

Early ontogeny of the Cambrian trilobite *Sao hirsuta* from the Skryje-Týřovice Basin, Barrandian area, Czech Republic

LUKÁŠ LAIBL, OLDŘICH FATKA, CATHERINE CRÔNIER & PETR BUDIL



Preservation of ontogenetic stages of trilobites from the Cambrian of the Skryje-Týřovice Basin (Barrandian area) has been known from several localities in the upper part of the Buchava Formation. The most complete information on exoskeletal changes during ontogeny was based on material assigned by Barrande (1852) to *Sao hirsuta*. Based on quantitative methods and detailed study of the morphology of the exoskeleton, we recognize three protaspis and two early meraspis instars of *Sao hirsuta*. We also describe the protaspis stages of two indeterminate taxa of Ptychopariida, one originally determined as the protaspides of *Sao hirsuta* and the other referred to by Růžička (1943) as “Barrande’s larva”. Protaspides of *Sao hirsuta* have an adult-like morphology, and their presumed benthic mode of life is consistent with the restricted palaeogeographic distribution of this genus. • Key words: trilobites, ontogeny, Skryje-Týřovice Basin, Buchava Formation, Barrandian area, Cambrian.

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Lukáš Laibl & Oldřich Fatka, Charles University, Faculty of Science, Institute of Geology and Palaeontology, Albertov 6, 128 43 Prague 2, Czech Republic; lukaslaibl@gmail.com, fatka@natur.cuni.cz • Catherine Crônier, Université Lille 1, UFR Sciences de la Terre, UMR 8217 Géosystèmes, 59655 Villeneuve d’Ascq, France; catherine.cronier@univ-lille1.fr • Petr Budil, Czech Geological Survey, Klárov 3, Praha 1, 118 21 Czech Republic; petr.budil@geology.cz

A short preliminary announcement and diagnosis of a spectacular solenopleurid trilobite *Sao* were published by Barrande (1846). A more comprehensive account was provided by Hawle & Corda (1847) who, however, did not use Barrande’s generic name because they considered it to be preoccupied. Unfortunately, these two preliminary studies contained numerous mistakes criticized by Barrande (1852), who provided the first thorough study of the ontogeny of *Sao* and several other trilobites. New data on the early ontogeny of *Sao hirsuta* was provided by Růžička (1943), based on large new collections of immature specimens including anaprotaspides. He also distinguished the so-called “Barrande’s larva”, a protaspis stage of uncertain affinity (Růžička 1943, text-figures on pages 14 and 31). Whittington (1957) argued that the smallest stages described by Růžička (1943, pl. 4, figs 7, 8, pl. 5, fig. 5) probably belong to “Barrande’s larva” rather than to *S. hirsuta*. In the following year, Šnajdr (1958) summarized all earlier data on Cambrian trilobites of the Barrandian area, including the ontogeny of *S. hirsuta*, provided new observations and illustrated many early ontogenetic specimens of the species. Since then, no new information on the ontogeny of

S. hirsuta or any other trilobites from the Skryje-Týřovice Basin have been published, with the exception of a short comment by Valíček & Šarič (2001) on *Luhops expectans* (Barrande, 1852).

Recent methods of investigation of exceptionally preserved fossil material combined with intensive study of trilobite ontogeny have made it possible to evaluate trilobite ontogenies more comprehensively and to compare them with those of other arthropods. Ontogenetic data have been important for our understanding of the palaeobiogeographic distribution of trilobites (Chatterton & Speyer 1989), their systematics (Fortey 1990, 2001), and their phylogenetic relationships (Edgecombe *et al.* 1988, Fortey & Chatterton 1988, Park & Choi 2009). They have also enabled the exploration of topics as different as survivorship during extinction events (Chatterton & Speyer 1989, Lerosey-Aubril & Feist 2005) and the evolution of trilobite body patterning (Hughes 2007, Feist & Lerosey-Aubril 2008).

The objectives of the present study are: (1) to investigate the immature specimens assigned to *S. hirsuta* by previous authors, using modern techniques (*e.g.*, scanning

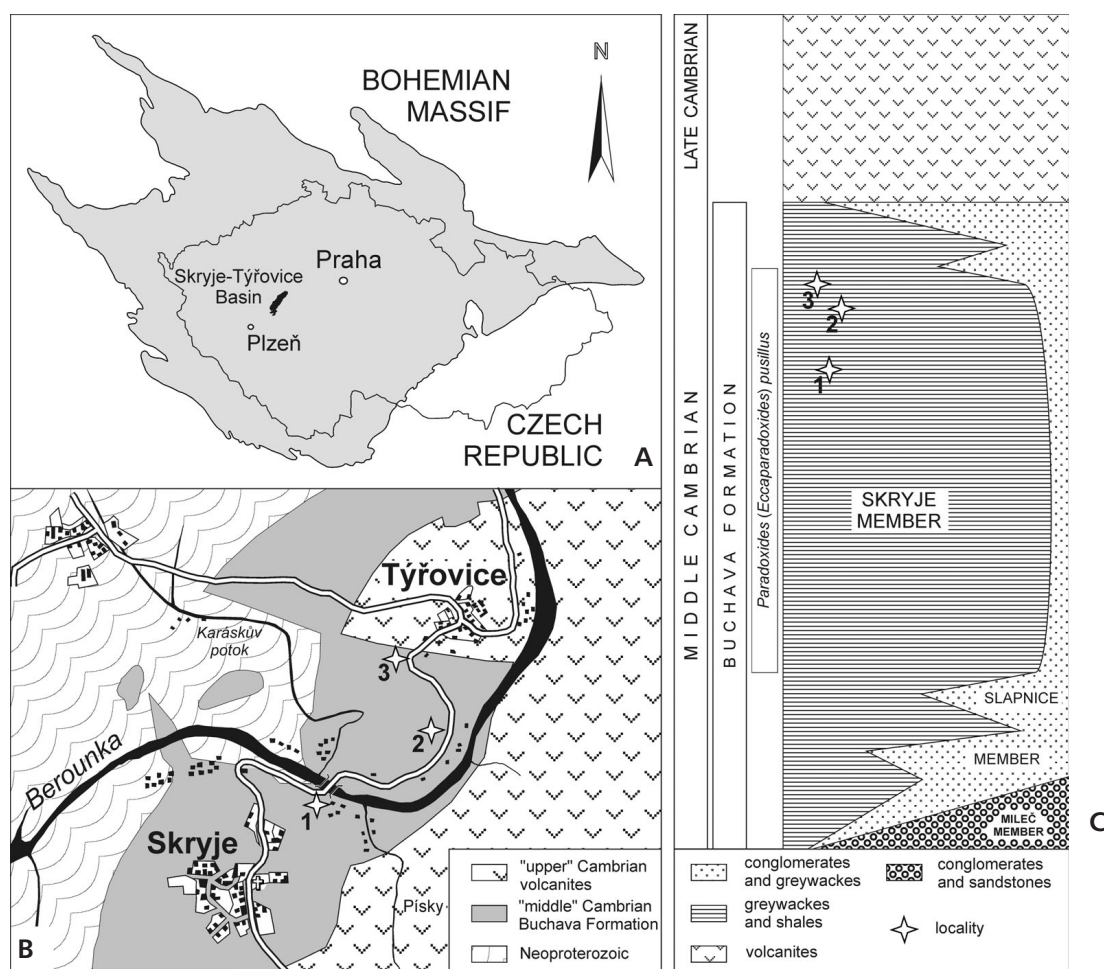


Figure 1. Geological setting. • A – map of the Bohemian Massif (shaded) showing the Czech Republic and the Cambrian of the Skryje-Týřovice Basin. • B – Cambrian of the Skryje-Týřovice Basin with location of the following fossil sites in the Buchava Formation: Skryje – Luh (1), Týřovice – Pod hrůškou (2) and Týřovice – Lúmek (3); geology modified after Mašek *et al.* (1997). • C – stratigraphic positions of the three localities within the Buchava Formation of the Skryje-Týřovice Basin; stratigraphy after Fatka *et al.* (2011b).

electron microscopy, quantitative methods); (2) to assess whether the specimens are all truly conspecific; (3) to provide accurate descriptions of the morphological changes during the early ontogeny of *S. hirsuta*; and (4) to infer life-history strategy and its possible implication for the palaeobiogeographic distribution of this species.

Geological setting

The Cambrian Buchava Formation (Fatka *et al.* 2011b) consists of about 200 m of fossiliferous siliciclastic sediments (fine shales and graywackes with subordinate lenses of sandstones and conglomerates) in the Skryje-Týřovice Basin, situated northeast of the town of Plzeň (Fig. 1A). The formation, which crops out in a narrow zone around the middle course of the Berounka River, unconformably overlies slightly metamorphosed Neoproterozoic rocks and is overlain by Furongian to earliest Ordovician extru-

sive rocks (dacites, andesites and rhyolites) of the Křivoklát-Rokycany Complex (Havlíček 1971, Drost *et al.* 2004).

The basal part of the Buchava Formation is composed of poorly fossiliferous, white to grey conglomerates and sandstones containing only fragmentary remains of trilobites, brachiopods and gastropods (Havlíček 1971). This sequence is usually overlain by darker conglomerates associated with greyish green graywackes and shales with fragmentary but locally common trilobites and brachiopods (*e.g.* Mergl & Kordule 2008) and some exceptionally preserved fossils such as graptoloids and *Wiwaxia* (Maletz *et al.* 2005, Fatka *et al.* 2011a). The sequence of graywackes and clayey shales with occasional silty to sandy intercalations is the most widespread lithofacies, reaching a thickness of nearly 200 m in the north-eastern part of the basin. A rich assemblage of well-preserved fossils including trilobites, agnostids, echinoderms, brachiopods, hyolithids, molluscs,

sphenothallids, organic-walled microfossils and ichnofossils has been recorded from numerous outcrops of these fine-grained sediments (e.g. Šnajdr 1958, Lefebvre & Fatka 2003, Álvaro *et al.* 2004, Fatka 2004, Fatka & Szabad 2011). In the northeastern part of the Skryje-Týřovice Basin, several tongue-like bodies of dark conglomerate are developed in the upper part of the Buchava Formation. Fine shales overlying and underlying these conglomerates are exposed at several outcrops. An abundant and diverse fauna was collected at three of these outcrops, at Skryje – Luh, Týřovice – Pod hrůškou and Týřovice – Lůmek (Fig. 1). Most of the growth stages of *Sao hirsuta* described by Hawle & Corda (1847), Barrande (1852), Růžička (1943), Whittington (1957) and Šnajdr (1958), as well as by us in the present study, came from the Týřovice – Pod hrůškou locality (see Fatka 2004). The specimens from Týřovice – Pod hrůškou were supplemented in our study by less well preserved ones that are rare at the other two outcrops.

Material and methods

Material. – The specimens, preserved as internal and external moulds in very fine-grained shales, were either coated with ammonium chloride and photographed under an optical microscope (Nikon SMZ 1500, Olympus SZX 12) and/or photographed using a scanning electron microscope in a low vacuum mode (JEOL-6380 LV, Hitachi S-3700N). Drawings were produced from the photographs. The specimens are housed in the National Museum, Prague (NM), the Czech Geological Survey (CGS), Prague, and in the Museum of Dr Bohuslav Horák at Rokycany (MBHR).

Biometric measurements. – One hundred and one of the best preserved protaspids and early meraspids were selected for biometric studies (Tables 1–3). The maximum length and width of the exoskeleton (Fig. 2), excluding spines, were measured using optical image analyzer *TpsDig2* (Rohlf 2006a).

Landmarks and centroid size. – Landmark-based geometric morphometrics were performed to obtain the centroid size of protaspids of *S. hirsuta*. Three landmarks (all type 2 of Bookstein 1991) were selected on the protaspid exoskeleton (see Fig. 2). The 2D projections of landmarks were obtained using *TpsDig2*, and the centroid size calculated using *TpsRelw* (Rohlf 2006b).

Graphs. – All bivariate plots and the frequency histogram, as well as the linear regression, linear correlation and the *p* value, have been made using the PAST package (Hammer *et al.* 2001).

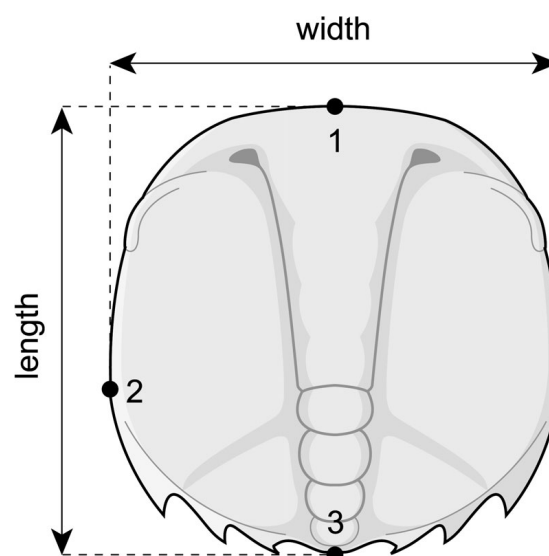


Figure 2. Measured parameters. The landmarks are defined as: 1) anteriormost point of the exoskeleton; 2) maximum lateral extent of the exoskeleton; 3) posterior end of the exoskeleton.

Growth. – For *S. hirsuta*, four growth metrics have been calculated: Dyar's index (*Di*), the average per-moult increment (*AGI*), the average per-moult growth rate (*AGR*) and the index of conformity to Dyar's rule (*IDC*). Dyar's index is a post-moult *vs.* pre-moult size ratio between the two successive instars (Dyar 1890). For detailed calculation of *AGI*, *AGR* and *IDC*, see Fusco *et al.* (2011).

Systematic palaeontology

Terminology. – Morphological terminology generally follows Whittington & Kelly (1997), with the following exceptions. The terms anaprotaspis, metaprotaspis and paraprotaspis (*sensu* Beecher 1895) are not used, following the recommendation of Chatterton & Speyer (1997); protaspis instars are instead referred to as stages 1, 2 and 3, as in Lee & Chatterton (2005). The terminology of the posterior cranial border furrow and posterior cephalic marginal furrow follows Lee & Chatterton (2005). Terminology of the post-cephalic part of the exoskeleton during ontogeny is based on Hughes *et al.* (2006). The following abbreviations are used: P1, P2 and P3 for protaspis stages 1, 2 and 3; M1-4 and M1-5 for meraspis degree 1 with respectively four or five segments in the meraspis pygidium.

Order Ptychopariida Swinnerton, 1915
Family Solenopleuridae Angelin, 1854
Subfamily Solenopleuropsinae Thorall, 1947

Remarks. – We provisionally follow Álvaro & Vizcaíno (1997) in regarding the subfamily Saoinae Hupé, 1953 as invalid.

Table 1. Dimensions and trunk segment numbers of protaspid and early meraspid stages of *Sao hirsuta* Barrande, 1846.

Institution	Number	Stage	Width (mm)	Length (mm)	Centroid size	Segment number	Institution	Number	Stage	Width (mm)	Length (mm)	Centroid size	Segment number
CGS	3173	P1	0.66	0.62	5,11E-01	?	CGS	3487	P3	0.98	0.93	7,67E-01	4
CGS	3229	P1	0.68	0.63	5,26E-01	?	CGS	3505	P3	0.9	0.93	7,49E-01	4
NM	L3550	P1	0.7	0.67	5,48E-01	?	MBHR	89940	P3	1	0.91	7,60E-01	4
NM	L3555	P1	0.7	0.67	5,47E-01	?	MBHR	89980	P3	1.1	1.01	8,48E-01	4
NM	L3686	P1	0.76	0.68	5,74E-01	?	MBHR	89981	P3	0.94	0.99	7,99E-01	4
NM	L3689	P1	0.72	0.69	5,68E-01	?	MBHR	89985	P3	0.96	0.98	7,95E-01	4
NM	L3690	P1	0.72	0.66	5,51E-01	?	NM	L19014	P3	0.98	0.96	7,83E-01	4
NM	L3691	P1	0.78	0.67	5,69E-01	?	NM	L3727	P3	0.92	0.98	7,83E-01	4
NM	L3692	P1	0.74	0.62	5,39E-01	?	NM	L3729	P3	1.04	1.04	8,42E-01	4
NM	L3698	P1	0.72	0.71	5,83E-01	?	NM	L3732	P3	1	0.98	8,11E-01	4
NM	L3704	P1	0.72	0.71	5,78E-01	?	NM	L3734	P3	1.08	0.97	8,13E-01	4
NM	L3705	P1	0.72	0.61	5,21E-01	?	NM	L3736	P3	1.06	1.09	8,86E-01	4
NM	L3708	P1	0.74	0.63	5,36E-01	?	NM	L3739	P3	1.04	0.96	7,97E-01	4
NM	L3718	P1	0.7	0.7	5,70E-01	?	NM	L3742	P3	0.92	0.95	7,71E-01	4
CGS	3164	P2	0.86	0.77	6,60E-01	3	NM	L3744	P3	0.96	1.03	8,24E-01	4
CGS	3490	P2	0.8	0.72	6,13E-01	3	NM	L3750	P3	1.02	1.04	8,35E-01	4
CGS	3521	P2	0.76	0.76	6,28E-01	3	NM	L3752	P3	0.96	0.99	8,05E-01	4
MBHR	89959	P2	0.88	0.82	6,84E-01	3	NM	L3754	P3	1.04	0.92	7,84E-01	4
MBHR	89992	P2	0.84	0.86	7,02E-01	3	NM	L3755	P3	1.02	0.94	7,80E-01	4
NM	L12500	P2	0.88	0.75	6,48E-01	3	CGS	MS11478	P3	1.04	1.03	8,42E-01	4
NM	L12501	P2	0.8	0.76	6,28E-01	3	CGS	MS568	P3	0.92	0.94	7,47E-01	4
NM	L19012	P2	0.92	0.83	7,03E-01	3	CGS	MS569	P3	0.9	1.02	8,10E-01	4
NM	L3534	P2	0.84	0.82	6,74E-01	3	CGS	MS570	P3	0.94	0.95	7,72E-01	4
NM	L3537	P2	0.84	0.85	7,00E-01	3	CGS	MS572	P3	1.02	0.92	7,69E-01	4
NM	L3539	P2	0.76	0.83	6,71E-01	3	CGS	MS572_1	P3	1.02	0.99	8,16E-01	4
NM	L3544	P2	0.82	0.81	6,65E-01	3	CGS	MS9536	P3	1.06	1.08	8,83E-01	4
NM	L3546	P2	0.84	0.74	6,29E-01	3	CGS	MS9544	P3	0.92	0.94	7,61E-01	4
NM	L3548	P2	0.78	0.79	6,41E-01	3	NM	L19015	M1-4	1.16	1.18	–	5
NM	L3554	P2	0.8	0.82	6,62E-01	3	CGS	MS573	M1-4	1.12	1.12	–	5
NM	L3566	P2	0.84	0.84	6,90E-01	3	CGS	MS575	M1-4	1.08	1.21	–	5
CGS	MS563	P2	0.88	0.82	6,93E-01	3	NM	L19016	M1-5	1.22	1.31	–	6
CGS	MS564	P2	0.82	0.8	6,60E-01	3	CGS	MS574	M1-5	1.23	1.37	–	6
CGS	3140	P3	0.94	0.96	7,68E-01	4	CGS	MS579	M1-5	1.24	1.31	–	6

Genus *Sao* Barrande, 1846

[*nom. conserv.*, *non Sao* Billberg, 1820; ICZN Opinion 512]

Type species. – *Sao hirsuta* Barrande, 1846; Buchava Formation, Drumian, Skryje-Týřovice Basin, Barrandian area, Czech Republic.

Emended diagnosis. – A genus of Solenopleuropsinae with the following combination of characters: (1) cephalic border vaulted, delimited by deep furrow; (2) glabella

with three deep transverse lateral glabellar furrows and a sagittal furrow; (3) exoskeleton densely covered with tubercles and small hollow spines; (4) preglabellar field concave without any tubercles or spines.

Occurrence. – In addition to the occurrence in the Skryje-Týřovice Basin, the genus has been recorded from the Liptergrün Formation (Drumian) of the Franconian Forest, Germany (Sdzuy 2000) and from the middle part of the Playón Beds (Drumian?) of the Ossa-Morena Zone, Spain (Gozalo *et al.* 1994).

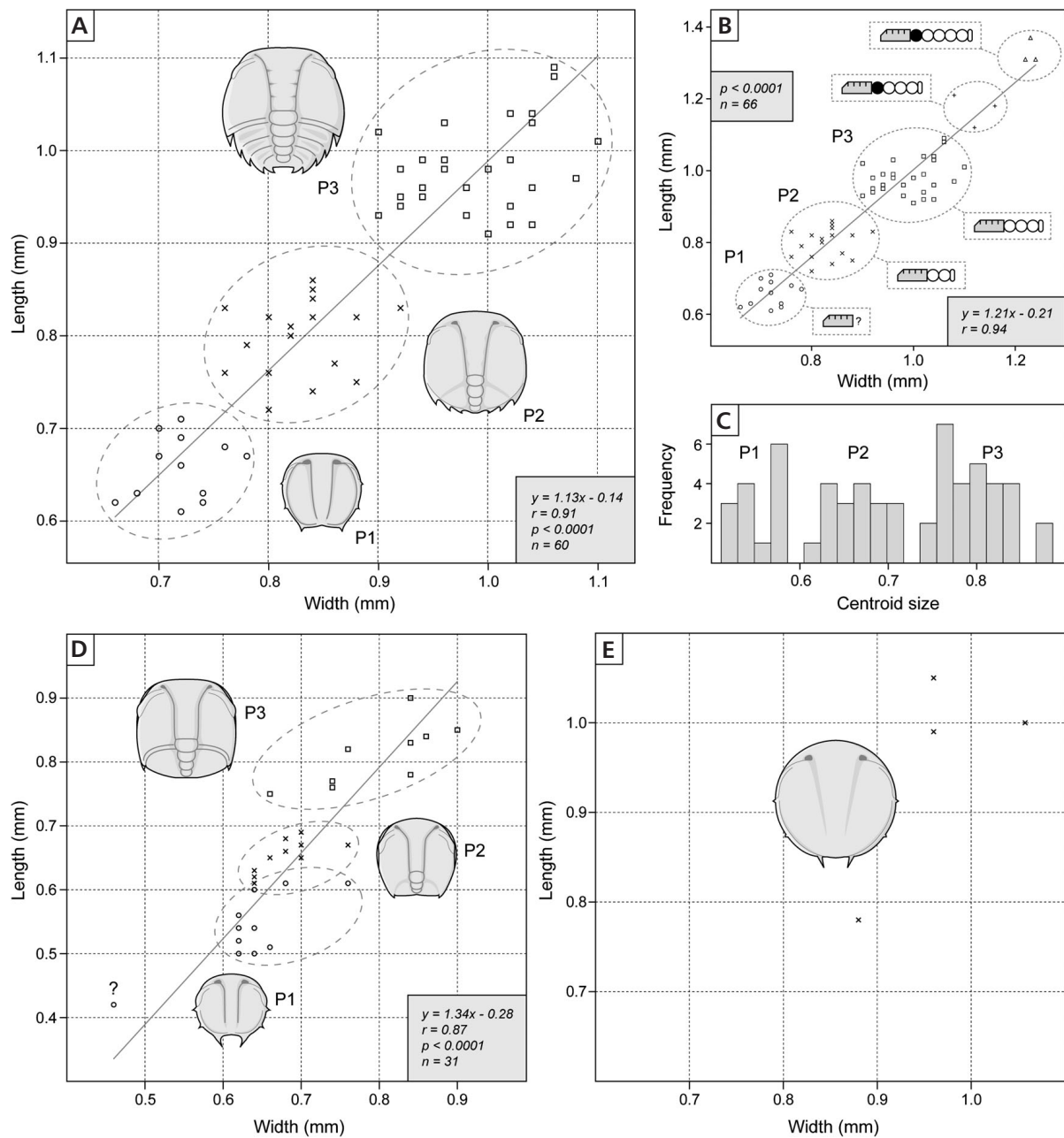


Figure 3. Graphs. • A – scatter plot diagram of length versus width of 60 protaspides of *Sao hirsuta*. • B – scatter plot diagram of length versus width of 60 protaspides and 6 early meraspides of *Sao hirsuta*. Cephalon (grey pentagons), articulated segments (black circles) and fused segments (white circles) are figured. • C – size frequency histogram of centroid size of 60 protaspides of *Sao hirsuta*. • D – scatter plot diagram of length versus width of 31 protaspides of *Ptychopariida* sp. A. • E – scatter plot diagram of length versus width of 4 protaspides of *Ptychopariida* sp. B.

Sao hirsuta Barrande, 1846

Figures 4–6, 8A–F

1846 *Sao hirsuta* Barr.; Barrande, p. 13.

1852 *Sao hirsuta* Barr. – Barrande, p. 384, pl. 3, fig. 6, pl. 4, fig. 12, pl. 7, figs 1a–c, 2–32 (non pl. 7, fig. 1d, e = *Ptychopariida* sp. A).

1943 *Sao hirsuta* Barrande. – Růžička, p. 11, pl. 4, figs 11,

13–15, 17 (non pl. 4, figs 7–10, 12, 16, pl. 5, fig. 5 = *Ptychopariida* sp. A).

1957 *Sao hirsuta* Barrande. – Whittington, pp. 937–940, pl. 115, figs 21, 22; pl. 116, figs 16, 17, 19 (non pl. 116, figs 14, 15, 18, 20, 21 = *Ptychopariida* sp. A).

1958 *Sao hirsuta* Barrande. – Šnajdr, pp. 21, 23, 204–214, figs 44, 45, pl. 43, figs 7–9, 13–23, 26–33, 35 (non

- figs 1–6, 10–12, 24, 34 = *Ptychopariida* sp. A), pl. 44, pl. 45, figs 1–24 (see for complete synonymy prior to 1957).
- 1959 *Sao hirsuta* Barrande. – Whittington, pp. 130, 142, fig. 88.
- 1959 *Sao hirsuta* Barrande. – Poulsen, pp. 276–277, figs 204, 13.
- 1970 *Sao hirsuta* Barrande. – Horný & Bastl, pp. 157–164, pl. 4, fig. 4.
- 1971 *Sao hirsuta* Barrande. – Havlíček, p. 35.
- 1988 *Sao hirsuta* Barrande. – Whittington, pp. 591, 592, fig. 13, pl. 53, figs 5–7.
- 1990 *Sao hirsuta* Barrande. – Šnajdr, pp. 10, 26, 32, 36, 44, 102, 104, 258.
- 1994 *Sao hirsuta* Barrande; Gozalo *et al.*, pp. 44, 45, 48, 50.
- 1994 *Sao* aff. *hirsuta* Barrande. – Gozalo *et al.*, pp. 48–50, pl. 1, figs 2–6, pl. 2.
- 1997 *Sao hirsuta* Barrande. – Chatterton & Speyer, p. 174.
- 2000 *Sao hirsuta* Barrande. – Sdzuy, pp. 301, 305, 310, pl. 5, figs 7–12.
- 2004 *Sao hirsuta* Barrande. – Álvaro *et al.*, p. 145.
- 2004 *Sao hirsuta* Barrande. – Fatka, p. 112.
- 2006 *Sao hirsuta* Barrande. – Kordule, pp. 290, 296–302.
- 2009 *Sao hirsuta* Barrande. – Fatka & Mergl, p. 79.

Lectotype. – NM L12525, selected by Šnajdr (1958), from the Buchava Formation (Drumian), Skryje-Týřovice Basin, Czech Republic. Figured by Barrande (1852, pl. 7, fig. 15), Šnajdr (1958, pl. 44, fig. 10), Fig. 6D herein. This specimen was also designated lectotype of *Ellipsocephalus nanus* Barrande, 1846 by Marek (*in* Horný & Bastl 1970, p. 212).

Diagnosis. – As for the genus.

Ontogeny. – The length-width dimensions of sixty protaspis specimens assigned to *S. hirsuta* were plotted (Fig. 3A). Three distinct protaspis stages (P1, P2 and P3) are recognized on the basis of size and morphological features. The protaspis stages are clearly distinguishable also in the frequency histogram (Fig. 3C). For postprotaspis development, six articulated early meraspides (degree 1) were plotted with the protaspides (Fig. 3B). This graph suggests the presence of two distinct stages within meraspis degree 1, with four (M1-4) and five (M1-5) segments

Table 2. Dimensions and trunk segment numbers of protaspis and early meraspis stages of *Ptychopariida* sp. A.

Institution	Number	Stage	Width (mm)	Length (mm)	Centroid size	Segment number
NM	L3688	P1	0.62	0.56	–	?
NM	L3699	P1	0.64	0.54	–	?
NM	L3700	P1	0.76	0.61	–	?
NM	L3703	P1	0.62	0.52	–	?
NM	L3706	P1	0.68	0.61	–	?
NM	L3717	P1	0.64	0.6	–	?
NM	L3722	P1	0.62	0.54	–	?
NM	L3729	P1	0.66	0.51	–	?
NM	L19008	P1	0.66	0.51	–	?
NM	L19009	P1	0.62	0.5	–	?
CGS	MS559	P1	0.46	0.42	–	?
CGS	MS11486	P1	0.64	0.5	–	?
CGS	3155	P2	0.7	0.67	–	2
CGS	3217	P2	0.68	0.68	–	2
CGS	3507	P2	0.64	0.62	–	2
CGS	3522	P2	0.64	0.61	–	2
NM	L3547	P2	0.66	0.65	–	2
NM	L3551	P2	0.7	0.69	–	2
NM	L3563	P2	0.68	0.66	–	2
NM	L19010	P2	0.76	0.67	–	2
CGS	MS561	P2	0.7	0.65	–	2
CGS	MS562	P2	0.64	0.63	–	2
CGS	3280	P3	0.66	0.75	–	3
NM	L3540	P3	0.74	0.76	–	3
NM	L3549	P3	0.76	0.82	–	3
NM	L3726	P3	0.84	0.83	–	3
NM	L19011	P3	0.9	0.85	–	3
NM	L19013	P3	0.86	0.84	–	3
CGS	MS565	P3	0.74	0.77	–	3
CGS	MS572	P3	0.84	0.9	–	3
CGS	MS11476a	P3	0.84	0.78	–	3

respectively in the meraspis pygidium. We found no individuals that could be assigned to meraspis degree 0.

Protaspis stage 1 (Figs 4A, B, 8A): Exoskeleton circular in outline, 0.61–0.71 mm long and 0.66–0.78 mm

Figure 4. *Sao hirsuta* Barrande, 1846. Buchava Formation, Skryje-Týřovice Basin. • A – protaspis stage 1; CGS 3229. • B – NM L3704, protaspis stage 1 with exposed hypostome (h). • C – CGS MŠ564, protaspis stage 2 with fixigenal and marginal spines on the trunk (arrows). • D – CGS MŠ563, protaspis stage 2 with fixigenal and marginal spines on the trunk (arrows). • E, F – NM L19012, protaspis stage 2; E – general view showing hypostome (h) and librigena (lb); F – detail of hypostome with rostral plate (rp) and marginal spines (arrows). • G – NM L3727, protaspis stage 3. • H – CGS MŠ572, protaspis stage 3. • I – CGS MŠ568, protaspis stage 3. • J–L – CGS MŠ569, protaspis stage 3 with displaced librigena and hypostome; J – detail of doublure with spines; K – general view of specimen with librigena (lb) and hypostome (h); L – detail of hypostome with marginal spines (arrows) of protaspis stage 3. Scale bars represent 0.2 mm in A–E, G–I, K; 0.1 mm in F, J, L.

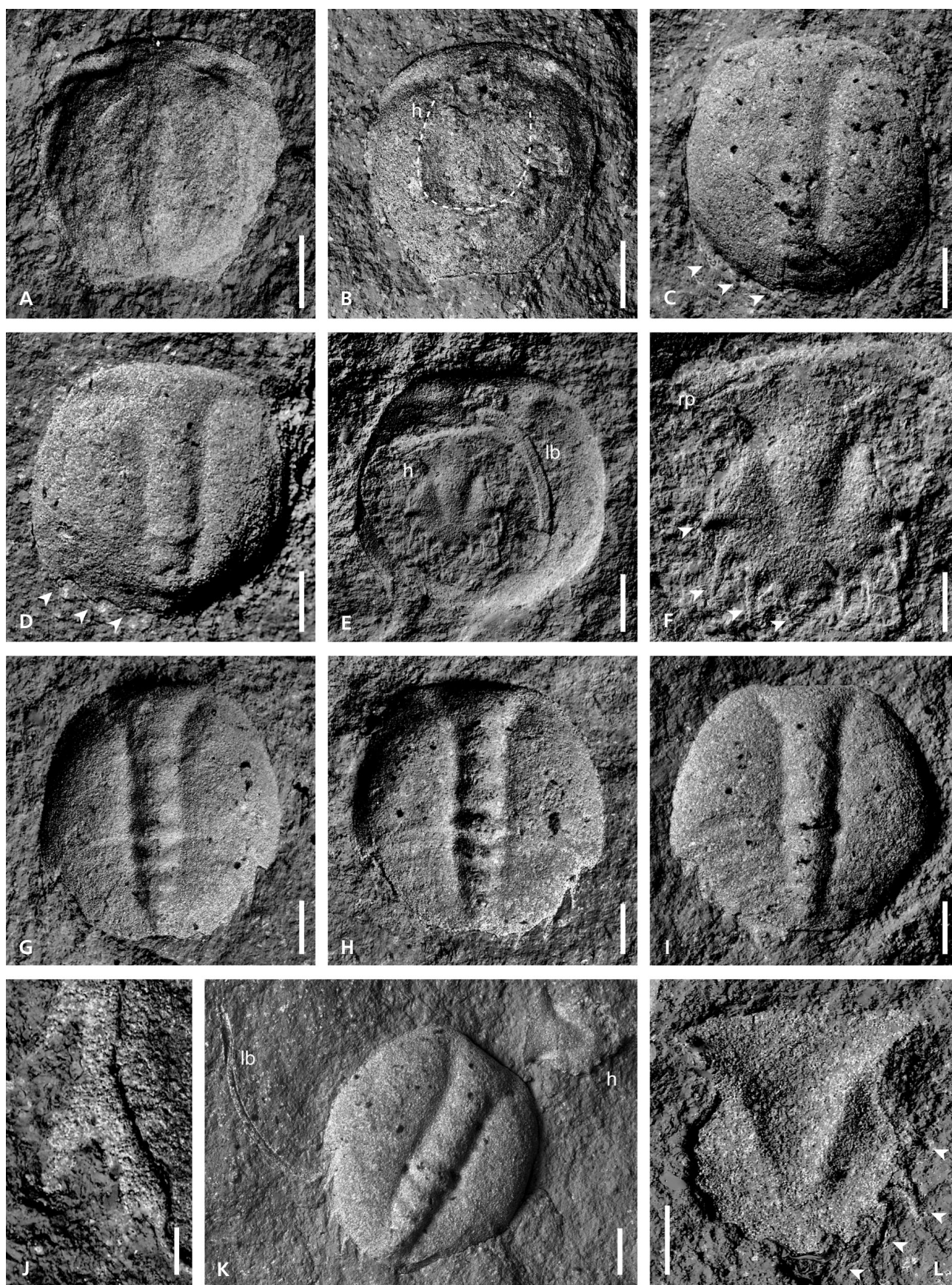


Table 3. Dimensions and trunk segment numbers of protaspid and early meraspid stages of *Ptychopariida* sp. B.

Institution	Number	Stage	Width (mm)	Length (mm)	Centroid size	Segment number
CGS	3475	P	0.88	0.78	–	?
CGS	MS9646	P	0.96	0.99	–	?
CGS	MS9647	P	0.96	1.05	–	?
NM	L11427	P	1.05	1	–	?

wide, gently vaulted; axial furrows weakly developed; anterior fossulae large; eye ridges slender; posterior exoskeletal margin slightly concave in dorsal view. Three pairs of short fixigenal spines present: anterior fixigenal spine situated in anterior third (exsag.) of exoskeletal length, pointed laterally; mid-fixigenal spine occurring at posterior third (exsag.) of exoskeletal length, pointed postero-laterally; posterior fixigenal spine projecting from the posterior end of the exoskeleton (exsag.), pointed posteriorly. Ventral surface of the exoskeleton poorly known; hypostome reaching *ca* two-thirds of exoskeletal length (sag.).

Protaspid stage 2 (Figs 4C–F, 8B): Exoskeleton 0.72–0.86 mm long and 0.76–0.92 mm wide, moderately vaulted; axial part widening anteriorly; S1–S3 weakly defined, SO distinct; fossulae placed laterally from LA; facial suture marginal; LO approximately in posterior third of exoskeleton; posterior fixigenal spine located opposite two-thirds of exoskeletal length (sag.), oriented posteriorly. Hypostome conterminant, central lobe parabolic, posterior lobe circular with nine horizontally directed marginal spines. Trunk broadly rhombic (tr.) with two pairs of posterior spines; axis consisting of three segments; pleural parts smooth. Doublure narrow.

Protaspid stage 3 (Figs 4G–L, 5A–C, 8C): Exoskeleton circular to subhexagonal in outline, 0.91–1.09 mm long and 0.9–1.1 mm wide; LA expanding (tr.) forward, reaching (sag.) anterior border of cranidium; fossulae minute; eye ridges narrow; facial suture opisthoparian running mostly marginally; posterior cranidial border furrow weakly developed; LO slightly wider than L1; posterior cephalic marginal furrow located at exoskeletal mid-length, running transversally from LO and distally slightly curved backward. Hypostome similar as in P2. Trunk semi-circular to subtrapezoidal with four pairs of marginal spines;

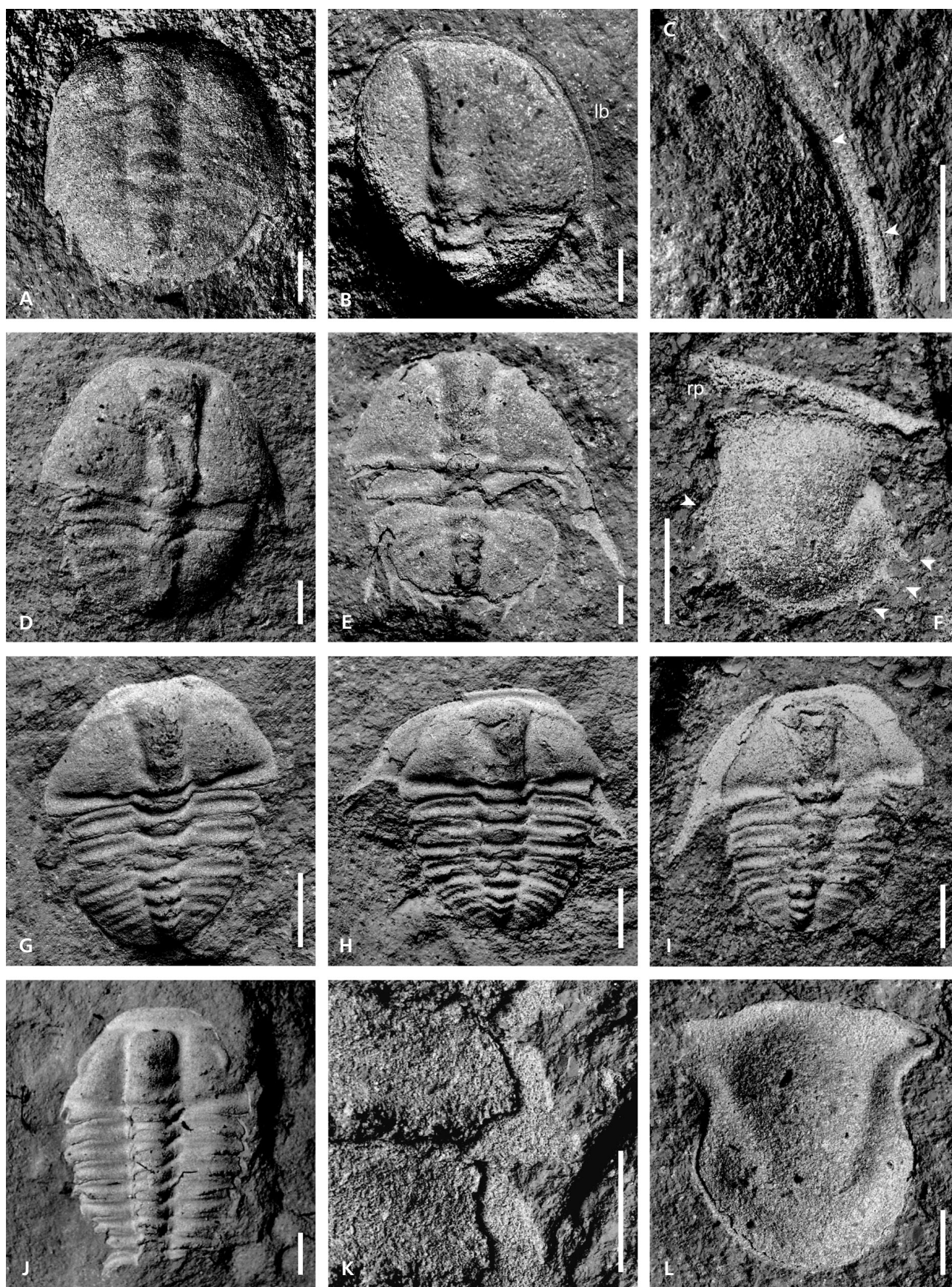
axis narrowing posteriorly, consisting of four segments; pleural furrows weakly developed. Doublure narrow with fine terrace ridges on librigena.

Postprotaspid development (Figs 5D–L, 6, 8D–F): The smallest cranidium is subtrapezoidal in outline, 0.66 mm long and 1.08 mm wide; later cranidia are proportionally wider. Throughout ontogeny the cephalon displays the following changes: glabella becomes relatively shorter; LA widens anteriorly until meraspid degree 6, narrows in the following degrees (7–8) so all glabellar lobes are approximately of the same width (tr.); in late meraspides and holaspides the glabella is forwardly tapering; lateral glabellar furrows become deeper and transverse; sagittal glabellar furrow appears in late meraspides; LO becomes proportionally wider; anterior border first appears as small projections anterolaterally from LA in meraspid degree 2; in subsequent stages the whole border increases in length (sag.) and the preglabellar furrow becomes distinct; in late ontogeny, preglabellar furrow deepens and forms a concave preglabellar field; palpebral lobes move backward slightly in early ontogeny and subsequently rapidly become arched laterally; anterior branch of facial suture extends, posterior branch curves inwards; in meraspid degree 2 distinct node appears close to proximal part of posterior cranidial border furrow and remains up to holaspid stages; tubercles appear in late ontogeny, firstly on glabella and genae and afterwards on whole cephalic border; narrow early meraspid librigenae become broad; genal spines proportionally shorten; cephalon becomes strongly vaulted and its anterior border convex in frontal view.

The hypostome undergoes the following changes during ontogeny: early meraspid hypostome is conterminant, bears marginal spines which subsequently disappear; later meraspid and holaspid hypostomes lack marginal spines; the separation of hypostome from rostral plate probably appears during the middle meraspid period; in later ontogeny the anterior hypostomal wings slightly extend transversely.

Thoracic segments of early meraspid stages show moderately vaulted axial part; pleural parts are almost flat, with small distal pleural spine; pleural furrows are distinct; in later stages the pleural parts become more vaulted; the pleural spines shorten in the late meraspides and they are truncated in holaspid period; the number of segments increases from one to seventeen.

Figure 5. *Sao hirsuta* Barrande, 1846. Buchava Formation, Skryje-Týřovice Basin. • A – NM L3732, protaspid stage 3. • B, C – CGS MŠ567, protaspid stage 3; B – showing librigena (lb); C – detail of librigenal doublure with fine terrace ridges (arrows). • D – CGS MŠ573, meraspid degree 1–4. • E – CGS MŠ574, meraspid degree 1–5. • F – CGS 350, hypostome probably of meraspid degree 1 with rostral plate (rp) and marginal spines (arrows). • G – CGS MŠ578, meraspid degree 2. • H – CGS MŠ581, meraspid degree 4. • I – MBHR 89976, meraspid degree 4. • J, K – CGS MŠ588, middle meraspid stage; J – general view; K – detail of distal parts of thoracic pleurae showing doublure. • L – CGS MŠ600, hypostome of middle meraspid stage. Scale bars represent 0.2 mm in A–F, K, L; 0.5 mm in G–J.



The pygidium shape changes from semicircular in early meraspides to broadly subhexagonal (tr.) in holaspid; the number of segments is four in meraspid degree 1 and subsequently increases to five. In early meraspid ontogeny, five pygidial segments generally remain, while the number of segments is usually four in second the half of meraspid ontogeny; starting with meraspid degree 15, the number of segments in meraspid pygidium gradually decreases to one segment plus a terminal piece in holaspid pygidium.

Remarks on ontogeny. – The protaspid period of *S. hirsuta* is composed of three morphologically distinct stages (Fig. 3A). A similar three-stage protaspid period has been described in other species within the suborder Ptychopariina, such as in the menomoniid *Bolaspidella housensis* (Walcott, 1886) and *Alataspis sesongensis* Park & Choi, 2011 (see Lee & Chatterton 2005, fig. 4; Park & Choi 2011, fig. 8A). The ptychopariid *Spencella?* sp. also shows three comparable protaspid stages (Chatterton & Speyer 1997, fig. 170/1–9). However, some other trilobites such as calymenids (Chatterton *et al.* 1990) and proetids (Chatterton 1994) also have a three-stage protaspid period, so this character is not distinctive for Ptychopariina.

Šnajdr (1958) illustrated several specimens of *S. hirsuta* that he regarded as belonging to meraspid degree 0. We reinterpret them as protaspid stage 3, since the presence of an articulation between the protocranidium and the trunk could not be demonstrated in any of them, even when using SEM (*cf.* Figs 4G–I, K, 5A, B). Accordingly, we hypothesize that the ontogeny of *S. hirsuta* did not include a meraspid degree 0 (Fig. 3B). This is a unique feature, although in some other trilobites with well-known ontogeny, the meraspid degree 0 still remains undiscovered. It could not be excluded that this feature was not so exceptional (for instance the ontogeny of *Triarthrus eatoni* in Hughes *et al.* 2006). However, it has been shown that more than one articulation apparently became operational in between two instars in some trilobites, resulting in the release of two segments in the thorax (*e.g.* Chatterton 1971). If something similar happened at the protaspis/meraspis transition in *S. hirsuta*, this could explain the absence of meraspid degree 0 specimens in our sample. This hypothesis is supported by the AGI, AGR, IDC and Dyar's index values (Table 4), which are comparable with those observed in other trilobites (*e.g.* Chatterton *et al.* 1990, Hunt & Chapman 2001, Fusco *et al.* 2011). Moreover, the Dyar's index values are similar between successive instars, from P1 to M1-5, suggesting that no growth stages are missing. The ontogeny of *S. hirsuta* is also remarkable in having two meraspid degree 1 stages, having four and five segments respectively in the meraspid pygidium. Comparable multiple-stage meraspid degrees are known in other trilobites (Hughes *et al.* 2006).

Genus uncertain

Ptychopariida sp. A

Figures 7A–K, 8H–J

Remarks. – Protaspides of this species were assigned to *S. hirsuta* by Barrande (1852, pl. 7, fig. 1d, e), Růžička (1943, pl. 4, figs 7–10, 12, pl. 5, fig. 5), Whittington (1957, pl. 116, figs 14, 15, 18) and Šnajdr (1958, pl. 43, figs 1–6, 10–12). However, the specimens differ from protaspides of *S. hirsuta* in having larger palpebral lobes, and in the morphology of the trunk including the absence of marginal spines. In addition, the individual protaspid stages of *Ptychopariida* sp. A are comparatively smaller than the corresponding stages of *S. hirsuta*; stages 1 and 2 of *S. hirsuta* are approximately the same size as stages 2 and 3 respectively of *Ptychopariida* sp. A. Several early meraspides assigned to *S. hirsuta* by previous authors (Růžička 1943, pl. 4, fig. 16; Whittington 1957, pl. 116, figs 20, 21; Šnajdr 1958, pl. 43, figs 24, 34) may also belong to *Ptychopariida* sp. A, as suggested by their large palpebral lobes and their modest pleural spines.

Ontogeny. – Three protaspid stages can be recognized on the basis of exoskeletal morphology, but compared with *S. hirsuta* they are not as clearly differentiated by size (Fig. 3D).

Protaspid stage 1 (Figs 7B, C, 8H): Exoskeleton circular in outline, 0.5–0.61 mm long and 0.62–0.76 mm wide, slightly vaulted; axial part widening anteriorly, delimited by well-developed furrows; fossulae large; distinct palpebral lobes reaching exoskeletal mid-length (exsag.), posterior margin concave in dorsal view. Anterior fixigonal spine located behind the palpebral lobe; mid-fixigonal spine situated in posterior quarter of the exoskeleton; posterior fixigonal spine relatively long and located at the posterior end of exoskeleton (exsag.).

Protaspid stage 2 (Figs 7D, E, 8I): Exoskeleton circular in outline, 0.61–0.69 mm in length and 0.64–0.76 mm in width, moderately vaulted; glabella widening anteriorly in anterior quarter; short pair of posterior fixigonal spines present; LO in posterior third of exoskeleton; posterior cephalic marginal furrow weakly defined, running transversally from LO and then suddenly curving backward. Trunk bearing two axial rings; pleural parts effaced.

Protaspid stage 3 (Figs 7F–H, 8J): Exoskeleton circular to subtrapezoidal in outline, 0.75–0.9 mm long and 0.66–0.86 mm wide; anterior part of glabella widening anteriorly; palpebral lobes large; facial suture opisthoparian; librigena narrow, curved, with fine terrace ridges on the doublure; LO approximately in posterior third of exoskeleton; posterior

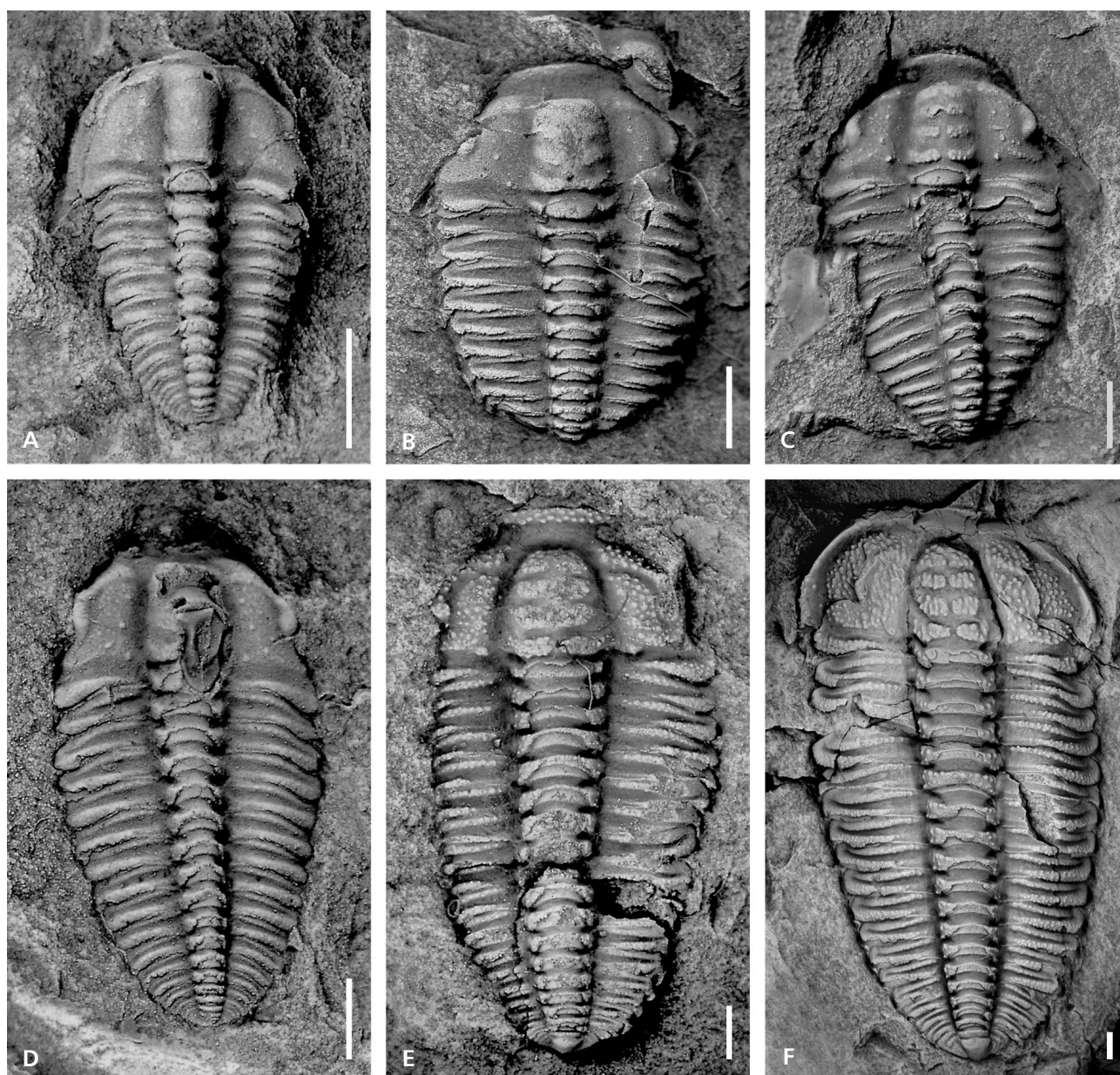


Figure 6. *Sao hirsuta* Barrande, 1846. Buchava Formation, Skryje-Týřovice Basin. • A – NM L12517, meraspid degree 8. • B – NM L12521, late meraspid stage. • C – NM L12524, meraspid degree 14. • D – NM L12525, lectotype, meraspid degree 14. • E – NM L12530, early holaspid stage. • F – NM L12537, late holaspid stage. Scale bars represent 1 mm.

cephalic marginal furrow distinct, deflected posteriorly. Trunk with three segments; posterior margin without spines.

Meraspid degrees 0–2 (Figs 7I–K): Cranidia of degrees 0–2 subrectangular in outline, 0.6–1.0 mm long and 1.2–1.51 mm wide; glabella slightly widening anteriorly; glabellar furrows moderately impressed; short (sag.) anterior border developed; palpebral lobes large, reaching backwards to approximately level with glabellar midlength (sag.); posterior cranidial border furrows slightly widening distally; free cheeks narrow with short posteriorly oriented

genal spine; doublure narrow. Thorax moderately vaulted (tr.); pleurae ending distally in small spines; number of thoracic segments increasing from zero to two. Meraspid pygidium semicircular; axis composed of six segments; pleural furrows weak; pleural spines modest.

Remarks on ontogeny. – One very small protaspis, indicated by a question mark in Fig. 3D, may represent an additional stage. It is rather similar in morphology to specimens that we have assigned to protaspis stage 1 except that the posterior fixigenal spines are slightly longer (Fig. 7A).

Table 4. Average values of length (*L*), width (*W*) and centroid size (*CS*), and the results of growth formulas (see Material and methods for detailed information) of protaspid and early meraspid stages of *Sao hirsuta* Barrande, 1846.

Stage	<i>L</i> (mm)	<i>W</i> (mm)	<i>CS</i>	<i>Di</i> (l)	<i>Di</i> (w)	<i>Di</i> (cs)	<i>IDC</i> (l)	<i>IDC</i> (w)
P1	0.66	0.72	0.55	–	–	–	–	–
P2	0.80	0.83	0.66	1.21	1.16	1.20	0.97	0.99
P3	0.98	0.99	0.80	1.22	1.19	1.20	0.92	0.88
M1-4	1.17	1.12	–	1.19	1.13	–	0.91	0.90
M1-5	1.33	1.23	–	1.14	1.10	–	–	–
	AGI (l)	0.08	AGI (w)	0.06	AGR (l)	1.19	AGR (w)	1.14

Some small protaspides illustrated by Růžicka (1943, pl. 4, figs 7, 8, pl. 5, fig. 5) as *S. hirsuta* were considered by Whittington (1957, p. 940) possibly to belong to the taxon we designate Ptychopariida sp. B. However, we consider it more likely that they belong to the protaspid stage 1 of Ptychopariida sp. A, because they share a large palpebral lobe with stages 2 and 3 of that taxon. Moreover, stage 1 protaspides of Ptychopariida sp. A are more common in the Buchava Formation than protaspides of Ptychopariida sp. B, as also observed by Šnajdr (1958).

These early ontogenetic stages cannot be assigned with confidence to any of the other trilobite taxa that occur with *S. hirsuta* in the *Paradoxides* (*Eccaparadoxides*) *pusillus* Zone in the Skryje-Týřovice Basin. However, considering their comparatively high abundance and their characteristically distinct palpebral lobes, they probably belong to one of the normal-eyed taxa common at the Týřovice – Pod hrůškou locality (e.g. *Agraulos*, *Skreiaspis*; cf. Fatka 2004, table 1).

Ptychopariida sp. B

Figures 7L, 8G

Remarks. – This protaspid stage of uncertain affinity was briefly described and illustrated by Růžicka (1943, text-figs on pp. 14, 31) as his so-called “Barrande’s larva”. Šnajdr (1958) listed additional material but did not provide any new observations.

Ontogeny. – Protaspides of Ptychopariida sp. B are represented by only four specimens, all of similar shape and size (Fig. 3E).

Protaspid stage (Figs 7L, 8G): Protaspides circular in outline, 0.78–1.05 mm long and 0.88–1.06 mm wide,

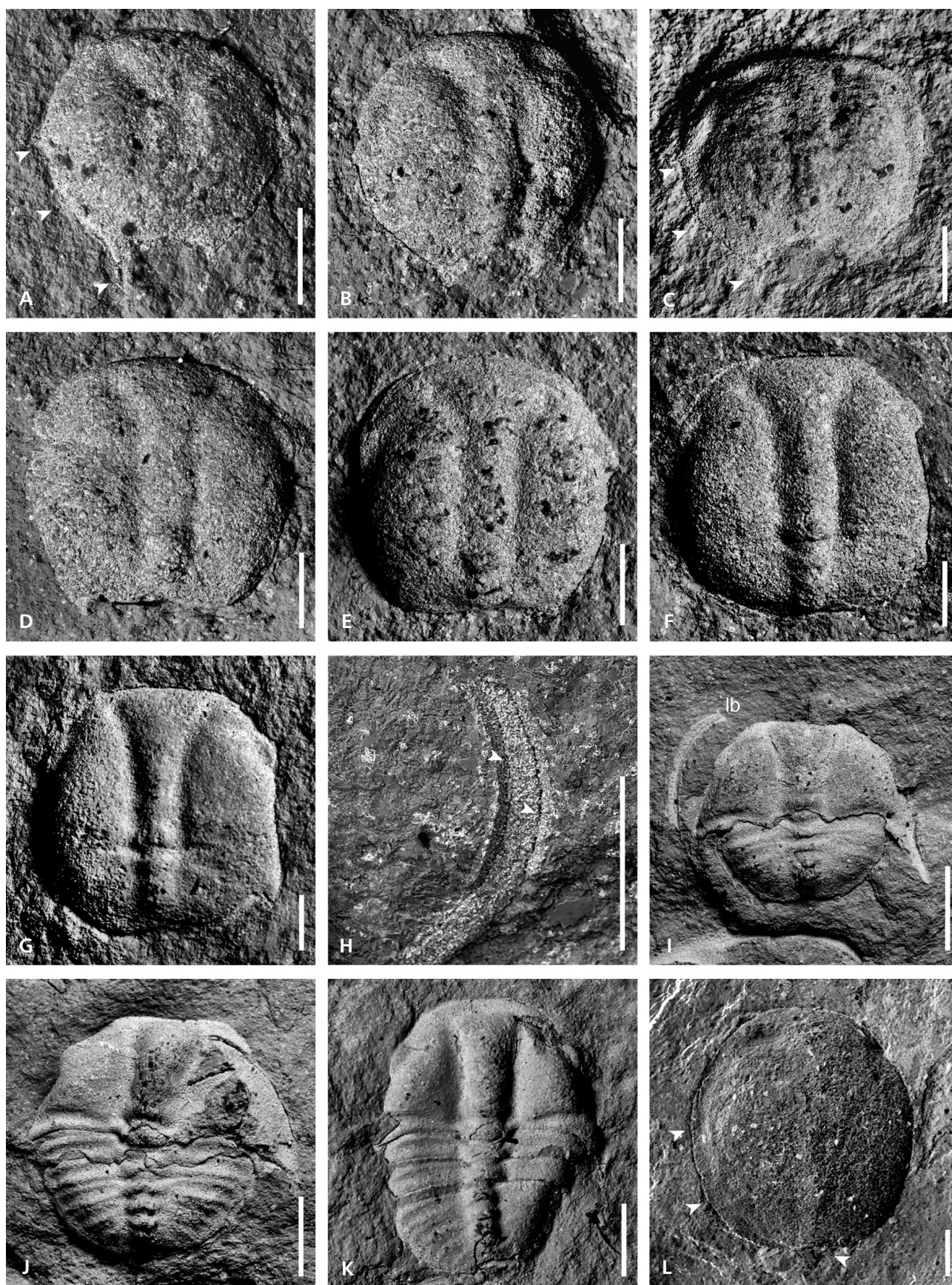
moderately vaulted; axis weakly defined; fossulae large; eye ridge narrow; posterior exoskeletal margin moderately convex. Diminutive anterior fixigenal spine located opposite exoskeletal mid-length; short mid-fixigenal spine opposite posterior quarter (sag.) of exoskeleton; slightly larger postero-ventrally oriented fixigenal spine projecting from the posterior end of exoskeleton.

Remarks on ontogeny. – The exact affinities of these protaspides are uncertain. Only members of the Order Ptychopariida or the Superfamily Paradoxidoidea are known from the Skryje-Týřovice Basin. We assign the present specimens to the Ptychopariida because protaspides of the Paradoxidoidea are quite different in morphology (cf. Šnajdr 1958, figs 20, 23; Chatterton & Speyer 1997, fig. 168).

Mode of life of protaspides and possible implication for palaeobiogeography

Several workers have focused on trilobite life history strategies during ontogeny (Speyer & Chatterton 1989; Chatterton & Speyer 1989, 1997; Chatterton *et al.* 1990; Leroosey-Aubril 2006; Crônier 2007, *etc.*). Speyer & Chatterton (1989) established a dichotomy in the protaspid body plan – the adult-like and nonadult-like plans. Adult-like protaspides are usually disk-shaped, with a more or less planar ventral surface, a comparatively small hypostome, and an intumed doublure commonly bearing terrace ridges. Nonadult-like protaspides are globular, with an enrolled doublure and a hypostome commonly with long spines directed obliquely downwards. Based on these features, Speyer & Chatterton (1989) suggested a benthic life style for the adult-like protaspides and a planktic life style for the nonadult-like protaspides.

Figure 7. All specimens from Buchava Formation, Skryje-Týřovice Basin. • A–K – Ptychopariida sp. A. • A – CGS MŠ559, smallest specimen showing fixigenal spines (arrows). • B – CGS MŠ560, protaspid stage 1. • C – NM L19008, protaspid stage 1 with fixigenal spines (arrows). • D – CGS MŠ561, protaspid stage 2. • E – CGS MŠ562, protaspid stage 2. • F – CGS MŠ565, protaspid stage 3. • G – CGS MŠ572, protaspid stage 3. • H – NM L3549, librigenal doublure with fine terrace ridges (arrows) of protaspid stage 3. • I – CGS MŠ577, meraspid degree 0 with librigena (lb). • J – CGS MŠ576, meraspid degree 1. • K – CGS MŠ577, meraspid degree 2. • L – Ptychopariida sp. B, CGS MŠ9647, protaspid stage showing fixigenal spines (arrows). Scale bars represent 0.2 mm in A–H, L; 0.5 mm in I–K.



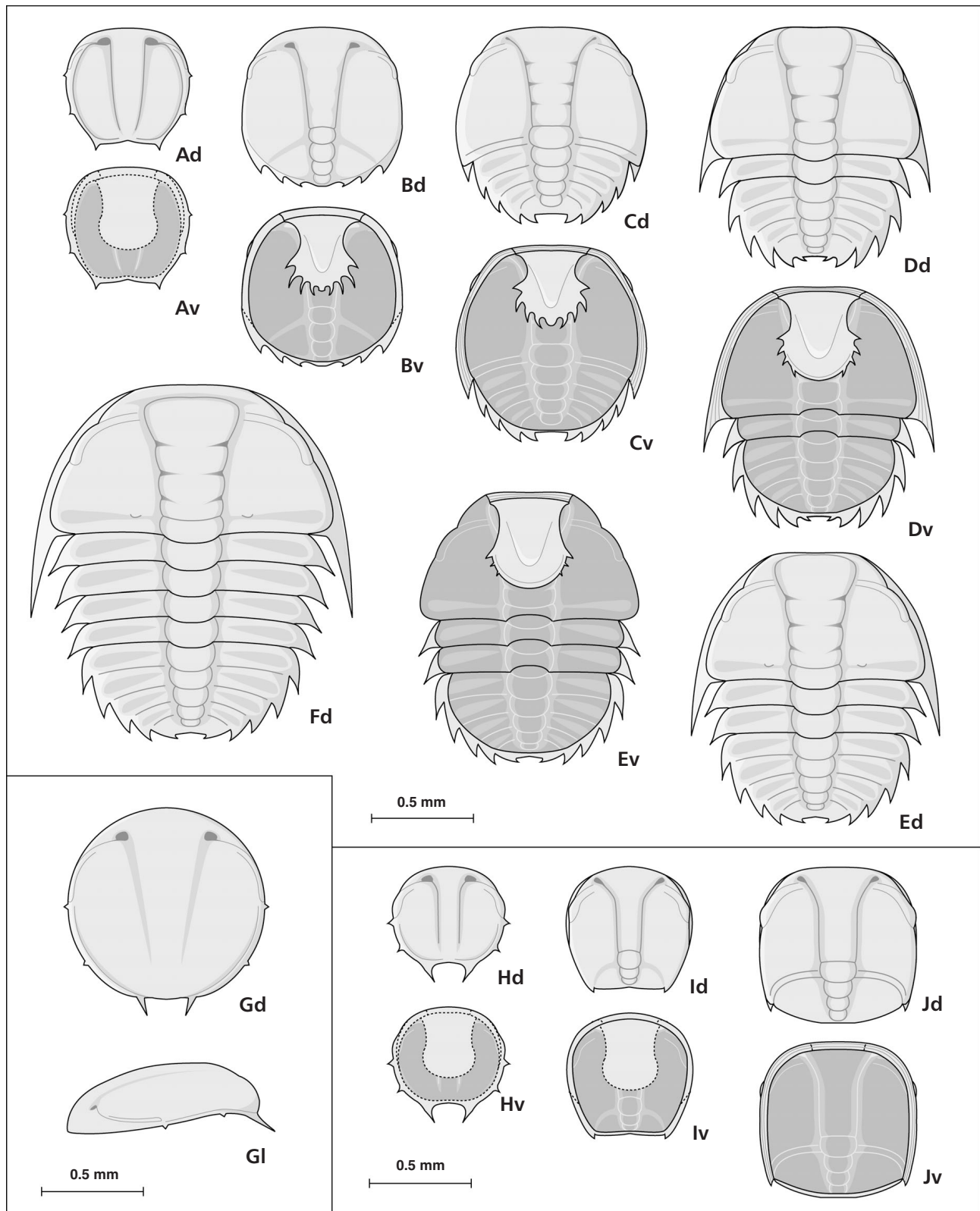


Figure 8. Reconstruction of the exoskeleton of early ontogenetic stages of *Sao hirsuta* Barrande, 1846 (A–F), *Ptychopariida* sp. B (G) and *Ptychopariida* sp. A (H–J), in dorsal (d), ventral (v) or lateral (l) views. • A – protaspis stage 1. • B – protaspis stage 2. • C – protaspis stage 3. • D – meraspid degree 1–5. • E – meraspid degree 2–5. • F – meraspid degree 4–5. • G – protaspis stage. • H – protaspis stage 1. • I – protaspis stage 2. • J – protaspis stage 3. Inferred features are shown by stippled line.

Protaspid stages 2 and 3 of *S. hirsuta* and Ptychopariida sp. A have an adult-like morphology. They share the dorso-ventrally flattened exoskeleton, a comparatively small hypostome with horizontally oriented spines, a planar ventral surface and an inturned doublure. Moreover, protaspid stage 3 of both *S. hirsuta* and Ptychopariida sp. A bear fine terrace ridges on the ventral doublure surface (Figs 5C, 7H). All these characters suggest that these protaspid stages were probably benthic. In the protaspid stage 1 of both *S. hirsuta* and Ptychopariida sp. A the doublure between the posterior spines seems to be inturned and, despite diagenetic flattening, it is also obvious that the exoskeleton was very slightly arched and had a planar ventral surface. Chatterton & Speyer (1997) considered that protaspides of this shape were benthic rather than planktic, although several earlier workers supposed that they had a planktic lifestyle. We therefore consider that *S. hirsuta* and Ptychopariida sp. A had a life-history strategy corresponding to type IIIa of Chatterton & Speyer (1997), characterized by an entirely benthic protaspid period. This could explain why the palaeogeographic distribution of *S. hirsuta* is restricted to the western margin of Gondwana. Other members of the Solenopleuropsinae are also restricted to West Gondwana (Álvaro & Vizcaíno 1997), possibly due to the similarly limited dispersal capabilities of their larval stages.

Protaspides of Ptychopariida sp. B have morphology typical of a comparatively early protaspid stage (three pairs of fixigenal spines, trunk portion not distinguishable) but are very large for such an early stage (Fig. 3E). There are two possible explanations for their large size, as proposed also by Lerosey-Aubril (2006) for proetoid protaspides: (1) a taphonomic explanation – there were smaller protaspid stages but they were uncalcified and/or they are not preserved; or (2) a lecitotrophic explanation – lecitotrophic larvae are usually much larger than planktotrophic ones (e.g. Thorson 1950), so the protaspides of Ptychopariida sp. B may have been nourished with a large yolk. The lecitotrophic explanation seems more probable because of the early protaspid morphology of the specimens.

Conclusions

The detailed and quantitative description of the early ontogeny of *Sao hirsuta*, Ptychopariida sp. A and Ptychopariida sp. B allows the following conclusions to be drawn:

1. *S. hirsuta* had three protaspid instars. The adult-like morphology of the protaspides indicates they had a benthic mode of life, explaining the very restricted palaeogeographic distribution of the species.
2. The apparent absence of the meraspid degree 0 in *S. hirsuta* is unique in trilobite ontogeny. Instead of the meraspid degree 0 there are two stages in degree 1, with

four and five segments respectively in the meraspid pygidium.

3. Ptychopariida sp. A, previously considered part of the ontogenetic sequence of *S. hirsuta*, is classified as a separate taxon. It has at least three protaspid stages characterized by large palpebral lobes.

4. The protaspis of Ptychopariida sp. B has the morphology of an early protaspid stage but is of unusually large size, suggesting that the larvae may have been lecitotrophic.

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