REMAINS OF THE ALIMENTARY TRACT IN THE LATE ORDOVICIAN TRILOBITE *DALMANITINA* (PRAGUE BASIN, BARRANDIAN AREA, CZECH REPUBLIC)

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Abstract. Preservation of digestive structures in trilobites is generally rare; remains of the alimentary tract have been documented in about eighty of more than twenty thousand described species. Several tens of specimens belonging to five Cambrian and nine Ordovician species from the Barrandian area, Czech Republic, have markedly contributed to the knowledge of the trilobite digestive system. Here, we describe seven exceptionally preserved late holaspid trilobite specimens of species of the genus *Dalmanitina* collected from Upper Ordovician strata of the Barrandian area. All studied specimens are preserved as internal moulds and exhibit a narrow strip-like structure that runs sagitally or sub-sagitally under the axial lobe of the thoracopygon. These strip-like structures are markedly different from scavenger burrows and are interpreted as remains of the alimentary canal. A slightly expanded anterior-most part of the digestive system is preserved in the cephalic shield of six specimens and is interpreted as a remainder of the anterior midgut. A dark area is seen in the glabellar lobes of three specimens. These dark areas do not represent pyrite concentrations in the hypostome–glabellar cavity, because they contain only small amounts of Fe and S. These areas are interpreted as the remainder of cephalic digestive midgut diverticula, or the "perigastric organ". Quantitative chemical analyses show that in species of *Dalmanitina* the digestive system is preserved as dark matter containing partly digested food particles and most probably also a higher amount of clay minerals. The described specimens constitute the first well-documented example of digestive structures in the subfamily Dalmanitininae.

INTRODUCTION

The Cambrian and Ordovician succession of the Teplá-Barrandian Unit (Czech Republic) has contributed markedly to documentation of the morphology of trilobite digestive systems (Budil & Fatka 2022). The record of Czech Ordovician trilobites preserving remains of the digestive system is comparatively extensive and includes nine Early, Middle and Late Ordovician taxa (Budil & Fatka 2022). The highest number of such specimens has been reported from the Letná Formation (Fatka et al. 2013). Remains of the digestive system represented by a pouch-like structure usually called the crop (Kraft et al. 2023; Lerosey et al. 2011) associated with remains of the intestine gut are known in more than 20 articulated specimens of the trinucleid *Deanaspis goldfussii* (Barrande, 1846) (see Beyrich 1846; Barrande 1852; Raymond 1920; Přibyl &

Vaněk 1969; Šnajdr 1990, 1991; Shaw 1995; Fatka & Budil 2022). From the Veselá locality near Beroun, Šnajdr (1991, fig. 14) figured one internal mould of *Dalmanitina socialis* (Barrande, 1846) with a narrow strip-like structure that he interpreted as incompletely preserved remains of the intestinal tube (= the alimentary canal of the digestive tract). However, this specimen was unnumbered, and it has never been deposited in an institutional collection. Remains of the gut associated with paired diverticula were recently described in one specimen of *Selenopeltis buchi* (Barrande, 1846) by Fatka et al. (2013), who also documented a holaspid specimen of *Birmanites ingens* (Barrande, 1846) (= *Nobiliasaphus*? *ingens* sensu Gutiérrez-Marco et al. 2022) with a phosphatised gut preserved in the thoracic and pygidial axis.

In this paper, we describe examples of fossilised digestive structures in seven specimens of *Dalmanitina socialis* (Barrande, 1846) from four localities in the Letná Formation. This work is the first report of the preservation of such structures in the subfamily Dalmanitininae.

GEOLOGICAL SETTING AND PRESERVATION OF NON-MINERALISED FOSSIL REMAINS

The geological setting of the Letná Formation and the preservation of skeletal fossils and faunal and ichnofossil assemblages in the formation have been summarised by Fatka et al. (2013, 2021) and Drage et al. (2018). In the north-western limb of the Prague Basin, remains of non-mineralised and lightly mineralised fossils have been collected at several outcrops of the Letná Formation (Van Roy et al. 2021, 2022). Many of these species had been described by Barrande in the nineteenth century, particularly the bivalved arthropods *Nothozoe pollens* Barrande, 1872, *Zonozoe drabowiensis* Barrande, 1872, *Drabovaspis complexa* (Barrande, 1872), the more or less problematic *Triopus draboviensis* Barrande, 1872 and *Caryon bohemicum* Barrande, 1872. The cheloniellid arthropod *Duslia insignis* Jahn, 1893 and the marrellomorph *Furca bohemica* Fritsch, 1908 were described only slightly later. After a long gap, two other taxa, *"Nothozoe" barrandei* Chlupáč, 1970 and *Zonoscutum solum* Chlupáč, 1999, were established. Nearly all these taxa have been subsequently re-examined and re-interpreted (see Chlupáč 1988,

1999a, b; Rak et al. 2009, 2013; Ortega-Hernández et al. 2010; Van Roy et al. 2021, 2022). Two new genera of thylacocephalans were described by Van Roy et al. (2022). Most of the Letná non-trilobite arthropods, including those with non-mineralised exoskeletons, were collected at outcrops of the *Dalmanitina–Deanaspis* Association (e.g., Chlupáč 1965; Rak et al. 2009; Ortega-Hernández et al. 2010; Bicknell & Pates 2020). This pattern suggests that conditions conducive to soft-tissue fossilisation were not uncommon.

Fossilised gut remains have been observed in four of the more than twenty trilobite species in the *Dalmanitina–Deanaspis* Association, or the *Modiolopsis draboviensis* Community of Kříž & Steinová (2009) (= *Modiolopsis draboviensis* Association of Polechová 2022), and the *Drabovia dux* Community of Havlíček (1982 and 1998). These associations are characteristic of rather proximal and shallow-marine environments in the middle part of the Letná Formation (Vaněk & Valíček 2001; Fatka & Mergl 2009; Fatka et al. 2013). Gut remains possibly had the highest preservation potential in these settings. These associations are characterised by excellent preservation of individual ichnofossil specimens (Mikuláš 1998). This preservation implies that the overall bioturbation was very weak, because otherwise the ichnofossils would have been damaged by subsequent bioturbation.

Distribution of species of *Dalmanitina* in the Prague Basin

Numerous species of *Dalmanitina* Reed, 1905, and related genera are widespread in Upper Ordovician strata of European peri-Gondwana; however, a review and analyses of the phylogenetic relations of *Dalmanitina* are beyond the scope of this paper.

In the Prague Basin, dalmanitid trilobites range from the uppermost Dapingian/lowermost Darriwilian to the uppermost Hirnantian (Mergl 1991; Budil 1996, 1999; Budil et al. 2011). The genus *Dalmanitina* has a much shorter stratigraphical range, as species of this genus have been found exclusively in sediments of the Berounian Regional Stage, corresponding to the Sandbian to lower–middle Katian of the international chronostratigraphic system (see Havlíček & Marek 1973; Bergström et al. 2009; Fatka et al. 2013). The Berounian Stage comprises five different lithostratigraphic units, the Libeň, Letná, Vinice, Zahořany and Bohdalec for-
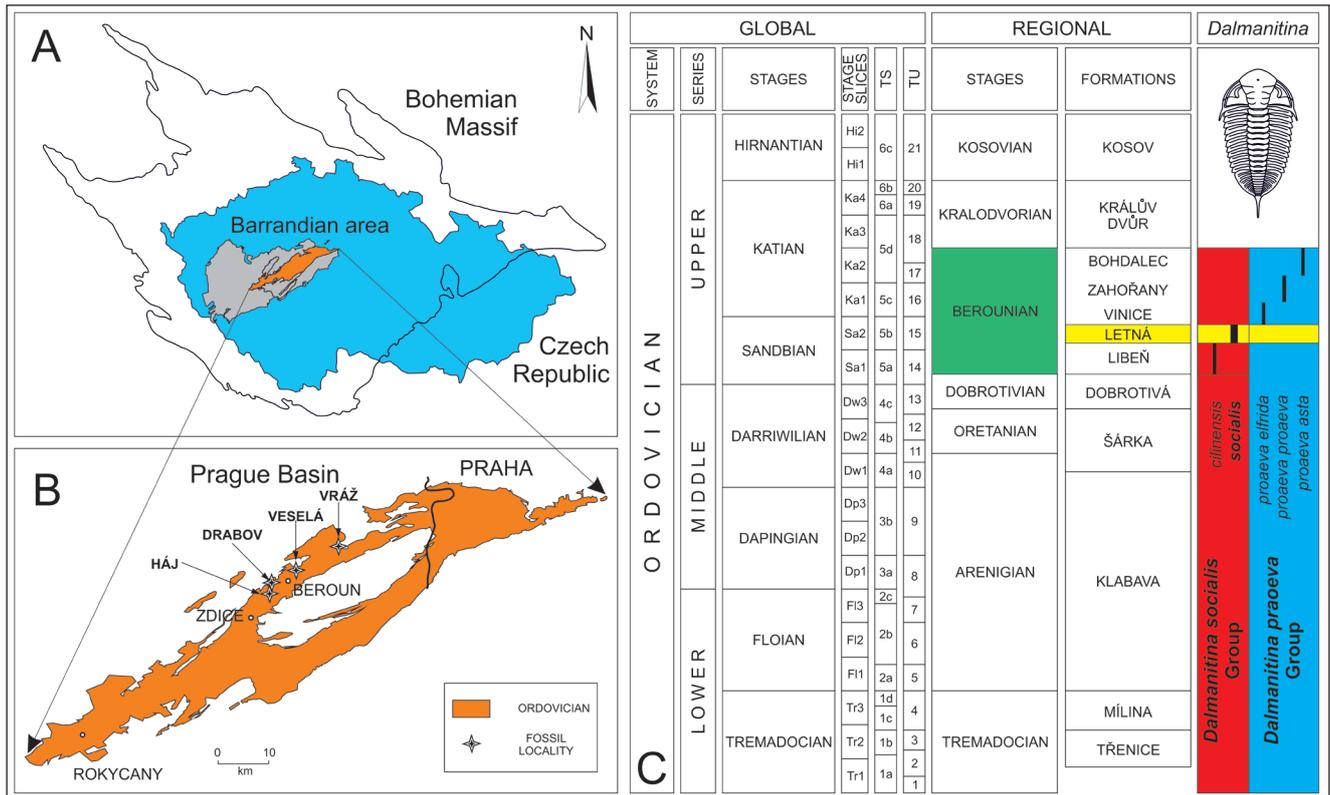
Fig. 1 - Geographic location and stratigraphic distribution of specimens discussed in this study. A) A sketch map of the Czech Republic and the Barrandian area. B) A sketch map of the Prague Basin showing the location of the Háj near Zahořany, Drabov (Děd), Veselá and Vráž localities at which the studied exceptionally preserved trilobites with soft parts were found. C) The stratigraphy of the Ordovician System of the Prague Basin. The levels at which the studied trilobite specimens were collected are marked (stratigraphy modified from Fatka & Budil 2021).

mations (Fig. 1C). Despite lithological differences, the skeletal fauna is taxonomically comparable in all these units (Havlíček & Vaněk 1966). The systematics and stratigraphical range of *Dalmanitina* were studied by Šnajdr (1956, 1982a, b, 1987, 1990) and more recently by Vaněk & Vokáč (1997). Some aspects of trilobite autecology and synecology were discussed by Přibyl & Vaněk (1972, 1976).

Two groups of *Dalmanitina* species can be informally distinguished among Barrandian taxa (see Drage et al. 2018 and Fatka & Budil 2021):

1) The *Dalmanitina socialis* Group occurs in the Sandbian Libeň and Letná formations (Fig. 1C) and comprises two species, *D. socialis* (Barrande, 1846) and the ancestral *D. cilinensis* Šnajdr, 1956. Both species are characterised by large eyes, a noticeably anteriorly expanded anterior glabellar lobe, comparatively long genal and pygidial spines, a slightly higher number of pygidial axial rings than in representatives of second *Dalmanitina* group, and well-developed, deeply impressed interpleural furrows on the lateral pygidial lobes.

2) The *D. proaeva* Group is known from the Katian Vinice, Zahořany and Bohdalec formations and includes *D. proaeva proaeva* (Emmrich, 1839), *D. proaeva elfrida* Šnajdr, 1982 and *D. proaeva asta* Šnajdr, 1982. Šnajdr (1982a, b, 1987, 1990) regarded the last two taxa as separate species (Fig. 1C).

MATERIAL AND METHODS

Material

The studied specimens are housed in three institutional collections. One specimen is deposited in the collection of the Naturhistorisches Museum Wien, Austria (abbreviation NMW), two specimens are housed in collections of the Museum für Naturkunde Berlin, Germany (abbreviation MB), and the other four specimens are in the original collection of Joachim Barrande housed in the National Museum Prague (abbreviation NM L). All seven studied specimens were collected from the Upper Ordovician Letná Formation at the Háj near Zahořany, Drabov (Děd), Vráž and Veselá localities (Fig. 1B, C).

Documentation method

Photographs were taken using a NIKON D 300 digital camera (Nikon). In the first stage, specimens were left uncoated and photographed to make visible colour differences between the internal mould and the remains of the digestive tract. Three spec-
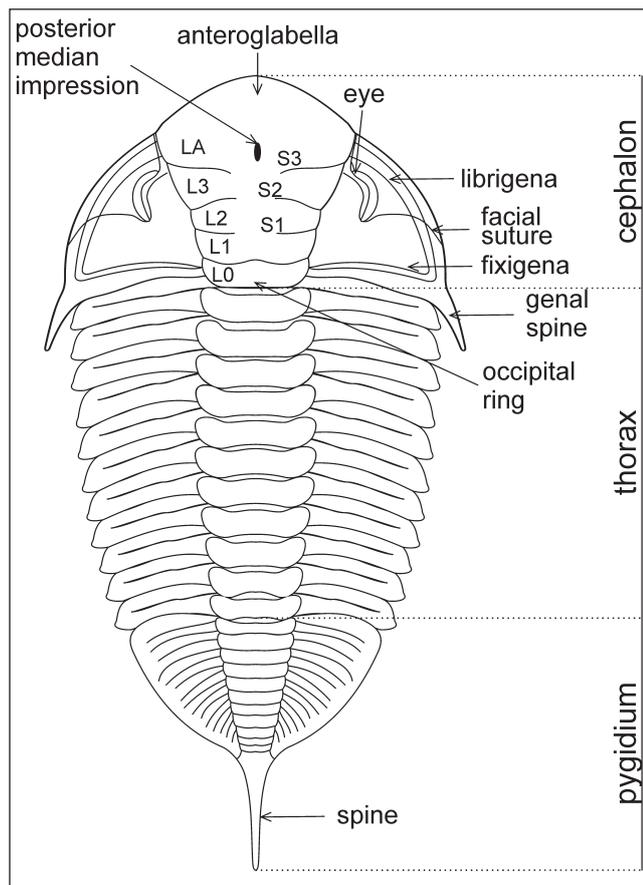
Fig. 2 - Morphology of the exoskeleton of the trilobite *Dalmanitina socialis* (Barrande, 1846) (after Fatka et al. 2021). Abbreviations: LA, anterior lobe; L0 to L3, lateral lobes; S1 to S3, transverse furrows.

imens (NMW 1906/008/008 (1906.VIII.8), MB 1965.2.13 and MB 1994.1.95 MB.T.2015) were photographed under polarised light (Figs 4E-G, 5A-C, E-G). In the second stage, internal moulds were coated with ammonium chloride sublimate before photographing. The drawings were made from photographs using Corel Draw X3 and Photoshop CS5.

The chemical analyses were performed using a Scan TESCAN Vega, EDS X-MAX 50 (Oxford Instruments) at the Institute of Petrology and Structural Geology, Faculty of Science, Charles University in Prague. The studied specimens of *Dalmanitina* are preserved in deeply weathered quartzose sandstone. This makes the interpretation of chemical analyses quite difficult. Despite this, two of the studied specimens were examined by energy dispersive X-ray (EDAX) analysis, to look for surface elemental differences associated with separate parts of the digestive structures. Both samples were uncoated and analysed under a low vacuum.

The EDAX analyses were undertaken at six places in specimen 1 (NM L 51954) and six different places in specimen 2 (NM L 51953). The exact placement of the analysed points is described in Tab. 1.

The terminology used below follows that proposed by Whittington (1997), including the following abbreviations: exsag. (exsagittal), sag. (sagittal), tr. (transversal), agl (anteroglabella), $dc_1 - dc_4$ (possible cephalic diverticula), dt_1 (possible trunk diverticula), g (gut), gl (glabella), hy (hypostome), mg (midgut), or (occipital ring), pmi (posterior medial impression), LA (anterior lobe), L0-L3 (lateral lobes), S1-S3 (transverse furrows), 1-11 (thoracic segments), 1-9 (pygidial segments). Morphological terms are summarised in Fig. 2.

RESULTS

Description of specimens

All specimens are preserved as internal moulds in quartzose sandstone. Six articulated exoskeletons have eleven thoracic segments and attain 50 to more than 85 mm in sagittal length. The seventh specimen is incomplete and the length of a complete exoskeleton would range around 80 mm.

Consequently, all studied specimens represent a holaspid to late holaspid growth stage. Only internal moulds were studied, as the external moulds were usually not collected in the 19th century and are absent in historical collections. The perfect articulation of all exoskeletal elements, the occurrence of librigenae *in situ* (commonly ankylosed in adult specimens of *Dalmanitina*; see Drage et al. 2018), and the *in situ* hypostome beneath the glabella indicate a lack of disturbance of trilobite exoskeletons and suggest that the studied specimens are carcasses (Fortey 1974, 1990; Daley & Drage 2016).

Specimen 1 (Figs 3A–D, 7A, 8A)

NM L 51954, Veselá locality near Beroun.

Description. An irregularly polygonal sample of a quartzose sandstone, which is about 36 mm wide and 50 mm long, bears an originally complete, now partly damaged brown to dark brown internal mould of a trilobite.

The slightly damaged cephalon includes the remains of *in situ* preserved left and right librigena; the cephalon is connected to a perfectly articulated thorax and pygidial shield (Fig. 3A–C). The left antero-lateral and anterior-most parts of the cephalon, the distal pleural tips of the sixth to eleventh thoracic segments, and the left postero-lateral and posterior-most parts of the pygidium have been broken off. The cephalon, thorax and pygidium are somewhat flattened, but glabellar furrows as well as thoracic and pygidial segments and pleural furrows are distinct (Fig. 3A–C).

A dark grey smooth strip, ca. 19.0 mm long and a maximum of 1.25 mm wide, is clearly visible in the right side of the axis from the first to ninth thoracic segments (Fig. 3A–C). Isolated irregularly shaped bodies are developed in the first and second thoracic segments (a and b in Fig. 3D), whereas the smooth surface is uninterrupted in the axis from the third to the ninth segments (c in Fig. 3D). This smooth surface is not seen in the tenth and eleventh segment, and is also missing in the anterior part of
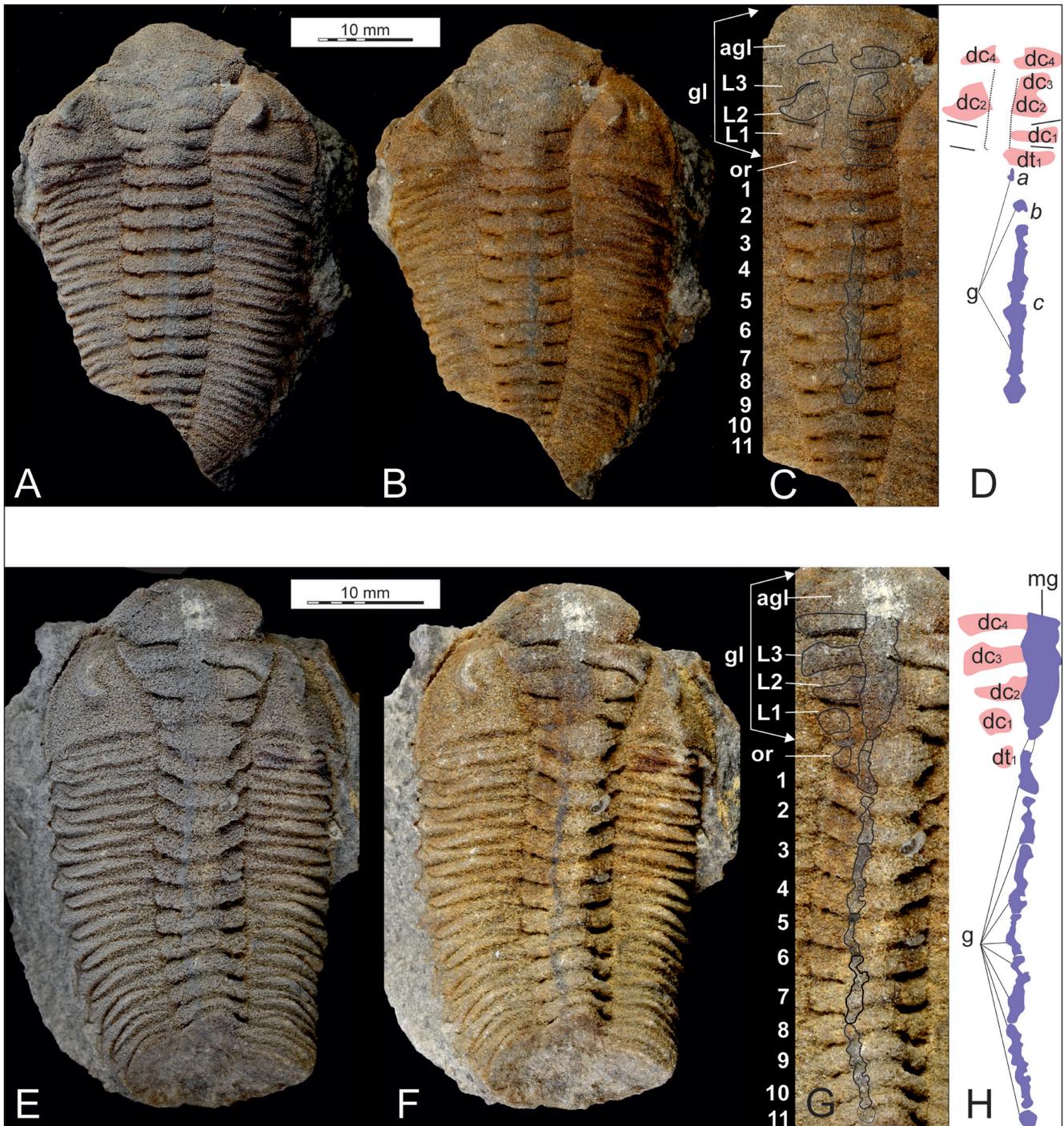
Fig. 3 - Partly damaged internal moulds of *Dalmanitina socialis* (Barrande, 1846), Upper Ordovician, Sandbian Stage (= Berounian Regional Stage), Letná Formation. Both specimens exhibit a narrow strip-like structure that runs under the axial lobe of the thoracopygon. A–D) Specimen 1, NM L 51954, Veselá locality near Beroun. A) Internal mould, uncoated. B) Internal mould, uncoated. C) Detail of the axial part of glabella and thorax with marked remains of the alimentary tract, coated with ammonium chloride sublimate. D) Interpretative sketch of remains of the alimentary tract. E–H) Specimen 2, NM L 51953, Drabov locality (Děd near Beroun). E) Internal mould, coated with ammonium chloride sublimate. F) Internal mould, uncoated. G) Detail of the axial part of glabella and thorax with marked remains of the alimentary tract, uncoated. H) Interpretative sketch of remains of the alimentary tract. Abbreviations: a, b, c, irregularly shaped smooth areas in the axis of the thorax; agl, anterior glabellar lobe; gl, glabella; g, gut; mg, midgut; or, occipital ring; dt_1 and dc_1 to dc_4, diverticula; L1 to L3, glabellar lobes; 1–11, thoracic segments.

the pygidial axis (Fig. 3C). One or two dark-coloured areas of apparently paired structures are pre-served in the occipital ring and at one or both sides of the glabellar lobes (dt_1 and dc_1 to dc_4 in Fig. 3D).

Specimen 2 (Figs 3E–H, 7B, 8B)

NM L 51953, Drabov locality (Děd near Beroun).

Description. An irregularly polygonal sample of quartzose sandstone, which is approximately 37 mm wide and 45 mm long, bears one originally complete, now partly damaged internal mould of a trilobite exoskeleton on its surface.

The remains of the completely articulated internal mould of the exoskeleton include the cephalon and thorax, which have a total sagittal length of 42 mm and a maximum transverse width of 25.5 mm. The left side of the cephalon is complete and includes the *in situ* librigena and the left eye (Fig. 3E, F), but the left genal spine is broken off. The right side of the cephalon includes a complete fixigena and the posterior part of the *in situ* librigena, but the eye and anterior portions of both fixigena and librigena are missing (Fig. 3E, F); the right genal spine is partly preserved. The thorax is complete and includes all 11 thoracic segments, but the pygidium is missing. Both cephalon and thorax are well vaulted; glabellar furrows and thoracic segments are clearly distinct (Fig. 3E–G).

A dark grey smooth strip, approximately 33 mm long and 0.9–2.8 mm wide, is clearly visible in the central area of the glabella and in the thoracic axis (mg and g in Fig. 3E–H). This dark strip is absent in the anterior-most part of the glabella. Is it possible that the smooth strip was originally present in this area, but is not visible because of the damage to the anteriormost part of the glabella. The strip appears anteriorly from S3, where it is ca. 2.8 mm wide. More posteriorly, the strip exhibits an approximately consistent width to L1, where it suddenly narrows to less than 1 mm wide in the occipital ring ("or" in Fig. 3G). The width of the strip is approximately 0.9 mm in all thoracic segments; the preserved length is 25.5 mm (g in Fig. 3G). At the left side of the glabella, an inconspicuous but clearly visible dark grey-coloured area is seen in the anteroglabella (= agl) and in L2 and L3; this area covers a large part of the glabellar surface (dc_1 to dc_4 in Fig. 3F–H). Similar grey-coloured area occurs also in the occipital ring (dt_1 in Fig. 3F–H).

Specimen 3 (Fig. 4A–D, 8C)

NM L 51951, Drabov locality (Děd near Beroun).

Description. An irregularly pentagonal sample of quartzose sandstone, ca. 84 mm long and nearly 60 mm wide, bears on its lower part a complete, partly covered internal mould of a trilobite. All exoskeletal parts are dorsally slightly flattened, and glabellar furrows and thoracic and pygidial segments are distinct (Fig. 4A–C).

The articulated internal mould of the exoskeleton measures 61.0 mm in sagittal length and a maximum of 31 mm in transverse width. The right librigena and part of the fixigena are covered by the surrounding rock. The thorax was broken behind the ninth thoracic segment and across the pygidium (arrows in Fig. 4A); both parts of the exoskeleton are now glued together. On the right side, a small, posterior-most part of the pygidium is missing.

Both left fixigena and librigena are complete and include the eye and complete left genal spine. The glabella is incompletely preserved, because the central glabellar area is cracked between S1 and S3 and the frontal glabellar lobe is broken off. The lower external surface of the *in situ* preserved hypostome is exposed in the anterior-most part of the cephalon (hy in Fig. 4D), in the area under the missing anterior glabellar lobe. More posteriorly, a small part of the hypostome body lies in the lower level of the hypostome–glabellar cavity. Inside the more posteriorly developed fissure, in the area between S3, the hypostome–glabellar cavity (= space between the hypostome body and the internal surface of the glabellar exoskeleton) is filled by fine-grained material (mg in Fig. 4D). Between L1 and L3, inconspicuous but discernible dark grey markings are visible (dc_1 to dc_4 in Fig. 4D).

A dark grey, posteriorly slightly narrowing strip ca. 33 mm long and a maximum of 1.2 mm wide is well developed at the exposed surface of the articulating half-rings in the middle of the thoracic axis (Fig. 4A–D). This strip starts in the first thoracic segment and continues through all thoracic segments to the ninth ring of the pygidial axis (g in Fig. 4D). This strip is not seen in the second, third and eleventh thoracic segments. The darker surface is slightly displaced to the right side (Fig. 4A–D) and its total length in the thorax and pygidium is about 42 mm.

Specimen 4 (Fig. 4E–H)

NMW 1906/008/008 (1906.VIII.8), Veselá locality near Beroun.

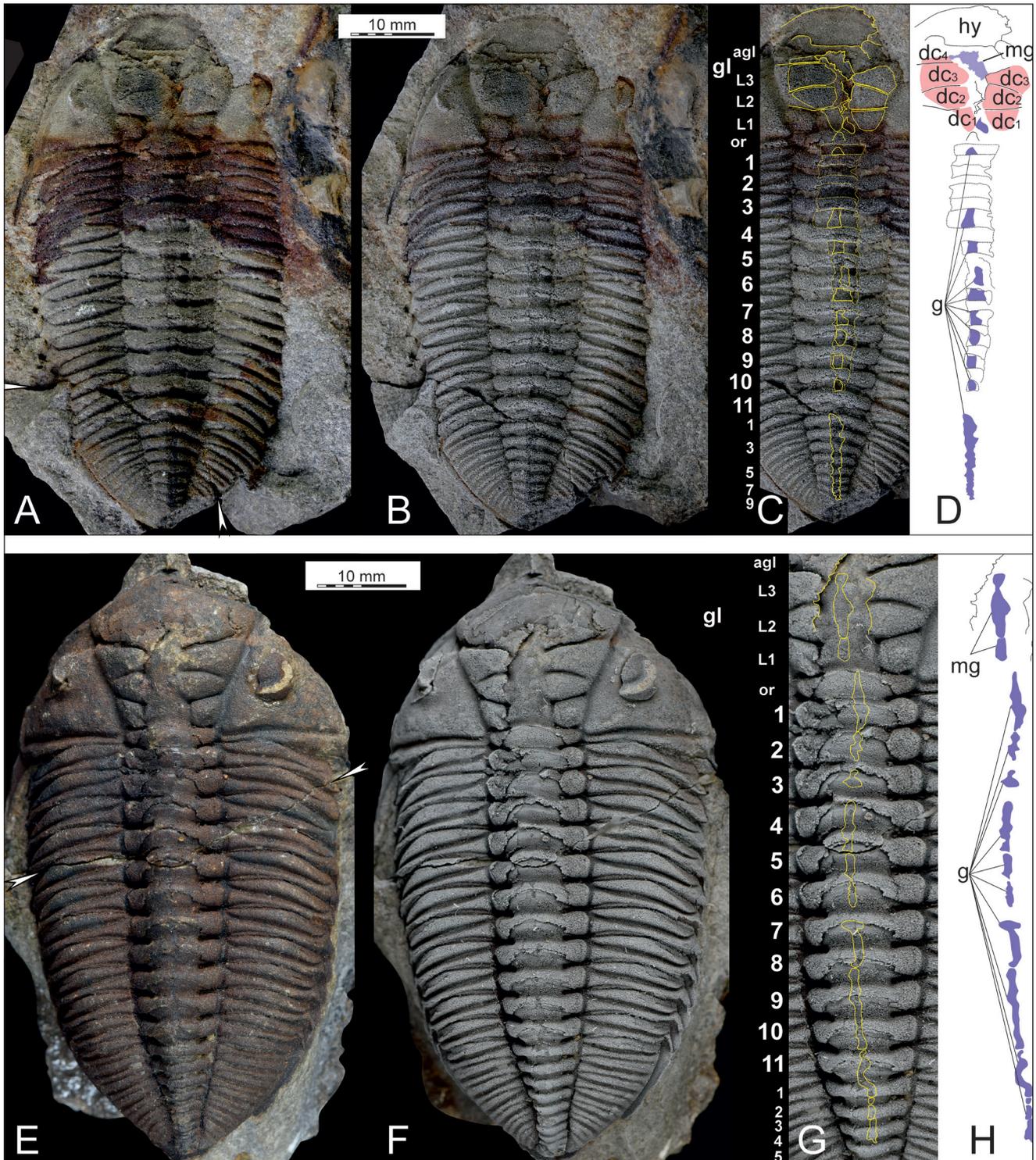*Description.* This 58 mm long and nearly 34

Fig. 4 - Internal moulds of *Dalmanitina socialis* (Barrande, 1846), Upper Ordovician, Sandbian Stage (= Berounian Regional Stage), Letná Formation. Both specimens exhibit a narrow strip-like structure that runs under the axial lobe of the thoracopygon. A–D) Specimen NM L 51951, Drabov locality (Děd near Beroun). A) Internal mould, uncoated. B) Internal mould, coated with ammonium chloride sublimate. C) Detail of the axial part of the glabella and thorax, coated with ammonium chloride sublimate. Remains of the alimentary tract are indicated by yellow outlines. D) Interpretative sketch of remains of the alimentary tract. E–H) Specimen NMW 1906/008/008 (1906.VIII.8), Veselá locality near Beroun. E) Internal mould, uncoated, photographed under polarised light. F) Internal mould, coated with ammonium chloride sublimate, photographed under polarised light. G) Detail of the axial part of the glabella and thorax, coated with ammonium chloride sublimate, photographed under polarised light. Remains of the alimentary tract are indicated by yellow outlines. H) Interpretative sketch of remains of the alimentary tract. Abbreviations: agl, anterior glabellar lobe; g, gut; gl, glabella; hy, *in situ* preserved hypostome; mg, midgut; or, occipital ring; dt_1 and dc_1 to dc_2: diverticula; L1 to L3, glabellar lobes; 1–11, thoracic segments; 1–5 and 1–9, pygidial segments. Arrows in (A) and (E) mark rock breakage.

mm wide sample of quartzose sandstone bears a complete and excellently preserved trilobite on its surface. The brown internal mould represents a very slightly damaged exoskeleton. Both eyes were broken off and have been glued roughly in their original position; similarly, the thorax was broken, and both its parts are now glued together (arrows in Fig. 4E). The pygidial spine is missing. The entire exoskeleton measures 55.1 mm in length (sag.) and 29.7 mm in width (tr.).

In the slightly squeezed glabellar area, an inconspicuous smoother sausage-like, very slightly sunken surface can be traced between L1 and S3 (mg in Fig. 4G–H). In the middle of the thoracic and pygidial axis, a dark brown, glossy strip, ca. 34.5 mm long and a maximum of 2 mm wide, is clearly visible (g in Fig. 4H). The surface of this strip is finer-grained than the surrounding matrix. The strip starts near the anterior margin of the occipital ring ("or" in Fig. 4G), runs through the axis of all eleven thoracic segments, and continues to the fourth pygidial segment (g in Fig. 4G, H).

Specimen 5 (Fig. 5A–D)

MB 1965.2.13, Drabov locality (Děd near Beroun).

Description. A sample of grey quartzose sandstone approximately 62 mm wide and 45 mm long bears on its surface an originally complete, but slightly damaged post-collection, internal mould of a trilobite.

The articulated internal mould of the exoskeleton measures 47 mm in sag. length (without pygidial spine) and 29 mm in tr. width. The left anterior-most margin of the cephalon, the left eye, and the right posterior-most margin of the pygidium are missing. All exoskeletal parts are slightly flattened. All glabellar furrows are well cut and deep, and the surface of the glabellar lobes is smooth. Anteriorly from the posterior median impression (pmi in Fig. 5C), the smooth surface of the anterior glabellar lobe is interrupted by a shallow transversal furrow.

Posteriorly from the pmi, a pouch-like area delimited by a poorly visible shallow furrow is visible (mg in Fig. 5D). In the posterior part of the glabella, two small smooth areas are present between L1 and in the occipital ring. In the middle of the thoracic and pygidial axis, a dark strip, about 36.5 mm long and no more than 1.2 mm wide, is clearly visible in some places (Fig. 5A–D); its surface is fin-

er-grained than the surrounding matrix (Fig. 5B, C). This structureless strip can be observed in all eleven thoracic segments, and continues to the ninth pygidial segment (Fig. 5B–D).

Remark. This excellently preserved specimen was figured by Kowalski (1992: 100–101, fig. 137). However, no remark on the remains of the digestive system was made.

Specimen 6 (Fig. 5E–H)

MB 1994.1.95 MB.T.2015, Drabov locality (Děd near Beroun).

Description. A sample of grey quartzose sandstone, ca. 101.5 mm long and 45 mm wide, bears an originally complete, slightly flattened and slightly damaged internal mould of a trilobite on its surface.

The articulated internal mould of the exoskeleton measures 83.5 mm in sagittal length (including the partially preserved pygidial spine) and 38.5 mm in tr. width. On the right side, the right gena and the distal ends of the anterior three pleura are missing. The thorax was broken behind the fifth thoracic segment and across the pygidium; both these exoskeletal parts are now glued together (arrows in Fig. 5E). All glabellar furrows are well cut and deep, and the surface of glabellar lobes is smooth, except for L1 and L2 that are covered by fine granules. Posteriorly from the posterior median impression (pmi in Fig. 5G), the smooth surface of the anterior glabellar lobe is interrupted by a shallow, narrow transverse crack. A sagittal, inconspicuous fissure marks out a sausage-like central glabellar area between the posterior-most part of the anterior glabellar lobe and S1 (mg in Fig. 5H).

In the middle of the axis, an orange-coloured strip about 57 mm long and around 1 mm wide is seen (Fig. 5E–G). This strip starts in the occipital ring, then runs sagitally through the axis of all eleven thoracic segments and continues to the ninth pygidial segment (Fig. 5G, H).

Specimen 7 (Fig. 6A, B, 8D)

NM L 36820, most probably the Háj at Zahořany locality.

Description. An irregularly shaped sample of brown siltstone measures 58 by 76 mm and bears an incomplete exoskeleton of the trilobite on its surface.

The strongly flattened internal mould of the cephalon is articulated with seven anterior-most
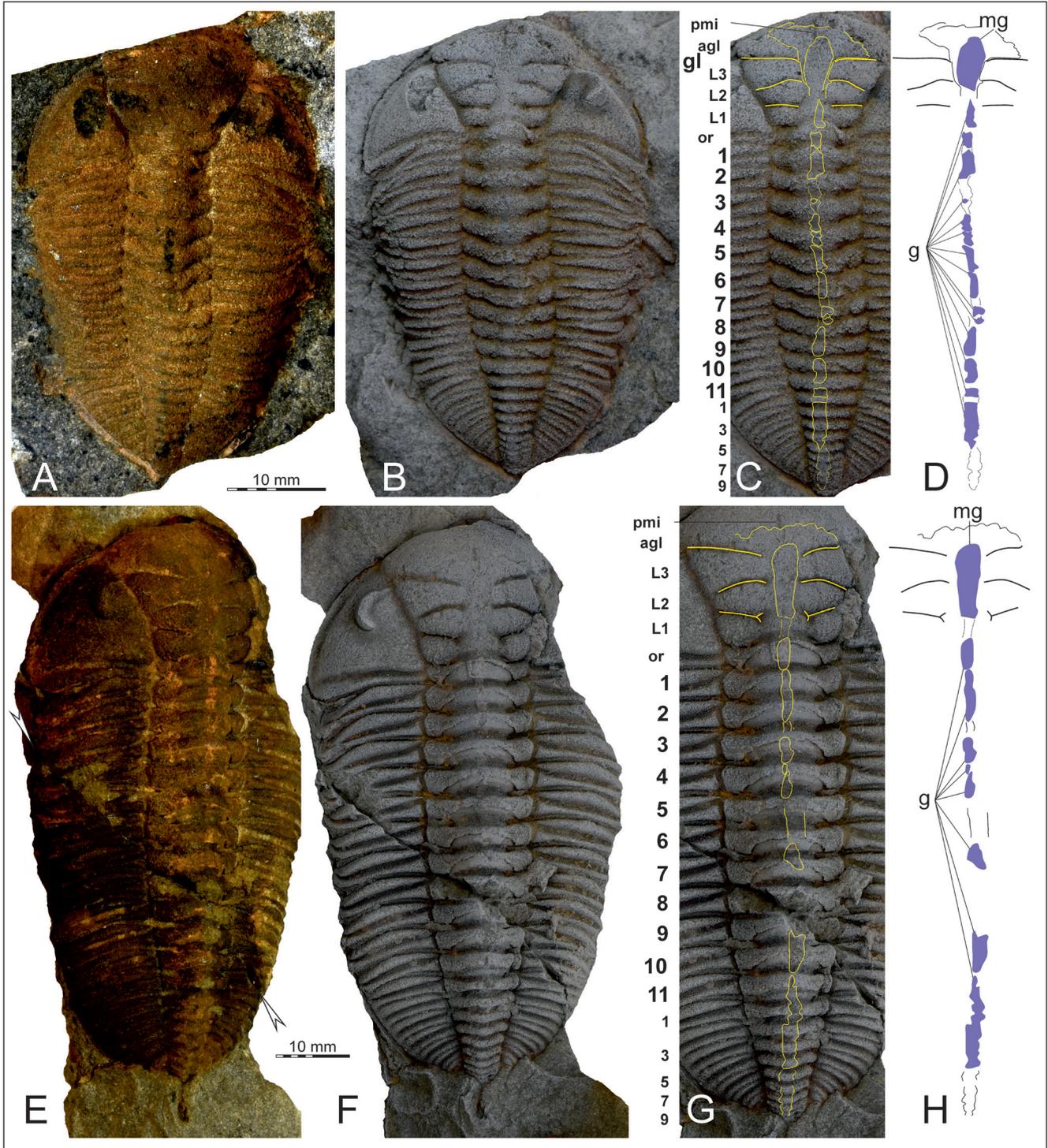
Fig. 5 - Internal moulds of *Dalmanitina socialis* (Barrande, 1846), Upper Ordovician, Sandbian Stage (= Berounian Regional Stage), Letná Formation. Both specimens exhibit a narrow strip-like structure that runs under the axial lobe of the thoracopygon. A–D) Specimen MB 1965.2.13. Drabov locality (Děd near Beroun). A) Internal mould, uncoated, photographed under polarised light. B) Internal mould, coated with ammonium chloride sublimate, photographed under polarised light. C) Detail of the axial part of the glabella and thorax, coated with ammonium chloride sublimate, photographed under polarised light. Remains of the alimentary tract are indicated by yellow outlines. D) Interpretative sketch of remains of the alimentary tract. E–H) Specimen MB 1994.1.95 MB.T.2015. Drabov locality (Děd near Beroun), photographed under polarised light. E) Internal mould, uncoated, photographed under polarised light. F) Internal mould, coated with ammonium chloride sublimate, photographed under polarised light. G) Detail of the axial part of glabella and thorax, coated with ammonium chloride sublimate, photographed under polarised light. Remains of the alimentary tract are indicated by yellow outlines. H) Interpretative sketch of remains of the alimentary tract. Abbreviations: pmi, posterior median impression; agl, anterior glabellar lobe; g, gut; gl, glabella; mg, midgut; or, occipital ring; L1 to L3, glabellar lobes; 1–11, thoracic segments; 1–9, pygidial segments.
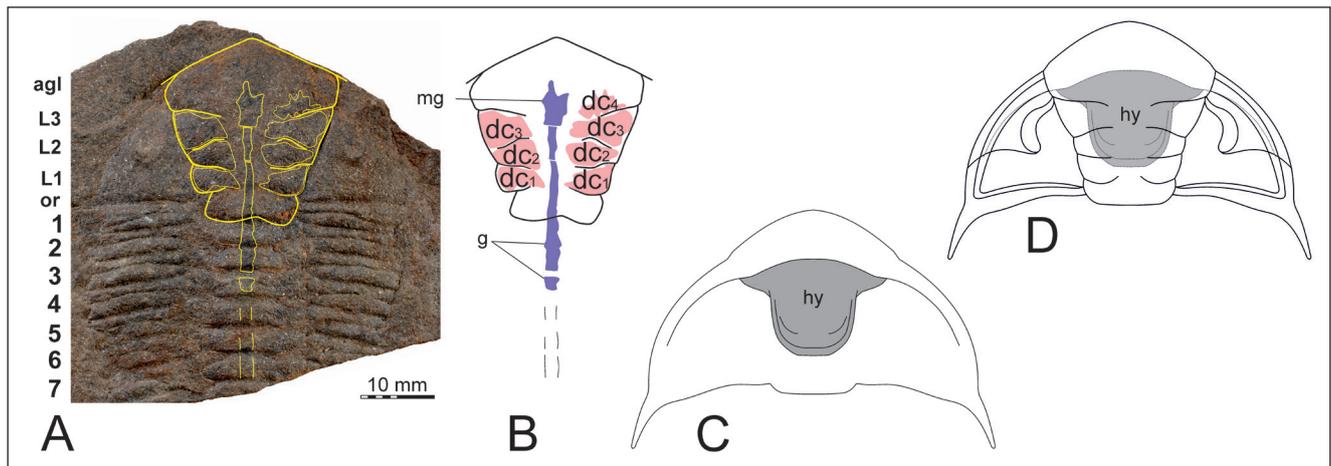
Fig. 6 - Incomplete internal mould of *Dalmanitina socialis* (Barrande, 1846), Upper Ordovician, Sandbian Stage (= Berounian Regional Stage),
Letná Formation and morphology of the cephalic shield of *Dalmanitina*. A–B) Specimen NM L 36820 exhibits a narrow strip-like
structure that runs under the axial lobe of the thoracic segments. Háj at Zahořany locality. A) Internal mould, uncoated. B) Interpreta-
tive sketch of remains of the alimentary tract. C–D) Morphology of the cephalic shield of *Dalmanitina socialis* (Barrande, 1846) (after
Barrande 1846 and Fatka et al. 2021). C) Ventral view. D) Dorsal view. Abbreviations: agl, anterior glabellar lobe; mg, midgut; g, gut;
hy, hypostome (grey); or, occipital ring; dc_1 to dc_4, diverticula; L1 to L3, glabellar lobes; 1–7, thoracic segments.

thoracic segments; the posterior part of the thorax
and pygidium are broken off. The preserved part of
the exoskeleton is 55.1 mm long (sag.) and 29.7 mm
wide (tr.); the length of the complete specimen can
be estimated as approximately 80 mm. The presence
of *in situ* preserved librigenae and well-articulated
thoracic segments demonstrate that the specimen
represents a carcass and not an exuvia.

A dark, irregularly shaped area is seen in the
central part of the anteroglabella (mg in Fig. 6A,
B). Paired dark structures are preserved in L1, L2
and L3 on the left side of the glabella and on the
right side in L1, L2 and probably also in the right
posterior part of the anterior glabellar lobe (dc_1 to
dc_4 in Fig. 6B). In the 41-mm long-remains of the
thorax, a narrow, almost sagitally running, 1.1-mm-
wide dark strip is seen (g in Fig. 6B).

DISCUSSION

Alimentary tract preservation in trilobites
In peri-Gondwanan Ordovician strata, pres-
ervation of digestive structures in trilobites is ex-
tremely rare (Budil & Fatka 2022). The morphology
and preservation of remains of the alimentary tract
in trilobites are briefly summarised below, and the
possible occurrence of digestive glands, or divertic-
ula, is discussed.

Morphology. Chatterton et al. (1994) and Lero-
sey-Aubril et al. (2010, 2012) distinguished two mor-
phological types of alimentary tract in trilobites: (1)
a simple tube differentiated into the anterior crop;
and (2) a simple tube flanked laterally by metamer-
ically paired caeca. Recently, Gutiérrez-Marco et al.
(2017) and Hopkins et al. (2017) discussed a possi-
ble third type of alimentary tract, characterised by
the co-occurrence of both a crop and metamerical-
ly paired caeca. This third type of alimentary tract
was subjected to a thorough discussion by Lero-
sey-Aubril & Peel (2018), who disagreed with the
interpretation of Gutiérrez-Marco et al. (2017) and
Hopkins et al. (2017).

Preservation. Four different types of preserva-
tion of digestive structures have been distinguished:
(1) infillings, (2) cavities, (3) dark markings on the
exoskeleton or internal mould and (4) precipitation
of a mineral coating over nonbiomineralized tis-
sues (see Robison & Babcock 2011; Lerosey-Aubril
et al. 2012; Fatka et al. 2013; Wang et al. 2018). At
least two other types of preservation, like pyritiza-
tion (Stürmer & Bergström 1993; Bartels et al. 1998;
Vayda 2019; Babcock 2003) and clay mineral replica-
tion presumably resulting from late-stage diagenesis
(English & Babcock 2010) are also possible. How-
ever, the both last-named processes are still poorly
understood (e.g. English & Babcock 2007, 2010).

Alimentary tract in phacopids and dalmanitids. Campbell (1975) analysed the functional anatomy of phacopid trilobites and suggested the presence of a widened anterior part of the alimentary tract which he called the stomach (= crop in later terminology). He also proposed the presence of hypothetical digestive glands surrounding the crop anteriorly and laterally (Campbell 1975, figs 2A and 3). Unfortunately, the specimens leading Campbell to the reconstruction of digestive glands were never described in detail; thus, it is not possible to determine whether those remains were preserved as infillings, cavities or dark markings. Later, Stürmer & Bergström (1993, figs 4, 5, 20, 23) and Bartels et al. (1998) observed structures recalling those reconstructed by Campbell (1975) in pyritised specimens of species of *Phacops* and *Asteropyge* from the Hunsrück Slate, Germany. Stürmer & Bergström (1993) and Bartels et al. (1998) called these pyritised infillings intestinal diverticula or "liver" or "hepatopancreas". The occurrence of "liver" was accepted in the generalised model of a phacopid cephalon proposed by Bergström in Whittington (1997, fig. 94).

By contrast, Otto (1994) and Bruton & Haas (1997, 1999, 2003) did not confirm the interpretation of Stürmer & Bergström (1993) and Bartels et al. (1998). Bruton & Haas (1999: 73–74) interpreted the dark paired structures under the phacopid glabella as "*possible growth of acicular pyrite or even disseminated pyrite grains following the terrace line pattern of the hypostoma and doublure*"; they further concluded that "*Areas of pyrite concentration under the mid-body of hypostoma and inside the doublure of the hypostoma outline various shapes and form... but none outlines a bag-like stomach nor an oesophagus. Darker diffuse areas however form a centrally placed bilobed structure... and shadows of what might be the oesophagus.*"

Recently, Wendruff et al. (2020, fig. 3d, f) illustrated four specimens showing remains of a gut and paired digestive diverticula surrounding the anterior part of the digestive tract in cephala of an undescribed dalmanitid from the Silurian Waukesha Lagerstätte, U.S.A. Problematic remains of possible soft tissue of the digestive tract are seemingly present also in the anterior part of the thorax. Unfortunately, the authors did not interpret the morphology of the digestive tract in detail, but it is apparently preserved as an infilling.

An articulated specimen of species *Dalmanites* with remains of appendages associated with a 3-D preserved digestive tract was recently described by Siveter et al. (2021) from the Silurian Herefordshire Lagerstätte, UK. In the only studied specimen, much of the digestive system is preserved, especially a narrow straight intestine with no observable lateral diverticula in the thorax (Siveter et al. 2021, fig. 4E, F, H, J, K). In the cephalon, two pairs of well-delimited, transversely directed lateral diverticula infill glabellar lobes L2 and L3; all diverticula are situated above the supposed oesophagus (Siveter et al. 2021: 2249, figs 1I–K, 4B–F, K). Remains of a crop are not seen in this specimen of species of *Dalmanites*. The digestive tract is preserved as cavities and/or as infillings.

Earlier reports of alimentary tract preservation in Letná Formation trilobites

As discussed above, a simple digestive tract associated with a crop under the glabella was described in the asaphid *Nobiliasaphus*? *ingens* and the trinucleid *Deanaspis goldfussii* from the Letná Formation. In contrast, the odontopleurid *Selenopeltis buchi* is an example of a trilobite with a gut associated with digestive caeca (Fatka et al. 2013; for further discussion, see also Gutiérrez-Marco et al. 2022). These observations agree with the previously established morphological types of trilobite alimentary tracts (Chatterton et al. 1994; Lerosey-Aubril et al. 2010) as well as with preservation as infilling in *N.*? *ingens* and *D. goldfussii* and as cavities in *S. buchi*.

Morphology and interpretation of the alimentary tract in *Dalmanitina*

Remains of the digestive system are preserved in the cephalic shield, thorax and pygidial shield of all seven studied specimens.

Cephalic shield. In six specimens, a sausage-like, smooth, dark-coloured or orange area is preserved in the middle part of the glabella. A dark, sagitally prolonged surface is seen in specimen NM L 51953 (mg in Fig. 3E–H). In specimen NM L 51951, fine-grained material is preserved between S3 (mg in Fig. 4A–D). A smooth sausage-like surface located near the middle of the glabella that fills the cavity between the hypostome and the glabella is developed in three specimens, specimen NMW 1906/008/008 (1906.VIII.8) (mg in Fig. 4E–H), specimen MB 1965.2.13 (mg in Fig. 5A–D), and specimen MB 1994.1.95 MB.T.2015 (mg in Fig. 5E–H). A dark polygonal surface is seen in the posterior part of the anterior glabellar lobe in specimen NM L 36820 (mg in Fig. 6A, B).

Interpretation – In agreement with earlier studies by Chatterton et al. (1994), Shu et al. (1995) and Lerosey-Aubril et al. (2010, 2012), we interpret these sausage-like structures as remains of the stomach part of the alimentary canal, corresponding to a presumed cephalic midgut (mg in Figs 3H; 4D, H; 5D, H; 6B).

In three of the studied specimens (NM L 51954, NM L 51951, NM L 36820), irregular, paired, dark-coloured areas are discernible in the occipital ring as well as in glabellar lobes L1, L2, L3 and in the anterior glabellar lobe (dt_1 and dc_1 to dc_4 in Figs 3C, D, 4C, D, 6A, B). In the fourth specimen (NM L 51953), five dark-coloured areas are seen in the occipital ring and in glabellar lobes L1, L2, L3 and in the anterior glabellar lobe (dt_1 and dc_1 to dc_4 in Fig. 3 G, H). The morphology and placement of these darker spots in the glabellar lobes recall those interpreted as pyrite concentration by Bruton & Haas (1997, 1999, 2003). In *Dalmanitina*, however, these surface spots do not contain infilling, and they are preserved as dark markings.

Interpretation – The explanation of these dark-coloured areas is problematic and is discussed in the following section *EDAX analysis*.

Thorax. In all seven studied specimens, an orange, grey or dark brown, glossy, structureless, sagitally or exsagitally oriented strip is preserved in the posterior-most part of the cephalon (in the occipital ring) and in thoracic segments; this strip is always located near the middle line of the axis (Figs 3–6). This location fits well with the areas where gut remains have previously been identified in trilobites (e.g., Lerosey-Aubril et al. 2012; Fatka et al. 2013; Budil & Fatka 2022).

Interpretation – We interpret these structures as remains of the median tube of the post-stomach part of the alimentary canal corresponding to a simple gut.

Pygidial shield. A dark strip is visible in the axis from the first to the ninth pygidial segment in specimen 3 (NM L 51951, Fig. 4A–D), and a glossy, structureless band is present in the axis between the first and the third pygidial segments in specimen 4 (NMW 1906/008/008 (1906.VIII.8), Fig. 4E–H). Comparable structures are preserved in the pygidial axis in specimen 5 (MB 1965.2.13, Fig. 5A–D) and specimen 6 (MB 1994.1.95 MB.T.2015, Fig. 5E–H).

In the other three studied specimens, the pygidium is missing.

Interpretation – As in the cases of the cephalic shield and thorax, we interpret these structures as remains of the median tube corresponding to the simple gut. In all specimens, the simple strip preserved in the thoracopygon is transversally narrower than the sausage-like area observed in the glabella.

Preservation

In the studied specimens of species of *Dalmanitina*, two preservational styles of digestive-system remains could be distinguished.

1) In five specimens, the axial part of the digestive system is preserved as a narrow, fine-grained, dark-coloured, straight strip seen in all segments of the thoracopygon. This narrow strip starts as a slightly wider sausage-like body under the posterior part of the glabella; this body is composed of dark-coloured, fine-grained material (Figs 3H, 4H, 5H, 6B). The medially placed darker strip in the axial region of the thoracopygon corresponds to the gut, as known in other trilobites. The wide sausage-like body in the cephalon most probably represents the midgut (for discussion see Shu et al. 1995; Gutiérrez-Marco et al. 2022). Both these parts of the alimentary tract are preserved as infillings in all studied specimens of species of *Dalmanitina*.

2) Dark-coloured areas in the glabellar lobes positioned abaxially of the sausage-like body are preserved in three specimens (Figs 3H, 4D, 6B). The occurrence of such markings evokes the question of preservation of cephalic digestive midgut diverticula, or of the "perigastric organ" of Cervellione et al. (2017). Comparable structures in *Phacops* from the Devonian Hunsrück Slate were explained as pyrite concentrations in the mid-body of the hypostome by Otto (1994: 54) and Bruton and Haas (1999: 73). In *Dalmanitina*, the dark-coloured areas are transversally wider than the hypostome–glabellar cavity (compare Figs 3F–H; 4A–D, 6A–D).

To understand what the dark-coloured areas represent in *Dalmanitina*, a total of twelve places on two specimens were chemically analysed (Fig. 7).

EDAX analysis

All herein studied specimens of species of *Dalmanitina* are preserved in deeply weathered

Fig. 7 - EDAX analytical points for two specimens of *Dalmanitina socialis* from the Upper Ordovician Letná Formation. A) Specimen NM L 51954. B) Specimen NM L 51953.
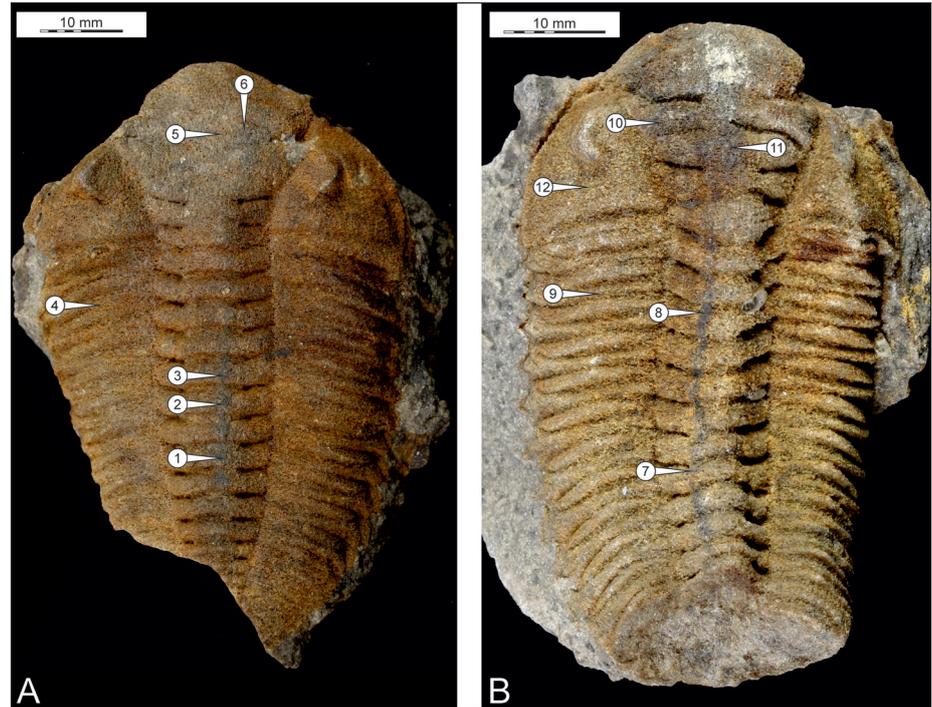
quartzose sandstone characterised by a low silt content. This deep weathering makes interpretation of chemical analyses quite difficult.

Results and discussion. The EDAX analyses revealed that the digestive structures and the surrounding rock are composed predominantly of C, O, Si and Al, with minor amounts of Fe, K and P. Na, Mg, Ca and Ti were also repeatedly detected, but not in all analysed places (Tab. 1). The analyses did not reveal conspicuous elemental differences between separate parts of the digestive structures and the material making up other parts of the trilobite internal mould, i.e., there are no statistically important differences in the percentages of most of the analysed elements. The only exceptions are slight enrichment of Al in the gut (point 1), cephalic midgut (point 6), and dark-coloured area (point 5) of specimen NM L 51954 and a higher level of C in the cephalic midgut of NM L 51953 (point 11, Tab. 1).

The interpretation of these results is difficult, because the contents of all other elements vary only very slightly. We do not have a reasonable explanation for the low level to absence of Na, S and Cl in various areas of the internal mould. However, filling by different materials at death or soon after is the most plausible explanation. The higher content of C in one midgut sample might reflect filling of the midgut by digested food particles (point 11, see Tab. 1).

The slightly higher levels of Al in the gut and midgut could mean filling of these parts by a slightly higher amount of clay minerals (Tab. 1).

The low content of Fe combined with the very low content to absence of S in the dark-coloured areas and in other parts of the glabella in specimen 1 (points 5 and 6 in Tab. 1) and in specimen 2 (points 10 and 11 in Tab. 1) do not support the occurrence of pyritisation in the hypostome–glabellar cavity.

Interpretation - (1) Based on the EDAX analysis, we hypothesise that both the cephalic midgut and the gut contain infill including remains of food mixed with fine-grained sediment (= clay minerals) that entered the gut post-mortem or was ingested either together with food particles. (2) The dark-coloured areas surrounding the cephalic midgut could be interpreted as remains of the soft tissue belonging to cephalic digestive midgut diverticula (= "perigastric organ" *sensu* Cervellione et al. 2017).

PALAEOECOLOGY OF *DALMANITINA*

Dalmanitina was classified as vagrant benthos by Havlíček & Vaněk (1966) and Přibyl & Vaněk (1976). Specimens of species of this genus were certainly not able to live on the sea floor in an incompletely enrolled position (see Bruton & Haas 1999 for discussion of such positions in phacopid

BODY PART	ELEMENT / POINT	C	O	Na	Mg	Al	Si	P	S	Cl	K	Ca	Ti	Fe	TOTAL
MIDGUT	5	14.33	51.94	0.08	0.30	9.58	17.10	0.18	-	-	3.11	0.20	0.33	2.85	100.00
MIDGUT	11	31.71	49.92	-	0.07	2.82	9.87	0.61	-	-	0.59	0.21	-	4.21	100.00
dc4	6	14.59	53.84	0.04	0.34	9.08	14.59	0.31	-	-	2.83	0.12	0.28	3.97	100.00
dc3	10	20.53	52.89	0.10	0.08	2.79	17.61	0.43	0.11	0.11	0.69	0.34	0.13	4.20	100.00
GUT	1	14.07	48.49	0.13	0.42	10.01	16.80	0.29	-	-	3.79	0.35	0.46	5.20	100.00
GUT	2	19.62	47.98	0.05	0.25	7.18	15.16	0.36	0.14	0.13	2.62	0.45	0.37	5.70	100.00
GUT	3	20.53	48.10	0.10	0.30	7.80	12.02	0.50	-	-	2.61	0.36	0.31	7.36	100.00
GUT	7	24.22	48.92	-	0.22	6.57	13.18	0.66	-	-	2.24	-	0.41	3.57	100.00
GUT	8	19.53	50.70	-	0.26	7.06	11.91	0.74	0.09	0.10	2.25	-	0.35	7.02	100.00
MATRIX, PLEURA	4	14.38	53.54	0.07	0.24	7.51	15.51	0.35	-	-	2.26	0.05	0.23	5.86	100.00
MATRIX, PLEURA	9	27.57	49.38	-	0.12	2.15	16.37	0.25	0.13	-	0.53	0.22	-	3.29	100.00
MATRIX, FIXIGENA	12	24.95	53.70	-	-	1.90	14.76	0.56	-	-	0.38	0.21	0.15	3.39	100.00

Tab. 1 - Results of EDAX analyses of the digestive structures and matrix in two specimens of *Dalmanitina socialis* (points 1–6, NM L 51954; points 7–12, NM L 51953) from the Upper Ordovician Letná Formation.
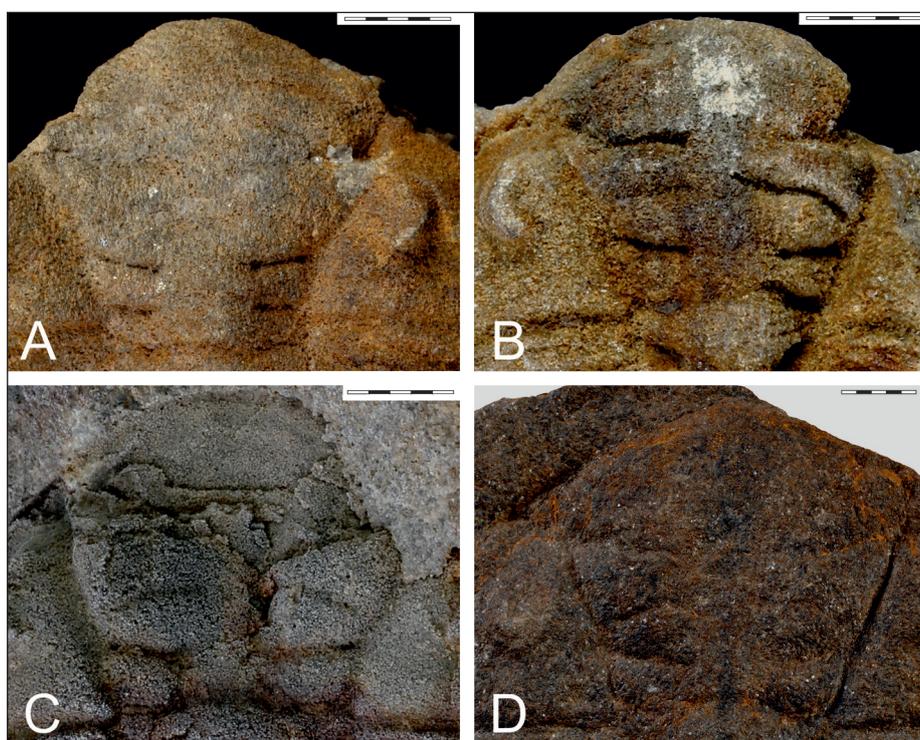

Fig. 8 - Details of internal moulds of *Dalmanitina socialis* (Barrande, 1846), Upper Ordovician, Sandbian Stage (= Berounian Regional Stage), Letná Formation. A) Specimen 1, NM L 51954. B) Specimen 2, NM L 51953. C) Specimen NM L 51951. D) Specimen NM L 36820.

trilobites), because the exoskeletal morphology of *Dalmanitina* does not enable such a posture. A medium-sized scavenger/occasional predator scenario *sensu* Fortey & Owens (1997) seems to be the most parsimonious life strategy for this genus. This interpretation is consistent with the presence of ingested food and clay minerals in the infill of both the cephalic midgut and the gut.

Ichnofossils

Mikuláš (1998) concluded that the ichnofossil *Rusophycus* isp., which is abundant at several localities in the Letná Formation, originated by the activity of *Dalmanitina socialis*. Direct field evidence

at the Chrustenice locality shows that *Rusophycus* occurs in siltstone and fine-grained greywacke that are intercalated between layers of greywacke and quartzose sandstone with a low proportion of siltstone (Mikuláš & Stachacz, observations 2019; Fatka et al. in press). The greywacke and quartzose sandstone layers are interpreted as intertidal (Stachacz, personal communication, 2019), and the *Rusophycus*-rich layers represent a shallow subtidal setting with a well-illuminated but sometimes muddy bottom.

Brief remarks about the danger of misinterpreting *Planolites*- or *Skolithos*-like ichnofossils as gut remains of trilobites were published by Fatka

et al. (2013) and Kraft et al. (2020). In the Ordovician System of the Prague Basin, association of *Planolites*- or *Skolithos*-like ichnofossils and trilobites is common for *Placoparia* and several trinucleids (Shaw 1995). This kind of ichnofossil may mimic remains of a trilobite digestive tract that was left empty after dissolution of its original infill. A careful examination reveals that in most cases, ichnofossils differ from gut infillings (see also Fatka et al. 2013) in one or more of the following features: (1) all simple horizontal to sub-horizontal tubular ichnofossils (repichnia, domichnia, fodinichnia), unlike gut contents, have a more-or less-constant diameter, which also appears to be much larger than the presumed digestive tubes of trilobites described here; (2) ichnofossils commonly extend outside the axis, or even outside the trilobite body; and (3) ichnofossils frequently display a tortuous course, whereas the digestive tract of trilobites is essentially straight. However, as noticed by Babcock & Peel (2007) and confirmed by the investigation of various Ordovician trilobites, including *Dalmanitina* (Mikuláš, Budil, Fatka, unpublished observation), vermiform scavengers might have preferentially targeted the alimentary tract of the trilobite carcass. Therefore, it is particularly important to be very careful when interpreting a semi-tubular cavity under the axial region of a trilobite, especially when the cavity is preserved under only a short portion of the axial lobe and when it is not associated with other remains of the alimentary tract.

Trilobite cololites, pre-coprolites and coprolites

In addition to the standard palaeontological approach, it is possible to characterise fillings of the digestive tubes in terms of ichnology; thus, to facilitate future research, it is appropriate to consider the ichnological status of the described gut fillings. Gastrointestinal fillings can be considered from an ichnological perspective because they are the result of substrate disturbance. Přikryl et al. (2012), Knaust (2020) and Bertling et al. (2022) provided the most detailed ichnological classification of gastrointestinal fossil fillings to date. They adopted the term "cololite", which means all the contents of the digestive tract found inside the body of an organism. They also applied the traditional name "coprolite" to fossil faeces. Further-

more, they added the term pre-coprolite to refer to a cololite within the producer's body that is ready in shape and consistency to be eliminated from the animal as a coprolite. This term, if used consistently, should gradually lead to the correlation of coprolites and their producing organisms. Přikryl et al. (2012) described the contents of the digestive tracts of fish; the same approach may also be useful for research on trilobite digestive tracts. In our material, especially in the two individuals shown in Figure 4, the pygidial ends of the digestive tracts are terminated by a form that could represent pre-coprolites of *Dalmanitina*. Such remains have been found, for example, in small fossiliferous nodules of the Bohdalec Formation at the Na Strži locality in Prague 4 (Mikuláš 1982).

Conclusions

The studied specimens of *Dalmanitina* contain a straight, simple and narrow strip under the axis of all segments of the thoracopygon. The strip starts in the anterior part of the occipital ring and reaches the tip of the pygidial axis. This strip is preserved as a dark grey, fine-grained infill and is interpreted to correspond to the remains of a simple gut (Fig. 9).

In the middle and rear parts of the glabella, a transversely slightly expanded, sausage-like, smooth area is preserved in six of studied specimens. This infill is preserved in the same way as the remains of the gut; consequently, we interpret these smooth areas as representing the remains of an enlarged part of the tube-like and medially positioned part of the digestive system.

In the glabella of three specimens, remains of the enlarged tube-like system are laterally surrounded by dark-coloured areas in the glabellar lobes and occipital ring. We interpret these structures as remains of cephalic diverticula; hence, the tube-like body in the cephalon is identified as the midgut. We propose naming the cephalic digestive midgut diverticula the "perigastric organ", as earlier proposed for Decapoda by Cervellione et al. (2017).

The described specimens of *Dalmanitina* constitute the first well-documented example of digestive structures in the subfamily Dalmanitininae.
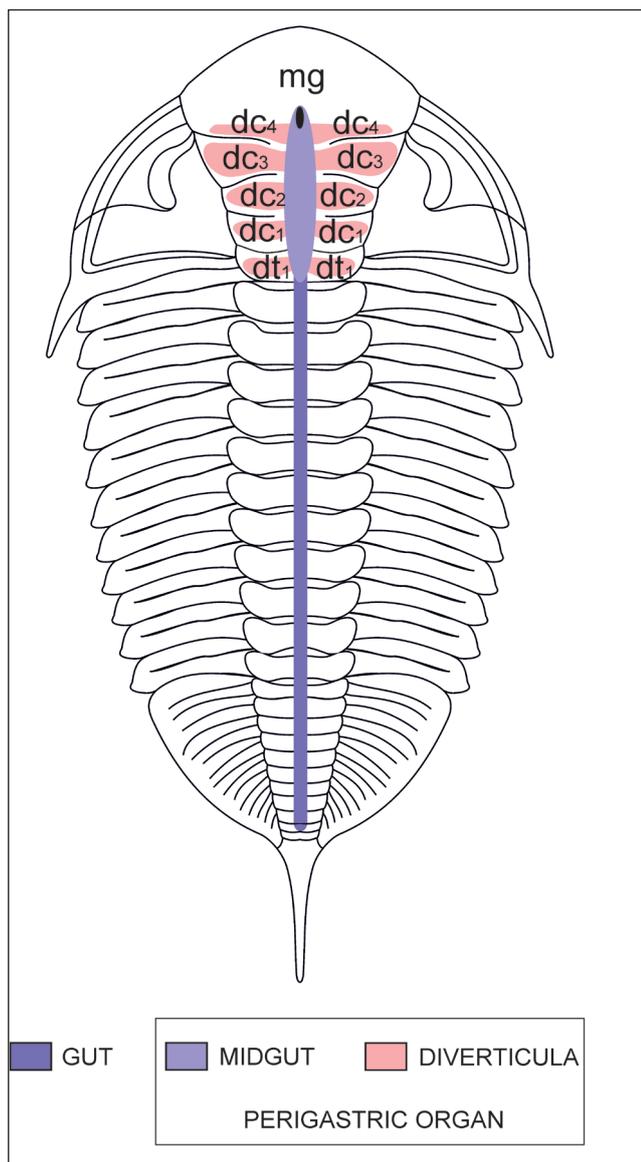
Fig. 9 - Sketch reconstruction of *Dalmanitina* showing the morphology of the digestive system in the cephalic, thoracic and pygidial regions. Abbreviations: mg, midgut; dc_1 to dc_4, cephalic midgut diverticula; dt_1, trunk midgut diverticula.

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