**Charles University**

**Faculty of Science**

Ph.D. study program: Geology

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# Vertebrates of the Lower Palaeozoic from the Barrandian area (Bohemian Massif) and their comparison with faunas of adjacent areas

# Vertebrata spodného paleozoika barrandienskej oblasti (Český masív) a ich porovnanie s faunami priľahlých oblastí

Doctoral thesis

Supervisor: doc. RNDr. Petr Kraft, CSc.

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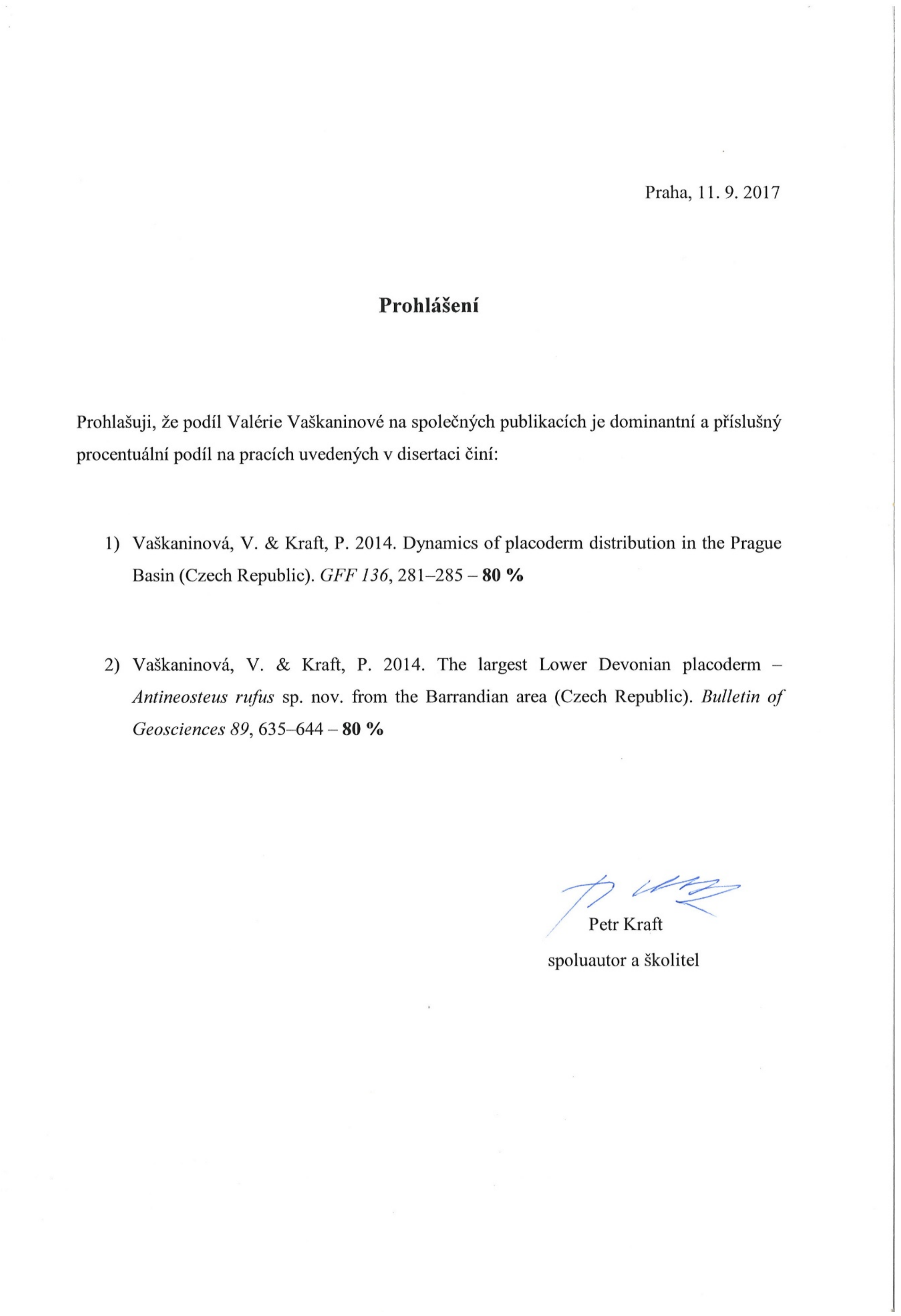

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1) Vaškaninová, V. & Kraft, P. 2014. Dynamics of placoderm distribution in the Prague Basin (Czech Republic). *GFF 136*, 281–285 – **80 %**

2) Vaškaninová, V. & Kraft, P. 2014. The largest Lower Devonian placoderm – *Antineosteus rufus* sp. nov. from the Barrandian area (Czech Republic). *Bulletin of Geosciences 89*, 635–644 – **80 %**

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I declare that the share of Valéria Vaškaninová in our joint paper is dominant and the percentage of the work on the paper mentioned in the dissertation is the following:

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Vaškaninová, V. & Ahlberg, P.E. 2017. Unique diversity of acanthothoracid placoderms (basal jawed vertebrates) in the Early Devonian of the Prague Basin, Czech Republic: A New Look at *Radotina* and *Holopetalichthys*. *PLoS ONE 12(4)*, e0174794 – **80 %**

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# Abstract

This thesis deals with early vertebrate fossil remains from the Lower Palaeozoic strata of the Barrandian area (Bohemian Massif). It is presented as a compilation of four papers that were published or submitted in scientific peer-reviewed journals with impact factor. All included papers are focused on the most abundant and diverse vertebrate fauna from the Barrandian area – the placoderms. Placodermi are early vertebrates characterized by articulated head and trunk shields composed of dermal bony plates. In the Barrandian area, they occur exclusively in the Devonian of the Prague Basin. The main objectives of the thesis are modern taxonomic revisions of the placoderm taxa from the Prague Basin as well as discussions about trends in their abundance, diversity, and distribution in space and time, taphonomy, and the evolutionary and phylogenetic implications of their morphology.

Two characteristic placoderm associations were distinguished. In the Lochkovian and Pragian, members of the group Acanthothoraci dominate the placoderm record. Acanthothoracid placoderms are among the most basal jawed vertebrates and thus a detailed study of their morphology has a great potential to illuminate the relationships and evolutionary patterns among the stem jawed vertebrates. They are most abundant in the Lochkovian, where they constitute an unusually diversified association of four genera – *Radotina*, *Tlamaspis*, *Sudaspis*, and *Kosoraspis*. Two genera (*Radotina* and *Holopetalichthys*) occur in the Pragian. Placoderms are less abundant in the Pragian than in the Lochkovian.

All the determinable specimens from the Emsian belong among the homostiid arthrodire placoderms – large filter feeders. Two species of two genera (*Antineosteus* and *Johannaspis*) could be distinguished. *Antineosteus rufus* is the largest known Early Devonian placoderm. The placoderm record in the Emsian is scarce. The significant decrease in diversity and abundance of placoderms in the Prague Basin throughout the Early Devonian is in contradiction to the general trend in placoderm faunas worldwide. It is interpreted as a factor of specific local paleogeography. The revisions significantly changed the previous view of the taxonomic composition and diversity of placoderms in the Lower Devonian of the Prague Basin.

# Abstrakt

Predkladaná dizertácia sa zameriava na fosílne zvyšky raných stavovcov pochádzajúce zo spodnopaleozoických vrstiev barrandienskej oblasti (Český masív). Dizertácia je kompiláciou štyroch vedeckých článkov publikovaných alebo odoslaných k publikácii v recenzovaných časopisoch s impakt faktorom. Všetky publikácie, ktoré tvoria jadro dizertačnej práce, sa zameriavajú na najhojnejšiu a najdiverzifikovanejšiu skupinu stavovcov z barrandienskej oblasti – plakodermy (panciernaté ryby). Plakodermy sú rané rybovité stavovce charakteristické prítomnosťou artikulovaného hlavového a hrudného panciera zloženého z dermálnych kostných dosiek. V barrandienskej oblasti sa vyskytujú výhradne v devóne pražskej panvy. Hlavnými cieľmi dizertácie sú moderné taxonomické revízie taxónov plakoderm z pražskej panvy ako aj diskusie o trendoch v početnosti, diverzite a distribúcii fosílií v čase a priestore, ich tafonómii a evolučných a fylogenetických aspektov ich morfológie.

Rozlišujeme dve typické asociácie plakoderm. V lochkove a pragu prevládajú zástupcovia bazálnej skupiny plakoderm Acanthothoraci. Acanthothoraci patria medzi najbazálnejšie čeľustnaté stavovce, a preto má detailné štúdium ich morfológie veľký potenciál osvetliť vzťahy a evolučné vzorce v stem group čeľustnatých stavovcov. Najhojnejšie sú zastúpené v lochkove, kde tvorili nezvykle diverzifikovanú asociáciu štyroch rodov – *Radotina*, *Tlamaspis*, *Sudaspis* a *Kosoraspis*. Dva rody (*Radotina* a *Holopetalichthys*) sa vyskytujú v pragu. Plakodermy sú v pragu menej početné ako v lochkove.

Všetky určiteľné fosílie plakoderm z emsu patria medzi homostiidné arthrodiry – veľké planktonofágne formy. Boli určené dva druhy dvoch rodov (*Antineosteus* a *Johannaspis*). *Antineosteus rufus* je najväčším spodnodevonským plakodermom vôbec. Plakodermy sú v emse veľmi vzácne. Výrazný pokles početnosti a diverzity plakoderm v pražskej panve v priebehu spodného devónu je v rozpore s celosvetovým trendom fáun plakodermov. Vysvetľujeme to ako faktor špecifickej miestnej paleogeografie. Predkladané revízie výrazne zmenili tradičný pohľad na druhové zloženie a diverzitu plakoderm v spodnom devóne pražskej panvy.

# Contents

# List of papers

This thesis is based on the following papers, referred to in the text by Roman numerals:

I. **Vaškaninová, V.** & Kraft, P. 2014. Dynamics of placoderm distribution in the Prague Basin (Czech Republic). *GFF 136*, 281–285.

II. **Vaškaninová, V.** & Kraft, P. 2014. The largest Lower Devonian placoderm – *Antineosteus rufus* sp. nov. from the Barrandian area (Czech Republic). *Bulletin of Geosciences 89*, 635–644.

III. **Vaškaninová, V.** & Ahlberg, P.E. 2017. Unique diversity of acanthothoracid placoderms (basal jawed vertebrates) in the Early Devonian of the Prague Basin, Czech Republic: A New Look at *Radotina* and *Holopetalichthys*. *PLoS ONE 12(4)*, e0174794.

IV. **Vaškaninová, V.** 2017. New genus of homostiid arthrodire contributes to the revision of placoderm diversity and faunal interchange in the Early Devonian of Prague Basin (Czech Republic) – Under review in *Alcheringa*.

The following peer-reviewed papers were published during the Ph.D. study and are also discussed in the thesis:

V. **Vaškaninová, V.** & Kraft, P. 2016. A unique occurrence of a psammosteid heterostracan on the peri-Gondwanan shelf in the Lower/Middle Devonian boundary marine deposits. *Fossil Imprint 72*, 155-160.

VI. Mergl, M., **Vaškaninová, V.** & Žigaite, Ž. 2017. Vertebrate microremains from the Pragian, Emsian and Eifelian of the Prague Basin (Czech Republic). *Folia Musei Rerum Naturalium Bohemiae Occidentalis, Geologica et Paleobiologica, 51(1-2)*. DOI: 10.1515/fbgp-2017-0001.

# Introduction

Vertebrate fossil collecting has had a long tradition in Bohemia (part of the present day Czech Republic). Particularly in the Prague Basin, a part of the Barrandian area (Teplá-Barrandian Unit, Bohemian Massif) rich and renown for Lower Palaeozoic fossil invertebrates, early vertebrate fossils were reported already in the 19th century. At that time, many quarries were operating in that area and the stone blocks were processed by hand. The quarry workers had close contacts with the local fossil collectors and were well instructed and skilled in detecting precious finds, such as early vertebrates. Tracing their history, the majority of the specimens have become parts of private and subsequently (as donations or inheritances) public collections.

Lower Palaeozoic macroscopic vertebrate fossils are known exclusively from the Devonian of the Prague Basin. The first one to figure and describe placoderm, acanthodian, and indeterminate vertebrate fossils from the Devonian was Barrande (1872). His determinations were revised by Eastman (1897) who described the Prague Basin placoderm material housed in the Museum of Comparative Zoology (Harvard University). The revised taxonomy was published in Czech by Bayer (1905). Perner (1918) presented a list of supposed vertebrate genera from the Lochkovian without descriptions or illustrations. Individual specimens of placoderms and heterostracans were described by von Koenen (1895) and Růžička (1929; revised by Tarlo 1965). The most extensive descriptive work was done by Gross (1950, 1958, 1959) who described all the placoderm specimens from the Lochkovian and Pragian of the Prague Basin known and accessible at that time. His determinations were slightly revised by Westoll (1967).

Since then no taxonomic study was made on the Lower Palaeozoic early vertebrates from the Barrandian area except for a revision of the acanthodian genus *Machaeracanthus* by Burrow et al. (2010) including material from the Prague Basin, and **papers II–IV**. The Early Devonian placoderm material was especially in need of a throughout taxonomic revision because of the confusions the past descriptions had caused (Moy Thomas & Miles 1971, Stensiö 1969; see discussion in **paper III**).

Apart from numerous placoderm specimens and a single appearance of a psammosteid heterostracan (**paper V**); only members of the vertebrate group Acanthodii (sensu Janvier 1996) are present in the Lower Palaeozoic of the Barrandian area (specifically the Devonian of the Prague Basin) as macroscopic fossils. The fin spines and scapulocoracoids of *Machaeracanthus bohemicus* (Barrande, 1872) from the collections of the Národní Muzeum, Prague (Czech Republic) were partly revised by Burrow et al. (2010). Along with the problematic and scarce fin spines attributed to the genus *Onchus* they are currently being studied by my consultant Dr. Jaroslav Zajíc (for a revision of stratigraphic occurrences of acanthodians see Zajíc 1988). The occurrence of microscopic vertebrate elements in the Silurian and Devonian of the Prague Basin is discussed below. No other vertebrate remains are known from the Lower Palaeozoic of the Barrandian area.

## Aim of the thesis

The thesis is mostly focused on the richest and most diverse vertebrate fauna from the Lower Palaeozoic of the Barrandian area – the placoderms. Their occurrence is restricted to the Devonian of the Prague Basin. All the determinable specimens originate from the Lower Devonian strata (Lochkovian – Emsian). The main objectives of the thesis are the following:

a) A modern taxonomic revision of the Early Devonian placoderm faunas. **Paper III** focuses on the Lochkovian and Pragian mainly acanthothoracid placoderms, **paper II** and **IV** focus on homostiid arthrodire placoderms from the Emsian.
b) Evolutionary and phylogenetic implications of the new morphological observations of the Prague Basin acanthothoracid placoderms (**paper III**) and their potential to illuminate the origin of jaws and dermal macromery within the stem gnathostomes.
c) Tracing the trends in abundance and diversity of placoderm faunas from the Prague Basin throughout the Early Devonian (**papers I** and **IV**) with a discussion about taphonomy and its potential to influence the observed data (**papers I, III** and **IV**).
d) Biogeographical distribution of selected vertebrate groups (**paper III–V**) with respect to the specific local palaeographical development of the Prague Basin area in the Early

Devonian (**paper IV**) and employment of vertebrate distribution data for specifying local environmental conditions (**paper V**).

## Material and methods

The material studied in this thesis originates from the Devonian strata of the Prague Basin. One additional specimen discussed in **paper III** comes from the Lower Devonian Taunus Quartzite near Rüdesheim (Rheinish Slate Massif, Germany).

All the published material is deposited in public collections, the majority as a part of the vertebrate collection in the Národní Muzeum, Prague (abbrev. NM). Additional material described in **paper III** is housed in the Natural History Museum, London (NHM) and Humboldt Museum für Naturkunde, Berlin (HMN). Part of the material described in **paper IV** is housed in the Museum of Comparative Zoology, Harvard University, Cambridge, MA (MCZ), the Naturhistorische Museum Wien (NHMW) and Chlupáčovo Muzeum Historie Země of the Charles University, Prague (ChMHZ). The material described and figured in **paper VI** is housed in the palaeontological collections of the Centre of Biology, Earth and Environmental Sciences at the Faculty of Education of the University of West Bohemia, Plzeň (PCZCU).

Most of the described material has not been prepared during the course of this study, with the exception of ChMHZ-VV-001, which was dissolved in 8 % formic acid, but the bone was too fragile to complete the preparation (**paper IV**). Fragments of rock cut off from selected specimens were dissolved in acetic acid to provide index microfossil samples (**paper II** and **V**). The specimens were studied using standard palaeontological methods, observed under the optic microscope Olympus SZX9, photographed with the digital camera Canon EOS 6D, and figured using the drawing attachment Olympus SZH-DA (**paper II** and **III**). Some specimens were photographed after being coated with ammonium chloride (**paper III** and **IV**). Line drawings were produced from hand drawings and photographs in Adobe Photoshop CS6 (**paper III–V**). The surface sculpture and fine details of selected specimens from the NM collection were observed and photographed with the scanning electron microscope Hitachi S-3700N (**paper II–V**) and the digital microscope Keyence VHX-2000 (**paper III** and **V**).

# Evolutionary and phylogenetic implications: Acanthothoraci as stem gnathostomes and model jawed vertebrate ancestors

The early evolution of vertebrates has currently become a major research topic in vertebrate biology (Brazeau 2009, Davis *et al.* 2012, Gai *et al.* 2011, Giles *et al.* 2015, Oisi *et al.* 2013, Zhu *et al.* 2013). Crucial to the debate is the origin of jawed vertebrates (gnathostomes), one of the most important events in vertebrate evolution and a key to our own ancestry. The gnathostome stem group (Figure 1) has long been a subject of debate. In the last decades, several early vertebrates were being considered as possible candidates for the common ancestor of jawed vertebrates.

The group Acanthodii in a traditional sense (sensu Janvier 1996) comprises jawed vertebrates known from the Silurian to the end of the Palaeozoic. They are characterized by spines in front of every fin but the caudal, and a micromeric dermal cover (composed of small scales or platelets). The group was previously regarded as a paraphyletic array of stem gnathostomes, stem osteichthyans, and stem chondrichthyans (Brazeau 2009, Davis *et al.* 2012) but more recent phylogenetic analyses resolve them entirely as stem chondrichthyans (Brazeau & de Winter 2015, Dupret *et al.* 2014, Giles *et al.* 2015, Zhu *et al.* 2013).

As an effect of this assumption, the upper part of the gnathostome stem group is now occupied exclusively by the placoderms (Figure 1). The traditional group ´Placodermi´ (sensu Janvier 1996) is known from the Silurian and Devonian. The most characteristic feature of its members is a head and thoracic shield of thick macromeric dermal plates (larger plates composed of numerous dermal layers) usually covered by tubercles or ridges composed of semidentine (Denison 1978). Recently the group is being regarded as a paraphyletic segment of stem gnathostomes rather than a clade branching off the stem gnathostome group (Qiao *et al.* 2016). Some ´placoderms´, the so-called ´maxillate placoderms´ (Figure 1, *Qilinyu* and *Entelognathus*) from the Silurian of Yunnan (China), display a combination of placoderm anatomy with osteichthyan features such as marginal jawbones (maxilla, premaxilla, and dentary; Zhu *et al.* 2013, 2016). In phylogenetic analyses, they are resolved close to the last common ancestor of osteichthyans (bony fishes and tetrapods; Figure 1).

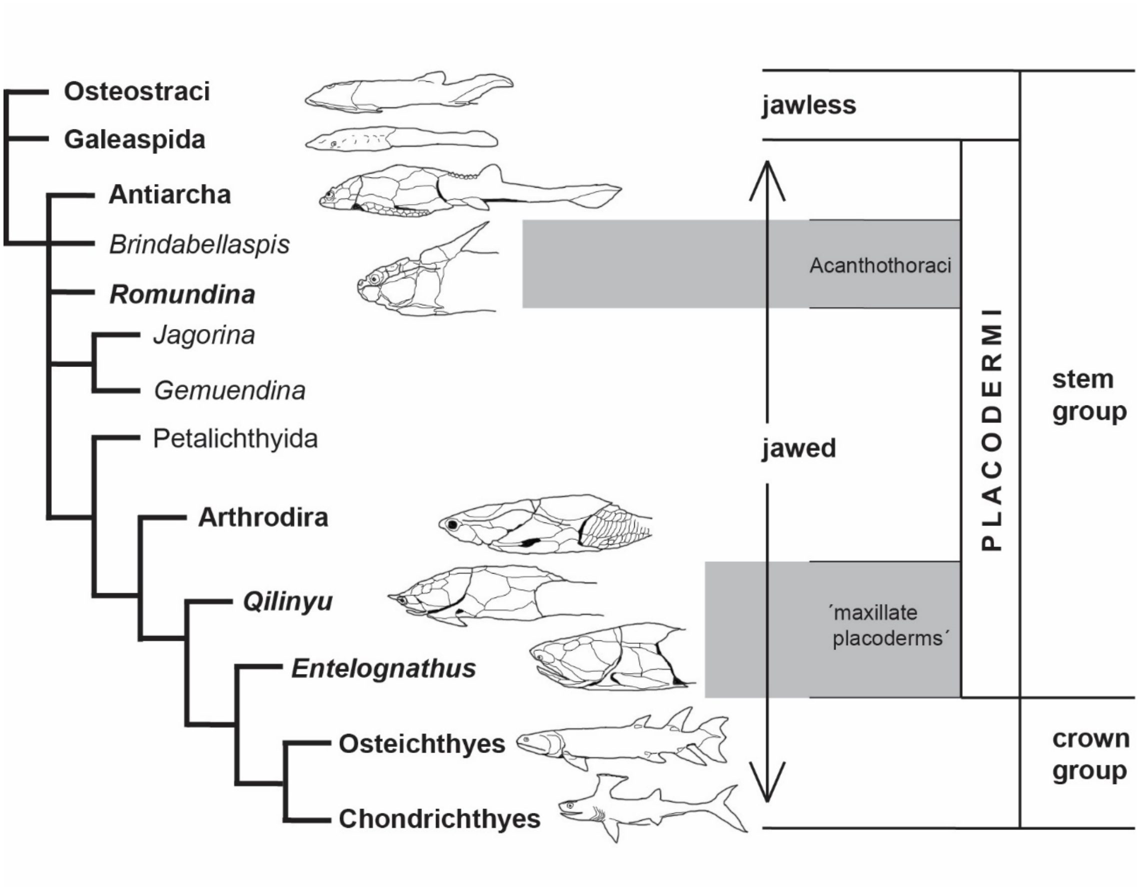

**Figure 1.** Summary vertebrate phylogeny, figured groups/genera in bold (modified from Zhu *et al.* 2016).

The placoderm group Acanthothoraci is resolved (along with the group Antiarcha) among the most primitive jawed vertebrates (Figure 1; Qiao *et al.* 2016, Zhu *et al.* 2016). Although the phylogenetic relationships within the group are still problematic, they can be characterized by a distinctive cranial anatomy. All of them possess a so-called ´upper lip´ - a prolonged trabecular region of the braincase protruding anteriorly to the nasal capsules, with a corresponding dermal cover of a premedian dermal plate or fields of tesserae (Dupret *et al.* 2010, 2014). The ´upper lip´ is absent in any other gnathostome group (or non-ossified and therefore poorly known in antiarchs; comp. Zhu & Janvier 1996) but it resembles the condition in jawless vertebrates (Figure 1; Oisi *et al.* 2013). Although previously regarded as a derived character (Denison 1978) the presence of the ´upper lip´ suggests that acanthothoracids are close to jawless vertebrates, which display similar cranial features (Dupret *et al.* 2014).

However, acanthothoracids continue to be poorly understood anatomically except for the genus *Romundina* (Dupret *et al.* 2017). A more detailed knowledge of their anatomy could thus provide crucial information for unravelling the chain of evolutionary events that constitutes the origin of jawed vertebrates. **Paper III** is an important first step of an extensive morphological description of the Prague Basin acanthothoracid fauna.

The reinterpretation of placoderms resurrected the debate about the homology between the macromeric dermal skeleton (composed of larger dermal plates containing numerous bony layers) of placoderms and osteichthyans with an idea of a ′placoderm-osteichthyan continuum′ (Zhu *et al.* 2013, 2016; comp. Janvier 1996). It suggests that osteichthyans continued the development of the placoderm body plan whereas chondrichthyans secondarily lost their macromeric dermal bones (Ryll *et al.* 2014, Zhu *et al.* 2016). This extends the origin of our own set of macromeric dermal bones down to the upper part of the gnathostome stem group (Figure 1: jawed stem group). The lower part of the gnathostome stem group is occupied by the jawless vertebrates known as ostracoderms (Figure 1: Osteostraci, Galeaspida). Among them distinctive dermal bones with individual identities and pattern (e.g. in relation to the sensory line canal system) are absent, except in heterostracans (see discussion in **paper III**). Heterostracans have macromeric shields (**paper V**) but their dermal bones show no homology with either placoderms or osteichthyans (Janvier 1996).

Acanthothoracid placoderms, especially the Prague Basin genera (*Radotina, Tlamaspis,* and *Kosoraspis*; **paper III**), display another important feature of the dermal skeleton – the tesserae (also present in placoderm groups Rhenanida and Stensioellida, sensu Denison 1978). Tesserae are small platelets resembling the body scales but situated on the head where they separate the larger dermal bones. Their microanatomy and relations with the macromeric bones are still poorly known, but they are generally considered to be built of only one superficial layer of bone (Gross 1959). Tesserae were previously regarded as a derived character acquired through fragmentation of the macromeric dermal bones (Gardiner 1984, Stensiö 1969, Westoll 1967) although sometimes as a primitive character that might have given rise to the macromeric dermal skeleton (Denison 1978, Gross 1959).

In **paper III** we demonstrate the possible relationship of the macromeric dermal and the tesserate domains by comparing the prenasal areas of the acanthothoracid genera *Romundina* and *Radotina*. In *Romundina* the prenasal area is fused and appearing as a single bone. However, its internal vasculature is divided into two discrete domains: an anterior thick area with a more elaborate radial vasculature in several superimposed layers with an anterior medial radiation centre and a posterior one with more linear canals in one layer only (Dupret *et al.* 2010, Fig. 2B). This pattern corresponds well to the one observed in *Radotina*, with a premedian anterior dermal bone followed posteriorly by a band of tesserae. The premedian plate has its ossification centre at the anterior midline (**paper III**, Fig. 2) at the same spot as the radiation centre of vascular canals in *Romundina*. This observation can guide our further research on the evolution and development of the dermal domain.

The presence of tesserae is clearly a character that associates the acanthothoracids with jawless stem gnathostomes. The lack of obvious homologies in the macromeric dermal bones of placoderms and heterostracans suggests the origin of macromeric bones typical for placoderms and osteichthyans within the gnathostome stem group contemporary with the origin of jaws. However, in psammosteid heterostracans (such as *Schizosteus*, **paper V**) bands of tesserae are present between the macromeric bones in a manner very similar to the condition in *Radotina* (**paper III**, Fig. 2). Given their position among the most basal jawed vertebrates in the recent phylogenetic analyses (Figure 1; Dupret *et al.* 2014, Giles *et al.* 2015, Qiao *et al.* 2016, Zhu *et al.* 2016) the skull roof pattern of acanthothoracids is most likely to be the plesiomorphic feature for all jawed vertebrates.

Acanthothoracids have the potential to directly illuminate a key evolutionary novelty of gnathostomes – the origin of jaws and teeth. Although the dermal cheek plates were known in *Romundina* (Ørvig 1975) only two supposed acanthothoracid dental elements have been described. One of them (Rücklin & Donoghue 2015) has been shown to be a dermal tessera (Burrow *et al.* 2016); the other one (Goujet & Young 2004, Fig. 3A) comprises a pair of anterior supragnathal plates preserved in articulation on a placoderm neurocranium, but it is not clear that this belongs to an acanthothoracid. Our preliminary study (Vaškaninová & Ahlberg 2017) has revealed the presence of dental elements in three genera of acanthothoracid placoderms (*Radotina, Tlamaspis*, and *Kosoraspis*; **paper III**) from the Lochkovian and Pragian of the Prague Basin. They differ fundamentally from the published examples, resembling more closely the dentitions of crown gnathostomes (chondrichthyans and osteichthyans; Figure 1).

In addition, other parts of the visceral arches such as the gill skeleton or the hyoid arch are preserved in certain semi-articulated specimens of the acanthothoracid placoderm genera

*Tlamaspis* (**paper III**, Fig 6) and *Kosoraspis* from the Lochkovian of the Prague Basin. The gill arch skeleton was poorly known in basal placoderms until recently (Brazeau *et al.* 2017). Since the visceral arch skeleton is a part of the anatomy that changed most drastically during the transition from jawless to jawed vertebrates, a detailed description of the genera occurring in the Prague Basin will be of great benefit to understand this transition.

## Vertebrates of the Lower Palaeozoic from the Barrandian area

### Placodermi

All the placoderm specimens known from the Barrandian area were found in the Devonian strata in various localities of the Prague Basin. Most of the material was undescribed before and along with the previously studied specimens, it was in need of a thorough taxonomic revision. This revision is the core of this thesis as well as the **papers II–IV**. The revision significantly changed the previous view of the taxonomic composition and diversity of placoderms in the Lower Devonian of the Prague Basin. The Prague Basin placoderm fauna could be divided into two associations – the Lochkovian and Pragian mainly acanthothoracid placoderm association, and the homostiid arthrodire association from the Emsian.

The Lochkovian placoderms were discovered in a single locality, Černá rokle near Kosoř (southwest of Prague), where they occur in the Radotín Limestone of the Lochkov Formation (**paper I** and **III**). The preservation in this locality is very specific, the specimens are embedded in dark platy limestone and appear to be considerably dorsoventrally flattened and disarticulated. Our synchrotron microtomography investigation (see Conclusions) has shown that the degree of compression is much lower than previously thought (Gross 1959). Most of the specimens are at least semi-articulated or the individual elements were moved not far from their original life position. Černá rokle is the richest of all the placoderm bearing localities in the Prague Basin (**paper I**). However, this could be due to taphonomical factors as well as selective collecting at the different localities. It is probable that most of the specimens come from a certain layer or accumulation exposed at the time of active quarrying in the area (see discussion in **paper III**).

The acanthothoracid placoderms from the Lochkovian of the Prague Basin form a diversified association untypical for the Early Devonian time. Instead of two genera *Radotina* and *Kosoraspis* originally described by Gross (1950, 1958, 1959) we were able to unambiguously distinguish four genera of acanthothoracids – *Radotina*, *Tlamaspis*, *Sudaspis*, and *Kosoraspis* (**paper III**). Some specimens of *Tlamaspis* and *Sudaspis* were previously included in the genus *Radotina* that was based on a very confusing diagnosis with variable character states of the skull roof composition (more or less tessellated; Gross 1959). We demonstrated that *Radotina kosorensis* (sensu Gross 1950, 1958, 1959) also known as *Holopetalichthys kosorensis* (Moy Thomas & Miles 1971) is in fact a multitaxon chimaera combining characters from different genera, each with its own characteristic and stable skull roof pattern (**paper III**). Therefore, all the previous interpretations of acanthothoracid placoderms (apart from references to holotypes) from the Prague Basin should be disregarded.

The species *Radotina kosorensis* Gross, 1950 is now confined to a few specimens that share unique characteristics with the holotype. Their skull roof is covered by large tesselate areas separating the macromeric dermal bones. The individual scales from Černá rokle attributed to *Radotina* (Burrow & Turner 1999, Gross 1959, Stensiö 1969) belong in fact to the genus *Kosoraspis* based on their characteristic dermal ornament. *Tlamaspis inopinatus* Vaškaninová & Ahlberg, 2017 has a very long facial region and no tesserae between the large central and nuchal plates. It lacks a premedian dermal plate. *Sudaspis chlupaci* Vaškaninová & Ahlberg, 2017 has a long prenasal region with a characteristic stepped lateral profile. The posterior part of its skull roof is macromeric with protruding paranuchal plates. The taxonomic distinctness of the enigmatic genus and species *Kosoraspis peckai* Gross, 1959 is not in dispute. All these taxa can be included among the acanthothoracids based on the presence of a projecting "upper lip" (Dupret *et al.* 2014).

The Pragian placoderms were discovered in the Koněprusy area. They are embedded in the white Koněprusy Limestone (Praha Formation) of bioherm origin (**paper I** and **III)**. The preservation is perfectly three-dimensional, most of the specimens were found within the sedimentary infill of large orthocone cephalopod shells. The abundance of placoderms in the Pragian is far lower than in the Lochkovian (**paper I**). The taxonomic composition was also revised in **paper III**. *Radotina tesselata* Gross, 1958 shares detailed similarities with the holotype of *Radotina kosorensis*. Since no other specimen could be assigned to *R. tesselata* it remained a single specimen species. We have resolved the taxonomic confusion of the so-called *′Radotina′ prima* (previously known as *Coccosteus primus* Barrande, 1872; *Holopetalichthys novaki* von Koenen, 1895; and *Radotina tuberculata* Gross, 1958) and established the name combination *Holopetalichthys primus* (Barrande, 1872). *Holopetalichthys* was excluded from the acanthothoracids based on the absence of a prenasal area, but its higher taxonomic affinities remain unknown. It displays a number of unusual characters (**paper III**).

All the acanthothoracid and *Holopetalichthys* specimens from the Lochkovian and Pragian of the Prague Basin are well suited to microtomographic examination, because of the homogeneity of the matrix and the good contrast between the matrix and bone (see Conclusions). Preliminary results from the synchrotron tomography investigation of the placoderms from the Lower Devonian of the Prague Basin confirm the taxonomy proposed in **paper III**. The reconstructed data have a great potential to enhance our understanding of basal placoderm anatomy and morphological diversity. The detailed investigation is expected to add substantially to the discussion about early gnathostome cranial evolution as well as the evolution of dermal bone macromery.

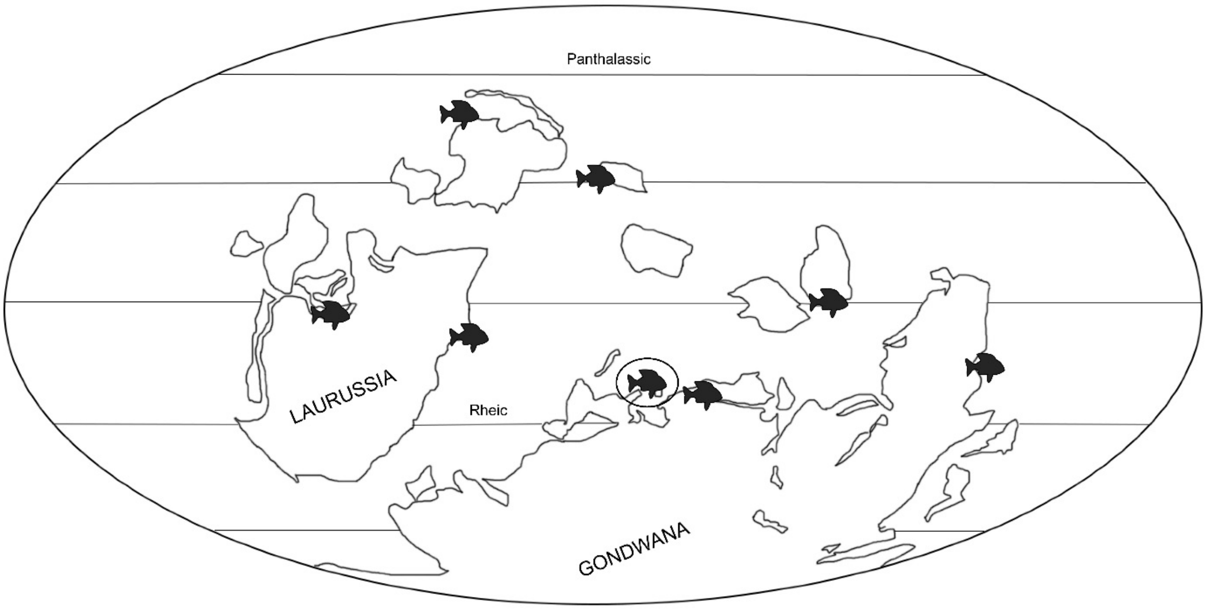

**Figure 2.** Map of acanthothoracid placoderm distribution in the Lochkovian and Pragian, the occurrence in the Prague Basin in circle (map after Torsvik & Cocks 2013; for data references see **paper III** and **IV**).

Acanthothoracid placoderms were distributed worldwide in the Early Devonian (**paper IV**). They are known from both hemispheres, from tropical as well as moderate climates (Figure 2). The Prague Basin acanthothoracid fauna is by far the most abundant (**paper I**) and diversified (**paper III**) but this may be influenced by selective sampling or a need for systematic revisions of acanthothoracid specimens in other areas of the world. The acanthothoracid genera *Radotina*, *Tlamaspis*, *Sudaspis* and *Kosoraspis* are known exclusively from the Prague Basin.

The taxonomical composition of the Emsian placoderm fauna from the Prague Basin has been misunderstood for more than a hundred years. Some of the specimens were initially determined as four species of three genera (*Coccosteus*, *Asterolepis*, *Dinichthys*; Barrande 1872, Eastman 1897), many were never described. The determinations were soon rejected and for a long time the specimens remained in open nomenclature (Denison 1978, Vaškaninová 2009). The abundance of the Emsian placoderm fauna is very low in the Prague Basin (**paper I**), only a few specimens are known from each locality. However, they occur at a number of localities of Emsian age in the Prague Basin and in different environments, from very shallow (**paper II**) to relatively deeper (**paper IV**) marine environments. All the occurrences are in limestones (**paper I**).

The diversity of the Emsian placoderm assemblage is lower than previously thought (**paper IV**). We were able to distinguish two species of two genera, both belonging among the homostiid arthrodires (sensu Denison 1978). *Antineosteus rufus* Vaškaninová & Kraft, 2014 from the upper Emsian of the Prague Basin is the largest known Early Devonian placoderm, inferred to exceed three meters in length (**paper II**). It was found in the Červený lom Quarry where the Suchomasty Limestone of the Daleje-Třebotov Formation is exposed (**paper I–II**). The sediments were deposited in a very shallow lagoon environment. Although *A. rufus* was described based on two fragments of large dermal plates it can be assigned to homostiid arthrodires with certainty. Given its gigantic body size and the general lack of teeth or biting edges among the homostiids (Lelièvre 1984), we propose a filter-feeding strategy for the group. This would make homostiids the first vertebrates to invade this nutrient-rich ecospace, however in a period of collapsed diversity in the planktonic communities (**paper II**).

*Johannaspis bohemicus* (Barrande, 1872) belongs to a new genus established based on Barrande´s (1872) and Eastman´s (1892) originals and some previously unpublished specimens. All of them originate from a number of localities in the Emsian strata (Zlíchov and Daleje-

Třebotov formations; **paper I**). The previous taxonomic splitting of the material into various genera is explained as a factor of specific taphonomical preservation at different localities in the Prague Basin. Another factor enabling the artificial splitting was the present location of the material in different institutions around the world (**paper IV**).

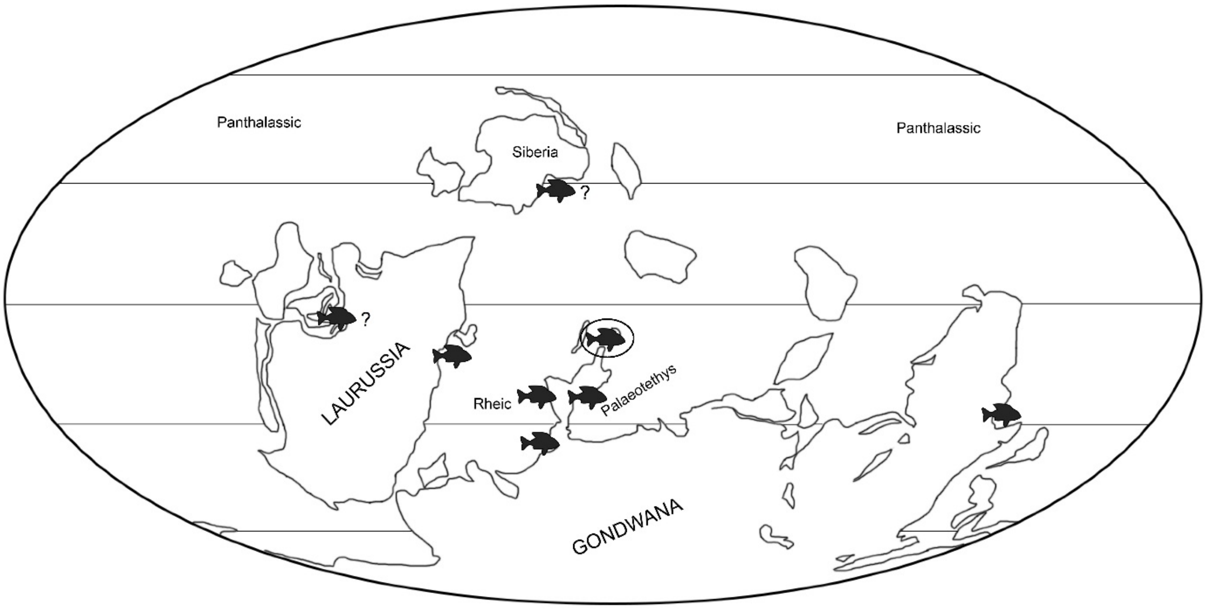

**Figure 3.** Map of homostiid arthrodire placoderm distribution in the Emsian, the occurrence in the Prague Basin in circle, problematic occurrences with question mark (map after Torsvik & Cocks 2013; for data references see **paper IV**).

The palaeogeographical distribution of homostiids in the Early Devonian was limited to tropical and subtropical shallow marine environments, mainly in the southern hemisphere; the reported occurrences on the northern hemisphere are questionable and could in fact originate from the Middle Devonian (**paper IV**). The prevailing record is concentrated on the northern and eastern continental margins of Gondwana (Figure 3). The genus *Antineosteus* is known from the upper Emsian of the Prague Basin (**paper II**), Morocco (Lelièvre 1984) and Algeria (Lelièvre 1988); *Johannaspis* is known only from the Prague Basin (**paper IV**).

Homostiids are no longer recorded in the northern peri-Gondwana in the Middle Devonian yet they appear in Laurussia and Siberia. Some genera presumably migrated from northern to eastern Gondwana (Young 2003). This distribution pattern in the Eifelian is most probably a factor of environmental changes. The disappearance of environments with abundant food resources favourable for these large suspension feeders in the Prague Basin could be related to the narrowing of the oceanic realm and gradual emerging of dry land as an early manifestation of the approaching Variscan orogeny (Havlíček 1998, **paper IV**). This specific local palaeogeographical development could also explain the decrease in diversity and abundance of placoderms in the Prague Basin throughout the Early Devonian, which is in contradiction to the general trend in placoderm faunas (**paper I**).

## Agnatha

The only confirmed and determinable aganthan (jawless) vertebrate remains from the Lower Palaeozoic of the Barrandian area are two head carapace plates discovered in the Emsian-Eifelian boundary interval (Daleje-Třebotov or Choteč Formation) in the Prastav Quarry (Prague-Hlubočepy). They were figured and described already by Růžička (1929) and taxonomically revised as *Schizosteus perneri* (Růžička, 1929) by Tarlo (1965). Their biogeographical occurrence was discussed in **paper V** where the better preserved of the two plates was refigured with a number of detailed views.

Psammosteid heterostracans are considered freshwater dwellers (Lebedev *et al.* 2010) or coastal brackish or continental-water inhabitants (Lukševičs *et al.* 2010). However, only purely marine sediments occur in the Devonian of the Prague Basin (Havlíček 1998). Thus, the rare occurrence of a psammosteid heterostracan in the Emsian/Eifelian boundary beds of the Prague Basin is indicative of a dry land influence in the vicinity of the preserved relic of Devonian rocks in the Teplá-Barrandien unit. This inference was already supported by the occurrence of the coeval vascular plants (see references in **paper V**), but the vertebrate remains allow us to suppose a temporarily favourable habitat with probably brackish conditions. This assumption is based on the argument that in spite of the increasing number of terrestrial plant fossils throughout the Middle Devonian strata (related to the rising Variscan orogeny) heterostracan vertebrates never reappeared in the Prague Basin. The presence of vertebrate remains thus proved to be a valuable factor for reconstructing the character of regional palaeoenvironments and aspects of local palaeogeography.

This occurrence is significant also in a broader biogeographical and stratigraphical sense. The psammosteid heterostracans are known mostly from Laurussia and they are very rare in the Lower Devonian strata (Lukševičs *et al.* 2010). The specimen discovered in the Prague Basin is the first record of the genus *Schizosteus* in the Lower Devonian and it represents the easternmost occurrence of the group Psammosteidae.

## Vertebrate microremains

Despite the extensive micropalaeontological collecting in the Silurian strata of the Barrandian area, no vertebrate microremains have been reported yet. The only known description published are fragments of acanthodian scales (genera *Nostolepis* and *Gomphonchus*) dissolved from a few rock samples collected in the Silurian/Devonian boundary beds during a post-conference field trip (Märss 1997). Gross (1950) mentioned the presence of acanthodian scales in the ´Liteň Beds´ and ´Budňany Limestone´ (Wenlock and upper Přídolí; Märss 1997). The author of this thesis performed test sampling on selected Silurian localities (Vaškaninová 2014) and among the collected microscopic fragments some rare findings of indeterminable (S. Turner, pers. comm. 2015) thelodont scales were recorded from the Ludfordian of the Požáry Quarry (Praha-Řeporyje). It is remarkable that although the accompanying conodont fragments are well preserved the preservation of vertebrate elements is much worse as they are often damaged and corroded.

Microscopic fragments of presumable vertebrates from the Devonian strata of the Prague Basin were collected by specialists in micropalaeontology as a by-product of sampling phosphatic elements (e.g. conodonts, brachiopods). However, none of this material was published except for the acetic acid isolated scales of *Machaeracanthus bohemicus* Barrande, 1872 from the Lochkov Formation from Kosoř described and illustrated by Gross (1973) and acanthodian scales illustrated by Märss (1997). **Paper VI** is a preliminary attempt to fill this gap. It focuses on the material collected from selected localities in four stratigraphical horizons of the Prague Basin (Pragian, lower Emsian, upper Emsian and the Eifelian/Givetian boundary interval). Apart from acanthodian and placoderm fragments, which occur also as macroscopic fossils in the same strata, chondrichthyan and probable sarcopterygian (onychodont) elements are figured and described. **Paper VI** is thus the first record of these vertebrate groups in the Lower Palaeozoic of the Barrandian area.

## Conclusions and future direction of the study

The main conclusions of this thesis are the following:

a) In the Lochkovian of the Prague Basin, the placoderm fauna was composed exclusively of acanthothoracids. It is the most abundant (**paper I**) and the most diverse of all placoderm faunas in the Prague Basin. Instead of the previously described two genera (*Radotina* and *Kosoraspis*), it was possible to unambiguously distinguish four acanthothoracid genera (*Radotina, Tlamaspis, Sudaspis,* and *Kosoraspis*; **paper III**). All of them display primitive characters of high importance for understanding the relationships and evolutionary patterns among the stem jawed vertebrates.

b) The Pragian placoderm fauna is much less abundant (**paper I**) and is dominated by *Holopetalichthys*, a disputed genus of uncertain taxonomical affinities that was finally proven valid after being synonymised with *Radotina* by many previous authors. *Radotina tesselata* remained a single specimen species (**paper III**). However, its excellent preservation allows a detailed description of the cranial and visceral morphology of the genus.

c) In the Emsian, a turnover in the taxonomic composition of placoderm faunas has happened in the Prague Basin. Only the members of the most diverse placoderm order Arthrodira were recorded (**paper I**). In contrast to the previously published data only two genera of homostiid arthrodires (large suspension-feeding forms) are confirmed – *Antineosteus* (**paper II**) and *Johannaspis* (**paper IV**). *Antineosteus rufus* is the largest known placoderm from the Lower Devonian strata worldwide.

d) The abundance and diversity of the Prague Basin placoderms decreased significantly throughout the Early Devonian which is in contradiction to the general trend (**papers I** and **IV**). Judging from the biogeographical distribution of the respective placoderm groups, the Prague Basin was supposedly more open to faunal exchange with both hemispheres in the Lochkovian and Pragian, because members of the globally distributed group Acanthothoraci are present (Figure 2). The fauna of homostiid arthrodires was more restricted to tropical and subtropical shallow marine environments of the southern hemisphere in the Emsian (Figure 3). In the Eifelian homostiids disappeared from the northern continental margin of Gondwana and are recorded in Laurussia, Siberia and eastern Gondwana. This distribution pattern is interpreted as an effect of the palaeogeographical changes related to the proceeding Variscan orogeny (**paper IV**).

The research of acanthothoracid placoderms from the Prague Basin has numerous future perspectives. Because of the perichondral bone lining of the internal structures and an overall heavy ossification in acanthothoracids, the material is very suitable for tomography. In 2016, twenty specimens from the Lochkovian and Pragian strata have been synchrotron scanned in various resolutions at the European Synchrotron Radiation Facility in Grenoble, France. Another experiment is scheduled for November 2017 focusing on spot scans of selected specimens in histological (submicron) resolution.

The preliminary 3D rendered data have already yielded exceptional results, providing novel and detailed information about the cranial morphology, visceral skeleton, and postcranial anatomy never observed in a basal jawed vertebrate before. The synchrotron data also confirmed our diagnoses published in **paper III**. Further data on the microanatomy and histology of teeth, dermal bones, and tesserae, emerging from synchrotron microtomography investigation of the Prague Basin placoderms, will provide an outstanding dataset for future hypotheses about deep vertebrate phylogeny and the evolution of macromery, jaws, and dentition. Future investigation of the Prague Basin acanthothoracids will greatly enhance the understanding of our own body plan evolution and developmental pathways and will therefore be of broad interest to the (palaeo)biological research community.

Another future direction of early vertebrate research in the Prague Basin is the study of microscopic vertebrate elements. Our preliminary reports (**paper VI**, Vaškaninová 2014) have shown that vertebrate elements are more common in the residues from the Silurian and Devonian strata of the Prague Basin than previously thought. The study of microscopic vertebrate elements from carefully selected localities could enhance our understanding of the diversity of early vertebrate fauna in the Prague Basin, adding new jawed and possibly jawless vertebrate groups to the record. Considering the very good biostratigraphical zonation in the

Barrandian area, a larger number of vertebrate microfossil data could enable biostratigraphical correlations with the areas of the world where invertebrate index fossils are absent.

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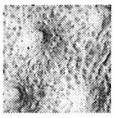
# Paper II

# The largest Lower Devonian placoderm – *Antineosteus rufus* sp. nov. from the Barrandian area (Czech Republic)

VALÉRIA VAŠKANINOVÁ & PETR KRAFT



*Antineosteus rufus* sp. nov. from the upper Emsian of the Czech Republic is described based on two fragments of large dermal plates discovered in the Suchomasty Limestone. The original length of the animal is inferred to have exceeded that of *Tityosteus rieversae* – the largest Lower Devonian placoderm recorded so far. The occurrence of *A. rufus* in the Prague Basin is consistent with other giant homostiids in several areas. These animals were apparently adapted to plankton-feeding, although they appeared in the conditions of collapsed diversity of the planktic communities during the "Devonian Nekton Revolution". This successful feeding strategy made them the first vertebrates occupying the nutrient-rich ecospace producing the largest animals up to the present. • Key words: Vertebrata, Placodermi, *Antineosteus,* Emsian, Barrandian area, nekton revolution.

VAŠKANINOVÁ, V. & KRAFT, P. 2014. The largest Lower Devonian placoderm – *Antineosteus rufus* sp. nov. from the Barrandian area (Czech Republic). *Bulletin of Geosciences 89(3)*, 635–644 (6 figures). Czech Geological Survey, Prague. ISSN 1214-1119. Manuscript received May 20, 2013; accepted in revised form April 12, 2014; published online June 4, 2014; issued June 9, 2014.

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Placoderms make up a minor component of the fauna from the Devonian of the Barrandian area, Czech Republic. The Devonian of this area is globally renowned for its rich invertebrate fossil associations with brachiopods, trilobites, corals, bryozoans, goniatites, tentaculites, and conodonts as the significant faunal components. The Barrandian placoderms have been known since the second half of the 19th century with the first description by Barrande (1872). The most abundant placoderm remains occur in the basal Lochkov Formation whilst higher up in the section they are rare. The section records a sudden overturn of the placoderm fauna at the time of the Pragian-Emsian transition. The less derived Acanthothoraci are fairly numerous in the Lochkovian and continue through to the Pragian, but in reduced numbers and body size (Gross 1958, 1959; Westoll 1967; Vaškaninová 2011). In the Emsian, members of the more derived order Arthrodira appeared in the Barrandian area, completely displacing the former acanthothoracid fauna (Vaškaninová & Kraft in press). The majority of the arthrodire specimens can be assigned to the family Homostiidae (or clade Migmatocephala, see phylogenetic remarks), found in the Devonian strata of Europe, Morocco, Siberia, Spitsbergen, Greenland, Canada (Denison 1978) and southeastern Australia (White 1978).

The present paper is the first contribution to the revision of placoderm fauna from the Barrandian area. It describes a giant species, not only an extreme member of the vertebrate communities but also in the late Early Devonian marine ecosystems. Its importance is that the specimen occurs in sedimentary sequence with excellent stratigraphic control and in one of the key areas for Devonian stratigraphy because of global stratotypes as well as other sections.

## Material

Although fossil fish remains are rare, as a result of sustained collecting throughout the 19th and 20th centuries, the National Museum in Prague (NM) now houses a large collection. In addition to a partly described historical collection from the 19th century (Barrande 1872, Eastman 1897, Bayer 1905, Perner 1918) several collectors such as A. Schubert, F.J. Pecka, W. Kolář, R. Růžička and I. Chlupáč in the first half of the 20th century were able to substantially add to the collections, when quarrying in the Barrandian area was still active (Perner 1918).

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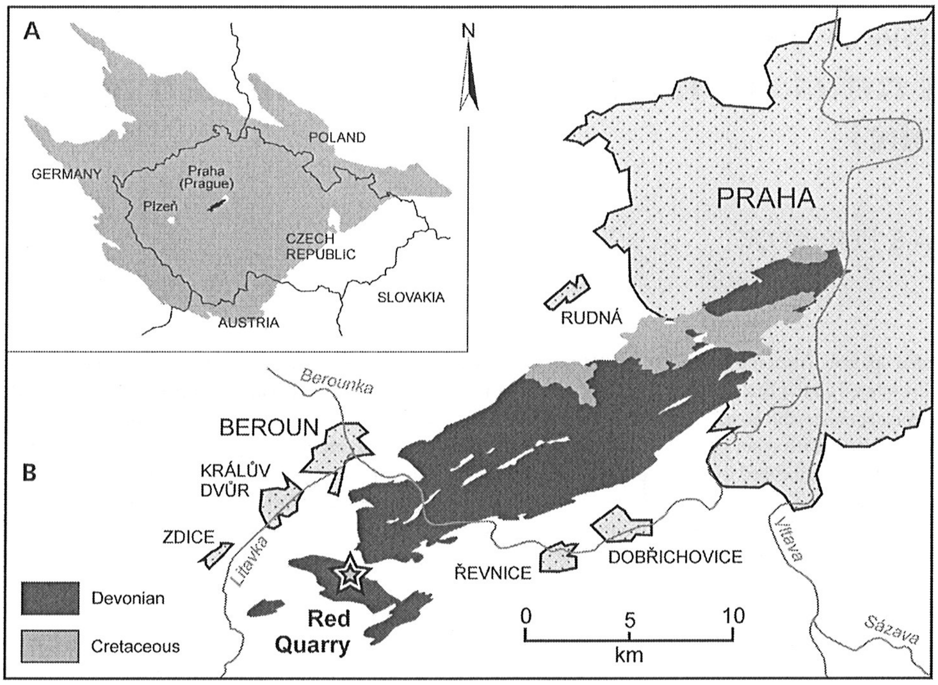

**Figure 1.** Sketch map of the Devonian in the Prague Basin. • A – location of Devonian sediments (black) in the central part of the Bohemian Massif (grey shaded) on the territory of the Czech Republic. • B – simplified map of the Devonian distribution with the fossil site marked with an asterisk. Some rivers, towns and cities are selected with respect to the overall picture; tectonics is omitted; only the significant marine Cretaceous cover is displayed, younger continental units are omitted.

The specimens described here were discovered in the Červený lom (Red Quarry) near the villages of Suchomasty and Koněprusy, south west of Prague (GPS coordinates 49° 54´ 38˝N, 14° 4´ 36˝E), Czech Republic (Fig. 1). Both specimens were donated to the National Museum by J. Kácha, a private fossil collector, in the 1990's, however, as the specimens were given to him by the Červený lom quarry workers the exact layer is not known (J. Kácha, oral communication). However, acid digestion (see below) has provided age diagnostic conodonts.

Each specimen comprises a single dermal plate, where the bone structure is preserved in its original thickness without compression, atop a limestone slab. The surface structure of the dermal plates is well preserved including the ornamentation of dermal tubercles. One specimen (Lc 126) is partly exfoliated and exhibits its inner bone layers partly exposed in the thickest area of the plate. Both plates are incomplete, especially their margins which are broken off in an irregular manner. This mode of preservation is as a result of a post-mortem transport across a short distance.

The studied material is deposited in the collections of the National Museum in Prague.

## Geological and palaeontological settings

The studied fossils were discovered at "Červený lom" Quarry near Suchomasty (Fig. 1) in the Suchomasty Limestone, a local facies of the upper Emsian Daleje-Třebotov Formation (Fig. 2) in the Koněprusy area (for the description of the locality see Chlupáč *et al.* 1979, Chlupáč 1993, Berkyová 2009 and Berkyová *et al.* 2009; a detailed analysis of various aspects was provided by Dieken 1996). It is a lectostratotype of the Suchomasty Limestone (Chlupáč 1981; for the section of the entire sequence see Chlupáč *et al.* 1979, fig. 14) and exposes a complete sequence of the so-called Suchomasty Marble, used as a decorative stone. It comprises reddish and grey bioclastic (mainly crinoidal) and micritic, mostly well-bedded limestones with common stromatactis structures (*e.g.* Havlíček & Kukal 1990; for microfacies and some other characteristics see Dieken 1996, Koptíková 2011 and Vodrážková *et al.* 2013; the stromatactis structures were studied in detail by Kukal 1972, recently by Dieken 1996, Hladil 2005 and Hladil *et al.* 2006), its thickness is 20–30 m. Coarser detritus dominates both the lowest and uppermost parts of the sequence (Chlupáč *et al.* 1979, Chlupáč 1998, Koptíková 2011). The sediments were deposited on the weathered and corroded surface of the Koněprusy Reef, represented by the Koněprusy Limestone (*e.g.* Chlupáč 1976, fig. 1; Chlupáč *et al.* 1979, fig. 15; Havlíček & Kukal 1990, fig. 2; Chlupáč 1998, fig. 68), covering the former reef flat and lagoon of this submerging "dead" reef after a short gap from the early to mid Emsian. The Suchomasty Limestone reflects a shallow, purely marine environment with a high level of turbulence and rapid changes between low and high-energy stages of the current intensity (Chlupáč *et al.* 1979, Chlupáč 1998, Havlíček & Kukal 1990) but probably below the storm-wave (Vodrážková *et al.* 2013).

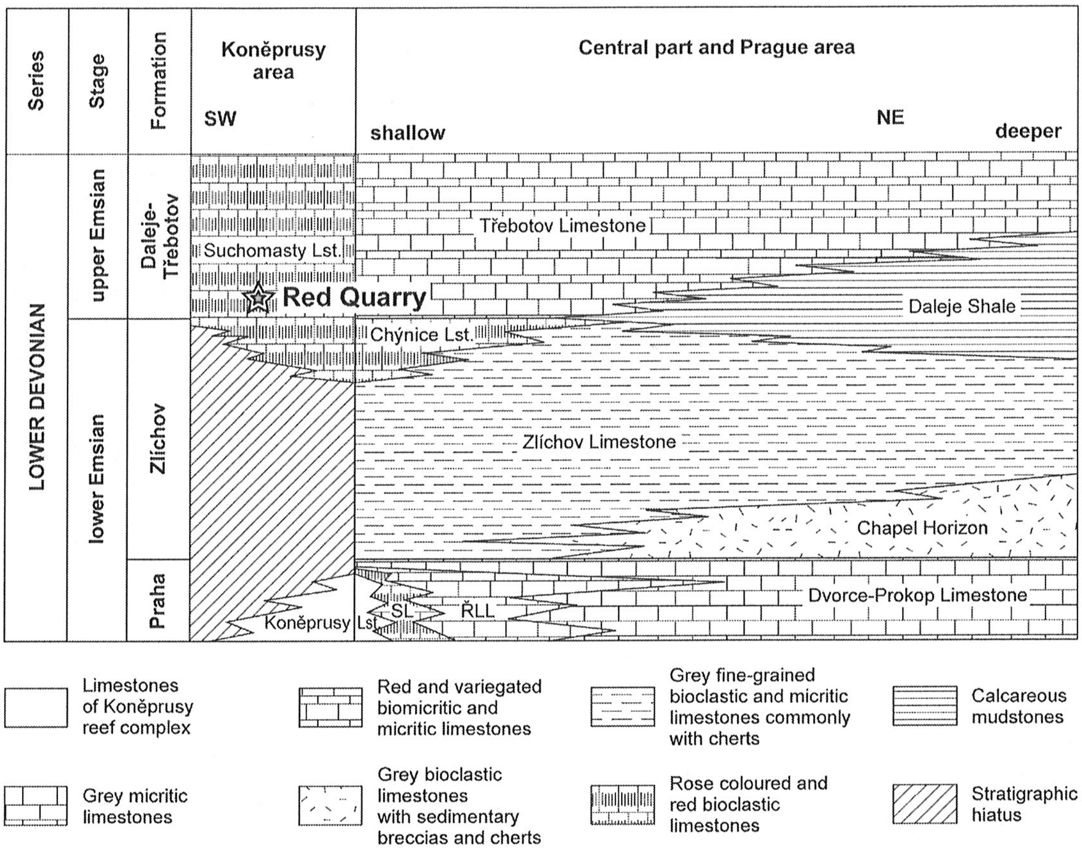

**Figure 2.** Stratigraphic chart of the Emsian in the Prague Basin with the position of the fossil site marked with an asterisk (modified after Budil *et al.* 2013). Abbreviations: Lst. – Limestone, SL – Slivenec Limestone, ŘLL – Řeporyje-Loděnice Limestone.

The fauna of the Suchomasty Limestone at the Červený lom Quarry is rich in benthos. The invertebrate fauna is abundant in certain layers and contains mainly echinoderms, and also tentaculites, ostracods, trilobites (Chlupáč *et al.* 1979; Chlupáč 1993, 1998) and brachiopods (Chlupáč *et al.* 1979, Havlíček & Kukal 1990, Mergl & Vodrážková 2012) as the significant components (for all groups see Dieken 1996). Only a few taxa of microflora and microfaunal foraminifera were identified by Dieken (1996). Lack of other microelements, calcispheres and peloids (in contrast to its deeper water equivalent – the Třebotov Limestone) was proved by Berkyová & Munnecke (2010).

The Suchomasty Limestone at the quarry has been constrained to the interval of the *Novakia elegans-N. cancellata-N. richteri-N. holynensis* tentaculite zones (Chlupáč *et al.* 1979, Ferrová *et al.* 2012) and the *Polygnathus laticostatus-P. serotinus-P. costatus patulus* conodont zones (Chlupáč *et al.* 1979, Dieken 1996, Berkyová 2009). No associated index fossils, such as tentaculites, were found on the slabs on which both placoderm specimens occur. A piece of rock from the specimen Lc 125 was digested using acetic acid and several fragments of conodonts were discovered in the residue. S. Vodrážková (oral communication) determined the elements as *Belodella* sp., which is not stratigraphically diagnostic and a single fragment of *Icriodus beckmanni* (subspecies unknown) indicative of the *serotinus* Zone (Dalejan, upper Emsian). In addition, according to Berkyová (2009), *I. beckmanni* is confined to this stratigraphical level in the Prague Basin and thus the studied placoderm remains, at least specimen Lc 125, can be assigned to the *serotinus* Zone.

## Systematic palaeontology

Class Placodermi McCoy, 1848
Order Arthrodira Woodward, 1891
Suborder Brachythoraci Gross, 1932
Family Homostiidae Jaekel, 1903; emend. Mark-Kurik & Carls, 2004

### Genus *Antineosteus* Lelièvre, 1984a

*Type species. – Antineosteus lehmani* Lelièvre, 1984a.

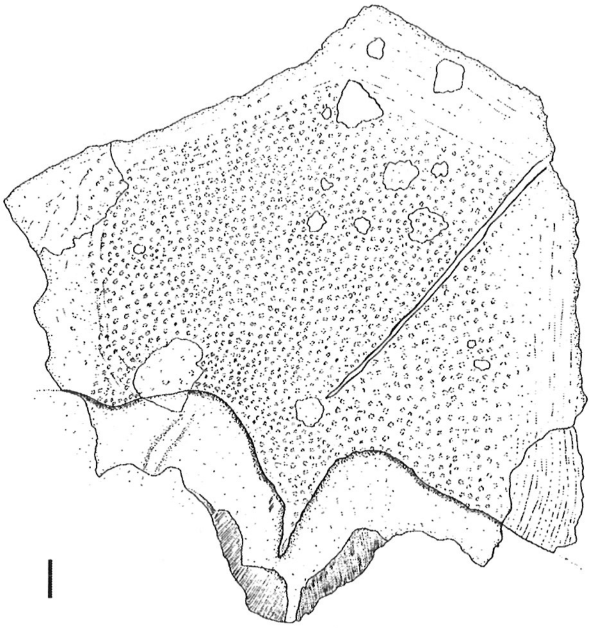

**Figure 3.** *Antineosteus rufus* sp. nov. NM Lc 125, holotype. Right central plate. Scale bar 1 cm.

*Emended diagnosis.* – The genus *Antineosteus* belongs to the family Homostiidae (Brachythoraci) and is characterized by the pineal plate with two lateral expansions reaching towards the preorbital plates. The dorsal margin of the orbital notch is formed by the lateral margin of a single postorbital plate. The anterior and lateral margins of the central plates are straight. The supraorbital sensory line is absent on the central plates. Dermal ornament consists of round tubercles with tips separated by a shallow ridge.

*Remarks.* – *Antineosteus* was described as a monospecific genus and no separate diagnoses were provided by Lelièvre (1984a). For the purpose of describing a new species we erected the genus diagnosis of selected features observed by Lelièvre (1984a) extended by our new observations.

*Species assigned.* – *Antineosteus lehmani* Lelièvre, 1984a; *Antineosteus rufus* sp. nov.

*Geographic and stratigraphic occurrence.* – Morocco, Algeria and Czech Republic; Upper Emsian (Dalejan).

### *Antineosteus rufus* sp. nov.

Figures 3–6

*Derivation of name.* – From the Latin *rufus* (red) after the colour of the limestone as well as the name of the type locality – the Red Quarry (Červený lom).

*Holotype.* – Nearly complete right central head shield plate NM Lc 125 figured in Figs 3, 5B, 6.

*Type locality.* – Red Quarry near Suchomasty (Czech Karst, Czech Republic).

*Material.* – Right central plate (NM Lc 125), right anterior dorsolateral plate (NM Lc 126).

*Diagnosis.* – The following combination of characters: right central plate of approximately equal width and length; absence of pit lines on the central plates; the suture between both central plates curved; the posterior process of the central plate narrow and more acutely pointed than in *A. lehmani*; the dermal tubercles smaller and sparsely distributed than in *A. lehmani*.

*Description.* – Central plate (C). The anterior and lateral margins of the right central plate of the head shield (Figs 3, 5B) are not preserved. Thus, the original size of the plate was larger than the preserved area, with the preserved width and length, both approximately 13 cm. The medial suture with the left central plate is poorly preserved, but appears to be curved.

The well-preserved posteromesial margin illustrates the overlap areas, where the nuchal and paranuchal plates sutured. It indicates that the anterior margin of the nuchal plate was concave. In the overlap area for the nuchal plate a transverse thickening is preserved, extending towards the right anterior lobe of the nuchal plate. The posterolateral overlap area was covered by the paranuchal plate; its shape indicates an acute anterior margin of the plate.

Lateromesially to the sharp posterior process of the central plate separating the overlap areas for the nuchal and paranuchal plates runs the central sensory line canal. It is preserved as two parallel grooves, partly exposed, because the sensory line was originally porous. No trace of supraorbital sensory line or pit lines is observable on the surface of the plate. The average thickness of the plate is 1 mm, reaching maximum 5 mm anteromesially.

Anterior dorsolateral plate (ADL). The right anterior dorsolateral plate (Figs 4, 5A) is slender anteriorly and widens gradually posteriorly. The anterior part of the plate along with the articular condyle has the inner bone structure exposed forming a spiny projection in the midline. The articular condyle points dorsally almost in the same axis as the surface of the plate. The articular area is partly preserved; being long, slender and concave ventrally. The preserved dorsal margin of the ADL is straight and a trace of the overlap area for the median dorsal plate is visible. Most of the ventrolateral part of the anterior dorsolateral along with the overlap areas for the surrounding plates is not preserved. The length of the plate fragment is 16 cm.

The main sensory line canal runs medially. Its preserved posterior part is straight, and formed as one shallow groove. The maximum thickness at the posterodorsal margin of the plate reaches 5 mm.

Both plates are covered with dermal ornament, although this has suffered some damage. In a few areas the typical arthrodire ornament of round tubercles with a shallow ridge separating the tip (detail Fig. 6) is visible. Towards the outer margins of both plates, the tubercles tend to be arranged in lines. The ornament on the uppermost dermal bone layer of the anterior and lateral margins of the central plates has been eroded away revealing linear ridges, possibly lines of arrested growth. The sensory lines cross through some of the tubercles.

*Remarks.* – The preserved outline of the anterior margin of the nuchal plate indicates that the left central plate was narrower than the right one (a situation comparable to the skull roof of *Antineosteus lehmani* Lelièvre, 1984a and *Tityosteus rieversae* Gross, 1960).

Both plates indicate a homostiid affinity: 1) Large Coccosteina with broad, depressed head and trunk shields (Denison 1978). This character is supported by the position of the articular condyle, its axis following the anterior margin of the plate, which supports a nearly horizontal position of the plate (Young 2005, p. 217) and thus of the dorsal part of the trunk shield as well as the skull roof. It indicates a dorsoventrally compressed armour of *A. rufus*. 2) Narrow anterior borders of the PNu and Nu plates, the strong posterolateral extensions of the central plates (Young 2004).

The determination of the new plates to the genus *Antineosteus* is supported by the characters in common with *A. lehmani:* the shape of the central plate, the course of the central sensory line canal and the dermal ornament. The shape of the anterior part of ADL and the outline of the overlap area for the median dorsal plate on the preserved part of the ADL of *A. rufus* are also very similar.

The course of the main sensory line on the ADL is straighter than on *A. lehmani* (compare Lelièvre 1984a) and runs medially on the contrary to the lc of *A. lehmani* that runs parallel to the dorsal margin of the plate. However, this character can be highly variable. The notable size difference between the two species cannot be used as a diagnostic character either as this may represent continuous variation.

However, the posterior outline of the central plate is more curved than on *A. lehmani* with a longer and sharper posterior process (in addition to a more acute anterior outline of the paranuchal plate). Another character which justifies the erection of a new species is the absence of pit-lines on the central plate of *A. rufus.*

The absence of the supraorbital canals on the central plates is a typical character shared by the primitive brachythoracids *Homostius, Burrinjucosteus* (White 1978), *Dhanguura* (Young 2004) as well as most dolichothoracids (Lelièvre 1984a). However, it is not considered a phylogenetically significant character, rather a plesiomorphy of the clade *Taemasosteus-Antineosteus* (Lelièvre 1984a) or a reversion of evolution (Young 1981). The extension of supraorbital canals onto the centrals is listed as one of the brachythoracid characters by Denison (1984).

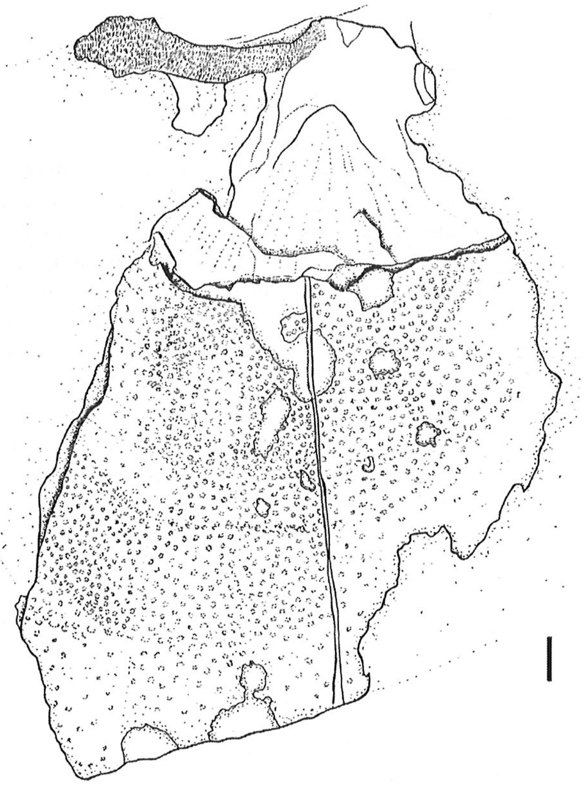

**Figure 4.** *Antineosteus rufus* sp. nov. NM Lc 126. Right anterior dorsolateral plate. Scale bar 1 cm.

The anterior dorsolateral plate of *Homostius* (Heintz 1934) has a different shape with the main lateral line running parallel to the ventral edge of the plate (Denison 1978). In general, *Homostius* is unique among homostiids in a different skull roof pattern due to the dorsal position of the orbits. *Burrinjucosteus asymetricus* also shows characters similar to *A. rufus,* such as the absence of supraorbital sensory lines on the C plates or the outline of the anterior margins of the Nu and PNu (White 1978). *Taemasosteus,* despite of the presence of supraorbital canals on the C plates, has a very similar shape of the ADL plate (White 1978).

*Phylogenetic remarks.* – Most authors have dealt with the relationship and evolution among the whole group of placoderms (*e.g.* Denison 1983, Goujet & Young 1995), the arthrodires (Denison 1984) or rather the more advanced brachythoracid arthrodires (Young 1981, Carr 1991, Trinajstic & Dennis-Bryan 2009).

The genus *Antineosteus* was originally included in the family Homostiidae (Lelièvre 1984a after the definition proposed by Young 1981). According to the more recent phylogenetic analysis of Lelièvre (1995, fig. 14) it was included among a "primitive brachythoracid" clade Migmatocephala (erected by White & Toombs 1972 on the basis of "mixed" characters between arctolepids, brachythoracids and pachyosteomorphs), sharing a synapomorphy of absent posterior ventral plates of the thoracic armour (Lelièvre 1995, character 36) with *Homostius*. This condition results in the posterior opening of the pectoral fenestra. Young (2003) places *Atlantidosteus* provisionally among the migmatocephalans as a sister taxon of *Homostius*, on the basis of an elongate suborbital lamina of the suborbital plate. This character, as well as the characters linking *Antineosteus* and *Homostius* to the remaining migmatocephalans (*Tityosteus* and *Taemasosteus*) and *Holonema* (Lelièvre *et al.* 1990), is not observable on the preserved material of *A. rufus*.

Some characters are detectable on the material despite its poor state of preservation: character 1 of Lelièvre (1995) "dermal plates of the skull-roof with overlapping surfaces", character 8 "shape of the anterior nuchal margin on the dorsal surface: convex", character 12 "paranuchal plate process onto the central plate determining a lateral lobe", character 17 "posterior lobe of the central plate protruding between the nuchal and paranuchal plates" and character 44 "supraorbital sensory line on the central plate: absent". However, Trinajstic & Dennis-Bryan (2009) have observed all these characters, except character 1, showing polymorphism within the eubrachthytoracid arthrodires.

*Remarks on body size.* – Gross (1960) estimated the total length of *T. rieversae* to a maximum of 250 cm but he had only the posterior part of the skull roof available. Thus, he inferred the size from the proportions of *Coccosteus* and mentioned the possible range of the skull roof of *T. rieversae* from 35 up to 50 cm in length without knowledge of the dimensions of the anterior part. He however admits, that the position and shape of the nuchal and paranuchal plates of *T. rieversae* resemble a member of Homostiidae where those plates are prolonged compared to Eubrachythoraci (up to two thirds of the whole head shield). Later, Otto (1992) described a new material of *T. rieversae* containing the anterior head shield plates associating the genus more closely with the Homostiidae (length of central plate 19 cm and ADL 11 cm; total length of the head shield approximately 45 cm). Therefore the body dimensions proposed by Gross (1960) were overestimated.

The size and shape of the plate Lc 126 indicates an anterior dorsolateral plate of a larger specimen than Lc 125 as only approximately one half of the right ADL is preserved. However, the completely preserved ADL of *T. rieversae* is shorter than the preserved part of the ADL of the larger specimen of *A. rufus* n. sp. We calculated the skull size based on comparison with the reconstruction of the complete head shield of *A. lehmani* and size ratios of its plates (Lelièvre 1984a) and the dimensions and plate pattern of *T. rieversae* listed by Otto (1992). The potential allometric growth changes were omitted because plates of large, *i.e.* presumably adult specimens were compared. In addition, the known ontogenetic data indicate that length proportions of most plates were constrained in different growth stages despite of allometry in other directions (*e.g.* Werdelin & Long 1986, Cloutier 2010). The length of the skull roof of *A. rufus* specimen Lc 125 based only on the size of the fragment of the C plate is at least 45 cm. However, we assume the fragment represents only a half of the original plate. In such case the length of the skull roof must be doubled. The calculations based on the fragmentary specimen Lc 126 resulted even in a larger dimension of the skull roof. Minimum size considering the present fragment length would be some 70 cm. However, it is evident (see above) that at least one half of the plate is missing. Thus the skull should exceed 1 m in length.

According to the calculated dimensions of the skull, the total length of the fish when it was alive is inferred to have exceeded 3 metres (considering the extreme calculations and in accordance with Gross 1960 even 6 metres), which makes it the largest Lower Devonian placoderm known so far. It was much larger than the Australian (Wee Jasper, New South Wales) *Dhanguura* and *Cathlesichthys*, considered by Young (2004) to be comparable in size to *Tityosteus rieversae*. The large brachythoracid *Confractamnis johnjelli* from the Broken River area in Queensland (Australia) originates most probably from Middle Devonian strata (Young 2005).

## Discussion

The earliest record of the Homostiidae (*sensu* Young 2004) is of Emsian age. The youngest, *Homostius sulcatus* (Kutorga, 1837) (taxonomic assignment according to Mark-Kurik pers. comm. 2013), is from the lower Givetian of Laurussia (Baltic area, Scotland, Canada; Mark-Kurik 1992). These primitive brachythoracid arthrodires are known from the Lower Devonian strata of various regions: northern and eastern continental margins of Gondwana – Rhineland, Aragón and Minusinsk Basin (*Tityosteus*, Mark-Kurik & Carls 2004); the Emsian of south eastern Australia (*Goodradigbeeon, Burrinjucosteus, Taemasosteus*, White 1978; *Dhanguura, Cathlesichthys*, Young 2004), Morocco and Algeria (*Antineosteus, Atlantidosteus*; Lelièvre 1984a, 1984b, 1988) and Czech Republic (*Antineosteus*; studied herein), and from Laurussia – Spitsbergen (*Homostius*; Mark-Kurik & Carls 2004, fig. 5) and Severnaya Zemlya (Mark-Kurik 1991). In these areas they occupied mostly shallow tropical

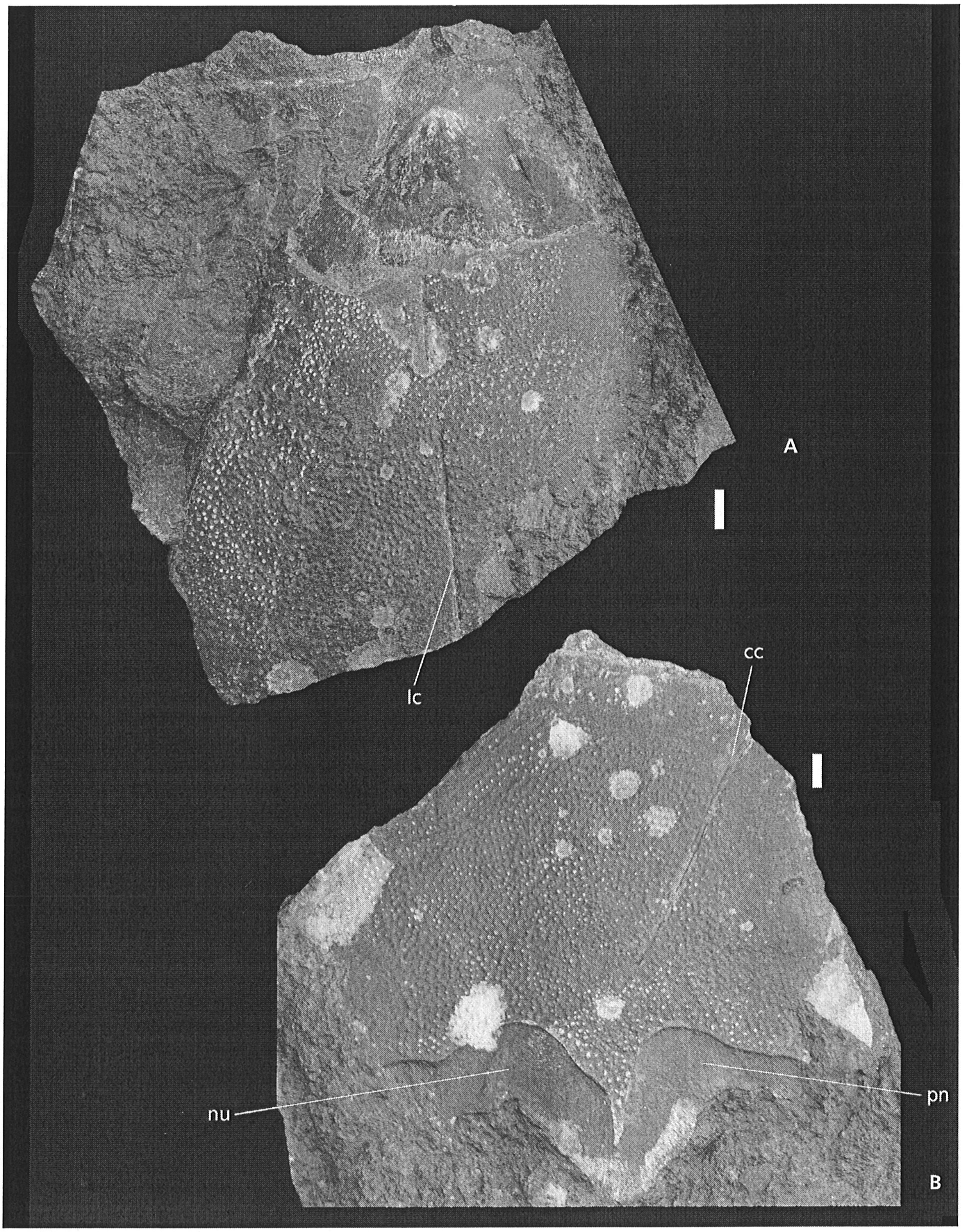

**Figure 5.** *Antineosteus rufus* sp. nov. • A – NM Lc 126. Right anterior dorsolateral plate. • B – NM Lc 125, holotype. Right central plate. Scale bar 1 cm. Abbreviations: cc – central sensory line canal, lc – main sensory line canal, pn – overlap area for the paranuchal plate, nu – overlap area for the nuchal plate.

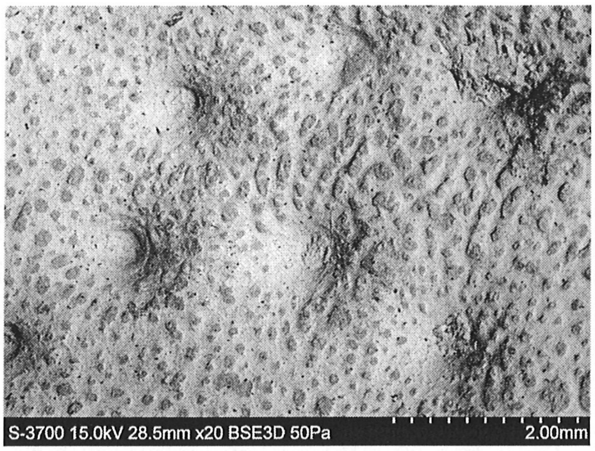

**Figure 6.** *Antineosteus rufus* sp. nov. NM Lc 125, holotype. SEM detail of dermal sculpture from the medial margin of the plate.

to subtropical marine environments (White 1978, Young 2003) with good connections to open seas (Mark-Kurik & Young 2003). Lelièvre (1984a) discussed the possible migration routes along the northern (Turkey, Iran, Afghanistan) or southern (South America) continental margins of Gondwana. The occurrence of *A. rufus* supports a northern migration route rather than southern. Considering the occurrence of the coeval and relative genus *Atlantidosteus* (Young 2003) in the Emsian of Morocco on the southern hemisphere and in the Eifelian of Australia (Queensland) that was close to the palaeoequator, makes this pattern of distribution more probable. The distribution of the seemingly endemic faunas (Denison 1984) could be in connection with the maximum transgression in the Emsian (Young 1987) thus related to the Daleje Event (House 1985, Chlupáč & Kukal 1988, Ferrová *et al.* 2012 and references therein). Mark-Kurik & Young (2003) note that the presence of large fishes in various strata is an indicative of palaeoclimatic conditions rather than of the palaeogeography.

The homostiids in general possessed edentulous jaws and were large sized (Mark-Kurik & Carls 2004). This combination of features is typical for planktivorous vertebrates. Such a mode of life was supposed by Denison (1978) for three arthodire genera including *Homostius*. Mark-Kurik (1992) compared the feeding strategy and the body size of this taxon to the modern whale shark. Mark-Kurik & Carls (2004) discussed a microphagous feeding behaviour of *Homostius* and *Antineosteus* with respect to the direct fossil evidence of their toothless jawbones. In the latter, the preserved inferognathal of *A. lehmani* is toothless or covered by dermal tubercles (Lelièvre 1984a, fig. 14, pl. IV. C, D). *A. rufus* and other large arthodires can be reasonably supposed as planktivorous (suspension feeders) as well even though their jawbones are unknown yet.

The occurrence of the giant *A. rufus* in the Emsian of the Prague Basin, in addition to other giant placoderms in the Lower Devonian worldwide suggests abundant food resources. It is significant that the very large homostiids such as *Tityosteus rieversae* Gross, 1960, *Dhanguura johnstoni* Young, 2004, *Cathlesichthys weejasperensis* Young, 2004, and *Antineosteus rufus* sp. nov., among which *A. rufus* is the largest, occurred globally in the Emsian and appeared almost coevally. This occurrence is considered to be another hitherto overlooked aspect (not to be confused with dominating giant predaceous placoderms in the Late Devonian; see Signor & Brett 1984) of a global event labelled as the Devonian Nekton Revolution (Klug *et al.* 2010).

The mentioned appearance of several giant homostiids during the Early Devonian represents an initial occupation of the free ecospace, which was repeatedly refilled by large bony fishes in most of the Mesozoic and by baleen whales, some rays and sharks in the Cenozoic (Friedman *et al.* 2010). Large homostiids, including *A. rufus*, are thus the oldest members of this ecological guild of large-bodied planktivorous vertebrates. These specialised forms appeared in such a stage of vertebrate evolution that allowed an effective reflection of the planktivourous feeding habit on the body size. This evolutionary advantage appeared in period of general plankton decline in diversity (Klug *et al.* 2010, Fig. 1). However, the occurrence of these placoderms is an indirect evidence that the water column was rich in nutrients and *e.g.* larvae and fry had to be abundant (naturally, not analysed by Klug *et al.* 2010).

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# Paper III

PLOS | ONE

RESEARCH ARTICLE

# Unique diversity of acanthothoracid placoderms (basal jawed vertebrates) in the Early Devonian of the Prague Basin, Czech Republic: A new look at *Radotina* and *Holopetalichthys*

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## Abstract

The taxonomy of Early Devonian placoderm material from the Lochkovian and Pragian of the Prague basin, previously attributed to the genera *Radotina* and *Holopetalichthys*, is revised. The Pragian species *Radotina tesselata* Gross 1958 shares detailed similarities with the holotype of the Lochkovian *Radotina kosorensis* Gross 1950, which is also the holotype of the genus; the assignation of both species to *Radotina* is supported. However, the Lochkovian material previously attributed to *Radotina kosorensis* also contains two unrecognised taxa, distinguishable from *Radotina* at the generic level: these are here named *Tlamaspis* and *Sudaspis*. The disputed genus *Holopetalichthys*, synonymised with *Radotina* by some previous authors, is shown to be valid. Furthermore, whereas *Radotina*, *Tlamaspis* and *Sudaspis* can all be assigned to the group Acanthothoracii, on the basis of several features including possession of a projecting prenasal region of the endocranium, *Holopetalichthys* lacks such a region and is probably not an acanthothoracid. Skull roof patterns and other aspects of morphology vary greatly between these taxa. *Radotina* has a substantially tesselated skull roof, whereas the skull roofs of *Tlamaspis* and *Holopetalichthys* appear to lack tesserae altogether. *Tlamaspis* has an extremely elongated facial region and appears to lack a premedian plate. *Sudaspis* has a long prenasal region, but unlike *Tlamaspis* the postnasal face is not elongated. Past descriptions of the braincase of '*Radotina*' and the skull roofs of '*Radotina*' and '*Holopetalichthys*' incorporate data from more than one taxon, giving rise to spurious characterisations including an apparently extreme degree of skull roof variability. These descriptions should all be disregarded.

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## Introduction

The early evolution of vertebrates has recently become a major research topic in vertebrate biology [1–8]. One of the main areas of interest is the gnathostome (jawed vertebrate) stem group, which is important from both evolutionary and phylogenetic perspectives. In evolutionary terms, the gnathostome stem group encompasses the origin of jaws and associated major changes in facial architecture [3,5,7]; in phylogenetic terms, it is a segment of the vertebrate tree whose content and topology has long been the subject of debate [9,10,11,1,2,3,4,6,7]. A key development in the understanding of this stem group has been the recognition that the placoderms (armoured jawed fishes of Silurian to Devonian age), which until recently were regarded as a clade branching off the gnathostome stem group, probably form a paraphyletic segment of that stem group [2,7,8] (but see [12]). Some groups of placoderms appear to be very primitive and close to jawless vertebrates [7] whereas others possess what were previously regarded as osteichthyan autapomorphies (notably a maxilla, premaxilla and dentary) and are probably close to the gnathostome crown-group node [6, 13].

Associated with this reinterpretation of the placoderms has been the recognition of homologies between the macromeric dermal skeleton of placoderms and osteichthyans [6], previously regarded by most workers as independently evolved ([14] but see [15] and [9]). Another Palaeozoic vertebrate group, the acanthodians ("spiny sharks"), which were previously seen as stem osteichthyans [16] or as a multiply paraphyletic array of stem gnathostomes, stem osteichthyans and stem chondrichthyans [2,4], are in the most recent analyses assigned in their entirety to the chondrichthyan stem group [6,7,8,17]. This leaves the upper part of the gnathostome stem group occupied entirely by placoderms, and gives rise to the idea of a "placoderm-osteichthyan continuum", where osteichthyans essentially continued the gradual development of the placoderm bauplan whereas chondrichthyans departed more radically from it, *inter alia* by losing their perichondral and macromeric dermal bones [18]. Detailed studies of primitive placoderms therefore have the potential to provide crucial information about the early evolutionary steps on the path leading to our own body plan.

Acanthothoracids display many morphological features which could be considered as basal for jawed vertebrates [13,19]. Yet their morphology is poorly known except for the genus *Romundina* [7,20,21] and they occur scarcely in the fossil record (e.g. [22–30]). The Prague Basin acanthothracid collection, as reinterpreted herein, is outstanding both in diversity of species and abundance of specimens.

Early vertebrate fossils have been collected in Bohemia (part of the present day Czech Republic) for more than 150 years. Most of the specimens are now housed in public collections (Národní Muzeum (National Museum) in Prague, Czech Geological Survey and the Faculty of Science, Charles University). The collections can be considered as non-selective because almost all the rare specimens were included [31]. The best preserved remains were discovered in the period of active, especially manual quarrying in the Prague Basin (see below). The majority of the specimens described here are deposited in the Národní Muzeum in Prague (abbreviated NM in text) and most of them belong to historical collections assembled since the second half of the 19th century. The most recent well-preserved specimens were collected during the second half of the 20th century. Only scarce fragments have been collected in recent decades.

The Bohemian placoderms were first described by Barrande [32]. He studied several specimens from the Pragian and Emsian (Lower Devonian), among them one acanthothoracid specimen. Another specimen from the Pragian was described by von Koenen [33]. The first descriptions of acanthothoracids from the Lochkovian were accomplished by Gross [34–36] during his several stays in Prague. He described all the specimens known and accessible at that time from the Lochkovian and Pragian in detail and erected four new species (genera *Radotina* and *Kosoraspis*). The last extensive study of the Lower Devonian material from the Bohemian collections by Westoll [37] was focused on morphological terminology and phylogenetic relationships rather than taxonomy of the studied material. No other attempt to revise the Prague Basin placoderm material had been made prior to the recent studies by one of the current authors [31,38,39].

This paper examines all specimens formerly assigned to the genus *Radotina* either in published papers or in the catalogue of the NM. The published data have often been mentioned in studies on phylogenetic relationships [10] or systematics [25,40]. However, our current research on this material is uncovering a great deal of new information, both from the previously described specimens and from the extensive undescribed material in the NM collections, that not only augments but frequently contradicts the published accounts. This paper represents the first step in a complete revision of the Bohemian acanthothoracid material. In a later paper we will also be examining the enigmatic genus *Kosoraspis* [35,36], but as its taxonomic distinctness from *Radotina* is not in dispute it will not be considered here.

## Material and methods

The majority of specimens considered in this paper belong to the Národní Muzeum (NM) in Prague (the collections of the Czech Geological Survey and Charles University contain no acanthothoracid material or specimens relevant to this study). Additional specimens from the collections of the Natural History Museum, London (NHM) and Humboldt Museum für Naturkunde, Berlin (HMN) are also discussed. The specimen numbers are listed in the Systematic palaeontology section below. No permits were required for the described study, which complied with all relevant regulations.

The collections of the NM house some 300 placoderm remains; among them 25 fragments are labelled as the genus *Radotina*, three as *Holopetalichthys* and another 30 as *Macropetalichtys*. 47 samples (each with a unique catalogue number; some of them counterparts or separately numbered broken pieces), catalogued either as belonging to one of these three genera or as "Placodermi indet.", were investigated for the purposes of this revision. All the studied specimens are of Devonian age and come from two localities in the Prague Basin.

All the specimens originally labelled *Radotina kosorensis* (most of them herein reclassified as the new genera *Tlamaspis* and *Sudaspis*) were found in the Radotín Limestone, a member of the basal Devonian (Lochkovian) Lochkov Formation (Fig 1B1) at the quarries in Černá rokle (Fig 1A1). The bony elements are very indistinct in the dark grey fine-grained matrix of the limestone when dry. Therefore all the specimens were coated with ammonium chloride before being photographed and illustrated. Some of them were mechanically prepared in the 1950s. Preparation with acetic acid (5–10%) was also tested by one of us (V.V.) on a single specimen of an isolated dermal plate, but it was unsuccessful as the bone tended to dissolve along with the matrix.

A smaller number of specimens described herein are from the Koněprusy Limestone, a member of the Lower Devonian (Pragian) Praha Formation (Fig 1B2), which is exposed in several localities near the village of Koněprusy (Fig 1A2). As the limestone is pure white and the bone elements have a reddish surface (caused by ferric oxide coating), the material could be photographed successfully without ammonium chloride coating. The Koněprusy Limestone is the only shallow water photic zone reef facies in the Prague Basin containing placoderms. The preserved specimens are distinctly smaller in size than the Lochkovian placoderms.

All the specimens were studied with an Olympus SZX9 optic microscope and the drawing in Fig 2A was made with a drawing attachment Olympus SZH-DA. The surface sculpture and fine details of suitable specimens were observed under the scanning electron microscope Hitachi S-3700N and Keyence VHX-2000 digital microscope.

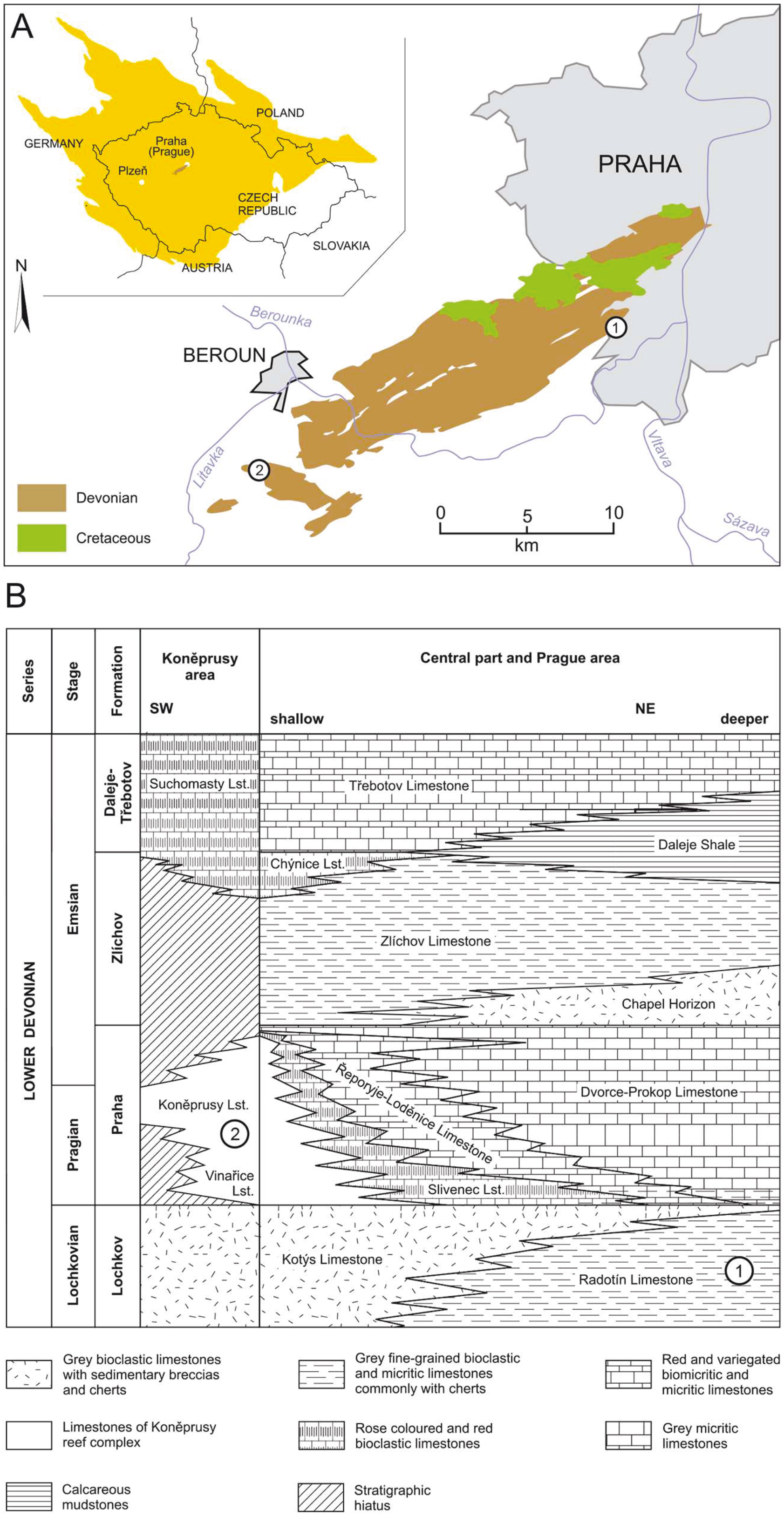

**Fig 1. Devonian of the Prague Basin.** (A) Upper left: Location of Devonian sediments (brown) in the central part of the Bohemian Massif (yellow). Right: Simplified map of the Devonian distribution. Tectonics omitted,

the marine Cretaceous cover is displayed with respect to the known extent of the Devonian, younger continental units omitted; (B) Stratigraphic chart of the Lower Devonian in the Prague Basin. Numbers represent the fossil sites: 1 Černá rokle near Kosoř; 2 Koněprusy. Modified from [31] after [41].

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### Nomenclatural acts

The electronic edition of this article conforms to the requirements of the amended International Code of Zoological Nomenclature, and hence the new names contained herein are available under that Code from the electronic edition of this article. This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the ICZN. The ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information viewed through any standard web browser by appending the LSID to the prefix "http://zoobank.org/". The LSID for this publication is: urn:lsid:zoobank.org:pub:ADCE-BED8-B1A1-42E6-B20A-C2DF1FEDB072. The electronic edition of this work was published in a journal with an ISSN, and has been archived and is available from the following digital repositories: PubMed Central, LOCKSS.

## Geological and palaeontological settings

The Černá rokle (= Black Gorge) quarries are situated in the south-eastern part of the Prague Basin in the Radotín Valley (Fig 1A1). Several quarries were operating there from the 19th century until the 1960s. Perner [42] noted a major increase in fossil fish discoveries at the beginning of the 20th century when closer contacts were established between the quarry workers and the local fossil collectors. The rocks were being quarried and processed by hand to make paving setts, and the workers were instructed and well trained in detecting precious finds. Those were then sold to the collectors, recruited from the local intellectual elite. The largest collections were amassed by A. Schubert (postmaster), F. J. Pecka (local teacher), W. Kolář (clerk) and R. Růžička (engineer); the collection of the late professor I. Chlupáč also contained a few finds acquired in his youth. The majority of these collections were donated to the NM, over the course of several decades. Crucially, important material was donated after Walter Gross had finished his studies of the NM placoderm collections in 1959, and is described here for the first time. After the quarrying ceased only collecting in debris was possible at the locality.

The outcrop represents a parastratotype of the Lochkovian/Pragian boundary and the stratotype of the boundary between the Lochkov and Prague formations [41]. The Devonian succession starts in the eastern quarries with the uppermost layers of the Lochkov Formation (Fig 1B1) composed of dark greyish platy fine-grained limestone alternating with calcareous shale facies (Radotín Limestone; [43]). Both facies are rich in invertebrate fossils [41], including bivalves (genera *Panenka*, *Neklania*, *Hercynella*, *Leiopteria*), gastropods (genera *Loxonema*, *Raphistomina*), hyoliths (*Orthotheca suavis*), tentaculites (*Paranowakia intermedia*, *P. geinitziana*, *Nowakia kobylica*), orthocone cephalopods, eurypterids (genus *Acutiramus*), phyllocarid crustaceans (genus *Ceratiocaris*), trilobites (genera *Spiniscutellum*, *Lochkovella*, *Lepidoproetus*, *Leonaspis*), brachiopods (genera *Howellella*, *Areostrophia*, *Plectodonta*) and graptolites (genus *Monograptus*). Vertebrate fossils include placoderms [41] and acanthodians (*Machaeracanthus bohemicus;* [44]).

The historical specimens with the lithological unit "upper part of the Koněprusy Limestone" written on the original label were most probably found at Houba´s Quarry on the southern slope of the Zlatý kůň Hill near the village of Koněprusy (Fig 1A2). Houba´s Quarry was among the first quarried in the area, exposed from 1869, and the locality is considered to

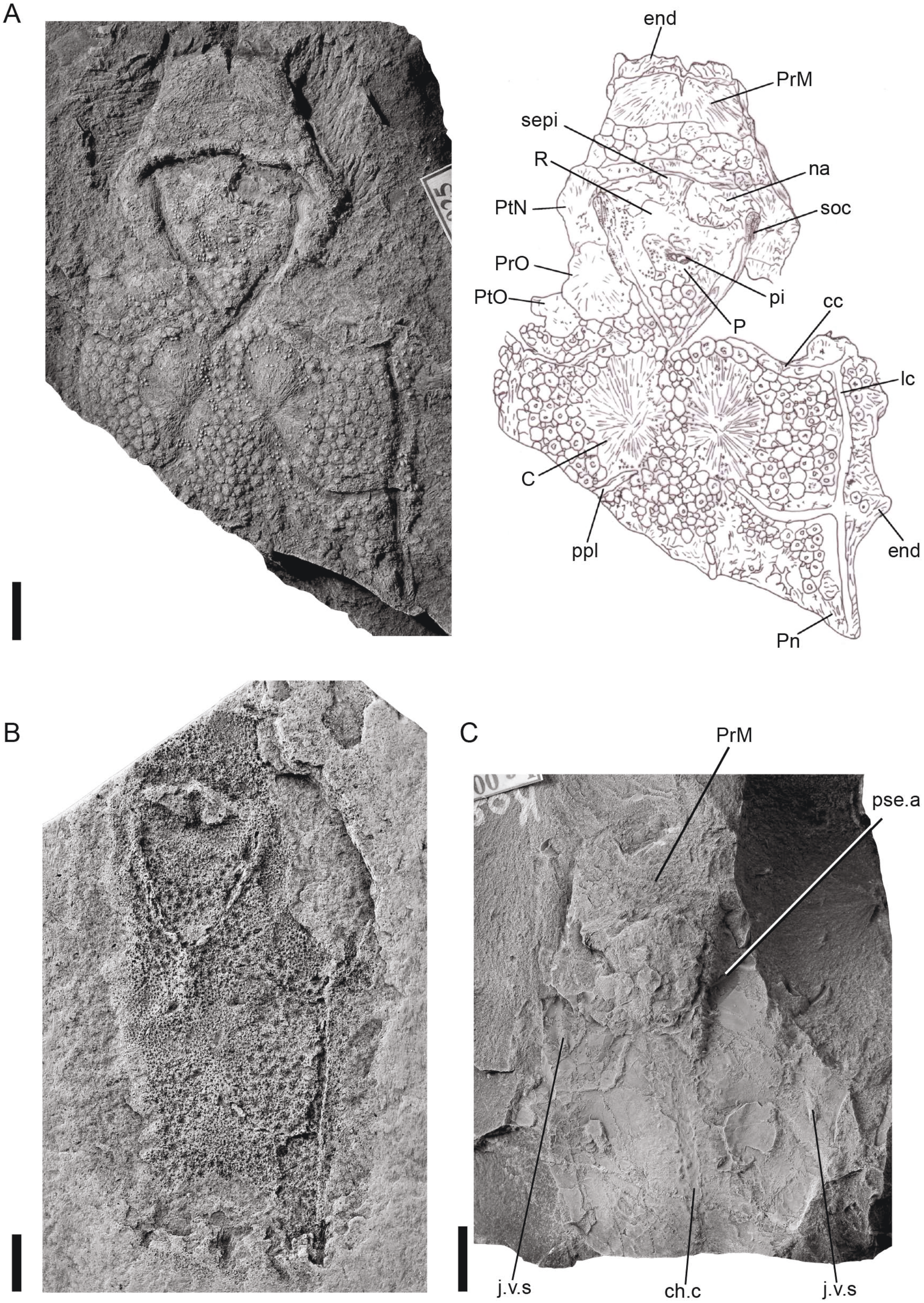

**Fig 2. *Radotina kosorensis* Gross, 1950.** (A), holotype, NM Lc 25, skull roof; (B), natural mould of external surface of skull roof, NHM P.12829; (C), anterior part of skull roof with endocranial base, NM Lc 461. Scale bars = 10 mm. Abbreviations: C central plate; cc central sensory line groove; ch.c chordal canal; end endocranium; j.v.s secondary jugular vein; lc lateral sensory line groove; na nasal openings; P pineal plate; pi pineal organ; Pn paranuchal plate; ppl

posterior pitline; PrM premedian plate; PrO preorbital plate; pse.a efferent pseudobranchial artery; PtN postnasal plate; PtO postorbital plate; R rostral plate; sepi internasal septum; soc supraorbital sensory line groove.

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be the one visited by J. Barrande [45]. The white massive limestones are either of biogenic origin, built by reef forming activities of visually recognisable sessile organisms surrounded by fine-grained micrite matrix, or coarse-grained bioclastic limestone composed of solid organic remains (Fig 1B2). They contain rich invertebrate fauna of around 500 species including stromatoporoids (genus *Actinostroma*), corals (genera *Favosites*, *Heliolites*, *Xystriphyllum*, *Pseudochonophyllum*), gastropods (genus *Platyceras*), bivalves, rostroconchs (genus *Conocardium*), trilobites (genera *Radioscutellum*, *Lioharpes*, *Gerastos*), brachiopods (genera *Sieberella*, *Hysterolites*, *Stenorhynchia*, *Eoglossinotoechia*, *Cymostrophis*, *Rynchospirina*), bryozoans (genera *Fenestella*, *Hemitrypa*, *Utropora*, *Semicoscinium*) and phyllocarid crustaceans [41]. Placoderms occur with rare specimens of large acanthodians (the genus *Machaeracanthus* may have reached 2 metres in length; [44]) and orthoconic cephalopods (genus *Ptenoceras*) in the Koněprusy Limestone.

## Systematic palaeontology

Class **Placodermi** M'Coy, 1848 [46]

Order **Acanthothoraci** Stensiö, 1944 [22]

Family **Palaeacanthaspidae** Stensiö, 1944

Genus ***Radotina*** Gross, 1950 [34]

(Figs 2 and 3)

**Diagnosis.** Jawed vertebrate possessing a broad, flat endocranium with an anterior prenasal expansion of the trabecular region. Skull roof composed of individual small plates separated by fields of tesserae. The rostronasal capsule in dorsal position, posterior to a trapezoidal premedian area. Dorsal margin of orbit formed by three dermal plates. The rostral plate wide but anteroposteriorly short, forming a transverse bar above the dorsal margins of the nostrils. The small pineal plate, bounded by tesserae posteriorly, has a smoothly curved posterior margin, prominent lateral corners, and a transverse anterior margin. No pineal foramen. The central plates small, widely separated and of oval shape. The ornament on the dermal plates and tesserae composed of small star-shaped tubercles, each with five to six ridges that are large relative to the central body of the tubercle.

**Type species.** *Radotina kosorensis* Gross, 1950

***Radotina kosorensis* Gross, 1950**

(Fig 2)

1950 *Radotina kosorensis* Gross; Gross [34]: pp. 113–118, fig. 1A.
1958 *Radotina kosorensis* Gross; Gross [35]: pl. 1, fig. 1–2, pl. 2, fig. 1–2; textfig. 1–2.
1959 *Radotina kosorensis* Gross; Gross [36]: pl. 3, fig. 6; textfig. 1A
1967 *Radotina kosorensis*; Westoll [37]: pp. 83–98, fig. 2A.
1969 *Radotina kosorensis* Gross; Stensiö [47], fig. 106A.
1971 *Holopetalichthys kosorensis*; Moy-Thomas & Miles [48], p. 185, fig. 8.18B.
1975 *Radotina kosorensis* Gross; Ørvig [40], pp. 45–48, 53, 66, fig. 1C.
1978 *Radotina kosorensis* Gross; Denison [25], p. 36, fig. 22B.
1984 *Radotina kosorensis* Gross; Goujet [10], pp. 228–231, fig. 8A, 12.
1993 *Radotina kosoriensis*; Lelièvre et al. [27], p. 156, fig. 7.6O.
1996 *Radotina kossorensis*; Janvier [49], p. 170, fig. 4.57H.
1998 *Holopetalichthys kosorensis* (Gross); Chlupáč [41], p. 107.
2002 *Radotina kosorensis*; Roček [50], p. 148–149, fig. 208.

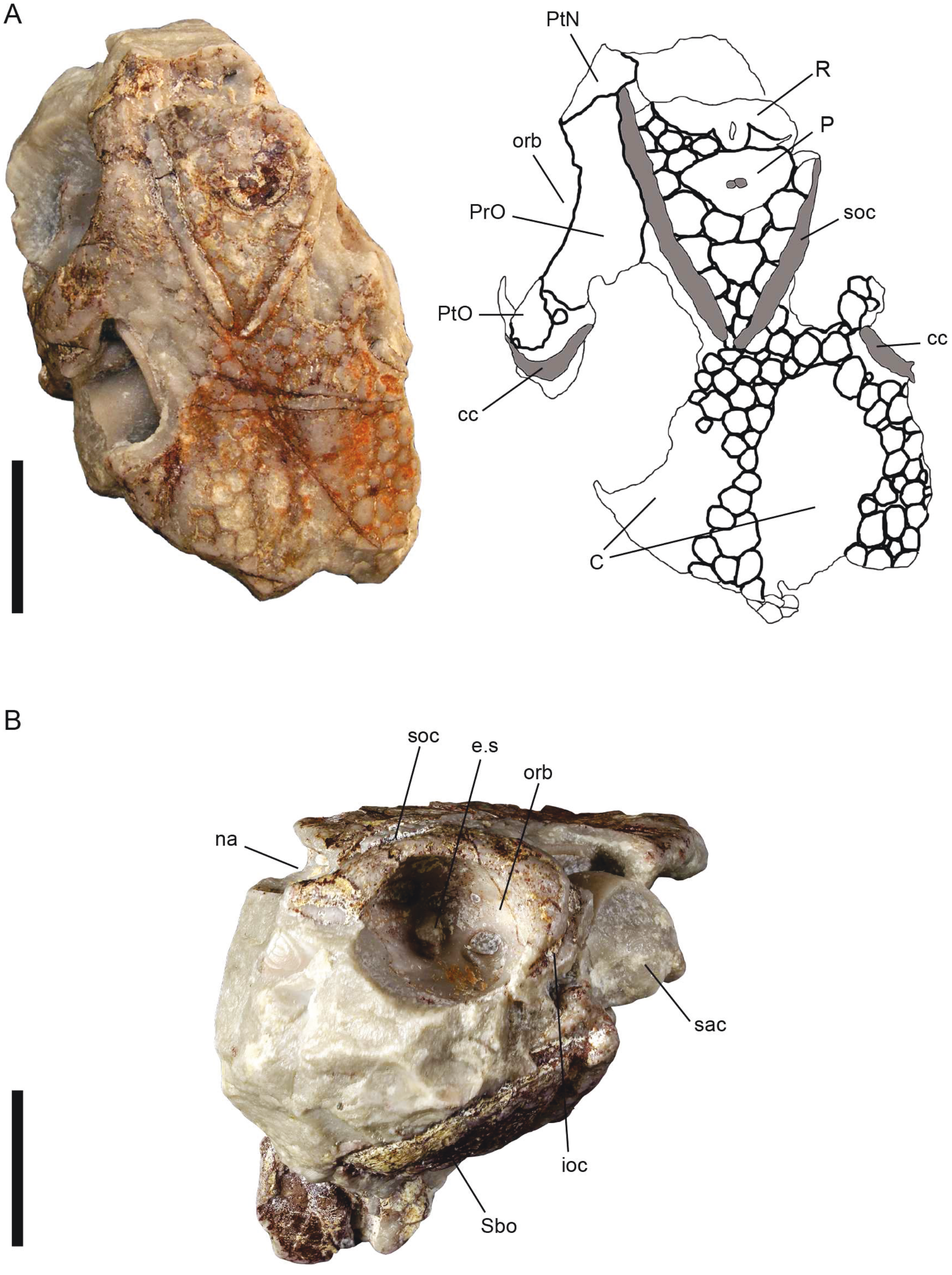

**Fig 3. *Radotina tesselata* Gross, 1958; holotype, NM Lc 95.** (A), dorsal view; (B), left lateral view; Scale bars = 10 mm. Abbreviations: C central plate; cc central sensory line groove; e.s eye stalk; ioc infraorbital sensory line groove; na nasal openings; orb orbit; P pineal plate; PrO preorbital plate; PtN postnasal plate; PtO postorbital plate; R rostral plate; sac sacculus of the inner ear; Sbo suborbital plate; soc supraorbital sensory line groove.

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2009 *Radotina kosorensis* Gross; Vaškaninová [51], p. 195.

2011 *Radotina kosorensis* Gross; Vaškaninová [38], p. 52.

**Diagnosis.**The trapezoidal prenasal part of the skull roof is formed by a short premedian plate and a posterior band of tesserae. The slightly curved central sensory line parallels the anterior margin of the central plate.

**Holotype.** Incomplete skull roof. Figured by: Gross [35], tab. 1, fig. 1, 2; tab. 2, fig. 1; textfig. 1, 2; Gross [36], tab. 3, fig. 6; textfig. 1A. Housed in the Národní Muzeum in Prague with inventory number NM Lc 25 (Fig 2A).

**Type horizon.** Lower Devonian, Lochkovian; Lochkov Formation, Radotín Limestone.

**Type locality.** Černá rokle quarries near Kosoř in Prague-Radotín.

**Material.** Skull roofs NM Lc 25, NHM P.12829 (Natural History Museum, London); endocranium NM Lc 461 (and counterpart NM Lc 462).

**Remarks.** Much of the material formerly assigned to *Radotina kosorensis* is here split off into the new genera *Tlamaspis* and *Sudaspis* (see below). These new taxa differ from *Radotina* in major aspects of cranial morphology, justifying separation at the generic level. NHM P.12829 and NM Lc 461 are, along with the holotype, the only specimens that can securely be referred to *Radotina kosorensis*. The scales attributed to *Radotina kosorensis* by Gross [36] and subsequent authors are not associated with any of these specimens. For the present they should formally be regarded as indeterminate, but their characteristic tubercle morphology suggests that they may belong to *Kosoraspis* (pers. obs. VV).

**Description.** The holotype (Fig 2A) and the so-called London specimen [35] (NHM P.12829; Fig 2B) are both incomplete skull roofs, exposed in dorsal view, that extend from the premedian plate posteriorly to the anterior part of the paranuchal plate. The holotype consists of an actual dermal skeleton whereas the London specimen is a natural mould. They do not represent the same individual.

The skull roof is composed of several dermal plates separated by fields of tesserae. In contrast to the dermal plates, the tesserae are composed of a single superficial shallow layer and are very similar to body scales [35,36]. The trapezoidal premedian plate (Fig 2A and 2C) is twice as wide as long. The ossification centre lies at its anterior border. A band of tesserae borders the posterior margin of the premedian plate and reaches towards the nostrils. The nostrils face dorsally, and the orbits are positioned posterolaterally to the nostrils. In the holotype the dorsal margins of the orbits are formed by three smaller well developed plates interpreted as the postnasal, preorbital and postorbital plates. The postorbital does not reach the posterior margin of the postorbital process and does not carry the infraorbital sensory line groove. In NHM P.12829 only two plates form the orbital margin, but a possible third plate lies between these two plates and the supraorbital lateral line groove (Fig 2B). However, it is difficult to understand the pattern as the specimen is an imperfect natural mould.

The supraorbital sensory lines emerge close to the ossification centres of the postnasal plates and continue along the mesial margins of the postnasal and preorbital plates. The supraorbital sensory lines and the nostrils outline the rostropineal area. The rostral plate is wide and anteroposteriorly short, forming a transverse bar above the dorsal margins of the nostrils. It is better preserved on the London specimen, where it touches the anterior margin of the pineal plate (Fig 2B). The small pentangular pineal plate has a smoothly curved posterior margin, prominent lateral corners, and a transverse anterior margin. There are twin recesses for the pineal and parapineal organs, positioned side by side, but no pineal foramen. The posterior part of the rostropineal area is covered by tesserae.

The central plates are oval and show slight elevations anteriorly, posteromesially and posterolaterally that appear to correspond to the underlying auditory capsules with semi-circular canals [37]. They are separated by a narrow band of tesserae and occupy the position between the central and the posterior sensory lines. Posterior to the central plates only tesserae are present. However, Gross [36] noted some faint radiating striae resembling the middle layer of a bony plate in the posterolateral corner of the holotype near the main sensory line canal (Fig 2A). We interpret this as the anterior end of the paranuchal plate. (Note that we refer to the plate that forms the posterolateral corner of the skull roof as a "paranuchal" or "posterior paranuchal" in different taxa, depending on whether a bone identified as an "anterior paranuchal" is present. This is somewhat unsatisfactory but follows standard usage in the placoderm literature [25].) The anterior part of the skull roof, from the premedian plate as far back as the centrals, has proportions very similar to *Romundina stellina* [21]; the only noteworthy difference is that *Radotina kosorensis* has smaller orbits. However, the posterior part of the skull roof appears to be considerably longer in *R*. *kosorensis* than in *Romundina stellina*.

The ornament on the dermal plates and tesserae is composed of small star-shaped tubercles, each with five to six ridges that are large relative to the central body of the tubercle. On the central plates the tubercles are restricted to the marginal areas, where they are arranged concentrically. The tesserae are tiny plates, each carrying an individual tubercle or a small group.

The sensory lines have the form of deep, wide-open grooves. They do not cross the ossification centres of the bony plates. Their pattern is most clearly seen on the holotype (Fig 2A). The supraorbital sensory lines are deep, gradually widening in the anterior part. The anterior part of the main sensory line and the central sensory lines are separated from the postorbital plate by a band of tesserae. The central sensory line is gently S-shaped and runs towards the connection of the supraorbital grooves. The posterior sensory line curves anteriorly, ending just posterior to the central plate. Where a sensory line groove passes through a tesserate area, it passes between rather than through individual tesserae, and the pattern of the tesselation is somewhat disturbed. In a few areas, notably on the main sensory line posterior to its junction with the posterior sensory line, a separate lining for the sensory canal itself is preserved within the groove. This lining is composed of very thin bone with fine transverse striations and presumably lay within the membranous wall of the sensory line canal.

The median part of the endocranial base is preserved on the specimen NM Lc 461 (and its counterpart NM Lc 462; Fig 2C). This specimen does not show the dermal skull roof, but is assigned to *Radotina kosorensis* because of the similar proportions of the premedian region. As is frequently the case in specimens from Černá rokle, the split between slab and counterslab does not follow a single plane; in the middle and posterior parts, the split mainly follows the internal face of the perichondral bone floor of the braincase (though it jumps to the floor of the sacculus on both sides), but anteriorly it rises through the telencephalic region of the braincase before entering the basal layer of the dermal bone of the premedian region. The endocranium has a roughly rhombic shape with markedly projecting postorbital processes. The most striking feature of the endocranium is the imprint of the notochordal canal that is surrounded by a vascular web and several openings. The notochord reaches far forward, ending anterior to the postorbital processes. Other prominent features are traces of canals on the lateral margins of the endocranial base, possibly branches of the jugular vein, and anteriorly a curved transverse groove for the pseudobranchial artery. The telencephalic recesses and olfactory nerve canals can be seen in section.

***Radotina tesselata* Gross, 1958**

(Fig 3)

1950 *Radotina* sp. Gross; Gross [34], pp. 113–118, fig. 1C.
1958 *Radotina tesselata* n. sp.; Gross [35], pl. 2, fig. 3, 4, pl. 3, fig. 1–4; textfig. 3–5.
1959 *Radotina tesselata;* Gross [36], pp. 3, 4, 9.
1967 *Radotina tesselata;* Westoll [37], pp. 83–85, 88.
1969 *Radotina tesselata* Gross; Stensiö [47], fig. 51, 104 B.

1975 *Radotina tesselata* Gross; Ørvig [40], pp. 45, 48, 63, 64, 66.
1978 *Radotina tesselata* Gross; Denison [25], p. 36.
1984 *Radotina tesselata*; Goujet [10], pp. 230, 231, fig. 12.
1986 *Radotina tesselata*; Young [11], p. 17, fig. 7C.
2009 *Radotina tesselata* Gross; Vaškaninová [51], p. 195.
2011 *Radotina tesselata* Gross; Vaškaninová [38], p. 52

**Diagnosis.** The only known specimen is much smaller than *R. kosorensis*. The central sensory line canals point anteriorly and do not parallel the margins of the central plates. The supraorbital canals form a more acute angle than in *R. kosorensis*. Tesserae in the rostronasal area bigger than tesserae on the rest of the skull roof.

**Holotype and only specimen.** Anterior part of the cranium, missing the prenasal region. Figured by Gross [35], pl. 2, fig. 3, 4; pl. 3, fig. 1–4; textfig. 3–5. Housed in the Národní Muzeum in Prague with inventory number NM Lc 95 (Fig 3).

**Type horizon.** Lower Devonian, Pragian; Praha Formation, Koněprusy Limestone.

**Type locality.** Koněprusy near Beroun, south-east of Prague, probably the area of the present day Houba´s Quarry.

**Remarks.** Gross [35] describes one specimen of this species only–the holotype. It is a three-dimensional cranium with badly preserved ornamentation of the skull roof plates. The prenasal region and the area posterior to the centrals are missing. Both orbits and nostrils were prepared by a technician of W. Gross. Later a part of the endocranial base was prepared away by an unknown technician to expose the posterior part of the perichondrally lined brain cavity and ventral parts of the inner ear cavities. Although this specimen is much smaller than the holotype and other specimens of *Radotina kosorensis*, it has a partly ossified braincase (missing only the premedian region) and is thus presumably close to adult size.

**Description.** The pattern of the skull roof plates is similar to *R. kosorensis* (Fig 3A), although the premedian plate is unknown. Postnasal, preorbital and postorbital plates border the dorsal margin of the orbits. The supraorbital sensory line emerges at the posteromesial margin of the small postnasal plate and continues posteriorly along the mesial margin of the large preorbital plate. The postorbital plate is small and does not carry any sensory line canal. The pineal plate is small with prominent anterolateral corners. It covers both recesses for the pineal and parapineal organs and does not display a pineal foramen. The rest of the rostropineal area is covered by tesserae substantially larger than the ones covering the rest of the skull roof. The outline of the rostral plate is unclear, but it is evident that tesserae are present also anterior to the pineal plate. The central plates are oval with no sensory lines crossing. They are separated by tesserae.

The supraorbital sensory lines form a more acute angle (approx. 60˚) than in *R. kosorensis* (70˚ on the holotype). The infraorbital sensory line groove runs along the posteroventral margin of the postorbital plate. A similar groove on the ventral margin of the postnasal plate may represent its anterior continuation. The central sensory line parallels the orbit and the posteromesial margin of the postorbital plate, pointing anteromesially towards the spot where the supraorbital sensory line touches the margin of the preorbital plate. This contrasts with the condition in *R. kosorensis* (see above), where the central sensory line is transverse and gently S-curved. All sensory lines are developed as deep and wide canals. In a few areas the grooves are covered by a thin bony lamina representing the wall of the canal itself, as described for *R. kosorensis*.

Two dermal plates are clearly visible on the left lateral side of the holotype (Fig 3B). Gross [35] described them tentatively as "mandibulare". A slightly curved sensory line is detectable on both plates. We interpret the larger plate as the left suborbital, which is supported by its position relative to the orbit. The second plate could be a broken and displaced right suborbital plate.

The nasal cavities, which face anteriorly, are placed medially to the anterior ends of the supraorbital sensory lines. They have an oval shape and were separated by a thin, incompletely closed septum internasale ([35]; unpreserved at present). The posterior wall of each cavity is formed by a lamina cribrosa pierced by numerous perichondrally lined canals for branches of the olfactory nerve. Imprints of blood vessels supplying the olfactory organ are preserved on the capsulae walls.

The orbits, which are relatively larger than in *Radotina kosorensis*, occupy an anterior lateral position, posterior to the nostrils. Their inner space is wider than the opening and reaches beyond it towards the area of the central sensory lines. Medially the orbit reaches the level of the supraorbital sensory lines. The internal surface of the orbits shows apertures for nerves and blood vessels, as well as a small triangular eye stalk (Fig 3B). A large opening for the optic nerve lies anterior to the eye stalk. The aperture for the jugular vein is situated in the postero-lateral area of the orbit.

The otic part of the cranial cavity in the posterior ventral part of the holotype (posterior to the orbits and the dislocated suborbital plate) has been prepared by an unknown technician. The ventral and partly lateral sides of the cavities lined by a thin perichondral lamina are exposed. Anteriorly the remains of a narrow endocranial base—the medullar part of the endocranial cavity—are visible. The most prominent structures are the sacculi with the semicircular canals.

**Genus *Tlamaspis* gen. nov.** *urn:lsid:zoobank.org:act:E4B78421-D50B-4D38-BDB3-16B34C37E489*

(Figs 4–6)

**Diagnosis.** Jawed vertebrate possessing a broad, flat endocranium with an anterior prenasal expansion of the trabecular region. Prenasal area very long, occupying at least one quarter of the whole length of the endocranium. Premedian area of the endocranium contains an elaborate canal network. Glenoid region of endocranium broad. Grooves of lateral aortae on ventral wall of endocranium deeply impressed, lyre-shaped, continuing forward to hypophysial fossa. Endocranial surface rugose between grooves of lateral aortae. Grooves of secondary jugular veins deeply incised, narrow, s-curved, main mesial branch attached posterior to crossing of efferent pseudobranchial artery. Dermal skull roof contains one pair of large oval central plates, meeting in the midline anteriorly but posteriorly separated by the nuchal plate. Premedian plate absent. Posterior margin of dermal skull roof forms a projecting midline point created by the nuchal. Dermal ornament consists of small, rounded tubercles with eight to nine moderately prominent ridges.

**Derivation of name.** After the Czech/Slovak word for large mouth–“tlama”, and the Greek “aspis” (shield).

**Type and only known species.** *Tlamaspis inopinatus* sp. nov.

**Remarks.** Most of the specimens we redescribe as a new genus *Tlamaspis* were originally included in *Radotina kosorensis* by Gross [36]. In fact they differ from this taxon in numerous respects including the absence of a premedian plate, very large central plates that contact each other and the nuchal plate without intervening tesserae, tubercles of a distinctive morphology, and an elongate prenasal region. Previous authors [35,36,37,10] have explained the absence of tesserae in the *Tlamaspis* specimens, in contrast to their presence in *Radotina kosorensis*, either as individual variation or as due to taphonomic processes. However, taphonomic loss can be ruled out, because the marginal areas of the central and nuchal plates of *Tlamaspis* (which, under the taphonomic hypothesis, would in the holotype of *Radotina kosorensis* lie underneath fields of tesserae) are covered with firmly attached tubercles and have clearly not been exposed

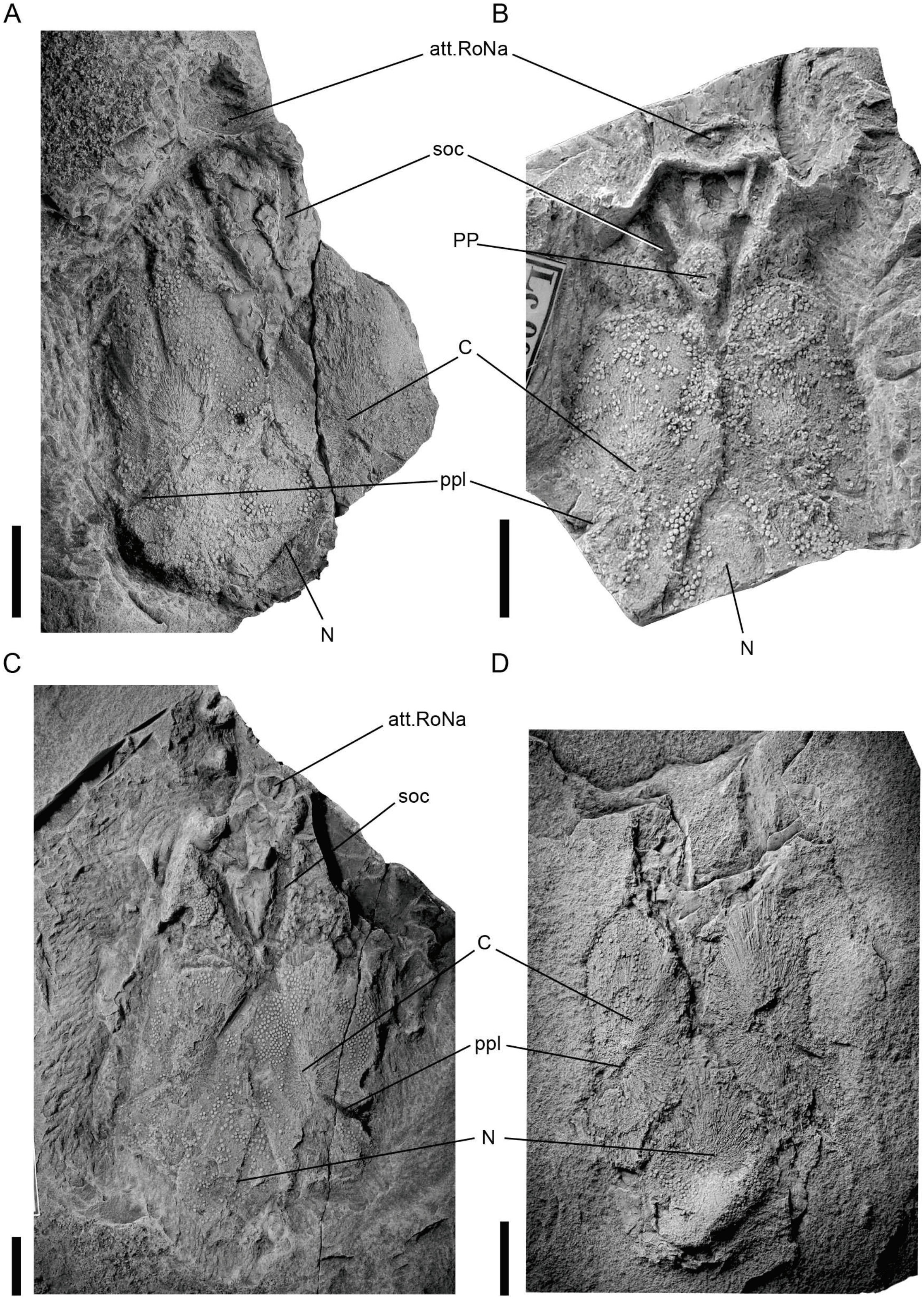

**Fig 4. *Tlamaspis inopinatus* gen. et sp. nov. Skull roofs.** (A), holotype, NM Lc 34, skull roof attached to endocranium; (B), central part of skull roof, NM Lc 29; (C), nearly complete skull roof, NM Lc 22; (D), skull roof, NM Lc 491. Scale bars = 10 mm. Abbreviations: att.RoNa attachment for rostronasal capsule; C central plate; N nuchal plate; PP postpineal plate; ppl posterior pitline; soc supraorbital sensory line groove.

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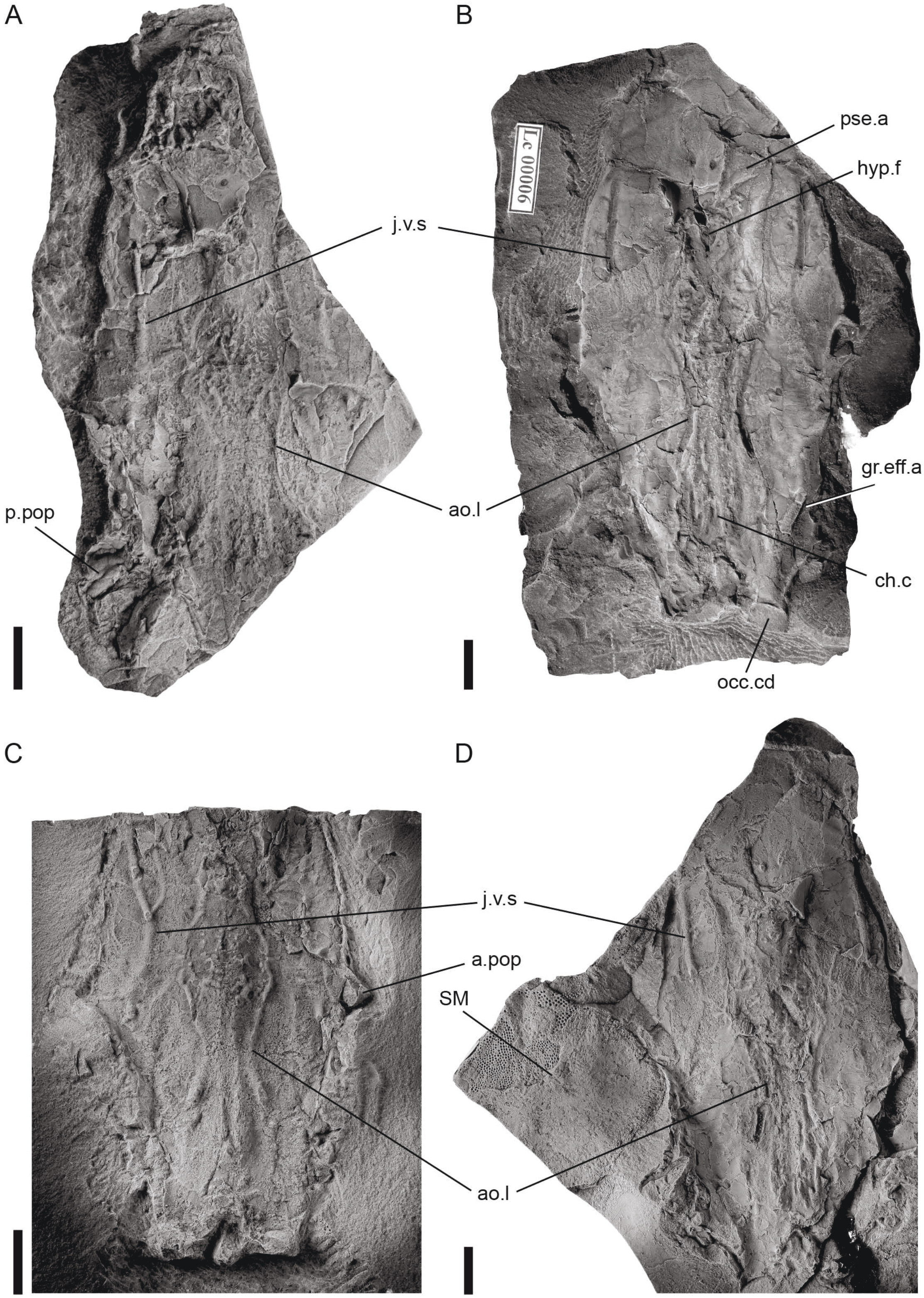

**Fig 5. *Tlamaspis inopinatus* gen. et sp. nov. Endocrania.** (A), holotype, NM Lc 35, endocranial base with rostronasal region; (B), endocranial base (counterpart of NM Lc 7), NM Lc 6; (C), posterior part of endocranial base, NM Lc 9; (D), endocranial base with rostronasal region and inner cast of submarginal plate, NM Lc 7. Scale bars = 10 mm. Abbreviations: ao.l lateral aorta; a.pop anterior postorbital process; ch.c chordal canal; gr.eff.a groove for the common efferent artery; hyp.f hypophyseal fenestra; j.v.s secondary jugular vein; occ.cd occipital condyle; p.pop posterior postorbital process; pse.a efferent pseudobranchial artery; SM submarginal plate.

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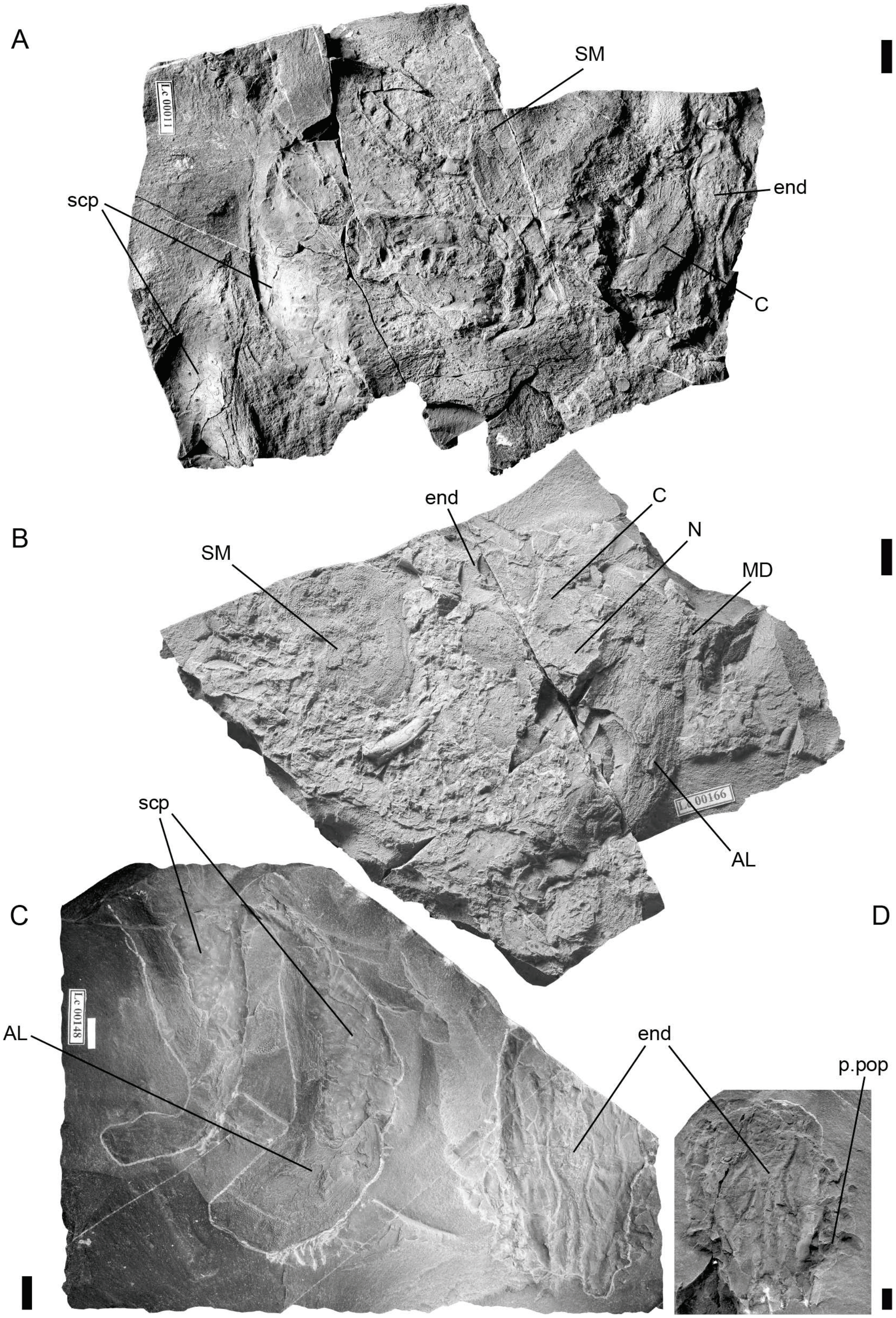

**Fig 6. *Tlamaspis inopinatus* gen. et sp. nov. Associated skull roofs, cheek and thoracic plates.** (A), NM Lc 11; (B), NM Lc 166; (C), posterior part of endocranial base associated with both shoulder girdles, NM Lc 148; (D), posterior part of endocranial base (counterpart of NM Lc 148), NM Lc 467. Scale bars = 10 mm. Abbreviations: AL anterior lateral plate; C central plate; end endocranium; MD median dorsal plate; N nuchal plate; p.pop posterior postorbital process; scp scapulocoracoid; SM submarginal plate.

https://doi.org/10.1371/journal.pone.0174794.g006

by post mortem stripping-off of tesserae. Individual variation is difficult to formally disprove without a statistically significant morphometric sample, but we note that all the *Tlamaspis* specimens are consistently similar, and different from *Radotina kosorensis*, with respect to the characters mentioned above.

***Tlamaspis inopinatus* sp. nov.** *urn:lsid:zoobank.org:act:874093B8-ED0C-4133-8418-1DCA118E945E*

(Figs 4–6)

1959 *Radotina kosorensis* Gross [36]; Gross, pl. 1; pl. 2, fig. 1–5; pl. 3, fig, 1–4, 7; pl. 4, fig. 3; pl. 5, fig. 3–4; textfig. 1B-E; 2A, D-E; 3; 4A;

1969 *Radotina kosorensis* Gross [47]; Stensiö, fig. 9B, 105A, 193A.

1975 *Radotina kosorensis* Gross; Ørvig [40], fig. 1B.

1978 *Radotina kosorensis* Gross; Denison [25], fig. 2E, 6E.

2002 *Radotina kosorensis*; Roček [50], fig. 205.

**Diagnosis.** As for genus.

**Derivation of name.** From Latin *unexpected*.

**Holotype.** Endocranium with medial skull roof plates. Figured by Gross [36] tab. 2, fig. 1,3, textfig. 1B. Housed in the Národní Muzeum in Prague with inventory number NM Lc 34 (and counterpart Lc 35; Figs 4A and 5A).

**Type horizon.** Lower Devonian, Lochkovian; Lochkov Formation, Radotín Limestone.

**Type locality.** Černá rokle near Kosoř in Prague-Radotín.

**Material.** endocrania NM Lc 6 (and counterpart NM Lc 7), NM Lc 8 (and counterpart NM Lc 9), NM Lc 10, NM Lc 34 (and counterpart NM Lc 35); endocrania with attached skull roof plates NM Lc 22 (and counterpart NM Lc 23), NM Lc 29, NM Lc 491; endocranium associated to shoulder girdle NM Lc 148 (and counterparts NM Lc 467 and NM Lc 471); endocrania associated to shoulder girdle, cheek and other dermal plates and bony elements NM Lc 11 (and counterparts NM Lc 12 and NM Lc 13), NM Lc 165 and NM Lc 168 (and counterpart NM Lc 489), NM Lc 166 (and counterpart NM Lc 167); shoulder girdle NM Lc 19 (and counterpart NM Lc 20), NM Lc 463 (and counterpart NM Lc 464); shoulder girdle associated with scales NM Lc 174 (and counterpart NM Lc 175), NM Lc 197.

**Description.** The skull roof is dominated by a pair of large, oval central plates, which meet in the midline but are separated posteriorly by a teardrop-shaped nuchal plate (NM Lc 22, NM Lc 29, NM Lc 34, NM Lc 491; Fig 4). Each central plate has a distinct, raised area in the middle, with a strongly radial texture and few or no tubercles. The nuchal plate is large, tapering anteriorly, and has a posterior oval projection that covers the underlying occipital process of the endocranium. The central and nuchal plates all have well-defined margins, but they are not quite as tightly joined as the bones of a typical sutured skull roof (see for example *Holopetalichthys*, below). Tesserae are absent between these plates. No premedian plate is present in any specimen, even though the premedian region is preserved; we infer that it is genuinely absent. The rostronasal capsule is not preserved, but its attachment area on the braincase is small. A small rhombic postpineal plate situated between the supraorbital sensory lines is known only in one specimen (NM Lc 29; Fig 4B). The supraorbital sensory lines are deep, and usually leave impressions on the dorsal side of the endocranium (Fig 4A–4C). They form a narrow V shape and meet behind the small postpineal plate. The central plates carry anteromedially directed posterior sensory lines running in the direction of the ossification centres, as well as middle and anterior pit lines. The remaining sensory lines and the openings for the endolymphatic ducts are unknown. The dermal ornament consists of small, rounded tubercles with eight to nine moderately prominent ridges.

On specimen NM Lc 7 (Fig 5D) the inner surface of a relatively large submarginal plate is exposed adjacent to the postorbital process. Similar large oval submarginal plates are present in specimens NM Lc 11–13, NM Lc 165 and NM Lc 166 (Fig 6A and 6B). Anteriorly and posteriorly to the submarginal plate of NM Lc 7, and laterally to the endocranium, lie two other damaged plates that are difficult to identify. The posterior one could be the dorsal margin of the anterior lateral plate.

Specimens NM Lc 11–13, NM Lc 165 and NM Lc 166 (Fig 6A and 6B) display a cluster of tubular bony endoskeletal elements in various states of preservation in the area between the endocranium and the suborbital plate. We interpret them as elements of the visceral skeleton, most probably the gill arches.

The thoracic shield of *Tlamaspis* is incompletely known. The most frequently preserved shoulder girdle element is the anterior lateral (AL) plate with the perichondrally ossified scapulocoracoid firmly attached to its mesial side, which is seen more or less clearly in NM Lc 11, NM LC 148 and NM Lc 166 (Fig 6). Gross [36] was unsure about the taxonomic identity of the few isolated anterior lateral plates from Černá rokle that he was able to study. Their determination to the genus *Tlamaspis* is now confirmed by specimen NM Lc 148 (Fig 6C), which was unknown to him. The anterior lateral plate is narrow, tall and crescent shaped with the postbranchial lamina situated on the concave margin. Anteroventrally it appears to taper to a point. In overall appearance it somewhat resembles an early osteichthyan cleithrum, such as that of an onychodont [52] or porolepiform [53]. The tubercles on the postbranchial lamina are fine and dense. The ossification centre lies in the anterior area of the plate. The shape of the scapulocoracoid follows the shape of the AL plate. The scapulocoracoid is composed of an anterior coracoid process and a dorsal scapular blade (Fig 6A and 6C). Numerous imprints and openings for blood vessels and nerves are clearly visible on the surface. It is possible to recognize dorsal and ventral groups ([47], figure 193A).

In NM Lc 166 the AL, which is preserved in approximate life position relative to the braincase (Fig 6B), is overlapped dorsally by the median dorsal plate (MD). This positional relationship is likely to be slightly disturbed, as it leaves no room for the dorsolateral thoracic plates that would be expected to carry the main lateral line canal of the trunk, separating the AL from the MD. The median dorsal plate has anterolateral projections that give the bone a butterfly-like outline (Fig 6B). The dorsal spine is broken off. The remaining plates of the thoracic shield are as yet unknown or unrecognisable.

The most abundant remains of *T*. *inopinatus* are the dorsoventrally compressed, perichondrally ossified endocrania. Most commonly the rock slab containing the specimen has split horizontally along the ventral face of the endocranium, with the crack sometimes running above and sometimes below the thin ventral layer of perichondral bone, so that the bone is divided in patches between slab and counterslab. Curiously, in all specimens examined to date the crack rises dorsally in the prenasal region, so that at least part of this region ends up attached to the counterslab (Fig 5B and 5D). The dorsal surface of the endocranium is largely covered by the central and nuchal plates of the skull roof (see above), except anteriorly where the rostronasal-prenasal region is exposed. (Figs 4B, 4C and 5A). In ventral view, the outline of the endocranium is clearly visible, but the actual lateral walls are difficult to reconstruct because of the strong dorsoventral compression of the specimens.

The endocranium is relatively slender. The facial region, from the postorbital processes to the anterior margin of the endocranium, is remarkably long. It comprises more than 50% of the length of the endocranium, whereas the corresponding proportion in *Romundina stellina* is approximately 42% (measurements taken from endocranium in [21]). The pre- and postnasal parts of the facial region appear in proportional terms to be equally elongated relative to the condition in *Radotina kosorensis* or *Romundina stellina*. In other words, the facial region of *Tlamaspis* appears isometrically "stretched" compared to these taxa. In general morphological terms the prenasal area is reminiscent of that in *Romundina* [7,21], with broad suborbital shelves separated in the midline by a raised, anteriorly flaring region that carries the attachment for the rostronasal capsule posteriorly and the premedian area anteriorly (Figs 4B, 4C and 5A). Unlike in *Romundina* and *Radotina*, there is no premedian plate in *Tlamaspis*, but a distinct premedian area can be recognised in the region where a premedian plate would be expected (Fig 5A). The dorsal surface of the endocranium lacks external perichondral ossification in this area, exposing a complex internal network of perichondrally lined canals.

The endocranium is widest at the level of the short anterior postorbital process (Fig 5B and 5C). The posterior postorbital process is robust but appears to be relatively short (Figs 5A and 6D). Posterior to this process, the occipital region is proportionately much shorter than in *Romundina* [21] and the condyles are strikingly wide. Mesial to the posterior postorbital process, the ventral surface of the endocranium carries a wide but not very deep longitudinal groove, bounded mesially by a ridge (Fig 5B, gr.eff.a). A similar groove in *Romundina* has been interpreted as housing a common efferent branchial artery [21].

The hypophyseal opening is slightly posterior to the rostronasal area. Anterior to the hypophysial foramen and mesial to the pseudobranchial arteries two smaller openings are situated. These can be matched in *Romundina* ([20], figures 2B,3D), where they communicate with the dorsal surface of the rostronasal area through two perichondrally lined canals that pass vertically through the cartilage of the endocranium. Their function remains uncertain.

Deeply impressed imprints of paired blood vessels are visible on the ventral surfaces of all the endocrania. The grooves for the efferent pseudobranchial arteries (Fig 5B, pse.a) originate anterior to the hypophysial fossa and follow a curved transverse trajectory similar to that in *Romundina* [7, 21]. Posteriorly there are lyre-shaped imprints of the lateral aortae. The endocranial surface between the grooves of the lateral aortae is rugose. The grooves of the secondary jugular veins (Fig 5, j.v.s) are deeply incised, narrow, and s-curved, and their main mesial branch is attached posterior to the crossing with the efferent pseudobranchial artery. The course of the notochord is visible posteromedially.

**Remarks.** Gross [36] described some anterior lateral plates of smaller individuals as *R. kosorensis*. The plates are very similar in shape to the AL of *T. inopinatus*, but always lack the dermal ornament and other diagnostic features and are always found in isolation. Therefore, these finds (nos. NM Lc 3, 187 and counterpart 472, 465 and counterpart 466; [36], pl. 5, f. 2, textfig. 4B) must be left in open nomenclature.

**Genus *Sudaspis* gen. nov.** *urn:lsid:zoobank.org:act:4949C1DA-BFD6-4FAE-B85F-EFFED9517D8B*

(Fig 7)

**Diagnosis.** Jawed vertebrate possessing a broad, flat endocranium with an anterior prenasal expansion of the trabecular region. Prenasal region long. Suborbital shelf narrows abruptly at junction with prenasal region, creating distinct"shoulder" in endocranial margin. Endocranium tapering strongly posteriorly to a narrow glenoid region with prominent condyles. Grooves of lateral aortae on ventral face of endocranium narrow, shallow, together forming hourglass shape, branching anteriorly, ending anteriorly in two clearly visible foramina at level of anterior postorbital process and efferent hyoid artery. Endocranial surface between aorta grooves not rugose. Grooves of secondary jugular veins very obvious, wide, nearly straight, giving off several minor branches laterally, main mesial branch attached anterior to crossing of efferent pseudobranchial artery. Posterior part of skull roof relatively short. Large paranuchal plates form projecting posterior corners of skull roof. Dermal ornament composed of small, close-spaced, round tubercles without ridges.

**Derivation of name.** After the name of the street "V Sudech" (in barrels) in Prague-Radotín, which runs parallel to the quarries, its name reflecting the characteristic shape of the upper

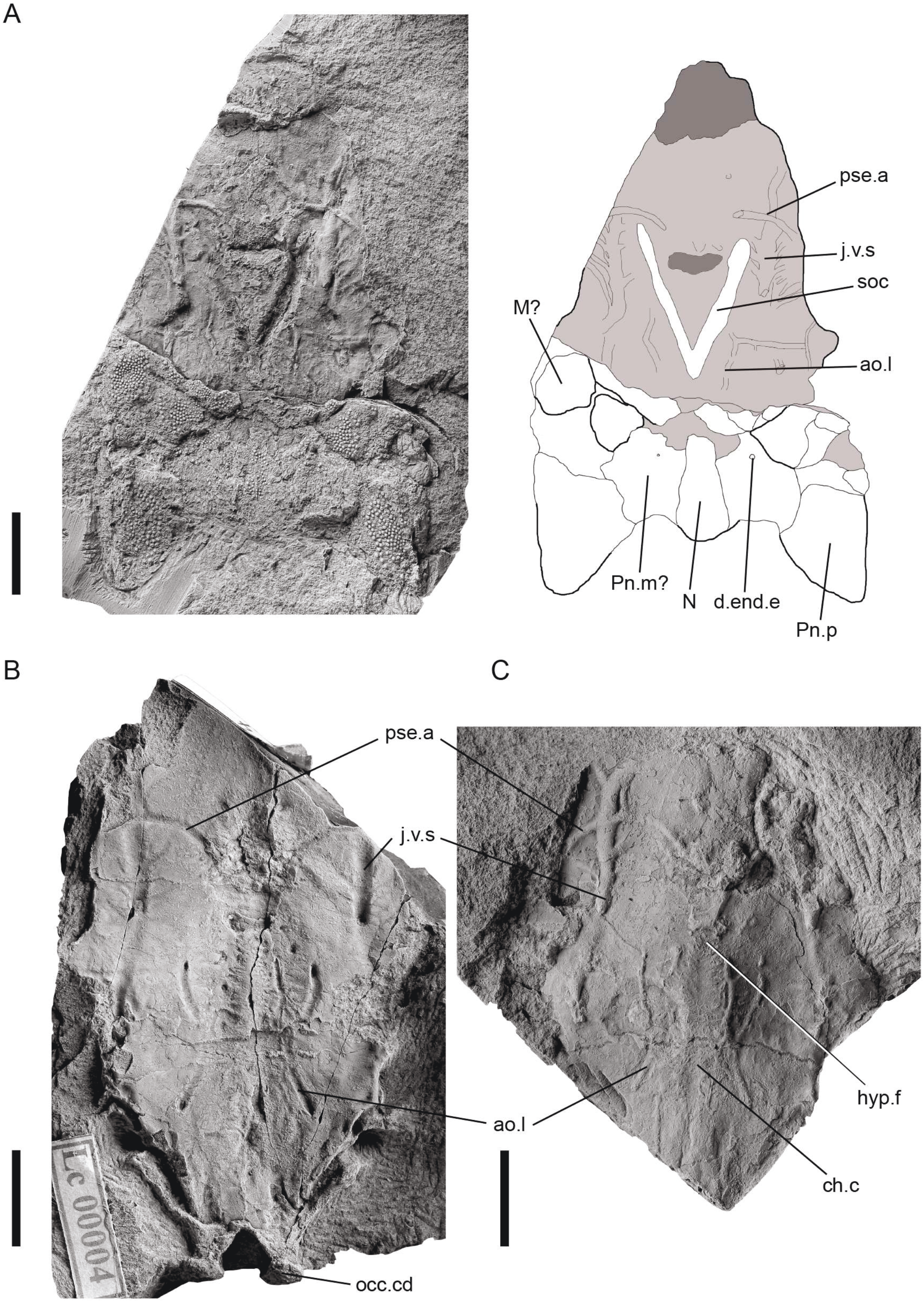

**Fig 7. *Sudaspis chlupaci* gen. et sp. nov.** (A), holotype, NM Lc 27, posterior part of skull roof attached to endocranium; (B), endocranial base, NM Lc 4; (C), endocranial base, NM Lc 496. Scale bars = 10 mm. Abbreviations: ao.l lateral aorta; ch.c chordal canal; d.end.e external foramen for the endolymphatic duct; hyp.f hypophyseal fenestra; j.v.s secondary jugular vein; M marginal plate, N nuchal plate; occ.cd occipital condyle; Pn.m medial paranuchal plate; Pn.p posterior paranuchal plate; pse.a efferent pseudobranchial artery; soc supraorbital sensory line groove.

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part of the profile resembling three barrels as well as the shape of the endocranium of *S. chlupaci*; and the Greek “aspis” (shield).

**Type and only known species.** *Sudaspis chlupaci* sp. nov.

***Sudaspis chlupaci* sp. nov.***urn:lsid:zoobank.org:act:386A13CD-82D5-412F-9B7E-D06015C508DF*

(Fig 7)

1959 *Radotina kosorensis* Gross; Gross [36]: pl. 2, fig. 6–7; pl. 3, fig. 5; pl. 4, fig. 1–2, textfig. 1F; 2C; –5.

1969 *Radotina kosorensis* Gross; Stensiö [47], fig. 105B.

**Diagnosis.** As for genus.

**Derivation of name.** In honour of late professor Ivo Chlupáč, a famous Czech invertebrate palaeontologist and stratigrapher, and a great enthusiast for early vertebrate research in the Czech Republic.

**Holotype.** Base of endocranium with posterior dermal skull roof cover. Figured by Gross [36], pl. 3, fig. 5, textfig. 1F. Housed in the Národní Muzeum in Prague with inventory number NM Lc 27 (Fig 7A).

**Type horizon.** Lower Devonian, Lochkovian; Lochkov Formation, Radotín Limestone.

**Type locality.** Černá rokle near Kosoř in Prague-Radotín.

**Material.** Endocrania NM Lc 4 (and counterpart NM Lc 32), NM Lc 469; endocranium with skull roof plates NM Lc 27.

**Description.** The holotype (Fig 7A) has the posterior part of the dermal skull roof preserved, but this is not easy to interpret. Prominent paranuchal plates, similar to those of *Romundina* [28], form the posterolateral corners of the roof. The nuchal appears to be narrow and small. It is certainly separated from the paranuchals, but it is not clear whether the intervening space is occupied by a single medial paranuchal (posterior central), as in *Romundina*, or by a mosaic of smaller bones. Anterior to the paranuchals, the region occupied in *Romundina* by marginals, anterior paranuchals and centrals [28] appears to consist of a greater number of smaller bones. A full interpretation of the skull roof must await the discovery of additional material, but it is already clear that the skull roof of *Sudaspis* is diagnostically different from those of both *Tlamaspis* and *Radotina*. The dermal ornament is composed of small, close-spaced, round tubercles without ridges.

The facial region of the endocranium is differently proportioned to *Romundina*, *Radotina* and *Tlamaspis*. As in *Tlamaspis*, the length of the facial region is just over 50% of the total endocranial length, contrasting with approximately 42% in *Romundina*, but in *Sudaspis* the extra length is due entirely to the elongated prenasal region; the proportions of the postnasal region are similar to *Romundina* [21] and *Radotina*. The suborbital shelf narrows abruptly at its anterior end, creating a distinct”shoulder” in the endocranial margin. Posteriorly, the endocranium tapers strongly to a narrow glenoid region with prominent condyles. The shallow, narrow, anteriorly branching grooves for the lateral aortae form an hourglass shape. The area between these grooves is smooth, not rugose as in *Tlamaspis*, but further anteriorly there is a low and narrow midline ridge flanked by numerous small transverse "scratches", that extends forwards towards the hypophysial region. The secondary jugular vein grooves are wide and nearly straight, branching laterally and mesially, the main mesial branch attaching anterior to the crossing with the canal of the efferent pseudobranchial artery. A transverse vascular groove running medially from the postorbital processes and crossing the jugular vein canal is interpreted as transmitting the efferent hyoidean artery. The posterior postorbital process is visible but difficult to interpret in the available material. Posterior to this process, the occipital region is both longer and more strongly tapering than in *Tlamaspis*. It shows a curious double margin, with an external crista on each side that posteriorly joins with the condylar region of the occiput. This clearly reflects an anatomical feature, but it is not possible to say whether it retains its natural shape or has been modified by dorsoventral compression.

Order and Family indet.

**Genus *Holopetalichthys* von Koenen, 1895**

(Fig 8)

**Diagnosis.** Jawed vertebrate with perichondrally ossified endocranium. Endocranium with long preorbital region incorporating fused nasal capsule. Dermal skull roof entirely macromeric, tesserae absent. Supraorbital and preorbital margin of skull roof formed by single elongate supraorbital ossification. Paired rostral plates. Posterior end of postpineal plate contacts nuchal plate, separating the central plates in the midline. Central plate elongated, reaches posterior margin of skull roof. The tubercles of the dermal ornament round, composed mainly of bone. Median dorsal plate complex composed of a spine-shaped posterior median dorsal, a broad butterfly-shaped anterior median dorsal, and a posterolaterally positioned plate.

**Type and only known species.** *Holopetalichthys primus* (Barrande, 1872)

**Remarks.** The specimens described herein as the genus *Holopetalichthys* had originally been split into three separate species. Barrande [32] erected the species *Coccosteus primus* based on specimen NM Lc 40 (Fig 8A). Its generic identification was challenged by Bayer [54]. Specimen NM Lc 136 (Fig 8B) was described by von Koenen [33] as a monospecific new genus and named *Holopetalichthys novaki*. Gross [35], without knowledge of the published specimens, described NM Lc 33 (Fig 8D) as a new species of the genus *Radotina* with the species name *tuberculata*. Westoll [37] was the first to note the common characters of NM Lc 40 and 33 and united them in a single species using the name *Radotina prima*. He never mentioned NM Lc 136 or the generic name *Holopetalichthys*. Ørvig [40] pointed out this fact of priority, but suggested to dismiss the older name as a nomen nudum. Although Denison [25] repeated this suggestion, none of them applied to officially accept the younger name *Radotina*. However, this would not be possible, as the name *Holopetalichtys* had been widely used in contemporary literature (e.g. [48]; [41] and references therein). Goujet [10] doubted the determination of *R. prima* to the genus *Radotina*, based on the absence of tesserae and the premedian plate, which has been added to the reconstruction by Denison ([25] figure 22C) without supporting evidence. According to Goujet [10] the differences in histology and the shape of the dermal sculpture are strong arguments to exclude the species *R. prima* from the order Acanthothoraci. However, he did not suggest any taxonomic or systematic solution.

Our examination of the material historically assigned to *Coccosteus primus*, *Holopetalichthys novaki* and *Radotina tuberculata* shows that it represents a single species, which is so different from *Radotina kosorensis* and *R. tesellata* that assignation to *Radotina* is out of the question. It is also very different from *Coccosteus*. We establish the combination *Holopetalichthys primus* for this species. It has already been used by Chlupáč [55,56], with the nomination of a lectotype (NM Lc 40, Barrande's holotype of *Coccosteus primus*), but without a formal diagnosis; we present a diagnosis to complete the taxonomic process. The assignation of *Holopetalichthys* to the Acanthothoraci must be regarded as doubtful, given that there is no evidence for a projecting prenasal area or a premedian plate.

Zhu and Wang [57] described a new species of the order Macropetalichthyidae named *Holopetalichthys longhuaensis*. Their diagnosis is not in accordance with the former description [33], which is not even cited in the paper, and the genus *Holopetalichthys* is considered a genus novum. Therefore *Holopetalichthys longhuaensis* must be considered a preoccupied taxon and thus the determination by Zhu and Wang is invalid.

***Holopetalichthys primus* (Barrande, 1872)**

(Fig 8)

1872 *Coccosteus primus*. Barr.; Barrande [32], pp. 640–641, pl. 29–1, 2.

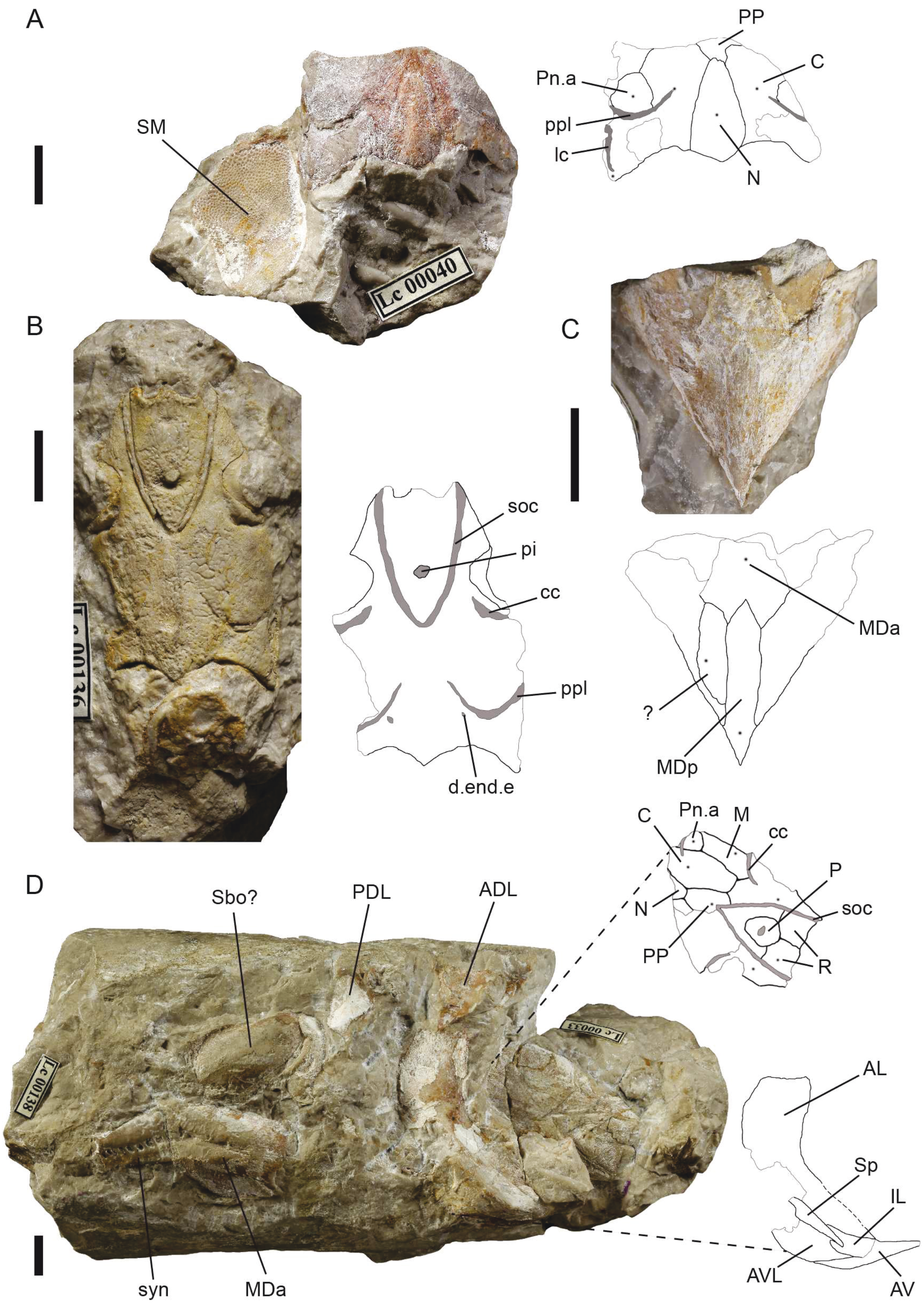

**Fig 8.** ***Holopetalichthys primus*** **(Barrande, 1872).** (A), holotype, NM Lc 40, posterior part of the skull roof, inner cast of submarginal plate; (B), skull roof, NM Lc 136; (C), median dorsal plate complex, NM Lc 139 (D), head and thoracic shield, NM Lc 33 and 138. Scale bars = 10 mm. Abbreviations: ADL anterior dorsolateral plate; AL anterior lateral plate; AV anterior ventral plate; AVL anterior ventrolateral plate; C central plate; cc central sensory line groove; d.end.e external

foramen for the endolymphatic duct; IL interolateral plate; lc lateral sensory line groove; M marginal plate; MDa anterior median dorsal plate; MDp posterior median dorsal plate; N nuchal plate; P pineal plate; PDL posterior dorsolateral plate; pi pineal organ; Pn.a anterior paranuchal plate; PP postpineal plate; ppl posterior pitline; R rostral plate; Sbo suborbital plate; SM submarginal plate; soc supraorbital sensory line groove; Sp spinal plate; syn synarcuale.

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1895 *Holopetalichthys Novaki* v. Koenen; von Koenen [33], pp. 25–27, pl. IV, 2 a, b.

1905 *Coccosteus primus* Barr. ("doubtfully belonging to genus *Coccosteus*"); Bayer [54], p. 29.

1905 *Holopetalichthys Novaki* Koen; Bayer [54], p. 33.

1950 *Radotina* sp. Gross; Gross [34], pp. 113–118, fig. 1B.

1958 *Radotina tuberculata* n. sp; Gross [35], pp. 21–23, pl. 1, fig. 3; pl. 3, fig. 5–6; textfig. 6.

1967 *Radotina prima* (Barrande); Westoll [37], pp. 83–88, fig. 2B.

1969 *Radotina tuberculata* Gross; Stensiö [47], fig. 104A.

1971 *Holopetalichthys kosorensis*; Moy-Thomas & Miles [48], fig. 8.18A.

1975 *Radotina tuberculata* Gross; Ørvig [40], pp. 48, 49, 66, fig. 1D.

1978 *Radotina prima* (BARRANDE); Denison [25], pp. 36, 79, fig. 1B, 22C.

1984 „*Radotina*" *prima*; Goujet [10], pp. 224, 228, 230, 235, 238, 239, fig. 8B, 9, 12.

1996 '*Radotina' prima*; Janvier [49], p. 170, fig. 4.57D.

2002 *Coccosteus primus* Barr. = *Holopetalichthys primus* (Barrande, 1872); Chlupáč [55], explication to pl. 29, fig. 1, 2 (no page number).

2002 *Holopetalichthys primus;* Chlupáč et al. [56], fig. 83, 2.

2009 *Radotina prima* (Barrande); Vaškaninová [51], p. 195.

2011 "*Radotina*" *prima* (Barrande, 1872); Dupret et al. [29], fig. 3C, pp. 531–532, 537.

2011 *Holopetalichthys primus* (Barrande, 1872); Vaškaninová [38], p. 52.

**Diagnosis.** As for genus.

**Holotype.** The posterior part of the skull roof with associated submarginal plate. Figured by Barrande [32], pl. 29–1, 2. Housed in the NM with the catalogue number NM Lc 40 (Fig 8A).

**Type horizon.** Lower Devonian, Pragian; Prague Formation, upper Koněprusy Limestone.

**Type locality.** Koněprusy near Beroun, south-east of Prague, probably the area of the present day Houba Quarry.

**Material.** Head and associated thoracic region NM Lc 33+NM Lc138 (ČF 5 of Westoll [37]); skull roof NM Lc 40 (ČF 6 of Westoll [37]), NM Lc 136; cheek plate NM Lc 145; median dorsal plate NM Lc 139 (ČF 2 of Westoll [37]), NM Lc 141 (ČF 1 of Westoll [37]); thoracic shield plates NM Lc 134 (ČF 3 of Westoll [37]) and counterpart NM Lc 135 (ČF 4 of Westoll [37]).

**Remarks.** Gross [35] described only one specimen, NM Lc 33 ([35], pl. 1, f. 3, textfig. 6A), as *Radotina tuberculata*. It was known as an anterior part of the skull roof; its posterior part was thought to be lost after deposition, as glue marks were still visible on the fracture surface. We have discovered that NM Lc 33 is a part broken off specimen NM Lc 138, which contains the thoracic region and a synarcual ossification (described but not figured by Westoll [37]). The two pieces had already become separated by the 1950s when Gross started to study the material.

Specimen HMN f 633 in the Humboldt Museum für Naturkunde, Berlin, from the Lower Devonian Taunus Quartzite near Rüdesheim, Rheinish Slate Massif, Germany, is identifiable as the anterior right side of the skull roof of *Holopetalichthys*. It was decribed as *Radotina* sp. by Gross [35]. Although its attribution to *Holopetalichthys* is unproblematic, its incompleteness, together with the fact that it is much larger than the Koněprusy specimens and derives from another locality, means that we cannot confidently identify it as the species *Holopetalichthys primus*. We provisionally designate it *Holopetalichthys* sp.

**Description.** The skull roof is composed of macromeric dermal plates, tesserae are absent. The plates are clearly recognisable by their ossification centres visible in the vascular middle layer (Fig 8A, 8C and 8D). The nostrils are positioned anterior to paired rostral plates and face anterodorsally. The skull roof probably terminated at this point, as we have no record of a premedian plate. The rostronasal capsule was clearly not loosely attached as in *Romundina* or *Tlamaspis*, where it tends to become detached from the rest of the endocranium.

The dorsal rim of the orbit carries a narrow, sharply delineated encircling groove, lying close to the orbital margin anteriorly and posteriorly but diverging away mesially from it in the middle (Fig 8B). The preorbital and supraorbital area is formed by a single elongate supraorbital ossification bounded by the supraorbital sensory line mesially, by a suture with the central plate posteriorly, and by the central sensory line groove posterolaterally (Fig 8D). The central sensory line runs towards the ossification centre of the central plate. The paired rostral plates are bounded by the supraorbital sensory lines laterally, and by a suture with the round pineal plate posteromesially. In the pineal area medially to the supraorbital sensory lines lies the pineal plate. The pineal organ was originally positioned in the ossification centre of this plate, but there is no pineal opening.

Posterior to the central sensory line the ossification centres of another two plates are recognisable—the marginal and anterior paranuchal plates [37]. The marginal plate extends posteriorly separating the anterior paranuchal plate from the skull roof margin (Fig 8A and 8D). The anterior and posterior paranuchal plates are separated by the posterior pit lines, but the posterior paranuchal is not well preserved.

The central plates are elongated, oval, wider anteriorly, and do not meet mesially. The obliquely oriented posterior pit lines extend towards the ossification centres of the plates in NM Lc33 and NM Lc 40; in NM Lc 136 they appear to cross the ossification centres and continue towards the posterior meeting point of the suborbital canals. The centrals are separated in the midline by the nuchal plate and the elongated postpineal plate. The supraorbital sensory lines meet close to the ossification centre of the postpineal plate. The nuchal plate is relatively short and widens posteriorly, terminating in a blunt midline point. The sensory lines occupy deep grooves, recessed into to the dorsal surface of the endocranium. The matrix fill of the canal itself is preserved in some places, notably in the supraorbital canals of NM Lc 136 (Fig 8B); it is surrounded by an extremely thin mineralized boundary layer that appears to represent the membranous walls of the canal. Sensory lines may follow sutures (as in the case of the supraorbital canal following the suture between the rostral and supraorbital plates), but their ends always point towards the ossification centres of bones. The endolymphatic duct opening is clearly visible on the specimen NM Lc 136 (Fig 8B).

Only one plate from the cheek area is known, the submarginal plate preserved as an imprint on the specimen NM Lc 40 (slightly displaced posteriorly; Fig 8A). It has a typical shape for this bone, widening anteriorly with an oval projection dorsally. A fragment of similar submarginal plate occurs also on the specimen NM Lc 145.

The median dorsal plate complex, which at first sight might be interpreted as a single bone, is in fact composed of a spine-shaped posterior median dorsal, a broad butterfly-shaped anterior median dorsal and an un-named posterolaterally positioned plate. The posterior dorsal has a triangular cross section, with a dorsal crest ornamented by oblong ridges (Fig 8C). Specimen NM Lc 138 (ČF 5 of Westoll [37]; Fig 8D) displays a complete thoracic complex preserved in 3D along with isolated trunk shield plates. Overall, the thoracic armour is very short anteroposteriorly, taking the form of a narrow shoulder girdle, somewhat as in acanthothoracids and ptyctodonts. The damaged anterior lateral plate resembles the shape of the AL plates found in

*Tlamaspis inopinatus* or *Palaeacanthaspis vasta* [22]. Anteroventrally it appears to taper to a point. The anteroventral ramus of the AL is bounded ventrally by a spinal plate, which carries a short posterolaterally directed pectoral spine, and anterior to the spinal plate an interolateral plate with a forked posterior end that clasps the spinal plate. Remarkably, the area ventral to the spinal and interolateral plates is occupied not by a single anterior ventrolateral plate, but by two plates. We tentatively interpret them as the anterior ventral and anterior ventrolateral plates (AV, AVL; Fig 8D), resembling the condition reconstructed in *Romundina* cf. *stellina* [28]. The AL plate is ornamented with badly preserved tubercles in the mesial area and on the postbranchial lamina. Dorsally to the AL plate lie two smaller isolated plates, probably the anterior and posterior dosolateral plates. The median dorsal plate complex has the dorsal spine broken off and its inner bone layer is exposed along with the spine cavity (compare the preservation of *P. vasta* [22]). The median dorsal plate is connected to a robust bony element in the area of the former dorsal spine, the synarcual [37], which appears to be slightly displaced. The synarcual has a joint surface on the posterior end. Medially, there is a band of small openings —the accreted vertebrae. In the vicinity of the MD plate lies a larger, oval plate, probably a displaced suborbital plate.

The surface sculpture of specimen NM Lc 136 (Fig 8B) is mostly abraded, broken off or destroyed by polishing. Specimen NM Lc 33, also strongly polished, has the tubercles most clearly visible on the rostral plates. They are poorly preserved, but they evidently were rather bulky, not star shaped or striated. Similar tubercles are very well preserved in the imprint of the submarginal plate of the holotype (Fig 8A) and have been examined on a latex peel. They seem to be built mostly of a vascular bone layer, the semidentine is restricted only to the top. This type of tubercle occurs also on the probable spinal plate of the specimen NM Lc 134, which was found in the same piece of rock as the imprint of a median dorsal plate complex of *Holopetalichthys*. The counterpart of the MD complex is found on specimen NM Lc 135. Median dorsal plate complexes of the same shape can be found on specimens NM Lc 139 (Fig 8C) and NM Lc 141; both have a distinctive dermal ornament. Specimen NM Lc 136 (Fig 8B) has a fragment of another plate attached to the posterior border of the skull roof. Its position suggests that it may be part of a median dorsal complex, but it is too incomplete to identify.

## Discussion

### Phylogenetic and evolutionary implications

We do not present a phylogenetic analysis in this paper because it would be premature at this stage. Detailed anatomical investigations of all the Lochkovian and Pragian placoderms of the Prague Basin are under way, on the basis of synchrotron microtomography, and will produce large amounts of new phylogenetic data within the next few years. However, our taxonomic findings already have a major impact on the phylogenetic significance of the Prague Basin placoderms, because they show that past interpretations have been based on multi-taxon chimaeras. This is especially important because they have been widely recognized as very primitive placoderms, potentially informative about questions such as the origin of a macromeric skeleton. For example, Moy-Thomas and Miles [48] consider at some length the significance of dermal bone variability in "*Holopetalichthys kosorensis*", which is described (following [37]) as having a skull roof that shows individual variation between fully macromeric and largely tesselated conditions. But as we have shown above, this "*Holopetalichthys kosorensis*" is a multi-taxon composite that includes aspects of *Radotina kosorensis*, *Tlamaspis inopinatus* and *Holopetalichthys primus*, three very different placoderms, each with its own characteristic (and apparently stable) skull roof pattern. The extreme individual variability posited by Westoll [37] and Moy-Thomas and Miles [48] simply does not exist. Given this unusual situation, with its potential for seriously corrupting phylogenetic and evolutionary data sets relating to early gnathostomes, we urge that all previous descriptions and interpretations of the Prague Basin placoderms be excluded from the current discussion of these questions.

Our taxonomic revision reveals that the Early Devonian of the Prague Basin contains a remarkable richness of acanthothoracids, especially in the Lochkovian where the placoderm fauna can now be seen to consist of at least four acanthothoracids (*Radotina kosorensis*, *Tlamaspis inopinatus*, *Sudaspis chlupaci* and *Kosoraspis peckai*) with no other placoderm groups known to be represented in the assemblage. This is interesting from an ecological perspective (see below) but also with regard to the evolution of dermal bone macromery.

The last few years have seen a remarkable about-turn as regards the evolution of macromery, from an almost universally held belief that the macromeric skeletons of placoderms and osteichthyans are independently evolved (e.g. [14,49]) to widespread acceptance that they are homologous (e.g. [6,13]). This extends the homologue set of our own macromeric skeleton down into the upper part of the gnathostome stem group, with the implication that the absence of homologous bones in chondrichthyans is secondary [13]. The lower part of the gnathostome stem group comprises jawless bony vertebrates known as ostracoderms. Among these, thelodonts and anaspids are entirely covered with scales, and are thus micromeric in the same sense as chondrichthyans. Galeaspids and osteostracans have dermal head shields that are normally solid one-piece structures in the adult, but are composed of tesserae that fuse late in ontogeny [58,59]. This can also be considered as a type of micromeric skeleton, because the tesserae do not appear to have conserved individual identities, but in osteostracans at least the anterior rim of the head shield is composed of larger, morphologically distinctive bones [59]. Heterostracans have macromeric dermal headshields, but these show no pattern similarities with either placoderms or osteichthyans [49]. However, bands of tesserae are sometimes present between the macromeric bones (notably in the psammosteid *Drepanaspis* [49]), in a manner very reminiscent of *Radotina*.

The lack of obvious homologies between the macromeric patterns of heterostracans and placoderms suggests that the macromeric bones that characterize placoderms and osteichthyans evolved de novo within the gnathostome stem group, at approximately the same time as the origin of jaws. However, the head-shield tesserae of osteostracans, galeaspids and some heterostracans are strongly reminiscent of those in acanthothoracid placoderms such as *Radotina*, raising the intriguing possibility that their presence in acanthothoracids could be a primitive character retained from agnathan ancestors. The fact that many recent phylogenetic analyses recover acanthothoracids as among the most basal jawed vertebrates [7,8,13,19] makes this hypothesis all the more interesting.

Given our limited understanding of the skull roof patterns in some Prague Basin placoderms, especially *Sudaspis*, and the current lack of microanatomical data for the tesselated regions, it is too early to venture on a detailed interpretation of these patterns and their significance. However, one striking observation that is worth highlighting is the relationship between the premedian plates of *Radotina kosorensis* and *Romundina stellina*. *Romundina* has a unitary premedian plate without obvious sutures, but synchrotron microtomography reveals that its internal vasculature divides into two discrete domains ([20], figures 1C and 2B). The thick anterior part of the plate contains several superimposed layers of internal vasculature, all with a radial pattern originating at a midline point near the anterior margin. By contrast, the much thinner posterior half of the plate has a non-radial vasculature with a largely anteroposterior orientation, principally occupying the contact surface between the dermal bone and the underlying endoskeleton. In *Radotina kosorensis* (Fig 2A), the premedian dermal bone cover consists of two discrete components: a premedian plate anteriorly and a field of tesserae posteriorly. The premedian plate shows a clear radial structure, originating from the same place in the anterior midline as the radial vascular pattern of *Romundina*. This suggests that the seemingly unitary premedian plate of *Romundina* incorporates the same combination of an anterior plate and a posterior field of tesserae as the premedian dermal skeleton of *Radotina*, but that the sutures have become obscured. Further data on dermal bone microanatomy, which should emerge from the synchrotron microtomography investigation of the Prague Basin acanthothoracids, will provide a more robust basis for future hypotheses about the evolution of macromery.

## Taphonomy

The large number of morphologically diverse and well preserved placoderm specimens from the localities Černá rokle (Lochkovian) and Koněprusy (Pragian) provides a good database for studies of taphonomy and subsequent diagenetic effects. The strongly dorsoventrally flattened skulls with partly exposed endocranial structures represent the best preserved specimens from the Černá rokle quarries. In life, the endocrania were built of unmineralized cartilage, covered by a thin layer of perichondral bone; after death the cartilage decayed and was replaced with sedimentary infill. The endocrania are flattened to a thickness of only a few millimetres [36], contrasting with the three-dimensional preservation of similar endocrania of *Romundina* in the Lochkovian of Prince of Wales Island [7,28,40] and *Radotina tesselata* in the Pragian Koněprusy limestone (see below). The endocrania display openings and imprints of nerves and blood vessels. The slabs containing the specimens were usually split in the horizontal plane, so the inner cast of the specimen represents the base of the endocranium, i.e. the inner ventral surface. Although the compression is strong, some prominent features (e.g. the prenasal area of *T*. *inopinatus*) have retained their threedimensionality. No endocranium is laterally compressed, even in semi-articulated specimens where the adjacent shoulder girdle is preserved in lateral view (Fig 6). This probably reflects the fact that acanthothoracid endocrania, like those of most placoderms, were rather broad and flat even in life (e.g. [21]) and thus tended to settle in a horizontal position in the sediment.

In most cases, the dorsal endocranial surface is covered by at least the central and nuchal plates of the skull roof. The cheek plates (e.g. the submarginal) are preserved separately. They were not attached to the endocranium as firmly as the skull roof plates and are found associated to the endocranium or the thoracic plates with their ventral surfaces exposed. Also the anterior lateral plates are preserved isolated with the strongly compressed scapulocoracoid always firmly attached. Other thoracic plates are found isolated as well; the median dorsal plate has the spine broken off as a rule.

A number of specimens of *Tlamaspis inopinatus* show a specific form of preservation where the specimen, despite being flattened, is complete with the head closely associated to the shoulder girdle and the visceral skeleton pushed from beneath the head laterally (Fig 6A and 6B). The process can be reconstructed as a dorsoventral or semi-lateral compression of a complete anterior body of the fish, e.g. head and thoracic shield. The ventral thoracic plates are unknown; the complete posterior body has not yet been discovered. Some specimens show scattered disarticulated body scales associated to separate dermal plates or their fragments.

The postmortem transport of placoderms found in the Černá rokle quarries was apparently only over a short distance. The model of the prevailing taphonomic processes can be reconstructed from the patterns of fragment distribution. The carcasses were being transported to the anoxic basin from a supposed platform by turbidite currents. During the process of decay, before the specimens were covered by sediment, another short distance transport of smaller and lighter parts (e.g. fragments of dermal plates or scales) may have occurred. The strong compression was a part of the subsequent diagenetic process. However, the accompanying fauna, including other fish (e.g. fin spines of *Machaeracanthus* [44]), does not display such strong compression [41]. In rare cases the specimens display a slight horizontal displacement of the dermal plates (e.g. NM Lc 29; Fig 4B). The overlap increases but the plate position is constant.

The Koněprusy material is preserved three-dimensionally. The most common specimens are skull roofs along with median dorsal plate complexes. The dermal plates are split through their middle vascular bone layer; the surface sculpture was preserved in the missing counterparts, but can be reconstructed from a few areas of natural mould present on the specimens. The recently associated specimens NM Lc 33 and NM Lc 138 (Fig 8D) display a fully preserved head situated inside the thoracic region with adjacent separate plates and vertebral column, all deposited within the infill of an orthocone cephalopod shell.

## Palaeoecology

The Černá rokle quarries yielded the most abundant placoderm material, greatly exceeding the number of specimens from the remaining localities of the Prague Basin [31]. It is uncertain whether this abundance is a taphonomic effect, the result of intensive collecting of all fragments during the period of active quarrying, or if the placoderms were genuinely more abundant in the Lochkovian of the Prague Basin. Perner [42] and Gross [36] supposed the existence of a "fish bearing" layer or accumulation exposed at the time of active quarrying, nowadays inaccessible, but probably belonging to a relatively short overlap of the *Paranowakia bohemica* and *P. intermedia* tentaculite zones (for more details see [31]). Only scarce fragments of placoderm fossils can be found nowadays. *Contra* King et al. [12], who argue that phylogenetically basal placoderms were benthic, we suggest that the Lochkovian acanthothoracids were most probably nektonic active swimmers, considering the shape of their crania and trunk armours, and the lateral position of the orbits [25, 28]. The environment in the Lochkovian of the Černá rokle is supposed to be relatively deep water [43].

In the bioherm environment of the Koněprusy quarries in the Pragian the small placoderms may represent prey for larger predators (e.g. the acanthodian genus *Machaeracanthus* found in the same strata [44]). Often the placoderm remains are preserved in the infill of large orthoconic cephalophod shells (e.g. Fig 8B and 8D). The prominence of acanthothoracids in these assemblages is remarkable, especially in the Lochkovian Radotín Limestone where at least four morphologically divergent acanthothoracids (*Radotina*, *Tlamaspis*, *Sudaspis* and *Kosoraspis*) occur side by side. We are not aware of another example of such an acanthothoracid-dominated placoderm fauna. By contrast, Emsian and later placoderm assemblages from the Prague Basin contain only arthrodires [31].

## Conclusions

This paper has significantly changed the view of the systematic structure of the Prague Basin Lower Devonian (Lochkovian and Pragian) placoderm fauna, finally resolving the long prevailing confusion about the variable character states in individual taxa. Four genera (*Radotina*, *Tlamaspis*, *Sudaspis* and *Holopetalichthys*) have been established and provided with unambiguous diagnoses based on well documented unique characters. The species name *Radotina kosorensis* Gross, 1950 is now limited to a few specimens that share unique characters with the holotype. *Radotina tesselata* Gross, 1958 remains a single specimen species. *Radotina* has a skull roof with large tesselated areas separating the macromeric bones. *Tlamaspis* is characterised by a very long facial region and a dermal skull roof lacking tesserae. *Sudaspis* has a long prenasal region with a distinctive, stepped lateral profile. The skull roof is essentially macromeric, including large and prominent paranuchals. We consider all the previously published attempts to reconstruct or interpret the "radotinid" material, apart from references to holotypes, as invalid because they inadvertently combine information from more than one taxon.

We have also resolved the taxonomic confusion following the generic determination of the so-called "*Radotina*" *prima* (previously known as *Coccosteus primus*, *Holopetalichthys novaki* and *Radotina tuberculata*) and its problematic position within the acanthothoracids. We establish the name combination *Holopetalichthys primus* (Barrande, 1872) for a number of specimens displaying the same unique characters. The genus *Holopetalichthys* is excluded from the acanthothoracids on the basis of the probable absence of the prenasal area as well as other distinct characters listed above. However, it displays many unusual features in its dermal skeleton. We interpret *Holopetalichthys* as a basal placoderm of uncertain affinities.

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## Author Contributions

**Conceptualization:** VV PEA.

**Data curation:** VV.

**Formal analysis:** VV PEA.

**Funding acquisition:** VV PEA.

**Investigation:** VV PEA.

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**Project administration:** VV.

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**Supervision:** PEA.

**Validation:** VV PEA.

**Visualization:** VV PEA.

**Writing – original draft:** VV PEA.

**Writing – review & editing:** VV PEA.

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# Paper V

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# A UNIQUE OCCURRENCE OF A PSAMMOSTEID HETEROSTRACAN ON THE PERI-GONDWANAN SHELF IN THE LOWER/MIDDLE DEVONIAN BOUNDARY MARINE DEPOSITS

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**Abstract:** A rare psammosteid heterostracan (Agnatha) occurrence in the Devonian of the Prague Basin is indicative of a dry land influence in the regional palaeogeography. This argument is strongly supported by the appearance of vascular plants, but the studied vertebrates allow us to presume a local brackish water environment. These conditions are considered to be related to a supposed land in the vicinity of the preserved relic of Devonian rocks in the Teplá-Barrandian unit. Such unique conditions were not repeated in the area despite the increasing extent of continental environment related to the rising Variscan Orogeny.

**Key words:** Agnatha, Psammosteida, Devonian, Prague Basin, local palaeogeography

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## Introduction

The volcano-sedimentary deposits forming the infill of the Prague Basin are situated in the central part of the Czech Republic. Although preserved as a small denudation relic in the Teplá-Barrandian unit of the Bohemicum, they represent one of the most significant palaeontological areas in the European Variscides, with more than a century and a half of fossil collecting history. In spite of this extensive collecting activity, agnathan remains were not known from the intensively studied Silurian strata of the Prague Basin until recently, and even now only as microfossils (Vaškaninová (2014) described rare findings of indeterminable thelodont scales from the Ludfordian of the Požáry Quarry).

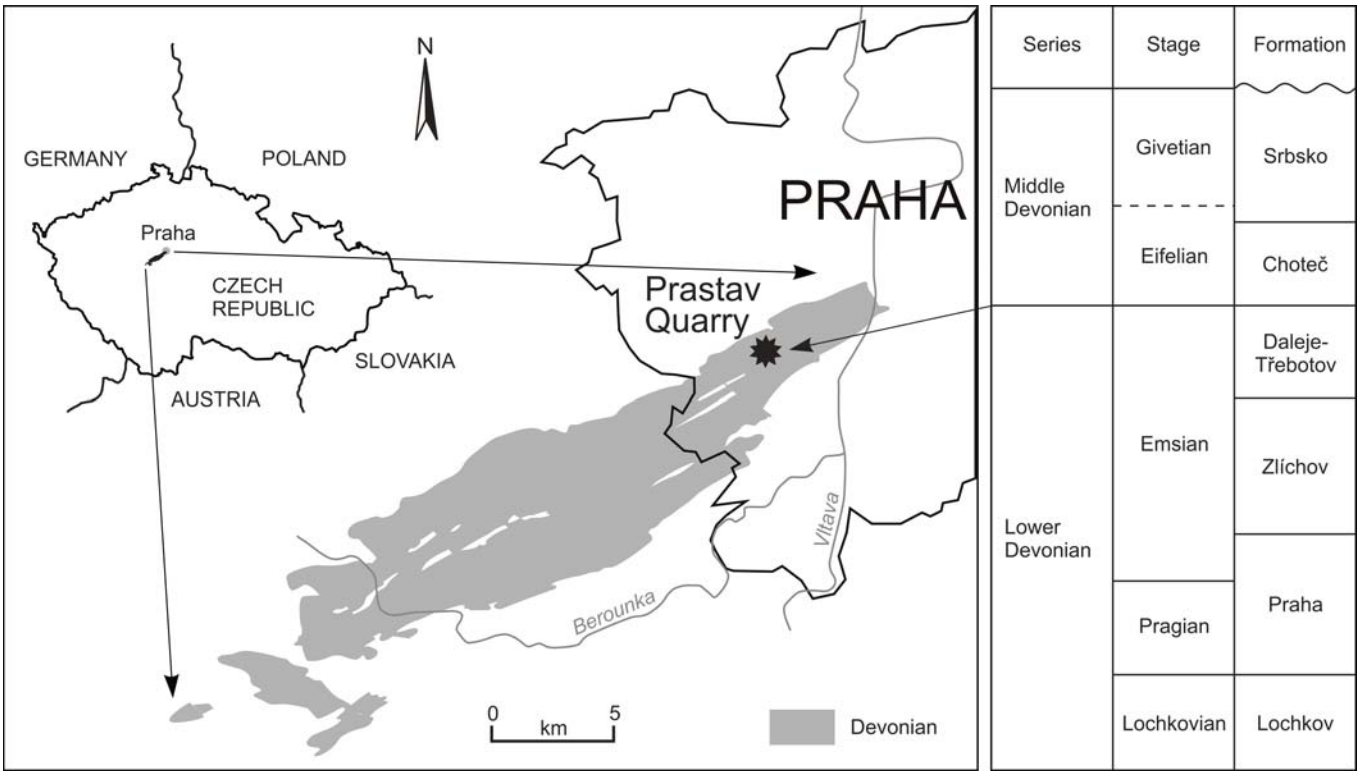
In the Devonian, the only agnathan remains known are two separate head carapace plates of psammosteid heterostracans. Both were found at the same locality (Prastav Quarry, see below) and are currently stored in the National Museum in Prague (for the specimen not described herein see Růžička 1929: fig. I.2). The larger and more easily determinable specimen (National Museum inventory number Lc 62) was originally described as *Psammosteus* (*Ganosteus*) *perneri* Růžička, 1929. Tarlo (1965) assigned the specimen to the genus *Schizosteus* Obruchev, 1940 and based the species diagnosis on a unique dermal ornamentation of regular, well-separated tubercles. No new material has been found or, at least, available for study and revision. However, the occurrence of psammosteids in the Prague Basin itself will be briefly discussed in this paper.

## Geological and palaeontological settings

Both psammosteid carapace plates were discovered at a single locality – the Prastav Quarry near the village Holyně south-west of Prague (Text-fig. 1; also named Holině by Růžička (1929) or Holin, Hlubocepy near Prague by Tarlo (1965)). The quarry is now abandoned, but its walls are well-accessible and preserved, because it is a part of the NPP U Nového mlýna area protected by State Law. The section in the Prastav Quarry is the international parastratotype of the Lower/Middle Devonian boundary, comprising the upper part of the Emsian Třebotov Limestone and the basal portion of the Eifelian Choteč Limestone (Text-fig. 1).

The upper part of the Třebotov Limestone is developed as light grey micritic nodular limestones, containing a rich fauna with goniatites (e.g. genera *Mimagoniatites*, *Agoniatites*, *Gyroceratites*), trilobites (genera *Phacops*, *Scabriscutellum* a.o.), bivalves (genera *Panenka*, *Kralovna*, *Pantata*) and tentaculites (*Nowakia richteri*, *N. holynensis*) (Chlupáč et al. 1979).

The basal portion of the Choteč Limestone is lithologically quite different from the uppermost part of the Třebotov Limestone (Chlupáč et al. 1979, Koptíková 2011) in relative deep-water facies of the shelf (Chlupáč 1998) or



| Series | Stage | Formation |
|---|---|---|
| Middle Devonian | Givetian | Srbsko |
| | Eifelian | Choteč |
| Lower Devonian | Emsian | Daleje-Třebotov |
| | | Zlíchov |
| | Pragian | Praha |
| | Lochkovian | Lochkov |

**Text-fig. 1. Sketch map of Devonian in Prague Basin; position of Prastav Quarry marked with asterisk; stratigraphy of Devonian in Prague Basin (after Chlupáč 1998); Emsian/Eifelian boundary beds preserved in quarry related to locality with arrow.**

slope (Koptíková 2011). It consists of grey to dark-grey micritic limestone, with thin intervals of dark calcareous shales. The fauna is characterized by the appearance of index goniatites *Pinacites jugleri* and *Fidelites occultus*, trilobites (e.g. genera *Cyphaspides*, *Aulacopleura*, *Thysanopeltis*) (Chlupáč et al. 1979), and brachiopods (e.g. linguliform genus *Paterula*, rhynchonelliform genera *Chlupacina*, *Holynetes*) (Havlíček and Racheboeuf 1979, Mergl 2001). Tentaculites (*Nowakia sulcata*) and other fauna also occur (Chlupáč et al. 1979). No other vertebrate remains are known from this locality.

## Systematic palaeontology

### *Schizosteus perneri* (Růžička, 1929)

Pl. 1

For synonymy see Tarlo (1965: 63).

Holotype. NM-Lc 62 (National Museum, Prague).

Type locality. Prastav Quarry near Holyně, southwest of Prague.

Type horizon. Lower/Middle Devonian boundary beds, Emsian/Eifelian; Třebotov/Choteč limestones (see Discussion).

Description and remarks. Růžička (1929) acquired the specimen NM-Lc 62 from the quarry workers without being told about the exact circumstances of the discovery. He presumed the origin on the basis of contemporary labours in the central part of the quarry wall. We refer to the previous determination of the specimen to *Schizosteus perneri* (Růžička, 1929) as published by Tarlo (1965). We have no new data or observations to alter the diagnosis or the systematic position of the specimen, but we include remarks on some non-diagnostic features we have observed on the specimen.

The specimen represents a well preserved left branchial plate, with its dorsal surface exposed (Pl. 1, Fig. 1). It is covered with superficial dermal ornament laterally, whereas in the mesial area, the ornament is exfoliated, and the inner vascular bone surface exposed (Pl. 1, Fig. 2c). The plate is ca. 17 cm long, slightly convex, except for the anterior-most margin, which is concave (Pl. 1, Fig. 2a). The overall convex shape is increasing towards the posterior end (Pl. 1, Fig. 2b). Posterior to the concave area, a transverse fracture is visible. The ornament is composed of well-bordered roundish tubercles with radially oriented ribs, slightly almond-shaped in cross section. Meeting points of the ribs are oriented towards the lateral margin of the plate (Pl. 1, Fig. 2d–e) on each well preserved tubercle. The tubercles are small at the anterior margin of the plate, and gradually enlarge towards the posterior end. In the anterior displaced area, a cross section of the dermal layers is visible (Pl. 1, Fig. 2f), as well as the shape of the tubercles, which are narrower at the base. The tubercles tend to be arranged in diagonal rows on most of the plate surface.

## Discussion

As mentioned above, the exact stratigraphic layer which yielded the two specimens is unknown. However, Růžička

(1929) stated that the strata being quarried at the time of the discovery contained numerous goniatite fossils. He also wrote his assumption about the stratigraphic position on the original specimen label, where the type horizon is determined as the Choteč Limestone, horizon gγ (G-g$^3$), of Eifelian age. This information was borrowed by Tarlo (1965). On the contrary, Chlupáč et al. (1979) considered the find to belong to the upper part of the Třebotov Limestone (*N. richteri* or *N. holynensis*-Zone), based on the lithotype. Chlupáč's interpretation would place its origin in the uppermost Emsian strata. Lukševičs et al. (2010) agreed with Chlupáč, although they were citing Tarlo (1965).

This controversy has so far proven impossible to resolve conclusively, as there are no visible index fossils in the matrix surrounding the plate. We dissolved several small samples taken from the limestone slab with the specimen NM-Lc 62, but neither conodonts nor determinable tentaculites were found in the residuum. We identified only a number of very small, narrow cones as internal moulds of tentaculite shells, representing complete apical portions or their fragments. We subsequently tried to find tentaculites directly in the rock. We used the remaining small rock pieces from the slab with the fossil. After a short acid treatment, plenty of cross-cuts or internal and external moulds appeared on the corroded surface. As the external moulds seem to be smooth, without transversal rings, they can be assigned to the genus *Styliolina*, but the material does not allow species determination. Since this genus occurs in both the Třebotov and Choteč limestones, the value of the discovered tentaculites for precise stratigraphy is almost nil. The only argument we can present, however weak, supports Chlupáč's premise: *Styliolina* was more diversified and abundant in the Emsian than the Eifelian of the Prague Basin (Chlupáč et al. 1979). Since the sample was small, finding any such fossils at all in it indicates a relative abundance in the stratum.

Nevertheless, the lack of exact stratigraphic position of the specimens is not too serious. It is certain that both specimens were found in the Emsian/Eifelian boundary interval. In spite of lithological change, the limestones of this interval are of similar origin from turbidites or distal tempestites (Koptíková 2011).

Psammosteid heterostracans are known mainly from Laurussia (Lukševičs et al. 2010), and are quite rare in the Lower Devonian. The genus *Drepanaspis* Schlüter, 1887 is one of the few genera known from the Pragian and Emsian. *Drepanaspis* occurs in south-western England and the Rhenish Slate Massif in western Germany (Tarlo 1965), both of which are considered Avalonian terranes, and in the middle-upper Emsian strata of the Ardenne Massif (Delsate et al. 2004), forming a part of Armorica.

The presence of a psammosteid heterostracan in the Prague Basin on the peri-Gondwanan shelf represents the easternmost occurrence of the group. It is also the earliest occurrence of the genus *Schizosteus*, which is otherwise known from the Eifelian and Givetian of Laurussia (Tarlo 1965, Lukševičs et al. 2010, Glinskiy 2014). Lukševičs et al. (2010) mentioned this occurrence, but associated it with the faunal interchanges with Armorica. However, Young (1990) supposes the faunal communication between Gondwana and Laurussia to commence in the Frasnian.

The Lower-Middle Devonian boundary deposits in the Prague Basin represent a purely marine succession of carbonates and calcareous shales, rich in fossils. Most of them are indicative of a marine environment, e.g. cephalopods (goniatites and "orthocones") are exclusively marine, and generally even stenohaline (Boyle and Rodhouse 2005).

Psammosteids are considered freshwater dwellers by Lebedev et al. (2010); coastal brackish-water or continental inhabitants by Lukševičs et al. (2010). The occurrence of two psammosteid dermal plates, one of them quite large, indicates the proximity of dry land. Its existence is also strongly supported by the occurrence of terrestrial plants, which first appeared in the Prague Basin during the Silurian (Obrhel 1962, 1968, Libertín et al. 2003). The occurrence of these plants in the Silurian and lowermost Devonian can be correlated with emerged volcanic islands (Měska and Kratochvíl 1946, Fiala 1970, Kříž 1992). In the Devonian, the existence of dry land was apparently caused mainly by tectonic activity (cf. Havlíček 1998).

Obrhel (1968) illustrated the diversity and frequency of occurrence of terrestrial plants in the marine sediments of the Prague Basin. He demonstrated a significant increase in both aspects toward the Srbsko Formation, the terminal unit of the basin, yielding abundant terrestrial plants, such as genera *Protopteridium*, *Protolepidodendron*, *Pseudosporochnus* (Obrhel 1961, 1968), often preserved in large fragments. This formation has a different character than other Devonian units. It is represented by a rhythmic siliciclastic succession, while other units are predominantly carbonate. This character of the Srbsko Formation is considered to be caused by the Variscan movements in the neighbouring areas (Chlupáč 1998). In fact, it reflects a supply of material transported from the near, continually approaching and uplifting Variscan Orogeny.

While the rich Givetian flora was related to large marginal areas of the emerged Variscan range, the upper Emsian and Eifelian terrestrial plants (Obrhel 1960, 1968, 1991) could originate from the limited continental conditions of islands. A lack of terrestrial plants in the Pragian and lower Emsian of the Prague Basin (Obrhel 1968, 1991) indicates an absence of dry land conditions near the area where the Devonian strata in the central Teplá-Barrandian Unit were deposited.

Psammosteids would be expected to follow the same trend as we can observe in terrestrial plants. They occur in sediments of the age when only the restricted habitats of scattered islands could exist. The subsequent expanding continental areas have not yielded any evidence of their presence. It is quite enigmatic with respect to a more complicated migration between islands, compared to the easily followable pathways along the Variscan coast in the period when the psammosteids flourished (Lebedev et al. 2010). It is a question which remains to be studied, because the limited occurrence of psammosteids in the Prague Basin indicates a complicated local palaeogeography. It also raises questions about the fresh and brackish water environments, their extent and the character of the dry lands and their coastal areas in the discussed period. Even if a carcass, postmortem transported from a far area, cannot be safely excluded, it can only raise questions about the distance, rather than existence of the suitable environment itself. As we are not able to estimate that distance, taking both aspects into account, we can estimate hundreds of meters to tens of kilometres. However, the occurrence of not a single but two independent remains of psammosteids and their absence in other parts of the Devonian section in the Prague Basin both indicate a temporary existing favourable habitat not far from the site of their discovery, rather than an accidental, unrepeated transport of two almost coeval carcasses from a long distance.

## Conclusions

The occurrence of a psammosteid heterostracan in the Prague Basin during the Emsian/Eifelian turn supports the assumption about the existence of dry land nearby. In that time, probably a brackish coastal environment (Lukševičs et al. 2010) enabled the penetration of psammosteids to the area. The conditions suitable for this vertebrate group were apparently of very short duration, because psammosteids never reappeared in the Prague Basin.

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## Explanations of the plate

## PLATE 1

*Schizosteus perneri* (Růžička, 1929), Prastav Quarry near Holyně, No. NM-Lc 62

1a. Left branchial plate in dorsal view.
1b. Schematic drawing of the plate, grey colour indicating areas with preserved dermal ornament.
2a. Anterior view.
2b. Posterior view.
2c. Detail of vascular bone layer.
2d–e. Details of dermal ornament in posterior area of plate.
2f. Detail of dermal ornament in anterior area of plate.
Scale bars = 1 cm; in 2c–f scale bars = 1 mm.

# PLATE 1