

MORPHOLOGY, LIFE-HISTORY STRATEGY, AND AFFINITY OF THE BARRANDE'S LARVA

Lukáš Laibl & Václav Micka²

¹ Czech Academy of Sciences, Institute of Geology, Rozvojová 269, 165 00 Prague 6, Czech Republic; laibl@gli.cas.cz

² Šaturova 662, 142 00 Prague 4, Czech Republic, mickav@seznam.cz

Abstract: *Barrande's larva is an early developmental trilobite stage (protaspis) characterized by an effaced, gently vaulted circular exoskeleton about 1 mm in diameter. This early stage was described in 1943 by Robert Růžička. The reinvestigation of all known specimens provides new insights into morphology, ecology, and systematic assignment of this peculiar trilobite stage. The absence of palpebral lobes and eye ridges in Barrande's larva suggests this protaspis stage belongs to a blind trilobite species. Moreover, the meraspides of a blind conocoryphid trilobite Conocoryphe, which comes from the same strata, fit well the estimated size of the meraspis specimens of Barrande's larva. It is therefore assumed, that Barrande's larva is a protaspis stage of Conocoryphe. The large size of Barrande's larva, its slightly inflated exoskeleton with wide glabella, and low abundance at the type locality indicate lecithotrophic development.*

Keywords: Trilobita, Skryje-Týřovice Basin, Cambrian, *Conocoryphe*, lecithotrophy

INTRODUCTION

In 1943, Robert Růžička described an early developmental trilobite stage (protaspis) from the Cambrian sediments of the Skryje-Týřovice Basin (Růžička 1943) labeling it as anaprotaspis stage of unknown systematic affinity. An “anaprotaspis” is a descriptive term to designate the earliest simple-shaped trilobite stage with an unrecognizable trunk (see Chatterton & Speyer 1997 for discussion). Růžička (1943) also noticed that this early stage is rather large, comparable by size to much later developmental stages of other trilobites. Despite Růžička (1943) mentioning and figuring out one specimen, he apparently collected more of them before 1945, as evidenced by several other specimens discovered in the National Museum, Prague collections. In 1957, Whittington briefly mentioned this anaprotaspis specimen and noted it might represent a later stage of smaller anaprotaspides assigned by Růžička (1943) to solenopleurid trilobite *Sao hirsuta* Barrande, 1846 (cf. Whittington 1957a). Later, Šnajdr discovered several other specimens of this anaprotaspis giving it an informal name Barrande's larva (Šnajdr 1958). The affinity of Barrande's larva was unknown

until the work of Laibl *et al.* (2014) who assigned it to the order Ptychopariida (Ptychopariida sp. B in Laibl *et al.* 2014) based on morphological similarities with some other “ptychopariid” species and referring to trilobites known from the Skryje-Týřovice Basin. Since Ptychopariida is a paraphyletic or (more likely) polyphyletic group (Fortey 2001, Paterson *et al.* 2019, Paterson 2019) this assignment provides no useful information regarding the affinity of Barrande's larva.

In this contribution, we present new morphological data on the Barrande's larva based on the observation of all available specimens from the National Museum, Prague (prefix L, collected by Robert Růžička in 1940s), and the Czech Geological Survey (prefix MŠ, collected by Milan Šnajdr in 1950s). Subsequently, we discuss the life-history strategy of these protaspides and, based on several lines of evidence, we suggest their affinity to the trilobite genus *Conocoryphe* Hawle & Corda, 1847.

Morphological terminology used in this paper follows Whittington & Kelly (1997), with some modifications according to Hughes *et al.* (2006) for the term trunk.

RESULTS

Occurrence and preservation

Eight so far known specimens of the Barrande's larva all come from the Týřovice – Pod hrůškou locality (Buchava Formation, Miaolingian, *e.g.* Fatka & Kozák 2023) in the Skryje-Týřovice Basin (Czech Republic). They are all preserved as internal moulds in fine shales, dorsoventrally flattened, slightly deformed, and covered by iron hydroxides. For more details about the geology, stratigraphy, and environment of the Buchava Formation and the Týřovice – Pod hrůškou locality see Růžicka (1943), Fatka (2004), Fatka *et al.* (2011) and Laibl *et al.* (2014).

Description

Detailed measurements of the available specimens of Barrande's larva suggest that two protaspis stages are present in the ontogeny of this species. Most of the specimens are 0.91–1.10 mm wide and 0.88–1.05 mm long (Table 1, Figure 1A) and overlap by size with the latest (third) protaspis stage of co-occurring trilobite *S. hirsuta* (that is, however, of very different morphology, see Laibl *et al.* 2014). One small specimen of Barrande's larva (no. L 4456) is 0.76 mm wide and 0.77 mm long (Table 1, Figure 1A) and probably represents an earlier developmental stage. Morphologically, this earlier stage is identical to the larger specimens (*cf.* Plate I, fig. 1 and Plate I, fig. 7) and the following description thus applies to both protaspis stages.

The protaspis are circular in dorsal view, effaced, and gently vaulted, with well-developed marginal rim, anterior pits, and three pairs of fixigenal spines (Figure 2, Plate II). The anterior pits are distinct, positioned near the anterior margin of the exoskeleton, spaced ca. 0.4–0.5 mm from each other. Shallow, almost indistinct, axial furrows run posteriorly from the anterior pits, slightly converge backward, and reach a bulged sub-circular area which is herein interpreted as the occipital ring. The occipital ring is positioned one-fourth from the posterior margin (*sag.*). No palpebral lobes nor eye ridges are visible. The marginal rim is developed around the lateral and posterior margins of the exoskeleton. The anterior fixigenal spines are short (ca. 0.03 mm long), located in the protaspis mid-length (*exsag.*), and pointed laterally. The mid-fixigenal spines are minute, in most cases preserved as tiny nodes approximately opposite the occipital ring (*exsag.*). The posterior fixigenal spines are comparatively long (reaching about 0.07 mm), located at the posterior margin of the exoskeleton, spaced about 0.25 mm at their bases, and orientated posteroventrally; their distal tips slightly converge towards the medial axis. The posterior margin of the exoskeleton is slightly bulged posteriorly and curled ventrally. The doublure is narrow. The librigenae are ventral, separated by marginal facial sutures. The rostral plate is wide (about 0.75 mm), separated by rostral sutures from the rest of the doublure. The hypostome is conterminant, comparatively large, 0.54 mm

Table 1. Measured parameters of Barrande's larva and *Conocoryphe* from the Buchava Formation, Skryje-Týřovice Basin, Czech Republic. Abbreviations: ExL, exoskeletal length; ExW, exoskeletal width; P1, first protaspis stage; P2 second protaspis stage; M3–5, meraspis degrees 3–5.

Taxon	Stage	Spec. No.	ExW (mm)	ExL (mm)
Barrande's larva	P1	L 4456	0.76	0.77
Barrande's larva	P2	L 4439	0.91	0.88
Barrande's larva	P2	MŠ 9646	0.96	0.99
Barrande's larva	P2	MŠ 9647	0.96	1.05
Barrande's larva	P2	L 4453	1.01	0.97
Barrande's larva	P2	L 4440	1.02	1.04
Barrande's larva	P2	L 11427	1.05	1
Barrande's larva	P2	L 4448	1.1	0.91
<i>Conocoryphe gerlinda</i>	M3	L 68588	1.85	2.31
<i>Conocoryphe</i> sp.	M5	L 28222	2.05	2.91

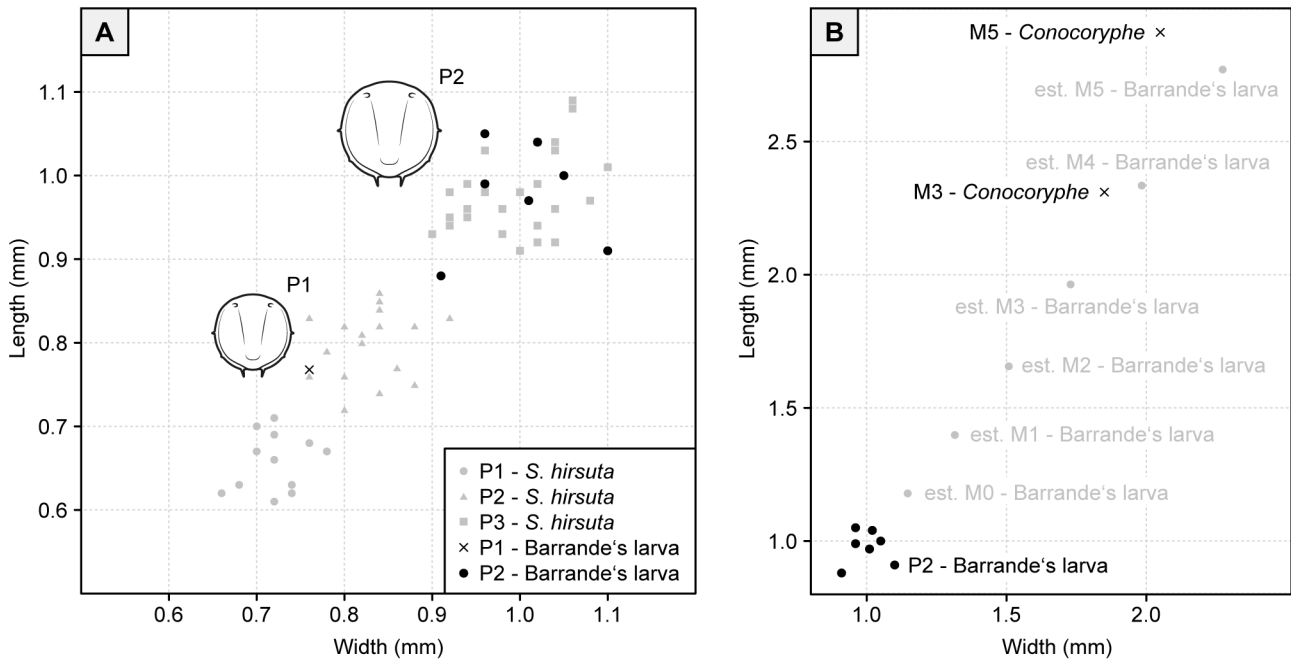


Figure 1. Bivariate scatter plots of Barrande's larva, *Sao hirsuta* and *Conocoryphe* from the Buchava Formation, Skryje-Týřovice Basin, Czech Republic. **A** – Scatter plot of exoskeletal length vs. width of Barrande's larva and *S. hirsuta*; note that the first (P1) and second (P2) protaspis stages of Barrande's larva are morphologically comparable to P1 of *S. hirsuta*, while the size cluster P2 of Barrande's larva overlaps with size cluster P3 of *S. hirsuta*. **B** – Scatter plot of exoskeletal length vs. width of the second protaspis stage of Barrande's larva, estimated size of its meraspides (M0–M5), and comparison with meraspides (M3 and M5) of *Conocoryphe*.

long, and about the same maximal width, covering about 25% of the ventral opening. The anterior hypostomal margin is gently curved and laterally extended into anterior hypostomal wings. The central lobe of the hypostome is parabolic, and the posterior lobe is circular and bears nine marginal spines; the lateral spines are the longest and the more posterior pairs are shorter; the medial spine is unpaired.

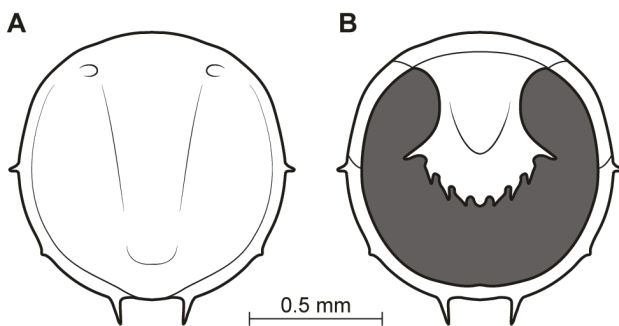


Figure 2. Reconstruction of the dorsal (**A**) and ventral (**B**) protaspis morphology of Barrande's larva from the Buchava Formation, Skryje-Týřovice Basin, Czech Republic.

DISCUSSION

Discussion on the morphology

Barrande's larva is characterized by a unique combination of characters that is not present in other early developmental trilobite stages from the Skryje-Týřovice Basin, namely large size, effaced exoskeleton, absence of palpebral lobes, bulged posterior margin, and tightly spaced posterior fixigenal spines. It has a proportionally longer lateral pair of hypostomal spines than the protaspis stages of *S. hirsuta* (cf. Laibl *et al.* 2014).

Whittington (1957) suggested Barrande's larva may be a later stage of smaller anaprotaspides assigned by Růžicka (1943) to *S. hirsuta*. However, Laibl *et al.* (2014) proved these small anaprotaspides (= *Ptychopariida* sp. A of Laibl *et al.* 2014) belong most likely to *Agraulos* Hawle & Corda, 1847 or *Skreiaspis* Růžicka, 1944. They are characterized by distinct palpebral lobes and flat posterior margin (cf. Laibl *et al.* 2014, fig. 7C, 8Hd, and Figure 3C herein) and are, therefore, unlikely to be part of the developmental sequence of Barrande's larva.

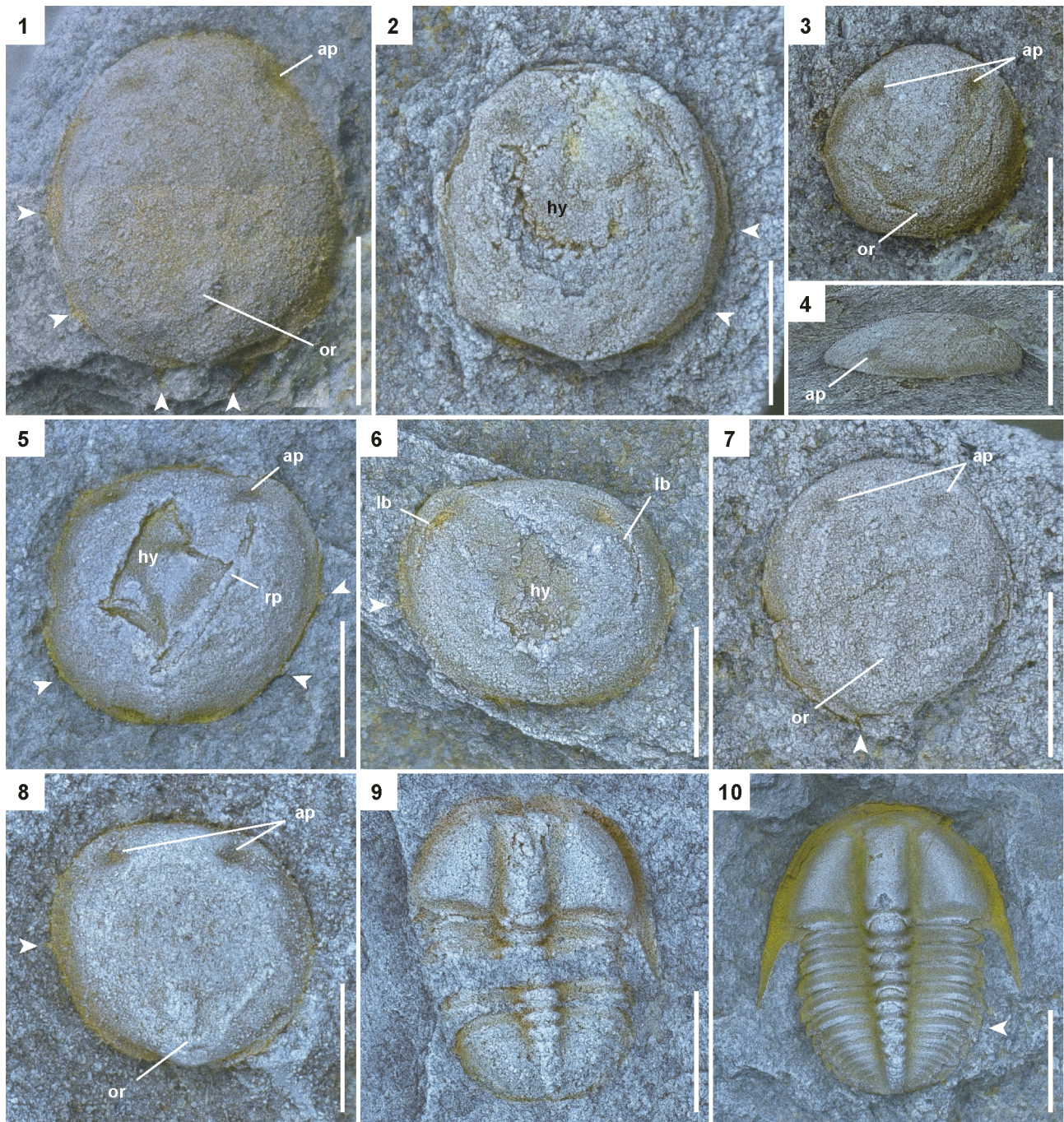


Plate I. Protaspid stages of Barrande's larva and meraspides of *Conocoryphe* from the Buchava Formation, Skryje-Týřovice Basin, Czech Republic. **1–6, 8** – second protaspid stage of Barrande's larva from dorsal (1–3, 5–6, 8) and lateral view (4), Týřovice – Pod hrůškou. 1 – MŠ 9647 (figured by Laibl *et al.* 2014, fig. 7L). 2 – L 4440. 3, 4 – L 4439. 5 – L 4453. 6 – L 4448. 8 – L 11427 (original specimen, figured by Růžicka 1943, p. 14, 31, figured by Šnajdr 1958, pl. 45, fig. 25). **7** – first protaspid stage of Barrande's larva from dorsal view, Týřovice – Pod hrůškou, L 4456. **9–10** – early meraspides of *Conocoryphe* from dorsal view. 9 – meraspid degree 3 of *Conocoryphe gerlinda* Šnajdr, 1982, Skryje – Luh, L 68588. 10 – meraspid degree 5 *Conocoryphe* sp., Skryje, L 28222. Abbreviations: ap, anterior pits; hy, hypostome; lb, librigena; or, occipital ring; rp, rostral plate. Arrows point to the fixigenal spines in 1–8 and to the thoracic-pygidial boundary in 10. The scale bar is 0.5 mm in 1–8, and 1 mm in 10.

Růžicka (1943) noted marginal eye ridges in his description of Barrande's larva (=Protaspis on p. 14 and 31 in Růžicka 1943). Similarly, Laibl *et al.* (2014) mentioned and reconstructed a narrow eye ridge in the same taxon (=Ptychopariida sp. B on p. 304 and in fig. 8GL–8GD in Laibl *et al.* 2014). The present investigation of new material confirms no eye ridges or palpebral lobes are present in Barrande's larva, even in the original specimen of Růžicka (1943, see Plate I, fig. 8 herein). We believe that Růžicka (1943) probably erroneously interpreted the anterior portion of the marginal rim as the eye ridges. The interpretation of Laibl *et al.* (2014) is likely based on the artifacts from the SEM images.

Affinity of Barrande's larva

Despite the simple morphology of Barrande's larva, these protaspis stages undoubtedly belong to Trilobita because of the presence of several typical trilobite features, namely anterior pits, trilobate exoskeleton, three pairs of fixigenal spines, librigenae and a spiny hypostome (cf. Whittington 1957b, Palmer 1962a, Chatterton & Speyer 1997). From the trilobite taxa that occur in the Skryje-Týřovice Basin, Barrande's larva does not belong to Agnostina, because protaspides of these forms are unknown and were most likely uncalcified or absent (Robison 1964, Chatterton & Speyer 1997). Barrande's larva also cannot be assigned to Ellipsocephalidae or Paradoxididae, as these families have particular protaspis morphologies, with non-effaced exoskeletons, well-developed glabellae, and distinct palpebral lobes (cf. Šnajdr 1958, Laibl *et al.* 2017, 2018). Early meraspides of Centropleuridae are in many aspects similar to those of Paradoxididae (Babcock 1994), and such an assignment is also unlikely. Protaspides of Solenopleuridae and possibly also of Agrauidae and Ptychopariidae are known from the Skryje-Týřovice Basin, all seem to have distinct palpebral lobes and are much smaller than Barrande's larva (see Šnajdr 1958, Laibl *et al.* 2014, 2015).

The absence of palpebral lobes in Barrande's larva suggests this protaspis stage might belong to a blind trilobite species of the family Conocoryphidae that is represented in the Skryje-Týřovice Basin by several species (Vokáč & Míčka 2024). Although palpebral lobes are not always distinct in all early

protaspides due to their small size and poor preservation even in species whose adults possess well-developed eyes (e.g. Whittington 1957a, Lee & Chatterton 2005a, b), this is likely not the case for Barrande's larva given its large size and fine preservation. The absence of the palpebral lobes thus seems to be genuine character of this taxon. Of the conocoryphid genera that co-occur with protaspides of Barrande's larva in the same locality, the most abundant is *Conocoryphe* (Fatka 2004). Except for the shared absence of palpebral lobes in both taxa, the early meraspides of *Conocoryphe* fit well the expected size for meraspides of Barrande's larva (Table 1, Figure 1B). We calculated the expected mean size for the individual meraspis stages of Barrande's larva (Table 2), based on the mean size of the large protaspis stage of Barrande's larva and the mean growth rate of *S. hirsuta* (cf. Laibl *et al.* 2014) to test if the *Conocoryphe* meraspides are of similar dimensions as expected meraspides of Barrande's larva. *S. hirsuta* seems to be a good model for meraspis growth, as the protaspis growth and proportions are comparable to Barrande's larva. The recorded early meraspides of *Conocoryphe* fit well with the calculated mean dimensions of Barrande's larva (Figure 1B). It is therefore likely, that Barrande's larva represents a protaspis stage of *Conocoryphe*.

Table 2. Measured and estimated dimensions of the individual meraspis degrees of Barrande's larva and *Conocoryphe* from the Buchava Formation, Skryje-Týřovice Basin, Czech Republic. Note that 1.145 and 1.19 constants for width and length are consistent with the mean growth rates between individual stages of *Sao hirsuta* (cf. Laibl *et al.* 2014). Abbreviations: ExL, exoskeletal length; ExW, exoskeletal width; P2 second protaspis stage; M1–5, meraspis degrees 1–5.

Stage	Measured dimensions (mean)		Estimated dimensions	
	ExW	ExL	ExW * 1.145	ExL * 1.19
P2	1	0.977	1	0.977
M0	-	-	1.145	1.1626
M1	-	-	1.3110	1.3835
M2	-	-	1.5011	1.6464
M3	1.85	2.31	1.7188	1.9592
M4	-	-	1.9680	2.3315
M5	2.05	2.91	2.2534	2.7744

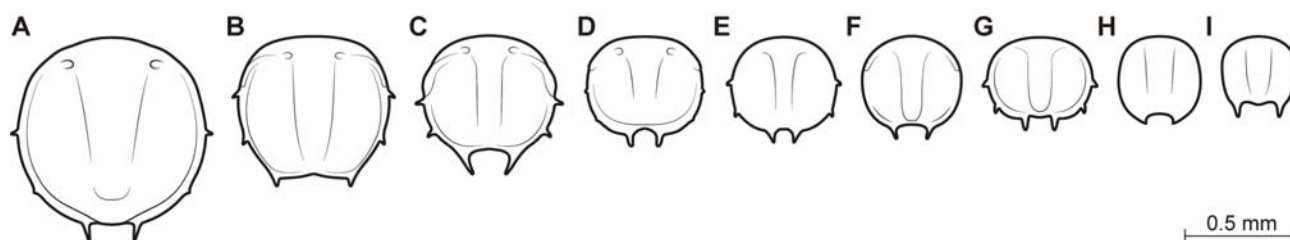


Figure 3. Comparison of the morphology and size of various Cambrian trilobite protaspides. **A** – the first protaspid stage of Barrande's larva, Czech Republic. **B** – the first protaspid stage of *Sao hirsuta*, Czech Republic (redrawn from Laibl *et al.* 2014). **C** – the first protaspid stage of *Ptychopariida* sp. A, Czech Republic (redrawn from Laibl *et al.* 2014). **D** – the first protaspid stage of *Spencella?* sp., USA (redrawn from Chatterton & Speyer 1997). **E** – the first protaspid stage of *Blainia gregaria* Walcott, 1916, USA (redrawn from Whittington 1957a). **F** – the first protaspid stage of *Crassifimbria walcoti* (Resser, 1937), USA (redrawn from Palmer 1958). **G** – the first protaspid stage of *Aphelaspis brachyphasis* Palmer, 1962b, USA (redrawn from Lee & Chatterton 2005a). **H** – the first protaspid stage of *Bolaspidea housensis* (Walcott, 1886), USA (redrawn from Lee & Chatterton 2005b). **I** – the first protaspid stage of *Glaphyraspis parva* (Walcott, 1899), USA (redrawn from Lee & Chatterton 2005b).

Life-history strategy

The unusual feature of Barrande's larva is the large size of this early developmental stage. In reality, most other trilobite protaspides of similar morphology are half the size of Barrande's larva or even smaller (Figure 3). The extraordinary dimensions of Barrande's larva have already been noticed by Růžička (1943) and Laibl *et al.* (2014). The latter authors also suggested that such a large size might reflect the amount of yolk in the egg and possible lecithotrophic development. Laibl *et al.* (2017) comprehensively reviewed lecithotrophy in trilobites. Except for the large size, Laibl *et al.* (2017) listed several other additional characteristics that help to recognize lecithotrophy in trilobites, these are: 1, low or almost no growth increment between individual instars; 2, accelerated or abbreviated development; 3, lower frequency (rarity) of protaspides at the locality reflecting fewer large eggs per parent; and 4, inflation of the glabella to store lipid reserves from the yolk. Barrande's larva is quite a rare element at the Týřovice – Pod hrůškou locality, especially when compared with taxa that are extremely abundant in the same site [e.g. *S. hirsuta* or even *Eccaparadoxides pusillus* (Barrande, 1846), cf. Fatka 2004, Laibl *et al.* 2014, 2017], suggesting fewer eggs per parent than some of the other co-occurring trilobite species. The exoskeleton of Barrande's larva is also slightly inflated resulting in the effacement of axial furrows. Considering also the wide anterior part of the glabella, this morphology suggests

similar modifications as in lecithotrophic protaspides of *Hydrocephalus carens* Barrande, 1846 (Laibl *et al.* 2017). To sum up, the large protaspid size, inflated exoskeleton with wide glabella, and low abundance at the locality all suggest the lecithotrophic development of Barrande's larva.

ACKNOWLEDGEMENTS

The manuscript benefited from constructive reviews by Jana Bruthansová and Michal Mergl. The research was conducted within institutional support RVO 67985831 of the Institute of Geology of the Czech Academy of Sciences.

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