Digestive structures in Ordovician trilobites *Colpocoryphe* and *Flexicalymene* from the Barrandian area of Czech Republic

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Abstract. Two recently discovered specimens of the abundant calymenoid trilobite *Colpocoryphe* Novák in Perner, 1918 from the Middle Ordovician Šárka Formation and one specimen of *Flexicalymene* (*Flexicalymene*) *pragensis* Vaněk & Vokáč, 1997 from the Upper Ordovician Bohdalec Formation, all from the Prague Basin, display remains of the digestive system. In *Colpocoryphe*, an internal mould of an articulated exoskeleton contains a post-stomach part of the alimentary canal preserved through the narrow axial region of the occipital ring, all thoracic segments as well as in the axial part of the pygidial shield. The anterior part of the digestive system is poorly known as the specimen shows the hypostome preserved in situ and the space between the glabella and the hypostome is represented by an empty cavity associated with probable remains of gut diverticulae on both sides of the cephalon. The second, incomplete specimen consists of five posterior thoracic segments articulated with the pygidium. The axial region of this specimen is preserved with a clearly discernible segmented intestine which terminates at the axial tip and then bends ventrally. In an enrolled specimen of *Flexicalymene pragensis*, supposed remains of the alimentary tract are comparatively poorly preserved but discernible in the middle and posterior parts of the thoracic axis and in the anterior part of the pygidial axis. Digestive structures within the family Calymenidae have not been described previously. Earlier discoveries of the digestive system in Ordovician trilobites of the Barrandian area are briefly reviewed.

Key words: *Colpocoryphe*, *Flexicalymene*, digestive tract, Ordovician, Barrandian area, Czech Republic.

INTRODUCTION

Skeletal remains of invertebrates, including trilobite exoskeletons, are abundant in the Barrandian area (e.g. Barrande 1852, 1872; Chlupáč et al. 1998; Bruthansová et al. 2007 and references therein). More than 900 trilobite species have been described from Cambrian to Devonian rocks of this area (Valíček & Vaněk 2001; Vaněk & Valíček 2002) but remains of their soft parts are extremely rare (e.g. Šnajdr 1990). Exceptionally preserved trilobites with remains of the digestive system were discovered in the Cambrian Buchava and Jince formations of the Skryje–Týřovice and Příbram–Jince basins as well as from the Ordovician Mílina and Letná formations of the Prague Basin (Fatka et al. 2014; Fig. 1C herein).

Here, we describe the remains of an undoubted digestive system in three specimens of calymenoid trilobites; *Colpocoryphe bohemica* (Vaněk, 1965), *C.* cf. *bohemica* and *Flexicalymene* (*F.*) *pragensis* Vaněk & Vokáč, 1997. Both specimens of the genus *Colpocoryphe* were recently collected at two localities situated in the lower levels of the Middle Ordovician Šárka Formation (Darriwilian = Oretanian Regional Stage; see Fig. 1C) in the western part of the Prague Basin (Fig. 1B); the specimen of *Flexicalymene* (*F.*) *pragensis* was collected by the junior author at the Brumlovka locality in shales of the Upper Ordovician Bohdalec Formation (Katian = Late Berounian Regional Stage; see Fig. 1C) in the eastern part of the Prague Basin (Fig. 1B). Two specimens are deposited in the palaeontological collections of the Czech Geological Survey Prague (ČGS MD 001, 007). The third specimen is stored in the West-Bohemian Museum in Plzeň (specimen number WBM S 06 160).

GEOLOGICAL SETTING

Šárka Formation

The Šárka Formation has been established by Kettner & Kodym (1919) and contains a highly diverse skeletal fauna (e.g. Havlíček & Vaněk 1966, 1990; Fatka & Mergl 2009). Its thickness ranges from several metres in the marginal parts of the basin to nearly 300 m in segments with supposedly rapid synsedimentary subsidence (Havlíček 1981). General overviews of the

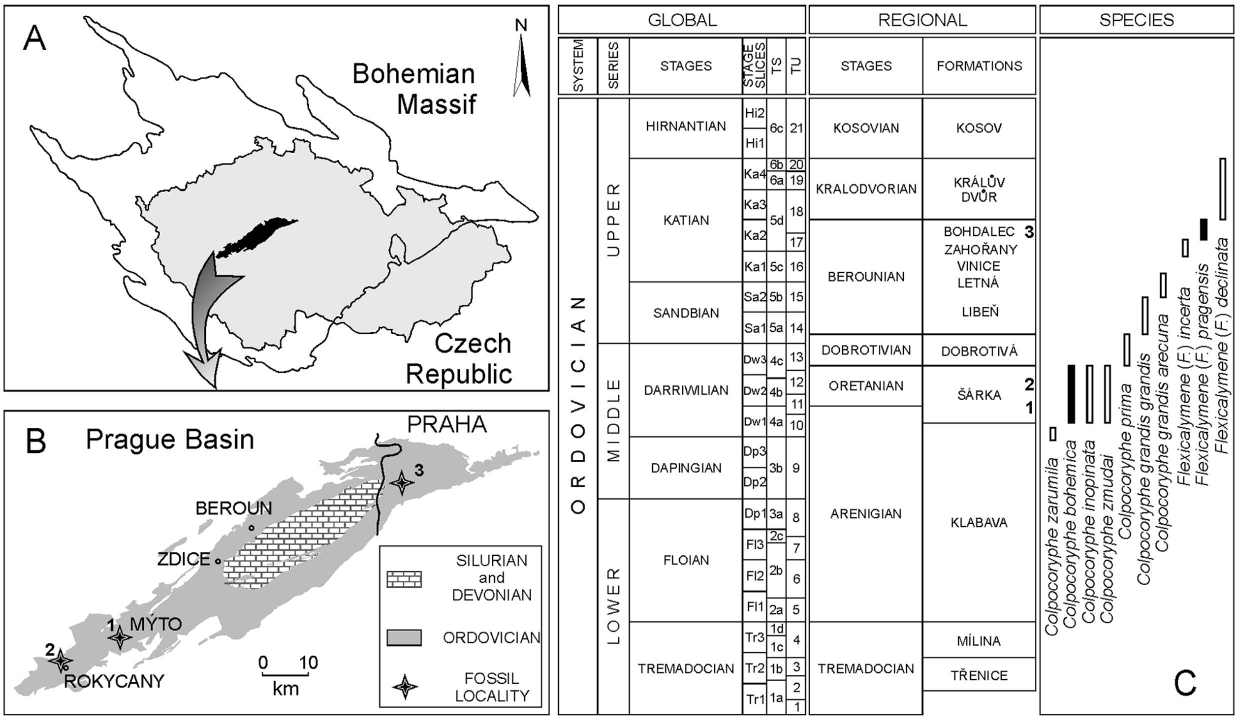

Fig. 1. Location of discovery sites, and the Ordovician stratigraphy in the Barrandian area. **A**, map of the Czech Republic and the Bohemian Massif showing the distribution of Ordovician rocks in the Barrandian area. **B**, Ordovician of the Prague Basin with the location of three outcrops that yielded the studied specimens: 1, field near Mýto; 2, fields north of Rokycany; 3, Brumlovka locality. **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, and ranges of species of *Colpocoryphe* and *Flexicalymene* (stratigraphy modified from Bergström et al. 2008, Fatka et al. 2013 and Vodička et al. in press).

stratigraphy and depositional setting of the Šárka Formation are available in Kukal (1962), Havlíček & Vaněk (1966), Havlíček (1982, 1998), Havlíček & Fatka (1992) and Servais et al. (2008). Traditionally, the Šárka Formation was supposed to be time equivalent with the British Llanvirn (e.g. Havlíček & Vaněk 1966); later, it was proposed that it corresponds to the interval from late Arenig to early Llanvirn (e.g. Kraft et al. 2001). Fatka et al. (2013) correlate the Šárka Formation with the Oretanian Regional Stage which is equal to the middle Darriwilian (Bergström et al. 2008). This formation is divided into two graptolite biozones, the *Corymbograptus retroflexus* and *Didymograptus clavulus* biozones (Kraft et al. 2001).

With the exception of several probably heterochronous, stratigraphically and geographically restricted horizons, the dark shales of the Šárka Formation are usually quite sparsely fossiliferous. Our knowledge of the contained fauna comes mainly from loose siliceous nodules. These nodules have long attracted the attention of private collectors by an abundant occurrence of well- to excellently preserved fossils. Unfortunately, such loose nodules do not provide information about their stratigraphic position and/or about the depositional setting (see Budil et al. 2007; Mergl et al. 2008).

Fossil associations of the Šárka Formation

Well-diversified trilobites, brachiopods, gastropods, echinoderms, phyllocarids, ostracods, bivalves, agnostids, hyoliths, cephalopods and conulariids, associated with graptolites and ichnofossils, have been studied for more than 150 years (see Barrande 1872; Havlíček & Vaněk 1966, 1990; Mikuláš 1991; Mergl 2002; Chlupáč 2003; Kraft & Kraft 2003; Budil et al. 2007; Manda 2008; Mergl et al. 2008; Fatka & Mergl 2009; Steinová 2012; Polechová 2013; Aubrechtová 2015). Non-trilobite associations of the Šárka Formation have been analysed by numerous authors.

Havlíček (1982) recognized the *Euorthisina* Community, inhabiting a widely distributed subtidal, soft-bottom environment. This term was later replaced by the *Euorthisina–Placoparia* Community by Havlíček & Vaněk (1990). The fauna of the deeper-water graptolite black shale was assigned to the 'pelagic fauna dominated by graptolites' of Havlíček & Vaněk (1990) and Havlíček (1998). Mergl (2002) proposed that the generally poorly fossiliferous shales with phyllocarids (*Caryocaris*), graptolites, conulariids, nautiloids and trilobites should be classified as the *Rafanoglossa* Community within his *Paterula* Community Group. Vavrdová (1982) assigned samples from the Šárka Formation to the MPM (assemblage with dominant *Micrhystridium*) as well as to the SPH (assemblage with a dominance of small sphaeromorphs) phytoplankton communities. Mikuláš (1991, 1998) ranged the ichnofossil assemblages, though with some reservations, to a transition from the *Cruziana* to the *Zoophycos* ichnofacies. Lefebvre (2007, p. 164) distinguished two biofacies based on stylophoran echinoderms. The western part of the Prague Basin was assigned to the comparatively shallower Mitrocystitid Biofacies representing the Echinoderm Taphofacies D, the eastern part of the basin was classified as an example of the deeper Lagynocystitid Biofacies of the Echinoderm Taphofacies E (Fig. 2).

Mitrocystites mitra and other echinoderm taxa occur in the fields at Mýto and Rokycany, e.g. in the area from which both exceptionally preserved trilobite specimens originate, and the faunal association fits well with the Mitrocystitid Biofacies. However, *M. mitra* and *Lagynocystis pyramidalis*, i.e. typical forms of different echinoderm biofacies, are known to occur together in fields north of Rokycany as well as in the eastern part of the basin. Both taxa occur together with typical representatives of the *Euorthisina–Placoparia* Association.

Trilobite associations of the Šárka Formation

More than 50 species of trilobites occur as dominant elements of these fossil associations (Havlíček & Vaněk 1966; Budil et al. 2007; Mergl et al. 2007). Mergl et al. (2008) prefer the name *Placoparia* Association instead of the *Euorthisina–Placoparia* Community of Havlíček & Vaněk (1990); associations with common cyclopygids, *Bohemilla* and *Girvanopyge* were interpreted as an indication of the proximity of the Cyclopygid Biofacies of Fortey (1985). Bruthansová (2003) briefly discussed associations of Ordovician illaenid trilobites and preferred the designation 'dalmanitid–illaenid–calymenacean

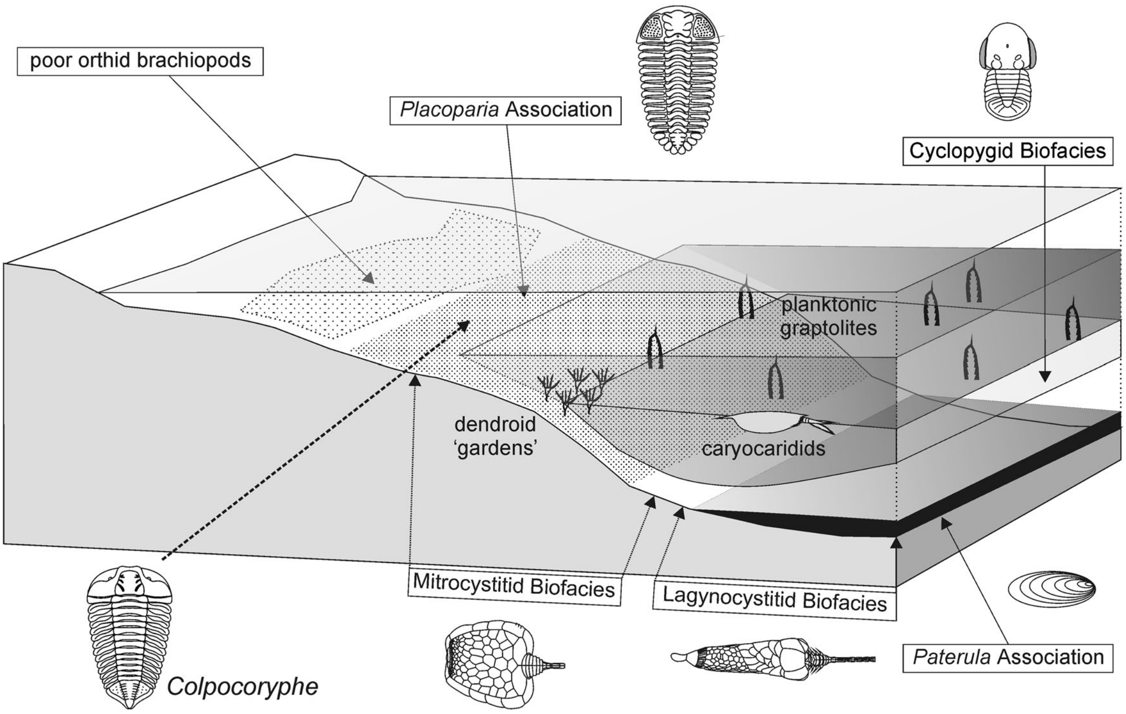

Fig. 2. Sketch showing the distribution of major biofacies associated with the late Darriwilian Šárka Formation. The shallowest part of the basin was inhabited by a sparse orthid brachiopod association. In the offshore direction it was replaced by the *Placoparia* Association which is characterized by a rich skeletal fauna with trilobites and brachiopods. In the offshore slope settings it grades into a low-diversity atheloptic trilobite association that also includes 'gardens' of benthic dendroids. The water column was inhabited by planktonic graptolites and taxa of the poorly diverse Caryocarid and Cyclopygid biofacies. Poorly oxygenated black shales in the central part of the basin were dominated by the *Paterula* Association. Modified after Fatka & Mergl (2009, fig. 11d).

assemblage'; she also noted that illaenids do occur together with cyclopygids. Fatka & Mergl (2009) compared the *Euorthisina* Community of Havlíček with the atheloptic trilobite association of Fortey & Owens (1987) and considered the Middle Ordovician trilobite fauna for an example of the Dalmanitid–Calymenacean Fauna of Cocks & Fortey (1988).

The studied specimens of *Colpocoryphe* were collected from loose siliceous nodules at two localities in the western part of the Prague Basin. The diverse skeletal fauna found in nodules occurring at both localities belongs to the *Placoparia* Association of Mergl et al. (2008). The presence of the ichnogenus *Arachnostega* in the left part of the cephalon of the *Colpocoryphe* cf. *bohemica* specimen (Fig. 3) excludes deposition in an anoxic environment.

Bohdalec Formation

The Bohdalec Formation was established by Bouček (1928). Locally it contains an abundant skeletal fauna (e.g. Havlíček & Vaněk 1966, 1990; Fatka & Mergl 2009). The thickness of this formation ranges from about 20 m in the marginal parts of the basin to nearly 500 m in segments characterized by supposedly rapid synsedimentary subsidence, e.g. within the territory of Prague (Havlíček 1981). General overviews of the stratigraphy and depositional setting of the Bohdalec Formation are available in Röhlich (1957), Havlíček & Vaněk (1966, 1990), Havlíček (1982, 1998), Havlíček & Fatka (1992) and Servais et al. (2008). Traditionally, the Bohdalec Formation was assigned to ther British Caradoc Series (e.g. Bouček 1928, 1937; Kettner & Prantl 1947; Havlíček & Vaněk 1966). Later on, the Bohdalec Formation was proposed to represent the youngest part of the Berounian Series by Havlíček & Marek (1973) and/or of the Berounian Regional Stage (Fatka et al. 1995). Fatka et al. (2013) correlate the Bohdalec Formation (late Berounian Regional Stage) with the middle Katian (Bergström et al. 2008). The formation has not been divided biostratigraphically and shows a complicated lithofacies development (Röhlich 2006).

Fossil associations of the Bohdalec Formation

Comparatively well diversified trilobites, brachiopods, bivalves, bryozoans, gastropods, ostracods, echinoderms, hyoliths, cephalopods, conulariids, rare agnostids and graptolites, associated with locally abundant ichnofossils from the Bohdalec Formation, have been studied for more than 150 years (see Barrande 1872; Havlíček & Vaněk 1966, 1990; Mikuláš 1988; Fatka & Mergl 2009). In the first comprehensive study of the Bohemian Upper Ordovician sequences, Bouček (1928) separated and described richly fossiliferous sediments of the so-called *Polyteichus* Facies, which is characterized by a dominance of carbonate-cemented silty shale. Within the *Polyteichus* Facies, two major skeletal assemblages have been distinguished by Havlíček (1982, 1998) and Havlíček & Vaněk (1990), namely (1) the *Hirnantia plateana* and (2) the *Svobodaina ellipsoides* 'communities'. Black shale, which originated in a comparatively deeper environment, contains the *Onniella michlensis* Community, which is associated with a poor dalmanitid–calymenacean trilobite fauna of Cocks & Fortey (1988). The lower part of the formation contains characteristic elements of the widely distributed *Paterula* Association, such as small epiplanktic brachiopods, atheloptic trilobites and sparse ichnofossils (Mikuláš 1988; Havlíček 1998; Fatka & Mergl 2009). At several outcrops, poor planktonic graptolites and trilobites of the Cyclopygid Biofacies occur in this association.

Trilobite associations of the Bohdalec Formation

More than 20 species of trilobites are abundant in fossil associations in the Bohdalec Formation (Havlíček & Vaněk 1966, 1990; Vaněk & Vokáč 1997). Two associations have been distinguished on the basis of trilobites: the *Onnia abducta* Community, defined originally by Havlíček & Vaněk (1990), and the interval with *Declivolithus alfredi* established in the lower part of the formation (see Röhlich 2006). This comparatively deeper environment provided rare pelagic elements such as *Cyclopyge*, *Bohemilla* and *Sculptaspis*, associated with scarce shallow-water elements.

The enrolled specimen of *Flexicalymene* (*F.*) *pragensis*, described here, is preserved as internal and external moulds. The dark shale in which it occurs represents a typical lithology of the lower part of the *Polyteichus* Facies (*Onniella michlensis* Community, Bohdalec Formation). The absence of ichnofossils in the sample with this trilobite argues for poorly oxygenated depositional environment.

METHODS

The methods used to analyse all trilobite specimens include standard light microscopy of external surfaces (Microscope NIKON SMZ 1500, Leica S8APO). Photographs were taken using digital cameras NIKON D 300 and Olympus SZX-ILLB200 after coating the samples with ammonium chloride. Drawings were made from photographs using Corel Draw X3 and Adobe Photoshop CS5. The terminology follows that proposed by

Whittington & Kelly (1997), including the following abbreviations: sag. (sagittal), tr. (transverse). The chemical analyses was performed using Scan TESCAN Vega, EDS X-MAX 50 (Oxford Instruments).

STUDIED MATERIAL

Systematic palaeontology

Family CALYMENIDAE Burmeister, 1843
Subfamily COLPOCORYPHINAE Hupé, 1955
Genus *Colpocoryphe* Novák in Perner, 1918

Type species. *Calymene arago* Rouault, 1849; Llanvirn–Llandeilo (= Darriwilian), La Couyere, Ille-et-Vilaine, Brittany, France. By original designation.

Remarks. Vaněk (1965) placed *Colpocoryphe* in the synonymy of *Plaesiacomia* Hawle & Corda, 1847. In agreement with Dean (1966, p. 304), Hammann (1983), Šnajdr (1988, 1991), Pek & Vaněk (1989), Vaněk (1995), Valíček & Vaněk (2001) and other authors, we maintain them as separate genera. The systematic revision of *Colpocoryphe* is, however, beyond the scope of this paper.

Discussion. Seven species and subspecies of the genus have been recorded in the Barrandian area (Fig. 1C; Table 1). The two specimens described herein are preserved as internal moulds in hard siliceous nodules, which represents a typical lithology of the Middle Ordovician Šárka Formation (Kukal 1962; Chvátal 2003; Drost et al. 2003). External moulds of both specimens were destroyed during the splitting.

Palaeoecology. Hammann (1983, p. 29, text-fig. 11) suggested a burrowing mode of life for *Colpocoryphe*; this lifestyle is generally accepted (e.g. Fortey & Owens 1987; Šnajdr 1988; Havlíček & Vaněk 1990). Gutiérrez-Marco et al. (2002) and Vidal (1998) used the designation *Colpocoryphe* Biofacies, but its composition was not specified.

Specimen ČGS MD 001, *Colpocoryphe* cf. *bohemica*
(Vaněk, 1965)
Figure 3

Description. It represents a late meraspid (M-10), preserved as an internal mould of an articulated thorax associated with the cephalon and pygidium. The right pleural part of the thorax and pygidium are partly covered by rock matrix; the original exoskeletal material is dissolved. The left side of the cephalon bears an about 1 mm long cavity, representing a tiny ichnofossil of the genus *Arachnostega* (see Fatka et al. 2011; *Ar* in Fig. 3B).

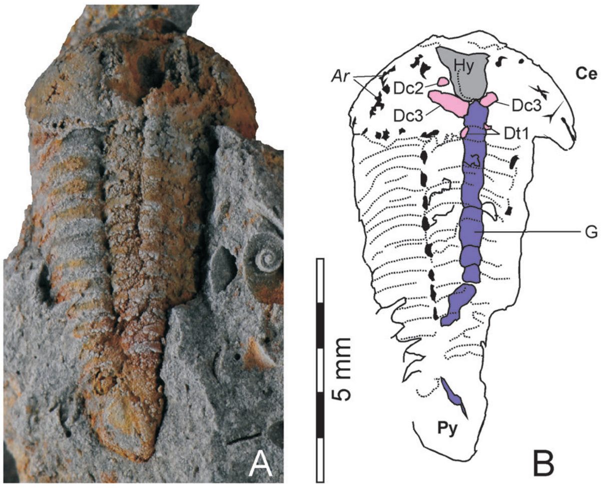

Fig. 3. Morphology of the preserved parts of the digestive system in the cephalic and thoracic regions of *Colpocoryphe* from the Šárka Formation (Middle Ordovician, Darriwilian = Oretanian Regional Stage). **A**, internal mould of *Colpocoryphe* cf. *bohemica* (Vaněk, 1965) in dorsal view; Czech Geological Survey Prague, ČGS MD 001; fields north of Rokycany (locality 2 in Fig. 1B). **B**, interpretative sketch of the specimen in **A**. Abbreviations: Ar, ichnofossil *Arachnostega*; Ce, cephalon; Hy, hypostome; G, gut; Dc, cephalic gut diverticulae; Dt, thoracic gut diverticula.

Table 1. Species of the genus *Colpocoryphe* Novák in Perner, 1918 in the Ordovician of the Prague Basin

Species	Formation	Number of specimens
Colpocoryphe zarumila Šnajdr, 1988	Klabava	<10
Colpocoryphe bohemica (Vaněk, 1965)	Šárka	>500
Colpocoryphe inopinata (Novák in Perner, 1918)	Šárka	±60
Colpocoryphe zmudai Vaněk, 1995	Šárka	<10
Colpocoryphe prima (Barrande, 1872) [= *C. adisol* Šnajdr, 1985]	Dobrotivá	±50
Colpocoryphe grandis grandis (Šnajdr, 1956)	Libeň	±150
Colpocoryphe grandis arecuna Šnajdr, 1988	Letná	±60

The exoskeleton is preserved in a prone attitude; it is 9.7 mm long (sag.) and reaches 5.1 mm in maximum width (tr.). The width of the axial region of the thoracic segments ranges from 2.2 mm in the first segment to 1.1 mm in the tenth segment. The glabella is broken off, revealing an external mould of a complete hypostome. Posteriorly the axial part of the internal mould preserves a slightly narrowing tube-like structure, which we interpret as a remnant of the alimentary canal.

Alimentary canal. A comparatively narrow, three-dimensionally preserved tube-like relic is visible inside the thoracic and pygidial axes. This centrally placed and nearly parallel-sided tube extends from the posteriormost part of the glabella, through the occipital ring to the sixth thoracic segment. In the seventh and eighth segments, the alimentary canal bends to the left and seems to be interrupted in the ninth and tenth segments (G in Fig. 3B). Remains of the alimentary canal reappear in the left anterolateral part of the pygidial axis. The alimentary canal is visible on the occipital ring, but its anterior continuation on the glabella is not known, as the axial part of the cephalon shows only the lower ventral surface of the hypostome (Hy in Fig. 3B). The major part of the glabella is broken off and consequently the anteriormost parts of the alimentary canal are preserved only in narrow postero-lateral borders of the glabella, where imprints of two cephalic gut diverticulae are seen on the left side (Dc2 and Dc3 in Fig. 3B); one cephalic gut diverticula is developed in the right side (Dc3 in Fig. 3B). Small cavities developed left and right from the gut in the occipital ring most probably belong to thoracic gut diverticulae (Dt1 in Fig. 3B).

In dorsal view, the transversal width of the alimentary canal ranges from 0.47 to 0.52 mm in the thorax. The canal is narrower in the pygidium, where it measures only about 0.4 mm in tr. width. In dorsal and lateral views, the alimentary canal shows a bead-shaped contour.

Locality. This specimen was collected by the junior author (M. D.) at a small field SW of Mýto – rybník svatého Štěpána (= St. Stephan pond; locality 1 in Fig. 1B).

Remarks. Because of relatively poor preservation, this specimen is affiliated to *Colpocoryphe bohemica* only tentatively. Assignment to this species is, however, the most parsimonious because the two other species identified from the Šárka Formation, *C. inopinata* (Novák in Perner, 1918) and the poorly known *C. zmudai* Vaněk, 1995, have been found only from the eastern part of the Prague Basin. In addition, these species are very rare, whereas *C. bohemica* is known from several hundred specimens (see Table 1).

Specimen WBM S 06 160, *Colpocoryphe bohemica* (Vaněk, 1965)
Figure 4

Description. The posterior five thoracic segments are articulated with the pygidium. The preserved part of the exoskeleton is 9.4 mm long (sag.) and 8.8 mm wide (tr.); the pygidium measures 4.8 mm in sag. length and 6.4 mm in tr. width. The axis of the thoracic segments as well as the pygidial axis display a distinct, axially placed, three-dimensionally preserved tube-like relic (Fig. 4), which we interpret as a remnant of the alimentary canal.

Alimentary canal. This structure extends through the thorax and pygidium to the axial tip. In dorsal view, the transversal width of the alimentary canal ranges around 1.4 mm in the thorax, being narrower in the pygidium, where it measures only about 0.85 mm in tr. width. The alimentary canal shows a bead-shaped contour in dorsal as well as in lateral view (Fig. 4). Fine and short transversal constrictions producing the bead-shaped contour of the alimentary canal seem to be related to the segmentation of the exoskeleton.

Although only incompletely preserved, this specimen shows morphological features indicating that it was partly or fully enrolled when entombed. A comparable preservation of the gut in an enrolled Cambrian trilobite *Jiumenia anhuiensis* was recently described and discussed by Zhu et al. (2014), who stressed the importance of enrollment for the preservation of trilobite soft parts.

Locality. This specimen was collected by the late V. Kordule (amateur collector of fossils in Příbram). After his sudden death the sample was purchased by the West-Bohemian Museum in Plzeň in 2010. The outcrop

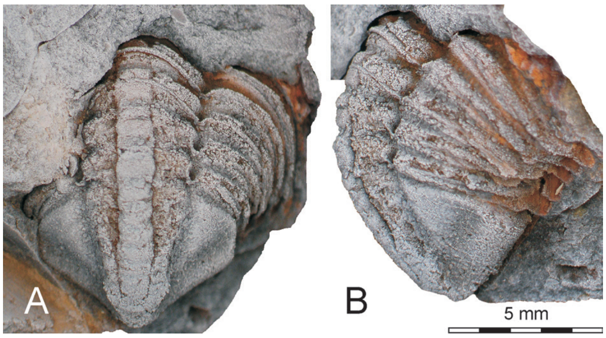

Fig. 4. Internal mould of *Colpocoryphe bohemica* (Vaněk, 1965) from the Šárka Formation (Middle Ordovician, Darriwilian = Oretanian Regional Stage); West-Bohemian Museum in Plzeň, WBM S 06 160; fields near Mýto (locality 1 in Fig. 1B). **A**, dorsal view. **B**, lateral view.

from which the specimen was collected was not registered. However, the lithological characters of the nodule and the composition of the associated fossils agree with concretions occurring in fields north of Rokycany (P. Kraft, pers. comm. 2013; locality 2 in Fig. 1B).

Remarks. The affiliation of this specimen to *Colpocoryphe bohemica* is, in comparison with the previous sample, more reliable because the pygidium has 7–8 rings and a distinct postaxial elevation reaching the pygidial margin.

Based on a comparison with complete specimens of *Colpocoryphe bohemica*, the length (sag.) of the studied specimen is estimated to have been approximately 18 mm. The missing part of the body was likely destroyed during diagenetic processes, because it was situated outside the boundary of the nodule. Such a type of preservation suggests that the nodules were formed during early diagenesis (for a detailed discussion see Dabbard & Loi 2012).

Subfamily FLEXICALYMENINAE Siveter, 1977
Genus *Flexicalymene* Shirley, 1936

Type species. *Calymene blumenbachii* var. *caractaci* Salter, 1865; Marshbrookian, Caradoc (= Sandbian), England. By original designation.

Remarks. Only three Upper Ordovician species of the genus *Flexicalymene* have been recorded from the Barrandian area (Fig. 1C, Table 2). The studied specimen is assigned to *Flexicalymene* (*F.*) *pragensis* Vaněk & Vokáč, 1997, the only species of this genus known from the Bohdalec Formation. The systematic status of *F.* (*F.*) *pragensis* is somewhat problematic, as the species was established on more or less flattened specimens preserved in fine silty shale.

Specimen ČGS MD 007, *Flexicalymene* (*F.*) *pragensis* Vaněk & Vokáč, 1997
Figure 5

Description. The exoskeleton is enrolled and strongly flattened; the cephalon and pygidium are visible on one surface, whereas the articulated thorax is visible on the opposite side of the mould (Fig. 5). Enrolment combined with flattening preclude direct measurement of some dimensions and allows of only approximate assessment of the original size. The specimen reaches 47 mm in maximum width (tr.). The length of the exoskeleton in a prone attitude is estimated to be about 105 mm (sag.).

Alimentary canal. A comparatively narrow but quite prominent swelling is visible along the inner axial surface of the external mould in the middle and posterior parts of the thorax (G in Fig. 5A). A furrow

Table 2. Species of the genus *Flexicalymene* Shirley, 1936 in the Ordovician of the Prague Basin

Species	Formation	Number of specimens
Flexicalymene (*F.*) *incerta* (Barrande, 1846)	Zahořany	>300
Flexicalymene (*F.*) *pragensis* Vaněk & Vokáč, 1997	Bohdalec	±100
Flexicalymene (*F.*) *declinata* (Hawle & Corda, 1847)	Králův Dvůr	>250

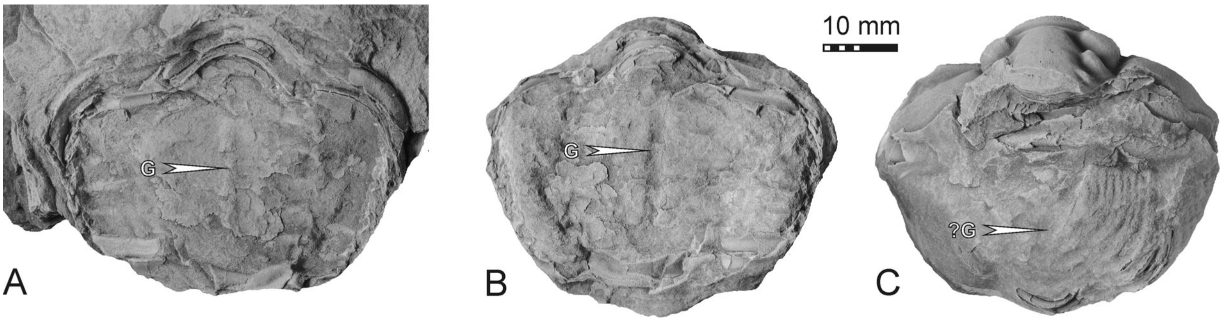

Fig. 5. Morphology of the preserved parts of the digestive system in the thoracic and pygidial regions of *Flexicalymene* (*F.*) *pragensis* Vaněk & Vokáč, 1997 from the Bohdalec Formation (Upper Ordovician, Katian = Late Berounian Regional Stage); Czech Geological Survey Prague, ČGS MD 007; Brumlovka locality (locality 3 in Fig. 1B). **A**, **B**, dorsal views; **C**, anterior view. Abbreviation: G, gut.

of comparable width and length is developed on the surface of the internal mould of the counterpart (G in Fig. 5B). A shallow, poorly cut furrow is seen also in the axial part of the internal mould of the pygidium (?G in Fig. 5C).

We interpret the axially placed and nearly parallel-sided structures that have developed as swellings and furrows as a poorly preserved remnant of the alimentary tract. This tube-like structure occurs in the medial part of the thorax, whereas its anterior continuation in the cephalon is not preserved. In dorsal view, the alimentary canal seems to have a bead-shaped contour, as in the two specimens of *Colpocoryphe* described above (cf. Fig. 4).

Locality. This specimen was recently collected by the junior author (M. D.) at the Brumlovka locality in Prague (locality 3 in Fig. 1B, C).

DISCUSSION

Decay of soft parts

Experiments on modern *Limulus* show that decay of the internal soft parts begins only a few hours after death and lasts for no more than one month (Babcock & Chang 1997; Babcock et al. 2000). The preservation of the gut in both specimens of *Colpocoryphe* and in *Flexicalymene* means that the processes of mineral precipitation leading to the preservation of delicate remains of internal soft parts must have started very early after the entombment of carcasses.

Dabbard & Loi (2012, pp. 100–101) suggested a model, in which the early diagenetic phosphogenesis linked to carbonate fluor-apatite (CFA) precipitation was more intensive in the upper few centimetres (5–10 cm) of sediment under oxic to suboxic conditions. The following silicification invokes a decrease in pH linked to sulphate reduction and pyrite precipitation in the anoxic zone.

Morphology of the alimentary tract

Recently, Lerosey-Aubril et al. (2011) distinguished two major morphological types of the alimentary tract: (1) a simple tube with a crop and (2) a simple tube flanked laterally with metamerically paired caeca (= gut diverticulae). Both morphologies have been found in Ordovician trilobites of the Prague Basin (Fatka et al. 2014).

As in the recently described Cambrian specimen of *Jiumenia anhuiensis* (see Zhu et al. 2014), a bell-shaped, anteriorly narrow glabella is present in *Colpocoryphe*. Metamerically paired caeca could be expected in such a glabella. We also agree with Zhu et al. (2014), who noted that the preservation of the gut as a sediment-like infilling is more common (see also Šnajdr 1991) than the phosphatization of metamerically paired digestive caeca.

Preservation by phosphatization

Two of the studied specimens (ČGS MD 001 and ČGS MD 007) were collected from strongly weathered rocks which preclude chemical analyses. The third specimen (WBM S 06 160) is preserved in a dark grey, comparatively lightly weathered siliceous nodule. We have examined this specimen using scanning electron microscopy (SEM) and energy dispersive X-ray (EDX) analyses with the intention of testing the suspected preservation of the digestive system by phosphatization (see Lerosey-Aubril et al. 2012; Zhu et al. 2014).

The *SEM examination* did not show any apparent differences between the enclosing rock matrix and the internal mould of the trilobite specimen.

The *EDX analyses* were undertaken at four different areas of the rock sample. Two spots were placed inside the supposed gut (guts 1 and 2 in Table 3), and two spots were located outside the trilobite body (matrices 1 and 2 in Table 3). This investigation did not show statistically important differences in the percentages of

Table 3. Results of the energy dispersive X-ray (EDX) analyses performed on the gut and the surrounding sediment. The composition is expressed in weight percentage (wt%). Some elements were not detectable and/or the estimated proportions was below the equipment's lower limit of reliability (referred as n)

Sample	C	O	Na	Mg	Al	Si	P	S	K	Fe
Matrix 1	7.26	53.91	n	n	4.42	29.02	9.54	6.86	1.04	3.26
Matrix 2	12.26	49.00	n	n	4.1	17.1	0.55	0.73	0.96	14.23
Gut 1	31.54	43.69	0.37	n	1.47	13.1	n	n	0.35	8.1
Gut 2	25.72	49.22	n	10	1.02	18.14	n	n	n	4.41

most of the analysed elements. The chemical composition of the material in the supposed gut and the surrounding rock matrix are very similar (Table 3).

The only exception is the distinctive enrichment by C and the relative depletion of Al inside the supposed gut. The interpretation of these data is quite difficult as the content of all other elements varies only very slightly. We do not have any explanation for the depletion of Al. It could not be excluded, however, that the enrichment by C reflects the differences in the initial composition of the bottom mud (= surrounding matrix) and the gut filled by partly digested food particles.

CONCLUSIONS

Two specimens belonging to *Colpocoryphe* show a simple tube in the occipital ring as well as in all thoracic segments and in the pygidium. In a complete specimen of *Colpocoryphe*, possible relics of two cephalic diverticulae and one thoracic diverticula are visible.

The glabella expands posteriorly and thus a simple gut associated with gut diverticulae is the preferred morphology of the intestine in *Colpocoryphe* (Fig. 6).

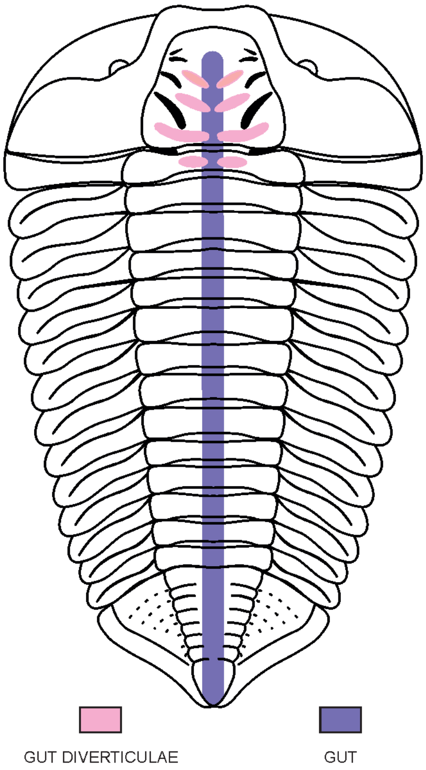

Fig. 6. Reconstruction of the morphology of the preserved parts of the digestive system in the cephalic, thoracic and pygidial regions of *Colpocoryphe* in dorsal view.

The anterior part of the digestive tract is not preserved in *Flexicalymene*, but the posterior part shows a morphology comparable with that of *Colpocoryphe*.

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Barrandeumi piirkonnas Tšehhi Vabariigis Ordoviitsiumi trilobiitidel *Colpocoryphe* ja *Flexicalymene* leitud seedetrakti elemendid

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Seedetrakti elemente leiti kahel eksemplaril tavaliselt rohkesti esineval calymenoidsel trilobiidil *Colpocoryphe* Novák in Perner, 1918 Kesk-Ordoviitsiumi Šárka kihistust ja ühel eksemplaril *Flexicalymene* (*Flexicalymene*) *pragensis* Vaněk & Vokáč, 1997 Ülem-Ordoviitsiumi Bohdaleci kihistust. Kõik kolm leidu jäävad Praha basseini piiresse. *Colpocoryphe* liigendatud välisskeleti sisevalatis näitab maojärgset torujat seedekulgla osa, mis on säilinud kuklalüli piirkonnas, samuti kõigil rindmiku ja pügiidiumi lülide telgmises osas. Seedekulgla eesmist osa tuntakse halvasti, sest hüpostoomi paiknemine takistab vaatlust. Teine, ebatäielik eksemplar koosneb viiest tagarindmiku lülist, mis on liigendatud pügiidiumiga. Nende telgmises osas on selgesti eristatav segmenteeritud torujas moodustis, mida tõlgendatakse jämesoolena. Keerdunud asendis *Flexicalymene pragensis*'e eksemplaril on seedekulgla elemendid halvasti säilinud, kuid on siiski jälgitavad kesk- ja tagarindmiku ning pügiidiumi eesosa telje alal. Calymenidae seedetrakti elemente ei ole varem kirjeldatud. On kommenteeritud varasemaid analoogilisi leide teiste sugukondade trilobiitidel Barrandeumi piirkonnas.