formation of the extrascapular bone band also varies between species. In all species of the family Amblypteridae, the extrascapular bone band is formed by an unpair median extrascapular and a pair of lateral extrascapular bones. These bones are often joined by additional extrascapular bones (postparietal in the sense of BLOT (1966), ŠTAMBERG (1976), GAD (1988), additional extrascapulars in the sense of DIETZE (1999, 2000). In *Amblypterus latus*, 2 additional extrascapular bones may be present (ŠTAMBERG 2013b), *P. decorus* possesses up to 3 additional paired lateral extrascapular bones (DIETZE 2000), *P. duvernoyi* and *P. gelberti* has 2 to 4 pairs of additional lateral extrascapulars (GAD 1988, DIETZE 1999). Sometimes also a duplication of the median extrascapular is described *in P. duvernoyi* and *P. gelberti* from the Saar-Nahe Basin. However, duplication of the median extrascapular has never been observed in *P. rohani* from the basins of Bohemia and, on the contrary, the median extrascapular always occurs as an unpaired bone of stable shape.

The skull roof bone assemblages described by HEYLER (1971) from the Surmoulin locality of the Autun Basin as *P. rohani* are identical in morphology and sculpture to the above

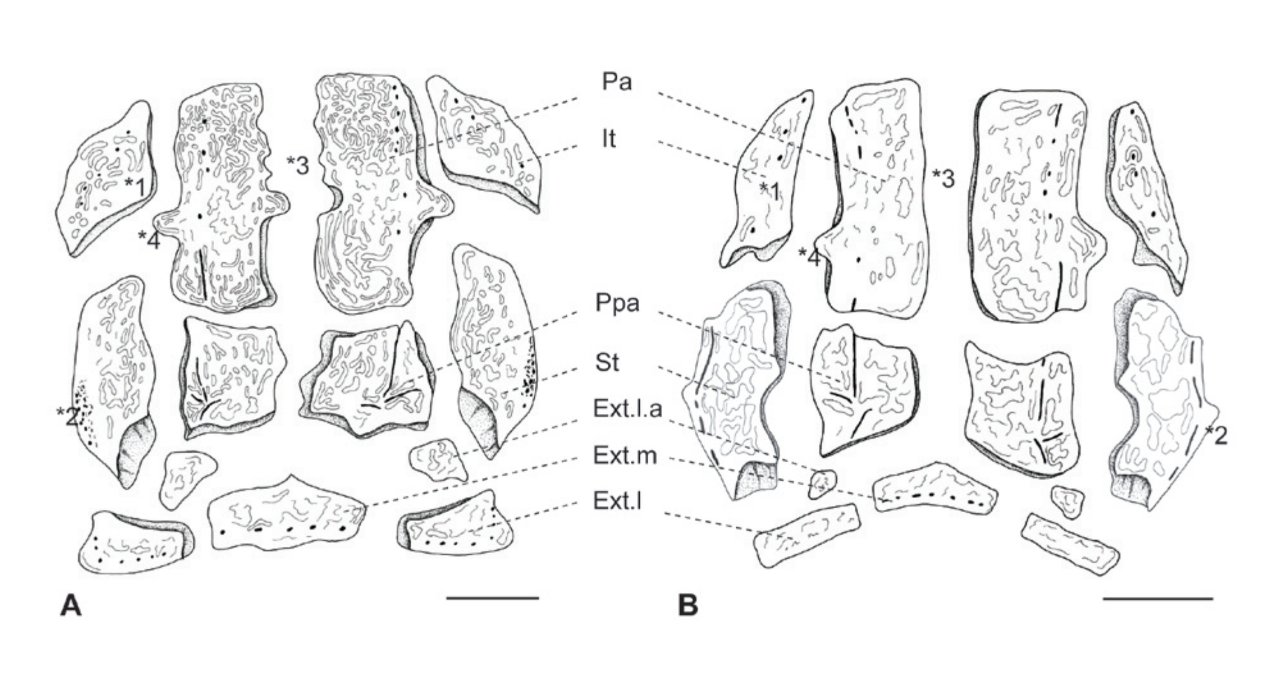


Fig. 8. *Schematic drawings of the skull roof in dorsal view, showing the position of overlapped areas of Paramblypterus rohani (Heckel & Kner, 1861) (A) and Paramblypterus sp. (B). The differences record following marks: *1 – Shape of the intertemporal; *2 – Shape of the supratemporal (presence or absence of lateral process); *3 – Shape of the interparietal suture; *4 – Position of lateral process of the parietal. Figure A is arranged on the basis of specimens MHK–P 64665, MHK–P 80198, MHK–P 80194, MHK–P 81461 etc. Figure B is arranged on the basis of specimens MHK–P 30754, MHK–P 81404, MHK–P 81409, MHK–P 81420 etc. Scale bars 5 mm.*

Obr. 8. *Schematické kresby klenby lebeční v pohledu dorsálním ukazující jejich kloubící plochy u Paramblypterus rohani (Heckel & Kner, 1861) (A) a Paramblypterus sp. (B). Rozdílné znaky jsou označeny následujícími značkami: *1 – Tvar intertemporale; *2 – Tvar supratemporale (přítomnost nebo chybění laterálního výběžku); *3 – Tvar interparietálního švu; *4 – Pozice laterálního výběžku na parietale. Obr. A je vytvořen na základě jedinců MHK–P 64665, MHK–P 80198, MHK–P 80194, MHK–P 81461 a dalších. Obr. B je vytvořen na základě jedinců MHK–P 30754, MHK–P 81404, MHK–P 81409, MHK–P 81420 a dalších. Měřítka 5 mm.*

Abbreviations: *Ext.l – extrascapular lateral; Ext.l.a – accessory extrascapular lateral; Ext.m – extrascapular medial; It – intertemporal; Pa – parietal; Ppa – postparietal; St – supratemporal.*

described bones of *P. rohani* from the Bohemian Massif as with *P. duvernoyi* from the Saar-Nahe Basin.

Together with the species *P. rohani*, a large group of specimens comes from the Rudník Horizon of the Krkonoše Piedmont Basin, whose characteristic feature is a straight or only slightly wavy interparietal suture, lateral parietal process is displaced posteriorly to about 1/3 of the length of the lateral margin in the direction from the posterior margin of the bone, intertemporal of triangular shape but not wide posteriorly and supratemporal with lateral process (Fig. 8B). During the course of the study, I initially assumed that this was a variation of the bones of the skull roof within the species *P. rohani*. However, the displacement of the lateral process of the parietal is associated with a change in the shape of the intertemporal, which is triangular in shape as in *P. rohani*, but is markedly elongated antero-posteriorly and the posterior margin of the intertemporal is significantly shorter than in *P. rohani*. Moreover, individuals with skull roof bones shaped in this manner have a significantly deeper operculum than *P. rohani*. For this reason, I consider the individuals described above to be members of a distinct species and will be studied separately. Now they are ranged as *Paramblypterus* sp. At the same time, the skull roof bones thus formed are an example of the fact that it is sometimes very difficult to distinguish true bone variation in one species from a character that already characterizes another taxon. Comparison of the skull roofs characters of *Paramblypterus rohani* and *Paramblypterus* sp. shows Fig. 8.

Circumorbital series

The orbit of the middle size is surrounded by the series bones including preorbital, dermosphenotic, infraorbital posterior, jugal, ventral infraorbital and rostro-premaxillo-lacrymal. The bones of the sclerotic ring are rarely preserved. They are very thin and only two interlocking bones of the sclerotic ring have ever been found. According to their proportions, it is clear that the sclerotic ring consisted of four arcuate fine bones that were wedged together (MHK-P 81380). The preorbital surrounding the orbit anteriorly and partly dorsally was described together with the bones of the rostral region. The preorbital of crescent shape (MNH-P 64854, MNH-P 81399, MNH-P 81442) is in contact posteriorly with the intertemporal and dermosphenotic (infraorbital in the sense of BLOT (1966), infraorbital superius in the sense of ŠTAMBERG (1976), infraorbital superior in the sense of ŠTAMBERG (2021), dermosphenotic 2 in the sense of DIETZE (1999, 2000). The rim of the dermosphenotic flanking the orbit is arcuate. The dermosphenotic is anteriorly pointed, ventroposteriorly it widens slightly and ventrally it touches the posterior infraorbital. The sculpture on the bone consists of only a few round-shaped tubercles. The small posterior infraorbital (infraorbital in the sense of BLOT (1966), jugal 2 in the sense of DIETZE (1999, 2000) is of oval shape and slightly dorsoventrally elongated flanking the orbit posteriorly (Fig. 9A, B). This bone forms a junction between the dermosphenotic and the jugal. The jugal (infraorbital in the sense of BLOT (1966), jugal

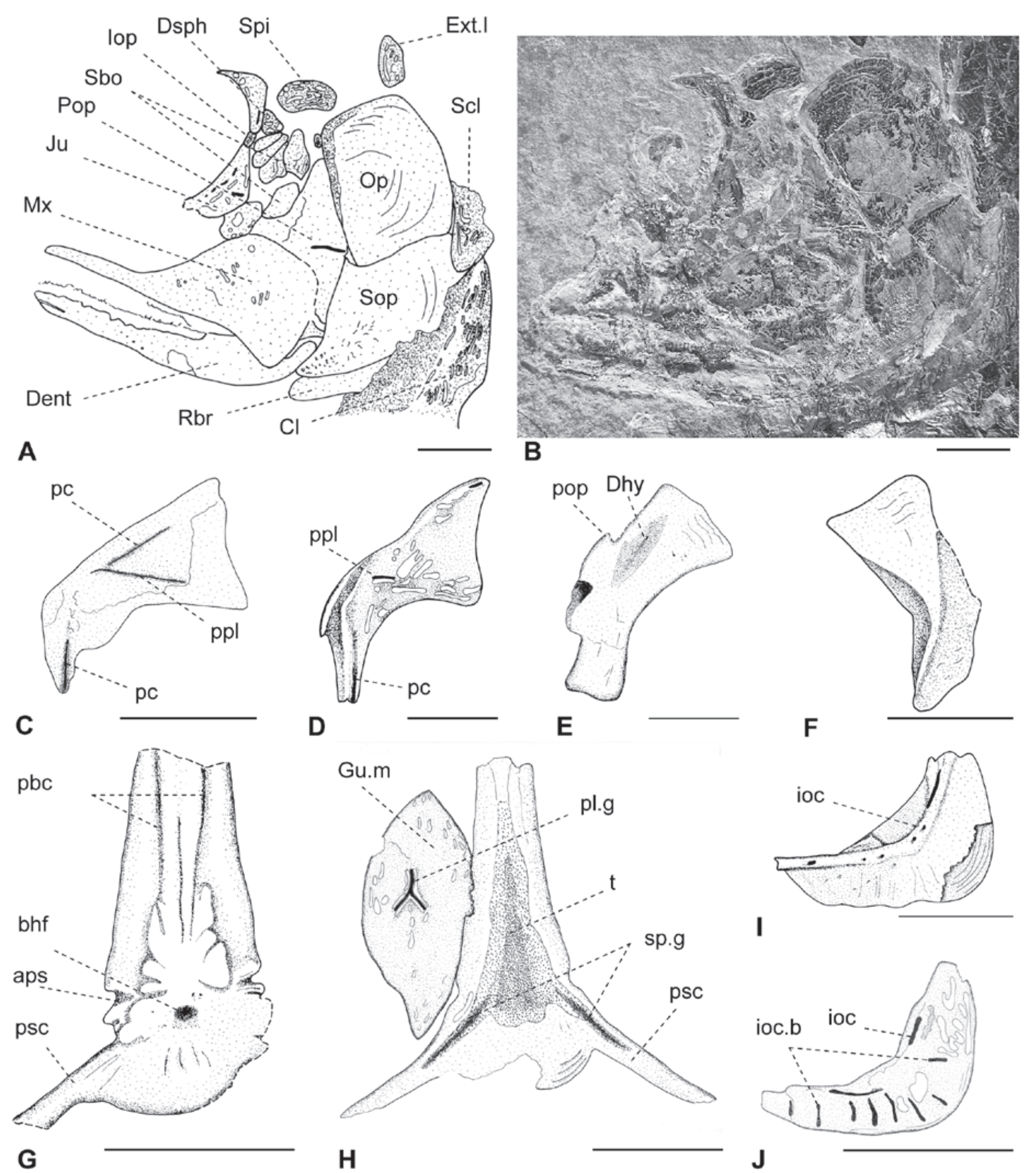


Fig. 9. *Paramblypterus rohani (Heckel & Kner, 1861). Scale bars 5 mm. A, B – Drawing and photograph of the cheek, jaws and opercular apparatus in lateral view. MHK–P 64854. C – Right preoperculum in lateral view. MHK–P 81380. D – Right preoperculum in lateral view. MHK–P 81451. E – Right hyomandibula in lateral view with a small processus opercularis and obscure trace of the dermohyal. MHK–P 81464. F – Left hyomandibula in lateral view. MHK–P 81451. G – Parasphenoid in dorsal view. MHK–P 30755. H – Parasphenoid and mesial gular in ventral view. Ventral surface of the parasphenoid bears small granular teeth. MHK–P 81810. J – Right jugal in medial view with conspicuous infraorbital canal. MHK–P 81412. J – Left jugal in lateral view with grooves of the infraorbital canal and several short grooves of sensory canals branching off posteriorly from the infraorbital canal. MHK–P 80193.*

Obr. 9. *Paramblypterus rohani (Heckel & Kner, 1861). Měřítka 5 mm. Kresba a fotografie lící, čelistí a operkulárního aparátu v pohledu laterálním. MHK–P 64854. C – Pravé preoperkulum v pohledu laterálním. MHK–P 81280. D – Pravé preoperkulum v pohledu laterálním. MHK–P 81451. E – Pravá hyomandibula v pohledu laterálním s malým operkulárním výběžkem a nejasným otiskem dermohyale. MHK–P 81464. F – Levá hyomandibula v pohledu laterálním. MHK–P 81451. G – Parasfenoid v pohledu dorsálním. MHK–P 30755. H – Parasfenoid a gulare mediale v pohledu ventrálním. Ventrální povrch parasfenoidu nese drobné granulární zoubky. MHK–P 81810. J – Pravé jugale v pohledu mediálním s výrazným infraorbitálním kanálem. MHK–P 81412. J – Levé jugale v pohledu laterálním se žlábky infraorbitálního kanálku a několika krátkými žlábky odstupujícími posteriorně z infraorbitálního kanálu. MHK–P 80193.*

Abbreviations: *Apc – notch for internal carotid arteries; bhf – bucco-hypophysial foramen; Cl – cleithrum; Dent – dentary; Dhy – dermohyal; Dsph – dermosphenotic; Ext.l – extrascapular lateral; Gu.m – gular medial; ioc – infraorbital canal; ioc.b – branches of the infraorbital canal; Iop – infraorbital posterior; Ju – jugal; Mx – maxilla; Op – operculum; pbc – parabasal canal; pc – preopercular canal; pl.g – gular pit line; Pop – preoperculum; pop – processus opercularis; ppl – preopercular pit line; psc – posterior ascending process; Rbr – branchiostegal rays; Sbo – suborbital; Scl – supracleithrum; Sop – suboperculum; sp.g – spiracular groove; Spi – spiracular; t – teeth.*

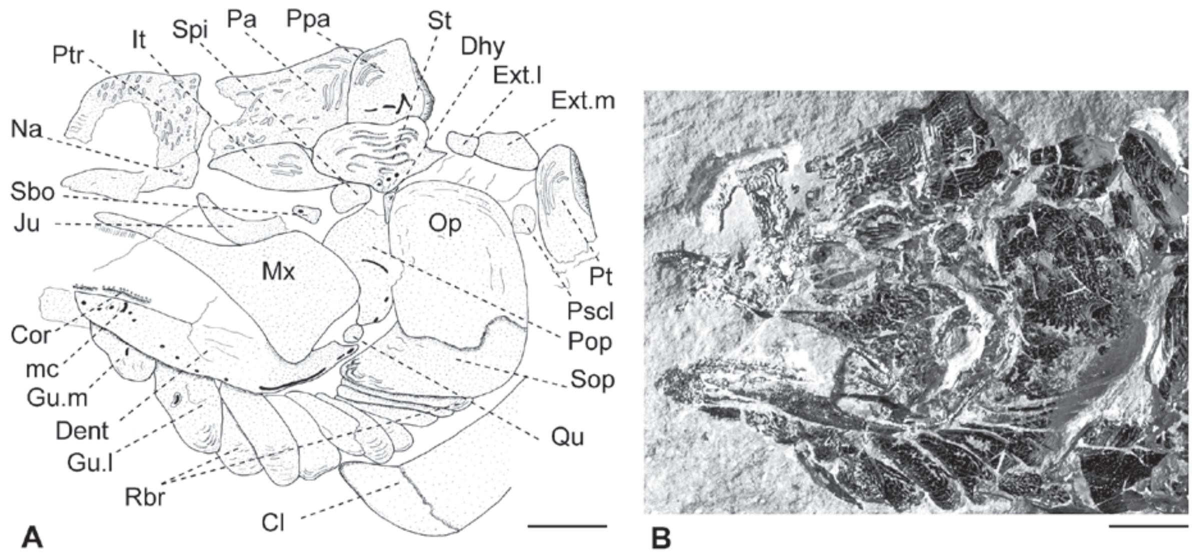


Fig. 10. *Paramblypterus rohani (Heckel& Kner, 1861). A, B – Drawing and photograph of the skull. DP 4529. Scale bars 5 mm.*
Obr. 10. *Paramblypterus rohani (Heckel & Kner, 1861). A, B – Perokresba a fotografie lebky. DP 4529. Měřítka 5 mm.*
Abbreviations: *Cl – cleithrum; Cor – coronoid; Dent – dentary; Dhy – dermohyal; Ext.l – extrascapular lateral; Ext.m – extrascapular medial; Gu.l – gular lateral; Gu.m – gular medial; It – intertemporal; Ju – jugal; mc – mandibular canal; Mx – maxilla; Na – nasal; Op – operculum; Pa – parietal; Pop – preoperculum; Ppa – postparietal; Pscl – presupracleithrum; Pt – posttemporal; Ptr – postrostral; Qu – quadratum; Rbr – branchiostegal rays; Sbo – suborbital; Sop – suboperculum; Spi – spiracular; St – supratemporal.*

1 in the sense of DIETZE (1999, 2000), infraorbitale inferius in the sense of ŠTAMBERG (1976) is of crescent shape lining the orbit partly posteriorly and ventrally (MNH-P 64854; MNH-P 81412). The posterior margin extends partially over the suborbital and overlaps the anterior margin of the maxillary plate. The jugal is in contact anteriorly with the narrow, antero-posteriorly extended ventral infraorbital (infraorbital in the sense of Blot 1966; lacrymal in the sense of DIETZE (1999, 2000), ŠTAMBERG (2021). The rostro-premaxillo-lacrymal, which is shortly in contact with the orbit in its antero-ventral corner, was described together with the preorbital in the paper on rostral part of the skull.

The infraorbital canal passes along the orbit from the intertemporal across the dermosphenotic, infraorbital posterior, jugal, infraorbital inferior to the rostro-premaxillo-antorbital. The infraorbital canal on the dermosphenotic and infraorbital posterior is preserved in the form of short grooves oriented dorsoventrally. The canal is indicated by pores on the jugal located in an arc parallel to the anterior margin of the bone (MNH-P 30867, MNH-P 80156) with 6–8 short sensory canals oriented posteriorly branching off from the canal (Fig. 9I, J). Through the ventral infraorbital, the infraorbital canal passes from the jugal to the rostro-premaxillo-lacrymal.

The preorbital and the dermosphenotic flanking the dorsal margin of the orbit and separating the orbit from the intertemporal is a character identical to *P. duvernoyi*, and the same position of the bones is found in both *P. gelberti* (GAD 1988, DIETZE 1999) and *P. decorus* (BLOT 1966). The same bones in *P. vratislaviensis* do not touch and the intertemporal forms the dorsal margin of the orbit (ŠTAMBERG 2021).

Contrary to the conclusions of DIETZE (1999, 2000) who states that the sclerotic ring is absent in both *P. duvernoyi* and *P. gelberti* from the Saar-Nahe Basin, the presence of a sclerotic ring is documented in *P rohani*. In the type species *P. decorus*, BLOT (1966) shows a sclerotic ring composed of four bones, and the presence of sclerotic bones is confirmed in *Amblypterus latus* (DIETZE 2000) or *P. vratislaviensis* (ŠTAMBERG 2021). Since the sclerotic bones are very thin, their preservation is very rare and it is possible that the sclerotic ring may have been present in the Saar-Nahe Basin specimens of *P. duvernoyi* and *P. gelberti* but did not resist the processes during fossilization.

In the author's previous work (ŠTAMBERG 1976), which provided insights on *P. rohani* and other species included in the present revision study, the posterior infraorbital is not identified and a direct contact of the dermosphenotic with the jugal is supposed. The material now studied documents the presence of a posterior infraorbital in this group of fish as well. It is a small bone that is very rarely preserved on the material.

Cheek

The suborbital bones, the spiracular, the preoperculum and the dermohyal fill the space between the bones surrounding posteriorly the orbit and the opercular apparatus (Figs 9A–F, 10A, B). The large anamnestic spiracular bone is rectangular in shape with rounded corners. It medially lines the supratemporal and intertemporal and anteriorly is in contact with the dermosphenotic. A set of small anamnestic suborbital bones extends ventrally from the spiracular. These bones fill the space anterior to the preoperculum and as the specimen (MNH-P 64854) shows (Fig. 9A, B), 7 small suborbital bones may also be present.

The cheek space filled by the small suborbital bones is posteriorly bounded by the anterior deep part of the preoperculum. The preoperculum (Figs 9A–D, 10A, B) is the

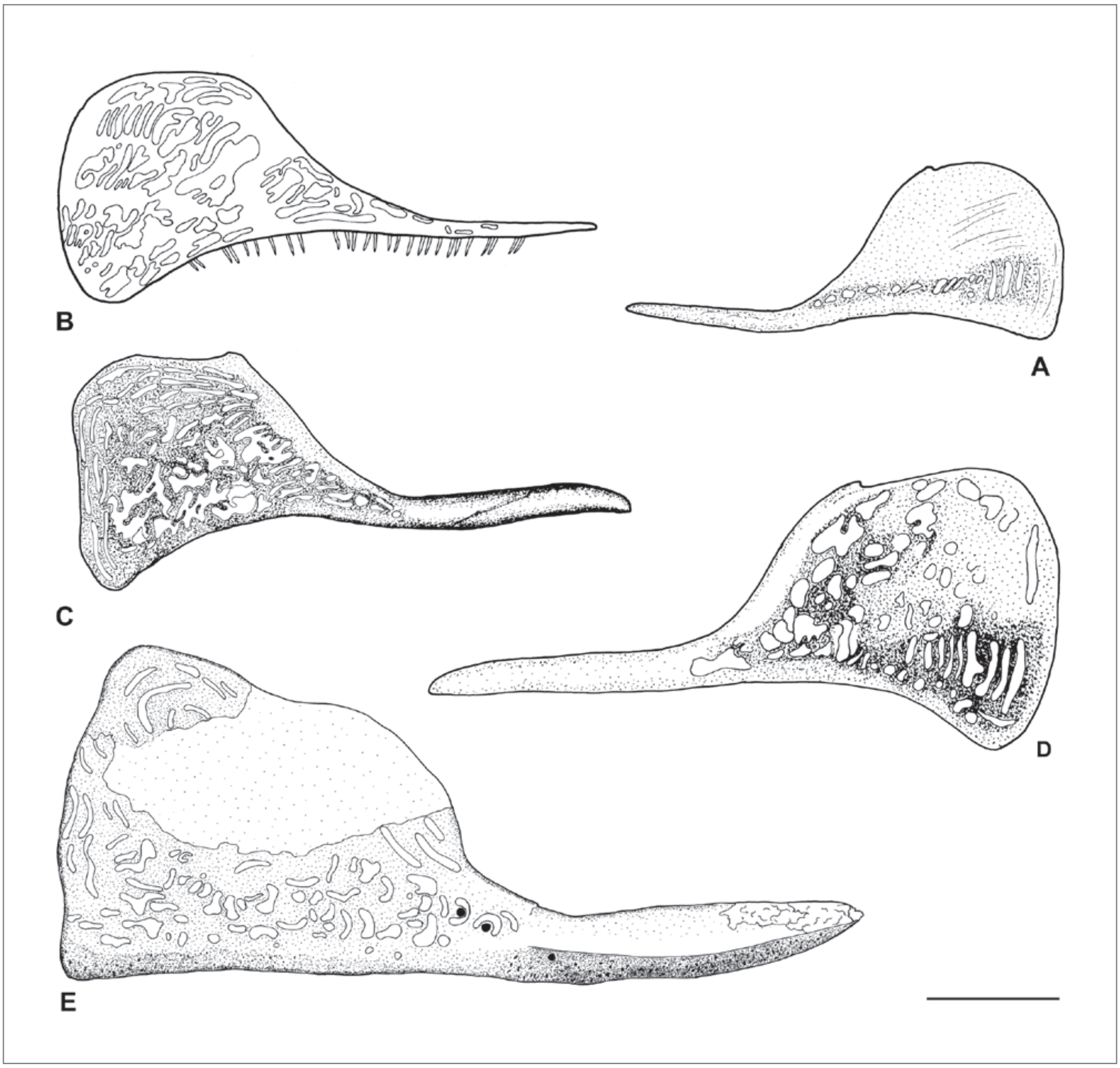


Fig. 11. *Paramblypterus rohani (Heckel & Kner, 1861). Maxillae of specimens of different ages. Scale bar 5 mm.*
A – MHK–P 81446a; B – NHMW 1866/XXII/5; C – MHK–P 81446b; D – MHK–P 81451; E – MHK–P 64914.
Obr. 11. *Paramblypterus rohani (Heckel & Kner, 1861). Maxily jedinců různého stáří. Měřítko 5 mm.*
A – MHK–P 81446a; B – NHMW 1866/XXII/5; C – MHK–P 81446b; D – MHK–P 81451; E – MHK–P 64914.

bone surrounding the maxillary plate posteriorly and dorsally and is therefore a bone markedly bent according to this plate (MNH-P 81451, MNH-P 64854). Thus, the preoperculum is morphologically divided into a narrow, dorsoventrally extended posterior portion inserting between the maxillary plate and the suboperculum, and a deep antero-dorsal portion flanking the maxillary plate dorsally. The ventral margin of the anterior extended part of the preoperculum makes a 90° angle with the anterior margin of the posterior narrowed part of the bone. The dorsal and posterior margins of the bone together form a bend angle of the preoperculum of about 130°. The anterior margin of the dorsally lying greatly expanded part of the preoperculum is concave and reaches the anterior level of the maxillary plate. The preoperculum overlaps the dorsal margin of the maxillary plate in a narrow strip. The connection between the preoperculum and the maxillary plate is quite firm, as a small projection can be traced on the maxillary plate in front of its dorsal margin (Fig. 11A, C, D), which probably strengthened the connection between these two bones. The preopercular canal runs from the ventral margin of the bone along the posterior margin of the bone towards the dorsal and continues along the dorsal margin of the bone. The course of the canal is indicated by longitudinal depressions or, conversely, by bowing of the bone at the point of passage of the preopercular sensory canal. At the site of the preopercular bend, the preopercular pit line runs anteriorly, oriented horizontally. The angle of inclination of the preoperculum (i.e. the angle of the dorsal edge of the preoperculum with the horizontal plane) is about 40°. The slight tilt of the preoperculum can also be judged by the slightly tilted suspensorium (DIETZE 2001).

Quadratojugal is quite sporadically preserved on MHK-P 10979, DP 4529 – Fig. 10A, B). It is oval in shape and its ventroanterior margin is adjacent to the posterior margin of the maxilla. In its anterior part it is thickened and with remains of indistinct sculpture, the dorsoposterior part is enlarged and was probably covered by the ventral part of the preoperculum.

The dermohyal of triangular shape is inserted between the postero-dorsal margin of the preoperculum and the anterior margin of the operculum (DP 4529). This small bone is preserved quite sporadically and reaches up to two-thirds of the height of the operculum with the dorsal side. The dermohyal attaches to the hyomandibula as shown in specimen MHK-P 81464 – Fig. 9E).

The hyomandibula is a thick and relatively short bone. It is slightly flexed and the tapered ventral and expanded dorsal portions together form an angle of 150°. Specimens MHK-P 81451 and MHK-P 81464 show the hyomandibular in lateral view (Fig. 9D, E). On the posterior margin, there is a small bump representing the processus opercularis about midway at the level of the bone bend. On the anterior margin of the hyomandibula, on the other hand, there is a depression where the posterior part of the palatoquadrate has encroached.

If we compare the cheek bones of the studied specimens with some other species and genera, it can be concluded that the described large spiracular is characteristic of the family Amblypteridae. The described spiracular of *P. rohani* is identical to the spiracular of *P. decorus* (BLOT 1966, DIETZE 2000), *P. duvernoyi*, *P. gelberti* (GAD 1988, DIETZE 1999), *P. vratislaviensis* (ŠTAMBERG 2021) as well as with *Amblypterus latus* (DIETZE 2000, ŠTAMBERG 2013b). It is always a large rectangular bone located posteriorly from the dermosphenotic and laterally from the intertemporal and supratemporal. The area between the circumorbital bones and the opercular apparatus is subject to fragmentation of the larger bones into smaller ones, probably in connection with improved grasping ability and mobility of the maxillary apparatus. For this reason, an increased number of small suborbital bones can be found in this area, the number of which varies considerably. Both GARDINER (1963) and DIETZE (2000) report only two suborbital bones in *Amblypterus latus* but ŠTAMBERG (2013b) finds 4 suborbital bones behind the circumorbital bones. *P. decorus* has 6–9 suborbitals and a larger number of dermohyals (BLOT 1966, DIETZE 2000). *P. duvernoyi* and *P. gelberti* may have about 6 suborbital bones (GAD 1988, DIETZE 1999) and one to two dermohyals in front of the operculum.

Fragmentation of the cheek area is well known also in the family Aeduellidae where *Aeduella blainvillei* has up to 8 suborbital bones in the cheek area (HEYLER 1969), *Neslovicella rzehaki* 6 suborbital bones and *Bourbonnella hirsuta* 5 suborbital bones (ŠTAMBERG 2007a).

The preoperculum has a stable shape in all species of the genus *Paramblypterus* and in *Amblypterus latus*. The 40° angle of inclination of the properculum found here also corresponds to the inclination of the preoperculum of *P. duvernoyi* (DIETZE 1999) and *Amblypterus latus*. BLOT (1966) figured *P. decorus* with a preoperculum inclination angle of 36°. In aeduellid species, e.g. *Aeduella blainvillei,* the posterior margin of the preoperculum is in a vertical position (HEYLER 1969), likewise in *Neslovicella rzehaki* (ŠTAMBERG 2007a). In *Bourbonnella guilloti* Heyler, 1969 the angle of inclination of the preoperculum is 61° (HEYLER 1969) and similar (68°) is in *Bourbonnella hirsuta* (ŠTAMBERG 2007a).

The dermohyal of the specimens of *P. duvernoyi* and *P. gelberti* from the Saar-Nahe Basin is usually present as only one bone, but the occurrence of two or three small bones between the preoperculum and operculum has also been rarely found (DIETZE 1999). A single dermohyal of *P. vratislaviensis* is narrow and conspicuously dorsoventrally elongated and a very similar slender dermohyal is found in *Amblypterus latus* (DIETZE 2000). In contrast, seven to ten small dermohyals lie anterior to the operculum of *P. decorus* (BLOT 1966, DIETZE 2000).

The hyomandibula is not known in other species of the genus *Paramblypterus* or in *Amblypterus latus*. A similar shape to the hyomandibula described here is depicted by POPLIN (1974) in Actinopterygii from the Carboniferous of Kansas, and the short and thick hyomandibula is also present in *Amia calva* (GRANDE & BEMIS 1998), *Polypterus* (ARRATIA & SCHULTZE 1991) and many others. However, we find a diametric difference in the shape of the hyomandibula in a number of other Permo-Carboniferous actinopterygians (*Elonichthys crassidens* Giebel, 1848, *Rhabdolepis saarbrueckensis* Gardiner, 1963, *"Elonichthys" krejcii* (Fritsch, 1895), *Letovichthys tuberculatus* Štamberg, 2007a (see ŠTAMBERG 2007a, 2010b), which have a very narrow, dorso-ventrally elongated hyomandibula.

Parasphenoid

The parasphenoid is a characteristically shaped bone composed of the corpus parasphenoidis, which ends behind the large paired processus ascendens posterior and is not significantly stretched posteriorly (Fig. 9G, H). MHK-P 64809, MHK-P 80245, MHK 81446, MHK 81464 and others show the parasphenoid in dorsal view. The corpus parasphenoidis is partially divided anteriorly by a paired parabasal canal into three lobes of which the middle lobe is dorsally arcuate. In the posterior third of the corpus parasphenoidis is the bucco-hypophysial canal, which passes through the centre of ossification. On either side of the corpus parasphenoidis at approximately the level of the bucco-hypophysial foramen are the folds through which the pseudobranchial artery passes. The parasphenoid *Kansasiella eatoni* shows similar folds and subsequent grooves (POPLIN 1974, Fig. 8B). Specimen MHK-P 30755 (Fig. 9G) also shows fine patterns on its dorsal apex, which are impressions of the ventral side of the neurocranium. Unfortunately, no remnants of the neurocranium could be found on any of the specimens. A very well-developed large processus ascendens posterior protrudes in the posterior part of the corpus parasphenoidis. This paired process, directed latero-posteriorly, makes an angle of 60–72° with the coprus parasphenoidis. Variations in the angle at which the processus ascendens posterior is oriented are caused during fossilization. Specimen MHK-P 81810 (Fig. 9H) shows the ventral surface of the parasphenoid with a field of granular teeth which extends along the middle of the corpus parasphenoidis. This field of teeth is wide around the ossification centre of the corpus parasphenoidis and the field of teeth narrows anteriorly. Paired spiracular grooves run from the root of the processus ascendens posterior to the centre of the corpus parasphenoidis.

The parasphenoids described above are identical in shape to the parasphenoids described so far in *P. duvernoyi* (DIETZE 2000, 2001), *P. gelberti* (BOY 1976, GAD 1988, DIETZE 2000, 2001), paramblypterids of the group incertain from the Autun Basin (HEYLER 1969), *P. vratislaviensis* (ŠTAMBERG 2021) as well as *A. latus* (ŠTAMBERG 2013b). A deviation in the shape of the parasphenoid can be seen in *Paramblypterus comblei* (HEYLER 1969) from

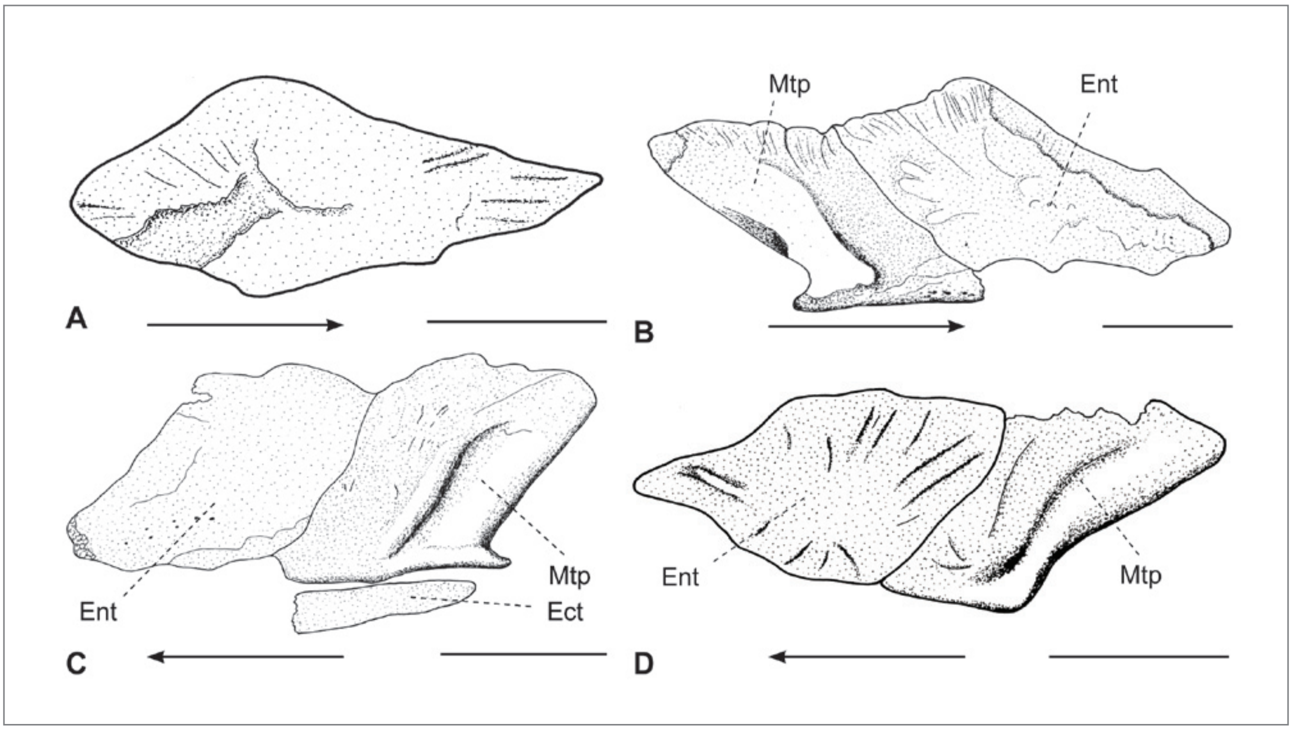


Fig. 12. *Paramblypterus rohani (Heckel & Kner, 1861). Dermal palatal bones. The arrows indicate the front for all bones. Scale bar 5 mm. A – MHK–P 81450; B – MHK–P 81464; C – MHK–P 81490; D – MHK–P 81401.*
Obr. 12. *Paramblypterus rohani (Heckel & Kner, 1861). Dermální patrové kosti. Šipky označují přední část kostí. Měřítko 5 mm. A – MHK–P 81450; B – MHK–P 81464; C – MHK–P 81490; D – MHK–P 81401.*
Abbreviations: *Ect – ectopterygoid; Ent – entopterygoid; Mtp – metapterygoid.*

the Autun Basin, where the processus ascendens posterior branches off from the corpus parasphenoidis at an angle of 90°, while the parasphenoids of the other species at an angle of 60°– 70°.

Maxilla

Maxilla is composed of a low anterior suborbital part and deep posterior maxillary plate (Figs 3C, 9A, B, 10, 11). The depth of the maxillary plate increases slightly posteriorly, it has straight dorsal edge and it extends postero-ventrally to a small blunt process. In the anterior part of the dorsal edge of the maxillary plate there is a small projection which served to connect the maxilla more firmly to the anterior part of the preoperculum. The ratio of the length of the plate to its height varies around 1.2, and the ratio of the total length of the maxilla to the length of the maxillary plate varies around 2.15. The sculpture on the bone consists of flat mounds and tubercles. The anterior margin of the plate is without sculpture and has been overlain by the jugal and suborbital bones; likewise the dorsal margin of the maxillary plate has a narrow band without sculpture and has been overlain by the preoperculum. Usually, three pores of the sensory canal are situated in the transition zone between the maxillary plate and the narrowed suborbital part of the maxilla anteriorly.

The maxillary plate of *P. rohani* has a characteristic basic shape, and no differences from the maxilla of *P. duvernoyi* (DIETZE 1999, 2000) are noted. In the past, variations in plate shape were often considered as characters characterizing different species (HEYLER 1969, ŠTAMBERG 1976). The study of a large number of specimens of different ages of *P. duvernoyi* from the Saar-Nahe Basin (DIETZE 1999, 2000) and the present study of specimens of *P. rohani* from the Bohemian Massif have shown that the shape of the maxillary plate, although stable in its basic shape, is highly variable in proportion. However, the dorsal margin of the maxillary plate is always straight and there is never any significant stretching of the ventro-posterior corner of the plate. Sometimes the shape of the maxillary plate is close to a square, but usually it is rectangular in shape with a slight anteroposterior stretch. The dimensions of several maxillary plates are shown in Table 1.

Observation of a larger number of individuals shows some differences between the maxillae of *P. rohani* and *P. vratislaviensis*. The maxillary plate of *P. vratislaviensis* is shorter relative to the total length of the maxilla and its length is contained in the total length of the maxilla 2.5 to 3 times, the ratio of the length of the maxillary plate to its height fluctuates around 1. In addition, the dorsal margin of the maxillary plate of *A. vratislaviensis* is dorsally convex (ŠTAMBERG 2021). The distinct shape of the maxillary plate was described by HEYLER (1969) in *Paramblypterus comblei.* The maxillary plate in this species is high and extended ventrally as well.

A large maxillary plate of square or slightly rectangular shape is characteristic of the genus *Paramblypterus*. It differs fundamentally from the actinopterygian family Elonichthyidae, where the plate is elongated and forms a distinct postero-ventral process (SCHINDLER 1993, 2017, 2018a, b). The maxillary plate of the paramblypterids is distinctly different from the same bone in fishes of the family Aeduellidae, where the maxillary plate is triangular in shape, a feature that very easily distinguishes these fishes, which are sometimes found together in the same strata (HEYLER 1969, ŠTAMBERG 2007a, 2010a).

Tab. 1. *Paramblypterus rohani (Heckel & Kner, 1861). Dimensions of maxillae of different ages (in mm).*
Tab. 1. *Paramblypterus rohani (Heckel & Kner, 1861). Rozměry svrchních čelistí (v mm) jedinců různého stáří.*

	Lenght of the maxilla	Lenght of maxillary plate	Deep of maxillary plate
MHK-P 30885	8.5	4	3
MHK-P 30900	11	5.5	4
MHK-P 81446(B)	17	8	7
MHK-P 82451	19	9.5	8
MHK-P 81446(A)	22	10	9
MHK-P 81442	23	10.5	9
MHK-P 80193	24	11	9
MHK-P 81451	24	12	11
MHK-P 81459	25	12.5	10
MHK-P 64854	27	12	11
MHK-P 64914	33	16	14

Dermal palatal bones. The palatoquadrate is not preserved on any of the individuals studied because it was not ossified. The dermal bones, the ectopterygoid, entopterygoid and metapterygoid which cover the palatoquadrate medially are preserved in isolation (MHK-P 81401, MHK-P 81464, MHK-P 81490 – Fig. 12). The narrow ectopterygoid is antero-posteriorly elongated and sutures medial to the metapterygoid. The metapterygoid is dorso-ventrally elongated, markedly thickened in the postero-ventral part and forms the posterior cover of the palatoquadratum. It is found isolated or even in solid association with the entopterygoid. So far it has always been found in dorso-lateral view and thus without teeth. The distinct thickening of the bone in its postero-ventral part and the prominent protruding edge continuing postero-anteriorly support the idea that the metapterygoid described here is a solid union of the pars metapterygoidea as documented by ARRATIA & SCHULTZE (1991) and partly of the pars quadrata. The metapterygoid sutures anteriorly with the entopterygoid. The entopterygoid is approximately of rhombic shape, anteroposteriorly elongated and tapering anteriorly.

The designation of these dermal bones is based on the situation described by NIELSEN (1942) in *Pteronisculus aldingeri* (Nielsen, 1942), where not only the dermal bones of the medial side of the palatoquadrate but also the entire palatoquadrate is preserved. Thus, the position of the dermal bones relative to the palatoquadrate can also be determined.

The above described dermal bones of the medial side of the palatoquadrate are identical to the same bones in *P. duvernoyi* and *P. gelberti* (GAD 1988, DIETZE 2001).

Lower jaw

The lower jaw is rather weak tapering anteriorly. The posterior part of the lower jaw is deep and dorsally forms a process. The base of the lower jaw was meckelian bone, which is not preserved on the material and on the medial side of the lower jaw there is only a groove where this cartilaginous part was deposited. The largest dermal bone in lateral view is the dentalosplenial, which is followed posteriorly by the angular (Figs 9A, B, 10A, B). The angular is extended along the entire posterior part of the mandible dorsally. The mandible thus forms a large dorsally directed process in the posterior part, built up by the endochondral components of the meckelian bone which are enveloped posteriorly by the angular. In the medial view, the coronoid bones and prearticular are preserved in firm union with the entire lower jaw on the material from the Bohemian Massif and the contours of the individual bones cannot be discerned (MHK-P 64854). Distinct pores of the mandibular sensory canal are evident on a number of specimens and the canal ran dentalosplenial from the anterior margin of the bone along its ventral margin and through the angular where it bent dorsally passing to the preopercular (MHK-P 82451). There is also a distinct angular pit line at the bend of the mandibular canal to the angular (Fig. 10A, B). Sometimes a distinct dentary pit line (Fig. 10A, B) is observed in the anterior third of the dentary closer to its dorsal edge (DP 4529, MHK-P 70075).

Teeth

On the maxilla and mandible we find two types of denticles, namely marginal teeth attached to the maxilla and dentalosplenial and short teeth covering the coronoid bones and prearticular of the mandible and dermal bones of the palate. The dentalosplenial of the lower jaw and maxilla of the upper jaw bear marginal teeth which consist of a long tube on which a short sharply pointed acrodinine tooth sits (Fig.13). This type is well illustrated by the adult specimen MHK-P 70046 of the total body length 190 mm with maxilla which is 23 mm long. The tooth consits of a long tubule which is termianted by sharply pointed acrodin apex. The acrodin apex has a conical shape but on the teeth in the anterior part of the jaws is more slender and curved posteriorly (Fig. 13D). Whole tooth including tubule is 1.2 mm long. Another specimen MHK-P 27571 exhibits isolated maxilla 16 mm long and lower jaw. Jaws bear set of tubular teeth which are 2 mm long. The length of the acrodin apex is only 0.3 mm long (Fig. 13A–C). Tubular teeth (tubular teeth in the sense of BLOT 1966, BLOT & HEYLER 1963, HEYLER 1969) are ranged probably in two rows and they are very numerous, hence the term “brush teeth” was often used in the past. They are embedded in the jaws in the bone mass. Only a short part of the tube with a tooth protruded above the jaw. A similar maxilla of *Paramblypterus* with the teeth described in MHK-P 27571 is figured by HEYLER (2000, fig. 1) from the beds of Igornay (Autun Basin, France).

Tubular teeth are one of the diagnostic features of the family Amblypteridae. This was confirmed in *A. latus* and *A. lateralis* from the Saar -Nahe Basin (HEYLER 1976, 2000; DIETZE 2000; ŠTAMBERG 2013b), *P. decorus* from the Stephanian of Commentry, France (BLOT 1966, DIETZE 2000), *P. gaudryi* (Sauvage, 1890), and other species of the genus *Paramblypterus* from the Autun Basin, France (HEYLER 1969, 1971), *P. duvernoyi* and *P. gelberti* from the lower Permian of Germany (BOY 1976, GAD 1988, DIETZE 2000), *P. vratislaviensis* (ŠTAMBERG 2021) and in other to this time not described species of *Paramblypterus* of the lower Permian of the Bohemian Massif (ŠTAMBERG 2020). Tubular teeth are also well developed in the species of the family Aeduellidae (BLOT 1966, HEYLER 1969, ŠTAMBERG 2007a, 2010a).

There are small short teeth on the coronoid bones, prearticular and palatine bones. The teeth are with a relatively wide base attached directly to the bone. These teeth, although short

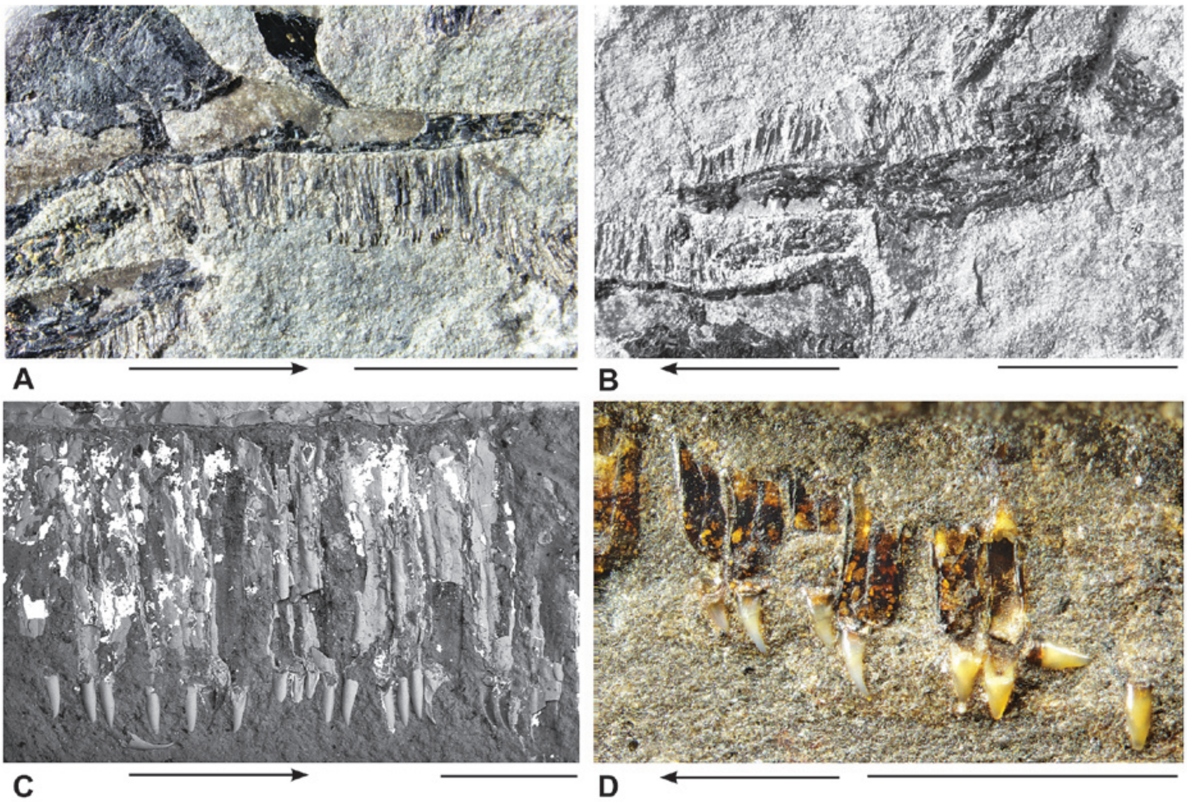


Fig. 13. *Paramblypterus rohani (Heckel & Kner, 1861). The arrows indicate the front for all bones. A – Right maxilla with tubular teeth. MHK–P 27571. Scale bar 5 mm. B – Left lower jaw with tubular teeth. MHK–P 27571. Scale bar 5 mm. C – Detail of tubular teeth on right maxilla. MHK–P 27571. Scale bar 1 mm. D – Tubular teeth on left maxilla. Long tubules are terminated by sharply pointed acrodin tooth which in the anterior part of the jaw are more slender and curved posteriorly. MHK–P 70046. Scale bar 1 mm.*

Obr. 13. *Paramblypterus rohani (Heckel & Kner, 1861). Šipky označují přední část kostí. A – Pravá maxila s tubulárními zuby. MHK–P 27571. Měřítko 5 mm. B – Levá spodní čelist s tubulárními zuby. MHK–P 27571. Měřítko 5 mm. C – detail tubulárních zubů na pravé maxile. MHK–P 27571. Měřítko 1 mm. D – Tubulární zuby na levé maxile. Dlouhé tubuly jsou zakončeny ostře zašpičatělým akrodinovým zoubkem, který je v přední části čelisti štíhlejší a zahnutý dozadu. MHK–P 70046. Měřítko 1 mm.*

are more robustly built than the acrodinine spikes at the end of the tubules.

The dentition of the specimens described here, assigned to the species *P. rohani*, has recently been described from a number of specimens including juvenile specimens (ŠTAMBERG 2020). However, continuing research indicates that some of the individuals cited in that paper as *Paramblypterus* cf. *rohani* belong to other, previously undescribed species.

Opercular apparatus

The operculum, suboperculum, branchiostegal rays, paired lateral gular and unpaired median gular form the dermal part of the opercular apparatus (Fig. 14). The operculum is a flat large bone with rounded corners, always deeper than its length (e.g. MHK-P 64795 – depth 12 mm, length 8.5 mm; MHK-P 81451 – depth 14 mm, length 11 mm). The depth of the operculum is 1.23 to 1.4 times greater than its length, and the depth of the operculum is 1.3–1.4 times greater than the depth of the suboperculum (Fig. 14). The operculum is sculptured with flat irregular mounds and bumps. The ventral margin of the bone is straight or slightly concave, whereas the dorsal margin is convex. The shape of the operculum is quite variable and the antero-ventral corner may be in some individuals slightly elongated anteriorly. The dorsal margin of the operculum reaches the supratemporal and extrascapular lateral, the anterior margin of the operculum is in contact with the dermohyal and preoperculum. The suboperculum is always lower than the operculum and its shape is slightly variable. The dorsal margin of the suboperculum is concave and the anterodorsal corner of the suboperculum projects in a prominent pointed process. This prominence is not always conspicuous on fossil material, but if the preservation of this part of the bone is good, this prominence can always be noted (Fig. 14D, G). The antero-ventral corner of the suboperculum projects into a large, bluntly terminated process. The sculpture on the suboperculum consists of flat mounds and bumps. The suboperculum is anteriorly in contact with the preoperculum.

Eight wedge-shaped branchiostegal rays continue ventrally to the suboperculum (MHK-P 30883). Very often they are preserved isolated. The largest branchiostegal ray of the length 18 mm is shown by MHK-P 81433. Branchiostegal rays are always smaller in area than the anteriorly situated lateral gular and median gular (Fig. 14I). The sculpture on the branchiostegal rays is similar to that on the suboperculum and operculum.

Lateral gular is an antero-posteriorly elongated bone, anteriorly pointed, and posteriorly tapered with a rounded posterior end. The lateral margin of the bone is convex, whereas

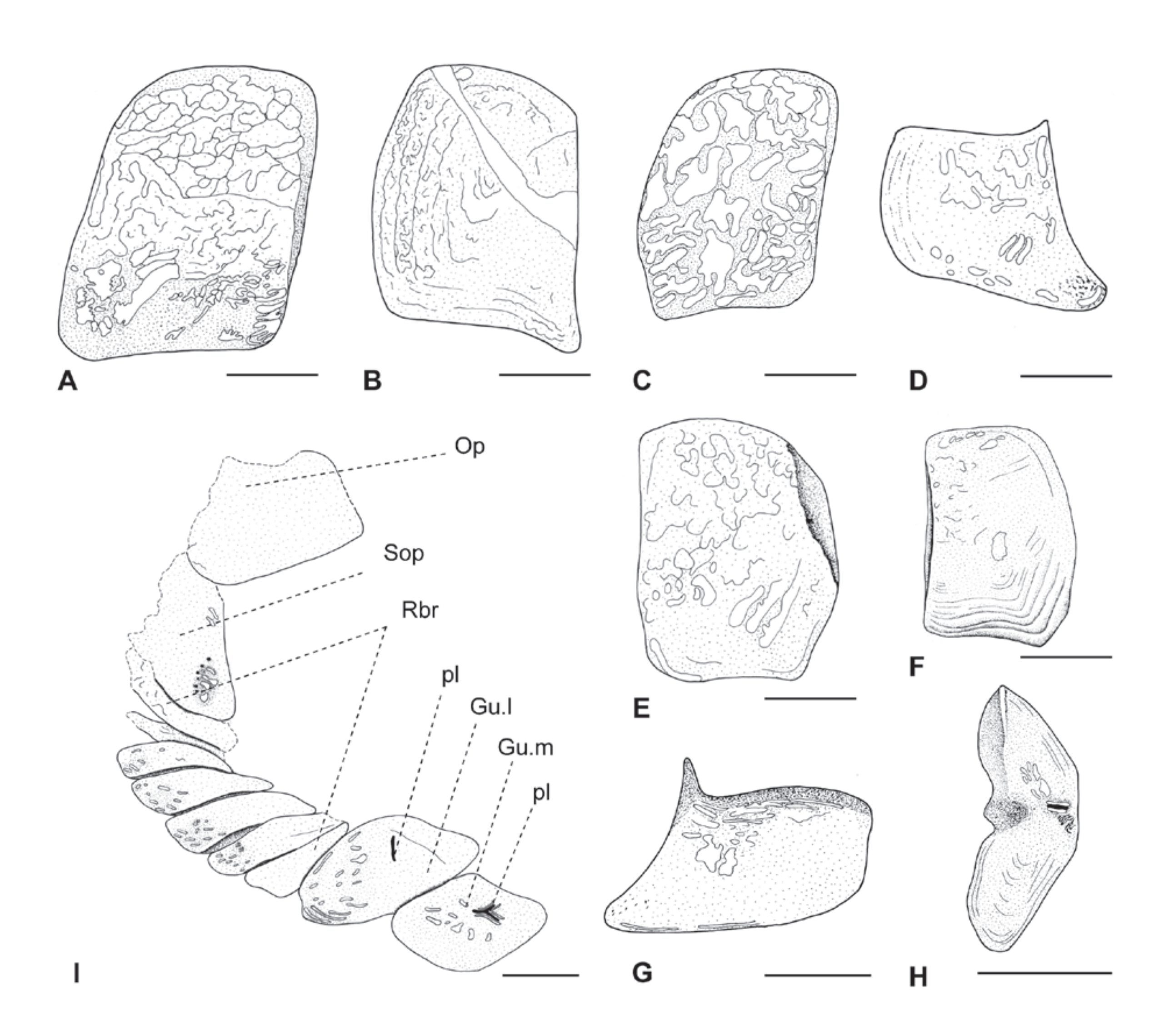


Fig. 14. *Paramblypterus rohani (Heckel & Kner, 1861). Dermal bones of the opercular apparatus. Scale bars 5 mm. A – Right operculum. MHK–P 81431; B – Right operculum. MHK–P 81450; C – Right operculum MHK–P 64753.; D – Right suboperculum. MHK–P 81451; E – Left operculum. MHK–P 81451; F – Left operculum. MHK–P 81380; G – Left suboperculum. MHK–P 81446; H – Left gular lateral in ventral view. MHK–P 81446; I – Opercular apparatus in lateral view. MHK–P 81797.*
Obr. 14. *Paramblypterus rohani (Heckel & Kner, 1861). Dermální kosti operkulárního aparátu. Měřítka 5 mm. A – Pravé operkulum. MHK–P 81431; B – Pravé operkulum. MHK–P 81450; C – Pravé operkulum MHK–P 64753.; D – Pravé suboperkulum. MHK–P 81451; E – Levé operkulum. MHK–P 81451; F – Levé operkulum. MHK–P 81380; G – Levé suboperkulum. MHK–P 81446; H – Levé gulare laterale v pohledu ventrálním. MHK–P 81446; I – Operkulární aparát v pohledu laterálním. MHK–P 81797.*
Abbreviations: *Gu.l – gular lateral; Gu.m – gular medial; Op – operculum; pl – pit line; Rbr – branchiostegal rays; Sop – suboperculum.*

the medial margin is concave (MHK-P 81446). The short gular pit line is located about half the total length of the bone and runs in a latero-medial direction. The anterior part of the medial margin is overlapped by the median gular (MHK-P 81446). The median gular (MHK-P 81446, MHK-P 81810) is rhombic in shape with a tapered posterior and anterior part. Its posterior part is wedged between the anterior parts of the paired gular lateral and partially overlaps them. The prominent gular pit line of the V or Y-shaped is located in the middle of the bone at the level where the bone is widest. The sculpture consists of sparsely placed short mounds oriented antero-posteriorly.

The formation of the opercular apparatus described above is identical to the characteristics of these bones in *P. duvernoyi* from the Saar-Nahe Basin, and there are not too many differences in other species of the family Amblypteridae either. Only variations in the number of branchiostegal rays can be noted from species to species, ranging from seven to ten, with GAD (1988) reporting 7 to 9 branchiostegal rays in *P. gelberti*, ŠTAMBERG (1976) in *P. rohani* also 7, ŠTAMBERG (2021) 7 rays in *P. vratislaviensis*, DIETZE (2000) 10 rays in *A. latus*, whereas ŠTAMBERG (2013b) 8 rays in the same species, BLOT (1966) 8 rays in *P. decorus*, whereas DIETZE (2000) 9 rays in the same species.

Pectoral girdle

Dermal bones of the pectoral girdle are composed of the posttemporal, supracleithrum, presupracleithrum, postcleithrum, cleithrum and clavicle (Fig. 15). The oval-shaped posttemporal follows the anteriorly lying strip of extrascapular bones. A prominent antero-lateral process on the posttemporal extends between the extrascapular lateral and operculum.

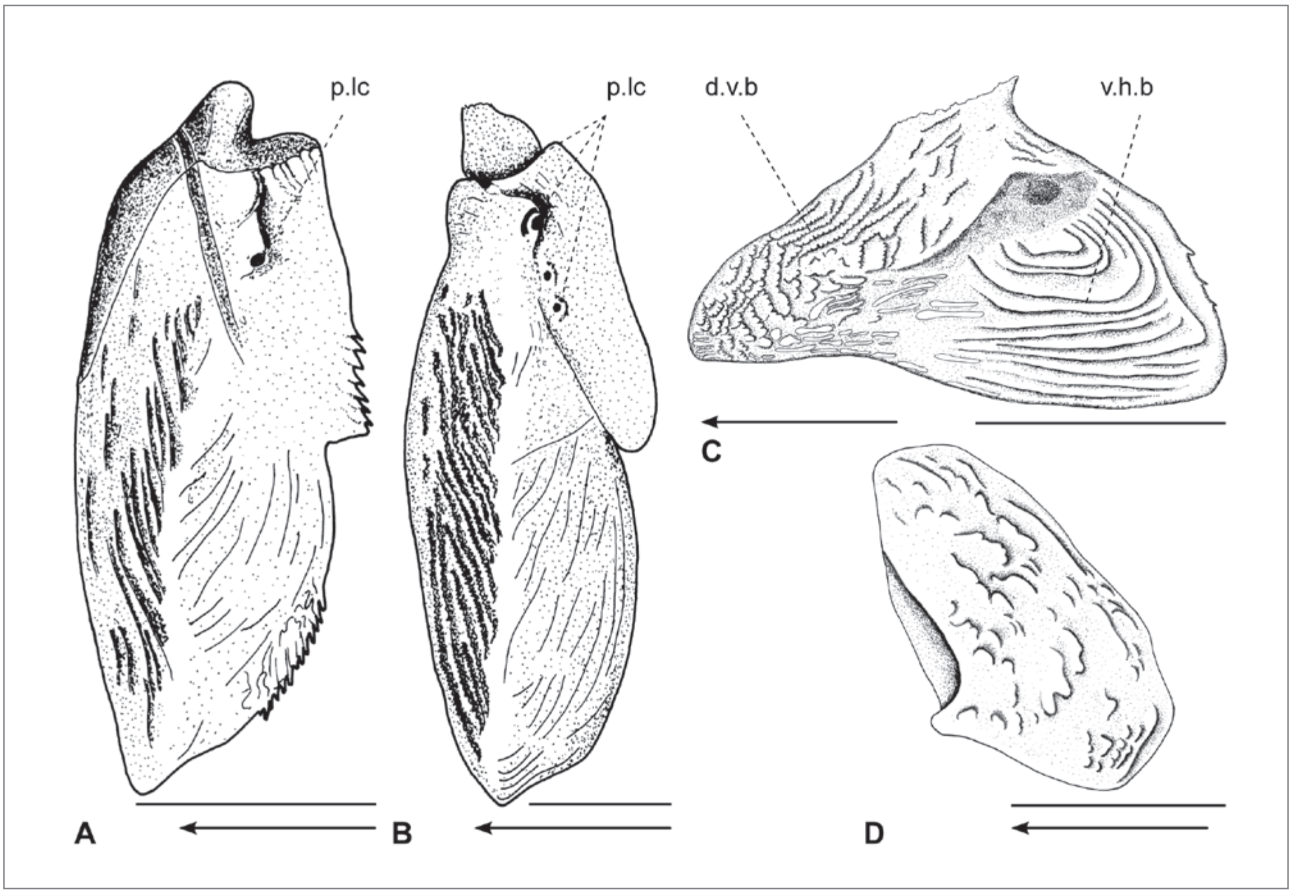


Fig. 15. *Paramblypterus rohani (Heckel & Kner, 1861). Dermal bones of the pectoral girdle. The arrows indicate the front for all bones. Scale bars 5 mm. A – Left supracleithrum in lateral view. MHK–P 64804; B – Left supracleithrum in lateral view. MHK–P 64805; C – Left clavicle in lateral view with ventral horizontal branch sculptured with strong concentrically arranged ridges. Dorsal vertical branch bears finely denticulated short ridges. MHK–P 81432; D – Left posttemporal in dorsal view. MHK–P81380.*
Obr. 15. *Paramblypterus rohani (Heckel & Kner, 1861). Dermální kosti prsního pletence. Šipky označují přední část kostí. Měřítka 5 mm. A – Levé suprakleithrum v pohledu laterálním. MHK–P 64804; B – Levé suprakleithrum v pohledu laterálním. MHK–P 64805; C – Levá klavikula v pohledu laterálním s ventrální horizontální větví skulpturovanou koncetricky uspořádanými silnými valy. Dorsální vertikální větev nese krátké valy jemně zoubkované. MHK–P 81432; D – Levé posttemporale v pohledu dorsálním. MHK–P 81380.*
Abbreviations: *d.v.b – dorsal vertical branch; p.lc – pores of the lateral sensory canal; v.h.b – ventral horizontal branch.*

Lateral sensory canal passes from the extrascapular lateral across the lateral process of the posttemporal to the supracleithrum. A small rounded presupracleithrum (postspiracular in the sense of ŠTAMBERG 2021) occupies a position among the posttemporal, supracleithrum and operculum. This small bone is observed only rarely (NM-M 1983, DP 4529 – Fig. 10) as it is usually covered by the surrounding large bones. The supracleithrum is one of the largest bones and the most commonly preserved. The dorsoventrally elongated oval-shaped bone flanks the operculum posteriorly and extends to about half the height of the suboperculum. The dorsal margin of the bone bears a large process similar to the peg and socket type articulation on the scales and certainly contributes to the interlocking of the dermal bones of the pectoral girdle. This process and the dorsal margin of the bone are overlain by the posttemporal. The supracleithrum bears a distinct sculpture over the entire surface of the bone consisting of dorsoventrally oriented long ridges. The lateral sensory canal, manifested by prominent pores, runs diagonally across the supracleithrum in the dorsal third of the bone (Fig. 15A, B). On the inner side of the supracleithrum, the sensory canal is in the form of a continuous mound beginning at the dorsal margin of the bone just anterior to the dorsal process and running diagonally in a posteroventral direction and arising in the dorsal 1/3 of the posterior margin of the supracleithrum (MHK-P 64799). The posterior margin of the supracleithrum is often markedly serrated, especially dorsally from the lateral sensory canal. The postcleithrum (anocleithrum in the sense of ŠTAMBERG (1976) is located just posterior to the contact between the supracleithrum and cleithrum (NM-M 1983, NM-M 4915, MHK-P 82451). It is an enlarged one or two scales of the scale row behind the cleithrum and certainly served to reinforce the interconnection of the dermal bones of the pectoral girdle.The cleithrum is very often preserved, as it is one of the largest and additionally reinforced bones and thus resists fossilization quite well. The cleithrum is always considerably dorso-ventrally elongated. Morphologically, it is a complicated bone, since the cleithrum in lateral view consists of a dorsal branch, dorso-ventrally elongated, and an anterior branch, which is elongated antero-posteriorly and bent medially. The larger dorsal branch is divided by a relatively sharp edge into a posterior part, which is distinctly sculptured with mounds that are additionally serrated, and a medial part, which is bent medially and borders the gill cavity posteriorly. The clavicle forms an anterior part of the dermal bones of the shoulder girdle. It curves strong inwards ventrally and forms the ventral horizontal branch and dorsal vertical branch (MHK-P 81432, MHK-P 81432, MHK-P 81423 – Fig. 15C).

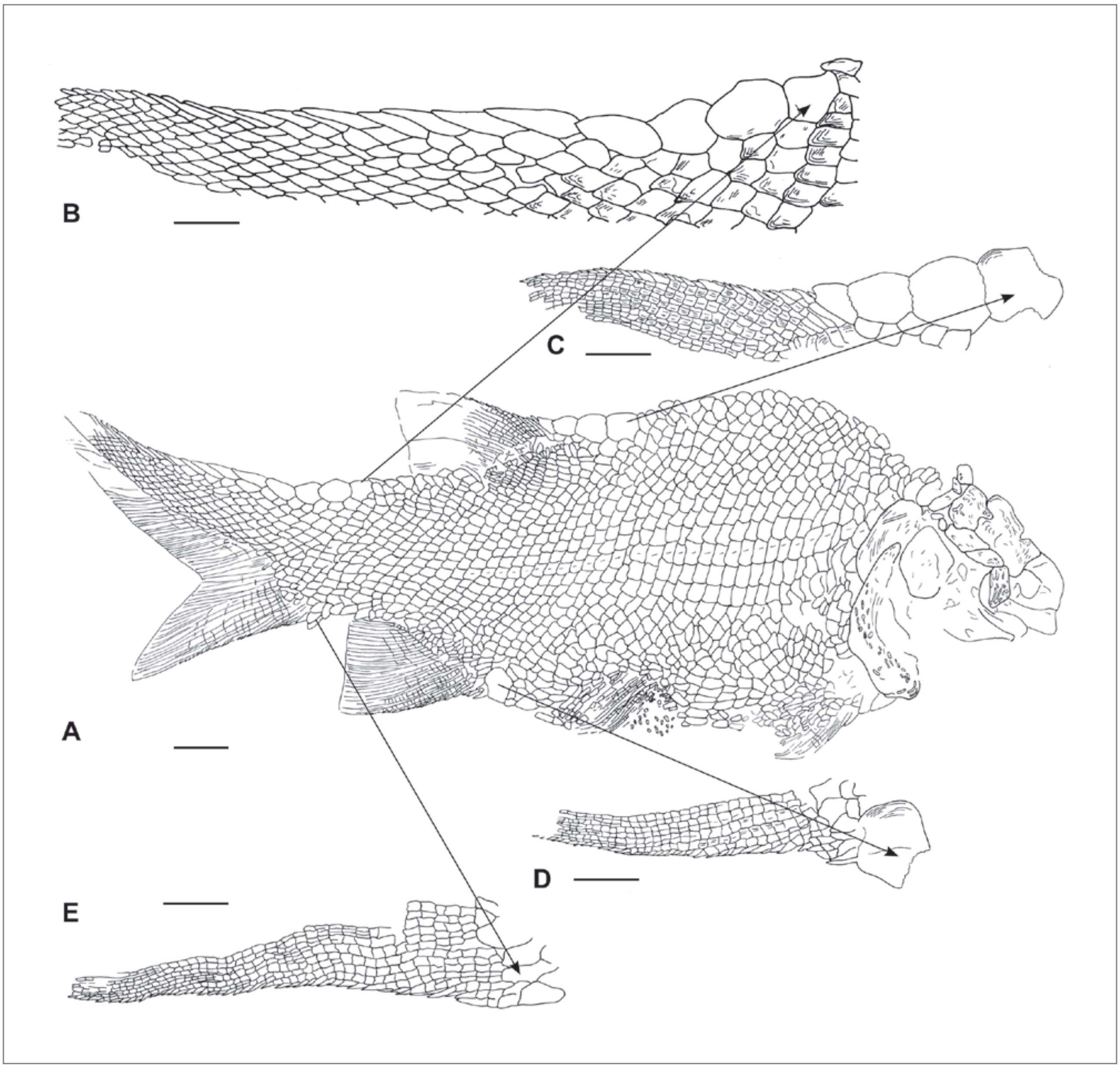


Fig. 16. *Paramblypterus rohani (Heckel & Kner, 1861). A – E – Drawing of whole specimen NM–M 484 (A) with drawings of the dorsal border of the caudal fin (B), large ridge scutes and dorsal border of the dorsal fin (C), anterior border of the anal fin (D) and anterior border of the ventral lobe of the caudal fin. Scale bars 5 mm.*
Obr. 16. *Paramblypterus rohani (Heckel & Kner, 1861). A – E – Kresba celého jedince NM–M 484 (A) s kresbami dorsálního okraje ocasní ploutve (B), velkých kýlových šupin a dorsálního okraje hřbetní ploutve (C), anteriorního okraje řitní ploutve (D) a předního okraje ventrálního laloku ocasní ploutve. Měřítka 5 mm.*

Clavicle is concave posteriorly and overlocks the anterior part of the cleithrum. Similarly, as the cleithrum it is composed of a ventral and a dorsal branch. The ventral branch, which is in the horizontal position, is triangular in shape, wide posteriorly and tapering anteriorly. It bears on its ventral outer surface strong ridges concentrically arrange which are parallel with posterior and medial margins. At the point of flexion between the ventral and dorsal branches the ridges pass onto the dorsal branch of the clavicle. The dorsal branch is triangular in shape, deep posteriorly and tapering anteriorly. The ridges on the dorsal branch of the clavicle are finely denticulated. The set of described dermal bones of the pectoral girdle corresponds to observations found in *P. duvernoyi* and *P. gelberti* from the Saar-Nahe Basin. In addition, a narrow interclavicle is determinate in *P. duvernoyi* (DIETZE 2000). Regarding the position of the postcleithrum, it can be noted that DIETZE (1999) delineates the postcleithrum between the supracleithrum and the cleithrum in the reconstruction of *P. duvernoyi* and GAD (1988) placed this bone in the same position in *P. gelberti.* I am convinced that the postcleithrum is located posteriorly from the contact of the supracleithrum and cleithrum. A large postcleithrum with a large process including additional enlarged scales located underneath each other can also be observed very well not only in *P. rohani* but also on many specimens of a hitherto undescribed species of the genus *Paramblypterus* from the Boskovice Basin. This position suggests that the postcleithrum and possibly other large scales behind the cleithrum were formed by enlarging the scales of the scale row behind the cleithrum as inferred by GARDINER (1984). The postcleithrum ventrally from the supracleithrum is connected to the supracleithrum by a large process, and any additional enlarged scales are

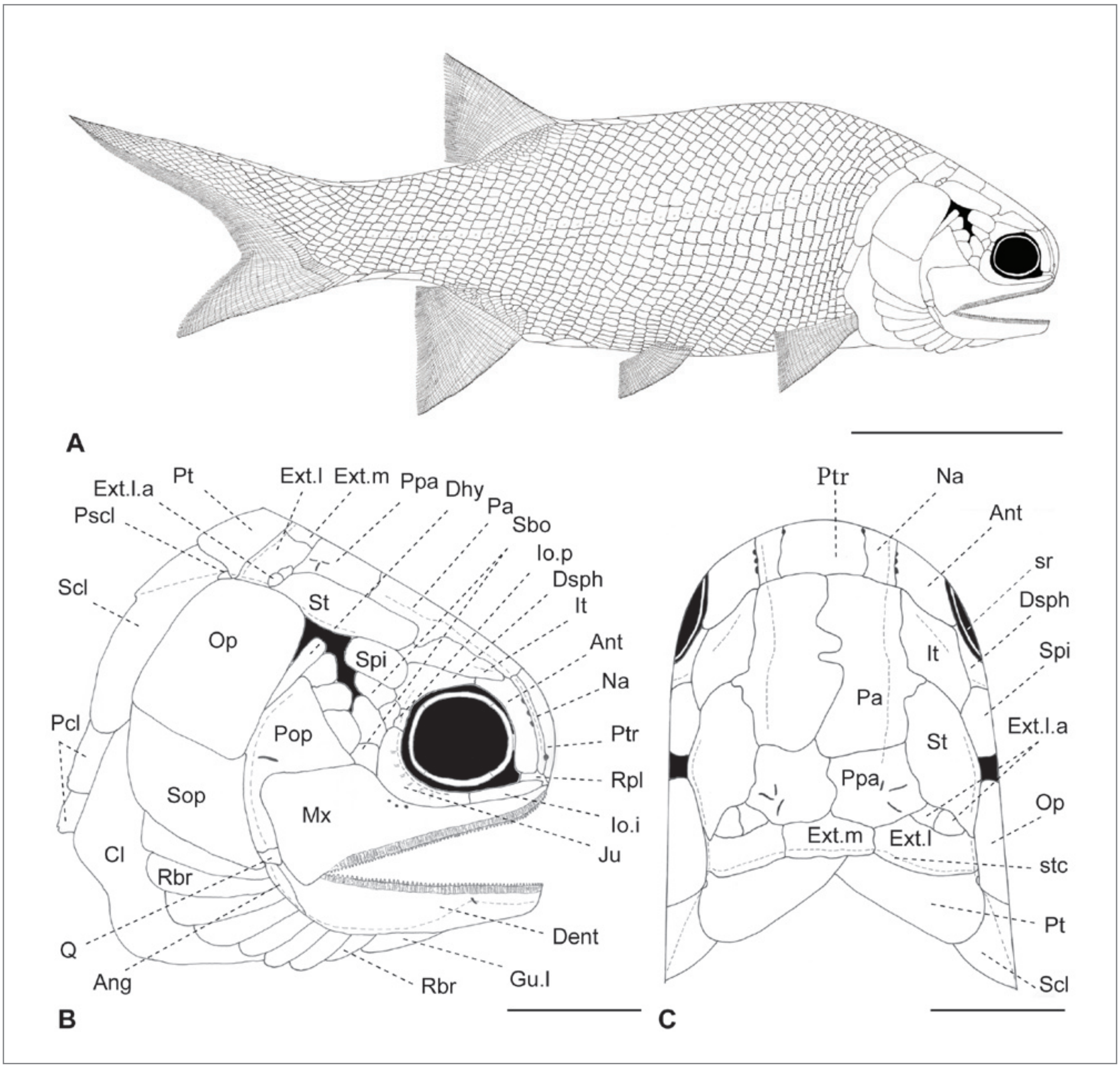


Fig. 17. *Paramblypterus rohani (Heckel & Kner, 1861). A – Restoration of the body in lateral view, scale bar 50 mm; B – Restoration of the skull in lateral view, scale bar 10 mm; C – Restoration of the skull in dorsal view, scale bar 10 mm.*
Obr. 17. *Paramblypterus rohani (Heckel & Kner, 1861. A – Rekonstrukce těla v pohledu laterálním, měřítko 50 mm; B – Rekonstrukce lebky v pohledu laterálním, měřítko 10 mm; C – Rekonstrukce lebky v pohledu dorsálním, měřítko 10 mm.*
Abbreviations: *Ang – angular, Ant – antorbital, Cl – cleithrum, Dent – dentalosplenial, Dhy – dermohyal, Dsph – dermosphenotic, Ext.l – extrascapular lateral, Ext.l.a – accessory extrascapular lateral, Ext.m – extrascapular medial, Gu.l – lateral gular, Io.i – infraorbital inferior, Io.p – infraorbital posterior, It – intertemporal, Ju – jugal, Mx – maxilla, Na – nasal, Op – operculum, Pa – parietal, Pcl – postcleithrum, Pop – preoperculum, Ppa – postparietal,Pt – posttemporal, Ptr – postrostral, Rbr- branchiostegal rays, Rpl – rostro-premaxillo-lacrimal, Sbo – suborbital, Scl – supracleithrum, Sop – suboperculum, Spi – spiracular, sr – sclerotic ring, St – supratemporal, stc – supratemporal commissure.*

connected to the preceding ones in the vertical row by a peg and socket articulation. A large postcleithrum adjacent to the ventral part of the supracleithrum and three further enlarged postcleithral scales are present in *P. decorus* (BLOT 1966, DIETZE 2000). The cleithrum is not preserved in *P. decorus* and thus the relative positions of the supracleithrum, cleithrum and postcleithral scales are not clear. Small presupracleithrum is very rarely observed on material from the Krkonoše Piedmont Basin and the Inner-Sudetic Basin, similar to the *P. duvernoyi* from the Saar-Nahe Basin. I believe that this bone is preserved in adult specimens but is probably covered by surrounding larger bones and thus escapes attention. Also, this situation can be shown in a hitherto undescribed species of the genus *Paramblypterus* from the Boskovice Basin, where presupracleithrum can be observed in many adults.

Paired fins. The small pectoral fin is composed of lepidotrichia articulated from its base. There are more than 15 lepidotrichia but exact number could not be established. Anteriorly the fin is provided with numerous fulcral scales which alternate with the terminal segments of lepidotrichia (MHK-P 82369). The pectoral fin does not possess a scaly lobe as mentioned by ŠTAMBERG (1976) in specimen NM-M 490. The presence of small scales around the base of the pectoral fin was erroneously assessed as a scaly lobe, but these are only small scales of the ventral part of the trunk.

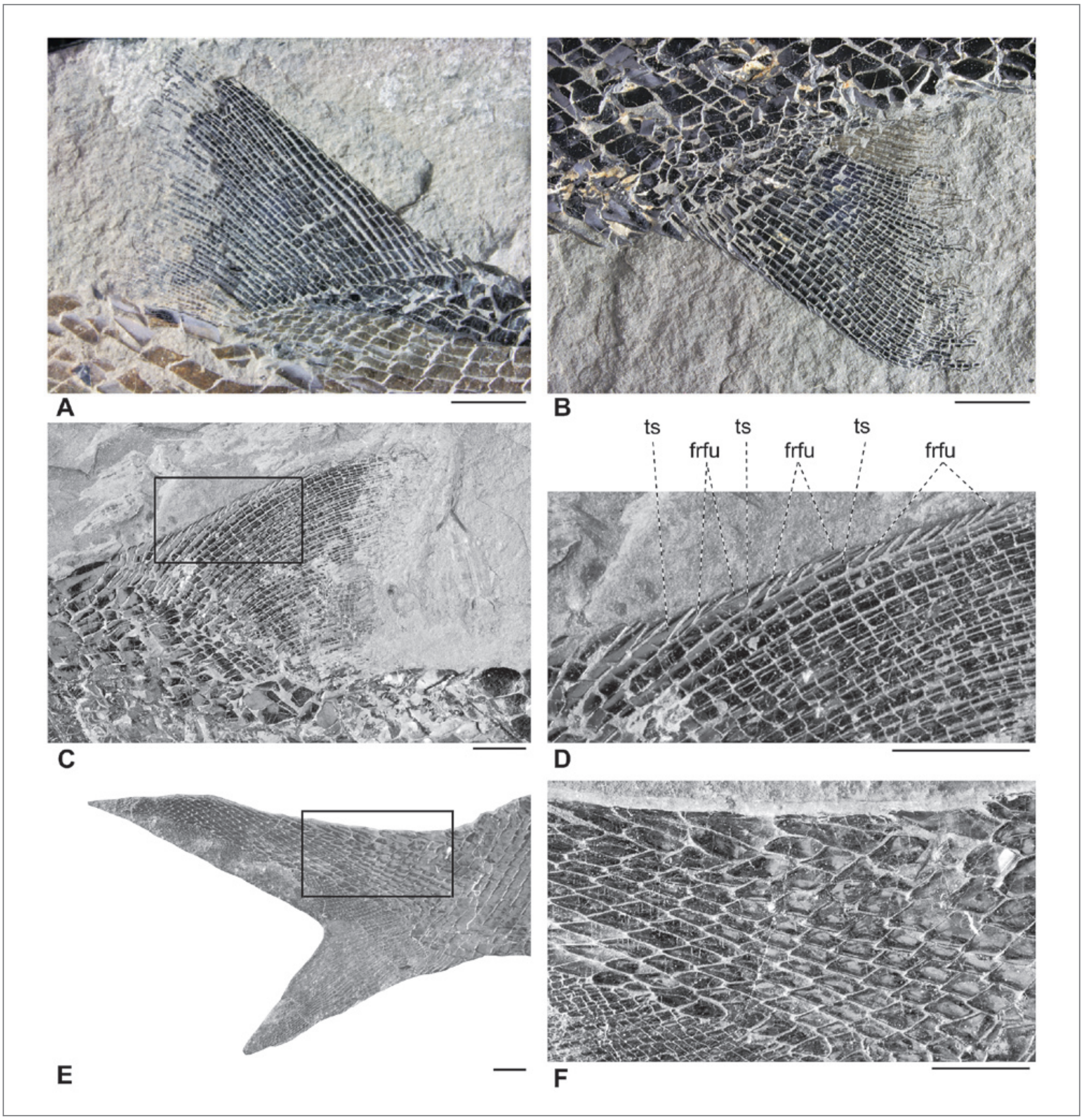


Fig. 18. *Paramblypterus rohani (Heckel & Kner, 1861). Scale bars 5 mm. A – Dorsal fin, NM–M 4916; B – Anal fin, DP 4529; C – Dorsal fin of old animal. The frame marks the view at D of this figure. MHK–P 82356. D – Anterior border of the dorsal fin with numerous fringing fulcra which form together with few terminal segments of the lepidotrichia the anterior border of the fin. MHK–P 82356; E – Caudal fin. The frame marks the view at F of this figure. MHK–P 19837; F – Arrangement of dorsal scutes on the dorsal edge of the caudal peduncle and dorsal lobe of the caudal fin. MHK–P 19837.*
Obr. 18. *Paramblypterus rohani (Heckel & Kner, 1861). Měřítka 5 mm. A – Hřbetní ploutev, NM–M 4916; B – Řitní ploutev, DP 4529; C – Hřbetní ploutev starého zvířete. Obdélník vyznačuje detail D na tomto obrázku. Anteriorní okraj hřbetní ploutve, který je tvořen početnými fulkrami a méně početnými koncovými segmenty lepidotrichií. MHK–P 82356. E – Ocasní ploutev. Rámeček označuje detail F tohoto obrázku. MHK–P 19837.*
Abbreviations: *frfu – fringing fulcra; ts – total segement of the lepidotrichium.*

The scaly lobe of the pectoral fin has not yet been identified on other specimens either.

The pelvic fin consists of about 18 segmented lepidotrichia (MHK-P83130, MHK-P 64687, DP 4529). The pointed terminal segments of first four lepidotrichia forms anterior border of the pelvic fin where they alternate with numerous fulcral scales. Base of the pelvic fin extends over 4 scale row and along the base of the fin are developed two rows of small scales (MHK-P 81463, MHK-P 83130).

Unpaired fins. The dorsal and anal fins are triangular in shape and approximately the same size (Fig. 18). Both are significantly larger than the paired fins. More than half of the base of the dorsal fin is located anterior to the base of the anal fin. The base of the dorsal fin extends along 7–8 scale rows (MHK-P 82356, NM-M 4916, NM-M 4928). A field of minute scales is located along the base of the fin (MHK-P 19837, MHK-P 82384, MHK-P 83125, NM-M 484). The dorsal fin consists of about 32 segmented lepidotrichia dichotomously branched. The terminal segments of the first 7–9 lepidotrichia terminate at the anterior edge of the fin where they alternate with numerous fulcral scales (MHK-P 82356, MHK-P 82354). The longest lepidotrichium of the fin consists of 35 segments. The segments have straigth sutures (Fig. 18D) unlike the sigmoid sutures of the actinopterygians of the family Aeduellidae.

The anal fin of triangular shape is large and its base extends over a length of 8–9 scale rows (MHK-P 83118, DP 4529). A field of minute scales is located along the anal in base. The structure of the anal fin is identical with the dorsal fin and 32 segmented lepidotrichia dichotomically branching are observed. Posterior margin of the fin is similarly as in the dorsal fin straight and vertically oriented.

Deeply cut caudal fin is significantly heterocercal (MHK-P 19837, MHK-P 83118). The dorsal lobe contains more than 50 lepidotrichia in addition to the rhombic scales and is 1.4–1.6 times longer than the ventral lobe. The dorsal margin of the caudal peduncle and the dorsal margin of the dorsal lobe of the caudal fin are covered by 3 ridge scutes which transition into elongate basal fulcra. The large ridge scutes begin just behind the hinge line of the trunc scales. The dorsal lobe forms an angle 23° with the horizontal plane and the ventral lobe forms an angle 25° with the horizontal plane. No flap was noted on the point of the dorsal lobe. The ventral lobe consists of 20 segmented and dichotlomically branching lepidotrichia. The pointed segments of the first nine lepidotrichia of the ventral lobe of the caudal fin terminate at the anterior border of the fin where they alternate with fulcral scales (NM-M484, DP 4529). In general, in old specimens, the lepidotrichia are very numerous, short and wide in all fins and the anterior margin of the fin has numerous fulcral scales. On the other hand, in young specimens the lepidotrichia are few, long, narrow and the anterior edge of the fin contains significantly fewer fulcral scales. The position and structure of the paired and unpaired fins described above are not significantly different from those of *P. duvernoyi*, nor are they significantly different from those of other species of the genus *Paramblypterus*. The position of the dorsal fin appears to be more anterior to the anal fin than in *P. duvernoyi* and no flap were found on the point of the dorsal lobe of the caudal fin which is present in *P. duvernoyi* (DIETZE 1999, 2000). The main defining character for the species *P. reussi* (Fig. 22B) was the relative position of the dorsal and anal fins whose bases are placed perpendicularly above each other. I believe that this is only a partial deformation of the body and a displacement of the dorsal part slightly posteriorly. This displacement is evidenced by the inclination of the scale rows, where in undeformed specimens the inclination of the scale row in front of the anal fin is about 60°, in the type specimen of *P. reussi* this inclination is almost 78°, indicating a posterior displacement of the dorsal fin. A slightly higher number of lepidotrichia of paired and unpaired fins has been recorded (BLOT 1966, DIETZE 2000) in *P. decorus*. *Amblypterus latus* which has larger anal and dorsal fins relative to body size also contains a higher number of lepidotrichia, 40 in the dorsal and anal fins (ŠTAMBERG 2013b).

Squamation

The squamation is formed by thick scales with peg and socket articulation. The scales are arranged in diagonal rows (Figs 16, 17A, 19, 20). The scale row anterior to the anal fin makes an angle 60-65° with the horizontal plane. The scale pattern

$$\frac{28\text{–}31}{9\text{–}11 \quad 23\text{–}26 \quad 38\text{–}40}\ 41\text{–}43$$

has been found on a number of relatively well-preserved specimens MHK-P 82451, MHK-P 81457, MHK-P 83108, MHK-P 64925, MHK-P 82353, NM-M 490, NM-M 484, NM-M 849, NM-M 1252, and others.

The scale row in front of the anal fin contains 13 scales above the lateral sensory line and 14 below the lateral sensory line. The shape of the scales depends on their location on the body. Large rectangular scales, which are taller than their length, cover the trunk in front of the body and especially along the lateral sensory line. Posterior to them on the side of the body, the scales are diamond-shaped while the very narrow long scales cover the ventral region of the body. The scales covering most of the trunk have a smooth surface, but the scales in the anterior part of the body bear relatively pronounced sculpture and serration on their posterior edge (MHK-P 30945, NM-M 4915, NM-M 4924 and others). Specimens MHK-P 64796, MHK-P 81462, MHK-P 82451, NM-M 4915 demonstrate squamation in more detail. The scales of the first five rows below the lateral sensory line have the whole posterior edge serrated and they have up to12 denticles (Fig. 19). The posterior edge of the scales bearing pores of the lateral sensory canal also bears serrations. The scales behind the skull located dorsal to the sensory line usually have only 5 denticles (MHK-P 82451). There are pronounced diagonal ridges on the outer surface of the scale which lead to each denticle. The degree of serration on the posterior edge of the scales decreases in a posterior direction. Denticles are absent on the scale of eighth row of the lateral sensory line. In other scales serration is significantly decreased and the last scale with several denticles occurs in the 15th row (MHK-P 64796). Serration of the posterior edge of the scales is also exhibited in the minute scales occurring along the base of the anal and dorsal fins (DP 4529); on the contrary this serration is missing in other specimens (NM-M 4928). Some specimens have all scales smooth (MHK-P 64910, MHK-P 82353). Sometimes the ridges on the surface of the scales and serration of their posterior edge are observable on only a limited number of scales just behind the skull or only on some scales. I am convinced that these differences are not a sign of species difference, but are variation within species. It can also be observed that serrations and fine sculpturing on the scales are absent especially in old adults. This is probably due to the abrasion of the scales during the animal's lifetime.

Specialised scales lie in front of the dorsal and anal fins and on the caudal fin in addition to the scales arranged in diagonal rows. Four large smooth ridge scutes (Figs 16A, C, 21A), rarely 5 ridge scutes (MHK-P 64910), without serration precede the base of the dorsal fin (NM-M 484, NM-M 4929, P 80178). One median and one pair of large scutes with fine serration and fine concentrically aranged lines (Fig. 21B, C, D) are located around the cloacal aperture in front of the anal fin (MHK-P 64821, MHK-P 64813). The dorsal edge of the caudal peduncle and dorsal lobe of the caudal fin cover three dorsal scutes which begin immediately behind the hind line. A series of basal fulcra cover the dorsal margin of the dorsal lobe (Fig. 16B). Two large ventral scutes cover ventral edge of the caudal peduncle.

Squamation on juveniles develops gradually, beginning on the dorsal lobe of the caudal fin and progressing along

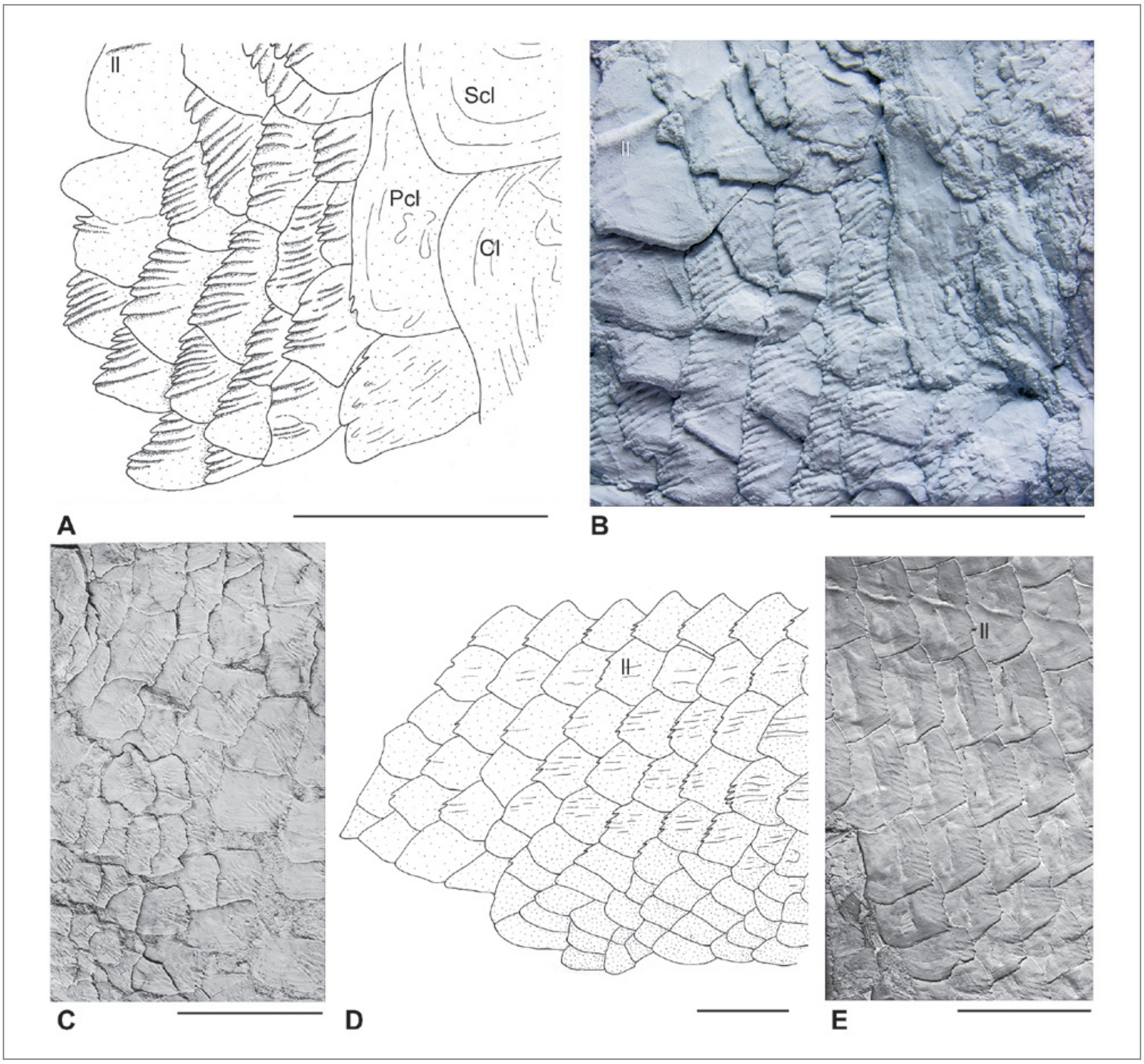


Fig. 19. *Paramblypterus rohani (Heckel& Kner, 1861). Scale bars 5 mm. A, B – Drawing and photograph of the postcleithrum and the scales behind the pectoral girdle. The scales bear ridges on their outer surfaces; well preserved large postcleithrum is without ridges. NM–M 4915; C – Scales behind the pectoral girdle. MHK–P 64796; D – Scale rows from the area between the pectoral and pelvic fins, outer surface bear fine ridges terminating as denticles on the posterior edge of the scales. NM–M 4916; E – Scales of the lateral sensory line and below the line from the area behind the pectoral girdle. MHK–P 81462.*
Obr. 19. *Paramblypterus rohani (Heckel & Kner, 1861). Měřítka 5 mm. Kresba a fotografie poskleithra a šupin za pletencem prsní ploutve. Šupiny nesou valy na svém vnějším povrchu; velmi dobře zachované postkleithrum je bez valů. NM–M 4915; C – Šupiny za pletencem prsní ploutve. MHK–P 64796; D – Šupinové řady z oblasti mezi prsní a břišní ploutví, vnější povrch nese valy končící jako zoubky na zadním okraji šupin. NM–M 4916; E – Šupiny boční smyslové linie a šupiny pod linií z oblasti za pletencem prsní ploutve. MHK–P 81462.*
Abbreviations: *Cl – cleithrum; ll – lateral sensory line; Pcl – postcleithrum; Scl – supracleithrum.*

the lateral sensory line anteriorly. The beginnings of body squamation can already be observed on individuals with a total body length of 27–37 mm (MHK-P 70084, MHK-P30947, MHK-P 80197). In such large juveniles, scales are developed only on the dorsal lobe of the caudal fin and a number of scales bearing the lateral sensory canal. Well-developed are the scales forming the base of the ridge scutes in front of the dorsal and anal fins. The future ridge scutes are composed of individual scales that gradually coalesce (Fig. 21 E, F). Individuals of total body length 37–50 mm have the scales on nearly the entire surface of the body, the scales are missing or very thin, almost indistinct along the dorsal and ventral margins of the body. The specimens over 50 mm of total body size (MHK-P 30885, NM-M2695, MHK-G241) have scale cover on the whole surface of the body.

A ganoine surface of the scales bears microtubercles which has circular base and they are arranged in regular distances (Fig. 20F). The microtubercles of the same shape and arrangement were described by ŠTAMBERG (2018, 2021) in *Paramblypterus vratislaviensis* or *Aeduella blainvillei*. Monitoring of the size and distance microtubercles can be possibility use to identify the species as already MEUNIEUR et al. (1986) demonstrated in recent and fossil genera of Lepisosteiformes and Polypteriformes. Significantly different shaped microtubules with an oval base were described by ŠTAMBERG (2018) on *Progyrolepis heyleri* Poplin, 1999,

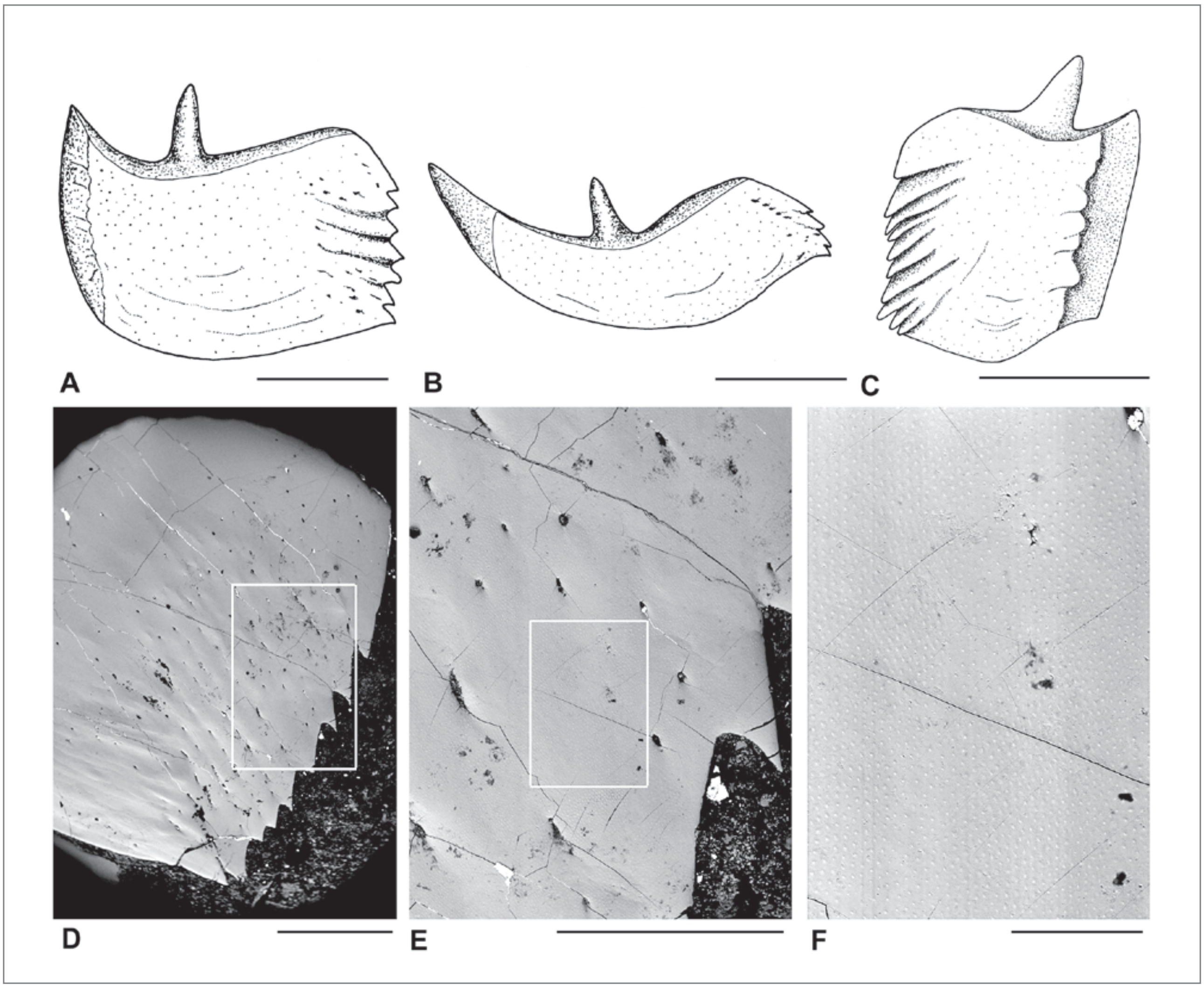


Fig. 20. Paramblypterus rohani (Heckel & Kner, 1861). A – Scale from the 10th row below the lateral sensory line. MHK–P 80193, scale bar 2 mm; B – Scale from the pelvic area. MHK–P 80193, scale bar 2 mm; C – Scale from the row behind the pectoral girdle. MHK–P 30945, scale bar 2 mm; D – Lateral surface of the scale from anterior area of the body. The frame marks the view at E of this figure. MHK–P 80193, scale bar 1 mm; E – Detail of posterior edge of the scale. The frame marks the view at F of this figure. MHK–P 80193, scale bar 0.5 mm; F – Ganoine surface of the scale with microtubercles which have circular base and they are arranged in regular distances. MHK–P 80193, scale bar 0.1 mm.
***Obr. 20.** Paramblypterus rohani (Heckel & Kner, 1861). A – Šupina z desáté řady ventrálně od boční smyslové linie. MHK–P 80193, měřítko 2 mm; B – Šupina z břišní oblasti. MHK–P 80193, měřítko 2 mm; C – Šupina z řady za pletencem prsní ploutve. MHK–P 30945, měřítko 2 mm; D – Vnější povrch šupiny z přední části těla. Obdélník označuje detail E na tomto obrázku. MHK–P 80193, měřítko 1 mm; E – Detail posteriorního okraje šupiny. Obdélník označuje detail F na tomto obrázku. MHK–P 80193, měřítko 0,5 mm; F – Ganoinový povrch šupiny s mikrotuberkuly, které mají kruhovitý základ a jsou rozmístěny v pravidelných vzdálenostech. MHK–P 80193, měřítko 0,1 mm.*

Igornichthys bohemicus Štamberg, 2016 or by RICHTER (1995) on *Palaeoniscum freieslebeni* Blainville, 1818.

The scale pattern of *P. rohani* does not differ from the scale pattern of *P. duvernoyi* reported by DIETZE (2000) and also agrees with the scale pattern found in *P. vratislaviensis* and *P. zeidleri* (ŠTAMBERG 2021). A slightly higher number of scale rows was found in *P. decorus* (BLOT 1966) and, conversely, a lower number of scale rows in front of the anal fin is shown by *Amblypterus latus* (ŠTAMBERG 2013b). The sculpture on the scales, consisting of fine ridges running out on the posterior margin in the denticles, is more pronounced than in *P. duvernoyi* described by DIETZE (2000, Fig. 5A), and in contrast, it is close to the sculpture in *P. gelberti*. The sculpture on the scales in *P. rohani* is more pronounced compared to the scales in *P. vratislaviensis* and *P. zeidleri* (ŠTAMBERG 2021), *P. decorus* (BLOT 1966, DIETZE 2000) and *Amblypterus latus* (DIETZE 2000). Different features of the sculpture on the scales can be observed in specimen NM-M1352 of *Paramblypterus feistmanteli* (Fritsch, 1895). This individual, reaching a total length of about 70 mm, has scales distinctly sculptured with fine lines. In contrast to the scales of *P. rohani*, where fine ridges of antero-posterior direction predominate, in P. *feistmanteli* fine lines parallel to the posterior margin of the scales are running in serration on the posterior margin, and they are combined with lines parallel to the ventral margin of the scales. The fine sculpture of *P. feistmanteli* is developed just posterior to the head on all scales of the total trunk height, and posteriorly the sculpture and serration become progressively restricted to the scales along the lateral sensory line, terminating on the 16-scaled line.

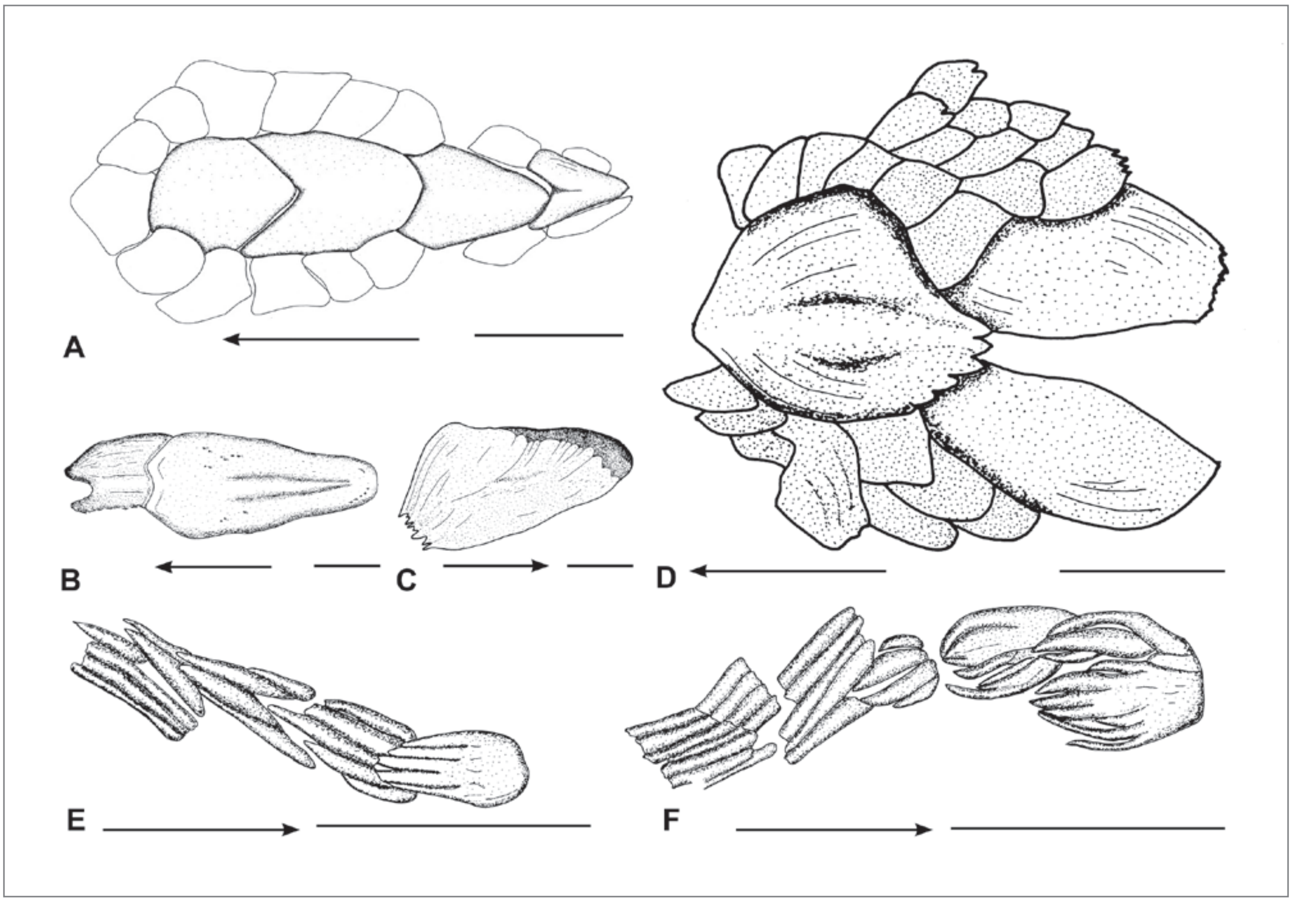


Fig. 21. *Paramblypterus rohani (Heckel & Kner, 1861). Arrows indicate directio cranialis. A – Four ridge scales in front of the dorsal fin base. MHK–P 80178, scale bar 5 mm; B – Dorsal scute from the dorsal lobe of the caudal fin. MHK–P 80193, scale bar 2 mm; C – Right large scale lateral to the cloaca. MHK–P 64821, scale bar 2 mm; D – Large ridge scale anterior to the cloaca and paired large scales lateral to the cloaca. MHK–P 64813, scale bar 2 mm; E, F – Ridge scales of juvenile specimen anteriorly to the dorsal (E) and anal (F) fins are composed of individual scales that gradually coalesce. MHK–P 80197, scale bars 2 mm.*

Obr. 21. *Paramblypterus rohani (Heckel & Kner, 1861). Šipky označují směr kraniální. A – Čtyři kýlové šupiny před bazí hřbetní ploutve. MHK–P 80178, měřítko 5 mm; B – Dorzální kýlová šupina z dorzálního laloku ocasní ploutve. MHK–P 80193, měřítko 2 mm; C – Pravá velká šupina ležící laterálně od kloaky. MHK–P 64821, měřítko 2 mm; D – Velká kýlová šupina ležící anteriorně od kloaky a párové velké šupiny ležící laterálně od kloaky. MHK–P 64813, měřítko 2 mm; E, F – Kýlové šupiny juvenilního jedince ležící anteriorně od hřbetní (E) a řitní (F) ploutve jsou složené z jednotlivých šupin, které postupně srůstají. MHK–P 80197, měřítka 2 mm.*

Conclusions

Several conclusions can be drawn from the study of the *P. rohani* material from the Rudník Horizon and the Kalná Horizon of the Krkonoše Piedmont Basin and the Otovice limestone of the Olivětín Member of the Intra-Sudetic Basin.

1. Synonymy of the species *P. rohani*

Actinopterygii from the Permian sediments of the Krkonoše Piedmont basin originally described under the species names *Palaeoniscus rohani* Heckel & Kner, 1861, *Palaeoniscus luridus* Heckel & Kner, 1861, *Palaeoniscus obliquus* Heckel & Kner, 1861 and *Palaeoniscus caudatus* Heckel & Kner, 1861 were revised by ŠTAMBERG (1977, 2013a) and included in the species *Paramblypterus rohani*. On the basis of the present study, the species originally described as *Palaeoniscus reussi* Heckel & Kner, 1861 is also included in *P. rohani*. This species, known as the only specimen of NM-M 1215, has so far been distinguished from *P. rohani* by the presence of a short maxillary plate, the absence of lateral processes on the parietal and by the position of the dorsal fin base above the base of the anal fin (ŠTAMBERG1976, 2013a). The present study of a large number of specimens has shown considerable deformation of the cadavers during fossilization. The bodies of some specimens are greatly flattened by pressure, and the position of the fins is also deformed. The angle taken by the scale row in front of the anal fin of *Paramblypterus reussi* demonstrates a posterior displacement of the dorsal fin. In addition, a large variability was found especially in the bones of the cranial vault and maxilla. For this reason, not only all the above-mentioned species but also *P. reussi* belong to only one species, namely *Paramblypterus rohani*.

During the study of the species *Paramblypterus rohani*, a group of individuals from the Rudník Horizon characterized by several distinct features on the bones of the cranial vault (Fig. 8B) and the shape of the operculum were isolated. These are mostly smaller individuals than the adults of *Paramblypterus rohani*. I believe that the characters of these individuals cannot be considered as mere bone variability, but probably represent characters of a different species of the genus *Paramblypterus*.

2. Relationships between *P. rohani* and *P. duvernoyi*

The study demonstrates, on the one hand, considerable similarity in a number of anatomical and morphological characters, but also some differences between *P. rohani* and *P. duvernoyi*.

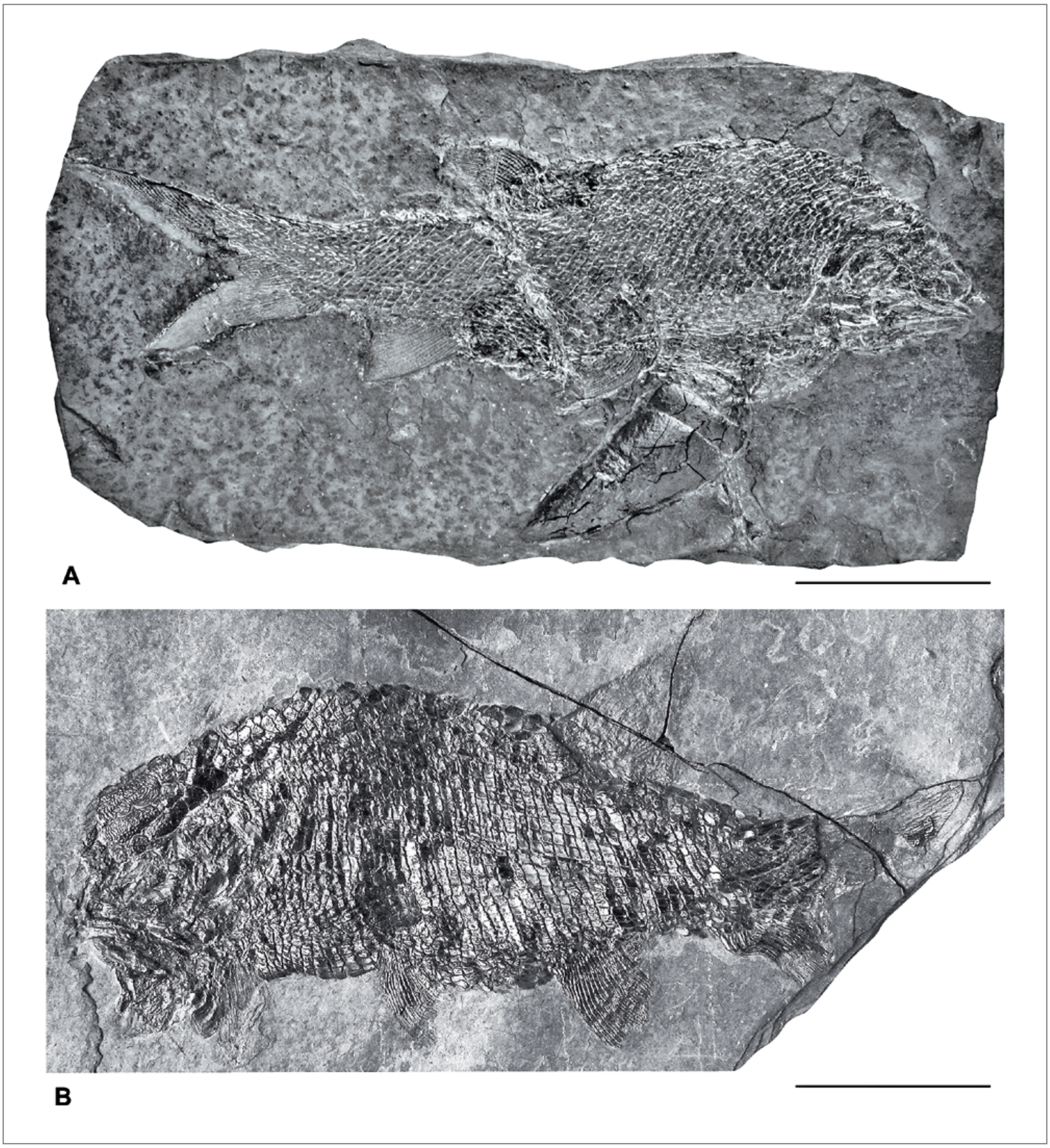


Fig. 22. *Paramblypterus rohani (Heckel & Kner, 1861). Scale bars 50 mm. A – Well preserved whole specimen together with a coprolite of xanacanthid shark. NM–M 1252; B – The holotype of Paramblypterus reussi (Heckel & Kner, 1861) which is ranged to the synonymy of P. rohani. NM–M 1215.*
Obr. 22. *Paramblypterus rohani (Heckel & Kner, 1861). Měřítka 50 mm. A – Celý jedinec spolu s koprolitem xenakanthidního žraloka. NM–M 1252; B – Holotyp Paramblypterus reussi (Heckel & Kner, 1861) který je zahrnut do synonymiky P. rohani. NM–M 1215.*

The structure of the rostral region in both species is identical, and there is also great agreement in the shape, variability and sculpture of the bones of the skull roof. Two median extrascapulars have been described on material from *P. duvernoyi* (DIETZE 1999, fig. 2), in contrast to *P. rohani*, where a single extrascapular median of stable rectangular shape with an anterior process projecting between the right and left postparietals is always present. The present study also confirms the similarity of *P. rohani* and P. duvernoyi in the position of the bones surrounding the orbit. In the circumorbital region, there is a distinct preorbital, which in *P. rohani* is always compact entire with distinct mounds, sometimes coalescing with the nasal. The division of the preorbital into supraorbital and preorbital as documented by DIETZE (1999) in *P. duvernoyi* has not been observed in any specimen. The sclerotic ring in the orbit was confirmed in *P. rohani* whereas it is missing in *P. duvernoi*.

No significant differences were noted in the bones of the cheek, jaws, opercular apparatus and dermal bones of the shoulder girdle except in the postcleithrum position. The postcleithrum is derived from the scale row continuing ventrally from the supracleithrum and is located behind

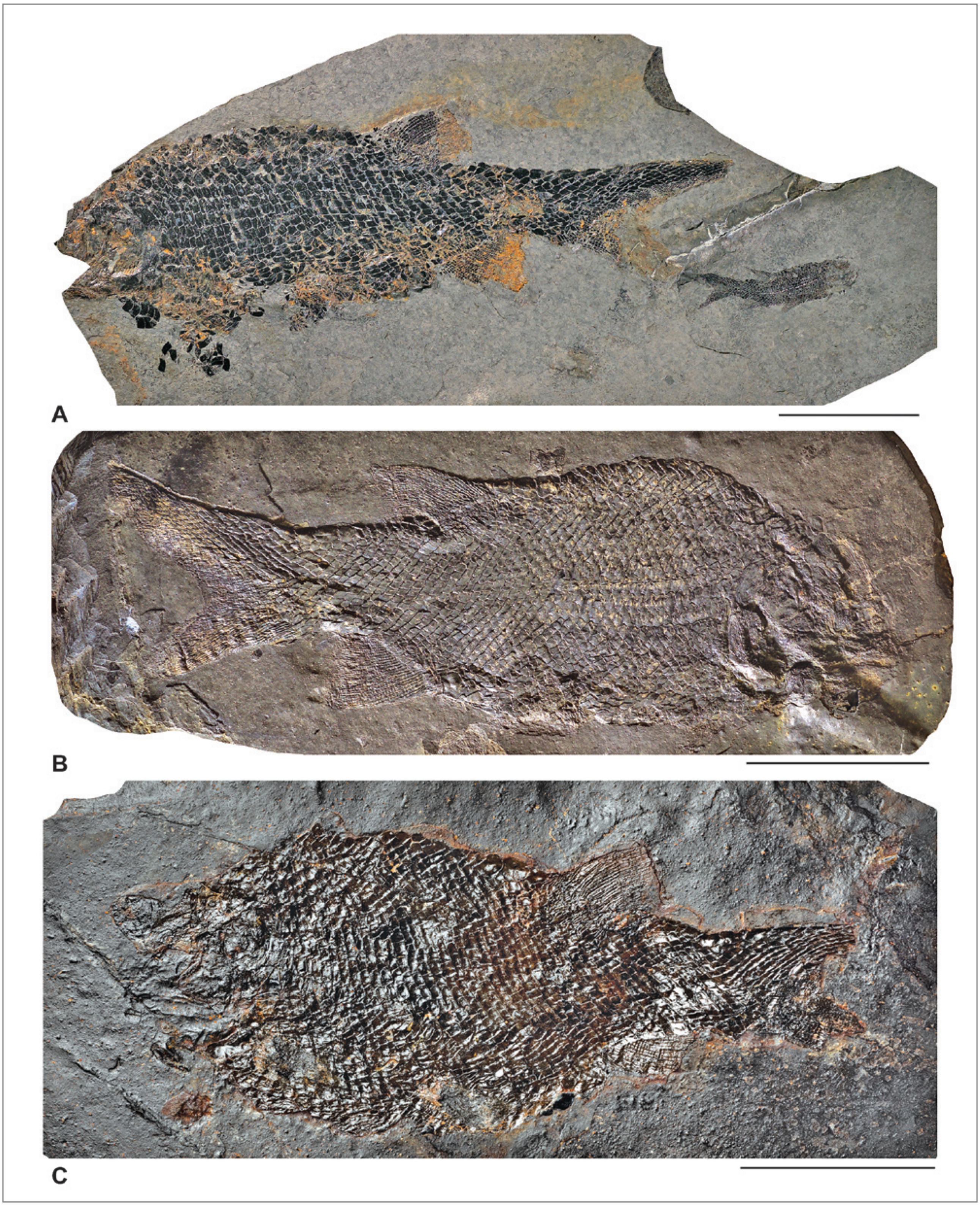


Fig. 23. *Paramblypterus rohani (Heckel & Kner, 1861). Scale bars 50 mm. A – Whole specimen together with a small Neslovicella elongata Štamberg, 2010. MNP 167; B – Whole specimen. Drawing of the specimen is on the Fig. 15. NM–M 484; C – Whole specimen with conspicuously arched trunk due to a deformation during fossilization. MHK–P 81196.*

Obr. 23. *Paramblypterus rohani (Heckel & Kner, 1861). Měřítka 50 mm. A – Celý jedinec spolu s malou rybou Neslovicella elongata Štamberg, 2010. MNP 167; B – Celý jedinec. Kresba tohoto jedince je na obr. 15. NM–M 484; C – Celý jedinec s výrazně vyklenutým tělem zapříčiněným deformací jedince během fosilizace. MHK–P 81196.*

the contact of the supracleithrum and cleithrum in *P. rohani*. The postcleithrum is presented by one or more enlarged scales that have serration on their posterior edge similar as on the following scales. The location of the postcleithrum between the ventral part of the supracleithrum and the dorsal margin of the cleithrum as drawn by DIETZE (1999, 2000) on *P. duvernoyi* was not found on any specimen.

The position and structure of paired and unpaired fins of *P. rohani* and *P. duvernoyi* do not differ significantly. The material of *P. rohani*, although often very deformed,

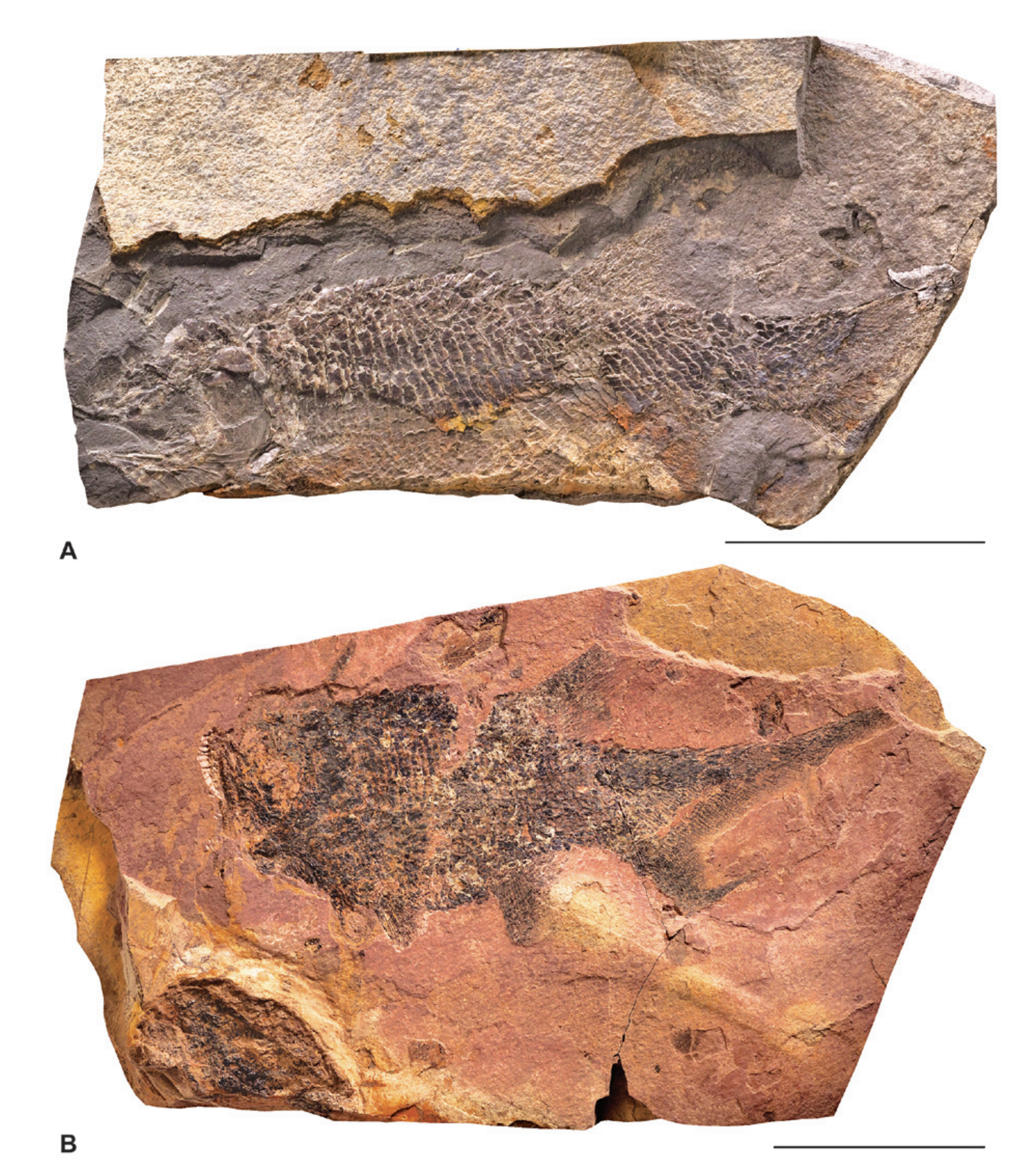


Fig. 24. Paramblypterus rohani (Heckel & Kner, 1861). Scale bars 50 mm. A – Whole specimen MHK–P 10979 with well preserved skull. Initially misinterpreted (ŠTAMBERG 1993) as Paramblypterus gelberti (Goldfuss, 1847). B – Whole specimen with a significantly deformed trunk and caudal fin. MHK–P 64954.
Obr. 24. Paramblypterus rohani (Heckel & Kner, 1861). Měřítka 50 mm. A – Celý jedinec MHK–P 10979 s velmi dobře zachovanou lebkou. Původně byl chybně určen (ŠTAMBERG 1993) jako Paramblypterus gelberti (Goldfuss, 1847). B – Celý jedinec s výrazně deformovaným trupem a ocasní ploutví. MHK–P 64954.

shows the position of the base of the dorsal fin slightly displaced anterior to the base of the anal fin than in *P. duvernoyi*. The posterior tip of the dorsal lobe of the caudal fin of *P. rohani* does not protrude to the flap as in *P. duvernoyi*.

The scale pattern of the two species does not differ significantly. The scale cover of *P. rohani* shows a more pronounced sculpture consisting of fine mounds projecting on the serration in the posterior edge of the scales and the last serrated scales occur just posterior to the pelvic fin. On some specimens, especially old specimens, the scales are thick without any grooves or wrinkles on the outer surface, and the serration on the posterior margin of the scales is also greatly reduced.

The fusiform body of *P. rohani* is slightly arched anteriorly to the dorsal fin at a level perpendicular to the space between the pectoral and pelvic fins.

3. Occurrence of *P. rohani*.

P. rohani occurs in the basins of the Bohemian Massif only in sediments of Permian age. Its most abundant occurrence is associated with the grey-black, organic-rich clays of the Rudník Horizon of the Vrchlabí Formation of the Krkonoše Piedmont Basin. However, isolated occurrences of this species have also been documented in the grey claystones and pinkish limestones of the Kalná Horizon of the Prosečné Formation of the Krkonoše Piedmont Basion. Recent studies (ŠTAMBERG 2021) have also shown the presence of *P. rohani* in the sediments of the Intra-Sudetic Basin, namely in the grey-black organic-rich Otovice Limestone of the Olivětín beds of the Broumov Formation. On the other hand, it is completely absent in the Ruprechtice Horizon of the Olivětín Member of the Broumov Formation, where it is replaced by *Paramblypterus vratislaviensis* and *P. zeidleri*. The age of the Vrchlabí Formation with the Rudník Horizon, Prosečné Formation with the Kalná Horizon of the Krkonoše Piedmont Basin and Olivětín Member with Otovice Limestone of the Intra-Sudetic Basin can be supposed to be Asselian. It can be derived from the radioisotope study of the volcanic rock in both basins (Opluštil et al. 2016).

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Souhrn

Paprskoploutvá ryba *Paramblypterus rohani* (Heckel a Kner, 1861) tvoří velice významnou složku rybí fauny v sedimentech spodního permu podkrkonošské a vnitrosudetské pánve a je rovněž jedním z nejdéle známých druhů obratlovců ze sedimentů mladších prvohor Českého masívu. HECKEL & KNER (1861) popsali *Paramblypterus rohani* původně jako *Palaeoniscus rohani* spolu s dalšími druhy *P. caudatus, P. reussii, P. luridus* a *P. obliquus* ze spodního permu podkrkonošské pánve. FRITSCH (1894, p. 100) rozpoznal blízkou podobnost výše uvedených druhů k *Amblypterus duvernoyi* (Agassiz, 1833). FRITSCH (1894) však považoval dva jedince, které vyobrazil AGASSIZ (1833) za dva různé druhy a zároveň postrádal detailnější popisy kostí hlavy, šupin a ploutví. Z toho důvodu uvedl výše popsané druhy jako určité formy druhu *Amblypterus duvernoyi* pod rodovým jménem *Amblypterus*, a to jako *A. rohani, A. obliquus, A. caudatus*, a *A. luridus*. Pouze *Palaeoniscus reussi* je uveden odděleně jako *Amblypterus reussi*. Podrobně byly studovány druhy popsané původně v práci HECKEL & KNER (1861) autorem této práce (ŠTAMBERG 1976). Byly řazeny do rodu *Paramblypterus*, a to jako *P. rohani, P. caudatus, P. reussi, P. luridus* a *P. obliquus*. Následně řadí ŠTAMBERG (1977) druhy *P. luridus* a *P. obliquus* do synonymiky druhu *P. rohani*. Rozdíly mezi *P. rohani, P. reussi* a *P. caudatus* byly spatřovány (ŠTAMBERG 1977) především v odlišnostech ve tvaru dermálních kostí klenby lebeční (tvar parietálních kostí a jejich laterálních výběžků, průběh interparietálního švu, tvar supratemporale), odlišnosti ve tvaru maxillární desky a ve tvaru těla.

V minulosti byla opakovaně zmiňována velká podobnost *Paramblypterus rohani* z Českého masívu a *Paramblypterus duvernoyi* ze sárské pánve v Německu (FRITCH 1894, WOODWARD 1891, ŠTAMBERG 1976, 2013a, DIETZE 1999, 2000). Nyní předkládaná studie založená na materiálu zahrnující typové jedince, které studovali HECKEL & KNER (1861) a FRITSCH (1894, 1895) a na obsáhlém materiálu získaném v posledních 50 letech, si klade následující základní cíle, a to:

1. Pokud možno co nejkompletnější poznání druhu *P. rohani,* který patří k nejhojnějším v permských sedimentech Českého masívu.
2. Vyhledání shodných nebo rozdílných znaků mezi *P. rohani* a *P. duvernoyi* a vyjasnění, zda *P. rohani* a *P. duvernoyi* jsou dva různé druhy, nebo *P. rohani* patří do synonymiky *P. duvernoyi.*

Ze studia materiálu *P. rohani* z rudnického obzoru a kalenského obzoru podkrkonošské pánve a otovického vápence olivětínských vrstev vnitrosudetské pánve lze vyvodit několik závěrů:

1. Paprskoploutvé ryby z permských sedimentů podkrkonošské pánve popsané původně pod druhovými názvy *Palaeoniscus rohani* Heckel & Kner, 1861, *Palaeoniscus luridus* Heckel& Kner, 1861, *Palaeoniscus obliquus* Heckel & Kner, 1861 and *Palaeoniscus caudatus* Heckel & Kner, 1861 revidoval ŠTAMBERG (1977, 2013a) a zahrnul je do druhu *Paramblypterus rohani*. Na základě současného studia je řazen ke druhu *P. rohani* i druh původně popsaný jako *Palaeoniscus reussi* Heckel & Kner, 1861. Tento druh známý jako jediný kus NM-M 1215 byl dosud odlišován od *P. rohani* krátkou maxilární deskou, nepřítomností laterálního výběžku na parietale a pozicí dorsální ploutve nad ploutví anální (ŠTAMBERG 1976, 2013a). Současné studium velkého množství jedinců prokázalo značné deformace těl uhynulých jedinců během fosilizace. Těla některých jedinců jsou značně tlakem roztažena v anteriorní části do výšky a tím je deformována i pozice ploutví. Úhel, který svírá šupinová řada před anální ploutví *Paramblypterus reussi* dokazuje posunutí dorsální ploutve posteriorním směrem. Navíc byla zjištěna velká variabilita především kostí klenby lebeční a svrchní čelisti. Z tohoto důvodu patří všechny výše jmenované druhy pouze jednomu druhu *Paramblypterus rohani*.

Během studia druhu *Paramblypterus rohani* byla vyčleněna na základě odlišných znaků kostí klenby lebeční (Obr. 8B) a odlišného tvaru operkula skupina jedinců pocházejících z rudnického obzoru. Tato skupina zahrnuje většinou menší jedince, než jsou adultní jedinci druhu *Paramblypterus rohani*. Domnívám se, že znaky na klenbě lebeční a na operkulu nejsou pouhým projevem variability kostí, ale pravděpodobně se jedná o zástupce odlišného druhu rodu *Paramblypterus*.

2. Vztahy mezi *P. rohani* a *P. duvernoyi*. Studie dokládá na jedné straně značnou shodu v řadě anatomických a morfologických znaků, ale rovněž i některé odlišnosti druhu *P. rohani* a *P. duvernoyi*.

Stavba rostrální oblasti u obou druhů je shodná, rovněž tak panuje velká shoda ve tvaru, variabilitě i skulptuře kostí klenby lebeční. Na materiálu *P. duvernoyi* byly popsány dvě kosti extrascapulare mediale (Dietze 1999, fig. 2) na rozdíl od *P. rohani*, kde je vždy přítomno liché extrascapulare mediale stabilního obdélníkovitého tvaru s anteriorním výběžkem vybíhajícím mezi pravé a levé postparietale. Nynější studie potvrzuje též shodu *P. rohani* a *P. duvernoyi* v postavení kostí obklopujících orbitu. V cirkumorbitální oblasti se uplatňuje výrazné preorbitale, které u *P. rohani* je vždy kompaktní celistvé s výraznými valy, někdy srůstající s nasale. Na žádném jedinci nebylo zaznamenáno dělení preorbitale na supraorbitale a preorbitale, jak dokládá DIETZE (1999) u *P. duvernoyi*. U *P. rohani* byla potvrzena přítomnost kůstek sklerotikálního kruhu, zatímco u *P. duvernoyi* sklerotikální kruh chybí. Žádné výrazné rozdíly nebyly zaznamenány v kostech líce, čelistí, operkulárního aparátu nebo dermálních kostí pletence prsní ploutve kromě pozice postcleithrum. Postcleithrum je zvětšená šupina ventrálně od supracleithra. Postcleithrum u *P. rohani* je umístěno posteriorně od kontaktu supracleithra s cleithrem a je prezentováno jednou či více zvětšenými šupinami, které mají skulpturu i zoubkování na svém posteriorním okraji podobné jako na následujících šupinách. Na žádném jedinci nebylo nalezeno umístění postcleithrum mezi ventrální částí supracleithra a dorsálním okrajem cleithra které zakreslila DIETZE (1999, 2000) u *P. duvernoyi*.

Pozice a stavba párových a nepárových ploutví *P. rohani* a *P. duvernoyi* se výrazně neliší. Materiál *P. rohani*, i když je často velice deformovaný, ukazuje postavení základny dorsální ploutve mírně posunuté anteriorně vůči základně anální ploutve než je u *P. duvernoyi*. Posteriorní konec dorsálního laloku ocasní ploutve *P. rohani* nevybíhá v jakýsi prapor jako u *P. duvernoyi*.

Šupinový vzorec obou druhů se výrazně neliší. Šupinový pokryv *P. rohani* ukazuje někdy výraznější, někdy méně výraznou až chybějící skulpturu tvořenou jemnými valy vybíhajícími v zoubkování na posteriorním okraji šupin.

Tělo kapkovitého tvaru *P. rohani* je mírně vyklenuté dorsálně před dorsální ploutví na úrovni začátku břišní ploutve.

3. *Paramblypterus rohani* se vyskytuje v pánvích Českého masívu pouze v sedimentech permského stáří. Jeho nejhojnější výskyt je vázán na šedočerné na organiku bohaté jílovce rudnického obzoru vrchlabského souvrství podkrkonošské pánve. Ojedinělé výskyty tohoto druhu byly však dokázány i v šedých jílovcích a narůžovělých vápencích kalenského obzoru prosečenského souvrství podkrkonošské pánve. Nedávné výzkumy (ŠTAMBERG 2021) prokázaly přítomnost *P. rohani* i v sedimentech vnitrosudetské pánve, a to v otovickém vápenci olivětínských vrstev broumovského souvrství. Tento druh naopak zcela chybí v ruprechtickém obzoru olivětínských vrstev broumovského souvrství, kde jej nahrazuje především druh *Paramblypterus vratislaviensis* a *P. zeidleri*. Stáří vrchlabského souvrství s rudnickým obzorem, prosečenského souvrství s kalenským obzorem podkrkonošské pánve a olivětínských vrstev s otovickým vápencovým obzorem vnitrosudetské pánve lze odvodit ze studie radioisotopů vulkanických hornin v obou pánvích jako assel (OPLUŠTIL et al. 2016).

Lokality, na kterých je doložena přítomnost druhu *Paramblypterus rohani*:

Podkrkonošská pánev, vrchlabské souvrství, rudnický obzor: Čistá; Košťálov; Košťálov „Kovářův mlýn“; Košťálov „Za hospodou“; Kovářsko; Kundratice „Doly“; Kundratice „Rokle v lese“; Dolní Lánov „Kovářsko“; Prostřední Lánov „Za továrnou“; Příkrý „Honkův potok“; Semily „Levý břeh Jizery“; Rybnice „Hrádecký potok“; Vrchlabí „Zářez silnice“.

Podkrkonošská pánev, prosečenské souvrství, kalenský obzor: Arnultovice; Veselá „Veselský potok“; Horní Kalná „Odvaly dolu Adam“.

Vnitrosudetská pánev, broumovské souvrství, olivětínské vrstvy, otovický vápenec: Otovice „Černý potok“; Otovice „Stěnava“; Otovice „Chmelnice“; Otovice „Vápenka“.

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