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# Remains of the digestive system in the middle Cambrian trilobite *Ptychoparioides henkli* Kordule, 2006 (Barrandian area, Czech Republic)

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**ABSTRACT**
Preservation of the digestive system in trilobites is extremely rare: from the Barrandian area, such remains have been recorded in two Cambrian and eight Ordovician trilobite genera. In this contribution we describe eight new examples of articulated trilobites displaying remains of the digestive system in the axial parts of the cephalon and thorax from the middle Cambrian Buchava Formation of the Skryje-Týřovice Basin. All studied specimens are identified as *Ptychoparioides henkli* Kordule, 2006 and exhibit up to four pairs of cavities or light-coloured markings under the central and posterior parts of the glabella, one pair in the occipital ring and up to six pairs in the axis of the anterior thoracic segments. These cavities or light-coloured markings are interpreted as remains of metamerically paired digestive caeca of the «perigastric organ». An anteriorly rounded, posteriorly widely V-shaped body preserved in the frontal glabellar lobe of a conical glabella in one specimen most probably represents a remnant of the foregut chamber. These specimens constitute the first example of digestive structures observed in Cambrian ptychopariid trilobites in the Barrandian area. A dark-coloured axial surface preserved in eight thoracic segments between and behind paired cavities or markings is present in two specimens; this surface is interpreted as remains of the hindgut. The occurrence of trilobites preserving digestive-system remains together with locally abundant articulated echinoderms and ontogenetic stages of trilobites, as well as previously described bivalved arthropods, confirm that the depositional environment of the Buchava Formation was favourable for exceptional preservation of fossils, including soft-tissue preservation.

**KEY WORDS**
Trilobita,
Drumian,
digestive system,
Barrandian area,
Skryje-Týřovice Basin,
Czech Republic.

**RÉSUMÉ**
*Restes du système digestif du trilobite du Cambrien moyen* Ptychoparioides henkli *Kordule, 2006 (région du Barrandien, République tchèque).*
La conservation du système digestif des trilobites est extrêmement rare : dans la région du Barrandien, de tels restes ont été découverts, correspondant à deux genres de trilobites du Cambrien et huit genres de l'Ordovicien. Nous décrivons huit nouveaux exemples de trilobites articulés présentant des restes de système digestif dans les parties axiales du céphalon et du thorax. Tous proviennent de la Formation de Buchava (Cambrien moyen), du bassin de Skryje-Týřovice. L'ensemble des spécimens étudiés sont identifiés comme *Ptychoparioides henkli* Kordule, 2006 et présentent jusqu'à quatre paires de cavités ou de marques de couleur claire sous les parties centrale et postérieure de la glabelle, une paire dans l'anneau occipital et jusqu'à six paires dans l'axe des segments thoraciques antérieurs. Ces cavités, ou marques de couleur claire, sont interprétées comme des restes de *caeca* digestifs appariés métamériquement de « l'organe périgastrique ». Chez un spécimen, un corps arrondi à l'avant, et en forme de large V à l'arrière, conservé dans le lobe glabellaire frontal d'une glabelle conique, représente très probablement un vestige de la chambre de l'intestin antérieur. Ces spécimens constituent le premier exemple de structures digestives observées chez les trilobites ptychopariidés du Cambrien dans la région barrandienne. Une surface axiale de couleur foncée préservée dans huit segments thoraciques entre et derrière des cavités ou des marques appariées est présente dans deux spécimens ; cette surface est interprétée comme des restes de l'intestin postérieur. La présence de trilobites présentant des restes de système digestif, d'échinodermes articulés (localement abondants), de stades ontogénétiques de trilobites, ainsi que d'arthropodes bivalves décrits dans une étude précédente, confirment que l'environnement de dépôt de la Formation de Buchava était favorable à une conservation exceptionnelle des fossiles, y compris des tissus mous.

**MOTS CLÉS**
Trilobita,
Drumien,
système digestif,
région barrandienne,
bassin de Skryje-Týřovice,
République tchèque.

## INTRODUCTION

Exceptionally preserved specimens from the lower Paleozoic strata of the Barrandian area (Czech Republic) have significantly contributed to the documentation of poorly sclerotized and soft-bodied organisms (e.g. Chlupáč 1988; Rak *et al.* 2009; van Roy *et al.* 2021, 2022), including the morphology of trilobite digestive systems (Budil & Fatka 2022). Remains of trilobite digestive structures have been described or illustrated in two Cambrian and eight Ordovician trilobite genera. Three specimens of *Ptychoparia* Hawle & Corda, 1847 showing digestive-system remains were mentioned or briefly discussed by Jaekel (1901a), Šnajdr (1958) and Kordule (2006), and two specimens of *Conocoryphe* Hawle & Corda, 1847 with some gut preservation were figured by Budil & Fatka (2008) and Fatka *et al.* (2008). Detailed analyses of these five specimens were, however, not published.

Specimens of the Late Ordovician trilobite *Deanaspis goldfussii goldfussii* (Barrande, 1846) with remains of the digestive system interpreted as a crop associated with gut were described for the first time by Beyrich (1846). The original specimens and other materials were figured or discussed by Barrande (1852), Přibyl & Vaněk (1969), Šnajdr (1990, 1991), Shaw (1995), Lerosey-Aubril *et al.* (2011) and Fatka & Budil (2022). Šnajdr (1991) figured and briefly described one specimen of *Dalmanitina socialis* (Barrande, 1846) with a narrow grey strip interpreted as gut remains. Several other specimens with remains of the digestive system were recently studied by Fatka *et al.* (2024). One specimen of the Early Ordovician harpidid *Harpides grimmi* (Barrande, 1852) was described by Fatka *et al.* (2013b). From Middle Ordovician strata, two specimens of *Colpocoryphe bohemica* (Vaněk, 1965) and one specimen of the bathycheilid *Prionocheilus vokovicensis* (Šnajdr, 1956) were studied by Fatka *et al.* (2015) and Fatka & Budil (2018). Fatka *et al.* (2013a, 2015) described gut remains in three Late Ordovician trilobites, particularly in the odontopleurid *Selenopeltis buchi* (Barrande, 1846), *Birmanites*? *ingens* (Barrande, 1852) and *Flexicalymene* (*Flexicalymene*) *pragensis* Vaněk & Vokáč, 1997. Recently, crops and gut remains were discovered in several specimens of the Middle Ordovician dionidid *Trinucleoides reussi* Barrande, 1872 (Fatka and Budil, unpublished data).

In this contribution, we described eight articulated specimens of *Ptychoparioides* Růžička, 1940 showing well-preserved remains of digestive structures. These specimens were collected from the Buchava Formation at the "Jestřábí" locality on the slope of the Dlouhá hora Hill.

## EXCEPTIONALLY PRESERVED FOSSILS IN THE BUCHAVA FORMATION

The trilobites described herein that exhibit remains of the digestive system are not the only exceptionally preserved specimens collected from the Buchava Formation. Exceptionally preserved fossils have been described from numerous levels of this unit; for example, Jaekel (1901a) figured and discussed an internal mould of *Ptychoparia dubinka* Kordule, 2006 with partly preserved remains of the digestive system from the Pod trním locality. Lower

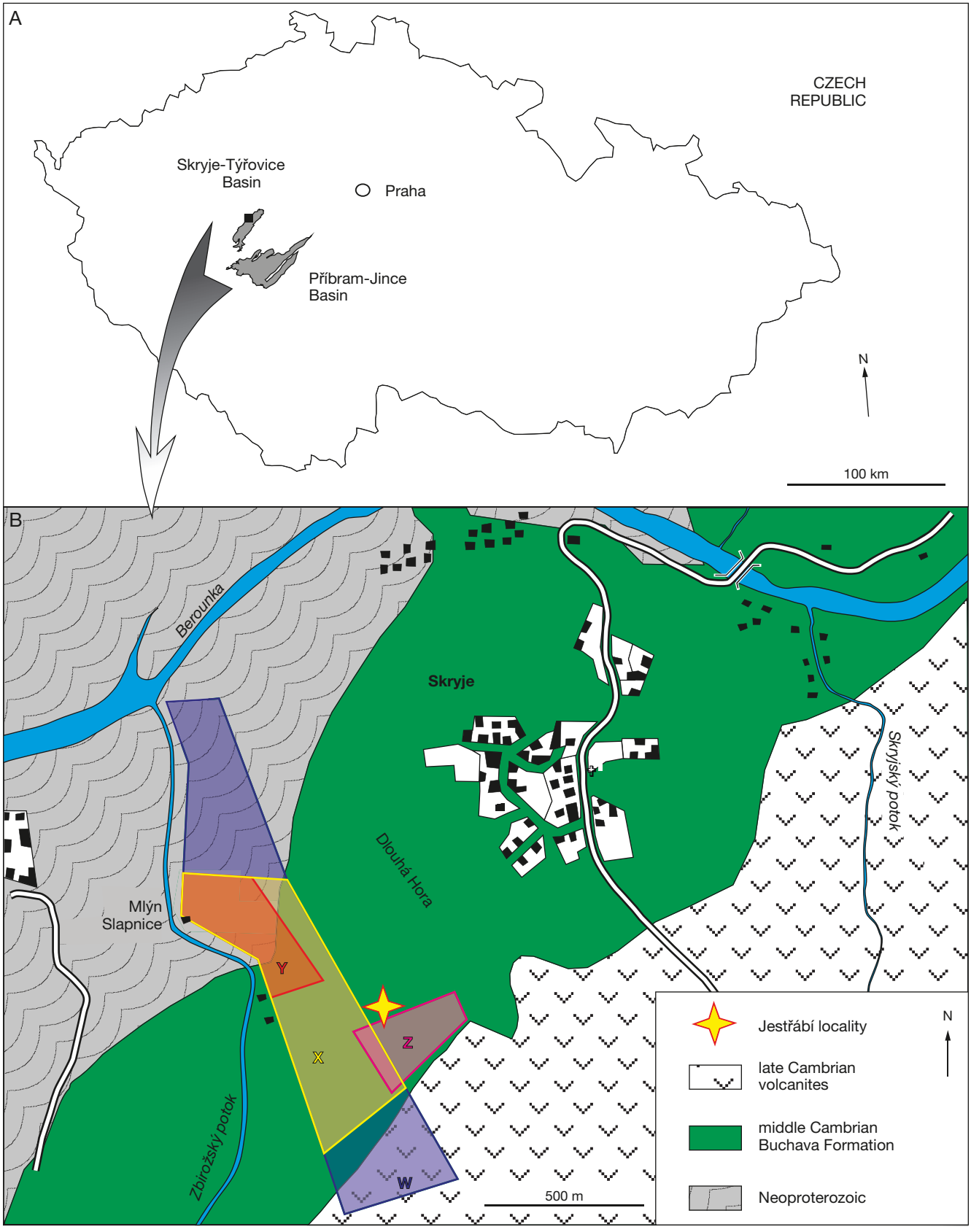


FIG. 1. — Maps showing the collecting location of the studied trilobite material: **A**, The Czech Republic and Cambrian rocks of the Skryje-Týřovice and Příbram-Jince basins; **B**, Detailed map showing the distribution of the middle Cambrian Buchava Formation in the vicinity of Skryje and the location of the "Jestřábí" locality. Geology modified after Mašek *et al.* (1997) and Vorel *et al.* (2018). The positions of sections on the right bank of the Zbirožský potok brook were described by: **W**, Jahn (1896: 734-741, fig. 8); **X**, Kettner (1923: fig. 1), **Y**, Kettner (1923: fig. 3); **Z**, Jarka (1941). Figure by O. Fatka.

stratigraphic levels of the Slapnice Member contain rare remains of the pterobranch *Rhabdotubus robustus* Maletz, Steiner & Fatka, 2005 and the bizarre metazoan *Wiwaxia* sp. cf. *W. corrugata* (Matthew, 1899), see Maletz *et al.* (2005) and Fatka *et al.* (2011a).

Articulated eocrinoid, stylophoran and cinctan echinoderms collected at several outcrops in middle and higher stratigraphic levels of the Skryje Member were studied by Barrande (1846, 1887), Jaekel (1901b), Ubaghs (1967a, b), Prokop & Fatka (1985) and Parsley & Prokop (2004). Locally abundant hyolith conchs with either an *in situ* operculum and helens or a conch associated with the operculum were studied by Marek (1981), Valent *et al.* (2012) and more recently by Martí Mus & Bergström (2005); these fossils occur at several stratigraphic levels. Higher levels of the Skryje Member contain rare specimens of Burgess Shale-type organisms, such as the non-biomineralized bivalved arthropod *Tuzoia* Walcott, 1912 (see Fatka & Herynk 2016). An ichnofossil preserved behind the posterior part of its assumed tracemaker, an intact exoskeleton of the trilobite *Agraulos ceticephalus*, was interpreted as a fodichnial association by Fatka & Szabad (2011).

### Succession at the Dlouhá hora Hill near Skryje

Numerous natural exposures and excavations on the eastern slope of the Dlouhá hora Hill (Fig. 1B) have been studied during the last 150 years by Jahn (1896, 1897), Jarka (1941), Šnajdr (1958), Kordule (2006), Fatka *et al.* (2011a, b) and Vorel *et al.* (2018). The exposed succession is about 180 m thick; the lower levels contain poorly fossiliferous deposits of the *Pompeckium kuthani* brachiopod Zone (see Jahn 1897; Havlíček 1971). Higher in the succession, the first valves of the stratigraphically important brachiopod *Bohemiella romingeri* appear, associated with poor remains of other skeletal organisms. Higher yet in the succession, the first remains of the abundant trilobites *Paradoxides* (*E.*) *pusillus* (Barrande, 1846) and *Paradoxides* (*Hydrocephalus*) *carens* (Barrande, 1846) are associated with abundant brachiopods (*B. romingeri* (Barrande, 1846)) and a moderately diverse fauna dominantly consisting of trilobite remains (*Conocoryphe* Hawle & Corda, 1847, *Ctenocephalus* Hawle & Corda, 1847, *Paradoxides* Brongniart, 1822, *Ptychoparia* Hawle & Corda, 1847, *Skreiaspis* Růžička, 1946, *Lobocephalina* Růžička, 1940, *Ptychoparioides* Růžička, 1940, *Ellipsocephalus* Zenker, 1833, *Jincella* Šnajdr, 1957), agnostids (*Peronopsis* Hawle & Corda, 1847, *Phalagnostus* Howell, 1955), echinoderms (*Ceratocystis* Jaekel, 1901, *Lichenoides* Barrande, 1846, *Trochocystites* Barrande, 1887) and hyoliths (*Buchavalites* Marek, 1975, *Maxilites* Marek, 1972, *Slapylites* Marek, 1980). In the upper part of the exposed succession, the association is supplemented by *Sao hirsuta* (Barrande, 1846) and *Solenopleurina tyrovicensis* Růžička, 1939 (see Jarka 1941: 8). However, the youngest levels of the sections are poorly accessible, because they are covered by weathered erosion debris.

Barrande (1887) and his collectors designated material collected in the area of the Slapnice mlýn Mill and Dlouhá hora Hill as "*Slap*" or "*Slapy*" (see Šnajdr 1958: 26; Chlupáč 1999: 11). Outcrops in the wider surroundings of the hillslope Dlouhá hora Hill were studied for the first time by Jahn (1896: 734-741, fig. 8), who published a detailed description of part of the section on the right bank of the Zbirožský potok brook; the section starts not far from the Berounka River and continues around the mlýn Slapnice mlýn Mill to the north-eastern slope of the Dlouhá hora Hill (Fig. 1B[W]). Only two years later, Jahn (1897: 15-16) briefly discussed his newest fossil finds at the Dlouhá hora Hill section and reported for the first time the occurrence of the stratigraphically important brachiopod *Orthis kuthani* (Pompeckj, 1896) (basionym: *Pompeckium kuthani* Pompeckj, 1896) from lower stratigraphic levels of the section. A section approximately 1600 m long along the Zbirožský potok brook valley was studied by Kettner (1923: fig. 1), who published a schematic drawing of this section starting in Proterozoic rocks in the Berounka River valley and reaching the volcanites of the Křivoklát-Rokycany Volcanic Complex (Fig. 1B[X]). In that contribution, the Cambrian part of the section was elaborated in greater detail (Kettner 1923: fig. 3; Fig. 1B[Y]). However, only exposures above the bottom of the Zbirožský potok brook, i.e. the lowermost parts of the slope of the Dlouhá hora Hill were considered in detail in the sections studied by Jahn (1896) and Kettner (1923). Jahn (1896: fig. 8) compiled a list of taxa established in the Dlouhá hora Hill section; this list was partly repeated by Pompeckj (1896: 566-567). The only detailed list of taxa collected from numerous isolated outcrops on the hill-slope of the Dlouhá hora Hill (Fig. 1B[Z]) was compiled by Jarka (1941: 13).

### The "Jestřábí" locality

Three narrow and forested valleys cut the slope on the right side of the Zbirožský potok brook above the cottage area Na slapnici (between localities no. 22 and 23 of Fatka *et al.* 2011a). In the margin of the middle valley, a small area of debris containing small (*c.* 15 cm diameter) rock fragments was accessible (Fig. 1B). This margin of the forest is called "Jestřábí". The upper part of the middle valley and the surrounding forest and fields do not contain natural outcrops of Cambrian sediments. The material at the "Jestřábí" locality could have originated from two possible sources: 1) rock fragments were carried from the surrounding fields and deposited at the margin of the forest; or 2) rock fragments were generated during reconstruction of the old nearby forest-trail.

Within the rock fragments, three lithotypes could be distinguished: 1) hard quartz sandstone, which does not contain fossil remains; 2) sandy, light green greywacke characterised by abundant internal and external moulds of articulated specimens of the ptychopariid trilobite *Ptychoparioides henkli* Kordule, 2006 associated with disarticulated remains of other trilobites and rare articulated eocrinoid echinoderms; and 3) grey-blue shale containing disarticulated trilobites together with abundant specimens of the brachiopod *Bohemiella romingeri*.

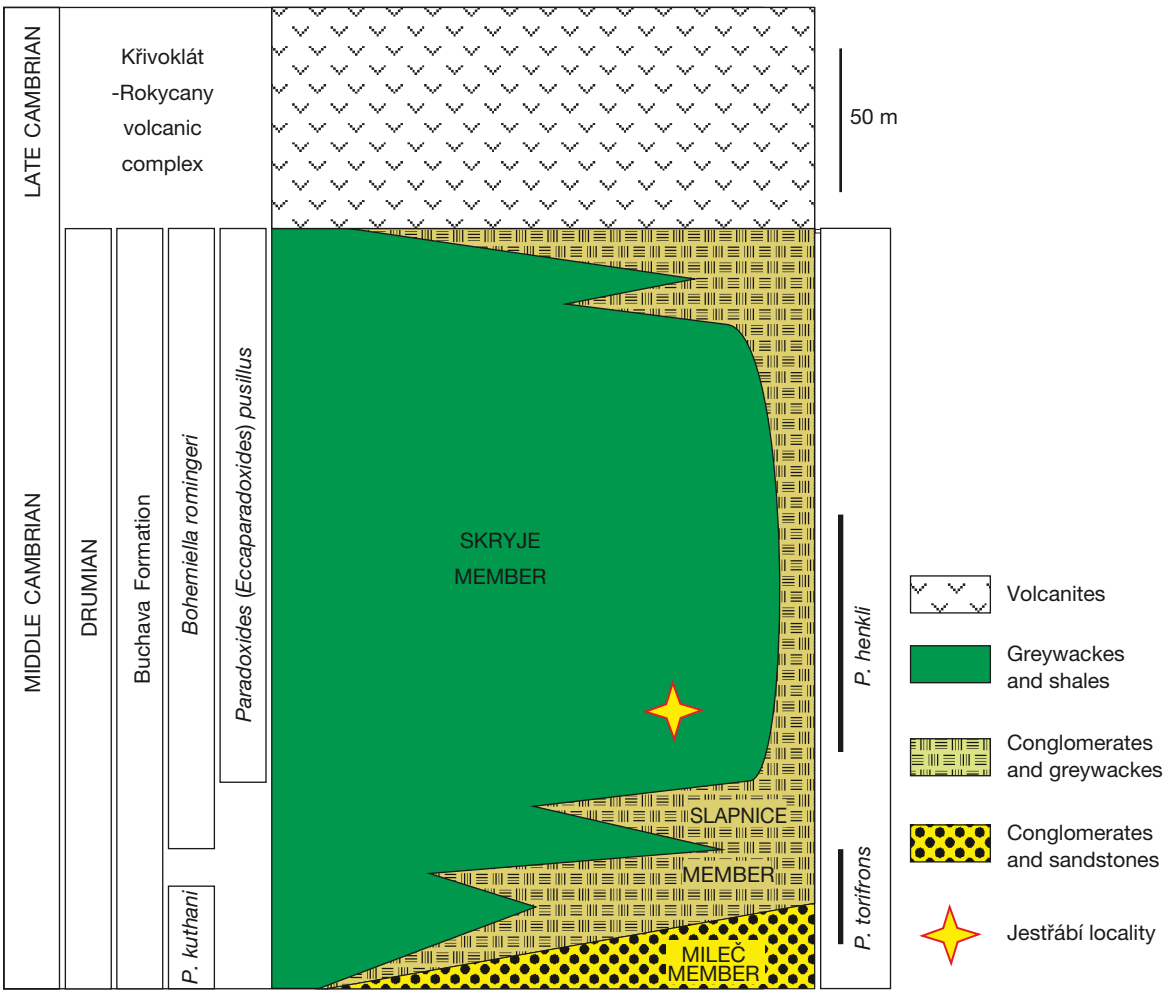


FIG. 2. — Synthetic stratigraphic column of the Buchava Formation (Drumian) in the Skryje-Týřovice Basin with the stratigraphic position of the "Jestřábí" locality and the distribution of *Ptychoparioides torifrons* (Pompeckj, 1896) and *P. henkli* Kordule, 2006 marked. Diagram modified after Fatka *et al.* (2011a). Figure by O. Fatka.

## MATERIAL AND REPOSITORY

All studied specimens of *Ptychoparioides henkli* were collected at the "Jestřábí" locality by one of the authors (VM) in the years 2007 to 2009. The "Jestřábí" locality lies in the middle stratigraphic levels of the Buchava Formation, corresponding to the lower part of the *Paradoxides* (*Eccaparadoxides*) *pusillus* Zone (Fig. 2). These levels of the Buchava Formation are correlated with the Drumian Stage (Geyer *et al.* 2008).

All studied samples are housed in the collections of the Czech Geological Survey, Prague, under inventory no. CGS MV 26 to CGS MV 32.

## METHODS AND TERMINOLOGY

The methods used to analyse the studied specimens included standard light microscopy of internal moulds using a NIKON SMZ 1500 microscope (Nikon Corporation, Amstelveen, Netherlands). Photographs were taken using a NIKON D 300 digital camera (Nikon Corporation, Ayuthaya, Thailand). Internal moulds of eight specimens were photographed both uncoated and coated with ammonium chloride; subsequently, the internal moulds were compared with the photographs. Finally, the results of the comparison were applied to produce detailed descriptions and interpretative line drawings made using Corel Draw X3.

### TERMINOLOGY

The terminology used herein follows that proposed by Whittington & Kelly (1997), Lerosey-Aubril *et al.* (2017) and Cervellione *et al.* (2017), and includes the following abbreviations:

| | |
|---|---|
| CE | cephalic shield; |
| Dc | cephalic digestive glands; |
| Dt | thoracic digestive glands; |
| FC | foregut chamber; |
| GL | glabella; |
| HY | hypostome; |
| FL | frontal glabellar lobe; |
| L1 to L3 | lateral glabellar lobes; |
| MG | midgut; |
| OR | occipital ring; |
| PO | perigastric organ; |
| PY | pygidial shield; |
| sag. | sagittal; |
| tr. | transverse; |
| TS | thoracic segment. |

Numbers of cephalic digestive glands follow the numbering used recently by Lerosey-Aubril *et al.* (2017).

The term perigastric organ (PO) is used for cephalic and thoracic digestive glands (Dc and Dt) in the same way as for decapods by Cervellione *et al.* (2017). Similarly, we apply the descriptive term foregut chamber (FC) as used by McLaughlin (1983) and other authors.

## SYSTEMATICS

Class TRILOBITA Walch, 1771
Order PTYCHOPARIIDA Swinnerton, 1915
Suborder PTYCHOPARIINA Richter, 1932
Superfamily PTYCHOPARIOIDEA Matthew, 1887
Family PTYCHOPARIIDAE Matthew, 1887
Subfamily PTYCHOPARIINAE Matthew, 1887

Genus *Ptychoparioides* Růžička, 1940

TYPE SPECIES. — *Solenopleura torifrons* Pompeckj, 1896 by original designation, Drumian, Buchava Formation, Mileč Member, *Pompeckium kuthani* brachiopod Zone.

SPECIES INCLUDED. — Three species of the endemic genus *Ptychoparioides* have been described: two species (*Ptychoparioides torifrons* (Pompeckj, 1896) and *Ptychoparioides henkli* Kordule, 2006) are known from the Skryje-Týřovice Basin, and the third (*Ptychoparioides chlupaci* Kordule, 2006) was established only in the Příbram-Jince Basin.

### REMARKS

*Ptychoparioides torifrons* (Pompeckj, 1896) comes from higher levels of the Mileč Member and lower layers of the Slapnice Member of the Buchava Formation (Fig. 2). Kordule (2006: 292) reported the occurrence of this species from five outcrops: the Malá Pleš locality near Kouřimecká hájovna; the Na Kamenných hůrkách locality near Týřovice; the slopes of Mileč Hill; the Slapnický mlýn Mill locality and the Hlohovice locality. Vokáč (1997: pl. 1, fig. 6) and Vokáč & Micka (2004: 14) discussed one slightly damaged cephalon of this species from the Terešovská huť locality.

*Ptychoparioides henkli* was described from the lower part of the *Paradoxides* (*Eccaparadoxides*) *pusillus* Zone at the hillslope of the Dlouhá hora Hill (Figs 1; 2). The species is also present at unspecified outcrops on the hill slope of the Dlouhá hora Hill, at the Dubinky Hill locality, at outcrops near the Podmokelský mlýn Mill, and at the Mlečice locality (= Terešovská huť locality) (Kordule 2006: 294).

Rare finds of *Ptychoparioides chlupaci* Kordule, 2006 have been documented from the lower and middle parts of the *Paradoxides* (*Eccaparadoxides*) *pusillus* Zone of the Jince Formation at the Potůček and Ve žlutých localities near Rejkovice (see Kordule 2006: 296).

### MATERIAL EXAMINED

A total of approximately 40 outstretched, very slightly to substantially damaged but originally fully articulated exoskeletons of *Ptychoparioides henkli* were collected from rock fragments of sandy light-green greywacke at the "Jestřábí"' locality. It is possible that all trilobites were preserved in one large cluster. All specimens belong to the holaspid growth stage and contain remnants of digestive structures. We selected eight specimens showing the best-preserved remains of the digestive system for detailed study.

## RESULTS

### SPECIMEN CGS MV 32 (Figs 3; 10D)

*Description*

A nearly complete, anteriorly slightly damaged cephalon with both *in situ* preserved librigenae is articulated with fourteen thoracic segments; left pleura of the ninth to fourteenth thoracic segments are not exposed, the pygidium is missing (Fig. 3A, B)

*Soft tissue*

The central and posterior glabellar surface bears three pairs of clearly visible, rounded, white-coloured markings positioned in L1 to L3 (Figs 3; 10D[Dc1 to Dc3]); slightly larger markings are preserved also in the occipital ring (Figs 3; 10D[Dc0]) as well as in the axial part of the six anterior-most thoracic segments (Figs 3; 10D[Dt1 to Dt6]).

The central area between the white markings is widest and uncoloured in the glabella. In contrast, a quite narrow median strip is seen in the occipital ring and the six anterior thoracic segments (Fig. 3A, B); this narrow strip continues in the seventh and eight axial rings and is slightly darker in colour than the surface of the axial rings (marked only part of outline of the strip, Figs 3A, B; 10D).

*Remarks*

The anterior-most white-coloured left and right markings bear at least three fine, sagittally oriented scratches on its surface. Up to six similarly fine but transversally oriented scratches are seen in the other more posterior cephalic and thoracic white-coloured markings (Fig. 3B). The scratches did not form as a result of mechanical cleaning of the surface and their origin remains unknown.

### SPECIMEN CGS MV 26 (Figs 4; 10B)

*Description*

Incomplete, strongly flattened and considerably damaged remains of a thorax containing eleven articulated axial rings connected with three nearly complete anterior-most pleurae and small remains of other eight pleurae at the left side and ten pleurae at the right side. The posterior part of the strongly damaged cephalon is bent down at an angle of about 70 degrees. The left librigena is strongly weathered but its remains are still preserved *in situ*. A large part of the right librigena is broken off, and only a small part remains. The pygidium and the posterior parts of the thorax are missing.

*Soft tissue*

Small, irregular, whitish spots are preserved in the occipital ring and in the posterior part of the incomplete glabella (Figs 4; 10B[Dc0 and Dc1]). The flattened, only slightly vaulted axial

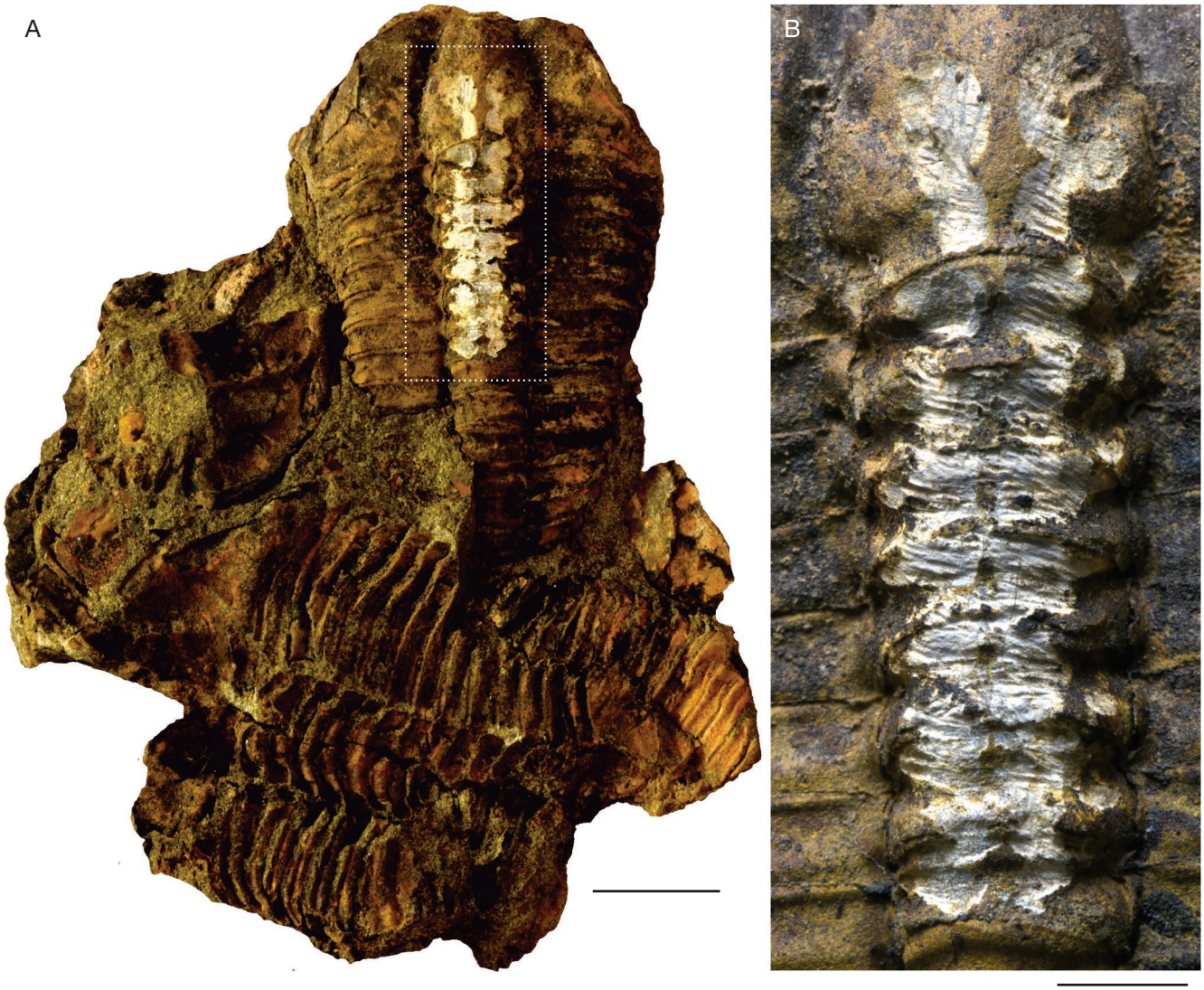


Fig. 3. — *Ptychoparioides henkli* Kordule, 2006, CGS MV 32, incomplete, moderately damaged cephalon articulated with thirteen thoracic segments. Specimen coated in ammonium chloride sublimate prior to photography: **A**, general view; **B**, detailed view. Scale bars: A, 10 mm; B, 5 mm. Photos by P. Budil, arranged by O. Fatka.

rings bear prominent light markings in the first to the sixth thoracic segments (Fig. 4). These markings are paired and range from small and rounded (Figs 4; 10B[Dt5r]) through ellipsoidal and sagittally prolonged (Fig. 10B[Dt4r]) to large and rounded (Fig. 10B[Dt6l]). In the first to third thoracic segments, the surface of the axial rings is barely perceptible to be darker between the light markings (Fig. 10B[G]).

Specimen CGS MV 27 (Figs 5; 10A)

*Description*

Strongly damaged but originally complete articulated exoskeleton with remains of both librigenae preserved *in situ* (Fig. 5A). A small remnant of the *in situ* hypostome is seen in the left antero-lateral part of the glabella (Fig. 10A[HY]). The anterior-most part of the cephalon is broken off. The axis and fourteen pleurae are visible at the right side of the thorax, while only four pleurae are preserved at the left thoracic side; four more posterior pleurae are only partially preserved (Fig. 5A). Remains of the axis and pygidial pleural lobe are preserved on the right side (Fig. 5A).

*Soft tissue*

The surface of the flattened glabella bears three white areas in L2 and L3 (Figs 5; 10A[Dc2l, Dc2r and Dc3r]), two other light, quite poorly visible areas are preserved in L1 (Figs 5; 10A[Dc1l and Dc1r]). White spots are seen also in the occipital ring (Figs 5; 10A[Dc0l and Dc0r]). Comparatively small, paired, irregularly elliptical white spots are preserved in the first to fourth axial rings (Figs 5; 10A[Dt1 to Dt6]). The colour of the surface between the paired spots and holes is identical to the colour of other parts of the thorax.

Specimen CGS MV 28 (Figs 6; 10C)

*Description*

Very slightly damaged cephalon with hypostome and both librigenae preserved *in situ* and with eleven incomplete,


Fig. 4. — *Ptychoparioides henkli* Kordule, 2006, CGS MV 26, an incomplete, strongly flattened and damaged specimen preserving eleven thoracic segments: **A**, general view; **B**, detailed view. Scale bars: A, 10 mm; B, 5 mm. Photos by P. Budil, arranged by O. Fatka.

slightly disarticulated and posteriorly retracted thoracic segments; the pygidium and posterior thoracic segments are missing (Fig. 6A). The U-shaped narrow groove in the middle of the glabella represents the posterior margin of the hypostome (Figs 6; 10C[HY]).

*Soft tissue*

One small cavity occurs on each side of the hypostome (Figs 6; 10C[Dc3]). Two pairs of large, polygonal, light-coloured spots are situated in L1 and L2 of the glabella (Figs 6; 10C[Dc1 and Dc2]). Two other light-coloured, irregular areas are present in the occipital ring (Figs 6; 10C[Dc0]). An elliptical, sagittally prolonged grey-coloured spot is preserved in the anterior-most third of the glabella (Figs 6; 10C[E]). Seven small to large, rounded white spots are preserved in the axes of the first to fifth thoracic segments (Figs 6; 10C[Dt1 to Dt5]). The colour of the surface between all the light spots is identical to the colour of other parts of the thorax.

Specimens CGS MV 29a and CGS MV 29b
(Figs 7; 10G)

Remains of two damaged articulated specimens are preserved on the surface of a rock fragment 58.6 mm long, 41.3 mm wide and a maximum of 15 mm thick.

*Description of CGS MV 29a*

The more damaged specimen includes a nearly complete cephalon with both librigenae (Figs 7A; 10Ga), which is articulated with remains of four anterior thoracic segments. A partly exposed external surface of the *in situ* hypostome is seen in the anterior part of the glabella (Figs 7Aa; 10Ga[HY]).

*Soft tissue*

The postero-lateral margins of the hypostome are bordered by a pair of yellow-brown, large, antero-laterally oriented ellipsoidal depressions in L3 (Figs 7A; 10Ga[Dc3]). In L1 and L2, two pairs of yellow-brown spots are seen in the posterior part of the glabella; these spots are shallow, transversally narrow and sagittally short (Figs 7A; 10Ga[Dc1 and Dc2]). The whole surface of the occipital ring and the axis of the anterior thoracic segment are replaced by sagittally short and transversally wide, yellow-brown cavities (Figs 7A; 10Ga[Dc0 and Dt1]). Posteriorly from the hypostome, the central posterior surface of the glabella between Dc3 and Dc0 exhibits a wide sausage-like elevation (Figs 7A; 10Ga[G]). The axis of the fourth thoracic segment as well as all the more posterior thoracic segments and the pygidium are missing.

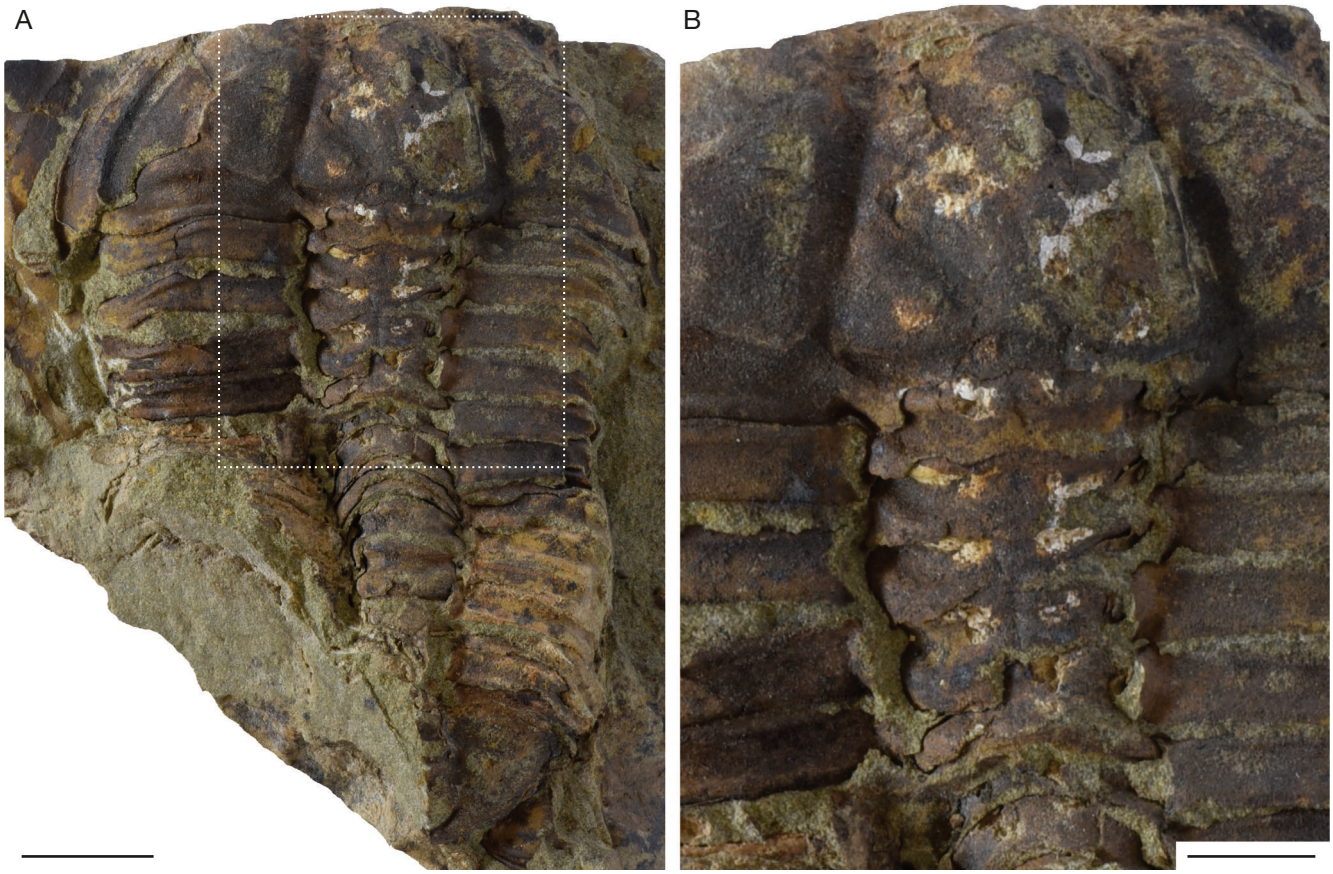


Fig. 5. — *Ptychoparioides henkli* Kordule, 2006, CGS MV 27, strongly damaged articulated exoskeleton with hypostome and remains of both librigenae: **A**, general view; **B**, detailed view. Scale bars: A, 10 mm; B, 5 mm. Photos by P. Budil, arranged by O. Fatka.

*Description of CGS MV 29b*

A strongly damaged and only partly uncovered cranidium is articulated with remains of twelve thoracic segments. The external mould of the *in situ* preserved hypostome is exposed under the broken-off anterior half of the glabella (Figs 7B; 10Gb[HY]).

*Soft tissue*

Inside L3, laterally from the *in situ* hypostome, rounded, yellow-brown spots are developed on both sides of the glabella (Figs 7B; 10Gb[Dc3]); two other yellow-brown, ellipsoidal depressions are present behind the postero-lateral margin of the hypostome (Figs 7B; 10Gb[Dc2]). Generally comparable, transversally slightly wider depressions are also developed in the postero-lateral surface of the glabella in L1 (Figs 7B; 10Gb[Dc1]). The occipital ring is broken off and is replaced by a tiny brown-coloured surface (Figs 7B; 10Gb[Dc0]). The axial parts of the second to fourth thoracic segments are obscured by an external surface of a remnant of an indeterminable trilobite. The axis of the fifth thoracic segment is broken off (Fig. 7B). A rectangular elevated area is clearly visible in the central glabellar surface between the posterior hypostomal margin and the anterior margin of the occipital ring (Figs 7B; 10Gb[G]).

Specimen CGS MV 30 (Figs 8; 10E)

*Description*

A slightly damaged cephalon with both librigenae is preserved together with a damaged thorax consisting of eleven axial rings associated with 14 pleurae on the right side and remains of three pleurae on the left side (Fig. 8A).

*Soft tissue*

A small cavity is seen in the right antero-lateral part of the conical glabella (Figs 8; 10E[Dc3]). Two much larger and deeper cavities are preserved in both L2 of the glabella (Figs 8; 10E[Dc2]). Two additional quite large cavities are developed in the postero-lateral glabellar surface of L1 (Figs 8; 10E[Dc1]). A shallow, ellipsoidal, yellow-coloured cavity is seen in the occipital ring (Figs 8; 10E[Dc0l]). Three pairs of small to large, yellow-coloured cavities are preserved in the axis of the first to third thoracic segments (Figs 8; 10E[Dt1 to Dt3]). Similarly, the axis of the fourth to sixth thoracic segments bears paired, shallow, large depressions (Figs 8; 10E[Dt4 to Dt6]). Below the well-preserved surface of the central part of the glabella, between Dc3r and Dc2l, a sausage-like transversal widening is seen (Figs 8; 10E[G]). In the area between Dc2 and middle of the posterior margin of the anterior glabellar lobe is developed a narrow bulge (Fig. 8B[arrow]). The colour of the

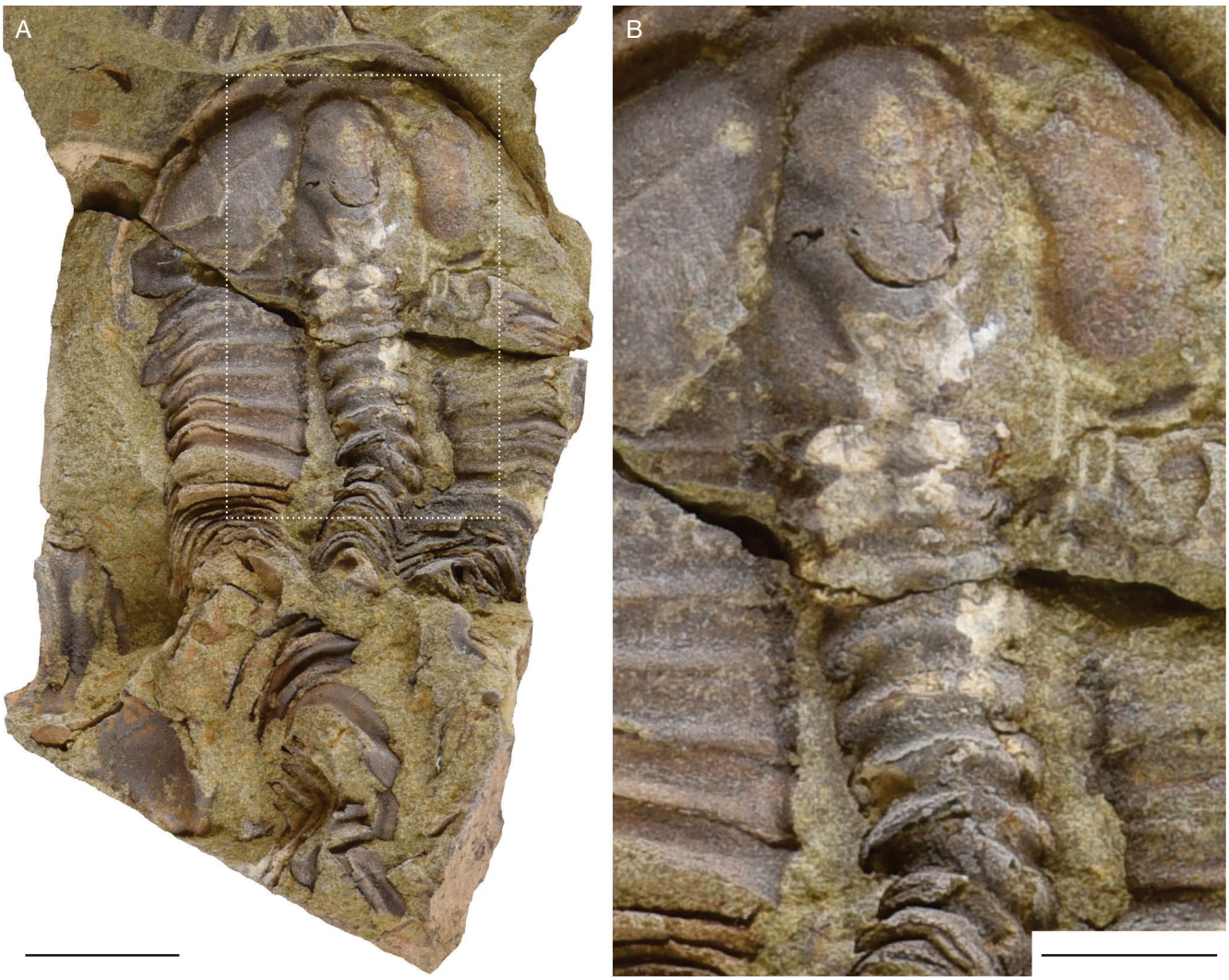


Fig. 6. — *Ptychoparioides henkli* Kordule, 2006, CGS MV 28, specimen consisting of a slightly damaged cephalon with *in situ* hypostome and both librigenae, and an incomplete thorax: **A**, general view; **B**, detailed view. Scale bars: A, 10 mm; B, 5 mm. Photos by P. Budil, arranged by O. Fatka.

surface between the paired cavities is identical to the colour of other parts of the thorax.

Specimen CGS MV 31 (Figs 9; 10F)

*Description*

A polygonal rock sample bears the anterior part of a damaged articulated specimen (Fig. 9A[a]) preserved together with remains of articulated but incomplete thoraxes of four other specimens (Fig. 9A[b to e]). Exceptionally preserved specimen is composed of a very slightly damaged cephalon with both *in situ* librigenae articulated with incompletely preserved remains of the three anterior thoracic segments. Specimen a contains remains of the digestive system; specimens b to e do not show digestive-system remains.

*Soft tissue*

The surface of the well-preserved conical glabella bears an anteriorly arched bulge in the frontal glabellar lobe (Figs 9A, B; 10F). Posteriorly, this bulge continues as a wide, V-shaped, sagittally prolonged and posteriorly gradually narrowing tube-like extension in the central part of the glabella (Figs 9A, B; 10F[G]). At the left side, a small depression is developed in L3 just near the tube-like extension (Figs 9; 10F[Dc3l]). Laterally from the bulge, the course of the V-shaped tube-like body becomes broader in front of Dc3. Even more anteriorly, the bulge is bluntly ended (Fig. 9B[arrow]). A pair of kidney-shaped imprints is seen at both sides of the tube-like extension in the middle of the glabella (Figs 9; 10F[Dc2]). Another pair of small rounded pits is preserved in L1 in the postero-lateral surface of the glabella (Figs 9; 10F[Dc1]). The axis of the first thoracic segment is situated below the chipped-off occipital ring and bears a transversally wide whitish spot (Figs 9; 10F[Dt1r]). A pair of small rounded, whitish spots is seen in the axis of the second, slightly clockwise-rotated thoracic segment (Figs 9; 10F[Dt2]). Another pair of similar, slightly larger spots is preserved in the axis of the third thoracic segment (Figs 9; 10F[Dt3]). The rest of the thorax of this specimen is missing.


Fig. 7. — *Ptychoparioides henkli* Kordule, 2006, CGS MV 29a and CGS MV 29b, two damaged specimens: **A**, specimen CGS MV 29a consists of a nearly complete cephalon with both librigenae articulated and remains of four anterior thoracic segments; **B**, specimen CGS MV 29b is strongly damaged with a partly uncovered cranidium articulated with remains of twelve thoracic segments and with an *in situ* hypostome. Scale bar: 10 mm. Photos by P. Budil, arranged by O. Fatka.

## DISCUSSION

### Morphology of soft tissue in the studied specimens

*Median strip*

A dark-coloured median strip between paired spots occurs on the surface of the glabella and the thoracic axis in two specimens (CGS MV 32, Fig. 3; Fig. 10D[G] and CGS MV 26; Figs 4; 10B[G]). In two other specimens, a wide sausage-like elevation is present in the posterior half of the glabella between Dc1 and the posterior margin of Dc3 (CGS MV 29a, b; Figs 7A, B; 10Ga[G], b[G]).

**Interpretation.** The placement of these structures between paired spots inside the axial part of the glabella makes it possible to interpret them as remains of the centrally placed gut.

*Paired cavities*

All the specimens of *P. henkli* considered in the present work show one to six cavities or whitish or yellow-brown spots arranged in three symmetrical pairs in the glabella. One pair of such spots is also seen in the occipital ring, and up to six pairs of spots occur in the axis of the anterior six thoracic segments. Both cavities and coloured spots are embedded inside the internal moulds. In several specimens, it is evident that paired spots occur immediately below the internal surface of the exoskeleton (Figs 5B[Dt1]; 10A; 6B[Dc1], 10C[Dc1]; 8[Dc2 and Dc1]; 10E[Dc2 and Dc1]).

The surfaces of the coloured spots in the well-preserved specimen CGS MV 32 bear numerous, clearly visible, transversely oriented wrinkles and depressions (Dc0 to Dc3 and Dt1 to Dt6 in Figures 3 and 10D).

**Interpretation.** The arrangement of paired spots combined with their placement inside the axial part of the cephalon and thorax makes it possible to interpret these structures as remains of paired digestive glands. The transversely oriented wrinkles most probably originated during early diagenetic changes of the tissue of the digestive system.


Fig. 8. — *Ptychoparioides henkli* Kordule, 2006, CGS MV 30, a slightly damaged cephalon with both librigenae preserved together with five separate incomplete parts of the thorax: **A**, general view; **B**, detailed view. The arrow in B indicates the low bulge within the glabella. Scale bars: A, 10 mm; B, 5 mm. Photos by P. Budil, arranged by O. Fatka.

*Other structures*

The morphology seen in the anterior half of the glabella of specimen CGS MV 31 (Figs 9A, B; 10F), with an anteriorly arched bulge developed in the middle of the frontal glabellar lobe (Figs 9B[arrow]; 10F[green area]), is remarkable. This bulge continues posteriorly as a V-shaped tube-like prolongation between L3 and L0. In front of Dc3, the tube-like structure (bulge) shows antero-lateral widening and its margin runs to the glabellar furrow.

A very similar configuration, with a low bulge appearing in the middle of the frontal glabellar lobe (Figs 8B[arrow]; 10E[green area]) and continuing to the area between L1, is developed in specimen CGS MV 30 (Fig. 10E). The elliptical, sagittally prolonged white-coloured spot in specimen CGS MV 28 occupies a comparable position in the anterior-most third of the glabella (Figs 6; 10C[E]).

**Interpretation.** The identical morphology preserved in the glabella of these three specimens could be interpreted in the following way:

– the antero-lateral widening developed in the anterior-most part of the glabella most probably represents the remains of a chamber situated in the frontal lobe.

– the arched bulge and/or white spot seen in the posterior margin of the frontal lobe represents the anterior-most part of the gut.

– posteriorly, the gut continues as a sagittally prolonged tube-like extension in the middle and rear parts of the glabella.

*Summary*

The alimentary canal preserved in the middle and posterior parts of the glabella is associated with three pairs of large lobate imprints; the fourth pair occurs in the occipital ring. All these imprints are interpreted as paired cephalic digestive glands, des-

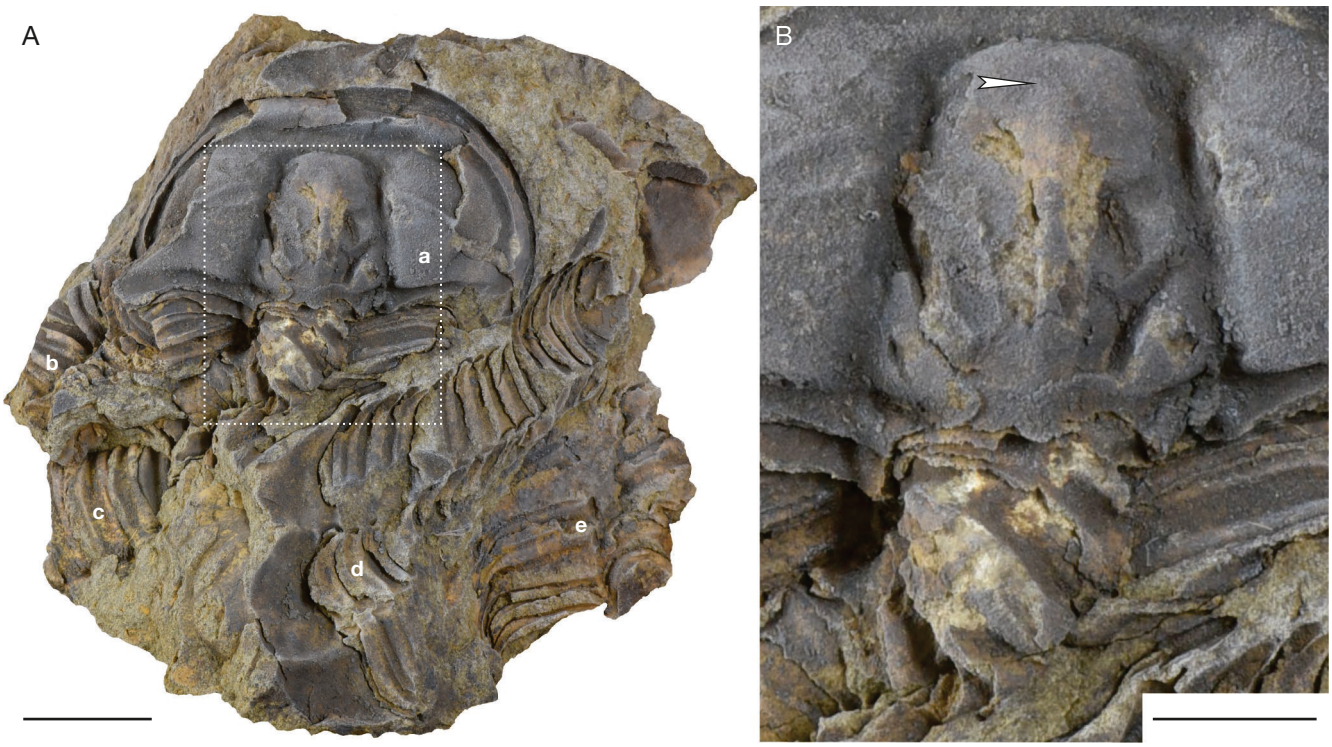


Fig. 9. — *Ptychoparioides henkli* Kordule, 2006, CGS MV 31, anterior part of articulated specimen with remains of incomplete articulated thoraxes of four other specimens: **A**, general view; **B**, detailed view. The arrow in B indicates the bulge within the glabella. **a**, damaged articulated specimen; **b**-**e**, remains of articulated incomplete thoraxes of four specimens. Scale bars: A, 10 mm; B, 5 mm. Photos by P. Budil, arranged by O. Fatka.

ignated Dc0 to Dc3 (Fig. 11). The spots or cavities developed on both sides of the gut in the axial region of the six anteriormost thoracic segments belong to partially preserved, paired thoracic digestive glands, designated Dt1 to Dt6 (Fig. 11). The number of paired digestive glands, and their morphology and positioning, are the same as the remains of the digestive system described in previous work (e.g. Chatterton *et al.* 1994; Lerosey-Aubril *et al.* 2011, 2012; Fatka *et al.* 2013a, b, 2015).

*Final interpretation*

The body in the frontal glabellar lobe we interpret to belong to the foregut chamber. This morphology is consistent with the proposal of Lerosey-Aubril & Peel (2018: 751), who argued that the anteriormost pair of digestive glands occurs immediately posterior to the frontal glabellar lobe. These authors also hypothesised that the digestive glands belong to the midgut and the boundary between the foregut and midgut was located under the posterior margin of the frontal lobe; consequently, the part of the gut associated with paired digestive glands preserved in the cephalon and thorax corresponds to the midgut.

Following Cervellione *et al.* (2017) and Fatka *et al.* (2024), the paired digestive glands in the cephalon (Dc0 to Dc3) and in the thorax (Dt1to Dt6), are together called the "perigastric organ" (Fig. 11).

## Taphonomy

*Formation of the trilobite accumulation*

A large part of the Skryje Shales belongs to the conocoryphid biofacies of Álvaro & Vizcaïno (2003), with episodic common reworked, rarely amalgamated trilobite and brachiopod shells reflecting numerous storm disruption events. Mud deposits with articulated skeletons were accumulated from suspension. The fossil association of the Skryje Shales includes only trilobites with well-developed eyes such as *Ptychoparioides* and diverse paradoxidids; blind trilobites characteristic of the conocoryphid biofacies, such as the widely distributed and abundant *Conocoryphe* or the locally common *Ctenocephalus*, are entirely absent. This composition of the skeletal fauna suggests deposition within the photic zone, and the absence of bioturbation indicates poor oxidation of the sea floor.

The sandy light green greywacke at the "Jestřábí" locality from which the studied articulated specimens of *Ptychoparioides henkli* were obtained also contains disarticulated remains of other trilobites and rare articulated eocrinoid echinoderms. This unit does not exhibit current sorting. The studied specimens come from a monospecific accumulation that contained the remains of approximately 50 articulated and disarticulated exoskeletons of adults of *Ptychoparioides henkli*. At least two different processes could have been responsible for producing this type of accumulation.

1) The accumulation represents a mass transportation event of living individuals. The killing and mass deposition of their bodies most probably resulted from a debris flow (see Cisne 1973; Brett *et al.* 2012; M. Eliáš, personal communication 2008).

2) The preserved accumulation originated from a large monospecific, size-segregated assemblage of fully articulated

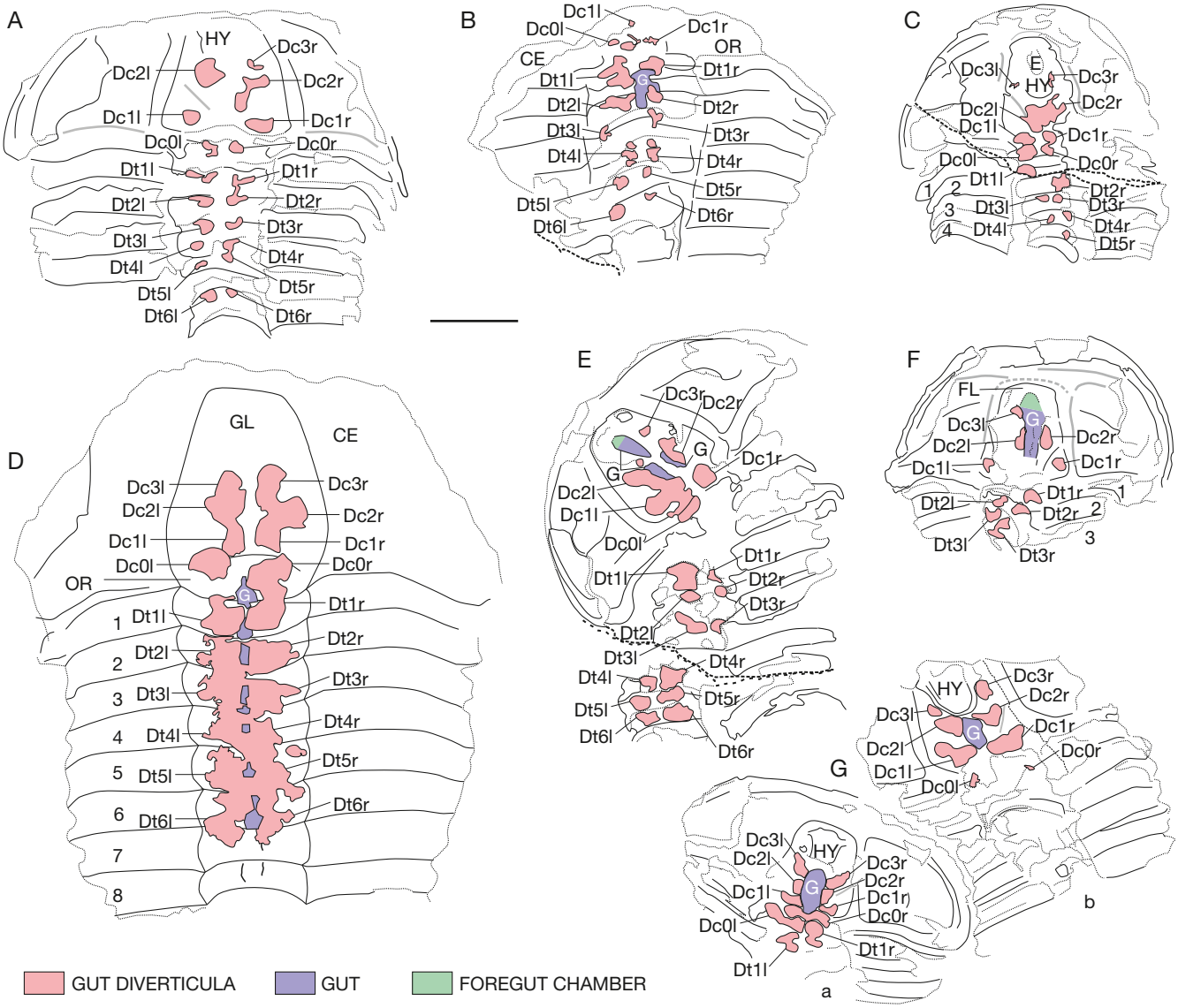


FIG. 10. — Interpretative line drawings of studied specimens: **A**, CGS MV 27; **B**, CGS MV 26; **C**, CGS MV 28; **D**, CGS MV 32; **E**, CGS MV 30; **F**, CGS MV 31; **G**, CGS MV 29. Abbreviations: **CE**, cephalon; **Dc**, cephalic digestive glands; **Dt**, thoracic digestive glands; **e**, sagittally prolonged grey-coloured spot; **FL**, frontal glabellar lobe; **G**, gut; **GL**, glabella; **HY**, hypostome; **OR**, occipital ring; **1-8**, thoracic segments. Scale bar: 10 mm. Drawing by O. Fatka.

specimens that was rapidly buried *in situ*. This type of accumulation was named a body cluster by Speyer & Brett (1985).

Due to apparent monospecific aggregation of size-segregated and fully articulated exoskeletons, we interpret the studied association as a body cluster of Speyer & Brett (1985).

*Trilobite preservation*

All studied specimens of *P. henkli* show *in situ* preserved librigenae, various stages of disarticulation of the thoracopygon, and partially preserved remains of the digestive system. The exoskeletons of at least three specimens (Figs 3-5) show a well-articulated thorax. In contrast, three other specimens (Figs 6; 8; 9) show evident disarticulation of the exoskeleton. The remaining two specimens (e.g. Fig. 7) are strongly damaged and it is not possible to determine the completeness of their exoskeletons.

Partially or completely preserved sets of cephalic and thoracic diverticula with remains of the gut are preserved in six specimens. Just diverticula, without remains of the gut, are seen in two specimens (CGS MV 27, Figs 5; 10A and CGS MV 28, Figs 6; 10C). The most complete remains of the digestive system are seen in specimen CGS MV 32, in which four pairs of cephalic and six pairs of thoracic diverticula are associated with gut remains and are seen in the occipital ring and in six anterior thoracic segments (Figs 3; 10D[Dc0-Dc3, Dt1-6 and G]). All ten pairs of diverticula are also preserved in the incomplete and strongly damaged specimen CGS MV 30 (Figs 8; 10E[Dc0-Dc3, Dt1-6]); however, no remains of the gut are detectable in this specimen. Only one cephalic diverticulum (Dc3l) is missing in specimen CGS MV 27 (Fig. 5; 10A). Complete sets of cephalic diverticula are preserved in three specimens: CGS MV 29a,

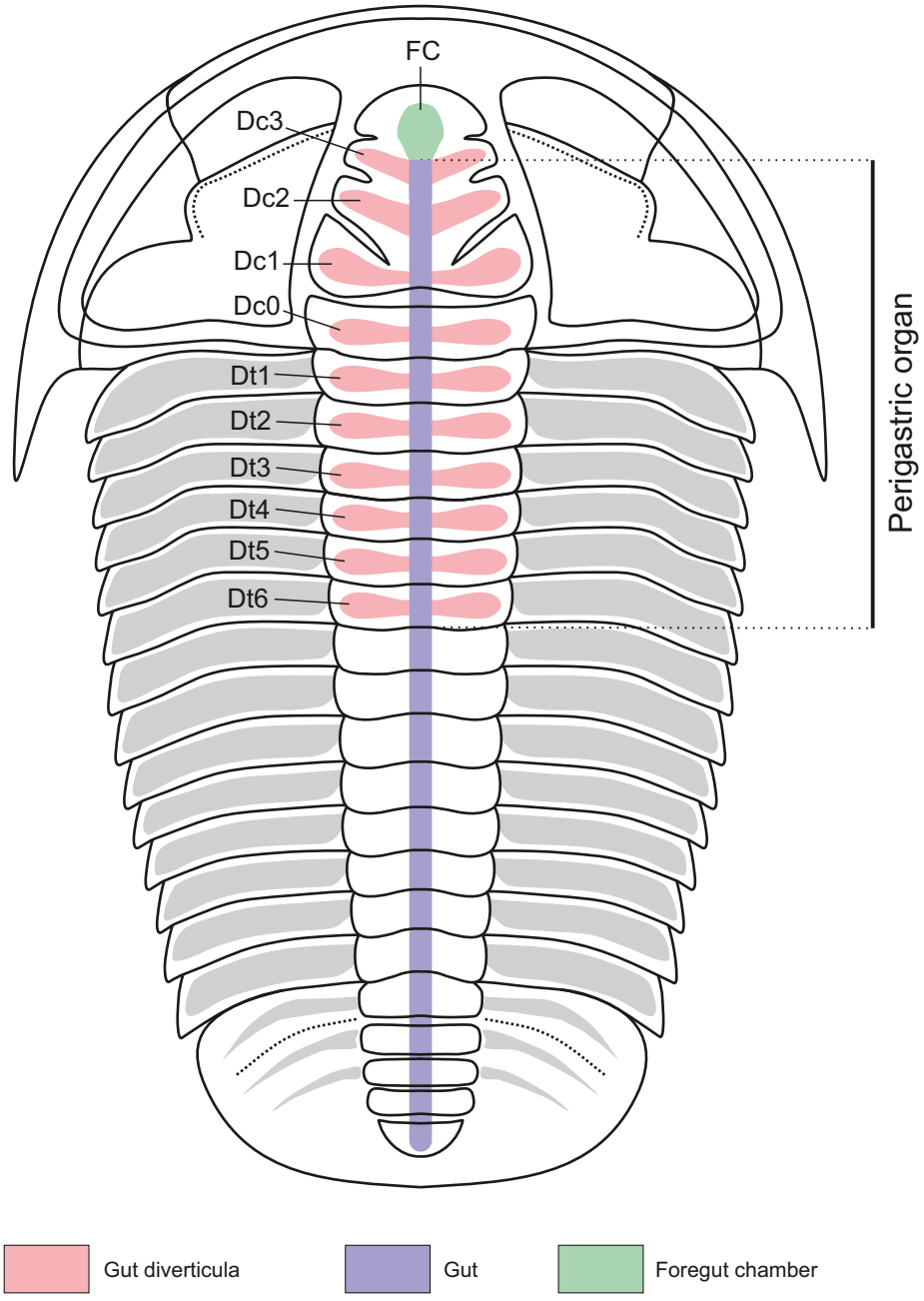


FIG. 11. — Reconstruction of the digestive systems of *Ptychoparioides henkli* Kordule, 2006 in dorsal view. The midgut tract in blue-violet, the hindgut in light blue-violet and the midgut caeca/glands in lavender. Abbreviations: **CE**, cephalon; **Dc0**-**Dc3**, cephalic digestive glands; **Dt1**-**Dt6**, thoracic digestive glands; FC, foregut chamber. Drawing by O. Fatka.

CGS MV 29b (Figs 7; 10G) and CGS MV 31 (Figs 9; 10F). One pair of thoracic diverticula is preserved in the specimen CGS MV 29a (Figs 7; 10G) and six pairs are seen in CGS MV 26 (Figs 4; 10B).

In the cephalon, small parts of the gut are preserved in five specimens (CGS MV 26, Figs 4, 10B; CGS MV 30, Figs 8, 10E; CGS MV 31, Figs 9, 10F; CGS MV 29a and CGS MV 29b, Figs 7, 10G); gut remains in the anterior six thoracic segments are seen in one specimen (CGS MV 32, Figs 3, 10D). Gut remains in more posterior thoracic segments and in the pygidium are absent in all studied specimens.

The question of how remains of the digestive system could be preserved despite the substantial differences in the degree of exoskeletal disarticulation must be addressed. To answer this question, we compared our specimens with the results of the experimental taphonomic work of Butler *et al.* (2015) and Klompmaker *et al.* (2017, 2018).

Butler *et al.* (2015) concluded that endogenous gut bacteria are the main factor controlling decay in the brine shrimp *Artemia salina*. They showed that the carcass of this shrimp was consumed rapidly by endogenous bacteria after rupture of the gut wall and that the developed biofilm mediated

authigenic mineralization of soft tissues, including the gut and body cavity. In their experimental conditions, the wall of the gut failed at the mid- to hindgut junction, allowing gut-derived microbes to spread into the body, where they proliferated (see Butler *et al.* 2015: 7). This observation explains the preservation of cephalic and thoracic diverticula as well as the absence of the hindgut in specimens of *Ptychoparioides*.

Klompmaker *et al.* (2017) studied the decay of eight marine arthropods by means of experiments; in this work, we compare the preservation of *Ptychoparioides* with the degree of exoskeletal disarticulation and the completeness of the digestive system in stomatopods. In stomatopods, disintegration of the carapace commenced after approximately 50 days and the soft tissue had entirely decayed after about 100 days (Klompmaker *et al.* 2017: 779, figs 3c; 4). This comparison makes it possible to explain the observed exoskeletal disarticulation and partial preservation of the digestive system in *Ptychoparioides* as resulting from embedding earlier than 50 days after the death of the trilobites.

*Palaeoecology*

The occurrence of paired digestive glands implies slow digestion of ingested particles, which agrees with a hypothesised detritus-feeding habit (see Fatka & Budil 2018).

## CONCLUSIONS

1) Rare remains of the digestive system are for the first time documented in the middle Cambrian trilobite *Ptychoparioides henkli* from the Skryje-Týřovice Basin in the Barrandian area. Preservation of the digestive system is restricted to the cephalon and the anterior part of the thorax. The studied specimens show a convincing presence of the gut, associated with symmetrically arranged digestive glands (four pairs of cephalic digestive glands and six pairs of thoracic digestive glands) (Fig. 11).

2) The gut associated with paired digestive glands preserved in the cephalon and thorax is part of the midgut. In agreement with Fatka *et al.* (2024), we name this structure the "perigastric organ".

3) The descriptive term "foregut chamber" is proposed for the widening of the digestive system in the anterior-most glabellar lobe (Fig. 11).

4) Remains of the digestive system are missing in the axis of the posterior thoracic segments and in the pygidium, i.e., in the parts of the digestive system representing the hindgut. This absence of soft parts is most likely associated with spreading of endogenous bacteria after rupture of the gut wall at the mid- to hindgut junction, as observed in the extant brine shrimp *Artemia salina*.

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