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Mgr. Lukáš Laibl

**Ontogeneze vybraných taxonů trilobitů a agnostoidů
ze středního kambria barrandienské oblasti**

**Ontogeny of selected taxa of middle Cambrian
trilobites and agnostoids of the Barrandian area**

Disertační práce

Školitel: doc. RNDr. Oldřich Fatka, CSc.

Konzultant: RNDr. Petr Budil, Ph.D.

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Prohlášení:

Prohlašuji, že jsem závěrečnou práci zpracoval samostatně a že jsem uvedl všechny použité informační zdroje a literaturu. Tato práce ani její podstatná část nebyla předložena k získání jiného nebo stejného akademického titulu.

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Mgr. Lukáš Laibl

Abstract

This thesis deals with the ontogeny of trilobites and agnostoids from the Cambrian of the Skryje-Týřovice and Příbram-Jince basins (Barrandian area, Bohemian Massif). Thesis is presented as a compilation of four papers that were published in scientific peer-reviewed journals. The introduction of the thesis serves as a general overview of the trilobite post-embryonic development and connects all published papers together.

All four papers presented here are focussed on modern description of the post-embryonic development of *Sao hirsuta*, Ptychopariida sp. A, Ptychopariida sp. B, Ptychopariida sp. C, *Ellipsocephalus hoffi*, *Ellipsocephalus polytomus*, *Hydrocephalus carens* and *Eccaparadoxides pusillus*. In addition, a discussion about the life-history strategies of early developmental trilobite stages is presented. It has been suggested that *Sao hirsuta* and Ptychopariida sp. A had benthic protaspides and that the early ontogenetic stages of Ptychopariida sp. B, *Eccaparadoxides pusillus* and *Hydrocephalus carens* were likely lecithotrophic. Consequently, it has been documented that species with benthic protaspides show a strongly restricted geographic distribution and that lecithotrophic taxa seem to be associated with higher latitude areas. The developmental patterns of *Ellipsocephalus hoffi* and *Ellipsocephalus polytomus* were used for inferring a close phylogenetic relationship between Ellipsocephalidae and Redlichiida.

Abstrakt

Předkládaná práce se zabývá ontogenezí trilobitů a agnostidů, pocházejících ze skryjsko-týřovické a příbramsko-jinecké pánve (Kambrium, Barrandien, Český masiv). Práce je prezentována jako soubor čtyř samostatných článků, které byly publikovány v recenzovaných odborných časopisech. Úvodní část práce slouží jako obecný přehled postembryonálního vývoje trilobitů a propojuje prezentované publikace dohromady.

Publikované studie jsou zaměřeny na moderní popis postembryonálního vývoje druhů *Sao hirsuta*, Ptychopariida sp. A, Ptychopariida sp. B, Ptychopariida sp. C, *Ellipsocephalus hoffi*, *Ellipsocephalus polytomus*, *Hydrocephalus carens* a *Eccaparadoxides pusillus*. Kromě toho je zde diskutována životní-historie raných vývojových stádií vybraných trilobitů. U druhů *Sao hirsuta* a Ptychopariida sp. A je předpokládáno, že měly bentická protaspidní stádia. Druhy Ptychopariida sp. B, *Eccaparadoxides pusillus* a *Hydrocephalus carens* byly pravděpodobně lecitotrofní. Bylo rovněž prokázáno, že druhy s bentickými protaspidními stádii měly silně omezené zeměpisné rozšíření a že lecitotrofní druhy se vyskytovaly převážně ve vyšších zeměpisných šířkách. Vývoj druhů *Ellipsocephalus hoffi* a *Ellipsocephalus polytomus* ukazuje na blízké fylogenetické vztahy mezi čeledí Ellipsocephalidae a řádem Redlichiida.

Contents

Introduction	6
List of papers	6
Aim of the thesis	7
Material and methods	8
Material	8
Methods	8
Ontogeny of trilobites	9
Outline of the trilobite post-embryonic development	9
Growth	11
Segmentation	13
Life-history strategies	15
Ontogeny of Cambrian trilobites and agnostids from the Barrandian area	20
Ontogenetic stages from the Skryje-Týřovice Basin	20
Ontogenetic stages from the Příbram-Jince Basin	22
Conclusions and future directions of the study	23
Acknowledgements	24
References	25

Introduction

The first detailed description of the post-embryonic development of trilobites was published more than 160 years ago by Barrande (1852). Material for his ontogenetic studies comes from the Central Bohemia called the Barrandian area. This material was subsequently studied by several workers, most comprehensively by Šnajdr (1958). Since that time, no modern revision of the Cambrian trilobite development from the Barrandian area has been published, despite the increasing knowledge in this field worldwide. Fortey (2001) stressed the importance of Cambrian trilobite ontogenies for better understanding of the phylogenetic relationships within Trilobita.

This thesis deals with the post-embryonic development of trilobites and agnostids from the traditional mid-Cambrian (Cambrian Series 3) strata of the Barrandian area. The exceptional preservation of this material and its amount enable to study Cambrian trilobite development in astonishing detail. Species from this area also comprise members of the trilobite groups (e.g. Ptychopariida, Redlichiida) that are crucial for understanding the early evolution and diversification of the group itself. They also provide sufficient data for resolving the origin of certain life-history strategies that appear already in the Cambrian period.

List of papers

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

- I. **Laibl, L.**, Fatka O., Crônier C., Budil P. 2014. Early ontogeny of the Cambrian trilobite *Sao hirsuta* from the Skryje-Týřovice Basin, Barrandian area, Czech Republic. *Bulletin of Geosciences* 89, 293–309.
- II. **Laibl, L.**, Fatka, O., Budil, P. 2015. Unusual Cambrian trilobite larva from the Skryje-Týřovice Basin, Czech Republic. *Palaeoworld* 24, 71–74.
- III. **Laibl, L.**, Fatka, O., Budil, P., Ahlberg, P., Szabad, M., Vokáč, V., Kozák, V. 2015. The ontogeny of *Ellipsocephalus* (Trilobita) and systematic position of Ellipsocephalidae. *Alcheringa* 39, 477–487.
- IV. **Laibl, L.**, Esteve, J., Fatka, O. 2017. Giant postembryonic stages of *Hydrocephalus* and *Eccaparadoxides* and the origin of lecithotrophy in Cambrian trilobites. *Palaeogeography, Palaeoclimatology, Palaeoecology* 470, 109–115.

Aim of the thesis

This thesis is focused on the post-embryonic development of selected trilobites and agnostids from the middle Cambrian of the Skryje-Týřovice and Příbram-Jince basins and its implications for trilobite biogeographic distribution and phylogeny. Specifically, the main objectives of the thesis are the following:

- a) A modern description of developmental sequences or individual stages, using appropriate imaging techniques (high resolution optical microscopy, scanning electron microscopy), detailed biometrics and statistical analysis. **Papers I-IV** tackle these themes and methods.
- b) A discussion about life-history strategies, in particular about mode of life of the earliest trilobite stages (protaspides), based on functional morphology and developmental patterns. This is the main topic of the **paper I** (benthic protaspides) and **paper IV** (lecithotrophy).
- c) An investigation of how life-history strategies can influence the biogeographical distribution of particular species. More specifically, whether trilobites with benthic protaspides tend to have more restricted palaeogeographical distributions (discussed in **paper I**), and the validity of “Thorson’s rule” (that the percentage of direct developers or lecithotrophic species increases with higher latitudes; discussed in **paper IV**).
- d) The utility of developmental data for resolving phylogenetic relationships at various taxonomical levels. Developmental patterns were suggested as evidence of phylogenetic closeness in **paper III**. The developmental modification probably caused by differing selective pressures, and the differing morphologies this produced in closely-related taxa, were discussed in **paper IV**.

Note: The ontogenetic development of agnostids, in particular of the species *Condylopyge rex*, was preliminarily also studied during the course of this Ph.D. However, the amount of material and the necessity to compare it with additional material found worldwide means additional work is required before manuscript preparation. Therefore, the paper is not included in this thesis, although the material has been statistically evaluated and the manuscript is in preparation.

Material and methods

Material

The majority of the studied material in this thesis and **papers I–IV** comes from the Drumian strata from either the Skryje-Týřovice Basin or the Příbram-Jince Basin (Barrandian area, Bohemian Massif, Czech Republic). Additional material used in **paper III** was collected from the Cambrian Stage 5 limestones of the Jämtland area (Sweden). The material from both Bohemian basins is preserved as internal and/or external moulds in fine lithic arenites to shales. The surface of both internal and external moulds from the Skryje-Týřovice Basin is usually covered by iron hydroxides.

All published material is deposited in the collections of the National Museum, Prague (prefix NM), the Czech Geological Survey, Prague (prefix CGS), and in the Museum of Dr. Bohuslav Horák at Rokycany (prefix MBHR). Further study material is deposited in the Museum of Comparative Zoology – Harvard University, Cambridge (Massachusetts, USA) and in the Natural History Museum, London (UK).

Methods

All studied material was photographed using a scanning electron microscope in low vacuum mode (JEOL-6380 LV, Hitachi S-3700N, material for the **paper I**), under an optical microscope (Keyence VHX-2000, Nikon SMZ 1500, Olympus SZX 12, material for **papers I–IV**) or using a digital camera (Canon EOS 6D, material for the **paper III**). Samples imaged using both the optical microscope and digital camera were coated with ammonium chloride prior to photography. When necessary, line drawings were produced from photographs in Adobe Illustrator CS2.

The material was subsequently measured using the optical image analyser TpsDig2 (Rohlf 2006). Measured specimens were plotted on width vs. length scatterplots in order to recognise individual instars (**papers I, IV**), plotted on size frequency histograms to illustrate the size distributions (**papers I, IV**), or on boxplots to compare selected groups with other parameters (**paper IV**). The measured parameters were also used to calculate growth patterns. In **paper IV** one-way ANOVA and post-hoc Tukey (HSD) tests were used to investigate the differences between selected groups. All statistical analyses were performed in R 3.0.3 (R

Core Team 2014, in the **paper IV**) or using the PAST package (Hammer et al. 2001, in **paper I**).

Ontogeny of trilobites

Outline of the trilobite post-embryonic development

Trilobite post-embryonic development is traditionally divided into three successive periods – the protaspid, meraspid and holaspid periods (introduced and defined by Beecher 1895 and Raw 1925, for a summary see Chatterton and Speyer 1997, see Fig. 1). This basic division is usually used for description of trilobite life-cycles in the scientific literature. These periods, however, are defined purely on the articulation of the dorsal exoskeleton, and therefore probably do not represent corresponding life phases in different trilobites (Chatterton and Speyer 1997, Hughes et al. 2006). Therefore, the boundaries between the protaspid-meraspid periods and meraspid-holaspid periods often do not co-occur with the timing of metamorphosis, onset of the epimorphic growth mode, or onset of the adult cranidial morphology (e.g. Hughes and Chapman 1995, Chatterton and Speyer 1997, Hughes et al. 2006).

The protaspid period comprises the earliest, widely accepted, mineralised postembryonic stages (Beecher 1895, but see Fortey and Morris 1978). The size of protaspid instars usually varies between 0.2 and 1.0 mm in length (Whittington 1957a, **paper IV**) but it can reach up to 2.5 mm in some species (**paper IV**). By definition, the protaspid period is characterised by the cephalon and trunk being conjoined as one shield (Raw 1925, Edgecombe et al. 1988), and having functional facial sutures (Hughes et al. 2006). The latter character is, however, not recognisable in all supposed protaspides (e.g. *Eodiscina*, cf. Zhang and Clarkson 2012). Protaspides are known virtually from all trilobite groups with the exception of *Agnostina* and *Olenellina*. The protaspid period can be subdivided into individual protaspid stages (stage 1, stage 2, etc.), usually recognisable by their differing morphology and dimensions (Fig. 2). Beecher's (1895) subdivision of the protaspid period into anaprotaspides, metaprotaspides and paraprotaspides is currently little used, mainly due to inconsistency in their definition and problems with homology of these stages in all trilobites (Edgecombe et al. 1988). The morphology of protaspid stages is diverse and is generally related to taxonomy, mode of life

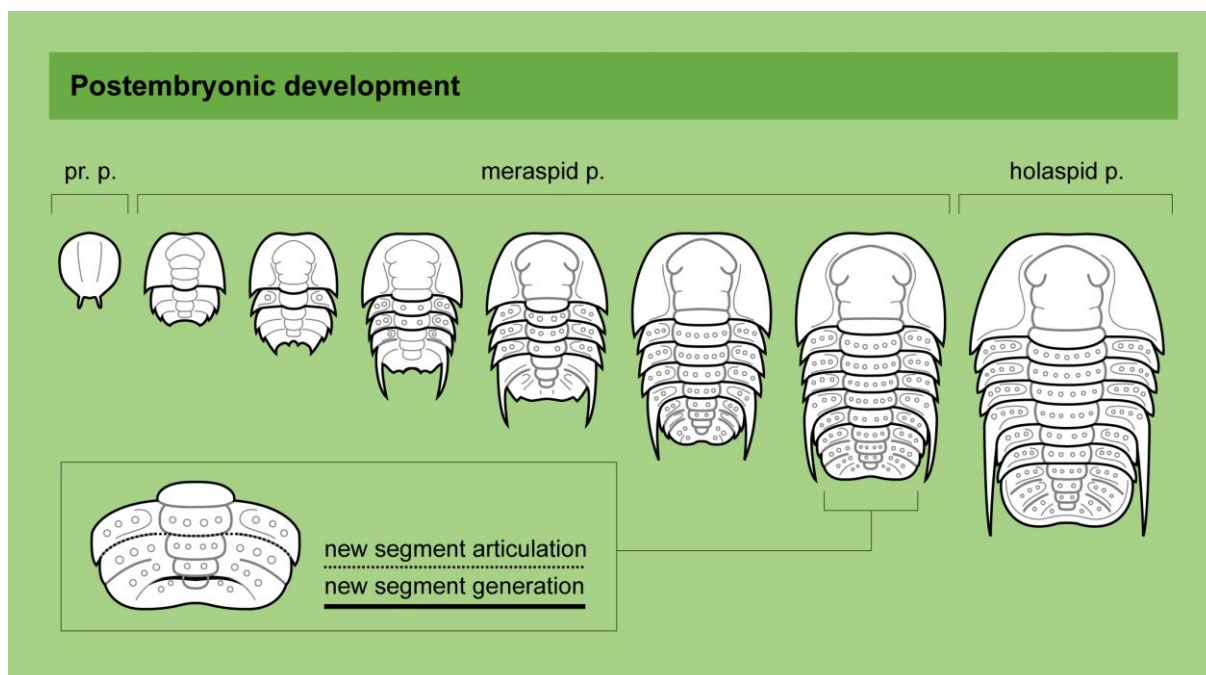


Figure 1 – Postembryonic development of *Shumardia (Conophrys) salopiensis*; modified according Stubblefield (1926) and Waisfeld et al. (2001). Abbreviations: holaspis p., holaspis period; meraspis p., meraspis period; pr. p., protaspis period.

and to particular protaspis stage (see chapter “Life-history strategies” and Fig. 2 for basic terminology and morphological descriptions).

The onset of the meraspis period begins when the first articulation structure between cephalon and trunk is developed (Raw 1925, Whittington 1957a, Chatterton and Speyer 1997, see Fig. 1). In some taxa, like *Sao hirsuta*, the meraspis period apparently starts with the development of two articulations (**paper I**). During the meraspis period new segments were progressively released from the anterior margin of the pygidium into the thorax (Stubblefield 1926, Chatterton and Speyer 1997). The meraspis period is subdivided into meraspis degrees based on the number of thoracic segments (degree 1 = one thoracic segment developed, degree 2 = two thoracic segments developed, etc.). The number of meraspis degrees, however, does not always directly correspond to the number of instars during the meraspis period (Chatterton and Speyer 1997). In most of the trilobites, one segment was released from the pygidium with each moult, but there are some exceptions when two segments could be released as in *Dentaloscutellum campbelli* (see Chatterton 1971), or no segments released as in *Sao hirsuta* and *Shumardia (Conophrys) salopiensis* (**paper I**, Fortey and Owens 1991, respectively). With the exception of radical metamorphoses, most of major morphological changes occurred during the meraspis period.

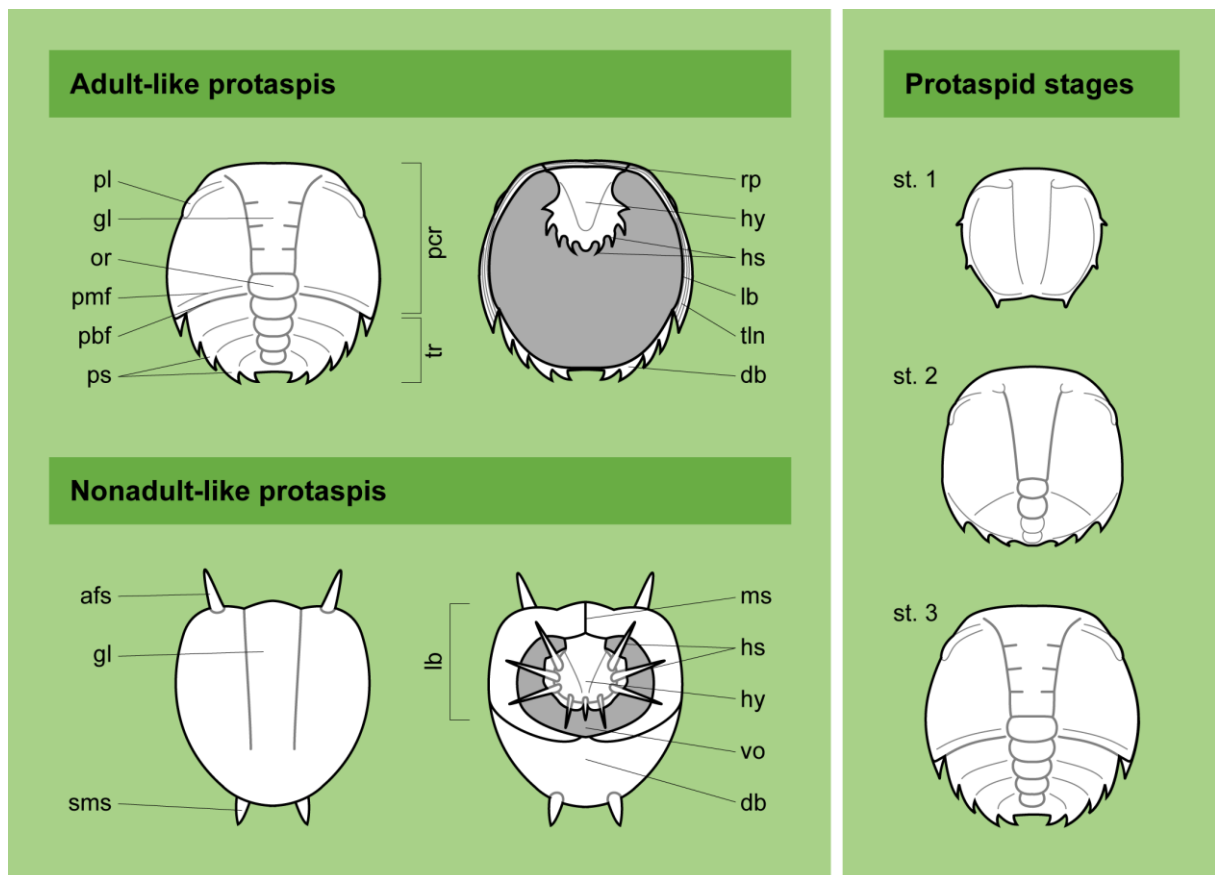


Figure 2 – A typical morphology of the adult-like (benthic) and nonadult-like (planktonic) protaspid stage from the dorsal and ventral view; modified according Speyer and Chatterton (1989) and **paper I**. Abbreviations: afs, anterior fixigenal spine; db, doublure; gl, glabella; hs, hypostomal spine; hy, hypostome; lb, librigena; ms, median suture; or, occipital ring; pbf, posterior border furrow; pcr, protocranium; pl, palpebral lobe; pmf, posterior marginal furrow; ps, trunk spines; rp, rostral plate; sms, submarginal spines; st. 1-3, stage 1-3; tln, terrace lines, tr, trunk; vo, ventral opening.

A trilobite is considered to be in the holaspid period when all the thoracic segments, that are characteristic for the given species, are separated (Raw 1925, but see Stubbelfield 1926). This definition is, however, inapplicable for some species because they show variation in the number of thoracic segments, such as *Aulacopleura konincki* (see Hughes and Chapman 1995, Fusco et al. 2004), *Monkaspis daulis* (see Yuan et al. 2014), *Paradoxides davidis* (see Bergström and Levi-Seti 1978), *Elrathia kingii* (see Bright 1959) and numerous other examples in Hughes et al. (1999). Some trilobites also continued to add segments into the holaspid pygidium (see protarthric development in the chapter “Segmentation”).

Growth

Trilobites, like other ecdysozoans, grew discontinuously by a series of moulting events. Two basic traits are used to describe growth in trilobites – the growth increment and the growth

rate. The growth increment (GI) is the absolute linear increase of the body size and can be defined as

$$GI = a_n - a_{n-1}$$

where a is a linear dimension of the n^{th} instar. Alternatively, the average growth increment (AGI) can be calculated for all instars in the ontogeny of a particular species, and is defined as

$$AGI = \frac{a_n - a_1}{n - 1}$$

where a is a linear dimension of the n^{th} or the 1^{st} instar and n is the number of instars. The growth rate (GR) is a pre-moult/post-moult size ratio, and can be defined as

$$GR = \frac{a_n}{a_{n-1}}$$

where a is a linear dimension of the n^{th} instar. The average growth rate in trilobites falls within standard values that are known for other arthropods (Fusco et al. 2011). Although some workers suggested higher growth rates earlier in ontogeny (e.g. Chatterton et al. 1990), modern data suggest that the growth rate was relatively consistent during the whole of development (Fusco et al. 2011). Only the growth increment during radical metamorphosis of certain species (see below) seems to be slightly higher than during the rest of the development (Lerosey-Aubril and Feist 2005, Chatterton 1980, but see Chatterton et al. 1990). On the other hand, in some, possibly lecithotrophic species (**paper IV**), the growth increment between protaspid stages is rather lower (see chapter “Life-history strategies”).

Dyar’s rule argues that the linear dimensions of successive instars of a particular arthropod species increase at a constant rate (Dyar 1890, see also Palmer 1962). Generally, Dyar’s rule is considered the null hypothesis for arthropod growth (e.g. Klingenberg and Zimmermann 1992). The level of consistency of the constant ratio during development can be quantifying by the index of conformity with the Dyar’s rule (IDC , see Fusco et al. 2011), and is defined as

$$IDC = 1 - \frac{|a_n - b_n|}{AGI(n - 2)}$$

where a is a measured linear dimension of the n^{th} instar, b is a linear dimension of the expected n^{th} instar under the constant growth, AGI is average growth increment and n is the

number of instars. This index can reach values from zero (maximal divergence from Dyar's rule) to one (perfectly constant size ratio). The majority of trilobites (~80% with sufficient developmental data) apparently grew at a relatively constant rate during their life cycle (i.e. generally following Dyar's rule), since their index of conformity with Dyar's rule is larger than 0.8 (Fusco et al. 2011, **paper I**).

Segmentation

Trilobite development can be considered as hemianamorphic, i.e. the generation of new segments (anamorphic phase) during the early ontogeny is subsequently followed by a stable number of segments (epimorphic phase) later in development (Minelli et al. 2003, Fusco et al. 2004, Hughes et al. 2006, see Fig. 3).

Beside growth and morphological changes, two main processes took place during the postembryonic development of trilobites – segment generation and segment articulation. Generally, all segments that form the trilobite cephalon were already developed in the earliest protaspides (Hughes et al. 2006, but see Lee and Chatterton 1996). New segments of the trunk were generated at the anterior part of the terminal segment (i.e. subterminally, see Fig. 1), as can be observed in some trilobites bearing a macropleural segment, such as *Shumardia (Conophrys) salopiensis* (cf. Stubblefield 1926, Fortey and Owens 1991). Although the usual pattern of segment addition during the early ontogeny of trilobites was one segment per moult, cases where none, two, three, or more segments being added between successive moults are also known (cf. Hughes et al. 2006, Crônier 2010, Hou et al. 2015, Dai et al. 2014, 2015, **paper IV**).

Both segment generation and segment articulation were likely independent processes, decoupled from one another. Such decoupling would mean that segment generation was faster, similar to, or slower than segment articulation. This enables us to recognise three phases – the accumulation, equilibrium and depletion phases (Kopaska-Merkel 1987, Simpson 2005). During accumulation phase the rate of segment generation was faster than segment articulation, and consequently the number of segment in the pygidium increased. In equilibrium phase, the rates of segment generation and articulation were equal and the number of pygidial segments therefore remained constant. Finally, in the depletion phase the segments were released into the thorax faster than they were generated and so segment number in the

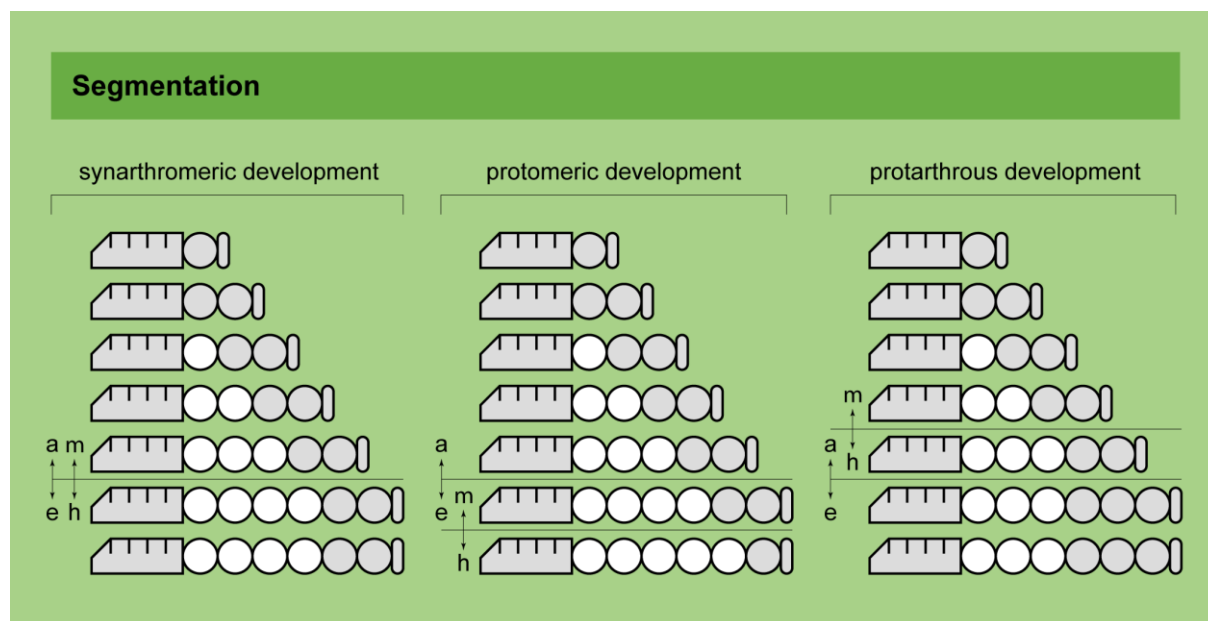


Figure 3 – Types of the trilobite development that are based on the comparative timing of the last articulation and onset of the epimorphic phase of segmentation; modified according Hughes et al. (2006). Abbreviations: a, anamorphic phase; e, epimorphic phase; h, holaspisid period; m, meraspid period.

pygidium decreased. The depletion phase was operational usually during the terminal part of the meraspid period of some trilobites (Hughes et al. 2006).

Based on the comparative timing of the last articulation and onset of the epimorphic phase of segmentation, Hughes et al. (2006) defined several modes of trilobite development – protomeric, synarthromeric and protharthrous (Fig. 3). Protomeric development occurs when the epimorphic phase of the development precedes the onset of the holaspisid period. This is probably the most common mode of development in trilobites, known in species such as *Aphelaspis brachyphasis*, *Scutellum calvum*, *Dimeropyge speyeri*, *Hintzeia plicamarginis*, *Sao hirsuta*, etc. (see Simpson et al. 2005, Hughes et al. 2006, **paper I**). In synarthromeric development, the onset of the holaspisid period and the epimorphic phase are synchronous. This is typical for *Triarthrus eatoni*, *Aulacopleura konincki*, *Trimercephalus lelievrei*, etc. (Hughes et al. 2006, Crônier 2010). Finally, protharthrous development is characterised by an earlier onset of holaspisid period than the onset of epimorphic phase. This mode of development is known in *Ctenopyge ceciliae*, *Cryptolithus tessellatus*, *Cryphops ensae*, *Eoredlichia intermediata*, *Zhangshania typica*, etc. (Hughes et al. 2006, Crônier 2010, Dai and Zhang 2013, Hou et al. 2017).

Life-history strategies

With few exceptions (e.g. Fortey 1974, McCormick and Fortey 1998, Shino et al. 2014), adult trilobites were generally mobile benthic scavengers or particle feeders (Fortey and Owens 1999). Comparable life-styles can be suggested for the late meraspid trilobites in which the overall morphology was similar to the adult. A different life-style and ecology can be determined for the protaspides and earliest meraspides.

Since the first description of trilobite ontogeny, and in particular the protaspid period, trilobite workers have generally considered all early stages of trilobites (protaspides, earliest meraspides) to be planktonic (e.g. Beecher 1895, Whittington 1957a, Cisne 1973). Although this was certainly true for some trilobites, there were also trilobites likely with benthic early developmental stages. Speyer and Chatterton (1989) established two general morphological types of trilobite protaspides that are based on the overall similarity to the later developmental stages – the adult-like and nonadult-like protaspides (Fig. 2). Adult-like protaspides resemble adult (holaspid) trilobites in overall appearance; they are dorso-ventrally flattened, with a planar ventral surface, and have a sharply inturned doublure, often with terrace ridges. The ventral opening is large and the hypostome comparatively small. These protaspides can bear marginal spines that are oriented generally in the horizontal plane. Nonadult-like protaspides are usually bulbous or globular, with an incurved doublure. The ventral opening is small and is mostly covered by a comparatively large hypostome with obliquely directed needle-like spines. The subdivision of the dorsal shield into a protocranidium and trunk is usually indistinct in nonadult-like protaspides. Unlike adult-like forms, spines of the nonadult-like protaspides can be projected in all three dimensions. The prosopon (surface texture) of nonadult like protaspides may have pits, polygonal ridges or fingerprint patterns.

Based on this functional morphology (e.g. flattened vs. bulbous exoskeleton, size of the ventral opening, size and orientation of the spines, presence vs. absence of terrace ridges), Chatterton (1980) and Speyer and Chatterton (1989) inferred that nonadult-like protaspides were likely planktonic, while adult-like ones were benthic. This presumption is also supported by a radical metamorphosis during the life-cycle of trilobites with nonadult-like protaspides (Speyer and Chatterton 1989), which may correspond with a change in mode of life as in extant crustaceans. The timing of such metamorphosis, and supposed switch from a planktic to benthic mode of life, varies taxonomically. In some species this metamorphosis occurs

within the protaspid period, usually after one or two moults (e.g. *Flexicalymene senaria*, *Osmolskabole prima* and *Tsinania canens*, cf. Chatterton et al. 1990, Lerosey-Aubril and Feist 2005 and Park and Choi 2009, respectively). In others, such as *Isotelus parvirugosus* (see Chatterton 1980) and *Crypholithus tessellatus* (see Chatterton et al. 1994), the metamorphosis co-occurs with the protaspid–meraspid boundary. In rare cases, the metamorphosis took place during the earliest meraspid period (e.g. *Remopleurides caphyroides*, cf. Whittington 1959). The adult-like protaspides did not pass through any radical metamorphosis and they are believed to have had relatively direct development.

The majority of Cambrian trilobites had adult-like protaspides (e.g. most members of Ptychopariida, Redlichiida, Corynexochida, cf. **paper I**, Dai and Zhang 2012, Hou et al. 2015, respectively). However, members of the suborder Eodiscina (cf. Zhang and Clarkson 2012) and some Furongian species from the order Corynexochiida (cf. early protaspides of *Tsinania canens* of Park and Choi 2009) are considered to have nonadult-like protaspides. Interestingly, the typically nonadult-like protaspides seem to have evolved independently in several trilobite lineages (Remopleuridioidea, Trinucleioidea, Asaphida, Calymenina and Proetoidea) likely during the Ordovician (cf. Park et al. 2016, Chatterton et al. 1990, Edgecombe et al. 1997). Park et al. (2016) suggested that independent evolution of planktonic nonadult-like protaspides in Trinucleioidea, Remopleuridioidea and Asaphida during the Furongian and Early Ordovician could be associated with increasing ecological pressure near the onset of the Global Ordovician Biodiversification Event (GOBE).

Trilobites with planktonic early stages should have been more widespread than ones with purely benthic stages (Chatterton and Speyer 1990). However, this presumption has not been properly tested, although the relationship between protaspid ecology and distribution has been studied by Chatterton and Speyer (1989). **Paper I** discusses the relationship between protaspid functional morphology and the biogeographic distribution of the solenopleurid trilobite *Sao hirsuta*. It has been shown (**paper I**), that all protaspid stages of *S. hirsuta* have an adult-like morphology and were most likely benthic. Therefore, they should have quite restricted dispersal capabilities and consequently, a restricted palaeogeographic distribution. Indeed, this species is known only from three isolated areas along the West Gondwanan margin – from the Ossa-Morena Zone (Spain), Skryje-Týřovice Basin (Bohemia) and Franconian Forest (Germany). Moreover, subsequent studies of the holaspid morphology have

revealed considerable morphological variability in surface sculpture between these three populations (Laibl, unpublished data).

There are several issues with the planktic–benthic division of early developmental stages. Firstly, beside stages that are typically adult-like or nonadult-like there are some protaspides which are not easily assigned to either group. This is especially evident in Cambrian forms, since the basic division by Speyer and Chatterton (1989) was proposed mainly on the basis of post-Cambrian trilobites that already show protaspid stages well adapted either for the benthic or planktonic mode of life. For example, the Furongian remopleuridioid trilobite *Haniwa quadrata* had slightly bulbous protaspides that seem neither of the typically adult-like morphology nor nonadult-like one (Park and Choi 2011). The earliest protaspid stages of certain ptychopariid trilobites can be either inverted saucer shaped (see Lee and Chatterton 2005a, **paper I**), or more bulbous so that they resemble some nonadult-like protaspides (cf. Ptychopariide sp. A of Lee and Chatterton 2005b). Secondly, there are protaspid or even meraspid stages that show the adult-like morphology, but have comparatively long spines that are directed almost ventrally. Protaspid stage 1 of genus and species indet. 2 of Zhang and Pratt (1999), assigned to *Estaingia sinensis* by Dai and Zhang (2012), shows long postero-ventrally oriented pleural spines. Early meraspid cranidia of *Olenellus gilberti* have similarly oriented intergenal spines (Webster 2014). Both Zhang and Pratt (1999) and Webster (2014) suggest that stages with such spines lived in the water column rather than on the seafloor.

While the planktic or benthic nature of early developmental stages can therefore be inferred from numerous morphological characters, the recognition of feeding (planktotrophic, detritotrophic) and non-feeding (lecithotrophic) strategies is difficult. Generally, the feeding strategies of early developmental stages of marine benthic invertebrates are based mainly on the size of the earliest stage, as this should reflect the egg size (and therefore the amount of yolk, e.g. Jablonski and Lutz 1983).

It can be assumed that most trilobites with comparatively small first stage protaspides (0.20–0.40) were feeding (either planktotrophic or detritotrophic). Although this is speculative, the majority of recent crustaceans have comparatively small feeding larvae (Anger 2001, see also the numerous examples in Martin et al. 2014), and it can be inferred that trilobites were similar. There are, however, some trilobite protaspides of a size that is considerably exceeding that of most other protaspides. These large protaspides may be lecithotrophic, as has been

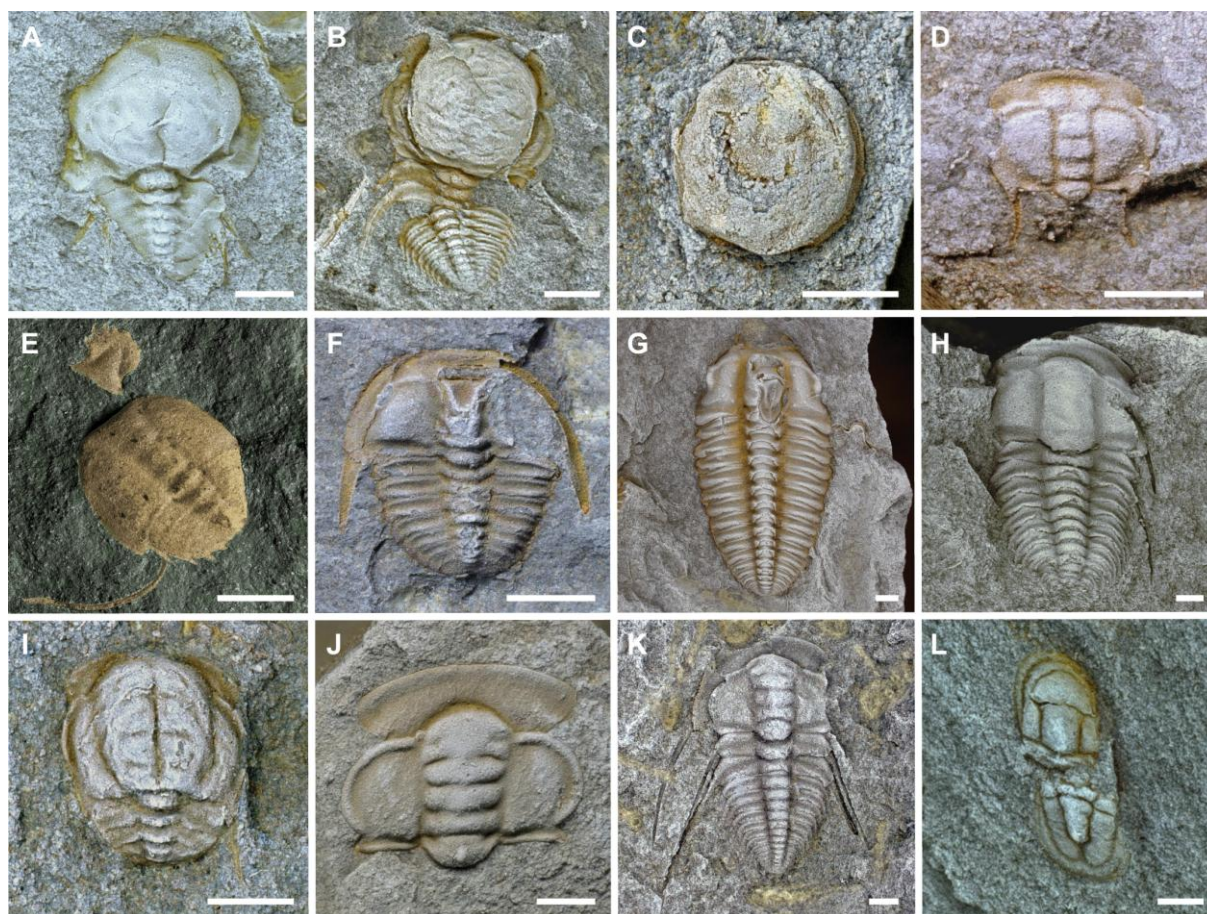


Figure 4 – Ontogenetic stages of selected mid-Cambrian trilobites and agnostoids from the Barrandian area (A-G, I, J, L from the Skryje-Týřovice Basin; H, K from the Přebram-Jince Basin). A, second protaspid stage of *Hydrocephalus carens*, CGS; B, early meraspid stage of *Hydrocephalus carens*, NM; C, protaspid stage of Ptychopariida sp. B, NM; D, early meraspid cranium of Ellipsocephalida sp. A, NM; E, third protaspid stage of *Sao hirsuta*, CGS; F, early meraspid stage of *Sao hirsuta*, NM; G, late meraspid stage of *Sao hirsuta*, NM; H, early holaspid stage of *Ellipsocephalus hoffi*, CGS; I, second protaspid stage of *Eccaparadoxides pusillus*, NM; J, middle meraspid cranium of *Eccaparadoxides pusillus*, NM; K, late meraspid stage of *Paradoxides paradoxissimus gracilis*, NM; L, meraspid stage of *Condylopyge rex*, NM. Specimens from the National Museum (NM) and the Czech Geological Survey (CGS). Scale bar = 0.5 mm.

suggested in several papers. Chatterton et al. (1990) inferred large embryos with yolky eggs for the Middle Ordovician species *Brongniartella*. Lerosey-Aubril (2006) suggested that the enlargement of proetoid protaspides during the Devonian may have been caused by lecithotrophy. In **paper I**, large protaspides of an undetermined Cambrian ptychopariid trilobite are also suggested to be lecithotrophic. However, this is potentially problematic because in trilobites, as well as in other arthropods, it is nearly impossible to recognise the earliest developmental stage in the fossil record. In each discovered protaspid stage, there may be a preceding stage that has not been discovered, was not preserved or was not calcified. Therefore, in trilobites, the size of the protaspid stage itself cannot be used as the only evidence of feeding strategy. A possible solution to this problem is to compare protaspid sizes of closely related taxa, in which we can recognise homologous individual stages. For

example, the first known protaspid stages of *Eccaparadoxides* and *Hydrocephalus* are morphologically quite similar and possess the same number of segments (see **paper IV**), but they are of different sizes. Similarly, the large stage of *Ptychopariida* sp. B sensu Laibl et al. (**paper I**) is morphologically comparable with the smaller earliest known stages of ptychopariids (e.g. *Spencella?* sp., *Sao hirsuta*, *Aphelaspis brachyphasis*, cf. Chatterton and Speyer 1997, **paper I**, Lee and Chatterton 2005a, respectively).

In addition to the large size of the earliest postembryonic instars, there are other developmental characters that could indicate possible lecithotrophic development in trilobites. These are: low growth increment, abbreviation or acceleration of the development and inflation of the exoskeleton. All of these developmental characters are based on the direct comparison with extant crustaceans.

Lecithotrophy in crustaceans is frequently associated with an abbreviation of development (Rabalais and Gore 1985, Anger 2001, Thatje et al. 2003). Rabalais and Gore (1985) defined abbreviated development as a developmental sequence that is of shorter duration than that normally seen in the majority of related species to a taxon. Consequently, the number of instars is lower and/or the duration of ontogeny is shorter. This may involve various developmental types such as hatching at an advanced stage or elimination of certain stages within the sequence (e.g. accelerated development, for more detail see Rabalais and Gore 1985). The Ordovician *Brongniartella* sp. and the Silurian *Platycoryphe sinensis* apparently lacked the planktonic protaspid stages that are typical for other calymenids and likely hatched at an advanced benthic stage (Chatterton et al. 1990). They can therefore be considered to have an abbreviated type of development. The Cambrian species *Eccaparadoxides pusillus* and *Hydrocephalus carens* both added more segments (four and six, respectively) between the first and second protaspid stage, than is usual in the majority of trilobites (**paper IV**), and showed an acceleration of the early development.

The growth increment and growth rate in trilobites have recently been intensively studied, resulting in a large amount of data on trilobite ontogeny (see Fusco et al. 2011, or chapter “Growth”). The median value of average per-moult growth rate for trilobite protaspides is 1.32 for length (range 1.04–1.77) and 1.25 for width (range 1.00–2.21). At least one trilobite in which lecithotrophy is suggested (*Hydrocephalus carens*) had a lower growth rate between the protaspid stages (1.29 for length and 1.02 for width) than the median for Trilobita (**paper**

IV). Recent decapod larvae that are lecithotrophic tend to have similarly lower growth rates (1.03–1.08 for length) than the planktotrophic forms (1.11–1.22 for length) (see Taishaku and Konishi 2001). Some lecithotrophic nauplii of Acrothoracica even do not increase in size during subsequent moults (Kolbasov et al. 2014). Comparisons such as this can be used as an additional tool in supporting lecithotrophy, but should be used carefully, since the differences are relatively minor and trilobite growth is still not entirely understood (Fusco et al. 2011, 2014).

Recent crustaceans whose larvae or juveniles are lecithotrophic, usually store yolk or lipids from yolk in the hepatopancreatic region under the carapace (Anger 2001, Taishaku and Konishi 2001, Watts et al. 2006, Chan et al. 2014, see also numerous examples in Martin et al. 2014). In some cases, the amount of yolk caused a prominent inflation of the carapace (Goy 2014). There exists reasonably good knowledge about the morphology of the digestive tract in adult trilobites (Chatterton et al. 1994, Lerosey-Aubril et al. 2011, 2012, Fatka et al. 2013), and it can be assumed that a similar morphology was present in the early postembryonic stages. The inflated glabella may therefore in some trilobite protaspides (e.g. *Eccaparadoxides pusillus* and *Hydrocephalus carens*, see **paper IV**) represent a similar adaptation for storing lipids from the yolk.

Ontogeny of Cambrian trilobites and agnostids from the Barrandian area

Ontogenetic stages from the Skryje-Týřovice Basin

In the Skryje-Týřovice Basin early ontogenetic stages of trilobites occur at several localities that are situated in the upper stratigraphical levels of the Buchava Formation (upper levels of the *Eccaparadoxides pusillus* Zone, for geological settings see Fatka 2004, Fatka et al. 2011). These localities are situated near Týřovice (localities Týřovice – Pod hruškou, Týřovice – Lůmek, cf. Prantl 1947, Fatka 2004, **paper I**), or Skryje (localities Skryje – Luh, Dlouhá Hora Hill, Vosník Hill, cf. Jahn 1898, Jarka 1941, Chlupáč et al. 1998, Fatka 2004). The species in which the juveniles are known are listed below.

Sao hirsuta Barrande, 1846 – The complete post-embryonic development of *S. hirsuta* (Figs 4E–G) is known. The development of this species was described already by Barrande (1852). Růžička (1943) provided some new data, including description of early protaspid stages. Later, the development was discussed by Whittington (1957b) and revised by Šnajdr (1958). The last comprehensive description of the ontogeny of *S. hirsuta* has been published in **paper I**. Early developmental stages of *S. hirsuta* are the most common specimens found in the aforementioned localities of the Skryje-Týřovice Basin.

Ptychopariida sp. A. – Only protaspid and early meraspid stages are known. These stages were originally described as belonging to *S. hirsuta* (cf. **paper I**) by Barrande (1852), Růžička (1943), Whittington (1957b) and Šnajdr (1958). In **paper I**, they were described as a separate species (based on the dimensions, morphology of the paleobral lobes and trunk) of uncertain affinity.

Ptychopariida sp. B – This taxon is so far known from protaspid stages only (Fig. 4C). It was initially described by Růžička (1943) as the so-called “Barrande’s larva” and then re-described by Šnajdr (1958). New data has been collected and published in **paper I**. The affinity of this taxon is uncertain, but based on the recently discovered specimens it may belong to the family Conocoryphidae.

Ptychopariida sp. C – Only one protaspid individual of Ptychopariida sp. C has been described and discussed in **paper II**. A more specific affinity of this specimen is uncertain.

Skreiaspis spinosus (Jahn, 1895) – The meraspid and holaspis stages of *S. spinosus* are known. Barrande (1852) described late meraspid and holaspis stages of *S. spinosus* as belonging to *Agraulos ceticephalus*. Šnajdr (1958) discovered early meraspides of this species and comprehensively described its ontogeny.

Eccaparadoxides pussilus (Barrande, 1846) – The complete post-embryonic development of this species (Figs 4I–J) is known. Early ontogenetic stages of *E. pusillus* were described by Barrande (1852) as *Hydrocephalus saturnoides*. Later on, Ford (1881) for the first time suggested these stages may be juveniles of *Paradoxides*. Subsequently, the development of this species has been studied by Pompeckj (1895), Raymond (1914), Raw (1925), Šuf (1926), Růžička (1943) and Šnajdr (1958). Šnajdr (1958) provided the first comprehensive

description of *E. pusillus* post-embryonic development. Recently, the protaspid stages of this taxon were studied in **paper IV**.

Hydrocephalus carens Barrande, 1846 – The complete post-embryonic development of *H. carens* (Figs 4A–B) is known. The protaspid and early meraspid stages was described by Barrande (1852). Šuf (1926) discovered early protaspid stage of this species. Development of *H. carens* was studied also by Pompeckj (1895), Raymond (1914), Raw (1925), Růžička (1943) and Šnajdr (1958). The protaspid development was investigated in **paper IV**.

Ellipsocephalida sp. A – The early meraspid stages (Fig. 4D) were originally described by Raymond (1914) as protaspides belonging to Paradoxididae. Růžička (1943) provided complementary material and named this taxon “Raymond’s larva”. Růžička (1943) and Whittington (1957b) assigned these stages to *Paradoxides rugulosus* (= *Eccaparadoxides pusillus*). In contrast, Šnajdr (1958) noted that these stages resemble early stages of Protolenidae. Valíček and Šarič (2001) published a short comment, in which they assigned this taxon to *Luhops expectans*. Since these stages resemble some juvenile cranidia of Ellipsocephalidae (see **paper III**), I assign them to this group.

Agnostids – The ontogenetic development (meraspid to holaspid stages) from the Skryje-Týřovice Basin is known for the species *Condylopyge rex* (Barrande, 1846) (Fig. 4L), *Pleuroctenium granulatum* (Barrande, 1846), *Peronopsis cuneifera* (Barrande, 1846), *Phalacroma bibullatum* (Barrande, 1846) and *Phalagnostus nudus* (Beyrich, 1845). The development of these agnostid species was described by Barrande (1852) and Šnajdr (1958). Currently, the ontogeny and morphological variability of *C. rex* is studied by the author of this thesis.

Ontogenetic stages from the Příbram-Jince Basin

In the Příbram-Jince Basin early ontogenetic stages of trilobites are comparatively rare presumably due to sampling bias and unfavourable taphonomy. Already described material as well as some new findings comes mainly from the *Paradoxides paradoxissimus gracilis* Zone and from the *Ellipsocephalus hoffi-Lingulella-Rejkocephalus* Zone (for geological settings see Fatka and Szabad 2014). Juveniles are known in following species.

Ellipsocephalus hoffi (Schlotheim, 1823) – Despite adult specimens of *E. hoffi* (Fig. 4H) are extremely common, particularly in the upper levels of the Jince Formation (*Ellipsocephalus*

hoffi-*Lingulella-Rejkocephalus* Zone), early developmental stages of this taxon are rare. Only late ontogenetic stages are known and have been described in **paper III**.

Paradoxides paradoxissimus gracilis (Boeck, 1827) – Novák figured two meraspid stages of *P. paradoxissimus gracilis* (Fig. 4K) in his unpublished supplement to the *Système silurien du centre de la Bohème*. Some additional data were published by Šuf (1926). The late meraspid and holaspid development of this species was comprehensively described by Šnajdr (1958). Recently, new material comprising the early meraspid stages has been discovered in the collections of the National Museum, Prague.

Hydrocephalus minor (Boeck, 1827) – Only the late meraspid stages of this species were figured by Šnajdr (1958). They are morphologically alike to *H. carens*. Additional material is available in the collections of the National Museum, Prague.

Conocoryphe sulzeri (Schlotheim, 1823) – Two late meraspid stages of *C. sulzeri* supposedly from the *Paradoxides gracilis* Zone were figured by Šnajdr (1958, pl. 33, figs 6, 7). Some additional material is deposited in the collections of the National Museum, Prague.

Conclusions and future directions of the study

The main conclusions of this thesis are the following:

- a) The post-embryonic development, its part, or early ontogenetic specimens have been described for *Sao hirsuta*, Ptychopariida sp. A, Ptychopariida sp. B (**paper I**), Ptychopariida sp. C (**paper II**), *Ellipsocephalus hoffi*, *Ellipsocephalus polytomus* (**paper III**), *Hydrocephalus carens* and *Eccaparadoxides pusillus* (**paper IV**). The individual instars of the early development were recognised in *Sao hirsuta*, Ptychopariida sp. A (**paper I**), *Hydrocephalus carens* and *Eccaparadoxides pusillus* (**paper IV**). Three different developmental phases during late ontogeny of *Ellipsocephalus hoffi* were recognised (**paper III**).
- b) Life-history strategies of early developmental stages of *Sao hirsuta*, Ptychopariida sp. A, Ptychopariida sp. B (**paper I**), *Hydrocephalus carens* and *Eccaparadoxides pusillus* (**paper IV**) were discussed. Benthic protaspides were inferred for *Sao hirsuta* and Ptychopariida sp. A (**paper I**). Lecithotrophic development was suggested for

Ptychopariida sp. B (**paper I**), *Eccaparadoxides pusillus* and for *Hydrocephalus carens* (**paper IV**).

- c) The relationship between biogeographical distribution and life-history strategies was studied and discussed. *Sao hirsuta* with entirely benthic protaspides show strongly restricted geographic distributions (**paper I**). The distribution of supposedly lecithotrophic trilobite species with large protaspides seems to be associated with higher latitudes along the West Gondwanan margin (**paper IV**).
- d) The development of *Ellipsocephalus hoffi*, *Ellipsocephalus polytomus* and other members of the Ellipsocephalidae show numerous similarities with the order Redlichiida. This may suggest close phylogenetic relationship between these groups (**paper III**). On the other hand, different selective pressures are believed to be responsible for modification of the early ontogeny of *Hydrocephalus carens* and *Eccaparadoxides pusillus* (**paper IV**).

Research on the presented topic has numerous future perspectives. Currently, a paper about comparative development of *Eccaparadoxides pusillus*, *Eccaparadoxides pradoanus*, *Hydrocephalus carens*, *Paradoxides gracilis* and *Acadoparadoxides pinus* is under preparation. Consequently, a cladistic matrix for phylogenetic analysis of the family Paradoxididae is being assembled.

Future work is necessary to understand fully the developmental patterns of *Sao hirsuta*. The amount of articulated specimens of this taxon in various developmental stages makes it a perfect model organism such as *Aulacopleura koninckii* (see Fusco et al. 2004). *S. hirsuta* also shows geographical variability of the surface sculpture that is worth to study in detail.

Another three manuscripts about ontogeny of *Ellipsostrenua* from Scandinavia, *Fritzolenellus* from Newfoundland and *Condylopyge* from the Czech Republic are in progress. The author would like also perform a comprehensive review of the trilobite life-history strategies.

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