

# Hypostomes in Cambrian agnostids from the Barrandian area (Czech Republic)

OLDŘICH FATKA & VLADISLAV KOZÁK†



Remains of agnostid hypostomes are rare and have only been reported in about fifty specimens assigned to ten Cambrian species. A large collection of several thousand specimens of a Cambrian skeletal fauna from the Barrandian area includes articulated agnostids with *in situ* preserved hypostomes in two species from the Příbram–Jince Basin and in one species from the Skryje–Týřovice Basin. Unequivocal remains of hypostomes are described in *Condylopyge rex* (Barrande, 1846), *Peronopsis integra* (Beyrich, 1845) and *Onymagnostus hybridus* (Brögger, 1878). The material provides the first information on the hypostomal morphology in the superfamily Condylpygoidea Raymond, 1913 and adds new data in two other Cambrian agnostid genera. The chemical composition and placement of agnostid hypostomes are briefly discussed. • Key words: Agnostida, hypostomes, middle Cambrian, Jince Formation, Buchava Formation, Barrandian area, Czech Republic.

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Hypostomes in agnostids are found only very rarely. Up to now, these ventral structures have been documented worldwide only in seven Cambrian genera: *Acadagnostus* Kobayashi, 1939; *Aagnostus* Brongniart, 1822 in Brongniart & Desmarest (1822); *Onymagnostus* Öpik, 1979; *Peronopsis* Hawle & Corda, 1847 (including *Redeaagnostus* Naimark, 2012); *Proagnostus* Butts, 1926; *Ptychagnostus* Jaekel, 1909; and *Triplagnostus* Howell, 1935. The majority of the described agnostid hypostomes is preserved due to early diagenetic silicification and/or phosphatisation in limestones and limestone nodules (Robison 1972, Müller & Walossek 1987). So far, only two agnostids with the hypostome preserved in siliciclastic rocks have been reported by Rushton (1979) and Fatka *et al.* (2009b). Hypostomes are still entirely unknown in Ordovician agnostids (Tab. 1).

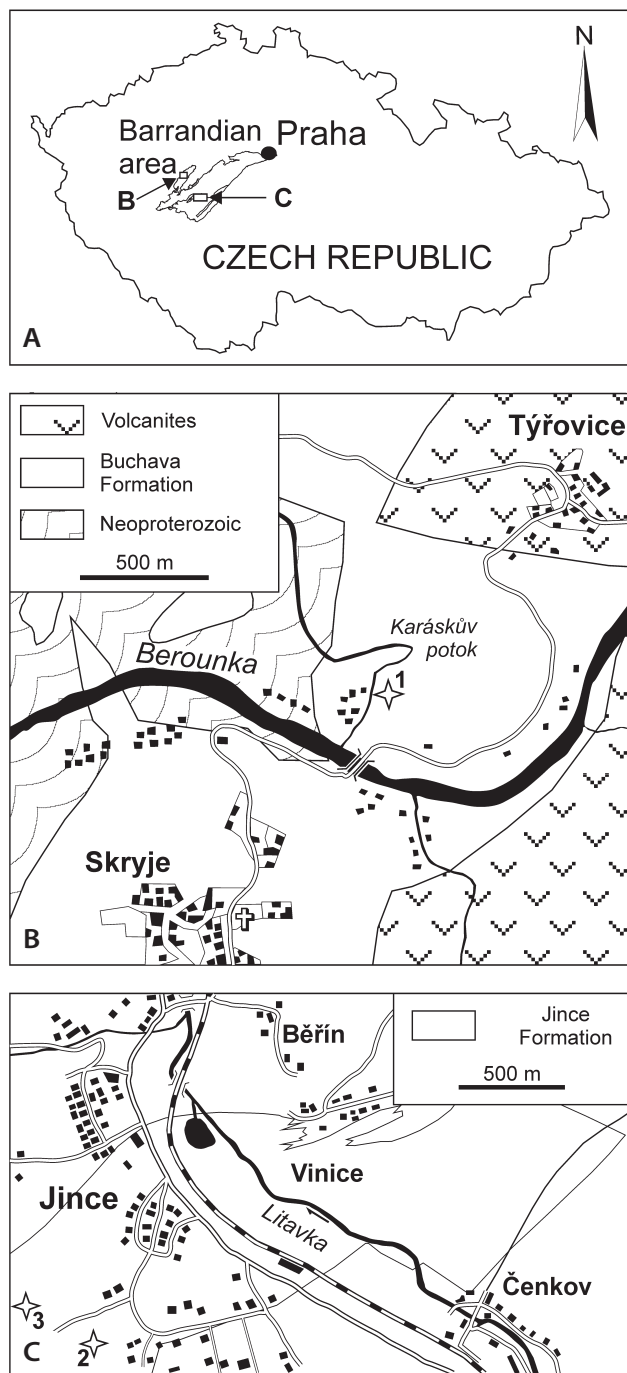
The aim of this paper is to describe four exceptionally preserved agnostid specimens belonging to the genera *Condylopyge* Hawle & Corda, 1847, *Peronopsis* and *Onymagnostus*, all of them showing remains of the hypostome. The material has been recently collected in middle Cambrian shales of the Barrandian area (Fig. 1).

## Preservation of agnostid hypostomes

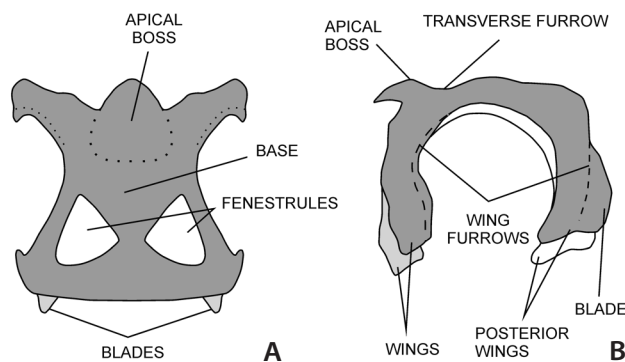
Aagnostid hypostomes can be preserved in three diverse ways: (i) as secondarily silicified or (ii) as secondarily

phosphatised skeletal elements occurring in limestone, and (iii) as *in situ* preserved natural moulds in fine siliciclastics.

*Preservation due to silicification.* – Silicified agnostid hypostomes were first identified by Robison (1972), who found them attached to the ventral surface of articulated exoskeletons in *Peronopsis* and *Ptychagnostus* from the Wheeler Shale (now Wheeler Formation) in the Drum Mountains, Utah, U.S.A. The remarkable morphology of the agnostid hypostome led Robison (1972, fig. 1) to introduce a specific terminology (Fig. 2), based on a comprehensive study of hypostomes in ten specimens of *Peronopsis fallax ferox* (Tullberg, 1880) (see Robison 1972, pp. 242, 243, fig. 2). The classification of *P. fallax ferox* has been discussed by Robison (1982), Axheimer & Ahlberg (2003), Naimark (2012) and Weidner & Nielsen (2014). Ritterbush (1983) discussed and figured ventral views of cephalae associated with hypostomes also in *Peronopsis interstricta* (White, 1874), a species recently assigned to *Euagnostus* Whitehouse, 1936 (see Weidner & Nielsen 2014, p. 55). A single specimen of *Ptychagnostus* n. sp.? with a poorly preserved hypostome was figured by Robison (1972, fig. 3c); subsequently, Robison (1982, p. 142) classified this specimen as *Ptychagnostus gibbus* (Linnarsson, 1869). Robison (1982, p. 142, pl. 4, fig. 5) also figured the ventral surface of a small holaspide specimen of *Ptychagnostus seminula* (Whitehouse, 1939);



**Figure 1.** Geological setting. • A – map of the Czech Republic showing the distribution of Cambrian outcrop areas in the Příbram–Jince and Skryje–Týřovice basins. • B – simplified sketch map showing the location of fossil sites in the mid-Cambrian Buchava Formation in the north-eastern part of the Skryje–Týřovice Basin (geology modified from Mašek *et al.* 1997). • C – simplified sketch map showing the location of fossil sites in the mid-Cambrian Jince Formation in the northern part of the Příbram–Jince Basin (geology modified from Havlíček 1971). Legend: Buchava Formation, 1 – Karáskův potok valley near Týřovice; Jince Formation, 2 – Obalovna on the southern slope of the Vysrkov hill, east of Jince; 3 – excavation on the northern slope of the Vysrkov hill, east of Jince.



**Figure 2.** Morphology of agnostid hypostome in ventral (A) and lateral view (B) (after Robison 1972).

this species has subsequently been assigned to the genus *Onymagnostus* (e.g. Robison 1984).

**Preservation due to phosphatisation.** – The most comprehensive study on the agnostid ventral morphology, including a detailed description of the morphology and position of the hypostome, was published by Müller & Walossek (1987). Several tens of phosphatised specimens of the widely distributed species *Agnostus pisiformis* (Wahlenberg, 1818) were extracted from Guzhangian nodular limestones in the Alum Shale Formation of southern Sweden (see Nielsen & Schovsbo 2007). However, this material comprises only small specimens representing exclusively early developmental stages; the soft ventral cuticle of later stages other than the first holaspide stage has not been recorded (Müller & Walossek 1987, p. 4).

A partly phosphatised ventral surface covered with a coarse phosphatic material roughly indicating the location of the hypostome and appendages in a cephalic shield of *Proagnostus bulbosus* Butts, 1926 was figured by Babcock *et al.* (2005, fig. 1c) and Maas *et al.* (2006, fig. 4d). Both specimens were collected from the stratotype section (the Paibi section) marking the base of the Paibian Stage and Furongian Series in the Huaqiao Formation, Hunan Province, China.

Robison (1988, p. 40, fig. 9) described a morphologically distinctive hypostome in *Oidagnostus trispinifer* Westergård, 1946 from a limestone and lime wackestone of the Holm Dal Formation of North Greenland. However, the mode of preservation was not discussed.

**Preservation in clastic sediments.** – Rushton (1979, fig. 5e) figured a damaged internal mould of the exoskeleton of *Ptychagnostus* (*P.*) *triangulatus* (Illing, 1916) from the Abbey Shale Formation of central England; this specimen shows the external mould of an incomplete hypostome. The species was later transferred to the genus *Onymagnostus* (e.g. Robison 1984, p. 51).

Fatka *et al.* (2009b, p. 483, fig. 4) figured and briefly discussed remnants of a hypostome preserved below the posteroglabella in an articulated specimen of *Peronopsis integra* (Beyrich, 1845). This specimen is re-figured and described herein (Fig. 4D).

Moysiuk & Caron (2019a, b) studied more than fifty specimens of *Peronopsis columbiensis* (Rasetti, 1951) and *Ptychagnostus praecurrens* (Westergård, 1936) from the Burgess Shale, some of them showing remains of the hypostome. Moysiuk & Caron (2019a) discussed the taphonomy of these specimens and stressed that rapid burial at various angles and partial decay produced subtle asymmetries in many specimens. A comparable situation is seen in middle Cambrian siliciclastic rocks in the Barrandian area (e.g. Šnajdr 1958, pl. 2, fig. 2; Fatka *et al.* 2015, fig. 2d). Such taphonomic processes could produce a slight lateral shifting of the hypostome relative to the dorsal exoskeleton. However, the displacement appears to be minimal and does not significantly impact on the original placement of the hypostome.

## Agnostids in the Barrandian area

In the Barrandian area, Cambrian agnostids have been known for more than 170 years (see Beyrich 1845, Barrande 1846, Hawle & Corda 1847). Since these pioneer works, hundreds of articulated agnostid exoskeletons and disarticulated sclerites have been collected from numerous outcrops (e.g. Šnajdr 1958, Pek 1977, Fatka *et al.* 2004, Budil *et al.* 2011).

Such a large material has provided important information on the mode of life of agnostids as well as their ontogeny. Middle and Late Ordovician agnostids arranged in a natural cluster or aligned in a row were repeatedly described. Such natural clusters of articulated and disarticulated agnostid exoskeletons were suggested to represent agglutinated polychaete worm-tubes by Prantl (1948), whereas articulated agnostid exoskeletons arranged in a row were interpreted as specimens that have been attached to an algal strand (Příbyl & Vaněk 1976, Pek 1977). Slavičková & Kraft (2001) discussed several enrolled Middle Ordovician agnostids attached to an enigmatic fossil, most probably representing a branched axis of a putative octocoral. Articulated agnostids entombed inside the exoskeleton of various invertebrates have been interpreted as examples of a cryptic behaviour associated with feeding and moulting (Fatka *et al.* 2009b, Fatka & Szabad 2011, Fatka & Kozák 2014). Morphological modifications in the only known malformed agnostid described by Fatka *et al.* (2009a) were explained as a failed attack by a durophagous predator. Mantis shrimp-like animals like *Yohoia*, *Jianfengia* or *Fortiforceps* may represent potential predators (compare

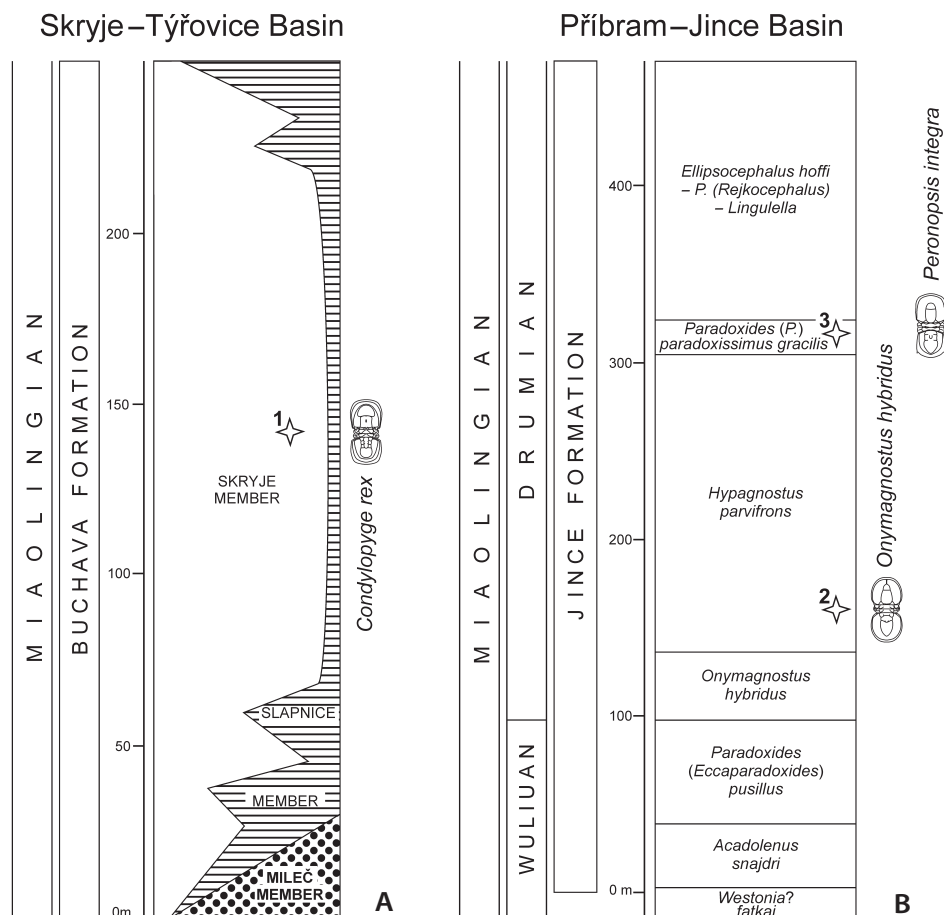
Haug *et al.* 2012). The ontogeny of agnostids from the Barrandian area has been studied by Barrande (1852), Šnajdr (1958) and Laibl & Fatka (2017).

In the Barrandian area, agnostids are preserved as external and internal moulds in siliciclastic rocks (e.g. Šnajdr 1958, Pek 1977, Fatka *et al.* 2015). Up to now, no exceptionally preserved agnostids showing remains of soft or poorly mineralized tissue have been documented, with the exception of one specimen of *Peronopsis integra* with a hypostome (Fatka *et al.* 2009b).

## Geological setting

The material described herein was collected at an outcrop with blue-green shales of the Buchava Formation (Skryje–Týřovice Basin), and at two fossil sites with greenish shales to fine greywackes of the Jince Formation (Příbram–Jince Basin) (see Figs 1, 3). At all outcrops, the host sediments of the examined agnostids consist of fine greywackes to mudstones containing well-preserved, often articulated agnostids, trilobites, echinoderms, bivalved arthropods, hyolithids and other skeletal faunas (Fatka *et al.* 2004, Geyer *et al.* 2008, Fatka & Szabad 2014). The high proportion of articulated specimens suggests minimal post-mortem transport of the assemblages.

*Karáskův potok valley near Týřovice (site 1 in Figs 1B, 3A).* – Natural outcrops on the eastern slope of the brook named Karáskův potok north of Skryje expose the lower half of the Buchava Formation (section 15 in Fatka *et al.* 2011). The geology of this valley was studied by numerous authors, including Jahn (1896), Prantl (1941), Šnajdr (1958) and Havlíček (1971). However, there is no detailed description of the Cambrian succession and its fossil content, with the exception of a brief remark by Jahn (1896, p. 697, fig. 4), who published a schematic section and listed the presence of the following taxa: *Lichenoides priscus* (Barrande) [= *Lichenoides vadosus* Parsley & Prokop]; *Trochocystites bohemicus* Barrande, *Orthis Romingeri* Barrande [= *Bohemiella romingeri*], *Agnostus integer* Beyrich (= *Peronopsis integra*), *Agnostus rex* Barrande [= *Condylopyge rex*], *Paradoxides spinosus* Boeck [= *Paradoxides (Hydrocephalus) carens* (Barrande)], *Conocoryphe sulzeri* (Schlothheim), *Conocoryphe (Ctenocephalus) coronata* (Barrande) [= *Ctenocephalus (C.) coronatus*], *Ptychoparia striata* (Emmrich) [= *Ptychoparia dubinka* Kordule], *Agraulos ceticephalus* (Barrande), *Agraulos spinosus* Pompeckj [= *Skreiaspis spinosus*] and *Sao hirsuta* Barrande. Recently, Mikuláš & Fatka (2017) assigned the enigmatic fossil *Medusites cf. radiatus* Linnars. of Pompeckj (1896) to the ichnogenus *Astropolichnus* Crimes & Anderson from the “Pod trním” locality in the Karáskův potok valley.



**Figure 3.** A, B – lithostratigraphic subdivision of Cambrian rocks in the Skryje–Týřovice Basin (modified after Fatka *et al.* 2011) and biostratigraphy of the Jince Formation in the Příbram–Jince Basin (after Fatka & Szabad 2014), with stratigraphic position of fossil sites at which the materials were collected. • A – Buchava Formation, 1 – Karáskův potok valley near Týřovice. • B – Jince Formation, 2 – Obalovna on the southern slope of the Vystrkov hill, east of Jince; 3 – excavation on the northern slope of the Vystrkov hill, east of Jince.

The specimen of *Condylopyge rex* (CGS CW19a, b; Fig. 4A, B herein) originates from outcrops at the eastern slope of the Karáskův potok valley.

*Obalovna on the eastern slope of the Vystrkov hill, east of Jince (site 2 in Figs 1C, 3B).* – The approximately 400 m thick succession is accessible at the eastern slope of the Vystrkov hill near Jince. It is one of the most complete and richly fossiliferous sections through the Jince Formation in the Litavka river valley. Numerous small outcrops and the contained fauna have been subjects of palaeontological and stratigraphical studies for more than 150 years. Fossils collected from these outcrops were described and discussed by Barrande (1852) and numerous other authors (see Šnajdr 1958, Fatka & Szabad 2014, summary in Chlupáč 1999). The stratigraphy was studied by Želízko (1897, 1911), Šuf (1926), later on also by Šnajdr (1958) and Havlíček (1971). Fatka & Kordule (1992) published a brief summary of fossils collected from nine small outcrops on the eastern slope of the Vystrkov hill.

The specimen of *Onymagnostus hybridus* (NML 46515; Fig. 4E herein) was collected from the *H. parvifrons* Zone at one of these outcrops.

*Excavation at the northern slope of the Vystrkov hill, south-east of Jince (site 3 in Figs 1C, 3B).* – Recently Fatka *et al.* (2014, pp. 148, 149) reviewed the history of research and the composition of the fossil fauna from this large exposure with greenish, fine-grained greywackes and shales of the *Paradoxides (P.) paradoxissimus gracilis* trilobite Biozone and the lower levels of the overlying *Ellipsocephalus hoffi*–*Lingulella*–*Paradoxides (Rejkocephalus)* Interval Zone.

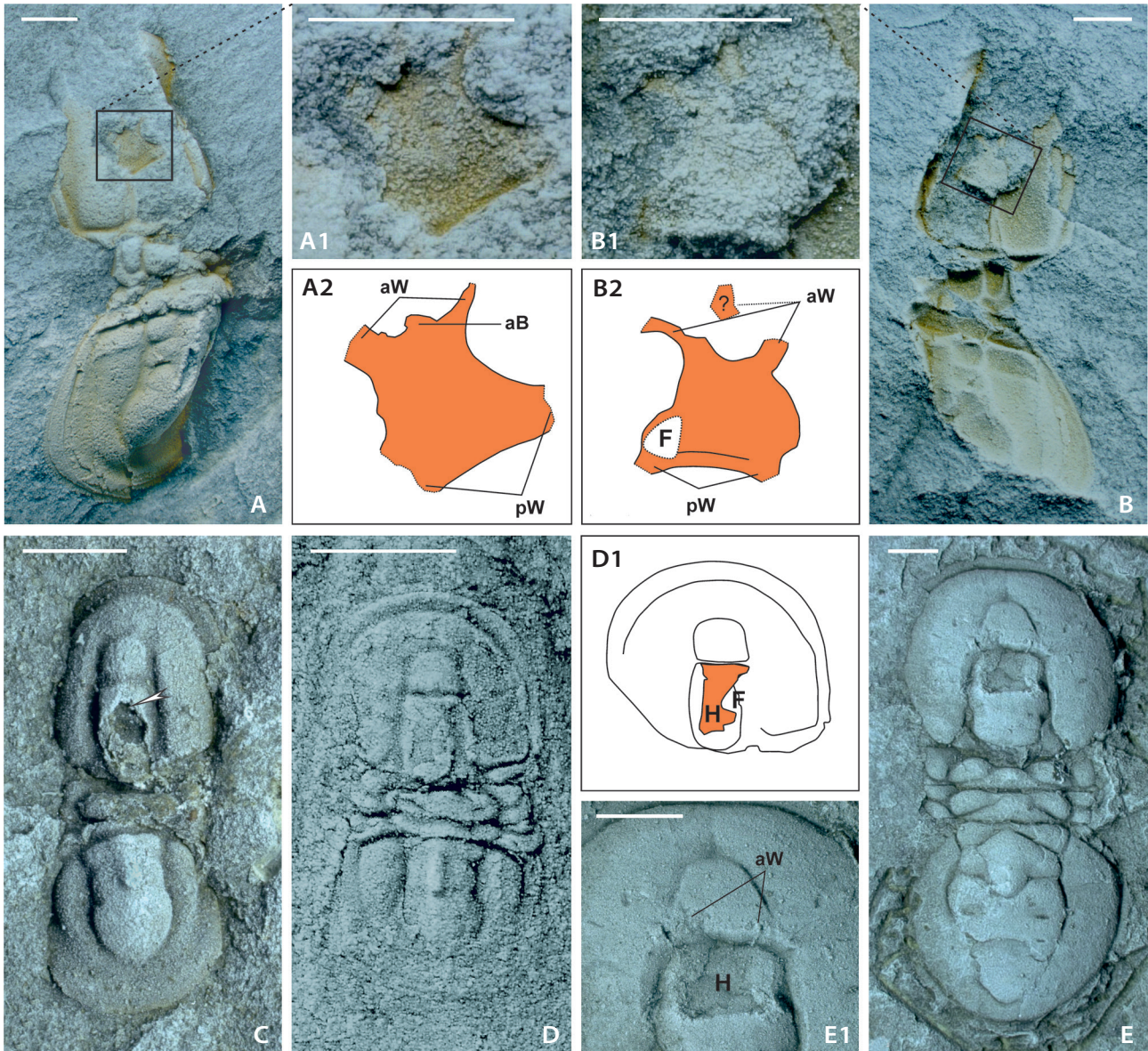
Both of the herein studied specimens of *Peronopsis integra* (Beyrich, 1845), numbered CGS CW24 (Fig. 4C) and VV001B (Fig. 4D), were collected from this outcrop.

## Material and methods

Internal moulds were coated with ammonium chloride and photographed using the digital microscope Keyence VHX-2000.

**Terminology.** – The morphological terms of Whittington (1997) are used. The terminology for the agnostid hypostome follows Robison (1972).





**Figure 4.** A, B – *Condylopyge rex* (Barrande, 1846) with hypostome. Karáskův potok valley near Týřovice, Buchava Formation, Skryje–Týřovice Basin, Barrandian area, Czech Republic; A – partially damaged internal mould CGS CW19a; A1 – detail of hypostome; B – partially damaged external mould, CGS CW19b; B1 – detail of hypostome. • C, D – *Peronopsis integra* (Beyrich, 1845) with hypostome, on the northern slope of the Vystrkov hill, east of Jince, *Paradoxides* (*P.*) *paradoxissimus gracilis* Zone, Jince Formation, Příbram–Jince Basin, Barrandian area, Czech Republic; C – internal mould of articulated exoskeleton, CGS CW24; D – internal mould of articulated exoskeleton, CGS VV001B. • E – *Onymagnostus hybridus* (Brøgger, 1878) internal mould with possible remains of the hypostome and well visible notulae in the pygidial axis. Obalovna on the northern slope of the Vystrkov hill, east of Jince, *Onymagnostus hybridus* Zone, Jince Formation, Příbram–Jince Basin, Barrandian area, Czech Republic, NML 46515; A2, B2, D1 – drawing of hypostome. Specimens CGS CW19a, CGS CW19b, CGS CW24 and VV001B housed in the Czech Geological Survey, Prague, specimen NML 46515 stored in the collection of the National Museum in Prague. All scale bars represent 1 mm. Specimens were whitened with ammonium chloride sublimate prior to photography. Abbreviations: aB – apical boss; aW – anterior wings; F – fenestrule; H – hypostome; pW – posterior wings.

**Repositories.** – Figured specimens are housed in collections of the Czech Geological Survey, Prague, Czech Republic (collection numbers CGS VV001B, CGS CW 19a, b, CGS CW24) and in the collections of the Palaeontological Department of the National Museum, Prague, Czech Republic (collection number NML 46515).

**Measurements.** – Measurements were made from highly enlarged digital images. The morphology and dimensions of the broken or covered exoskeletal parts were estimated in cases where the preservation of the mould made it possible (for example, the mirroring). All measurements were repeated two times in order to eliminate possible

errors. The following abbreviations have been used:  $E_L$  = length of exoskeleton;  $C_L$  = length of cephalic shield;  $C_W$  = width of cephalic shield;  $H$  = hypostome;  $P_L$  = length of pygidial shield;  $P_W$  = width of pygidial shield;  $PG_L$  = length of posteroglabella;  $PG_W$  = width of posteroglabella;  $aB$  = hypostomal apical boss;  $aW$  = hypostomal anterior wings;  $pW$  = hypostomal posterior wings.

## Studied material

### *Condylopyge rex* (Barrande, 1846)

Figure 4A, B

*Material and locality.* – Specimen ČGS CW19a, b; Karáskův potok valley near Týřovice (site 1 in Fig. 1B).

*Description.* – A complete, anteriorly partly damaged and slightly disarticulated exoskeleton of a holaspid. It is comparatively small and preserved as external and internal moulds in a hard, moderately weathered shale.

The cephalon is slightly displaced in relation to the well-articulated thoracic segments, which are connected to a complete pygidium. The glabella is broken away, thus revealing the underlying hypostome, which is nearly complete.

The base of the hypostome is 0.70 mm long and 0.56 mm wide; possible fenestrula is seen on the internal hypostome mould (F in Fig. 4B1, B2). Narrow anterolateral outgrowths are preserved on both sides of the anterior margin of the hypostome. These represent proximal parts of the hypostomal anterior wings ( $aW$  in Fig. 4A2, 4B2). The anterior margin is nearly straight with a small medial arch, suggesting the presence of an hypostomal apical boss in condylopygids ( $aB$  in Fig. 4A2). Wide but short postero-lateral widenings on both sides of the posterior margin of the hypostome represent proximal parts of posterior wings ( $pW$  in Figs 4A2, B2).

*Dimensions.* –  $E_L$  = 8.59 mm;  $C_L$  = 3.66 mm,  $C_W$  = 3.10 mm;  $P_L$  = 4.16 mm,  $P_W$  = 3.9 mm.

*Remarks.* – The hypostome shows the presence of an apical boss, anterior and posterior wings and a wide base and a possible fenestrula.

### *Peronopsis integra* (Beyrich, 1845)

Figure 4C

*Material and locality.* – Specimen ČGS CW24; excavation at the eastern slope of the Vystrkov hill, south-east of Jince (site 3 in Fig. 1C).

*Description.* – A tectonically slightly deformed internal

mould of an articulated middle-sized holaspid specimen preserved in a fine-grained greywacke.

The cephalon and the pygidium are slightly displaced in relation to the thorax. The central part of the posteroglabella is broken and a smooth surface is displayed below the collapsed exoskeleton (arrow in Fig. 4C).

*Dimensions.* –  $E_L$  = 4.27 mm;  $C_L$  = 2.00 mm,  $C_W$  = 1.73 mm;  $P_L$  = 1.85 mm,  $P_W$  = 1.71 mm.

*Remarks.* – The smooth surface seen below the collapsed part of the posteroglabella most probably represents a partially preserved hypostome. The hypostome is apparently situated under the posteroglabella.

### *Peronopsis integra* (Beyrich, 1845)

Figure 4D

*Material and locality.* – Specimen ČGS VV001B; excavation at the eastern slope of the Vystrkov hill, south-east of Jince (site 3 in Fig. 1C).

*Description.* – A complete, dorso-ventrally flattened and tectonically slightly deformed articulated exoskeleton of a middle-sized holaspid specimen entombed inside a hyolithid conch (see Fatka *et al.* 2009b).

The surface of both the external and internal moulds of the posteroglabella shows an incomplete hypostome displaced slightly to the left ( $H$  in Fig. 4D1); the right side of the posteroglabella is slightly broken. The visible part of the hypostome is about 0.57 mm long and less than 0.20 mm wide; the apical boss can not be distinguished. The large embayment seen at the right side of the hypostome most probably corresponds to the fenestrula (F in Fig. 4D1). The base of the hypostome shows a slightly curved outline, most probably because of an oblique placement of this skeletal part. Both the anterior and posterior wings of the hypostome are partly preserved on the surface of both moulds (Fig. 4D); dorsally directed parts of hypostomal anterior and posterior wings are most probably flattened and not visible.

*Dimensions.* –  $E_L$  = 2.76 mm;  $C_L$  = 1.33 mm,  $C_W$  = 1.51 mm;  $P_L$  = 1.1 mm,  $P_W$  = 1.35 mm.

*Remarks.* – The hypostome is apparently situated under posteroglabella.

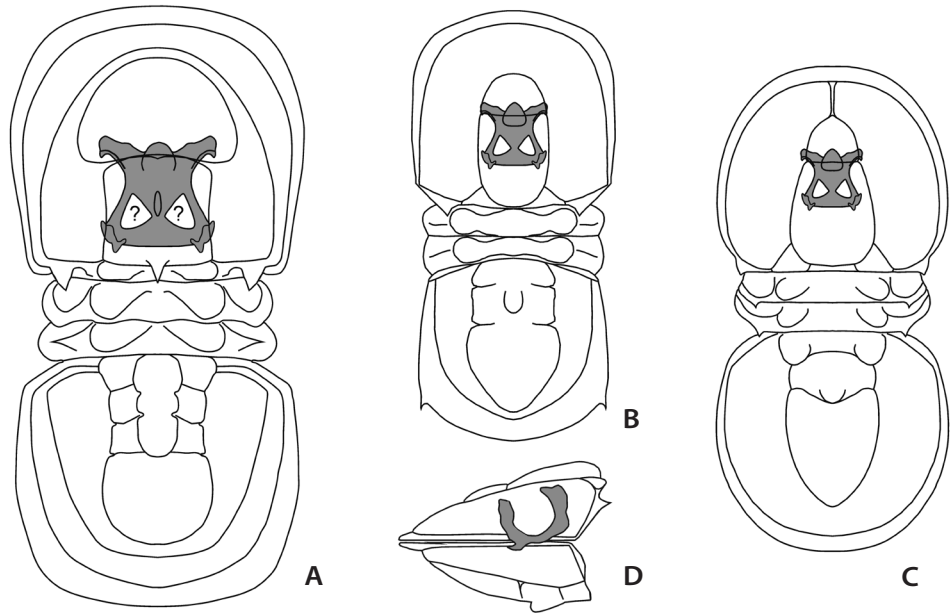
### *Onymagnostus hybridus* (Brøgger, 1878)

Figure 4E

*Material and locality.* – Specimen NML 46515; Obalovna on the eastern slope of the Vystrkov hill, east of Jince (site 2 in Fig. 1C).



**Figure 5.** A–C – supposed position of hypostome in dorsal view. • A – *Condylopyge rex* (Barrande, 1846). • B – *Peronopsis integra* (Beyrich, 1845); supposed position of hypostome in lateral view (D). • C – *Onymagnostus hybridus* (Brögger, 1878).



**Description.** – A complete articulated exoskeleton preserved as an internal mould in mudstone.

The anterior half of the posteroglabella is collapsed and shows a flat area with a quadrangular outline. The transglabellar furrow, the posterior part of the anteroglabella and the surrounding surface of the acrolobe are slightly damaged and depressed. Tiny depressions are seen in both postero-lateral corners of the anteroglabella.

**Dimensions.** –  $E_L = 9.44$  mm;  $C_L = 4.09$  mm,  $C_W = 4.65$  mm;  $P_L = 4.09$  mm,  $P_W = 4.33$  mm,  $PG_L = 1.95$  mm,  $PG_W = 1.60$  mm. The hypostome is 1.15 mm long.

**Remarks.** – The conspicuous, quadrangular flattening restricted to the anterior half of the posteroglabella agrees well with the supposed outline and expected position of the hypostome (H in Fig. 4E1). The depressions developed in the anteroglabella fit well with the area where the anterior hypostomal wings were attached (aW in Fig. 4E1).

## Discussion

### Position of the hypostome in agnostids

In the first description of an agnostid hypostome, Robison (1972, pp. 242, 243) supposed that the hypostome was situated beneath the anteroglabella. Öpik (1979, p. 34), however, suggested that the hypostome was situated beneath the posteroglabella. Later on, Robison (1982, p. 150) suggested a scenario when “the dead animal was probably deposited with its dorsal surface resting on the seafloor. After decay of the soft tissue, the

labrum collapsed against the dorsal exoskeleton and was cemented in place by subsequent silicification. The amount of anterior or posterior displacement of the labrum is unknown”. Ritterbush (1983, p. 309) was convinced about an *in situ* position of hypostomes in her silicified specimens and suggested a position of the labrum (= in actual terminology hypostome) beneath the second glabellar lobe; Ritterbush (1983) also speculated about a posterior migration of the mouth in agnostids. Müller & Walossek (1987, p. 44) stated that the outline of the hypostome in *A. pisiformis* approximately corresponds “to the anterior glabellar lobe and projects ventrally and, in the enrolled condition, reaches far into the concavity of the pygidial shield, the deepest point corresponding approximately to the culmination point of the axis”. Such description fits well with the situation seen in the smallest specimens of the meraspid degree 1, stage 1b (compare Müller & Walossek 1987, pl. 7, fig. 1; pl. 28, fig. 6). In this stage, the cephalic shield is about 350 µm long and the position of the hypostome corresponds to the area of the anteroglabella. In comparison, two slightly larger cephalae of the meraspid degree 1, stage 1c (450 µm and 600 µm long) show a more posteriorly situated hypostome (compare Müller & Walossek 1987, pl. 10, fig. 1; pl. 13, fig. 1); the position of the hypostome agrees with a placement under both the anteroglabella and the posteroglabella. Two other figured cephalae with the hypostome *in situ* are at least 480 µm long and belong to the meraspid degree 2, stage 2a (Müller & Walossek 1987, pl. 11, figs 3, 4; pl. 22, fig. 2); in these two specimens the hypostome has moved even more posteriorly, and its position is between the anteroglabella and the posteroglabella, with the main portion of the hypostome

situated under the posteroglabella. Larger growth stages of *A. pisiformis* are not preserved and thus were not studied by Müller & Walossek (1987). Whittington (1988, fig. 1; 1997, fig. 27/1b) published an outline of the cephalon of the Middle Ordovician agnostid *Arthrorhachis* sp., including a possible outline of the hypostome placed under the anterior portion of glabella. The position of hypostomes in holaspis specimens figured by Rushton (1979) and Fatka *et al.* (2009b) as well as in silicified specimens described and figured by Robison (1972, 1982) and Ritterbush (1983) is more or less posteroglabellar. Similarly, all herein examined holaspis specimens of *C. rex* (Fig. 4A, B), *P. integra* (Fig. 5C, D), and *O. hybridus* (Fig. 4E) show that the main portion of the hypostome is placed under the posteroglabella; only the anterior third of the hypostome lies under the anteroglabella.

Based on the available material, we suppose that the position of the hypostome changed during ontogeny. In early ontogenetic stages, the hypostome was located under the anteroglabella (see Müller & Walossek 1987). In holaspis stages, the hypostome was largely situated under the posteroglabella; only the anterior wings reached under the anteroglabella (Figs 4, 5).

The position of the hypostome figured in specimens of *Peronopsis* cf. *columbiensis* by Moysiuk & Caron (2019a, fig 1a, b, c, d) as well as in the specimen of *Ptychagnostus* cf. *praecurrens* by Moysiuk & Caron (2019b, fig. 2e) is more posterior when compared with the interpretative diagram of *Peronopsis* (Moysiuk & Caron 2019a, fig. 2e). Such a more posterior position of the hypostome fits well with the situation observed in the herein studied specimen of *O. hybridus* (Fig. 4E) and in *P. integra* (Fig. 4C, D). Consequently, the hypostome in holaspis specimens of both last-named taxa and also in *C. rex* is reconstructed under the posteroglabella, while only anterior wings extended under the posteriormost portion of the anteroglabella (Fig. 5A–D).

## Chemical composition of the agnostid hypostome

Rasetti (1952, p. 887) supposed that after embedding, the muscle contraction hold the individual exoskeletal parts together and consequently interpreted the tightly enrolled agnostids as almost certainly buried alive. He also noted that if the agnostid had a calcified hypostome, it should now be present inside the enrolled exoskeleton. Robison (1972, p. 243) discussed the possible calcification of the hypostome. A light calcification of the hypostome was suggested also by Babcock *et al.* (2005, p. 10, but see Maas *et al.* 2006, p. 275).

The agnostids studied herein are preserved as internal and external moulds in quite strongly weathered

siliciclastic sediments. The original biomineralised parts have been completely dissolved and replaced by secondary minerals, such as carbonates and iron-oxides. Hence, the original chemical composition of the exoskeleton and the hypostome cannot be analyzed in the here studied specimens. Following Müller & Walossek (1987, p. 44), however, we suppose that the hypostome of the agnostids was chitinous and only lightly biomineralised.

## Conclusions

In the Barrandian area, thousands of articulated agnostids have been collected from the Jince and Buchava formations, but only four exoskeletons assigned to three species contain remains of hypostome. The scarcity of hypostomes in agnostids reflects their small size combined with their poor preservation potential and a weak attachment to the ventral body surface.

The observed differences in preservation of the mineralized dorsal exoskeleton and the hypostome *in situ* could be explained by a weak (if any) mineralization of this ventral element.

It is apparent that during the ontogeny, the position of the hypostome in agnostids changed from being situated beneath the anteroglabella to a more posterior position beneath the posteroglabella.

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