Geologica Acta, Vol.16, N° 1, March 2018, 65-73
DOI: 10.1344/GeologicaActa2018.16.1.4

geologica acta

Digestive structures in the Middle Ordovician trilobite *Prionocheilus* Rouault 1847, from the Barrandian area of Czech Republic

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ABSTRACT

Remains of a digestive system from a slightly damaged articulated specimen of the comparatively rare bathycheilid trilobite *Prionocheilus vokovicensis* (Šnajdr, 1956) are described for the first time. The specimen comes from the Middle Ordovician Šárka Formation of the Prague Basin and contains the midgut region of the digestive system preserved through the axial region of glabella and six anterior thoracic segments. The anterior-most part of the digestive system is unknown as the anterior glabellar lobes are not preserved in the studied specimen. In the cephalic shield, the remains of two pairs of gut diverticulae are seen in the posterior region of the glabella. Remains of five pairs of small cavities developed in the axis of the first six thoracic segments represent the remains of thoracic gut diverticulae. The discussed specimen possess the first undoubted remain of digestive structures established within the family *Bathycheilidae* (Přibyl, 1953).

KEYWORDS *Prionocheilus*. **Digestive tract. Ordovician. Barrandian area. Czech Republic.**

INTRODUCTION

Nearly one thousand trilobite species have been described from the Cambrian to Devonian aged rocks of the Barrandian area of the Czech Republic (Valíček and Vaněk, 2001; Vaněk and Valíček, 2002) but remains of soft parts are extremely rare (*e.g.* Šnajdr, 1990; Fatka *et al.*, 2014). About twenty exceptionally preserved articulated trilobite exoskeletons with remains of digestive system have been collected from Cambrian Buchava and Jince formations (fms.) of the Skryje-Týřovice and Příbram-Jince basins (Jaekel, 1901; Fatka *et al.*, 2014). Similar number of trilobite specimens with undoubted remains of gut, cephalic and thoracic diverticulae and/or crop were recently documented in Ordovician specimens from the Mílina (Tremadocian), Šárka (Darriwilian), Letná (Sandbian), and Bohdalec (Katian) fms. of the Prague Basin (for summary see Fatka *et al.*, 2014) (Fig. 1C).

Here, we describe the morphology of the digestive system in the rare bathycheilid trilobite *Prionocheilus vokovicensis* (Šnajdr, 1956). A slightly damaged internal mould of an originally complete and well articulated exoskeleton was recently identified by the junior author in collections housed in the National Museum of Prague (housed under the inventory number NM L35774). The external mould of the studied specimens is not stored in the National Museum collections. This extraordinary specimen was collected near the town of Rokycany, particularly in the fields of the Osek locality. In these fields, diverse Middle Ordovician fossils, preserved in silicified nodules of the Šárka and Dobrotivá fms., have been collected since the middle of the 19th century (Lajblová and Kraft, 2014).

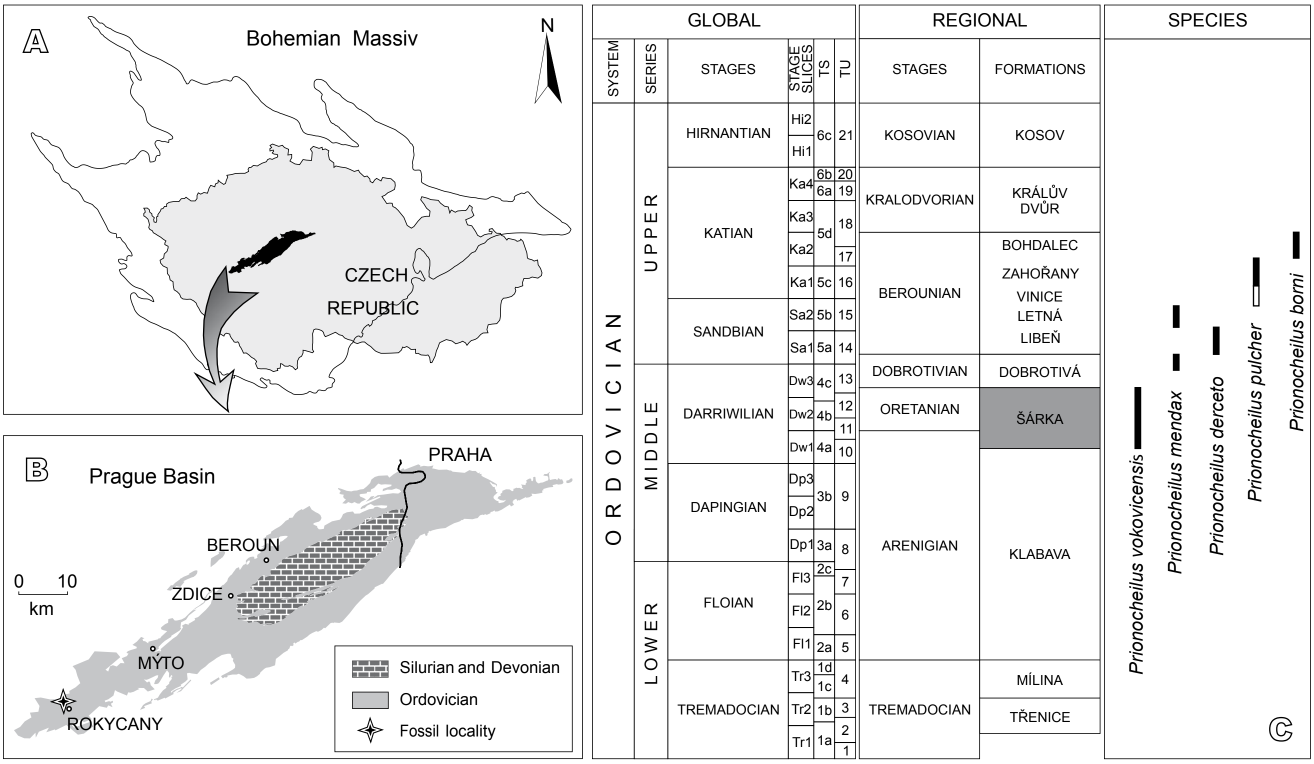

FIGURE 1. Maps showing the location of the discovery site and Ordovician stratigraphy in the Barrandian area: A) Map of the Czech Republic and the Bohemian Massif with the Ordovician rocks of the Barrandian area; B) Ordovician of the Prague Basin showing the location of the Osek locality at which the studied specimen was found. C) Chart showing the correlation between global series, stages, stage slices, Time Slices (TS), Time Units (TU), and the regional chronostratigraphic and lithostratigraphic units recognized in the Ordovician of the Prague Basin with marked ranges of the species of *Prionocheilus* (stratigraphy modified from Bergström *et al.*, 2008; Fatka *et al.*, 2013). Ranges of the species of *Prionocheilus* based on Šnajdr (1956), Vaněk (1965), Budil and Kraft (2003), Mergl *et al.* (2008), Peršín and Budil (2009), Vokáč *et al.* (2015).

GEOLOGICAL SETTING

The Šárka Formation

The Šárka Formation (Fm.) contains a highly diverse skeletal fauna (*e.g.* Havlíček and Vaněk, 1966, 1990; Fatka and Mergl, 2009). The thickness of this formation ranges from several metres in the marginal parts of the basin to nearly 300 metres in segments of supposed rapid synsedimentary subsidence (Havlíček, 1981). The stratigraphy and depositional setting of the Šárka Fm. have been discussed by numerous authors (*e.g.* Kukal, 1962; Havlíček and Vaněk, 1966; Kraft and Kraft, 1992, 1999; Havlíček and Fatka, 1992; Havlíček, 1998; Servais *et al.*, 2008). In earlier schemes, the Šárka Fm. was correlated with the British Llanvirn Series (*e.g.* Havlíček and Vaněk, 1966); later, it was supposed to correspond to the late Arenig to early Llanvirn interval (*e.g.* Kraft *et al.*, 2001). Fatka *et al.* (2013) correlated the Šárka Fm. with the Oretanian Regional Stage which is equal to the middle Darriwilian (Bergström *et al.*, 2008). Based on the restricted ranges of graptolites, the Šárka Fm. has been divided into two biozones: the older *Corymbograptus retroflexus* and the younger *Didymograptus clavulus* biozones (Kraft *et al.*, 2001). The Šárka Fm. typically consist of poorly fossiliferous dark shales. Our knowledge about fauna is generally based on specimens collected from siliceous nodules, which have attracted the attention of amateur collectors. However, such loose nodules do not provide information about the stratigraphic position and original palaeoenvironment (Budil *et al.*, 2007; Mergl *et al.*, 2008).

Fossil associations

Abundant remains of brachiopods, gastropods, trilobites, agnostids, phyllocarids, ostracods, bivalves, hyoliths, cephalopods, echinoderms, and conulariids associated with graptolites and ichnofossils have been studied for more than 150 years (Barrande, 1872; Havlíček and Vaněk, 1966; Chlupáč, 1970, 2003; Mikuláš, 1991; Horný, 2001; Mergl, 2002; Kraft and Kraft, 2003; Budil *et al.*, 2007; Manda, 2008; Mergl *et al.*, 2008; Fatka and Mergl, 2009; Steinová, 2012; Polechová, 2013; Aubrechtová, 2015). The intensively studied and diverse fauna made possible to distinguish several trilobite and non-trilobite associations of the Šárka Fm. (Havlíček, 1982, 1998; Havlíček and Vaněk, 1990; Mergl, 2002; Lefebvre, 2007). Mikuláš (1991, 1998) studied assemblages of ichnofossils, which he assigned to a transition from *Cruziana* to *Zoophycos* ichnofacies.

Trilobite associations

More than 50 species of trilobites have been described from the Šárka Fm. (Havlíček and Vaněk, 1966; Budil *et al*., 2007; Mergl *et al*., 2007). Remains of trilobite exoskeletons together with gastropod, brachiopod and bivalve shells are common elements in fossil associations. Trilobite associations have been discussed by Havlíček and Vaněk (1990), Havlíček (1998), Bruthansová (2003), Budil *et al*. (2007), Mergl *et al*. (2008), Fatka and Mergl (2009) and Mergl and Kozák (2016). All earlier proposals of trilobite associations were recently summarized by Fatka *et al*. (2015) and are shown in Figure 2.

The discussed damaged internal mould of an originally complete exoskeleton of *Prionocheilus vokovicensis* is preserved in a siliceous nodule that is known from the shallower part of the *Placoparia* Association of the Šárka Fm. (Fig. 2).

METHODS

Methods used to analyse the trilobite specimen included standard light microscopy of the external surface of the internal mould (Microscope NIKON SMZ 1500, Leica S8APO); photographs were taken using digital cameras (a NIKON D 300 and an Olympus SZX-ILLB200) after coating with ammonium chloride. The drawing was made from a photograph using Corel Draw X3 and Adobe Photoshop CS5. The terminology used follows that proposed by Whittington and Kelly (1997), including the following abbreviations: sag. (sagittal), tr. (transverse). The specimen is housed in the National Museum of Prague, under the inventory number NML 35774.

SYSTEMATIC PALAEONTOLOGY

Family: Bathycheilidae Přibyl, 1953
Subfamily: Pharostomatinae Hupé, 1953
GENUS ***Prionocheilus*** Rouault, 1847

Type of species. *Prionocheilus verneuili* (Rouault, 1847), Sandbian/Katian, Formation de Riadan in the Martigné-Ferchaud South of Rennes, Caradocian, Brittany, France (by original designation).

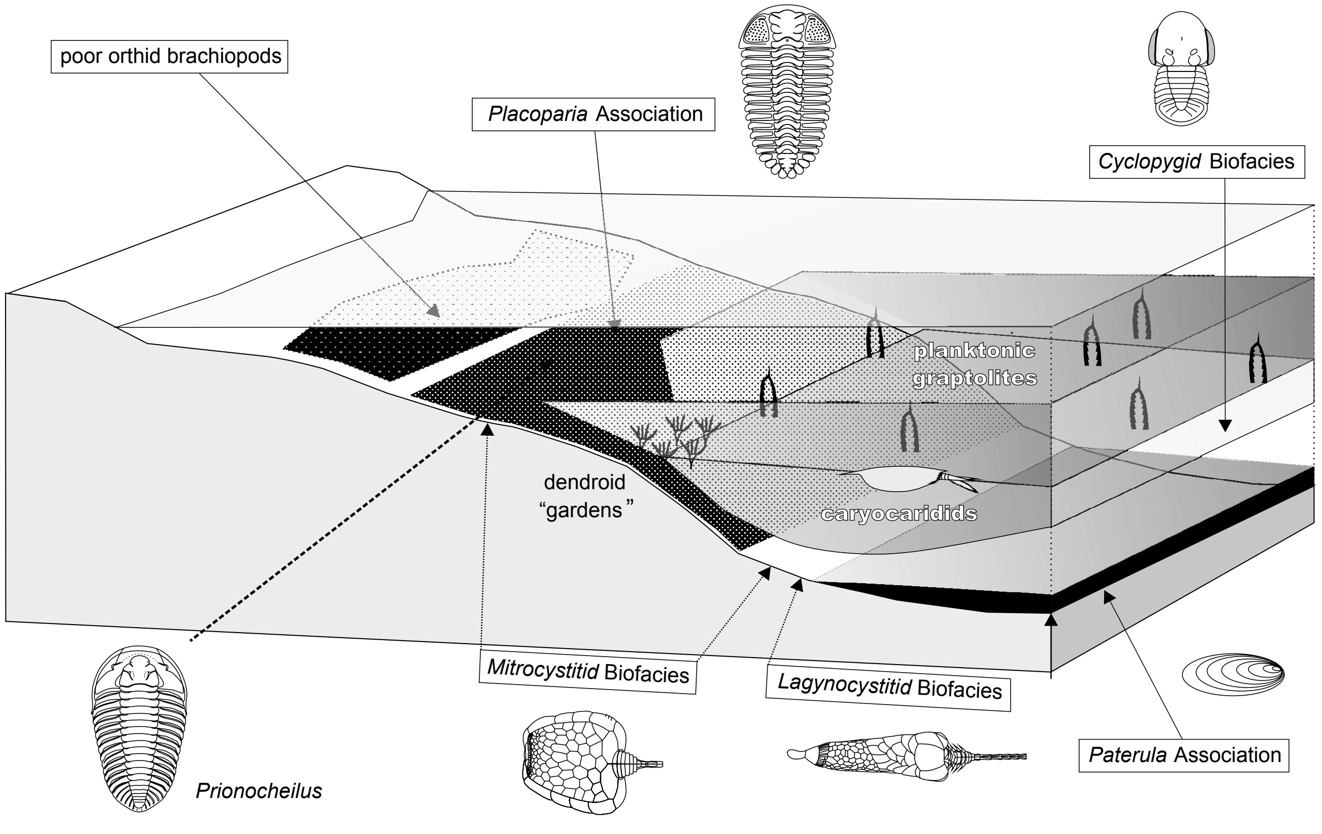

FIGURE 2. Sketch representing the distribution of the major biofacies associated with the late Darriwilian Šárka Fm. and occurrence of *Prionocheilus*. The shallowest part of the basin was inhabited by the poor orthid brachiopod association, in the offshore areas the *Placoparia* Association rich with trilobites, brachiopods and other skeletal fauna; in the offshore, downslope, it gradationally passes into the poor atheloptic trilobite association (not represented in this figure), which includes also the poor benthic dendroid 'gardens'. The water column was inhabited by poor planktonic graptolites and taxa of the poorly diverse *Caryocarid* and *Cyclopygid* biofacies. Poorly oxygenated black shales in central parts of the basin are dominated by the *Paterula* Association. Modified from Fatka and Mergl (2009, fig. 11D) and Fatka *et al.* (2015, fig. 2).

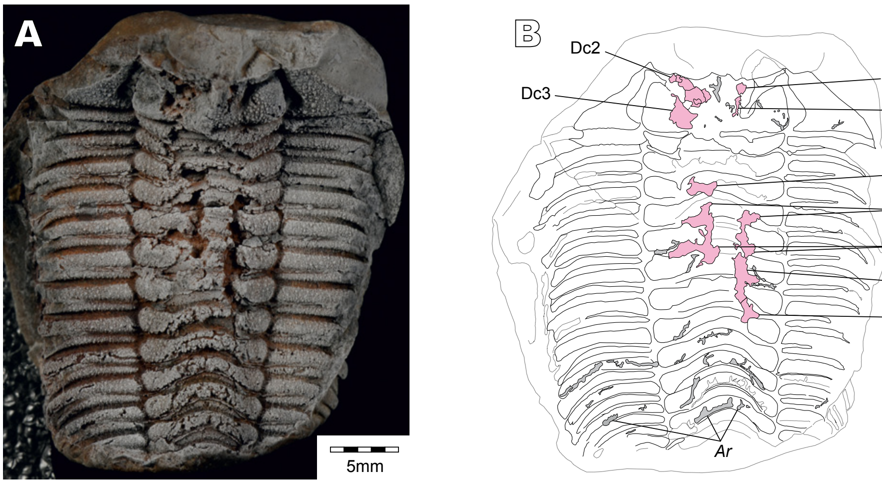

FIGURE 3. Morphology of the preserved parts of the digestive system in the cephalic and thoracic regions of *Prionocheilus* from the Šárka Fm. (Middle Ordovician, Darriwilian= Oretanian Regional Stage). A) Internal mould of *Prionocheilus vokovicensis* (Šnajdr, 1956) in dorsal view; National Museum of Prague, NML 35774; fields North of Rokycany (Osek locality). B) Interpretative sketch. Dc: cephalic gut diverticulae; Dt: thoracic gut diverticula; *Ar*: ichnofossils *Arachnostega*.

Remarks. The validity of *Prionocheilus* (Rouault, 1847) and *Pharostoma* (Hawle and Corda, 1847) has been discussed for a long time. Šnajdr (1956), Vaněk (1965), Whittington (1965), and Siveter (1973, 1976) placed *Prionocheilus* in the synonymy of *Pharostoma*. However, Dean (1964) showed that the contribution of Rouault (1847) predates that of Hawle and Corda (1847). Ingham (1977) followed the proposal of Dean (1964) bringing the argumentation that *Prionocheilus* was used in zoological publications. However, in an addendum, Siveter (1976, pg.: 393) stressed the information about decision published in the Bulletin of Zoological Nomenclature bearing on the question of the usage of *Prionocheilus* instead of *Pharostoma*. In agreement with the scientific revisors in Horný and Bastl (1970), Hammann and Henry (1978), Hammann (1983), Zhou *et al*. (1984), Rábano (1989) and other authors, we follow the use of *Prionocheilus*. The systematic revision of *Prionocheilus* is, however, out of the scope of this paper.

Species. Siveter (1973, pg.: 2) assigned 19 species to *Pharostoma* (syn. of *Prionocheilus*). Sixteen years later, Rábano (1989, pg.: 93) listed 18 species classified under *Prionocheilus*. In comparison, Lemke (unpublished) provided the most complete list of 27 species assigned to *Prionocheilus*. Evaluation of their lists and detailed discussion is, however, out of the scope of this contribution.

Distribution. *Prionocheilus* has been established in West Gondwana (Argentina, Mendoza area; Morocco), European peri-Gondwana (France, Iberian Peninsula, Czech Republic, Great Britain, Ireland), Baltica (Estonia), Laurentia (Canada), Kazakhstania, SW China (Guizhou Province).

Prionocheilus ranges from the Tremadocian of France and Spain [*P. languedocensis* (Courtessole and Pillet, 1975)] to the Ashgillian of Canada [*P. rarus* (Cooper and Kindle, 1936)], Ireland [*P. obtusum* (McCoy, 1846)], and Kazakhstan [*P. solitus* (Apollonov, 1974)].

In Ordovician sequence of the Prague Basin, five species have been assigned to *Prionocheilus*: *P. borni* (Vaněk, 1995), *P. derceto* (Vaněk, 1995), *P. mendax* (Vaněk, 1965), *P. pulcher* (Barrande, 1846), and *P. vokovicensis* (Šnajdr, 1956). Stratigraphically, they range from the Middle Ordovician Šárka Fm. (Darriwilian) to the Upper Ordovician Bohdalec Fm. (Late Berounian Regional Stage = mid Katian) (Fig. 1C);

Prionocheilus vokovicensis (Šnajdr, 1956) (Figs. 3, 4 and 5).

Description. The studied specimen is preserved in a hard siliceous nodule, which represents one of litholotypes of the Middle Ordovician Šárka Fm. (Kukal, 1962; Chvátal, 2003; Drost *et al*., 2003). It is a slightly incomplete, partly damaged, internal mould of posterior part of cephalon associated with a nearly complete articulated thorax of a middle-sized holaspid specimen.

The exoskeleton is preserved in a prone attitude; the preserved part is 28mm long (sag.) and reaches 24mm in maximum width (tr.). The width of the axial region of thoracic segments ranges from 10mm in the first segment to 7mm in the eleventh (=posterior-most preserved) segment.

The anterior border and preglabellar field were situated outside the siliceous nodule and, as a result, are not preserved. The surface of the fixigena and the anterior part of the glabella are strongly weathered. The pygidium and the posterior-most thoracic segment were situated outside the siliceous nodule and are not preserved.

Two, quite deep, lobate cavities are developed in the left posterior part of the glabella; one narrow, sagitally oriented cavity is seen in the right posterior part of the glabella. Similar paired and quite deep cavities are developed also in the axial part of the third and fourth thoracic segment; unpaired, morphologically comparable cavities are seen also in the left part of the second segment axis as well as in the right part of the axis in the fifth and sixth thoracic segment.

Comparatively narrow, centrally placed and nearly parallel-sided remains of the dorsal exoskeleton are visible in several segments of the axial part of the thorax. These remains extend from the second to the sixth thoracic segment.

Interpretation. The above described cavities in the glabella and in the anterior part of the thorax recall the earlier described remains of trilobite digestive system (Lerosey-Aubril *et al*., 2011, 2012; Fatka *et al*., 2013, 2015). The placement inside the axial part of the cephalon and thorax combined with an apparent arrangement in pairs makes it possible to interpret these stuctures as paired gut diverticulae supposedly associated with a centrally placed gut (most probably not preserved in this specimen, the original position of the gut was under the parallel-sided and narrow area seen between paired cavities).

The alimentary canal, preserved in the posterior part of the glabella, is associated with two larger, separated, lobate imprints (left) and one longer and narrow cavity. All of these imprints are interpreted as two pairs of cephalic gut diverticulae (Dc2-3 in Fig. 3B). The small cavities developed on either side of the gut in the axial region of the second to sixth thoracic segments belong to partially preserved, paired thoracic gut diverticulae (Dt2 to Dt6 in Fig. 3B). The slight shift of thoracic diverticulae on the left side is, most probably, caused by decay of soft tissue during early diagenesis.

The thin fissure developed ventrally in the axis of the fourth and fifth segments, separates dorsally positioned, a sagitally elongated body which could represent the remains of a tubular gut (arrow in Fig. 4).

Remarks. The cephalon and all preserved thoracic segments are well articulated and the remains lack any signs of disarticulation in the posterior part of the thorax. Therefore, the disarticulation along the posterior part of the thorax in an unspecific location, *sensu* Daley and Drage (2016), could be excluded. Consequently, this specimen represents partly preserved internal mould of an originally complete carcass.

Based on comparison with other complete specimens of *Prionocheilus vokovicense*, sag. length of the herein described specimen could be estimated to range from 35 to 40mm; it apparently represents a late holaspid stage.

Fine, branched and curved tunnels of the ichnospecies *Arachnostega gastrochaenae* BERTLING, 1992, are developed directly below the exoskeletal surface in different parts of the mould, especially in the eighth to eleventh thoracic segment (*Ar* in Fig. 3B). *Arachnostega* tunnels associated with body fossils have been reported from numerous Ordovician areas, including the Šárka Fm. of the Barrandian area (for summary see Fatka *et al*., 2011).

Similarly, in specimens of *Colpocoryphe bohemica* described from the Šárka Fm. of the Barrandian area, as well as in the herein studied specimen of *Prionocheilus*, it is possible to suppose that the missing parts of the exoskeleton were situated outside of the nodule and were destroyed during diagenetic processes (compare Fatka *et al*., 2015). Such a type of preservation agrees well with the very early diagenetic formation of siliceous nodules (for detailed discussion see Dabbard and Loi, 2012 and the following section of this paper).

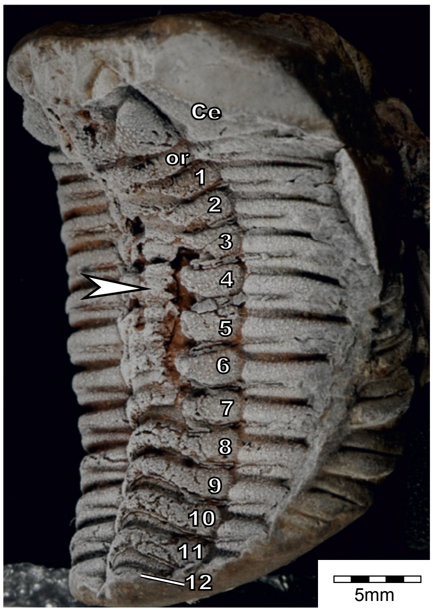

FIGURE 4. Morphology of the preserved parts of the digestive system in the cephalic and thoracic regions of *Prionocheilus* from the Šárka Fm. (Middle Ordovician, Darriwilian=Oretanian Regional Stage). Internal mould of *Prionocheilus vokovicensis* (ŠNAJDR, 1956) in dorso-lateral view; National Museum of Prague, NML 35774; fields North of Rokycany (Osek locality). Ce: cephalic shield; or: occipital ring; 1 to 12: thoracic segments; arrow: sagitally elongated body which could represent the remains of a tubular gut.

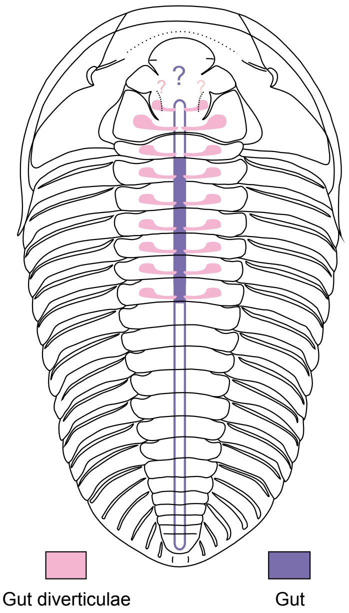

FIGURE 5. Reconstruction of the morphology of the digestive system in *Prionocheilus* in dorsal view.

DISCUSSION

Decay of soft parts

Babcock and Chang (1997) and Babcock *et al.* (2000) showed, that the decay of internal soft parts started only a few hours after death in modern *Limulus* and the decay did not last more than one month. Also, other decay experiments have shown a rapid destruction of internal organs in marine arthropods by the activity of microbes associated with phosphatization of internal tissues (Butler *et al.*, 2015; Strang *et al.*, 2016). Similarly, as in other trilobites with preserved soft parts, the processes leading to preservation of the delicate remains of soft tissue should be initiated very shortly after the entombment of carcasses. This agrees with the model of early diagenetic phosphogenesis linked to Carbonate Fluor-Apatite (CFA) precipitation in upper levels of the sediment (Dabbard and Loi, 2012). Such type of preservation of soft parts could be explained by a rapid mineralisation of the gut associated with the early diagenetic formation of the siliceous nodule. This process was later on followed by a diagenetic removal of the original gut mineral phase, possibly due to weathering. The exoskeleton may have been dissolved at the same time.

Morphology of alimentary tract

Two major morphological types of alimentary tract have been distinguished by Lerosey-Aubril *et al.* (2011): i) simple tube with a crop, and ii) simple tube with metamerically paired caeca (=gut diverticulae). Both morphologies have been observed in Ordovician trilobites of the Prague Basin (Fatka *et al.*, 2014). Recently, Gutiérrez-Marco *et al.* (2017) described a third type of alimentary tract characterised by a co-occurrence of both crop and metamerically paired caeca in large asaphid *Megistaspis* (*Ekeraspis*) *hammondi* from the Fezouata Lagerstätte of Morocco.

In *Prionocheilus*, similarly as in the Cambrian specimen of *Jiumenia anhuiensis* (Zhu *et al.*, 2014), the blind *Conocoryphe* (Budil and Fatka, 2008) and the small-eyed Middle Ordovician *Colpocoryphe* (Fatka *et al.*, 2015), a bell-shaped, anteriorly narrowing glabella is developed. Due to this glabellar morphology, metamerically paired caeca could be expected. We also agree with Zhu *et al.* (2014), who explained the more abundant preservation of guts as sediment-like infilling (Šnajdr, 1990), while more rarely preserved metamerically paired digestive caeca is connected with a susspected phosphatisation of this part of the digestive system (for discussion see Lerosey-Aubril *et al.*, 2012 and Fatka *et al.*, 2013).

Palaeoecology

Based on general morphology of exoskeleton and hypostome, Hammann (1983, pg.: 34, text-fig. 12) suggested an epibenthic mode of life for *Prionocheilus*; this is generally accepted (*i.e.* Mergl *et al.*, 2008, pg.: 279) (Fig. 2). Budil *et al.* (2007, pg.: 68) classified *P. vokovicensis* as a scavenger-predator. The occurrence of paired diverticulae, however, implies a long-standing digestive process of ingested particles, which is in agreement with a detritus feeding habit.

CONCLUSIONS

i) Remains of the digestive system are, for the first time, documented in an Ordovician bathycheilid trilobite.

ii) The studied carcass of *Prionocheilus vokovicensis* shows an apparent presence of two cephalic and at least six thoracic diverticulae (Fig. 5). In the studied specimen, preservation of the gut tract is questionable.

iii) The alimentary tract observed in *Prionocheilus* is known in trilobites with diverse visual abilities. Comparable tracts have been reported in the contemporaneous genus *Colpocoryphe*, as well as in the Cambrian genera *Conocoryphe* and *Jiumenia*.

ACKNOWLEDGMENTS

We thank Thomas Hegna (Western Illinois University, U.S.A.) and an anonymous reviewer for their helpful reviews and the linguistic improvements made on our text. This study was supported by PROGRES Q45 of the Ministry of Education, Youth and Sports of Czech Republic and the Czech Geological Survey internal project No 339900. This paper is a contribution to the project IGCP 653 "Filling the gap between Cambrian Explosion and the GOBE".

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Manuscript received March 2017;
revision accepted June 2017;
published Online October 2017.