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Review of early developmental stages of trilobites and agnostids from the Barrandian area (Czech Republic)

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Abstract: This contribution briefly summarizes the history of research, modes of preservation and stratigraphic distribution of 51 trilobite and five agnostid taxa from the Barrandian area, for which the early developmental stages have been described.

Keywords: Trilobita, Agnostida, development, Barrandian area, Czech Republic

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Introduction

Fossils from the Barrandian area have played a crucial role in studies focussed on trilobite and agnostid postembryonic development, because the first description of both trilobite and agnostid ontogeny was based on material from this area, and was published in middle of the 19th century (Barrande 1852). The very abundant record of the well-preserved early developmental stages of trilobites and agnostids has been documented from various stratigraphic levels and lithologies in the Barrandian area.

This contribution briefly summarizes all early developmental stages of trilobites (protaspides and meraspides; for terminology, see below) and agnostids (meraspides) described from the Barrandian area. It also provides a complete list of references for all papers dealing with the ontogenetic development of trilobites and agnostids from this area, and provides comprehensive information about housing of the originally-published material. We believe that such a review can be a useful source of information about the character and housing of this published material.

Outline of trilobite ontogeny

Traditionally, trilobite post-embryonic development is divided into three successive periods – (1) the protaspid, (2) meraspid and (3) holaspid periods (for comprehensive overview see Whittington 1957a, Chatterton & Speyer 1997, Hughes et al. 2006).

The protaspid period

This period is widely accepted as encompassing the earliest mineralised postembryonic stages (Beecher 1885, but see Fortey & Morris 1978). Protaspides are characterised by the cephalon and trunk being conjoined as one shield (Raw 1925, Edgecombe et al. 1988). Based on overall similarity to later developmental stages, two general morphological types of protaspides can be distinguished – the adult-like (probably benthic) and the nonadult-like (probably planktonic) protaspides (Speyer & Chatterton 1989).

The meraspid period

This period begins when the first articulation structure between the cephalon and trunk is developed (Raw 1925; Chatterton & Speyer 1997). During the meraspid period, new segments were progressively released from the anterior margin of the pygidium into the thorax (Stubblefield 1926). The majority of morphological changes usually occur during the meraspid period.

The holaspid period

This period begins when all the thoracic segments that are characteristic for adults of the given species are separated from the pygidium (Raw 1925). During the holaspid period, however, trilobites continued to grow, and sometimes even show considerable alometric changes.

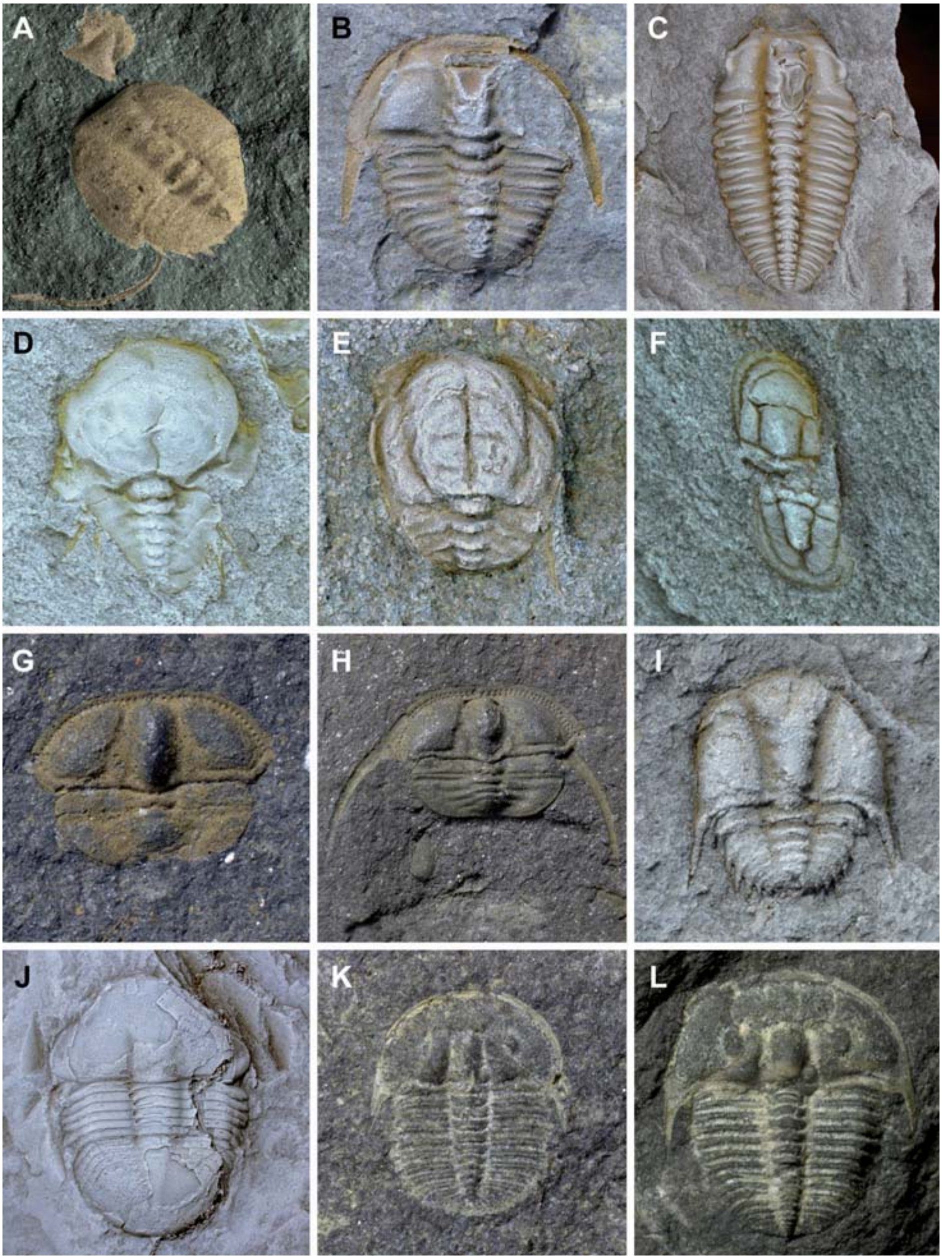
Outline of agnostid ontogeny

In comparison with trilobites, only two post-embryonic periods can be recognised in agnostids (excl. Eodiscina): (1) meraspid and (2) holaspid periods. The definitions of both meraspid and holaspid periods are the same as those used for trilobites. Protaspides of agnostids have not been found, and it is generally accepted that agnostids lack the free-living protaspid stages (Robison 1964, Müller & Walossek 1987, Chatterton and Speyer 1997).

Historical overview of the ontogeny of trilobites and agnostids from the barrandian area

The first description of trilobite and agnostid ontogeny was published by Barrande (1852). He, however, admitted that some palaeontologists had discussed the development of trilobites even earlier (e.g. Sternberg, Burmeister, Salter, etc., Barrande 1852, pp. 257–259). Barrande (1852) described and illustrated more or less complete postembryonic developmental sequences in four trilobite species: (*Sao hirsuta*, pl. 7; *Deanaspis senftenbergi*, pl. 30; *Dalmanitina elfrida*, pl. 26; and *Aulacopleura koninckii*, pl. 18), and also illustrated a few early developmental stages in nine other species (*Skreiaspis spinosus*, pl. 10; *Conocoryphe sulzeri*, pl. 26; *Otarion diffractum*, pl. 18; *Raphiophorus rouaulti*, pl. 30; *Marrolithus ornatus*, pl 29; *Cyclopyge rediviva*, pl. 34; *Heterocyclopyge pachycephala*, pl. 34; *Zetillaenus wahlenbergianus*, pl. 34; *Vysocania oblita*, pl. 30). He also illustrated some trilobite species that were subsequently recognised as juveniles of other species (*Eccaparadoxides pusillus*, pl. 13, pl. 49; *Hydrocephalus carens*, pl. 13, pl. 49). Barrande (1852) provided a comprehensive description of developmental sequences in five Cambrian agnostids (*Condylopyge rex*, pl. 49; *Pleuroctenium granulatum granulatum*, pl. 49; *Peronopsis cuneifera*, pl. 49; *Phalacroma bibul-*

Fig. 1. A hodgepodge of early postembyonic stages of trilobites. A) protaspid stage of *Sao hirsuta* Barrande, 1846; B) early meraspid stage of *Sao hirsuta* Barrande, 1846; C) late meraspid stage of



Sao hirsuta **Barrande, 1846 (lectotype); D) protaspid stage of** ***Hydrocephalus carens*** **Barrande, 1846; E) protaspid stage of** ***Eccaparadoxides pussilus*** **(Barrande, 1846); F) meraspid stage of** ***Condylopyge rex*** **(Barrande, 1846); G) early meraspid stage of** ***Deanaspis senftenbergi*** **(Hawle & Corda, 1847); H) early meraspid stage of** ***Deanaspis senftenbergi*** **(Hawle & Corda, 1847); I) early meraspid stage of** ***Dalmanitina elfrida*** **Šnajdr, 1982; J) late meraspid stage of** ***Ectillaenus benignensis*** **(Novák in Perner, 1918); K) early meraspid stage of** ***Aulacopleura koninckii*** **(Barrande, 1846); L) meraspid stage of** ***Aulacopleura koninckii*** **(Barrande, 1846). A–F) Buchava Formation of the Skryje-Týřovice Basin; G–I) Vinice Formation of the Prague Basin; J) Dobrotivá Formation of the Prague Basin; K–L) Motol Formation of the Prague Basin.**

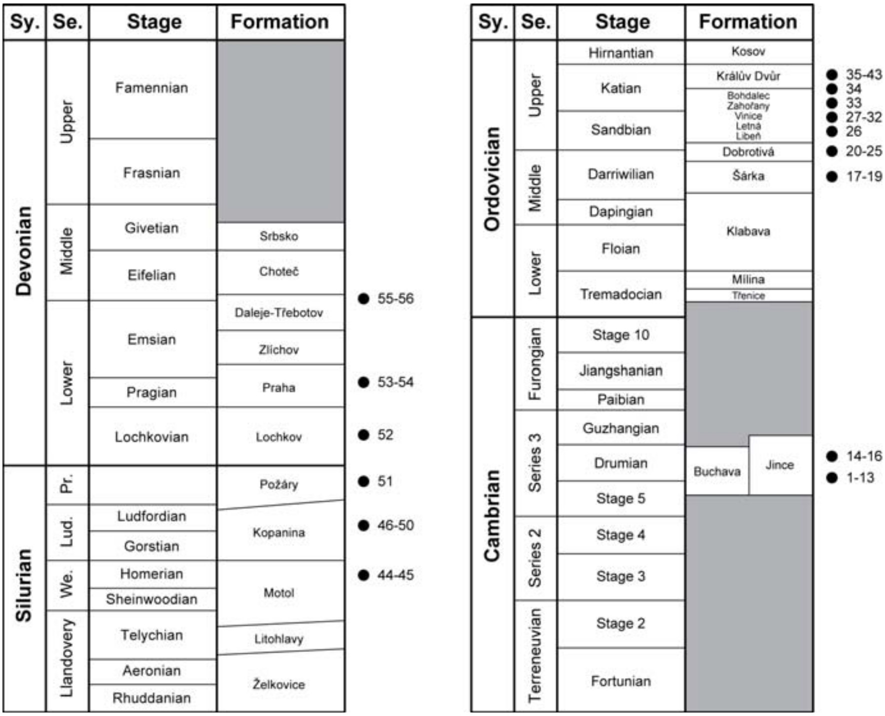


Fig. 2. Lithostratigraphy of Příbram-Jince, Skryje-Týřovice and Prague basins and correlation with the international chronostratigraphy (modified after Kříž 1992, Chlupáč 1998, Geyer et al. 2008 and Fatka et al. 2013). The individual numbers on the right side of the column refer to the particular trilobite or agnostid species in the Tab. 1. Abbreviations: Lud. – Ludlow; Pr. – Pridoli; Se. – Series; Sy. – System; We. – Wenlock.

latum, pl. 49; *Phalagnostus nudus*, pl. 49). Subsequently, Barrande (1872) described some additional developmental stages of *Degamella princeps* (pl. 14), *Zdicella zeidleri* (pl. 3) and *Microparia speciosa* (pl. 2).

Later, several authors focused on the development of Barrandian trilobites in order to understand the general trends in trilobite ontogeny, as well as to discuss their phylogeny and systematics (Raymond 1914, Raw 1925, Størmer 1942, Whittington 1957a). Whittington (1957b) and some other palaeontologists (Šuf 1926, Růžička 1943, Šnajdr 1958) restudied and re-described certain trilobite ontogenies from the Cambrian strata of the Barrandian area; ontogeny of some Ordovician species was studied by Whittington (1940, 1956).

During the second half of the 20th century, the ontogeny of many Barrandian trilobites was described as a part of several extensive monographic studies, such as those of the family Cyclopygidae (Marek 1961), Trinucleidae (Přibyl & Vaněk 1969), Phacopidae (Chlupáč 1977) and Odontopleuridae (Šnajdr 1984). Some shorter papers about trilobite ontogenetic development were also published separately (Kříž & Pek 1974, Šnajdr 1975, 1981, Kácha & Šarič 1991).

At the end of the 20th century, and especially in the beginning of the 21st century, Bohemian material started to be extensively reinvestigated. Some trilobites eventually became so-called model species, such as *Aulacopleura koninckii*. Detailed papers dealing with various aspects of development in this species were published by Nigel C. Hughes, Giuseppe Fusco, Paul S. Hong and others (Hughes & Chapman 1995, Hughes et al. 1999, Hughes & Chapman 2001, Fusco et al. 2004, Fusco et al. 2014, Hong et al. 2014, Fusco et al. 2016, Hughes et al. 2017). Most recently, Laibl et al. (2014, 2015a, 2015b, 2017) studied and described the ontogenetic

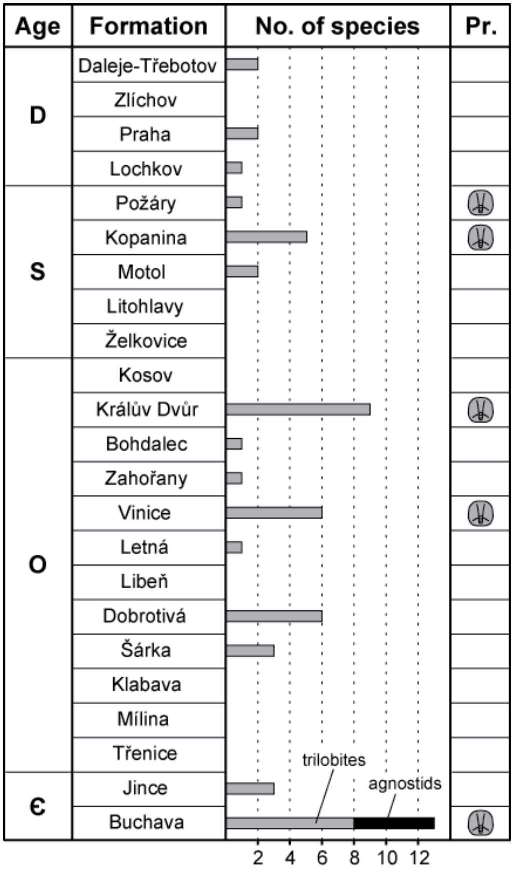


Fig. 3. Distribution and abundance of the early developmental stages of trilobites and agnostids in the Cambrian (Є) to Devonian (D) strata of the Barrandian area. The column labelled "Pr." indicates levels from which the protaspid stages are known.

development of selected Cambrian trilobites from the Skryje-Týřovice and Příbram-Jince basins; meanwhile Budil et al. (2013) have focussed on the Devonian phacopid trilobites.

Preservation of developmental stages of trilobites and agnostids from the barrandian area

In the Barrandian area, the early postembryonic stages of trilobites and agnostids are known to be preserved in three different ways, all reflecting a particular lithology.

The first mode of preservation is characteristic for material from Cambrian and Ordovician strata (juvenile individuals from the Buchava, Jince, Šárka, Dobrotivá, Letná, Vinice, Zahořany, Bohdalec and Králův Dvůr formations). This mode of preservation also occurs, though rarely, in several stratigraphic levels of the Silurian and Devonian (juveniles from the Motol, Kopanina and Daleje-Třebotov formations). Specimens are usually preserved as internal and external moulds in siliciclastic sediments (sandstones to shales). The original material of the exoskeleton is either completely absent, being dissolved (both types of moulds are usually covered by iron or manganese hydroxides, e.g. Šnajdr 1958), or is preserved as partly decalcified remains of the exoskeletons (e.g. in shales of the Motol and the Daleje-Třebotov formations, cf. Hughes et al. 2014, Budil et al. 2013, respectively). Material from shales, siltstones or greywackes is often articulated, but nearly always shows strong flattening, due to sediment compaction. Some specimens can be deformed by shear stress. Despite the compaction and deformation, specimens collected from very fine grained shales sometimes show astonishing details (Fig. 1A–D).

The second mode of the preservation of the early developmental stages of trilobites is characteristic for limestones (sometimes weathered into the decalcified residuum, so called "white beds"). This is typical especially for late Silurian (juvenile stages from the Kopanina and Požáry formations) and Devonian strata (juveniles from the Lochkov, Praha, Daleje-Třebotov and Choteč formations). Specimens from limestones have their exoskeleton recrystallised and/or peeled off from the internal moulds and attached to the negative counterparts. Early developmental stages from limestones are usually disarticulated (with the exception of enrolled specimens of *P. insequens*), but they often maintain their original relief. The last mode of the preservation is the replacement of the original exoskeleton by other

No.	Taxon	Formation	First recognised	Also studied	Originals stored	Material
1	*Sao hirsuta* Barrande, 1846	Buchava	Barrande (1852)	Růžička (1943), Whittington (1957a, b), Šnajdr (1958), Laibl et al. (2014)	NM, CGS, MCZ	P, M
2	*Hydrocephalus carens* Barrande, 1846	Buchava	Raw (1925)	Raymond (1914), Šuf (1926), Růžička (1943), Šnajdr (1958), Laibl et al. (2017)	NM, CGS	P, M
3	*Eccaparadoxides pusillus* (Barrande, 1846)	Buchava	Raymond (1914)	Raw (1925), Šuf (1926), Růžička (1943), Šnajdr (1958), Laibl et al. (2017)	NM, CGS	P, M
4	Ptychopariida sp. A	Buchava	Laibl et al. (2014)	-	NM, CGS, MCZ	P, M
5	Ptychopariida sp. B	Buchava	Růžička (1943)	Šnajdr (1958), Laibl et al. (2014)	NM, CGS	P
6	Ptychopariida sp. C	Buchava	Laibl et al. (2015b)	-	CGS	P
7	Ellipsocephalida sp. A	Buchava	Raymond (1914)	Růžička (1943), Whittington (1957a), Šnajdr (1958), Valíček & Šarič (2001)	NM, CGS, MCZ	P, M
8	*Skreiaspis spinosus* (Jahn, 1895)	Buchava	Barrande (1852)	Šnajdr (1958)	NM, CGS	M
9	*Condylopyge rex* (Barrande, 1846)	Buchava	Barrande (1852)	Šnajdr (1958)	NM, CGS	M
10	*Pleuroctenium granulatum granulatum* (Barrande, 1846)	Buchava	Barrande (1852)	Šnajdr (1958)	NM, CGS	M
11	*Peronopsis cuneifera* (Barrande, 1846)	Buchava	Barrande (1852)	Šnajdr (1958)	NM, CGS	M
12	*Phalacroma bibullatum* (Barrande, 1846)	Buchava	Barrande (1852)	Šnajdr (1958)	NM, CGS	M
13	*Phalagnostus nudus* (Beyrich, 1845)	Buchava	Barrande (1852)	Šnajdr (1958)	NM, CGS	M
14	*Paradoxides paradoxissimus gracilis* (Boeck, 1827)	Jince	Šnajdr (1958)	-	NM	M
15	*Hydrocephalus minor* (Boeck, 1827)	Jince	Šnajdr (1958)	-	NM	M
16	*Conocoryphe sulzeri* (Schlotheim, 1823)	Jince	Barrande (1852)	Šnajdr (1958)	NM	M
17	*Parabarrandia bohemica* (Novák, 1884)	Šárka	Šnajdr (1975)	-	CGS	M
18	*Pricyclopyge binodosa* (Salter, 1859)	Šárka	Marek (1961)	-	NM	M
19	*Ectillaenus sarkaensis* (Novák in Perner, 1918)	Šárka	Bruthansová (2003)	-	NM	M
20	*Parabarrandia crassa* (Barrande, 1872)	Dobrotivá	Šnajdr (1975)	-	CGS	M
21	*Zbirovia arata* (Barrande, 1872)	Dobrotivá	Šnajdr (1990)	-	CGS	M
22	*Nobiliasaphus repulsus* (Přibyl & Vaněk, 1968)	Dobrotivá	Kříž & Pek (1974)	-	CGS	M
23	*Ectillaenus benignensis* (Novák in Perner, 1918)	Dobrotivá	Novák in Perner (1918)	Bruthansová (2003)	NM	M
24	*Degamella princeps* (Barrande, 1872)	Dobrotivá	Barrande (1872)	Marek (1961)	NM	M
25	*Cyclopyge umbonata* (Angelin, 1854)	Dobrotivá	Marek (1961)	-	NM	M
26	*Deanaspis goldfussi* (Barrande, 1846)	Letná	Přibyl & Vaněk (1969)	-	CGS	M
27	*Deanaspis senftenbergi* (Hawle & Corda, 1847)	Vinice	Barrande (1852)	Whittington (1940), Přibyl & Vaněk (1969), Shaw (1995)	NM, CGS, MCZ	M
28	*Dalmanitina elfrida* Šnajdr, 1982	Vinice	Barrande (1852)	Whittington (1956), Šnajdr (1990)	NM, MCZ	P, M
29	*Cyclopyge rediviva* (Barrande, 1846)	Vinice	Barrande (1852)	Marek (1961)	NM	M
30	*Cekovia goetzi* Šnajdr, 1957	Vinice	Bruthansová (2003)	-	CGS	M
31	*Selenopeltis buchi* (Barrande, 1846)	Vinice	Šnajdr (1984)	-	NM, CGS	M
32	*Heterocyclopyge pachycephala* (Hawle & Corda, 1847)	Vinice	Barrande (1852)	Marek (1961)	NM	M
33	*Marrolithus ornatus* (Sternberg, 1833)	Záhořany	Barrande (1852)	Přibyl & Vaněk (1969)	NM, CGS	M
34	*Vysocania vaneki* (Šnajdr, 1958)	Bohdalec	Pereira et al. (*In press*)	-	NM	M
35	*Selenopeltis vultuosa* Přibyl & Vaněk, 1966	Králův Dvůr	Šnajdr (1984)	-	CGS	M
36	*Nankinolithus granulatus* (Wahlenberg, 1818)	Králův Dvůr	Přibyl & Vaněk (1969)	-	CGS	M
37	*Onnia ultima* (Barrande, 1852)	Králův Dvůr	Přibyl & Vaněk (1969)	Shaw (1995)	CGS	M
38	*Mucronaspis grandis* (Barrande, 1852)	Králův Dvůr	Budil (1996)	-	NM, CGS	P, M
39	*Zetillaenus wahlenbergianus* (Barrande, 1852)	Králův Dvůr	Barrande (1852)	Bruthansová (2003)	NM	M
40	*Vysocania oblita* (Barrande, 1872)	Králův Dvůr	Barrande (1852)	Bruthansová (2003), Pereira et al. (*In press*)	NM, CGS	M
41	*Cyclopyge marginata* (Hawle & Corda, 1847)	Králův Dvůr	Marek (1961)	-	CGS	M
42	*Zdicella zeidleri* (Barrande, 1872)	Králův Dvůr	Barrande (1872)	-	NM	M
43	*Microparia speciosa* (Hawle & Corda, 1847)	Králův Dvůr	Barrande (1872)	Marek (1961)	NM	M
44	*Raphiophorus rouaulti* (Barrande, 1852)	Motol	Barrande (1852)	-	NM	M
45	*Aulacopleura koninckii* (Barrande, 1846)	Motol	Barrande (1852)	Hughes & Chapman (1995), Hughes et al. (1999), Hughes & Chapman (2001), Fusco et al. (2004), Fusco et al. (2014), Hong et al. (2014), Fusco et al. (2016), Hughes et al. (2017)	NM, CGS, MCZ, NHM, USNM	M
46	*Otarion diffractum* Zenker, 1833	Kopanina	Barrande (1852)	Hughes et al. (1999)	NM, CGS	M
47	*Eophacops buliceps buliceps* (Barrande, 1846)	Kopanina	Chlupáč (1977)	-	CGS	M
48	*Scharyia* sp.	Kopanina	Šnajdr (1981)	-	CGS	P
49	*Kosovopeltis svobodai* (Šnajdr, 1960)	Kopanina	Šnajdr (1960)	Kácha & Šarič (1991)	CGS	P, M
50	*Scharyia micropyga* (Hawle & Corda, 1847)	Kopanina	Šnajdr (1981)	-	CGS	P, M
51	*Scharyia nympha* Chlupáč, 1971	Požáry	Šnajdr (1981)	Šnajdr (1990)	CGS	P
52	*Spiniscutellum umbelliferum* (Beyrich, 1845)	Lochkov	Prantl (1949)	Šnajdr (1960)	NM	M
53	*Prokops hoeninghausi* (Barrande, 1846)	Praha	Chlupáč (1977)	Budil et al. (2013)	NM	M
54	*Reedops* cf. *bronni* (Barrande, 1846)	Praha	Budil et al. (2013)	-	NM	M
55	*Pedinopariops superstes* (Barrande, 1852)	Daleje-Třebotov	Budil et al. (2013)	-	CGS	M
56	*Pedinopariops insequens* (Chlupáč, 1977)	Daleje-Třebotov	Chlupáč (1977)	-	NM	M

Tab. 1. A list of 51 trilobite and five agnostid taxa from the Barrandian area for which the early developmental stages (P – protaspides, M – meraspides) were described so far. The first recognition of ontogeny refers to the publication in which the particular individuals were recognised as part of developmental sequence of a trilobite species (e.g. it does not necessarily refer to the first publication where the individuals were illustrated or described). Note that in the first description of the ontogeny the particular taxon may be given under different name. Abbreviations: CGS – Czech Geological Survey, Prague, Czech Republic; MCZ – Museum of Comparative Zoology, Cambridge, USA; NHM – Natural History Museum, London, UK; NM – National Museum, Prague, Czech Republic; USNM – National Museum of Natural History, Washington, D.C., USA.

minerals, most commonly by silica or pyrite. Silicification of trilobite exoskeletons is known from several stratigraphic levels of the Barrandian area, but has not yet been extensively studied (for detailed information see Mergl 2010). Pyritization of trilobites generally does not provide specimens sufficiently preserved for suitable detailed study of small specimens (Mergl & Budil 2011).

Distribution of developmental stages of trilobites and agnostids from the Barrandian area

In the Barrandian area, early developmental stages of trilobites and agnostids are known from the Cambrian strata of the Skryje-Týřovice and Příbram-Jince basins, as well as from Ordovician to Devonian strata of the Prague Basin (Figs 2, 3 and Tab. 1).

In the Skryje-Týřovice Basin, early ontogenetic stages of both trilobites and agnostids occur at several localities that are situated in the upper stratigraphic levels of the Buchava Formation (for details see Fatka et al. 2011, Laibl et al. 2014). Protaspides and meraspides are known in *Eccaparadoxides pusillus* (Fig. 1E), *Hydrocephalus carens* (Fig. 1D), *Sao hirsuta* (Fig. 1A–C), Ptychopariida sp. A and Ellipsocephalida sp. A. Only protaspid stages were described for Ptychopariida sp. B and Ptychopariida sp. C. Meraspides are known in *Skreiaspis spinosus*, and in the agnostids *Condylopyge rex* (Fig. 1F), *Pleuroctenium granulatum granulatum*, *Peronopsis cuneifera*, *Phalacroma bibullatum* and *Phalagnostus nudus* (Barrande 1852, Růžička 1943, Šnajdr 1958, Laibl et al. 2014, 2015b, 2017).

Within the Příbram-Jince Basin, early developmental stages of trilobites are comparatively rare, presumably due to sampling bias in combination with unfavourable lithology. Described material comes exclusively from the *Paradoxides paradoxissimus gracilis* Zone (for geological settings and stratigraphy, see Fatka & Szabad 2014). Uncommon meraspides are known in *Conocoryphe sulzeri*, *Hydrocephalus minor* and *Paradoxides paradoxissimus gracilis* (cf. Tab. 1, Šnajdr 1958).

In the Ordovician strata of the Prague Basin, numerous material containing early developmental trilobite stages is known especially from the Dobrotivá, Vinice and Králův Dvůr formations (Figs 2 and 3; for outline of geology and stratigraphy see Havlíček 1982, 1998). Some other material also comes from the Šárka, Letná, Zahořany and Bohdalec formations. Protaspides and meraspides are known in *Dalmanitina elfrida* (Fig. 1I) (e.g. Barrande 1852) and in *Mucronaspis grandis* (Budil 1996); articulated meraspides or individual meraspid sclerites in *Cekovia goetzi*, *Cyclopyge marginata*, *Cyclopyge rediviva*, *Cyclopyge umbonata*, *Deanaspis goldfussi*, *Deanaspis senftenbergi* (Fig. 1G–H), *Degamella princeps*, *Ectillaenus benignensis* (Fig. 1J), *Ectillaenus sarkaensis*, *Heterocyclopyge pachycephala*, *Marrolithus ornatus*, *Microparia speciosa*, *Nankinolithus granulatus*, *Nobiliasaphus repulsus*, *Onnia ultima*, *Parabarrandia bohemica*, *Parabarrandia crassa*, *Pricyclopyge binodosa*, *Selenopeltis buchi*, *Selenopeltis vultuosa*, *Vysocania oblita*, *Vysocania vaneki*, *Zbirovia arata*, *Zdicella zeidleri* and *Zetillaenus wahlenbergianus* (cf. Tab. 1, Barrande 1852, 1872, Přibyl & Vaněk 1969, Marek 1961, Šnajdr 1975, 1984, Bruthansová 2003). Currently, no pre-holaspid agnostid specimen is known from Ordovician sediments of the Prague Basin (cf. Pek 1977).

In Silurian strata, early ontogenetic stages of trilobites are known mainly from the Kopanina Formation, but abundant material also comes from the Motol Formation (Figs 2 and 3; for outline of geology and stratigraphy see Kříž 1992, 1998). Only in one species from the Požáry Formation have the early stages been recorded. Protaspides, meraspid cranidia and pygidia are known in *Kosovopeltis svobodai* and *Scharyia micropyga* (Kácha & Šarič 1991, Šnajdr 1981, respectively). Only protaspides are known in *Scharyia nympha* and *Scharyia* sp. (Šnajdr 1981). Meraspides and their sclerites in astonishing amounts are known for *Aulacopleura koninckii* (Fig. 1K–L) (e.g. Hughes & Chapman 1995). Some meraspid stages are also known in *Otarion diffractum*, *Eophacops buliceps buliceps* and *Raphiophorus rouaulti* (Barrande 1852, Chlupáč 1977).

In Devonian strata of the Prague Basin, developmental stages are known in species from the Lochkov, Praha and Daleje-Třebotov formations (Figs 2 and 3; for outline of geology see Chlupáč 1998, 2003). Meraspides of Devonian species are known in *Spiniscutellum umbelliferum*, *Prokops hoeninghausi*, *Reedops* cf. *bronni*, *Pedinopariops superstes* and *Pedinopariops insequens* (cf. Tab. 1, Šnajdr 1960, Chlupáč 1977, Budil et al. 2013).

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